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THIRTY YEARS OF PRIMARY SUCCESSION ON THE

STORBREEN GLACIER FORELAND, JOTUNHEIM, NORWAY:

SPECIES POPULATIONS, COMMUNITY DYNAMICS AND ENVIRONMENTAL INFLUENCES

VOLUME I

MARGARET ANN NICHOLLS, B.Sc

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Abstract

Changes in arctic-alpine vegetation composition over 30 years in a successional sequence on the Storbreen glacier foreland, Southern Norway, and in the adjacent regional vegetation, are analysed. The study is based on a repeat survey of 410 permanent sites and 24 new sites (located on land exposed since 1970). Classification (TWINSPAN) and ordination (Canonical Correspondence Analysis), diversity indices and transition probabilities, are used to identify changes at the species level, to examine successional dynamics at the community level and to assess the role of the environment in compositional change.

Species population changes are extensive, cannot be explained solely in terms of successional change, and appear to be influenced by regional climatic change since 1970. Changing successional patterns are attributed to species-specific effects on performance. In the dense vegetation of the low altitude dwarf-shrub heath, this involves shifts in relative abundance. Some species are increasing in abundance at relatively high-altitude and on relatively young sites, where vegetation is relatively sparse.

The study follows the dynamics of the successional sequence over 30 years using a spatio-temporal chronosequence approach to succession. Three spatially-determined successional trajectories are associated with the major landforms in the study area. These trajectories are tending towards: (1) a species-rich, dwarf-shrub heath at low-altitude and at higher altitude, north-facing sites; (2) a species-rich snowbed community at high-altitude, south-facing sites and at lower altitude, north-facing sites; and (3) a species-poor snowbed community at high-altitude, north-facing sites. Mesoscale gradients of altitude and aspect govern qualitative differentiation from an early pioneer stage. Subsequent increases in successional distance indicate divergence. Community-scale compositional changes are influenced by five complex environmental gradients reflecting development, topography, moisture/snowlie, disturbance and substrate. Within individual communities, environmental variables apparently govern the rate of successional development. The development of the successional sequence is influenced by environmental variables operating at several scales.

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Chapter 1: Background and study area

1.1 Introduction

This study examines changes occurring in a successional vegetation sequence over a 30-year time increment. The study area is the foreland of a retreating glacier (Storbreen) in south central Norway. Such sites are particularly useful for successional studies due to:

(1) The incremental release of new land for colonization, producing a zonation in space that represents a sequence in time;

(2) Dating of moraines deposited by the glacier during its overall retreat provides a temporal framework for the development of the successional sequence.

Land emerging from glacial cover is generally denuded of propagules and developed soils, although complete sterility is unlikely (Matthews, 1999). This work therefore concerns primary rather than secondary succession, where the disturbance initiating development is relatively minor, leaving soils and propagules *in situ.*

The site has been the focus of an ongoing research programme since 1970 examining successional vegetation patterns and dynamics using a network of permanent quadrats. This previous work is integral to and is built upon in this study. In particular, data from the first study (Matthews, 1976) has been made available for comparative purposes. The following section considers the findings of this past research and how the present study relates to and arises from this work. Subsequent sections of the introduction concern the physical context: the location, glacial history and soils; geology and climate; and finally, evidence of changing climatic conditions.

1.2 Previous successional studies at Storbreen

Four primary studies mark the development of vegetation research at Storbreen:

(1) The initial study by Matthews (1976) identified vegetation patterns in relation to terrain age at both the individual species and community levels. He used the patterns to reconstruct successional pathways, recognised the importance of altitude, aspect and microtopography, and discussed the implications for models of primary succession.

(2) Whittaker (1985) focussed on environmental relationships and species populations. He also repeated part of the 1970-71 survey (controlling for altitude), identified age and microtopographic environmental factor complexes as important influences on vegetation development, and investigated species roles and relationships.

(3) Crouch (1992) compared phanerogram and cryptogam sequences, and also related them to a wider range of influential environmental variables than had been attempted by Whittaker.

(4) Foskett (1998) examined the role of microtopography in detail, again relating community structure to environmental variables. Her study also compared the sequence at Storbreen with several other glacier forelands at higher and lower altitudes.

Particular themes, central to these studies, are discussed below and placed within the wider context of successional studies in the next chapter.

1.2.1 The importance of environmental variables and the role of geoecology

Matthews (1976) examined spatial variation in species distribution and community patterning, finding complex zones and gradients separated by ecoclines (rather than ecotones). Both time and the environment were considered causal, with environmental heterogeneity (particularly altitude, aspect and microtopography) generating variation in successional rate and the duration of successional stages.

Integrating population and community level approaches, Whittaker (1985) found that individualistic species distributions and behaviour affect community patterns and dynamics but also that species groups have common community roles and responses to environmental variation. He identified two complexes of environmental factors related to terrain-age and microtopography (the latter including snowlie duration, exposure and moisture), while controlling for altitude and aspect. A subsequent review concluded that a simple time sequence is inadequate to determine the complexity of successional vegetation patterning (Matthews and Whittaker, 1987). Environmental gradients were found to be strongly influential, particularly the two factor complexes, altitude and aspect. This emphasis on spatial variation and vegetation-environment interactions as explanatory influences on successional trajectories, rates of change and assemblage patterns is termed geoecology, and was developed/considered further in Matthews (1992).

Crouch (1992) found that age-related factors are of primary importance, while environmental gradients generate secondary patterns; cryptogam distributions being most strongly influenced by microscale and phanerograms by macroscale variation. Coarse scale distribution patterns correlate with environmental gradients, corresponding to the model proposed in R. H. Whittaker's (1953) climax pattern hypothesis, but vary individualistically when considered in greater detail (Crouch, 1992; 1993). Crouch's consideration of cryptogams (which were not investigated by either Matthews or Whittaker) also provided a justification for separate investigations of the phanerograms in the previous studies.

The importance of spatial variation in shaping the sequence has implications for the use of the chronosequence concept in successional studies. This concept assumes space and time to be equivalent, with spatial patterns representing time elapsed. However, where spatial variations influence successional trajectory or rate, the concept is only of limited usefulness. Whittaker (1989, 1991) and Crouch (1992) found that age represents the predominant influence, but that the environment also constitutes a successional driving force. Whittaker concluded that the chronosequence is an imperfect predictor of the pattern of succession at a specific location.

These studies also examined the relative importance of allogenic (environmental) and autogenic (plant-mediated) influences. On young land with pioneer assemblages (and at high-altitude), allogenic factors tend to predominate, while in later stages and/or at lower altitude autogenic influences become increasingly important (Whittaker, 1985; Matthews and Whittaker, 1987; Whittaker, 1989, 1993). Additionally, Whittaker (1993) found that allogenic factors, particularly climate, hydrology and disturbance, could generate short-term dynamics. He argued that both types of influence underlie species turnover, with increasingly unfavourable physical conditions for early species tending to reduce populations, and that replacements occur when declining populations are subject to competitive interactions.

Clementsian theory characterises successional change as solely progressive, culminating in a stable climax (Clements, 1916, 1936). However, based on reanalysis of some of Matthews' sites after 12 years, Whittaker (1985) found considerable variation in the rate of development due to interruptions and reversals. Progression was clearly identified on young sites (20 - 50 years), but older sites frequently showed no significant change, with a minority retrogressing due to disturbance or experiencing compositional shifts due to changing moisture availability (Matthews and Whittaker, 1987; Whittaker, 1991). Whittaker (1985) questioned whether the 12-year time interval was sufficient to detect progressive change on older sites. Mature sites were not found to be fixed endpoints, but are better described as a mosaic of vegetation types responding to a fluctuating environment (Whittaker, 1985; Foskett, 1998). Foskett distinguished retrogression from disturbance, the latter occurring rapidly due to physical changes and responsible for creating younger ground on old terrain allowing pioneers to persist. Processes classed as disturbance include soil erosion and sediment deposition while retrogression results from the slow degradation of soils.

Whittaker (1985, 1987, 1993) detected differences in reproductive behaviour, with seed dispersal predominating on successional sites but vegetative reproduction in the regional vegetation outside the glacier foreland. Asexual clones were thought to have a competitive advantage over seedlings in dense vegetation due to their greater development at release, allowing pre-emption of resources.

Finally, Matthews (1976) questioned whether successional sites would ever match the regional vegetation. Factors considered to have the potential to change trajectories include climatic change, different parent materials and altitude, the last generating developmental differences as the glacier retreats onto higher ground.

1.2.2 Sequences related to altitude

Matthews (1976) identified two successional sequences according to altitude. At high-altitude (mid-alpine) sites, there is a relatively simple, two-stage sequence, with few species and pioneers present in mature vegetation. There is greater complexity at lower elevation with three successional stages and greater differences between endpoints. Foskett (1998) explored the role of variables associated with the microtopographic complex, finding that terrain age decreases while microtopography increases in importance with increasing altitude. In explanation, she suggested that the severity of conditions determines the level of vegetation cover, which acts as a buffer against environmental perturbation when cover is substantial. This buffering effect diminishes in effectiveness as vegetation becomes increasingly sparse.

Matthews' (1976) major finding was that the successional sequence diverges. He attributed this to an increase in the species pool during the course of the successional sequence and to variation in the microtopographic controls amongst mature community types. Matthews (1992) and Foskett (1998) related divergence to environmental stress on alpine sites, convergence occurring where vegetation cover provides micro-environmental amelioration at low-altitude (particularly at subalpine sites where the tree canopy enhances the effect).

1.2.3 Study aims

The main aim of the present study was to carry out a comprehensive reanalysis of the permanent quadrats at Storbreen after a time interval of 30 years. Apart from Whittaker's reanalysis of a small proportion of the quadrats, this would provide the first *direct* evidence of succession at Storbreen. The specific objectives of the study can be stated as follows:

(1) To describe 30 years of temporal change in the species population distributions;
(2) To analyse the community dynamics of the successional sequence; and
(3) To investigate the role of environmental parameters in the compositional changes.

A further comparative study is considered important for the opportunity it provides to expand understanding of the dynamics of the Storbreen glacier foreland geoecological system. Some of the areas of interest include the following:

(1) Whittaker (1985) suggested that 12 years would be insufficient to detect progressive change at older successional sites. Would 30 years be sufficient to detect such changes and what form would these take?
(2) Is the compositional discontinuity at the foreland boundary still apparent after another time increment?
(3) Did the differences in reproductive behaviour found by Whittaker indicate qualitative differences between the older and younger sites in terms of successional trajectory?
(4) Matthews (1976) suggested that environmental factors affect the rate of successional change and the duration of seres. Would this be confirmed from the directly measured changes, and might qualitative change also be found?
(5) How are the environmental factor complexes identified by Matthews (1976), Whittaker (1985), Crouch (1992) and Foskett (1998) reflected in the directly measured successional changes?
(6) Can the directly measured changes shed light on the relative importance of the autogenic and allogenic controls on succession?
(7) Climatic change has been cited as likely to generate changes in successional trajectory. Could evidence of this be found? How closely would the results parallel the predictions?

1.3 Study area

The study area lies in western Jotunheimen, central Southern Norway (61°35'N, 8°11'E), approximately 150km from the west coast. The Storbreen glacier foreland forms a subsidiary, partly hanging valley to the U-shaped Leirdalen on the eastern flank of the Smørstabb massif (Figure 1.1). Jotunheimen contains the two highest mountains in northern Europe (Galdhøppigan, 2469m and Glittertind, 2452m), and Storbreen is backed to the south and west by several peaks exceeding 2000m.

In the middle of the eighteenth century, the glacier extended as far as the River Leira (Matthews, 1977), but since then it has progressively retreated to its present position. The glacier snout is currently at 1400m asl, and the exposed foreland exceeds 1.5km in length. The main channel of the principal meltwater stream, the Storbreagrove, is central to the foreland, with minor channels irrigating peripheral areas (Figure 1.2), some fed by the main channel, others by permanent snow patches on the surrounding slopes. As seen in Figure 1.2, the valley has an overall northeast-facing aspect.

The generally shallow gradient of the Storbreagrove steepens where the stream crosses a rocky bar around 1200m. On younger ground above this are fluted moraines, which parallel the direction of glacier retreat. More peripherally, minor standstills and readvances have produced arcuate terminal and lateral moraines. Consequently, at higher altitude on the flanks of the foreland, age increases with elevation, but within the central trough, age decreases as altitude increases. The outermost moraine forms the foreland boundary, marking a temporal discontinuity beyond which a consistently higher level of vegetation cover and the presence of deeper soils distinguish the regional vegetation from that within the foreland. The dating of these moraines by historical evidence and lichenometry (Matthews, 1974, 1975) (see also section 3.2.1) has contributed substantially to the areal chronology used in this study and which is illustrated in Figure 1.3.

The whole study area is situated in the alpine zone above the (birch) treeline, which lies at about 1000m in Leirdalen. The altitudinal range of the study area is between 1100 and 1550 masl, within both low- and mid-alpine belts. The division approximately coincides with the 1930 moraine, so that present pioneer assemblages occur within the mid-alpine belt (Foskett, 1998). High-altitude sites on the north-facing flank of the foreland may mark the start of the high-alpine belt (Matthews, 1976).

1.3.1 Glacial history

Pleistocene glaciations caused many of the present-day landforms, including the deep, steep-sided Leirdalen. Following the Erdal advance ca 10000 calibrated years BP (Matthews et al., 2000), regional deglaciation occurred in central Norway during the Boreal, from ca 9000 years BP and was complete by ca 8000 years BP, when there is evidence that the mountain passes in Hardangervidda were wooded (Andersen, 1980). Temperatures are estimated to have been 2.5°C higher than at present, resulting in the glacier equilibrium line altitude (ELA) being above the highest point of Jostedalsbreen (Nesje and Kvamme, 1991). The chronology determined by Matthews et al. (2000) for Bøverbreen on the western side of the Smørstabb massif indicates that glaciers were absent until ca 5300 years BP and remained small until 2500 years BP. Mild conditions were then interrupted by advances known as Bøvertun I (2400-1600 years BP) and

Bøvertun II (1400-800 years BP), before a return to warmer conditions during the Medieval Warm Period (800-600 years BP). Evidence of peat formation at Storbreen from ca 3000 years BP indicates deteriorating climatic conditions (Matthews et al., 2000) that culminated in an advance that extended close to the Little Ice Age (LIA) maximum at ca 1800 years BP (Bøvertun I). All such advances since the Erdal advance and prior to the Little Ice Age (LIA) were, however, relatively small.

Declining temperatures in the fifteenth century marked the start of the LIA advance. The maximum age of this advance at Storbreen according to radiocarbon dating is AD1450 (Matthews, 1991; Matthews et al., 2000). However, the LIA maximum is generally accepted as being reached ca AD1750 on the basis of historical evidence and lichenometry. It marks the most extensive advance since the Erdal Event, overriding peat at Bøverbreen which had accumulated since ca 5760 years BP (Matthews et al., 2000). The outer moraine at Storbreen is attributed to this advance (Matthews, 1976, 1977; Matthews et al., 1986).

Since the mid-eighteenth century, there has been an overall retreat, though the moraines provide evidence that standstills or minor advances interrupted this. The present extent of the glacier is described by Andreassen (1999) (area, 5.4km^2; length, 3km; slope, 14°). During this century, the glacier has decreased in area by 25% and in length by 40% of its maximum LIA extent, 800m of this retreat occurring between AD1940 and 1997. Between 1949 and 1997, it lost 11 metres of water equivalent (mweq), averaging 0.22 mweq/a^{-1} (Nesje et al., 2000). However, during the mid 1980s and early 1990s, positive mass balances thickened the glacier by 25m (between 1800 and 1950 masl), and small push moraines were formed. In 1997, the glacier had been in balance for at least 10 years and the front was considered stationary or to be making minor advances. Recent observations of the glacier by the author suggest that ablation rates have increased since 1997, with particularly high levels in 2003 (Matthews: personal communication).

1.3.2 Soil

Mellor (1984) and Messer (1984) have investigated soil development in the foreland and the immediately surrounding area. Outside the foreland, soils are classified as Brown Soils, and while foreland sites appear to be progressing towards this endpoint, the soils are still much thinner after nearly 250 years of development.

Mellor (1985) found slow decomposition rates: while surface organic material accumulates over time (up to 25mm on the 1750 moraine), soil organic carbon is low even on the oldest foreland sites (15% compared to 30% outside the boundary). The range of weathering processes are restricted in the study area; clay particles generally comprise less than 1% of the till substrate and evidence of chemical weathering (etching by organic acids and changes in biotite hydration) is found only outside the foreland boundary. Within the foreland, translocation is important, particularly of organic carbon and Fe, which may form organo-metallic complexes contributing to increasing acidity. Illuvial coatings on grains and peds are interpreted as forming following the thawing of ice lenses in the soil. The absence of bleaching of lower horizons is attributed to high

Fe levels in the parent material, low rainfall, seasonal frozen ground and frost heave. It is also suggested that after 100 years, initially slow rates of development increase with increasing vegetation cover and surface stability. Messer (1984, 1988) also found slow rates of soil development and low cation exchange capacity. On newly deglaciated till, pH was 7.0-7.3, falling to 5.8 after 40 years and 4.5 on the 1750 moraine. Outside the foreland the maximum pH was 5.65. She also identified an altitudinal gradient attributed to climatic severity: rates of pedological processes increased with decreasing altitude on land of a similar age. Darmody and Thorn (1997) suggest microclimate and aspect as the main factors underlying these differences.

1.3.3 Geology and climate

Storbreen occurs on the upper Jotun Nappe, emplaced during the Caledonian orogeny (Strand, 1960). The rocks in the study area show evidence of intense regional metamorphism, comprising predominantly pyroxene-granulite gneiss, occurring in several sheets with mylonites marking the shear zones of thrust planes between them, and minor lenses of intrusive peridotite (Strand, 1960; Battey, 1975; Andersen, 1998; Matthews et al., 2000). The parent material tends to be of intermediate composition, and there are no calcareous rocks in the study area.

There are no weatherstations in the immediate vicinity of Storbreen, the nearest are at Fanaråken, 16 km to the southwest at 2062 masl, and at Bøverdalen, 14 km to the northwest at 701 masl. Using Matthews' (1976) calculations based on interpolations between mean temperatures from these weatherstations, Foskett (1998) estimates mean temperatures at Storbreen as –0.78°C at 1140 masl and –1.7°C at 1310 masl. Further calculations in Matthews and Whittaker (1987) based on interpolation between Fanaråken and Elvester, 14 km to the northeast at 674 masl, were used by Crouch (1992) to estimate mean temperature as -0.6°C at 1100 masl and –2.2°C at 1400 masl. Matthews and Whittaker (1987) use an altitudinal gradient of –5.45°C per km increase. Crouch (1992) quotes a mean June temperature of +4.2°C and a mean December temperature of –11.3°C, based on Messer (1984).

Mean precipitation has been calculated as 1500mm by Mellor (1985). Foskett (1998), using interpolation based on the Fanaråken (123cm) and Bøverdalen (49cm) data, estimates mean snowfall as 75cm (1140 masl) and 95cm (1310masl).

The length of the growing season depends on the timing of snowmelt and therefore on regional weather patterns (Billings, 1974b), together with local conditions that govern snow accumulation. Snowmelt may not occur until the second week in July and temperatures are likely to fall below zero by the end of September, giving approximately eight to ten weeks for plants to complete that year's phenological cycle. However, there is great variability, both interannually and spatially within the study area. As found by Whittaker (1985), the growing season may be severely reduced in years of late snowlie as occurred in 1983. Spatial variability depends on altitude and microtopography, which controls the accumulation of snow at a local level. As pointed out by Matthews (1992), ridgetops may remain snowfree for most of the year, while growing seasons of three months or less have been found for snowbed sites elsewhere in southern Norway.

1.4 Climatic change

Climatic change is a factor that Matthews (1976, 1999) considers likely to generate changes in successional trajectory. Such changes may affect the vegetation both directly and indirectly; in particular, changes in either the date of snowmelt and/or timing of the onset of snow in the autumn will affect growing season length. The nature of anticipated responses to such change are discussed in the next chapter, with evidence of climatic change in south central Norway presented below.

It is particularly important to establish whether conditions during the 30 years preceding the 1970 survey are similar to those during the 30 years preceding the present survey, as these indicate the boundary conditions under which the vegetation in each survey has developed. A long time series is therefore required, covering the period from at least 1940. Although data from weather stations relatively close to the study area were made available by Det Norske Meteorologiske Institutt (DNMI) in Oslo, they were incomplete. That for Sognefjell (16km to the southwest, 1413 masl), for example, had a temperature record dating back to only 1968 and data between 1990 and 1997 were missing.

A longer time series was available from the DNMI reports: 'Annual and seasonal temperature variations in Norway 1876 – 1997 (Report No. 25/98)' and 'Annual and seasonal precipitation variations in Norway 1896 – 1997 (Report No. 27/98)' (Hanssen-Bauer and Nordli, 1998; Hanssen-Bauer and Førland, 1998). Both reports are in the form of a collection of regional records; the south west region, relevant to this study, is based on data from 12 weather stations for the temperature series and 10 weather stations for the precipitation series.

Temperature variation. Figure 1.4 is reproduced from the report and shows the standardised annual mean temperature time series, together with seasonal time series, for each of the six regions (the south west is R2). The report found temperature increases of 0.4 - 1.2°C between 1876 and 1997, that were statistically significant (at the 5% level) in every region, except the northern inland region. The extent of the increase in temperature is not specified for individual regions, except in terms of standard deviations. The time series comprises a number of trends that are consistent in all regions: temperatures increase significantly from 1876 to the 1930s, followed by a significant decrease to the late 1960s, after which temperatures again increase significantly up to the end of the time series. The highest mean temperatures occur in the mid 1930s and in 1990. In the south west region, these annual trends reflect significant increases in both spring and autumn temperatures.

Variation in precipitation. The overall increase in precipitation in Norway is between 5 and 18%, but the highest increases occur in the north west, where increases exceeded 15%. Although there is positive trend in the south west, this comprises a period of relatively stable precipitation receipt between 1896 and approximately 1960, but a significant increase from 1960 to the end of the time series (1997). Seasonally, the increase reflects increased precipitation in the autumn, which is significant despite a decrease since the 1980s, and in the winter, which has increased significantly since 1960.

Their report also assesses evidence of a correlation between temperature and precipitation changes. In the southwest, temperature and precipitation are correlated with onshore winds, reflecting a change since the 1930s from southerly to southwesterly winds being precipitation bearing. The cause is thought to be the change, since the 1970s, to positive values in the North Atlantic Oscillation (NAO) index, pushing North Atlantic storm tracks further to the north (Hurrell, 1995; Beniston, 2000; Nesje et al., 2000; Yoo and D'Odorico, 2002).

1.4.1 Vegetation distribution changes

Further evidence of regional climatic change, together with the vegetation response, is provided in a series of studies by Kullman that monitor treeline changes in the Swedish Scandes. The studies reconstruct birch, pine and spruce tree limit chronologies since the Holocene. Early work (Kullman, 1993, 1998) using data from 1972 to 1991, detects a recent treeline advance, despite declining populations. Regeneration is low with evidence of defoliation and retarded growth. The most important influence is found to be early winter snowfall; if absent, low ground temperatures and frozen soils result in frost damage and desiccation. The birch belt was found to be expanding at its lower limit and a number of shrubs experiencing local dieback and altitudinal descent (e.g. *Betula nana, Empetrum hermaphroditum, Juniperus communis, Salix glauca* and *Vaccinium myrtillus*) (Kullman, 1998).

Temperatures were low at the start of the century, increasing until the 1930s and birch establishment was common until the 1950s but has been rare since then. Temperatures from 1961 to 1990 declined by 0.9°C compared to those between 1931 and 1960. Between the 1970s and the early 1990s, 30% of birch have perished, heath expanded and mortality is high amongst spruce and pine established in the 1920s and 1930s. Trees involved in the advance are those established in the 1950s. Cold winters in the 1980s and snow-free ones (e.g. 1995/96) are found to be most damaging, although the research does not take account of any effects from acid deposition. Kullman sees the climate as undergoing long-term cooling (Kullman, 1993) and hypothesises that the LIA may have been the leading trough in a neoglaciation, subsequent cooling being masked by anthropogenic warming (Kullman, 1998).

A similar pattern is discussed in Kullman and Kjallgren (2000), but increasing winter temperatures in the 1990s are now detected and described as anomalous against the trend of cooling. However, a search in 1998 and 2000 of an area first surveyed by Kilander in 1955, found 60 saplings of seven species above the limits cited in 1955 (Kullman, 2002). This represents an advance from 1095m to 1370m for birch. Shrub species also occurring at higher elevation include *Juniperus communis, Salix glauca, S. lanata, S. phylicifolia* and *Vaccinium myrtillus.* Ring counts show that the saplings have established since 1987. Factors contributing to this advance are cited as reduced summer snow duration, mild winters with reduced desiccation and reduced frost damage, leading to enhanced establishment, survivorship and growth. Birch, juniper and willow were not found at this altitude in the 1970s or in experimental plots during the period 1981-1992. While the absence of reindeer grazing contributes, increasing temperatures are cited as the principal cause and are associated with a shift from clonal to generative reproduction, the species involved being wind disseminated. Kullman concludes that vegetation appears as responsive as some physical parameters (glaciers, permafrost) rather than experiencing the expected inertia. Trees and shrubs are responding more rapidly and sensitively than the field layer.

1.4.2 Summary of section 1.4

The DNMI records indicated a significant overall increase in temperature between 1876 and 1997 that comprised three trends. Temperatures increased between 1876 and the 1930s, subsequently declining from the 1930s to the late 1960s after which they again increased to the end of the time series. Overall, there has been an increase in temperature of 0.4-1.2°C, and this reflected increases during the spring and autumn. Precipitation has also increased, but this was only significant from the 1960s in the south west region, and mainly reflects increases during the autumn and winter. Precipitation has increased in Norway by 5-18%, but the largest increases are in the north west.

The DNMI reports indicated that increasing temperature and precipitation are intercorrelated in the south west region, and both are correlated with onshore winds. The reports found that the climatic changes reflected a shift from southerly to south westerly winds being precipitation bearing, and associated this with a change to positive values in the NAO index since the 1970s. Nesje and Dahl (2003) considered this to be superimposed on climatic warming and Yoo and D'Odorico (2002) found separate signals from the NAO and what is described as CO_2 warming, that affected the date of ice break up in the Baltic. While there is evidence of climatic warming, the underlying causal processes are still subject to controversy. Karlén (1998), for example, found correlations between proxy climatic indicators and variation reflecting solar rather than anthropogenic forcing, decreasing temperatures between the 1940s and 1970s being cited as evidence.

Vegetation changes, including evidence of an increase in tree line elevation in the Swedish Scandes (Kullman and Kjallgren, 2000; Kullman, 2002) and increasing species richness on summits in the Jotunheim (Klanderud and Birks, 2003), have been attributed to increasing temperatures in Scandinavia

1.5 The scope of this study

This study is based on a repeat survey of an extensive range of long-term permanent plots, which were first surveyed in 1970. Both compositional change since 1970 and environmental conditions on the individual sites are included in the dataset. This dataset is unusual in terms of the opportunity it provides to follow successional development under a variety of environmental conditions. This section outlines a number of specific issues, arising from the study aims (section 1.2.3), to which this study may contribute.

(1) In examining species distributions and how they change over a period of 30 years, this study is expected to provide direct evidence of successional changes. However, as discussed in section 1.4, there is evidence of a change in climatic conditions during those 30 years compared

to the period immediately preceding the 1970 survey. Temperature and precipitation were significantly lower during the period from the 1930s to the late 1960s than they have been since 1970. Changes in species distributions since 1970 may be, at least in part, a response to that climatic signal.

Does this study detect evidence of a vegetation response to this climatic warming?

(2) Whittaker (1993) hypothesised that differences in plant physiological responses to the differing conditions on the major landforms within the study area might result in differences in developmental histories. In examining the dynamics of communities from each of these landforms, this study provides a test of this hypothesis.

Are there differences in terms of community dynamics between the major landforms within the study area?

(3) This study will examine the role of environmental variables within the vegetation groups that represent the different communities. This is a relatively fine-scale analysis and, combined with the coarser scale analysis of community dynamics, may detect differences in the ways that environmental variables operate at the different scales.

Does the environment have a different role in successional development when viewed at a coarse compared to a fine scale? How do the effects at each scale relate to each other?

(4) The geoecology model as defined by Matthews (1992) was based on research carried out on small glacier foreland systems in Scandinavia, particularly that at Storbreen.

Do the findings in this study support the geoecology model and in what ways do they contribute to its development?

Chapter 2: Literature review

2.1 Introduction

This chapter is not intended as a comprehensive account of successional theory, for which two recent reviews are particularly useful, that of Matthews (1992) and Walker and del Morel (2003). This discussion is focused on three areas. Initially there is a discussion of successional theory and attempts to understand the mechanisms of species replacements. Secondly, the relationship between the environment and vegetation patterning is examined. Finally, there is a consideration of the effects associated with climatic change, involving sources from palaeoecology and manipulation experiments. The literature cited is preferentially drawn from studies on glacier forelands and work undertaken in similar habitats. A review of analytical techniques is included in Chapter 3 (sections 3.6 to 3.8).

2.2 Divisions in successional theory

A fundamental division in the development of successional theory arose from differences between the ideas of Clements and Gleason. Clements takes a holistic, autogenic approach (Clements, 1916, 1928), characterising succession as driven by the vegetation, deterministic and directional, always progressive and converging to a stable climatic climax (Clements, 1936). The vegetation is considered as an organism, integrated and interdependent, undergoing development in a repeatable, deterministic and irreversible way. Gleason on the other hand, employs a species-level, reductionist approach (Gleason, 1917, 1926, 1927, 1939). He finds that distributions are individualistic, succession is indeterminate, unpredictable and not irreversible. Although emphasising chance in migration and variability in communities, he does not, however, propound entirely random assemblages nor deny the importance of competition (as thought by many of his opponents).

Clements' approach has been persistently influential, despite studies casting doubt on some important tenets of his work (Matthews, 1992; Walker and del Morel, 2003). This appears largely due to the importance of the processes identified in the theory: nudation, migration, ecesis, competition, reaction and stabilization (Clements, 1928). Gleason, on the other hand, attracted criticism from the outset, see Matthews (1996), and there was a general resistance to his ideas, although evidence supporting them is accumulating.

Clements' continuing influence is seen in holistic accounts of succession from the 1960s. Odum (1969, 1971) provides a checklist of factors that are expected to change predictably over the course of succession, culminating in a stable climax. Margalev (1968) has a systems ecology approach, seeing succession in terms of internal energy flow, information acquisition and increasing resistance to environmental perturbation.

The biological processes defined by Clements continue to dominate many successional studies, particularly those that seek a unifying theory: examples include Initial Floristic Composition (IFC) and Relay Floristics (Egler, 1954), Facilitation, Tolerance and Inhibition (Connell and Slatyer, 1977), Vital Attributes (Noble and Slatyer, 1980) and Successional

Hierarchy (Pickett et al., 1987, 1989). These models attempt to provide a unifying framework, but none have found general acceptability (Miles, 1987; Walker and Chapin III, 1987). The principal criticisms being that they are overly simplified, regard succession solely as a biotic process and describe the result or net effect of the mechanism (Connell et al., 1987; Walker and Chapin III, 1987; Matthews, 1992; Walker and del Morel, 2003).

Underlying these divergent approaches is the difference in scale at which the vegetation is examined. Clements adopts a coarse scale, focusing at the biome level (Clements, 1936); while Gleason studies the fine-scale detail of species distributions. Coarsening of the scale results in a loss of detail (Giller and Gee, 1987; Clark, 1993; Levin, 1993; Antonovics et al., 2001). While Clements (1936) recognises environmental discontinuities and anthropogenic disturbance as generating variation in the vegetation, small-scale heterogeneity is considered of little importance.

While Clementsian theory is considered holistic, it focuses almost exclusively on the plants, treating the environment as a subsidiary influence. Earlier work by Cowles (1899, 1901) had emphasised the roles of disturbance and 'physiography' (the interaction between the environment and the biota he sees as driving succession). Gleason continues this theoretical line, focusing on the relationship between species distributions and environmental variability. Rather than the Clementsian large-scale climax, no two communities are considered to be identical, although similar environments generate similar communities. This paved the way for a methodological change from an approach involving classification to one that used ordination, recognising continuous variation along environmental gradients (Curtis and McIntosh, 1951; Whittaker, 1967, 1975; Matthews, 1996). This association of vegetation patterning with environmental gradients is frequently restricted to a focus on a few factors, particularly disturbance and the generation of patches (Watt, 1947; Whittaker, 1953, 1975; Burrows, 1990). Disturbance has been seen as initiating, interrupting, redirecting and reversing succession (Matthews and Whittaker, 1987; Whittaker, 1991; Glenn-Lewin and van der Maarel, 1992; Foskett, 1998), but few authorities consider it in detail. As stated by Walker and del Morrel (2003), disturbance has not been fully integrated into successional theory.

Walker and del Morel (2003) also suggest that Gleason's focus on spatial difference and Clements' on temporal change should be integrated. Despite work on patch dynamics (Pickett and White, 1985; 1987) and the climax pattern hypothesis (Whittaker, 1953), many studies treat spatial and temporal variation as unrelated (Pickett, 1987; Whittaker, 1993).

2.3 Dispersal and establishment

In the absence of a seedbank, colonization depends on dispersal ability, subsequent germination and establishment in adverse conditions. Generally in primary succession, initial colonizers reach sites as seeds, occasionally as vegetative propagules (Bazzaz, 1987; Fenner, 1987; Gray, 1987a; Grubb, 1987a; Mortimer, 1987; Whittaker, 1993). However, the proportions of species that are present at the outset and those arriving as waves of colonizers vary in different systems, Initial Floristic Composition (IFC) or Relay Floristics (Egler, 1954). Dispersal ability may also impact on subsequent sequence development.

Studies of seed rain have found that dispersal generally occurs over distances of only a few metres from the parent plant (Ryvarden, 1971; Fenner, 1987; Stocklin and Baumler, 1996; Law et al., 2001) and may frequently be restricted to an area close to the parent plant (van der Valk, 1992). Longer distance dispersal may however be underestimated (Fort and Richards, 1998; Ennos, 2001) with secondary dispersal possibly exceeding that of primary (Johnson and Fryer, 1992), which has been discussed in relation to long-distance Holocene migrations by Cain et al. (1998). Ryvarden (1971, 1975) working in the Finse area, found that the most frequently occurring species present in the vegetation were present in the seed rain close to the glacier. His study involved relatively small glacier forelands (Kongsnutbreen and Blåisen).

Other authorities consider dispersal to be a more variable and stochastic process. Fastie (1995) found that proximity to seed source determined site composition at Glacier Bay, together with the subsequent trajectory of the sequence and the nature of the endpoint (Bormann and Sidle, 1990; Chapin III, 1993a). Late successional species have been found to be negligible in the seed rain on young land at this site (Chapin III et al., 1994). Whittaker and Bush (1993) attribute the slow development and depauperate nature of the vegetation on Krakatoa to the depletion of the source areas. Similarly at Mount St Helens, dispersal beyond a few metres from surviving vegetation is dependent on stochastic events, leaving many potential sites unoccupied (del Morel and Bliss, 1993; del Morel, 1993; del Morel et al., 1995). Development is further slowed by those species most able to disperse being intolerant of the harsh conditions (Wood and del Morel, 1987).

It appears that the size of the system is critical. When larger areas are involved (Glacier Bay, Mount St Helens and Krakatoa) with distance to sources exceeding several kilometres, dispersal presents a greater obstacle and becomes increasingly stochastic. Small systems, particularly where land becomes available progressively (as on glacier forelands), have much closer seed sources that increase in proximity over time. The foreland at Storbreen is such a system and dispersal ability is not expected to be a driving force even in the initial stages of colonization.

Harsh conditions on young land may prevent those species reaching it being able to establish without some mitigation (Franklin, 1987). Small-scale heterogeneity may provide "safe sites" with contrasting conditions to those prevailing in the area, the precise qualities varying according to the type of system. Moisture retention is important at Storbreen (Whittaker, 1993) and in the drought conditions of Mount St Helens (del Morel, 1993). In conjunction with nutrients, moisture may increase root development (Chapin III, 1993a), high root:shoot ratios are frequently seen amongst early pioneers, allowing access to more reliable, deeper sources of moisture (del Morel and Bliss, 1993; Matthews, 1992). Moisture is also seen as critical in the sandy soils in front of the Morteratsch Glacier in the Swiss Alps, while shade (in fissures, from stones and established plants) is important elsewhere on the foreland (Stocklin and Baumler, 1996). Surface undulations and established plants also trap seeds and other wind blown particles, and are important at Glacier Bay (Walker, 1993) and at Mono Lake, California, where strong winds and a smooth surface combine to delay establishment (Fort and Richards, 1998). Jumpponen et al. (1999) working at the Lyman Glacier, Washington give a more detailed assessment of attributes associated with safe sites: collecting and retaining moisture, preventing desiccation and therefore promoting germination while bird perches and faecal deposits provide seeds with a ready source of nutrients (cf. Niederfriniger Schlag and Erschbamer, 2000). Hodkinson et al. (2002) found safe sites concentrated imported invertebrates and allonchthonous detritus, improving nutrient and moisture status, and possibly being the sites of initial soil formation. Species may have particular requirements from such sites and this may contribute to early species patterning (van der Valk, 1992; Titus and Tsuyuzaki, 2003). Although competition is generally regarded as being reduced on young compared to old ground (Margalev, 1968; Krebs, 1985; Bazzaz, 1987; Peet, 1992; Chapin III, 1993a; Kupfer and Runkle, 1996; Lichter, 2000; Guo, 2003), Parrish and Bazzaz (1982) found species characteristic of early sites capable of strongly competitive interactions. This may allow uptake of unpredictably occurring pulses of nutrients (Bazzaz, 1987) pre-empting resources otherwise available for faster-growing species (van Wijk et al., 2003). High levels of competition may result from the concentration of seedlings in safe sites (Mortimer, 1987; Chapin III and Körner, 1995b).

Cryptogams are often amongst initial or early colonizers, e.g. black crusts at Glacier Bay (Chapin III et al., 1994) and cyanobacteria on Svalbard (Hodkinson et al., 2003), although they are not normally essential prerequisites. They have been associated with substrate stabilization (i.e. filamentous binding, rafts), chemical dissolution and physical exfoliation of bare rocks (Grubb, 1987a; Mazzoleni and Ricciardi, 1993; Vestal, 1993; Walton, 1993; Wynn-Williams, 1993). They have also been found to trap aeolian material (Frenot et al., 1995, 1998), and where mats develop, soil aggregation, microclimate amelioration, nitrogen-fixing and moisture retention may result, generating safe sites that may subsequently be colonized by higher plants (Billings, 1974a; Mazzoleni and Ricciardi, 1993; Sprent, 1993; Vestal, 1993; Walker, 1993; Walton, 1993; Wynn-Williams, 1993; Vetaas, 1997). However, Hahn et al. (1996) suggest that they may provide competition with higher plants at Imnavait Creek (Alaska).

Clements (1928) considered that succession operated through successive waves of invading species. Distinguishing this process as 'Relay Floristics', Egler (1954) put forward an alternative hypothesis of 'Initial Floristic Composition' (IFC), in which all species occurring in a successional sequence were present at or near the outset, the changing pattern of dominants resulting from differing life history traits, particularly growth rate and longevity. According to this theory, as mortality increases amongst early species, later ones replace them. Reaction is thought to be implicit in Relay Floristics (Pickett et al., 1987; Matthews, 1992), while IFC indicates that initial conditions are suitable for the establishment of all species.

From the available literature, examples of IFC occur more frequently in secondary succession: for example in the *Calluna* cycle (Miles, 1987), in the broom/bracken sequence in the Portland Hills, New Zealand (Partridge, 1992) and in Central New England following the destruction of the canopy in a hurricane (Hibbs, 1983). Matthews (1992) quotes examples from primary succession at Glacier Bay, but the normally later-colonizing species are stunted and show signs of nutrient deficiency, being unlikely to be the same individuals that dominate later. At Mount St Helens, late species act as pioneers in some situations where seed sources are nearby (del Morel and Bliss, 1993). Whittaker (1993) found occasional, healthy examples of later species growing on young land, but this was infrequent and did not include all species, some never occurring on young land.

Burrows (1990) considers that as a general rule, late species do not occur on young land in primary succession because propagules are unable to reach it. However, as seen above, the seed rain in small systems is likely to contain all species, although later species may be less numerous. Whittaker (1993) on the other hand considered that there was a filter to establishment of later species at Storbreen (see also Foskett (1998) and Vetaas (1994) at Bodalsbreen). Such a filter may involve the need for specific conditions in safe sites or competitive interactions with early species (Parrish and Bazzaz, 1982).

It appears that IFC is more characteristic of secondary succession, while Relay Floristics typically occurs in primary sequences. This may be due to the harsh and limiting conditions or, possibly, competition at safe sites. Lichter (2000) at Lake Michigan, found that late species were able to tolerate conditions on young land, but seed predation and weather conditions constrained their establishment. Primary succession pioneers have some of the characteristics of late species, rather than the differential life history traits of IFC, often being slow-growing, long-lived and tolerant of low nutrients (Grubb, 1987a; Chapin III, 1993a). It appears that generally the classic model of Relay Floristics applies in primary succession, although the precise cause of the failure to establish on young land varies between sites depending on local conditions.

2.4 Resources

Dispersal constraints are generally regarded as limited to initial stages, with other processes responsible for subsequent replacements, unless IFC occurs. A process that has been connected with these replacements is the response to changing resource levels (i.e. nutrients, moisture and light). Early in the sequence most nutrients and light are generally in good supply (Vitousek and Walker, 1987). It is often stated, however, that nutrients are low in initial stages of succession (e.g. Whittaker, 1975; Pickett et al., 1987), possibly because nitrogen is frequently limiting (Chapin III, 1993a; Chiba and Hirose, 1993; Miles and Walton, 1993; Walker, 1993; Chapin III et al., 1994). Phosphorous is likely to be at maximal levels, being produced by weathering (Walker and Syers, 1976; Vitousek and Walker, 1987; Chapin III et al., 1994). Moisture may be low or poorly retained (Chapin III, 1993a). As more plants become established, nutrient uptake increases and availability depends increasingly on mineralization and cycling. The plants provide organic material to the soil, improving water and nutrient retention (Whittaker, 1975; Vitousek and Walker, 1987; Blundon et al., 1993; Bradshaw, 1993; Chapin III et al., 1994). Nitrogen accumulates from atmospheric deposition, fixers and nitrifying bacteria (Huston and Smith, 1987; Marrs and Bradshaw, 1993; Walker, 1993; Chapin III et al., 1994). Light and phosphorous decrease in availability as a result of plant activities (Chapin III et al., 1994), and both nitrogen and phosphorous are subject to leaching, immobilization in unavailable forms, in plant and in microbial biomass (Walker and Syers, 1976; Vitousek and Walker, 1987; Schimel et al., 1996; Hobbie et al., 1998). Late in a sequence, availability of light and nutrients is likely to be low, and specialization in resource acquisition is increasingly prevalent e.g. vertical root segregation (Bazzaz, 1987).

The autogenic changes in soil conditions over time are the basis of 'reaction' (Clements, 1928) i.e. the effect of plants on the environment. It has been described at the Franz Josef Glacier, New Zealand (Burrows, 1990); at Glacier Bay (Bormann and Sidle, 1990; Burrows, 1990; Hobbie et al., 1998); and at the Lyman Glacier Foreland, Washington (Jumpponen et al., 1998). The processes identified have contributed to the concept of 'facilitation' (Connell and Slatyer, 1977). This is an active process thought to drive species replacements; early species creating conditions favourable for later species but disadvantageous for themselves (Connell and Slatyer, 1977). An alternative view is that changes are passive, coincident to the presence of vegetation, giving rise to the term 'amelioration' (Grubb, 1987a). Neither Connell and Slatyer (1977) nor Matthews (1992) can find substantial evidence of 'facilitation' driving replacements. There is, however, a growing body of evidence to suggest that early invaders, particularly N-fixers, resist invasion by later species, with the net immediate effect of their presence resembling the 'inhibition' model (Connell and Slatyer, 1977; Walker and Chapin III, 1987; Connell et al., 1987). Examples include *Alnus crispa* thickets at Glacier Bay (Chapin III, 1993a; Walker, 1993; Chapin III et al., 1994), *Lupinus lepidus* patches on Mount St Helens (Wood and del Morel, 1987; Morris and Wood, 1989; del Morel, 1993; del Morel et al., 1995) and *Salix* spp. on the foreland of the Lyman Glacier, Washington (Jumpponen et al., 1998). This process involves control of resources belowground, with shading and physical interference aboveground. Later species may be unable to establish or, if present, are disadvantaged and 'tolerate' the conditions until the death of the incumbent plant(s) releases resources (particularly nitrogen and light) (Wood and del Morel, 1987; Jumpponen et al., 1998). This may subsequently ease establishment constraints for later species (particularly those with higher nitrogen requirements) and may increase the rate of successional replacement.

2.4.1 The role of mycorrhiza

The models discussed above expand a Clementsian concept but retain the fundamental assumption of autogenic (plant-mediated) control of succession. Recent work that explores plant relationships with mycorrhiza suggests that plant access to resources may involve greater complexity and an element of environmental interaction.

Infection by mycorrhiza is widespread, affecting an estimated 95% of plants (Read, 1999). The relationship is thought to be particularly important in increasing availability in nutrient-poor soils. Mycorrhiza occur extensively at high latitude (Woodward and Kelly, 1997), although high ratios of root to shoot mass (R:S ratios) suggest they may be absent from extreme high-altitude sites (Körner and Larcher, 1988). They have been shown to occur as a successional sequence (Grubb, 1987a; Pickett et al., 1987), increasing in frequency and undergoing compositional change (Jumpponen et al., 2002). They have low frequency on young land (Chapin III, 1993a; Read, 1999; Jones and Henry, 2003), occurring rarely before 40 years on the Lyman Glacier foreland (Jumpponen et al., 2002; Hodkinson et al., 2003). There is disagreement concerning the reason for this. Read (1999) considers that the fungi are destroyed by disturbance. Chapin (1993a) conducted transplants of *Alnus crispa* to young soils finding that the ectomycorrhiza were lost. This he attributed to high pH, although the reverse pattern is quoted by Crawley (1997) (lack of infection amongst late species being attributed to low pH). In any case, early species (such as *Saxifraga cespitosa*) are rarely infected, while later ones (particularly *Salix* spp.) generally are (Jumpponen et al., 1998; Ohtonen et al., 1999). The establishment of later species may be slowed by a low level of soil infection (Jones and Henry, 2003).

Pornon and Doche (1994), working in the Swiss Alps, consider the presence of mycorrhiza to obviate the need for within-stage competition. Schimel et al. (1996) on the other hand, show that the competitive ability of some later successional species is enhanced, citing the advantage of late successional grasses over earlier species.

Different types of mycorrhiza affect different functional types and take up different forms of nutrients (Chapin III et al., 1995b). In addition to nutrient uptake, mycorrhiza are involved in active foraging, producing enzymes that directly attack the substrate, protecting against disease (the fungal mantle physically protecting the roots and producing an antifungal compound), improving water supply and increasing reproductive success (Read, 1999). The experimental work of Fitter et al. (2000) shows mycorrhizal proliferation in nutrient-rich soil patches, increasing the speed of response by reducing the need to initiate additional roots. The cost to the plant is 10-85% of photosynthate according to Rossow et al. (1997), although the infection acts as a carbon sink, stimulating photosynthesis by up to 15% (Read, 1999).

Rossow et al. (1997) investigating browsing on willow and balsam poplar at the Tanama River, Alaska found that infection was reduced where herbivory was intense, resulting in a shift in dominance to less palatable alder and spruce.

The presence of mycorrhiza is important late in the sequence as concentrations of phosphorous decrease (Vitousek and Walker, 1987; Read, 1999). As indicated above, *Salix* spp. have high levels of infection, they also have the greatest rates of phosphorous uptake in tundra ecosystems (Shaver, 1995). The restriction of *S. herbacea* to snowbeds, despite the ability to grow rapidly at the edges (Wijk, 1986b), is seen as resulting in part from the low levels of mycorrhiza in the peripheral soils (Stanton et al., 1994).

This process may therefore be directly involved in species replacements and contribute to the general restriction of late successional species to more developed soils. Relationships are species-specific and the various types take up different forms of nutrients, contributing to specialization in later stages of the sequence. They are sensitive to photosynthate supply and may be lost if grazing pressure is high. A change in mycorrhizal availability in soils may affect competitive interactions, particularly involving the various *Salix* spp..

2.4.2 Competition for limiting resources

Another Clementsian concept that has been used in explanations of species replacements is that of 'competition'. Early species are seen as being outcompeted by later ones (Fitter, 1987; Gray, 1987b; Chapin III, 1993a; Chapin III et al., 1994; Rees et al., 2000). Experimental work by

Parrish and Bazzaz (1982) concludes that competition acts as a selection pressure amongst later species; increasing plant density leads to specialization, allowing coexistence and maximizing resource use. Amongst early species, however, the ability to survive in an unpredictable and harsh environment is seen as the predominant selection pressure. This has contributed to marked differences found in a wide range of traits between early and late species.

Early species have generalist strategies, high plasticity and broad niches, overlap not being of importance when plant density is low; this allows utilization of a broad range of habitats in changing conditions (Margalev, 1968; Leigh, 1975; Edwards and Gillman, 1987; Burrows, 1990; Peet, 1992; Whittaker, 1992). Specific requirements increase (Gray, 1987b), and plasticity (particularly in reproductive allocation and photosynthesis) falls, later in the sequence (Margalev, 1968; Bazzaz, 1987; Gray, 1987b; Burrows, 1990), niches are narrower and specialization increases. This reduction in niche breadth (or narrower Gaussian curves on environmental gradients) reduces overlap and therefore competition (Leigh, 1975; Burrows, 1990; Crawley, 1997).

Contrasting environmental selection pressures therefore result in contrasting plant life history traits. Early, generalist species with plastic responses are better able to react opportunistically and tolerate unpredictable and often stressful conditions. Environmental amelioration and increased plant density accompany successional development so that selection pressure is subsequently for traits that allow coexistence; specialization leads to niche separation and, while species may be strongly competitive within that range, the general level of competition falls e.g. by vertical segregation of rooting systems.

2.4.3 Tilman's resource-ratio hypothesis

Tilman describes his hypothesis as an allogenic model explaining species replacements (Tilman, 1985), but his focus is on the restricted range of environmental factors directly contributing to changing resource levels (Tilman, 1981, 1985, 1986, 1988). Resource changes form a gradient in time to which species have evolved (Tilman, 1985), resulting in differing requirements and competitive ability (Tilman, 1981, 1986). The principal resources are light and a soil resource (usually nitrogen), availability of the two being seen as inversely correlated. Species are superior competitors for one, but inferior for the other, with the ratio between the two governing a shifting sequence of dominants as disturbance, cycling and consumption alter the relative proportions (Tilman, 1985, 1988). Species with lower equilibrial requirements for a particular resource reduce it to a level insufficient for a species with a higher requirement (Tilman, 1985). The hypothesis does not suggest that one resource becomes more important as a limiting factor, but that different species are superior competitors at particular ratios (Tilman, 1985).

The resource-ratio hypothesis has been criticised by Thompson (1987) as it treats competition as important in all habitats and as a variable species attribute, rather than being a consistent species strategy only in nutrient-rich ones, as propounded by Grime (1977, 1979). Tilman (1987) however presents evidence of variable responses, which may be reversed or vary proportionally, largely as a result of differential allocation to above- and below-ground structures (R:S ratio).

However, Cahill (2003) subsequently found that root mass does not respond directly to increased competition, although the results of experimental work suggest that response varies with the level of competition (Chapin III, 1980; Parrish and Bazzaz, 1982; McGraw and Chapin III, 1989; Chapin III and Shaver, 1995; Pugnaire and Luque, 2001).

Grime (1977, 1979) and Thompson (1987) argue that rather than competing, plants in low resource environments adopt a 'stress' strategy of low growth rate and endurance of low nutrients. Take-up is seen as limited by diffusion rate, so that high R:S ratios will be of little benefit. McGraw and Chapin (1989) however found a reversal in competitive ability between *Eriophorum vaginatum* (low-resource) and *E. scheuchzeri* (high resource); in transplant experiments, *E. vaginatum* outcompeted *E. scheuchzeri* on nutrient-poor sites having greater resource-use, rather than uptake efficiency. Chapin and Shaver (1995) suggest that competition is more intense at low nutrient levels.

Lichter (2000) tests Tilman's hypothesis in the context of the primary successional sequence of the Lake Michigan sand dunes. He states Tilman's principal argument as being that soil development drives succession, testing this by reciprocal transplants between early and late sites. Late species were able to establish on young land, when seed predation and climate allowed this; early species rarely established on mature sites (attributed to light competition exacerbated by litter burial). He concludes that succession is driven not by soil development but (initially) by dispersal ability with competition becoming important subsequently. There is no testing of species requirements or nutrient availability, and it is not clear whether late species are directly competing with early ones on the young sites. Tilman (1985, 1994) and Tilman and Wedin (1991) have acknowledged the importance of dispersal ability, applying the hypothesis to sequence replacements. Tilman generally equates 'soil resources' with nitrogen (rather than 'soil quality') and this increases in most primary systems over time. Lichter (2000) does not discuss changing ratios over time between two resources, but accepts that competition for light plays a major role in later stages. The work seems to be primarily a test of facilitative effects and the results may support Tilman in that they provide evidence that competition for resources drives succession.

While experimental evidence supports some areas of the hypothesis, without knowledge of species requirements (Matthews, 1992) and taking into account the prevalence of stochastic events, it has a limited usefulness as a predictive tool. It explains pattern rather than the complexity and detail of the replacements (Olff et al., 1993). To provide a realistic and predictive model, incorporating variation in important resources between stages, for different plants and within an environmental context, Tilman (1985) accepts that the forest-gap simulations of Botkin and Shugart might be more useful.

Tilman (1985, 1988) attempts to integrate autogenic and allogenic factors, recognising the importance of interactive processes. It marks a broader approach than is seen in purely biological explanations, with the understanding that plant life history traits have evolved in response to the environment. The full range of environmental effects is not included; physical and climatic severity, the effects of site history, microsites and disturbance may result in constraints that differ between habitat types.

2.4.4 Positive interactions

Several examples of 'facilitation' discussed above had a net inhibitory outcome (Walker and Chapin III, 1987; Connell et al., 1987; Wood and del Morel, 1987; Morris and Wood, 1989; del Morel, 1993, 1993, 1995). Competitive interactions may occur generally (Walker and Chapin III, 1987; Lichter, 2000) rather than restricted to productive (low disturbance, low stress) environments (Grime, 1977, 1979). Experimental work associated with Tilman's Resource Ratio Hypothesis has shown that plant-plant relationships can vary along environmental gradients of changing resource levels (Chapin III, 1980; Chapin III and Shaver, 1995). A recent reassessment of interactive processes has brought these strands together in a consideration of 'positive interactions' (Bertness and Callaway, 1994; Callaway et al., 2002).

The role of nitrogen-fixers such as *Alnus crispa* and *Lupinus lepidus* was initially assumed to be facilitative (nurseplants). Similar in effect to safe sites, discussed in section 2.3, the potential benefits include increased nutrient availability, trapping of particles and seeds, perches for birds and moisture retention (Morris and Wood, 1989; del Morel, 1993; Franco-Pizana et al., 1996; Pugnaire and Luque, 2001). However, the presence of the established plant complicates this, with accompanying detrimental effects such as shading, root competition and litter accumulation. The net effect may be inhibitory, as discussed above (Walker and Chapin III, 1987; del Morel and Bliss, 1993), but the mechanism may be more complex. Compared to exposed sites, those associated with nurseplants may show improved germination success (Franco-Pizana et al., 1996). Where fewer seeds germinate or are able to establish, those that do may grow larger and be more likely to flower (Morris and Wood, 1989). Increased survival is also associated with patches (Walker and Chapin III, 1987) possibly due to protection from insect herbivory (Jumpponen et al., 1998; Bishop, 2002).

Carlsson and Callaghan (1991) investigating aggregations of plants in arctic and alpine situations looked at the shelter effects of shrubs on *Carex bigelowii* in Swedish Lapland. The net effect appears facilitatory, the shrubs increasing protective snow cover, preventing desiccation, improving microclimate and increasing nutrients (trapping litter and intercepting detritus). Similar effects are associated with growth within *Racomitrium lanuginosum* mats (Billings, 1974a; Press et al., 1998; Lee, 1999; Niederfriniger Schlag and Erschbamer, 2000). It was hypothesised that beneficial aboveground effects dominated resulting in net facilitation, while competitive belowground interactions were minor.

This and other experimental work reveals a complex gradient of responses to multiple environmental factors, the net outcome varying with a shifting pattern of positive and negative contributions. The balance of facilitation to competition/inhibition changes with the extent and direction of changing availability, limiting factors and whether the resource can be substituted (Bertness and Callaway, 1994; Holmgren et al., 1997). The position on this gradient varies with the level of stress or site severity experienced by the plants.

Evidence of such gradients is drawn from habitats that allow comparison of high to low stress or severity. Experimental work by Hacker and Bertness (1995) tests the relationship between *Juncus gerardii* and the shrub *Iva frutescens* in salt marshes. *I. frutescens* was unable to grow at low positions without the mitigating effects of *J. gerardii*, primarily the release of 0_2 (alleviating anoxia) and shading (reducing evaporation and therefore hypersalinity). *I. frutescens* extends its distribution into harsh conditions it would not otherwise have the morphological or physiological plasticity to tolerate. At higher elevations where conditions were less harsh, *I. frutescens* outcompetes *J. gerardii.* Callaway (1997) found competition between *Pinus albicaulis* and *Abies lasiocarpa* at low elevation, but at higher sites *A. lasiocarpa* was aggregated around *P. albicaulis.* He suggests that the relationship also changes temporally, in response to climatic stress. Callaway et al. (2002) describe a comparative study of the effects of neighbour removal between high and low sites associated with eleven mountain peaks. Competition dominated at low elevation, but at high-altitude with severe conditions, higher levels of biomass and productivity were associated with the presence of neighbours. He identifies amelioration of microclimate (raising temperature, protection from wind scour) and disturbance (increased soil stability, protection from herbivory). Pugnaire and Luque (2001) studied relationships along a gradient of increasing moisture stress in northeastern Spain. Belowground competition occurred ubiquitously, while aboveground effects varied between facilitative (shade, increased moisture availability in high stress sites) and competitive, lower moisture stress reducing the benefit of shade.

2.4.5 Relationship with other work

Callaway (1997) sees positive interactions as indicative of interdependence, conflicting with Gleason's concept of individualistic distributions (Gleason, 1939). However, the examples quoted appear to be opportunistic; not dependent on a specific mutualism or the result of coevolution, but taking advantage of physical amelioration in severe conditions. Shelter by rocks or wooden fences (Carlsson and Callaghan, 1991) may produce similar responses. Callaway (1997) suggests that some relationships may be more specific (shared mycorrhiza or pollinators).

Competition in stressful conditions and involving differential above- and belowground effects conflicts with Grime (1977, 1979), who sees competition as confined to fertile habitats with the whole plant behaving consistently. Grime's view is supported, but only partially, in a recent study by Bonser and Reader (1995): competition increased with biomass, but nonetheless occurred in all environments tested.

This work advocates the consideration of interactions coupled to their environmental setting, recognising that they cannot be understood in isolation (Bertness and Callaway, 1994). It therefore represents a broadening of the purely biological approach, but does not develop a methodology by which this can be applied.

2.4.6 Gradient analysis

Callaway (1997) sees inconsistencies between his work and Whittaker's gradient analysis (Whittaker, 1953, 1967, 1975). Gradient analysis expresses species response to their environment and is related to the concept of individualistic species distributions propounded by Gleason (1926, 1939). Plotting a sequence of species distributions on an influential environmental gradient should ideally produce a series of bell-shaped Gaussian curves, indicating normal distributions and having relatively little overlap (Connell and Slatyer, 1977; Whittaker, 1985; Giller and Gee, 1987; Pickett et al., 1987; Guo, 2003). The species curves are considered to represent niches, with the maxima indicating optimal conditions and the breadth of the curve showing the extent of tolerances (Whittaker, 1967; ter Braak, 1987a), while the degree of overlap indicates the extent of interspecific competition (Burrows, 1990). However, the work discussed above suggests that relationships vary along the gradients, undergoing shifts with the severity of conditions and the availability of a complex of resources.

There are other exceptions to the idealized form of gradient analysis. Burrows (1990) discusses Gleason's concept of temporary, fluctuating and constantly varying associations. Pickett et al. (1987) suggest that competitive ranking can be affected by disturbance. Wolda (1987) finds tolerance is affected by seasonal fluctuations. Digby and Kempton (1987) emphasise the importance of secondary gradients and species interactions. Clark (1993) discusses neighbour effects that influence plant interactions via humidity, wind resistance, groundwater and subsurface flow. Stability may be needed for these relationships to develop fully (Tilman, 1987), while in a fluctuating environment they are the result of transient dynamics.

Changing relationships and plant-environment interactions suggest mechanisms by which the environment can influence community development and species replacements.

2.5 Environmental resistance and the geoecological approach

Gradient analysis describes species reaction to particular environmental factors, but does not explain replacements. Svoboda and Henry (1987) view succession as driven by a biological driving force (BDF) opposed by environmental resistance (ER). The initial balance determines the type of succession seen, so that in severe environments the strength of the ER may prevent the development of a significant BDF, resulting in non-directional, non-replacement succession (Jones and Henry, 2003) (cf. Muller, 1952). It also contributes to an understanding of directional replacements, which occur as BDF increases relative to ER, allowing more of the available species to enter the sequence. As pointed out by Matthews (1992) however, plant-environment interactions may enhance or reinforce vegetation development as well as resist it.

Geoecology, as defined by Matthews (1992), involves a coupling of the environment and biota and emphasises landscape processes. Viewing succession from this standpoint produces a model where autogenic influences increase in strength over successional time while allogenic ones diminish. In severe systems, allogenic factors will continue to dominate while autogenic factors do not develop sufficiently to exert an important influence, resulting in non-directional, non-replacement succession. In habitats that are less severe, some overlap will occur so that autogenic factors dominate, particularly in the final stages. This trend becomes more pronounced with increasingly favourable conditions. Additionally, environmental factors are not seen as simply resisting autogenic development, but may enhance it. As well as influencing successional rate, environmental effects are more pervasive, affecting the nature of the successional sequence (Matthews, 1992): system complexity (the number of developmental stages); whether mature stages become more or less similar (converging or diverging); which species and growth forms are able to colonize and the biomass they produce; and the extent to which pioneer and mature assemblages differ. While this provides a framework by which environmental factors can be incorporated into a model, it is a general statement rather than a detailed approach (Walker and del Morel, 2003). The single curves used to depict the model (Matthews, 1992) may confound the variety of disparate and interacting allogenic and autogenic factors.

2.6 Progression towards the climax

There has been a considerable debate over the concept of the 'climax', the culmination or 'highest' developmental point of the sequence. Some authors feel that the term's meaning is ambiguous and preferentially use the term 'mature vegetation' (Foskett, 1998) or endpoint (Krebs, 1985; Fastie, 1995). Both of these terms are used in this study because of various connotations, particularly those of homogeneity, autogenic dominance and stability.

This section considers the classic view of the nature of the endpoint of successional changes and ways in which subsequent work has contributed to its development.

2.6.1 The classic view of the climax

Clements saw the climax as climatically determined, stable indefinitely (unless perturbed by man), covering large continental areas and unified by the nature of its dominants (Clements, 1928, 1936). Variability results from gradual climatic changes between boundaries, in the composition of subdominant species, various sub-, pro- and post-climaxes, which may be maintained stably by disturbance. Clements propounds a holistic and organismic view of succession applied at a large scale; much of the criticism has emerged as successional systems are considered at a more detailed level (Matthews, 1992; Walker and del Morel, 2003).

The climatic monoclimax rarely receives support in modern literature. Even Margalev (1968) and Odum (1969), do not accept that a uniform climax vegetation type covers wide areas. They see the climax as comprising organisational units in a state of dynamic tension and separated by relatively sharp boundaries or ecotones.

Tansley (1920, 1935) was among early workers who acknowledged that the landscape comprises a variety of vegetation types. In his concept of the polyclimax, other types of mature vegetation occur regionally, in addition to the climatically controlled climax, and are controlled by different environmental conditions. The polyclimax concept visualised the landscape as a mosaic, with patches of differing vegetation marked by discontinuities.

Watt (1947) describes what is subsequently termed cyclic succession. Plant aggregates form a patch mosaic as a result of differing climatic and soil conditions. This develops by alternating periods of upgrading and downgrading, as vigour changes. This process is seen as initially stochastic, depending on chance dispersal, becoming increasingly ordered over time.

2.6.2 Spatial-temporal patterning and disturbance

Whittaker's (1951, 1953, 1967, 1975) climax pattern model describes and seeks to explain vegetation that varies continuously. Vegetation composition is related to underlying environmental gradients, with species populations individualistically distributed along them. As stated by Matthews (1992) p 290:

> "Succession at any point in the landscape and the resulting climax communities depend on the precise combination of environmental factors at that point."

The resulting pattern is of continuous, gradational changes, rather than a mosaic, and boundaries that are blurred rather than sharp (ecoclines rather than ecotones). Many of Whittaker's concepts have been generally accepted and provide a realistically complex interpretation of community composition (Matthews, 1992).

Clements (1936) saw disturbance as influencing vegetation patterning transiently, unless anthropogenically induced. This view has been expanded, particularly by Horn (1974, 1976, 1987) as generating discrete, scattered patches due to small-scale, frequent events.

Four causal processes have been discussed: environmental discontinuities, patch mosaic cycles, interacting and overlapping environmental gradients and disturbance-initiated patches. Various combinations of these factors are used to explain spatial patterning. Burrows (1990) describes the vegetation as an environmentally controlled mosaic, modified by the plants, and interrupted by disturbance, environmental discontinuities and intense competition. Mature vegetation withstands small-scale disturbance, but intense events reset succession, possibly maintaining a subclimax. Disturbance is seen as irregular, unpredictable and limiting the influence of the dominant species. Krebs (1985) sees two fundamental patterns superimposed on one another; a continuum of environmental gradients and patches bounded by discontinuities including those where disturbance has resulted in retrogression. Crawley (1997) considers patches to be generated by disturbance, dispersal and pathogens, resulting in cycles that are out of synchrony. Wiens (2000) describes disturbance as disrupting a matrix comprising environmental gradients, producing patches at both fine- and coarse-scales.

At Storbreen, Matthews (1976) found that vegetation changed continuously along environmental gradients rather than occurring as discrete units. A similar view is held by Crouch (1992), but with disturbance creating 'younger ground', where pioneers persist, and cycles of succession on the oldest ground.

Disturbance has been seen as creating 'regeneration gaps' (Grime, 1979), interrupting and resetting succession (Matthews and Whittaker, 1987). Although frequently destructive, disturbance may act as a selection pressure, as proposed by Brandani (1983) in his discussion of *Salix* and *Betula* spp., while Matthews (1999) sees it as a continuum ranging from beneficial to detrimental effects (e.g. cryoturbation, which both damages plants and creates new microsites).

Disturbance also produces a temporal dimension to patterns of spatial heterogeneity. Patches out of synchrony with the surrounding vegetation change over time, possibly integrating with it but new pathways may be opened. Both Greig-Smith (1983) and Clark (1993) emphasise this temporal dimension (Crawley, 1997; Wiens, 2000).

The vegetation response to these environmental gradients has been seen as involving both reaction and interaction (Connell, 1975; Bazzaz, 1987). Gradients change temporally and plants may survive in suboptimal conditions for substantial periods of time; the patterning may therefore involve both current and historical gradients (Brown, 1988).

Patterning is therefore more complex than a monoclimax uniformly covering extensive areas (Clements, 1936). It involves the vegetation response to environmental gradients (Whittaker, 1953, 1967) with gradual transitions (ecoclines) when they occur sequentially in space. Against this pattern, or matrix (Wiens, 2000), various environmental and biotic factors create patches with sharp boundaries (ecotones), including disturbance, environmental discontinuities, pathogens, clumped dispersal and intense competition. Disturbance is generally viewed as being destructive but may be integral to successional processes. There is also a temporal dimension; the development of disturbed patches and interactions prompting changes in the gradients.

2.6.3 Convergence and divergence

Rather than increasing similarity and convergence to a monoclimax (Clements, 1928, 1936) , the gradients discussed above suggest separate developmental strands that may alternatively diverge over time. Examples of both convergence and divergence occur, the particular trajectory depending on site conditions.

In southern Norway, examples of convergence occur on glacier forelands in the Jotunheimen and Jostedalsbreen regions (Foskett, 1998) and at Bødalsbreen (Vetaas, 1994), while Matthews (1976) considered that divergence occurred at Storbreen (cf. Whittaker, 1993; Foskett, 1998). The principal difference involves environmental severity and the extent to which plant-mediated processes are able to develop (Matthews, 1992, 1999). In practical terms, this appears to depend critically on the growth form comprising the canopy. Divergence has been associated with a shrub canopy at high-altitude (Matthews, 1999), where environmental stress limits the cover (Foskett, 1998). At lower altitude, trees form the canopy, which tends to insulate the system from environmental influences (Vetaas, 1994; Matthews, 1999). Kupfer and Runkle (1996) examine gap dynamics in Hueston Woods Preserve, Ohio. The process involves initial divergence followed by convergence as the canopy closed and competitive sorting produced more uniform vegetation. The canopy both buffers against environmental perturbation (Vetaas, 1994; Foskett, 1998; Matthews, 1999) and provides conditions where plant-mediated processes can operate.

Divergent systems may also result from differing stable endpoints due to persistent compositional effects caused by resource variation (Inouye and Tilman, 1988), dispersal and stochastic events at Mount St Helens (del Morel and Bliss, 1993) and Glacier Bay (Fastie, 1995), and disturbance-related shifts in composition (Pickett et al., 1987; Peet, 1992). Convergence occurs where dominance (Brandani, 1983) or competition (Peet, 1992) is high. Initial site differences may persist throughout the sequence, but composition becomes increasingly differentiated as specialisation increases within the mature vegetation.

2.6.4 Stability

Clements (1936) saw the climatic climax remaining stable indefinitely unless disturbed by man, natural disturbance being rapidly repaired. Since the 1960s this concept has been subject to critical examination with the increasing focus on variation and heterogeneity (Wiens, 2000).

Stability implies both resistance to change and constancy in composition. While it is generally accepted that temporal change decreases during succession (e.g. Peet, 1992), there is disagreement as to the reasons. Margalev (1968) considers that 'information acquisition' by the vegetation reduces the effects of environmental impacts and fluctuations, responses becoming indirect and specialisation increasing, leading to an integrated, interdependent and efficient system that resists change. Grime (1979) sees 'inertia' as resulting from permanent environmental amelioration (changes in mineral status, soil structure and microclimate). Whittaker (1975) ascribes increased resistance to the change from short- to long-lived species and the loss of directionality. Each emphasises different aspects of increasing maturity in the vegetation.

Equilibrium (or dynamic equilibrium) with the connotation of oscillation around a stable mean (Burrows, 1990; Walker, 1997) may be a preferable term to stability. Whittaker (1975) uses the term 'steady-state' (equilibrium) to denote a relatively constant population generated by a flow of individuals (Watt, 1947; Krebs, 1985). Equilibrium is therefore perceived as an autogenic quality maintained in the face of environmentally derived perturbation. While the discussion of climax patterning primarily concerned spatial variation, in discussing its attainment and maintenance, the emphasis is on temporal variation.

Some authorities consider that environmental perturbation is continual and pervasive, sufficient to prevent equilibrium being attained (Williamson, 1988; Crawley, 1997; Huggett, 1998). Krebs (1985), summarises the environmental factors that maintain 'disequilibrium' as grazing, climatic instability and disturbance-induced mortality. Such disturbance-related factors may result in a permanent transition state (Brandani, 1983; Pickett et al., 1987; Brown, 1988; Glenn-Lewin and van der Maarel, 1992). Alternatively, disturbance is seen as generating microcycles within the landscape, the climax representing a summation of the communities and being maintained by homeostasis (Watt, 1947; Schoener, 1988; Burrows, 1990; Walker, 1997). So that in addition to causing retrogression, disturbance may maintain the climax (Matthews, 1999).

Clements considers the climate as the principal control on the climax (Clements, 1936). However, some authorities consider that continual climatic fluctuations and changing long-term trends prevent mature vegetation attaining equilibrium (Walker, 1997). Brown (1988) sees vegetation responding to both past and present conditions, while Walker (1997) finds that plant responses lag behind current conditions by several decades (Eriksson and Ehrlen, 2001), so that ecosystems are out of phase and contain an unstable mixture of species.

Additionally, gradual, degenerative processes may affect equilibrium vegetation. Matthews (1999) identifies such processes as waterlogging, nutrient deficiency, accumulation of toxins and excessive siltation. Waterlogging (following ironpan formation) and nutrient depletion are seen as leading to muskeg formation at Glacier Bay, Alaska (Burrows, 1990; Matthews, 1999). Rather than retrogression (Miles, 1987), i.e. returning to a previous developmental stage, this may represent an edaphically driven, alternative endpoint (Krebs, 1985).

Rather than a stable climax (Clements, 1936), mature vegetation is therefore better described as maintaining a dynamic equilibrium by homeostasis or approaching a 'steady state' in population terms (Whittaker, 1975). The picture emerging is of two types of interaction with the environment; (1) a set of processes in response to which the vegetation changes gradually approaching, but rarely attaining, equilibration; (2) relatively abrupt disturbances, which damage the vegetation, opening patches where succession is reinitiated. Equilibration may take several decades if populations persist in suboptimal conditions. Mature vegetation can degenerate where changing resources no longer provide suitable conditions. Scale of observation again affects the extent of changes that are seen.

2.7 The chronosequence concept

The chronosequence concept involves the substitution of space for time. Spatial separation is assumed to represent temporal distance; a sequence is then constructed without the need to observe changes actually occurring through time. If the assumption that space and time are equivalent (Pickett, 1987) is not valid, effects in time are not those seen in space (Whittaker, 1993). However, rather than being ignored, the differences between the two may provide insights into the operation of successional processes (Whittaker, 1987, 1989).

This methodology is frequently used in relation to prograding systems, such as glacier forelands and dunes, where substrate becomes available for colonization progressively and stages within the sequence can be dated. There are many examples where the chronosequence concept has been used for such systems: at Storbreen (Matthews, 1976; Hawker, 2000); Glacier Bay (Cooper, 1923, 1931, 1939; Bormann and Sidle, 1990); Twin Glacier, Ellesmere Island (Jones and Henry, 2003); Lyman Glacier, Washington (Jumpponen et al., 1998), Kerguelen Islands, Antarctica (Frenot et al., 1995, 1998); with prograding dunes, at Lake Michigan (Cowles, 1899, 1901; Olson, 1958; Lichter, 1998, 2000) and Schiermonnikoog, The Netherlands (Olff et al., 1993).

The methodology usually assumes that environmental conditions are homogeneous, with environmentally dissimilar sites treated as if they were identical (Olff et al., 1993; Bakker et al., 1996). As discussed above, environmental variability is widespread (e.g. Gauch, 1982; Bradshaw, 1993; Bakker et al., 1996; Stewart et al., 2000; Wiens, 2000), and disturbance generates patches (Miles, 1987; Burrows, 1990; Grimm, 2000). At Storbreen, more recently exposed sites occur at increasingly high-altitude, where differences in the sequence led Matthews (1976) to express doubt as to whether the pathway will be identical to that at low-altitude. Spatial heterogeneity marks differences in the nature and rate of succession (Glenn-Lewin and van der

Maarel, 1992), making the chronosequence an imperfect predictor (Whittaker, 1991). Additionally, conditions may vary temporally and result in changes to the successional trajectory (Pickett, 1987; Glenn-Lewin and van der Maarel, 1992; Bakker et al., 1996). Such redirection is unlikely to be evident (Burrows, 1990) and an interpretation that does not take it into account may be erroneous (Bormann and Sidle, 1990). As pointed out by Matthews (1976), conditions (particularly climatic) may vary between time stages, which may be characterised by fundamentally different constraints. While heterogeneity in space and time is the rule, there may be rare exceptions (Lichter, 1998).

A test of the significance of this variability is the extent to which age controls the sequence. Composition is not simply a function of distance/time since deglaciation at Storbreen (Matthews, 1976; Matthews and Whittaker, 1987). Huggett (1998) expresses a similar view in relation to soil development. He concludes that the development of soil is best described as evolution rather than a progressive process. Foskett (1998) finds the influence of age exceeded by that of microtopography with increasing altitude. A study by Darmody and Thorn (1997) (also at Storbreen), found soils of the same age, but of contrasting altitudes, have significantly different properties, leading them to warn against 'over-interpretation of the distance for time analogue'. Age may not provide a complete explanation, but it is often the most important gradient (Whittaker, 1985; Hawker, 2000).

It appears that use of the chronosequence concept normally obscures the detailed effects of environmental heterogeneity on successional processes such as species replacements. This has led to warnings against its use other than for generalizations, qualitative statements and for formulating hypotheses (Pickett, 1987), that inferences drawn from chronosequences are likely to be unreliable (Bakker et al., 1996) or invalid (Glenn-Lewin and van der Maarel, 1992). Chronosequences have rarely been tested, but in an examination of the sequence at Glacier Bay, Fastie (1995) using stand reconstruction shows that rather than one, there are several sequences in the study area. The particular pathway followed depended on proximity to seed source (cf. Bormann and Sidle, 1990; Chapin III et al., 1994). The use of the chronosequence therefore led to simplification and to a misleading interpretation.

Estimating the length of time that the substrate has been available for colonization is a further potential source of error. Only rarely are direct records such as photographs available, and these provide 'spot ages'. Plants can be used, as in lichenometry or dendrochronology, to assess surface age, but establishment immediately on exposure is unlikely, delays are variable and increase with altitude (Sigafoos and Hendricks, 1969). Matthews (1992) (and references therein) discusses proxy records, particularly those suitable for use on glacier forelands. Stabilization of waterlogged substrates varies between sites and may extend to several decades. Organic material and propagules may be transported on the surface of the glacier or uncovered with its retreat. Such additions may promote development within areas of deposition as seen at the Twin Glacier Foreland (Jones and Henry, 2003). Dates may be calculated for moraines, but intermoraine areas are generally dated by extrapolation assuming a constant rate of retreat (Matthews, 1992, 1999). Maizels and Petch (1985) use lichens to determine the relative ages of intermoraine deposits, but such painstaking methodology is rarely employed. Dating is therefore likely to contain inaccuracies: the size of the cumulative error is impossible to estimate and will vary between sites.

While the chronosequence is useful to obtain a generalized overview of changes in community structure, a reductionist approach may be more useful at a local scale. Repeat surveys of permanent quadrats are likely to provide a greater depth of understanding, particularly of causal mechanisms and the response to changing conditions (Franklin, 1987; Pickett, 1987; Herben, 1996; Jones et al., 1997; Gottfried et al., 1999).

2.8 The environmental variables

Environmental controls and influences comprise an important element in this study and some background is given in this section. The principal sources of information are drawn from work in similar habitats, including that carried out at Storbreen, but are not restricted to successional studies. The main focus is on environmental influences on vegetation composition.

2.8.1 General assessments of the plant:environment relationship

An initial point not often emphasised is that arctic and alpine plants are well adapted to their environments (Körner and Larcher, 1988; Körner, 1999a, 1999b; Lee, 1999). Körner (1999a, 1999b) finds these plants are limited by reproduction opportunity, rather than productivity or resource availability, which are similar to lowland plants if considered per month of growing season rather than per year. Optimal temperatures for photosynthesis are similar (Lee, 1999) and efficiency is higher (greater carbon binding capacity and higher nitrogen content). While the vegetation responds to fertilizer addition, it is not nutrient limited (cf. Chapin III et al., 1995a). Lee (1999) discusses adaptations, including: frost tolerance; low canopy stature producing a warmer microclimate for metabolic processes and maintaining hydration (Billings, 1974a; Burrows, 1990); dark pigments (anthocyanins) which also increase temperature; increased longevity and pseudovivipary, which increase successful reproduction. These adaptations involve predictable effects, short-term fluctuations are likely to be within tolerance limits, but the plants may be vulnerable to changes in long-term climatic trends (Körner, 1999a).

While the regional scale climate constrains all vegetation, environmental gradients operate at a finer scale, differentially affecting species distributions (Körner, 1995). These gradients involve interactions both with other gradients and via feedbacks with the vegetation itself (Billings, 1974a; Whittaker, 1985; Matthews and Whittaker, 1987; Southwood, 1987; Whittaker, 1989; Brown, 1988; Crouch, 1992; Shugart, 1997; Foskett, 1998; Pickett et al., 2000). Shugart (1997) sees these interactions as having the potential to alter ecosystem function, differentially affecting functional groups which determine system attributes e.g. variation in litter quality affects decomposition and nutrient cycling rates (Chapin III, 1993b). Spatially, the vegetation composition at any particular location results from the position in relation to a number of gradients (Whittaker, 1953; Matthews, 1976; Matthews and Whittaker, 1987; Crouch, 1992). Temporally, changes in these environmental conditions (driven by species and/or physical agents)

(Southwood, 1987; Burrows, 1990; Pickett et al., 2000) are seen as initiating species dynamics (Matthews and Whittaker, 1987; van der Valk, 1992; Hobbs, 1997; Shugart, 1997; Foskett, 1998; Silvertown, 2001).

Several authorities identify different variables as being effective at different scales: a coarse-scale control operating via a cascade of finer-scale effects that directly affect the plants (Fitter, 1987; Williamson, 1988). Whittaker (1989) discussing Storbreen, considers snowlie as a surrogate, effective through differences in growing season length, moisture regime and nutrient availability. Wiens (2000) found that pattern and response change with scale; coarse-scale controls involve geology, topography and climate, while at a finer-scale microtopography and soil variables led to cover and microclimate variation. Large-scale gradients set a framework, with smaller-scale gradients superimposed. Bauert (1996) sees macrogradients of altitude and latitude with superimposed ecological gradients. Antonovics et al. (2001) found fine-scale mapping to reveal important stochastic factors while at a larger scale environmental variables exert control. Wookey et al. (2002), examining succession on the Lambardalur Glacier Foreland in northern Iceland, described successional change as a chronosequence with superimposed multidirectional environmental changes, using soil evolution as a model (Huggett, 1998). Despite differences within the individual systems, the above discussion indicates that macroscale landscape variables (climate, altitude, latitude, and geology) provide a control framework, while at a local level, meso- or microscale gradients influence vegetation patterning more directly.

Additionally, initial conditions and site history are influential (Whittaker, 1985; Pickett et al., 1987; Huggett, 1998). Whittaker (1991) working at Storbreen, develops this further, seeing the different landform units as experiencing different environmental histories (e.g. topography, or climate change over time) and considers that this may lead to temporal differences in the nature of succession.

2.8.2 Altitude

In the last section, altitude was described as a major environmental control on distribution and composition (e.g. Pickett et al., 1987; Crouch, 1992). Generally, the severity of conditions increases with altitude. The delay between deposition and plant establishment was found to be longer at Mount Rainier, Washington, at higher sites (Sigafoos and Hendricks, 1969). Darmody and Thorn (1997) found chemical weathering and soil development to be reduced at high-altitude on the Storbreen foreland to the extent that they suggested that high-altitude conditions might inhibit pedogenesis. In both cases altitude is seen as operating via climatic effects.

Increasing altitude is accompanied by a fall in temperature, reduced partial pressure of both CO_2 and O_2 and increased radiation (including a higher UV component) (Billings, 1974b; Körner, 1994, 1999b; Beniston, 2000). The effects of windscour are more severe and precipitation can be higher (Billings, 1974b; Körner, 1994; Callaway et al., 2002). Foskett (1998) noted the redistribution of snow from exposed to more sheltered sites. Large rocks and exposed bedrock occur more frequently at high-altitude (Billings, 1974b; Foskett, 1998). Del Morel and Bliss (1993) also discuss the difficulties of dispersal to higher elevation as constraining development at Mount St Helens.

Occasionally, studies compare conditions for plants at high and low-altitude via reciprocal transplants and manipulations. Plants respond most strongly to temperature at high-altitude but to nutrients at low-altitude (e.g. Stenstrom et al., 1997; Callaway et al., 2002). Grabherr et al. (1995) found that species richness fell with altitude in a series of discontinuities, caused by changes such as increasing cryoturbation in the nival zone.

The study area at Storbreen has an altitudinal range of ca 1150 to 1550 masl. Younger sites occur at higher altitude due to the glacier retreat onto higher land. Age and altitude are therefore negatively correlated (Whittaker, 1989) except where old sites occur at high-altitude on lateral moraines. Matthews (1976) considers succession at Storbreen to be simpler and more predictable at high-altitude, while Foskett (1998) found that microtopography replaced age as the most influential variable at high-altitude. This was related to lower temperatures, greater exposure and higher precipitation, compounded by lower vegetation cover, compared to sites at low-altitude. Vegetation and soil developed more rapidly at low-altitude.

2.8.3 Duration of snowlie

Snow is distributed unevenly within a site as accumulation involves an interaction between wind and topography (Johnson and Billings, 1962; Billings, 1974a; Wijk, 1986b; Hahn et al., 1996; Foskett, 1998). As wind direction is relatively consistent year to year, so is the position of snowbanks and patches (Mordaunt, 1999). The duration of snowlie is governed by the amount accumulating (deep snow maintaining a low temperature) and how it is packed (Foskett, 1998; Mordaunt, 1999; Beniston, 2000). Snow accumulates in depressions and on leeslopes (Stanton et al., 1994) and may be thicker on north-facing slopes (Matthews, 1978; Auerbach and Halfpenny, 1991). Although position may be constant, the annual melting date varies with the depth of accumulation (Stanton et al., 1994), and is earlier on lower or convex slopes (Burrows, 1990).

The duration of snowlie affects plants both directly and indirectly via a number of environmental factors. Direct effects include physical protection from frost, abrasive and desiccating winds and extremely low temperatures (Billings, 1974a; Carlsson and Callaghan, 1991; Stanton et al., 1994; Körner, 1995; Hahn et al., 1996; Beniston, 2000), although the mechanical action of snow and ice may damage plants (Hahn et al., 1996).

Indirect effects occur through influences on other gradients. Growing season length depends in part on depth of accumulation and conditions early in the year (Johnson and Billings, 1962; Peterson, 1994; Foskett, 1998; Beniston, 2000). Respiration costs increase when snowmelt is delayed and affect carbon balance (Stanton et al., 1994).

Galen and Stanton (1995) manipulated growing season length in a snowbed on Penn Mountain, Colorado. Snowmelt acted as a phenological cue, with a few species able to respond opportunistically. *Sibbaldia procumbens* is one of these species with active primordia maintained below the snow, involving a respiration cost if snowmelt is delayed. In the short-term, there was little difference in vegetation cover with changes in the melt date, but longer-term changes are expected through changes in soil conditions.

Walker et al. (1995) measured responses to annual variation in snowmelt date on the Front Range, Colorado. Particularly striking in this study is the effect of the 1983 ENSO event, which increased snow cover; counterintuitively, this was associated with an increase in leaf length and leaf births. He found that phenology was linked to snowmelt date but that development was more rapid when melt was late allowing the cycle to be completed within the available time. However when snowmelt was early, the period of maximum growth tended to occur in dry conditions; later melt resulted in this coinciding with the release of moisture and nutrients.

Melting snowbanks/patches release moisture and nutrients and may provide a reliable source throughout the growing season (Johnson and Billings, 1962; Billings, 1974a; Seppelt et al., 1988; Carlsson and Callaghan, 1991; Taylor and Seastedt, 1994; Galen and Stanton, 1995; Walker et al., 1995; Walker and Walker, 1996; Foskett, 1998; Lee, 1999; Beniston, 2000). Deep soils characteristic of mature sites may be formed with high levels of organic material, nitrogen, phosphorous and pH (Stanton et al., 1994). Late melting sites may, however, become waterlogged, inhibiting decomposition and resulting in poor soils (Wijk, 1986b). Wynn-Williams (1993) describes the precipitation of snow algae onto the soil surface with snowmelt, their decomposition contributing nutrients, particularly nitrogen. Johnson and Billings (1962) in a study on Beartooth Ridge, Colorado, identified the receipt of moisture from melting snowbeds as being a common feature of sites with frost activity.

The same interaction between wind direction and topography that results in the accumulation of snow has also been identified as leading to the deposition of allochthonous material and invertebrates (Carlsson and Callaghan, 1991; Hodkinson et al., 2002) and diaspores (Ryvarden, 1975). As the snow melts, these are concentrated in the centre of the shrinking snowbed where nutrient deposition may exceed the nutrient inputs typically used in manipulation experiments (Hodkinson et al., 2002). More detrimentally, pathogens can accumulate with the snow (Stanton et al., 1994) and snowbanks provide protection for small mammals in the winter so that high levels of herbivory may be associated with them (Wijk, 1986b; Auerbach and Halfpenny, 1991; Stanton et al., 1994; Foskett, 1998).

Snowbeds are associated with a gradient of effects; adverse conditions are associated with long duration of snowlie, with central areas remaining covered in some years, subject to waterlogging and slow rates of decomposition. Peripheral sites benefit from nutrient and moisture inputs and a longer growing season, receiving winter protection but more likely than central areas to experience competition (Stanton et al., 1994) and herbivory (Wijk, 1986b). Conditions on slopes surrounding the snowbed show consistent patterns; land is dry, exposed and sparsely vegetated above the snowbed and moist, nutrient-rich but densely vegetated below it (Johnson and Billings, 1962; Billings, 1974b). Foskett (1998) found a differential effect depending on altitudinal position; at low-altitude the presence of snow may be beneficial particularly for moisture availability, but at higher altitude long snowlie may have adverse impacts.

2.8.4 The glacier climate

The mechanism by which this mesoscale influence is generated is described in Matthews (1992). Cold air sliding down the glacier surface generates a down-valley wind that is restricted during the day by the up-valley wind caused by heating of the valley sides. On small glacier forelands like Storbreen, the main effect is limited to 50m (Lindroth, 1965; Ballantyne and Matthews, 1982). Conditions are warmer at night, when the up-valley wind is reversed, and below the soil surface (Ballantyne and Matthews, 1982). The distance covered by the effect depends on the size of the glacier, being limited to ca 200m for small valley and cirque glaciers (Matthews, 1992, 1999), although Whittaker (1989) quotes 500m.

The temperature effect may not impact greatly on the vegetation as the warmer night temperatures narrow the range of temperatures experienced (Ballantyne and Matthews, 1982). Persson (1964) and Lindröth (1965) found 'southern' species growing close to the snout at Skaftafellsjökull, Iceland and concluded that conditions were not strongly adverse.

Other effects may be more important. Boulton and Dent (1974) working at Breidamerkurjökull in Iceland, found that aeolian deflation left a stony lag immediately in front of the glacier, the material being deposited patchily amongst the mature vegetation, which acted as a windbreak (Matthews, 1999). Plants may be stunted and deformed where they are exposed (Heusser, 1956) or may suffer abrasion from windblown particles (Matthews, 1999).

Vetaas (1997) at Bodalsbreen, found that the glacier wind could be strong enough to remove plant cover. Specifically, he associated it with the generation of patch dynamics and cyclic succession that could inhibit heath development.

Matthews (1976) argued that variation in the rate of glacier retreat resulting in early vegetation being subject to the 'cold air dome' for differing lengths of time, with long-lasting, differential effects on vegetation development.

2.8.5 Disturbance

Three measures of disturbance have been used in this study: fluvial disturbance, frost heave and solifluction. These were found to be the principal agents of disturbance operating in the study area by previous workers at Storbreen (Whittaker, 1985; Crouch, 1992). This section includes brief discussions of how particular types of disturbance occur and the effects on the vegetation. This is followed by a more general discussion of the role of disturbance in succession.

Fluvial disturbance (flooding, channel switching) This may occur during snowmelt or periods of intense ablation from the glacier. Nutrients (Vitousek and Walker, 1987; Matthews, 1999) and fine sediment (Foskett, 1998) may be deposited, in extreme cases a site may be inundated with sediment, covering the vegetation present (White, 1979). On sloping or free-draining sites, fines may be removed from higher areas leaving a coarse lag (White, 1979; Matthews et al., 1998). Frenot et al. (1995) working on the subantarctic Kerguelen Islands, found that flooding washed fine particles down the soil profile.

Brandani (1983) found flood tolerant species where flooding was predictable. White (1979) describes differential tolerance of flooding along floodplain gradients and early dissemination of seeds onto open sites following spring flooding.

Frost heave (cryoturbation) This requires moisture (Billings, 1974a) and fluctuating temperatures generated by seasonal or diurnal freeze-thaw cycles, the latter causing the formation of needle-ice (Johnson and Billings, 1962). The frequency of frost heave falls on older sites at Storbreen (Whittaker, 1989; Crouch, 1992), and Frenot et al. (1995) found intensity increased with proximity to the glacier snout where freeze-thaw cycles are most frequent. Shallow soils are more susceptible (Whittaker, 1989) with substrate texture and type also being important controls (Bliss et al., 1994). At the Lyman Glacier foreland in Washington, Jumpponen et al. (1999) found that needle-ice formed in silts but not coarser material, while Matthews et al. (1998) found it to be associated with medium-coarse silt and fine sand. Matthews et al. (1998) working at Styggedalsbreen, most frequently detected cryoturbation on exposed sites on ridgetops and low mounds.

Vegetation cover can prevent cryoturbation by transpiring excess moisture, binding soil and insulating it: examples include cryptogam crusts (Bliss et al., 1994) and particularly deciduous species (Johnson and Billings, 1962; White, 1979; Chapin III et al., 1995b; Matthews et al., 1998). Where cover is low, cryoturbation may prevent colonization (Johnson and Billings, 1962), and damage rooting systems (White, 1979; Brandani, 1983; Matthews, 1999), particularly affecting seedlings (Whittaker, 1985; Frenot et al., 1995; Niederfriniger Schlag and Erschbamer, 2000). However, there may also be beneficial effects, e.g. the creation of safe sites for germination and establishment (Johnson and Billings, 1962; White, 1979; Brandani, 1983; del Morel and Bliss, 1993; Matthews, 1999). It may lead to soil mixing and prevent the loss of fines and nutrients by leaching (Matthews, 1999), which may also be described as disrupting soil development (Wookey et al., 2002). The overall effect depends on the balance between plant ability to tolerate disruption and requirement for nutrients (Jonasson, 1986).

Solifluction Johnson and Billings (1962) describe solifluction as the viscous flow of saturated soil over an impermeable surface due to cryoturbation-induced loss of strength. The greatest movement takes place during spring thaw, when ice lenses melt and thaw consolidation occurs. Solifluction lobes form on sloping land where moisture levels are high (Matthews, 1999) and the surface is cohesive (Matthews et al., 1998).

Disturbance is generally described as detrimental. Tissue may be damaged (Burrows, 1990) and where extreme, plant mortality may result (Brown, 1988), with the loss of vegetation patterning, nutrients and material (Wiens, 2000). In successional terms, this may lead to retrogression (Matthews and Whittaker, 1987), a slowing of successional rate or a redirection (Whittaker, 1991; Peet, 1992; Matthews, 1999). Walker and Chapin (1987) see the intensity as determining the level of associated change; infrequent, high intensity disturbance reversing succession, while at moderate levels delay or modification result. However, damaging effects on particular components of the vegetation may be beneficial to others or the system as a whole.

Disturbance that perturbs substrate integrity may expose unweathered material and nutrients (Sousa, 1984; Whittaker, 1985; Pickett et al., 1987; Burrows, 1990; del Morel and Bliss, 1993; Matthews, 1999). Where tissue is damaged or removed, open patches may allow immigration and limit dominance (Sousa, 1984; Burrows, 1990), promote coexistence and diversity (Matthews, 1999) and result in cyclic succession (Whittaker, 1985). At Storbreen, Whittaker (1993) found that disturbance was important for forb establishment.

Disturbance is most important on younger ground, declining with age (Southwood, 1987; Whittaker, 1989, 1993) but is responsible for maintaining pioneer species on old sites at Storbreen (Whittaker, 1985; Foskett, 1998). Vegetation types may be associated with a particular disturbance regime (Matthews, 1999) and disturbance types are associated with or facilitate one another (Brandani, 1983). Intermediate levels of disturbance are seen as generating maximum diversity (Grime, 1973; Fox, 1981; Sousa, 1984; Whittaker, 1985; Chapin III and Körner, 1995a); both extremes requiring specialists (Grime, 1979; White, 1979; Brandani, 1983).

Disturbance may therefore be viewed as either detrimental or advantageous. This may partly be due to comparison of disturbance events of a different nature. It is measured by the parameters of intensity, frequency and predictability (Brandani, 1983), all of which are variable. Papers by White (1979) and Sousa (1984) develop the concept of disturbance in relation to vegetation development:

1. Disturbance (including all but the most severe events) is viewed as an environmental gradient (Whittaker, 1953, 1967), and related to the coencline (Whittaker, 1975) by the addition of a temporal axis.
2. Disturbance occurs ubiquitously, at least at mild/moderate levels. It has therefore acted as a selection pressure in relation to which plants have evolved and adapted. Minor disturbance is frequent and regular, and plants have adapted to it. Moderate events are less frequent but more irregular; plants having an adaptive response. At the highest levels of intensity, plants are destroyed and vegetation dynamics lost.
3. Rather than being caused solely by exogenous, physical agents, disturbance may be initiated or promoted by the biota. Vegetation varies in susceptibility (i.e. seasonally) to regular events, particularly fire and unusual frosts that are damaging during the growing season but not when plants are acclimated. Purely exogenous events are those occurring too rarely to be important in evolutionary terms i.e. in relation to generation time.
4. The climax is often thought of as being disturbance-free and succession as being perturbed by disturbance. White (1979) considers both to be shaped by moderate disturbance, a normal part of the environment for most plants.

Elsewhere discussions generally focus on high intensity events, which cause mortality (Brown, 1988) and which are the result of exogenous events (Brandani, 1983). Disturbance overrides other environmental gradients, although organisms may actively modify disturbance (Wiens, 2000). Walker (1996) sees disturbance as initiated by external factors, and important in evolution, diversity and productivity.

2.8.6 Moisture

The contribution from snowmelt is discussed above, together with the consequent effects on vegetation patterning around snowbanks. Moisture is linked with all three disturbance variables, although the moisture requirement in cryoturbation is lower than for fluvial disturbance or solifluction. Adequate moisture supply contributes to the importance of safe sites on young land, where the developing root systems of seedlings make them susceptible to drought.

The high level of moisture availability following snowmelt is important in many systems (i.e. Seppelt et al., 1988; Callaghan and Johasson, 1995), particularly where the contribution from melting snowpatches continues throughout the growing season (Taylor and Seastedt, 1994). Moisture availability has additional controls: relief and canopy (Körner, 1995) and temperature, precipitation and wind/humidity (evapotranspiration) (Krebs, 1985). Topography has an effect on total receipt of precipitation, which generally increases with altitude but decreases on exposed and leeward slopes (Beniston, 2000). Soil permeability influences moisture retention, which is low on gravel and glacial till (Ballantyne and Matthews, 1982), so that glacier forelands are often xeric. Impeded drainage caused by permafrost or ironpan formation, i.e. muskeg at Glacier Bay, results in waterlogging.

Available moisture is seen as generally adequate in arctic/alpine ecosystems to avoid drought, at least for established plants on developed soils (Körner, 1994; Taylor and Seastedt, 1994; Beniston, 2000). However, Chapin et al. (1988) found that soil moisture was strongly correlated with productivity at a tundra site near Barrow, Alaska, although availability generally exceeded field capacity and the optima for microbial activity. Running water in subsurface pipes contains high levels of nutrients (particularly nitrogen) and may increase soil warmth. This relationship of moisture (especially of meltwater) and nutrients is widely recognised (Whittaker, 1985; Walker et al., 1995; Hahn et al., 1996; Matthews, 1999; Jones and Henry, 2003).

As mentioned above, glacial tills are generally free draining (Ballantyne and Matthews, 1982). Although early soils on glacier forelands tend to have poor moisture retention, this improves as soils age, with the input of organic material (Burrows, 1990; Crouch, 1992). The surface layers of soils are prone to drying particularly where cover is low (Körner, 1999a; Ewing, 2002), although moisture may be available at depth (del Morel and Bliss, 1993). Carlsson and Callaghan (1991) note that windblast may result in desiccation, while sheltered sites have higher moisture levels. Free draining early sites with low cover open to the glacier wind, are likely to be susceptible to surface desiccation.

Plants have varying responses to the level of moisture availability. Rapid root growth amongst seedlings enables tapping of deeper moisture, avoiding surface drought (Burrows, 1990; del Morel and Bliss, 1993). Varying moisture availability has been associated with particular growth forms by Hahn et al. (1996) at Imnavait Creek: deciduous species where there is running water, evergreen on dry sites and sedges where waterlogging occurs. Whittaker (1993) observed that shrub distributions were partly determined by moisture at Storbreen, some occurring principally along meltwater streams (*Salix lanata),* on marshy (*S. glauca*) and driėr sites (*Phyllodoce caerulea*). Shrub invasions of early communities tap deeper resources as surface moisture is consumed by shallower rooting species (Mooney, 1997), deeper rooting deciduous species having a greater effect (Chapin III et al., 1995b). Hydraulic lift of moisture from deeper soil layers by trees and shrubs may leak into adjoining soils (Wilson, 2000).

Physical controls and vegetation effects on moisture distribution and differential soil characteristics generate patterns of availability, which in turn affects vegetation pattern. At the Ellesmere and Devon Islands, Canada, increased cover and species richness were associated with an area of 'seepage' (Bliss et al., 1994); on Niwot Ridge, Alaska, particular communities were related to growing season moisture availability (Taylor and Seastedt, 1994). Temporal variability is governed by changing receipt from precipitation (including seasonally), increased retention as soils develop, glacier retreat (Ballantyne and Matthews, 1982) and lower mobility of meltwater stream courses with age (Whittaker, 1989; Gurnell et al., 1999). Moisture therefore contributes both to spatial and temporal dynamics (Whittaker, 1985).

2.8.7 Age

Previous studies at Storbreen have found that age, and age-related factors (altitude, disturbance, soil variables) (Whittaker, 1985) are important determinants of vegetation composition and changes (Matthews, 1976; Crouch, 1992, 1993; Whittaker, 1989). The decease in the importance of age as altitude increased (Foskett, 1998), and the masking of the effect of age by altitude (Darmody and Thorn, 1987) have been discussed above. Age is of considerable importance, but environmental factors, particularly altitude, also contribute (Matthews, 1978).

Pickett (1987) considers that time is a surrogate for 'past operational environments'; understanding succession depends on knowledge of these and changes in them. Wookey et al. (2002), working at Lambardalur Glacier in northern Iceland, found no clear signs of classic succession in a study of the relationship between age, vegetation and soil evolution. Reworking of organic material by decomposers, intense cryoturbation and grazing are superimposed and distort the influence of age.

Age/age-related factors (including altitude) have been found to be important determinant(s) at Storbreen, but there is a body of opinion that considers it a surrogate for site history and other environmental factors. The differences in measurement units between age and such factors are considerable and will contribute to the greater weight given to age. Age provides a coarse-scale summary of changes that are due to fine-scale dynamics.

2.8.8 Soil variables

This section considers soil as an environmental variable, and which soil properties undergo change, how they differ over time and the nature of controls on spatial variability.

Soil provides a controlled environment within which mineralization takes place and nutrients are stored (Burrows, 1990; Hahn et al., 1996). Soils in mountain areas are often shallow and nutrient-poor (Beniston, 2000). Messer (1988) working in southern Norway found brown soils topped by organic material with a dark A horizon to be typical. Nutrient sources are: atmospheric deposition; plant and animal remains; microbial biomass (Walker, 1993; Schimel et al., 1996);

and weathering of parent material, particularly for phosphorous (Vitousek and Walker, 1987). Various forms of nitrogen are available to plants including nitrate, ammonium, atmospheric nitrogen and organic nitrogen (amino acids and simple proteins) (Kielland, 1994; Shaver, 1995; Raab et al., 1996; Schimel et al., 1996; Lee, 1999).

Microbial activity is reduced where soil conditions are cold and/or wet (Marion et al., 1997; Fitter et al., 2000), so that undecomposed material accumulates (Messer, 1988), often to significant levels where conditions are unfavourable. This organic material (OM) retains moisture (Vitousek and Walker, 1987; Burrows, 1990; Lichter, 2000). Increase in the organic content of soils affects texture and may result from incorporation of higher quality litter. Hydrogen ion concentration is measured as pH, and results from the presence of organic acids, atmospheric deposition and parent material (Beniston, 2000). Hydrogen ions can replace cations on cation exchange complexes and may affect nutrient availability (Krebs, 1985).

Recently deposited or exposed substrates are unstable, inhibiting plant colonization (Matthews, 1992). Early colonization by cyanobacteria and/or algae may bind the surface (Wynn-Williams, 1993), as discussed in Matthews (1992). The presence of deeper-rooted vegetation improves substrate cohesion (Beniston, 2000; Callaway et al., 2002).

Soil properties change over time in response to processes such as weathering, leaching and the incorporation of organic material. Some nutrients, particularly nitrogen, accumulate over time due to atmospheric deposition and the activities of fixers (Burrows, 1990). However, some nutrients, particularly phosphorous, are likely to occur at high concentrations early in succession, with the principal contribution being from weathering; over time phosphorous is sequestered, leached or is present only in forms unavailable to plants (Vitousek and Walker, 1987). Nutrients are increasingly sequestered in the biomass with cycling and mycorrhiza assuming greater importance (Burrows, 1990).

Cycling in cold, wet soils is slow so that OM accumulates (Whittaker, 1975; Vitousek and Walker, 1987; Schimel et al., 1996; van Wijk et al., 2003). At Imnavait Creek, OM amounted to 30-55% of aboveground biomass, with turnover exceeding two years, and at Glacier Bay the organic content of soils increases tenfold in the first 200 years (Chapin III et al., 1994). Soil depth increases with age (Whittaker, 1975; Marion et al., 1997), increasing up to ca 10cm on foreland sites at Storbreen (Whittaker, 1989). Messer (1988), investigating soils on 18 glacier forelands in southern Norway, found that CEC and OM increased while pH decreased with soil depth and time since deglaciation, but there was not a simple linear relationship between the three variables. Huggett (1998) investigates environmental influences on soil; rather than representing a consistent, directional driving-force, he found that environmental conditions undergo continuous, multidirectional changes that result in soil heterogeneity.

Altitudinal effects on pedogenesis at Storbreen are mentioned above. Steep slopes increase drainage rate with accompanying leaching and erosion (Beniston, 2000). Sites proximal to the ice sheet on Signy Island, Antarctica were found to receive propagules and invertebrates from detritus on the ice (Smith and Lewis, 1993). The presence of nutrients in meltwater was mentioned in section 2.8.6. At the Lambardalur cirque, Wookey et al. (2002) found that disturbance resulted in the loss of OM; in the harsh environment, such material was not hummified and was therefore subject to leaching or aeolian erosion. Wind shear can affect shallow roots in exposed areas, reducing temperatures and impairing decomposition and cycling (Körner, 1994).

These examples illustrate the relationship between environmental conditions and soil heterogeneity. The vegetation also forms part of the soil environment. The species themselves influence soils through the quality of the litter input, particularly lignin, secondary metabolites and C:N ratio, which affects decomposition rate and cycling. Deciduous species have more abundant and higher quality litter than evergreen ones, grasses and forbs being superior to shrubs (Chapin III et al., 1980, 1986;,1995a, 1995b; Chapin III and Shaver, 1989; Chapin III, 1993b; Shaver and Laundre, 1997; Woodward and Kelly, 1997). Wilson (2000) conducted transplant experiments between forest and prairie soils in Saskatchewan. Transplanted soils rapidly assumed the characteristic properties of soils at their destination, attributed to root structure, stem flow and the effect of the canopy on moisture reaching the ground. He concluded that species clumping might result in soil heterogeneity. Jumpponen et al. (1998) found that organic content increased twofold under *Salix* spp. compared to bare ground. Brubaker et al. (1995) compare *Salix* spp. litter to evergreen; higher soil organic content under evergreen species led to a fall in pH and the loss of redox sensitive elements (Fe, Ma and Al). The presence of deep rooted, deciduous shrubs also increases soil stability. Ewing (2002) associates nutrient retention with deciduous shrubs and grasses and leaching with evergreen shrubs.

Rooting system properties and depths vary between species, separating belowground resource acquisition, particularly late in succession (Bazzaz, 1987; Fitter, 1987; Chapin III and Shaver, 1995; Fitter, 1999; Fitter et al., 2000). Long, unbranched taproots allow species access to deeper resources i.e. *Eriophorum vaginatum* tapping underground water pipes (Chapin III et al., 1988). Deciduous shrubs have most roots 5-25cm below the surface, while evergreen shrubs are shallower and subject to fluctuating temperature and moisture (Schimel et al., 1996). Species on ridgetops, such as *Loiseleuria procumbens*, typically have thin, highly branched roots able to tap large volumes of soil (Billings, 1974a). Variation in species rooting depth allows the tracking of fines down a soil profile in the Subantarctic Kerguelen Islands (Frenot et al., 1995, 1998). Differences in rooting systems are advantageous in different environmental locations. Fitter et al. (2000) found a species-specific response to nutrient heterogeneity in terms of the number of roots, their length, the quantity of secondary laterals and/or fine hairs, the pattern of branching and the up-regulation of nutrient transporters.

Soils may vary in a consistent way over time, but spatial heterogeneity can be superimposed by environmental conditions, including the nature of the vegetation, which has an interactive relationship with the soil.

2.8.9 Herbivory

Herbivory has been classed as a disturbance, with results similar to those discussed in section 2.8.5, i.e. loss of pattern, material and nutrients for particular species (Wiens, 2000; Wookey et al., 2002), and again these may be viewed as detrimental or beneficial depending on the perspective. Additionally, there are broader-scale community effects.

The effects on individual, damaged plants are generally adverse. Crawley (1999) discusses the effects of leaf damage, including stomatal closure, reduction in root biomass, increased susceptibility to mortality, energetic costs of regrowth and delayed bud burst; all are of greater importance when water or nutrients are limited. Establishment may be prevented (Edwards and Gillman, 1987), but the most frequently quoted effect is the removal of tissue (Margalev, 1968; Burrows, 1990; Marrs and Bradshaw, 1993), particularly damaging when meristem tissue is targeted (Ehrlen, 1995). However, some consequences may not be immediately obvious. At the Tanama River, Alaska, Rossow et al. (1997) found that browsing by moose and snowshoe hare reduced ectomycorrhizal infection by 16% due to the reduction in carbohydrate flow to the roots. Reindeer grazing is associated with increased deflation in the Swedish Scandes (Kullman, 1998). Arnalds (1987) describes the devastating effect that clearance and grazing has had on Icelandic vegetation since settlement in 874 AD; with low-altitude *Betula pubescens* woodland reduced from 65% to 1% and only 25% of the landmass now having vegetation cover. Bishop (2002) investigating the short duration of initial population expansion on Mount St Helens, found high rates of insect herbivory on the periphery of patches increasing mortality there to the extent that succession was retarded.

From the perspective of other plants in the vicinity, herbivory may increase resource availability (Crawley, 1999); maintain diversity (Chapin III and Körner, 1995b) and reduce competition, particularly when dominant species are targeted (Connell, 1975; Davis et al., 1985; Edwards and Gillman, 1987; Tilman, 1994; Wilson, 2000). The removal of biomass opens the canopy allowing light to penetrate to understorey or suppressed species, encouraging germination and releasing unpalatable species from constraint (Burrows, 1990). For example in the Tanama River experiment, Rossow et al. (1997) found compositional shifts from the browsed willow and balsam to the less palatable alder and spruce.

Benefits may accrue even to targeted species. Edwards and Gillman (1987) discuss seeds and fruits deposited with nutrients and seed caches protected from desiccation. Grazed plants may also have mechanisms to minimize the effects of damage. Defoliation may stimulate compensatory growth (Edwards and Gillman, 1987; Burrows, 1990), although as Crawley (1999) points out, in the case of grasses this results in delayed flowering and is indicative of reduced fitness.

Some species are preferentially grazed (Burrows, 1990), palatability being related to herbivore requirements, involving high nutrient content (Pastor, 1995) and low levels of chemical defences (phenolics and other secondary metabolites which inhibit gut microbes) (Chapin III, 1993b; Chapin III et al., 1995b). Deciduous species, particularly grasses, are preferred to evergreen species for this reason (Hobbie, 1995; Chapin III et al., 1986). In succession, early species concentrate resources on growth rather than protection (Chapin III, 1993a), while later ones contain higher levels of secondary metabolites. Preferential consumption of early species has been seen as opening the habitat to later invaders (Edwards and Gillman, 1987). A similar allocation pattern occurs amongst highly productive and competitive plants, which may also be targeted (Chapin III, 1993b; Bonser and Reader, 1995; Tilman, 1994). Differential patterns of species selection result in the preferential targeting of deciduous, early and competitive/productive species, all of which are associated with high availability of soil nutrients and low levels of chemical defences. Unpalatable species may nonetheless be targeted by a restricted, more specialized group of herbivores (Edwards and Gillman, 1987; Lawton, 1987; Walker and Chapin III, 1987).

Selective grazing may be detected from the genotypes present at a site (Edwards and Gillman, 1987). Variation in chemical defences amongst willow and birch species has been attributed to selective browsing during the Holocene (Jeffries and Bryant, 1995). McIntire and Hik (2002) studied the effects of grazing history at a site in Southwest Yukon using three alpine perennials. Historically grazed plants were able to tolerate removal of 58-61% of the present year's growth; the plants had a variety of responses including early season growth (avoiding predominantly late-season herbivory, coincident with low levels of shading), delayed senescence and increased productivity. Effects differ seasonally. Winter browsing was found to stimulate plant growth and nutrient concentration, whereas severe damage resulted from similar levels during the summer (Crawley, 1997). In addition to spatial differences, temporal effects involve variable plant responses that may be adaptive.

Herbivory has a variety of effects at the community level. Heavy grazing may increase dominance, as at Hardangervidda, Norway (Pastor, 1995). More often dominant species appear to be targeted, increasing coexistence and diversity (Chapin III and Körner, 1995b; Wilson, 2000). A decrease in density may reduce competition (Connell, 1975). Preferential consumption of seeds/seedlings may influence the age structure of a community (Edwards and Gillman, 1987; Lichter, 2000). More generally, grazing is an important influence in determining species composition, relative abundance, spatial organization and genetic make-up (Krebs, 1985; Edwards and Gillman, 1987).

2.9 Climatic change

2.9.1 Introduction

As seen in Chapter One, there is evidence of decadal scale, regional climate change in southern Norway since 1970, which involves increasing precipitation and warmer temperatures during winter and spring. This study does not present evidence or speculate as to the cause of these changes. In this section the potential effects on vegetation are examined, using studies undertaken to investigate anticipated anthropogenically-induced warming, some of which involve experimental manipulation of climatic features. Palaeoecological studies provide another source of information on the effects on vegetation of warming following the last glacial. Many of these studies use arctic or subarctic sites e.g. the International Tundra Experiment (ITEX) sites and while some of the species discussed occur in the study area, the community constraints are likely to differ. Additionally, these studies do not involve the complication of including successional change.

Temperature change The mean temperature is estimated as having increased by 0.5-0.7°C in the past century (Hansen et al., 1981; Chapin III and Körner, 1995b; Grabherr et al., 1995; Houghton et al., 2001). Temperature increases are considered to be in response to a 25% increase in CO_2 levels since the mid nineteenth century (Körner, 1994; Vitousek, 1994). However, the global mean masks spatial, particularly latitudinal, variation. Chapin et al. (1995a) found that there had been an increase of 4°C over the preceding 50 years at Toolik Lake, Alaska. Matthews (1992) mentions an increase of 1-2°C globally since the LIA glacier maximum. Fluctuations may occur over decadal rather than a century timescale: for example temperatures in Svalbard increased by 6°C between 1900 and 1930 (Matthews, 1992). Hansen et al. (1981) discuss a temperature increase of 0.8°C over the period 1880 to 1940 followed by a decrease of 0.5°C between 1940 and 1970 at high latitude in the northern hemisphere (reflecting the pattern seen in Chapter One). Generally the range of the anticipated increase is given a wide amplitude, examples include 1.5-4.5°C (Beniston, 2000), 1.4-5.8°C from the IPCC Third Assessment Report (Houghton et al., 2001) and 2-4°C in summer and 1-5°C in winter (Press et al., 1998), by 2100. This rise in temperature is expected to be greater at both high latitude (particularly in the north and over land) (Hansen et al., 1981; Halpin, 1994; Callaghan and Johasson, 1995; Chapin III and Körner, 1995a; Henry and Molau, 1997; Molau and Alatalo, 1998; Houghton et al., 2001) and at high-altitude (Bugmann and Fischlin, 1994; Haeberli and Beniston, 1998; Beniston, 2000). This may be of particular importance as high latitude/altitude systems are seen as having temperature as their primary control, while at lower latitude, nutrients (Callaghan and Johasson, 1995; Jones et al., 1997) or biotic interactions are of greater influence (Woodward, 1988; Körner, 1999a). The IPCC indicate that increases in minimum temperature are expected to be twice that for the maximum (Houghton et al., 2001). Haeberli and Beniston (1998) cite an increase of 2°C in minimum temperature since the beginning of the twentieth century, 1°C since the 1980s. Similarly, Beniston (2000) looking at the interaction of climate with mountain systems, finds an amplification of 2°C in the minimum temperature. Rather than the long-term mean, it is the present conditions (temperature extremes and regime) that influence vegetation (Bugmann and Fischlin, 1994; Holtmeier, 1994). Increases in precipitation are expected to accompany those in temperature (Bugmann and Fischlin, 1994; Taylor and Seastedt, 1994; Beniston, 2000).

CO_2, ozone depletion and N deposition In addition to the temperature effects expected, higher levels of CO_2 might have a direct effect on plants. Other pollutants also affect vegetation systems: ozone depletion due to chemicals such as CFCs and nitrous oxide contributing to continued acid precipitation. Ozone depletion reduces the extent to which short wavelength (280-320nm) UV-B is screened. Beniston (2000) cites depletion of 1.7-3.0% over the last 20 years with the peak occurring in winter when the radiation pathway is long, damage therefore being minimized. Caldwell et al. (1999) discuss the long record of ozone levels from Arosa in Switzerland; from 1926 to 1973 increases averaged 0.1% per decade, but from 1973 to 1993 decreases averaged 2.9%. Bjorn et al. (1997; 1998) find that ozone depletion is greatest at high latitude and altitude, particularly over Scandinavia and in the Arctic, where levels had decreased since 1979 by 45-64% up to the late 1990s. Nitrogen deposition may provide a limiting resource to high latitude/altitude systems, but is associated with detrimental effects. It has been implicated in the leaching of nitrate and acidification of mountain lakes in Norway (Skjelkvale and Wright, 1998) and damage to forests in the Swiss Alps (Innes, 1994).

2.9.2 Changes in physical parameters expected to accompany climatic change

Snowmelt and the growing season An increase in temperature is likely to prompt early snowmelt, extending the length of the growing season (Peterson, 1994), particularly if increases in the winter or minimum temperature are involved (Woodward, 1988; Stenstrom et al., 1997; Suzuki and Kudo, 1997). While there is evidence from the Scottish Highlands that the duration of snowlie is already decreasing (Mordaunt, 1999), the effect may be negated by increased precipitation (Henry and Molau, 1997; Beniston, 2000). Molau (1997), working at Latnjajaure, Sweden, reports earlier snowmelt over the preceding decade that was often followed by blizzards.

The brevity of the growing season in many arctic and alpine systems imposes a constraint on growth and productivity (Körner, 1994; Walker et al., 1995; Molau, 1997; Woodward et al., 1997). Walker et al. (1995), in the Front Range, Colorado found that some species growth patterns were related to interannual climatic fluctuations, depending on carbohydrate storage in the preceding season. Molau (1997) found that 15-40% of phytomass depended on such fluctuations, particularly on early season weather and therefore the timing of snowmelt. Welker et al. (1997) simulated an extended growing season finding an associated growth increase, accelerated phenology, greater seed set, colonization of bare ground, carbon sequestration and biomass. Temperature-induced extension of the growing season would not, however, result in universal advantage (Körner, 1994). Species will be differentiated according to life history traits, some being directly disadvantaged, snowbed species in particular being detrimentally affected due to the loss of protective winter cover and a water source in spring (Peterson, 1994; Beniston, 2000). Such effects are likely to alter the present balance in interactions.

Glacier retreat This has occurred in many systems since the LIA maximum (e.g. Haeberli and Beniston, 1998) and may accelerate with a continued rise in temperature, unless increased ablation is matched or exceeded by increased accumulation. Nesje et al. (2000) and Nesje and Dahl (2003) found that increased accumulation has resulted in advances of maritime glaciers in western Norway, although glacier retreat continues in the east of Norway. In the Alps, Haeberli and Beniston (1998) and Beniston (2000) anticipate mass wasting of 30-50% of the present volume by 2100, accompanied by an upward shift of the equilibrium line by 200-300m and a loss in thickness of 1-2m per annum. Meltwater discharge will increase and vegetation shifts are expected to follow. Such an accelerated retreat would expose an increased area of young land, with longer dispersal distances potentially slowing colonization. Also, the retreat may be onto higher land, and increased disturbance may accompany the increased volume of meltwater.

Nutrients It is frequently assumed that rising temperature will increase mineralization rates (Pornon and Doche, 1994; Callaghan and Johasson, 1995; Hobbie, 1995; Pastor, 1995; Beniston, 2000). Nadelhoffer et al. (1991) incubated six Arctic soils at different temperatures.

This confirmed that mineralization increased with temperature, but the level of organic material present caused greater variability. Nitrogen levels increased, but so did losses to leaching, denitrification and immobilization in microbial biomass. Therefore availability to plants might not increase greatly (Callaghan and Johasson, 1995).

Arctic and alpine systems are often considered as nutrient limited (Pornon and Doche, 1994; Callaghan and Johasson, 1995; Jones et al., 1997; Shaver et al., 1997). However, plants are adapted to low resource levels, physiologically and through life history traits (Körner and Larcher, 1988; Lee, 1999), and may not find increases in nutrient availability to have advantageous effects. Callaghan and Johasson (1995) report increased mortality in response to nitrogen and phosphorous additions, while Körner and Larcher (1988) discuss increased production of starch leading to differences in bud ripening and increased winter frost damage. Körner (1994) finds compositional changes, but also weakening of stress tolerance and phenological changes that are out of phase with seasonal trends.

Experimental manipulation to mimic climate change often involves both increasing temperature and nutrient addition (e.g. Callaghan and Johasson, 1995; Chapin III and Shaver, 1995; Chapin III et al., 1995a; Henry and Molau, 1997; Alatalo and Totland, 1997; Press et al., 1998) and the results generally indicate a greater response to nutrient change (Press et al., 1998). Species may specialize in utilization of different nutrient sources (Callaghan and Johasson, 1995); if climatic changes preferentially increase availability of one form, particular species may sequester a greater share of a limited pool of resources (Chapin III et al., 1995a). Shaver (1995) sees this process as underlying differential species changes in productivity and consequently in competitive ability and dominance at Toolik Lake, Alaska; in the long-term community composition changes are expected to follow. This may establish a positive feedback loop through changes in litter quality and cycling rate, enhancing the changes taking place (Chapin III et al., 1995a; Hobbie, 1995; Pastor, 1995; Henry and Molau, 1997; Press et al., 1998). However, there is also evidence of 'luxury consumption' i.e. uptake and storage of nutrients in excess of growth requirements (Wooky et al., 1994; Lee, 1999; van Wijk et al., 2003).

Chapin et al. (1995a) found that despite compositional changes in response to temperature increases, overall productivity and biomass remained consistent; differential species success compensated for changes when considered at a community level (Shaver and Chapin III, 1986).

In summary, mineralization is expected to increase with an increase in temperature, although availability to plants may not be commensurate with the increase in rate, while higher availability may have adverse effects on plants adapted to low resource levels. Uptake of different nutrient forms is species-specific and climatic changes are expected to have differential effects on the various forms; the overall effect being a differing division of a limited nutrient pool. Species will therefore experience differential changes in growth and productivity, altering their relative competitive ability and subsequently the dominance patterns, ultimately resulting in changes to community composition. There may be reinforcing feedbacks through changes in litter quality, but due to compensatory effects it is not anticipated that community productivity will change radically.

Direct temperature effects The above discussion focuses on indirect temperature effects. Direct effects may be small due to acclimation, growing season and snowfall effects being more important (Körner, 1995; Woodward and Kelly, 1997). However, a small change in mean temperature has been seen to have a disproportionate effect on plant growth, Grace (1988) found an increase of 1°C raised productivity by 10%. Photosynthesis is inhibited at lower temperatures than growth, probably through changes in cell wall extensibility (Woodward, 1988; Woodward and Kelly, 1997), so that growth ceases earlier than photosynthesis in the autumn and photosynthate becomes available to other sinks, particularly storage (Körner and Larcher, 1988). Temperature may act in conjunction with other factors such as photoperiod, as a phenological cue (Holtmeier, 1994).

Wooky et al. (1994) found higher temperature to result in an increase in sexual reproduction, but anticipates differential effects depending on the availability of bare ground, with a closed canopy likely to have a buffering effect. Sexual reproduction has been seen as vital in arctic and alpine systems, to enable plants to reach suitable microsites (Bauert, 1996).

Bergman et al. (1996) examined pollinator activity in Latnjajaure, Sweden, finding a correlation with temperature and solar radiation. Such pollinators are important for the success of early flowering, outbreeding species (Molau, 1993).

Temperature effects are therefore seen as principally indirect, but with direct effects on growth and the success of sexual reproduction. This may enhance the likelihood of range expansion in open systems, particularly near the limit of species distributions (Grace, 1988).

Increased CO_2, ozone depletion and nitrogen deposition Plants at high-altitude have a greater uptake efficiency of CO_2 due to its reduced partial pressure, so that increased concentration may have a profound effect (Körner and Larcher, 1988), although Holtmeier (1994) considers that it may be dissipated in the windier conditions. The principal effect anticipated is one of fertilization; stimulating photosynthesis (Reynold et al., 1993; Beniston, 2000; Poorter and Nevas, 2003), however, enhanced production of photosynthate may be stored rather than increasing growth (Körner, 1994). Enhanced CO_2 may also improve water-use efficiency by prompting the partial or complete closure of stomata, therefore limiting transpiration (Reynold et al., 1993; Beniston, 2000; Poorter and Nevas, 2003). Finally there may be an increase in the C:N ratio reducing the quality of litter.

Ozone depletion and the resulting increase in incidence of UV-B causes damage to vegetation, particularly of the photosynthetic machinery and to DNA, and changes in the microbial community (Callaghan and Johasson, 1995). More specifically this involves, DNA lesions (Britt, 1997; Taylor et al., 1997), photoxidative effects producing free radicals (Jenkins et al., 1997; Caldwell et al., 1999), inhibition of photosynthesis (probably due to a decrease in Rubisco activity) followed by damage to PS II (Barnes et al., 1987; Baker et al., 1997). Increased UV-B prompts the up-regulation of several biochemical pathways; those of repair enzymes such as photolyases and antioxidant enzymes (Britt, 1997; Taylor et al., 1997) and screening compounds, particularly flavonoids, which can absorb up to 90% of incident UV-B (Barnes et al., 1987; Bornman et al., 1997; Jenkins et al., 1997; MacKerness et al., 1997; Caldwell et al., 1999).

Structural changes can also result due to altered resource allocation, including: thicker leaves, changes in cuticle waxes, shorter internode lengths and increased tillering (MacKerness et al., 1997; Caldwell et al., 1999). Experiments using high intensity UV-B have caused growth defects, leaf curling and bronzing (Britt, 1997). There have been criticisms of some of this work as the vegetation is often screened from receiving photosynthetically active radiation (PAR) and UV-A, which has been shown to increase plant resistance and more closely resembles field conditions (Bjorn et al., 1998; Caldwell et al., 1999).

Stimulatory effects due to CO_2 enhancement are often found to be short-lived as plants acclimatize to changing conditions (Callaghan and Johasson, 1995; Beniston, 2000; Poorter and Nevas, 2003), while the damage caused by increased incidence of UV-B may accumulate over time (Callaghan and Johasson, 1995; Caldwell et al., 1999). High latitude plants may be particularly disadvantaged because they are not adapted to high levels of UV-B, are often perennials (accumulating damage) while repair enzymes are cold sensitive (Barnes et al., 1987; Bjorn et al., 1997, 1998). It has been suggested that stimulatory effects of enhanced CO_2 may cancel out the inhibitory effects of increased UV-B (Moody et al., 1997).

Work on the effects of nitrogen deposition is comparatively scarce. Apart from lake acidification and forest damage, more moderate effects involve increased fertility (Holtmeier, 1994; Theodose and Bowman, 1997). Similar to the effects anticipated from increasing nutrient availability, this may lead to compositional change and the displacement of dominants (Körner, 1999a). Additionally, nutrient-poor communities may become vulnerable to invasion by more competitive species, particularly grasses (Theodose and Bowman, 1997).

2.9.3 Distribution changes expected to result from climatic change

Changing growth and reproductive success are expected to accompany warmer, longer growing seasons and changing resource availability. However, all species are not expected to respond in identical ways, some have physiological or life history traits that enable them to perform well, for others the effects will be neutral or disadvantageous. This differentiation is expected to lead to differences in resource acquisition and competitive ability, and to result in differential compositional changes. Factors contributing to this differentiation are considered in this section together with the nature of anticipated community changes in response to changing climatic trends.

McGraw (1995), working on buried seedbanks in solifluction lobes, found microevolutionary changes in temperature response on a century timescale. She hypothesises that within-species diversity might allow expansion in response to climatic change not possible for a homogenous population. Silvertown (2001) discusses studies at the Rothampstead Grass Park experimental plots. Soil conditions changed slowly and were interspersed with climatic events prompting intensification of the gradual response. There were four categories of response: decrease, fluctuation, outbreak and increase. Decreasing and fluctuating populations were adversely affected to various degrees, the response depending on periodic amelioration of other factors. Outbreak species were selfing ruderals, taking advantage of favourable climatic conditions but declining subsequently as they lacked the genetic variability enabling them to perform well under changing conditions. Those increasing (including *Anthoxanthum odoratum*) were outbreeding species. He concludes that a higher level of genetic variability allowed rapid local adaptation, which might result in rapid expansion of boundaries under climatic amelioration, provided that gene flow from the resident population was low. Reduced gene flow to peripheral populations results from distance, altitude and polyploidism (Antonovics et al., 2001; Petit et al., 2001; Silvertown, 2001). 30-40% of arctic and alpine plants are polyploids (having multiple sets of chromosomes), suggesting advantage conferred in previous population expansions, particularly postglacial migration (Murray, 1995; Petit et al., 2001). While outbreeding may result in local adaptation, polyploidism prevents gene flow from the resident population and increases the likelihood of selfing or pollen flow from other locally adapted plants (Chapin III and Körner, 1995b), stabilizing the edge of the range and enhancing exploitation of new environments (Murray, 1995). Outbreeding species have high levels of within-species genetic diversity and the potential to adapt to local conditions. Distance, altitude and polyploidy effectively isolate a locally adapted species from continued gene flow from the resident population.

Antonovics et al. (2001) modelled the boundary of an expanding population that was physiologically tolerant of an adjacent habitat but also subject to continuing evolution. Local adaptation was important together with distance from the resident population. Expansion occurred via stochastic events, rather than diffusion, and was revealed by fine-scale mapping. A similar pattern is discussed in Petit et al. (2001) in relation to postglacial migration. Again, expansion is not considered diffusive but is dependent on rare long-distance events: an ‘advance guard’ being established on favourable sites in front of the colonizing front, spreading from these initial foci and later merging.

Phenological cues contribute to the extent of the response to an extended growing season. These frequently involve both temperature and photoperiod (Mooney and Billings, 1961; Richardson and Salisbury, 1977; Grime, 1979; Krebs, 1985; Woodward, 1988; McGraw, 1995; Zhang and Welker, 1996; Welker et al., 1997). Walker et al. (1995) consider that the response to climate change may depend on the balance between genetically predetermined and environmentally prompted cues.

Community changes in response to climatic changes are not expected to involve simple linear migrations (Halpin, 1994; Brubaker et al., 1995; Beniston, 2000; Lawton, 2000); but small-scale patterns due to interactions, soil development differences and species-specific environmental requirements (Amman, 1995; Westoby and Leishman, 1997; Petit et al., 2001). Changes are anticipated in altitudinal ranges, producing stress as environmentally tolerant species come into contact and compete with established populations whose adaptation to nutrient-poor conditions may no longer confer the same advantage (Halpin, 1994; Körner, 1994; Chapin III and Körner, 1995b; Westoby and Leishman, 1997; Woodward et al., 1997; Beniston, 2000). Disadvantaged species are likely to remain at favourable microsites (Halpin, 1994); despite being poorly adapted to the changing conditions, specialized, slow reproducers or poor dispersers (Beniston, 2000; Petit et al., 2001).

The rate of change is likely to exceed migration capacity (Smith et al., 1992; Körner, 1994; Chapin III and Körner, 1995b; Beniston, 2000). Changes depend on interspecific variation (Smith et al., 1992; Shaver et al., 1997; Lee, 1999), with patterns expected to be unpredictable and individualistic (Graumlich, 1994; Körner, 1994; Amman, 1995; Chapin III and Körner, 1995b; Henry and Molau, 1997; Suzuki and Kudo, 1997; Lawton, 2000). Disruption is expected amongst established community types, with the new assemblages that emerge having different ecosystems properties and characteristics (Smith et al., 1992; Amman, 1995; Brubaker et al., 1995; Murray, 1995; Caldwell et al., 1999; Beniston, 2000; Lawton, 2000).

Grabherr et al. (1995) found increases of 25% in species richness since 1900 in response to a temperature increase of 0.5 – 0.7 °C on the summits of the Austrian Alps. Such changes required migration routes or corridors, but rates did not approach those of isotherm elevation. Competition with established species and the availability of safe sites are thought to be important influences. The process is seen as one of space filling rather than moving.

Differential species responses to climatic change are expected to produce individualistic distribution changes influenced by dispersal ability, soil development and species-specific requirements. Migration capability is therefore thought unlikely to keep pace with isotherm shifts. Interactions with existing vegetation and the availability of suitable microsites are likely to introduce further complexity. Species associations are expected to change and new assemblage types are anticipated.

Chapter 3: Methods

This chapter discusses the decisions concerning research design and numerical analysis. The initial sections involve sampling design and considerations related to operator error and identification. Later sections concern multivariate analytical techniques, initially reviewing available techniques followed by a discussion of those selected.

The identification of changes in species distributions since 1970-71 (Aim 1) requires that the present dataset be directly comparable to that of Matthews (1976). Sampling strategy is therefore constrained by decisions taken in relation to that study.

3.1 Research design

3.1.1 The strategy adopted in 1970-71

Matthews (1976) selected quadrat in preference to nearest neighbour sampling. Two factors influenced this decision. Firstly, nearest neighbour sampling detects pattern at a detailed level and is therefore time consuming. The survey aimed to detect the broad scale pattern, requiring a large number of sampling points, but was constrained by the time available. Secondly, a consistent area was considered preferable to the variation inherent in nearest neighbour sampling.

Quadrat size relative to plant size and the scale of patterning influences the relationships that are detected (McIntosh, 1967; Pielou, 1977; Greig-Smith, 1983; Crawley, 1997). Matthews (1976) used nested multiples of 1m^2 quadrats to investigate scale, resembling the 'grid' analysis of Goodall (1970), and the contiguous quadrats described by Greg-Smith (1983).

The 'stratified random sampling' technique used by Matthews (1976) combines elements of random and stratified sampling, neither of which were considered optimal individually. Inferential statistics assume independent, random sampling. Random samples are unbiased, and can be added as required (Jager and Looman, 1995). Although coverage is efficient overall, it may be uneven locally and therefore not effective for examining spatial variation (Matthews, 1976; Kent and Coker, 1992). Stratified sampling ensures evenness of coverage and is appropriate for inferential statistics, provided the interval does not correspond to periodicity in the vegetation, leading to sample bias (Matthews, 1976; Greig-Smith, 1983). However, samples can only be added or removed across complete strata (Crouch, 1992), making design changes difficult to implement (Matthews, 1976). 'Stratified, random sampling' involves a division of the study area into grid squares, within which a set number of sites are selected randomly. It is statistically valid, flexible and provides good coverage (Matthews, 1976; Greig-Smith, 1983; Crouch, 1992; Kent and Coker, 1992; Jager and Looman, 1995).

Common measures of species occurrence are density, cover and frequency. Matthews (1976) measured both cover and frequency, but only used the latter in his analysis. Density is a count of individual plants (Digby and Kempton, 1987; Kent and Coker, 1992), difficult to identify where spread is by ramets or tillering (Goodall, 1970; Magurran, 1988; Crouch, 1992), and such counts are extremely time-consuming. Cover subjectively assesses the percentage of the quadrat occupied, while frequency measures presence/absence in subdivisions of the quadrat (Kent and Coker, 1992). Matthews (1976) considers frequency to be complex, combining number, size and pattern, but closer to an overall quantitative measure than cover. Frequency provides a stable measure of sparse and seasonal vegetation, whereas cover increases markedly when plants come into leaf (Goodall, 1970; Crouch, 1992). However, frequency underestimates common and large species compared to rare and small ones (Magurran, 1988; Foskett, 1998) and is influenced by the relationship between quadrat size and distribution pattern (Goodall, 1970; Crouch, 1992). Importantly, frequency is objective and therefore relatively consistent when measured by different individuals; cover involves greater subjectivity and is found to vary widely (Matthews, 1976). Both Crouch (1992) and Foskett (1998) preferred cover, as data were collected by one individual and the studies were not comparative, so that the disadvantages associated with frequency outweigh those of using cover. However, the present study is comparative and uses several field assistants, increasing the importance of consistency (cf. Whittaker, 1985). Frequency was therefore selected as most appropriate.

3.1.2 Factors that influenced the decisions on sampling design in 2000-01

The outcomes of this study rely on the ability to determine changes in species populations over the 30 years since 1970. For there to be confidence in the results, the two surveys must be equivalent and, while errors are to be expected in both, they must be small and random enough that they do not obscure emerging patterns or generate such patterns themselves.

In addition to the comparative vegetation survey, the study examines the relationship between compositional change and environmental conditions, requiring supplementary data collection. While information collection is kept simple, an increase in survey time is unavoidable. Additionally, fewer field assistants were involved than in the original survey.

While it was necessary to reduce the workload, this had to be achieved without jeopardising the accuracy and equivalency of the study. It was considered important to incorporate a broad range of environmental variation while substantially retaining the detail of the vegetation survey to maximize the options for analysis.

Factors influencing the decisions on the sampling strategy adopted in this study therefore included the following:

(a) The 1970-71 survey used 638 sites at which 16 m^2 quadrats were recorded (Matthews, 1976), representing the upper limit.

(b) Smaller sampling units are associated with increased sampling error. Matthews (1976) calculated this as 4.0% for 1 m^2, 1.0% for 4 m^2, 0.44% for 9 m^2 and 0.25% for 16 m^2. Whittaker (1985), repeating part of the 1970-71 survey, cites this in support of his decision to retain the 16 m^2 quadrat sampling unit while restricting his survey by aspect and altitude.

(c) Crouch (1992), comparing cryptogam and higher plant successional sequences at Storbreen, used a 'minimal area test'. She selected 4 m^2 as a sampling unit as this coincided with the slope break in the species-area curve, though species number continued to increase at a decreasing rate up to 16 m^2. Additionally, the number of sites was reduced by a third within age and altitude zones.

(d) In a random sample of the 1970-71 data, the species count in 64% of sites increased by zero or one species with the increase in area from 9 to 16 m^2 (Figure 3.1):

(e) Crouch (1992) excluded sites on cliffs and all those above 1400masl as inaccessible and potentially dangerous.

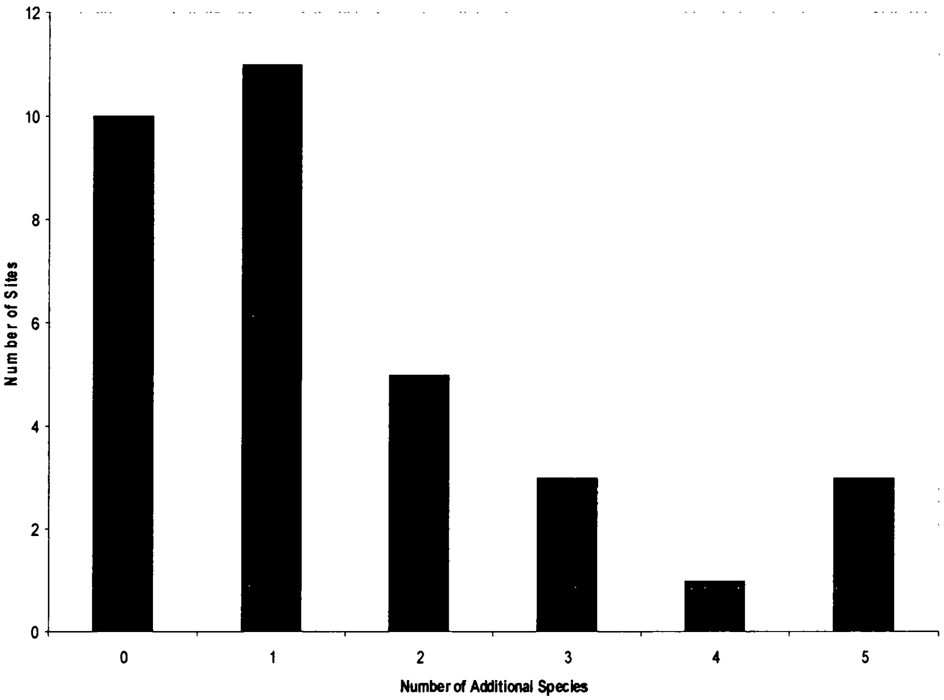

Figure 3.1: The number of additional species resulting from an increase in sample unit size from 9 m^2 to 16 m^2:
A random sample of 33 sites from the 1970-71 dataset was used.

(f) Matthews (1976) found that a 16 m^2 sampling unit corresponded to the scale of patterning in the vegetation. This pattern was recoverable at 9 m^2 with some loss of resolution, but not at smaller sampling units.

(g) In the literature, the preferred size of sampling unit generally corresponds to natural vegetation units, avoiding different parts of the within-site mosaic being treated as independent (Pielou, 1977; Greig-Smith, 1983; Crawley, 1997). Kent and Coker (1992) suggest 1 x 1m^2 for grassland and dwarf heath and 2 x 2m^2 – 4 x 4m^2 for shrubby heath, tall herbs and grassland. Chytry and Optykova (2003) find considerable variation in the sizes of sampling units in use in European phytosociology and propose standardisation at 16 m^2 for grassland, heath, herbaceous and low shrub vegetation, 50 m^2 for scrub and 200 m^2 for woodland. Mueller-Dombois and Ellenberg (1974), on the other hand, suggest 1-2 m^2 for herbs and 4 m^2 for low shrubs and tall herbs. Jager (1995) and Jongman (1995) discuss the balance between statistical power required for interpretation and unnecessarily large samples.

The scale of aggregation and the size of the vegetation units are therefore important criteria in selecting sample size. While 16 m^2 most closely approximates the scale of patterning, 9 m^2 is also acceptable. Examination of within-site spatial patterning is not a primary aim of this study, making a modest loss of resolution acceptable. Maximising the range of environmental variation sampled is important, but reduced statistical power and increasing sampling error suggest that smaller units are less useful despite containing most species found in larger units.

Therefore the strategy adopted involved no systematic rejection of sites by environmental criteria, apart from inaccessible high-altitude sites. Instead the sampling unit is reduced from 16 to 9 m^2 and the number of sites by approximately one third. In both surveys, numbered quadrats were recorded individually; the quadrats selected for the 2000 survey could therefore be compared directly to the same quadrats in the 1970 survey.

Figure 3.2 shows the selected quadrats. At the site, a red 'X' marks the north corner with filled red circles at each of the other corners.

13	14	15	16
12	11	10	9
5	6	7	8
4	3	2	1

Figure 3.2: The 9-m^2 quadrats selected as the sampling unit in this study
additional quadrats included in 1970-71 are shown in red.

Where a site could not be located on the ground (generally due to vegetation overgrowth, rarely by channel switching or slope collapse), the closest neighbouring site, surveyed in 1970 but not selected for this survey, was used instead. In the field, many of the highest altitude sites proved accessible; those on the cliffs were potentially dangerous and therefore avoided. Figure 3.3 shows the location of those sites resurveyed, including new sites established in 2000-01.

3.1.3 New sites on land deglaciated since 1970-71

Sites representative of the pioneer stage are required for comparisons of sequence stages. The 1970-71 map of the study area (Matthews, 1976) is based on aerial photographs taken in 1968. This was extended using the 1997 Storbreen glacier map produced by the Norwegian Water Resources and Energy Directorate (Norges vassdrags-og energidirektorat (NVE)) in Oslo, and updated by field survey in 2000. The area of newly deglaciated land is small compared to that supporting pioneer vegetation in 1970-71, as the glacier has retreated onto higher ground relatively slowly. For the data to be equivalent, it was necessary to replicate both site density and selection. The earlier survey uses a 7 x 13 grid with eight sites randomly selected within each square. A similar grid was constructed, but the number of sites per square reduced to six so that 24 new sites were randomly selected. Location on the ground used compass bearings and pacing from at least two known reference points (i.e. meltwater stream junctions, position on the ice front and other sites). Some potential sites were abandoned due to the presence of rocks and streams; where a suitable location was not found within 5m, another random point was selected (Matthews, 1976).

Of the original 638 sites, a total of 410 were resurveyed. Twenty-four additional sites were established and surveyed on land deglaciated since 1970.

3.1.4 Operator error

Both studies used field assistants, mainly undergraduates from Kings College, London and Swansea University. Time in the field is short and assistants are consequently inexperienced. Additionally, some sites are particularly difficult i.e. cover is complete, species lists long and vegetation stratified. Therefore, there is the potential for high cumulative error rates. To avoid this both studies attempted to control errors.

Matthews (1976) tested for 'operator error' in both qualitative (species identified) and quantitative (counts) terms. Qualitative errors generally involved omissions rather than adding species not present. On average, one species was missed per 16m^2 site, with error rates increasing with site complexity (a maximum of four on a site containing 30 species). Species missed tend to be small and infrequent. Quantitative errors involved under- rather than over-counting. Inconspicuous, moderately abundant species were affected rather than conspicuous species of low or high abundance. He concluded that the error rate is likely to over- rather than under-estimate that for the whole study area. Matthews also examined use of cover rather than frequency as the sampling measure. Frequency is associated with undercounting, while errors in cover show greater variability, occurring in either direction.

Whittaker (1985) also used a number of assistants but, rather than testing in the field, he compared ordination results, using data recorded by himself, by Matthews with two assistants and by operators working independently. The direction and extent of change are similar on all but one site. He pointed out that infrequent species have little overall influence, error rates were low in the context of a large multivariate dataset, but contributed to 'noise', and concluded that the rationale underlying the study was tenable.

The present study therefore attempted to keep both qualitative and quantitative error rates low. In both studies, there was a period of training and the principal operators were involved in species identification. With fewer field assistants in the present study, the group generally worked together, particularly in surveys of complex sites; including those close to the River Leira and at low-altitude on south-facing land, where shrub layers frequently exceed 2metres, ground flora is well developed and species lists exceed 30. Direct checks of the work were made once a week; small quantitative errors being found most frequently, while qualitative ones were rare. As discussed above, frequency is objective, associated with low variability and a tendency to omission and undercounting. Its use contributes to low error rates and ensures a known, directional trend. Finally, Professor Matthews provided advice during the early stages of this study and was involved in surveying some of the early sites, allowing a crosscheck between the principal operators.

In conclusion, the present study uses methods that do not differ in principle from those of 1970-71. Errors are similar in type and rates do not exceed those of the earlier survey. For practical purposes, it is considered that the surveys are equivalent and that their use in a comparative study is justified. While errors in both surveys compound the error rate; being similar in direction and likely to involve the same species, it is argued that they will not materially affect this conclusion.

3.1.5 Species identification and taxonomy

While most species were identified at the sites, where necessary, small samples were taken for identification. Generally, such samples used specimens adjacent to the marked site.

Matthews' (1976) use of composites for several closely related species is followed in the present study involving:

Carex spp. (mainly *Carex bigelowii*)
Festuca spp. (*F. ovina, F vivipara*)
Poa spp.
Pyrola spp. (*P. minor, P. norvegicum, P. rotundifolia, P. secunda*)

Two additional composites are used in the present study: *Arenaria* spp. and *Arctostaphylos* spp. The first was considered necessary as two species of Sandwort (*A. norvegica* and *Minuartia biflora*) and one Pearlwort (*Sagina saginoides*) were identified on these quadrats in 2000-01 but only one Sandwort (*A. norvegica*) in 1970-71. While population expansions may have occurred, the species closely resemble one another and occur in similar situations. Misidentification appears more likely and hence grouping these species is the safer option.

A rather different problem was found in the identification of the two *Arctostaphylos* spp., *A. alpina* and *A. uva-ursa*. *A. alpina* was recorded almost exclusively in 2000-01; but in 1970-71 *A. uva-ursi* was most frequent while *A. alpina* occurred rarely. From observation, the predominant species in 2000-01 did not have leathery (coriaceous) leaves but did show a strong red colouration by the end of the season. While it is possible that these two species experienced a reversal in relative frequency (the evergreen *A. uva-ursi* declining while the deciduous *A. alpina* increases), resulting in the substantial change in overall frequency, this conjecture lacks conclusive evidence.

Hybridization amongst the three *Salix* spp. (*S. glauca, S. lanata* and *S. phylicifolia*) is discussed by Matthews (1976). Whittaker (1985) also referred to this problem, but includes only *S. glauca* and *S. lanata*. Both studies however record these species individually. Evidence of hybridization was found in 2000-01, primarily involving *S. glauca* and *S. lanata*. Criteria were therefore established to allocate specimens to appropriate species: differences in catkins; leaf length to width ratio (a value less than two suggesting *S. lanata*); and the extent and nature of leaf hairs (fine and silky indicating *S. glauca*, thick and woolly *S. lanata*). *S. phylicifolia* was rarely affected by hybridization, and was distinguished by a bright green leaf colouration and narrow, shiny and hairless leaves. Many specimens appeared young, with a single stem and no developed branching.

Luzula arcuata and *L. spicata* are mentioned by both Matthews (1976) and Whittaker (1985) as being difficult to distinguish when not in flower. This was also found in the present study, particularly on sites surveyed early in the growing season. Despite this, these species are identified separately, a practice followed in the previous studies.

Erigeron uniflorum has completely different distributions in the two surveys, strongly suggesting that it was misidentified. Fortunately the species is rare and has been excluded from the analysis.

The nomenclature adopted in this study is that of Lid (1963). A full list of species names and abbreviations is given in Appendix 1.

3.2 Recording the environmental variables

In Chapter Two, the vegetation-environment relationship is described as a two-way interactive system, maintained by feedbacks (section 2.8.2). An aim of this study is to explore this relationship in the context of vegetation changes occurring since 1970. Previous work has identified the most influential environmental variables in the system (Whittaker, 1985; Crouch, 1992; Foskett, 1998). However, it is not known whether these variables continue to predominate in subgroups representing sequence stages. Information was consequently collected for as wide a range of variables as possible, although this increases the likelihood of multicollinearity. Additionally, some environmental variables are surrogates for more influential factors, act indirectly, or contribute to broad environmental gradients (Greig-Smith, 1983; Myers and Giller, 1988b; Whittaker, 1989; Burrows, 1990).

This section describes the recording of these variables. Chapter Two, sections 2.8.2-2.8.9, discusses interactions with the vegetation in more detail.

3.2.1 Age

The LIA glacier advance reached its maximum extent ca AD 1750 (Matthews, 1976, 1977, 1991, 1992). Minor advances interrupted the subsequent retreat, leaving a series of arcuate moraines (Matthews, 1992). Site age is based on dates calculated by Matthews (1976) for the deglaciation of these moraines and interpolation between them.

Moraines formed since 1900 are dated using evidence from Liestøl (1967), particularly mass balance calculations; Øyen's reports from farmers and guides; annual measurements since 1900 (largely the work of Øyen and the Norsk Polarinstitutt); a 1908 photograph; and maps (1936, 1940, 1951 and 1968) based on surveys and aerial photographs (1955, 1966 and 1968) (Matthews, 1976). The associated error is estimated at ±5 years (Matthews, 1976).

Direct evidence is scarce prior to 1900 and dating relies largely on lichenometry (c.f. Beschel, 1950, 1961). This proxy assumes a relationship between lichen size and time since exposure. Curves are constructed using lichen sizes from independently dated moraines, lichens from undated moraines are then compared to these curves giving approximate ages. At Storbreen, Matthews (1974, 1975, 1976, 1977) used the mean size of the five largest *Rhizocarpon geographicum* on the proximal moraine slope. Distal slopes may be considerably older and contain lichen-bearing rocks transported by the glacier. This methodology conflicts with that of Webber and Andrews (1973), who advocate the use of only the single largest lichen. Matthews (1974, 1976) considers the response to longer exposure time likely to be more accurately reflected in the use of several lichens, single specimens possibly representing anomalies or deposited from supraglacial material (Matthews, 1973). His view is supported by testing using families of curves and has been validated by supplementary evidence (Matthews, 1974, 1975, 1976). Median dates from the families of curves reflect this evidence more closely than isolated predictions.

Overall, it is estimated that the dating of the moraines is accurate to within ±10 years. Error rates are larger on terrain where glacier movements are least, particularly for lateral moraines on steep slopes at high-altitude, and on relatively old terrain.

An appropriate age for land outside the foreland presents greater difficulties. Regional deglaciation took place approximately 9 000 radiocarbon years BP (Andersen, 1980). However, the advance of the glacier to the LIA maximum severely affected local climate in terms of temperature depression, exposure to the glacier wind, disturbance from meltwater streams and the activation of solifluction/gellifluction lobes (Ballantyne and Matthews, 1982; Matthews et al., 1986). Additionally, an advance close to the LIA maximum may have occurred approximately 1800 years BP (Matthews, 1991). Previous studies have used ages only slightly older than that within the foreland. Whittaker (1985, 1989) used 300 years and Crouch (1992) used 250 years, citing the detrimental conditions during the LIA as justification. Both authors found that using older dates in the analysis reduced the explanatory power of age, but did not affect other variables.

However, Matthews (1976) found soil profiles outside the 1750 moraine generally exceeded 50cm, those inside being rarely more than a few cms. Similarly lichens were frequently larger than 300mm outside the foreland, but rarely exceed 100mm inside. Matthews (1976) considers this land to be at least an order of magnitude older than that within the foreland.

Soil depth and lichen growth therefore indicates a considerable age difference though this may not be reflected in the species compositional discontinuity (Whittaker, 1985, 1989; Crouch, 1992). It is not disputed that the presence of the glacier would cause vegetation damage, but seed sources in close proximity to the moraine are likely to reduce the vegetational distinctiveness of the discontinuity.

The above discussion suggests that extra-foreland terrain is markedly older than that within the foreland. While the LIA and any preceding advances produced detrimental effects both in terms of climate and increased disturbance, the glacier did not override the land. It was therefore considered that an age greater than those used previously would reflect the situation more accurately. A number of test runs (CCA) were used to determine the effects of various ages; once age exceeds a few hundred years, it makes little difference to the overall result, as discussed by Crouch (1992). Rather than ascribing an intermediate, but arbitrary, date, the oldest possible date, 9 000 years, has therefore been used.

3.2.2 Altitude (section 2.8.2)

Altitude was calculated by interpolation from existing 10m contour maps (Matthews, 1976; Whittaker, 1985; Crouch, 1992), including the 1997 glacier map (NVE).

3.2.3 Aspect

The Storbreen foreland has a broad division between NE and SW facing land.

Whittaker (1985) did not use aspect, sites often lacking a preferred orientation and no clear pattern emerged. However, aspect influences microclimatic effects; south-facing slopes receive greater insolation and tend to be drier than more northerly facing slopes (Billings, 1974b; Amman, 1995; Körner, 1995, 1999b; Beniston, 2000), vegetation is consequently more prolific (Hobbs, 1997). Additionally, south-facing land is found to have higher levels of phosphorous (Walker and Syers, 1976), enhanced soil development and chemical weathering (Darmody and Thorn, 1997). The timberline on south-facing slopes can be up to 100 m higher than on north-facing slopes (Bruun and Moen, 2003). Bickerton and Matthews (1992) found lichens on the south-facing side of Nigardsbreen foreland gave older dates than those on correlated moraines facing north. Aspect may therefore exert a considerable influence on vegetation development and assessing this variable is considered worthwhile.

Measurement was made of the direction of the predominant slope to the nearest 1°, or that of the surrounding land if the site was flat (Crouch, 1992). The resulting values are circular; the largest angles representing values similar to the lowest ones, and therefore inappropriate for multivariate analysis. Foskett (1998) converted the values into deviation from north and east using a five-point ordinal scale. The method used in this study is based on Batschalet (1981) and generates two variables, northness and eastness. Northness uses the cosine of the angle giving a figure between +1 (due north) and –1 (due south) with values close to zero indicating east or west; eastness uses the sine, giving +1 for sites facing east, -1 for those facing west and zero for north or south (cf. Crouch 1992).

3.2.4 Slope

Increasing slope gradient indirectly influences vegetation via effects on other variables:

(1) Increased solifluction (section 2.8.5);
(2) Improved drainage reducing moisture availability;
(3) Reduced snow accumulation (Foskett, 1998) (although topographical configuration may produce snow patches on steep slopes);

(4) Downslope movement retarding soil development; although rarely severe, evidence of soil loss frequently suggests small but continuous increments. The shallow soils support pioneer communities even on the oldest land.

Flat sites are more likely to have higher moisture levels, snow accumulation and thicker soils.

Slope was measured as deviation from the horizontal using a clinometer, accurate to the nearest degree. Where slope angle varied across the site, an average was calculated weighted proportionally to area.

3.2.5 Exposure

This variable is related to wind effects (desiccation, abrasion and temperature) and snow accumulation (Whittaker, 1985; Foskett, 1998). Crouch (1992) and Foskett (1998) used broadly similar ordinal scales, but Crouch has an additional increment and this is used in this study:

0 = sheltered on 4 sides
1 = " 3 sides
2 = " 2 sides
3 = open hillside (i.e. shelter 1 side)
4 = flat, no shelter
5 = ridge or hilltop

3.2.6 Glacier Climate (section 2.8.4)

This combines exposure and proximity to the glacier. The effect is negligible beyond a distance of approximately 500m (Whittaker, 1985), being most influential within 50m of the glacier snout. Given the pattern of wind distribution in the foreland (Matthews, 1992), such effects are strongest within the central axis when the site is exposed in the direction of the glacier. The measurement uses an ordinal scale:

0 = further than 600m from the glacier
1 = 600 -50m, not exposed to the glacier, not in the central axis
2 = " " , exposed to the glacier, not in the central axis
3 = " " , not exposed, in the central axis
4 = " " , exposed, in the central axis
5 = within 50m, not directly exposed, not in the central axis
6 = within 50m, exposed to the glacier and in the central axis

3.2.7 Moisture (section 2.8.6)

Crouch's (1992) 'finger test' was preferred to an instrumented measurement, mainly because it is simple, easy to apply, and rapid, not involving bulky equipment that may breakdown. Foskett (1998) compared the results of this test to those obtained using a capacitance probe, finding the former relatively accurate, convenient and comparable between sites. She relied largely on the finger test due to the mechanical failure of the probe.

Initially two measurements were made, one after four days without rain, another after two days of rain. The results were similar with a maximum difference of one point where sites were dry. This procedure was revised due to lack of useful information and the necessity for repeated site visits. Subsequently one measurement was taken after two days without rain. The scale is as follows:

1 = dry, friable, no moist soil at 1cm depth (finger not visibly wet)
2 = dry, friable but moist at 1cm depth
3 = surface moist to touch but not visibly wet
4 = soil surface wet, but no puddling, surface water caused by pressing reabsorbed rapidly
5 = pressing soil causes puddling, but no standing water
6 = standing water, wet and boggy

3.2.8 Duration of snowlie (section 2.8.3)

The measurement uses a methodology developed by previous workers at Storbreen, involving the ratio of the green lichen *Rhizocarpon* spp. to that of the brown *Umbilicaria* spp.. *Rhizocarpon* spp. has been found to require a reliable moisture source, growing preferentially around snowpatches, at the bases of boulders and the foot of moraine slopes (the 'green zone hypothesis') (Haines-Young, 1983, 1985; Crouch, 1992; Foskett, 1998). The brown *Umbilicaria* spp. is found in drier, more exposed positions, on the tops of boulders and on ridge crests (Crouch, 1992). Benedict (1990) tested resistance to snowkill, transplanting lichen encrusted rocks to various positions in snowpatches on the Colorado Front Range. *Rhizocarpon* tolerated longer snowlie (up to 40 weeks), and took longer to die than *Umbilicaria.* The difference is related to growth rate. Moisture is available below deep snow but light does not penetrate; the lichens respire but cannot photosynthesise. Without replenishment, stored carbon is consumed more rapidly at high compared to low growth rates. Mortality amongst fast growing species, such as *Umbilicaria*, occurs more rapidly. While confirming that *Rhizocarpon* has greater tolerance of late snowlie, the faster growth rate of *Umbilicaria* may distort the ratio under less extreme conditions. Time lags occur in the response to climatic change; *Rhizocarpon* taking up to 14years to die when transplanted to deep snow and lichen-free areas around snowpatches being attributed to conditions in the 1950s.

The ratio is the percentage of green to brown lichen. A high value indicates late snowlie:

90:10 = 9
80:20 = 4
70:30 = 2.3
60:40 = 1.5
50:50 = 1
40:60 = 0.67
30:70 = 0.43
20:80 = 0.25
10:90 = 0.11

3.2.9 Humus, soil and rooting depths (section 2.8.8)

'Humus' is the depth of surface organic material. It reflects the balance between inputs and decomposition rate, which affect nutrient availability. At some sites this forms a continuous layer, while elsewhere it occurs intermittently, filling irregularities or accumulating around the base of boulders. Crouch (1992) combined continuity with depth in a three point ordinal scale. Jonasson (1986) discussed the disruption of surface organic material by frost heave, although interruptions also result from the presence of irregularities (due to erosion or the size/shape of clasts in the substrate). In this study, the depth of the organic layer was measured, with evidence of frost heave collected separately.

'Soil' measures the depth of brown staining or that of mixing of organic and mineral soils (Whittaker, 1985; Foskett, 1998).

'Rooting' measures the maximum depth at which roots occur. Surface roots are generally fine, forming a mat where well developed, while deeper roots are woody, associated with the presence of shrubs. A maximum rather than average (Whittaker, 1985) or representative depth (Foskett, 1998) was chosen as it is objective and reflects the extent of vegetation development.

The measurements were taken from a small pit dug adjacent to the site, avoiding disruption of the vegetation. While variation may occur over short distances, only one pit was used per site, although the location was selected as representative of site conditions. Measurements are accurate to the nearest millimetre.

3.2.10 pH (section 2.8.8)

pH interacts with climate and vegetation, influencing cation exchange capacity and therefore nutrient availability (Whittaker, 1985).

A soil sample was taken from below the humus layer in the pit described above. Stones and organic material were removed and the soil thoroughly mixed with de-ionized water in ratio of 2:5. A portable pH meter was used (Camlab 501), the reading recorded to one decimal place. Spatial variability and dependence on weather conditions are discussed by Foskett (1998), who concluded that it was not worthwhile to make multiple recordings of pH.

3.2.11 Texture (section 2.8.8)

Soil particle size and cohesiveness affects soil temperature, moisture and susceptibility to frost heave (Foskett, 1998).

Material from the soil sample was used, employing a similar ordinal scale (based on the USDA triangular diagram) to those of Crouch (1992) and Foskett (1998).

1 = sand, could not be rolled into a ball
2 = loamy sand, could not be rolled into a cylinder 5mm in diameter
3 = sandy loam, could not be rolled into a thread 1mm in diameter
4 = loam, thread (3) could not be shaped into a horseshoe
5 = silt/clay loam, thread (3) could not be shaped into a circle
6 = silts and clays, thread could be shaped into a circle

In practice, few soils scored 5 and none above that. Tills behave like clays but do not represent well-developed soils and are classified as sand.

3.2.12 Compaction

This variable may affect seedling germination, establishment and water infiltration/runoff. A penetrometer was used to measure compressive soil strength, but as discussed by Crouch (1992), many readings were needed to cover the range found at most sites (40 provided an average over 4 m^2). The readings vary widely over short distances, with a similar range at most sites. The spatial scale is finer than that of the sampling unit, rendering the measurements virtually meaningless. The variable was therefore abandoned.

3.2.13 Clasts

Substrate clast sizes contribute to the frequency of safe sites for plant establishment, varying in the capacity to trap seeds, particulate matter and moisture (section 2.3). Both Crouch (1992) and Foskett (1998) collected data on three clast sizes; Crouch did not identify boulders separately while Foskett combined medium sized clasts as 'gravels and cobbles'. Boulders exert a microtopographic influence due to the shelter they provide (Foskett, 1998). Gravel and cobbles are likely to impact differently on vegetation, affecting moisture retention and finer material being more susceptible to frost heave than coarser substrate (Matthews, 1999; Foskett, 1998). Cobbles have a greater microtopographic influence compared to the limited shelter provided by gravel. Four categories of substrate were therefore used in this study: fines (<2mm); gravel (2mm-60mm); cobbles (60mm-256mm); and boulders (>256mm). The frequency (0 – 25) of clasts was measured per quadrat, excluding substrate beneath the vegetation due to avoid damage.

3.2.14 Bare Ground

This is an inverse measure of vegetation cover. The extent influences the severity of frost heave (the number of freeze-thaw cycles, depth of freezing) (section 2.8.5); retention of soil moisture (the level of percolation/runoff, surface evaporation/desiccation) (section 2.8.6); susceptibility to temperature fluctuations and wind effects (Foskett, 1998); but other plants compete for moisture and nutrients (sections 2.4.2 and 2.4.4).

Foskett (1998) measured both % vegetation cover and % bare ground. This study only assesses bare ground as the variables effectively measure the same factor. Bare ground is measured as frequency (0 – 25) per quadrat, in the same way that the vegetation was measured. As clasts were only counted where there is no vegetation cover, the counts for clasts sum to the bare ground total, necessitating the exclusion of one of the clast categories from subsequent analysis (Johnston, 1980).

3.2.15 Frost heave (section 2.8.5)

Whittaker (1985) initially used a five point ordinal scale to measure all disturbance but subsequently introduced separate scales for frost heave and slope movement. Crouch (1992) used a three point scale assessing visible effects at each site; while Foskett (1998) measured current frost activity by means of an index related to dowel displacement. Visible effects confound current and recent activity, but reflects the strength of the influence during vegetation development (Foskett, 1998) and is of greater relevance to this study. The scale is based on that of Crouch (1992):

0 = none visible
1 = slight, surface undulation but no broken ground
2 = moderate, surface uneven and cracked, no patches of bare soil > 10mm
3 = severe, very uneven, patches of bare soil > 10mm, vegetation displaced

Initially a fourth category was included involving extreme disturbance (patches of bare soil exceeding 100mm), but no sites had evidence of such intensive disruption. Each quadrat was scored, the site total being the sum over the nine quadrats with a maximum of 27.

3.2.16 Solifluction (section 2.8.5)

Solifluction and gellifluction are not distinguished in this study (Foskett, 1998) as the effects are similar. Both Crouch and Foskett used similar ordinal scales:

0 = none visible
1 = slight, small lobes, risers up to 10mm
2 = moderate, lobes with risers 10-100mm
3 = severe, large lobes with risers over 100mm

While Foskett assessed the variable in each 20cm square, it was considered sufficient in this study to score each quadrat.

3.2.17 Fluvial Disturbance (section 2.8.5)

Crouch used a four-point scale, not including channel switching and flooding, which form part of Foskett's expanded scale. The latter is used in this study and applied to each quadrat:

0 = none evident
1 = slight, flushing but no stream channels formed
2 = moderate, flowing water forming streams < 100mm wide
3 = severe, part of the quadrat occupied by stream channels > 100mm wide
4 = extreme, evidence of site flooding and/or stream switching.

3.2.18 Trampling

Direct effects include damage to and displacement of vegetation, while indirect effects involve substrate changes particularly compaction, restricting infiltration and damaging surface roots.

Whittaker (1985) included trampling as part of the disturbance variable. Crouch (1992) used a four point scale and Foskett (1998) measured the frequency of paths, broken vegetation and prints in each 20cm square.

Initially it was intended to record frequency, intensity and type of disturbance. As recording progressed, it became apparent that damage occurred rarely, almost exclusively associated with the glacier path (except for some valley bottom sites grazed by cattle), and was extreme (complete loss of vegetation, surface compaction or poaching). Recording was therefore limited to the occurrence of such damage within each quadrat.

3.2.19 Grazing and browsing (section 2.8.9)

Grazing/browsing was considered important by previous workers at Storbreen (Whittaker, 1985; Crouch, 1992), but only Foskett (1998) collected data on the variable. She measured the frequency of nibbled leaves/seedheads and of faeces, although her study sites avoided areas of extreme herbivory.

In this study, herbivory is categorised as grazing where plants are damaged (nibbled) or browsing if parts were removed. Severe browsing may result in mortality, while grazed plants experience a reversal in development, often temporarily, with some species increasing production in response. The plant species affected was also recorded as preferential herbivory may contribute to differential species responses. The variable was measured as frequency per 20cm subdivision.

3.2.20 Droppings

Data on this variable were collected for several reasons:

(1) It indicates the presence of particular species, possibly linked to patterns of herbivory;

(2) Some plants are dispersed via animal vectors i.e. ptarmigan and *Empetrum hermaphroditum* (Tybirk et al., 2000);

(3) Droppings provide localised nutrient inputs, important on nutrient-poor sites.

Foskett (1998) used the presence of faeces as evidence of grazing, but otherwise such data have not previously been collected.

Five types of droppings were recorded: sheep, cow, hare, ptarmigan and vole, 'vole' including several species of vole and lemming. Hare and ptarmigan droppings most frequently contained berries/seeds, but source plants were not identified. Frequency was recorded per 20cm subdivision.

3.3 Species distributions

This section discusses the maps used to investigate changes in species distributions.

3.3.1 Species distribution maps

Mapping species distributions is often used initially in an ecological study to summarise data and allow hypothesis generation (Myers and Giller, 1988a), to indicate spatial relationships

(Matthews, 1981) and to aid interpretation (Crouch, 1992). In this study, it is used to examine spatially coarse-scale changes in frequency. Each species is illustrated by three maps: the 1970 and 2000 distributions and net changes between the two.

The map is based on that of Matthews (1976) using the 1968 aerial photographs. It was updated from the 1997 Storbreen glacier map (Norges vassdrags-og energidirektorat (NVE), Oslo) and by fieldwork in 2000-2003. It was digitalized using the Map Viewer Programme (1995). Counts and the differences between them were converted to circle areas by dividing the square root by 40 (Monkhouse and Wilkinson, 1963). This conversion factor is selected as: small counts are easily distinguished; overlap in circle size is minimal for large counts; the range is clearly represented; and the circles do not obscure the map. This was preferred to an octave scale (Crouch, 1992) due to the greater detail and sensitivity.

Large 'colonization' events or species losses are treated cautiously, but are included on the map unless there are compelling grounds for exclusion. Increasing and decreasing populations are considered more reliable as identification is corroborated in the two surveys. One site had a radically different species list in 2000 compared to 1970; the site was apparently misidentified and was therefore excluded from the analysis.

3.4 The measurement of diversity

The analyses in Chapter Five examine community structure to determine changes since 1970. The initial section comprises a comparative examination of 'within-habitat' (MacArthur, 1965) or α diversity (Whittaker, 1967, 1975). Various diversity measures provide information on species number, the extent of dominance and equitability of distribution.

3.4.1 Analytical techniques for the measurement of diversity

Diversity involves both species number and the distribution of individuals amongst these species (relative abundance) (MacArthur, 1965; Bazzaz, 1975; May, 1975a, 1975b; Magurran, 1988; Kent and Coker, 1992). There are two approaches to examining diversity: (1) plots of species in rank order against abundance; and (2) the reduction of site data to one or a few single statistic(s) or indices.

The first approach involves a comparison of the curve with a series of models, which characterise the number of influential environmental variables and the manner of resource partitioning (Peet, 1974; Bazzaz, 1975). The curves vary with the number of species and the evenness of distribution and the models are interpreted as representing a successional progression. Severe, early successional sites with few species and strong dominance generate the steep curve of the geometric model (Bazzaz, 1975; May, 1975a, 1975b; Magurran, 1988), the increase of rare species in intermediate stages producing the concave curve of the log series model (Kempton and Taylor, 1976; Magurran, 1988), while equitable distributions are represented by the broken-stick model (Lloyd and Ghelardi, 1964; MacArthur, 1965; May, 1975a; Magurran, 1988). However, this is complicated by the use of the log normal model (Preston, 1948), which has been criticised as a statistical construct rather than being ecologically interpretable (May, 1975a; Krebs, 1985; Magurran, 1988), although some consider the S-shaped curve as representing mature successional communities with many rare species (Bazzaz, 1975; May, 1975b; Whittaker, 1975). It does, however, encompass a wide range of site types.

3.4.2 The advantage of indices in a comparative study

While these curves are of interest ecologically and include more information (May, 1975b), indices are considered more appropriate to identify and characterise change:

(1) Calculating an index reduces the data, providing a useful summary (Clifford and Stephenson, 1975; May, 1975b; Kempton and Wedderburn, 1978; Magurran, 1988; Kent and Coker, 1992), which is easier to handle than the greater complexity of the curves (Kempton, 1979).

(2) Using only four ecological models/interpretations, the curves are less sensitive in detecting change than the absolute values of the indices. Indices avoid dependence on a limited range of distribution types (Krebs, 1985).

(3) Sites may be intermediate or not conform to any models (Matthews, 1976; Morris and Lakhani, 1979; Magurran, 1988).

(4) The wide range of community types encompassed by the lognormal model overlaps with other distributions, particularly the log series (Greig-Smith, 1983). This was found when the models were tested using data from this study. While goodness of fit statistics could be used (Magurran, 1988), sites are then compared using a single number.

(5) Several indices could be calculated, which describe a variety of aspects of diversity. This is considered of greater interest, flexibility and sensitivity than a comparison of relative similarity to a small range of models.

3.4.3 Criteria used for the selection of indices

Numerous indices have been formulated, but many have been extensively criticised and some duplicate information. Diversity involves both species number and relative abundance of individuals, giving three types of indices (Berger and Parker, 1970; Peet, 1974; Matthews, 1976):

(1) species richness;

(2) evenness of distribution or equitability; and

(3) combinations of these components.

Many authorities consider that combining species richness with relative abundance comes closest to describing diversity (MacArthur, 1965; Whittaker, 1967; Hurlbert, 1971; Clifford and Stephenson, 1975; May, 1975a, 1975b; Pielou, 1977; Kempton, 1979; Krebs, 1985).

In this study, diversity measures are used as comparative descriptors, to detect change in assemblage structure. Despite criticisms and reservations (Hurlbert, 1971; Hill, 1973a), this is considered useful taking into account the following considerations:

(1) Rather than directly characterising assemblages, mean diversity within age groups is used to identify changing patterns during succession and trends between the surveys.

(2) Several indices are used and cover a range of attributes representative of various aspects of diversity, rather than relying on a single statistic.

3.4.4 The selection of indices used in this study

***The Shannon-Wiener Index* (1949)** Obtained from:

$$H' = -\sum_{i=1}^{S} P_i \ln P_i$$

$P_i = n_i/N$ the Maximum Likelihood Predictor (Kent and Coker, 1992); n_i is the number of individuals in the ith species; N is the total number of individuals; In is $\log_e$

This assumes a random sample from an infinitely large population, for which the total number of species is known (Magurran, 1988; Kent and Coker, 1992). As this is not generally the case, the similarly calculated Brillouin index is suggested as an alternative (Magurran, 1988), being a sample rather than a community parameter (Peet, 1974; Greig-Smith, 1983). If used inappropriately, the Shannon index is judged to give a biased result, underestimating species number and overestimating the index (Peet, 1974; Pielou, 1977). However, in comparisons with the Brillouin index, the Shannon index is considered more satisfactory (Peet, 1974; Greig-Smith, 1983), and the two have been found to be correlated over a wide range of values (Clifford and Stephenson, 1975). Mouillot (1999) found that the Shannon index was associated with small errors regardless of the underlying model and sample size.

The index arises from Information Theory, representing the information content per unit of code (Clifford and Stephenson, 1975; Kempton and Wedderburn, 1978). It is generally considered a measure of uncertainty (MacArthur, 1965; Hurlbert, 1971; Peet, 1974; Matthews, 1976; Greig-Smith, 1983) although Hill (1973a) and Krebs (1985) classed it as a measure of system order or entropy. It is generally regarded as combining species number with relative abundance (Berger and Parker, 1970; Krebs, 1985; Brown, 1988), although Magurran (1988) classed it as solely a measure of proportional abundance.

High values indicate even distributions (Pielou, 1977), although such values also indicate large numbers of rare species (Peet, 1974; Kempton and Taylor, 1976; Greig-Smith, 1983; Putman and Wratten, 1984; Magurran, 1988), as the log term reduces the relative contribution of abundant species. May (1975a) found that large numbers of species were required for high values where distributions are equitable, the index being insensitive when species were few. In Hill's family of indices (1973a), this index is intermediate to species number and the reciprocal of the Simpson index, influenced by rare and common species respectively, but Hill considered it to contain little additional information. While recognising its shortcomings, Bazzaz (1975) still used the index for comparative purposes as it continues to be widely used by field ecologists (Usher, 1987; Kent and Coker, 1992; del Morel et al., 1995).

The sensitivity to rare species is of particular interest in this study. However, due to the above reservations (particularly that use of the Brillouin index is more appropriate) it was considered necessary to compare the two indices. They followed a similar pattern over a wide range of site types, suggesting that there was little advantage in using Brillouin. The behaviour of the index was also observed. Although having no term for species number, the index increased with this parameter. Species-poor sites gave low values, particularly where most individuals belonged to one species. Values increased with the number of species and/or the evenness of distribution, particularly as the proportion of individuals comprising the dominant species decreased. The highest values occurred on sites with no strongly dominant species, and with many rare species.

The Shannon-Weaver index has therefore been used in this study to reflect changes in less abundant species.

The Shannon Equitability Index Obtained from:

$$E = \frac{H'}{H'_{max}} = -\sum_{i=1}^{S} \frac{P_i \ln P_i}{\ln S}$$

Where S is the number of species in the habitat, otherwise the notation is the same as above

The index scales the value obtained for the Shannon index to that obtained if individuals are distributed equally amongst the species (Hill, 1973a; Peet, 1974; Pielou, 1975, 1977; Putman and Wratten, 1984).

Several equitability indices have been constructed using a similar rationale, but scaling or relativisation is criticised due to the magnification of weaknesses with the multiplication of index terms (Whittaker, 1975), particularly when there is dependence on species number (Sheldon, 1969; Peet, 1974, 1975). Sheldon (1969) tested a number of such indices and found the Shannon Equitability index to be the most stable in relation to fluctuations in species number.

An independent measure of equitability was considered useful in this study. The Shannon Equitability index is the most stable and unusually, it emphasises rare species.

The Simpson index (Simpson, 1949) Obtained from:

$$D = \sum_{i=1}^{S} P_i^2$$

Where P_i is n_i/N; n_i being the number of individuals in the ith species and N the total number of individuals.

This index measures dominance concentration (Hill, 1973a; Peet, 1974; Whittaker, 1975; Greig-Smith, 1983; Begon et al., 1986; Magurran, 1988), the squared term emphasising the contribution of common species, effectively weighting the index (May, 1975a). It measures the probability that two individuals, drawn randomly, are from the same species (Simpson, 1949; Berger and Parker, 1970; Hurlbert, 1971; Peet, 1974; Matthews, 1976; Pielou, 1977; Kempton and Wedderburn, 1978; Morris and Lakhani, 1979; Greig-Smith, 1983; Krebs, 1985). This probability is low where species number is high and abundance evenly distributed (Clifford and Stephenson, 1975). Simpson (1949) considers this a population constant rather than a sample statistic and therefore independent of sample size.

Some consider it to combine species number with relative abundance (Clifford and Stephenson, 1975; Brown, 1988), possibly due to the summation over all species. However, Berger and Parker (1970) found only a moderate correlation with species number.

Hill (1973a) used it to represent the common species extreme of a continuum of relative abundance. Morris and Lakhani (1979) preferred to emphasise common rather than rare species, which may be chance migrants. However, other authorities found that common species experienced considerable fluctuations, with the index reflecting this rather than overall site processes (Kempton and Taylor, 1976).

To measure diversity directly, the index is subtracted from one or the reciprocal used (Hill, 1973a) becoming the probability that two individuals are not of the same species. It increases with both higher richness and equitability (Whittaker, 1975), but is more generally found to depend on equitability. Samples with high species richness but low equitability therefore have lower values than those with low richness but high equitability (Begon et al., 1986). Where species number exceeds 10, it is influenced by abundance distribution, changing little if this fits a log series but rising sharply where the broken stick model applies (Magurran, 1988).

The Simpson index primarily reflects relative abundance and is most strongly influenced by common species. It has been used to complement the Shannon index and as part of an examination of changes in site dominance.

The Berger-Parker index (Berger and Parker, 1970) Obtained from:

$$d = \frac{N_{max}}{N}$$

Where N_{max} is the number of individuals in the most abundant species and N is the total number of individuals

This index measures the concentration of dominance in the single most abundant species (Magurran, 1988). The reciprocal is used so that the index increases as dominance decreases.

It is not used frequently, but is favoured by May (1975a), who characterised it as a simple index, which is at least as effective as those of Shannon and Simpson. Berger and Parker (1970) found that it was correlated with the Simpson index.

As the index is based on the proportion of individuals in the first species, it is therefore sensitive to changes only in these parameters, rather than to other sources of change (Magurran, 1988). Additionally, the emphasis on a single dominant may mask codominance.

In this study it characterises the level of single species dominance, while codominance is detected via the Simpson index.

Species number or richness This is a count of the number of species in a sample. It is frequently considered the most unambiguous measure of diversity (Matthews, 1978; Gray, 1987b; Brown, 1988), not subject to bias or mathematical inconsistencies as with the more complex indices. Alternatively, lacking a measure of relative abundance, it is seen as providing only a partial description of diversity (MacArthur, 1965; May, 1975b; Kempton, 1979; Putman and

Wratten, 1984). Hill (1973a) found high levels of richness to be correlated with rare species. While some authorities consider this to reflect site conditions (e.g. Clifford and Stephenson, 1975; Brown, 1988), for others rare species are relatively unimportant (Hurlbert, 1971; Morris and Lakhani, 1979).

Species number has been found to depend on sample size (MacArthur, 1965; Margalev, 1968; Berger and Parker, 1970; Hill, 1973a; Peet, 1974; Whittaker, 1975). Hurlbert (1971) discussed its capacity to vary independently of evenness i.e. increasing with sample size while evenness falls. Some authorities see a dependence on sample size and/or stochastic factors that does not reflect organisational change (Sheldon, 1969; Peet, 1974, 1975) and advocate use of a constant area/number of individuals (Clifford and Stephenson, 1975; Kempton, 1979).

Species number is used in this study in relation to an area of constant size. The number of species/individuals a site has the capacity to support is a variable characteristic indicative of factors such as the availability of microhabitats and resources. Changes suggest differences in conditions and/or organisation that can be verified and explored using a range of measures. The relationship between species number and total individuals is examined further through the Margalev index, discussed below.

The Margalev index Obtained from:

$$D_{Mg} = \frac{(S-1)}{\ln N}$$

Where S is the number of species; ln is $\log_e$ and N is the total number of individuals

This index is not used frequently. Although strongly related to species number (Magurran, 1988), there is also a term for the number of individuals (Clifford and Stephenson, 1975) although the log term weights small numbers (Putman and Wratten, 1984). The index increases with species number and/or decreases in the number of individuals and can distinguish sites with differing numbers of species but similarly sized populations.

It is used in this study to examine the relationship between species number and the total number of individuals. Additionally, it discriminates well between relatively similar sites (Magurran, 1988), particularly important in older age groups.

In addition to those indices discussed above, both log series α (Fisher et al., 1943) and the Q statistic (Kempton and Taylor, 1976) were considered due to their focus on moderately abundant species (Kempton and Taylor, 1976; Kempton and Wedderburn, 1978; Kempton, 1979; Magurran, 1988). Neither were used; the first due to interpretation difficulties and concern over the assumed model (MacArthur, 1965; Pielou, 1977), while the second is not widely used, making its properties not well known. Moreover, it is apparently related to both the Shannon and Simpson indices (Kempton and Wedderburn, 1978).

Indices were selected from each of the three categories (section 3.4.3): species number and the Margalev index reflect species richness; the Shannon, Simpson and Berger-Parker indices combine species richness with evenness of distribution; and the Shannon Equitability index is based on the equitability component. Both S and the Margalev indices were included to examine changes in species number in relation to changes in the number of individuals. Use of both the Shannon and Simpson indices enables changes in relative abundance to be attributed to changes in either rare or common species (respectively), while the Berger-Parker index detects changes in the dominance component related to single species.

The indices were applied to age classes to identify changes over the course of each sequence and between the two. The indices were not used to characterise the sequence as this was not a primary aim of this study.

Within-group changes between the surveys are tested for significance using both the t-test for paired samples and the Wilcoxon signed rank test. Such paired 'quasiexperiments' are appropriate for significance testing (James and McCulloch, 1990). The nonparametric Wilcoxon test is considered more appropriate, avoiding the assumptions of the parametric t-test (Kent and Coker, 1992), particularly normality of distribution. Both tests are used to compare the results in view of the weaker inferential power of the Wilcoxon test (Kent and Coker, 1992). The indices are calculated using the Species Diversity and Richness package (Henderson and Seaby, 2001) and the tests using SPSS (1999).

3.5 Multivariate analysis: classification

3.5.1 Introduction

The data generated by this study are largely observational, providing indirect evidence of causal processes (Connell, 1975) rather than the definitive answers possible from experimental testing of hypotheses (James and McCulloch, 1990; Jager and Looman, 1995). Nonetheless, such work may be used to test hypotheses and to generate models. The multivariate techniques used are generally not considered appropriate for significance testing as they do not identify causal factors (Gauch, 1982; James and McCulloch, 1990). The strategy adopted involves a combined or complementary use of classification and ordination (see section 3.6.1) to identify and describe vegetation units and relate these to environmental factors. These subsets are also used to examine the functioning of the system since 1970. The following sections review the methods and techniques available, together with the rationale underlying the particular choices made.

Classification covers a range of techniques that identify discrete classes (Kent and Coker, 1992), particularly useful in initial exploration (Hill et al., 1975; Jager and Looman, 1995). However, clusters are found even if they are artificially imposed (Matthews, 1981; Gauch, 1982; Kent and Coker, 1992; Jongman, 1995; van Tongeren, 1995).

Classification has been linked to concepts that assume the presence of distinct communities and, in particular, with the organismic theories of Clements (1916, 1928, 1936) and Tansley (1920, 1935) (Kent and Coker, 1992) and the Zurich-Montpelier and Uppsala schools of phytosociology (Poore, 1955a, 1955b, 1956; Braun-Blanquet, 1964; Daubenmire, 1966) (Greig-Smith, 1983). An alternative conceptual approach proposes that environmental gradients are marked by continuous variation in community composition (the continuum theory), based on individualistic species distributions as propounded by Gleason (1917, 1926, 1927, 1939), and explored using gradient analysis techniques developed e.g. by Curtis (1951) and Whittaker (1967, 1975). These fundamental differences underlie the separate development of classification and ordination techniques (section 2.2).

Proponents of the continuum theory preferred ordination, rejecting classification as artificial (Gauch, 1982; Burrows, 1990). Gradients are seen as abstract, not necessarily occurring in space (McIntosh, 1967; Greig-Smith, 1983). Communities at gradient extremes differ in type but intervening changes are ecoclinal with gradational transitions of varying intermediate composition (McIntosh, 1967; Greig-Smith, 1983). Critics have claimed the continuum to be an artefact of ordination techniques and that disturbed and seral sites are deliberately selected to provide intermediates (Looman, 1963; Poore, 1964; Daubenmire, 1966). In response, the method is defended as using the total vegetation rather than selecting sites for internal homogeneity, representative of particular endpoints (McIntosh, 1967).

More recently this debate has been at least partially resolved (Whittaker, 1985; Crouch, 1992) through the development of numerical classification using large heterogeneous datasets (McIntosh, 1967; Hill et al., 1975). The prevalence of the continuum is generally accepted and the purpose of classification revised as 'continuum segmentation' (McIntosh, 1967). Complementary analyses are frequent, with classification used to identify and examine vegetation types and ordination to assess the relationship between the vegetation and environmental variables (McIntosh, 1967; Matthews, 1981; Gauch, 1982; Digby and Kempton, 1987; Crouch, 1992; Kent and Coker, 1992; Caseldine and Pardoe, 1994; Vetaas, 1994; Pardoe, 1996; Foskett, 1998; Rosales et al., 2001; Jones and Henry, 2003). The methods are increasingly seen as consistent (i.e. McIntosh, 1967; Hill et al., 1975), providing a broader picture and generating greater confidence in the results (Crouch, 1992; Kent and Coker, 1992). This combined approach is used in this study.

3.5.2 Differences between classification techniques

These primarily occur in three areas:

(1) Combining individual species/samples or dividing the full dataset into progressively smaller groups (agglomerative and divisive techniques, respectively).

Many early techniques were agglomerative, mainly due to the low computational requirement when computer time was limited (van Tongeren, 1995). Frequently, techniques involve initial conversion to a (dis)similarity matrix (Greig-Smith, 1983; van Tongeren, 1995), with the type of linkage selected from an array of methods i.e. single linkage/nearest neighbour, complete linkage/furthest neighbour and group centroid (Matthews, 1981; Gauch, 1982; Digby and Kempton, 1987). Each procedure has strengths/weaknesses and the selection is made subjectively.

Divisive techniques have become increasingly important with greater computer availability, although such methods are regarded as more efficient as they do not require the storage of a matrix and requirements increase linearly with the size of the dataset, rather than proportionally to the cube of the number of stands (Hill et al., 1975). The approach is top-down, initial divisions depend on major differences in the data, which determine the subsequent subgroups (Hill et al., 1975; Digby and Kempton, 1987; van Tongeren, 1995). Agglomerative techniques depend initially on small differences, possibly representing noise (Gauch, 1982; Digby and Kempton, 1987), and local differences predominate over larger ones (Hill et al., 1975; van Tongeren, 1995).

Divisive techniques are preferred due to the subjectivity of many agglomerative methods, the greater computational efficiency and superiority in detecting major trends.

(2) Whether relationships between groups are detected directly or in a subsequent step (hierarchical or non-hierarchical techniques).

A hierarchical technique provides a dendrogram so that relationships are determined objectively (van Tongeren, 1995), whereas non-hierarchical techniques require subjective construction of a plexus or constellation diagram (Kent and Coker, 1992). Non-hierarchical techniques may be used to construct composite groups, with relationships determined subsequently, and to identify outliers, reduce noise and redundancy (Gauch, 1982; van Tongeren, 1995). A number of early techniques are non-hierarchical: e.g. COMPCLUS (Gauch, 1979), CLUSLA (Louppen and van der Maarel, 1979), and FLEXCLUS (van Tongeren, 1986). All involve the detection of groups by clustering within a specified "distance" from a random point (van Tongeren, 1995).

The principal advantages of non-hierarchical techniques are greater within-cluster homogeneity and the absence of an imposed structure (van Tongeren, 1995), while interpretation of results from hierarchical techniques is easier and more objective (Greig-Smith, 1983; van Tongeren, 1995).

(3) Whether one or more than one variable(s) are used to determine group membership (monothetic or polythetic) (Kent and Coker, 1992).

The variables are usually indicator species. All monothetic methods are divisive while polythetic methods may be either divisive or agglomerative (Gauch, 1982). An early monothetic technique is the Association Analysis of Williams and Lambert (1959, 1960), based on positive associations using a χ^2 test (Matthews, 1981; Greig-Smith, 1983). The principal criterion for the selection of indicator species is maximal association with other species (van Tongeren, 1995). Subgroups identified are highly similar (Digby and Kempton, 1987), but the technique is weakened by the reliance on a single indicator species. Chance presence or absence may lead to misclassification (Gauch, 1982; Greig-Smith, 1983; Digby and Kempton, 1987; van Tongeren, 1995), less likely when a number of species are used

A more recent development is the use of ordination axes to divide the data. Van Tongeren (1995) discusses Williams' use of a Principal Components Analysis ordination (1976) and more notably, the work of Hill (Hill et al., 1975; Hill, 1979a), who used the first Correspondence Analysis (CA) axis as the basis for Two-Way Indicator Species Analysis (TWINSPAN). Hill (1975) considers this a general form of Association Analysis but polythetic and therefore avoiding high levels of misclassification (Kent and Coker, 1992).

3.5.3 The method of TWINSPAN

TWINSPAN uses a CA ordination axis, divided at the centre of gravity to form a dichotomy. Samples with values below the mean form the negative (left) group while those with values higher than the mean form the positive (right) group. The species are scored and ordered according to their preference for each group, and the highest scoring in each group are selected as indicators. Frequency classes are treated as 'pseudo-species', with preselected cut levels, each indicator being a different real species to avoid all indicators coming from the same species. The indicator scores are added, giving a crude site ordination, and threshold scores for inclusion in each group are calculated. The selected threshold level minimizes the number of discordant samples between the two ordinations. Where these differ, the original is assumed correct except in the 'zone of indifference' around the division, where classification is by indicator score.

Hill (1979a) and Hill et al. (1975) found misclassification levels of approximately 3%. Factors causing this include misclassification at a higher level and the presence of preferential (not indicator) species.

In its original form, the method was sensitive to rare species, which could dominate the classification yet may occur only by chance, making interpretation uncertain. Although downweighting of rare species is recommended (Hill et al., 1975; Kent and Coker, 1992), this criticism continues to be made (ter Braak, 1995a; van Tongeren, 1995)

TWINSPAN is amongst the group of techniques found by Tausch et al. (1995) to be unstable when the entry order varied, particularly at lower division levels and using complex data. Van Groenewoud (1992) reported similar instability, attributed to selection of species occurring first in the data matrix when the maximum number of indicator species is exceeded, and nonconvergence when axes have similar eigenvalues. Subsequently, Oskanen and Minchin (1997) corrected an order dependent programming bug affecting linear rescaling and lax convergence criteria.

TWINSPAN is seen as optimal and a broad improvement on earlier methods (Kent and Coker, 1992); a preferred method (Greig-Smith, 1983); and effective and robust (Gauch, 1982).

3.5.4 The use of TWINSPAN in this study

This technique is used for the following reasons:

(1) Divisive techniques reflect trends rather than local differences. Being polythetic, high levels of misclassification due to stochastic presence or absence are avoided. Testing showed non-hierarchical methods summarised data, but groups were difficult to interpret and relationships between them could be obscure. However, as a hierarchical method, TWINSPAN imposes structure i.e. it is assumed that a division is appropriate for each strand at each level.

(2) It is widely used (e.g. Caseldine and Pardoe, 1994; Vetaas, 1994; Pardoe, 1996; Rosales et al., 2001; Jones and Henry, 2003), and has been applied previously to the vegetation at Storbreen (Whittaker, 1985; Crouch, 1992; Foskett, 1998). Its properties are known, criticisms are minor and the method is found effective. Constrained Ordination Indicator

Species Analysis (COINSPAN), introduced by Carleton et al. (1996), uses a CCA ordination and while it compares favourably with TWINSPAN in providing indicator species for particular environmental conditions, its properties have not been widely tested.

Cut levels for the pseudo-species were set at 10, 20, 50, 75, 100, 150, 180 and 220, as the range in this study greatly exceeded the default maximum of 100. The intention is to distinguish infrequent, moderately abundant and abundant species, while minimizing the influence of rare species, which were also downweighted.

The total number of groups was considered carefully. Other workers at Storbreen have tended to use large numbers of groups, Whittaker (1985) for example used 32. A trial run using this number showed that there were difficulties in interpretation. Many of the small groups differed only marginally, suggesting amalgamation was appropriate. Fewer groups were more clearly interpretable. Eight was found to be optimal in terms of the balance between clarity and retention of detail; further reduction proved uninformative. A representative measure of the species composition of each group was calculated using mean frequencies, but excluding species with average frequencies of less than ten. This was used to aid interpretation.

The TWINSPAN programme was from the Community Analysis Package version 2.1 (Pisces Conservation, 2002), which is corrected in accordance with the findings of Oskanen and Minchin (1997).

3.5.5 Site trajectories and system transition probabilities

Vegetation assemblages and the relative location of the sites in each survey have been used to construct a web of pathways illustrating the system dynamics since 1970 (Greig-Smith, 1983; Miles, 1987; Brown, 1988). Whittaker (1985) constructed a similar diagram but covering a shorter time interval and the larger number of groups increasing pattern complexity (cf. van Groenedael et al., 1996).

Such data can potentially be used in Markov Chain Analysis to predict composition after a further time interval. Matrices of probabilities are calculated from observed transitions between representative states (Usher, 1987), by dividing the frequency of a particular transition by the total frequency (Greig-Smith, 1983; Mather, 1991). Future generations are calculated by multiplying the abundance of a particular state or species by the relevant probability (Horn, 1974; Krebs, 1985; Orloci and Orloci, 1988).

However, data for one time interval is an inadequate basis for this analysis (Usher, 1992) and the usefulness of this method has been criticised as follows:

(1) Appropriate time intervals. Work by Chidress et al. (1998) found annual constraints produced superior results due to the incorporation of year to year variation in species dynamics, particularly important for systems experiencing continuous change i.e. successional sequences.

(2) Generation of data. Long datasets are required to establish and test probabilities and transition states (Matthews, 1981; Usher, 1992), but are rarely available (Facelli and Pickett, 1990).

(3) Model assumptions. Stationary Markov chains, used most frequently, assume constant probabilities and independence from past pathways (Matthews, 1981; Krebs, 1985; Whittaker, 1985). Historical and spatial factors are not taken into account but they do influence and may change trajectories (Facelli and Pickett, 1990). Orloci and Orloci (1988) found the signature of a stationary Markov chain, with no inflection indicating a change in probabilities, in a secondary successional sequence, but developed soil and propagules may restrict the trajectory compared to primary sequences.

In this study, a simulation using Markov chain analysis was not therefore considered appropriate. Transition probabilities (calculated as above) are, however, used to determine the strength of particular trajectories within the system, to identify and examine pathways and to explore the process by which the system as a whole diverges.

3.6 Multivariate analysis: Ordination

Ordination is a statistical method to order species and/or samples in terms of similarity (McIntosh, 1967; Beals, 1973; Gauch, 1982; Austin, 1985; Whittaker, 1985; Kent and Coker, 1992; ter Braak, 1995a). The purpose is to identify assemblage pattern by summarising and reducing dimensionality (Gauch, 1982; Carleton, 1984; Whittaker, 1985; Kent and Coker, 1992) and relate this to environmental pattern (Matthews, 1981; Greig-Smith, 1983; Austin, 1985; ter Braak and Prentice, 1988; Crouch, 1992). More detailed examination, including experimental testing, requires greater sensitivity and uses techniques such as multiple regression and ANOVA (Matthews, 1981; Gauch, 1982; Jongman, 1995; ter Braak, 1995a).

3.6.1 The influence of data characteristics

The data comprise measures of species present in samples and the environmental context in which the sample develops. Species data vary widely between samples, and a large proportion are absent in a particular case (ter Braak, 1987a). The relationship between species and individual environmental variables is often found to be non-linear. With an extensive range of samples, species distributions are frequently unimodal (either symmetrical or skewed) (Westman, 1980; ter Braak, 1995a). However, where only a proportion of the full distribution is sampled, the relationship may be monotonic or linear (Gauch et al., 1981; ter Braak, 1987a; ter Braak and Prentice, 1988; Ejrnaes, 2000). The maximum of the unimodal distribution is seen as indicating optimal conditions, and the range covered by the curve as representing tolerances (ter Braak, 1986, 1987a, 1995a). Variables may operate indirectly via effects on other variables, possibly generating a cascade of effects i.e. topography influencing temperature, irradiance, exposure and moisture (Austin, 1985; Austin et al., 1994). Additionally, the influence may change over the course of the gradient; reflecting threshold effects (Gauch, 1982), changing interactions (Goodall, 1970; Digby and Kempton, 1987) or interdependence (Beals, 1973; ter Braak, 1987b). Therefore environmental variables rarely operate in isolation, but are interrelated and the nature of the interactions modifies their effects. While species responses to particular variables are seen as individualistic (Yarranton, 1967; Westman, 1980), in a broader sense species assemblages frequently respond collectively, but in individualistic ways.

The interrelatedness of variables and the collective or common response suggests that removal of correlated variables as 'superfluous' (ter Braak, 1995a) is inappropriate, although serving to simplify the analysis. Alternatively, retention of the complexity of the gradient is seen as strengthening the analysis, reflecting reality more closely (Westman, 1980; Carleton, 1984; James and McCulloch, 1990; Økland, 1996).

3.6.2 How general is the symmetrical, unimodal response curve?

The prevalent form of vegetation response to environmental variables is curvilinear, but debate concerns the frequency with which symmetrical, unimodal curves occur. Ejrnaes (2000) found distributions to be primarily linear, monotonic and unimodal, but bimodal, irregular, truncated and skewed distributions also occurred. 95% of the distributions examined by Austin (1976) were nonmonotonic and curvilinear; of these 26% were symmetrical and bell-shaped, 29% skewed, 16% shouldered or plateaued and 29% bimodal. Westman (1980) found that a Gaussian curve explained 95% of the variance for only 2.2% of distributions. However, many variables were used, some having no significant role, and by combining the variables the mean variance explained increased to 65.1%. Austin et al. (1994) found that skew was positive when optima are low and negative when high. Økland (1992) suggests that skew occurs due to differences in species responses to the same gradient, and may be removed by using complex factor gradients.

Species responses are therefore found to be predominantly unimodal; while skewing is common, symmetrical curves also occur frequently. The use of complex factor gradients apparently increases the incidence of symmetrical curves.

3.6.3 The effects of species absence

Section 3.6.1 noted the frequency of species absence. Zeros are assumed to indicate unfavourableness, but levels of this vary and absence may be due to stochastic factors i.e. dispersal, germination. The use of a single measure equates these various causes (Noy-Meir and Austin, 1970; Swan, 1970) and consequently applies a standard distance to all absences. Beals (1973) suggested that this underlies his finding that small scale differences in vegetation are related linearly to environmental factors but become exponential as levels increase.

3.6.4 Direct and indirect techniques

Many techniques involve forms of gradient analysis (Whittaker, 1967, 1975). Direct techniques integrate environmental variables with the vegetation composition. Early forms generally involved single environmental gradients against which a measure of species abundance or importance is plotted (Hill, 1973b; Digby and Kempton, 1987), although additional dimensions may be added. However, one or a few variables may not adequately represent a complex environment and subjectively selected gradients (Matthews, 1981; Greig-Smith, 1983; Carleton, 1984; Digby and Kempton, 1987) may fail to include those of greatest importance (Gauch, 1982; Austin, 1985) or may overestimate the importance of particular gradients (Matthews, 1981; Greig-Smith, 1983; Digby and Kempton, 1987; Kent and Coker, 1992; Økland, 1996). Interpretation is then unreliable. The recent development of direct techniques (e.g. as in canonical ordination) has allowed consideration of multiple variables that more effectively represent the complex environment (ter Braak, 1987b, 1995a; Økland, 1996).

Alternatively, indirect gradient analysis identifies primary gradients in vegetation composition, which are associated with variables in a subsequent step (McIntosh, 1967; Hill, 1973b; Carleton, 1984; ter Braak, 1986; Digby and Kempton, 1987; ter Braak, 1987a; James and McCulloch, 1990; Crouch, 1992; Kent and Coker, 1992; Jongman, 1995; Økland, 1996). The vegetation gradient is treated as a latent or theoretical variable (Austin, 1985; ter Braak and Prentice, 1988; Jongman, 1995; ter Braak, 1995a; Økland, 1996). Ter Braak (1995a) discussed several advantages of indirect, as opposed to direct, techniques, including the difficulty of measuring environmental variables and their importance whereas, collectively, species are often good environmental indicators (Økland, 1996).

Direct gradient techniques are therefore more appropriate where influential environmental variables are already identified, while indirect techniques are useful where this is not known and to establish the importance of measured variables (Økland, 1996).

3.7 The choice of techniques

Canonical Correspondence Analysis (CCA) was used in this study. It has been widely used in recent studies and is a development of Correspondence Analysis (CA). It is discussed more extensively in section 3.8. In this section, other techniques are examined and the reasons for their rejection.

3.7.1 Polar ordination

This is one of the earliest techniques, involving the choice of dissimilar sites to act as poles for each axis (Matthews, 1976; Gauch, 1982), with the remaining sites arranged between them according to values in a (dis)similarity matrix (Greig-Smith, 1983). The selection of endpoints is frequently criticised as subjective (Beals, 1973; Gauch et al., 1977; Palmer, 1993), and outliers may be chosen producing axes oblique to the main trend (McIntosh, 1967; Gauch, 1982; Greig-Smith, 1983). Although described as 'primitive' (Beals, 1973), comparisons indicate that it has useful properties: axes are calculated separately, avoiding distortion due to interdependence (Gauch et al., 1977), and long gradients, large patterns and clusters are represented without distortion (Gauch et al., 1974, 1977). It does not assume a linear distribution (Beals, 1973) and computation requirements are modest (Gauch et al., 1974).

3.7.2 Principal Components Analysis (PCA), Factor Analysis (FA) and Redundancy Analysis (RDA)

These three related techniques are based on a common algorithm. PCA calculates new components from interrelated groups of variables (Johnston, 1980; Kent and Coker, 1992; ter Braak, 1995a), using least squares regression and subsequent iteration (ter Braak, 1995a). FA examines the interrelatedness of the PCA components (Swan, 1970; Johnston, 1980; Greig-Smith, 1983; James and McCulloch, 1990), by excluding 'unique' variance. RDA is canonical PCA, including a multiple regression on the environmental variables in the algorithm (ter Braak and Prentice, 1988).

An important problem with this group of techniques is their assumption of linearity, which is mathematically inappropriate for curvilinear distributions (Beals, 1973; Ihm and van Groenewoud, 1975; Matthews, 1976; Gauch et al., 1977; Matthews, 1981; Gauch, 1982; Carleton, 1984; Austin, 1985; Wartenberg et al., 1987; Crouch, 1992; ter Braak, 1995a). Distortions occur with longer gradients (Hill, 1973b; Gauch et al., 1977; Austin, 1985; ter Braak, 1987a; Peet et al., 1988; James and McCulloch, 1990; ter Braak, 1995a). As discussed above, this involves interleaving of sites and the presence of a horseshoe (Goodall, 1970; Noy-Meir and Austin, 1970; Ihm and van Groenewoud, 1975; Westman, 1980; Gauch, 1982; Matthews and Whittaker, 1987; Palmer, 1993). Beals (1973) particularly criticised the use of Euclidean distance finding that no such relationship existed between species and environmental space (Williamson, 1978; Austin, 1985; Digby and Kempton, 1987; Wartenberg et al., 1987). Gauch (1977) found the method sensitive to clusters, and outliers, leading to compression and rotation, with disjunct groups frequently occurring on higher axes (Greig-Smith, 1983; James and McCulloch, 1990).

3.7.3 Principal Co-Ordinates Analysis (PCO) (Gower, 1966; Pielou, 1977)

This is based on the Q-mode algorithm of PCA (i.e using a site-by-site rather than a species-by species matrix) but may employ a distance measure other than Euclidean distance (Kent and Coker, 1992; ter Braak, 1995a). It is a metric form of multi-dimensional scaling (Williamson, 1978; Gauch, 1982; Digby and Kempton, 1987; Wartenberg et al., 1987; James and McCulloch, 1990; ter Braak, 1995a). The technique is used rarely and so difficult to assess, although it shares the assumption of linearity with PCA (Gauch, 1982; Austin, 1985).

3.7.4 Canonical Correlation Analysis, COR

This is based on species-environment correlations and is therefore a direct gradient technique (Johnston, 1980; Westman, 1980; Gauch, 1982; Greig-Smith, 1983; Carleton, 1984; Whittaker, 1985; Digby and Kempton, 1987). It has been described as a multivariate extension of multiple regression (Carleton, 1984; James and McCulloch, 1990; ter Braak, 1995a).

This technique again assumes linearity and distorts non-linear, nonmonotonic data (Goodall, 1970; Westman, 1980; Gauch et al., 1981; Gauch, 1982; Greig-Smith, 1983; ter Braak, 1986; ter Braak and Prentice, 1988; James and McCulloch, 1990). The technique becomes unreliable when species and environmental variables exceed the number of sites (ter Braak, 1995a).

3.7.5 Non Metric Multidimensional Scaling (Shepard, 1962; Kruskal, 1964)

This technique is based on the ranking of (dis)similarities, represented by distance (Gauch et al., 1981; Matthews, 1981; Gauch, 1982; Greig-Smith, 1983; Digby and Kempton, 1987; James and McCulloch, 1990; Kent and Coker, 1992; Økland, 1992). Initially, the method uses a random configuration or, more usually, an ordination (Gauch et al., 1981; ter Braak, 1995a). 'Stress' is an inverse measure of goodness of fit (Matthews, 1981; Austin, 1985; Whittaker, 1987; Kent and Coker, 1992; Økland, 1992), of the extent to which the scatter of points deviates from a monotonic curve (Matthews, 1976; Greig-Smith, 1983; Wartenberg et al., 1987; James and McCulloch, 1990; ter Braak, 1995a). Iterations continue until stress is minimized (Gauch et al., 1981; Digby and Kempton, 1987; ter Braak, 1995a).

NMDS assumes monotonicity rather than linearity in species response to environmental gradients (Matthews, 1976; Gauch et al., 1981; Austin, 1985; Whittaker, 1987), although this may still not be adequate (Gauch et al., 1981; Matthews, 1981). Distortions have been found, including an 'arch' (Gauch et al., 1981; Gauch, 1982; Digby and Kempton, 1987; Kent and Coker, 1992), and outliers may cause involution at gradient ends (Gauch et al., 1981; Wartenberg et al., 1987). The number of dimensions, the type of (dis)similarity coefficient used and whether there is an initial ordination are determined by subjective choices (Williamson, 1978; Gauch et al., 1981; Austin, 1985; Wartenberg et al., 1987; Palmer, 1993; ter Braak, 1995a). There may be several solutions or failure to converge (Kent and Coker, 1992).

Digby and Kempton (1987) did not recommend the use of NMDS as they found it rarely had an advantage over metric techniques and interpretation was difficult (cf. James 1990). Similarly, Gauch et al. (1981), while accepting that results may be informative, considered other methods superior, and concluded that the technique is of limited use to ecology. However, Matthews (1976) successfully used the technique in his initial analysis of the vegetation at Storbreen and it is preferred by Minchin (1987).

3.7.6 The maximum likelihood solution of Gaussian ordination

The fit of a particular model, i.e. Gaussian logit curves, is measured by its deviance from that observed (ter Braak and Looman, 1986), the sum of the deviance over all species providing a measure of the badness of fit (Gauch et al., 1974). Logit regression involves iterative calculations of a series of parameters (species optima, tolerances and maximum values) using least-squares regression (ter Braak, 1995a; ter Braak and Looman, 1995). Minimal deviance in the regression identifies the gradient that best explains the species composition (Gauch et al., 1974; Westman, 1980; ter Braak, 1987a; ter Braak, 1995a).

This technique is most useful where there is a known, single, strong gradient (Gauch et al., 1974; Gauch, 1982; ter Braak, 1995a). The additional parameters provide information on habitat space, overlap, packing on gradients and relative species importance (Gauch et al., 1974).

The Gaussian logit model is considered superior to other techniques (Gauch et al., 1981; Palmer, 1993) and is used to evaluate performance (Ihm and van Groenewoud, 1975; Westman, 1980; Wilson, 1981; ter Braak and Looman, 1986; ter Braak and Prentice, 1988). It detects and represents nonmonotonic, curvilinear relationships (Westman, 1980), and is generally free from distortion (ter Braak and Looman, 1986). However, the production of reliable programmes is hampered by the excessive computational cost (ter Braak, 1995a). This technique is most suitable for detailed examination of species responses rather than providing an overview as required in this study. Additionally, programmes are not readily available.

3.8 An overview of Correspondence Analysis (CA) and related techniques

These techniques were inspired by Whittaker's (1967) direct gradient analysis, using weighted averaging (WA). Species optima (indicator values) and tolerances are calculated in relation to environmental gradients (ter Braak, 1987b), as the average value of the environmental variable over those sites at which the species is present, weighted proportionally to species abundance (Austin, 1985; ter Braak and Looman, 1986; ter Braak and Barendregt, 1986; ter Braak and Looman, 1995). This approximates to the maximum likelihood solution of Gaussian logistic regression, assuming narrow ecological amplitudes (tolerances) and homogenous distribution of environmental variables over the range of species occurrence (ter Braak, 1985; ter Braak and Looman, 1986; ter Braak and Barendregt, 1986; ter Braak and Prentice, 1988; ter Braak and Looman, 1995).

Hill (1973b) included two-way weighting, or reciprocal averaging (RA) in a procedure known as Correspondence Analysis (CA) (Gauch et al., 1977; ter Braak, 1985; Palmer, 1993). Although simpler than Gaussian logistic regression, it similarly assumes a unimodal response (ter Braak, 1987a; James and McCulloch, 1990) and approximates to it when:

(1) maxima are equally spaced;
(2) tolerances are equal;
(3) optima are homogeneously distributed over a large interval (A) compared to tolerances; and
(4) sites are homogeneously distributed over an interval contained within A.

These conditions are unlikely to be fully satisfied but the technique is considered robust to violations (ter Braak, 1985, 1986; ter Braak and Prentice, 1988; ter Braak, 1995a).

DCA was introduced by Hill (1979b) and Hill and Gauch (1980) to remove distortions found in CA (Gauch, 1982; Greig-Smith, 1983; Austin, 1985; ter Braak, 1985; Whittaker, 1985; Wartenberg et al., 1987; ter Braak and Prentice, 1988; James and McCulloch, 1990; Kent and Coker, 1992; ter Braak, 1995a). More recently CCA has been developed, whereby ordination axes are constrained to be linear combinations of the environmental variables through a multiple regression step within the algorithm (ter Braak, 1986; 1987b; ter Braak and Prentice, 1988; Kent and Coker, 1992; Carleton et al., 1996; Økland, 1996).

Development of WA and subsequent refinement, has produced a powerful and widely used range of techniques. The canonical ordination technique represents a return to the direct gradient form of analysis, but now involving a multivariate assessment of both environmental variables and species (ter Braak, 1986).

3.8.1 The principles of CA

CA uses the RA algorithm with a species/samples matrix (Kent and Coker, 1992). Using initially arbitrary species scores, site scores are calculated from the average, weighted species scores. Improved species scores are then calculated as the weighted average of sites on which they occur and rescaled between 1 and 100, counteracting the reduction in range due to averaging. Ideally, iterations continue until the scores stabilise/converge (Hill, 1973b; Gauch, 1982; Digby and Kempton, 1987; Kent and Coker, 1992; Palmer, 1993; ter Braak, 1995a). The first axis is the theoretical variable maximising the dispersion of the species scores; subsequent axes function similarly using remaining variability but with an additional step ensuring that the scores are uncorrelated with preceding axes (ter Braak, 1995a). Eigenvalues indicate axis importance, variance accounted for, or score dispersion (Gauch, 1982; Whittaker, 1985; ter Braak, 1986; Crouch, 1992; ter Braak, 1995a; Jones and Henry, 2003), and values fall with successive axes (Kent and Coker, 1992). As an indirect technique, the axes are latent, theoretical variables, related to environmental variables in a subsequent multiple regression or correlation step (Carleton, 1984; ter Braak, 1985; 1986; ter Braak and Barendregt, 1986; Whittaker, 1987; ter Braak and Prentice, 1988; Økland, 1996). There are similarities with the PCA algorithm (Hill, 1973b), particularly in the iterative procedure (Gauch et al., 1977; Gauch, 1982; Whittaker, 1985), although absent species do not influence CA (ter Braak and Barendregt, 1986).

An 'arch' may occur on second and higher axes due to a quadratic (cubic, etc) relationship with the preceding axis, despite it being orthogonal and uncorrelated (Hill, 1973b; Austin, 1985; ter Braak, 1986; 1987a; Wartenberg et al., 1987; Kent and Coker, 1992; ter Braak, 1995a). Detrending (DCA) in the DECORANA programme (Hill, 1979b; Hill and Gauch, 1980) involves segmentation and adjustment of sample scores to zero mean and unit variance (Gauch, 1982; Greig-Smith, 1983; Whittaker, 1985; Wartenberg et al., 1987; Crouch, 1992; Palmer, 1993). However, ter Braak and Prentice (1988) and ter Braak (1995a) found the arch likely to occur when the eigenvalue of the folded first axis exceeds that of a weak second gradient. Therefore, in CANOCO (ter Braak, 1987c), later axes are uncorrelated with both earlier axes and their polynomials (ter Braak and Prentice, 1988; ter Braak, 1995a).

Compression at the axis extremes results from the edge effect; all species are included but some are assumed to lie beyond the gradient range (ter Braak, 1985; ter Braak and Prentice, 1988). DECORANA rescales the axis to zero mean and unit variance, dividing scores by average curve width making the units multiples of the curve standard deviation (Gauch, 1982; Austin, 1985; ter Braak, 1995a).

CCA incorporates multiple regression into the algorithm constraining the axes as linear combinations of the environmental variables. Site scores are regressed against the variables at each iteration producing new site scores (ter Braak, 1986, 1995a). Integral standardisation of the variables allows joint analysis of variables measured in differing units (ter Braak, 1986, 1987b, 1995a). The results contain both canonical coefficients and intraset correlations, quantifying the correlation of variables with the axes (ter Braak, 1986; ter Braak and Prentice, 1988). However, canonical coefficients assume other variables are held constant, while the intraset correlations assume covariance as in the dataset. Multicollinearity causes instability in the canonical coefficients while the intraset correlations can still be used.

3.8.2 The interpretation of biplots

These techniques produce biplots of species and site points (Kent and Coker, 1992). Site points lie at the centroid of the species occurring there (Crouch, 1992; ter Braak, 1995a), while species points indicate the optima of Gaussian response curves (ter Braak, 1986; ter Braak and Prentice, 1988). The relative positions suggest which species comprise site composition, the probability of species presence decreasing with distance from the species point (ter Braak, 1986). Peripheral species tend to be rare, characteristic of extreme conditions, and not influential. Centrally placed species may be ubiquitous, unrelated to the axes, not unimodal or have their optima there (ter Braak and Prentice, 1988; ter Braak, 1995a). Intermediate positions indicate a closer relationship to the axes (ter Braak, 1995a). The distance between the species points is proportional to the χ^2 distance, indicating the level of association (Gauch, 1982; Bliss et al., 1994; del Morel et al., 1995).

In CCA, vectors represent environmental variables. Vector length or importance is proportional to the rate of compositional change associated with that variable, the direction being that of maximum change (ter Braak, 1986, 1987b; ter Braak, 1995a). Position in relation to other vectors and the axes show the level of correlation (Kent and Coker, 1992), the cosine of the intervening angles being equivalent to a correlation coefficient (Gauch, 1982). The origin represents the variable mean, so that the site or species point can be related to higher (on the same side as the arrowhead) or lower (closer to the arrow tail) than average values (ter Braak, 1986; Kent and Coker, 1992; ter Braak, 1995a). Perpendiculars from the species point to the vector indicate the species ranking on that variable (ter Braak, 1986; Kent and Coker, 1992; ter Braak, 1995a), species distance from the vector indicating influence by other factors (ter Braak, 1987b).

The biplot shows the pattern of compositional variation, restricted in CCA to that related to the environmental variables. CA and DCA present the major vegetation gradients, not all of which are related to measured variables.

3.8.3 Problems associated with the CA family of techniques

Debate concerns both the justification and the procedures involved in detrending and rescaling in DCA. Wartenberg et al. (1987) found no justification for DCA, considering the 'arch' a data attribute, reported in other disciplines and caused by qualitative compositional differences. James (1990) shared this view, seeing the arch as the result of successive replacement and changing favourability.

Peet et al. (1988) responded by arguing that different causes underlie the arch in CA/DCA and the more severely distorted horseshoe in PCA. The latter is considered to result from an inability to represent the data adequately, distances between extremes being equal to those between centrally placed sites and the extreme, while the former reflects a quadratic relationship between two axes (Hill, 1973b; Gauch et al., 1977; Gauch, 1982; Greig-Smith, 1983; Austin, 1985; ter Braak, 1986, 1987a; ter Braak and Prentice, 1988; Kent and Coker, 1992; ter Braak, 1995a). DCA is found to order long gradients more effectively than PCA (Hill, 1973b; Gauch et al., 1977; Gauch, 1982; Kent and Coker, 1992); DCA producing meaningful, interpretable results, while axis two of CA was uninterpretable.

However, criticism of detrending in DECORANA is widespread:

(1) Information is lost and meaningful higher order axes removed (Pielou, 1977; Minchin, 1987; Peet et al., 1988; Kent and Coker, 1992; Palmer, 1993) or deferred (Gauch, 1982; ter Braak, 1995a).

(2) Mathematical artefacts may result, making DCA prone to distortion in the face of increasing β diversity (James and McCulloch, 1990; van Groenewoud, 1992; Tausch et al., 1995).

Pielou (1977) described detrending as overzealous, while Podani (1997) considered it ill-defined and needing improvement.

Axis rescaling leading to a constant rate of species turnover is useful in interpretation (Hill and Gauch, 1980; Peet et al., 1988; Whittaker, 1991; ter Braak, 1995a). However, it is criticised as imposing an unrealistic model (Kent and Coker, 1992; Palmer, 1993), and in view of changing α diversity, not representing actual intersample distance (Wartenberg et al., 1987).

Digby and Kempton (1987) and Wartenberg (1987) described both procedures as arbitrary. Ter Braak (1995a) suggested the omission of rescaling and detrending by making higher order axes uncorrelated with both those preceding and their polynomials (Peet et al., 1988; ter Braak and Prentice, 1988). Detrending by polynomials (CANOCO) appears preferable to the procedure used in DECORANA (Hill, 1979b).

Tausch et al. (1995) found instability with differing entry order in ordination methods based on RA. The problem was considered intractable, linked to data complexity and mathematical artefacts from detrending. However, Podani (1997) criticised the limited testing, suggesting that the problem was due to computational problems; in particular, convergence criteria (iterations ceasing arbitrarily if differences are deemed negligible or after a pre-selected number), and floating point arithmetic (leading to arbitrary rounding errors). Testing carried out by Oskanen and Minchin (1997) confirmed lax convergence criteria as responsible for the instability in CA. Correction of a bug in the linear rescaling programme together with stricter convergence criteria increased the stability of DCA substantially. However, problems were found where higher order axes had similar eigenvalues and where there are many rare species, where variability contributes little to residuals.

The overemphasis of the contribution of rare species is noted by Gauch (1982), while Digby and Kempton (1987) suggested it was caused by scaling to the species mean. Ter Braak (1995a) related this to the ability of CA to identify compositionally differing blocks even when the 'block' comprises a single species at a single site. Even with downweighting, it is sensitive to aberrant, species-poor sites (Gauch et al., 1977; Matthews, 1981), making removal of such outliers important (ter Braak and Prentice, 1988).

As discussed, these techniques assume a unimodal response curve and, under particular circumstances, approximate to the maximum likelihood solution of Gaussian logistic regression (ter Braak, 1995a). However, although symmetrical, Gaussian curves occur frequently, they are not universal (Matthews, 1981; Austin et al., 1994) (section 3.8.1), although it is also asserted that these techniques are robust to violations (Hill and Gauch, 1980; ter Braak and Prentice, 1988). However, WA is inconsistent when these assumptions are violated i.e. given variably spaced optima, and skewed or uneven curves (ter Braak and Barendregt, 1986). In CA, violations result in the arch and the edge effect (ter Braak, 1995a). DCA is seen as forcibly imposing these assumptions through detrending and rescaling; but both Minchin (1987) and Austin et al. (1994) questioned whether even DCA is robust under severe violations. However, work by Ejrnaes (2000) has confirmed that DCA was robust in such circumstances.

Testing against PCA has shown DCA to produce superior results, attributed to its unimodal, rather than linear, assumptions (Hill and Gauch, 1980; Gauch, 1982; Austin, 1985; ter Braak, 1995a). Gauch et al. (1977) found RA relatively stable to increasing β diversity, the arch effect being preferable to the complex surfaces, involutions and unpredictable distortions of distance inherent particularly in non-standardised PCA. RA separated outliers, clustering the remaining data, but in PCA compression and rotation resulted in the outliers occurring on higher order axes, difficult to interpret in terms of community variation. Gauch et al. (1981) compared RA, DCA and NMDS, finding neither RA nor NMDS to have a consistent advantage, but DCA superior to both. Compared to Gaussian ordination, DCA sample placement was inferior, although an appropriate configuration was retained.

In conclusion:

(1) Detrending and rescaling in DECORANA impose unrealistic assumptions, detrending by polynomials appears preferable;
(2) Rare species are overemphasised, requiring downweighting and the removal of outliers;
(3) DCA appears to be robust to violations of the assumption of symmetrical, unimodal response curves;
(4) Testing of DCA finds it produces superior results to most techniques except Gaussian ordination.

3.8.4 A comparison between DCA and CCA

Økland (1996) suggested that functional differences between the two techniques make them suitable for differing purposes, despite the shared methodology. Specific considerations included:

(1) Subjective decisions determine the inclusion of environmental variables, such that important variables may be excluded or inappropriate ones used;
(2) The ordination configuration is determined by the particular groups of variables included;
(3) Compositional variation not accounted for by the selected variables is discarded; and

(4) Multiple regression assumes a linear relationship.

However, DCA is interpreted using a set of measured environmental variables, similarly chosen subjectively. Variation, unrelated to these variables, is not directly interpretable, resulting from unspecified other causes. CCA is particularly useful when the principal causes of variation are already established and allows direct examination of relationships between variables. Del Morel et al. (1995), for example, preferred CCA to DCA for the direct insight into environmental controls on vegetation.

Ter Braak (1987a) pointed out that indirect methods do not incorporate environmental variables into the algorithms, relationships may be missed or poorly represented and relatively minor variation may occur on higher order axes (ter Braak, 1987b, 1995a). In particular, the construction of complex gradients, may prove difficult (ter Braak, 1995a). Both are specifically detected by CCA.

In CCA, early gradients relate directly to the measured variables and may therefore result in differing configurations to those recovered by DCA, if measured variables do not fully explain the most important vegetation trends (Whittaker, 1989). Comparison of the two ordination diagrams and eigenvalues for the relevant axes indicate relative explanatory power, providing useful insights (ter Braak, 1995a). Eigenvalues for CCA axes are often lower than for DCA (ter Braak, 1987b; Crouch, 1992; ter Braak, 1995a; Pardoe, 1996).

Rather than being discarded, residual variation is shown on higher order, non-canonical axes (ter Braak, 1986, 1988; ter Braak and Prentice, 1988).

Multiple regression or correlation coefficients are often used to interpret DCA gradients. CCA incorporates the regression into a non-linear technique (ter Braak, 1995a) rather than assuming a linear relationship between variables and species abundance (ter Braak, 1986; ter Braak and Prentice, 1988).

Palmer (1993) compared the two in terms of the effects of detrending and rescaling and ability to handle skewed distributions and unusual sample designs. CCA recovered gradients more accurately than DCA when distributions were skewed, there was considerable noise and with unbalanced sampling, DCA warping and distorting the gradient. CCA was unaffected by multicollinearity. He considered that artificial arches occur rarely, finding that DCA destroyed a true arch, which was retained in CCA, and concluded that detrending is generally not necessary and may be detrimental.

Statistical inference tests have been used to assess the importance of identified gradients. In CCA the Monte Carlo permutation test is used (Bliss et al., 1994; del Morel et al., 1995; ter Braak, 1995a; Økland, 1996). Such testing is dubious for large datasets (Foskett, 1998) and given that these techniques are exploratory rather than confirmatory (James and McCulloch, 1990; Kent and Coker, 1992; Palmer, 1993).

Log transformation of skewed distributions is suggested to improve the approximation to normality (ter Braak and Barendregt, 1986). However, these techniques are not strictly parametric (Palmer, 1993) although they are more effective with symmetrical distributions. Digby and Kempton (1987) consider that the scaling by species and site means has a similar effect (Gauch et al., 1977).

3.8.5 The choice of technique

Of widely available techniques, the CA family is most appropriate where data shows a unimodal response curve. Within this family, DCA and CCA appear the strongest and most highly developed. However, all the techniques discussed have limitations and defects (Matthews, 1981; Peet et al., 1988; Økland, 1996).

CCA directly examines the role of specific environmental variables. The importance of the variables used in this study has been established in previous work (Whittaker, 1985, 1987, 1989, 1991; Crouch, 1992; Foskett, 1998). Whittaker (1989) found DCA preferable in detecting overall structure, while CCA draws out interwoven variables. CCA is resilient to multicollinearity, allowing correlated variables to be retained. CCA is therefore the preferred option for an examination of relationships between predetermined variables.

In addition to the full dataset, subsets of the data (the TWINSPAN groups) are used to investigate relationships amongst the variables over the course of the sequence. Short gradients are more likely to reflect a linear or monotonic relationship (section 3.8.1), suggesting that a linear technique might be more appropriate for small groups. However, larger groups with longer gradients are more likely to have a unimodal relationship. Linear techniques are of limited usefulness for even monotonic gradients. The CA family is however robust to differing distribution types. It was therefore considered acceptable to use CCA in the analysis of the subsets.

Another factor contributing to the decision involves the extent to which CCA has been used since its introduction by ter Braak in the 1980s. Birks et al. (1994) list 379 papers using this and related techniques between 1986 and 1993. Its use has continued to increase since the 1990s (i.e. Bliss et al., 1994; Stanton et al., 1994; Vetaas, 1994; Amman, 1995; Pardoe, 1996; Gottfried et al., 1999; Rosales et al., 2001; Lyon and Sager, 2002; Jones and Henry, 2003). Such widespread use allows evaluation of the properties.

Detrending by polynomials was found to have no discernible effect on CCA (ter Braak, 1987c; ter Braak and Prentice, 1988) and so was not used in the analysis. As discussed above, the Monte Carlo test was not used and rare species were downweighted, but otherwise the defaults were used.

3.9 Correlations amongst the environmental variables

These are used to detect covarying environmental factors and to examine changes in the overall pattern when the dataset is divided into subgroups. The use of ordinal rather than interval/ratio scales and a preliminary examination showing that many variables are not normally distributed led to the selection of a non-parametric coefficient (Matthews, 1981; Whittaker, 1987; Kent and Coker, 1992).

Spearman's rho is found to be less rigorous as the number of tied ranks increase, due to the use of ordinal data (Whittaker, 1985; Foskett, 1998). Kendall's tau is more robust and the programme (SPSS, 1999) contains a modified formula that enhances this (Whittaker, 1985). Data were standardised, ensuring that differing scales are directly comparable (Digby and Kempton, 1987).

Chapter 4: Changes in species frequency and distribution

4.1 Introduction

This chapter considers changes to species populations. However, before examining these in detail, the validity of the data needs to be considered. Inherent in surveys that use a number of operators is the potential problem of errors, both of miscounting and misidentification. Steps were taken in both surveys to minimize errors, but inevitably some will have been included. Precise identification/ quantification of errors is impossible so that these results need to be considered in a way that avoids placing weight on counts that are not corroborated, as is explained below.

Matthews (1976) tested operator error and found that the principal mistakes involved under- rather than over-counting, particularly of small stature, rare plants. A similar tendency was found in the 2000 survey (see Chapter 3). Species occurring at low frequency are not therefore considered in detail.

A potential source of error that may have important implications for this study is that of systematic error, where species may be identified differently in the two surveys. This is most likely to involve species that are morphologically similar, two possible examples considered in Chapter 3 involve the shrub *Salix* spp. and the graminoid *Luzula* spp.. Positive identification of the same species at a particular site in both surveys provides corroboration: in many instances the species was found on the same or adjacent quadrats. More weight is therefore given in the following discussion to sites where changes in frequency occur. Additionally, colonizations and losses associated with clusters of sites containing increases or decreases (respectively) are considered to be more convincing. The rare cases where particular counts were excluded are discussed in Chapter 3. It is recognised that it is impossible to screen out all errors, but by focusing on consistent patterns it is intended to minimize the effects of these and consider real changes that have occurred in the distributions.

Section 4.2 presents an initial overview, with the summation of total population frequencies, identifying species undergoing substantial change and whether this involves expansion or contraction. Site age is then incorporated in section 4.3 to relate the changes to the successional sequence and to consider the level of explanatory power age has as a driving force.

Distribution changes affecting individual species are assessed in section 4.4 using the mesoscale parameters of site age, altitude and aspect. Where the dominant influence is succession, two patterns may result: (1) migration, where species associated with successional stages remain on ground of a particular age, so that their entire distributions move up the foreland as the sites age; (2) expansion, where species found on the oldest land expand their range, moving up the foreland once a threshold age has been reached while remaining on the original sites. However, the pattern of change may indicate other influences. Change that is limited spatially suggests an underlying change occurring in a finer scale variable, for example a watercourse may have changed position. However, consistent, foreland-scale change may indicate a process operating at a larger, regional scale. Substantial population increases may in themselves provide a further influence, affecting species with which such a population is in contact through the intensification of interspecific interactions. The assessment of distribution changes in terms of these particular variables may therefore indirectly suggest the nature of the driving influence, in particular whether this represents a generalised change in background conditions or a more localised source. Simple functional groups have been used to divide the species (woody shrubs, grasses and related species, forbs and pioneers). These may be useful in two ways. They represent structural components (woody shrubs for example provide the main canopy-forming species) and, additionally, certain physiological attributes are consistent within the groups, for example grasses and shrubs use different forms of nitrogen (Pornon and Doche, 1994). Comparison within and between these groups therefore provides a further source of information by which the changes can be characterised and may suggest explanations for the observed changes.

Section 4.5 looks at associations between the species and how these have changed during the course of 30 years. This allows the importance of the changes to be assessed in a wider community context. Although individual species changes are of interest, they may make only a marginal difference to the assemblages present. This also allows a further source of potential explanation to be explored; changes predominantly affecting a particular habitat type may reflect a coarser scale change, for example differences in snowbed species would follow from a change in the extent of permanent snow patches.

4.2 Overall changes in frequency

An initial assessment of the extent of the changes has been made by totalling individual species frequency in each dataset. Species undergoing the highest percentage increases and decreases are shown in Tables 4.1 and 4.2 respectively (the full list is given in Appendix 2).

Nine of those species increasing (Table 4.1) are woody shrubs (*Betula nana*, *Empetrum hermaphroditum*, *Juniperus communis*, *Loiseleuria procumbens*, *Salix glauca*, *S. herbacea*, *S. phylicifolia*, *Vaccinium myrtillus*, and *V. uliginosum*), six of which are deciduous. Of the three evergreens, *J. communis* and *L. procumbens*, show small numerical rises, but *E. hermaphroditum* has the second largest increase. Three of the remaining species are grasses (*Anthoxanthum odoratum*, *Deschampsia cespitosa* and *Phleum alpinum*) mainly associated with older sites, together with *Carex* spp. Of the five forbs, all may be found on older sites, although the late pioneer *Oxyria digyna* also occurs on young sites and is associated with disturbance and high moisture levels on older land (Whittaker, 1993).

Species that have declined (Table 4.2) are more numerous, but large changes in frequency are fewer. A wide range of species is involved, but only one deciduous shrub, *Salix lanata*. There are three evergreen shrubs (*Arctostaphylos* spp., *Phyllodoce caerulea*, *Vaccinium vitis-idaea*), seven pioneer species, including three grasses (although the number and area of very young sites have also decreased), with the remaining nine being forbs (*Antennaria alpina*, *Bartsia alpina*, *Cardamine bellidifolia*, *Cardaminopsis petraea*, *Hieracium alpinum*, *Leontodon autumnalis*, *Polygonum viviparum*, *Sibbaldia procumbens*, and *Tofieldia pusilla*).

Table 4.1: Species with increased frequency in 2000

Species	Total 1970 (410 sites) **	Total 2000 (410 Sites) **	Total 2000 (434 Sites) **	Change (410 Sites)	%	Change (434 Sites)	%
Sal phy	383	2406	2416	+2023	+528.20	+2033	+530.81
Pyr spp	114	536	536	+422	+370.18	+422	+370.18
Are spp	374	650	957	+276	+73.80	+583	+155.88
Ran acr	127	260	260	+133	+104.72	+133	+104.72
Tri eur	296	551	551	+255	+86.15	+255	+86.15
Epi ana	105	192	192	+87	+82.86	+87	+82.86
Sax riv	119	193	210	+74	+62.18	+91	+76.47
Sal myr	158	247	247	+89	+56.33	+89	+56.33
Oxy dig*	2463	3404	3816	+941	+38.21	+1353	+54.93
Sal gla	9651	14497	14588	+4846	+50.21	+4937	+51.16
Vac myr	3204	4745	4745	+1541	+48.10	+1541	+48.10
Des ces	281	413	413	+132	+46.98	+132	+46.98
Jun com	359	525	525	+166	+46.24	+166	+46.24
Aco sep	141	205	205	+64	+45.39	+64	+45.39
Ped lap	787	1117	1117	+330	+41.93	+330	+41.93
Vac uli	4969	6632	6632	+1663	+33.47	+1663	+33.47
Phl alp	743	927	953	+184	+24.76	+210	+28.26
Sal her	22874	29121	29278	+6247	+27.31	+6404	+28.00
Emp her	23449	28929	28950	+5480	+23.37	+5501	+23.46
Rum asa	306	357	358	+51	+16.67	+52	+16.99
Ant odo	1522	1718	1720	+196	+12.88	+198	+13.01
Car spp	9279	10389	10401	+1110	+11.96	+1122	+12.09
Ver alp	987	1067	1102	+80	+8.11	+115	+11.65
Loi pro	1422	1574	1574	+152	+10.69	+152	+10.69
Hup sel	240	257	257	+17	+7.08	+17	+7.08
Gna nor	356	373	373	+17	+4.78	+17	+4.78
Bet nan	9707	10080	10080	+373	+3.84	+373	+3.84
Sol vir	958	967	967	+9	+0.94	+9	+0.94

*Pioneer species

** Note:

(1) 9 x 1m^2 quadrats were used per site. The maximum frequency per quadrat was 25. The second total frequency column for 2000 (noted 434 sites), gives the total including the new pioneer sites surveyed in 2000 only, while the first column (noted 410 sites) includes only those sites that were also surveyed in 1970. The numbers represent summed frequency, which could, theoretically, be (9 x 25 x 410) 92 250 or (9 x 25 x 434) 97 650.

(2) Species with a summed frequency exceeding 100 are included here, the totals for the remaining species are given in Appendix 2

Table 4.2: Species with Reduced Frequency in 2000

Species	Total 1970 (410 sites) **	Total 2000 (410 Sites) **	Total 2000 (434 Sites) **	Change (410 Sites) **	%	Change (434 Sites)	%
Ara alp*	355	44	85	-311	-87.61	-270	-76.06
Sil aca	282	74	78	-208	-73.76	-204	-72.34
Lyco alp	382	106	106	-276	-72.25	-276	-72.25
Sax ces*	809	67	277	-742	-91.72	-532	-65.76
Car pet	537	181	228	-356	-66.29	-309	-57.54
Ant alp	521	227	227	-294	-56.43	-294	-56.43
Luz arc	1632	714	714	-918	-56.25	-918	-56.25
Cas hyp	6741	3829	3829	-2912	-43.20	-2912	-43.20
Des alp*	1750	739	995	-1011	-57.77	-755	-43.14
Luz spi	1306	725	749	-581	-44.89	-557	-42.65
Tof pus	590	350	350	-240	-40.68	-240	-40.68
Sal lan	5133	3227	3227	-1906	-37.13	-1906	-37.13
Arc spp	1092	715	715	-377	-34.52	-377	-34.52
Car bel	482	306	316	-176	-36.51	-166	-34.44
Pol viv	5321	3574	3575	-1747	-32.83	-1746	-32.81
Jun tri	1581	1082	1082	-499	-31.56	-499	-31.56
Sed ros	201	132	139	-69	-34.33	-62	-30.85
Poa spp*	4423	2457	3136	-1966	-44.45	-1287	-29.10
Hie alp	980	704	704	-276	-28.16	-276	-28.16
Vio pal	125	92	92	-33	-26.98	-33	-26.98
Vac vit	4196	3138	3138	-1058	-25.21	-1058	-25.21
Phy cae	12217	9385	9385	-2832	-23.18	-2832	-23.18
Leo aut	1011	806	806	-205	-20.28	-205	-20.28
Cer alp*	343	243	274	-100	-29.15	-69	-20.12
Ger syl	356	286	286	-70	-19.66	-70	-19.66
Sib pro	785	651	654	-134	-17.07	-131	-16.69
Eri ang	923	786	786	-137	-14.84	-137	-14.84
Tri spi*	2062	1808	1894	-254	-12.32	-168	-8.15
Fes spp	6314	5770	5803	-544	-8.62	-511	-8.09
Bar alp	2435	2261	2262	-174	-7.15	-173	-7.10
Sax opp*	259	191	241	-68	-26.25	-18	-6.95
Sau alp	405	377	377	-28	-6.91	-28	-6.91
Pin vul	1225	1150	1150	-75	-6.12	-75	-6.12
Ran gla	961	931	931	-30	-3.12	-30	-3.12
Gna sup	1100	1032	1068	-68	-6.18	-32	-2.91
Sax ste	724	635	706	-89	-12.29	-18	-2.49
Cer cer*	1712	1314	1836	-398	-23.25	+124	+7.24

*Pioneer species

** Note:

(1) 9 x 1m^2 quadrats were used per site. The maximum frequency per quadrat was 25. The second total frequency column for 2000 (noted 434 sites), gives the total including the new pioneer sites surveyed in 2000 only, while the first column (noted 410 sites) includes only those sites that were also surveyed in 1970. The numbers represent summed frequency, which could, theoretically, be (9 x 25 x 410) 92 250 or (9 x 25 x 434) 97 650.

(2) Species with a summed frequency exceeding 100 are included here, the totals for the remaining species are given in Appendix 2

While the changes in frequency are extensive, increases are largely confined to species already occurring in high numbers, while decreases often involve less numerous ones. It has been suggested that adjustments to changing conditions may occur by a compensatory mechanism involving moderately abundant species (Mortimer, 1987). This is examined in Table 4.3, where changes in frequency exceeding 10% are partitioned into frequency classes.

The abundant and rare groups have more species increasing than decreasing and higher overall totals, with the opposite pattern amongst the moderately abundant and uncommon classes. The increases in the 'abundant' group are dominated by those affecting the woody shrubs, having a net increase of 11440. Moderately abundant species that have declined in abundance are mostly forbs, the net decrease being 3936. More species are invading than have been lost and many of these new colonizers now have counts amounting to several 10s. All species lost were rare (frequency < 10 in 1970), except for *Melandrium apetalum* with 40.

For a compensatory mechanism to be operating, the changes in frequency should be accommodated within a similarly sized population. Total frequency was 167 874 in 1970 and 173 624 (410 sites) (176 839 for 434 sites) in 2000, representing an increase of only 3.4%. Calculated as a site average, this gives 409.45 (1970) and 423.47 (2000) for the 410 sites sampled in both surveys (the increase may be explained by frequency increases with the ageing of the youngest sites). The 2000 average falls to 407.46 when the sparsely-vegetated new sites are included. The changes in frequency are therefore accomplished by redistribution amongst abundance classes with no major change in total frequency.

4.2.1 Summary of section 4.2

(1) Some very large changes in frequency are identified, associated with particular groups of species.

(2) The group with the largest overall increase in absolute terms is that including the woody shrubs, although some forbs and grasses associated with old sites also show large rises. The shrub species involved are predominantly deciduous, although *Empetrum hermaphroditum* provides a notable exception.

(3) Decreases affect a wide range of species, comprising evergreen shrubs, most of the pioneers, and a group of later-occurring forbs.

(4) A compensatory mechanism may accommodate these population changes. Evidence for this includes increases mainly involving abundant and rare species, while moderately abundant and uncommon species show net decreases. Despite these changes, totals for the two surveys differ by only 3.4%.

4.3 Changes in frequency partitioned into age groups

The species data have been divided into ten age groups in order to consider whether population changes are spread evenly or concentrated on sites of a particular age, whether successional change can be detected and if so, whether this satisfactorily explains the changes. There were nearly twice as many sites within the regional vegetation as in any other single age

Table 4.3: Changes in species frequency related to abundance class

- **Changes greater than 10%**

Abundance Category		**Species**	Total change in frequency	
			+	-
High (1000s)	Positive	Car spp, Emp her, Oxy dig (P), Sal gla, S. her (P), S. phy, Vac myr, V. uli	+23851	
	Negative	Cas hyp, Phy cae, Poa spp (P), Pol viv, Sal lan, Vac vit		-12411
Moderate (100s)	Positive	Aco sep, Ant odo, Are spp, Des ces, Jun com, Loi pro, Ped lap, Phl alp, Pyr spp, Ran acr, Rum asa, Sal myr, Sax riv, Tri eur, Ver alp	+2962	
	Negative	Ant alp, Ara alp(P), Arc spp., Car bel, Car pet, Cer alp(P), Des alp(P), Eri ang, Ger syl, Hie alp, Jun tri, Leo aut, Luz arc, L. spi, Lyco alp, Sax ces(P), Sed ros, Sib pro, Sil aca, Tof pus		-6347
Low (10s)	Positive	Ach mil, Alc alp, Bet pub, Cal vul, Cys fra, Dry oct, Epi ana, Sax niv	+247	
	Negative	Cam rot, Cry cri, Epi als, Equ spp, Eri uni, Eup alp, Lyco ann, Rub arc, Tha alp, Vio pal, Woo alp		-441
Rare and Losses/Gains	Positive	Alc glo, Ast alp, Coe vir, Com pal, Cre pal(l), Eri sch, Jun big(l), Mel pra(l), Nar str(l), Ped oed(l), Pot cra(l), Pul ver, Rum ala(l), Sil doi(l)	+277	
	Negative	Adi cap(L), Ang arc(L), Bot lun(L), Des fle(L), Mel ape(L), Sax cer(L)		-61
		Total	+27882	-20317

- **Changes less than 10%**

	Species	Total change in frequency	
Positive	Bet nan, Cer cer(P) Gna nor, Hup sel, Ran pyg, Sol vir	+545	
Negative	Bar alp, Epi ang, Fes spp, Gna sup, Pin vul, Ran gla (P), Sal ret, Sau alp, Sax opp (P), S. ste, Tri spi(P)		-1057

Notes: All species occurring in the study area are included.
The abundance categories used are based on total frequency in 2000
A list of the abbreviations and full species names is given in Appendix 1
(P) denotes pioneer species; (l) a species gained and (L) a species lost

group. The sites were therefore divided between two groups, depending on their proximity to the outer moraine: those on or adjacent to the moraine formed group 9, while those at a greater distance comprised group 10. A list of sites comprising these groups is given in Appendix 3 and their spatial locations are shown in Figure 4.1.

Figures 4.2 and 4.3 compare increases and decreases in terms of numbers of species and overall frequency for each age group. Both figures indicate trends related to terrain age; on the youngest ground (up to 58 years) there is an increase in both the number of species and the total frequency, but both decrease on the oldest ground. Intermediate aged terrain has a more complex, variable pattern and may indicate a transition between the two.

4.3.1 Age-related patterns in species frequency

The general trend of net increases on younger ground and net decreases on older terrain, particularly in the regional vegetation, has a more variable pattern when considered in detail (Table 4.4). Underlying species changes are listed where net increases or decreases exceeded 100 counts (age > 42 years) or 50 where counts are lower (age 5-42 years). The focus is therefore on larger changes and more abundant species, which have greater input to the community.

Age Group 1 (30-42 years). Pioneer species have increased (e.g. *Arenaria* spp., *Cerastium cerastoides* and *Trisetum spicatum*), together with some species more characteristic of older ground (e.g. *Carex* spp., and *Salix glauca*). The only species declining on this very young ground is the early pioneer, *Arabis alpina*.

Age Group 2 (42-58 years). Increases occur in the heath species *Empetrum hermaphroditum* and *Phyllodoce caerulea*, and also amongst *Salix* spp., including *S. lanata* (which increases only in Groups 2 and 3). Early pioneer species decline.

Age Group 3 (59-70). This Group is characterised by large increases in a small number of species, dominated by that for *S. herbacea* (2355) and including both *Empetrum hermaphroditum* and *Salix glauca*. A further heath species, *Vaccinium uliginosum*, shows a more modest increase. Pioneers are decreasing, including *Cerastium cerastoides* and *Saxifraga cespitosa*, and particularly *Poa* spp..

Age Group 4 (71-113). Species increasing include many heath species, the late pioneer *Ranunculus glacialis,* and the forb *Pinguicula vulgaris*. Both *Cassiope hypnoides* and *Salix lanata* decrease in numbers (a pattern also apparent in older groups).

Age Group 5 (115-147). Heath species increase and now include *Betula nana* and *Salix phylicifolia*. Losses continue amongst pioneers together with *Cassiope hypnoides*, *Salix lanata*, and *Luzula* spp.. This is the youngest terrain on which *Phyllodoce caerulea* and *Polygonum viviparum* exhibit a decrease.

Age Group 6 (149-186). This group is also dominated by increases in heath species, together with *Hieracium alpinum* and *Phleum alpinum*. Losses also affect species such as *Cassiope hypnoides* and *Phyllodoce caerulea*.

Table 4.4: Changes in Species Frequency between 1970 and 2000 divided according to the ages of the sites

Group	Age: 1970	2000:	Increases	Decreases
1 n = 43	0-12	30-42	Are spp +140, Car pet +49, Car spp +48, Cer cer +83, Des alp +142, Epi ana +160, Fes spp +55, Gna sup +63, Luz spi +92, Oxy dig +424, Poa spp +350, Sal gla +131, Sal her +383, Sax opp +77, Sax ste +75, Tri spi +393, Ver alp +84.	Ara alp –89.
2 n = 44	12-28	42-58	Are spp +126, Car spp +345, Emp her +391, Fes spp +150, Gna sup +159, Oxy dig +857, Phy cae +118, Sal gla +579, Sal her +2094, S. lan +153, Ver alp +102.	Ara alp –210, Car pet –235, Cer cer –346, Poa spp –289, Sax ces -611
3 n = 44	29-40	59-70	Car spp +468, Emp her +773, Phy cae +293, Sal gla +896, S. her +2355, S. lan +283, S. phy +401, Vac uli +109	Are spp. –139, Cer alp –234, Cer cer –371, Des alp –781, Fes spp –247, Luz arc –110, L. spi –101, Oxy dig –294, Poa spp –645, Sax ces –111, Sax ste –147, Tri spi –601.
4 n = 43	41-83	71-113	Car spp +283, Emp her +992, Pin vul +113, Ran gla +151, Sal gla +540, S. her +729, S. phy +325, Vac uli +165.	Cas hyp –171, Fes spp –133, Luz spi –115, Oxy dig –109, Poa spp –289, Sal lan –367.
5 n = 41	85-117	115-147	Ant odo +174, Bar alp +122, Bet nan +143, Car spp +160, Emp her +942, Sal gla +509, S. her +443, S. phy +169.	Car bel –113, Cas hyp –456, Fes spp –212, Luz arc –237, L. spi –121, Phy cae –182, Poa spp –190, Pol viv –164, Ran gla –192, Sal lan –609.
6 n = 46	119-156	149-186	Bet nan +296, Emp her +963, Hie alp +234, Phl alp +109, Sal gla +463, S. her +226, S. phy +276, Vac myr +245, V. uli +192.	Cas hyp –539, Luz spi –161, Phy cae –590, Sal lan –499.
7 n = 44	157-191	187-221	Emp her +501, Sal gla +753, S. phy +368, Vac myr +500, V. uli +302.	Ant alp –141, Bar alp –210, Bet nan –132, Cas hyp –913, Gna sup –100, Hie alp –161, Jun tri –142, Luz arc –101, L. spi –118, Phy cae –949, Pin vul –222, Poa spp –194, Pol viv –135, Sal her –335, S. lan –494, Tof pus –180.
8 n = 44	193-221	223-251	Bet nan +207, Car spp +132, Emp her +853, Fes spp +119, Ped lap +182, Sal gla +194, S. her +178, S. phy +189, Vac uli +509, V. vit +162.	Cas hyp –167, Jun tri –145, Luz arc –150, Phy cae –856, Poa spp –142, Pol viv –105, Sal lan –250, Sil aca –117.
9 n = 41	All 9 000*		Bet nan +113, Des ces +157, Emp her +252, Phl alp +117, Sal gla +427, S. phy +104, Vac myr +274, V. uli +115.	Ant alp –119, Cam rot –185, Car spp –199, Cas hyp –387, Fes spp –280, Hie alp –270, Jun tri –101, Luz arc –191, Lyco alp –184, Ped lap –150, Phy cae –438, Poa spp –273, Pol viv –832, Sal her –210, S. lan –148, Vac vit –660.
10 n = 44	All 9 000*		Fes spp +192, Jun com +117, Ran acr +112, Sal gla +276, S. her +317, S. phy +159, Tri eur +515, Vac myr +310, V. uli +228.	Arc alp –237, Cas hyp –211, Eri ang –203, Gna sup –144, Hie alp –142, Leo aut –141, Luz arc –146, Phy cae –267, Poa spp –167, Pol viv –251, Sau alp –165, Sol vir –356,Vac vit –422, Ver alp –266.

Note: A list of abbreviations and full names is given in Appendix 1.The numbers are the net change in frequency between 1970 and 2000.

* Groups 9 and 10 contain sites within the regional vegetation; those in group 9 are within 10 metres of the 1750 moraine, while those in Group 10 are at a greater distance.

Age Group 7 (187-221). This is the youngest group to show decreases in both numbers of species and total counts. Few species show increases and these are all heath dominants. *Cassiope hypnoides*, *Luzula* spp., *Phyllodoce caerulea*, *Poa* spp., *Polygonum viviparum* and *Salix lanata* have declined, as have the forb species *Bartsia alpina*, *Hieracium alpinum*, *Pinguicula vulgaris* and *Tofieldia pusilla.*

Age Group 8 (223-251). Increases are found amongst a wider range of species than in the previous Group including *Festuca* spp. and *Pedicularis lapponica.* Decreases continue to affect the same species as above, but include *Silene acaulis*, which has declined to very low levels in the study area.

Age Groups 9 and 10 (9000). The main trend in both Groups is of decreasing numbers of species and total frequency. Those species mentioned above continue to decline and decreases also affect the shrubs *Arctostaphylus* spp. and *Vaccinium vitis-idaea*, together with the forbs *Campanula rotundifolia*, *Hieracium alpinum*, *Pedicularis lapponica*, *Pyrola* spp., *Saussurea alpina*, *Solidago virgaurea* and *Veronica alpina.* Group 10 does not show any decline for *Salix lanata.* Increases occur amongst heath shrubs, the grasses, *Deschampsia cespitosa* and *Festuca* spp., the forb *Ranunculus acris* and the evergreen shrub, *Juniperus communis.*

4.3.2 Temporal trends

The youngest ground is characterised by changes involving pioneers as would be expected in an ageing successional sequence. However, some late successional species appear to be increasing in the youngest age groups, well outside their centres of distribution. These include the heath dominants *Empetrum hermaphroditum* and *Salix glauca*, together with *Carex* spp. and *Gnaphalium supinum.*

To test whether these species were colonizing younger land, distributions in 1970 and 2000 were compared on young terrain, the latter including the newly established sites. The data are presented in Figure 4.4 and include the late heath dominant *Betula nana.* With the exception of *Gnaphalium supinum*, where the distribution is bimodal (with peaks on very young and on old terrain), the data do not support this conjecture in relation to very young land. Rather, it indicates that frequency of these typically late species is lower in 2000 compared to 1970 on land younger than about 50 years. In each case frequency shows a marked increase compared to 1970 on slightly older land, the precise timing being species-specific.

Three factors may be contributing to this delay: (1) newly exposed sites are at higher altitude in 2000 compared to 1970 as the glacier retreats onto higher ground; (2) the area occupied by young land is reduced in 2000 compared to 1970; and (3) much of the youngest land in 1970 comprised the fluted moraines. These are flat and relatively featureless with few safe sites (section 2.3). A study by Ballantyne and Matthews (1982), which measuring moisture availability close to the snout, showed that the till dried rapidly once the glacier had retreated beyond ca50m. Whittaker (1985) noted the lack of *Salix* spp. seedlings in this area. The fluted moraines are now 32-49 years old and form a substantial proportion of sites less than 50 years old. It is suggested therefore that these later species are experiencing establishment difficulties due to lack of available moisture and the scarcity of suitable microsites. This, possibly combined with the increasing altitude, has lead to diminished performances compared to 1970. Figure 4.4 also shows a contrasting pattern on land exceeding ca 50 years, where populations have increased appreciably.

Species that show the highest overall increases do so over a wide range of terrain ages. *Salix glauca* increases in every age group but particularly on land of intermediate age. *S. phylicifolia* and *Vaccinium uliginosum* increase on terrain older than 60 years and *Vaccinium myrtillus* on older ground, from ca. 150 years. *S. herbacea* increases up to ca. 200 years, particularly on terrain aged 40-70 years, falling in the regional vegetation of Group 9 but then increasing at greater distance from the 1750 moraine in Group 10. *Empetrum hermaphroditum* increases on ground of all ages, except the youngest and oldest, with no age category showing a decrease. The final heath species, *Betula nana*, has not shown a large overall change (an increase of 3.84%), but the changes suggest a shift onto younger ground (increases in Groups 5 and 6 aged 115-186 years and a decline in Group 7 187-221).

Similarly, those species declining show a persistent pattern over a wide range of terrain ages. *Cassiope hypnoides* declines on terrain older than 70 years, *Phyllodoce caerulea* and *Polygonum viviparum* after 115 years, *Salix lanata* after 70 years until Group 9, *Luzula* spp. after 59 years and *Poa* spp. after ca 40 years.

In addition to *Betula nana*, some species seem to be moving onto younger ground, for example *Gnaphalium supinum*, *Oxyria digyna*, *Phyllodoce caerulea* and *Salix lanata*. This is a theme that is examined more thoroughly with respect to individual distribution patterns in the next section.

Salix phylicifolia was a moderately common species in 1970 but has subsequently increased by 538%. Increases have occurred throughout the sequence from ca. 59 years so that this species is now a major component of the vegetation, although this species may have been misidentified (section 3.1.5).

The decline affecting *Salix lanata* is not typical of the trend amongst other *Salix* spp.. Hybridization with *S. glauca* (section 3.1.5) as a potential source of misidentification and this is discussed in greater detail below.

The older terrain is characterised by a large number of species each exhibiting a small decrease. This decline involves species that appear to be performing poorly across the whole sequence together with species that are declining solely on old terrain. The pioneer, *Poa* spp., has decreased substantially on the oldest ground, where it may previously have been associated with transitory disturbance. This suggests that there may have been a reduction in disturbance on these sites, possibly linked to the increases in woody shrubs and suggesting an increase in autogenic control. Although rare, *Betula pubescens carpatica* is the only tree species present and its seedlings have increased by 91%. The life histories of some major heath dominants may make them more amenable to cyclic changes. *Empetrum hermaphroditum*, for example, can adopt a circular form, spreading outward but dying in the centre (Whittaker, 1993). Although this was not noted in the present survey, its propensity for vegetative propagation was, with adventitious stems rooting several metres from the parent plant.

4.3.3 Summary of section 4.3.

(1) Numbers of species and total frequencies have increased on the youngest sites, but both appear to have decreased in the regional vegetation. Intermediate sites show greater complexity.

(2) Young sites show a clear successional pattern, with wave-like increases and decreases in pioneers (e.g. *Arenaria* spp., *Cerastium cerastoides* and *Trisetum spicatum*).

(3) A test of the performance of several species associated with old, low-altitude sites (*Betula nana, Carex* spp.*, Empetrum hermaphroditum* and *Salix glauca*) on young land showed poorer performance on land younger than ca 50 years in 2000 (largely comprising the fluted moraines), but improvement on land older than this. It is suggested that changing moisture conditions on the flutes and a scarcity of safe sites is constraining colonization of this land.

(4) Heath species (e.g. *Empetrum hermaphroditum* and *Vaccinium uliginossum*) exhibit increases on a wide range of sites throughout the sequence.

(5) Certain species are showing a wide-ranging decline on terrain of all ages (e.g. *Cassiope hypnoides* and the evergreen shrub, *Phyllodoce caerulea*).

(6) Older sites, particularly within the regional vegetation, exhibit individually small but extensive declines particularly amongst small forbs (e.g. *Campanula rotundifolia*, *Hieracium alpinum*, *Leontodon autumnalis* and *Saussurea alpina*).

4.4 Species distributions

4.4.1 Introduction

In this section changes in species distributions will be assessed by describing the pattern in 1970 and considering how this has changed by 2000. Species of low abundance are generally not included as their contribution to the community is slight, stochastic events are likely to exert excessive influence and trends are difficult to identify.

Three maps have been produced for each species, showing the distributions in 1970 and 2000, together with the amount and direction of changes occurring between the surveys. General patterns are identified and defined in terms of broad scale site parameters: age of terrain, altitude (increasing up the foreland and onto the flanks at either side), and aspect. These factors are generally sufficient to describe the distribution at this scale of resolution, but some patterns suggest a strong mesoscale spatial influence from additional variables. Factors operating at a finer scale, with effects at the local level, such as soil depth and pH, will be examined in Chapter 6.

The species are divided by growth form (shrubs, graminoids and forbs), with pioneers treated as a further group. These occupy broadly similar functional positions within the assemblages and may provide evidence of compensatory changes or differing strategies within or between functional groups. The heading includes the frequencies in 1970 and 2000, the second figure for

2000 indicates the revised total where the species also occurred on the newly established sites. Throughout, the focus is on general patterns and these are summarised in Tables 4.5 and 4.6.

4.4.2 Shrubs and subshrubs

Many of these 16 species are dominant at sites throughout the study area and are therefore amongst the most numerous species. 15 have at least several hundred counts. *Betula pubescens* ssp *carpatica* is also discussed, as the population increase may have implications for the position of the treeline. Each description involves a brief summary of the distribution and the main changes that have occurred.

***Arctostaphylos* spp.** (Figure 4.5: 1970-1092; 2000-715)

Distribution: This species is associated with old terrain (off-foreland and old foreland sites), modified by altitude (decreasing in frequency up to mid-altitude) and fine-tuned by aspect (higher altitude sites are occupied when south-facing).

Change: Conditions within the 1970 centre of distribution appear to have become less favourable, while those within the foreland appear a little less restrictive, with some colonization of relatively young terrain at high-altitude. Expansion in this area has not, however, compensated for the decreasing frequency on older ground. The changes are patchy, with areas in which the population is maintained against a background of declining performance, suggesting that there is an important contribution from microscale influences. If a range shift is occurring, it is as yet poorly developed.

Betula nana (Figure 4.6: 1970-9707; 2000-10080)

Distribution: This is primarily influenced by terrain age as the species occurs with maximum abundance on the oldest sites, at low to mid-altitude. Frequency decreases at higher elevation and on younger terrain within the foreland, with evidence of a gap on north-facing, mid-altitude sites.

Changes: Increases and particularly colonization on younger, higher ground (especially on the south-facing part of the foreland) has more than compensated for the poorer performance on relatively old, low-altitude sites. A range shift may be underway, with the change in pattern suggesting an easing of the age and altitude limitations.

Betula pubescens* ssp *carpatica (Figure 4.7: 1970-34; 2000-65)

Distribution: This species is scattered and occurs at low frequency, covering a wide range of site ages (from 19 years to the regional vegetation). It is predominantly at low-altitude on north-facing land, but occurs up to mid-altitude on south-facing land.

Change: While still found mainly at low-altitude, decreases have occurred on north-facing land but increases where this faces south. The age of occupied sites has become more restricted, with losses from the oldest land and a failure to colonize younger sites. Frequency has increased

Table 4.5: Frequency of distribution types within functional groups

Distribution Type	Species with this distribution in each functional group			
	Shrubs	Pioneers	Grasses	Forbs
1. Continuous distribution on old/off-foreland sites often with a south facing asymmetry, moderate frequency on younger sites in the foreland and may be at higher altitude within the foreland compared to outside	*Salix glauca* ↑ *Salix lanata* ↓		*Festuca* spp ↓	
2. Continuous distribution on old/off-foreland sites often with a south facing asymmetry, lower frequency on younger sites and often at lower altitude within the foreland	*Arctostaphylos* spp ↓ *Betula nana* ↑ *Empetrum hermaphroditum* ↑ *Loiseleuria procumbens* ↑ *Phyllodoce caerulea* ↓ *Vaccinium myrtillus* ↑ *V. uliglossum* ↑ *V. vitis-idaea* ↓		*Carex* spp ↑ *Juncus trifidus* ↓	*Bartsia alpina* ↓ *Pedicularis lapponica* ↑ *Pyrola* spp ↑ *Solidago virgaurea* ↑
3. In 2 groups on old, flanking sites at mid altitude with a south facing asymmetry	*Cassiope hypnoides* ↓ *Salix herbacea* ↑		*Anthoxanthum odoratum* ↑ *Huperzia selago* ↑ *Luzula arcuata* ↓	*Antennaria alpina* ↓ *Gnaphalium supinum* ↓ *Hieracium alpinum* ↓ *Leontodon autumnalis* ↓ *Polygonum viviparum* ↓ *Sibbaldia procumbens* ↓ *Veronica alpina* ↑
4. Low altitude, old and off-foreland sites	*Juniperus communis* ↑		*Deschampsia cespitosa* ↑	*Tofieldia pusilla* ↓
5. On foreland sites below a diagonal from low altitude north facing to mid altitude south facing sites				*Pinguicula vulgaris* ↓
6. A diagonal crossing the foreland at mid altitude, higher on north facing sites	*Salix myrsinites* ↑ *Salix phylicifolia* ↑			
7. As 6 but higher on south facing sites			*Luzula spicata* ↓ *Phleum alpinum* ↑	
8. Central sites covering a wide age range	*Betula pubescens* ssp *carpatica* ↑			
9. Central sites, young and at high altitude		*Cerastium alpinum* ↓ *Saxifraga cespitosa* ↓		*Saxifraga stellaris* ↓
10. As 9 but with a second group on the north facing flank at mid altitude		*Cerastium cerastoides* ↑ *Deschampsia cespitosa* ssp *alpina* ↓ *Oxyria dygnia* ↑ *Poa* spp ↓ *Saxifraga oppositifolia* ↓ *Trisetum spicatum* ↓		*Cardamine bellidifolia* ↓ *Cardaminopsis petraea* ↓
11. As 9 but with a south facing asymmetry at high altitude		*Arabis alpina* ↓		
12. As 9 but on north and south facing sites at mid altitude		*Arenaria* spp ↑		
13. On the north facing flank at mid-high altitude		*Ranunculus glacialis* ↓		

Note:
The direction of the overall population change is indicated by the arrow following the species name.

Table 4.6: Summary of change types within functional groups

Type of Change	Species undergoing this type of change in each functional group			
	Shrubs	Pioneers	Grasses	Forbs
1. Decreasing on old ground, largely at low altitude; increasing on higher ground and on younger sites within the foreland; population is declining	*Arctostaphylos* spp ↓ *Vaccinium vitis-idaea* ↓			
2. Decreases may occur on old ground at low altitude; substantial increases within the foreland on younger and higher ground; population is increasing	*Betula nana* ↑ *Empetrum hermaphroditum* ↑ *Salix glauca* ↑ *S. herbacea* ↑ *V. myrtillus* ↑ *V. uliginosum* ↑		*Carex* spp. ↑ *Huperzia selago* ↑	*Solidago virgaurea* ↑
3. Decreases on both flanks; increases on central, higher sites	*Cassiope hypnoides* ↓ *Loiseleuria procumbens* ↑ *Phyllodoce caerulea* ↓			*Antennaria alpina* ↓ *Gnaphalium supinum* ↓ *Hieracium alpinum* ↓ *Pinguicula vulgaris* ↓ *Polygonum viviparum* ↓ *Pyrola* spp. ↑
4. Increases on both flanks at mid altitude	*Juniperus communis* ↑			
5. Decline on the north facing flank; negligible increases	*S. lanata* ↓		*Festuca* spp.↓ *Luzula arcuata* ↓ *L. spicata* ↓	
6. As 5 but increases centrally and on south facing sites			*Anthoxanthum odoratum* ↑	*Bartsia alpinum* ↓ *Veronica alpina* ↑
7. Decline on south facing sites, but may increase at low altitude and on north facing land			*Deschampsia cespitosa* ↑	*Sibbaldia procumbens* ↓ *Pedicularis lapponica* ↑
8. Decreases at low altitude on north facing, off-foreland sites			*Eriophorum angustifolium* ↓	
9. Decrease at low altitude within the foreland; minor increases on both flanks			*Juncus trifidus* ↓	*Leontodon autumnalis* ↓ *Tofieldia pusilla* ↓
10. A widening diagonal band at higher altitude on north facing sites	*B. pubescens* ssp. *carpatica* ↑ *S. myrsinites* ↑ *S. phylicifolia* ↑			
11. Colonizing on newly exposed land; decreases centrally and on north facing land; population declining		*Arabis alpina* ↓ *Deschampsia cespitosa* ssp. *alpina* ↓ *Poa* spp. ↓ *Saxifraga cespitosa* ↓ *Saxifraga oppositifolia* ↓		*Cardamine bellidifolia* ↓ *Cardaminopsis petraea* ↓
12. Substantial increases and colonization on young land and on the north facing flank		*Ranunculus glacialis* ↓ *Trisetum spicatum* ↓ *Arenaria* spp. ↑ *Cerastium cerastoides* ↑ *Oxyria dygnia* ↑		
13. Colonization on newly exposed land and on older ground; decreases on central sites		*Cerastium alpinum* ↓	*Phleum alpinum* ↑	*Saxifraga stellaris* ↓

but the species now occurs in clusters, suggesting a consolidation on favourable habitat, where it appears less ephemeral.

Cassiope hypnoides (Figure 4.8: 1970-6741; 2000-3829)

Distribution: This species is strongly influenced by age, occurring on older sites but rarely outside the foreland. It is found predominantly at mid-altitude, restricted to older and south-facing sites with increasing elevation. This suggests a physiological limitation that may be compensated on older land or by favourable aspect. This low-growing subshrub may be at a disadvantage in the competitive environment outside the foreland and at low-altitude.

Changes: There has been a comprehensive decline indicating that conditions are generally less favourable. Some younger, central sites have been colonized but only at mid-altitude and not compensating for decreases elsewhere.

Empetrum hermaphroditum (Figure 4.9: 1970-23449; 2000-28929 (28950))

Distribution: This occurs predominantly on off-foreland and older foreland sites from mid-altitude, north-facing to high-altitude, south-facing ground. Within the foreland it occurs at lower altitude on north-facing sites, so that on younger ground its distribution shows a greater altitudinal limitation than on older terrain.

Change: There is an overall increase in abundance due to higher site counts and colonization on central and north-facing sites above mid-altitude together with recently exposed land. This results in a more even distribution across the foreland boundary and the disappearance of the south-facing asymmetry at low to mid-altitude. The species has colonized young ground at high-altitude to a greater extent than would be expected from the distribution in 1970. Minor decreases occurred on older land below mid-altitude. There has been a marked expansion of the range.

Juniperus communis (Figure 4.10: 1970-359; 2000-525)

Distribution: This species occurs mainly on off-foreland and old foreland sites at low-altitude. It is scattered on younger ground up to 62 years old.

Change: Although generally increasing, this species but has been lost from several sites where it had been a minor component and does not occur on land younger than 148 years. It now occurs on both flanks but is confined to the oldest foreland sites.

Loiseleuria procumbens (Figure 4.11: 1970-1422; 2000-1524)

Distribution: The centre of distribution is on old foreland sites (220-160 years) at low-altitude, with a south-facing asymmetry at higher altitude. It occurs infrequently on off-foreland sites.

Changes: There is a decrease within the centre of distribution, particularly on the flanks and on south-facing sites at higher altitude. It increases centrally at low-altitude, with colonization on younger, higher land involving a south-facing asymmetry. It appears more numerous on land slightly younger than its central range in 1970. The range appears to be expanding except at low-altitude.

Phyllodoce caerulea (Figure 4.12: 1970-12217; 2000-9385)

Distribution: The centre of the distribution is on foreland sites up to about 62 years at low-altitude, spreading onto the flanks up to mid-altitude on north-facing and high-altitude on south-facing sites but occupying older ground than at low-altitude. Off-foreland sites are occupied sparsely. It occurs occasionally on younger land, but with a south-facing asymmetry.

Change: There is a marked decline, especially at low-altitude. However, the species is increasing along a central strip, which broadens at mid-altitude with some colonization on younger, higher land. Occupied sites are more clustered. The central sites where the species increases lie close to a major meltwater stream. Additionally, increases occur on north-facing, foreland sites where other shrub species decline (see discussion of *Salix lanata*). This species decreases on both low-altitude and old flanking sites, where populations of some dominant shrubs are increasing (see discussion of *S. glauca*). This suggests a species that does not compete strongly unless on optimal sites, but is able to occupy suboptimal sites when competition is reduced. Whatever has caused the depletion of the *S. lanata* population on the north-facing flank does not have a similar effect on this species.

There has been a contraction onto optimal, moist sites, suggesting a relative decline in performance, with the species failing to occupy sites as young as those in 1970.

Salix glauca (Figure 4.13: 1970-9651; 2000-14497 (14588)

Distribution: This is a widespread species. Frequency falls with reducing age and increasing altitude, with flanking sites at mid-altitude having a south-facing asymmetry. Off-foreland sites are occupied with decreasing frequency above low-altitude and rarely at high-altitude.

Change: This species has increased throughout its range but particularly on younger ground, at mid-altitude and, notably, on off-foreland sites. Small decreases are interspersed across the foreland, becoming less frequent as sites become younger. Colonization occurs on young, high-altitude sites with a south-facing asymmetry. Performance has improved, although high-altitude remains limiting.

Salix herbacea (Figure 4.14: 1970-22874; 2000-29121 (29278))

Distribution: The centre of the distribution is on the old ground of both flanks, but with a greater altitudinal range where north-facing. There is no evidence of a discontinuity at the 1750 moraine.

Change: This is dominated by increases on mid-altitude, north-facing sites within the foreland and on younger land at high-altitude. Its performance has improved particularly on sites on the north flank. Despite making no major inroad at low-altitude (possibly hampered by its low stature), it increases on and colonizes some sites there.

Salix lanata (Figure 4.15: 1970-5133; 2000-3227)

Distribution: The centre of the distribution is on older foreland sites but it occurs with moderate frequency up to 34 years. There is a south-facing asymmetry in the distribution.

Change: There has been an extensive decline on sites at low and mid-altitude. This is particularly severe on the north-facing flank, so that by 2000 the south-facing asymmetry extends to low-altitude. The remains of shrubs were found on and adjacent to many of these sites (personal observation). While there may have been some confusion with *S. glauca* (particularly due to hybridization), which may contribute to an apparent decline, there is evidence of extensive mortality affecting a shrub species in this area. These *Salix* spp. comprise the majority of the shrubs on the north-facing flank. Declines are seen amongst other species there, including both *Luzula* species, while increases occur amongst *Carex* spp. and *S. herbacea*, together with the pioneers *Cerastium cerastoides* and *Oxyria digyna.* The species does increase on a few sites at low-altitude but these are scattered and small. It occurs with increasing frequency on younger ground, but has failed to colonize newly exposed land, that had been colonized in 1970.

Salix myrsinites (Figure 4.16: 1970-158; 2000-247)

Distribution: An unusual distribution involving an uneven diagonal band across the foreland at mid-altitude, higher on north-facing ground than south-facing. It mainly lies within the 160-year isochrone, but with outliers on young (3-16) and old (160-220) ground.

Change: The band is wider but still evident. Change generally involves loss from 1970 sites and colonization of those nearby, although decreases and increases do occur. Newly occupied sites are both higher and lower, but the outliers in 1970 have been lost so that the distribution is entirely within the 190-year isochrone. The range of sites occupied has increased suggesting a modestly improved performance.

Salix phylicifolia (Figure 4.17: 1970-383; 2000-2406 (2416))

(Note: This is another Salix spp. that may have been misidentified, although leaf colour and thickness contrast with those mentioned above and no hybrids were observed. Additionally, many of the specimens found in 2000 were young.) (See Whittaker (1993) and section 3.1.5 for a further discussion.)

Distribution: A largely central distribution, although similar to that of *S. myrsinites* in 2000, with sites largely confined within the 160-year isochrone and at higher altitude on north-facing ground compared to south-facing.

Change: Widespread colonization has occurred below low-altitude, north-facing to high-altitude south-facing sites although the distribution is clustered within this area. Sites occupied in 1970 might be acting as nucleii as they are surrounded by colonized sites in 2000. Frequency is lower on north-facing ground and the 1970 sites there tend to be lost by 2000. It is still rare at high-altitude, particularly on the highest flanking sites and occurrences are infrequent on north-facing sites down to low-altitude (a similar pattern to *S. lanata* possibly resulting from local conditions). Off-foreland sites have now been colonized, but only at low-altitude. Younger ground is occupied with increasing frequency compared to 1970.

There is an improvement in performance but the south-facing asymmetry has become more pronounced due to the failure of extensive colonization on north-facing sites.

Vaccinium myrtillus (Figure 4.18: 1970-3204; 2000-4745)

Distribution: This is centred on off-foreland and old sites mainly at low-altitude. Small occurrences are scattered over younger ground, becoming increasingly rare with falling age. Above mid-altitude, there is a south-facing asymmetry.

Change: This species has increased throughout its range, but particularly on north-facing sites at low-altitude. Frequency has increased on foreland sites and younger, particularly central sites are colonized. Although it has not moved onto newly exposed sites, it is more numerous on young ground than in 1970. Decreases are infrequent and occur mainly at low-altitude. There is an improved performance throughout the range but only a modest expansion.

Vaccinium uliginossum (Figure 4.19: 1970-4969; 2000-6632)

Distribution: The distribution is continuous on old and off-foreland sites, from low-altitude where north-facing, to high-altitude where south-facing. Frequency is lower within the foreland and decreases with increasing altitude and falling age.

Change: This species increases throughout its range, although interspersed with decreases at low-altitude, particularly on off-foreland sites. By 2000, frequency has risen within the foreland, but retaining the 1970 pattern, suggesting an improvement in performance without an expansion in range.

Vaccinium vitis-idaea (Figure 4.20: 1970-4196; 2000-3138)

Distribution: The centre of this distribution is outside the foreland from mid-altitude, north-facing to mid-altitude on south-facing sites. It occurs almost exclusively on off-foreland sites.

Change: This species decreases on almost every off-foreland site although this remains the centre of the distribution, with exceptions only at extremely low-altitude. This contrasts sharply with the increase in frequency within the foreland (on land up to 92 years). The resulting pattern of change within the foreland resembles that of *Phyllodoce caerulea*. The decline outside the 1750 moraine suggests deteriorating conditions within the centre of the range.

4.4.3 Summary of section 4.4.2

(1) Of the shrub species, 11 increase while five decrease in total frequency. Eight of those that increase are deciduous and this group is dominated by various *Salix* spp. Four of those that decrease are evergreen.

(2) A few species increase throughout their range, including on old, low-altitude sites (*Empetrum hermaphroditum* and *Salix glauca).*

(3) Some species increase on younger and higher ground, while decreasing on low-altitude, old sites that were previously central to the distribution (*Betula nana*, *Loiseleuria procumbens*, *Vaccinium myrtillus*, *V. uliginosum* and *V. vitis-idaea).* This pattern suggests an improving performance but not in relation to other species on the old sites.

(4) Decreasing frequency throughout the range indicates a weakening performance that appears to result from a macroscale change that affects the whole site.

(5) The patterns of change amongst the three *Vaccinium* spp. suggests that performance on foreland sites is critical to the extent of their overall expansion or contraction. *V. vitis-idaea* is largely confined to off-foreland sites, *V. myrtillus* has a moderate abundance on younger sites but *V. uliglossum* has a major component of its population on foreland sites.

(6) Species that increase overall tend to have a higher abundance on younger foreland sites than would be expected from a successional progression from 1970 (*Salix myrsinites* and *S. phylicifolia).*

(7) Species declining are strongly age limited but have typically fared poorly on old sites, while any occupation of foreland sites has been modest (*Arctostaphylos* spp. and *Cassiope hypnoides).*

4.4.4 Pioneer distributions

All 11 pioneer species have been included as counts amount to several hundred and all have shown significant changes in their distributions between the surveys. Generally the sites forming the centres of distribution in 1970 have aged and developed beyond the pioneer stage by 2000. The retreat of the glacier has slowed, particularly during the 1980s and 1990s, as it withdrew onto ground at higher altitude. Since ca.1984, retreat has occurred mainly on the north side exposing land that has a southerly aspect. Although sites have been surveyed on this more recently exposed land at a similar density to those on older ground, there are fewer of them as the area is smaller compared to such land in 1970. This needs to be taken into account when assessing any declines in pioneer populations.

Arabis alpina (Figure 4.21: 1970-355; 2000-44 (85))

Distribution: This species occupies central and south-facing sites on young ground at high-altitude, but occurs rarely and at low frequency on north-facing sites. Frequency increases with decreasing age.

Change: There is an extensive decline within the centre of the distribution. This species has moved onto newly exposed land in line with its position in 1970, but is less frequent there, with both the reduction in sampling area and the increased altitude of newly exposed land possibly contributing to this. Persistence on sites occupied in 1970 and rare colonization on older sites at low-altitude may indicate disturbance-created openings. It appears that decreasing opportunity may underlie this decline in frequency.

***Arenaria* spp.** (Figure 4.22: 1970-374; 2000-650 (957))

Distribution: These species are mainly found centrally on higher ground, largely on sites aged

19-34 years, rarely on younger land. They occur with moderate frequency on flank sites at mid-altitude.

Change: This is marked by colonization of younger sites at high-altitude with increased frequency compared to 1970. Although the distribution remains mainly central, flank sites are occupied throughout the mid-altitude range and occasionally at lower altitude. There has been an improvement in performance resulting in a population increase and a range expansion. Frequency on new sites is greater and the decline on central sites is lower than expected from the 1970 distribution.

Cerastium alpinum (Figure 4.23: 1970-343; 2000-243 (274))

Distribution: The species occurs on central sites at mid-altitude in the age range 19-62 years, rarely on younger or north-facing sites. It is not found on south-facing land.

Change: There has been a decrease in the centre of the 1970 range, but increases and colonization on both higher and lower sites. By 2000 the distribution has spread to high-altitude, newly exposed sites and those aged up to 148 years where these are central. Frequency at sites has fallen and the distribution has become diffuse. At lower altitude, there is a north-facing asymmetry, not seen at higher elevation. Low numbers make any range expansion difficult to detect.

Cerastium cerastoides (Figure 4.24: 1970-1712; 2000-1314 (1836))

Distribution: This species has a diagonal distribution from high-altitude, south-facing sites, switching to central sites at mid-altitude and onto north-facing ground at lower altitude.

Change: Reductions have occurred at the centre of the 1970 range, but increases on both younger, higher altitude sites and at mid-altitude on the north-facing flank. The latter corresponds to the area where *Salix lanata* declines. There is no longer a pronounced south-facing asymmetry at high-altitude. As a result of losses from central sites, the population is split between north-facing, mid-altitude sites and those on younger ground at high-altitude. Conditions on the north-facing flank have apparently improved for this species, coincident with loss of shrub dominants.

Deschampsia cespitosa* ssp. *alpina (Figure 4.25: 1970-1750; 2000-139 (995))

Distribution: This is centred on ground aged 19-34 years, at mid-altitude with a north-facing asymmetry and a separate, subsidiary distribution on older, north-facing sites.

Change: Performance has declined. There has been a contraction of the area occupied with a decline on north-facing sites, particularly at mid-altitude. A residual population remains on central sites and there has been some colonization on newly exposed land. On occupied sites, frequencies are generally lower than in 1970.

Oxyria digyna (Figure 4.26: 1970-2463; 2000-3404 (3816))

Distribution: This species mainly occurs on the north-facing flank from mid to high-altitude, with a subsidiary population on more central sites younger than 62 years, with a few large occurrences on the south-facing flank.

Change: There have been decreases on older, central sites, similar to the situation for *Cerastium cerastoides*. There has been an expansion onto mid-altitude sites on the north-facing flank, previously dominated by *Salix lanata*. This species is both colonizing and increasing on the youngest central sites. There has been an improvement in performance, suggesting that the range is expanding.

Poa spp. (Figure 4.27: 1970-4423; 2000-2457 (3136))

Distribution: This occurs on young, central sites from mid to high-altitude, on older ground on the north-facing flank where it extends to lower altitude and at low frequency on old, south-facing sites. It covers a wide range of site ages from off-foreland to newly exposed ground.

Change: There has been an extensive decline throughout the range. By 2000, the area of high frequency occupation is limited to central sites younger than 49 years with increases and colonization occurring only in this area.

Ranunculus glacialis (Figure 4.28: 1970-961; 2000-931)

Distribution: This mainly occupies flank sites from mid to high-altitude but is more numerous on north-facing land. Ground occupied is older than 62 years, but only occasionally outside the foreland and rarely on south-facing sites.

Change: Decreases and increases are interspersed on the north-facing flank. Colonization has occurred at high-altitude on north-facing sites, across the centre of the foreland and on south-facing sites at mid-altitude. Previously limited largely to the highest altitude sites on the north-facing side of the foreland, the colonization of younger sites at slightly lower altitude is as yet only modest, but indicates the possibility of a range shift or expansion.

Saxifraga cespitosa (Figure 4.29: 1970-809; 2000-67 (277))

Distribution: Occupied sites are central and younger than 34 years, with the highest frequency around 19 years.

Change: This predominantly involves decreases, resulting in almost complete absence from its 1970 distribution by 2000. The population shifts with exposure of new land rather than having any permanent population-base within the foreland. Newly exposed sites show a high level of colonization, and the fall in numbers may be largely attributable to the reduction in area of such land.

Saxifraga oppositifolia (Figure 4.30: 1970-259; 2000-191 (241))

Distribution: This species is mainly found on central, young (3-34 years) sites at mid-altitude, with a north-facing asymmetry. Frequency declines with increasing age.

Change: This species has decreased on central sites, largely in line with ageing, and at low-altitude. There has been significant colonization of young and newly exposed sites maintaining a similar population size to 1970 within a smaller area. The north-facing asymmetry has disappeared. There is an improved performance within the constricted range.

Trisetum spicatum (Figure 4.31: 1970-2062; 2000-1808 (1894))

Distribution: It is found on central sites aged 3-34 years at mid to high-altitude, frequency decreasing with increasing age. There is a subsidiary group on older, north-facing sites from low to mid-altitude and a scattering on south-facing, mid to high-altitude sites.

Change: Decreases affect central sites and the species is virtually absent at low-altitude by 2000. The north-facing, mid-altitude group is more distinct due to the reduced occupation of central sites and the colonization of additional older land. Young, high-altitude sites have been sparsely colonized. Older sites (32-49 years) now form the centre of the distribution. The absence from high-altitude, flanking sites and low frequency on newly exposed land suggests that this species may be approaching its tolerance limit.

4.4.5 Summary of section 4.4.4

(1) Eight pioneer species have decreased while only three have increased. All those increasing have a strong and consistent presence on the north-facing flank.

(2) Site age is of importance for most of these species, but the extent of this varies. Where it is the primary influence, the species only occurs on very young sites (*Arabis alpina*, *Saxifraga cespitosa* and *S. oppositifolia*).

(3) An altitudinal constraint is suggested by presence of the species on both young and older sites when these are north-facing (*Arenaria* spp., *Cerastium cerastoides* and *Oxyria digyna*).

(4) The north-facing flank and young, central sites appear to be equivalent for several species, but other species occur preferentially on one site type, e.g *Ranunculus glacialis*, which occurs almost exclusively on north-facing sites in 1970. Several species show differential changes between site types (*Deschampsia cespitosa* ssp. *alpina* and *Poa* spp.).

(5) Species with age as a primary constraint appear to have been affected by the reduction in available land as the glacier retreat has slowed in recent years.

(6) Some species may be reaching the limit of their tolerance of site severity (*Arabis alpina*, *Deschampsia cespitosa* ssp. *alpina* and *Trisetum spicatum*), while others have increased on newly exposed land in comparison with 1970, indicating either a higher tolerance of conditions or an improved performance (*Arenaria* spp. and *Oxyria digyna*).

(7) A spatial separation of populations is occurring as a result of losses from central, moderately young sites. Several pioneer populations have increased on sites on the north-facing flank (cf. section 4.4.2).

4.4.6 Distribution of grasses and related species (excluding pioneers)

10 of the 22 species are considered in detail. Most of the grasses show overall increases or

decreases of less than 10%, a pattern followed by the sedges (treated as a single group as in the 1970 survey), but not by cotton grasses (*Eriophorum* spp.), rushes or woodrushes. Club mosses also decline or increase marginally. Several ferns occur on the foreland, but numbers are very low and none are included here.

Anthoxanthum odoratum (Figure 4.32: 1970-1522; 2000-1718 (1720))

Distribution: There are two foci: on south-facing land at mid-altitude and at low-altitude on north-facing sites. Occupied sites are generally old (exceeding 118 years) including those outside the foreland.

Change: The south-facing group has expanded onto higher and lower ground, together with younger foreland sites. The range of the north-facing group has contracted with decreases above low-altitude, although frequency has increased on the lowest sites.

Decreases on the north-facing flank coincide with the area of *S. lanata* decline and may result from local conditions. Increased frequency and expansion in range elsewhere suggests that generally performance has improved.

***Carex* spp.** (Figure 4.33: 1970-9279; 2000-10389 (10401))

Distribution: These species mainly occur outside the foreland in a continuous distribution from mid-altitude, north-facing to high-altitude, south-facing sites. Frequency within the foreland is moderate compared to that outside and decreases with site age.

Change: These species are declining on many off-foreland and older flank sites, particularly where these are north-facing and on sites distant from the moraine. Within the foreland, there are increases above low-altitude and a markedly higher frequency by 2000, particularly on younger ground adjacent to the north-facing flank at mid-altitude. These species show a well-developed range shift; declining on older and lower land, accompanied by an increasing population on younger and higher ground. They require high moisture levels, and changing availability may underlie this shift.

Deschampsia cespitosa (Figure 4.34: 1970-281; 2000-413)

Distribution: This species occurs mainly on low-altitude, central sites and at mid-altitude on south-facing ground. It is found sparsely on older land, but rarely on off-foreland sites.

Change: The distribution is largely confined to low-altitude sites with a north-facing asymmetry by 2000. The distribution shows a shift towards older land with the inclusion of several off-foreland sites and the loss of some younger sites. There is a contraction in altitudinal range by 2000, and a shift to north- rather than south-facing sites.

Festuca* spp. *(F. ovina, F. vivipara) (Figure 4.36: 1970-6314; 2000-5770 (5803))

Distribution: These species occur on two site types: off-foreland sites with decreasing frequency up to high-altitude; and within the foreland above a diagonal from low-altitude on north-facing sites to mid-altitude where south-facing.

Change: The population on old land is persistent, except on the highest north-facing flank sites. That on younger land shows a marked decline at mid-altitude, particularly where sites are north-facing. There are however, increases at both higher altitude, including the youngest sites, and at low-altitude.

It appears that at least two species are present in this composite group, one a pioneer, the other a late successional species. The decline at mid-altitude therefore involves migration onto younger sites with decreases on both flanks, particularly that facing north (including sites where *Salix lanata* declined). The minor decrease in total frequency therefore combines decreases due to the reduction of space available for pioneers with a range contraction from mid-altitude sites. The increases at low and high-altitude provide only a partial compensation.

Juncus trifidus (Figure 4.37: 1970-1581; 2000-1082)

Distribution: This species occurs predominantly below a diagonal from low-altitude north-facing to high-altitude south-facing sites with a scattering on the north-facing flank at mid-altitude.

Change: This species shows a wide-ranging decline at low-altitude, although there are minor increases on the flanks at mid-altitude and on young, central sites. While the extent of the distribution shows no marked change, frequency has declined by a third, so that it appears that a range contraction may be underway. There is no compensatory shift in distribution.

Luzula arcuata (Figure 4.38: 1970-1632; 2000-714)

Distribution: This occurs mainly on old sites on both flanks and occasionally on newly exposed land. The range is greater on north-facing sites, extending from mid to high-altitude, but is limited to high-altitude sites on the south-facing flank.

Change: There is a marked decline on both flanks, although more extensive on north-facing sites, leaving a diffuse distribution by 2000. Increases occur on the youngest sites occupied in 1970 but it has not colonized land exposed since then. This species is in decline on the flanks, but is increasing on central sites and may be undergoing a range shift.

Luzula spicata (Figure 4.39: 1970-1306; 2000-725 (749))

Distribution: This species occurs in a continuous band across the foreland from mid-altitude, north-facing to high-altitude on south-facing sites, but is rare outside the foreland.

Change: The most marked feature is the reduction on both flanks, especially where north-facing, although it increases in frequency on central sites. By 2000, occurrences are scattered on the older sites of the flanks, the highest frequency being on younger ground with a south-facing asymmetry.

Both *Luzula* species declined on the north-facing flank, while *Carex* spp. increased, suggesting that these species may have been misidentified in one or other survey. However, *Luzula* spp. were classed as an intermediate snowbed species by Matthews (1976), while *Carex* spp. typically occupy boggy sites with low pH (Fitter et al., 1984). These changes may therefore indicate changes in the duration of snowlie.

Huperzia selago (Figure 4.40: 1970-240; 2000-257)

Distribution: Predominantly on old land (off-foreland to 160 years) from mid-altitude on the north flank, and scattered at low-altitude with a subsidiary population at mid-altitude on the south-facing flank.

Change: Frequency declines on old sites throughout the range with a shift onto younger, adjacent ground.

Phleum alpinum (Figure 4.41: 1970-743; 2000-927 (953))

Distribution: This runs diagonally from mid-altitude, north-facing to high-altitude, south-facing sites. Frequency is highest on south-facing land and the species is rare on off-foreland sites.

Change: The distribution has broadened at either extreme of the diagonal, particularly on older land. Frequency decreases on central sites suggesting a trend towards the separation of two groups. The range has expanded on older land compared to 1970.

4.4.7 Summary of section 4.4.6

(1) Five species increase in frequency (including all but one, *Festuca* spp., of the grasses), while five decrease (predominantly rushes and woodrushes).

(2) Site age is again a dominant influence, with many of these species having distributions centred on the oldest land, either continuously following the outer moraine or in two groups on the flanks, frequently showing a south-facing asymmetry i.e. occurring at higher altitude on south- compared to north-facing sites.

(3) Species undergoing major declines decrease on the north-facing flank (*Luzula* spp.) or at low-altitude (*Juncus trifidus*), which may result from a spatially specific deterioration in conditions. Increases elsewhere are inadequate to compensate for the reductions.

(4) Where populations have increased, a decrease frequently occurs over part of the range, but younger land has been extensively colonized (*Anthoxanthum odoratum*, *Carex* spp., *Deschampsia cespitosa*, *Huperzia selago* and *Phleum alpinum*).

4.4.8 Distribution of forbs (excluding pioneers)

This is the most numerous category with 53 species, but many occur at low frequency. 14 species occupy only low-altitude sites outside the foreland, have low frequency and little change in distribution since 1970. Several rare species appear or disappear since 1970. Excluding the above, 16 species have been selected with several hundred counts, although rarely exceeding a thousand. They are therefore moderately frequent species, many of which have declined (section 4.2).

Antennaria alpina (Figure 4.42: 1970-521; 2000-227).

Distribution: Old sites are occupied at mid to high-altitude on the south-facing flank and on north-facing land from low to mid-altitude.

Change: Frequency decreases on the north-facing flank and the lower sites of the south-facing group. Persistence is greater on south-facing land where frequency increases on younger, more central sites. Performance is deteriorating within the previous distributional range but minor increases on younger, central sites suggest a range shift, although this is poorly developed.

Bartsia alpina (Figure 4.43: 1970-2435; 2000-2261 (2262)

Distribution: This species occurs mainly on older, low-altitude land and at mid-altitude with a south-facing asymmetry. It is infrequent outside the 1750 moraine.

Change: A minor reduction in frequency occurs at low-altitude particularly on north-facing land, but the species increases at higher altitude on younger, south-facing sites. The distribution pattern is comparatively stable although conditions appear to be deteriorating at low-altitude. A progressive shift may be underway onto higher land with a southerly aspect.

Cardamine bellidifolia (Figure 4.44: 1970-482; 2000-306 (316)

Distribution: This occurs at mid-altitude on north-facing sites, continuing to higher altitude with a south-facing asymmetry. It is infrequent at low-altitude.

Change: This species has declined throughout its range, disappearing from all but one low-altitude site. There is a fall in frequency on newly exposed land compared to 1970, reflecting the decrease in available area and/or the increase in severity. While performance has declined, the range contraction is as yet only modest.

Cardaminopsis petraea (Figure 4.45: 1970-537; 2000-181 (228))

Distribution: This species occurs mainly on the youngest central sites, falling in frequency as age increases, but occupying older north-facing sites at lower altitude.

Change: Decreases occur on both the north-facing flank and the youngest sites occupied in 1970, although by 2000 several newly exposed sites have been colonized. These changes together with persistence on some of the more central, north-facing sites, have resulted in a bimodal distribution similar to that seen for several pioneers. Performance has declined with a moderate contraction on the north-facing flank.

Gnaphalium supinum (Figure 4.46: 1970-1100; 2000-1032 (1068))

Distribution: This species occurs on the north-facing flank from mid to low-altitude and on south-facing sites at mid to high-altitude, off-foreland and the oldest foreland sites with no obvious discontinuity.

Change: There is a decrease in frequency on off-foreland sites and at low-altitude, accompanied by increases on young land within the foreland, most notably on south-facing sites at high-altitude. There appears to be a range shift taking place from older to younger land, with increases compensating for the decreases.

Hieracium alpinum (Figure 4.47: 1970-980; 2000-704)

Distribution: This distribution again involves two groups on older land, at mid to low-altitude where this is north-facing, and at higher altitude on the south-facing flank. This species occurs with low frequency at low-altitude.

Change: By 2000 there has been an extensive decline in both groups, but particularly on north-facing sites and older terrain. Frequency increases within the foreland, where it occurred rarely in 1970, but with a south-facing asymmetry on the youngest land. The change in the relative frequency on old and young land suggests that a range shift is in progress.

Leontodon autumnalis (Figure 4.48: 1970-1011; 2000-806)

Distribution: This species again shows a distribution split between lower altitude, north-facing sites and those at higher altitude on south-facing land, both occupying old and off-foreland sites. It occurs occasionally at low-altitude and rarely on south-facing, young sites.

Change: There is a mixed pattern of increases and decreases affecting sites on both flanks but leaving both relatively intact, although frequency on off-foreland sites is lower than in 1970. The range is similar but performance is poor, particularly on off-foreland sites, with no compensatory shift onto younger land.

Pedicularis lapponica (Figure 4.49: 1970-787; 2000-1117)

Distribution: The distribution is continuous on off-foreland and old sites at low-altitude, with a scattering up to high-altitude on the south-facing flank. This species occurs rarely on younger land.

Change: Increases and decreases are balanced on flank sites, except at high-altitude on south-facing land where frequency falls. However, there is a marked increase in frequency on old central sites at low-altitude, irrespective of the foreland boundary.

Pinguicula vulgaris (Figure 4.50: 1970-1225; 2000-1150)

Distribution: This species occurs below a diagonal from low-altitude, north-facing sites to mid-altitude on the south-facing flank. It is most frequent within the foreland, and is scattered on off-foreland sites at low-altitude.

Change: The species decreases at low-altitude but increases on younger sites at mid-altitude with a south-facing asymmetry.

Polygonum viviparum (Figure 4.51: 1970-5321; 2000-3574 (3575))

Distribution: There are two groups on flank sites: at low to mid-altitude where these are north-facing and from low to high-altitude where south-facing. It occurs infrequently on central sites at low-altitude and rarely on land younger than 118 years.

Change: At low-altitude there is a relatively equal mix of increases and decreases, but above mid-altitude decreases predominate on both flanks. Despite this, the overall pattern persists. There are minor increases on younger sites, but frequency on land of this age has fallen compared to 1970. With relatively large decreases outside the foreland boundary, the highest frequencies now occur on the oldest foreland sites. It appears that performance is declining, but as yet there has been no major range contraction.

***Pyrola* spp.** (Figure 4.52: 1970-114; 2000-536)

Distribution: These species occur on old sites at low-altitude and up to mid-altitude with a south-facing asymmetry. The majority of sites are within the foreland.

Change: Increases in frequency predominate, with a more substantial population on younger, higher altitude land and the disappearance of the south-facing asymmetry compared to 1970. A series of bands of occupied sites may indicate the different distributions within this composite grouping. There appears to be a general improvement in performance, with the increasing range of site types occupied suggesting a moderately developed range expansion.

Saxifraga stellaris (Figure 4.53: 1970-724; 2000-635 (706))

Distribution: The focus of the distribution is on moderately young sites (19-34 years), suggesting that this may be a late pioneer species.

Change: This species declines within the previous centre of the distribution, increasing on younger ground but also colonizing lower sites on the north-facing flank. The occupation of younger sites and the scattered increase on north-facing land resemble the distributions of some pioneer species, although with greater persistence on ageing land. Although total frequency is similar, there is a change from the occupation of a few sites at high frequency to a wider distribution at lower frequency. The range appears to be expanding, possibly indicating changing conditions as this species preferentially occurs on wet sites.

Sibbaldia procumbens (Figure 4.54: 1970-785; 2000-651 (654))

Distribution: This species occurs in two areas: on north-facing sites at low to mid-altitude and, predominantly, on south-facing land from mid to high-altitude. The sites are old and mainly outside the foreland.

Change: Frequency on south-facing sites decreases, although this remains the larger concentration. The distribution is relatively stable with only a minor overall reduction in frequency.

Solidago virgaurea (Figure 4.55: 1970-958; 2000-967)

Distribution: This species has a continuous distribution on old, low-altitude sites, primarily outside the foreland, continuing up to mid-altitude on the south-facing flank.

Change: Frequency decreases on off-foreland sites, particularly those furthest from the 1750 moraine, balanced by increases closer to the moraine and within the foreland. By 2000, the distribution shows greater frequency on north-facing sites at low-altitude and on mid-altitude, south-facing sites. Frequency increases marginally on slightly younger land and at higher altitude, suggesting that performance is improving despite the decrease on the oldest sites.

Tofieldia pusilla (Figure 4.56: 1970-590; 2000-350)

Distribution: This species occurs on old, central sites at low-altitude and rarely on the south-facing flank at mid-altitude.

Change: There is a general decline, increases are few and small. The performance appears to be declining, with no compensatory shift in range.

Veronica alpina (Figure 4.57: 1970 987; 2000-1067 (1102))

Distribution: The distribution is centred on sites that are north-facing at low-altitude and south-facing at mid-altitude. This species occurs mainly on old foreland sites but is scattered across terrain of a wide range of ages and elevation.

Change: There is a decrease in frequency on the north-facing flank, on sites where *Salix lanata* has declined, and at low-altitude. Increases occur in the centre of the foreland and particularly on younger, south-facing sites. By 2000 a pronounced south-facing asymmetry has developed. The increases at high-altitude and on younger land suggest that the range may be expanding.

4.4.9 Summary of section 4.4.8

(1) Of the 16 species considered here, 12 decreased and only 4 increased in frequency.

(2) 75% of these forbs are associated with relatively old terrain, particularly that outside the foreland. All decrease on these old sites. Whether this results in an overall decline depends largely on the extent of any increase within the foreland.

(3) In contrast to the forbs considered here, several shrubs preferentially increase on these sites (section 4.4.2). Underlying causal factors may involve preferential grazing, a decrease in establishment opportunity and/or biotic interactions e.g. shading.

(4) Several forbs decrease overall, but increase and colonize on foreland sites that are more than thirty years younger than the youngest sites they occupied in 1970 (*Antennaria alpina*, *Bartsia alpina*, *Gnaphalium supinum* and *Hieracium alpinum*). Such differential changes suggest that there is a poorly developed compensatory shift. Other species (*Leontodon autumnalis*, *Polygonum viviparum* and *Tofieldia pusilla*) do not show any compensatory shift; and the decline seems likely to be far-reaching

(5) Species increasing have initially either a continuous distribution on old land or one where foreland sites already constitute a subsidiary component (*Pedicularis lapponica*, *Pyrola* spp. and *Veronica alpina*).

(6) Two species with pioneer-type distributions (*Cardamine bellidifolia* and *Cardaminopsis petraea*) decline, while *Saxifraga stellaris* maintains its population, apparently primarily controlled by moisture availability.

Chapter 5: Change at the assemblage level

5.1 Introduction

In the last section of Chapter 4, associations between species populations were considered as a measure of community structure, with the focus on relatively abundant species. In this chapter, the focus is on the composition found locally at a particular site, which will differ from that found in these groupings. The groups contain species with a variety of requirements, not all of which are met within any single 9m^2. There is a difference in scale from the overall distribution to a small part of the range; within the locality, differences in microtopography, stochastic factors and small-scale heterogeneity are likely to influence the specific composition and therefore the actual assemblage found. All species present are used in a site assessment, including those that are less abundant and rare. Additionally, the measure used to investigate species' associations was binary; presence/absence data contain no information about the relative frequency, which also characterises the type of assemblage.

Changes in species distributions may have a greater impact at a finer scale than shown by the association groups, which apply across the whole area. Broad-scale distribution changes are the sum of numerous local differences, which are seen at the site level by quantitative changes in species frequency. Large changes in frequency are likely to alter the relative species balance within the site, which is reflected in the pattern of dominance. In section 4.2, it was shown that most increases in species frequency exceeding 10% involved abundant and rare species, while decreases in frequency affected moderately abundant and uncommon ones. While adding weight to the conjecture that dominance patterns have changed, these changes involve totals which may not be reflected at individual sites and give no information concerning the pattern on terrain of different ages.

In section 5.2, a number of measures of diversity and equitability are used to assess the extent of changes in species richness and relative abundance, and the relationship with age structure. Section 5.3 examines changes in site composition using a TWINSPAN classification. Qualitative and quantitative differences in the groups identified in each dataset may contribute to an understanding of the changes that have taken place over the last 30 years. Finally, the groups with which individual sites are identified in each survey are compared to establish the nature of the transitions that occur and of group trajectories.

5.2 Diversity indices

This section involves an examination of the changes in diversity in both the successional sites and the regional vegetation. In the latter case, change would be expected to be minimal but the discussion of species distributions in Chapter 4 suggests that many populations are experiencing changes in frequency on the oldest land. Differences in diversity parameters might be expected to accompany such changes.

A number of measures of diversity are used as each has a particular emphasis: (1) overall richness using species number (S) and the Margalev index (D_{Mg}); (2) dominance of abundant species using the Berger-Parker index (d) together with the Simpson index, D, and (3) equitability, with the emphasis on rare species using the Shannon index (H^I and E). The various indices have been calculated for site composition in both 1970 and 2000. Using the age groups from Chapter 4, the means have been tested for significant differences using a t-test and the Wilcoxon test, both for matched pairs of samples. The age groups have been combined as the single groups contained too few samples to apply these tests. The differences in mean and standard deviation are shown in Tables 5.1-5.6 together with the results of the tests at the p = 0.05 level.

5.2.1 The Shannon index, H^I

High values of this index indicate that sites contain many rare species: increases suggest a greater contribution from less abundant and particularly rare species; decreases show a change in balance towards the more abundant species. The results discussed below are given in Table 5.1 and in Figure 5.1.

1970. The index initially increases, before decreasing in groups 5 and 6 (85-156 years) and rising again on the oldest sites. A comparison with Table 4.4 suggests that the pattern on young sites corresponds to the influx and subsequent decline of pioneer species together with increasing frequencies of early-occurring shrubs, such as *Salix* spp. and *Empetrum hermaphroditum* which persist in the intermediate successional stages. The value of the index is therefore higher in groups 5 and 6 compared to the very young sites. The increase on older sites (from ca 150 years) appears to involve invasions by later heath and snowbed species such as *Betula nana, Bartsia alpina* and the late successional grasses *Anthoxanthum odoratum* and *Phleum alpinum.* Pioneer sites have few rare species, while mature sites have a relatively large number.

2000. The pattern differs compared with that of 1970.The absence of very young sites results in the initial high mean (the influx of pioneers having already occurred). The lowest value of the index occurs on the intermediate sites of groups 5 and 6 (115-186 years in 2000), suggesting that the accumulation of later species is delayed compared to 1970. The values are lower and more consistent on older sites compared to 1970 and the mean decreases in the regional vegetation.

Changes between the surveys. The consistent pattern on foreland sites appears to reflect successional processes, as does the significant increase in the mean for groups 1 and 2 (a similar increase was seen between the pioneer sites and groups 3 and 4 in 1970). The significant decreases on older foreland sites and in the regional vegetation indicate a trend involving a loss of rare species since the 1970 survey. This reflects the changes seen in the species distributions (section 4.4) and may indicate changing conditions, perhaps involving a reduction in establishment opportunity.

5.2.2 The Shannon Equitability index, E

This index increases as the distribution of individuals amongst species becomes more even. The results are given in Table 5.2 and Figure 5.2.

Table 5.1 Changes in the Shannon Index between 1970 and 2000 on terrain of different ages

The table shows the mean and standard deviation for both 1970 and 2000 together with the results of the Wilcoxon and t-tests for differences between the two population means

Site Group	Year	Age	Mean	SD	Year	Age	Mean	SD	Wilcoxon	T-test
1 and 2	1970	0-28	**1.51**	**±0.24**	2000	30-58	**1.63**	**±0.21**	**0.002**	**0.001**
3 and 4		29-83	**1.65**	**±0.18**		59-113	**1.61**	**±0.15**	**0.024**	0.051
5 and 6		85-156	**1.62**	**±0.18**		115-186	**1.58**	**±0.23**	0.146	**0.032**
7 and 8		157-221	**1.65**	**±0.23**		187-251	**1.62**	**±0.26**	**0.008**	**0.008**
Off-Foreland		9000	**1.66**	**±0.25**		9000	**1.61**	**±0.32**	**0.004**	**0.004**
Foreland			1.62	±0.21			1.61	±0.22	0.086	0.433
All			**1.63**	**±0.22**			**1.61**	**±0.24**	**0.005**	0.051

Notes:

1. Differences in population means are significant where the test results are lower than 0.05 (ie the probability of the result occurring by chance is less than 5%). Significant test results are shown in bold, as are the means and standard deviations when at least one of the tests show a significant difference at this level.
2. The Wilcoxon and t-tests used were for matched pairs of samples.
3. The age groups used are those discussed in Chapter Four sections 4.2 and 4.3.

Table 5.2 Changes in the Shannon Equitability Index between 1970 and 2000 on terrain of different ages

The table shows the mean and standard deviation for both 1970 and 2000 together with the results of the Wilcoxon and t-tests for differences between the two population means

Site Group	Year	Age	Mean	SD	Year	Age	Mean	SD	Wilcoxon	T-test
1 and 2	1970	0-28	**0.66**	**±0.14**	2000	30-58	**0.65**	**±0.04**	**0.010**	0.476
3 and 4		29-83	0.63	±0.05		59-113	0.62	±0.08	0.207	0.278
5 and 6		85-156	**0.63**	**±0.05**		115-186	**0.62**	**±0.05**	**0.001**	**0.001**
7 and 8		157-221	**0.62**	**±0.04**		187-251	**0.62**	**±0.06**	**0.017**	0.291
Off-Foreland		9000	0.62	±0.04		9000	0.63	±0.05	0.076	0.105
Foreland			**0.64**	**±0.08**			**0.62**	**±0.06**	**0.000**	**0.014**
All			**0.63**	**±0.07**			**0.63**	**±0.06**	**0.000**	**0.046**

Notes:

1. Differences in population means are significant where the test results are lower than 0.05 (ie the probability of the result occurring by chance is less than 5%). Significant test results are shown in bold, as are the means and standard deviations when at least one of the tests show a significant difference at this level.
2. The Wilcoxon and t-tests used were for matched pairs of samples.
3. The age groups used are those discussed in Chapter Four sections 4.2 and 4.3.

1970 Distribution of individuals is comparatively equitable amongst species on pioneer sites, but this decreases with increasing age on land exceeding ca 30 years.

2000 The pattern is similar to that of 1970 in the early stages of the sequence, taking into account the effect of ageing on the youngest sites. The older foreland sites, from ca 120 years, show a greater consistency than in 1970, and the regional vegetation has a higher mean than the oldest foreland sites.

Changes between the surveys Both surveys show a decrease in the index mean with site ageing, although there are minor differences in the pattern. The mean differs significantly on the youngest sites mirroring changes from ca 30 years in 1970 (accompanying the influx of pioneers). Moderately young sites (groups 3 and 4) do not change significantly, reflecting the small increment seen in 1970 between this group and groups 5 and 6. The successional pattern appears to involve a large initial decrease in equitability as species invade young terrain, followed by relatively small subsequent decreases. However, on older foreland sites (from ca 120 years), the mean decreases significantly between 1970 and 2000, indicating a trend towards reduced equitability. Amongst the regional vegetation, the change in the index is non-significant, suggesting resistance to the underlying change despite the effect on the oldest foreland sites.

5.2.3 Species richness, S

This is a simple count of the number of species per plot. The results are presented in Table 5.3 and in Figure 5.3.

1970 The pattern involves an initial increase (from ca 30 years), followed by a further increase on older terrain. This resembles the pattern of the Shannon index in 1970 and reflects successional waves of species invasions as discussed above.

2000 The pattern is one of progressive increase in richness per plot on foreland sites with a minor down-turn in the regional vegetation. The wavelike pattern seen in 1970 is not apparent, but may be inferred from the changes with ageing seen in 1970: the first age increment being accompanied by an increase in the mean, the second by a decrease. The pattern in 2000 may therefore still reflect successional processes, except for the down-turn amongst the regional vegetation.

Changes between the surveys Significantly different means occur only amongst the pioneer sites and in the regional vegetation. The increase on young land reflects that occurring in 1970, suggesting the invasion by pioneer species and therefore involving a successional process. The decrease in the regional vegetation indicates a trend of species loss outside the foreland (section 4.4).

5.2.4 The Margalev index, D_{Mg}

This is another richness measure, but here the number of species is divided by the number of individuals at a site. The index increases with species number or a decrease in the number of individuals; conversely it decreases with a reduction in species number or an increase in the

Table 5.3 Changes in Species Richness between 1970 and 2000 on terrain of different age

The table shows the mean and standard deviation for both 1970 and 2000 together with the results of the Wilcoxon and t-tests for differences between the two population means

Site Group	Year	Age	Mean	SD	Year	Age	Mean	SD	Wilcoxon	T-Test
1 and 2	1970	0-28	**10.16**	**±4.62**	2000	30-58	**13.25**	**±4.87**	**0.000**	**0.000**
3 and 4		29-83	14.07	±3.98		59-113	13.52	±4.11	0.271	0.197
5 and 6		85-156	13.77	±4.72		115-186	14.02	±4.96	0.247	0.481
7 and 8		157-221	15.48	±5.95		187-251	15.49	±6.09	0.672	0.977
Off-Foreland		9000	**16.04**	**±6.84**		9000	**14.86**	**±7.59**	**0.000**	**0.009**
Foreland			**13.60**	**±5.20**			**14.14**	**±5.12**	**0.032**	**0.025**
All			14.10	±5.65			14.28	±5.71	0.668	0.401

Notes:

1. Differences in population means are significant where the test results are lower than 0.05 (ie the probability of the result occurring by chance is less than 5%). Significant test results are shown in bold, as are the means and standard deviations when at least one of the tests show a significant difference at this level.
2. The Wilcoxon and t-tests used were for matched pairs of samples.
3. The age groups used are those discussed in Chapter Four sections 4.2 and 4.3.

Table 5.4 Changes in the Margalev Diversity Index between 1970 and 2000 on terrain of different ages

The table shows the mean and standard deviation for both 1970 and 2000 together with the results of the Wilcoxon and t-tests for differences between the two population means

Site Group	Year	Age	Mean	SD	Year	Age	Mean	SD	Wilcoxon	T-Test
1 and 2	1970	0-28	**1.91**	**±0.78**	2000	30-58	**2.14**	**±0.81**	0.125	**0.049**
3 and 4		29-83	**2.23**	**±0.72**		59-113	**2.05**	**±0.66**	**0.026**	**0.013**
5 and 6		85-156	2.03	±0.70		115-186	2.04	±0.71	0.539	0.895
7 and 8		157-221	2.16	±0.84		187-251	2.17	±0.85	0.451	0.946
Off-Foreland		9000	**2.12**	**±0.95**		9000	**1.94**	**±1.04**	**0.001**	**0.007**
Foreland			2.10	±0.77			2.10	±0.76	0.983	0.997
All			2.10	±0.81			2.07	±0.82	0.166	0.277

Notes:

1. Differences in population means are significant where the test results are lower than 0.05 (ie the probability of the result occurring by chance is less than 5%). Significant test results are shown in bold, as are the means and standard deviations when at least one of the tests show a significant difference at this level.

number of individuals. A comparison with the preceding index, S, therefore indicates which parameter is changing. The results are presented in Table 5.4 and in Figure 5.6.

1970 Again there is a pattern of initial fluctuation, as described for species richness, but rather than a subsequent increase, the means are relatively stable on older terrain (after ca 150 years). The change on older land is therefore probably the result of the increasing numbers of individuals as sites age.

2000 The pattern amongst younger sites and the downturn in the regional vegetation resemble that of species number in 2000, indicating a close correspondence between the two indices.

Changes between the surveys There are significant differences on the younger foreland sites and within the regional vegetation. The increase on the pioneer sites reflects the 1970 pattern and the increase in species number, indicating a successional process of species invasions on young land. The decrease in groups 3 and 4 reflects the pattern in 1970 after ca 80 years, in neither case is the decrease matched by a significant decrease in species number, suggesting that the number of individuals is increasing. On older foreland sites the means have not changed significantly, suggesting relative stability. The decrease in D_{Mg} amongst the regional vegetation reflects the trend of species loss outside the foreland.

5.2.5 The Berger-Parker Dominance index, d

This index measures the proportional abundance of the single most abundant species in relation to the total number of individuals. The reciprocal is used so that an increase in the index represents an increase in diversity or a decrease in the dominance of this species. An increase in the number of individuals, without an increase in the frequency of the dominant species, also causes the index to increase. High values of the mean indicate stages in the sequence where single-species dominance is least, low values where this species accounts for a high proportion of the total number of individuals. The results are presented in Table 5.5 and in Figure 5.5.

1970 The pattern again involves fluctuations as the sites age. There is a low mean on the pioneer sites, which increases in groups 3 and 4 from ca 30 years, decreases in groups 5 and 6 (85 to 156 years) before increasing again on the older foreland sites and in the regional vegetation. This pattern shows high levels of single-species dominance where individuals and the number of species are low; decreases in dominance are associated with influxes of species and increasing numbers of individuals. This contrasts with the Shannon Equitability Index, which shows equitability to be falling over the course of the sequence. However, that index is calculated using all of the within-site distribution, rather than focusing on only one species. This discrepancy may be explained if increasing dominance is the result of changes involving a group of species.

2000 On young sites, the pattern resembles that in 1970, taking into account the changes associated with ageing. However, the mean for groups 5 and 6 has not increased since 1970 as would be expected from the transition to groups 7 and 8 seen previously. The result is an

Table 5.5 Changes in the Berger-Parker Dominance Index between 1970 and 2000 on terrain of different ages

The table shows the mean and standard deviation for both 1970 and 2000 together with the results of the Wilcoxon and t-tests for differences between the two population means

Site Group	Year	Age	Mean	SD	Year	Age	Mean	SD	Wilcoxon	T-Test
1 and 2	1970	0-28	**2.79**	**±1.18**	2000	30-58	**3.29**	**±1.37**	**0.029**	**0.020**
3 and 4		29-83	**3.47**	**±1.29**		59-113	**2.90**	**±0.97**	**0.000**	**0.000**
5 and 6		85-156	**3.20**	**±1.08**		115-186	**2.91**	**±1.25**	**0.001**	**0.008**
7 and 8		157-221	**3.37**	**±1.31**		187-251	**3.02**	**±1.28**	**0.000**	**0.001**
Off-Foreland		9000	**3.84**	**±1.47**		9000	**3.53**	**±1.65**	**0.001**	**0.011**
Foreland			**3.24**	**±1.24**			**3.01**	**±1.22**	**0.000**	**0.001**
All			**3.37**	**±1.31**			**3.12**	**±1.33**	**0.000**	**0.000**

Notes:
1. *Differences in population means are significant* where the test results are lower than 0.05 (ie the probability of the result occurring by chance is less than 5%). Significant test results are shown in bold, as are the means and standard deviations when at least one of the tests show a significant difference at this level.
2. The Wilcoxon and t-tests used were for matched pairs of samples.
3. The age groups used are those discussed in Chapter Four sections 4.2 and 4.3.

Table 5.6: Changes in the Simpson Index between 1970 and 2000 on terrain of different ages

The table shows the mean and standard deviation for both 1970 and 2000 together with the results of the Wilcoxon and t-tests for differences between the two population means

Site Group	Year	Age	Mean	SD	Year	Age	Mean	SD	Wilcoxon	T-test
1 and 2	1970	0-28	4.80	±2.38	2000	30-58	5.53	±2.65	0.125	0.086
3 and 4		29-83	**5.73**	**±2.30**		59-113	**4.85**	**±1.66**	**0.000**	**0.000**
5 and 6		85-156	**5.24**	**±1.97**		115-186	**4.85**	**±2.34**	**0.003**	**0.027**
7 and 8		157-221	**5.72**	**±2.60**		187-251	**5.27**	**±2.77**	**0.001**	**0.0.13**
Off-Foreland		9000	**6.13**	**±2.86**		9000	**5.85**	**±3.39**	**0.015**	0.180
Foreland			**5.42**	**±2.34**			**5.10**	**±2.38**	**0.000**	**0.012**
All			**5.57**	**±2.47**			**5.26**	**±2.63**	**0.000**	**0.040**

Notes:
1. Differences in population means are significant where the test results are lower than 0.05 (ie the probability of the result occurring by chance is less than 5%). Significant test results are shown in bold, as are the means and standard deviations when at least one of the tests show a significant difference at this level.
2. The Wilcoxon and t-tests used were for matched pairs of samples.
3. The age groups used are those discussed in Chapter Four sections 4.2 and 4.3.

extended intermediate period during which single-species dominance is high, before it decreases in association with the influx of late species.

Changes between the surveys All group means change significantly and involve decreases, except on the youngest sites. The latter is likely to represent a successional process: increasing species/individuals on young land (the transition to groups 3 and 4 in 1970). On all older sites, values of the mean are lower than in 1970 suggesting a significant increase in single-species dominance throughout the sequence, including amongst the regional vegetation.

5.2.6 The Simpson index, D

This is a measure of dominance concentration involving summation over all species. The reciprocal is used, so that an increase in the index again represents a fall in dominance or an increase in evenness. The emphasis is on equitability, rather than on numbers of species, so that a species rich but inequitable site has a lower value than one that is species poor but equitable. The results are presented in Table 5.6 and in Figure 5.6.

The pattern and changes follow those described above for the Berger-Parker Index in terms of the timing, direction and the trend of increasing dominance since 1970 on older sites. The discrepancy in pattern between these dominance indices and the Shannon Equitability index is not therefore explained by co-dominance. The explanation may relate to the differing emphasis of the indices (on common and rare species respectively) and to the increase in individuals. As the number of individuals rises, the proportion represented by dominant (common) species falls.

5.2.7 Summary of section 5.2

(1) The pattern within each sequence is largely consistent, taking site ageing into account, and can be explained by successional development, however, there are frequently significant differences in the trends between the two surveys.

(2) The dominance and equitability indices indicate two apparently contrasting tendencies within the data. Dominance concentration is lower amongst sites with many individuals, but distributions are less equitable. An explanation may involve the effect of increases in the number of individuals and the emphasis on common and rare species respectively. Changes in the dominance measures between 1970 and 2000 indicate a trend towards increased dominance affecting all age categories.

(3) All of the indices, except the Shannon Equitability Index, detect a wavelike pattern of species influxes: (a) between 30 and ca 60 years; and (b) between 150 and 180 years.

(4) Successional processes appear to predominate on land younger than 100 years; and are consistent in both surveys taking into account site ageing. Any effect of the changing trends seen in older groups is obscured by the intensity of the successional changes.

(5) Changes within the sequence are summarised as follows:

a) Young sites 0-83 years (1970); 30-113 years (2000)

(i) Species number increases on pioneer sites in both surveys largely due to rarer species (increases in the Shannon Index). Equitability decreases, as does dominance by one or a few common species (possibly influenced by the increase in individuals).

(ii) The significant decrease in the Margalev Index as groups 3 and 4 age is not reflected in species number, suggesting that increasing numbers of individuals cause the change.

(iii) This stage represents the early influx of pioneer species.

b) Older foreland sites 85-221 years (1970); 115-251 years (2000)

(i) Species number increases with a corresponding increase in rarer species (the Shannon Index), but is not reflected in the Margalev Index, suggesting compensation by increasing numbers of individuals. This corresponds to the invasion and increase of later heath species (Table 4.4).

(ii) In 2000, the number of species and the mean of the Margalev Index increase only marginally in groups 5 and 6 compared to 1970, possibly explained by the overlap in the ages of the groups. The Shannon Index decreases significantly, however, indicating a reduction in rarer species. In conjunction with the changes in groups 3 and 4, this extends the period of comparatively low values on intermediate sites.

(iii) The pattern of equitability and dominance in 1970 involves a decrease, from approximately 150 years, in equitability, but also in dominance (the Berger-Parker and Simpson Indices). This may be explained by the different emphasis of the two indices; the contribution from rare species having decreased, but dominance being shared amongst several species. Additionally, the dominance indices may be sensitive to the increasing numbers of individuals.

(iv) In 2000, equitability is relatively constant rather than decreasing as in 1970. Changes in the Shannon Equitability Index are only significant in groups 5 and 6, where the decrease takes the mean value of the index below that of groups 7 and 8 in 1970. In these groups the trends in equitability and dominance indicate an increase in dominance.

c) Off-foreland sites

(i) Changes would be expected to be minimal as these sites are compositionally mature. However, significant changes occur in all indices, except the Shannon Equitability Index.

(ii) The mean number of species decreases significantly between 1970 and 2000, reflecting significant decreases in both the Margalev and Shannon indices. This appears to involve less frequently occurring species.

(iii) Equitability does not change significantly on the oldest sites, while both of the dominance indices decrease significantly, indicating increasing dominance by one or a small group of species.

5.3 Reconstructing successional trajectories

5.3.1 Introduction

Trajectories are used to summarise community development in terms of progression through a series of stages towards an endpoint: examples are given in Matthews (1992) and Walker and del

Morel (2003). The objective in this section is to reconstruct the trajectories occurring at Storbreen, using the repeat survey to identify the inter-stage transitions that have taken place. This reconstruction can be used to test the sequence structure inferred by Matthews (1976) using a chronosequence approach. Additionally, the use of a repeat survey of permanent plots in this study allows temporal changes to be directly related to spatial location i.e. mesoscale gradients of age, altitude and aspect. This section, therefore, contributes to the study aim of investigating the influence of physical conditions in succession through a coarse-scale examination of community development.

The initial step in this reconstruction uses pooled data from both surveys in a TWINSPAN classification to identify the principal assemblages in 1970 and 2000. This 'pooled approach' classifies all sites on a common basis and allows the identification of transitions consistently. The following section describes the community structure produced by this pooled approach. Subsequent sections consider in detail the transitions between individual stages since 1970, and how these transitions interrelate across the study area in terms of trajectories.

5.3.2 TWINSPAN classification

The decision to use eight groups (level 3), discussed in section 3.5.4, was made on the grounds that it gives interpretable groups that represent meaningful divisions within the data. The output data are given in Appendix 5. Figures 5.7 and 5.8 show the spatial distribution of the groups in 1970 and 2000 respectively. Indicator species, used to make the divisions, are often uncommon and do not provide sufficient information to interpret group identity unambiguously. As an aid to interpretation, mean species frequencies have therefore been calculated for each group (Table 5.7). It was noted that, even though inclusion was restricted to species with frequencies of 10 or more, some of these species were absent from a substantial proportion of sites. In order to distinguish such species from those that are more typical, a cut point was used of presence in 75% of sites in the group. The species are identified separately in Table 5.7.

5.3.3 Ecological identity of the TWINSPAN groups

The groups are considered in order of increasing maturity in the following discussion.

Group 7

This group appears to represent the earliest stage in development. The mean composition contains a limited range of pioneers, all of which occur at low frequency (Table 5.7). Sites belonging to this group are most numerous on the youngest land, decreasing in frequency as age increases (Figures 5.7 and 5.8). They are flanked by sites of group 8 and interspersed with sites of group 5 on land in the centre of the foreland.

The group is interpreted as representing the early pioneer stage, characterised by *Poa* spp. and *Trisetum spicatum.*

Table 5.7: Species composition in TWINSPAN Groups 7 and 8

(including species with an average frequency exceeding 10%)

Species:	Average / site*:	The number of sites from which the species is absent:
Group 7 (90 sites)		
Species occurring on 75% or more of the sites:		
Poa spp.	24.5	3
Trisetum spicatum	21.2	19
Species occurring on less than 75% of the sites:		
Cerastium cerastoides	11.3	35
Group 8 (47 sites)		
Species occurring on 75% or more of the sites:		
Cerastium cerastoides	29.5	5
Deschampsia cespitosa ssp. *alpina*	33.4	11
Oxyria digyna	33.5	4
Poa spp.	22.4	5
Species occurring on less than 75% of the sites:		
S. herbacea	10.9	17
Saxifraga stellaris	20.5	16

Indicator species: *Des alp* (+), *Nar str* (+), *Cer cer* (+), *Tof pus* (-), *Sax opp* (+).
Group 7 is the negative and Group 8 the positive group.

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* Average frequency per site

Group 8

This group appears to be only slightly more advanced than that of group 7. The mean composition contains several pioneer grasses and forbs (Table 5.7 and Figures 4.24 – 4.27) at moderate frequencies, including *Oxyria digyna* and *Poa* spp. that are not restricted to newly exposed land. *Salix herbacea* occurs at low frequency as a subsidiary species, suggesting that it has recently commenced colonization. Sites of this group are most numerous on land aged 20 – 30 years and occur rarely on younger land (Figures 5.7 and 5.8). They occur on the periphery of the central area occupied by sites of group 7, at higher altitude on the flanks and, less frequently, at slightly lower altitude on central sites.

This group is interpreted as a late pioneer stage, characterised by *Cerastium cerastoides* and *Deschampsia cespitosa* ssp. *alpina.*

Group 6

The mean composition indicates a late pioneer community, but some sites contain species that are more typical of a snowbed composition (Table 5.8). *Oxyria digyna* (Figure 4.26) is distributed widely, but is most numerous on older pioneer sites and on the north-facing flank. *Ranunculus glacialis* (Figure 4.28) is largely confined to the north-facing flank. Colonization by *Salix herbacea* starts after approximately 40 years (Table 4.4) and its frequency increases rapidly thereafter. Among the subsidiary species, *Luzula arcuata* is regarded as a snowbed intermediate (Matthews, 1976) and *Polygonum viviparum* is associated with snowbed sites (Matthews, 1976; Whittaker, 1989).

Sites in this group occur almost exclusively on the north-facing flank (Figures 5.7 and 5.8) and are predominantly at high-altitude. At the highest altitude, sites of this composition occur within the regional vegetation suggesting that, under the most severe conditions, it may represent a late developmental stage. Elsewhere, the sites are interspersed with those of group 3 and, occasionally, with those of group 5.

This composition is dominated by *S. herbacea*, with *Oxyria digyna* and *Ranunculus glacialis* being characteristic. This group may represent an intermediate snowbed stage but, at least at high-altitude, it corresponds to an impoverished late developmental stage.

Group 5

The mean composition combines late pioneers with shrubs that are associated with intermediate stages (Tables 5.8 and 4.4). The three late pioneer species, *Oxyria digyna, Poa* spp. and *Salix herbacea,* occur most frequently on moderately young land, while *S. glauca* is a taller shrub characteristic of intermediate stages. All species have low frequencies, including S. herbacea, the most frequently occurring species in this group.

Sites in this group occur mainly on central land, aged from 20 to 60 years (Figures 5.7 and 5.8). They are infrequent on older land and rare outside the foreland boundary. They are interspersed with sites of group 2 in central locations at lower altitude.

Table 5.8: Species composition in TWINSPAN Groups 5 and 6
(including species with an average frequency exceeding 10%)

Species:	**Average / site*:**	**The number of sites from which the species is absent:**
Group 5 (124 sites)		
Species occurring on 75% or more of the sites:		
Oxyria digyna	23.9	22
Poa spp.	20.0	19
Salix glauca	33.4	16
S. herbacea	63.9	6
Species occurring on less than 75% of the sites:		
Carex spp.	12.8	64
Group 6 (37 sites)		
Species occurring on 75% or more of the sites:		
Oxyria digyna	24.5	6
Ranunculus glacialis	21.6	1
Salix herbacea	74.6	0
Species occurring on less than 75% of the sites:		
Cassiope hypnoides	10.0	14
Luzula arcuata	17.6	17
Polygonum viviparum	14.1	33

Indicator species: *Pyr* spp. (+), *Rum asa* (-), *Dry oct* (-), *Cer cer* (-).
Group 5 is the negative and Group 6 the positive group.

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* Average frequency per site

This group is interpreted as an early intermediate stage on a heath pathway, where shrubs have started to invade pioneer communities. *S. herbacea* has the highest frequency, with *Poa* spp. and *S. glauca* being characteristic.

Group 4

The mean composition indicates a low stature community that is often species-rich (Table 5.9). *Salix herbacea* is the dominant species, but *Carex* spp. also occurs at high frequency, indicating that moisture levels are high on many sites in this group. Many of the typical snowbed species identified by Matthews (1976) and Whittaker (1989) are present: *Anthoxanthum odoratum, Gnaphalium supinum, Leontodon autumnalis, Polygonum viviparum* and *Sibbaldia procumbens.* However, many are subsidiary species, while the typical composition includes several species that are not known snowbed specialists e.g. *Bartsia alpina* and *Festuca* spp.. The strongly developed ground flora, and modest frequencies of taller shrubs, indicates a different developmental pathway to that of the dwarf-shrub heath.

Sites of this group occur from low- to mid-altitude on the north-facing flank and from mid- to high-altitude on that facing south (Figures 5.7 and 5.8). They are predominantly outside the foreland boundary, and therefore a mature site type, although the number of sites of this group within the foreland increases from seven to eleven between 1970 and 2000.

This group includes typical snowbed sites together with other sites that are less typical, although the community is of low stature and the species present indicate moist conditions. A possible explanation may involve the inclusion of more than one variant.

This group is therefore interpreted as being a mature snowbed type, dominated by *Salix herbacea* and *Carex* spp..

Group 3

The mean composition is dominated by shrub species (Table 5.9), unlike the preceding groups, where forbs and grasses predominate. Modest frequencies of *Empetrum hermaphroditum* and high frequencies of *Salix herbacea* are typical of this group, while amongst the subsidiary species *Phyllodoce caerulea* and *S. glauca* are associated with intermediate stages (Matthews, 1976; Whittaker, 1985). The forb, Polygonum viviparum (Figure 4.51), and the graminoid, *Carex* spp. (Figure 4.33), also subsidiary species, are associated with snowbed and/or sites with high moisture availability. Both occur most frequently on old land on the flanks of the foreland.

Sites in this group occur predominantly within the foreland at mid- to high-altitude on both flanks, but are also fairly frequent on central land at mid-altitude (Figures 5.7 and 5.8). At high-altitude, on the north-facing flank, sites of this composition occur amongst the regional vegetation, suggesting that in this location it may represent a late successional stage.

This group is interpreted as a late intermediate stage on a heath trajectory, occurring predominantly on flank sites, and dominated by *S. herbacea.*

Table 5.9: Species composition in TWINSPAN Groups 3 and 4

(including species with an average frequency exceeding 10%)

Species:	**Average / site*:**	**The number of sites from which the species is absent:**
Group 3 (94 sites)		
Species occurring on 75% or more of the sites:		
Empetrum hermaphroditum	17.0	20
S. herbacea	131.5	0
Species occurring on less than 75% of the sites:		
Carex spp.	14.2	45
Cassiope hypnoides	25.2	30
Phyllodoce caerulea	22.5	23
Polygonum viviparum	10.5	65
Salix glauca	27.9	24
Group 4 (61 sites)		
Species occurring on 75% or more of the sites:		
Bartsia alpina	11.2	13
Carex spp.	117.8	6
Empetrum hermaphroditum	29.0	14
Festuca spp.	51.6	13
Polygonum viviparum	47.8	9
Salix herbacea	197.1	0
Species occurring on less than 75% of the sites:		
Anthoxanthum odoratum	22.4	32
Cassiope hypnoides	23.3	24
Gnaphalium supinum	17.7	23
Hieracium alpinum	14.7	20
Leontodon autumnalis	14.3	34
Phyllodoce caerulea	20.6	23
Poa spp.	12.7	34
S. glauca	18.9	44
Sibbaldia procumbens	19.7	24
Vaccinium myrtillus	20.8	32

Indicator species: *Rum ala* (+), *Pin vul* (+), *Car* spp. (-), *Sax ste* (+).
Group 3 is the negative and Group 4 the positive group.

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* Average frequency per site

Group 2

The mean composition includes only shrub species and indicates a late, but not mature, heath stage (Table 5.10). All the shrubs listed are associated with heath sites, but there is no evidence of a herbaceous understorey that might be expected on mature sites. *Empetrum hermaphroditum* is the dominant species and has a wide distribution (Figure 4.9), but the high mean frequency associates the group most strongly with older sites at low-altitude and therefore with a late developmental stage. Many of the other shrubs typical of the group composition are associated with intermediate stages of development e.g. *Phyllodoce caerulea*, *Salix glauca* and *S. lanata* (Figures 4.12 – 4.15), although the high frequencies preclude this being an early intermediate stage. Amongst the subsidiary species, *Betula nana* and *Vaccinium uliginosum* are predominantly associated with older land (Figures 4.4 and 4.19); the low frequencies and limited extent of occupied sites may indicate ongoing colonization.

Sites of this group occur mainly within the foreland boundary, at moderately low-altitude and with a south-facing asymmetry up to mid-altitude (Figures 5.7 and 5.8).

This group is interpreted as representing a post-intermediate, species-poor stage, where species typical of mature heath sites are invading. It is a species-poor heath, dominated by *Empetrum hermaphroditum* and characterised by shrubby *Salix* species.

Group 1

The mean composition indicates a species-rich, mature heath community (Table 5.10). *Betula nana*, a late successional shrub, occurs at high frequency on most sites. *Empetrum hermaphroditum* occurs widely within the study area, but the high frequency indicates a late stage in development. Subsidiary species include moderate frequencies of several intermediate stage shrubs e.g. *Phyllodoce caerulea* and *Salix glauca,* a situation consistent with their decline in frequency as development approaches maturity. Several low stature forbs and the grass, *Festuca* spp., are also present as subsidiary species. These species are associated with late successional sites and are likely to represent the development of a ground flora in the final stages of succession.

Sites of this group predominate on the oldest ground at low-altitude (Figures 5.7 and 5.8), but also occur amongst the regional vegetation on the flanks up to mid-altitude, with a south-facing asymmetry.

This group is interpreted as a mature species-rich heath. It is co-dominated by *Betula nana* and *Empetrum hermaphroditum* and characterised by *Vaccinium* spp. (c.f. Matthews 1976).

5.3.4 Summary of section 5.3

(1) The TWINSPAN Groups are interpreted as follows:

Group 7: an early pioneer stage, *Poa* spp. and *Trisetum spicata* are characteristic species.

Group 8: a late pioneer stage, *Cerastium cerastoides* and *Deschampsia cespitosa* ssp. *alpina* are characteristic.

Table 5.10: Species composition in TWINSPAN Groups 1 and 2

(including species with an average frequency exceeding 10%)

Species:	Average / site*:	The number of sites from which the species is absent:
Group 1 (95 sites)		
Species occurring on 75% or more of the sites:		
Betula nana	115.9	7
Carex spp.	77.7	7
Empetrum hermaphroditum	146.4	0
Festuca spp.	54.9	15
Vaccinium uliginosum	67.2	9
V. vitis-idaea	67.7	18
Species occurring on less than 75% of the sites:		
Bartsia alpina	11.7	53
Pedicularis lapponica	17.0	31
Phyllodoce caerulea	24.7	24
Polygonum viviparum	15.5	41
Salix glauca	35.4	29
S. herbacea	42.1	42
Solidago virgaurea	13.5	58
V. myrtillus	48.8	32
Group 2 (290 sites)		
Species occurring on 75% or more of the sites:		
Empetrum hermaphroditum	117.5	1
Phyllodoce caerulea	53.4	29
Salix glauca	42.5	12
S. herbacea	41.1	36
S. lanata	20.2	62
Species occurring on less than 75% of the sites:		
Betula nana	29.7	101
Cassiope hypnoides	20.1	86
Vaccinium uliginosum	16.2	76

Indicator species: *Vac myr* (-), *Car* spp. (-), *Bet nan* (-), *Oxy dig* (-), *Eup alp* (-).
Group 1 is the negative and Group 2 the positive group.

* Average frequency per site

Group 6: a late pioneer/intermediate snowbed composition, which occurs as a late successional stage at high-altitude on the north-facing flank. It is dominated by *Salix herbacea*; *Poa* spp. and *Ranunculus glacialis* are characteristic species.

Group 5: an early pioneer/heath intermediate stage, dominated by *S. herbacea*; *Poa* spp. and *S. glauca* are characteristic.

Group 4: a mature snowbed type composition, occurring on flank sites, dominated by *S. herbacea* and *Carex* spp..

Group 3: a late pioneer/heath intermediate stage, occurring most frequently on flank sites at mid-altitude, species-poor and dominated by *S. herbacea.*

Group 2: species-poor heath, occurring predominantly within the foreland, dominated by *Empetrum hermaphroditum*; *Phyllodoce caerulea* and *Salix* spp. are characteristic.

Group 1: a mature species-rich heath, occurring mainly amongst the regional vegetation and at low-altitude, co-dominated by *Betula nana* and *E. hermaphroditum*; *Vaccinium* spp. are characteristic.

(2) Sites comprising these groups are not confined within particular age bands, although there is generally a preferred age range, and compositional types are interspersed locally (Figures 5.7 and 5.8). Different groups occur on the flanks compared to more central locations, and those occurring at high-altitude on the north-facing flank differ from those on that face south.

(3) There is a general trend in both 1970 and 2000 from pioneer stages dominated by forbs and grasses to stages that are increasingly dominated by shrub species. However, mature stages (both species-rich heath and snowbed) are marked by an influx of late successional forbs and grasses. On heath sites, this corresponds to an increase in structural complexity with canopy formation and understorey development.

5.4 Comparison of within-group composition in 1970 and in 2000

The groups identified in the last section are distinguished by substantial compositional differences. Any within-group differences are minor in comparison, but may, nonetheless, indicate important compositional trends. In this section, differences in group composition between 1970 and 2000 are identified by comparing the mean frequencies of species on sites that constitute the groups in each survey. These mean frequencies are given in Tables 5.11 to 5.18.

Group 7

With the exception of *Saxifraga cespitosa*, all of these early pioneer species have increased in mean frequency since the 1970 survey (Table 5.11), despite the increase in the altitude at which sites of this group occur in 2000, as the glacier retreats onto higher land. This increase in mean frequencies suggests that conditions at high-altitude are not limiting the distributions of early pioneer species. The declines in overall frequency (section 4.2) are, therefore, the result of a decrease in area, rather than an environmental limitation.

Table 5.11: Group 7; a comparison of species mean frequencies in 1970 with those in 2000

Species are included where the mean frequency is 5 or more in at least one of the surveys

Species	**Mean frequency in 1970**	**Mean frequency in 2000**
Cerastium cerastoides	9.3	16.3
Poa spp.	23.1	28.3
Salix herbacea	4.6	14.0
Saxifraga cespitosa	10.7	5.8
Trisetum spicatum	18.7	28.0

Table 5.12: Group 8; a comparison of species mean frequencies in 1970 with those in 2000

Species are included where the mean frequency is 5 or more in at least one of the surveys

Species	**Mean frequency in 1970**	**Mean frequency in 2000**
Cerastium cerastoides	38.9	23.4
Deschampsia cespitosa ssp *alpina*	54.9	19.6
Luzula spicata	13.0	1.1
Oxyria digyna	28.7	36.7
Poa spp.	16.9	26.0
Salix herbacea	13.4	9.3
Saxifraga stellaris	32.3	13.0

Group 8

In contrast to the early pioneer group, there is a trend towards decreasing frequencies on late pioneer sites (Table 5.12). Some of these are substantial e.g. *Deschampsia cespitosa* ssp. *alpina* and *Saxifraga stellaris* (64.3% and 59.8% respectively), while *Luzula spicata* was no longer present on many of these sites by 2000. These species are early occurring or associated with moist, possibly snowbed, conditions and the decreases in frequency may therefore indicate a reduction in available moisture. *Oxyria digyna* and *Poa* spp. are the only species that increase in frequency and these have broad distributions, not restricted to either early or moist sites. Many sites in this group are located on the flanks of the central trough, at slightly higher altitude than the sites of the early pioneer group.

Group 6

Decreases in frequency also characterise the changes in mean composition occurring in this group(Table 5.13), but in this case typically late occurring and snowbed-related species are involved: *Cassiope hypnoides*, *Luzula arcuata* and *Polygonum viviparum*, the late pioneer, *Ranunculus glacialis* and the dominant, *Salix herbacea.* Only two species increase in frequency, the pioneers *Oxyria digyna* and *Trisetum spicatum.*

These changes are retrogressive and those species affected are, again, predominantly associated with moist, snowbed conditions. Sites in this group also occur on the flanks, in this case at high-altitude on north-facing land.

Group 5

Compositional changes in this group are mixed (Table 5.14), with decreasing frequencies of the pioneer grasses, *Deschampsia cespitosa* ssp. *alpina* and *Poa* spp., but increasing frequency of the dominant subshrub, *Salix herbacea.* Changes in frequency are otherwise small, even when this involves species increasing in frequency across the study area as a whole e.g. *Carex* spp. and *Oxyria digyna.*

A potential causal mechanism might involve interactions between the dominant, *Salix herbacea*, and the low-stature pioneer grasses. In 2000, many of these sites occur on the fluted moraines (Figure 5.8), where moisture availability had declined with the retreat of the glacier (Ballantyne and Matthews, 1982). Tall, woody shrubs are slow to colonise this land (section 4.3), so that competitive pressure on *S. herbacea* is likely to be lower in 2000 than in 1970. Additionally, the latter species spreads by underground stems and is frequently infected by mycorrhiza, both of which increase the area from which moisture can be drawn in comparison with that accessible to the pioneer grasses. *Oxyria digyna*, on the other hand, was often found in rock crevices and in the lee of boulders, locations where available moisture is likely to be concentrated, but rarely in close proximity with *S. herbacea* (personal observation). Similarly, *Carex* spp. is generally associated with impeded drainage, conditions in which *S. herbacea* rarely occurs. Both species may, however, be limited in terms of expansion onto new land.

Table 5.14: Group 5; a comparison of species mean frequencies in 1970 with those in 2000

Species are included where the mean frequency is 5 or more in at least one of the surveys

Species	Mean frequency in 1970	Mean frequency in 2000
Carex spp.	11.8	13.4
Deschampsia cespitosa ssp. *alpina*	10.6	3.2
Oxyria digyna	23.7	24.0
Poa spp.	28.6	14.6
Salix glauca	29.5	35.9
S. herbacea	49.1	73.3
S. lanata	12.4	4.0

Table 5.13: Group 6; a comparison of species mean frequencies in 1970 with those in 2000

Species are included where the mean frequency is 5 or more in at least one of the surveys

Species	Mean frequency in 1970	Mean frequency in 2000
Cassiope hypnoides	15.4	4.3
Luzula arcuata	29.2	5.3
Oxyria digyna	20.6	28.6
Polygonum viviparum	17.9	9.9
Ranunculus glacialis	24.5	18.6
Salix herbacea	79.4	69.6
Trisetum spicatum	5.0	10.4

Group 4

Decreases in frequency affect all but three species present in the 1970 composition (Table 5.15). The exceptions are *Salix glauca* and *Veronica alpina*, which increase in frequency, and *Vaccinium myrtillus*, which maintains its population at the 1970 level. All other species decrease in frequency, including even *Empetrum hermaphroditum* and *S. herbacea.* Although some decreases are small, for many species there is a reduction of at least a third e.g. *Gnaphalium supinum, Leontodon autumnalis* and *Polygonum viviparum.*

The pattern of decreasing frequencies, associated with location on the flanks of the foreland, is repeated in this group, where it involves sites predominantly occurring within the regional vegetation. Thus, a similar pattern of declining frequency can be recognised in relation to several different groups, representing different successional stages. These declines are, however, confined spatially, suggesting that they are related to a change in conditions within that specific area. Most of the species declining in group 4 are snowbed specialists, suggesting that an explanation is likely to involve a change in snowcover.

Group 3

Compared to the snowbed group, this group has a more balanced pattern of increasing and decreasing frequencies between species (Table 5.16). However, there is a tendency for shrubs to increase while snowbed species again decrease in frequency. *Luzula arcuata, L. spicata* and *Polygonum viviparum* are associated with snowbed sites (Matthews, 1976) and all undergo substantial decreases. On the other hand, *Salix herbacea* increases in frequency, despite also being associated with snowbed sites, although in this case the species is not restricted to these conditions (Wijk, 1986b; Beerling, 1998). Other species that increase in frequency include *Carex* spp., associated with mire sites; *S. glauca*, frequently occurring on streamsides (Whittaker, 1985); and *Empetrum hermaphroditum*, often found on dry heath, but virtually ubiquitous. On these sites, the decline of the snowbed species does not appear to be accompanied by a reduction in available moisture, as found in groups with distributions largely restricted to sites at high-altitude on the flanks.

Sites of this group occur on both flanks, but also across the centre of the foreland (Figures 5.7 and 5.8). On the flanks, they are often at slightly lower altitude than the snowbed sites, which occur predominantly within the regional vegetation. The decline affecting snowbed species in group 4, discussed above, suggests a change in site characteristics, as would accompany the loss of snowcover. In group 3, decreases in frequency are limited to specialist snowbed species, while more generalist species, including *S. herbacea*, increase in frequency. Early and extensive melting of high-altitude snowbeds would be expected to increase flushing and moisture availability on lower slopes, but is also likely to result in the loss of a source of moisture later in the season. Further evidence to support this explanation comes from the scarcity of permanent snowbeds on either flank observed during the 2000-01 survey (personal observation), in contrast with the many observed by Matthews (1976), particularly on the north-facing flank.

Table 5.16: Group 3; a comparison of species mean frequencies in 1970 with those in 2000

Species are included where the mean frequency is 5 or more in at least one of the surveys

Species	Mean frequency in 1970	Mean frequency in 2000
Carex spp.	8.5	19.3
Cassiope hypnoides	36.2	15.6
Empetrum hermaphroditum	14.7	19.0
Luzula arcuata	13.3	4.4
L. spicata	10.4	5.1
Phyllodoce caerulea	34.7	11.7
Polygonum viviparum	14.2	5.2
Salix glauca	24.5	30.8
S. herbacea	118.3	143.0

Table 5.15: Group 4; a comparison of species mean frequencies in 1970 with those in 2000

Species are included where the mean frequency is 5 or more in at least one of the surveys

Species	Mean frequency in 1970	Mean frequency in 2000
Anthoxanthum odoratum	23.1	20.2
Bartsia alpina	14.1	7.5
Carex spp.	119.8	110.1
Cassiope hypnoides	32.6	13.9
Empetrum hermaphroditum	30.9	25.7
Festuca spp.	60.0	39.7
Gnaphalium supinum	24.0	13.0
Hieracium alpinum	17.4	12.4
Leontodon autumnalis	16.7	10.8
Phyllodoce caerulea	26.3	13.7
Poa spp.	18.7	8.1
Polygonum viviparum	60.2	36.3
Salix glauca	7.7	29.2
S. herbacea	207.6	186.7
Sibbaldia procumbens	22.4	16.5
Vaccinium myrtillus	20.2	20.0
V vitis-idaea	11.8	1.2
Veronica alpina	3.8	12.1

Group 2

Most species undergo minor changes in mean frequency (Table 5.17). These changes are generally in accordance with the population changes occurring across the study area as a whole. *Cassiope hypnoides*, *Phyllodoce caerulea* and *Salix lanata* undergo the most substantial decreases in frequency, while *Empetrum hermaphroditum* and the remaining *Salix* spp. have the largest proportional increases.

Species interactions would be expected to be stronger on these relatively mature sites, compared to the earlier stages discussed above. Sites in this group occupy some of the most favourable land within the foreland boundary, mainly occurring at relatively low-altitude and on land with long exposure times. Cover is often substantial, although rarely reaching 100%. Individuals are therefore likely to be in close proximity to individuals of a range of other species.

In this context, increases in frequency are likely to impact on other populations. The taller *Salix* spp. are the main canopy-forming species in this group; *Betula nana* occurs too infrequently and other species are too low in stature to do so. Increasing frequencies of the taller *Salix* spp. are likely to increase the extent of the shrub canopy and, consequently, to contribute to the decreases in frequency of the low stature *Cassiope hypnoides* and the forbs, *Bartsia alpina* and *Polygonum viviparum.* Additionally, *Empetrum hermaphroditum* and *Phyllodoce caerulea* were generally found to co-occur (personal observation), indicating a potential interaction. The changes in frequency indicate strengthening of the *Salix* canopy, while other effects might be due to the resultant species interactions.

Group 1

The most substantial differences in the mean compositions of these sites involve changes amongst the moderately frequent shrubs and indicate a shift in importance from evergreen to deciduous species (section 4.4) (Table 5.18). Amongst *Vaccinium* spp., the evergreen, *V. vitis-idaea*, has a mean frequency 41.4% lower in 2000 compared to 1970, while the deciduous species, *V. myrtillus* and *V. uliginosum*, are 49.4% and 18.0% higher. Similarly, the deciduous *Salix glauca* and *S. herbacea* are 77.7% and 32.2% higher in frequency in 2000. However, amongst other shrubs and species groups changes in frequency are minor, for example the co-dominants, *Betula nana* and *Empetrum hermaphroditum,* change by less than 10%. Amongst graminoids, *Carex* spp. and *Juncus trifidus* occur at marginally lower frequency in 2000, while the mean frequency of *Festuca* spp. is unchanged. Similarly, changes in frequency amongst the forb species are minor, but four species occur at higher frequency, (*Bartsia alpina*, *Pedicularis lapponica*, *Polygonum viviparum* and *Trientalis europea*), while only one is lower, (*Solidago virgaurea*). For most species the mean frequencies are largely stable, despite the increase in importance of the deciduous shrubs.

These changes amongst the moderately occurring shrubs are consistent with the direction of change occurring in their population totals (section 4.2). However, several of the other species' mean frequencies are stable despite substantial changes in total frequency since 1970. Examples include *Empetrum hermaphroditum*, which increases in frequency over the study area

Table 5.18: Group 1; a comparison of species mean frequencies in 1970 with those in 2000

Species are included where the mean frequency is 5 or more in at least one of the surveys.

Species	Mean frequency in 1970	Mean frequency in 2000
Arctostaphylos spp.	11.8	6.1
Bartsia alpina	9.5	13.5
Betula nana	121.1	111.9
Carex spp.	82.3	74.1
Empetrum hermaphroditum	143.9	148.4
Festuca spp.	54.9	54.9
Juncus trifidus	11.9	7.2
Pedicularis lapponica	13.5	19.7
Phyllodoce caerulea	24.6	24.8
Polygonum viviparum	15.1	15.8
Salix glauca	24.7	43.9
S. herbacea	35.7	47.2
Solidago virgaurea	15.9	11.6
Trientalis europea	5.5	10.3
Vaccinium myrtillus	38.2	57.2
V. uliginosum	61.0	72.0
V. vitis-idaea	88.0	51.6

Table 5.17: Group 2; a comparison of species mean frequencies in 1970 with those in 2000

Species are included where the mean frequency is 5 or more in at least one of the surveys.

Species	Mean frequency in 1970	Mean frequency in 2000
Bartsia alpina	11.3	8.4
Betula nana	32.6	27.1
Cassiope hypnoides	25.6	15.0
Empetrum hermaphroditum	111.5	122.9
Phyllodoce caerulea	62.1	45.6
Polygonum viviparum	12.4	6.6
Salix glauca	39.4	45.3
S. herbacea	38.6	43.5
S. lanata	25.4	15.5
S. phylicifolia	2.3	10.9
Vaccinium uliginosum	15.2	17.1

as a whole, *Phyllodoce caerulea* and *Polygonum viviparum*, which decrease. Additionally, *Carex* spp. decrease in frequency on these sites, while overall the population increases markedly by 2000.

This presents a problem as to how these changes are explained. Increases in frequency far exceed decreases, both proportionally and in numbers of species, making reciprocal interactions unlikely. This group represents a mature assemblage, occurring largely within the regional vegetation, where further successional change is not anticipated. The co-dominant, *Betula nana*, forms a dense canopy at many of these sites, buffering against environmental perturbation and limiting opportunities for establishment from seed. Changes in frequency are most likely to occur by vegetative expansion (Whittaker, 1985). Of those species increasing in frequency, *Salix glauca* is most likely to form a canopy of a similar height to that of *Betula nana*, but high frequencies of the willow characterise the intermediate stage (c.f. Jumpponen, 1998) and the canopy is less dense than that of the birch. The canopies formed by *Vaccinium* spp. and by *S. herbacea* are of considerably lower stature. These species are unlikely to be successful in a competitive interaction with *Betula nana*, and the frequency changes do not suggest that *Betula* is being displaced.

The identification of several foreland sites with the species-rich heath group in 2000 suggests another way in which these frequency changes may occur. If frequencies in this subset of sites differed markedly from those in the rest of the group, they might have the effect of inflating or depressing the overall mean. Despite their inclusion in the group, they may still have some attributes of earlier developmental stages or the nature of their development may have resulted in there being compositional differences with the older sites of the regional vegetation. To test the validity of this conjecture, shrub mean frequencies were calculated for the foreland sites (Table 5.19). The frequencies indicate lower values for these foreland sites for *Betula nana* and *Vaccinium vitis-idaea*, but higher ones for *S. glauca*, *S. herbacea*, *V. myrtillus* and *V. uliginosum*, in line with the trend identified above.

Several features indicate a qualitative difference from the composition on sites outside the outer moraine, although there is also evidence that development is less advanced. *Betula nana* occurs on all but one of these foreland sites at frequencies that are often substantial. However, with one exception, *Empetrum hermaphroditum* exceeds the frequency of *Betula nana* by at least 50 counts, despite its increase of less than 10% in the group as a whole. On many sites it is strongly dominant, with a mean frequency that is higher than in any of the group compositions examined. *Salix* and *Vaccinium* species occur frequently and on most sites, although the former are only subsidiary species in the group. The moderate frequencies of *B. nana*, *S. glauca* and *S. herbacea* suggest a transition point between the species-poor and species-rich heath. Similarly, the scarcity of *Arctostaphylos spp.* and *V. vitis-idaea* may be explained by incomplete development. However, the importance of both deciduous *Vaccinium* species and the high frequency of *E. hermaphroditum* suggest that development may follow a somewhat different route. In this case it may result in a mixed shrub canopy that, apart from *E. hermaphroditum*, includes predominantly deciduous shrubs that are faster growing than and may inhibit the lower

Table 5.19: Shrub frequencies on foreland sites that changed to the species-rich heath in 2000

Species	Sites									Total frequency	Average frequency
	287	303	310	318	331	423	425	436	475		
Arctostaphylos spp.	0	4	0	1	0	0	0	0	5	10	1.1
Betula nana	4	128	69	178	25	68	0	151	107	594	66
Empetrum hermaphroditum	166	214	199	222	78	164	102	157	210	1512	168
Salix glauca	120	5	96	83	42	101	135	123	7	712	79.1
S. herbacea	86	0	96	5	205	30	162	0	10	594	66
Vaccinium myrtillus	189	0	108	41	88	132	45	0	69	672	74.7
V. uliginosum	95	114	57	187	21	84	9	83	108	758	84.2
V. vitis-idaea	5	0	4	0	0	0	0	0	0	9	1

stature of evergreen species. The end result is a composition strongly dominated by *E. hermaphroditum* and characterised by both deciduous *Vaccinium* species.

5.4.1 Summary of section 5.4

(1) The mean frequencies of most species occurring on early pioneer sites are higher in 2000 compared to 1970, indicating that these species are not limited by the increase in average site altitude. Reductions in the total frequencies of pioneer species are caused by a reduction in the area sampled in 2000 compared to 1970.

(2) Groups 3, 4, 6, and 8 have considerably lower mean frequencies of species associated with snowbeds in 2000 compared to 1970. These groups have a substantial proportion of sites that occur on the flanks of the foreland. The more mature groups (3 and 4) have higher frequencies of heath species, while the less mature groups have higher frequencies of pioneer species in 2000. Several factors indicate that early loss of snowcover contributes to these changes:

(a) the observed reduction in the duration of snowlie on the high-altitude flanks;

(b) decreases in frequency occur in groups with a preponderance of sites on the flanks;

(c) the mature snowbed group is both strongly associated with the presence of late-lying snow and undergoes the most substantial changes; and

(d) species specifically associated with snowbeds are preferentially affected.

(3) Compositional changes since 1970 in the species-poor heath (group 2) involve increasing frequencies of *Salix* spp. and *Empetrum hermaphroditum.* These expanding populations are likely to interact with other resident species as cover is high on many of these sites. Such interactions are likely to contribute to the decreasing frequencies of *Cassiope hypnoides*, *Phyllodoce caerulea* and *S. lanata*.

(4) Higher frequencies amongst a group of deciduous *Salix* and *Vaccinium* species appears to be associated with the inclusion of a number of foreland sites in the mature species-rich heath (group 1) in 2000. Differences between the group mean composition and that found on these foreland sites suggest that there may be differences in the developmental pathway, although some features resemble an earlier successional stage. These foreland sites have the highest frequencies of *Empetrum hermaphroditum* in the study area and are characterised by deciduous *Vaccinium* and *Salix* species. In contrast, evergreen species occur at considerably lower frequencies than in the group as a whole.

5.5 Transition frequencies between 1970 and 2000

Having established the ecological identity of the site groups identified in the TWINSPAN classification, this section considers the changes that occur in the groups between 1970 and 2000. This part of the analysis therefore focuses on site dynamics as a further step in reconstructing the successional trajectories.

Transition frequencies are calculated by comparing the groups with which sites are identified in 1970 and in 2000. The transition frequencies in this section are based on the proportions of sites within the 1970 group that had changed to a different group (or remained the same) by

2000. The total number of sites undergoing a particular transition are converted to a percentage of the original 1970 group. Results are summarised in Table 5.20.

Early pioneer group (7)

Several progressive transitions occur from the early pioneer group, indicating variation in the rate of change (Table 5.20). The majority of sites (53%) were associated with the early intermediate group (5) by 2000. Compositional changes associated with this transition typically involve colonization by the late pioneer species, *Oxyria digyna* and *Salix herbacea*, together with the intermediate shrub, *S. glauca*. The presence of two late pioneer species is also associated with the transition to the late pioneer group (8), which occurs on 14% of these sites. However, the latter transition is also marked by higher frequencies of *Cerastium cerastoides* compared to the early pioneers and by the presence of *Deschampsia cespitosa* ssp. *alpina*. A similar proportion of sites (11%) were identified with the species-poor heath by 2000 and, in this case, the change is from low frequencies of pioneer species to comparatively high frequencies of shrubs. While the first two transitions have some species in common, the latter involves a complete compositional change.

In contrast with the frequently substantial compositional changes discussed above, 18% of the sites remained identified with the early pioneer group in 2000. Thus relatively few sites undergo little or no compositional change.

Finally, there are rare progressive transitions to group 6 and the late intermediate group (3). Sites in these two groups occur mainly on the flanks of the foreland (Figures 5.7 and 5.8), while most sites with an early pioneer composition occur within the central trough, as do sites of the early intermediate and species-poor heath. It appears that particular transitions, as well as compositional differences, are spatially segregated in terms of the major landform divisions of the study area.

Late pioneer group (8)

This composition was relatively uncommon in 1970, occurring on only 17 sites (Table 5.20). Progressive transitions to the early intermediate group (5) occur on approximately half of the sites, a similar proportion to that found in the early pioneer group, and may also develop outside the central trough. The early intermediate group has no early pioneer species and low frequencies of the late pioneer species, *Oxyria digyna* and *Poa* spp., compared to the late pioneer composition. *Salix herbacea* typically occurs at high frequency and *S. glauca* is present on many early intermediate sites. Transitions occur rarely to the late intermediate group (3), where frequencies of *S. herbacea* are substantially higher, and several woody shrubs are likely to be present, including *Empetrum hermaphroditum* and *Phyllodoce caerulea*. Finally, 35% remain identified with the late pioneer group in 2000, a considerably higher proportion than in the early pioneer group.

Although more limited in extent than those from the early pioneer group, the range of transitions indicates considerable variation in the rate of development. The majority of transitions

Table 5.20: Frequency of transitions from the 1970 TWINSPAN Groups

a) Group 1 (42 Sites)

Number of Sites	Classification in 2000	Proportion of Group (%)
39	1	93
3	2	7

b) Group 2 (138 Sites)

Number of Sites	Classification in 2000	Proportion of Group (%)
10	1	7
2	4	1
120	2	87
3	3	2
3	5	2

c) Group 3 (44 Sites)

Number of Sites	Classification in 2000	Proportion of Group (%)
5	4	11
8	2	18
25	3	57
4	5	9
2	6	5

d) Group 4 (31 Sites)

Number of Sites	Classification in 2000	Proportion of Group (%)
4	1	13
23	4	74
1	2	3
2	3	7
1	5	3

e) Group 5 (48 Sites)

Number of Sites	Classification in 2000	Proportion of Group (%)
12	2	25
10	3	21
23	5	48
3	6	6

f) Group 6 (19 Sites)

Number of Sites	Classification in 2000	Proportion of Group (%)
1	2	5
5	3	26
1	5	5
12	6	63

g) Group 7 (66 Sites)

Number of Sites	Classification in 2000	Proportion of Group (%)
7	2	11
2	3	3
35	5	53
1	6	2
12	7	18
9	8	14

h) Group 8 (17 Sites)

Number of Sites	Classification in 2000	Proportion of Group (%)
3	3	18
8	5	47
6	8	35

are progressive, despite the greater tendency towards stability of composition compared to the early pioneer sites.

Late pioneer/snowbed intermediate group (6)

Although the composition indicates a late pioneer stage, the progressive trend is weak compared to that found in the pioneer groups and the majority of sites (63%) retain their 1970 composition (Table 5.20). The only progressive transition that occurs on more than one site is to the late intermediate group (3) and involves 26% of the sites. The most notable compositional differences between these groups are the absence of the late pioneer species, *Oxyria digyna* and *Poa* spp., and the presence of several woody shrubs in the late intermediate composition. Three species occur in both groups (3 and 6): *Cassiope hypnoides*, *Polygonum viviparum* and *Salix herbacea*, but higher frequencies of the latter species are typical of the late intermediate group. Rare transitions occur to the early intermediate and species-poor heath groups.

With one exception, sites in this group occur at mid- to high-altitude on the north-facing flank of the foreland (Figures 5.7 and 5.8). Physical conditions at this location are the least favourable in the study area for plant growth. High winds and precipitation, together with low temperatures (Foskett, 1998) are exacerbated by low insolation levels (section 3.2.3). Additionally, closely spaced moraines and associated boulders contribute to the inhospitability of the terrain (personal observation).

In contrast with the pioneer groups, where progressive transitions predominate, most sites in group 6 retain their 1970 composition. Where progressive transitions do occur, that to the late intermediate group (3) is the most likely. However, in the pioneer groups progressive transitions most frequently involve the early intermediate group (5).

The early intermediate group (5)

In this group. similar numbers of sites developed progressively by 2000 as retained their 1970 composition (Table 5.20). Slightly more sites changed to the species-poor heath (2) compared to the late intermediate group (3). This is the first group where retrogressive transitions occur.

The progressive transitions typically involve the loss of pioneer species and colonization by shrubs. Transitions to the species-poor heath involve more extensive compositional changes than those to the late intermediate group, particularly in terms of the higher frequencies and the greater range of shrub species present. Species common to both groups 2 and 3 occur at higher frequency in the species-poor heath e.g. *Empetrum hermaphroditum* and *Salix glauca*, and several additional species may be present e.g. *Betula nana* and *Vaccinium uliginosum*. *S. herbacea* is an exception, occurring at higher frequencies in the late intermediate group.

The transition to the late pioneer/snowbed intermediate group (6) is considered retrogressive due to the absence of the woody shrub, *S. glauca*. This transition may also involve colonization by the snowbed species, *Luzula arcuata* and *Polygonum viviparum*. The late pioneer species, *Oxyria digyna* and *S. herbacea* occur in both groups, but *Ranunculus glacialis*, rather than *Poa* spp., is more likely to be found at the sites of the late pioneer/snowbed intermediate group 6.

The proportion of sites in this group that retain their 1970 composition, nearly 50%, is higher than that in the pioneer groups, but lower than that in group 6.

The mature snowbed group (4)

This group contains mature sites and, as might be expected from the above discussion, the majority (74%) remained in the same group in 2000 (Table 5.20). Both progressive and retrogressive trends are relatively weak.

Progressive transitions occur infrequently to the species-rich heath (group 1). This involves considerable compositional change, from a low stature community to one dominated by tall woody shrubs. This is largely due to increases in the frequencies of shrubs that occur in both groups, e.g. *Empetrum hermaphroditum*, colonization by *Betula nana*, and decreases in the frequency of *Salix herbacea* and in species richness, particularly involving forb and graminoid species.

The retrogressive trend is similarly weak, but the transitions are more varied; to the species-poor heath and both the early and late intermediate groups. All involve a reduction in species richness and in the frequency of *S. herbacea*. However, the three transitions are distinguished by differences in the extent and type of compositional change. Higher frequencies of several shrubs characterize the transition to the species-poor heath; the transition to the late intermediate group involves reductions in species richness and frequency; while higher frequencies of the late pioneers, *Oxyria digyna* and *Poa* spp., accompany transitions to the early intermediate group.

The late intermediate group (3)

While the majority of sites (57%) remained in this group in 1970 (Table 5.20), this represents a smaller proportion than either the mature snowbed or late pioneer/snowbed intermediate groups. Progressive transitions occur on 29% of the sites, roughly twice the number that undergo retrogressive changes.

Progressive transitions occur from this group to both the snowbed endpoint and, more frequently, to the species-poor heath. The transition to the shrub composition of the species-poor heath involves increases in the frequency of several shrub species common to both e.g. *Empetrum hermaphroditum* and *Salix glauca*, and, on some sites, *Betula nana* and *Vaccinium uliginosum* may colonize. Where the transition is to the mature snowbed composition, the main feature is likely to be an increase in species richness due to increases in the number of forb and graminoid species e.g. *Bartsia alpina* and *Festuca* spp.. Additionally, there are changes amongst species already present e.g. increases in frequency of *Carex* spp. and *S. herbacea*. These transitions indicate the presence of alternative, qualitatively different pathways following the late intermediate stage.

Retrogressive transitions occur infrequently and involve either the early intermediate or late pioneer/snowbed intermediate groups. Both involve recolonization by the late pioneer species, *Oxyria digyna*, together with *Poa* spp. (group 5) or *Ranunculus glacialis* (group 6) and a reduction in the frequency of *S. herbacea*. *S. glauca* may persist in the early intermediate group, but sites in group 6 generally support only low stature species.

Species-poor heath group (2)

The predominant trend amongst these sites is to retain the 1970 composition (87% of sites) (Table 5.20). Both progression and retrogression consequently occur infrequently.

Progressive transitions occur to the species-rich heath group and, infrequently, to the mature snowbed group. The transition to the species-rich heath involves changes in frequency amongst the woody shrubs: lower frequencies of *Salix* spp. and *Phyllodoce caerulea*, higher frequencies of *Betula nana*, *Empetrum hermaphroditum* and *Vaccinium* spp.. Additionally, several graminoid e.g. *Carex* spp. and *Festuca* spp., and forb species, e.g. *Bartsia alpina,* are likely to colonize. This transition involves structural development, i.e. canopy formation and the presence of understorey species. Progressive development at this stage may also result in a low stature snowbed community (group 4). This transition is marked by lower frequencies of the taller, woody shrubs e.g. *Phyllodoce caerulea* and *S. glauca*, a substantially higher frequency of *S. herbacea* and an increase in the range of functional types present with the addition of graminoids and particularly forbs.

The progressive transitions to the mature species-rich heath occur predominantly within the foreland boundary and appear to mark the completion of successional development. In 1970, only one foreland site was identified with the species-rich heath. By 2000, the number of such sites rose to nine, all at low-altitude and on land older than 190 years. While this indicates a minimum period for such development, the majority of foreland sites, even on old land at low-altitude, remain identified with the less mature species-poor heath. Therefore, many foreland sites require in excess of 250 years before successional development is complete.

Retrogressive transitions are only half as frequent as progressive ones. These transitions involve a return to early and late intermediate compositions, with reductions in frequency or the loss of several taller woody shrubs. Only *Salix glauca* (early) and *Empetrum hermaphroditum* (late) occur at even moderate frequencies, although in both transitions, *S. herbacea* increases substantially in frequency. Species of other functional types typically occur in both intermediate groups: the graminoid, *Carex* spp. and forb, *Polygonum viviparum* in the late intermediate group and the late pioneers, *Oxyria digyna* and *Poa* spp., in the early intermediate group. In general terms, retrogression involves reductions in the frequency of taller woody shrubs, but increases in low stature graminoids and forbs.

Species-rich heath group (1)

93% of sites in this group continued to be identified with it in 2000 (Table 5.20). Only three sites changed their classification and all of these returned to the species-poor heath composition.

The principal compositional changes associated with this retrogression involve the loss of ground flora species and changes in frequency among the woody shrubs. The mean composition of the species-poor heath does not contain any graminoid or forb species at frequencies of ≥10.

Among the shrubs, decreases occurred in the frequency of *Betula nana*, *Empetrum hermaphroditum* and *Vaccinium* spp., while *Phyllodoce caerulea* and *Salix lanata* increase at some sites.

Thus, the species-rich heath has a highly stable composition, once it has been attained. Retrogression occurs rarely and such changes are small, involving a return to the immediately preceding stage. The group has increased in size by 26% since 1970, from 42 to 53 sites, as a result of transitions from the species-poor heath and the snowbed endpoint.

5.5.1 Summary of section 5.5

(1) Clear patterns of change and stability have been identified over the 30-year time interval between 1970 and 2000.

(2) Progressive transitions are dominant amongst pioneer groups but are less easily discerned among groups characteristic of intermediate successional stages. There is little evidence of progression amongst mature groups.

(3) There is considerable variability in the extent of compositional change represented by the progressive transitions from common start points in the individual groups. This variability indicates differences in developmental potential from similar initial compositions.

(4) Compositional inertia or stability, together with retrogressive transitions, lengthen successional pathways. These trends increase the uncertainty of successional rates and the predictability of successional changes at individual sites.

(5) Compositional inertia increases with maturity, from 18% in the early pioneer group to 93% in the mature species-rich heath. Directional transitions are correspondingly reduced. Successional rate therefore slows as sites approach the endpoint of development. However, even at the early pioneer stage, approaching 20% of sites undergo little compositional change over 30 years.

(6) Retrogression also increases with maturity, but does not involve a return to the pioneer compositions. Sites may, however, be recolonized by late pioneer species such as Oxyria digyna and Poa spp..

(7) Spatial location, in terms of position in the landscape, altitude and aspect, is an important determinant of group identity and, consequently, of the transitions likely to occur at a site. This finding suggests that the predictability of successional development at specific sites may be improved by combining spatial and temporal parameters. In the study area, groups can be divided between those occurring predominantly centrally and/or at low-altitude (groups 7, 5, 2 and 1) and those occurring on the flanks of the foreland (8, 6, 3 and 4). The early and late intermediate stages, together with the species-poor heath (groups 5, 3 and 2), have the most widespread distributions (Figures 5.7 and 5.8).

(8) Species changes that accompany the transitions can be characterised either as replacements or as fluctuations, where species occur in both the original and destination groups and increase or decrease as the site develops or retrogresses. Replacements usually involve graminoid or forb species, while fluctuations are found amongst woody shrubs. Transitions from early stages are most frequently characterised by complete replacements.

(9) Results represent the first direct evidence of the transition of foreland sites to mature communities and, therefore, indicate the timescale of succession. This includes all but one of the transitions from the species-poor to the species-rich heath and all of the transitions to the mature snowbed group. On the heath pathway, there is a minimum age of approximately 190 years for the completion of successional development. However, as the majority of foreland sites have not yet undergone this transition, many sites will require considerably longer than this, even at low-altitude.

5.6 Transition probabilities and successional trajectories

5.6.1 Introduction

The transition frequencies, discussed in the last section, are used in this section to calculate the probability of transitions in the context of the whole study area. A transition probability is here defined as the probability of any site in a particular group in 1970 changing to a specified group or remaining unchanged by 2000. The probabilities are calculated from the number of sites undergoing a particular transition as a proportion of the total number (407) of transitions occurring in the study area. Some sites were excluded from these calculations because no species were present in one or other survey, or due to probable site misidentification. The probabilities for each transition are listed in Table 5.21, where three categories are recognised: those representing little or no compositional change; those indicating development towards a more mature stage; and those where the composition returns to that of a previous stage. .

This section culminates in an attempt to combine these transitions in order to identify trajectories; the results are summarised in Figure 5.9. Generally, transitions with low probabilities, i.e. less than 0.010 (1%), contribute little to this reconstruction and reference to them will, therefore, be minimal. The transitions are interpreted in terms of two major trajectories: (1) the heath trajectory; and (2) the snowbed trajectory.

5.6.2 The heath trajectory

The strongest progressive transition probabilities combine to form the heath trajectory, shown on the left of Figure 5.9. This sequence comprises transitions from the early pioneer to the early intermediate stage (with a probability of 0.086 or 8.6%), to the species-poor heath (0.030 or 3%) and to the species-rich heath (0.025 or 2.5%). Branches leave this main trajectory at the early pioneer and the early intermediate stages to form subsidiary 'loops' that incorporate additional stages (late pioneer and late intermediate) before a return transition completes the loop. In each case, transitions forming the subsidiary loop are weaker than those on the main trajectory: 0.022 (2.2%) and 0.020 (2.0%) for the late pioneer stage and 0.025 (2.5%) and 0.017 (1.7%) for the late intermediate stage. 'Jumps' can also be recognised where a stage is omitted that normally forms part of the sequence. Generally, the probabilities are low, except that from the early pioneer group to the species-poor heath, which has a probability approximately equal to that of the

Table 5.21: The probability of transitions from the 1970 TWINSPAN Groups

These probabilities refer to the probability of any site in a particular group in 1970 changing to specified groups or remaining unchanged by 2000 (see section 5.6.1 for further explanation).

Group (1970)	No Change	Retrogressive	Progressive
1	1 - 1 = 0.096	1 - 2 = 0.007	
2	2 - 2 = 0.296	2 - 3 = 0.007 2 - 5 = 0.007	2 – 1 = 0.025 2 - 4 = 0.005
3	3 – 3 =0.062	3 -5 = 0.010 3 - 6 = 0.005	3 - 2 = 0.017 3 - 4 = 0.012
4	4 - 4 = 0.057	4 - 2 = 0.003 4 – 3 = 0.005 4 – 5 = 0.003	4 - 1 = 0.010
5	5 – 5 = 0.057	5 - 6 = 0.007	5 - 2 = 0.030 5 – 3 = 0.025
6	6 – 6 = 0.030		6 – 2 = 0.003 6 – 3 = 0.012 6 – 5 = 0.003
7	7 - 7 = 0.030		7 – 2 = 0.017 7 – 3 = 0.005 7 - 5 = 0.086 7 - 6 = 0.003 7 – 8 = 0.022
8	8 - 8 = 0.015		8 - 3 = 0.007 8 - 5 = 0.020
Total in each category	0.643	0.054	0.277

Note:

In calculating the transition probabilities, the total number of sites used was 407. 2 sites had no species in 1970, and 1 lost all species by 2000.

weaker loop (1.7%). This jump indicates an extremely rapid rate of successional development over the 30 years between the surveys.

The majority of sites appear to follow a four-stage trajectory, but the presence of the additional stages indicates variation in the system. From the available evidence, a maximum of six stages is required to complete development of a species-rich heath composition.

Most of the core transitions on this trajectory occur between groups where the majority of sites are centrally-located. However, the transitions comprising the subsidiary loops involve groups where sites also occur on the flanks, raising the possibility that at least some of these transitions might be part of a separate trajectory.

5.6.3 A snowbed trajectory?

This section examines whether the groups on the right-hand side of Figure 5.9, the late pioneer/snowbed intermediate group (6), the late intermediate stage and the snowbed endpoint, represent a second trajectory. The transitions on this pathway are both weak (0.012 or 1.2%) compared to those along the heath trajectory.

The late intermediate group is linked to the heath trajectory via the second subsidiary loop. Subsequent to this stage, transitions involve either a return to the heath pathway (0.017 or 1.7%) or to the mature snowbed (0.012 or 1.2%). Sites that progress via the second subsidiary loop occur mainly on the flanks of the central trough (Figures 5.7 and 5.8).

Compositionally, both group 6 and the late intermediate group resemble early snowbed assemblages, with group 6 apparently representing the earlier stage. The latter composition includes late pioneer and several snowbed species: *Luzula arcuata*, a snowbed intermediary (Matthews, 1976), *Polygonum viviparum* and *Salix herbacea*. The late intermediate stage includes several shrub species, present in both heath and snowbed compositions, and *S. herbacea* at higher frequency than in group 6. Both suggest a higher level of development in the late intermediate stage.

However, other features of the late pioneer/snowbed intermediate group are not consistent with an early developmental stage. Firstly, the sites occur on old land, with some located outside the foreland boundary (Figures 5.7 and 5.8). Secondly, there is a higher level of compositional inertia in the group compared to pioneer and intermediate groups (Table 5.21). This suggests that group 6 is more mature than is compatible with it being an early stage. Finally, most of the sites attaining this composition between 1970 and 2000 appear to be behaving retrogressively, only one transition is classed as progressive, from group 7. These are not characteristics that are readily associated with an early developmental stage. Combined with an immature composition and against a background of harsh conditions at high-altitude on the north-facing flank, they suggest, alternatively, a spatially constrained stage where development is limited in extent, extremely slow, continually reset or an early stage of retrogression.

Features of the spatial distribution of sites in the three groups (6, 3 and 4) also suggest that they are not directly related as a trajectory, at least at the present time. Sites of group 6 occur, with one exception, at high-altitude on the north-facing flank, while those of the mature snowbed group are more widely distributed on the flanks, occurring at low- but not high-altitude on north-facing land (Figures 5.7 and 5.8). Sites of the late intermediate group occupy intervening land in the regional vegetation, and are also distributed more widely across the foreland. There is, therefore, an altitude-related sequence of composition types in the regional vegetation on the north-facing flank: sites of the mature snowbed group are interspersed with those of the species-rich heath at low- to mid-altitude, followed by late intermediate and finally those of group 6 as altitude increases. Since 1970, there have been transitions from group 6 to the late intermediate stage at high-altitude on the north-facing flank. However, this evidence of continued development within the regional vegetation appears anomalous, given the length of time for which it has been exposed and some possible explanations are considered in Chapter 7. At high-altitude on the north-facing flank, the late intermediate stage represents the maximum level of successional development, suggesting that there is a ceiling on succession that makes it unlikely that a mature snowbed composition will occur in the near future.

The composition of the late intermediate group contains species typical of both heath and snowbed groups, consistent with it representing a stage in both trajectories. However, the preceding discussion indicates that at high-altitude on the north-facing flank it occurs as a trajectory endpoint, with transitions occurring from the group 6 composition. This situation does not occur elsewhere in the study area and suggests that the assumption of a single compositional group may not be valid. An alternative explanation, consistent with these findings, involves compositionally differing strands that are associated with environmental differences between different spatial locations. The late intermediate composition is, therefore, examined in detail below.

First, is there evidence from other locations in the study area of spatially-determined transitions involving the late intermediate group? Sites of group 6 composition are the source of late intermediate sites at high-altitude on the north-facing flank, but elsewhere in the study area, the early intermediate group is the main source of transitions to this group. These early intermediate sites occur on moderately young land within the foreland, indicating a rapid rate of development compared to that occurring on the older land associated with the transitions from group 6. Additionally, transitions from the late intermediate group are strongly related to spatial location (Figures 5.7 and 5.8). At low- to mid-altitude on the north-facing flank and at mid- to high-altitude on the south-facing flank, transitions are predominantly to the mature snowbed group and infrequently to the species-poor heath. However, on sites located more centrally within the foreland, transitions occur only to the species-poor heath. Therefore, there are two sources of sites, but three possible outcomes following a late intermediate composition, and this outcome depends largely on spatial location.

The above discussion does not rule out differentiation during the late intermediate stage, however, the predictability of the outcome in relation to location, raises the possibility that distinct developmental strands are present within a catch-all composition. Minor compositional differences are not distinguished in the classification, which was designed to detect major divisions within the dataset.

A further examination of the late intermediate composition has been undertaken by dividing the sites according i.e. whether they face north or south or occupy land in the centre of the foreland (i.e. in relation to aspect). The mean composition has been calculated in a similar way as in section 5.3, but species are included where the mean frequency is five or greater, rather than ten, to increase the sensitivity of the analysis. The results are shown in Table 5.22.

With the exception of *Empetrum hermaphroditum*, all of the species differ in frequency and show patterns consistent with there being three compositional strands determined by location. The highest frequencies of *Salix glauca* and *S. lanata* occur on central sites, consistent with their subsequent development as species-poor heath. 50% of species have their highest frequencies on south-facing sites and these species are associated either with the snowbed endpoint composition e.g. *Gnaphalium supinum*, *Polygonum viviparum* and *Veronica alpina*, or with high moisture availability e.g. *Carex* spp. and *Luzula spicata*. While there is some correspondence between the compositions on north- and south-facing land e.g. similar frequencies of *Luzula arcuata* and *Polygonum viviparum*, several features distinguish the two. *Carex* spp. and *L. spicata* occur at low frequencies on north-facing sites, suggesting that moisture availability is lower there. Although *Salix herbacea* occurs most frequently on north-facing sites, many other snowbed species have low frequencies and occur on few sites there e.g. *Gnaphalium supinum* and *Veronica alpina*. *S. herbacea* occurs least frequently on south-facing sites, despite being dominant in the snowbed composition, with a frequency 44% lower than on north-facing sites. Finally, *Cassiope hypnoides* and *Phyllodoce caerulea* have higher frequency on north- compared to south-facing sites.

The mean composition on central sites differs from those on the flanks and has an affinity with an early heath composition e.g. the highest frequencies of the taller *Salix* species, but the lowest frequencies of typical snowbed forbs. Both north- and south-facing sites have mean compositions that are related to the snowbed composition, but *Salix herbacea* dominance is stronger and frequencies of the snowbed forbs are lower on north-facing sites, while *Cassiope hypnoides* and *Phyllodoce caerulea*, more typical of a species-poor heath composition, occur more frequently there. South-facing sites, on the other hand, resemble more closely the typical species-rich composition of the mature snowbed group.

This evidence indicates that the late intermediate stage contains three spatially-determined compositional strands, rather than representing a single, amorphous group.

5.6.4 Summary of section 5.6

(1) A four-stage heath trajectory is reconstructed on central sites:

early pioneer -> early intermediate -> species-poor heath -> species-rich heath

Subsidiary loops add late pioneer and late intermediate stages to these core transitions, but the subsidiary transitions occur mainly on flank sites, while the core transitions occur predominantly on central ones. 'Jumps' are transitions that omit stages and indicate rapid successional development, the most notable being that from the early pioneer stage to the species-poor heath.

(2) A possible snowbed trajectory was examined that included the following transitions:

Table 5.22: Variation of the late pioneer/heath intermediate group composition with aspect.

Species	North-facing sites	Centrally located sites	South-facing sites
Carex spp.	10.0	20.2	32.0
Cassiope hypnoides	33.8	6.9	19.2
Empetrum hermaphroditum	16.3	18.3	17.7
Festuca spp.	10.8	5.8	5.7
Gnaphalium supinum	1.0	1.1	7.8
Juncus trifidus	1.0	1.5	7.5
Luzula arcuata	9.9	1.2	11.5
Luzula spicata	4.0	11.0	13.6
Phyllodoce caerulea	30.3	10.7	12.8
Polygonum viviparum	12.5	0.2	14.1
Salix glauca	21.5	53.2	23.0
S. herbacea	146.6	122.7	101.5
S. lanata	2.4	18.4	9.1
Veronica alpina	1.4	2.9	6.4

late pioneer/snowbed intermediate -> late intermediate -> mature snowbed group

However, this trajectory presents several problems of interpretation. In particular, despite its immature composition, group 6 is not an early stage on this trajectory, the composition occurs only at high-altitude on the north-facing flank and includes sites in the regional vegetation.

(3) There is a sequence of groups in the regional vegetation on the north-facing flank: from mid-altitude, sites of the snowbed endpoint are followed by late intermediate sites and then by those of group 6 as altitude increases. This may be a toposequence, but transitions have occurred at high-altitude from group 6 to the late intermediate stage. However, there may be evidence of cyclic succession e.g. retrogression from the early intermediate group to group 6 that involves the loss of *Salix glauca.*

(4) The late intermediate composition contains three strands:

(a) species-poor heath precursor on central sites;
(b) species-poor snowbed variant on the north-facing flank; and
(c) species-rich snowbed variant on the south-facing flank.

The strands are confounded in a catch-all late intermediate composition. The particular variant that occurs at a site is determined by location on the aspect gradient.

(5) These findings suggest that there are at least three trajectories in the study area: the heath trajectory at low-altitude and on central sites; a species-rich snowbed trajectory at high-altitude on south-facing, flank sites; and a species-poor snowbed trajectory, also at high-altitude, but on north-facing sites. Differences between these trajectories are related to spatial location, in particular to altitude and aspect.

(6) A complete reconstruction of these snowbed trajectories has not been attempted, but the additional stages represented by the subsidiary loops (Figure 5.9) occur predominantly on flank sites. From this evidence, the following trajectories are proposed for the species rich (south-facing) and the species-poor (north-facing) snowbed trajectories at high-altitude:

North-facing trajectory:
early pioneer -> late pioneer -> early intermediate -> group 6 -> late intermediate (north variant)
South-facing trajectory:
early pioneer -> late pioneer -> early intermediate -> late intermediate (south variant) -> snowbed endpoint

(7) The findings related to the compositional strands in the late intermediate group also indicate that this stage occurs on some, but not all, centrally-located sites, most of which follow the four-stage heath trajectory.

(8) The trajectories that occurred at low-altitude could not be reconstructed as only late stages occur there at the present time.

5.7 Progression, stability or retrogression

This section focuses on the relative importance of the three categories of transition identified in Table 5.12, namely: little or no compositional change (stability or inertia); development of a more mature composition (progression); and return to a composition typical of a previous stage (retrogression). The percentages of transitions in each category for each of the TWINSPAN groups are summarised in Figure 5.10.

An initial inspection of the figure suggests that there is an overall trend of gradually increasing stability of composition and decreasing rates of progression of sites through time. The exceptions to this trend are the late pioneer/snowbed intermediate and the mature snowbed groups. As discussed above, these groups seem to represent important stages in alternative trajectories. Excluding the entries for these two groups clarifies the complementary trends for stability and progression associating them predominantly with the heath trajectory.

Progression These results support those of Whittaker (1985), who concluded that there was a strongly progressive trend early in succession. Progression is the strongest trend in pioneer stages and matches the probability that sites remain identified with the group in the early intermediate stage. The probability of progressive change decreases with increasing maturity, from 83% in the early pioneer group, to 46% in the early intermediate group and reaching zero in the species-rich heath, where there is no subsequent stage to which succession can progress.

Stability or inertia The total probability of remaining identified with the same group over 30 years is more than twice as great as that of progressive change (Table 5.21). This probability increases with maturity up to 93 % amongst the species-rich heath. However, the value of 87% in the species-poor heath appears anomalously high compared to the trend amongst the other heath stages. This suggests that prolonged development is required for foreland sites before progression to the species-rich heath, or, alternatively, that the species-poor heath represents an endpoint for many foreland sites. Compositional maturity appears to confer increasing stability, suggesting that site development includes mechanisms that promote resistance to change. However, even at the early pioneer stage, stability accounts for almost 20% of the transitions. In this case, there has been little opportunity for development and vegetation is sparse. Rather than the community being resistant to change, this suggests that a community is unable to develop. Reasons for this failure of progressive development at such an early stage might include severity of conditions and/or disturbance.

Retrogression On the other hand, retrogression does not occur prior to the early intermediate stage, and the highest probabilities of this type of transition occur towards the end of the sequence. However, retrogression is not a strong trend at any stage in terms of the numbers of sites or the extent of the compositional change i.e. the transitions involve one or rarely two stages. It has a total probability across all stages of 5.4% compared to 27.7% for progressive transitions. While the timing of retrogressive changes corresponds with the findings of Whittaker (1985), the trend is much weaker than indicated in his work, although this may be the result of the stricter criterion used in this study to define this type of change.

There is an indication that retrogression is related to spatial location. Groups with sites at high-altitude on the flanks have the highest incidence of retrogressive transitions. This includes both intermediate groups and particularly the snowbed endpoint (but not group 6). These findings can be related to Figure 5.9. Progressive transitions with a probability of 0.012 and above, are generally accompanied by retrogressive transitions, except those involving the pioneer stages, where the only evidence of retrogression involved two sites that lost all species by 2000. Each retrogressive transition tends to have a lower probability than the corresponding progressive one. Outside the heath trajectory, progressive transitions of 0.012 (groups 6 – 3 and 3 – 4), 0.017 (group 3 – 2) and 0.025 (group 5 – 3) are accompanied by retrogressive ones of 0.005, 0.007 and 0.010 respectively; progression is therefore more than twice as likely as retrogression. Within the main heath trajectory, progressive transitions of 0.025 and 0.030 are both accompanied by retrogression of 0.007; progression is three or four times as likely as retrogression.

In the literature, retrogression is frequently depicted as a late-stage phenomena attributed to disturbance or to slowly occurring soil degradation, (e.g. Matthews, 1999). In this study, the pattern indicates that retrogression accompanies strong progressive transitions and involves at least 20% of the number of sites developing progressively. However, this pattern occurs only on major transitions and at stages subsequent to that of the pioneers. Retrogression is relatively commonplace compared to the frequency of disturbance that is intensive enough to remove the vegetation (disturbance is discussed in greater detail in the next chapter) and is not restricted to late successional stages. It is suggested, therefore, that as a widely occurring phenomena, retrogression may represent developmental failure where invading species or an expanding population fail to grow and survive following successful establishment. This failure might result from soil degradation (in later stages) or disturbance, but additionally might signify insufficient site amelioration, e.g. the absence of species with which there are positive interactions, such as mycorrhiza, and the effects of inadequate resources in stressful habitats.

5.7.1 Summary of section 5.7

(1) Progression is strongest amongst early stages, particularly in the pioneer groups, and declines with increasing maturity, as found by Whittaker (1985).

(2) Stability/inertia is the most common state and the increase with maturity suggests increasing resistance to change. However, values associated with early successional groups, attaining nearly 20% in the early pioneer stage, suggest that community development may be arrested at any stage. The high value of 80% associated with the species-poor heath suggests that prolonged successional development is required to attain the species-rich heath composition and that this may represent an endpoint for some foreland sites.

(3) Retrogression occurs most frequently in late successional stages. In contrast with the findings of Whittaker (1985), however, it was found to be a weak trend in this study. It occurs most frequently at high-altitude on the flanks of the foreland, where strongly progressive transitions also occur. It is suggested that in addition to disturbance and soil degradation, developmental failure due to inadequate site amelioration or other factors should be included in the definition of retrogression.

Chapter 6: Environmental influences on vegetation changes

6.1. Introduction

A principal aim of this thesis is to examine the relationship between environment conditions and vegetation changes occurring during the 30 years since the 1970 survey. The findings reported in the preceding Chapter indicated that location within the landscape i.e. on mesoscale gradients of altitude and aspect, largely determine the type of trajectory followed, while terrain age is broadly indicative of position on that trajectory. However, even where values of these parameters are similar, community types frequently form a mosaic within a locality (Figures 5.7 and 5.8). This Chapter examines the proposition that this local variation might be explained by the effects of environmental gradients that operate at a fine-scale. If this is the case, the influence of the physical environment could be characterised as a nested series of vegetation-environment interactions (c.f. Myers and Giller, 1988b; Stewart et al., 2000).

Local variation at a fine-scale characterises many environmental variables. Although these variables may operate singly, they may also form complex gradients (section 3.6.2), interact with each other, with the vegetation and with gradients operating at different scales. Changes may have strictly local causes and effects, as when bank failure results in the flooding of one or two sites. When a directional change occurs over a larger area, a coarser-scale causal process is implicated, but it is likely to operate at a local scale through a series of perturbations that are similar in type. Using the above example, retrogressive changes on a series of sites close to a meltwater stream may all be caused by bank failure locally, but have increased ablation from the glacier as an underlying cause.

In Matthews' initial work at Storbreen, he proposed that age, altitude and aspect were the principal variables governing vegetation type (Matthews, 1976). Subsequent studies have explored this further. The main sources of environmental influence at Storbreen identified by Whittaker (1985) involved two complexes of environmental variables; a *terrain age factor complex* comprising age, disturbance, soil depth and altitude and a *microtopographic factor complex* including exposure, moisture and snowmelt. However, this work used sites of restricted aspect and altitudinal range. The importance of microtopography, particularly at higher altitude, was emphasised in Foskett's (1998) thesis.

Although a wide range of environmental variables were measured and assessed in this study, there are factors that were omitted for technical reasons and due to time constraints. This includes a comprehensive survey of nutrient availability and the effects of species interactions, both of which are thought to influence species distributions (section 2.4). Additionally, factors operating at a regional scale may influence compositional change, such as the climatic changes discussed in section 1.4. Changes in such variables may impact locally by altering the operation of the finer-scale variables, examples include flooding, as discussed above, or a change in the duration of snowlie. Changes in interspecific relationships may follow where particular species are favoured or better able to take advantage of the change in conditions because of life history, phenology, and physiological or reproductive strategies. In this case, phenotypic plasticity, the ability to respond opportunistically and develop an exploitative capability, may favour particular species.

A series of analytical techniques are used in this chapter to examine the relationship between the environmental variables and compositional changes. Initially, Kendall's tau correlation coefficients are calculated in order to investigate relationships amongst the variables and to determine whether the terrain-age and microtopographic complexes (Whittaker, 1985) are appropriate descriptors in relation to the successional stages (section 6.2). In section 6.3, Canonical Correspondence Analysis (CCA) is applied to the change data in conjunction with the environmental parameters to identify specific variables and gradients associated with compositional change, firstly using the data for the whole study area and subsequently for each stage of the successional sequence. An expected result of using subsets of the data is to reduce the range of the environmental variables found in each group. Descriptive statistics are therefore used to identify this range and to assess differences between the groups. The explanatory power of this analysis is examined in section 6.4 and how this changes over the course of the sequence. In the final section, species ordinations are used to investigate the relationship between functional groups (sections 4.4 – 4.12) and the environmental gradients identified in section 6.3.

6.2. Interrelationships between environmental variables detected by Kendall's tau correlation coefficients

An initial overview is presented using all of the site data collected in 2000-01; followed by assessments for each of the TWINSPAN groups (section 5.3). The correlation coefficients, calculated using the SPSS programme (1999), are presented in Tables 6.1 – 6.9, which have been rearranged to bring together any major grouping of variables. Many of the coefficients are weak, even though they are significant, suggesting that the correlations only occur on a small proportion of sites and their significance is due to the large sample size. To avoid a lengthy discussion involving these relatively weak relationships, coefficients lower than 0.40 are generally omitted from this examination.

6.2.1. Environmental variables at all sites (Table 6.1)

The majority of highly significant correlations are associated with terrain age (Table 6.1), suggesting that it describes a fundamental source of variation. The variables form two groups; one positively, the other negatively, correlated with age. The positive group comprises soil, root and humus depths, and texture, while the negative one includes glacier climate, pH, gravel, cobbles and the extent of bare ground. This age-related complex primarily involves variables that affect progressive change. Bare ground and pH decrease as vegetation cover increases (Messer, 1988). High frequencies of gravel and cobble-sized substrate are associated with young sites. However, intercorrelations between bare ground and the substrate variables have higher coefficients than those with age, suggesting that some variation occurs independently of age. On the other hand, soil depth and maturity increase over time, with contributions from organic surface material and rooting systems. Finally, the influence of the glacier climate

Table 6.1: Kendall's tau correlation coefficients between environmental variables using data for the whole study area

Variable	Age	Glacier	Altitude	pH	Gravel	Cobbles	BG	Soil	Root	Humus	Texture	Slope	East	North	Exposure
Age	1.000														
Glacier	__-0.438**__	1.000													
Altitude	-0.380**	__0.487**__	1.000												
pH	__-0.417**__	0.299**	0.234**	1.000											
Gravel	__-0.601**__	0.377**	0.295**	0.398**	1.000										
Cobbles	__-0.441**__	0.208**	0.214**	0.239**	__0.455**__	1.000									
BG	__-0.626**__	0.378**	0.331**	0.376**	__0.632**__	__0.594**__	1.000								
Soil depth	__0.596**__	-0.362**	-0.291**	-0.363**	__-0.527**__	-0.378**	__-0.530**__	1.000							
Root	__0.426**__	-0.210**	-0.184**	-0.224**	__-0.424**__	-0.342**	__-0.429**__	__0.487**__	1.000						
Humus	__0.450**__	-0.354**	-0.300**	-0.371**	__-0.444**__	-0.309**	__-0.441**__	__0.564**__	0.393**	1.000					
Texture	__0.455**__	-0.235**	-0.093**	-0.347**	-0.399**	-0.287**	-0.385**	0.383**	0.265	0.337	1.000				
Slope	0.069	-0.095**	0.152**	-0.063	-0.032	0.089**	0.031	0.046	0.052	0.020	0.071	1.000			
East	-0.022	-0.006	0.001	0.001	-0.028	-0.015	-0.051	0.012	0.022	0.008	0.046	0.044	1.000		
North	0.052	0.003	0.013	-0.093**	0.009	0.044	0.071	0.085**	-0.070	-0.053	0.056	0.031	-0.200**	1.000	
Exposure	-0.187**	0.292**	0.078	0.162**	0.175**	0.031	0.123**	-0.176**	-0.098**	-0.150**	-0.168**	-0.196**	-0.029	0.036	1.000
Moisture	0.145**	-0.086**	-0.033	-0.132**	-0.256**	-0.179**	-0.173**	0.144**	0.110**	0.189**	0.141**	0.021	-0.052	0.120**	-0.037
Snowlie	0.246**	-0.256**	-0.121**	-0.164**	-0.197**	-0.002	-0.123**	0.221**	0.139**	0.207**	0.152**	0.083	0.009	0.089**	-0.231**
Trampling	-0.003	-0.052	-0.093**	-0.016	-0.004	-0.085	-0.010	-0.038	-0.030	0.037	0.066	-0.061	0.021	-0.035	-0.116**
Grazing	0.207**	-0.241**	-0.169**	0.008	-0.278**	-0.271**	-0.338**	0.248**	0.257**	0.183**	0.085	-0.025	0.083	-0.085	-0.074
Browsing	0.047	-0.004	0.052	0.081	-0.084	-0.105**	-0.114**	0.008	0.096**	-0.020	0.061	0.022	0.006	-0.018	-0.045
Hare	0.133**	-0.111**	0.008	-0.097**	-0.061	-.083	0.102**	0.064	0.074	0.054	0.070	0.073	0.080	0.096**	-0.076
Ptarmigan	0.093**	-0.022	0.065	-0.012	-0.069	-0.034	-0.043	0.024	0.080	0.003	0.086	0.098**	-0.025	0.048	-0.005
Vole	-0.046	0.010	0.093**	0.025	0.041	0.053	0.121**	-0.068	-0.018	-0.096**	0.008	0.112**	-0.027	0.103**	-0.055
Sheep	-0.018	-0.034	0.030	0.084	-0.024	-0.048	-0.056	-0.050	-0.024	-0.071	-0.034	-0.078	-0.006	0.041	-0.059
Cow	0.056	-0.026	-0.067	-0.044	-0.011	-0.056	-0.044	0.060	0.065	0.065	0.022	-0.005	-0.059	-0.037	-0.065
Frost	-0.211**	0.156**	0.049	0.162**	0.310**	0.196**	0.253**	-0.225**	-0.208**	-0.167**	-0.178**	-0.117**	-0.094**	0.129**	0.098**
Solifluction	0.147**	-0.085	0.118**	-0.038	-0.141**	-0.139**	-0.097**	0.081	0.163**	0.062	0.165**	0.171**	0.024	0.019	-0.038
Fluvial	0.000	-0.016	-0.039	-0.136**	-0.134**	-0.046	-0.028	0.034	0.008	0.107**	0.037	-0.036	-0.062	0.088	0.018
Fines	-0.228**	-0.004	0.024	0.083	0.167**	0.102**	0.296**	-0.215**	-0.232**	-0.126**	-0.144**	-0.024	-0.068	0.143**	-0.022
Boulders	-0.193**	0.014	0.127**	0.119**	0.116**	0.381**	0.354**	-0.168**	-0.172**	-0.144**	-0.123**	0.180**	0.025	0.016	-0.094**

(1) ** Correlation is significant at the 0.01 level (2 tailed).

(2) Coefficients greater than 0.400 are shown in bold and these correlations are discussed in the text.

(3) The number of sites used in this analysis is 431.

Table 6.1 (ctd): Kendall's tau correlation coefficients between environmental variables using data for the whole study area

Variable	Moisture	Snowlie	Tramplin	Grazing	Browsing	Hare	Ptarmig	Vole	Sheep	Cow	Frost	Solifluct	Fluvial	Fines	Boulders
Age															
Glacier															
Altitude															
pH															
Gravel															
Cobbles															
BG															
Soil depth															
Root															
Humus															
Texture															
Slope															
East															
North															
Exposure															
Moisture	1.000														
Snowlie	0.087	1.000													
Trampling	-0.025	-0.022	1.000												
Grazing	0.083	0.050	-0.105**	1.000											
Browsing	0.059	0.013	-0.004	0.192**	1.000										
Hare	0.023	-0.035	0.014	-0.037	0.026	1.000									
Ptarmigan	0.078	0.034	0.057	-0.049	-0.007	0.131**	1.000								
Vole	0.021	-0.001	0.020	-0.002	0.089**	0.071	0.059	1.000							
Sheep	0.042	0.053	0.026	0.036	0.195**	-0.105**	0.075	0.091**	1.000						
Cow	-0.023	0.037	-0.009	0.061	0.093**	0.069	-0.020	-0.015	-0.027	1.000					
Frost	-0.205**	-0.134**	0.059	-0.261**	-0.162**	0.027	-0.059	-0.049	-0.012	-0.038	1.000				
Solifluction	0.160**	0.084	-0.031	0.087	0.163**	0.115**	0.174**	0.139**	0.087	-0.030	-0.284**	1.000			
Fluvial	**0.406****	0.041	0.032	-0.062	0.030	-0.018	-0.004	-0.036	-0.029	-0.022	-0.135**	-0.012	1.000		
Fines	0.091**	-0.002	0.086	-0.181**	-0.078	-0.054	-0.085	0.181**	0.104**	0.006	0.115**	0.050	0.166**	1.000	
Boulders	-0.058	0.081	-0.125**	-0.091**	-0.032	-0.050	0.011	0.089**	-0.061	-0.049	0.055	-0.051	0.006	0.062	1.000

(1) ** Correlation is significant at the 0.01 level (2 tailed).

(2) Coefficients greater than 0.400 are shown in bold and these correlations are discussed in the text.

(3) The number of sites used in this analysis is 431.

decreases with distance from the glacier, with most old sites being beyond the distance over which such effects are likely (500-600m) (section 3.2.6).

The correlation coefficient between age and altitude, -0.380, although marginally below the cutpoint for, is mentioned in this section as it reflects the balance between two contradictory trends within the study area. On central sites, altitude increases as age decreases, but on the flanks, the two variables increase together. Other than age, altitude is strongly correlated only with the effect of the glacier climate and this relationship is positive, reflecting the presence of the glacier at high-altitude.

Finally, fluvial disturbance is positively correlated with moisture availability, although a coefficient of only 0.406, suggests that other factors are frequently important in the occurrence of this disturbance type. Neither of these variables is strongly correlated with site age.

These findings provide only limited support for Whittaker's age and microtopographic complexes. Three gradients are detected: (1) an age-related, progressive successional development gradient, reflecting increasing autogenic control and maturity, with the negative correlations between the bare ground/substrate and soil variable groups supporting the concept of an integrated soil-vegetation complex (c.f. Walker and del Morel, 2003); (2) a moisture-disturbance gradient that is weakly developed; and (3) an altitude gradient. The weakness of the relationship between age and altitude reflects the inclusion, in this study, of a substantial number of sites on the flanks.

The following sections examine the relationships amongst the variables in the individual stages of the successional sequence, as determined by the TWINSPAN groups. At a coarse-scale, individual groups were associated with a limited range of locations determined by position on mesoscale gradients of age, altitude and aspect (sections 5.3 – 5.7). By restricting this source of variation, it is expected to identify relationships amongst variables operating at a fine-scale, which may be masked in a coarse-scale examination. Additionally, this examination will test further the stability and importance of the relationships described by Whittaker's terrain-age and microtopographic complexes in individual stages during the successional sequence.

6.2.2 Environmental variables in the early-pioneer group (7) (Table 6.2)

Terrain age is strongly correlated with several variables, even though this group represents the earliest phase of succession on newly deglaciated surfaces. Altitude (-0.776), pH and bare ground are negatively correlated with age, while snowlie and soil depth are positively correlated. The negatively correlated variables are highly intercorrelated, and the coefficients are often slightly stronger than with age, particularly those including altitude. However, the importance of the altitude gradient most likely reflects the consistency of the relationship with age, as most sites in this group are located within the central trough, with little or no confounding effect from sites on the flanks.

Table 6.2: Kendall's tau correlation coefficients between environmental variables using data from the early pioneer group

Variable	Age	Altitude	pH	BG	Snowlie	Soil	Humus	Glacier	Slope	East	North	Exposure	Moisture	Root	Tramplin
Age	1.000														
Altitude	**-0.776****	1.000													
pH	**-0.547****	**0.589****	1.000												
BG	**-0.574****	**0.678****	**0.599****	1.000											
Snowlie	**0.455****	**-0.485****	-0.337	**-0.479****	1.000										
Soil	**0.415****	-0.251	-0.172	-0.205	0.195	1.000									
Humus	0.319	-0.238	-0.101	-0.186	0.094	**0.708****	1.000								
Glacier	-0.152	0.102	0.010	0.044	-0.237	-0.308	-0.194	1.000							
Slope	0.151	-0.131	-0.103	-0.029	-0.142	0.023	-0.045	-0.045	1.000						
East	-0.070	0.044	0.123	0.041	0.241	-0.101	-0.055	-0.334	-0.242	1.000					
North	0.122	-0.095	-0.019	-0.131	0.083	0.236	0.253	0.015	0.071	-0.189	1.000				
Exposure	0.285	-0.196	-0.111	-0.161	0.236	0.169	0.311	0.214	-0.183	-0.134	**0.422****	1.000			
Moisture	-0.148	0.055	-0.099	-0.160	-0.130	-0.146	-0.139	0.208	-0.104	-0.160	-0.106	-0.109	1.000		
Root	0.193	-0.200	-0.057	-0.157	0.132	0.204	0.136	0.147	-0.057	-0.092	-0.011	-0.013	-0.227	1.000	
Trampling	0.089	0.000	-0.155	-0.056	-0.055	0.245	0.123	0.050	0.284	-0.238	0.025	-0.135	0.333	-0.076	1.000
Grazing	0.053	-0.082	-0.076	-0.217	0.161	-0.030	-0.040	0.059	-0.008	0.282	-0.283	-0.239	-0.066	0.015	-0.077
Ptarmigan	0.153	-0.190	-0.155	-0.014	0.287	0.271	0.259	0.050	-0.232	0.013	0.164	0.090	-0.222	0.254	-0.043
Vole	0.089	0.000	-0.155	-0.056	-0.055	0.245	0.123	0.050	0.284	-0.238	0.025	-0.135	0.050	-0.076	**1.00****
Sheep	-0.053	0.060	0.099	0.058	0.105	0.091	0.032	-0.326	-0.236	0.370**	-0.238	-0.213	-0.393**	0.158	-0.077
Frost	0.196	-0.178	-0.097	-0.023	-0.036	0.381**	0.344	-0.038	-0.021	-0.379**	0.145	0.221	-0.125	0.200	-0.100
Solifluctior	0.068	-0.007	-0.122	-0.033	-0.194	0.000	-0.137	0.277	0.229	-0.326	-0.231	-0.239	**0.477****	0.023	**0.590****
Fluvial	0.008	-0.037	-0.122	-0.083	-0.161	-0.084	-0.217	-0.326	0.076	-0.015	-0.030	-0.372**	0.309	-0.128	-0.077
Fines	-0.148	0.172	0.240	0.287	-0.214	-0.150	-0.210	0.131	-0.034	-0.215	0.048	-0.026	-0.120	0.081	0.038
Gravel	0.070	-0.190	-0.265	-0.245	0.016	-0.097	-0.099	-0.131	0.206	-0.095	0.088	-0.200	0.142	-0.188	0.088
Cobbles	0.096	-0.055	0.015	-0.139	0.099	0.262	0.384**	0.092	-0.097	0.142	0.128	0.261	-0.083	0.140	-0.177
Boulders	-0.185	0.253	0.169	0.271	-0.099	0.067	-0.115	-0.044	-0.101	0.091	-0.179	-0.144	0.143	-0.221	0.114

(1) ** Correlation is significant at the 0.01 level (2 tailed).
(2) Coefficients greater than 0.400 are shown in bold and these correlations are discussed in the text.
(3) The number of sites used in this analysis is 24.

Table 6.2 (ctd): Kendall's tau correlation coefficients between environmental variables using data from the early pioneer group

Variable	Grazing	Ptarmiga	Vole	Sheep	Frost	Solifluct	Fluvial	Fines	Gravel	Cobbles	Boulders
Age											
Altitude											
pH											
BG											
Snowlie											
Soil											
Humus											
Glacier											
Slope											
East											
North											
Exposure											
Moisture											
Root											
Trampling											
Grazing	1.000										
Ptarmigan	-0.077	1.000									
Vole	-0.077	-0.043	1.000								
Sheep	0.288	-0.077	-0.077	1.000							
Frost	**-0.505****	0.271	-0.100	-0.118	1.000						
Solifluctior	0.227	-0.077	**0.590****	-0.136	-0.059	1.000					
Fluvial	-0.136	-0.077	-0.077	-0.136	0.042	0.197	1.000				
Fines	-0.134	0.215	0.038	-0.037	0.083	0.149	0.268	1.000			
Gravel	-0.074	-0.189	0.088	0.030	0.000	-0.052	0.112	-0.150	1.000		
Cobbles	0.089	0.114	-0.177	-0.022	0.041	-0.201	-0.164	-0.271	**-0.413****	1.000	
Boulders	0.119	-0.114	0.114	-0.052	-0.099	0.253	-0.022	-0.125	-0.245	0.007	1.000

(1) ** Correlation is significant at the 0.01 level (2 tailed).
(2) Coefficients greater than 0.400 are shown in bold and these correlations are discussed in the text.
(3) The number of sites used in this analysis is 24.

The frequency of late-lying snow increases with site age and as altitude decreases, probably due to the effects of local topography. This is consistent with Foskett (1998), who found that strong winds at high-altitude removed snow and redeposited it on sheltered sites at low-altitude. Vegetation cover increases with the duration of snowlie.

The correlation of soil depth with age is independent of the other age-related variables, including the extent of bare ground. The depth of the surface organic surface layer is, however, positively correlated with soil depth but independent of age. This relationship might be expected on young sites where soil development is minimal and humus constitutes a major proportion of the total soil depth. The decline of pH with increasing age suggests rapid leaching of bases in soils with a low cation exchange capacity, but high base saturation on initial deposition (Matthews, 1992).

Solifluction, trampling and vole droppings are all positively intercorrelated, but are independent of both age and altitude. While trampling and vole burrows may contribute to the formation of solifluction lobes, any process associating trampling and vole droppings is more obscure. Additionally, there is a positive correlation between solifluction and moisture availability, as might be expected from the process of lobe formation (section 2.8.5).

Finally, cobbles and gravel are negatively correlated, independently of age, suggesting that sites may be segregated according to predominant substrate type.

6.2.3 Environmental variables in the late-pioneer group 8 (Table 6.3)

Age-related variables are also numerous in this group despite the modest level of variation in site age, although the correlated variables are mainly physical descriptors rather than measures of biogenic development. Snowlie, humus and fluvial disturbance are positively correlated with age, while altitude, glacier climate and hare droppings are negatively correlated.

The relationship of age with snowlie and altitude resemble those in the early pioneer group, but the latter coefficient is weaker, -0.508 compared to -0.776. This difference is explained by the inclusion of sites on the lower slopes of the flanks in the late pioneer group.

Older sites mainly occur at lower altitude, have longer duration of snowlie, deeper surface organic material and are more likely to undergo fluvial disturbance than younger sites, which are exposed to the glacier climate and have a higher incidence of hare droppings. Humus and soil depths are positively correlated, as in the early pioneer group. Browsing is negatively correlated with soil depth, while the coefficient with humus depth (-0.395) is only marginally below the cutpoint. Even on young land, browsing is associated with a low level of surface organic material available for soil formation.

Sites are commonly subject to either frost heave or fluvial disturbance; the distinction depending on site conditions. Fluvial disturbance occurs mainly on older sites and is related to high moisture availability and more advanced successional development (positive correlation with humus depth; negative correlation with bare ground). The incidence of frost heave is not age-related, but occurs predominantly at high-altitude, where pH is high and snow cover is low.

Table 6.3: Kendall's tau correlation coefficients between environmental variables using data from the late pioneer group 8

Variable	Age	Glacier	Altitude	Hare	pH	Moistur	Snowlie	Soil	Humus	Fluvial	Slope	East	North	Exposur	Root
Age	1.000														
Glacier	__-0.427**__	1.000													
Altitude	__-0.508**__	0.255	1.000												
Hare	__-0.524**__	0.173	0.400**	1.000											
pH	-0.398**	0.182	0.390**	0.308	1.000										
Moisture	0.385**	-0.305	-0.082	-0.061	-0.125	1.000									
Snowlie	__0.512**__	-0.180	__-0.498**__	__0.426**__	-0.363**	0.155	1.000								
Soil	0.362**	-0.265	-0.199	-0.301	-0.099	0.295	0.386**	1.000							
Humus	__0.449**__	-0.163	-0.325	-0.395**	-0.262	0.289	__0.424**__	__0.471**__	1.000						
Fluvial	__0.454**__	-0.225	-0.281	-0.210	-0.334	__0.694**__	0.260	0.257	__0.487**__	1.000					
Slope	0.104	-0.335	0.169	-0.038	-0.201	0.162	-0.047	0.066	-0.096	0.110	1.000				
East	-0.083	-0.010	-0.056	0.130	-0.057	-0.061	0.008	0.115	0.164	0.020	-0.057	1.000			
North	-0.072	0.374**	0.162	0.121	0.030	0.096	-0.133	-0.234	-0.224	0.087	-0.161	-0.237	1.000		
Exposure	-0.365**	__0.465**__	0.138	0.126	0.220	-0.151	-0.253	-0.155	-0.120	-0.051	-0.254	-0.100	0.269	1.000	
Root	0.075	-0.042	0.011	-0.098	0.201	0.006	0.210	0.350**	0.235	-0.111	-0.115	-0.051	-0.061	-0.034	1.000
Texture	0.160	0.167	-0.010	-0.087	-0.243	0.240	0.137	0.191	0.285	0.237	-0.102	0.050	0.109	-0.233	0.189
Trampling	-0.120	-0.060	0.129	-0.087	-0.091	-0.261	-0.243	-0.130	-0.032	-0.137	0.112	0.268	-0.109	-0.233	-0.060
Grazing	-0.009	-0.195	0.142	-0.222	0.054	-0.142	-0.003	0.173	0.138	-0.285	0.133	-0.026	-0.337	-0.177	0.328
Browsing	-0.331	0.191	0.146	0.302	0.071	-0.281	-0.145	__-0.497**__	-0.395**	-0.184	-0.027	-0.076	0.183	0.043	-0.110
Ptarmigan	-0.242	0.018	0.339	0.054	0.157	0.011	-0.191	-0.202	-0.262	-0.110	0.221	-0.087	0.057	0.145	-0.113
Vole	-0.117	0.193	0.137	0.106	0.140	-0.066	-0.090	-0.354**	-0.394**	-0.228	0.070	-0.129	0.121	0.014	-0.109
Sheep	-0.023	0.272	0.198	-0.159	0.043	-0.021	0.062	-0.082	0.052	0.073	0.047	-0.023	0.146	0.229	0.088
Frost	-0.299	0.235	__0.490**__	0.271	__0.545**__	-0.191	__-0.555**__	-0.275	-0.329	-0.338	-0.052	-0.114	0.237	0.119	-0.092
Solifluction	-0.354**	0.097	0.128	0.194	-0.021	-0.265	-0.189	-0.085	-0.221	-0.300	-0.034	0.057	-0.131	0.087	0.118
Fines	0.054	0.010	-0.144	0.019	-0.130	0.217	-0.045	-0.075	-0.043	0.245	0.071	-0.067	0.222	0.147	-0.147
Gravel	-0.169	0.119	0.200	0.075	0.177	__-0.490**__	-0.219	-0.229	-0.267	__-0.443**__	-0.049	-0.027	0.011	0.075	-0.003
Cobbles	0.016	-0.061	-0.011	-0.042	0.081	-0.114	0.178	0.285	0.037	-0.241	0.120	-0.029	-0.242	-0.106	0.059
Boulders	-0.027	-0.124	-0.112	0.047	-0.043	0.216	0.105	0.188	0.133	0.140	-0.022	0.120	-0.157	-0.075	0.123
BG	-0.324	0.142	0.253	0.202	0.236	-0.311	-0.352**	-0.214	-0.371**	__-0.415**__	0.023	-0.148	0.204	0.152	0.014

(1) ** Correlation is significant at the 0.01 level (2-tailed).

(2) Coefficients greater than 0.400 are shown in bold and these correlations are discussed in the text.

(3) The number of sites used in this analysis is 28.

Table 6.3 (ctd): Kendall's tau correlation coefficients between environmental variables using data from the late pioneer group

Variable	Texture	Trampl	Grazing	Brows	Ptarmig	Vole	Sheep	Frost	Solifluct	Fines	Gravel	Cobbles	Boulder	BG
Age														
Glacier														
Altitude														
Hare														
pH														
Moisture														
Snowlie														
Soil														
Humus														
Fluvial														
Slope														
East														
North														
Exposure														
Root														
Texture	1.000													
Trampling	-0.037	1.000												
Grazing	0.165	0.275	1.000											
Browsing	-0.136	0.136	-0.247	1.000										
Ptarmigan	-0.077	-0.077	0.125	0.077	1.000									
Vole	-0.105	-0.105	0.040	0.241	0.233	1.000								
Sheep	0.085	-0.145	0.025	0.154	0.063	0.270	1.000							
Frost	-0.153	0.236	-0.025	0.162	0.104	0.105	0.073	1.000						
Solifluction	0.125	0.288	0.257	0.134	0.130	-0.025	-0.237	-0.104	1.000					
Fines	-0.179	-0.139	-0.272	-0.143	-0.005	0.327	0.120	-0.092	-0.125	1.000				
Gravel	-0.269	0.269	0.112	0.123	-0.036	-0.129	-0.020	0.384**	0.040	-0.332	1.000			
Cobbles	-0.129	-0.268	0.159	-0.070	0.113	0.044	-0.159	-0.073	-0.067	-0.192	-0.072	1.000		
Boulders	0.228	-0.189	0.065	0.010	0.097	0.020	-0.159	**-0.402****	0.285	0.064	**-0.558****	0.144	1.000	
BG	-0.277	0.051	0.046	-0.048	0.127	0.200	-0.101	0.223	0.215	0.235	0.251	0.036	-0.113	1.000

(1) ** Correlation is significant at the 0.01 level (2-tailed).

(2) Coefficients greater than 0.400 are shown in bold and these correlations are discussed in the text.

(3) The number of sites used in this analysis is 28.

Clast sizes are also specifically differentiated between the two disturbance types. Fluvial disturbance is negatively correlated with gravel, although not positively associated with finer material, possibly indicating effective water transport, with the washing out of fine sediments leaving the coarser grades as a lag deposit at the soil surface. Frost heave is positively correlated with gravel, marginally below the cutpoint (0.384), and negatively correlated with boulders. Both probably reflect frost sorting of the smaller clasts, with boulders providing shelter and being less likely to be displaced.

Disturbance is of primary importance on these young sites. The relationship between the two dominant types suggests differentiation between the youngest land at high-altitude (subject to frost heave) and wetter sites, where there is a higher level of vegetation development (and organic material accumulates).

6.2.4 Environmental variables in the late pioneer-snowbed intermediate group (6) (Table 6.4)

Compared to the preceding groups, there are few age-related variables and gradients that are independent of age assume greater importance. Altitude, soil depth and moisture are positively correlated with age. Older sites occur at higher altitude (off-foreland sites on the flank), have deeper soils and higher moisture availability than younger ones. The positive correlation between age and altitude is due to the spatial configuration of sites in this group, and reverses the negative relationship found in several other groups, where sites are predominantly located on central land.

Moisture availability increases with site age, and independently with rooting/humus depths and with fluvial disturbance. Wet sites are of two types; one where organic material accumulates (possibly on mire sites), the other where there is evidence of site flooding/flushing.

Browsing is central to an important gradient. It is positively correlated with texture, grazing and sheep droppings, and negatively correlated with bare ground, gravel and easterly aspect. Browsing/grazing is associated with mature soils and west-facing sites, where vegetation is extensive and there is little exposed gravel. Sheep droppings and slope are negatively correlated, indicating that the highest frequencies occur on flat sites.

The extent of bare ground represents another gradient that is independent of age. It is positively correlated with snowlie and gravel/cobbles. Where vegetation is sparse, the substrate is most often a mixture of gravel and cobbles. Sites where there is evidence of late-lying snow frequently have extensive bare ground, possibly due to deflation and the formation of lag deposits that are not conducive to colonization. Despite evidence of late-lying snow from the lichen proxy, few snowpatches were observed on the north-facing flank during 2000-01. As lichens are slow-growing, their response to changing conditions may be delayed.

Finally, there are several other correlated variables that are independent of these gradients. Ptarmigan droppings occur more frequently as humus depth increases. The correlation between frost heave and boulders probably reflects the mechanical uplift of boulders. The incidence of solifluction increases with rooting depth. Exposure and slope also increase together.

Table 6.4: Kendall's tau correlation coefficients between environmental variables using data from the late pioneer/snowbed intermediate group

Variable	Age	Altitude	Soil	Glacier	Slope	East	North	Exposure	Moisture	Snowlie	pH	Root	Humus	Texture	Grazing
Age	1.000														
Altitude	**0.495****	1.000													
Soil	**0.530****	0.184	1.000												
Glacier	0.077	**0.407****	0.180	1.000											
Slope	0.068	0.254	0.034	0.242	1.000										
East	-0.114	-0.118	-0.191	-0.047	0.154	1.000									
North	0.227	0.268	0.210	0.274	0.054	-0.236	1.000								
Exposure	0.080	-0.023	-0.071	-0.011	**0.432****	-0.110	-0.008	1.000							
Moisture	**0.434****	0.231	0.325	0.067	0.110	-0.131	0.216	0.332	1.000						
Snowlie	0.007	-0.014	-0.043	-0.271	-0.162	0.051	-0.144	-0.370**	-0.314	1.000					
pH	-0.363**	-0.113	-0.349	-0.062	0.152	0.178	-0.099	-0.102	-0.318	-0.023	1.000				
Root	0.244	0.126	**0.598****	0.230	0.244	-0.253	0.192	0.182	**0.445****	-0.036	-0.366**	1.000			
Humus	0.194	-0.142	**0.461****	-0.098	-0.208	-0.163	0.047	0.194	**0.447****	0.022	-0.345	**0.514****	1.000		
Texture	0.309	0.132	0.171	0.090	-0.127	-0.365**	0.395**	0.231	0.329	**0.486****	0.008	-0.063	0.104	1.000	
Grazing	0.032	-0.140	0.000	-0.270	-0.223	-0.351**	-0.156	0.223	-0.138	-0.043	-0.194	-0.024	0.040	0.221	1.000
Browsing	0.143	0.000	0.114	-0.126	-0.170	**-0.472****	0.174	0.281	0.298	-0.365**	-0.142	0.027	0.099	**0.568****	**0.425****
Hare	0.306	0.108	0.233	-0.120	-0.127	-0.133	0.141	-0.020	0.313	0.082	**-0.477****	0.227	0.120	0.049	0.355**
Ptarmigan	0.254	0.200	0.390**	0.324	0.012	-0.367**	0.035	0.254	0.209	-0.208	-0.192	0.347	**0.476****	0.265	0.000
Vole	-0.315	-0.308	0.000	-0.059	-0.189	-0.268	0.103	-0.098	-0.085	-0.057	0.290	0.094	0.096	0.122	0.208
Sheep	-0.116	-0.349	0.185	-0.297	**-0.494****	-0.268	-0.062	-0.049	0.061	-0.215	0.000	0.062	0.382**	0.268	0.306
Frost	0.195	0.095	0.103	0.149	0.065	0.135	0.000	0.104	0.103	0.157	-0.284	0.080	0.148	0.047	-0.028
Solifluction	0.048	0.047	0.150	0.023	0.080	-0.299	0.094	0.122	0.380**	0.112	-0.094	**0.422****	0.284	-0.121	-0.224
Fluvial	0.370**	0.117	0.351**	0.068	-0.060	-0.164	0.327	0.070	**0.647****	-0.219	-0.380**	0.378**	0.290	0.304	0.208
Fines	-0.201	-0.184	-0.099	-0.237	-0.141	0.033	-0.039	-0.102	0.178	0.058	0.249	0.027	0.163	-0.117	-0.289
Gravel	-0.296	0.033	-0.330	0.057	0.081	0.198	-0.243	-0.173	-0.303	0.174	0.385**	-0.327	-0.374**	-0.249	-0.258
Cobbles	-0.214	-0.033	-0.367**	-0.009	-0.094	0.052	-0.268	-0.148	**-0.509****	0.317	0.071	-0.431	**-0.453****	-0.209	0.047
Boulders	-0.054	-0.112	-0.251	-0.095	0.162	0.211	0.046	0.165	-0.272	0.225	0.143	-0.247	-0.109	-0.055	0.008
BG	-0.289	-0.105	-0.296	0.085	0.074	0.243	-0.289	-0.055	-0.317	**0.441****	0.206	-0.159	-0.122	**-0.412****	-0.289

(1) ** Correlation is significant at the 0.01 level (2 tailed).

(2) Coefficients greater than 0.400 are shown in bold and these correlations are discussed in the text.

(3) The number of sites used in this analysis is 18.

Table 6.4 (ctd): Kendall's tau correlation coefficients between environmental variables using data from the late pioneer/snowbed intermediate group

Variable	Browsing	Hare	Ptarmigan	Vole	Sheep	Frost	Solifluction	Fluvial	Fines	Gravel	Cobbles	Boulders	BG
Age													
Altitude													
Soil													
Glacier													
Slope													
East													
North													
Exposure													
Moisture													
Snowlie													
pH													
Root													
Humus													
Texture													
Grazing													
Browsing	1.000												
Hare	0.277	1.000											
Ptarmigan	0.094	-0.314	1.000										
Vole	0.000	0.143	-0.222	1.000									
Sheep	**0.561****	0.065	0.185	0.306	1.000								
Frost	-0.169	0.191	0.100	-0.149	-0.174	1.000							
Solifluction	0.063	-0.080	0.184	0.148	0.025	-0.286	1.000						
Fluvial	0.389**	**0.652****	-0.189	0.202	0.128	-0.042	0.154	1.000					
Fines	-0.009	-0.133	-0.213	0.330	0.227	-0.167	0.394**	0.059	1.000				
Gravel	**-0.412****	-0.359**	-0.047	-0.062	-0.269	-0.064	-0.024	**-0.493****	-0.053	1.000			
Cobbles	-0.244	-0.075	-0.200	-0.103	-0.267	-0.032	-0.173	-0.373**	-0.275	**0.493****	1.000		
Boulders	-0.184	-0.092	-0.178	-0.062	-0.217	**0.479****	-0.364**	-0.305	-0.053	0.033	0.059	1.000	
BG	**-0.507****	-0.300	-0.130	0.021	-0.309	0.199	0.071	**-0.421****	0.138	**0.449****	**0.472****	0.290	1.000

(1) ** Correlation is significant at the 0.01 level (2 tailed).

(2) Coefficients greater than 0.400 are shown in bold and these correlations are discussed in the text.

(3) The number of sites used in this analysis is 18.

The independent trends within the dataset suggest a mosaic of disturbance/disruption that is superimposed on consistently severe conditions at high-altitude on the north-facing flank.

6.2.5 Environmental variables in the early pioneer-heath intermediate group (5) (Table 6.5)

The decrease in the number of age-related variables, observed in the preceding group, is repeated in the early intermediate group. However, in this case, strongly correlated variables are few and no biogenic variables are age-related, but instead are central to independent gradients.

Age-related variables are altitude, glacier climate and snowlie. Older sites are at lower altitude, where late-lying snow is more frequent compared to the younger sites at higher altitude that are more likely to be exposed to the glacier climate. The sites are located predominantly towards the centre of the foreland, which maximises the confounding effect of old sites occurring at low-altitude in the foreland.

The bare ground and soil variables appear central to two independent, biogenic gradients. The frequency of bare ground increases with that of both cobbles and gravel, but the substrate types are not intercorrelated. This may differentiate sites on the fluted moraines, where the substrate is predominantly gravel, from sites at a greater distance from the central trough, where coarser substrate occurs more frequently (personal observation). Finally, soil depth is positively correlated with humus depth; a relationship that also occurs amongst the pioneer groups

6.2.6 Environmental variables in the mature snowbed group (4) (Table 6.6)

This is a mature composition that includes many sites within the regional vegetation, indicating that there is likely to be little variation in site age. However, there are, nonetheless, several age-related variables. This includes a gradient representing successional development, from well-vegetated sites with mature, deep soils on old land, to relatively sparsely-vegetated, young sites, where cobbles frequently form the substrate. There is also an age-related disturbance gradient; solifluction is more frequent on old sites and fluvial disturbance on young sites.

Several variables are related to an independent altitude gradient. Age and altitude are not positively correlated, despite these sites being located on the flanks (c.f. the late pioneer/ intermediate snowbed group), because old sites occur both at low-altitude on the north-facing flank (negative correlation between altitude and northerly aspect) and at high-altitude on the south-facing flank. High-altitude sites are associated with deep rooting depths, but are also more likely to be exposed to the glacier climate than those at low-altitude.

Finally, frost heave is negatively correlated with snowlie; there is a lower incidence of frost heave where snow is late-lying, a relationship also found amongst the pioneer sites.

6.2.7 Environmental variables in the late pioneer-heath intermediate group (3) (Table 6.7)

There are relatively few strongly correlated variables and only soil depth is correlated with age (positively). Soil depth has a number of correlated variables but these are independent of site

Table 6.5: Kendall's tau correlation coefficients between environmental variables using data from the early intermediate group

Variable	Age	Glacier	Altitude	Exposure	Gravel	Snowlie	Humus	Slope	Solifluct	East	North	Moisture	pH	Soil	Root
Age	1.000														
Glacier	**-0.624****	1.000													
Altitude	**-0.472****	**0.506****	1.000												
Exposure	-0.391**	**0.453****	0.198	1.000											
Gravel	-0.372**	0.328**	0.102	0.331**	1.000										
Snowlie	**0.468****	-0.319**	-0.222	-0.299**	-0.263**	1.000									
Humus	0.390**	-0.336**	-0.160	-0.263**	-0.307**	0.283**	1.000								
Slope	0.387**	-0.395**	-0.139	-0.376**	-0.211**	0.273**	0.256**	1.000							
Solifluction	0.309**	-0.294**	-0.071	-0.191	-0.256**	0.089	0.220	0.367**	1.000						
East	-0.005	-0.042	0.052	-0.036	-0.022	-0.048	-0.018	0.061	0.044	1.000					
North	0.247	-0.168	-0.359**	0.038	0.058	0.191	0.070	0.035	-0.039	-0.191	1.000				
Moisture	0.222	-0.173	-0.125	-0.160	-0.310**	0.169	0.256**	0.089	0.152	-0.150	0.227	1.000			
pH	-0.278**	0.189	0.213	0.209	0.232**	-0.332**	-0.294**	-0.111	-0.057	-0.001	-0.133	-0.142	1.000		
Soil	0.239**	-0.270**	-0.059	-0.386**	-0.284**	0.293**	**0.402****	0.262**	0.078	0.084	-0.138	0.132	-0.250**	1.000	
Root	0.123	-0.110	0.114	-0.244**	-0.237**	0.145	0.168	0.255**	0.215	0.129	-0.156	0.065	0.095	0.232**	1.000
Texture	0.235**	-0.227	-0.108	-0.323**	-0.165	0.187	0.175	0.124	0.108	0.062	-0.073	-0.005	-0.239**	0.216	0.182
Trampling	-0.013	-0.091	0.017	0.030	-0.124	-0.074	0.074	-0.124	-0.070	-0.141	-0.102	-0.062	0.085	-0.057	0.111
Grazing	-0.092	-0.116	0.124	-0.178	-0.194	-0.082	0.027	-0.082	0.085	0.099	-0.292**	0.030	0.091	0.231**	0.180
Browsing	0.083	-0.057	0.081	-0.082	-0.106	0.034	0.065	0.031	0.063	0.197	-0.083	0.047	0.129	-0.032	0.192
Hare	0.145	-0.198	-0.076	0.087	0.131	-0.052	0.145	0.203	0.148	-0.107	0.128	0.029	0.056	-0.055	-0.193
Ptarmigan	0.196	-0.227	-0.084	-0.134	-0.158	0.050	0.079	0.217	0.178	-0.047	-0.086	0.027	0.093	-0.005	0.131
Vole	0.170	-0.206	-0.087	-0.170	-0.059	0.120	0.174	0.071	0.164	0.113	0.108	0.243**	-0.059	0.026	0.147
Sheep	0.147	-0.039	0.022	-0.203	-0.247**	0.137	0.058	0.004	0.255**	-0.156	0.021	0.310**	0.103	-0.072	0.143
Frost	-0.152	0.191	0.005	0.135	0.231**	-0.127	-0.096	-0.152	-0.336**	-0.222	0.262**	-0.053	0.107	-0.308**	-0.089
Fluvial	0.072	-0.019	0.008	0.001	-0.241**	0.059	0.153	-0.047	-0.084	-0.013	-0.032	0.195	-0.192	0.104	0.052
Fines	0.126	-0.103	-0.211	-0.085	-0.144	0.081	0.092	-0.077	0.073	-0.142	0.244**	0.292**	-0.210	-0.056	-0.130
Cobbles	-0.143	0.057	-0.082	0.109	0.197	-0.043	-0.115	0.049	-0.033	-0.024	0.007	-0.175	0.105	-0.071	-0.036
Boulders	0.191	-0.290**	-0.141	-0.287**	-0.336**	0.228	0.171	0.242**	0.053	0.093	-0.119	-0.003	-0.198	0.279**	0.092
BG	-0.260**	0.164	-0.011	0.215	**0.430****	-0.159	-0.181	-0.067	-0.135	-0.124	0.023	-0.258**	0.149	-0.137	-0.129

(1) ** Correlation is significant at the 0.01 level (2 tailed).

(2) Coefficients greater than 0.400 are shown in bold and these correlations are discussed in the text.

(3) The number of sites used in this analysis is 76.

Table 6.5 (ctd.): Kendall's tau correlation coefficients between environmental variables using data from the early intermediate group

Variable	Texture	Tramplin	Grazing	Browsing	Hare	Ptarmig	Vole	Sheep	Frost	Fluvial	Fines	Cobbles	Boulders	BG
Age														
Glacier														
Altitude														
Exposure														
Gravel														
Snowlie														
Humus														
Slope														
Solifluction														
East														
North														
Moisture														
pH														
Soil														
Root														
Texture	1.000													
Trampling	-0.075	1.000												
Grazing	0.096	0.000	1.000											
Browsing	0.145	-0.060	0.179	1.000										
Hare	-0.107	-0.046	-0.115	-0.062	1.000									
Ptarmigan	0.052	-0.044	-0.046	-0.010	0.143	1.000								
Vole	0.124	-0.041	-0.002	-0.014	0.072	-0.011	1.000							
Sheep	-0.021	-0.071	0.177	0.303**	-0.101	0.123	0.191	1.000						
Frost	-0.225	0.193	-0.174	-0.143	-0.015	-0.105	-0.113	0.046	1.000					
Fluvial	0.099	0.312**	-0.101	0.043	-0.061	-0.151	-0.027	-0.139	-0.121	1.000				
Fines	-0.187	0.164	-0.056	-0.057	-0.007	-0.123	0.115	0.220	0.130	0.184	1.000			
Cobbles	-0.062	-0.155	-0.184	-0.209	0.117	-0.028	0.007	-0.174	-0.026	-0.107	-0.210	1.000		
Boulders	0.181	-0.163	0.071	0.078	-0.014	0.154	-0.001	-0.135	-0.240**	-0.015	-0.159	0.078	1.000	
BG	-0.213	0.065	-0.247**	-0.282**	0.132	-0.033	-0.031	-0.334**	0.142	-0.069	-0.025	**0.411****	-0.053	1.000

(1) ** Correlation is significant at the 0.01 level (2 tailed).
(2) Coefficients greater than 0.400 are shown in bold and these correlations are discussed in the text.
(3) The number of sites used in this analysis is 76.

Table 6.6: Kendall's tau correlation coefficients between environmental variables using data from the mature snowbed group

Variable	Age	Fluvial	Cobbles	Boulders	BG	Solifluct	Texture	Soil	Root	Glacier	Altitude	Slope	East	North	Exposure
Age	1.000														
Fluvial	**-0.455****	1.000													
Cobbles	**-0.583****	0.262	1.000												
Boulders	-0.391**	0.173	**0.474****	1.000											
BG	**-0.564****	0.280	**0.607****	**0.510****	1.000										
Solifluctior	**0.499****	-0.294	**-0.460****	-0.322	**-0.361****	1.000									
Texture	**0.494****	-0.260	-0.233	-0.192	**-0.364****	0.189	1.000								
Soil depth	**0.453****	-0.183	-0.338**	-0.206	**-0.343****	0.305	0.255	1.000							
Root	0.392**	-0.135	**-0.475****	-0.148	**-0.386****	0.324	0.075	**0.448****	1.000						
Glacier	0.010	-0.137	-0.152	-0.189	-0.204	0.157	0.227	0.197	0.278	1.000					
Altitude	0.216	-0.244	-0.366**	-0.313	-0.279	0.292	0.126	0.182	**0.421****	**0.609****	1.000				
Slope	-0.107	-0.033	0.024	0.076	-0.073	0.072	-0.105	0.040	0.134	0.227	0.214	1.000			
East	0.278	-0.216	-0.259	-0.089	-0.164	0.286	0.285	0.359**	0.228	0.081	0.234	0.097	1.000		
North	-0.019	0.077	0.193	0.159	0.141	-0.173	-0.052	-0.206	-0.209	-0.326	**-0.469****	-0.271	**-0.422****	1.000	
Exposure	0.055	0.065	-0.190	-0.081	-0.148	0.148	0.034	-0.082	0.025	0.118	0.203	0.322	0.130	-0.146	1.000
Moisture	-0.074	0.309	-0.051	-0.126	0.017	0.098	-0.323	-0.025	0.167	0.079	0.138	0.028	-0.003	-0.208	-0.119
Snowlie	0.055	-0.217	-0.242	-0.150	-0.137	-0.060	-0.167	0.085	0.151	0.025	0.075	-0.145	0.003	-0.023	-0.059
pH	0.068	-0.227	-0.208	0.030	-0.063	-0.005	0.018	-0.054	0.110	0.173	0.234	-0.139	0.051	-0.190	0.049
Humus	0.252	-0.270	-0.244	-0.139	-0.205	0.231	0.179	0.363**	0.301	0.173	0.270	0.149	0.318	-0.359**	0.022
Trampling	0.119	-0.112	-0.036	-0.045	-0.116	0.010	0.055	-0.152	-0.063	-0.099	-0.134	-0.145	-0.018	0.107	-0.053
Grazing	0.003	0.048	-0.265	0.012	-0.073	0.102	-0.094	0.022	0.195	-0.004	0.209	0.055	0.078	-0.273	0.305
Browsing	0.010	-0.314	-0.036	0.015	-0.018	0.150	0.013	-0.057	-0.144	0.062	0.072	0.149	0.205	-0.068	0.239
Hare	0.131	0.027	-0.140	-0.185	-0.110	0.393**	0.003	0.239	0.237	-0.089	-0.048	-0.023	0.231	0.045	-0.278
Ptarmigan	-0.028	0.338	-0.081	-0.034	-0.217	0.037	-0.234	-0.109	0.059	-0.232	-0.100	0.183	-0.042	0.096	0.304
Vole	-0.102	0.124	0.013	-0.090	0.248	0.063	-0.158	-0.235	-0.255	-0.141	-0.070	-0.194	-0.134	0.236	0.061
Sheep	0.039	-0.152	0.029	0.000	0.048	-0.131	0.008	-0.318	-0.345**	-0.321	-0.135	-0.249	-0.136	-0.010	-0.065
Frost	0.011	0.111	0.094	0.119	-0.092	0.005	0.239	-0.084	-0.113	-0.232	-0.242	0.064	-0.067	0.209	-0.015
Fines	-0.256	0.237	0.278	0.080	**0.572****	-0.161	-0.306	-0.170	-0.303	-0.356**	-0.275	-0.281	-0.200	0.137	-0.248
Gravel	-0.282	-0.073	0.192	-0.063	0.146	-0.133	0.105	-0.075	-0.147	0.170	0.172	0.036	0.075	-0.254	-0.093

(1) ** Correlation is significant at the 0.01 level (2 tailed).
(2) Coefficients greater than 0.400 are shown in bold and these correlations are discussed in the text.
(3) The number of sites used in this analysis is 30.

Table 6.6 (ctd): Kendall's tau correlation coefficients between environmental variables using data from the mature snowbed group

Variable	Moisture	Snowlie	pH	Humus	Tramplin	Grazing	Browsing	Hare	Ptarmig	Vole	Sheep	Frost	Fines	Gravel
Age														
Fluvial														
Cobbles														
Boulders														
BG														
Solifluction														
Texture														
Soil depth														
Root														
Glacier														
Altitude														
Slope														
East														
North														
Exposure														
Moisture	1.000													
Snowlie	0.031	1.000												
pH	-0.102	0.194	1.000											
Humus	0.031	0.055	-0.002	1.000										
Trampling	0.086	0.190	0.235	-0.216	1.000									
Grazing	0.102	0.068	0.311	0.224	-0.198	1.000								
Browsing	-0.077	0.048	0.193	-0.087	0.346**	0.060	1.000							
Hare	0.219	0.044	-0.214	0.045	0.250	-0.237	-0.052	1.000						
Ptarmigan	0.166	0.005	-0.137	-0.131	0.372**	0.088	0.162	0.066	1.000					
Vole	-0.069	0.143	-0.121	-0.064	-0.049	-0.054	0.118	0.093	-0.115	1.000				
Sheep	-0.193	-0.083	0.122	-0.133	0.336	-0.119	0.180	-0.243	0.093	0.106	1.000			
Frost	-0.231	**-0.413****	-0.185	-0.169	-0.081	-0.084	0.006	0.010	0.083	-0.115	-0.064	1.000		
Fines	0.147	-0.011	-0.101	-0.206	-0.093	-0.053	-0.130	0.114	-0.304	0.350**	0.053	-0.078	1.000	
Gravel	-0.183	-0.226	0.065	0.131	-0.113	-0.103	-0.131	-0.016	-0.265	-0.161	0.100	0.100	0.068	1.000

(1) ** Correlation is significant at the 0.01 level (2 tailed).

(2) Coefficients greater than 0.400 are shown in bold and these correlations are discussed in the text.

(3) The number of sites used in this analysis is 30.

Table 6.7: Kendall's tau correlation coefficients between environmental variables using data from the late intermediate group

Variable	Age	pH	Gravel	Soil	Texture	Boulders	Glacier	Altitude	Slope	East	North	Exposure	Moisture	Snowlie	Root
Age	1.000														
pH	-0.309**	1.000													
Gravel	-0.380**	0.389**	1.000												
Soil depth	**0.529****	-0.269**	-0.280**	1.000											
Texture	0.394**	-0.266**	**-0.487****	**0.476****	1.000										
Boulders	0.306**	-0.077	-0.233	0.274**	0.077	1.000									
Glacier	0.190	-0.149	0.003	0.129	0.132	0.050	1.000								
Altitude	0.202	-0.041	-0.070	0.099	0.169	0.088	**0.526****	1.000							
Slope	0.205	-0.134	-0.086	0.163	0.077	0.182	0.004	0.016	1.000						
East	-0.157	0.033	0.070	0.121	0.036	0.066	0.134	0.008	0.033	1.000					
North	0.257**	-0.267**	-0.155	0.105	0.053	0.008	0.058	-0.066	0.058	-0.121	1.000				
Exposure	-0.273**	0.120	0.175	-0.233	-0.164	-0.222	0.120	0.037	0.117	0.052	-0.024	1.000			
Moisture	-0.118	-0.323**	-0.315**	-0.062	0.211	-0.178	0.057	-0.133	0.018	0.101	0.125	0.023	1.000		
Snowlie	0.243	-0.049	-0.108	0.243	0.103	0.241	-0.027	0.050	-0.034	0.001	0.015	-0.299**	-0.150	1.000	
Root	0.245	-0.053	-0.121	0.273**	0.184	0.036	0.128	0.130	0.174	-0.001	0.072	-0.052	-0.008	0.002	1.000
Humus	0.208	-0.211	-0.194	**0.464****	0.397**	0.065	-0.128	-0.075	0.020	0.052	0.002	-0.106	0.108	0.129	0.086
Trampling	-0.224	0.057	0.006	-0.134	-0.024	-0.234	-0.098	-0.171	-0.270**	-0.067	-0.210	-0.095	0.045	-0.202	-0.187
Grazing	-0.148	0.190	0.080	-0.063	-0.080	-0.001	0.058	0.208	0.044	0.214	-0.341**	0.144	-0.091	-0.116	0.086
Browsing	-0.222	-0.019	0.011	-0.153	-0.137	-0.124	0.002	0.073	-0.115	0.166	-0.046	0.160	0.114	-0.049	0.080
Hare	0.038	0.076	0.001	0.002	-0.049	0.015	0.180	0.092	0.018	0.146	0.088	0.029	0.024	-0.083	0.077
Ptarmigan	0.232	-0.040	-0.238	0.265**	0.170	0.010	-0.089	0.010	0.074	0.093	0.046	-0.162	0.065	0.191	0.210
Vole	0.189	-0.120	-0.143	0.064	0.079	0.120	-0.084	0.018	0.192	0.074	0.143	-0.099	-0.046	-0.146	-0.046
Sheep	-0.081	0.043	-0.047	-0.079	-0.161	0.020	-0.224	-0.079	-0.178	0.019	-0.081	-0.008	0.088	0.210	-0.169
Frost	0.061	0.040	0.198	0.072	-0.106	0.095	0.068	-0.081	-0.176	-0.150	-0.004	-0.207	-0.333**	0.099	-0.080
Solifluction	0.092	0.065	-0.199	0.042	0.263	-0.141	-0.344**	-0.076	0.191	0.131	-0.033	0.079	0.085	-0.131	0.150
Fluvial	0.021	-0.394**	-0.253	0.058	0.132	-0.110	-0.072	-0.287	0.031	-0.016	0.254**	-0.093	**0.563****	0.013	0.046
Fines	-0.204	0.100	-0.007	-0.117	0.015	-0.191	-0.379**	-0.306**	-0.027	0.019	-0.089	-0.017	0.188	-0.160	-0.251**
Cobbles	-0.059	0.011	0.089	-0.080	-0.110	0.220	0.015	-0.026	0.153	-0.028	0.145	-0.028	-0.035	0.254**	0.026
BG	-0.269**	0.311**	0.350**	-0.204	-0.277**	0.151	-0.181	-0.301**	0.012	0.046	-0.109	-0.066	-0.153	0.077	-0.195

(1) ** Correlations are significant at the 0.01 level (2 tailed).

(2) Coefficients greater than 0.400 are shown in bold and these correlations are discussed in the text.

(3) The number of sites used in this analysis is 50.

Table 6.7 (ctd): Kendall's tau correlation coefficients between environmental variables using data from the late intermediate group 3

Variable	Humus	Tramplin	Grazing	Browsing	Hare	Ptarmig	Vole	Sheep	Frost	Solifluct	Fluvial	Fines	Cobbles	BG
Age														
pH														
Gravel														
Soil depth														
Texture														
Boulders														
Glacier														
Altitude														
Slope														
East														
North														
Exposure														
Moisture														
Snowlie														
Root														
Humus	1.000													
Trampling	0.018	1.000												
Grazing	-0.162	-0.103	1.000											
Browsing	-0.130	-0.107	0.298**	1.000										
Hare	-0.089	-0.128	0.059	0.085	1.000									
Ptarmigan	0.102	-0.120	-0.016	-0.041	0.396**	1.000								
Vole	-0.122	-0.086	0.171	-0.033	0.304**	0.214	1.000							
Sheep	-0.048	0.045	0.088	0.169	-0.179	0.083	0.004	1.000						
Frost	0.051	0.197	-0.257**	-0.168	-0.021	-0.128	-0.156	-0.125	1.000					
Solifluction	0.027	-0.171	0.180	0.095	0.106	0.213	0.305**	0.029	**-0.475****	1.000				
Fluvial	0.286**	0.052	-0.292**	-0.024	-0.180	-0.093	-0.126	0.051	-0.137	-0.036	1.000			
Fines	0.147	0.265**	-0.068	-0.170	-0.073	-0.005	0.056	0.060	-0.043	0.221	0.213	1.000		
Cobbles	-0.024	-0.214	-0.123	0.090	-0.117	-0.230	-0.128	-0.049	0.080	-0.162	0.186	-0.054	1.000	
BG	-0.056	0.105	-0.150	-0.205	-0.072	-0.187	-0.076	-0.046	0.237	-0.213	-0.006	0.253**	0.348**	1.000

(1) ** Correlations are significant at the 0.01 level (2 tailed).
(2) Coefficients greater than 0.400 are shown in bold and these correlations are discussed in the text.
(3) The number of sites used in this analysis is 50.

age. Mature, deep soils have a substantial surface organic layer, while immature soils are likely to have gravel as a substrate.

Both disturbance and altitude gradients are independent of age. Fluvial disturbance is correlated with moisture availability, a relationship repeated in other groups. Frost heave and solifluction are negatively correlated, suggesting that the two disturbance types occur in contrasting conditions. Finally, sites at high-altitude are more likely to be exposed to the glacier climate.

Few strongly correlated variables would be expected either where values vary little, or where relationships are inconsistent. The three compositional strands found in this group (section 5.6.3) suggest that the latter explanation is most likely.

6.2.8 Environmental variables in the species-poor heath group (2) (Table 6.8)

Once again, there are few correlated variables. Age-related variables are most numerous, with altitude, gravel, cobbles and bare ground all negatively correlated. While altitude is solely correlated with age, the bare ground/substrate variables are also intercorrelated and these coefficients are stronger than those with age. There is a gradient from young sites at high-altitude that are sparsely vegetated and have a substrate of gravel and cobbles, to older, low-altitude sites with greater vegetation cover. The relationship between the extent of bare ground and age/altitude is likely to be weakened due to extensive vegetation cover on old sites at relatively high-altitude on the flanks.

Finally, soil and humus depths are again positively correlated. In this case, the relationship indicates that the importance of organic material to soil formation is not restricted to young sites. Soil depth and the extent of vegetation cover are again not strongly correlated, suggesting that one or both have reached a near-'climax' condition.

6.2.9 Environmental variables in the species-rich heath group (1) (Table 6.9)

There are again few strongly correlated variables. Most of the sites in this group occur within the regional vegetation, and the resulting minimal variation in site age may explain the absence of age-related variables in this group.

Soil depth and the extent of bare ground provide two measures of successional development, but they are not strongly intercorrelated and therefore representing separate gradients. Soil depth is positively correlated with rooting depth, suggesting that deep-rooted shrubs occur where soil depths are greatest. However, humus depth is not correlated with soil depth on these mature sites, suggesting that other factors are of greater importance in the late stages of soil formation.

The extent of vegetation cover is strongly correlated with all four substrate types, although only boulders and cobbles are also intercorrelated. Where vegetation is sparse, the predominant substrate will be one of three types: cobbles/boulders, gravel or fines. This segregation according to substrate type may correspond to differences in site types, examples include: moraines or boulder fields, stream/river deposits and mature soils or mire sites respectively.

Table 6.8: Kendall's tau correlation coefficients between environmental variables using data from the species-poor heath group 2

Variable	Age	Altitude	Gravel	Cobbles	BG	Soil	Glacier	Slope	East	North	Exposure	Moisture	Snowlie	pH	Root
Age	1.000														
Altitude	**-0.549****	1.000													
Gravel	**-0.435****	0.306**	1.000												
Cobbles	**-0.407****	0.279**	**0.406****	1.000											
BG	**-0.491****	0.329**	**0.527****	**0.608****	1.000										
Soil depth	0.266**	-0.239**	-0.278**	-0.210**	-0.256**	1.000									
Glacier	-0.142	0.245**	0.036	0.171**	0.147	-0.152	1.000								
Slope	-0.153**	0.291**	0.061	0.117	0.135	-0.070	0.083	1.000							
East	-0.036	0.054	-0.096	-0.006	-0.064	-0.094	0.053	0.117	1.000						
North	0.076	-0.107	-0.012	-0.008	0.037	-0.112	-0.092	-0.091	-0.132	1.000					
Exposure	0.008	-0.039	0.041	-0.043	0.022	0.082	0.026	-0.181**	-0.093	0.012	1.000				
Moisture	0.201**	-0.175**	-0.298**	-0.243**	-0.257**	0.187**	-0.044	-0.132	-0.003	0.084	-0.033	1.000			
Snowlie	0.098	-0.122	-0.122	0.009	-0.039	0.136	-0.093	-0.022	-0.005	0.157**	-0.098	0.105	1.000		
pH	-0.181**	0.145	0.163**	0.111	0.142	-0.148**	0.076	0.035	0.055	-0.118	0.066	-0.061	0.042	1.000	
Root	0.140	-0.138	-0.216**	-0.159**	-0.125	0.226	0.061	-0.016	0.010	-0.017	0.076	0.062	0.041	-0.116	1.000
Humus	0.217**	-0.247**	-0.273**	-0.205**	-0.268**	**0.423****	-0.135	-0.103	-0.076	0.011	-0.002	0.245**	0.180**	-0.227**	0.228**
Texture	0.231**	-0.127	-0.191**	-0.165**	-0.166**	0.057	-0.155**	-0.014	0.036	0.091	-0.083	0.081	0.064	-0.179**	0.029
Trampling	0.086	-0.145	-0.013	-0.068	-0.058	-0.070	-0.045	-0.006	0.047	0.040	-0.223**	0.022	0.064	-0.063	-0.018
Grazing	0.135	-0.048	-0.260**	-0.275**	-0.310**	0.092	-0.090	0.025	0.144	-0.183**	0.008	0.172**	0.014	0.175**	0.097
Browsing	0.082	0.102	-0.077	-0.079	-0.100	-0.082	-0.058	0.152**	0.159**	-0.068	-0.170**	0.105	0.000	0.088	0.001
Hare	-0.028	0.129	0.093	-0.039	0.028	-0.166**	0.167**	0.046	0.057	0.139	-0.094	-0.078	-0.156**	-0.064	-0.021
Ptarmigan	0.020	-0.037	0.076	0.075	0.067	-0.120	0.210**	-0.032	0.003	0.110	0.019	-0.058	-0.001	0.030	0.031
Vole	-0.039	0.094	0.044	-0.010	0.092	0.008	0.092	0.163**	-0.035	-0.006	0.024	-0.116	-0.003	-0.009	0.068
Sheep	-0.018	0.002	0.061	-0.034	-0.014	-0.066	-0.094	-0.091	0.060	0.071	0.008	-0.034	-0.050	0.129	-0.088
Frost	-0.173**	0.024	0.263**	0.147	0.183**	-0.072	0.000	-0.150**	-0.081	0.102	0.087	-0.166**	-0.120	0.096	-0.089
Solifluction	-0.050	0.136	0.002	-0.072	0.053	-0.132	-0.001	0.095	0.082	0.041	-0.024	0.033	0.083	0.051	0.023
Fluvial	0.029	-0.043	-0.182**	-0.087	-0.072	0.046	-0.073	-0.072	-0.050	0.055	0.048	0.352**	0.030	-0.113	0.009
Fines	-0.075	-0.049	0.040	-0.059	0.124	0.002	-0.189**	0.023	-0.012	0.148**	-0.088	0.032	0.052	-0.065	-0.045
Boulders	-0.173**	0.165**	0.034	0.269**	0.375**	-0.112	0.122	0.124	0.017	-0.013	-0.003	-0.071	0.026	0.114	0.022

(1) ** Correlation is significant at the 0.01 level (2 tailed).

(2) Coefficients greater than 0.400 are shown in bold and these correlations are discussed in the text.

(3) The number of sites used in this analysis is 152.

Table 6.8 (ctd.): Kendall's tau correlation coefficients between environmental variables using data from the species-poor heath

Variable	Humus	Texture	Tramplin	Grazing	Browsing	Hare	Ptarmig	Vole	Sheep	Frost	Solifluct	Fluvial	Fines	Boulders
Age														
Altitude														
Gravel														
Cobbles														
BG														
Soil depth														
Glacier														
Slope														
East														
North														
Exposure														
Moisture														
Snowlie														
pH														
Root														
Humus	1.000													
Texture	0.151	1.000												
Trampling	0.075	0.224**	1.000											
Grazing	0.026	-0.064	-0.178**	1.000										
Browsing	-0.075	0.115	0.026	0.216**	1.000									
Hare	-0.058	0.044	-0.016	-0.127	-0.002	1.000								
Ptarmigan	-0.060	0.060	0.214**	-0.103	-0.099	0.078	1.000							
Vole	-0.149**	0.067	0.046	0.001	0.096	0.005	0.107	1.000						
Sheep	-0.172**	-0.042	0.015	0.036	0.045	-0.141	0.060	-0.037	1.000					
Frost	-0.052	-0.057	-0.049	-0.275**	-0.139	0.120	-0.026	-0.036	0.037	1.000				
Solifluction	-0.084	0.065	-0.054	0.062	0.160**	0.010	0.070	0.134	0.037	-0.236**	1.000			
Fluvial	0.163**	-0.012	0.061	0.027	0.061	-0.010	-0.021	-0.040	0.005	-0.135	-0.009	1.000		
Fines	-0.005	0.112	0.135	-0.150	-0.026	0.002	0.014	0.070	0.109	0.102	0.143	0.120	1.000	
Boulders	-0.094	-0.121	-0.164**	-0.016	0.012	-0.001	0.029	0.021	-0.098	0.004	0.021	0.053	-0.084	1.000

(1) ** Correlation is significant at the 0.01 level (2 tailed).
(2) Coefficients greater than 0.400 are shown in bold and these correlations are discussed in the text.
(3) The number of sites used in this analysis is 152.

Table 6.9: Kendall's tau correlation coefficients between environmental variables using data from the species-rich heath group

Variable	Age	Cobbles	Root	Texture	Glacier	Altitude	Slope	East	North	Exposure	Moisture	Snowlie	pH	Soil depth	Humus
Age	1.000														
Cobbles	-0.364**	1.000													
Root	0.338**	-0.098	1.000												
Texture	0.337**	-0.065	0.119	1.000											
Glacier	0.060	0.017	0.083	0.083	1.000										
Altitude	0.120	0.104	-0.046	0.229	0.195	1.000									
Slope	0.089	-0.094	0.062	0.203	0.192	0.322**	1.000								
East	0.030	0.018	-0.037	0.320**	-0.049	0.018	0.106	1.000							
North	0.023	-0.028	-0.183	0.193	-0.184	0.236	0.157	-0.053	1.000						
Exposure	-0.124	-0.047	-0.137	0.002	0.041	-0.104	-0.319**	0.169	0.053	1.000					
Moisture	0.121	-0.174	0.111	0.140	0.062	0.092	0.053	0.065	0.131	0.281	1.000				
Snowlie	-0.080	0.083	-0.002	0.106	-0.179	-0.129	-0.151	-0.002	0.071	-0.045	0.065	1.000			
pH	0.046	-0.081	0.143	-0.235	-0.178	-0.088	-0.032	-0.181	-0.066	-0.042	-0.034	0.096	1.000		
Soil depth	0.285	-0.170	**0.471****	-0.007	0.070	-0.170	-0.050	-0.261	-0.239	-0.071	0.070	0.097	0.146	1.000	
Humus	0.092	-0.110	0.289	0.034	0.128	-0.186	-0.008	-0.042	-0.244	-0.178	0.034	-0.052	-0.108	0.256	1.000
Trampling	-0.307**	0.090	-0.165	-0.183	-0.019	-0.112	-0.185	0.135	0.015	0.194	-0.223	-0.102	-0.131	-0.081	0.019
Grazing	0.013	-0.229	0.147	-0.128	-0.167	-0.236	-0.053	-0.113	-0.138	-0.158	0.054	0.104	0.347**	0.228	0.258
Browsing	0.142	-0.141	0.203	-0.192	-0.096	-0.208	0.052	-0.293	-0.147	-0.282	-0.186	0.105	0.335**	0.293	0.119
Hare	0.045	-0.006	-0.165	-0.088	-0.081	0.066	0.026	0.204	0.033	0.103	-0.051	-0.130	0.017	-0.261	-0.158
Ptarmigan	0.213	-0.028	0.039	-0.031	0.279	0.258	0.069	0.048	-0.136	-0.017	0.144	-0.063	-0.121	-0.060	-0.134
Vole	0.060	0.142	0.132	0.083	-0.019	0.060	0.146	0.157	-0.007	-0.207	-0.121	0.085	0.004	0.070	-0.053
Sheep	0.030	0.115	-0.091	0.015	-0.074	0.242	0.051	0.021	0.214	-0.189	-0.153	0.022	0.072	-0.065	-0.267
Cow	0.060	0.017	0.158	-0.070	-0.019	-0.172	0.038	-0.150	-0.097	-0.207	-0.121	0.138	-0.058	0.070	0.158
Frost	-0.297	0.313**	-0.260	-0.110	-0.048	-0.189	-0.271	0.178	0.044	0.246	-0.186	0.167	-0.086	-0.251	-0.127
Solifluctior	0.291	-0.235	0.056	-0.050	0.167	0.205	-0.001	-0.070	0.065	0.112	0.322**	0.070	0.224	0.071	-0.173
Fluvial	-0.151	0.103	-0.027	-0.023	-0.064	-0.122	-0.221	-0.138	0.060	0.145	0.369**	0.284	-0.010	0.017	0.012
Fines	-0.096	0.158	-0.276	-0.102	-0.146	0.001	-0.128	-0.157	0.238	0.061	0.069	0.228	0.052	-0.152	-0.153
Gravel	-0.043	0.138	-0.002	-0.143	-0.044	-0.168	-0.046	-0.033	0.007	0.113	0.033	0.184	-0.023	-0.085	-0.017
Boulders	-0.199	**0.416****	-0.059	-0.136	0.063	-0.062	0.103	-0.129	0.037	-0.103	-0.059	0.035	0.163	-0.104	-0.003
BG	-0.198	**0.437****	-0.173	-0.114	-0.057	-0.018	-0.094	-0.157	0.110	0.025	0.044	0.198	0.101	-0.113	-0.062

(1) ** Correlation is significant at the 0.01 level (2 tailed).

(2) Coefficients greater than 0.400 are shown in bold and these correlations are discussed in the text.

(3) The number of sites used in this analysis is 53.

Table 6.9 (ctd): Kendall's tau correlation coefficients between environmental variables using data from the species-rich heath

Variable	Trampling	Grazing	Browsing	Hare	Ptarmigan	Vole	Sheep	Cow	Frost	Solifluction	Fluvial	Fines	Gravel	Boulders	BG
Age															
Cobbles															
Root															
Texture															
Glacier															
Altitude															
Slope															
East															
North															
Exposure															
Moisture															
Snowlie															
pH															
Soil depth															
Humus															
Trampling	1.000														
Grazing	-0.167	1.000													
Browsing	-0.096	0.320**	1.000												
Hare	0.259	-0.182	-0.056	1.000											
Ptarmigan	-0.068	-0.200	-0.175	0.201	1.000										
Vole	-0.019	0.076	0.192	-0.081	-0.068	1.000									
Sheep	0.228	-0.222	0.097	0.089	0.062	-0.074	1.000								
Cow	-0.019	0.030	0.158	0.189	-0.068	-0.019	-0.074	1.000							
Frost	0.363**	-0.228	-0.242	0.127	-0.044	-0.048	0.091	-0.048	1.000						
Solifluctior	-0.093	0.137	0.126	0.001	0.240	-0.093	0.272	-0.093	-0.148	1.000					
Fluvial	-0.064	0.064	0.059	-0.005	-0.029	-0.064	-0.246	-0.064	-0.046	0.127	1.000				
Fines	0.067	0.060	0.056	-0.056	-0.224	0.178	-0.033	0.158	0.133	0.147	0.234	1.000			
Gravel	-0.044	-0.073	-0.004	0.288	-0.023	-0.044	-0.169	**0.457****	0.284	-0.072	0.160	0.116	1.000		
Boulders	-0.078	0.011	0.119	-0.044	-0.107	0.125	-0.007	0.039	0.115	-0.163	0.120	0.172	0.116	1.000	
BG	0.019	0.061	0.076	-0.072	-0.151	0.166	-0.018	0.155	0.156	0.006	0.227	**0.635****	0.143	**0.504****	1.000

(1) ** Correlation is significant at the 0.01 level (2 tailed).

(2) Coefficients greater than 0.400 are shown in bold and these correlations are discussed in the text.

(3) The number of sites used in this analysis is 53.

Finally, gravel and cow droppings are positively correlated. Cows have not been observed to cross the Leira and, therefore, did not have access to most of the study area. They were observed most often close to the river, where sparsely vegetated gravel deposits occurred in the floodplain (personal observation).

6.2.10 Summary of section 6.2

The nature of the environmental gradients

The relationships that emerge from this discussion are complex and vary over the course of the sequence. However, several consistent associations suggest the presence of four compound environmental gradients, distinguished by their functional characteristics, rather than the relatively simple age-related and microtopographic complexes found by Whittaker (1985).

(a) *Developmental variables (age, soil, humus, rooting depths, texture, pH and bare ground).*

These are principally biologically governed, and can be interpreted as varying in a broadly predictable way related to the length of time over which a site has developed. Soil depth increases and textural grain size decreases with development, while pH and bare ground (the inverse of vegetation cover) decrease. If these factors operated in consort, age would be an accurate surrogate, but site history and conditions interfere with this progressive trend (Burrows, 1990; Glenn-Lewin and van der Maarel, 1992). They reflect the level of autogenic modification that has been possible and the directional 'driving force' resulting from the presence of the plants themselves - akin to the Biological Driving Force (BDF) of Svoboda and Henry (1987; Jones and Henry, 2003).

(b) *Topographic variables (altitude, slope, aspect and exposure).*

These variables do not change in importance over the successional timespan, unless by violent perturbation. They represent measures of underlying site severity against which successional development operates. Extremely harsh conditions will delay and slow successional change in the sense of environmental resistance (Vetaas, 1997; Svoboda and Henry, 1987; Jones and Henry, 2003) and Hawker's (2000) initial conditions. However, each variable represents a continuum, from harsh to moderate conditions, with some parts of the gradient being more favourable to the vegetation. Although dominated by the effects of the coarse-scale gradients, altitude and aspect, microtopographic variables, slope and exposure, may reinforce or counteract these effects locally.

(c) *Disturbance variables (frost heave, solifluction, fluvial disturbance, grazing and browsing).*

All have the capacity to interrupt, delay, reset or enhance succession (Whittaker, 1985; Matthews and Whittaker, 1987; Matthews, 1999; Glenn-Lewin and van der Maarel, 1992). Frost and fluvial disturbance are reduced by vegetation buffering and substrate stabilisation - occurring as soil and rooting systems develop (Matthews, 1999). Grazing and browsing can severely damage plants, more subtly alter composition (Crawley, 1999), or even stimulate growth (Krebs, 1985) and the incidence of herbivory has been found to increase with biomass (Edwards and Gillman, 1987; Margalev, 1968). All are governed by a number of disparate contributory factors e.g. frost by altitude, exposure, weather conditions and soil moisture.

(d) *Moisture variables (moisture, snowlie).*

Both increase with successional development, but are causally independent of it. There is a trend towards drying with the retreat of the glacier (Ballantyne and Matthews, 1982; Whittaker, 1991; Frenot et al., 1998; Matthews, 1999), but soils retain higher levels of moisture with the accumulation of organic material (Burrows, 1990). Windier conditions at high-altitude result in snow being redeposited at lower elevation (Foskett, 1998), even though snowfall may increase with altitude generally. Both moisture and snowlie are governed spatially by local microtopography, which determines the location of channel courses, areas of waterlogging or aridity, and the accumulation of snowpatches. Extreme conditions may be perturbing early in succession, but in later stages will lead to mature site differentiation. Moderate values are most conducive to increased vegetation development.

These variables represent four interacting environmental gradients. The topographic variables generate a passive framework, which constrains the operation of autogenic, successional development. They may also increase susceptibility to disturbance (for example frost heave occurs more frequently at high-altitude and solifluction on steep slopes) and generate extreme conditions of moisture or late snowlie. However, topography may also provide protection or generate favourable conditions i.e. on south-facing slopes (Körner, 1999b), in which case successional development is enhanced. Plant-mediated processes lead to progressive successional change, which may ameliorate severity, buffer against the effects of disturbance and modify the topographic influence. Perturbing variables can destroy or damage soils and vegetation, but may stimulate growth or check dominant species (Grime, 1979; Chapin III and Körner, 1995b). They operate at a variety of spatial and temporal scales: minor disruptions are frequent while intense, extensive events have longer return times (Pickett, 1987). Where moisture/snowlie conditions are extreme, they may restrict occupation to specialist species and contribute to mature site differentiation, but more moderate levels may encourage vegetation development. The environmental conditions do not solely restrain or perturb development (Svoboda and Henry, 1987), but may reinforce or promote it (Matthews, 1992) as they represent a continuum of variation, rather than only the most severe conditions.

(1) When all of the sites were examined together, three gradients were detected in the analysis: an age-related, successional development gradient (age, bare ground/substrates and soil variables); an independent topographic gradient (altitude); and a combined moisture/disturbance gradient. The association between disturbance and moisture appears to result from differences in the causal processes underlying the disturbance variables.

(2) In the detailed examination of the correlations within individual groups, the two components of successional development (soil variables and the extent of bare ground) are frequently not strongly intercorrelated, even when they are both correlated with age (groups 4 and 7).

(3) It appears that correlations between altitude and age are coincidental and due to the spatial configuration of landforms within the study area. Three differing associations between age and altitude were found: (1) a negative relationship where sites occur mainly within the central trough (groups 2, 5, 8 and 7); (2) a positive relationship where sites occur on one flank (group 6); and (3) no strong relationship where sites occur in both locations (groups 1 and 3), or with a south-facing asymmetry so that old land occurs at both high- and low-altitude (group 4). Altitude is associated with the effects of the glacier climate (groups 3, 4 and 5), but not in the pioneer groups, where such effects are likely to be uniformly severe.

(4) Disturbance was included in the terrain-age complex as a result of Whittaker's analysis, but in this study, correlations with age are rare (only in groups 4 and 8). Apart from the relationship between fluvial disturbance and moisture (whole study area, groups 3, 6 and 8), disturbance-related variables tend to be specific to particular groups and reflect conditions in them. For example, frost heave is correlated with solifluction (group 3), altitude, pH (group 8), snowlie (positively in group 4, negatively in group 8) and boulders (positively in group 5, negatively in group 8). Correlations involving browsing/grazing occur only in group 6, despite the inhospitable location of these sites. Finally, there are no correlations involving disturbance variables in groups 1, 2 and 5. Correlations involving disturbance variables are more numerous in groups with a high proportion of sites either on the flanks (groups 3, 4 and particularly 6), or on young ground (groups 7 and 8). In these locations, slopes are likely to be steep and/or the substrate is newly deposited and consequently unstable.

(5) Although moisture occurs as part of Whittaker's microtopographic complex, correlations involving moisture are restricted spatially, in this study, to groups with sites at high-altitude on the north-facing flank (groups 3 and 6) or on young land (groups 7 and 8), perhaps due to available water sources in these locations, snowbeds on the north flank and glacier meltwater on young terrain. The relationships with fluvial disturbance and solifluction are likely to reflect causal processes. Other relationships involve substrate types (groups 6 and 8) and root/humus depth (group 6).

(6) Snowlie was also included in Whittaker's microtopographic complex, but, in this study, the variable is more frequently associated with age and altitude. Negative correlations involving snowlie occur in groups containing sites at high-altitude and/or on young land (groups 5, 7 and 8). This concurs with Foskett (1998), who found that strong winds at high-altitude result in redeposition of snow onto lower altitude, older sites. There are strong negative correlations between snowlie and frost heave in groups 4 and 8, probably due to the protection from freezing provided by the snowcover. In group 6, there is a positive correlation between snowlie and bare ground, that is reversed in group 7. It appears that late-lying snow is disappearing from the north-facing flank, while in group 7, late snowlie is associated with more extensive vegetation on older ground.

(7) Strongly correlated variables are most numerous in the pioneer groups. Additionally, age-related variables predominate in groups 7, 8, 4 and 2, while gradients independent of age are more numerous in groups 6, 5, 3 and 1. These trends apparently correspond to a greater uniformity in physical conditions in the former, compared to the latter, subdivision. Examples include a range of disturbance types (group 6), differing substrate types (groups 5 and 1) and locational differences (group 3).

6.3 Environmental influences on changes in community composition

6.3.1. Introduction

This section presents the results of the Canonical Correspondence Analysis (CCA), a direct gradient technique, which relates patterns of variation in composition to variation in the environment. The analysis is discussed using the intraset correlations between environmental variables and the ordination axes (ter Braak, 1986) and a series of biplots (section 3.8.2). The vectors indicate the direction in which each variable increases, while its length represents its importance in explaining species/community composition (ter Braak, 1986; ter Braak and Prentice, 1988). The angle between the vector and the axes indicate the importance of the variable as a contributor to the axes (ter Braak, 1987b).

This analysis uses the net change data (i.e. the differences in species frequencies between 1970 and 2000). As negative values cannot be used with this method, the resulting data have been transformed by adding a constant (250, as the lowest value was –225). This has the benefit of distinguishing ties, where a species occurred at the same frequency in both surveys and 250 is added, from species that were absent, which remain as zero.

The purpose of this analysis is to detect those variables that are associated with compositional change, to determine differences between the groups and to consider whether generalisations can be drawn that have a wider application. The sites have been classified according to their TWINSPAN group in 2000 and the analysis is of compositional change, or flux, that has occurred since 1970. The sites have also been categorised according to the type of transition i.e. progressive, stable, or retrogressive (section 5.7) to distinguish conditions associated with rapid development, with the maintenance of a particular composition and with reversals. The analysis has been carried out for the whole dataset and on a group by group basis. By applying the analysis to the individual groups, any differences that occur over the course of the successional sequence, or associated with particular locations, can also be identified. Subsequent simplification of the results involves categorising the variables according to gradient type and the scale at which they operate.

No measurement of environmental variables was made in 1970, so that net changes in them cannot be determined. Some variables, such as altitude and exposure, are constant, while for others substantial changes may have accompanied those in frequency and composition. The environmental data, therefore, represent conditions in 2000, showing the culmination of any changes occurring over the thirty years.

Most of the variables used in section 6.2 have been retained, as many facets of the environmental context may influence and shape the changes that occur and these are likely to differ according to the group examined. However, some variables were removed from the analysis in order to improve clarity. The data on droppings have not been used as the effect is localised (with regards to nutrient input) although these data may identify herbivores that are likely to be grazing particular sites. The 'cobbles' variable has also been omitted, as the clasts would otherwise sum to the bare ground total. An initial exploratory analysis showed that many of the remaining variables had some explanatory power, either in relation to the whole dataset or for particular groups. Although there is multicollinearity in several groups, this should present no practical difficulties as intraset correlations are used to determine the identity of the axes, rather than the canonical coefficients (section 3.8.5). The first assumes covariance, while the latter assumes all other environmental variables are held constant and becomes unstable in the event of multicollinearity (ter Braak, 1986, 1987b; ter Braak and Prentice, 1988). The discussion is restricted to the first two axes: subsequent axes contributed little additional information, as the eigenvalues were low, and the axes are uninterpretable.

Initially, the results for the whole study area are presented, showing site identity in terms of TWINSPAN group membership (2000) (section 5.3). Each group is subsequently considered individually, except for group 6, which contained too few sites to be used in a separate analysis. Tables of descriptive statistics (range, mean and standard deviation) are used in this discussion, as the division of the dataset reduces the range of the variables within each group and this may alter their relative meaning. For example, bare ground varies between 0 and 103 in group 1 but between 196 and 225 in group 7; a high frequency of bare ground in the former will be lower than the lowest frequency seen in the latter. In some groups, this reduction may result in the relationship being linear rather than unimodal, but the method is robust to such violations, although the explanatory power may be weakened (ter Braak, 1986) (section 3.8.5).

The final part of this section examines the explanatory power of this analysis, using the eigenvalues and the total percentage variance explained by all of the canonical and the noncanonical axes separately.

6.3.2. The whole chronosequence (Table 6.10, Figure 6.1)

Figure 6.1 is a biplot of changes in composition on the first two CCA Axes, with the sites categorized according to their TWINSPAN groups in 2000. Although there is some overlap, each group occupies a limited area of the biplot and therefore, contains a defined section of the total variation.

Axis 1

The strongest intraset correlations (Table 6.10) are with soil depth (negative) and bare ground (positive), indicating a gradient of successional maturity, from poorly developed sites with thin soils and sparse vegetation, to mature sites that have thick soils and are well-vegetated. This gradient can be interpreted as one governed by the plants themselves, corresponding to the autogenic driving force in successional development that was discussed in section 6.2.10. In Figure 6.1, clasts (particularly gravel) and pH increase with bare ground, while humus, rooting depth and texture increase with soil depth. Age also increases with soil depth, but the low intraset correlation suggests that age is a secondary influence, in contrast to its position as central to a group of variables representing successional development in section 6.2.1. Successional development is not simply a linear temporal function, but appears to have controls operating independently of age.

Altitude and glacier climate both have stronger intraset correlations with Axis 1 than age, and both increase with bare ground. However, the vectors are separated from the bare ground

Table 6.10. The full dataset: intraset correlations and canonical coefficients between the environmental variables and Canonical Correspondence Analysis Axes 1 and 2

Environmental variable	Intraset correlation Axis 1	Intraset correlation Axis 2	Canonical coefficient Axis 1	Canonical coefficient Axis 2
Age	-0.295	-0.220	0.049	-0.167
Glacier	0.391	-0.075	0.107	-0.135
Altitude	0.417	-0.149	0.186	-0.177
Slope	0.0303	-0.082	-0.017	-0.048
Aspect E	0.0110	0.024	-0.035	0.043
Aspect N	0.051	0.016	0.052	-0.031
Exposure	0.157	0.065	0.009	0.068
Moisture	-0.0144	-0.034	0.057	0.020
Snowlie	-0.072	-0.039	0.009	0.024
pH	0.302	0.026	0.035	0.042
Soil depth	-0.426	-0.156	-0.154	-0.066
Root	-0.319	-0.166	0.020	-0.014
Humus	-0.275	-0.060	-0.015	0.045
Texture	-0.251	-0.145	-0.033	-0.079
Trampling	-0.034	0.045	-0.017	0.014
Grazing	-0.276	-0.132	-0.027	-0.143
Browsing	0.040	-0.079	0.050	-0.049
Frost	0.157	0.133	-0.041	0.076
Solifluction	-0.023	-0.095	0.019	0.013
Fluvial	0.035	-0.018	0.020	-0.028
Fines	0.172	0.066	0.040	-0.001
Gravel	0.423	0.061	0.095	0.045
Boulders	0.195	0.039	0.035	0.006
Bare Ground	0.486	0.102	0.181	-0.103

Notes: Canonical Coefficients are included for reference

cluster due to their position on Axis 2 (Figure 6.1). This suggests that the topographic gradient broadly reinforces the successional development gradient, but represents an independent influence. The topographic configuration of the study area frequently coincides with the autogenic gradient, adding a spatial dimension to the temporal one represented by age. However, some older sites occur at high-altitude on the flanks, so that altitude and influence from the glacier climate do not simply increase as sites become younger. Altitude is a surrogate for a number of factors that increase in severity with elevation; for example, temperature decreases and wind speed increases (Foskett, 1998), factors which persist over time. Thus, conditions at high-altitude sites of all ages remain harsh compared to those at low-altitude.

Axis 2

A group of relatively short vectors lie close to the position of Axis 2, showing that they are influenced almost exclusively by this second gradient (Figure 6.1). These are frost heave, trampling and exposure (positive) and solifluction, slope, moisture, and browsing (negative), with frost heave and solifluction having the highest intraset correlations (Table 6.10). This indicates an independent moisture/disturbance gradient as found in section 6.2, but including different disturbance variables, that coincides with a microtopographic gradient (exposure and slope), which was not detected using the correlation coefficients in section 6.2.

Many of the vectors that are highly correlated with Axis 1 occur as diagonals, indicating that they are also influenced by the gradient represented by Axis 2. Bare ground and thin soils are associated with drier conditions and an increased frequency of frost heave, while deeper soils and extensive vegetation are related to high values for moisture and solifluction. Moisture availability and the incidence of solifluction increase, while the incidence of frost heaves decreases, with increasing site maturity, as vegetation cover expands, soils thicken and stabilizing root systems develop.

These gradients broadly represent an autogenic driving force and the various allogenic factors with which it interacts. While these allogenic factors clearly contribute to the harshness of a site or to creating conditions more conducive to plant establishment and survival, the effects appear to be more complex than this and vary depending on the overall conditions. For example, although large clasts provide shelter and trap material on the lee side, they present difficulties for ongonig colonization; additionally, they are free draining, so that sites where larger clasts predominate tend to have lower surface moisture availability.

The cluster of sites shows that a divergence in compositional change accompanies increasing maturity (Figure 6.1). Sites are separated along the successional development axis, in accordance with their level of maturity, but site separation also occurs on the moisture/disturbance gradient. Pioneer groups (7 and 8) occupy similar positions on Axis 2. Sites of the intermediate groups (3, 5 and 6) are interspersed but occupy an increasingly broad range of positions in terms of moisture/disturbance. Differentiation becomes more pronounced late in the sequence (groups 1, 2 and 4). The species-rich heath and the snowbed groups (1 and 4) have the highest levels of moisture, with the species-poor heath (group 2) lying towards the drier extreme of the gradient.

6.3.3 The individual groups

Three lines of evidence are used in this section to determine the identity of the first two CCA axes in the individual TWINSPAN groups (section 5.3). These are: (1) the CCA biplots/intraset correlations; (2) the Kendall's tau correlation coefficients (section 6.2); and (3) the descriptive statistics, which include the mean and ranges of the environmental variables that occur in each group. This identifies the variables or compound environmental gradients that correspond most strongly to the compositional changes. Additionally, the analysis provides an assessment of the physical conditions occurring in each group and examines how these conditions differ between them. Table 6.26 summarises group mean, standard deviation and ranking relative to other groups, and Table 6.27 summarises the gradients associated with each axis. The tables supplement those for the individual groups. Finally, biplots showing the species ordinations are included in the analysis in order to examine species positions in relation to the environmental gradients and to known affinities. Species centroids are used in the ordination diagrams. These represent the optima of the species response, with frequency decreasing with distance from the point (ter Braak, 1986). The highest values in this analysis will generally indicate increases in frequency but, where a species declines throughout the group, it may correspond to the smallest decrease in frequency, although this is rare. Additionally, it should be borne in mind that changes in frequency are unlikely to coincide with the highest levels of the species' populations. Instead the analysis indicates, in most cases, conditions under which the population is able to expand.

6.3.3.1 Early-pioneer group (7) (Tables 6.11, 6.12; Figure 6.2)

Axis 1

The strongest intraset correlations on Axis 1 are with fines and pH (positive) and age (negative) (Table 6.11). The bare ground (positive) and moisture/exposure (negative) vectors are closest to the position of the axis (Figure 6.2), although the intraset correlations are modest. Age was found to be central to a group of correlated variables in section 6.2, but only the relationships with pH and bare ground are reflected on this axis.

Axis 1 is therefore interpreted primarily as an age-related gradient of successional development; from young, sparsely vegetated sites to older, more extensively vegetated ones. Where the substrate is exposed, it tends to be fine-grained, glacial till. This gradient is accompanied by a fall in pH, from approximately neutral to moderately acidic (Table 6.12). Even the most extensively vegetated sites in this group have only sparse cover (Table 6.12), so that this initial decrease in pH may well reflect leaching rather than cation exchange. Although variation in age and the extent of bare ground is modest on early pioneer sites, these variables, nonetheless, are likely to reflect the primary source of variation in compositional change.

Gradients of moisture and exposure are also associated with Axis 1 and indicate conditions that vary during early colonization. Seedlings require surface moisture as they are susceptible to drought prior to the development of substantial rooting systems (section 2.8.6). Sparsely vegetated sites tend to be sheltered, while more exposed sites are older and have more

Table 6.11. TWINSPAN group 7 (early pioneer): intraset correlations and canonical coefficients between the environmental variables and Canonical Correspondence Analysis Axes 1 and 2

Environmental variables	Intraset correlations Axis 1	Intraset correlations Axis 2	Canonical coefficients Axis 1	Canonical coefficients Axis 2
Age	-0.233	-0.167	-0.239	-0.135
Glacier	0.038	0.108	-0.009	-0.187
Altitude	0.144	0.157	0.014	-0.766
Slope	0.076	-0.204	-0.111	-0.522
Aspect E	-0.113	0.189	-0.506	0.240
Aspect N	-0.043	-0.155	0.017	0.676
Exposure	-0.161	-0.005	-0.475	-0.268
Moisture	-0.144	-0.088	-0.212	-0.459
Snowlie	-0.003	0.114	0.342	-1.065
pH	0.215	0.093	0.128	-0.506
Soil depth	-0.059	-0.152	-0.255	-0.716
Root	-0.010	0.002	-0.019	0.077
Humus	-0.068	-0.074	0.601	-0.260
Trampling	-0.020	-0.241	-0.099	0.224
Grazing	0.024	0.183	-0.520	1.365
Frost	-0.067	-0.150	-0.372	0.411
Solifluction	-0.006	-0.055	0.023	0.025
Fluvial	-0.071	-0.118	-0.094	-0.263
Fines	0.233	-0.098	0.197	-0.408
Gravel	-0.024	-0.073	0.169	-0.543
Boulders	0.080	0.122	0.233	-0.415
Bare Ground	0.180	0.067	-0.340	1.184

Notes: Canonical Coefficients are included for reference

Table 6.12: Descriptive statistics for measured environmental variables on constituent sites of the early pioneer group

	Mean	Std Dev	Min	Max	Median
Age	30.17	13.87	6.00	52.00	31.50
Glacier	3.96	0.81	3.00	6.00	4.00
Altitude	1359.21	19.95	1324.00	1405.00	1355.00
Slope	10.50	6.26	2.00	23.00	10.00
Aspect E	0.23	0.67	-1.00	1.00	0.51
Aspect N	0.30	0.67	-0.99	1.00	0.56
Exposure	3.67	1.01	2.00	5.00	3.00
Moisture	1.71	0.69	1.00	3.00	2.00
Snowlie	0.46	0.93	0.00	4.00	0.09
pH	6.65	0.54	5.90	7.70	6.55
Soil depth	0.92	0.68	0.00	2.40	0.80
Root	3.93	1.28	2.00	5.90	3.80
Humus	0.32	0.29	0.00	1.20	0.20
Texture	1.00	0.00	1.00	1.00	1.00
Trampling	0.38	1.84	0.00	9.00	0.00
Grazing	0.46	1.38	0.00	6.00	0.00
Browsing	0.00	0.00	0.00	0.00	0.00
Hare	0.00	0.00	0.00	0.00	0.00
Ptarmigan	0.04	0.20	0.00	1.00	0.00
Vole	0.21	1.02	0.00	5.00	0.00
Sheep	0.83	2.78	0.00	12.00	0.00
Cow	0.00	0.00	0.00	0.00	0.00
Frost	7.46	4.85	0.00	18.00	9.00
Solifluction	0.71	2.14	0.00	8.00	0.00
Fluvial	0.29	0.91	0.00	4.00	0.00
Fines	33.04	24.95	0.00	93.00	31.00
Gravel	104.88	27.40	52.00	163.00	101.50
Cobbles	56.46	25.62	22.00	107.00	49.50
Boulders	26.04	18.68	3.00	75.00	20.50
Bare Ground	220.42	6.85	196.00	225.00	223.50

extensive vegetation cover. Shelter was found to be an important attribute of 'safe-sites' in section 2.3, but as vegetation cover increases, shelter from the plants themselves provides additional opportunities for germination/establishment (section 2.4.4).

Axis 1 is therefore influenced by three gradient types: successional development (terrain age, pH and the extent of bare ground); moisture; and microtopography (exposure).

Axis 2

Those variables with the strongest intraset correlations are grazing, east-facing aspect, altitude (positive), slope, north-facing aspect, soil depth, trampling and frost heave (negative). Grazing and trampling are closest to the position of the axis, while many of the other variables occur as diagonals, also associated with the gradient on Axis 1 (Figure 6.2). The associations between age and soil depth/altitude identified in section 6.2, are reflected on this axis, with which age is also correlated.

Three interrelated gradients are therefore interpreted as being associated with Axis 2. The first is a gradient relating age and soil depth/altitude, from young, high-altitude sites, where soils tend to be shallow, to older sites at lower altitude, where soils are likely to be deeper. The position of the diagonal altitude vector is close to that of bare ground indicating that as altitude decreases, the extent of vegetation cover tends to increase. The second is a disturbance gradient, distinguishing sites according to whether grazing or trampling predominates, with grazed sites tending to be at high-altitude and trampled ones at lower altitude. Grazing is associated with shallow soils, possibly due to effects on organic inputs. The path to the glacier crosses the area where these sites occur and the reduction in grazing may, therefore, be due to physical damage and/or the presence of people. Finally, both frost heave and slope have higher values on sites where levels of grazing are low and soils are relatively deep, despite both variables having the capacity to disrupt the substrate. Many of the variables associated with this axis may be broadly described as disturbance and (micro)topographic factors, with high values representing conditions under which progressive development is likely to be slowed or perturbed.

Soil variables and the extent of bare ground are correlated with different axes. The independence of the two gradients may reflect the minimal level of soil development and the capacity of pioneer species to establish on glacial till (personal observation).

Those sites established in 2000-01 occur to the right of Figure 6.2, indicating sparse vegetation cover and high-altitude. Those sites remaining in the group since 1970 tend to be on older land with more extensive vegetation. Most of the spread on Axis 2 occurs at the centre of the cluster and primarily involves such sites. Both extremes of the gradient represented by Axis 2 reflect conditions that are likely to retard successional development i.e. grazed sites at high-altitude and trampled, north-facing sites where frost heave occurs frequently.

Species ordinations (Figure 6.3)

There are three groupings of species in Figure 6.3; one associated with the gradient on Axis 1 and two with that on Axis 2. Early pioneer species, including *Saxifraga oppositifolia*, *S. cespitosa* and *Cardaminopsis petraea*, occur on the youngest land where vegetation is sparse (Axis 1). A gradient of species is associated with increasing age, moisture and vegetation cover, from late pioneers e.g. *Poa* spp. and *Arenaria* spp. to the intermediate shrub, *Salix glauca.* Species also occurring on older land, but as a cluster associated with deep soils and low-altitude (Axis 2), include typically later species such as the shrubs, *Empetrum hermaphroditum* and *Salix herbacea*, the grass *Festuca* spp. and the forb, *Saxifraga rivularis.* Finally, a group of predominantly grass species are associated with grazed sites at high-altitude, these include *Deschampsia cespitosa* ssp. *alpina* and *Anthoxanthum odoratum.*

Environmental conditions (Tables 6.12 and 6.26)

These are young sites, with the lowest mean age in the sequence, where successional development is slight and allogenic factors are often extreme in comparison with those in other groups. Soil development is the least advanced, and bare ground the most extensive, in the study area. The sites are dry and have high means, with small standard deviations, for altitude, glacier climate and exposure, indicating consistently adverse conditions. Low values for the duration of snowlie suggest that snow is driven off and redeposited lower down the foreland.

In terms of disturbance, these sites have the highest incidence of frost heave in the study area. However, neither fluvial disturbance nor solifluction occur frequently, perhaps due to the low level of moisture availability. Grazing has the lowest frequency in the study area. These are severe sites with little autogenic amelioration. Allogenic influences are numerous and conditions are often severe. Variation in the range of the environmental factors is limited, but differences in compositional change correspond to these small differences.

6.3.3.2 Late-pioneer group (8) (Tables 6.13, 6.14, Figure 6.4).

Axis 1

The strongest intraset correlations are with grazing (positive) and aspect north (negative), while there are also relatively high correlations with root and soil depths, aspect east (positive), and fines (negative) (Table 6.13). None of these variables were found to be strongly intercorrelated in section 6.2. The fines vector is closest to the position of the axis in Figure 6.4, while the aspect north and grazing vectors occur as opposite poles of a gradient that shows only a slight influence from the gradient on Axis 2.

Many sites with a late-pioneer composition are located on the lower slopes of the north- and south-facing flanks (section 5.3, Figure 5.8). Differences in aspect are associated with contrasting compositional changes even at this early stage in succession. Grazing is associated with the opposite pole of aspect north, so that the most heavily grazed sites tend to be south-facing. These gradients also coincide with soil and rooting depths, with deeper soils and rooted species also occurring on south-facing sites. The frequency of fines as a substrate is highest on north-facing sites where soils are thin, but as in the early pioneer group, this substrate is likely to be glacial till rather than developed soil.

This Axis is, therefore, interpreted as a topographic gradient from north- to south-facing sites, with accompanying gradients of disturbance (grazing) and successional development (soil variables).

Table 6.13. TWINSPAN group 8 (late pioneer): intraset correlations and canonical coefficients between the environmental variables and Canonical Correspondence Analysis Axes 1 and 2

Environmental variables	Intraset correlations Axis 1	Intraset correlations Axis 2	Canonical coefficients Axis 1	Canonical coefficients Axis 2
Age	-0.174	-0.285	-0.026	0.090
Glacier	0.084	0.260	0.125	0.147
Altitude	0.078	0.124	0.251	0.324
Slope	0.013	-0.187	-0.154	-0.246
Aspect E	0.230	0.055	-0.085	-0.087
Aspect N	-0.296	0.096	-0.585	0.012
Exposure	0.022	0.160	0.180	-0.068
Moisture	-0.136	-0.260	0.263	-0.168
Snowlie	0.148	-0.150	-0.106	-0.088
pH	0.134	0.097	-0.227	0.055
Soil depth	0.267	-0.168	0.359	0.154
Root	0.298	-0.145	0.214	-0.176
Humus	0.128	-0.182	-0.412	0.192
Texture	-0.069	-0.060	0.217	-0.230
Trampling	0.070	0.194	0.238	0.185
Grazing	0.332	-0.061	-0.117	-0.300
Browsing	-0.129	0.060	0.106	-0.157
Frost	-0.117	0.157	-0.197	-0.194
Solifluction	0.113	0.134	-0.266	0.136
Fluvial	-0.128	-0.157	-0.010	-0.205
Fines	-0.221	0.005	-0.116	0.211
Gravel	0.042	0.212	0.120	0.248
Boulders	0.15	-0.103	0.134	0.168
Bare Ground	0.116	0.099	0.308	-0.232

Notes: Canonical Coefficients are included for reference

Table 6.14: Descriptive statistics for measured environmental variables on constituent sites of the late pioneer group

	Mean	Std Dev	Min	Max	Median
Age	39.57	17.10	19.00	81.00	35.50
Glacier	2.71	1.63	0.00	4.00	3.50
Altitude	1354.61	32.94	1282.00	1417.00	1353.50
Slope	12.43	7.84	4.00	34.00	10.00
Aspect E	0.21	0.66	-0.99	1.00	0.16
Aspect N	0.39	0.63	-1.00	1.00	0.70
Exposure	3.11	0.92	1.00	5.00	3.00
Moisture	3.29	1.78	1.00	6.00	3.00
Snowlie	1.39	2.34	0.00	9.00	0.43
pH	6.54	0.54	5.50	7.70	6.50
Soil depth	2.24	1.87	0.40	8.50	1.65
Root	5.83	2.37	1.80	11.40	5.15
Humus	0.65	0.55	0.10	2.40	0.40
Texture	1.07	0.38	1.00	3.00	1.00
Trampling	0.07	0.38	0.00	2.00	0.00
Grazing	4.61	7.25	0.00	25.00	1.00
Browsing	5.82	11.73	0.00	51.00	0.00
Hare	0.46	1.20	0.00	5.00	0.00
Ptarmigan	0.36	1.10	0.00	5.00	0.00
Vole	1.50	3.83	0.00	17.00	0.00
Sheep	4.46	10.26	0.00	42.00	0.00
Cow	0.00	0.00	0.00	0.00	0.00
Frost	3.00	4.18	0.00	13.00	0.00
Solifluction	2.04	3.73	0.00	14.00	0.00
Fluvial	6.68	11.54	0.00	36.00	0.00
Fines	46.82	38.07	3.00	161.00	32.00
Gravel	73.68	45.82	7.00	184.00	65.00
Cobbles	52.14	26.54	9.00	99.00	56.50
Boulders	33.11	24.81	0.00	91.00	31.00
Bare Ground	205.75	27.01	131.00	225.00	216.00

Axis 2

The variables that have the highest intraset correlations with Axis 2 are glacier climate and gravel (positive) and age and moisture (negative), while several other variables are only weakly correlated. Fluvial disturbance, snowlie and glacier climate were found to be correlated with age in section 6.2, and the associations are reflected here. However, altitude was correlated with age in section 6.2, but is not correlated with these axes, although age/glacier climate does appear to relate to the topographic configuration of the study area.

Most of the vectors occur in one of two diagonal clusters (Figure 6.4). The first is interpreted as a moisture/fluvial disturbance gradient that is coincident with gradients of age/glacier climate and microtopography (exposure/slope). Older sites have higher moisture availability, but fluvial disturbance occurs more frequently and sites are likely to be steeper, compared to younger sites, which are drier, likely to have gravel as a substrate and are more exposed, particularly to the glacier climate. Each extreme is associated with variables that may delay progressive development. This gradient is interpreted as reflecting differences between sites on the flanks and those in the central trough, particularly in terms of topography, moisture and disturbance.

Although soil and root depths are most strongly correlated with Axis 1, they are also associated with the gradient on Axis 2 and, with humus/snowlie, form a further diagonal cluster. Frost heave occurs at the opposite pole of this cluster, and is, therefore, associated with thin soils and the early loss of snowcover. This second gradient is interpreted as representing variables that have an additional impact on soil development.

The cluster of sites is separated on both axes, in terms of aspect/grazing, but additionally by variation on the age/moisture to exposure/glacier climate gradient. Progressive development since 1970 occurs on the youngest land, where moisture availability is low and sites are exposed to the glacier climate. Although sites remaining in the group occur mainly on older land, where moisture availability is higher, they are more likely to be north-facing and/or have a high incidence of fluvial disturbance.

Species ordinations (Figure 6.5)

The majority of species in Figure 6.5 occur on a diagonal that follows the line of the age gradient. Early pioneers are associated with young land and are exposed to the glacier climate e.g. *Saxifraga oppositifolia* and *S. cespitosa.* There is a cluster of species on slightly older land, associated with the frost heave and aspect north variables. This cluster includes the late pioneer species *Salix herbacea*, *Poa* spp. and *Oxyria digyna.* On older land and associated with increasing moisture availability, there is a linear sequence of typically later-occurring and moisture requiring species including *Salix glauca*, *Saxifraga stellaris*, *Saxifraga rivularis* and *Salix lanata.*

Environmental conditions (Tables 6.14, 6.26)

Conditions at sites in this group are frequently only slightly less severe than those in the early pioneer group (Table 6.26). These are also consistently young sites, at high-altitude, with little evidence of autogenic amelioration i.e. there has been little soil or vegetation development. Levels of exposure and the influence of the glacier climate are high and protective, late-lying snow is infrequent. Furthermore, sites are more likely to face north than those in the early pioneer group and this group has the highest mean for browsing in the study area, although there is little evidence of grazing. There is a high incidence of vole and sheep droppings, which may be related to the high frequency of browsing. Finally, these sites have the highest mean for moisture availability in the study area and this is associated with a high incidence of fluvial disturbance.

6.3.3.3 Late pioneer/snowbed intermediate group (6) (Tables 6.15, 6.26)

There are too few sites in this group in 2000 to run the CCA analysis (n = 18 sites). However, the descriptive statistics can be used to obtain an impression of the environmental conditions amongst sites of this group.

67% of sites change little compositionally between 1970 and 2000, while retrogressive transitions account for 28% of the sites in 2000, compared to only one site (6%) that has progressed to this composition. This is the highest proportion of retrogressive transitions in the study area and it is the only group where retrogression is a stronger trend than progression.

While this group contains predominantly old sites, mean age is the third highest in the study area, physical conditions are in several respects the most severe (Tables 6.15, 6.26). The means for slope, aspect north and altitude are the highest in the study area, as are those for both boulders and cobbles. Therefore, conditions associated with harsh topography are frequently combined with an inhospitable substrate, reflecting the presence of closely-spaced moraines at high-altitude on the north-facing flank. However, the moraines also provide shelter and the mean for exposure is the lowest in the study area. Additionally, only the late intermediate and snowbed groups have greater evidence of late-lying snow.

Despite the severity of these conditions, only the species-rich heath and the snowbed endpoint groups have deeper soils, although humus and rooting depths are relatively shallow. With reference to disturbance, browsing and solifluction have high means, but fluvial disturbance and frost heave occur infrequently. The incidence of hare and vole droppings are also high compared to other groups, although sheep droppings are ranked fourth.

On many of these sites, the apparently immature composition is, therefore, the result of a long period of successional development under harsh physical conditions. This conforms with the views of several authorities concerning vegetation development at high-altitude (e.g. Matthews, 1976, 1992).

6.3.3.4 Early pioneer-heath intermediate group (5) (Table 6.16, 6.17, Figure 6.6)

Axis 1

The strongest intraset correlations on Axis 1 are with soil depth (negative) and the extent of bare ground (positive), while there are moderate correlations with rooting depth, grazing, slope (negative), exposure and gravel (positive) (Table 6.16). Gradients involving soil depth and bare ground were identified in section 6.2, but were independent both of each other and of age. The only relationship reflected in this analysis is that between bare ground and gravel. Bare ground

Table 6.15: Descriptive statistics for measured environmental variables on constituent sites of the late pioneer/snowbed intermediate group

	Mean	Std Dev	Min	Max	Median
Age	2129.44	3779.25	40.00	9000.00	206.00
Glacier	0.50	0.92	0.00	3.00	0.00
Altitude	1365.50	82.14	1224.00	1525.00	1370.00
Slope	23.72	12.58	5.00	55.00	20.50
Aspect E	0.11	0.45	-0.91	0.67	0.09
Aspect N	0.79	0.43	-0.81	1.00	0.96
Exposure	2.17	0.92	0.00	3.00	2.00
Moisture	2.78	1.11	1.00	6.00	3.00
Snowlie	2.18	1.36	0.11	4.00	2.33
pH	6.00	0.19	5.50	6.20	6.05
Soil depth	8.41	8.05	1.20	28.60	4.65
Root	6.33	3.81	2.10	18.40	6.25
Humus	1.00	0.88	0.20	2.80	0.70
Texture	1.89	0.96	1.00	4.00	2.00
Trampling	0.00	0.00	0.00	0.00	0.00
Grazing	4.44	7.67	0.00	26.00	0.00
Browsing	2.67	7.25	0.00	30.00	0.00
Hare	3.39	9.85	0.00	42.00	0.00
Ptarmigan	0.28	0.67	0.00	2.00	0.00
Vole	1.06	2.67	0.00	10.00	0.00
Sheep	3.22	10.82	0.00	46.00	0.00
Cow	0.00	0.00	0.00	0.00	0.00
Frost	3.56	4.42	0.00	12.00	0.00
Solifluction	4.72	5.84	0.00	17.00	0.00
Fluvial	1.06	2.67	0.00	10.00	0.00
Fines	31.72	26.82	0.00	87.00	28.00
Gravel	25.28	18.37	0.00	58.00	21.50
Cobbles	60.17	34.11	0.00	129.00	55.50
Boulders	56.89	28.14	1.00	107.00	58.00
Bare Ground	174.00	59.45	47.00	223.00	203.50

Table 6.16. TWINSPAN group 5 (early intermediate): intraset correlations and canonical coefficients between the environmental variables and Canonical Correspondence Analysis Axes 1 and 2

Environmental variables	Intraset correlations Axis 1	Intraset correlations Axis 2	Canonical coefficients Axis 1	Canonical coefficients Axis 2
Age	-0.115	-0.014	0.089	0.065
Glacier	0.085	0.199	-0.162	0.032
Altitude	-0.116	0.278	-0.038	0.146
Slope	-0.225	-0.114	-0.175	-0.007
Aspect E	-0.070	0.026	-0.045	-0.007
Aspect N	0.164	-0.138	0.053	-0.036
Exposure	0.236	0.156	0.062	0.083
Moisture	-0.021	-0.094	-0.028	0.047
Snowlie	-0.125	-0.175	-0.084	-0.009
pH	0.018	0.244	-0.032	0.089
Soil depth	-0.254	-0.069	-0.090	0.034
Root	-0.242	-0.011	0.008	-0.147
Humus	-0.165	-0.161	-0.011	-0.107
Texture	-0.149	0.019	-0.123	0.099
Trampling	0.046	0.025	-0.056	0.064
Grazing	-0.229	0.028	-0.115	0.126
Browsing	-0.086	0.025	-0.018	0.053
Frost	0.187	0.034	0.049	0.085
Solifluction	-0.166	-0.005	-0.018	0.131
Fluvial	0.041	0.023	0.071	0.054
Fines	0.095	-0.127	0.026	-0.137
Gravel	0.227	0.146	0.139	-0.018
Boulders	-0.075	-0.078	0.099	-0.029
Bare Ground	0.243	0.027	0.010	0.097

Notes: Canonical Coefficients are included for reference

Table 6.17: Descriptive statistics for measured environmental variables on constituent sites of the early intermediate group

	Mean	Std Dev	Min	Max	Median
Age	316.33	1437.86	30.00	9000.00	62.50
Glacier	1.41	1.81	0.00	4.00	0.00
Altitude	1312.61	55.35	1185.00	1459.00	1327.50
Slope	16.75	10.01	2.00	39.00	15.50
Aspect E	0.34	0.55	-0.99	0.99	0.51
Aspect N	0.22	0.74	-1.00	1.00	0.55
Exposure	2.88	1.28	1.00	5.00	3.00
Moisture	2.63	1.24	1.00	6.00	2.00
Snowlie	1.66	1.95	0.07	9.00	0.67
pH	6.03	0.49	4.60	7.20	6.00
Soil depth	3.96	4.28	0.20	26.70	2.45
Root	6.05	2.79	1.50	20.40	5.70
Humus	0.91	0.68	0.10	3.40	0.80
Texture	1.39	0.63	1.00	3.00	1.00
Trampling	0.08	0.69	0.00	6.00	0.00
Grazing	5.79	11.72	0.00	78.00	1.00
Browsing	1.86	4.95	0.00	23.00	0.00
Hare	0.68	2.48	0.00	17.00	0.00
Ptarmigan	0.32	1.04	0.00	7.00	0.00
Vole	0.72	3.53	0.00	29.00	0.00
Sheep	3.47	7.61	0.00	38.00	0.00
Cow	0.00	0.00	0.00	0.00	0.00
Frost	4.33	5.40	0.00	19.00	0.00
Solifluction	2.59	4.75	0.00	18.00	0.00
Fluvial	1.72	6.23	0.00	36.00	0.00
Fines	31.74	29.30	0.00	199.00	25.50
Gravel	48.62	39.18	0.00	155.00	42.50
Cobbles	56.18	27.16	0.00	125.00	53.50
Boulders	45.42	32.46	0.00	136.00	34.50
Bare Ground	181.96	43.57	14.00	224.00	198.00

and rooting depth are the closest vectors to the position of Axis 1 in Figure 6.6. The frost heave vector coincides with that of bare ground, although the intraset correlation is modest.

Soil/rooting depth and bare ground occur as opposite poles of Axis 1, indicating that it represents a gradient of successional development. The highest level of grazing occurs on the most extensively vegetated sites, and these sites have the deepest soils and rooted species in the group. However, these more highly developed sites are also on the steepest sloping land. Flatter land is associated with extensive bare ground, higher levels of exposure, a high incidence of frost heave and gravel as a substrate. This description appears to identify sites on the fluted moraines (c.f. section 6.2) where development has been slow (section 4.3), while more highly developed sites occur on sloping land outside the central trough. Gravel as a substrate is moderately fine-grained, but is free-draining and likely to offer few 'safe-sites' for germination or establishment.

Axis 1 is therefore interpreted as a gradient of successional development that combines soil and vegetation components. There are also associated gradients of microtopography (exposure/slope) and disturbance (frost heave/grazing).

Axis 2

The strongest intraset correlations on Axis 2 are snowlie (negative) and altitude (positive), while there are moderate correlations with humus depth, aspect north (negative), pH and glacier climate (positive). Exposure and gravel are more strongly correlated with Axis 1 (Table 6.16).

The pH vector lies closest to the position of Axis 2, while the other vectors occur as diagonals, indicating varying levels of association with the gradients on Axis 1 (Figure 6.6). High-altitude sites tend to be more advanced, compared to those at low-altitude, and are also more likely to be south-facing. Sites where there is evidence of late-lying snow tend to have deeper soil/more extensive vegetation cover, deeper humus and are less exposed, particularly to the glacier wind, than those where snow does not accumulate.

This axis is interpreted as combining gradients of topography (altitude/aspect) and microtopography/snowlie, that are also related to the extent of successional development (Axis 1).

The cluster of sites in this group are separated along Axis 1 in terms of successional development, with compositional changes that represent progression predominantly associated with shallow soils/sparse vegetation (Figure 6.6). In contrast, compositional changes representing both retrogression and stability are more widely distributed on Axis 1, but concentrated towards the pole indicating deeper soils/extensive vegetation. The separation on Axis 2 is also appreciable. Sites developing progressively generally occupy higher positions on the Axis i.e. where altitude, exposure to the glacier climate and pH have the highest values, but where late-lying snow is infrequent. Compositional changes representing retrogression and stability tend to be lower on this Axis i.e. at lower altitude, where snow is more likely to be late-lying.

Species ordinations (Figure 6.7)

Many of the species positions in Figure 6.7 reflect differences between sites on the fluted moraines and those on the flanks. Changes in frequency amongst a group of predominantly shrub species, e.g. *Empetrum hermaphroditum*, *Salix glauca* and *Vaccinium myrtillus*, occur on sparsely vegetated, exposed sites where gravel is the predominant substrate (the fluted moraines). Interspersed with these shrubs are late pioneer species such as *Oxyria digyna*, *Poa* spp. and *Trisetum spicatum*, indicative of the harsh conditions at this location. A further group of shrubs, including *Cassiope hypnoides*, *S. lanata* and *Phyllodoce caerulea*, are associated with north-facing aspect, low-altitude and fines as a substrate. A group of pioneer species, associated with land exposed to the glacier climate, occur in a linear sequence from early species such as *Saxifraga cespitosa* and *S. oppositifolia*, through *Cardaminopsis petraea* and *Arenaria* spp. to typically late pioneers such as *Cerastium cerastoides* and *Salix herbacea* as exposure decreases.

Environmental conditions (Tables 6.17, 6.26)

These sites are young and development is commensurate with an early successional stage. The low mean values for soil variables, the extent of vegetation cover and for age indicate that this group is only marginally more advanced than the pioneer groups. Similarly, exposure, glacier climate and the incidence of frost heave are only more severe on pioneer sites. However, the relatively high frequency of boulders may provide shelter at a site-scale.

On the other hand, the low mean values for altitude and aspect north indicate conditions conducive to rapid successional development. This is consistent with this being one of the core stages on the heath trajectory and a transition to the species-poor heath occurring on some of these sites over the next 30 years. The high incidence of fluvial disturbance and, particularly, frost heave, together with the inhospitability of the fluted moraines for plant establishment and growth may, however, impede rapid development.

6.3.3.5 Mature snowbed group (4) (Tables 6.18, 19, Figure 6.8)

Axis 1

The only variable with an intraset correlation exceeding 0.2 on Axis 1 is soil depth, and even this variable is marginally more strongly correlated with Axis 2. An age-related gradient of successional development/disturbance and an independent altitude-related gradient were identified in section 6.2. Both of these gradients occur in Figure 6.8, but as diagonals indicating a joint influence from both axes.

The frost heave and trampling vectors are closest to the position of the axis, and while both are short, the intraset correlations are higher than those with Axis 2. Other variables with higher intraset correlations on Axis 1, compared to Axis 2, are aspect east, grazing (negative), fines and gravel (positive). Although these correlations are modest, all of the vectors are close to the position of the axis.

Axis 1 is therefore interpreted as a disturbance gradient that is related to variation in soil depth. The deepest soils occur on east-facing sites where the frequency of trampling and grazing

Table 6.18. TWINSPAN group 4 (mature snowbed): intraset correlations and canonical coefficients between the environmental variables and Canonical Correspondence Analysis Axes 1 and 2

Environmental variables	Intraset correlations Axis 1	Intraset correlations Axis 2	Canonical coefficients Axis 1	Canonical coefficients Axis 2
Age	-0.194	0.249	-0.403	0.142
Glacier	0.046	0.154	-0.574	-0.114
Altitude	0.111	0.232	0.968	0.037
Slope	-0.011	-0.020	-0.161	0.018
Aspect E	-0.141	0.097	-0.229	-0.306
Aspect N	0.016	-0.118	0.068	0.067
Exposure	0.004	-0.024	0.162	0.071
Moisture	0.038	-0.007	-0.019	0.102
Snowlie	-0.035	-0.038	0.053	0.077
pH	-0.089	-0.053	-0.160	-0.140
Soil depth	-0.239	0.241	0.082	-0.103
Root	-0.071	0.224	-0.077	0.321
Humus	-0.097	0.220	-0.168	0.207
Texture	-0.167	0.243	0.297	0.465
Trampling	-0.077	0.006	0.063	0.016
Grazing	-0.129	-0.097	-0.183	-0.286
Browsing	-0.039	-0.197	0.238	0.291
Frost	0.104	-0.004	-0.076	-0.206
Solifluction	-0.012	0.137	0.311	0.059
Fluvial	0.115	-0.125	0.185	0.186
Fines	0.122	-0.114	-0.147	1.088
Gravel	0.142	0.100	0.058	0.436
Boulders	0.024	-0.200	-0.097	0.624
Bare Ground	0.140	-0.198	0.413	-1.195

Notes: Canonical Coefficients are included for reference

Table 6.19: Descriptive statistics for measured environmental variables on constituent sites of the mature snowbed group

	Mean	Std Dev	Min	Max	Median
Age	6060.10	4228.77	138.00	9000.00	9000.00
Glacier	0.37	0.72	0.00	2.00	0.00
Altitude	1322.20	101.05	1158.00	1486.00	1325.50
Slope	18.37	8.36	4.00	38.00	17.00
Aspect E	0.51	0.46	-0.93	0.99	0.63
Aspect N	0.36	0.65	-0.98	1.00	0.61
Exposure	2.20	0.89	1.00	4.00	2.00
Moisture	2.83	1.09	1.00	6.00	3.00
Snowlie	2.58	1.73	0.43	9.00	2.33
pH	5.34	0.38	4.70	6.10	5.40
Soil depth	16.12	6.77	4.20	29.20	16.60
Root	11.33	4.49	4.80	19.30	10.60
Humus	2.75	2.01	0.60	9.80	2.30
Texture	2.77	1.01	1.00	5.00	3.00
Trampling	0.10	0.55	0.00	3.00	0.00
Grazing	7.33	9.47	0.00	34.00	3.50
Browsing	0.93	2.45	0.00	10.00	0.00
Hare	3.60	7.26	0.00	24.00	0.00
Ptarmigan	0.67	2.11	0.00	11.00	0.00
Vole	0.13	0.57	0.00	3.00	0.00
Sheep	5.37	20.15	0.00	110.00	0.00
Cow	0.00	0.00	0.00	0.00	0.00
Frost	1.13	2.89	0.00	9.00	0.00
Solifluction	6.53	7.11	0.00	27.00	6.00
Fluvial	1.63	2.88	0.00	9.00	0.00
Fines	19.63	29.39	0.00	136.00	6.50
Gravel	0.87	1.57	0.00	6.00	0.00
Cobbles	12.20	13.37	0.00	46.00	6.00
Boulders	16.60	15.94	0.00	55.00	11.50
Bare Ground	49.30	44.15	1.00	201.00	40.50

is high. As soil depth decreases, frost heave becomes more frequent and gravel or fines are increasingly likely to form the substrate.

Axis 2

The highest intraset correlations on Axis 2 are with age (positive) and boulders/bare ground (negative), while there are moderate correlations with glacier climate, altitude, all the soil variables, solifluction (positive) and browsing (negative). The age- and altitude-related gradients, identified in section 6.2, are most strongly correlated with this axis, but occur as two diagonals. A disturbance/topographic gradient lies closest to the position of Axis 2 (Figure 6.8), comprising solifluction at one pole with boulders/aspect north at the other.

Contrasting environmental conditions appear to underlie differences in compositional changes in this group. Mature snowbed sites occur at two locations in the study area: at mid- to high-altitude on the south-facing flank and at low-altitude on that facing north (section 5.3, Figure 5.8). The position of the altitude vector, perpendicular to a gradient of successional development, suggests that these differences in location are associated with alternative trends in compositional change. The shorter vectors, more directly associated with the axes, are interpreted as environmental factors operating at a finer-scale within the particular locations. For example, the highest frequencies of solifluction in this group occur on south-facing land, where the frequency of boulders is low. Such sites tend to be at high-altitude, have deep soils and deeply rooted species. Similarly, sites where development is low i.e. there is extensive bare ground and soils are shallow, tend to be north-facing and are likely to be at low-altitude.

Sites undergoing progressive compositional changes are separated from sites that remain identified with the group since 1970 in Figure 6.8. The latter occur above the origin on Axis 2 and along the length of Axis 1, although sites tend to be concentrated at each extreme. This indicates two trends within the data: high-altitude sites where gravel frequently forms the substrate, there is a high incidence of frost heave and soils/vegetation are moderately developed; and mid-altitude sites, where soils are deep, vegetation cover is extensive and solifluction or trampling are frequent. Compositional changes on sites newly identified with this group in 2000 are associated with a similar altitudinal range, but vegetation tends to be sparse, soils to be thin and sites are more likely to face north.

Species ordinations (Figure 6.9)

Changes in frequency amongst typical snowbed forbs e.g. *Anthoxanthum odoratum*, *Hieracium alpinum* and *Leontodon autumnalis* occur at mid-altitude on old land that tends to face south. Adjacent to this cluster is another group of mainly forb species, including *Veronica alpina*, *Bartsia alpina* and *Cerastium cerastoides*. Changes in frequency amongst the latter species are associated with grazing, trampling and lower altitude compared to the former. Both clusters comprise low-stature species that occur predominantly on south-facing sites, the division appears to distinguish the species-rich snowbed composition from a lower altitude variant, subject to more extensive disturbance.

Most of the shrubs follow a gradient parallel to Axis 2, from high-altitude, south-facing sites to low-altitude, north-facing sites, where vegetation is sparse. This involves a progression from

Cassiope hypnoides, *Salix herbacea* and *Empetrum hermaphroditum* at the high-altitude extreme, *Phyllodoce caerulea*, *Vaccinium myrtillus* and *V. uliginosum* at mid-altitude to *Betula nana*, *S. glauca* and *S. lanata* at low-altitude on north-facing land.

Environmental conditions (Tables 6.19, 6.26)

In several respects, these snowbed sites have a similar level of maturity to that found in the species-rich heath e.g. soil variables and the extent of bare ground. However, the community is of lower stature than the species-rich heath (section 5.3), and this is associated with high mean altitude, higher frequency of solifluction and the longer duration of snowlie in the snowbed group. Additionally, although neither grazing nor browsing are extensive, there is a high incidence of hare, ptarmigan and sheep droppings, hare and sheep droppings have the highest means in the study area.

6.3.3.6 Late pioneer-heath intermediate group (3) (Tables 6.20, 6.21, Figure 6.10)

Axis 1

The strongest intraset correlation on Axis 1 is with pH (positive) and soil depth (negative), while there are moderate correlations with gravel (positive), slope, humus depth and texture (negative) (Table 6.20). This reflects the relationships with soil depth identified in section 6.2, except those with age, which is not strongly correlated with either of these axes. The gravel and texture vectors are closest to the position of the axis in Figure 6.10.

This axis is primarily associated with a gradient of soil depth and maturity that coincides with that of slope. Deep, mature soils, with low pH, occur more frequently on steeper sites, while shallow soils are associated with moderate slopes, where there is a higher incidence of gravel as a substrate. These differences may reflect conditions in the spatially determined, compositional strands comprising this group, with deeper soils on the sloping land of the flanks.

Axis 1 is interpreted as a gradient of increasing soil maturity (a component of successional development) combined with one representing microtopography (slope).

Axis 2

The strongest intraset correlations on Axis 2 are with moisture (negative) and altitude (positive), while there are moderate correlations with humus depth, fluvial disturbance, fines (negative), pH and rooting depth (positive). Humus depth and pH are more strongly correlated with Axis 1. Altitude and moisture/disturbance gradients were detected in section 6.2, but were not intercorrelated. Therefore, although the altitude and moisture vectors occur as the two poles of Axis 2 (Figure 6.10), it appears that the two gradients are independent.

Sites at low-altitude tend to have higher moisture availability, but also a higher frequency of fluvial disturbance compared to the relatively dry sites that occur at high-altitude. Humus depth and the frequency of fines as a substrate also tend to be higher on low-altitude/moist sites, while deeper-rooted species occur at high-altitude.

Axis 2 is interpreted as a topographic gradient (altitude) that coincides with a gradient of moisture/disturbance (fluvial).

Table 6.20. TWINSPAN group 3 (late intermediate): intraset correlations and canonical coefficients between the environmental variables and Canonical Correspondence Analysis Axes 1 and 2

Environmental variables	Intraset correlation Axis 1	Intraset correlation Axis 2	Canonical coefficients Axis 1	Canonical coefficients Axis 2
Age	-0.073	0.048	0.151	-0.088
Glacier	0.080	0.059	-0.058	-0.104
Altitude	0.027	0.248	0.030	0.364
Slope	-0.253	0.122	-0.146	0.021
Aspect E	-0.012	0.017	0.161	0.101
Aspect N	-0.085	0.005	-0.062	0.068
Exposure	0.130	0.010	0.079	0.021
Moisture	-0.029	-0.278	0.034	-0.283
Snowlie	-0.149	0.025	-0.129	-0.109
pH	0.242	0.188	0.224	0.133
Soil depth	-0.363	0.084	-0.291	0.051
Root	-0.169	0.186	0.018	0.132
Humus	-0.243	-0.147	-0.066	-0.148
Texture	-0.283	-0.026	-0.106	-0.063
Trampling	0.054	-0.116	-0.177	-0.096
Grazing	0.011	0.076	-0.051	-0.052
Browsing	-0.002	0.028	-0.060	-0.063
Frost	0.039	0.063	0.158	0.125
Solifluction	-0.179	-0.010	-0.118	-0.053
Fluvial	-0.146	-0.225	0.158	0.243
Fines	-0.031	-0.200	0.014	-0.009
Gravel	0.222	0.025	-0.084	-0.201
Boulders	-0.098	0.120	-0.0270	-0.012
Bare Ground	0.036	0.000	-0.093	0.057

Notes: Canonical Coefficients are included for reference

Table 6.21: Descriptive statistics for measured environmental variables on constituent sites in the late intermediate group

	Mean	Std Dev	Min	Max	Median
Age	1380.44	3106.13	50.00	9000.00	163.00
Glacier	0.34	0.80	0.00	4.00	0.00
Altitude	1330.48	79.60	1171.00	1537.00	1325.00
Slope	19.60	10.46	3.00	42.00	20.00
Aspect E	0.09	0.64	-0.97	0.99	0.21
Aspect N	0.42	0.65	-0.96	1.00	0.74
Exposure	2.40	0.99	0.00	5.00	3.00
Moisture	2.96	1.46	1.00	6.00	2.00
Snowlie	2.21	1.99	0.11	9.00	1.50
pH	5.84	0.51	4.60	7.00	5.80
Soil depth	6.85	4.95	0.40	21.70	6.05
Root	6.74	2.61	2.40	13.30	6.15
Humus	1.36	1.20	0.10	6.30	1.15
Texture	2.12	1.00	1.00	4.00	2.00
Trampling	1.08	5.41	0.00	31.00	0.00
Grazing	6.54	8.03	0.00	35.00	4.00
Browsing	1.00	2.52	0.00	13.00	0.00
Hare	1.52	3.85	0.00	18.00	0.00
Ptarmigan	1.40	6.66	0.00	47.00	0.00
Vole	0.36	1.08	0.00	6.00	0.00
Sheep	1.58	4.63	0.00	29.00	0.00
Cow	0.00	0.00	0.00	0.00	0.00
Frost	4.14	5.15	0.00	19.00	0.50
Solifluction	3.98	5.25	0.00	18.00	0.50
Fluvial	3.38	8.56	0.00	33.00	0.00
Fines	34.50	30.57	0.00	167.00	28.50
Gravel	34.54	33.60	0.00	147.00	25.00
Cobbles	46.54	21.22	2.00	89.00	48.00
Boulders	40.16	28.01	2.00	156.00	37.50
Bare Ground	155.74	42.97	33.00	218.00	158.50

Compositional changes are differentiated according to the type of transition that has occurred since 1970 (Figure 6.10). Where sites have undergone progressive transitions, they generally occur towards the shallow soil/extensive gravel pole of Axis 1, and towards the high moisture/low-altitude pole of Axis 2. However, a few of these sites occur at higher altitude, including those previously identified with group 6. Sites where retrogression has occurred also have high moisture availability (Axis 2), but soils tend to be deeper (Axis 1). Sites remaining in the group since 1970 are also associated with deep soils, but the majority are at high-altitude where moisture levels are lower. The compositional changes are separated on both axes, but separation on Axis 2 is greater amongst sites with deeper soils, possibly due to increasing differentiation of the various site types with increasing maturity.

Species ordinations (Figure 6.11)

Changes in species frequency in this group reflect differences between conditions in the central trough from those on the flanks. Frequency changes among shrub species occur on a gradient from moist, shallow soils (intermediate *Salix* spp.) to thicker but drier soils and steeper slopes (*Cassiope hypnoides* and *Phyllodoce caerulea*) with *Empetrum hermaphroditum* positioned close to the origin. This reflects the separation between central, early heath-type sites and the presence of later heath species on the flanks (particularly that facing north). A number of snowbed forbs are also associated with the steeper slope and deeper soil extreme e.g. *Gnaphalium supinum*, *Leontodon autumnalis* and *Veronica alpina.* These forbs were predominantly associated with south-facing sites (section 5.4) suggesting that this grouping combines species from both flanks.

Pioneer species are divided between those at high-altitude e.g. *Ranunculus glacialis* and *Trisetum spicatum* and a larger group associated with thin soils and gravel as a substrate e.g. *Arenaria* spp. and *Cerastium cerastoides.* Early species such as *Saxifraga cespitosa* do not occur in this ordination.

Environmental conditions (Tables 6.21, 6.26)

The values of several variables are consistent with the intermediate level of successional development suggested for these sites (section 5.3). These include pH, bare ground, rooting and humus depths. However, mean values of age and texture are higher than in the species-poor heath (Table 6.26). This disparity may be the result of the inclusion of mature sites at high-altitude on the north-facing flank.

Against this background of relative maturity, environmental conditions are frequently severe. Only the pioneer and the late pioneer-snowbed intermediate groups have higher mean values for altitude and mean values for slope and aspect north are only exceeded in the latter (Table 6.26). Moisture levels and the duration of snowlie are amongst the highest in the study area, and associated with this is a high incidence of fluvial disturbance, possibly the result of flushing. Steep slopes and high moisture levels are likely to underlie the high frequency of solifluction. There is also a high incidence of frost heave, the third disturbance variable. However, frost heave and solifluction were negatively correlated in section 6.2 and different conditions generate each disturbance type (sections 3.2.15 and 3.2.16). At least some of these perturbing variables may, therefore, be segregated on different sites, possibly reflecting conditions in the individual compositional strands.

Frequent disturbance, steep slopes, late snowlie, high-altitude and north-facing aspect combine to produce generally harsh conditions.

6.3.3.7 Species-poor heath group (2) (Tables 6.22, 6.23, Figure 6.12)

Axis 1

The strongest intraset correlations are with humus (negative) and bare ground (positive), while there are moderate correlations with age, soil depth, moisture (negative), and altitude (positive) (Table 6.22). Bare ground and altitude are, however, more strongly correlated with Axis 2. Age was found to be correlated with altitude and bare ground in section 6.2, but was not strongly related to the soil variables. The soil/humus depth, age and moisture vectors are all close to the position of Axis 1 in Figure 6.12, but they are all associated with the negative pole.

Axis 1 is interpreted as a gradient of successional development that includes age and only the soil parameter component, coincident with a moisture gradient. Older sites have deeper soils and surface organic material, and tend to have greater moisture availability compared to younger ones.

Axis 2

The strongest intraset correlation on this axis is with bare ground (negative), while there are moderate correlations with texture (positive), glacier climate, altitude, solifluction and gravel (negative). Texture and fines are closest to the position of Axis 2 in Figure 6.12, but the vectors are short. As for Axis 1, the principal gradients associated with this axis are represented by variables at only one pole.

The axis is interpreted as a gradient of vegetation cover; from low-altitude sites with extensive vegetation, where solifluction occurs rarely, to sparsely vegetated, high-altitude sites, where gravel frequently forms the substrate, the influence of the glacier climate is strong and there is a higher incidence of solifluction. This axis therefore combines gradients of successional development (the vegetation cover component), topography (altitude/glacier climate) and disturbance (solifluction).

The cluster of points occurs as a diagonal following the bare ground/altitude vectors to the origin, then flattening to trace the soil depth vector on Axis 1. The majority of sites along the diagonal are those newly identified with group in 2000, indicating that they tend to occur at high-altitude and are sparsely vegetated. Those sites remaining in the group since 1970 are separated by differences in humus/soil depth and are most numerous above the origin, indicating that vegetation cover is extensive. The few sites undergoing retrogressive transitions to this composition are scattered amongst the sites remaining in the group.

This division suggests a two-stage developmental process. On younger sites, separation depends on the extent of vegetation cover, which is associated with topographic position and the level of disturbance. On older sites where vegetation cover is substantial, separation is in terms of humus/soil depth and moisture availability.

Table 6.22. TWINSPAN group 2 (the species-poor heath): intraset correlations and canonical coefficients between the environmental variables and Canonical Correspondence Analysis Axes 1 and 2

Environmental variables	Intraset correlation Axis 1	Intraset correlation Axis 2	Canonical coefficients Axis 1	Canonical coefficients Axis 2
Age	-0.300	-0.063	-0.074	-0.061
Glacier	0.0703	-0.132	-0.006	-0.052
Altitude	0.207	-0.217	0.117	-0.124
Slope	0.112	-0.031	-0.030	0.014
Aspect E	0.082	0.048	0.004	0.055
Aspect N	0.026	-0.019	0.048	-0.036
Exposure	-0.075	-0.072	-0.008	-0.033
Moisture	-0.196	-0.024	-0.070	-0.047
Snowlie	-0.083	-0.017	-0.009	0.028
pH	0.062	-0.079	0.009	-0.012
Soil depth	-0.355	0.043	-0.091	0.073
Root	-0.056	0.049	0.104	0.013
Humus	-0.414	-0.098	-0.259	-0.165
Texture	-0.003	0.137	0.043	0.083
Trampling	-0.014	0.054	-0.041	0.030
Grazing	-0.104	0.105	-0.005	0.018
Browsing	0.031	-0.024	0.010	-0.037
Frost	0.018	0.011	-0.075	0.083
Solifluction	-0.137	-0.190	-0.070	-0.081
Fluvial	0.007	0.024	0.066	0.022
Fines	0.015	-0.103	0.013	-0.030
Gravel	0.142	-0.199	-0.057	0.065
Boulders	0.119	-0.121	-0.080	0.058
Bare Ground	0.219	-0.28	0.159	-0.317

Notes: Canonical Coefficients are included for reference

Table 6.23: Descriptive statistics for measured environmental variables on constituent sites in the species-poor heath

	Mean	Std Dev	Min	Max	Median
Age	564.88	1860.41	49.00	9000.00	178.50
Glacier	0.06	0.39	0.00	4.00	0.00
Altitude	1225.14	70.43	1122.00	1439.00	1201.00
Slope	14.63	8.83	2.00	46.00	13.00
Aspect E	0.37	0.61	-1.00	1.00	0.52
Aspect N	0.16	0.68	-1.00	1.00	0.41
Exposure	2.48	1.13	0.00	5.00	3.00
Moisture	2.39	1.25	1.00	6.00	2.00
Snowlie	1.63	1.81	0.11	9.00	1.50
pH	5.81	0.47	4.10	6.70	5.80
Soil depth	8.36	5.97	0.20	36.00	7.20
Root	7.21	2.67	1.70	18.90	6.80
Humus	2.03	3.48	0.20	36.00	1.40
Texture	1.70	0.85	1.00	4.00	1.00
Trampling	1.14	8.33	0.00	98.00	0.00
Grazing	13.05	17.49	0.00	81.00	5.00
Browsing	0.38	2.40	0.00	27.00	0.00
Hare	1.46	4.02	0.00	36.00	0.00
Ptarmigan	0.14	0.53	0.00	4.00	0.00
Vole	0.16	0.82	0.00	8.00	0.00
Sheep	1.95	6.83	0.00	65.00	0.00
Cow	0.00	0.00	0.00	0.00	0.00
Frost	3.92	4.35	0.00	13.00	1.50
Solifluction	1.63	3.78	0.00	18.00	0.00
Fluvial	1.26	4.00	0.00	21.00	0.00
Fines	25.43	19.90	0.00	100.00	22.50
Gravel	24.59	24.51	0.00	112.00	19.00
Cobbles	40.68	26.24	0.00	129.00	37.50
Boulders	33.77	23.74	0.00	112.00	28.00
Bare Ground	124.48	52.98	0.00	225.00	127.00

Species ordinations (Figure 6.13)

Most changes in species frequency are associated with one of two gradients that distinguish the development of a forb-rich, low stature heath from that of a taller, dwarf-shrub heath. The first occurs as a diagonal from sparsely-vegetated sites at high-altitude to more extensively vegetated sites at low-altitude (corresponding to the progressively developing sites in Figure 6.7). This is marked by a progression from pioneers, particularly forbs, at the bare ground extreme e.g. *Arenaria* spp. and *Arabis alpina*, to low stature shrubs, e.g. *Vaccinium myrtillus* and *V. vitis-idaea.*, and later successional forbs, e.g. *Bartsia alpina*, *Dryas octopetala* and *Pedicularis lapponica*, as vegetation becomes more extensive.

The second gradient follows Axis 1, from young sites with thin soils and low moisture availability, to older sites with deeper soils and higher moisture availability (corresponding to those sites remaining identified with the group in Figure 6.12). The species are predominantly shrubs, with *Cassiope hypnoides*, *Phyllodoce caerulea* and *Salix* spp. associated with younger sites, *Empetrum hermaphroditum*, *S. herbacea* and *S. glauca* close to the origin and *Betula nana*, *S. phylicifolia* and *Vaccinium uliginosum* on older sites, although *B. nana* is intermediate between the two gradients.

Environmental conditions (Tables 6.23, 6.26)

Although these sites represent the penultimate stage on the heath trajectory, several development variables have unexpectedly low means, particularly in comparison with the species-rich heath (Table 6.26). Most of the sites in this group are within the foreland boundary and this is reflected in the low mean age relative not only to the mature groups, but also to both late intermediate groups (6 and 3). Although soils are relatively deep, they tend to be immature texturally (the means are lower only in groups 7, 8 and 5). However, only the species-rich heath and the mature snowbed groups have lower means for the extent of bare ground. Despite extensive vegetation cover, there is still a considerable disjunction in terms of soil variables between these predominantly foreland sites and groups with sites located in the regional vegetation.

Many potentially perturbing variables occur at moderate levels e.g. altitude, glacier climate, aspect north and most of the disturbance variables, and such conditions are likely to be conducive to plant growth. However, grazing and trampling have high frequencies and may cause substantial damage. The glacier path crosses the area covered by these sites, and its effects are often severe, although limited in extent (personal observation). Grazing primarily involves insects, although on some sites the frequency of hare or sheep droppings was substantial. Moisture availability is frequently low and may constrain successional development. Finally, measurements of pH showed an extensive range, from approximately neutral to strongly acidic.

6.3.3.8 Species-rich heath group (1) (Tables 6.24, 25, Figure 6.14)

Axis 1

The strongest intraset correlations are with grazing (positive) and exposure/altitude (negative), there is also a moderate correlation with soil depth (positive). Soil depth represented an independent gradient in section 6.2, intercorrelated only with rooting depth. Grazing and exposure lie closest to the position of Axis 1 (Figure 6.14). Exposed sites tend to be at high-altitude, where grazing levels are low and the soils shallow. Sites where grazing frequency is high are sheltered, tend to be at low-altitude and have deeper soils.

This axis is interpreted as a gradient of disturbance (grazing) and (micro)topography (altitude/exposure), with an associated successional development gradient representing variation in soil depth.

Axis 2

The strongest intraset correlations are with age (positive) and the extent of bare ground (negative), while there are moderate correlations with the three substrate types (negative). While no variables were correlated with age in section 6.2, the substrate types were independently correlated with the extent of bare ground, suggesting that they represent different site types. This is reflected in Figure 6.14, where the gravel vector is closest to that of bare ground, while fines are associated with exposed sites and boulders with sheltered, grazed sites.

Vegetation cover is greatest on old sites, and its extent decreases as age decreases. On young, sparsely vegetated sites, there are three types of substrate and each is associated with a variable that may perturb successional development, although each intraset correlation is small. Fines are associated with frost heave and, as mentioned above, also with high levels of exposure. Young sites with gravel as a substrate are associated with fluvial disturbance, suggesting that some may represent lag deposits. Finally, boulders are associated with late-lying snow, consistent with there being a high level of shelter on these sites.

The axis is interpreted as a gradient of successional development (age/bare ground) combined with a range of substrate types and associated perturbing variables. The two components of successional development are again associated with separate axes. Unusually, the extent of bare ground coincides with the age variable, while in several other groups, soil variables are more closely related to age.

The cluster of sites in Figure 6.14 shows two trends, corresponding to separation on each of the axes. Those sites remaining identified with the group since 1970 have the greatest separation on Axis 1, corresponding to the gradient of soil depth/exposure. Vegetation cover is relatively extensive, as most sites are above the origin on Axis 2. Sites that have the highest positions on Axis 2 occur at high-altitude, are exposed and tend to have shallow soils and rooting depths, despite having higher than average vegetation cover. This suggests that there may be qualitative difference in terms of species rooting depths compared to sites at low-altitude.

Sites that have undergone progressive transitions to this group are sparsely vegetated, have shallow soils and tend to be exposed compared to sites remaining in the group. The substrate is predominantly fines, associated with frost heave and north-facing aspect.

Table 6.24. TWINSPAN group 1 (the species-rich heath): intraset correlations and canonical coefficients between the environmental variables and Canonical Correspondence Analysis Axes 1 and 2

Environmental variable	Intraset correlation Axis 1	Intraset correlation Axis 2	Canonical coefficient Axis 1	Canonical coefficient Axis 2
Age	0.092	0.206	0.101	0.196
Glacier	-0.034	0.022	0.084	-0.057
Altitude	-0.209	0.084	-0.176	0.038
Slope	0.038	0.004	0.149	0.002
Aspect E	-0.142	0.041	-0.216	0.090
Aspect N	-0.099	-0.038	0.014	-0.110
Exposure	-0.211	0.013	-0.093	0.119
Moisture	-0.122	-0.003	-0.062	-0.044
Snowlie	0.064	-0.075	-0.144	-0.069
pH	0.151	-0.020	-0.006	-0.034
Soil depth	0.199	0.089	-0.070	-0.006
Root	0.122	0.060	0.133	0.001
Humus	0.134	-0.015	-0.125	-0.042
Texture	0.001	0.038	0.134	-0.065
Trampling	-0.058	0.017	0.064	0.012
Grazing	0.321	0.006	0.380	-0.031
Browsing	0.099	-0.025	-0.034	-0.047
Frost	-0.075	-0.0841	0.049	-0.083
Solifluction	-0.122	0.059	-0.101	-0.058
Fluvial	-0.015	-0.077	0.024	-0.010
Fines	-0.102	-0.134	-0.262	0.341
Gravel	-0.046	-0.142	-0.142	-0.022
Boulders	0.072	-0.140	-0.175	0.284
Bare Ground	-0.064	-0.234	0.381	-0.639

Notes: Canonical Coefficients are included for reference

Table 6.25: Descriptive statistics for measured environmental variables on constituent sites in the species-rich heath

	Mean	Std Dev	Min	Max	Median
Age	7509.87	3326.34	207.00	9000.00	9000.00
Glacier	0.02	0.14	0.00	1.00	0.00
Altitude	1202.00	80.88	1107.00	1505.00	1166.00
Slope	12.00	7.07	3.00	40.00	12.00
Aspect E	0.19	0.68	-1.00	1.00	0.44
Aspect N	0.20	0.69	-0.98	1.00	0.48
Exposure	2.72	0.95	1.00	5.00	3.00
Moisture	2.87	1.23	1.00	6.00	3.00
Snowlie	1.53	2.11	0.11	9.00	0.67
pH	5.55	0.43	4.70	6.50	5.60
Soil depth	20.04	8.34	3.80	36.00	19.50
Root	13.34	4.44	3.80	28.00	13.40
Humus	3.15	2.18	0.10	9.70	2.70
Texture	2.45	1.01	1.00	5.00	3.00
Trampling	0.13	0.96	0.00	7.00	0.00
Grazing	38.08	42.43	0.00	184.00	26.00
Browsing	2.17	4.70	0.00	27.00	0.00
Hare	1.06	2.55	0.00	15.00	0.00
Ptarmigan	0.45	1.26	0.00	8.00	0.00
Vole	0.11	0.82	0.00	6.00	0.00
Sheep	2.17	6.18	0.00	30.00	0.00
Cow	0.32	2.34	0.00	17.00	0.00
Frost	0.70	2.28	0.00	10.00	0.00
Solifluction	3.49	5.30	0.00	19.00	0.00
Fluvial	1.08	2.96	0.00	15.00	0.00
Fines	9.94	13.06	0.00	67.00	4.00
Gravel	0.45	1.92	0.00	13.00	0.00
Cobbles	2.92	6.02	0.00	31.00	1.00
Boulders	6.36	7.79	0.00	30.00	3.00
Bare Ground	19.68	21.19	0.00	103.00	13.00

Table 6.26: Summary of the mean and standard deviation of the measured environmental variables, in individual TWINSPAN groups, showing the relative group position

Variable:	**Mean, standard deviation and ranking:**							
	Group 1	Group 2	Group 3	Group 4	Group 5	Group 6	Group 7	Group 8
	n = 53	n = 152	n = 50	n = 30	n = 76	n = 18	n = 24	n = 28
Age/yrs	7510	565	1380	6060	316	2129	30	40
	±3326	±1860	±3106	±4229	±1438	±3779	±14	±17
	1	5	4	2	6	3	8	7
Altitude/masl	1202	1225	1330	1322	1313	1366	1359	1355
	±81	±70	±80	±101	±55	±82	±20	±33
	8	7	4	5	6	1	2	3
Slope/°	12	15	20	18	17	24	11	12
	±7	±9	±10	±8	±10	±13	±6	±8
	7	5	2	3	4	1	8	6
Aspect N	0.20	0.16	0.42	0.36	0.22	0.79	0.30	0.39
	±0.7	±0.7	±0.7	±0.7	±0.7	±0.4	±0.7	±0.6
	7		2	4	6	1	5	3
Exposure	2.72	2.48	2.40	2.20	2.88	2.17	3.67	3.11
	±0.95	±1.13	±0.99	±0.89	±1.28	±0.92	±1.01	±0.92
	4	5	6	7	3	8	1	2
Moisture	2.87	2.39	2.96	2.83	2.63	2.78	1.71	3.29
	±1.23	±1.25	±1.46	±1.09	±1.24	±1.11	±0.69	±1.78
	3	7	2	4	6	5	8	1
Snowlie	1.53	1.81	2.21	2.58	1.66	2.18	0.46	1.39
	±2.11	±1.63	±1.99	±1.73	±1.95	±1.36	±0.93	±2.34
	6	5	2	1	4	3	8	7
Soil depth/cm	20.04	8.36	6.85	16.12	3.96	8.41	0.92	2.24
	±8.34	±5.97	±4.95	±6.77	±4.28	±8.05	±0.68	±1.87
	1	4	5	2	6	3	8	7
Grazing	38	13	7	7	6	4	0.5	5
	±42	±17	±8	±9	±12	±8	±1	±7
	1	2	4	3	5	7	8	6
Frost heave	0.70	3.92	4.14	1.13	4.33	3.56	7.46	3.00
	±2.28	±4.35	±5.15	±2.89	±5.40	±4.42	±4.85	±4.18
	8	4	3	7	2	5	1	6
Solifluction	3.49	1.63	3.98	6.53	2.59	4.72	0.71	2.04
	±5.30	±3.78	±5.25	±7.11	±4.75	±5.84	±2.14	±3.73
	4	7	3	1	5	2	8	6
Fluvial disturbance	1.08	1.26	3.38	1.63	1.72	1.06	0.29	6.68
	±2.96	±4.00	±8.56	±2.88	±6.23	±2.67	±0.91	±11.54
	6	5	2	4	3	7	8	1
Bare ground	19.68	124.48	155.74	49.30	181.96	174.00	220.42	205.75
	±21.19	±52.98	±42.97	±49.30	±43.57	±59.45	±6.85	±27.01
	8	6	5	7	3	4	1	2

Species ordinations (Figure 6.15)

Most of the species changes in this group occur along a diagonal from low-altitude sites associated with boulders and late snowlie, to those at higher altitude that tend to be exposed and are more likely to face north. Species associated with the low-altitude extreme include predominantly snowbed species such as *Anthoxanthum odoratum*, *Leontodon autumnalis* and *Veronica alpina* together with the shrubs *Juniperus communis*, *Salix phylicifolia* and *S. lanata*. Most heath shrubs, including the co-dominants *Betula nana* and *Empetrum hermaphroditum*, are associated with the higher altitude extreme.

Other species are scattered across the diagram, suggesting that changes in frequency respond to a range of specific requirements, possibly associated with the different substrate types found in this group. For example *Bartsia alpina*, *Gnaphalium supinum* and *Pinguicula vulgaris* are associated with gravel as a substrate on sparsely vegetated land where fluvial disturbance is likely to occur.

Environmental conditions (Tables 6.25, 6.26)

Many of the mean values reflect the maturity of sites in this group and the generally low frequency/intensity of perturbing variables. The species-rich heath has the highest mean age, the deepest soils and the most extensive vegetation cover in the study area (Table 6.26). Soils are texturally mature and the mean pH is low, although the range includes some values approaching neutral (Table 6.25), both means are only exceeded in the mature snowbed group. Topographically, sites have the lowest mean altitude and are the least exposed to the glacier climate in the study area. Sites tend to be flat and infrequently face north. However, exposure has a relatively high mean, exceeded only in the pioneer and intermediate groups. The sites tend to be moist, but snow is not generally late-lying; the mean for the duration of snowlie is lower only amongst the pioneers, but for the species-rich heath this is likely to reflect early snowmelt, rather than the redistribution of snow. The sites undergo little substrate disturbance, e.g. frost heave has the lowest mean in the study area, but browsing and, particularly, grazing occur relatively frequently.

These are mature sites with conditions that are likely to be favourable for plant growth, particularly for shrub species, with deep soils, moderately high moisture and little substrate disturbance. The growing season is long relative to much of the study area, as the sites are at low-altitude and snowmelt is early. Although grazing frequency is high, there was no evidence of extensive insect infestation, and the relatively high level of exposure is mitigated where canopy formation occurs.

6.4 The importance of the measured environmental variables to species compositional change

Table 6.27 summarises the eigenvalues and Kendall's tau correlation coefficients between the species and environmental axes 1 and 2 for the above analysis. The eigenvalues indicate the variation in species composition (dispersion of the species scores) accounted for by the ordination Axis, and are therefore a measure of its importance (ter Braak, 1986, 1995a).

Table 6.27: Canonical Correspondence Analysis eigenvalues and species-environment correlation coefficients for Axes 1 and 2 and total explained variance for all canonical and non-canonical Axes

Group	Measure	Axis 1	Axis 2	% Explained Variance (Canonical Axes)	% Explained Variance (Non-Canonical Axes)
All Sites	Eigenvalue	0.334	0.128	20.6	79.4
	Kendall's tau	0.749	0.558	(24 axes)	(101 axes)
Species-rich heath Group 1	Eigenvalue	0.200	0.129	59.78	40.22
	Kendall's tau	0.607	0.727	(24 axes)	(52 axes)
Species-poor heath Group 2	Eigenvalue	0.221	0.169	29.17	70.83
	Kendall's tau	0.611	0.651	(24 axes)	(89 axes)
Late intermediate Group 3	Eigenvalue	0.231	0.193	55.53	44.5
	Kendall's tau	0.693	0.806	(24 axes)	(49 axes)
Mature snowbed Group 4	Eigenvalue	0.225	0.184	84.73	15.27
	Kendall's tau	0.844	0.931	(24 axes)	(29 axes)
Early intermediate Group 5	Eigenvalue	0.167	0.131	39.95	60.05
	Kendall's tau	0.623	0.582	(24 axes)	(72 axes)
Early pioneer Group 7	Eigenvalue	0.233	0.203	95.55	4.45
	Kendall's tau	0.899	0.891	(22 axes)	(23 axes)
Late pioneer Group 8	Eigenvalue	0.246	0.202	90.41	9.59
	Kendall's tau	0.825	0.852		
				(24 axes)	(27 axes)

Note. The correlation coefficients are those between the species and the environmental axes 1 and 2. Kendall's tau is provided, in addition to Pearson's correlation coefficients, in the ECOM programme.

Although rather modest, the eigenvalues indicate that the trends are of consequence. The correlation coefficients between the species and the environmental variables are strong.

This was examined further by considering the percentage variance explained by both the 7canonical and the non-canonical axes (Table 6.27). This is the sum over all of the axes extracted in the analysis; most of the individual contributions are small on higher order axes, the main explanatory power being in the first two, or sometimes three, axes. The canonical axes total shows how much of the variance is explained by the environmental variables used, while the non-canonical axes total indicates the level of residual variance. Factors that contribute to this include 'noise' (reflecting the use of flux data and errors), and variables that were not measured, such as plant interactions, dispersal capability and climatic variability. The level of variance explained differs over the sequence, but is low when all of the sites are considered together. When the data are divided, the percentage variance explained in each group is higher than that seen overall. This appears to be because the system as a whole is too complex to be summarised by a small number of orthogonal axes, whereas the particular combination of variables occurring in the groups approximate more closely to a small number of orthogonal axes.

The highest percentage variance explained occurs in the two pioneer groups (95.55% and 90.41%). The lowest value is for the species-poor heath (29.17%), which may in part reflect the size of the group (with 25% of the sites) and therefore be due to the same effects discussed for all sites. The value of 39.95% for the early intermediate group is also low, possibly reflecting the transitions in this group that involve species replacements and first appearances and which, therefore, depend on dispersal capability and proximity to source areas. Apart from these anomalous low values, there is a reduction over the sequence from the high explanation achieved in the pioneer groups to more modest values in the species-rich heath (59.78%), where a higher level of species interactions would be expected in generally more complex communities.

The environmental variables measured comprise allogenic factors that were considered likely to influence composition. It is expected that poorly developed or severe sites would show a high level of influence, particularly where vegetation/soil development is minimal, with little buffering capacity. However, the mature snowbed group has an explained variance of 84.73% reflecting a primary control in terms of site characteristics.

Thus, in all groups, except the pioneers and the snowbed groups, where the allogenic factors measured account for almost all of the variation, noise and the omission of important factor(s) contributing to the changes combine with the increasing complexity of the system to reduce the percentage variance explained. Important omitted factors may include autogenic factors such as interactions and dispersal capability, but additionally climatic variation since 1970 (section 1.4) may have influenced the changes that have been recorded.

6.5 Summary and conclusions relating to environmental variables and environmental gradients for sections 6.3 and 6.4

(1) A summary of the means and standard deviations of the environmental variables is given in Table 6.26 and of environmental gradients in Table 6.28.

Table 6.28: Summary of the gradients identified in the Canonical Correspondence Analysis biplots

Group	Axis	Key Variables and Intraset Correlation		Major Gradients
All Sites	1	Bare ground (0.486)/Gravel (0.423)	Soil Depth (-0.426)	Successional
		Altitude (0.417)/Glacier Climate (0.391)		Topography
	2	Frost Heave (0.133)	Grazing (-0.132)	Disturbance
Early pioneer Group 7	1	pH (0.215)/Bare Ground (0.180)	Age (-0.233)/Moisture (-0.144)	Successional/Moisture
		Fines (0.233)		Substrate
			Exposure (-0.161)	Microtopography
	2	Grazing (0.183)	Trampling (-0.241)	Disturbance
		Altitude (0.157)	Frost heave (-0.150)/Aspect N (-0.155)	Topography/Disturbance
			Slope (-0.204)	Microtopography
Late pioneer Group 8	1	Soil (0.267)/Root (0.298) depths		Successional
		Grazing (0.332)	Aspect north (-0.296)	Disturbance/Topography
	2	Glacier climate (0.260)	Age (-0.285)	Topography
			Moisture (-0.260)/Fluvial disturbance (-0.157)	Moisture/Disturbance
		Exposure (0.160)	Slope (-0.187)	Microtopography
		Frost heave (0.157)	Snowlie (-0.150)/Soil (-0.168)/Humus (-0.182)	Disturbance

Table 6.28: Summary of the gradients identified in the Canonical Correspondence Analysis biplots (sheet 2)

Group	Axis	Key Variables and Intraset Correlation		Major Gradients
Early intermediate Group 5	1	Bare ground (0.243)	Soil (-0.254)/Rooting depth (-0.242)	Successional
		Exposure (0.0.236)/Gravel (0.227)	Slope (-0.225)	Microtopography/Substrate
		Frost heave (0.187)	Grazing (-0.229)	Disturbance
	2	Altitude (0.278)	Aspect North (-0.138)/Fines (-0.127)	Topography/Substrate
		Glacier climate (0.199)/Exposure (0.156)	Snowlie (-0.175)	Snowlie/Microtopography
Mature snowbed Group 4	1		Soil depth (-0.239)	Successional
		Frost Heave (0.104)	Grazing (-0.129)/Gravel (minor)Trampling (minor)	Disturbance
	2	Age (0.249)/Soil (0.241)/Root (0.224)/Texture (0.243)	Bare Ground (-0.198)	Successional
		Altitude (0.232)/Glacier climate (0.154)	Aspect North (-0.118)	Topography
		Solifluction (0.137)	Browsing (-0.197)/Boulders (-0.200)	Disturbance/Substrate
Late intermediate Group 3	1	pH (0.242)	Soil Depth (-0.363)/Humus (-0.243)	Successional
		Gravel (0.222)	Texture (-0.283)/Slope (-0.253)	Substrate/Microtopography
	2	Altitude (0.248)	Moisture (-0.278)/Fluvial disturbance (-0.225)/Fines (-0.200)	Moisture/Disturbance/ Substrate

Table 6.28: Summary of the gradients identified in the Canonical Correspondence Analysis biplots (sheet 3)

Group	Axis	Key Variables and Intraset Correlation		Major Gradients
Species-poor heath Group 2	1		Age (-0.300)/Soil (-0.355)/Humus (-0.414)	Successional
			Moisture (--0.196)	Moisture
	2		Bare ground (-0.28)/Gravel (-0.199)	Successional/Substrate
			Altitude (-0.217)/Glacier climate (-0.132)	Topography
			Solifluction (-0.190)	Disturbance
Species-rich heath Group 1	1	Grazing (0.321)		Disturbance
			Altitude (-0.209)/Exposure (-0.211)	Microtopography
		Soil depth (0.199)		Successional (soil)
	2	Age (0.206)	Bare ground (-0.236)	Successional (vegetation)
			Boulders (-0.140)/Snowlie (minor) Gravel (-0.142)/Fluvial disturbance (minor) Fines (-0.134)/Frost heave (minor)	Substrate/Disturbance

Note: Where several variables have similar intraset correlations on a particular axis, the gradients have been separated by combining vectors that occur opposite to one another and using the relationships indicated by the Kendall's tau correlation coefficients in section 6.2. Where such a vector does not exist, the influence of the variable is assumed to represent a separate gradient.

(2) In these sections, Canonical Correspondence Analysis (CCA) was used to relate compositional change in the vegetation to environmental variables. In addition to the data from the whole study area, the analysis was applied to the individual TWINSPAN groups (section 5.3). Only the results from the first two CCA axes were used, as higher order axes were uninterpretable.

(3) Gradients of successional development, topography and disturbance were identified in every TWINSPAN group examined, while gradients of moisture/snowlie and substrate type were of importance in some, but not all of the groups (Table 6.28). Different substrate types were frequently associated with within-group differences in physical conditions e.g. in the early intermediate group, gravel is associated with sites on the fluted moraines, whereas boulders occurred more often on sites on the flanks. Different substrates also appear to be more susceptible to different forms of disturbance e.g. frost heave is associated with gravel (groups 8, 5 and 4) while fines is associated with fluvial disturbance (group 3).

(4) The soil and vegetation components of successional development (section 6.2.10) occurred on separate CCA axes except in the early intermediate group. Soil variables were generally associated with Axis 1, while the extent of bare ground/vegetation was associated with Axis 2, except in the early pioneer group where this was reversed. The identification of soil variables with Axis 1 suggests that they are more strongly associated with compositional change than the extent of bare ground/vegetation.

(5) While soil depth is not generally related to vegetation cover in section 6.3, there is other evidence in this study of an association between the vegetation and soil development. The measured soil variables include humus and rooting depth; humus indicates the amount and decomposability of plant-derived organic material, while increasing rooting depth stabilises the substrate. The three vectors (of soil, humus and rooting depths) generally occurred in close proximity in the ordination diagrams, except in the early pioneer group, although humus and rooting depths were associated with other, potentially controlling variables e.g. moisture/snowlie (groups 8, 5, 3 and 2) and disturbance (groups 8, 5 and 1). This suggests that an integrated soil-vegetation complex forms early in the successional sequence.

(6) It was expected that by restricting the analysis to within-group environmental effects, the influence of mesoscale topographic gradients of altitude and aspect would be substantially reduced. However, this is not the case in groups where sites are widely distributed within the foreland (groups 8, 5 and 2), or where subsets of sites are associated with the north- and south-facing flanks (groups 4 and 3). Differences in compositional change between subsets of sites with differing physical conditions suggest that distinct compositional strands are not restricted to the late intermediate group.

(7) Disturbance caused by biogenic processes includes grazing, browsing and trampling. Although grazing increases in frequency with increasing maturity (Table 6.26), it is associated with compositional change in all groups except the late intermediate group and the species-poor heath. Grazing occurred most frequently on sites where the levels of successional development (soil and/or the extent of vegetation cover) are highest. On the other hand, browsing occurred most frequently in groups which included sites on the flanks of the foreland (groups 8 and 6) (Table 6.26). Grazing and browsing targeted particular species e.g. *Oxyria digyna* and *Ranunculus glacialis* on young sites and *Salix* spp. on more mature ones (personal observation). Trampling is associated with sites on or close to the glacier path (groups 2, 3 and 7) or with the east side of the Leira (group 1), where cows graze.

(8) Physical processes causing disturbance are frost heave, fluvial activity and solifluction. Site-scale moisture availability and maturity are important controls on disturbance regime. Frost heave occurs most frequently in groups where moisture availability is low (groups 7, 5 and 2). Fluvial disturbance and solifluction are associated with groups where moisture levels are high and slopes are steep, although solifluction occurs more frequently within the regional vegetation (groups 6, 4, 3 and 1) (Table 6.26). These physical processes occur patchily in space and time and consequently intraset correlations are often modest. Generally, disturbance due to physical processes is associated with subsets of sites within groups e.g. solifluction on the high-altitude, south-facing sites in group 4, frost heave on the centrally-located sites in group 8 and on the fluted moraines in group 5.

(9) Microtopographic variables, exposure and slope, are most strongly associated with the CCA axes in early successional groups, particularly in groups 8 and 5, where they combine to form compound gradients. High levels of moisture availability are associated with older sites and deeper soils/humus (groups 7, 8 and 2).

(10) Important gradients in individual groups are often associated with a change from favourable to adverse conditions. For example in the late pioneer group, the gradient from north to south-facing land is accompanied by a progressive increase in soil depth, while in the species-poor heath, the gradient from high- to low-altitude, is accompanied by a decrease in solifluction and gravel, and an increase in vegetation cover. These gradients may indicate conditions that either promote or obstruct successional development.

(11) Differences in vegetation cover were frequently found to reflect variation amongst sites developing progressively (groups 7, 4, 3, 2 and 1). Additionally, amongst mature groups, sites remaining identified with the group in the two surveys were separated in terms of soil depth variables. This pattern, which was particularly well developed in the species-poor heath (Figure 6.12), also occurred in the mature snowbed and species-rich heath. This suggests that in late-successional groups, development following a progressive transition occurs in two stages. Stage one involves an increase in vegetation cover, while stage two involves soil development. Soil development includes increasing rooting depth, indicating the presence of deeper-rooted species, particularly shrubs. Therefore, compositional shifts appear to characterise stage two, rather than increases in cover.

(12) Species generally conform to known environmental affinities, the following examples are not exhaustive. Pioneer species are associated with harsh conditions, e.g. high-altitude and exposure to the glacier climate, not only in the early stages, but also throughout the sequence. *Carex* spp. is proximal to the moisture vector in every group. Snowbed forbs, e.g. *Leontodon* *autumnalis* and *Veronica alpina*, are associated with late snowlie. Shrubs are separated along a soil depth gradient in the late intermediate group.

(13) Although the eigenvalues are modest, the trends are meaningful and the correlation coefficients between the species and the environmental gradients are strong (Table 6.27). The variance explained by the canonical axes was low when large numbers of sites were included in the analysis e.g. for the whole dataset (20.6%) and the species-poor heath (29.17%), reflecting the complexity of even this relatively simple system. The higher explanation achieved for all other groups appears to reflect relatively simple systems with a more restricted range of environmental conditions within individual groups.

(14) Allogenic factors explain most of the variance in pioneer groups 7 and 8 (95.55% and 90.41% respectively) and in the mature snowbed group (84.73%). Lower explanations characterise the late intermediate (55.53%), the species-rich heath (59.78%) and, particularly, the early intermediate group (39.95%). These relatively low values may be the result of noise, the omission of important factors, such as species interactions, and the general, increasing complexity of the system.

(15) When data from the whole study area are analysed together, a simple pattern of important gradients is detected (Table 6.27) and the intraset correlations tend to be strong. The gradients associated with Axis 1 are successional development, reflecting both soil and vegetation components, together with altitude/glacier climate. Axis 2 is associated with a weakly developed disturbance gradient involving frost heave and grazing. Greater complexity is detected at the level of the individual groups. Examples include soil and vegetation components of successional development associated with different axes, differences in aspect separating subsets of sites (groups 8, 5, 4 and 3, section 6.3), and the inclusion of moisture, substrate type and additional disturbance variables. These differences appear to be the result of the different scales used in the analysis of the whole chronosequence compared to that in individual groups. At the study area scale, only gradients with a strong and consistent association with compositional change emerge as of importance, whereas examination at a group-scale detects smaller-scale interrelationships between the environmental variables

(16) Despite some similarities, there are also differences between the environmental interrelationships detected using Kendall's tau correlation coefficients and those detected by CCA, particularly involving the importance attributed to terrain age. Using the correlation coefficients (section 6.2), terrain age was frequently central to a group of variables and, although CCA identified similar groups of important variables, they were frequently not related to age e.g. altitude and snowlie (group 5). CCA extracts several orthogonal axes, with any one axis detecting only part of the whole pattern of relationships. On the other hand, the correlation coefficient measures the strength of the association of two variables over the whole dataset. It appears that age may frequently be associated with several different axes, as occurs in the early pioneer group. Additionally, CCA specifically detects gradients associated with compositional change, rather than measuring the strength of the relationship between the variables (section 6.2). Some strongly correlated variables may not be related to compositional change.

(17) Although the patterns that emerge from this discussion frequently involve complex associations of environmental variables, it is also possible to simplify this intricacy to a series of site types representing relatively minor compositional strands within each group e.g. those associated with substrate types in the species-rich heath. The variables examined in this Chapter operate at a site-scale, distinguishing a more detailed level of environmental variation compared to the mesoscale gradients discussed in Chapter 5. Environmental variation at both scales is related to compositional change, but while the mesoscale gradients determined trajectory type, finer-scale variation appears to be predominantly associated with differences in the rate of successional development. This association is the result of differential effects on progressive development that are related to site position on a number of environmental gradients i.e. the range from favourable to adverse conditions mentioned above. However, some environmentally-determined subsets of sites may indicate qualitative differences in the type of development, as found in the late intermediate group. These are frequently due to within-group differences in altitude and aspect, the gradients that were found in Chapter 5 to underlie the different trajectories, e.g. groups 5, 4, 3 and 1.

Chapter 7: Discussion

7.1 Introduction

In this chapter, results from the preceding chapters are discussed in the light of the study aims, which were (section 1.2.3):

1. To describe 30 years of temporal change in the species population distributions;
2. To analyse the community dynamics of the successional sequence;
3. To investigate the role of environmental parameters in the compositional changes.

These aims are considered in turn in the following discussion. Initially, the nature of the changes in species populations is discussed in relation to changes expected in a maturing successional sequence. In the next section, the contribution of this study to understanding the nature and functioning of the community dynamics is considered, particularly in relation to the major landforms occurring in the study area. Subsequently, the relationship of the environmental variables to compositional changes within the vegetation groups is examined and compared to the effects of the coarser scale gradients found on the individual landforms. Finally, the implications of this study are considered in the broader field of successional theory.

7.2 Patterns in the species distribution changes

The purpose of this section is to establish the principal characteristics of the distribution changes occurring between 1970 and 2000. The distribution maps in section 4.4 illustrate a dynamic system, changes being virtually ubiquitous.

Sections 4.2 and 4.3 identify important frequency changes: 66% of species in Tables 4.1 and 4.2 show changes in frequency exceeding 20%; 78% show changes greater than 10%. The latter percentage rises to 84% where all species are included (Table 4.3). Changes of less than 10% are few, 16% of species in Table 4.3 (17 species out of 105), and predominantly involve forbs (12 species). There is considerable variation between species in the direction and extent of the changes.

Both distributions and changes vary in detail but common patterns can be seen at a coarse scale (Tables 4.5 and 4.6). Distribution types are related to the species groupings discussed in section 4.5. For example, snowbed species often have two subpopulations: at high-altitude on the south-facing flank and at low to mid-altitude on the north-facing flank. Heath species and the tall herbs occur at low-altitude on old ground and pioneers on young, central sites at high-altitude. However, coarse-scale changes in spatial pattern are not characteristic (see distribution maps in section 4.4). Changes in population sizes are associated with broad divisions of the study area (age, altitude, aspect) e.g. decreases on old terrain and both decreases (amongst late successional species) and increases (amongst some pioneers) on the north-facing flank. Although a minority of late successional species show a trend of colonization on younger land than occupied in 1970, colonization and loss are not widespread. Frequency changes do not generally translate to major shifts in presence/absence.

For many species, the distributional changes are largely restricted to within-range variation, suggesting that changes involve performance for the majority of species. This may indicate inertia within the system; particularly resistance from established vegetation, clonal spread rather than sexual reproduction and dispersal difficulties.

7.2.1 The extent to which changes conform to typical successional patterns

In section 4.1, successional changes were characterised as migration (for pioneer and intermediate species) and expansion from mature sites (for late species). Table 4.4 shows wavelike increases and decreases in both frequency and occurrence, particularly amongst pioneers early in the sequence, while Section 4.4 contains examples of expansion from older to younger land. How far do the changes in the study area conform to the patterns typically associated with successional processes? The following discussion examines distributional changes that do not appear to conform to these patterns.

1. A few late species increase on old terrain in addition to expanding onto ageing terrain e.g. *Salix glauca* and *Empetrum hermaphroditum* (section 4.4.2).
2. Many species decrease within the regional vegetation, and often show a similar pattern amongst low-altitude, old foreland sites. These sites would be expected to change little and to resist change (section 2.6). Examples include *Cassiope hypnoides, Vaccinium vitis-idaea, Luzula arcuata, Huperzia selago, Hieracium alpinum, Leontodon autumnalis* and *Polygonum viviparum* (sections 4.4.2, 4.4.6 and 4.4.8). Section 5.2 shows that diversity parameters have changed significantly on these sites; with decreases in rare species, a reduction in species richness and an increase in dominance. The synchronization of these changes suggest that they are not caused by cyclic succession (Horn, 1974) (cf. Crouch 1992), but rather that the character of the mature vegetation may be changing. Continuing succession is not anticipated on land deglaciated for over 9000 years, although the regional vegetation close to the outer moraine will have been influenced by the presence of the glacier at the height of the LIA (Matthews, 1992 and references therein). While continuing recovery may contribute, it is suggested that these effects should be relatively minor as the glacier retreated from the vicinity 250 years ago and had not directly encroached on the land. There is no evidence that proximity to the outer moraine increases the intensity of the changes; sites furthest from the moraine are affected similarly to those adjacent to it. This suggests therefore, a more recent variation in conditions has occurred to which the vegetation is responding as a unit.
3. There are fewer pioneers (e.g. *Poa* spp. and *Trisetum spicatum*) and forbs on older land at low-altitude (sections 4.4.4 and 4.4.8). Crouch (1992) attributes the presence of pioneers on these sites to disturbance. Whittaker (1993) observed that forbs need openings within dense, shrub-dominated vegetation. Vetaas's study (1994, 1997) at Bødalsbreen, shows that a tree canopy can reduce successional cycles caused by the glacier wind. Increased development of a shrub canopy may act in a similar way.
4. Changes in frequency occur consistently within functional types. Tables 4.1 and 4.2 and section 4.4.2 show substantial increases amongst the majority of deciduous shrubs, while many evergreen shrubs decrease. Similarly most non-pioneer grasses and the sedges increase in frequency although other graminoid species decrease. In other groups, the response appears to

relate to the extent of the spatial location of the population. Most pioneers decrease, but the few species with ranges including a presence on the north-facing flank increase in frequency. The majority of forbs decrease, except where a substantial proportion of the distribution occurs within the foreland.

5. By 2000 some species occur on younger land at higher altitude or at increased frequency on younger sites compared to the earlier survey. Examples include *Antennaria alpina, Carex* spp., *Hieracium alpinum, Pyrola* spp., *Veronica alpina, Salix herbacea* and *Vaccinium uliginosum.* This is often accompanied by decreases in frequency on older land at low-altitude, so that by 2000 they may be better described as intermediate species, although most were previously classed as late successional.

6. Several late species (*Betula nana, Carex* spp., *Empetrum hermaphroditum* and *Salix glauca*) have not moved onto young land of a similar age to that occupied in 1970. Figure 4.4 and section 4.3 suggests that they might be encountering difficulties establishing on younger land, particularly on the drying surface of the fluted moraines (Ballantyne and Matthews, 1982; Whittaker, 1993). It has been suggested (e.g. (Whittaker, 1985 at Storbreen; del Morel and Bliss, 1993) that early colonizers act as seed sources for a more general population expansion. Young land may be effectively 'starved' of such seed sources, with long-term implications for vegetation composition on young land at Storbreen and potentially delaying successional development. However, they occur with substantially higher frequency in 2000 compared to 1970 on land over 50 years old.

7. Pioneer populations generally decline with the reduction in area of newly exposed land. However, a minority of such species - *Arenaria* spp., *Cerastium cerastoides* and *Oxyria digyna* – increase due to expansion on the north-facing flank. Various lines of evidence suggest that the cause is an environmental perturbation that affects many of the sites in that area (discussed in greater detail below).

8. The composition of the groups of associated species (Figures 4.58 and 4.59, section 4.5) indicates subtle shifts in affinities particularly among the forbs and some heath species resulting in some groups (especially low-altitude and snowbed forbs) being less distinct in 2000 compared to 1970.

Despite the underlying successional pattern of wavelike increases and decreases and expansions from older onto younger land seen in section 4.4, none of these changes characterise successional changes as previously described by Matthews (1976) and Whittaker (1985).

7.2.2 Causal mechanisms underlying the changes

Delayed establishment on the fluted till plain and the reduction in area of newly exposed land involve spatially restricted, mesoscale influences and clearly defined causal mechanisms. In other cases, the underlying process is less apparent. The discussion below initially considers the environmental change on the north-facing flank, moving on to examine whether there is evidence of more generally causative processes.

In terms of species populations, the main features of the changes on the north-facing flank are: (1) extensive mortality affecting shrub form *Salix* spp. (section 4.4.2); (2) a decline in *Luzula* spp., particularly *L. arcuata*, described by Matthews (1987) as a snowbed intermediate (section 4.4.6); (3) increasing pioneer populations, specifically *Cerastium cerastoides* and *Oxyria digyna,* together with the snowbed species *Salix herbacea* (section 4.4.4). Many of the late pioneer-snowbed intermediate sites are interspersed with sites that progressed rapidly or maintained a species-poor heath composition (Figures 5.7 and 5.8). These sites are relatively old, with well-developed soils (section 6.3), and there is evidence of late-lying snow, although there is also a positive correlation between snowlie and bare ground (section 6.2). Few late-lying or permanent snowpatches were observed in this area in 2000 or 2001, although Matthews (1976) mentions late-lying snow on the north-facing flank. This suggests that there has been a decrease in late-lying snow, but that the growth pattern of the lichen proxy had not yet adjusted to a change in conditions (section 6.2). Reduced snowcover or early snowmelt may leave shrubs and taller forbs exposed to adverse conditions that they are unable to tolerate (Billings, 1974a; Carlsson and Callaghan, 1991; Stanton et al., 1994; Körner, 1995; Hahn et al., 1996; Beniston, 2000) and/or deprive them of a source of moisture and nutrients during the summer (Johnson and Billings, 1962; Billings, 1974a; Billings, 1974b; Seppelt et al., 1988; Carlsson and Callaghan, 1991; Taylor and Seastedt, 1994; Galen and Stanton, 1995; Walker et al., 1995; Walker and Walker, 1996; Foskett, 1998; Lee, 1999; Beniston, 2000). While several shrubs have declined, pioneer species have increased in frequency (sections 4.4.2 and 4.4.8).

In the remainder of this section a number of potentially causal factors are examined to consider whether there is evidence that they have a role in generating the more general trends discussed above.

Moisture and snowlie Several pieces of evidence suggest that these variables may contribute to the changes that have occurred. The retreat of the glacier governs moisture supply on the fluted till plain (Ballantyne and Matthews, 1982). Reduced snowlie on the flanks of the foreland may prompt drying earlier in the growing season and explain the decreasing frequency of snowbed and moisture-requiring forbs (section 5.4). The decline of *Phyllodoce caerulea* outside an area adjacent to the meltwater stream (section 4.4.2) suggests that other parts of the foreland may also be drying, although Whittaker (1985) suggests that the species tolerates dry conditions, but is adversely affected by competition. Evergreen species may be more adversely affected by drying than deciduous ones due to shallow roots preventing access to deeper moisture (Schimel et al., 1996). On the other hand, some of the species increasing in frequency are moisture requiring, e.g. Whittaker (1985) describes *Salix glauca* as preferring boggy conditions and *Carex* spp. is typically associated with waterlogged sites.

This discussion indicates that these effects are spatially variable. Sites on the flanks appear to be drying, resulting in decreases in frequency amongst moisture-requiring species (section 5.4). Drying is also occurring on the fluted moraines with the retreat of the glacier. However, the increases in frequency of moisture-requiring species suggests that elsewhere in the study area moisture availability may be increasing.

Grazing Intensive herbivory has been conjectured to have resulted in past examples of extensive vegetation changes; for example the activities of the megaherbivores in the arctic (Chapin III and Körner, 1995b; Jeffries and Bryant, 1995). As discussed in section 2.8.10, grazing may affect genotype frequency, vegetation composition and species distribution (Krebs, 1985; Edwards and Gillman, 1987). However, it is virtually impossible to establish the effects of past grazing regimes that mould the present vegetation composition and structure (Edwards and Gillman, 1987).

Preferences in grazing/browsing can result in differential effects; targeted species may be reduced within the vegetation or removed completely (Connell, 1975; Davis et al., 1985; Edwards and Gillman, 1987; Tilman, 1994; Wilson, 2000), while unpalatable species may come to dominate (Burrows, 1990; Rossow et al., 1997).

Sheep are currently grazed on the foreland. The number brought to the study area in 2000/2001 was 19, although more than two were rarely observed together subsequently. They were generally found on the fluted moraines and in the surrounding area, occasionally at slightly lower altitude, but rarely in the regional vegetation or on south-facing sites, although some were observed to have crossed the meltwater stream late in the season. A small herd of reindeer (15-20) was seen briefly at low-altitude on the foreland in 2001. Cows grazed to the east of the Leira amongst the regional vegetation and could cause substantial damage locally, but ranged up and down the valley, limiting the intensity of their impact. The foreland supported several species of small mammals, evidence of which was found in the droppings data. Small populations of several bird species were also observed, and substantial numbers of insects.

Grazing most frequently involved insect damage and was most evident on old, low-altitude sites (Table 6.20). Data for browsing is shown in Table 7.1 below:

Table 7.1: Mean frequency per $9m^2$ quadrat of browsing for each of the TWINSPAN groups (2000 data)

Group	1	2	3	4	5	6	7	8
Mean Frequency	2.17	0.38	1.00	0.93	1.86	2.67	0	5.82

Note: Group identity is as used in Chapters 5 and 6

Browsing is most extensive amongst the late-pioneers and is moderately frequent amongst the sites of the late pioneer-snowbed intermediate group on the north-facing flank, where occasional examples of defoliated and debarked *Salix* spp. were found.

Herbivory is generally restricted to a limited range of plants (data on targeted species were collected as part of the survey). Those subject to both grazing and browsing were *Salix* spp. and some later successional grasses, at low-altitude, and including *Oxyria digyna* and *Ranunculus glacialis* at high-altitude. Additionally on young sites, pioneer grasses, particularly *Poa* spp., were browsed. Evergreen species rarely show evidence of herbivory; being of poorer nutritional quality with higher levels of chemical defences and structural tissue (e.g. lignin) than deciduous species (Chapin III et al., 1980; Chapin III et al., 1986, 1995b; Hobbie, 1995).

The most frequently grazed species are deciduous. All *Salix* spp. showed some evidence of grazing, but *S. glauca* and *S. lanata* were most often targeted; the first increased while the second decreased and appears to be the main heath species declining on the north-facing flank (problems with identification of these species were discussed in section 4.1). *Oxyria digyna* has increased particularly on young, central sites, while on the north-facing flank there is a mixed pattern, possibly due to the interspersion of site types there (section 5.3.7). *Ranunculus glacialis* shows a similar pattern but with weaker colonization on young terrain. Stimulation of vegetative growth from basal meristems has been noted when grasses have been grazed (Edwards and Gillman, 1987; Burrows, 1990), but results in delayed flowering (Crawley, 1999). Most later colonizing grasses have, however, increased in frequency and expanded their ranges. There is, however, no evidence of release from grazing pressure as a causal factor.

In conclusion, grazing/browsing may contribute to some of the changes seen, particularly on the north-facing flank. For most of the other changes recorded above, grazing does not provide a satisfactory explanation. Deciduous species that are subject to grazing, increase in frequency while ungrazed, evergreen ones decrease. Preferential grazing may contribute to the decline of *Poa* spp. on young sites, but not on older terrain where browsing frequency is low and sheep were rarely seen. Areas of particularly light grazing, e.g. the south-facing flank and mature heath sites, are nonetheless subject to distribution changes. There is no evidence that grazing intensity has substantially altered between the two surveys. However, as stated early in this discussion, grazing history contributes to present composition and structure, but tends to leave no clear evidence within the vegetation (Crawley, 1999).

Trampling This is mainly associated with the route to the glacier that was marked subsequent to the 1970 survey. The effects on the vegetation can be severe; as can be seen where it crosses two low-altitude sites that have species counts reduced by 50% compared to 1970. However the effects are strongly localised.

Disturbance While this will not target particular species, vegetation types may be associated with a particular disturbance regime (Matthews, 1999) and disturbance types tend to be limited in spatial extent; for example cryoturbation on young land close to the glacier snout (Frenot et al., 1995) and on exposed ridgetops (Matthews et al., 1998), and solifluction on sloping land (Matthews, 1999). It is impossible to judge how disturbance has changed, as such data were not collected in the 1970/71 survey. There is, however, no evidence of widespread, intensive disturbance (Tables 6.11-6.18 and Table 6.20).

Increased flooding might accompany high levels of ablation from the glacier. While this was seen in 2003 (J. A. Matthews, personal communication), there is evidence that the glacier has been relatively stationary from the mid 1980s at least to the late 1990s (Andreassen, 1999; Nesje et al., 2000). Few sites showed evidence of flooding or channel switching in the 2000/01 survey.

Disturbance has local controls, such as the presence of moisture (Billings, 1974a; Matthews, 1999), frequent freeze-thaw cycles (Johnson and Billings, 1962), substrate texture (Bliss et al., 1994) and slope (Matthews et al., 1998). It also has a macroscale control in the regional climate, which determines absolute temperature regime and precipitation receipt.

Climatic change Evidence presented in section 1.4 from weather stations and the Klima Reports (Hanssen-Bauer and Forland, 1998; Hanssen-Bauer and Nordli, 1998) discusses the climatic change that has taken place in southern Norway since 1876. Following a period of low temperatures from the 1930s to the late 1960s, temperatures have increased since 1970, particularly during the winter and spring, indicating an earlier onset of the growing season. Precipitation has increased by approximately 10%, also mainly in winter/spring. There are fluctuations in these trends, particularly in the 1980s when temperatures were frequently very low during the winter, but during the 1990s the rise has been pronounced. The North Atlantic Oscillation (NAO) appears to have contributed to climatic trends since the 1980s when it entered an extreme positive phase (Hurrell, 1995; Kaas and Frich, 1995; Beniston, 2000; Yoo and D'Odorico, 2002), bringing warm, moist air to western Norway resulting in the advance of maritime glaciers (Nesje et al., 2000; Nesje and Dahl, 2003).

Changes in snowlie, and possibly moisture availability appear likely to contribute to vegetation changes occurring on the high-altitude flanks. High levels of browsing may also contribute to the patterns of decreases and increases in frequency on the north-facing flank. However, the differential pattern of responses at low-altitude, particularly within the regional vegetation, and the shifts in some distributions onto land at higher altitude, indicate a widespread, consistent response by individual species that may be related to the change in boundary conditions discussed in section 1.4. In section 2.9, climatic change was associated with differential patterns of response from species and these are considered in more detail below.

7.2.3 The relationship between climatic and vegetation change

This section considers the distributional changes (section 7.2.1) in relation to the climatic changes described above. Additional material is drawn from experimental work examining the potential effects of anthropogenically-induced climate warming and the small number of studies that suggest such effects are already occurring.

Studies concerned with the effects of anthropogenically-induced warming relate warmer winter and spring temperatures to a reduction in duration of snowlie and an increase in growing season length. Differentiated species responses are expected due to differing life history traits enabling some species to take greater advantage of the longer season than others (Körner, 1994; Körner, 1995; Molau, 1997; Strenstrom and Jonsdottir, 1997; Suzuki and Kudo, 1997; Welker et al., 1997; Woodward and Kelly, 1997) together with variable effects on nutrient availability and species-specific nutrient uptake (Shaver and Chapin III, 1986; Nadelhoffer et al., 1991; Chapin III et al., 1995a; Shaver, 1995; Shaver et al., 1997). Experimental manipulations of temperature and nutrient availability show changes in growth rate, phenology and reproductive success, but generally these are short-term studies taking place over three years or less (Wooky et al., 1994; Chapin III et al., 1995a; Bauert, 1996; Henry and Molau, 1997; Jones et al., 1997; Stenstrom et al., 1997). Over the longer-term, more far-reaching community effects may occur as seen in the study by Chapin et al. (1995a) at Toolik Lake, Alaska. This study started in 1981 and continued for nine years. A variety of treatments were used, including temperature manipulation using greenhouses and nutrient additions; temperature increases also increased mineralization rates. Compositional changes occurred as a result of both nutrient and temperature manipulations, and the character of the site altered from *Eriophorum* tussock-tundra to a system dominated by *Betula nana.* A reinforcing, positive feedback was also found to operate through the improvement of litter quality and therefore of cycling rate with the increasing dominance of *B. nana.* At the end of the experiment, control plots were found to be undergoing the same changes seen in the manipulated plots; an increase in temperature of 4°C in permafrost temperatures over the past 50 years, the warmest air temperatures on record during the period of the study and a CO_2 efflux from the study area were cited as potential causal factors . The level and differential nature of the change is seen by Shaver and Laundre (1997) to result from the species-specific variation in growth response to the manipulation followed by subsequent competition (Chapin III and Shaver, 1995; Molau, 1997; Woodward and Kelly, 1997).

In the Toolik Lake study, the changes involved a strong compositional shift, which is not seen at Storbreen. This may be the result of initial differences in the characteristics of the ecosystem. Press et al. (1998) compared the effects of temperature and nutrient manipulations between subarctic (Abisko, Sweden) and high arctic (Ny Ålesund, Svalbard) sites. The subarctic dwarf-shrub community responded to temperature manipulation and nutrient addition by increased clonal and vegetative growth, the height of the canopy being raised by 86%, while in the high arctic the response involved both existing and invading species. The regional vegetation at Storbreen is dwarf-shrub and, as in this example, the response appears to be by changing dominance amongst species *in situ*, particularly the increasing frequency of deciduous species. At higher altitude, on younger land, vegetation is comparatively sparse and some forb species are able to find suitable sites.

Altitudinal shifts Distribution changes in response to warming are expected to involve shifts to higher altitude (Krebs, 1985; Grace, 1988; Halpin, 1994; Beniston, 2000), as reported in palaeoecological studies (Chapin III and Körner, 1995b). A few studies have already detected evidence of such changes. Grabherr et al. (1995) found species richness on summits in the Austrian Alps increased by 25% since the beginning of the century. Klanderud and Birks (2003) resurveyed 23 summits in the Jotunheim in 1998, 68 years after they were first surveyed, finding a similar increase in species richness on 19 summits. Such migrations are expected to be individualistic and unpredictable as species move into existing communities (Körner, 1994; Callaghan and Johasson, 1995; Chapin III and Körner, 1995b).

At Storbreen, increases in forb populations at higher altitude also reflects this pattern, the limited development of this trend may be due to the confounding of increasing altitude with decreasing age. Figure 4.3 shows intermediate and late species at higher frequency than in 1970 outside the area of the fluted moraines (*Betula nana, Carex* spp.*, Empetrum hermaphroditum* and *Salix glauca*). The abrupt truncation of the increased populations at ca 50years (Figure 4.3), suggest that increased population levels might continue onto higher land but for the constraint apparently associated with drying and a lack of safe sites on the fluted moraines (Whittaker, 1993).

7.2.4 Changes associated with functional groups

The results of experimental manipulations indicate that while the finescale detail of changing performance is species-specific, coarser-scale patterns are associated with the response of particular functional groups (section 4.4). As discussed by Shaver et al. (1997), there are fundamental attributes common to species within such groups and that differ between them. Examples include resource-use and efficiency (Shaver et al., 1997), photosynthetic capacity (Körner and Larcher, 1988; Chapin III, 1993b; Hobbie, 1995), litter quality (Hobbie, 1995; Pastor, 1995), growth rate (Körner, 1994; Chapin III et al., 1995a; Molau, 1997) and nutrient uptake (Shaver and Chapin III, 1986).

Shrubs As discussed above, large frequency increases preferentially involve deciduous shrubs, while decreases occur amongst evergreen ones (sections 4.2 and 4.4.2). Similar differential responses are also found in experimental studies (Chapin III et al., 1995a; Pastor, 1995; Shaver, 1995; Henry and Molau, 1997; Molau, 1997; Suzuki and Kudo, 1997; Lee, 1999).

Deciduous species predominantly occur on nutrient-rich sites, while evergreen ones are found in nutrient-poor conditions (Chapin III, 1980; Hahn et al., 1996; Chapin III et al., 1995b). Deciduous species also have a higher photosynthetic capacity than evergreen species (Körner and Larcher, 1988); they grow faster (Shaver, 1995) and are more responsive to nutrient addition (Körner, 1994; Molau, 1997; Suzuki and Kudo, 1997). Litter of deciduous species is also more copious and of higher quality than evergreen, having the potential to affect nutrient supply through changes in the rate of cycling (Chapin III et al., 1995a; Pastor, 1995), although increases in the C:N ratio might negate this (Henry and Molau, 1997; Welker et al., 1997). Deciduous species are therefore likely to be advantaged by a warmer, longer growing season, provided there is an adequate nutrient supply. Warming may increase nutrient supply through stimulation of the microbial community (Körner, 1994; Chapin III et al., 1995a; Zhang and Welker, 1996). However, a 3.5°C increase in air temperature on Svalbard was found to increase soil temperature by only 0.7°C, which was found to be insufficient to increase nutrient mineralization (Robinson et al., 1998).

E. hermaphroditum is one of only a few evergreen shrubs that have increased in frequency at Storbreen and occurs at particularly high frequencies at low-altitude on foreland sites (section 5.6). It can tolerate a wide range of moisture conditions (Tybirk et al., 2000), although it has been associated with drier conditions in the Jotunheim (Klanderud and Birks, 2003) and at Storbreen (Whittaker, 1991). Klanderud and Birks (2003) considered its increase to be due to loss of snowcover, although Tybirk et al. (2000) found that it required snowcover for winter protection and as a source of spring moisture. In this study, it is amongst those late species that have not colonized the fluted moraines (Figure 4.3), suggesting a relatively high moisture/snowlie requirement. It suffers little herbivory, although voles and lemmings may consume it in winter (Tybirk et al., 2000). It has a persistent seedbank (Molau and Larsson, 2000), and is dispersed long distances by birds (Tybirk et al., 2000). Additionally, it is resistant to pollution, tolerating soil pH as low as 3; and both it and *Carex* spp. increased in frequency in response to nitrogen deposition (Tybirk et al., 2000).

Outside of those areas that are drying, there is a trend towards increasing frequency of this species at Storbreen. Adventitious rooting from trailing stems was seen commonly, and elsewhere this has been found to be associated with expanding populations (Press et al., 1998). A population increase may have long term implications for the system at Storbreen. Several studies show that *E. hermaphroditum* produces an allelopathic secondary metabolite, a bibenzyl known as batatasin III (Wardle and Nilsson, 1997; Tybirk et al., 2000). Wallstedt et al. (2001) tested this on *Betula pendula* roots where it was found to inhibit NH_4 uptake and have persistent growth effects even after the compound was removed. It inhibited seedling germination and establishment of *Pinus sylvestris* (Nilsson et al., 2000) and *Betula pubescens* ssp. *czerepanoveii* (Weih and Karlsson, 1999). These effects were attributed to the inhibition of nitrogen acquisition due to a reduction in mycorrhizal infection and microbial biomass (Wardle et al., 1998; Nilsson et al., 2000). *E. hermaphroditum* itself exploits organic nitrogen through the proteolytic enzymes of its ericoid mycorrhiza (Tybirk et al., 2000). Michelsen et al. (1995) however, claim a similar inhibition was obtained using leaf extracts and is due to the stimulation of microbial activity and subsequent immobilization of nutrients in the microbial biomass, although the methodology employed has been criticised (Wardle and Nilsson, 1997). Wardle et al. (1998) found that changes in litter quality led to a series of ecosystem effects through the formation of a deep, allelopathic, organic humus, slowing decomposition and cycling through microbial inhibition, reducing plant nutrient acquisition and growth. In northern Sweden, Nilsson et al. (2002) found that by reducing *E. hermaphroditum* secondary metabolites they were able to change dominance in the system in favour of the grass *Deschampsia flexuosa*. *E. hermaphroditum* is able to dominate in low nutrient, acidic systems where diversity and plant numbers are low, reinforced by positive feedback from allelopathic compounds and the formation of a nutrient bank from which other species are excluded (Tybirk et al., 2000).

Such dominance is not a feature of the study area, where it is frequently associated with the deciduous *Vaccinium* species. Shevtosa et al. (1995) looked at the effects of neighbour removal on *E. hermaphroditum, Vaccinium myrtillus* and *V. uliginosum.* Their findings suggest that positive interactions may occur between the three (cf. Jonasson, 1992). *V. vitis-idaea*, however, responded favourably to the removal of *V. uliginosum*, suggesting the latter was competitively superior. This may contribute to an understanding of the declining performance of *V. vitis-idea* in this study, in areas where *V. uliginosum* performance is improving and the distributions overlap.

Grasses and related species Many of the late successional grasses have increased in frequency (*Anthoxanthum odoratum, Deschampsia cespitosa* and *Phleum alpinum*) (section 4.4.6 and Table 7.3).

In experimental studies, many grasses are found to respond to warming and/or nutrient additions in similar ways to deciduous shrubs, but more rapidly, through the expansion of existing leaves and tillering rather than changes in allocation and the development of new buds (Chapin III et al., 1995b; Shaver, 1995; Hobbs, 1997; Molau, 1997; Shaver et al., 1997). In some short-term experiments this is seen as the main response to warming and/or nutrient addition (Henry and Molau, 1997; Press et al., 1998), while in the longer-term the shrub response occurs after 5-10 years, at which point the grasses decline (Chapin III et al., 1995b; Chapin III et al., 1995a; Shaver and Laundre, 1997; Lee, 1999). Shaver and Chapin (1986) compare the effects of nutrient manipulation on four sites in Alaska; on two sites, grasses assumed dominance despite having been only a minor component previously.

Many of the other graminoid species have not performed well, particularly *Juncus trifidus* (Figure 4.35) and *Luzula* spp. (Figures 4.36 and 4.37), but with the exception of *Carex* spp. (Figure 4.31). The latter species show a mixed pattern on old sites, but increases in frequency on both the north-facing flank and young, high-altitude sites. Stenstrom et al. (1997) performed temperature manipulations with *Carex bigelowii* at Latnjajaure, Sweden, finding an accelerated growth response to the increased temperature that was likened to that of deciduous shrubs. Shaver and Laundre (1997) compared the responses of *Eriophorum vaginatum* and *C. bigelowii* to both temperature and nutrient increases at Toolik Lake, finding that plant size increased then stabilized at a higher biomass, ‘diluting’ the increased nutrient availability. Again, the response of *C. bigelowii* is likened to that of deciduous shrubs, involving the storage of increased photosynthate until the following season. Shaver (1995) considers that the early response of grasses will include sedges, which have similar patterns of resource allocation. Few other grass-related species have been used in manipulation experiments.

Grasses and sedges are likely to respond to both warming and increased nutrients in a similar way but more rapidly than the deciduous shrubs; other graminoid responses resemble those of evergreen shrubs. Where grasses coexist with deciduous shrubs, the taller shrub canopy is likely to overtop the grasses leading in the long-term to shrub dominance. While grasses are generally performing well in the study area, they are rarely dominants. This does not appear to have changed since 1970, with successional stages described in terms of the characteristic shrubs (Matthews, 1976). While grasses and sedges may have experienced greater population expansion than seen at present, there is no way of verifying this.

Forbs As a functional group, these species typically decrease and decline (sections 4.2, 4.3 and 4.4.8), particularly on old sites with which 75% are associated, apparently related to reduced establishment opportunity on these sites. The overall trend in forb frequency depends on performance on younger, higher altitude sites. Species with populations already present within the foreland in 1970 (*Pedicularis lapponica, Pyrola* spp. and *Veronica alpina*) have increased. Others appear to be in the process of establishing subpopulations there and frequencies may expand in the future (*Antennaria alpina, Bartsia alpina, Gnaphalium supinum* and *Hieracium alpinum*). A further group has made little if any encroachment on younger, high-altitude sites (*Leontodon autumnalis, Polygonum viviparum* and *Tofieldia pusilla*); and the decline may be far-reaching. Klanderud and Birks (2003) see a similar pattern: species with wide ecological tolerances migrating to higher altitude, while those with restricted ranges decline.

In the literature, forb performance parameters are often equated with those of deciduous shrubs in terms of photosynthetic capacity and growth rate (Körner and Larcher, 1988; Wooky et al., 1994; Molau, 1997) and in the short-term, reproductive success in response to manipulation experiments results in population increases (Henry and Molau, 1997; Welker et al., 1997). However, such studies are often monospecific, with a rather different pattern emerging from the community response. Hobbie (1995) and Press et al. (1998) found increases in growth in response to increases in nutrients and temperature amongst deciduous shrubs and grasses at the expense of forbs. Chapin et al. (1995a) found in the long-term that forbs and mosses were disproportionately disadvantaged compared to shrubs and grasses, to the extent that it was anticipated that whole functional groups could be lost. The principal mechanism appears to be shading and competition where vegetative growth of other species is enhanced (Alatalo and Totland, 1997; Molau, 1997). Hobbs (1997) mentions an association between forbs and disturbance (cf. Whittaker, 1993), together with the depletion of surface moisture due to the presence of grasses. Brubaker et al. (1995) found shrub increases during warming following the last glacial maximum at the expense of 'herbs', and expects a similar pattern at the present time. A similar pattern of decline is found amongst forbs at low-altitude in the dwarf-shrub heath at Storbreen.

7.2.5 Mature sites

As discussed above, *Empetrum hermaphroditum* dominance is associated with acidic conditions, low nutrient levels and allelopathic secondary metabolites that other species find difficult to tolerate. A similar inhibition was associated by Körner (1995) with the highly acidic litter under *Loiseleuria procumbens*, another evergreen species found to be increasing in the study area. Deciduous species on the other hand produce higher quality litter and are associated with higher nutrient levels. In both cases, the litter produced will feedback positively, reinforcing the conditions preferred by the species. This resembles the mechanisms discussed by Wilson and Agnew (1992) when describing positive feedback switches, suggesting an alternative to cyclic succession to explain the mosaic identified by Whittaker (1985) at Storbreen. Small-scale environmental heterogeneity might determine initial species composition; with positive feedback improving conditions for occupying species but these becoming increasingly inhibitory for species with differing requirements. With a lengthening growing season and strengthening patterns of dominance (section 5.2), intermediate compositions are more likely to conform to one endpoint or the other resulting in increased differentiation of the mosaic.

In the long-term manipulation of temperature and nutrient availability at Toolik Lake, Alaska, Chapin et al. (1995a) found that the biomass of *Betula nana* increased in both experimental and control plots, which he attributed to increasing regional temperatures. Additional work on growth patterns, showed that *Betula nana* achieved this through changes in allocation, converting short to long buds (Bret-Harte et al., 2001) and thereby increasing secondary rather than primary growth (Bret-Harte et al., 2002). The measure used in these surveys gives no indication of biomass so that it is not possible to establish whether such a change has occurred in the study area. The maintenance of the *Betula nana* population on older terrain, where most other species experience either substantial increases or decreases, may be indicative of such a process underlying the apparent stability.

7.2.6 *Salix herbacea*

This low stature shrub has increased in frequency by over 6000 counts since 1970 (Figure 4.12, Table 4.1). Increasing in frequency on the north-facing flank, and with a larger population than in 1970 on younger, high-altitude land, particularly that aged 30-60 years. This includes the area covered by the fluted moraines, where it is not affected by drying of this land (Ballantyne and Matthews, 1982), possibly benefiting from the failure of taller shrubs to colonize substantially or contributing to this (section 4.3).

Salix herbacea is often associated with snowbeds (Matthews, 1976), although also able to colonize open fellfields and ridgetops (Wijk, 1986a; Beerling, 1998). The restriction to snowbeds is thought to be due to poor competitive ability (Wijk, 1986a; Jones et al., 1997; Beerling, 1998). It may be blocked by the presence of *Vaccinium myrtillus* on adjacent land or by the lack of mycorrhizal infection (Wijk, 1986b; Stanton et al., 1994). While growing most strongly on the periphery of snowbeds (where thaw is early), it has more of its biomass in central positions (where thaw is late) (Wijk, 1986b; Stanton et al., 1994). However, there is evidence of a strong response to increased growing season length. Wijk (1986b) manipulated growing season length by removing snow and found that shoots increased threefold in length and fivefold in weight in response to an increase of 20%. Jones et al. (1997) found the species responded to warming by an acceleration of reproductive phenology and increasing the length and dry weight of leaves. Wijk (1986a) found a correlation between year to year variability in growth and temperature in the preceding May to June (the timing of snowmelt, and therefore growing season length), that was controlling the amount of carbohydrate stored for the next season's growth (Beerling, 1998). Beerling (1998) also discusses increased seed production during longer seasons, with predominantly vegetative expansion when temperatures were low. Large numbers of the plumed seeds were transported on upvalley winds towards the glacier at Storbreen late in the 2000 season (personal observation).

There appear to be three principal factors likely to underlie the expansion of the *Salix herbacea* population: (1) the strength of the growth response to increased growing season length;

(2) increased seed production, also in response to increased growing season length; and (3) the broad tolerance of physical conditions. The main areas of expansion, on the north-facing flank and the fluted moraines, are those where taller shrubs perform poorly. Lengthening shoots and larger leaves may give it the advantage in competition with other low stature species. The poor competitive ability, remarked in the literature, suggests that it is unlikely to be causally related to the decline of the taller shrubs (*Phyllodoce caerulea* and *S. lanata*); its expansion is more likely to be opportunistic, coincident with their decline.

7.2.7 Summary: species populations

(1) Among species with counts greater than 100, 66% of species exhibit changes in frequency since 1970 exceeding 20%, and 78% exceed 10%.

(2) Typically successional patterns are seen involving wavelike increases and decreases in frequency, and expansion onto younger land. However, other patterns are found that do not conform to these, including: (a) a group of late species including *Empetrum hermaphroditum* and *Salix glauca* that consistently increase on old terrain; (b) species that decline in the regional vegetation; (c) pioneer and forb populations that decrease on old terrain at low-altitude; (d) frequency changes that affect functional groups consistently; (e) species that increase in frequency on younger, higher-altitude land compared to their distribution in 1970; (f) several late species that do not occupy young land with the same frequency as in 1970 but occur with higher frequency on slightly older land; (g) pioneer populations that expand on the north-facing flank.

(3) On the north-facing flank, compositional changes are associated with an apparent reduction in duration of snowlie and high levels of browsing.

(4) Spatially restricted effects are associated with moisture and snowlie changes: drying on the fluted moraines; reduced snowlie on the north-facing flank; possibly restricting *Phyllodoce caerulea* to an area around the meltwater stream; and declining evergreen populations.

(5) Although grazing levels are not intensive, they may have increased since 1970. However, grazing is unlikely to provide a complete explanation as the most frequently grazed species are also those experiencing the largest population increases.

(6) The effects of trampling are severe but limited in extent.

(7) Most recorded disturbance was mild/moderate.

(8) The recent pattern of regional climatic change involves decreases in temperature and precipitation from the 1930s to the late 1960s, followed by increases in both temperature and precipitation from approximately 1970. Species-specific responses are anticipated to reduced snowlie and increased growing season length.

(9) Experimental studies elsewhere show short-term increases in growth rate, reproductive success and phenology in response to increasing temperatures or nutrient additions. In the long-term, compositional changes occur where the vegetation is open (at high latitude) and shifts in dominance where plant density is high (at low latitude). Similar changes occur at Storbreen, but at high and low-altitude (respectively).

(10) The preferential increases amongst deciduous shrubs may be related to their higher photosynthetic capability, faster growth rate and higher quality litter.

(11) The evergreen shrub, *Empetrum hermaphroditum,* increases in frequency and has been associated elsewhere with the production of deep, allelopathic humus that inhibits nutrient cycling at an ecosystem level. At Storbreen, the species is not widely dominant but is associated with the deciduous *Vaccinium* spp..

(12) The late-successional grasses and *Carex* spp. have increased in frequency in the study area while other graminoids have declined. In experimental work grasses and sedges are likened to deciduous shrubs but respond more rapidly to increases in temperature or nutrient additions via existing structures, although in the long-term, shrub dominance is expected as changing allocation patterns thicken the canopy.

(13) Forb species generally decrease in frequency, particularly on old terrain. The overall success of a species depends on its ecological amplitude in relation to younger, higher land. Long-term, community experimental studies, involving increasing temperatures in dense vegetation, frequently show forbs to be disadvantaged due to shading and competition from shrubs and grasses.

(14) The increasing frequency of *Salix herbacea* is likely to be opportunistic; it has wide ecological tolerances and responds favourably to an increase in growing season length, but competes poorly with taller shrubs. Its expansion is therefore likely to be coincidental to their decline.

7.3 Dynamics of the successional sequence

This study provides the opportunity to observe the dynamics of a successional sequence over a period of thirty years. This permits an assessment of actual changes occurring on particular sites, rather than reconstructing a sequence based on the assumption of space/time equivalence (section 2.7). In this section, the study findings concerning community dynamics are discussed in relation to interpretations in previous studies at Storbreen and in the broader context of successional theory.

7.3.1 The community structure of the sequence

Initially, the findings in this study are used to examine the interpretation of the system at Storbreen by Matthews (1976, 1978), and Whittaker's hypothesis that differing developmental histories on the various landforms result in distinct vegetation communities (Whittaker, 1993). This part of the study also has broader implications in terms of the effects of contrasting position on coarse-scale environmental gradients and in identifying factors that determine the nature of the successional trajectory (Walker and del Morel, 2003).

Matthews (1976, 1978) describes a three-stage low-altitude succession: an initial pioneer stage is followed by a species-poor (after 100 years) and then a species-rich heath (250 years). The species-poor heath sites are characterised by *Phyllodoce caerulea* and *Salix* spp., the species-rich heath by *Betula nana* and *Vaccinium* spp.. The sequence is simpler at high-altitude with only two stages, pioneer and snowbed, with pioneers more likely to persist in the 'climax' and the latter dominated by *S. herbacea* (Matthews, 1976, 1978; Matthews and Whittaker, 1987).

This study concurs with much of this interpretation, and although there are minor differences in detail, e.g. an additional intermediate stage is identified in this study, these are attributable to differences in methodological approach. More importantly, this study provides evidence of three, rather than two, trajectories (section 5.6). A heath trajectory occurs at low-altitude, the early stages of which occur on centrally-located sites at higher altitude. Snowbed trajectories occur on sites on the flanks of the foreland, but different communities are associated with north-facing (species-poor), compared to south-facing (species-rich), sites.

The major determinants of these trajectories are, therefore, altitude and aspect, which vary across the study area, so that these gradients vary at a mesoscale. Whittaker (1985) described altitude and aspect as surrogate gradients representing groups of variables that vary collectively with position on the gradient. The altitudinal range at Storbreen (1100 – 1500 m asl.) covers the transition from the low- to the mid-alpine zone (Matthews, 1976) and vegetation differences have previously been identified between sites developing at the extremes of this gradient (Matthews, 1976; Whittaker, 1985; Foskett, 1998). Increasing altitude is accompanied by increasing deflation, precipitation and exposure, decreasing temperature and an increased likelihood that snow is redeposited to lower altitude (Foskett, 1998). Pedogenesis proceeds more slowly (Darmody and Thorn, 1997), vegetation cover is less extensive (Matthews, 1976) and cryoturbation occurs more frequently (Matthews, 1999) at high- compared to low-altitude (sections 2.8.1 and 2.8.2).

In relation to aspect, the study area is broadly divided between land that faces north-west and that facing south-east (Figure 1.2), but aspect-related effects are likely to be more substantial on the exposed, higher altitude flanks compared to the relatively sheltered central trough. Associated microclimatic effects (section 3.2.3) include higher levels of insolation, lower moisture availability and enhanced soil development on south- compared to north-facing land. At Storbreen, depression systems are carried by southwesterly winds, while colder, sometimes snow bearing, systems are associated with north-easterlies (Matthews, personal communication). Although aspect has been documented as affecting growth rate, species richness and ameliorating altitudinal constraints (section 3.2.3), examples of its influence on successional trajectories are rare (one example is quoted in Matthews, 1992).

The model of high-altitude succession proposed by Matthews (1976) is of a shorter, simpler sequence than that occurring at low-altitude, with fewer stages and a greater similarity between pioneer and mature stages (Elven, 1975; Matthews, 1979a, 1979b; Birks, 1980). The decrease in growing season length with increasing altitude is considered a major constraint on the development of taller shrubs, so that *Salix herbacea*, forbs and cryptogams are of greater importance at high- compared to low-altitude (Matthews, 1992). These conclusions are supported in this study, e.g. late pioneer species occur in the mature groups, and *S. herbacea* is an important component of the composition. However, this study also contributes to the model by differentiating the two aspect-related trajectories on the individual flanks. Both are low-stature, snowbed communities, but successional development on the north-facing flank does not progress beyond a late-intermediate stage (section 5.6). Although both snowbed trajectories comprise at least four stages, in the methodology used in this study, each stage represents a smaller compositional step than is found on the four-stage heath trajectory. This is due to the inclusion of additional stages on the subsidiary loops and, on the north-facing flank, the apparently retrogressive transition from the early intermediate stage. On north-facing land, vegetation is sparse and species-poor, while on south-facing land the extensive vegetation is species-rich and characterised by snowbed forbs e.g. *Leontodon autumnalis.*

In associating the three trajectories with different landforms, the north- and south-facing flanks and low-altitude and/or on central land, this study provides evidence to support Whittaker's hypothesis. Whittaker (1993) suggested that species physiological responses to differences in environmental conditions, particularly disturbance, underlie the differences in vegetation communities on the individual landform units. As discussed above, increasing altitude is associated with increasingly harsh conditions, particularly in terms of weather patterns, temperature and the length of the growing season. South-facing aspect mitigates these conditions to some extent, while north-facing aspect exacerbates them. Qualitative differences distinguish not only mature sites, but also earlier stages e.g. the three compositional strands in the late pioneer-heath intermediate group. Disturbance, including browsing, occurs more frequently on the high-altitude flanks (section 6.3), as do retrogression and stasis (section 5.7), compared to land at low-altitude. The smaller inter-stage compositional differences and the low-stature of both communities at high-altitude, reflect harsh conditions, while greater species richness indicates amelioration on south-facing land.

It has been indicated in this discussion that centrally-located sites at high-altitude are likely to develop along the heath trajectory, in part due to the rapid progression of several early pioneer sites to the species-poor heath since 1970. However, many of those early pioneer sites were on the south-facing side of the central trough, where the glacier retreat has been most extensive, and favourable aspect may mitigate adverse conditions. Additionally, late-occurring species are colonising central sites on the fluted moraines more slowly than would be expected from their distributions in 1970 (section 4.3). Ultimately, these central sites may provide a further source of variation within the foreland.

7.3.2 Convergence and divergence

A divergent system occurs when the number of community types and/or the compositional distance between them increases during the course of successional development, while convergence involves increasing compositional similarity over time and has often been associated with the effects of canopy formation (Walker and del Morel, 2003) (section 2.6.3). Matthews and Whittaker (1987) and Matthews (1992) found the system at Storbreen to be divergent as a result of the limited species pool in early and intermediate stages, altitudinal and microtopographic control of mature communities and the greater variety of late-occurring species.

However, the findings in this study indicate that differentiation between sites occurs early in the successional sequence. The late pioneer group is associated mainly with flank sites (Figures 5.7 and 5.8) and compositional change was found to differ between north- and south-facing sites within the group (section 6.3), while the late intermediate group contained three compositional strands associated with central, north- and south-facing locations (section 5.6.3). In the early intermediate group, differences in compositional change were primarily associated with location on the lower flanks, compared to the fluted moraines, but north- and south-facing sites were also distinct in terms of compositional change (section 6.3).

The presence of these distinct compositional strands early in successional development on individual landforms may indicate parallel, rather than divergent, trajectories, at least in the post-pioneer stages. Parallel trajectories occur where habitat differences are strong enough to generate distinct trajectories that persist throughout the successional sequence and neither converge nor diverge (Matthews, 1992; Walker and del Morel, 2003). The increasing separation over time, from within-group compositional strands to individual mature groups, may be the result of sites accumulating at mature stages while numbers of sites early in the sequence remain consistent as sites progress through the stage. The number of sites at early stages is unlikely to be sufficient for the individual strands to be detected at the resolution used in this analysis. However, the compositional strands in the late intermediate group (section 5.6.3) were distinguished by differing frequencies among a group of species common to all three strands, while differences among the mature groups involve separate groups of species, with little overlap. This suggests that compositional distance increases with increasing maturity, perhaps following the influx of late successional species, and, therefore, that the trajectories are divergent rather than parallel.

Despite this representation of the system at Storbreen as three diverging trajectories, there is also evidence in this study of fine-scale variability that suggests that characterisation solely in terms of trajectories may impose too rigid a structure. The subsidiary loops (section 5.6) represent stages that occur predominantly on the flanks of the foreland, but these stages also occur on some centrally-located sites. Sites from both locations may subsequently undergo transitions to the heath trajectory, so that species-poor and species-rich heath sites occur at high-altitude on the flanks. However, a snowbed composition rarely occurs at locations other than on the flanks (Figures 5.7 and 5.8). Additionally, there is evidence of rapid progression that omits stages ('jumps', section 5.6) and the broad range of transitions that occur from each group (section 5.5). Such patterns resemble those found in a successional network, where there are few restrictions on the transitions that occur at any stage (Walker and del Morel, 2003).

Causal factors underlying the divergence at Storbreen appear to be related to environmental heterogeneity on the three principal landforms in the study area. Previous work done on small glacier forelands in Scandinavia indicates that alpine sites, where physical conditions are harsh, tend to diverge, while more favourable conditions at subalpine sites lead to convergence (Birks, 1980; Vetaas, 1986; Matthews, 1992), particularly where a tree canopy buffers the vegetation from environmental perturbation (Vetaas, 1986). Convergence tends to be associated with favourable conditions and the importance of autogenic processes, while divergence indicates that allogenic processes continue to exert a substantial influence.

An alternative view in Walker and del Morel (2003) emphasises the contribution of plant-mediated processes to divergence. Such processes include priority effects resulting from stochastic dispersal and the formation of mosaics due to the sporadic establishment of strongly dominant species; edaphic heterogeneity and other environmental influences are mentioned only briefly. They also suggest that divergent systems are likely eventually to converge, given enough time.

These differences in viewpoint appear to be related to differences in the type of system that is examined. Dispersal barriers and restrictions are unlikely to be major constraints in small glacier forelands, where seed rain has been found to contain most of the species occurring frequently in the surroundings (Ryvarden, 1971; 1975) and seed sources are often close to, and track, the retreating glacier. Dispersal frequency does, however, decrease with distance from the parent plant (section 2.3) and may, therefore, reinforce vegetation patterns on land adjacent to the seed source, but stochastic dispersal, resulting in long-lasting priority effects, does not appear to be a major determinant on small glacier forelands. However, following a volcanic eruption, where denudation occurs across an extensive area at one point in time, barriers to dispersal, including distance from seed sources, may be critical and result in the importance of stochastic dispersal found in these studies (del Morel, 1993; del Morel and Bliss, 1993; del Morel et al., 1995; Whittaker and Bush, 1993). A similar pattern occurs on larger moraine systems, if glacier retreat is rapid, as found by Fastie (1995) at Glacier Bay.

7.3.3 Cyclic succession

It was suggested (section 5.6.3) that cyclic succession (Watt, 1947) (section 2.6) may be occurring at high-altitude on the north-facing flank. This process involves a regenerative, upgrade phase that is followed by a degenerative, downgrade phase, where the system returns to its initial condition before the process is repeated. Contributory factors have been found to include resource limitation or disturbance that prevents the species dominant in the upgrade phase from reproducing (Watt, 1947). On the high-altitude, north-facing flank, transitions occur from the late pioneer-snowbed intermediate group to the late pioneer-heath intermediate group that involve colonization by the shrub, *Salix glauca* and, on some sites, by *Empetrum hermaphroditum.* Retrogressive transitions also occur in this location from both the early and late pioneer-heath intermediate groups to the late pioneer-snowbed intermediate group that involve the loss of these shrub species and colonization by the late pioneers, *Oxyria digyna* and *Ranunculus glacialis.* Retrogression was found to be a weak trend in the study area as a whole (Table 5.21) and the conditions generating it are unusual and likely to occur at irregular intervals. Nonetheless, the size of the late pioneer-snowbed intermediate group remains stable in the two surveys, despite transitions from it to the late pioneer-heath intermediate group. Finally, in the absence of such cycles, development of the late pioneer-heath intermediate composition has been extremely protracted. Physical conditions are severe at high-altitude on the north-facing flank, and shrub growth is likely to be limited by inadequate resources or dieback may occur once the shrub grows beyond the depth of winter snow cover. Retrogression may, therefore, have a high probability once a certain height has been attained. The observed decrease in the number and extent of snowpatches on the north-facing flank since 1970, together with the extensive mortality amongst *Salix* species (personal observation), may impact on this system in the longer term.

7.3.4 Retrogression

Retrogression involves vegetation changes that result in a return to a previous developmental stage, often as the result of environmental perturbation, particularly disturbance (Whittaker, 1985). The Clementsian paradigm does not include retrogression, but portrays succession as orderly and progressive (Clements, 1916, 1928). However, retrogressive changes were documented in successional systems by other early authorities e.g. Cowles (1899, 1901) and Gleason (1939).

Whittaker (1985) identified retrogression in the system at Storbreen at all successional stages, but found it to be strong enough to mask progression only in late stages. He associated it with disturbance, e.g. flooding or slope failure, that resulted in the delay or resetting of successional development (Matthews and Whittaker, 1987). The findings in this study support the pattern detected by Whittaker (1985) (section 5.7). However, retrogression is a weak trend in this study compared to both progression and stability of composition (Table 5.21). Stability of composition, rather than retrogression, dominates in late stages particularly on the heath trajectory (Figure 5.10) (as proposed by Clements, 1928, 1936; Margalev, 1968).

Evidence in this study suggests that, although retrogression may be associated with disturbance, it also occurs in other circumstances. Disturbance was found to occur most frequently on young sites and in vegetation groups with a high proportion of sites on the high-altitude flanks (section 6.3, Table 6.26). While retrogression is relatively frequent on sites on the flanks of the foreland, it does not involve the pioneer groups (section 5.6). Additionally, retrogression was found to accompany strongly progressive transitions, even at low-altitude where disturbance occurs less frequently, although retrogression occurs at a considerably lower frequency than the progressive transition (section 5.6, Figure 5.9). It is, therefore, suggested that retrogression might more generally involve developmental failure, where later-occurring species were able to begin growth, but full establishment and expansion was unsuccessful. Such failure may be the result of inadequate amelioration or severe conditions, in addition to disturbance.

Full retrogression to the pioneer compositions did not occur, although it frequently involved recolonization by late pioneer species, such as *Oxyria digyna* and *Poa* spp. that are also associated with old, disturbed land (Whittaker, 1985). However, further evidence of retrogression was found on two sites that lost all higher plant species since 1970, but had not been recolonized by 2000. This failure of colonization by early pioneer species may indicate that conditions are no longer suitable for their establishment due to ‘reaction’ on the environment associated with the presence of the previous community.

7.3.5 The timescale over which succession occurs

Previous work at Storbreen, e.g. Matthews (1976) and Matthews and Whittaker (1987), has estimated that at least 230 years are required for foreland sites to attain compositions similar to those occurring at mature stages within the regional vegetation. In this study, nine foreland sites attained the status of the species-rich heath and four that of the mature snowbed composition since 1970 (section 5.5). Those foreland sites identified with the species-rich heath in 2000 occur at low-altitude and on the oldest land within the foreland boundary (approximately 180-250 years old), while those identified with the mature snowbed group occur on younger land on the flanks, although this is probably related to the closer proximity of seed sources on the steeply sloping flanks.

This evidence suggests that the timescale for completion of successional development has decreased in comparison with previous studies up to 1982 (Whittaker, 1985). However, a comparison between the compositions of species-rich heath sites within the foreland boundary and those within the regional vegetation indicated that there were differences between the two (section 5.4). Some of the differences appear to indicate a less advanced level of development, e.g. high frequencies of *Salix* spp. and low frequencies of evergreen species, while others may reflect the development of an additional compositional type e.g. high frequencies of *Empetrum hermaphroditum* and *Vaccinium* spp.. This may indicate a response to changing conditions; as found by Whittaker (1985): endpoints may not be fixed, they may fluctuate with environmental changes.

Despite these transitions, many sites have not yet progressed from the species-poor heath, even at low-altitude, on land aged at least 250 years. The high level of inertia in the species-poor heath (section 5.7), may indicate that this represents a relatively stable composition for some of these sites.

7.3.6 Summary: community dynamics

(1) This study has found evidence of three spatially-differentiated successional trajectories within the study area at Storbreen: a heath trajectory at low-altitude and at higher altitude on central sites; a species-poor snowbed trajectory on the north-facing flank; and a species-rich snowbed trajectory at high-altitude on the south-facing flank. These trajectories are interpreted as being determined by mesoscale gradients of altitude and aspect.

(2) This study, therefore, agrees with Matthews' interpretation of the low-altitude, heath trajectory. However, at high-altitude, this study identifies a more complex pattern than the simple pioneer to snowbed trajectory found by Matthews (1976, 1978). Central sites at high-altitude appear to be following the low-altitude, heath trajectory, while distinct snowbed trajectories are associated with the north- and south-facing flanks.

(3) This study also provides evidence in support of Whittaker's hypothesis that different patterns of successional development are associated with the different landforms at Storbreen. Harsher climatic conditions and a shorter growing season at high- compared to low-altitude, and the amelioration of these conditions on south- compared to north-facing sites, appear to underlie the differences in development.

(4) Matthews and Whittaker (1987) and Matthews (1992) found the successional system at Storbreen to be divergent. In this study, there was evidence of differentiation at an earlier successional stage, but the possibility that this indicated the presence of parallel trajectories was rejected due to the increase in compositional distance over the successional sequence.

(5) The presence of subsidiary successional 'loops' and evidence of successional 'jumps' (where sites progress rapidly) indicates that characterisation of the system solely in terms of the three trajectories is an oversimplification (section 5.6). Variability at a fine-scale resembles the dynamics of a successional network. Thus, the successional system as a whole seems to possess 'fuzzy trajectories'.

(6) Divergence in this system is unlikely to be the result of long-lasting priority effects following stochastic dispersal, as barriers to propagule dispersal are few in a small glacier foreland system. At Storbreen, divergence appears to be the result of harsh physical conditions and the absence of a tree canopy acting as a buffer. Divergence is more likely to be the result of stochastic dispersal where extensive denudation follows a volcanic eruption or on a much larger glacier foreland system, where glacier retreat is rapid.

(7) It is suggested that cyclic succession is occurring at high-altitude on the north-facing flank. This appears to involve the establishment of intermediate shrubs, particularly *Salix glauca.* The subsequent loss of such species may be due to inadequate resources or to dieback once they grow beyond the protective cover of winter snowcover.

(8) This study has identified an increasing frequency of retrogression with increasing maturity, as was found by Whittaker (1985). Retrogression is weak in this study compared to both stability and progression. While retrogression occurs most frequently on sites that have a high incidence of disturbance, it also accompanies strongly progressive transitions, even at low-altitude. It is suggested, therefore, that retrogression may be more generally defined as developmental failure, where later species are able to establish but subsequently fail to thrive.

(9) The absence of full retrogression to a pioneer composition may indicate dispersal limitation of early pioneer propagules. Supporting evidence is provided by the restricted pioneer distributions (section 4.8) and the failure of recolonization on two sites that lost all higher plant species since 1970.

(10) Previous work at Storbreen has suggested that > 230 years are required for completion of the successional sequence (Matthews, 1976; Matthews and Whittaker, 1987). In this study, nine foreland sites have the status of the species-rich heath within 180 – 250 years and four attained the status of the mature, species-rich snowbed group within 90 years. However, the composition of sites newly identified with the species-rich heath suggests either that development remains less advanced than sites within the regional vegetation or that the development may represent a new compositional type.

7.4 The influence of environmental variables operating at a fine scale

Environmental variables operating at a fine scale are examined in this section, building on the summaries in sections 6.2.10 and 6.5. Firstly, the relationship between the mesoscale and fine-scale gradients is discussed. Secondly, the implications of this study are then considered in the broader context of successional theory.

7.4.1 The relationship between mesoscale and fine-scale environmental gradients

By examining the system at Storbreen in terms of both overall patterns and fine-scale detail, this study combines holistic and reductionist approaches. Many of the differences characterising the divisions discussed in section 2.2, particularly those between Clements and Gleason, may be ascribed to the differences between holistic and reductionist viewpoints (Walker and del Morel, 2003) and, therefore, to the different scales at which the system is viewed.

By viewing the system at a finer scale, the level of detail increases, but evidence of patterning becomes less obvious. Whittaker (1985) identified two complexes, related to terrain-age and to microtopography, which he used to describe environmental influences on vegetation development. In the present study there was evidence of these complexes when the study area was examined as a unit, but within the individual vegetation groups the pattern identified was more intricate. Group-scale variation in environmental conditions was related to the operation of four compound gradients: (1) successional development (age, soil, humus, rooting depths, texture, pH and bare ground); (2) topography (altitude, slope, aspect and exposure); (3) moisture (moisture, snowlie); and (4) disturbance (frost heave, solifluction, fluvial disturbance, grazing, browsing and trampling) (section 6.2.10). An additional gradient, (5) substrate type, was added when environmental conditions were related to compositional change (section 6.3). Consistent relationships between these gradients were rare, except for that between moisture availability and disturbance regime. In each group, compositional differences between sites were associated with variation on at least three of the compound gradients: successional development, topography and disturbance (Table 6.27).

Environmental gradients operating at different scales appear to govern different attributes of the system. Different positions on mesoscale gradients of altitude and aspect determine the trajectory followed for the majority of sites and, therefore, determine qualitative differentiation. Terrain age, a third mesoscale gradient, provides an indication of the stage on the trajectory that a site is likely to have attained. However, differences in the rate of development were identified during the examination of within-group transitions (section 5.5) and sites at different stages on a particular trajectory are often interspersed locally (Figure 5.8). Successional development is not, therefore, a simple, linear temporal function and there is no consistent or precise relationship between terrain age and the stage attained. The CCA axes, identified in section 6.3, are frequently associated with a gradient from adverse to favourable conditions. These gradients are related, in turn, to differences in the level of successional development, e.g. shallow to deep soils and sparse to extensive vegetation cover, and with different groups of species e.g. from intermediate to late-occurring shrubs in the species-poor heath. Different positions on group-scale environmental gradients appear, therefore, to be related principally to variation in the rate of successional development. This operates within the mesoscale framework generated by increasing age.

However, this study suggests that the influence of these gradients extends beyond the rate of development to include within-group qualitative differences. The topographic gradients of aspect and altitude, although mainly effective at a mesoscale, continue to be associated with within-group subdivisions of sites e.g. those on the north- and south-facing flanks (groups 3 and 4) and those on the flanks and in the central trough (groups 8 and 5). While these are within-group divisions, they are not completely independent of the influence of the mesoscale gradient.

Finally, there is also evidence of fine-scale qualitative differences that occur on proximal sites and affects the operation of the subsidiary loops (section 5.6). Examples are relatively rare but include species-poor heath sites at high-altitude on the north-facing flank and a late pioneer site at mid-altitude on the south-facing flank (Figures 5.7 and 5.8). The conditions generated by fine-scale variables within the locality contrast with those prevalent on the mesoscale landform. At high-altitude on the north-facing flank, watercourses follow the line of the closely spaced moraines. Sites in such locations are sheltered and have high moisture availability. The assemblages were generally low-stature and often dominated by *Salix herbacea,* but on some sites taller shrubs were present. The second example involves a south-facing site at mid-altitude, where there was evidence of persistent slope failure. On this site there was a sparse, late pioneer assemblage including *Oxyria digyna* and *Poa* spp.. Fine-scale variables can therefore counteract the influence of the mesoscale gradients and the conditions generated may be favourable or adverse. While mesoscale topographic gradients determine the trajectories, the locally effective variables in the examples quoted are microtopographic. Local modification by microtopographic variables has been documented in other studies, particularly shelter in exposed locations (section 2.4.4) (Bertness and Callaway, 1994; Callaway et al., 2002).

7.4.2 The nature of disturbance

There is a tendency for disturbance due to physical processes to decrease with increasing site maturity, while biological disturbance (grazing/browsing) increases in importance. This appears to be related to canopy effects, both as a buffer against physical disruption and as a food source. Much of the disturbance recorded involves frequent, minor events effective at a finescale; extreme events such as site flooding occurring rarely. This supports the conceptual model developed by White (1979) of a disturbance gradient as part of the coencline (see also R. H. Whittaker, 1953, 1967, 1975).

Disturbance recorded in this study, however, involves only evidence visible at the time of the survey. It therefore represents disturbances over a short timescale (usually the preceding weeks or months), although evidence of more intense events will be preferentially preserved e.g. large solifluction lobes. The disturbance recorded may, therefore, be a substantial underestimate of that occurring over 30 years. It has been suggested that there is a critical level at which stress/severity/disturbance prevents or reverses development (Whittaker, 1985; Matthews and

Whittaker, 1987; Whittaker, 1991). The role of disturbance is, therefore, unlikely to be fully appreciated.

7.4.3 The termination of primary successional processes

Walker and del Morel (2003) have proposed that there is a switch from primary to secondary processes late in primary succession. These secondary processes are seen as being reflected in increasing correspondence between composition and the environment. This includes an increase in the importance of competitive interactions that results in the increased abundance of those species best adapted to the conditions.

Evidence from this study suggests that such a switch could be represented by the change from increasing vegetation cover to increasing soil development as sites develop within mature groups (section 6.3). This was associated with compositional shifts amongst species once vegetation cover had become extensive and included increasing frequencies of deeper-rooted shrubs and higher levels of humus production. Such processes occur in the mature species-rich heath and snowbed groups, together with the species-poor heath (which may represent a stable stage for many foreland sites) (section 6.3).

7.4.4 A comparison of the chronosequence and combined spatio-temporal approaches

The chronosequence concept has received extensive criticism in some recent studies (Pickett, 1987; Glenn-Lewin and van der Maarel, 1992; Olff et al., 1993; Fastie, 1995; Bakker et al., 1996) (section 2.7). Criticisms primarily relate to the assumption of the equivalence of space and time, which leads to the discounting of spatial heterogeneity as an important influence on successional change. Sites with strongly differing compositions and environmental controls are equated due to their similar age. Averaging results in a loss of detail, and effective processes may be obscured. However, in many studies there is no option but to employ such a methodology due to time constraints in relation to the length of time over which the system develops. It has also been found useful in formulating hypotheses that can be tested in more detailed studies (Bakker, 1996).

The separation of temporal and spatial approaches is another effect of the division in successional theory (section 2.2), between Clements (1928, 1936), who emphasised temporal dynamics, and Gleason (1926) and later Whittaker (1953, 1975), who focused on spatial variation. However, heterogeneity occurs both spatially and temporally (section 2.6). Spatial variation prevents there being a simple space-time equivalence, but temporal variation also leads to spatial difference e.g. mosaics caused by the development of disturbance-related patches initiated at different times (section 2.6.2) (Krebs, 1987; Crawley, 1997).

Combined spatio-temporal approaches involve resurveying long-term permanent plots (as in this study), but the opportunities for such studies are few. This approach is useful in testing the hypotheses and conclusions based on chronosequence studies, and such investigations have found that the chronosequence approach may be misleading e.g. the multiple endpoints identified by Fastie (1995) at Glacier Bay within what had been considered a single chronosequence.

This study initially uses a chronosequence approach (Chapter 4 and section 5.2), but the data have been mainly examined using a combined spatio-temporal methodology (section 5.3 onwards). Although trends were identified using the chronosequence, a more detailed and informative assessment was possible by combining spatio-temporal analyses, in terms of both community dynamics and within-group variation. Many of the findings reported in this study would not have been possible by relying on a chronosequence approach, particularly that involved averaging. Examples from this study include the following:

(1) The presence of three spatially-determined trajectories would have been confounded due to the averaging effect. The controlling environmental gradients are unlikely to have been identified, resulting in a loss of information concerning the community dynamics.

(2) Temporal variation would have been obscured e.g. drying on the fluted moraines (section 4.3). Such causal processes and mechanisms indicate the importance of site history (Pickett, 1987; Bormann and Sidle, 1990; Burrows, 1990; Glenn-Lewin and van der Maarel, 1992; Bakker et al., 1996).

(3) Fine-scale spatial variation would be lost. This is virtually ubiquitous and is associated with compositional changes in this study.

7.4.5 Geoecology

The patterns of environmental influences, discussed above, resemble those proposed in the geoecology model (section 2.5). As defined by Matthews (1992), the model has two key aspects, p. 319:

> "...(1) the concept that biological and physical systems interact within the evolving glacier foreland landscape; and (2) the concept that glacier foreland landscapes are spatial systems within which the characteristics of succession and soil development vary broadly in relation to environmental severity."

The three trajectories associated with the different landform units have differences that can be ascribed to severity associated with high- and low-altitude, and at high-altitude with the amelioration provided by south-facing aspect and the exacerbation by conditions on north-facing land. 'Severity' is a rather general term and, at Storbreen, differences in severity are partly due to harsh mesoclimatic conditions and the short growing season at high-altitude, with aspect-related effects increasing the insolation, and therefore, the energy receipt, on south-facing sites.

The geoecology model associates successional development with a pattern of changes in the importance of allogenic and autogenic processes over time. In most systems, autogenic processes increase in importance as vegetation cover increases and soils develop. On the other hand, allogenic processes decrease in importance, for example as substrates stabilize and the effects of the glacier climate decline as the glacier retreats. Frequently, autogenic processes come to dominate the system, although this is less extensive and occurs later in successional time where allogenic conditions are severe, and may not occur where conditions are most harsh. This pattern is seen in the extent of successional development that occurs in the three trajectories described in this study. At low-altitude, the development of a shrub canopy both reflects the increasing importance of autogenic processes and contributes to this by physically buffering the system against environmental perturbation. The mature, species-rich snowbed group has moderate frequencies of several shrubs, but they do not dominate the community, which has a low-stature canopy. On the north-facing flank, the species-poor snowbed community is also of low-stature, but vegetation cover is sparse. Thus, the three mature community types show a decrease in the extent of buffering provided by the vegetation. In the species-poor snowbed community, the harsh physical conditions underlie the retarded development and the apparent cycling between successional stages. This is further illustrated by the differences in the level of variance explained by the canonical axes in the mature heath (59%) compared to the mature, species-rich snowbed group (84%) (Table 6.27). Among pioneer groups, this level exceeds 90%. The lower explanation achieved in relation to the two mature groups gives an indication of the extent of the increase in importance of autogenic processes.

In severe Arctic systems, Svoboda and Henry (1987) and Jones and Henry (2003) have developed a related concept involving a Biological Driving Force (BDF) that is opposed by Environmental Resistance (ER). In relatively favourable conditions, the BDF is seen as overcoming ER, resulting in directional successional development. However, in severe conditions, the BDF does not develop sufficiently to exceed the ER and, although species replacements may occur, they do not progress (c.f. non-directional succession Müller, 1952). However, the patterns associated with the environmental gradients in the present study, do not support the characterization of the environment as solely an impediment to successional development. Instead, the gradients generally represent a spectrum of effects, which include not only harsh, detrimental influences, but also favourable conditions that promote rapid, progressive development (section 5.5).

While the geoecology model reflects the dynamics of the system found in the present study, the mechanisms by which the physical system interacts with the biological system are not part of the model. This is an area in which Matthews (1992) considers that further research is needed. There are several models of successional development that incorporate allogenic processes, but these tend to emphasise only one aspect of the environment e.g. Tilman's resource ratio hypothesis (Tilman, 1988), and patch dynamics (e.g. Pickett, 1976). The present study found that several environmental gradients were associated with compositional change at each stage of development, including topography, disturbance and factors associated with successional development itself, such as increasing soil depth (section 6.3). While the importance of some of these gradients was found to diminish with increasing maturity, e.g. physical processes causing disturbance, even in the mature heath group environmental variables were associated with compositional change. While the physical environment is seen by many authorities to be of greatest importance during establishment (Walker and del Morel, 2003), e.g. due to its role in providing 'safe sites' (section 2.3), its effects are not limited to this stage. Other work has indicated that many aspects of the environment can influence plant growth and successional development e.g. R. H. Whittaker (1953) and Ellenberg (1979, 1991). At, or near, optimal conditions for a particular species, growth and development will proceed rapidly, but where conditions are suboptimal, retardation is likely to occur. Additionally, any particular set of conditions will impact differentially across a group of species (section 2.4).

From this discussion, it appears likely that, at a fine-scale, differences in plant physiological responses to environmental conditions may contribute to differences in vegetation patterning, as suggested by Whittaker (1993, section 7.3.1). However, such differences in response may also influence the outcome of interactions (van Andel et al., 1993). However, this was not an area researched in this study, and the role of the environment in species interactions can only be presented as a hypothesis that requires further investigation, perhaps involving experimental work (c.f. Matthews, 1992).

7.4.6 The broader theoretical context

The Clementsian paradigm has strongly influenced the development of successional theory and this is, as stated by Matthews (1992), largely due to the appeal of the unifying concepts that it contains. However, it presents a vegetation-based perspective and treats succession as orderly, predictable and consistently progressive (Clements 1928, 1936). Much of Clements' work involved vegetation patterns at a biome-scale and it appears likely that differences in scale may underlie some of the problems associated with the application of the paradigm to individual seres and sites. Many recent studies adopt a reductionist approach (Walker and del Morel, 2003) and contribute to accumulating evidence that challenges the paradigm (Wiens, 2000). Similarly, previous work at Storbreen has found evidence of the importance of fine-scale spatial (Matthews, 1976; Crouch, 1992; Foskett, 1998) and spatio-temporal (Whittaker, 1985) heterogeneity. At a fine scale, the findings of this study tend to support Gleason (1917, 1926, 1927) in terms of individualistic assemblages and species distributions that are strongly related to environmental variability. However, patterns have also been detected in this study e.g. the three trajectories, but these are discernible only when the successional system is viewed at a coarser scale. By examining the system at both fine and coarse scales (typifying the approaches of Gleason and Clements respectively), both the overall pattern and the underlying detail may be detected.

While identifying relatively coarse-scale patterns, this study does not find succession to be either orderly or predictable. Additionally, environmental conditions are associated with these patterns and may be causally related to their generation. Clements largely disregarded environmental factors as contributing to successional development in his focus on plant-mediated (autogenic) processes. Clements view has been a persistent influence on the development of successional theory, with the result that the preponderance of models that attempt to explain species turnover consider species interactions in isolation from the environment in which they take place (e.g. Connell and Slatyer, 1977; Noble and Slatyer, 1982). Where the environment is treated as more than a passive setting for 'reaction' to take place, the emphasis is frequently on one particular gradient e.g. Tilman's resource ratio hypothesis. However, in this study, as in previous work at Storbreen (e.g. Matthews, 1976; Crouch, 1992), vegetation patterns change continuously across the foreland, associated with position on a number of environmental gradients. These patterns are consistent with the climax pattern hypothesis of R. H. Whittaker

(1953), but applied to the whole successional sequence. The boundaries between vegetation types do not appear to represent discontinuities (Tansley, 1920, 1935) or abrupt ecotones (Margalev, 1968; Odum, 1969), but are gradational ecoclines (Figures 5.7 and 5.8) (Whittaker, 1953).

However, it appears that neither species interactions nor environmental conditions in isolation are adequate to explain successional changes. The answer appears to lie in a synthesis of biogenic and environmental factors; which might benefit from a re-examination of the work of even earlier authorities than Clements. Cowles (1899, 1901), for example, proposed that successional systems are driven by a combination of biotic and landscape variables, have a variety of regional and local causes and includes both retrogression and the repetition of stages.

7.4.7 Summary: influences of the environmental variables

(1) Five compound gradients (successional development, topography, moisture, disturbance and substrate type) were found to be associated with variation in compositional change at the scale of the vegetation groups.

(2) In general terms, several environmental gradient(s) are likely to be major constraints on the nature of successional development in any study area. Using this study as an example, the system occurs at both high-latitude and high-altitude, the growing season is short and conditions are generally harsh. The mesoscale gradients encompass a substantial range of values, e.g. four hundred metres altitudinal difference and from north- to south-facing land, and variations in these gradients occur across the study area. Environmental influences occur, however, at a variety of scales, from the mesoscale conditions associated with the different landforms to fine-scale differences between sites. There is also evidence of interactions between the different scales. The gradients effective at a mesoscale influence the qualitative nature of the trajectory (altitude and aspect) and the stage on the trajectory that the group has reached (age). Fine-scale gradients are mainly associated with differences in the rate of successional development on individual sites. This provides feedback to the group rate of development and therefore to the amount of development that is associated with a particular age zone. However, in several of the groups, sites can be subdivided into a number of compositional strands that are associated with group-scale differences in altitude and aspect related to different positions on the landforms. Additionally, fine-scale microtopography can influence the type of trajectory followed, and counteract, or reinforce, the mesoscale influence.

(3) Disturbance due to physical processes decreases with increasing site maturity, while biological disturbance increases in importance. However, most recorded disturbance involves minor events and these are poorly preserved. Therefore, the level of disturbance reported is likely to be a substantial underestimate of that which actually occurs.

(4) Following a transition to a mature vegetation group, development first involves increasing vegetation cover, which changes to increasing soil development as sites develop within the group. As this is associated with increasing shrub frequencies and rooting depth, it may indicate a switch from primary to secondary processes (Walker and del Morel, 2003).

(5) The spatio-temporal approach identifies both spatial and temporal heterogeneity, which is likely to be obscured or confounded using the chronosequence approach. While the chronosequence concept is useful in data exploration and to direct more detailed studies, it does not detect the spatial or temporal patterning that underlies many of the findings in the present study.

(6) The findings in this study generally support the geoecology model defined by Matthews (1992). This model emphasises the relationship between spatial variation, particularly that associated with environmental severity, and the characteristics of successional development. The three trajectories identified in this study relate a progressive decrease in community stature and vegetation cover to increasing severity in terms of climatic conditions and the length of the growing season as altitude increases and in differences between north- and south-facing sites. This is additionally related to a decrease in the importance of allogenic effects, and a concomitant increase in the importance of autogenic processes, at low- compared to high-altitude.

(7) The geoecology model does not stipulate the mechanisms and processes that relate the level of environmental severity to successional development. While it appears likely that differences in plant physiological responses contribute (Whittaker, 1993), plant performance also determines the outcome of interactions. Such a model requires a different approach, possibly involving experimental studies, to identify these mechanisms and processes.

Chapter 8: Conclusions

8.1 Introduction

This chapter draws together the main findings of this study and considers them in relation to the study aims from Chapter 1:

(1) to describe 30 years of temporal changes in the species population distributions;
(2) to analyse the community dynamics of the successional sequence; and
(3) to investigate the role of environmental parameters in successional changes.

The findings related to each of the study aims are considered in the initial sections. This is followed by an assessment of the methodology and of the wider implications of this study in relation to successional theory. In the final section, some potential areas of further research, arising from this study, are outlined.

8.2 Temporal change in species distributions

Species distributions in 1970 and 2000, and changes in frequency on individual sites, have been illustrated in a series of maps (Figures 4.5 to 4.57, and S1 to S52). These maps are an important part of this study and indicate the extent of the variability found amongst the species populations, with no two species having precisely the same distribution. However, most of the distributions were explicable in terms of age, altitude and aspect and there appeared to be a limited number of distribution types. Some species occurred predominantly on old land, at low-altitude, e.g. *Juniperus communis,* while others were rarely found outside of young sites at high-altitude, e.g. *Cerastium alpinum*, although some pioneer species showed a preference for the north-facing flank at high-altitude, e.g. *Cerastium cerastoides.* Another distribution type was largely restricted to sites on the north- and south-facing flanks, often with a south-facing asymmetry, e.g. *Anthoxanthum odoratum* and *Polygonum viviparum.* Many of the species that had this type of distribution are forbs and some have been associated with snowbed sites (c.f. Matthews, 1976; Matthews and Whittaker, 1987). Finally, there were species that occurred virtually ubiquitously throughout the study area, although often at lower frequency on the north-facing flank at high-altitude, e.g. *Salix glauca* and *Empetrum hermaphroditum.*

This study also provided direct evidence of successional patterns of species population changes. Two types of successional pattern were detected. The first involved shifts of the whole population onto younger land 2000 compared to 1970 and occurred mainly amongst pioneer species (Table 4.4). These wavelike increases and decreases in frequency are characteristic of relay floristics (Egler, 1954). Further evidence of this pattern was detected using the diversity indices (section 5.2), where two principal influxes of later species were detected on land aged 30-60 years and 150-180 years. The second wave involved species that expanded onto younger land as it aged, while maintaining the population on older land. This pattern was found mainly amongst later-occurring species, particularly shrubs.

However, some patterns were identified that could not be explained by successional processes. Although a few species, especially *Salix glauca* and *Empetrum hermaphroditum,* increased substantially, many typically late-occurring species declined on older land. Some of these species also increased in frequency either at low- or high-altitude within the foreland. These three patterns of response were predominantly associated with different species groups. Evergreen shrubs, e.g. *Vaccinium vitis-idaea,* and some forbs, e.g. *Leontodon autumnalis,* simply decline on older land. Deciduous shrubs, e.g. *V. myrtillus* and *V. uliginosum,* increase in frequency at low-altitude within the foreland, while forbs, e.g. *Hieracium alpinum,* increase in frequency at higher altitude. A south-facing asymmetry often accompanied these shifts in altitude. Changes within the regional vegetation were also detected using the diversity indices and showed species richness to have decreased while dominance increased between 1970 and 2000.

The patterns of change outlined above appear to reflect both differences in the type of community and particular attributes of the species. At low-altitude, vegetation cover is generally more extensive and reproduction is frequently due to vegetative expansion (Whittaker, 1985). Deciduous shrubs have fast growth rates compared to those of evergreen species (Körner and Larcher, 1988; Shaver, 1995). Faster growth rate may confer competitive advantage due to changes in relative position within the canopy. Forb and late-pioneer species have been found to require openings in the dense vegetation (Crouch, 1992), and decreasing frequencies may therefore reflect a reduction of such opportunities for establishment. However, at high-altitude, vegetation cover tends to be relatively sparse and some forbs have increased in frequency on this land.

Two other patterns were detected that appear to be related to landscape processes within the study area. Several species were found to decline on the north-facing flank, particularly later-occurring *Salix* shrubs, where they were absent from sites that they occupied in 1970. Some pioneer species, e.g. *Cerastium cerastoides*, on the other hand, increase in frequency on these sites. Additionally, snowbed and moisture-requiring species were found to have decreased in frequency on flank sites (section 5.4). There is observational evidence of a decrease in the frequency of late-lying snow and, in section 6.3, browsing was found to occur most frequently at high-altitude on the north-facing flank. Both factors may contribute to the species decreases occurring at this location. The second pattern involves conditions on the fluted moraines. While several late-occurring species have increased in frequency on young, centrally located sites, expansion onto land less than 50 years old appears to have been blocked (section 4.3). This was associated with evidence of drying on the fluted moraines (Ballantyne and Matthews, 1982; Whittaker, 1993). Both examples show spatially confined changes in distribution patterns that were directly related to processes occurring at a landscape scale.

8.3 Community dynamics of the successional sequence

This part of the study involved a reconstruction of the community dynamics since 1970 using the results of a TWINSPAN classification. Differences in composition were used to interpret the TWINSPAN groups in terms of successional stages (section 5.3):

An early pioneer stage (group 7), *Poa* spp. and *Trisetum spicata* are characteristic species.

A late pioneer stage (group 8), *Cerastium cerastoides* and *Deschampsia cespitosa* ssp. *alpina* are characteristic.

A late pioneer/intermediate snowbed stage (group 6), dominated by *Salix herbacea*; *Poa* spp. and *Ranunculus glacialis* are characteristic species.

An early pioneer/heath intermediate stage (group 5), dominated by *S. herbacea*; *Poa* spp. and *S. glauca* are characteristic.

A mature snowbed type stage (group 4), dominated by *S. herbacea* and *Carex* spp..

A late pioneer/heath intermediate stage (group 3), species-poor and dominated by *S. herbacea.*

A species-poor heath stage (group 2), dominated by *Empetrum hermaphroditum*; *Phyllodoce caerulea* and *Salix* spp. are characteristic.

A mature species-rich heath stage (group 1), co-dominated by *Betula nana* and *E. hermaphroditum*; *Vaccinium* spp. are characteristic.

When the vegetation groups were located on maps of the study area (Figures 5.7 and 5.8), it was found that although each group was associated with a particular range of terrain age, they were not confined to these bands and were interspersed locally. Additionally, different vegetation groups occurred primarily on the flanks of the foreland (groups 8, 6, 4 and 3) compared to those occurring on central sites and at low-altitude (groups 7, 5, 2 and 1).

The composition in each vegetation group was found to have undergone changes between 1970 and 2000. These changes were most substantial on the flanks of the foreland, where there were decreases in the frequency of snowbed and moisture-requiring species, while pioneer species increased in frequency in vegetation groups representing early stages and increases in shrubs occurred amongst more mature stages. It was considered that an explanation for these changes was likely to involve a reduction in late-lying snow.

The vegetation groups with which each site was identified in 1970 and in 2000 were used to calculate the transitions that had occurred during the 30 years between the two surveys. These were used (1) to identify the transitions that had occurred from each vegetation group and (2) in the construction of a transition diagram for the whole study area (Figure 5.9). Transitions from each individual vegetation group occurred to a number of other groups and showed considerable variability in the range of compositional change.

Direct evidence was presented of transitions of foreland sites from the species-poor heath to the mature species-rich heath and snowbed groups. These transitions were used to give a minimum timescale of 190 years for completion of successional development of a species-rich heath. However, a comparison of the species-rich heath composition within the foreland with that within the regional vegetation found that frequencies of *Empetrum hermaphroditum*, *Salix glauca* and deciduous *Vaccinium* species were higher on the foreland, but those of evergreen species were lower at the foreland sites. It could not be determined whether the foreland sites were less successionally advanced or whether this composition represented the development of a new mature site type. Many foreland sites remained classified as species-poor heath, even after 250 years.

These transitions were then used to construct a transition diagram for the whole study area (Figure 5.9) from which the main trajectories (developmental pathways) were reconstructed. A heath trajectory was identified at low-altitude and also inferred for sites at higher altitude that were located centrally.

Heath trajectory:
Early pioneer -> early pioneer-heath intermediate -> species poor heath -> species-rich heath

Subsidiary successional 'loops' were identified that incorporated additional stages (late pioneer and late pioneer-heath intermediate stages). Following completion of the late pioneer-heath intermediate stage, further transitions occurred either on the heath trajectory or to the mature snowbed group. The vegetation groups representing the additional stages occurred most frequently on the flanks of the foreland. Successional 'jumps' were also identified where rapid progressive development resulted in stages being omitted.

The development of the mature snowbed group appeared more complex but did not occur at high-altitude on the north-facing flank. The late pioneer-snowbed intermediate group was found not to represent an early stage in this snowbed trajectory, but was an intermediate stage that was confined to high-altitude on the north-facing flank. The late pioneer-heath intermediate group was the most successionally advanced stage attained on the north-facing flank and was found to contain three spatially-determined compositional strands: a heath precursor on central sites; a species-poor snowbed type on north-facing sites; and a species-rich snowbed type on south-facing sites. Two snowbed trajectories were therefore inferred:

North-facing species-poor trajectory:
Early pioneer -> late pioneer -> early intermediate -> late pioneer-snowbed intermediate (group 6) -> late intermediate (north variant)

South-facing species-rich trajectory:
Early pioneer -> late pioneer -> early intermediate -> late intermediate (south variant) -> snowbed endpoint

It was also suggested that cyclic succession might be occurring at high-altitude on the north-facing flank between the late pioneer-snowbed intermediate and late pioneer-heath intermediate groups. This appeared to be associated with the initial establishment and subsequent failure of taller shrubs, particularly *Salix glauca*. It was suggested that contributory factors might include low resource levels and/or the extent of protective winter snow cover.

Three types of transition were identified: 'progressive' where the site was identified with a more advanced successional stage in 2000; 'stability' or 'inertia' where sites continued to be identified with the same vegetation group in both surveys; and 'retrogressive' where the site was identified with a less advanced successional stage in 2000. Progression occurred most frequently at early successional stages and decreased with increasing maturity. Stability of composition occurred most commonly and increased with increasing maturity from 18% of the transitions in the early pioneer group to 93% in the mature species-rich heath. The high proportion of sites (80%) that retained the 1970 composition in the species-poor heath indicated the prolonged development required for these, mainly foreland, sites to attain the species-rich heath composition. Retrogression was a weak trend in the study area, but increased with increasing maturity and was found to accompany strongly progressive transitions. It was suggested that developmental failure might be a general cause of retrogression, in addition to disturbance and soil degradation. Directional transitions, both progressive and retrogressive, occurred most frequently on the flanks of the foreland.

8.4 The role of environmental parameters in successional change

Initially, relationships between the environmental parameters were investigated in both the full dataset and the individual vegetation groups using Kendall's tau correlation coefficients. This analysis identified four compound gradients representing successional development, topography, moisture and disturbance. When the full dataset was used, a relatively simple pattern was found involving an age-related successional development gradient, an independent altitude gradient and a combined moisture/disturbance gradient.

Greater complexity was found when the individual vegetation groups were analysed. Soil and vegetation cover (components of the successional development gradient) were not strongly related in the individual groups. The nature of the correlation between age and altitude varied with topographic configuration within the vegetation group and any relationship between them appeared to be coincidental. Correlations involving disturbance variables were specific to the conditions within the individual groups, with correlations between disturbance and moisture being more numerous on the high-altitude flanks and on young land. Factors that were inferred to contribute to this were: instability where the substrate is steeply sloping or has been recently deposited; the presence of snowbeds on the flanks; and glacial meltwater on young land. Duration of snowlie was negatively associated with age on young land, suggesting that snow had been redistributed to older land at lower altitude (Foskett, 1998).

Canonical Correspondence Analysis (CCA) was then used to explore the relationship between compositional change and the environmental variables, both in the dataset as a whole and in the individual vegetation groups. This analysis was supported by the use of species ordinations and descriptive statistics, calculated from values of the environmental variables that occurred within each of the vegetation groups. As with the Kendall's tau correlation coefficients, the pattern of related variables was simpler when the study area was considered as a unit, where successional development, topography and disturbance dominated the analysis, while greater complexity was found at the level of individual vegetation groups.

Topographic gradients of altitude and aspect were related to differences in within-group compositional change where there were spatial subdivisions of the vegetation groups, e.g. north-and south-facing sites within the late pioneer group. This suggested that spatially determined compositional strands might not be restricted to the late pioneer-heath intermediate group.

The compound gradients identified using the Kendall's tau correlation coefficients were also found to be important in this analysis, but with the additional factor of substrate type. Table 6.27 presents a summary of important gradients within the individual groups. Differences in substrate type were frequently associated with specific spatial locations, e.g. in the early pioneer-heath intermediate group, gravel was associated with the fluted moraines and boulders with the lower slopes of the flanks. Different substrate types were also associated with differences in disturbance regime e.g. disturbance by frost heave occurred most frequently where gravel formed the substrate.

There was evidence that an integrated soil-vegetation complex formed relatively rapidly following the early pioneer stage. In the early pioneer group, vegetation cover was found to be of greater importance (associated with axis 1) than soil variables, but in all but one of the other vegetation groups this relationship was reversed. Additionally, rooting and humus depths were associated with soil depth in every vegetation group, except the early pioneer group. Both rooting and humus depths are measures of specific attributes of the soil-vegetation relationship. The analysis identified what appeared to be a two-stage developmental process in mature groups. Following early progressive succession, vegetation cover increased until it reached at least the average for the group. Subsequent development involved increasing levels of soil development, including rooting and humus depth, which suggested that these changes were associated with compositional shifts amongst the species present. This was further supported by the frequent association of increasingly later-occurring species with this axis in the species ordinations.

The environmental gradients associated with the CCA axes in this analysis most frequently indicated a change from adverse to more favourable conditions. Such gradients were often accompanied by an increase of the level of successional development in terms of soil development and, in the species ordinations, by increasingly later-occurring species. This evidence suggested that environmental variables operating at the within-group scale were associated with differences in the rate of successional development.

Vegetation changes were associated with the various disturbance types in complex ways. Grazing was important to compositional change in every group examined, but increased in frequency with increasing maturity. Browsing occurred most frequently on young land and on the flanks of the foreland. Trampling was associated with the route of the glacier path and with cows grazing on the east side of the Leira. Frost heave was associated with low moisture availability, while both fluvial disturbance and solifluction occurred more frequently where moisture availability was high and slopes were steep. The incidence of solifluction was, however, highest on mature sites. Microtopography was most frequently associated with compositional change at early stages in the successional sequence.

The explanatory value of the canonical (environmental) compared to the non-canonical axes (Table 6.27) was found to be low where high numbers of sites were used in the analysis and where there was evidence that the vegetation groups were subdivided by compositional strands e.g. in the late pioneer-heath intermediate group. Low levels of explained variance therefore appeared to be associated with high levels of complexity that are not easily summarised on a few orthogonal axes. On the heath trajectory, high levels of variance explained amongst the pioneers (exceeding 90%) decreased with increasing maturity to approximately 59% in the mature species-rich heath group. However, this level remained high (84%) in the mature, species-rich snowbed group, indicating that allogenic factors remained important throughout development on this snowbed trajectory.

In section 1.4, evidence was presented of climatic changes that have occurred in this region of southern Norway since 1876 (Hanssen-Bauer and Forland, 1998; Hanssen-Bauer and Nordli, 1998). Following a statistically significant decrease in temperature from the 1930s to the late 1960s, there have been significant increases in temperature (0.4-1.2°C) and precipitation since 1970. Temperatures have increased primarily during the spring and autumn, and this is associated with an increase in growing season length (Hanssen-Bauer and Nordli, 1998). Several directional trends in composition changes were identified in this study, which have no clear explanatory mechanism within the study area. These include: evidence of increasing dominance and decreases in species richness on older land, within the regional vegetation where such changes would be expected to be minimal; increases in the frequency of fast-growing deciduous species on heath sites within the foreland, while evergreen species decrease; and up-altitude shifts amongst species, particularly forbs, that are declining at lower altitude. Similar patterns appear to be repeated at a regional scale e.g. Klanderud and Birks (2003) and therefore can be tentatively attributed to recent climatic change.

Several pieces of evidence suggest that environmental variables operating at a group-scale are related to differences in successional rate within the individual stages:

(i) although age provides a general indication of the successional stage attained, sites of similar ages are found to be at different stages within a locality;

(ii) within-group transitions indicate considerable variability in successional rate;

(iii) gradients identified with the CCA axes (section 6.3) frequently indicate a change from adverse to favourable conditions, which is in turn associated with an increase in the level of successional development and with changes in frequency amongst increasingly later-occurring species.

It is therefore proposed that variables defining the principal differences in conditions occurring within a study area are likely to govern qualitative differentiation, while those indicating fine-scale environmental variation largely determine the rate at which a site develops. The characteristics of successional development are therefore mediated by differences in physical conditions at a number of scales.

There is evidence of divergence as compositional differences, and therefore successional distance, increase over time (c.f. Matthews, 1976; Whittaker, 1985, 1993).

In summary, mesoscale gradients of altitude and aspect were found to control overall successional trajectories and therefore the qualitative nature of succession, environmental variables operating at the scale of individual vegetation groups appeared to relate primarily to differences in the rate of successional change.

8.5 Methodological implications

This study used a repeat survey of permanent plots that were established in 1970 and, therefore, a combined spatio-temporal approach. The more usual chronosequence approach relies on data collected at a single point in time and averages those data, so that a temporal dimension can be inferred, but in so doing takes no account of spatial heterogeneity. The chronosequence approach was expanded by Matthews (1976) to incorporate spatial location, but this still involved inferred temporal change. In this study, the combined spatio-temporal approach allows the assessment of both spatial and temporal heterogeneity. Both chronosequence and spatio-temporal approaches were used during this analysis, enabling a comparison to be made. Successional patterns were detected using the chronosequence approach, and spatial location could be included using Matthews' spatio-chronosequence approach, however, the combined spatio-temporal approach is only one of these methods that enables the operation of community dynamics to be followed over time and across the whole of the study area.

Ordination techniques identify continuous gradients of compositional change and, as seen in Figure 6.1, divisions within that continuous gradient may not be apparent. Divisions may be imposed by using a classification technique (e.g. Gauch, 1982; Kent and Coker, 1992; Jongman, 1995) but an alternative view classes this as 'continuum segregation' (McIntosh, 1975). Although the vegetation groups that were identified in this study result in a meaningful interpretation of the system, they actually represent an arbitrary division of the data.

The relationship of the environmental variables to temporal compositional change was a particular area of interest in this study. While the association of vegetation patterns with environmental variables in previous studies provides circumstantial evidence of the association with compositional change, it does not directly relate the two. However, the use of flux data in the CCA ordination is unusual and adds to the noisiness inherent in ecological data and is reflected in the modest eigenvalues. Nonetheless, the eigenvalues indicate that the trends are meaningful and the correlation coefficients between the environmental variables and the species axes are strong (Table 6.27). Additionally, the species ordinations associate species with known affinities. While the increased noisiness may weaken the analysis, it represents an attempt to directly relate different types of compositional change to the environment in which they occur.

8.6 Future research: some specific suggestions

Herbivory

Herbivory is considered of importance in shaping successional systems (section 2.8.9). Data was collected in this study concerning the frequency of herbivory at two intensities, termed 'grazing' (low intensity) and 'browsing' (high intensity, involving the removal of leaves and other parts). Additionally, the plant species that were targeted were identified, e.g. *Oxyria digyna*, *Ranunculus glacialis* and most of the pioneer grasses on young land, *Salix* spp. on mature sites.

This study found that the frequency of grazing increased with maturity, while browsing occurred most frequently on young sites and on the flanks of the foreland (Table 6.26).

It might be possible further to clarify spatial patterns in the incidence of herbivory e.g. whether herbivory is related to shelter or slope and whether it varies between the major landform units. Herbivory has been found to be important in opening gaps for the establishment of forbs and pioneer species, particularly on older, more extensively vegetated land (Connell, 1975; Davis et al., 1985; Edwards and Gilman, 1987). Such an association with species turnover might be indicated if herbivory were related to progressive transitions.

Herbivory may also be associated with decreases amongst several species at high-altitude on the north-facing flank (section 4.4). To test this hypothesis, an exclosure experiment could be set up at Storbreen, perhaps to compare effects on the different landform units or amongst different species. Similar experimental work at the Tanama River, Alaska, showed grazing to be associated with a reduction in palatable *Salix* spp., due to a reduction in ectomycorrhizal infection, and increases in less palatable evergreen species (Rossow et al., 1997).

Propagule dispersal via bird vectors

Bird dispersal is not generally considered to be of importance on young land in glacial moraine systems, due in part to the sparse vegetation cover and the absence of food sources. There has been little research in this field (Walker and del Morel, 2003). Birds were observed relatively frequently at Storbreen, e.g. ring ouzel and snowbunting, but most occurred at low-altitude, amongst the taller vegetation. However, ptarmigan droppings containing berries were found within a metre of the ice front at Storbreen. Although these berries have not been positively identified, ptarmigan are a known vector for the dispersal of *Empetrum hermaphroditum* (Tybirk et al., 2000). Dispersal accompanied by a nutrient source is likely to be advantageous on land with no developed soil. This may be an area worth investigating further, particularly with regards to intermediate species, where seeds are contained in berries and there is no apparent mechanism for their dispersal onto higher land.

Further monitoring at Storbreen

Several of the findings in this study have raised additional issues and generated hypotheses that could be tested by a continued programme of monitoring and observation of the system at Storbreen. These outstanding questions include:

(a) *The development of central sites at high-altitude.* It has been assumed in this study that these sites will progress along the heath trajectory. While the development of an early intermediate stage on many of these sites since 1970 suggests that such development is likely, there is also evidence that later species are slow to colonize sites on the fluted moraines younger than approximately 50 years. Slow colonization raises the possibility that these sites may undergo an extended period of stasis or that taller shrubs might fail to establish in sufficient numbers for development of the heath community type. These sites may consequently develop along one of the snowbed trajectories. Such sites may, therefore, further illuminate successional processes at high-altitude.

(b) *Successional development on low-altitude foreland sites.* Monitoring of these sites would establish whether transitions continue to occur to the mature species-rich heath and snowbed groups and whether the composition of foreland heath sites develops over time to more closely resemble that amongst the regional vegetation. In this study, sites that underwent the transition to the species-rich heath were more strongly dominated by *Empetrum hermaphroditum*, had higher frequencies of deciduous *Vaccinium* species but considerably lower frequencies of evergreen species, compared to the regional vegetation. It was not apparent whether this indicated a less advanced level of development or whether the sites were developing along a new pathway. Many old foreland sites continued to be identified with the species-poor heath in the 2000 survey, and this protracted period of development suggests that the widespread development of a species-rich heath composition, similar to that in the regional vegetation, may not occr.

(c) *A test of the hypothesis that cyclic succession (Watt, 1947) occurs at high-altitude on the north-facing flank.* Transitions were identified that appeared to represent the upgrade and downgrade phases of vegetational cycles (sections 5.6.3 and 7.3.3). However, this is inferred from only one transition. Species-rich snowbed sites occur at mid- to low-altitude on the north-facing flank and this composition may develop at higher altitude. Few late-lying snowpatches were observed in 2000 at high-altitude on the north-facing flank, although they appear to have been relatively common in 1970. If the presence of late-lying snow contributes to these cycles, and this reduction in late-lying snow is not reversed, retrogressive changes may occur on these sites.

(d) *Monitoring of changes in the duration and extent of late-lying snow.* Observational evidence suggests that snowpatches are less extensive on the north-facing flank than they were in 1970. Monitoring of changes in the duration of snowlie or snowpatches would provide direct evidence of ongoing changes. Parameters of interest include melting date, maximum depth at specified times in the season and the date of first snowfall.

(e) *Monitoring of the birch tree line in Leirdalen.* The frequency of *Betula pubescens* ssp. *carpatica* increased by 91% in this survey, compared to 1970 (Table 4.1), despite a decrease in the number of sites at which it occurred. Where the species persisted since 1970, it had frequently expanded onto adjacent quadrats, suggesting a trend towards greater aggregation. Kullman (2002), working in the Swedish Scandes, found an increase of 315 metres in the birch range margin, compared to a survey carried out in 1955, which he has associated with regional warming.

For much of this research, a full survey would not be necessary and monitoring of specific sites over 5-10 years would allow changes in vegetation patterning to be followed. However, a further full survey, using the spatio-temporal approach adopted here, in 30 years time would allow a direct comparison with the previous studies in terms of rate, amount and direction of change.

Bibliography:

Alatalo, J. M. and Totland, O. (1997). Response to simulated climatic change in an Alpine and Subarctic pollen-risk strategist, *Silene acaulis. Global Change Biology,* **3 (Suppl 1),** 74-79.

Amman, B. (1995). Palaeorecords of plant biodiversity in the Alps. In *Arctic and Alpine Biodiversity: Patterns, Causes and Ecosystem Consequences*, F. S. Chapin III and C. H. Körner (Eds.), Berlin: Springer-Verlag

Andersen, B. G. (1980). The deglaciation of Norway after 10000 BP. *Boreas,* **9,** 211-216.

Andersen, T. B. (1998). Extensional tectonics in the Caledonides of southern Norway: an overview. *Tectonophysics,* **285,** 333-351.

Andreassen, L. M. (1999). Comparing traditional mass balance measurements with long-term volume change extracted from topographical maps: A case study of Storbreen Glacier in Jotunheimen, Norway, for the period 1940-1997. *Geografiska Annaler,* **81A,** 467-476.

Antonovics, J., Newman, T. J. and Best, B. J. (2001). Spatially explicit studies on the ecology and genetics of population margins. In *Integrating Ecology and Evolution in a Spatial Context*, J. Antonovics and J. Silvertown (Eds.), Oxford: Blackwell

Antor, R. J. (1994). Arthropod fallout on high Alpine snow patches of the Central Pyrenees, Northeastern Spain. *Arctic and Alpine Research,* **26,** 72-76.

Arnalds, A. (1987). Ecosystem disturbance in Iceland. *Arctic and Alpine Research,* **19,** 508-513.

Auerbach, N. A. and Halfpenny, J. C. (1991). Snowpack and the subnivean environment for different aspects of an open meadow in Jackson Hole, Wyoming, USA. *Arctic and Alpine Research,* **23,** 41-44.

Austin, M. P. (1976). On non-linear species response models in ordination. *Vegetatio,* **33,** 33-41.

Austin, M. P. (1985). Continuum concept, ordination methods and niche theory. *Annual Review of Ecology and Systematics,* **16,** 39-61.

Austin, M. P., Nicholls, A. O., Doherty, M. D. and Meyers, J. A. (1994). Determining species response functions to an environmental gradient by means of a b-function. *Journal of Vegetation Science,* **5,** 215-228.

Baker, N. R., Nogues, S. and Allen, D. J. (1997). Photosynthesis and photoinhibition. In *Plants and UV-B: Responses to Environmental Change*, P. Lumsden (Ed.) Cambridge: Cambridge University Press

Bakker, J. P., Olff, H., Willems, J. H. and Zobel, M. (1996). Why do we need permanent plots in the study of long term vegetation dynamics? *Journal of Vegetation Science,* **7,** 147-156.

Ballantyne, C. K. and Matthews, J. A. (1982). The development of sorted circles on recently-deglaciated terrain, Jotunheimen, Norway. *Arctic and Alpine Research,* **14,** 341-354.

Barnes, P. W., Flint, S. D. and Caldwell, M. M. (1987). Photosynthetic damage and protective pigments in plants from a latitudinal Arctic Alpine gradient exposed to supplemental UV-B radiation in the field. *Arctic and Alpine Research,* **19,** 21-27.

Batschalet, E. (1981). *Circular Statistics in Biology.* London: Academic Press

Battey, M. H. (1975). (Unpublished) The geology of the area around Storbreen. Report of the 1974 Jotunheimen Research Expedition

Bauert, M. R. (1996). Genetic diversity and ecotypic differentiation in Arctic and Alpine populations of *Polygonum viviparum. Arctic and Alpine Research,* **28,** 190-195.

Bazzaz, F. A. (1975). Plant species diversity in old-field successional ecosystems in southern Illinois. *Ecology,* **56,** 485-488.

Bazzaz, F. A. (1987). Experimental studies on the evolution of niche in successional plant populations. In *Colonization, Succession and Stability,* A. J. Gray, M. J. Crawley and P. J. Edwards (Eds.), Oxford: Blackwell

Bazzaz, F. A. (1993). Scaling in biological systems: Population and community perspectives. In *Scaling Ecophysiological Processes: From Leaf to Globe*, J. R. Ehleringer and C. B. Field (Eds.), San Diego: Academic Press

Beals, E. W. (1973). Ordination: mathematical elegance and ecological naivete. *Journal of Ecology,* **61,** 23-35.

Beerling, D. J. (1998). *Salix herbacea L. Journal of Ecology,* **86,** 872-895.

Begon, M., Harper, J. J. and Townsend, C. R. (1986). *Ecology: Individuals, Populations and Communities,* Oxford: Blackwell

Benedict, J. B. (1990). Lichen mortality due to late-lying snow: results of a transplant study. *Arctic and Alpine Research,* **22,** 81-89.

Beniston, M. (2000). *Environmental Change in Mountains and Uplands.* London: Arnold

Berger, W. H. and Parker, F. L. (1970). Diversity of planktonic foraminifera in deep-sea sediments. *Science,* **168,** 1345-1347.

Bergman, P., Molau, U. and Holmgren, B. (1996). Micrometeorological impacts on insect activity and plant reproductive success in an Alpine environment Swedish Lapland. *Arctic and Alpine Research,* **28,** 196-202.

Bertness, M. D. and Callaway, R. (1994). Positive interactions in communities. *Trends in Evolution and Ecology,* **9,** 191-193.

Beschel, R. E. (1950). Flechten als altersmasstab rezenter moranen. *Zeitschrift fur Gletscherkunde und Glazialgeologie,* **1,** 152-161.

Beschel, R. E. (1961). Dating rock surfaces by lichen growth and its application to glaciology and physiography (lichenometry). In *Geology of the Arctic*, G. O. Rasch (Ed.), pp. 1044-62. Toronto: University of Toronto Press

Bickerton, R. W. and Matthews, J. A. (1992). On the accuracy of lichenometric dates: an assessment based on the 'Little Ice Age' moraine sequence of Nigardsbreen, southern Norway. *The Holocene,* **2,** 227-237.

Billings, W. D. (1974a). Arctic and Alpine vegetation: Plant adaptations to cold summer climates. In *Arctic and Alpine Environments*, J. D. Ives and R. G. Barry (Eds.), pp. 403-43. London: Methuen

Billings, W. D. (1974b). Adaptations and origins of Alpine plants. *Arctic and Alpine Research,* **6,** 129-142.

Birks, H. J. B. (1980). The present flora and vegetation of the Klutlan Glacier, Yukon Territory, Canada. *Quaternary Research*, **14**, 60-86.

Birks, H. J. B., Peglar, S. M. and Austin, H. A. (1994). An annotated bibliography of CCA and related constrained ordination methods 1986-1993. *Microcomputer Power Website.*

Bishop, J. G. (2002). Early primary succession on Mount St Helens: Impact of insect herbivores on colonizing lupines. *Ecology,* **83,** 191-202.

Bjorn, L. O., Callaghan, T., Gehrke, C., Gunnarsson, T., Holmgren, B., Johanson, U., Snogerup, S., Sonesson, M., Sterner, O. and Yu, S.-G. (1997). Effects on subarctic vegetation of enhanced UV-B radiation. In *Plants and UV-B: Responses to Environmental Change*, P. Lumsden (Ed.) Cambridge: Cambridge University Press

Bjorn, L. O., Callaghan, T. V., Gehrke, C., Johanson, U., Sonesson, M. and Gwynn-Jones, D. (1998). The problem of ozone depletion in Northern Europe. *Ambio,* **27,** 275-279.

Bliss, L. C., Henry, G. H. R., Svoboda, J. and Bliss, D. I. (1994). Patterns of plant distribution within two polar desert landscapes. *Arctic and Alpine Research,* **26,** 46-55.

Blundon, D. J., MacIsaac, D. A. and Dale, M. R. T. (1993). Nucleation during primary succession in the Canadian Rockies. *Canadian Journal of Botany,* **71,** 1093-1096.

Bonser, S. P. and Reader, R. J. (1995). Plant competition and herbivory in relation to vegetation biomass. *Ecology,* **76,** 2176-2183.

Bormann, B. T. and Sidle, R. C. (1990). Changes in productivity and distribution of nutrients in a chronosequence at Glacier Bay National Park, Alaska. *Journal of Ecology,* **78,** 561-578.

Bornman, J. F., Keuber, S., Cen, Y. -P. and Weissenbock, G. (1997). Ultraviolet radiation as a stress factor and the role of protective pigments. In *Plants and UV-B: Responses to Environmental Change*, P. Lumsden (Ed.) Cambridge: Cambridge University Press

Boulton, G. S. and Dent, D. L. (1974). The nature and rates of post-depositional changes in recently deposited till from southeast Iceland. *Geografiska Annaler,* **56(A),** 121-134.

Bradshaw, A. D. (1993). Fundamentals of primary succession. In *Primary Succession on Land*, J. Miles and D. W. H. Walton (Eds.), Oxford: Blackwell

Brandani, A. A. (1983). Glacial Processes and disturbance in vegetation richness. In *Tills and Related Deposits*, E. B. Evenson, C. Schluchter and J. Rabassa (Eds.), pp. 403-10. Rotterdam: Balkema

Bray, J. R. and Curtis, J. T. (1957). An ordination of the upland forest communities of Southern Wisconsin. *Ecological Monographs,* **27,** 325-349.

Bret-Harte, M. S., Shaver, G. R. and Chapin III, F. S. (2002). Primary and secondary stem growth in arctic shrubs: implications for community response to environmental change. *Journal of Ecology,* **90,** 251-267.

Bret-Harte, M. S., Shaver, G. R., Zoerner, J. P., Wagner, J. L., Chavez, A. S., Gunkleman IV, R. F., Lippert, S. C. and Laundre, J. A. (2001). Developmental plasticity allows *Betula nana* to dominate tundra subjected to an altered environment. *Ecology,* **82,** 18-32.

Britt, A. B. (1997). Genetic analysis of DNA repair in plants. In *Plants and UV-B: Responses to Environmental Change*, P. Lumsden (Ed.) Cambridge: Cambridge University Press

Brown, J. H. (1988). Species diversity. In *Analytical Biogeography*, A. A. Myers and P. S. Giller (Eds.), London: Chapman and Hall

Brubaker, L. B., Anderson, P. M. and Hu, P. S. (1995). Arctic tundra Biodiversity: A temporal perspective from late Quaternary pollen records. In *Arctic and Alpine Biodiversity: Patterns, Causes and Ecosystem Consequences*, F. S. Chapin III and C. H. Körner (Eds.), Berlin: Springer-Verlag

Bruun, H. H. and Moen, J. (2003). Nested communities of Alpine plants on isolated mountains: relative importance of colonization and extinction. *Journal of Biogeography,* **30,** 297-303.

Bugmann, H. and Fischlin, A. (1994). Comparing the behaviour of mountainous forest succession models in a changing climate. In *Mountain Environments in Changing Climates*, M. Beniston (Ed.) London: Routledge

Burrows, C. J. (1990). *Processes of Vegetation Change.* London: Unwin Hyman

Cahill, J. F. (2003). Lack of relationship between below-ground competition and allocation to roots in ten grassland species. *Journal of Ecology,* **91,** 532-540.

Cain, M. L., Damman, H. and Muir, A. (1998). Seed dispersal and the Holocene migration of woodland herbs. *Ecological Monographs,* **68,** 325-337.

Caldwell, M. M., Searles, P. S., Flint, S. D. and Barnes, P. W. (1999). Terrestrial ecosystem responses to UV-B radiation mediated by vegetation, microbes and abiotic photochemistry. In *Physiological Plant Ecology*, M. C. Press, J. D. Scholes and M. G. Barker (Eds.), Oxford: Blackwell

Callaghan, T. V. and Johasson, S. (1995). Implications for changes in Arctic plant diversity from environmental manipulation experiments. In *Arctic and Alpine Biodiversity: Patterns, Causes and Ecosystem Consequences*, F. S. Chapin III and C. H. Körner (Eds.), Berlin: Springer-Verlag

Callaway, R. M. (1997). Positive interactions in plant communities and the individualistic-continuum concept. *Oecologia,* **112,** 143-149.

Callaway, R. M., Brooker, R. W., Choler, P., Kividze, Z., Lortie, C. J., Michalet, R., Paolini, L., Pugnaire, F. I., Newingham, B., Aschehoug, E. T., Armas, C., Kikodze, D. and Cook, B. J. (2002). Positive interactions among Alpine plants increase with stress. *Nature,* **417,** 844-848.

Carleton, T. J. (1984). Residual ordination analysis: a method for exploring vegetation-environment relationships. *Ecology,* **65,** 469-477.

Carleton, T. J., Stitt, R. H. and Nieppola, J. (1996). Constrained indicator species analysis (COINSPAN): an extension of TWINSPAN. *Journal of Vegetation Science,* **7,** 125-130.

Carlsson, B. A. and Callaghan, T. V. (1991). Positive plant interactions in Tundra vegetation and the importance of shelter. *Journal of Ecology,* **79,** 973-983.

Caseldine, C. and Pardoe, H. (1994). Surface pollen studies from Alpine Subalpine Southern Norway-Applications to Holocene data. *Review of Palaeobotany and Palynology,* **82,** 1-15.

Chapin III, F. S. (1980). The mineral nutrition of wild plants. *Annual Review of Ecology and Systematics,* **11,** 233-260.

Chapin III, F. S. (1993a). Physiological controls over plant establishment in primary succession. In *Primary Succession on Land*, J. H. Miles and D. W. H. Walton (Eds.), pp. 161-78, Oxford: Blackwell

Chapin III, F. S. (1993b). Functional role of growth forms in ecosystem and global processes. In *Scaling Ecophysiological Processes: from Leaf to Globe*, J. R. Ehleringer and C. B. Field (Eds.), San Diego: Academic Press

Chapin III, F. S., Fletcher, N., Kielland, K., Everett, K. R. and Likens, A. E. (1988). Productivity and nutrient Ccycling of Alaskan Tundra: Enhancement by flowing soil water. *Ecology,* **69,** 693-702.

Chapin III, F. S., Hobbie, S. E., Bret-Harte, M. S. and Bonan, G. (1995b). Causes and consequences of plant functional diversity in Arctic ecosystems. In *Arctic and Alpine Biodiversity: Patterns, Causes and Ecosystem Consequences*, F. S. Chapin III and C. H. Körner (Eds.), Berlin: Springer-Verlag

Chapin III, F. S., Johnson, D. A. and McKendrick, J. D. (1980). Seasonal movement of nutrients in plants of differing growth form in an Alaskan Tundra ecosystem: Implications for herbivory. *Journal of Ecology,* **68,** 189-209.

Chapin III, F. S. and Körner, C. (1995a). Patterns and causes of Arctic plant community diversity. In *Arctic and Alpine Biodiversity: Patterns, Causes and Ecosystem Consequences*, F. S. Chapin III and C. Körner (Eds.), Berlin: Springer-Verlag

Chapin III, F. S. and Körner, C. H. (1995b). Patterns, causes, changes and consequences of biodiversity in Arctic and Alpine ecosystems. In *Arctic and Alpine Biodiversity: Patterns, Causes and Ecosystem Consequences*, F. S. Chapin III and C. H. Körner (Eds.), Berlin: Springer-Verlag

Chapin III, F. S., McKendrick, J. D. and Johnson, D. A. (1986). Seasonal changes in carbon fractions in Alaskan Tundra plants of differing growth form: Implications for herbivory. *Journal of Ecology,* **74,** 707-731.

Chapin III, F. S. and Shaver, G. R. (1989). Differences in growth and nutrient use among arctic plant growth forms. *Functional Ecology,* **3,** 73-80.

Chapin III, F. S. and Shaver, G. R. (1995). Individualistic growth response of Tundra plant species to environmental manipulations in the field. *Ecology,* **66,** 564-576.

Chapin III, F. S., Shaver, G. R., Giblin, A. E., Nadelhoffer, K. J. and Laundre, J. A. (1995a). Responses of Arctic tundra to experimental and observed changes in Climate. *Ecology,* **76,** 694-711.

Chapin III, F. S., Walker, L. R., Fastie, C. L. and Sharman, L. C. (1994). Mechanisms of primary succession following deglaciation at Glacier Bay, Alaska. *Ecological Monographs,* **64,** 149-175.

Chiba, N. and Hirose, T. (1993). Nitrogen acquisition and use in 3 perennials in the early stages of primary succession. *Functional Ecology,* **7,** 287-292.

Chidress, W. M., Crisafulli, C. M. and Rykiel, E. J. (1998). Comparison of Markovian matrix models of a primary successional plant community. *Ecological Modelling,* **107,** 93-102.

Chytry, M. and Otypkova, Z. (2003). Plot sizes used for phytosociological sampling of European vegetation. *Journal of Vegetation Science,* **14,** 563-570.

Clark, J. S. (1993). Scaling at the population level: Effects of species composition and population structure. In *Scaling Ecophysiological Processes: From Leaf to Globe*, J. R. Ehleringer and C. B. Field (Eds.), San Diego: Academic Press

Clements, F. E. (1916). *Plant Succession: An Analysis of the Development of Vegetation.* Washington DC: Carnegie Institute of Washington Publication 242

Clements, F. E. (1928). *Plant Succession and Indicators.* New York: H. W. Wilson

Clements, F. E. (1936). Nature and structure of the climax. *Journal of Ecology,* **24,** 252-284.

Clifford, H. T. and Stephenson, W. (1975). *An Introduction to Numerical Classification.* London: Academic Press

Connell, J. H. (1975). Some mechanisms producing structure in natural communities: a model and evidence from field experiments. In *Ecology and Evolution of Communities*, M. L. Cody and J. M. Diamond (Eds.), pp. 460-90, Cambridge Ms: Harvard University Press

Connell, J. H., Noble, I. R. and Slatyer, R. O. (1987). On the mechanisms producing successional change. *Oikos,* **50,** 136-137.

Connell, J. H. and Slatyer, R. O. (1977). Mechanisms of succession in natural communities and their role in community stability and organization. *The American Naturalist,* **111,** 1119-1144.

Cooper, W. S. (1923). The recent ecological history of Glacier Bay, Alaska: II. The present vegetation cycle. *Ecology,* **4,** 223-246.

Cooper, W. S. (1931). A third expedition to Glacier Bay, Alaska. *Ecology,* **12,** 61-95.

Cooper, W. S. (1939). A fourth expedition to Glacier Bay. *Ecology,* **20,** 130-155.

Cowles, H. C. (1899). The ccological relations of the vegetation on the sand dunes of Lake Michigan. *Botanical Gazette,* **27,** 95-117, 167-202, 281-308, 361-91.

Cowles, H. C. (1901). The physiographic ecology of Chicago and vicinity: A study of the origin, development and classification of plant societies. *Botanical Gazette,* **31,** 73-108, 145-182.

Crawley, M. J. (1997). Plant ecology. In *Plant Ecology,* M. J. Crawley (Ed.) Oxford: Blackwell

Crawley, M. J. (1999). Herbivory. In *Physiological Plant Ecology,* M. C. Press, J. D. Scholes and M. G. Barker (Eds.), Oxford: Blackwell

Crouch, H. J. (1992). Cryptogam distribution patterns and successional sequences on a glacier foreland in Southern Norway, PhD Thesis, London, University of Greenwich

Crouch, H. J. (1993). Plant distribution patterns and primary succession on a glacier foreland: A comparative study of cryptogams and higher plants. In *Primary Succession on Land,* J. H. Miles and D. W. H. Walton (Eds.), Oxford: Blackwell

Curtis, J. T. and McIntosh, R. P. (1951). An upland continuum in the Prairie-Forest Border Region of Wisconsin. *Ecology,* **32,** 476-496.

Darmody, R. G. and Thorn, C. E. (1997). Elevation, age, soil development and chemical weathering at Storbreen, Jotunheimen, Norway. *Geografiska Annaler,* **79A,** 215-222.

Darmody, R. G., Thorn, C. E. and Rissing, J. M. (1987). Chemical weathering of fine debris from a series of Holocene moraines: Storbreen, Jotunheimen, Southern Norway. *Geografiska Annaler,* **69 (A),** 405-413.

Daubenmire, R. (1966). Vegetation: identification of typal communities. *Science,* **151,** 291-298.

Davis, D. N. K., Lakhani, K. H., Brown, M. C. and Park, D. G. (1985). Early seral communities in a limestone quarry: an experimental study of treatment effects on cover and richness of vegetation. *Journal of Applied Ecology,* **22,** 473-490.

del Morel, R. (1993) Mechanisms of primary succession on volcanoes. In *Primary Succession on Land,* J. H. Miles and D. W. H. Walton (Eds.), pp. 79-100. Oxford: Blackwell

del Morel, R. and Bliss, L. C. (1993). Mechanisms of primary succession: Insights resulting from the eruption of Mount St Helens. *Advances in Ecological Research,* **24,** 1-66.

del Morel, R., Titus, J. H. and Cook, A. M. (1995). Early primary succession on Mt. St. Helen's, Washington. *Journal of Vegetation Science,* **6,** 107-120.

Dice, L. R. (1945). Measures of the amount of ecologic association between species. *Ecology,* **26,** 297-302.

Digby, P. G. N. and Kempton, R. A. (1987). *Multivariate Analysis of Ecological Communities.* London: Chapman and Hall

Edwards, P. J. and Gillman, M. P. (1987). Herbivores and plant succession. In *Colonization, Succession and Stability,* A. J. Gray, M. J. Crawley and P. J. Edwards (Eds.), pp. 295-314. Oxford: Blackwell

Egler, F. E. (1954). Vegetation Science Concepts 1. Initial Floristic Composition, a factor in old-field vegetation Development. *Vegetatio,* **4,** 412-417.

Ehrlen, J. (1995). Demography of the perennial herb *Lathyrus vernus* II: Herbivory and population dynamics. *Journal of Ecology,* **83,** 297-308.

Ejrnaes, R. (2000). Can we trust gradients extracted by DCA? *Journal of Vegetation Science,* **11,** 565-572.

Elven, R. (1975). Plant communities on recently deglaciated moraines at Finse, southern Norway. In *IBP in Norway, Methods and Results Section PT-UM Grazing Project, Hardangervidda Botanical Investigations. Appendix 1,* eds. Norwegian National IBP Committee, 381-467, Oslo: Norwegian IBP Committee. (Norwegian National IBP Committee, Report for 1974)

Ennos, R. A. (2001). Inferences about spatial processes in plant populations from the analysis of molecular markers. In *Integrating Ecology and Evolution in a Spatial Context*, J. Silvertown and J. Antonovics (Eds.), Oxford: Blackwell

Eriksson, O. and Ehrlen, J. (2001). Landscape fragmentation and the viability of plant populations. In *Integrating Ecology and Evolution in a Spatial Context*, J. Silvertown and J. Antonovics (Eds.), Oxford: Blackwell

Ewing, H. A. (2002). The influence of substrate on vegetation history and ecosystem development. *Ecology,* **83,** 2766-2781.

Facelli, J. M. and Pickett, S. T. A. (1990). Markovian chains and the role of history in succession. *Trends in Ecology and Evolution,* **5,** 27-29.

Fastie, C. L. (1995). Causes and ecosystem consequences of multiple pathways of primary succession at Glacier Bay, Alaska. *Ecology,* **76,** 1899-1916.

Fenner, M. (1987). Seed characteristics in relation to succession. In *Colonization, Succession and Stability,* P. J. Gray, M. J. Crawley and P. J. Edwards (Eds.), Oxford: Blackwell

Fisher, R. A., Corbet, A. S. and Williams, C. B. (1943). The relationship between the number of species and the number of individuals in a random sample of an animal population. *Journal of Animal Ecology,* **12,** 42-58.

Fitter, A., Hodge, A. and Robinson, D. (2000). Plant response to patchy soils. In *The Ecological Consequences of Environmental Heterogeneity,* M. J. Hutchings, E. A. John and A. J. A. Stewart (Eds.), Oxford: Blackwell

Fitter, A. H. (1987). Spatial and temporal separation of activity in plant communities: prerequisite or consequence of coexistence? In *Organization of Communities Past and Present,* J. H. R. Gee and P. S. Giller (Eds.), Oxford: Blackwell

Fitter, A. H. (1999). Roots as dynamic systems: the development ecology of roots and root systems. In *Physiological Plant Ecology,* M. C. Press, J. D. Scholes and M. G. Barker (Eds.), Oxford: Blackwell

Fitter, R., Fitter, A. and Farrer, A. (1984). *Grasses, Sedges, Rushes & Ferns of Britain and Northern Europe.* London: HarperCollins

Fort, K. P. and Richards, J. H. (1998). Does seed dispersal limit initiation of primary succession in desert playas? *American Journal of Botany,* **85,** 1722-1731.

Foskett, J. I. (1998). The nature and significance of microtopographic effects on vegetation succession on selected glacier forelands Jostadalen and Jotunheimen, Norway. PhD Thesis, London, University of Greenwich

Fox, J. (1981). Intermediate ievels of soil disturbance maximize Alpine plant diversity. *Nature,* **293,** 564-565.

Franco-Pizana, J. G., Fulbright, T. E., Gardiner, D. T. and Tipton, A. R. (1996). Shrub emergence and seedling growth in microenvironments created by the shrub. *Prosopis glandulosa. Journal of Vegetation Science,* **7,** 257-264.

Franklin, J. F. (1987). Importance and justification of long term studies in ecology. In *Long-Term Studies in Ecology*, G. E. Likens (Ed.)

Frenot, Y., Gloaguen, J. C., Cannavacciuolo, M. and Bellido, A. (1998). Primary succession on glacier forelands in the subantarctic Kerguelen Islands. *Journal of Vegetation Science,* **9,** 75-84.

Frenot, Y., Vliet-Lano, B. V. and Gloaguen, J. -C. (1995). Particle Translocation and Initial Soil Development on a Glacier Foreland, Kerguelen Islands, Subantarctic. *Arctic and Alpine Research,* **27,** 107-115.

Galen, C. and Stanton, M. L. (1995). Responses of snowbed plant species to changes in growing season length. *Ecology,* **76,** 1546-1557.

Gauch, H. G. (1979). COMPCLUS- A Fortran program for rapid initial clustering of large datasets. Ithaca, New York, Cornell University

Gauch, H. G., Chase, G. B. and Whittaker, R. H. (1974). Ordination of vegetation samples by Gaussian species distributions. *Ecology,* **55,** 1382-1390.

Gauch, H. G., Whittaker, R. H. and Singer, S. B. (1981). A comparative study of nonmetric ordinations. *Journal of Ecology,* **69,** 135-152.

Gauch, H. G., Whittaker, R. H. and Wentworth, T. R. (1977). A comparative study of reciprocal averaging and other ordination techniques. *Journal of Ecology,* **65,** 157-174.

Gauch, H. G. J. (1982). *Multivariate Analysis in Community Ecology.* Cambridge: Cambridge University Press

Giller, P. S. and Gee, J. H. R. (1987). The analysis of community organization: The influence of equilibrium, scale and terminology. In *Organization of Communities Past and Present*, J. H. R. Gee and P. S. Giller (Eds.), Oxford: Blackwell

Gleason, H. A. (1917). The structure and development of the plant association. *Bulletin of the Torrey Botanical Club,* **44,** 463-481.

Gleason, H. A. (1926). The individualist concept of the plant association. *The Bulletin of the Torrey Botanical Club,* **53,** 7-27.

Gleason, H. A. (1927). Further views on the succession concept. *Ecology,* **8,** 299-326.

Gleason, H. A. (1939). The individualistic concept of the plant association. *American Midland Naturalist,* **21,** 92-110.

Glenn-Lewin, D. C. and van der Maarel, E. (1992). Patterns and processes of vegetation dynamics. In *Plant Succession: theory and prediction*, D. C. Glenn-Lewin, R. K. Peet and T. T. Veblen (Eds.), pp. 11-59. London: Chapman and Hall

Golden Software Inc. (1995). Mapviewer for Windows, Connecticut, USA

Goodall, D. W. (1970). Statistical plant ecology. *Annual Review of Ecology and Systematics,* **1,** 99-124.

Gottfried, M., Pauli, H., Reiter, K. and Grabher, G. (1999). The Austrian research initiative: Global change effects at the low temperature limits of plant life: A progress report. In *Global Change in the Mountains*, M. Price (Ed.) London: Parthenon

Gower, J. C. (1966). Some distance properties of latent root and vector methods used in multivariate analysis. *Biometrika,* **53,** 325-338.

Grabherr, G., Gottfried, M., Gruber, A. and Pauli, H. (1995). Patterns and current changes in Alpine plant diversity. In *Arctic and Alpine Biodiversity: Patterns, Causes and Ecosystem Consequences*, F. S. Chapin III and C. H. Körner (Eds.), Berlin: Springer-Verlag

Grace, J. (1988). Temperature as a determinant of plant productivity. In *Plants and Temperature*, S. P. Long and F. I. Woodward (Eds.), Cambridge: The Company of Biologists Limited

Graumlich, L. J. (1994). Long-term vegetation change in mountain environments. Palaeoecological insights into modern vegetation dynamics. In *Mountain Environments in Changing Climates*, M. Beniston (Ed.) London: Routledge

Gray, A. J. (1987a). Genetic change during succession. In *Colonization, Succession and Stability*, A. J. Gray, M. J. Crawley and P. J. Edwards (Eds.), Oxford: Blackwell

Gray, J. S. (1987b) Species-abundance patterns. In *Organization of Communities Past and Present*, J. H. R. Gee and P. S. Giller (Eds.), Oxford: Blackwell

Greig-Smith, P. (1983). *Quantitative Plant Ecology.* Oxford: Blackwell

Grey-Wilson, C. and Blamey, M. (1995). *Alpine Flowers of Britain and Northern Europe.* London: HarperCollins

Grime, J. P. (1973). Competitive exclusion in herbaceous vegetation. *Nature,* **242,** 344-347.

Grime, J. P. (1977). Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *The American Naturalist,* **111,** 1169-1194.

Grime, J. P. (1979). *Plant Strategies and Vegetation Processes.* London: Wiley

Grimm, G. A. (2000). Vegetation succession on glacier forelands in the Jostedalsbreen region and the Jotunheimen, Southern Central Norway. PhD Thesis, University of Oxford

Grubb, P. J. (1987a). Colonization and succession in green plants and fungi. In *Colonization, Succession and Stability*, A. J. Gray, M. J. Crawley and P. J. Edwards (Eds.), pp. 81-102. Oxford: Blackwell

Grubb, P. J. (1987b). Global trends in species richness in terrestrial vegetation: a view from the Northern Hemisphere. In *Organisation of Communities Past and Present*, J. H. R. Gee and P. S. Giller (Eds.), Oxford: Blackwell

Guo, Q. (2003). Temporal species-richness-biomass relationships along successional gradients. *Journal of Vegetation Science,* **14,** 121-128.

Gurnell, A. M., Edwards, P. J., Petts, G. E. and Ward, J. V. (1999). A conceptual model for Alpine proglacial river channel evolution under changing climatic conditions. *Catena,* **38,** 223-242.

Hacker, S. D. and Bertness, M. D. (1995). Morphological and physiological consequences of a positive plant interaction. *Ecology,* **76,** 2165-2175.

Haeberli, W. and Beniston, M. (1998). Climate change and its impacts on glaciers and permafrost in the Alps. *Ambio,* **27,** 258-265.

Hahn, S. C., Oberbauer, S. F., Gebauer, R., Grulke, N. E., Lange, O. L. and Tenhunen, J. D. (1996). Vegetation structure and aboveground carbon and nitrogen pools in the Imnavait Creek watershed. In *Landscape Function and Disturbance in Arctic Tundra,* J. F. Reynolds and J. D. Tenhunen (Eds.), Berlin: Springer-Verlag

Haines-Young, R. H. (1983). Size variation of *Rhizocarpon* on moraine slopes in southern Norway. *Arctic and Alpine Research,* **15,** 295-305.

Haines-Young, R. H. (1985). Discussion of 'Size variation of *Rhizocarpon* on moraine slopes in southern Norway': a reply. *Arctic and Alpine Research,* **17,** 212-216.

Halpin, P. N. (1994). Latitudinal variation in the potential responses of mountain ecosystems to climatic change. In *Mountain Environments in Changing Climates*, M. Beniston (Ed.) London: Routledge

Hansen, J., Johnson, D., Lacis, A., Lebedeff, S., Lee, P., Rind, D. and Russell, G. (1981). Climate impact of increasing atmospheric carbon dioxide. *Science,* **213,** 957-966.

Hanssen-Bauer, I. and Forland, E. J. (1998). Annual and seasonal precipitation variations in Norway. 1896-1997. Oslo, Det Norske Meteorologiske Institutt

Hanssen-Bauer, I. and Nordli, P. O. (1998). Annual and seasonal temperature variations in Norway 1876-1997. Oslo, Norwegian Meteorological Institute

Hawker, A. (2000). Reconstructing primary vegetation succession on the Storbreen gletschervoldfeld. BSc Dissertation Thesis, University of Wales, Swansea

Henderson, D. P. A. and Seaby, D. R. M. H. (2001). Species Diversity and Richness. Lymington, Pisces Conservation Ltd

Henry, G. H. R. and Molau, U. (1997). Tundra plants and climate change: the International Tundra Experiment (ITEX). *Global Change Biology,* **3 (Suppl),** 1-9.

Herben, T. (1996). Permanent plots as tools for plant community ecology. *Journal of Vegetation Science,* **7,** 195-202.

Heusser, C. J. (1956). Postglacial environments in the Canadian Rocky Mountains. *Ecological Monographs,* **26,** 263-302.

Hibbs, D. E. (1983). Forty years of forest succession in Central New England. *Ecology,* **64,** 1394-1401.

Hill, M. O. (1973a). Diversity and evenness: A unifying notation and its consequences. *Ecology,* **54,** 427-432.

Hill, M. O. (1973b). Reciprocal averaging: An eigenvector method of ordination. *Journal of Ecology,* **61,** 237-249.

Hill, M. O. (1979a). TWINSPAN- A FORTRAN program for arranging multivariate data in an ordered two-way table by classification of individuals and attributes. Ithaca, New York, Cornell University

Hill, M. O. (1979b). DECORANA-A FORTRAN program for detrended correspondence analysis and reciprocal averaging. Ithaca, New York, Cornell University

Hill, M. O., Bunce, R. G. H. and Shaw, M. W. (1975). Indicator species analysis, a divisive polythetic method of classification and its application to a survey of native pinewoods in Scotland. *Journal of Ecology,* **63,** 597-613.

Hill, M. O. and Gauch, H. G. (1980). Detrended Correspondence Analysis, an improved ordination technique. *Vegetatio,* **42,** 45-58.

Hobbie, E. A., Macko, S. A. and Shugart, H. H. (1998). Patterns in nitrogen dynamics and N isotopes during primary succession in Glacier Bay, Alaska. *Chemical Geology,* **152,** 3-11.

Hobbie, S. E. (1995). Direct and indirect effects of plant species on biogeochemical processes in Arctic ecosystems. In *Arctic and Alpine Biodiversity: Patterns Causes and Ecosystem Consequences*, F. S. Chapin III and C. H. Körner (Eds.), Berlin: Springer-Verlag

Hobbs, R. J. (1997). Can we use plant functional types to describe and predict responses to environmental change? In *Plant Functional Types: Their Relevance to Ecosystem Properties and Global Change*, T. M. Smith, H. H. Shugart and F. I. Woodward (Eds.), Cambridge: Cambridge University Press

Hodkinson, I. D., Coulson, S. J. and Webb, N. R. (2003). Community assembly along proglacial chronosequences in the High Arctic: Vegetation and soil development in NorthWest Svalbard. *Journal of Ecology,* **91,** 651-663.

Hodkinson, I. D., Webb, N. R. and Coulson, S. J. (2002). Primary community assembly on land-the missing stages: Why are the heterotrophic organisms always there first? *Journal of Ecology,* **90,** 569-577.

Holmgren, M., Scheffer, M. and Husten, M. A. (1997). The interplay of facilitation and competition in plant communities. *Ecology,* **78,** 1966-1975.

Holtmeier, F. -K. (1994). Ecological aspects of climatically caused timberline fluctuations. Review and outlook. In *Mountain Environments in Changing Climates*, M. Beniston (Ed.) London: Routledge

Horn, H. S. (1974). The ecology of secondary succession. *Annual Review of Ecology and Systematics,* **5,** 25-37.

Horn, H. S. (1976). Succession. In *Theoretical Ecology: Principles and Applications*, R. M. May (Ed.), pp. 187-204. Oxford: Blackwell

Horn, H. S. (1987). Some causes of variety in patterns of secondary succession. In *Forest Succession: Concepts and Applications*, D. C. West, H. H. Shugart and D. B. Botkin (Eds.), pp. 24-35. New York: Springer-Verlag

Houghton, J. T., Ding, Y., Griggs, D. J., Noguer, M., van der Linden, P. J. and Xiaosu, D. (2001). Climate Change 2001: The Scientific Basis, Intergovernmental Panel on Climate Change.

Huggett, R. J. (1998). Soil chronosequences, soil development and soil evolution: a critical review. *Catena,* **32,** 155-172.

Hurlbert, S. H. (1971). The nonconcept of species diversity: a critique and alternative parameters. *Ecology,* **52,** 577-586.

Hurrell, J. W. (1995). Decadal trends in the North Atlantic Oscillation: Regional temperatures and precipitation. *Science,* **269,** 676-679.

Huston, M. and Smith, T. (1987). Plant succession: Life history and competition. *American Naturalist,* **130**, 168-198.

Ihm, P. and van Groenewoud, H. (1975). A multivariate ordering of vegetation data based on Gaussian type gradient response curves. *Journal of Ecology,* **63,** 767-777.

Innes, J. L. (1994). Design of an Intensive Monitoring System for Swiss Forests. In *Mountain Environments in Changing Climates*, M. Beniston (Ed.) London: Routledge

Inouye, R. S. and Tilman, D. (1988). Convergence and divergence of old field plant communities along experimental nitrogen gradients. *Ecology,* **69,** 995-1004.

Jager, J. C. and Looman, C. W. N. (1995). Data collection. In *Data Analysis in Community and Landscape Ecology*, R. H. G. Jongman, C. J. F. t. Braak and O. F. R. v. Tongeren (Eds.), pp. 10-28. Cambridge: Cambridge University Press

James, F. C. and McCulloch, C. E. (1990). Multivariate analysis in ecology and systematics: panacea or Pandora's box? *Annual Review of Ecology and Systematics,* **21,** 129-166.

Jeffries, R. L. and Bryant, J. P. (1995). The plant-vertebrate herbivore interface in Arctic ecosystems. In *Arctic and Alpine Biodiversity: Patterns, Causes and Ecosystem Consequences*, F. S. Chapin III and C. H. Körner (Eds.), Berlin: Springer-Verlag

Jenkins, G. I., Fuglevard, G. and Christie, J. M. (1997). UV-B perception and signal transduction. In *Plants and UV-B: Responses to Environmental Change*, P. Lumsden (Ed.) Cambridge: Cambridge University Press

Jenny, H. (1941). *Factors of Soil Formation.* New York: McGraw-Hill

Johnson, E. A. and Fryer, G. I. (1992). Physical characterization of seed microsites-movement on the ground. *Journal of Ecology,* **80,** 823-836.

Johnson, P. L. and Billings, W. D. (1962). The Alpine vegetation of the Beartooth Plateau in relation to cryopedogenic processes and patterns. *Ecological Monographs,* **32,** 105-135.

Johnston, R. J. (1980). *Multivariate Statistical Analysis in Geography.* Harlow: Longman

Jonasson, S. (1986). Influence of frost heaving on soil chemistry and the distribution of plant forms. *Geografiska Annaler,* **68A,** 185-195.

Jonasson, S. (1992). Plant responses to fertilization and removal in tundra related to community structure and clonality. *Oikos,* **63,** 420-429.

Jones, D. L. and Kielland, K. (2002). Soil amino acid turnover dominates the nitrogen flux in permafrost-dominated taiga forest soils. *Soil Biology and Biochemistry,* **34,** 209-219.

Jones, G. A. and Henry, G. H. R. (2003). Primary plant succession on recently deglaciated terrain in the Canadian High Arctic. *Journal of Biogeography,* **30,** 277-296.

Jones, M. H., Bay, C. and Nordenhall, U. (1997). Effects of experimental warming on Arctic willows (*Salix* spp.): a comparison of responses from the Canadian High Arctic, Alaskan High Arctic and Swedish Subarctic. *Global Change Biology,* **3 (Suppl 1),** 55-60.

Jongman, R. H. G. (1995). Introduction. In *Data Analysis in Community and Landscape Ecology*, R. H. G. Jongman, C. J. F. t. Braak and O. F. R. v. Tongeren (Eds.), pp. 1-9. Cambridge: Cambridge University Press

Jumpponen, A., Mattson, K., Trappe, J. M. and Ohtonen, R. (1998). Effects of established willows on primary succession on Lyman Glacier Forefront, North Cascade Range, Washington, USA:

Evidence for simultaneous canopy inhibition and soil facilitation. *Arctic and Alpine Research,* **30,** 31-39.

Jumpponen, A., Trapp, J. M. and Cazares, E. (2002). Occurrence of ectomycorrhizal fungi on the forefront of retreating Lyman Glacier (Washington, U.S.A.) in relation to time since deglaciation. *Mycorrhiza,* **12,** 43-49.

Jumpponen, A., Vare, H., Mattson, K. G., Ohtonen, R. and Trappe, J. M. (1999). Characterization of 'safe sites' for pioneers in primary succession on recently deglaciated terrain. *Journal of Ecology,* **87,** 98-105.

Kaas, E. and Frich, P. (1995). Diurnal temperature range and cloud cover in the Nordic Countries: Observed trends and estimates for the future. *Atmospheric Research,* **37,** 211-228.

Karlén, W. (1998). Climate variations and the enhanced greenhouse effect. *Ambio,* **27,** 270-274.

Kaufmann, R. (2001). Invertebrate succession on an alpine glacier foreland. *Ecology,* **82,** 2261-2278.

Kaufmann, R. (2002). Glacier foreland colonisation: distinguishing between short-term and long-term effects of climate change. *Oecologia,* **130,** 470-475.

Kempton, R. A. (1979). The structure of species abundance and measurement of diversity. *Biometrics,* **35,** 307-321.

Kempton, R. A. and Taylor, L. R. (1976). Models and statistics for species diversity. *Nature,* **262,** 818-820.

Kempton, R. A. and Wedderburn, R. W. M. (1978). A comparison of three measures of species diversity. *Biometrics,* **34,** 25-37.

Kent, M. and Coker, P. (1992). *Vegetation Description and Analysis: A Practical Approach.* London: Bellhaven Press

Kielland, K. (1994). Amino acid Aasorption by Arctic plants: implications for plant nutrition and nitrogen-cycling. *Ecology,* **75,** 2373-2383.

Klanderud, K. and Birks, H. J. B. (2003). Recent increases in species richness and shifts in altitudinal distributions of Norwegian mountain plants. *The Holocene,* **13,** 1-6.

Körner, C. (1994). Impact of atmospheric changes on high mountain vegetation. In *Mountain Environments in Changing Climates*, M. Beniston (Ed.) London: Routledge

Körner, C. (1999b). *Alpine Plant Life. Functional Plant Ecology of High Mountain Ecosystems.* Berlin: Springer-Verlag

Körner, C. and Larcher, W. (1988). Plant life in cold climates. In *Plants and Temperature*, S. P. Long and F. I. Woodward (Eds.), Cambridge: The Company of Biologists Limited

Körner, C. H. (1995). Alpine plant diversity: A global survey and functional interpretations. In *Arctic and Alpine Biodiversity: Patterns, Causes and Ecosystem Consequences*, F. S. Chapin III and C. H. Körner (Eds.), Berlin: Springer-Verlag

Körner, C. H. (1999a). Alpine plants: stressed or adapted? In *Physiological Plant Ecology*, M. C. Press, J. D. Scholes and M. G. Barker (Eds.), Oxford: Blackwell

Krause, G. H., Grafflage, S., Rumich-Bayer, S. and Somersalo, S. (1988). Effects of freezing on plant mesophyll cells. In *Plants and Temperature*, S. P. Long and F. I. Woodward (Eds.), Cambridge: The Company of Biologists Limited

Krebs, C. J. (1985). *Ecology: The Experimental Analysis of Distribution and Abundance.* New York: Harper Collins

Kruskal, J. B. (1964). Multidimensional scaling by optimizing goodness of fit to a nonmetric hypothesis. *Psychometrika,* **29,** 1-27.

Kullman, L. (1993). Pine (*Pinus sylvestris* L.) tree-limit surveillance during recent decades, Central Sweden. *Arctic and Alpine Research,* **25,** 24-31.

Kullman, L. (1998). Tree-limits and montane forests in the Swedish Scandes: Sensitive barometers of climate change and variability. *Ambio,* **27,** 312-321.

Kullman, L. (2002). Rapid recent range-margin rise of tree and shrub species in the Swedish Scandes. *Journal of Ecology,* **90,** 68-77.

Kullman, L. (2003). Recent reversal of Neoglacial climate cooling trend in the Swedish Scandes as evidenced by mountain birch tree-limit rise. *Global and Planetary Change,* **36,** 77-88.

Kullman, L. and Kjallgren, L. (2000). A coherent postglacial tree-limit chronology (*Pinus sylvestris* L.) for the Swedish Scandes: Aspects of palaeoclimate and 'Recent Warming'. *Arctic, Antarctic and Alpine Research,* **32,** 419-428.

Kupfer, J. A. and Runkle, J. R. (1996). Early gap successional pathways in *Fagus-Acer* forest. *Journal of Vegetation Science,* **7,** 247-256.

Law, R., Purves, D. W., Murrell, D. J. and Dieckermann, U. (2001). Causes and effects of small-scale Sspatial structure in plant populations. In *Integrating Ecology and Evolution in a Spatial Context*, J. Silvertown and J. Antonovics (Eds.), Oxford: Blackwell

Lawton, J. H. (1987). Assembly rules for successional communities. In *Colonization, Succession and Stability,* A. J. Gray, M. J. Crawley and P. J. Edwards (Eds.), Oxford: Blackwell

Lawton, J. H. (2000). Concluding remarks: A review of some open questions. In *The Ecological Consequences of Environmental Heterogeneity*, M. J. Hutchings, E. A. John and A. J. A. Stewart (Eds.), Oxford: Blackwell

Lee, J. A. (1999) Arctic plants: Adaptation and environmental change. In *Physiological Plant Ecology*, M. C. Press, J. D. Scholes and M. G. Barker (Eds.), Oxford: Blackwell

Leigh, E. G. (1975) Population Fluctuations, Community Stability and Environmental Variability. In *Ecology and Evolution of Communities*, M. L. Cody and J. M. Diamond (Eds.), pp. 51-73. Cambridge, Ms: Harvard University Press

Levin, S. A. (1993) Concepts of Scale at the Local Level. In *Scaling Physiological Processes: Leaf to Globe*, J. R.Ehleringer and C. B. Field (Eds.), San Diego: Academic Press

Lichter, J. (1998) Primary Succession and Forest Development on Coastal Lake Michigan Sand Dunes. *Ecological Monographs,* **68,** 487-510.

Lichter, J. (2000) Colonization Constraints During Primary Succession on Coastal Lake Michigan Sand Dunes. *Journal of Ecology,* **88,** 825-839.

Lid, J. (1963) *Norsk og sven flora,* Oslo: Det Norske Samlaget

Liestøl, O. (1967) Storbreen glacier in Jotunheimen, Norway. *Norsk Polarinstitutt Skrifter,* **141,** 1-63.

Lindroth, C. H. (1965) Skaftafell, Iceland: a living glacial refugium. *Oikos Supplementum,* **6,** 1-142.

Lloyd, M. and Ghelardi, R. J. (1964) A table for calculating the equitability component of species diversity. *Journal of Animal Ecology,* **33,** 217-226.

Looman, J. (1963) Preliminary classification of grasslands in Saskatchewan. *Ecology,* **44,** 15-29.

Louppen, J. W. M. and van der Maarel, E. (1979) CLUSLA: a computer program for the clustering of large phytosociological data sets. *Vegetatio,* **40,** 107-114.

Lyon, J. and Sager, C. L. (2002) Correspondence analysis of functional groups in a riparian landscape. *Plant Ecology,* **164,** 171-183.

MacArthur, R. H. (1965) Patterns of species diversity. *Biological Reviews,* **40,** 510-533.

MacArthur, R. H. and Wilson, E. O. (1967) *The Theory of Island Biogeography,* Princetown, N. J.: Princetown University Press

MacKerness, S. A. -H., Jordon, B. R. and Thomas, B. (1997) UV-B Effects on the Expression of Genes Encoding Proteins Involved in Photosynthesis. In *Plants and UV-B: Responses to Environmental Change*, P. Lumsden (Ed.) Cambridge: Cambridge University Press

Magurran, A. E. (1988) *Ecological Diversity and its Measurement,* Cambridge: Cambridge University Press

Maizels, J. K. and Petch, J. R. (1985) Age Determination of Intermoraine Areas, Austerdalen, southern Norway. *Boreas,* **14,** 51-65.

Margalev, R. (1968) *Perspectives in Ecological Theory,* Chicago: University of Chicago Press

Marion, G. M., Bockheim, J. G. and Brown, J. (1997) Arctic soils and the ITEX Experiment. *Global Change Biology,* **3 (Suppl 1),** 33-43.

Marrs, R. H. and Bradshaw, A. D. (1993) Primary succession on man-made wastes: the importance of resource acquisition. In *Primary Succession on Land*, J. H. Miles and D. W. H. Walton (Eds.), pp. 221-48. Oxford: Blackwell

Mather, P. M. (1991) *Computer Applications in Geography,* Chichester: J. Wiley

Matthews, J. A. (1973). Lichen growth on an active medial moraines, Jotunheimen, Norway. *Journal of Glaciology,* **12,** 305-313.

Matthews, J. A. (1974). Families of lichenometric dating curves from the Storbreen gletschervorfeld, Jotunheimen, Norway. *Norsk Geografisk Tidsskrift,* **28,** 215-235.

Matthews, J. A. (1975). Experiments on the reproducibility and reliability of lichenometric dates, Storbreen gletschervorfeld, Jotunheimen, Norway. *Norsk Geografisk Tidsskrift,* **29,** 97-109.

Matthews, J. A. (1976). A Phytogeography of a Gletschervorfeld: Storbreen-i-Leirdalen, Jotunheimen, Norway. Ph.D. Thesis, University of London, King's College.

Matthews, J. A. (1977). A lichenometric test of the 1750 end-moraine hypothesis: Storbreen gletschervorfeld, southern Norway. *Norsk Geografisk Tidsskrift,* **31,** 129-136.

Matthews, J. A. (1978). Plant colonization patterns on a Gletschervorfeld, southern Norway: a meso-scale geographical approach to vegetation change and phytometric dating. *Boreas,* **7,** 155-178.

Matthews, J. A. (1979a). The vegetation of the Storbreen gletschervorfeld, Jotunheimen, Norway. I. Introduction and approaches involving classification. *Journal of Biogeography,* **6,** 17-47.

Matthews, J. A. (1979b). The vegetation of the Storbreen gletschervorfeld, Jotunheimen, Norway. II. Approaches involving ordination and general conclusions. *Journal of Biogeography*, **6**, 133-67.

Matthews, J. A. (1981). Vegetation Studies. In *Quantitative Geography: A British View*, N. Wrigley and R. J. Bennett (Eds.), pp. 294-308. London: Routledge and Kegan Paul.

Matthews, J. A. (1991). The late Neoglacial ('Little Ice Age') glacier maximum in southern Norway: new ^{14}C-dating evidence and climatic implications. *The Holocene,* **1,** 219-233.

Matthews, J. A. (1992). *The Ecology of Recently Deglaciated Terrain.* Cambridge: Cambridge University Press

Matthews, J. A. (1996). Classics in physical geography revisited. *Progress in Physical Geography,* **20,** 193-203.

Matthews, J. A. (1999). Disturbance regimes and ecosystem response on recently-deglaciated substrates. In *Ecosystems of the World*, L. R. Walker (Ed.), pp. 17-37. London: Elsevier

Matthews, J. A., Dahl, S. O., Nesje, A., Berrisford, M. S. and Andersson, C. (2000). Holocene glacier variations in central Jotunheimen, southern Norway based on distal glaciolacustrine sediment cores. *Quaternary Science Reviews,* **19,** 1625-1647.

Matthews, J. A., Harris, C. and Ballantyne, C. K. (1986). Studies on a gelifluction lobe, Jotunheimen, Norway: ^{14}C chronology, stratigraphy, sedimentology and palaeoenvironment. *Geografiska Annaler,* **68A,** 345-360.

Matthews, J. A., Shakesby, R. A., Berrisford, M. S. and McEwan, L. J. (1998). Periglacial patterned ground on the Styggedalsbreen Glacier Foreland: Micro-topographic, Periglacial and Geoecological Controls. *Permafrost and Periglacial Processes,* **9,** 147-166.

Matthews, J. A. and Whittaker, R. J. (1987). Vegetation succession on the Storbreen Glacier Foreland, Jotunheimen, Norway: A Review. *Arctic and Alpine Research,* **19,** 385-395.

May, R. M. (1975a). Patterns of species abundance and diversity. In *Ecology and Evolution of Communities*, M. L. Cody and J. M. Diamond (Eds.), pp. 81-120. Cambridge: Harvard University Press

May, R. M. (1975b). Successional patterns and indices of diversity. *Nature,* **258,** 285-286.

Mazzoleni, S. and Ricciardi, M. (1993) Primary succession on the cone of Vesuvius. In *Primary Succession on Land*, J. H. Miles and D. W. H. Walton (Eds.), Oxford: Blackwell

McGraw, J. B. (1995) Patterns and Causes of Genetic Diversity in Arctic Plants. In *Arctic and Alpine Diversity: Patterns, Causes and Ecosystem Consequences*, F. S. Chapin III and C. H. Körner (Eds.), Berlin: Springer-Verlag

McGraw, J. B. and Chapin III, F. S. (1989) Competitive Ability and Adaptation to Fertile and Infertile Soils in Two *Eriophorum* Species. *Ecology,* **70,** 736-749.

McIntire, E. J. B. and Hik, D. S. (2002) Grazing History Versus Current Grazing: Leaf Demography and Compensatory Growth of Three Alpine Plants in Response to a Native Herbivore (*Ochotona collaris*). *Journal of Ecology,* **90,** 348-359.

McIntosh, R. P. (1967) The Continuum Concept of Vegetation. *The Botanical Review,* **33,** 130-187.

Mellor, A. (1984) An Investigation of Pedogenesis on Selected Neoglacial Moraine Ridge Sequences, Jostedalsbreen and Jotunheimen, Southern Norway, PhD Thesis, University of Hull

Mellor, A. (1985) Soil chronosequences on Neoglacial moraine ridges, Jostedalsbreen and Jotunheimen, southern Norway: a quantitative pedogenic approach. In *Geomorphology and Soils*, K. S. Richards, R. R. Arnett and S. Ellis (Eds.), pp. 289-308. London: George Allen and Unwin

Messer, A. C. (1984) A Geographical Investigation of Soil Development in Glacier Forelands in South-central Norway, PhD Thesis, University of Wales (University College Cardiff)

Messer, A. C. (1988) Regional Variations in Rates of Pedogenesis and the Influence of Climatic Factors on Moraine Chronosequences, Southern Norway. *Arctic and Alpine Research,* **20,** 31-39.

Michelsen, A., Graglia, E., Schmidt, I. K., Jonasson, S., Sleep, D. and Quarmby, C. (1999) Differential responses of grass and a dwarf shrub to long-term changes in soil microbial biomass C, N and P following factorial addition of NPK fertilizer, fungicide and labile carbon to a heath. *New Phytologist,* **143,** 523-538.

Michelsen, A., Schmidt, I. K., Jonasson, S., Dighton, J., Joes, H. E. and Callaghan, T. V. (1995) Inhibition of growth and effects on nutrient uptake of arctic graminoids by leaf extracts-allelopathy or resource competition between plants and microbes? *Oecologia,* **103,** 407-418.

Miles, J. (1987) Vegetation Succession- past and present perceptions. In *Colonization, Succession and Stability,* A. J. Gray, M. J. Crawley and P. J. Edwards (Eds.), pp. 1-29. Oxford: Blackwell

Miles, J. H. and Walton, D. W. H. (1993) Primary Succession Revisited. In *Primary Succession on Land*, J. H. Miles and D. W. H. Walton (Eds.), pp. 295-302. Oxford: Blackwell

Minchin, P. R. (1987) An evaluation of the relative robustness of techniques for ecological ordination. *Vegetatio,* **67,** 1167-1179.

Molau, U. (1993) Relationships Between Flowering Phenology and Life History Strategies in Tundra Plants. *Arctic and Alpine Research,* **25,** 391-402.

Molau, U. (1997) Responses to Natural Climatic Variation and Experimental Warming in Two Tundra Plant Species with Contrasting Life Forms: *Cassiope tetragona* and *Ranunculus nivalis. Global Change Biology,* **3 (Suppl 1),** 97-107.

Molau, U. and Alatalo, J. M. (1998) Responses of Subarctic-alpine Plant Communities to Simulated Environmental Change: Biodiversity of Bryophytes, Lichens and Vascular Plants. *Ambio,* **27,** 322-327.

Molau, U. and Larsson, E. L. (2000) Seed rain and seed bank along an alpine altitudinal gradient in Swedish Lapland. *Canadian Journal of Botany,* **78,** 728-747.

Monkhouse, F. J. and Wilkinson, H. R. (1963) *Maps and Diagrams,* London: Methuen

Moody, S. A., Coop, D. J. S. and Paul, N. D. (1997) Effects of Elevated UV-B Radiation and Elevated CO2 on Heathland Communities. In *Plants and UV-B: Responses to Environmental Change*, P. Lumsden (Ed.) Cambridge: Cambridge University Press

Mooney, H. A. (1997) Ecosystem Processes as a Function of Diversity: the Basis of the Viewpoint. In *Plant Functional Types: Their Relevance to Ecosystem Properties and Global Change*, T. M. Smith, H. H. Shugart and F. I. Woodward (Eds.), Cambridge: Cambridge University Press

Mooney, H. A. and Billings, W. D. (1961) Comparative Physiological Ecology of Arctic and Alpine Populations of *Oxyria digyna. Ecological Monographs,* **81,** 1-29.

Mordaunt, C. (1999) Association Between Weather Conditions, Snow-lie and Snowbed Vegetation in the Scottish Highlands. In *Global Change in the Mountains*, M. Price (Ed.) London: Parthenon

Morris, M. G. and Lakhani, K. H. (1979) Responses of grassland invertebrates to management by cutting. I. Species diversity of Hemiptera. *Journal of Applied Ecology,* **16,** 77-98.

Morris, W. E. and Wood, D. M. (1989) The Role of Lupine in Succession on Mount St Helens: Facilitation of Inhibition? *Ecology,* **70,** 697-703.

Mortimer, A. M. (1987) Contributions of plant population dynamics to understanding early succession. In *Colonization, Succession and Stability,* A. J. Gray, M. J. Crawley and P. J. Edwards (Eds.), Oxford: Blackwell

Mouillot, D. and Lepretre, A. (1999) A comparison of species diversity estimators. *Researches on Population Ecology,* **41,** 203-215.

Mueller-Dombois, D. and Ellenberg, H. (1974) *Aims and methods in vegetation ecology,* New York

Muller, C. H. (1952) Plant Succession in Arctic Heath and Tundra in Northern Scandinavia. *Bulletin of the Torrey Botanical Club,* **79,** 296-309.

Murray, D. F. (1995) Causes of Arctic Plant Diversity. In *Arctic and Alpine Biodiversity: Patterns, Causes and Ecosystem Consequences*, F. S. Chapin III and C. H. Körner (Eds.), Berlin: Springer-Verlag

Myers, A. A. and Giller, P. S. (1988a) Process, pattern and scale in Biogeography. In *Analytical Biogeography,* A. A. Myers and P. S. Giller (Eds.), London: Chapman & Hall

Myers, A. A. and Giller, P. S. (1988b) Biogeographic Patterns-Introduction. In *Analytical Biogeography,* A. A. Myers and P. S. Giller (Eds.), London: Chapman & Hall

Nadelhoffer, K. J., Giblin, A. E., Shaver, G. R. and Laundre, J. A. (1991) Effects of Temperature and Substrate Quality on Element Mineralization in Six Arctic Soils. *Ecology,* **73,** 242-253.

Nesje, A. and Dahl, S. O. (2003) The 'Little Ice Age'-Only Temperature? *The Holocene,* **13,** 139-145.

Nesje, A. and Kvamme, M. (1991) Holocene glacier and climate variations in western Norway: evidence for early Holocene glacier demise and multiple Neoglacial events. *Geology,* **19,** 610-612.

Nesje, A., Lie, O. and Dahl, S. O. (2000) Is the North Atlantic Oscillation Reflected in Scandinavian Glacier Mass Balance Records? *Journal of Quaternary Science,* **15,** 587-601.

Niederfriniger Schlag, R. and Erschbamer, B. (2000) Germination and establishment of seedlings on a glacier foreland in the Central Alps, Austria. *Arctic, Antarctic and Alpine Research,* **32,** 270-277.

Nilsson, M. C., Wardle, D. A., Zackrisson, O. and Jaderlund, A. (2002) Effects of Alleviation of Ecological Stresses on an Alpine Tundra Community over an Eight-Year Period. *Oikos,* **97,** 3-17.

Nilsson, M. -C., Zackrisson, O., Sterner, O. and Wallstedt, A. (2000) Characterization of the differential interference effects of two boreal dwarf shrub species. *Oecologia,* **123.**

Noble, I. R. and Slatyer, R. O. (1980) The Use of Vital Attributes to Predict Successional Changes in Plant Communities Subject to Recurrent Disturbances. *Vegetatio,* **43,** 5-21.

Noy-Meir, I. and Austin, M. P. (1970) Principal Components ordination and simulated vegetation data. *Ecology,* **51,** 551-552.

Odum, E. P. (1969) The Strategy of Ecosystem Development. *Science,* **164,** 262-270.

Odum, E. P. (1971) *Fundamentals of Ecology,* Philadelphia: Saunders

Ohtonen, R., Fritze, H., Pennanen, T., Jumponnen, A. and Trappe, J. (1999) Ecosystem properties and microbial community changes in primary succession on a glacier forefront. *Oecologia,* **119,** 239-246.

Økland, R. H. (1992) Studies in SE Fennoscandian mires: relevance to ecological theory. *Journal of Vegetation Science,* **3,** 279-284.

Økland, R. H. (1996) Are ordination and constrained ordination alternative or complementary strategies in general ecological studies. *Journal of Vegetation Science,* **7,** 289-292.

Olff, H., Huisman, J. and van Tooren, B. F. (1993) Species dynamics and nutrient accumulation during early primary succession in coastal sand dunes. *Journal of Ecology,* **81,** 693-706.

Olson, J. S. (1958) Rates of succession and soil changes on southern Lake Michigan sand dunes. *Botanical Gazette,* **119,** 125-170.

Orloci, L. and Orloci, M. (1988) On recovery, Markov chains and canonical analysis. *Ecology,* **69,** 1260-1265.

Oskanen, J. and Minchin, P. R. (1997) Instability of ordination results under changes in input data order: explanations and remedies. *Journal of Vegetation Science,* **8,** 447-454.

Palmer, M. W. (1993) Putting things in even better order: the advantages of Canonical Correspondence Analysis. *Ecology,* **74,** 2215-2230.

Pardoe, H. S. (1996) Micro-scale Patterns of Modern Pollen Deposition Within 3 Alpine Plant Communities. *New Phytologist,* **132,** 327-341.

Parrish, J. A. D. and Bazzaz, F. A. (1982) Competitive Interactions in Plant Communities of Different Successional Ages. *Ecology,* **63,** 314-320.

Partridge, T. R. (1992) Successional Interactions Between Bracken and Broom on the Port Hills, Canterbury, New Zealand. *Journal of Applied Ecology,* **29,** 85-91.

Pastor, J. (1995) Diversity of Biomass and Nitrogen Distribution Among Plant Species in Arctic and Alpine Tundra Ecosystems. In *Arctic and Alpine Biodiversity: Patterns, Causes and Ecosystem Consequences*, F. S. Chapin III and C. H. Körner (Eds.), Berlin: Springer-Verlag

Peet, R. K. (1974) The Measurement of Species Diversity. *Annual Review of Ecology and Systematics,* **5,** 285-307.

Peet, R. K. (1975) Relative diversity indices. *Ecology,* **56,** 496-498.

Peet, R. K. (1992) Community structure and ecosystem function. In *Plant Succession: Theory and Prediction*, D. C. Glenn-Lewin, R. K. Peet and T. T. Veblen (Eds.), pp. 103-51. London: Chapman and Hall

Peet, R. K., Knox, R. G., Case, J. S. and Allen, R. B. (1988) Putting things in order: the advantages of Detrended Correspondence Analysis. *The American Naturalist,* **131,** 924-934.

Persson, A. (1964) The vegetation at the margin of the receding glacier at Skaftafellsjokull, southeastern Iceland. *Botaniska Notiser,* **117,** 323-354.

Peterson, D. L. (1994) Recent Changes in the Growth and Establishment of Subalpine Conifers in Western North America. In *Mountain Environments in Changing Climates*, M. Beniston (Ed.) London: Routledge

Petit, R. J., Bialozy, R., Brewer, S., Cheddadit, R. and Comps, B. (2001) From Spatial Patterns of Diversity to Postglacial Migration Processes in Forest Trees. In *Integrating Ecology and Evolution in a Spatial Context*, J. Silvertown and J. Antonovics (Eds.), Oxford: Blackwell

Pickett, S. T. A. (1987) Space for time substitution as an alternative to long term studies. In *Long term studies in Ecology: approaches and alternatives*, G. E. Likens (Ed.), pp. 110-35. New York: Springer Verlag

Pickett, S. T. A., Cadenasso, M. L. and Jones, C. G. (2000) Generation of Heterogeneity by Organisms: Creation, Maintenance and Transformation. In *The Ecological Consequences of Environmental Heterogeneity*, M. J. Hutchings, E. A. John and A. J. A. Stewart (Eds.), Oxford: Blackwell

Pickett, S. T. A., Collins, S. L. and Armesto, J. J. (1987) Models, mechanisms and pathways of succession. *The Botanical Review,* **53,** 335-371.

Pickett, S. T. A. and McDonnell, M. J. (1989) Changing Perspectives in Community Dynamics: a Theory of Successional Forces. *Trends in Ecology and Evolution,* **4,** 241-245.

Pickett, S. T. A. and White, P. S. (1985) *The Ecology of Natural Disturbance and Patch Dynamics,* London: Academic Press

Pielou, E. C. (1975) *Ecological Diversity,* New York: John Wiley and Sons

Pielou, E. C. (1977) *Mathematical Ecology,* New York: Wiley

Pisces Conservation, L. (2002) Community Analysis Package Version 2.1, Lymington, Hampshire

Podani, J. (1997) On the sensitivity of ordination and classification methods to variation in the input order of data. *Journal of Vegetation Science,* **8,** 153-156.

Poore, M. E. D. (1964) Integration in the plant community. *Journal of Ecology,* **52 (Suppl.),** 213-226.

Poorter, H. and Nevas, M. -L. (2003) Plant Growth and Competition at Elevated CO_2: on Winners, Losers and Functional Groups. *New Phytologist,* **157,** 175-198.

Pornon, A. and Doche, B. (1994) Dynamics and Functioning of *Rhodedendron ferrugineum* Subalpine Heathlands (Northern Alps, France) (Mineral Nitrogen Availability in the Context of Global Climate Change). In *Mountain Environments in Changing Climates*, M. Beniston (Ed.) London: Routledge

Press, M. C., Callaghan, T. V. and Lee, J. A. (1998) How Will European Arctic Ecosystems Respond to Projected Global Environmental Change. *Ambio,* **27,** 306-311.

Preston, F. W. (1948) The commonness, and rarity, of species. *Ecology,* **29,** 254-283.

Pugnaire, F. I. and Luque, M. T. (2001) Changes in Plant Interactions along a Gradient of Environmental Stress. *Oikos,* **93,** 42-49.

Putman, R. J. and Wratten, S. D. (1984) *Principles of Ecology,* London: Croom Helm

Raab, T. K., Lipson, D. A. and Monson, R. K. (1996) Non-mycorrhizal Uptake of Amino Acids by Roots of the Alpine Sedge *Kobresia myosuroides*: Implications for the Alpine Nitrogen Cycle. *Oecologia,* **108,** 488-494.

Read, D. J. (1999) The Ecophysiology of Mycorrhizal Symbiosis with Special Reference to Plant Fitness. In *Physiological Plant Ecology*, M. C. Press, J. D. Scholes and M. G. Barker (Eds.), Oxford: Blackwell

Rees, M., Mangel, M., Turnbull, L., Sheppard, A. and Briese, D. (2000) The Effects of Heterogeneity on Dispersal and Colonization in Plants. In *The Ecological Consequences of Environmental Heterogeneity*, M. J. Hutchings, E. A. John and A. J. A. Stewart (Eds.), Oxford: Blackwell

Reynold, J. F., Hilbert, D. W. and Kemp, P. R. (1993) Scaling Ecophysiology from the Plant to the Ecosystem: a Conceptual Framework. In *Scaling Ecophysiological Processes: From Leaf to Globe*, J. R. Ehleringer and C. B. Field (Eds.), San Diego: Academic Press

Richardson, S. G. and Salisbury, F. B. (1977) Plant Responses to Light Penetrating Snow. *Ecology,* **58,** 1152-1158.

Robinson, C. H., Wookey, P. A., Lee, J. A., Callaghan, T. V. and Press, M. C. (1998) Plant community response to simulated environmental change at a high arctic, polar semi-desert. *Ecology,* **79,** 856-866.

Rosales, J., Petts, G. and Knab-Vispo, C. (2001) Ecological gradients within riparian forests of the Lower Caura River, Venezuela. *Plant Ecology,* **152,** 101-118.

Rosen, B. R. (1988) Biogeographical Patterns: A Perceptual Overview. In *Analytical Biogeography*, A. A. Myers and P. S. Giller (Eds.), London: Chapman & Hall

Rossow, L. J., Bryant, J. P. and Kielland, K. (1997) Effects of above-ground browsing by mammals on mycorrhizal infection in an early successional taiga ecosystem. *Oecologia,* **110,** 94-98.

Ryvarden, L. (1971) Trapping of diaspores in the Alpine zone at Finse, Norway. *Norwegian Journal of Botany,* **18,** 215-216.

Ryvarden, L. (1975) Winter-dispersed species at Finse, Norway. *Norwegian Journal of Botany,* **22,** 21-24.

Saetersdal, M. and Birks, H. J. B. (1997) A comparative ecological study of Norwegian mountain plants in relation to possible future climate change. *Journal of Biogeography,* **24,** 127-152.

Schimel, J. (1995) Ecosystem Consequences of Microbial Diversity and Community Structure. In *Arctic and Alpine Biodiversity: Patterns, Causes and Ecosystem Consequences*, F. S. Chapin III and C. H. Körner (Eds.), Berlin: Springer-Verlag

Schimel, J. P., Kielland, K. and Chapin, F. S. I. (1996) Nutrient availability and uptake by tundra plants. In *Landscape Function and Disturbance in Arctic Tundra*, J. F. Reynolds and J. D. Tenhunen (Eds.), pp. 203-22. Berlin: Springer-Verlag

Schoener, T. W. (1988) Ecological interactions. In *Analytical Biogeography*, A. A. Myers and P. S. Giller (Eds.), London: Chapman and Hall

Seppelt, R. D., Broady, P. A., Pickard, J. and Adamson, D. A. (1988) Plants and landscape in the Vestfold Hills, Antarctica. *Hydrobiologia,* **165,** 185-196.

Shannon, C. E. and Weaver, W. (1949) *The Mathematical Theory of Communication,* Urbana: University of Illinois Press

Shaver, G. R. (1995) Plant Function Diversity and Resource Control of Primary Productivity in Alaskan Arctic Tundras. In *Arctic and Alpine Biodiversity: Patterns, Causes and Ecosystem Consequences*, F. S. Chapin III and C. H. Körner (Eds.), Berlin: Springer-Verlag

Shaver, G. R. and Chapin III, F. S. (1986) Effect of Fertilizer on Production and Biomass of Tussock Tundra, Alaska, USA. *Arctic and Alpine Research,* **18,** 261-268.

Shaver, G. R., Giblin, A. E., Nadelhoffer, K. J. and Rasletter, E. B. (1997) Plant Functional Types and Ecosystem Change in Arctic Tundras. In *Plant Functional Types: their Relevance to Ecosystem Properties and Global Change*, T. M. Smith, H. H. Shugart and F. I. Woodward (Eds.), Cambridge: Cambridge University Press

Shaver, G. R. and Laundre, J. (1997) Exsertion, Elongation and Senescence of Leaves of *Eriophorum vaginatum* and *Carex bigelowii* in Northern Alaska. *Global Change Biology,* **3 (Suppl 1),** 146-157.

Sheldon, A. L. (1969) Equitability indices: dependence on the species count. *Ecology,* **50,** 466-467.

Shepard, R. N. (1962) The analysis of proximities: multidimensional scaling with an unknown distance function. II. *Psychometrika,* **27,** 219-246.

Shevtsova, A., Ojala, A., Neuvonen, S., Vieno, M. and Haukioja, E. (1995) Growth and reproduction of dwarf shrubs in a subarctic plant community: annual variation and aboveground interactions with neighbours. *Journal of Ecology,* **83,** 263-275.

Shugart, H. H. (1997) Plant and Ecosystem Functional Types. In *Plant Functional Types: their Relevance to Ecosystem Properties and Global Change*, T. M. Smith, H. H. Shugart and F. I. Woodward (Eds.), Cambridge: Cambridge University Press

Sigafoos, R. S. and Hendricks, E. L. (1969) The time interval between stabilization of alpine glacial deposits and establishment of tree seedlings. *Geological Survey Research (US),* **650B,** 89-93.

Silvertown, J. (2001) Plants Stand Still but Their Genes Don't: Non-trivial Consequences of the Obvious. In *Integrating Ecology and Evolution in a Spatial Context*, J. Silvertown and J. Antonovics (Eds.), Oxford: Blackwell

Simpson, E. H. (1949) Measurement of Diversity. *Nature,* **163,** 688.

Skjelkvale, B. L. and Wright, R. F. (1998) Mountain Lakes: Sensitivity to Acid Deposition and Global Climate Change. *Ambio,* **27,** 280-286.

Smith, R. I. (1993) Role of bryophyte propagule banks in primary succession. In *Primary Succession on Land*, J. H. Miles and D. W. H. Walton (Eds.), pp. 55-78. Oxford: Blackwell

Smith, T. M., Shugart, H. H., Bonan, G. B. and Smith, J. B. (1992) Modelling the Potential Response of Vegetation to Global Climate Change. *Advances in Ecological Research,* **22.**

Sousa, W. P. (1984) The Role of Disturbance in Natural Communities. *Annual Review of Ecology and Systematics,* **15,** 353-391.

Southwood, T. R. E. (1987) The concept and nature of the community. In *Organization of Communities Past and Present*, J. H. R. Gee and P. S. Giller (Eds.), Oxford: Blackwell

Sprent, J. I. (1993) The role of Nitrogen fixation. In *Primary Succession on Land*, J. H. Miles and D. W. H. Walton (Eds.), Oxford: Blackwell

SPSS (1999) SPSS for Windows

Stanton, M. L., Rejmanek, M. and Galen, C. (1994) Changes in Vegetation and Soil Fertility along a Predictable Snowmelt Gradient in the Mosquito Range, Colorado, USA. *Arctic and Alpine Research,* **26,** 364-374.

Stenstrom, M., Gugerli, F. and Henry, G. H. R. (1997) Response of *Saxifraga oppositifolia* L. to Simulated Climate Change at 3 Contrasting Latitudes. *Global Change Biology,* **3 (Suppl 1),** 44-54.

Stewart, A. J. A., John, E. A. and Hutchings, M. J. (2000) The World is Heterogeneous: Ecological Consequences of Living in a Patchy Environment. In *The Ecological Consequences of Environmental Heterogeneity*, M. J. Hutchings, E. A. John and A. J. A. Stewart (Eds.), Oxford: Blackwell

Stocklin, J. and Baumler, E. (1996) Seed rain, seedling establishment and clonal growth strategies on a glacier foreland. *Journal of Vegetation Science,* **7,** 45-56.

Strand, T. (1960) The Pre-Devonian Rocks and Structures in the Region of Caledonian Deformation. In *Geology of Norway*, O. Holtedahl (Ed.) Oslo: Aschehoug and Co

Strenstrom, A. and Jonsdottir, I. S. (1997) Responses of the Clonal Sedge, *Carex bigelowii*, to Two Seasons of Simulated Climate Change. *Global Change Biology,* **3 (Suppl 1),** 89-96.

Suzuki, S. and Kudo, G. (1997) Short-term Effects of Simulated Environmental Change on Phenology, Leaf traits and Shoot Growth of Alpine Plants on a Temperate Mountain, Northern Japan. *Global Change Biology,* **3 (Suppl 1),** 108-115.

Svoboda, J. and Henry, G. H. R. (1987) Succession in Marginal Arctic Environments. *Arctic and Alpine Research,* **19,** 373-384.

Swan, J. M. A. (1970) An examination of some ordination problems by use of simulated vegetation data. *Ecology,* **51,** 89-102.

Tansley, A. G. (1920) The classification of vegetation and the concept of development. *Journal of Ecology,* **8,** 118-149.

Tansley, A. G. (1935) The use and abuse of vegetational concepts and terms. *Ecology,* **16,** 284-307.

Tausch, R. J., Charlet, D. A., Weixelmax, D. A. and Zamudio, D. C. (1995) Patterns of ordination and classification instability resulting from changes in input data order. *Journal of Vegetation Science,* **6,** 897-902.

Taylor, L. R. (1978) Bates, Williams, Hutchison-a variety of diversities. In *Diversity in Insect Faunas: 9th Symposium of the Royal Entomological Society*, L. A. Mound and L. Warloff (Eds.), Oxford: Blackwell

Taylor, R. M., Tobin, A. K. and Bray, C. M. (1997) DNA Damage and Repair in Plants. In *Plants and UV-B: Responses to Environmental Change*, P. Lumsden (Ed.) Cambridge: Cambridge University Press

Taylor, R. V. and Seastedt, T. R. (1994) Short- and Long-Term Patterns of Soil Moisture in Alpine Tundra. *Arctic and Alpine Research,* **26,** 14-20.

ter Braak, C. J. F. (1985) Correspondence Analysis of Incidence and Abundance Data: Properties in Terms of a Unimodal Response Model. *Biometrics,* **41,** 859-873.

ter Braak, C. J. F. (1986) Canonical Correspondence Analysis: A new Eigenvector Technique for Multivariate Direct Gradient Analysis. *Ecology,* **67,** 1167-1179.

ter Braak, C. J. F. (1987a) *Unimodal Models to Relate Species to Environment,* Wageningen, The Netherlands: Groep Landbouwwiskunde

ter Braak, C. J. F. (1987b) The Analysis of Vegetation-Environment Relationships by Canonical Correspondence Analysis. *Vegetatio,* **69,** 69-77.

ter Braak, C. J. F. (1987c) CANOCO - a FORTRAN program for canonical ordination by [partial] [detrended] [canonical] correspondence analysis and redundancy analysis, Thesis, Wageningen, Agricultural Mathematics Group

ter Braak, C. J. F. (1988) Partial Canonical Correspondence Analysis. In *Classification and Related Methods of Data Analysis*, H. H. Bock (Ed.) Amsterdam: North Holland

ter Braak, C. J. F. (1995a) Ordination. In *Data Analysis in Community and Landscape Ecology*, R. H. G. Jongman, C. J. F. t. Braak and O. F. R. v. Tongeren (Eds.), pp. 91-173. Cambridge: Cambridge University Press

ter Braak, C. J. F. and Barendregt, L. G. (1986) Weighted Averaging of Species Indicator Values: Its Efficiency in Environmental Calibration. *Mathematical Biosciences,* **78,** 57-72.

ter Braak, C. J. F. and Looman, C. W. M. (1986) Weighted Averaging, Logistic Regression and the Gaussian Response Model. *Vegetatio,* **65,** 3-11.

ter Braak, C. J. F. and Looman, C. W. N. (1995) Regression. In *Data Analysis in Community and Landscape Ecology*, R. H. G. Jongman, C. J. F. t. Braak and O. F. R. v. Tongeren (Eds.), pp. 29-77. Cambridge: Cambridge University Press

ter Braak, C. J. F. and Prentice, I. C. (1988) A Theory of Gradient Analysis. *Advances in Ecological Research,* **18,** 271-317.

Theodose, T. A. and Bowman, W. D. (1997) Nutrient Availability, Plant Abundance and Species Diversity in Two Alpine Tundra Communities. *Ecology,* **78,** 1861-1872.

Thompson, K. (1987) The Resource Ratio Hypothesis and the Meaning of Competition. *Functional Ecology,* **1,** 297-303.

Tilman, D. (1981) Tests of Resource Competition Theory Using Four Species of Lake Michigan Algae. *Ecology,* **62,** 802-815.

Tilman, D. (1985) The Resource-Ratio Hypothesis of Plant Succession *American Naturalist,* **125,** 827-852.

Tilman, D. (1986) Resources, competition and the dynamics of plant communities. In *Plant Ecology*, M. J. Crawley (Ed.), pp. 51-75. Oxford: Blackwell

Tilman, D. (1987) On the Meaning of Competition and the Mechanisms of Competitive Superiority. *Functional Ecology,* **1,** 304-315.

Tilman, D. (1988) *Plant Strategies and the Dynamics and Structure of Plant Communities,* Princetown, New Jersey: Princetown University Press

Tilman, D. (1994) Competition and Biodiversity in Spatially Structured Habitats. *Ecology,* **75,** 2-16.

Tilman, D. and Wedin, D. (1991) Dynamics of nitrogen competition between successional grasses. *Ecology,* **72,** 1038-1049.

Titus, J. H. and Tsuyuzaki, S. (2003) Distribution of Plants in Relation to Microsites on Recent Volcanic Substrates on Mount Koma, Hakkaido, Japan. *Ecological Research,* **18,** 91-98.

Tsuyuzaki, S. and del Morel, R. (1995) Species attributes in early primary succession on volcanoes. *Journal of Vegetation Science,* **6,** 517-522.

Turnbull, L. A., Rees, M. and Crawley, M. J. (1999) Seed Mass and the Competition/Colonization Trade-off: a Sowing Experiment. *Journal of Ecology,* **87,** 899-912.

Tybirk, K., Nilsson, M.-C., Michelsen, A., Kristensen, H. L., Shevtsova, A., Strandberg, M. T., Johansson, M., Nielsen, K. E., Strandberg, B. and Johnsen, I. (2000) Nordic *Empetrum* Dominated Ecosystems: Function and Susceptibility to Environmental Changes. *Ambio,* **29,** 90-97.

Usher, M. B. (1987) Modelling successional processes in ecosystems. In *Colonization, Succession and Stability*, A. J. Gray, M. J. Crawley and P. J. Edwards (Eds.), Oxford: Blackwell

Usher, M. B. (1992) Statistical models of succession. In *Plant Succession: Theory and Prediction*, D. C. Glenn-Lewin, R. K. Peet and T. T. Veblen (Eds.), pp. 215-48. London: Chapman and Hall

van der Valk, A. G. (1992) Establishment, colonization and persistence. In *Plant Succession: Theory and Prediction*, D. C. Glenn-Lewin, R. K. Peet and T. T. Veblen (Eds.), London: Chapman and Hall

Van Groenedael, J. M., Roepers, R. G., Woltjer, I. and Zweers, H. R. (1996) Vegetation succession in lakes of West Connemara, Ireland: comparing predicted and actual changes. *Journal of Vegetation Science,* **7,** 211-218.

Van Groenewoud, M. (1992) The robustness of Correspondence, Detrended Correspondence and TWINSPAN analysis. *Journal of Vegetation Science,* **3,** 239-246.

Van Tongeren, O. (1986) FLEXCLUS, an interactive program for classification and tabulation of ecological data. *Acta Botanica Neerlandica,* **35,** 137-142.

Van Tongeren, O. F. R. (1995) Cluster Analysis. In *Data Analysis in Community and Landscape Ecology*, R. H. G. Jongman, C. J. F. t. Braak and O. F. R. v. Tongeren (Eds.), pp. 174-212. Cambridge: Cambridge University Press

Van Wijk, M. T., Williams, M., Gough, L., Hobbie, S. E. and Shaver, G. R. (2003). Luxury consumption of soil nutrients: a possible competitive strategy in above-ground and below-ground biomass allocation and root morphology for slow-growing Arctic vegetation? *Journal of Ecology,* **91,** 664-676.

Vestal, J. R. (1993) Cryptoendolithic Communities from Hot and Cold Deserts: Speculation in Microbial Colonization and Succession. In *Primary Succession on Land*, J. H. Miles and D. W. H. Walton (Eds.), Oxford: Blackwell

Vetaas, O. R. (1994) Primary succession of plant assemblages on a glacier foreland-Bodalsbreen, S. Norway. *Journal of Biogeography,* **21,** 297-308.

Vetaas, O. R. (1997) Relationships between floristic gradients in a primary succession. *Journal of Vegetation Science,* **8,** 665-676.

Vitousek, P. M. (1994) Beyond Global Warming: Ecology and Global Change. *Ecology,* **75,** 1861-1876.

Vitousek, P. M. and Walker, L. R. (1987) Resource availability: Ecosystem level interactions. In *Colonization, Succession and Stability*, A. J. Gray, M. J. Crawley and P. J. Edwards (Eds.), pp. 207-24Oxford: Blackwell

Volder, A., Bliss, L. C. and Lambers, H. (2000) The influence of temperature and nitrogen source on growth and uptake of two polar-desert species, *Saxifraga cespitosa* and *Cerastium alpinum. Plant and Soil,* **227,** 139-148.

Walker, B. H. (1997) Functional Types in Non-equilibrium Ecosystems. In *Plant Functional Types: their Relevance to Ecosystem Properties and Global Change*, T. M. Smith, H. H. Shugart and F. I. Woodward (Eds.), Cambridge: Cambridge University Press

Walker, D. A. (1996) Disturbance and recovery of arctic Alaskan vegetation. In *Landscape Function and Disturbance in Arctic Tundra*, J. F. Reynolds and J. D. Tenhunen (Eds.), pp. 35-72. Berlin: Springer-Verlag

Walker, D. A. and Walker, M. D. (1996) Terrain and vegetation of the Imnavait Creek Watershed. In *Landscape Function and Disturbance in Arctic Tundra*, J. F. Reynolds and J. D. Tenhunen (Eds.), pp. 73-108. Berlin: Springer-Verlag

Walker, L. R. (1993) Nitrogen fixers and species replacements. In *Primary Succession on Land*, J. H. Miles and D. W. H. Walton (Eds.), pp. 249-72. Oxford: Blackwell

Walker, L. R. and Chapin III, F. S. (1987) Interactions Among Processes Controlling Successional Change. *Oikos,* **50,** 131-135.

Walker, L. R. and del Morel, R. (2003) *Primary Succession and Ecosystem Rehabilitation,* Cambridge: Cambridge University Press

Walker, M. D., Ingersoll, R. C. and Webber, P. J. (1995) Effects of Interannual Climate Variation on Phenology and Growth of Two Alpine Forbs. *Ecology,* **76,** 1067-1083.

Walker, T. W. and Syers, J. K. (1976) The fate of Phosphorous during pedogenesis. *Geoderma,* **15,** 1-19.

Wallstedt, A., Sommarin, M., Nilsson, M.-C., Munson, A. D. and Margolis, H. A. (2001) The inhibition of ammonium uptake in exised birch (*Betula pendula*) roots by batatasin III. *Physiologia Plantarum,* **113,** 368-376.

Walton, D. W. H. (1993) The effects of cryptogams on mineral substrates. In *Primary Succession on Land*, J. H. Miles and D. W. H. Walton (Eds.), pp. 35-54. Oxford: Blackwell

Wardle, D. A. and Nilsson, M.-C. (1997) Microbe-plant competition, allelopathy and arctic plants. *Oecologia,* **109,** 291-293.

Wardle, D. A., Nilsson, M.-C., Gallet, C. and Zackrisson, O. (1998) An ecosystem-level perspective of allelopathy. *Biological Reviews,* **73,** 305-319.

Wartenberg, D., Ferson, S. and Rohlf, F. J. (1987) Putting things in order: a critique of detrended correspondence analysis. *The American Naturalist,* **129,** 434-448.

Watt, A. S. (1947) Pattern and Process in the Plant Community. *Journal of Ecology,* **35,** 1-22.

Webber, P. J. and Andrews, J. T. (1973) Lichenometry: a commentary. *Arctic and Alpine Research,* **5,** 295-302.

Weih, M. and Karlsson, P. S. (1999) The nitrogen economy of mountain birch seedlings: implications for winter survival. *Journal of Ecology,* **87,** 211-219.

Welker, J. M., Molau, U., Parsons, A. N., Robinson, C. H. and Wookey, P. A. (1997) Response of *Dryas octopetala* to ITEX Environmental Manipulations: a Synthesis with Circumpolar Comparisons. *Global Change Biology,* **3 (Suppl 1),** 61-73.

Westman, W. E. (1980) Gaussian analysis: identifying environmental factors influencing bell-shaped species distributions. *Ecology,* **61**, 733-739.

Westoby, M. and Leishman, M. (1997) Categorizing Plant Species into Functional Types. In *Plant Functional Types: their Relevance to Ecosystem Properties and Global Change*, T. M. Smith, H. H. Shugart and F. I. Woodward (Eds.), Cambridge: Cambridge University Press

White, P. S. (1979) Pattern, process and natural disturbance in vegetation. *The Botanical Review,* **45,** 230-299.

Whittaker, R. H. (1951) A criticism of the plant association and climatic climax concepts. *Northwest Science,* **25,** 17-31.

Whittaker, R. H. (1953) A Consideration of Climax Theory: The Climax as a Population and Pattern. *Ecological Monographs,* **23,** 41-78.

Whittaker, R. H. (1967). Gradient analysis of vegetation. *Biological Reviews,* **49,** 207-264.

Whittaker, R. H. (1975). *Communities and Ecosystems.* London: Collier MacMillan

Whittaker, R. J. (1985). Plant community and plant population studies of a successional sequence: Storbreen Glacier Foreland, Jotunheimen, Norway. PhD Thesis, University of Wales, Cardiff

Whittaker, R. J. (1987). An application of Detrended Correspondence Analysis and Non-Metric Multidimensional Scaling to the identification and analysis of environmental factor complexes and vegetation structures. *Journal of Ecology,* **75,** 363-376.

Whittaker, R. J. (1989). The vegetation of the Storbreen gletschervorfeld III, Vegetation-environment relationships. *Journal of Biogeography,* **16,** 413-433.

Whittaker, R. J. (1991). The vegetation of the Storbreen gletschervorfeld, Jotunheimen, Norway IV: Short-term vegetation change. *Journal of Biogeography,* **18,** 41-52.

Whittaker, R. J. (1992). Stochasticism and determinism in island ecology. *Journal of Biogeography,* **19,** 587-591.

Whittaker, R. J. (1993). Plant population patterns in a glacier foreland succession: pioneer herbs and later colonizing shrubs. *Ecography,* **16,** 117-136.

Whittaker, R. J. and Bush, M. B. (1993). Dispersal and establishment of tropical forest assemblages in Krakatoa. In *Primary Succession on Land*, J. H. Miles and D. W. H. Miles (Eds.), Oxford: Blackwell

Wiens, J. A. (2000). Ecological heterogeneity: An ontogeny of concepts and approaches. In *The Ecological Consequences of Environmental Heterogeneity*, M. J. Hutchings, E. A. John and A. J. A. Stewart (Eds.), Oxford: Blackwell

Wijk, S. (1986a. Influence of climate and age on annual shoot increment in *Salix herbacea. Journal of Ecology,* **74,** 685-692.

Wijk, S. (1986b). Performance of *Salix herbacea* in an Alpine snowbed gradient. *Journal of Ecology,* **74,** 675-684.

Williams, M. and Rastetter, E. B. (1999). Vegetation characteristics and primary productivity along an Arctic transect: Implications for scaling up. *Journal of Ecology,* **87,** 885-898.

Williams, W. T. and Lambert, J. M. (1959). Multivariate methods in plant ecology. I Association analysis in plant communities. *Journal of Ecology,* **47,** 83-101.

Williams, W. T. and Lambert, J. M. (1960). Multivariate methods in plant ecology. II The use of an electronic digital computer for association analysis. *Journal of Ecology,* **48,** 689-710.

Williamson, M. (1988). Relationship of species number to area, distance and other variables. In *Analytical Biogeography*, A. A. Myers and P. S. Giller (Eds.), London: Chapman and Hall

Williamson, M. H. (1978). The ordination of incidence data. *Journal of Ecology,* **66,** 911-920.

Wilson, J. B. and Agnew, A. D. Q. (1992). Positive-feedback switches in plant communities. *Advances in Ecological Research,* **26,** 263-336.

Wilson, M. V. (1981). A statistical test of the accuracy and consistency of ordinations. *Ecology,* **62,** 8-12.

Wilson, S. D. (2000). Heterogeneity, diversity and scale in plant communities. In *The Ecological Consequences of Environmental Heterogeneity*, M. J. Hutchings, E. A. John and A. J. Stewart (Eds.), Oxford: Blackwell

Wolda, H. (1987). Seasonality and the community. In *Organisation of Communities Past and Present*, J. H. R. Gee and P. S. Gill (Eds.), Oxford: Blackwell

Wood, D. M. and del Morel, R. (1987). Mechanisms of early primary succession in subalpine habitats on Mount St Helens. *Ecology,* **68,** 780-790.

Woodward, F. I. (1988). Temperature and the distribution of plant species. In *Plants and Temperature*, S. P. Long and F. I. Woodward (Eds.), Cambridge: The Company of Biologists Limited

Woodward, F. I. and Kelly, C. K. (1997). Plant functional types: Towards a definition by environmental constraints. In *Plant Functional Types: Their Relevance to Ecosystem Properties and Global Change*, T. M. Smith, H. H. Shugart and F. I. Woodward (Eds.), Cambridge: Cambridge University Press

Woodward, F. I., Smith, T. M. and Shugart, H. H. (1997) Defining Plant Functional Types: the End View. In *Plant Functional Types: Their Relevance to Ecosystem Properties and Global Change*, T. M. Smith, H. H. Shugart and F. I. Woodward (Eds.), Cambridge: Cambridge University Press

Wookey, P. A., Bol, R. A., Caseldine, C. J. and Harkness, D. D. (2002) Surface Age, Ecosystem Development and C Isotope Signatures of Respired CO_2 in an Alpine Environment, Northern Iceland. *Arctic and Alpine Research,* **34,** 76-87.

Wooky, P. A., Welker, J. M., Parsons, A. N., Press, M. C., Callaghan, T. V. and Lee, J. A. (1994) Differential Growth, Allocation and Photosynthesis Responses of *Polygonum viviparum* to Simulated Environmental Change at a High Arctic Polar Semi-Desert. *Oikos,* **70,** 131-139.

Wynn-Williams, D. D. (1993) Microbial processes and initial stabilization of fellfield soil. In *Primary Succession on Land*, J. H. Miles and D. W. H. Walton (Eds.), pp. 17-32. Oxford: Blackwell

Yarranton, G. A. (1967) Organismal and individualistic concepts and the choice of methods of vegetation analysis. *Vegetatio,* **15,** 113-116.

Yoo, J. C. and D'Odorico, P. (2002) Trends and Fluctuations in the Dates of Ice Break-Up of Lakes and Rivers in Northern Europe: the Effect of the North Atlantic Oscillation. *Journal of Hydrology,* **268,** 100-112.

Zhang, Y. and Welker, J. M. (1996) Tibetan Alpine Tundra Responses to Simulated Changes in Climate: Aboveground Biomass and Community Responses. *Arctic and Alpine Research,* **28,** 203-209.

Appendix 1: List of full species names

Abreviation	Full Name
Ach mil	Achillea millefolium
Aco sep	Aconitum septentrionale
Adi cap	Adiantum capillus-veneris
Alc alp	Alchemilla alpina
Alc glo	Alchemilla glomerulans
Ang arc	Angelica archangelica
Ant alp	Antennaria alpina
Ant odo	Anthoxanthum odoratum
Ara alp	Arabis alpina
Arc uva	Arctostaphylos uva-ursi
Are spp	Arenaria spp
Ast alp	Astragalus alpinus
Bar alp	Bartsia alpina
Bet nan	Betula nana
Bet pub	Betula pubescens carpatica
Bot lun	Botrychium lunaria
Cal vul	Calluna vulgaris
Cam rot	Campanula rotundifolia
Car bel	Cardamine bellidifolia
Car pet	Cardaminopsis petraea
Car spp	Carex spp
Cas hyp	Cassiope hypnoides
Cer alp	Cerastium alpinum
Cer cer	Cerastium cerastoides
Coe vir	Coeloglossum viride
Com pal	Comarum palustre
Cre pal	Crepis paludosa
Cry cri	Cryptogamma crispa
Cys fra	Cystopteris fragilis
Des ces	Deschampsia cespitosa
Des alp	Deschampsia cespitosa ssp. Alpina
Des fle	Deschampsia flexuosa
Dry oct	Dryas octopetala
Emp her	Empetrum hermaphroditum
Epi als	Epilobium alsinifolium
Epi ana	Epilobium anagallidifolium
Epi ang	Epilobium angustifolium
Equ spp	Equisetum spp.
Eri uni	Erigeron uniflorus
Eri ang	Eriophorum angustifolium
Eri sch	Eriophorum scheuchzeri
Eup alp	Euphrasia alpina
Fes spp	Festuca spp
Ger syl	Geranium sylvaticum
Gna nor	Gnaphalium norvegicum
Gna sup	Gnaphalium supinum
Hie alp	Hieracium alpinum
Jun big	Juncus biglumis
Jun tri	Juncus trifidus
Jun com	Juniperus communis
Leo aut	Leontodon autumnalis
Loi pro	Loiseleuria procumbens
Luz arc	Luzula arcuata
Luz spi	Luzula spicata
Lyc alp	Lychnis alpina
Lyco alp	Diphasium alpinum
Lyco ann	Lycopodium annotinum

Appendix 1: Sheet 2

Abreviation	Full name
Lyco sel	Huperzia selago
Mel pra	Melampyrum pratense
Mel ape	Melandrium apetalum
Nar str	Nardus stricta
Oxy dig	Oxyria digyna
Ped lap	Pedicularis lapponica
Ped oed	Pedicularis oederi
Phl alp	Phleum alpinum
Phy cae	Phyllodoce caerulea
Pin vul	Pinguicula vulgaris
Poa spp	Poa spp
Pol viv	Polygonum viviparum
Pot cra	Potentilla crantzii
Pul ver	Pulsatilla vernalis
Pyr spp	Pyrola spp
Ran acr	Ranunculus acris
Ran gla	Ranunculus glacialis
Ran pyg	Ranunculus pygmaeus
Rub arc	Rubus arcticus
Rum asa	Rumex acetosa
Rum ala	Rumex acetosella
Sal gla	Salix glauca
Sal her	Salix herbacea
Sal lan	Salix lanata
Sal myr	Salix myrsinites
Sal phy	Salix phylicifolia
Sal ret	Salix reticulata
Sau alp	Saussurea alpina
Sax cer	Saxifraga cernua
Sax ces	Saxifraga cespitosa
Sax niv	Saxifraga nivalis
Sax opp	Saxifraga oppositifolia
Sax riv	Saxifraga rivularis
Sax ste	Saxifraga stellaris
Sed ros	Sedum rosea
Sib pro	Sibbaldia procumbens
Sil aca	Silene acaulis
Sil dio	Silene dioica
Sol vir	Solidago virgaurea
Tha alp	Thalictrum alpinum
Tof pus	Tofieldia pusilla
Tri eur	Trientalis europaea
Tri spi	Trisetum spicatum
Vac myr	Vaccinium myrtillus
Vac uli	Vaccinium uliginosum
Vac vit	Vaccinium vitis-idaea
Ver alp	Veronica alpina
Vio pal	Viola palustris
Woo alp	Woodsia alpina

Appendix 2: Changes in species numbers 1970 to 2000

Species	Total 1970	Total 2000 (410 Sites)	Total 2000 (434 Sites)	Change (410 Sites)	%	Change (434 Sites)	%
Ach mil	15	42	42	27	180	27	180
Aco sep	141	205	205	64	45.39	64	45.39
Adi cap	13	0	0	-13	-100	-13	-100
Alc alp	13	21	21	8	61.54	8	61.54
Alc glo	1	6	6	5	500	5	500
Ang arc	1	0	0	-1	-100	-1	-100
Ant alp	521	227	227	-294	-56.43	-294	-56.43
Ant odo	1522	1718	1720	196	12.88	198	13.01
Ara alp	355	44	85	-311	-87.61	-270	-76.06
Arc spp	1092	715	715	-377	-34.52	-377	-34.52
Are spp	374	650	957	276	73.80	583	155.88
Ast alp	1	7	7	6	600	6	600
Bar alp	2435	2261	2262	-174	-7.15	-173	-7.10
Bet nan	9707	10080	10080	373	3.84	373	3.84
Bet pub	34	65	65	31	91.18	31	91.18
Bot lun	4	0	0	-4	-100	-4	-100
Cal vul	52	59	59	7	13.46	7	13.46
Cam rot	34	26	26	-8	-23.53	-8	-23.53
Car bel	482	306	316	-176	-36.51	-166	-34.44
Car pet	537	181	228	-356	-66.29	--309	-57.54
Car spp	9279	10389	10401	1110	11.96	1122	12.09
Cas hyp	6741	3829	3829	-2912	-43.20	-2912	-43.20
Cer alp	343	243	274	-100	-29.15	-69	-20.12
Cer cer	1712	1314	1836	-398	-23.25	124	7.24
Coe vir	3	38	38	35	1166.67	35	1166.67
Com pal	3	47	47	44	1466.67	44	1466.67
Cre pal	0	16	16	16		16	
Cry cri	132	59	59	-73	-55.30	-73	-55.30
Cys fra	3	51	51	48	1600	48	1600
Des ces	281	413	413	132	46.98	132	46.98
Des alp	1750	739	995	-1011	-57.77	-755	-43.14
Des fle	1	0	0	-1	-100	-1	-100
Dry oct	46	61	61	15	32.61	15	32.61
Emp her	23449	28929	28950	5480	23.37	5501	23.46
Epi als	37	11	11	-26	-70.27	-26	-70.27
Epi ana	105	192	192	87	82.86	87	82.86
Epi ang	26	24	24	-2	-7.69	-2	-7.69
Equ spp	36	15	15	-21	-58.33	-21	-58.33
Eri uni	81	15	15	-66	-81.48	-66	-81.48
Eri ang	923	786	786	-137	-14.84	-137	-14.84
Eri sch	5	6	6	1	20	1	20
Eup alp	40	32	32	-8	-20	-8	-20
Fes spp	6314	5770	5803	-544	-8.62	-511	-8.09
Ger syl	356	286	286	-70	-19.66	-70	-19.66
Gna nor	356	373	373	17	4.78	17	4.78
Gna sup	1100	1032	1068	-68	-6.18	-32	-2.91
Hie alp	980	704	704	-276	-28.16	-276	-28.16
Jun big	0	34	34	34		34	
Jun tri	1581	1082	1082	-499	-31.56	-499	-31.56
Jun com	359	525	525	166	46.24	166	46.24
Leo aut	1011	806	806	-205	-20.28	-205	-20.28
Loi pro	1422	1574	1574	152	10.69	152	10.69
Luz arc	1632	714	714	-918	-56.25	-918	-56.25
Luz spi	1306	725	749	-581	-44.49	-557	-42.65
Lyc alp	36	29	34	-7	-19.44	-2	-5.56

Appendix 2: Sheet 2

Species	Total 1970	Total 2000 (410 Sites)	Total 2000 (434 Sites)	Change (410 Sites)	%	Change (434 Sites)	%
Lyco alp	382	106	106	-276	-72.25	-276	-72.25
Lyco ann	143	52	52	-91	-63.64	-91	-63.64
Hup sel	240	257	257	17	7.08	17	7.08
Mel pra	0	6	6	6		6	
Mel ape	40	0	0	-40	-100	-40	-100
Nar str	0	52	52	52		52	
Oxy dig	2463	3404	3816	941	38.21	1353	54.93
Ped lap	787	1117	1117	330	41.93	330	41.93
Ped oed	0	1	1	1		1	
Phl alp	743	927	953	184	24.76	210	28.26
Phy cae	12217	9385	9385	-2832	-23.18	-2832	-23.18
Pin vul	1225	1150	1150	-75	-6.12	-75	-6.12
Poa spp	4423	2457	3136	-1966	-44.45	-1287	-29.10
Pol viv	5321	3574	3575	-1747	-32.83	-1746	-32.81
Pot cra	0	5	5	5		5	
Pul ver	9	21	21	12	133.33	12	133.33
Pyr spp	114	536	536	422	370.18	422	370.18
Ran acr	127	260	260	133	104.72	133	104.72
Ran gla	961	931	931	-30	-3.12	-30	-3.12
Ran pyg	60	65	65	5	8.33	5	8.33
Rub arc	87	29	29	-58	-66.67	-58	-66.67
Rum asa	306	357	358	51	16.67	52	16.99
Rum ala	0	55	55	55		55	
Sal gla	9651	14497	14588	4846	50.21	4937	51.16
Sal her	22874	29121	29278	6247	27.31	6404	28.00
Sal lan	5133	3227	3227	-1906	-37.13	-1906	-37.13
Sal myr	158	247	247	89	56.33	89	56.33
Sal phy	383	2406	2416	2023	528.20	2033	530.81
Sal ret	81	79	79	-2	-2.47	-2	-2.47
Sau alp	405	377	377	-28	-6.91	-28	-6.91
Sax cer	2	0	0	-2	-100	-2	-100
Sax ces	809	67	277	-742	-91.72	-532	-65.76
Sax niv	66	83	90	17	25.76	24	36.36
Sax opp	259	191	241	-68	-26.25	-18	-6.95
Sax riv	119	193	210	74	62.18	91	76.47
Sax ste	724	635	706	-89	-12.29	-18	-2.49
Sed ros	201	132	139	-69	-34.33	-62	-30.85
Sib pro	785	651	654	-134	-17.07	-131	-16.69
Sil aca	282	74	78	-208	-73.76	-204	-72.34
Sil dio	0	5	5	5		5	
Sol vir	958	967	967	9	0.94	9	0.94
Tha alp	101	48	48	-53	-52.48	-53	-52.48
Tof pus	590	350	350	-240	-40.68	-240	-40.68
Tri eur	296	551	551	255	86.15	255	86.15
Tri spi	2062	1808	1894	-254	-12.32	-168	-8.15
Vac myr	3204	4745	4745	1541	48.10	1541	48.10
Vac uli	4969	6632	6632	1663	33.47	1663	33.47
Vac vit	4196	3138	3138	-1058	-25.21	-1058	-25.21
Ver alp	987	1067	1102	80	8.11	115	11.65
Vio pal	125	92	92	-33	-26.98	-33	-26.98
Woo alp	22	18	18	-4	-18.18	-4	-18.18

Appendix 3: Age-groups and sites

Group	Age 1970	Age 2000	Sites
1	0-12	30-42	34, 39, 40, 41, 43, 44, 45, 49, 51, 52, 53, 54, 611, 613, 616, 617, 618, 636, 637, 705, 706, 710, 711, 712, 713, 714, 715, 716, 717, 718, 719, 720, 721, 722, 723, 724, 726, 727, 728, 729, 730, 731, 735.
2	12-28	42-58	36, 55, 57, 58, 59, 61, 62, 63, 64, 65, 66, 67, 68, 69, 72, 75, 76, 78, 81, 82, 83, 113, 117, 119, 120, 121, 122, 124, 532, 533, 535, 536, 537, 538, 595, 600, 601, 602, 606, 607, 608, 609, 612, 619.
3	29-40	59-70	19, 21, 22, 29, 30, 85, 108, 109, 110, 111, 112, 114, 115, 116, 118, 125, 127, 129, 131, 137, 138, 139, 140, 141, 149, 150, 511, 518, 520, 522, 524, 525, 526, 528, 529, 531, 539, 541, 570, 571, 598, 605, 639, 640.
4	41-83	71-113	24, 105, 107, 134, 135, 142, 143, 145, 147, 151, 153, 154, 155, 157, 158, 159, 160, 162, 163, 165, 171, 195, 196, 208, 209, 210, 211, 263, 463, 465, 467, 468, 469, 492, 494, 495, 509, 510, 513, 514, 516, 540, 544.
5	85-117	115-147	88, 102, 166, 167, 168, 169, 172, 173, 175, 176, 177, 183, 184, 185, 194, 198, 206, 212, 213, 214, 223, 257, 258, 261, 262, 265, 266, 449, 451, 459, 460, 461, 462, 464, 470, 489, 498, 506, 542, 551, 624.
6	119-156	149-186	90, 100, 178, 179, 180, 186, 199, 204, 205, 216, 217, 252, 254, 255, 270, 273, 274, 276, 277, 281, 283, 284, 293, 402, 403, 404, 405, 408, 409, 432, 448, 452, 454, 455, 456, 458, 472, 482, 488, 504, 547, 548, 549, 550, 586, 590.
7	157-191	187-221	96, 201, 218, 221, 224, 249, 271, 282, 285, 287, 288, 289, 290, 291, 292, 295, 296, 297, 300, 303, 310, 312, 320, 321, 323, 394, 395, 398, 400, 410, 411, 412, 421, 423, 429, 430, 434, 446, 487, 499, 552, 560, 577, 589.
8	193-221	223-251	13, 91, 92, 99, 187, 188, 189, 192, 193, 200, 203, 220, 298, 302, 304, 306, 307, 314, 315, 316, 317, 318, 319, 322, 356, 357, 378, 380, 382, 391, 392, 393, 413, 414, 418, 424, 436, 440, 445, 475, 476, 554, 569, 580.
9	All 10000		3, 12, 16, 93, 95, 225, 229, 231, 233, 234, 240, 242, 242, 246, 324, 330, 331, 332, 336, 337, 340, 364, 386, 390, 419, 420, 425, 437, 477, 480, 486, 502, 555, 558, 559, 563, 567, 576, 581, 585, 625.
10	All 10000		1, 7, 8, 9, 97, 227, 232, 235, 237, 239, 241, 244, 325, 326, 333, 334, 338, 341, 343, 344, 346, 347, 351, 354, 359, 362, 365, 367, 368, 369, 371, 372, 373, 375, 376, 438, 442, 478, 500, 565, 566, 575, 582, 583.

Appendix 4: Species abbreviations in Chapter Six

Species Increasing		**Species Decreasing**	
Abbreviation	Full Name	Abbreviation	Full Name
Ao	*Anthoxanthum odoratum*	Ant	*Antennaria alpina*
Are	*Arenaria* spp.	Ara	*Arabis alpina*
Bp	*Betula pubescens carpatica*	Arc	*Arctostaphylos* spp.
Cs	*Carex* spp.	Cb	*Cardamine bellidifolia*
Dc	*Deschampsia cespitosa*	Cp	*Cardaminopsis petraea*
Eh	*Empetrum hermaphroditum*	Ch	*Cassiope hypnoides*
Jc	*Juniperus communis*	Ca	*Cerastium alpinum*
Lp	*Loiseleuria procumbens*	Da	*Deschampsia cespitosa* ssp. *alpina*
Od	*Oxyria digyna*	Ha	*Hieracium alpinum*
Pl	*Pedicularis lapponica*	Jt	*Juncus trifidus*
Pa	*Phleum alpinum*	Leo	*Leontodon autumnalis*
Pyr	*Pyrola* spp.	La	*Luzula arcuata*
Ra	*Ranunculus acris*	Ls	*Luzula spicata*
Sg	*Salix glauca*	Phy	*Phyllodoce caerulea*
Sh	*Salix herbacea*	Ps	*Poa* spp.
Sp	*Salix phylicifolia*	Pol	*Polygonum viviparum*
Vm	*Vaccinium myrtillus*	Sl	*Salix lanata*
Vu	*Vaccinium uliginosum*	Sxcs	*Saxifraga cespitosa*
		Sib	*Sibbaldia procumbens*
		Sia	*Silene acaulis*
		Tp	*Tofieldia pusilla*
		Vv	*Vaccinium vitis-idaea*

Appendix 5: TWINSPAN output

Data is included up to the end of level 3 giving the eight groups used in Chapter 5
(the full output is 112 pages)

```
QUADRAT DIVISION 1  Number of quadrates in cluster = 838
eigenvalue = 0.4846  number of iterations = 3
Indicators and their sign
DRY_OCT [-];
PHY_CAE [+];
PED_OED [-];
NAR_STR [+];
CER_CER [+];
The maximum indicator score for the negative group = 0
The minimum indicator score for the positive group = 1
Negative group: 2 Number of objects = 540  comprising:

1, 8, 12, 13, 16, 19, 21, 22, 75, 91, 92, 93, 97, 100, 108, 109, 110, 112, 113, 115, 116, 117, 118, 127, 131, 134, 135, 137, 138, 139, 140,
143, 145, 147, 149, 150, 154, 155, 158, 160, 163, 165, 167, 168, 169, 173, 179, 185, 186, 187, 188, 189, 194, 195, 198, 200, 201, 203,
204, 205, 206, 209, 212, 213, 217, 218, 220, 223, 225, 227, 229, 231, 233, 234, 235, 237, 239, 240, 241, 242, 244, 246, 249, 252, 254,
255, 257, 258, 261, 263, 265, 266, 270, 271, 273, 274, 276, 277, 283, 284, 285, 287, 288, 289, 290, 291, 292, 293, 295, 296, 297, 298,
300, 302, 303, 304, 306, 307, 310, 312, 314, 315, 316, 317, 318, 319, 320, 321, 322, 323, 324, 325, 326, 330, 331, 332, 333, 334, 336,
337, 338, 340, 341, 343, 344, 346, 347, 351, 354, 356, 357, 359, 362, 364, 365, 367, 368, 369, 371, 372, 373, 375, 376, 378, 380, 382,
386, 390, 391, 392, 393, 394, 395, 398, 400, 402, 403, 404, 405, 408, 409, 410, 411, 412, 413, 414, 418, 419, 420, 421, 423, 424, 425,
429, 430, 432, 434, 436, 437, 438, 440, 442, 445, 446, 448, 449, 451, 452, 454, 455, 456, 458, 459, 460, 461, 462, 463, 464, 465, 467,
468, 469, 470, 472, 475, 476, 477, 478, 480, 482, 486, 487, 488, 489, 492, 494, 495, 499, 500, 502, 504, 506, 509, 510, 511, 513, 514,
516, 524, 525, 526, 528, 529, 540, 544, 547, 548, 549, 550, 551, 552, 555, 558, 559, 560, 563, 565, 566, 567, 571, 576, 577, 580, 581,
582, 583, 585, 586, 589, 590, 605, 606, 624, 625, 639, 13_1, 91_1, 92_1, 93_1, 97_1, 135_1, 138_1, 143_1, 145_1, 147_1, 151_1, 154_1,
158_1, 160_1, 165_1, 167_1, 168_1, 169_1, 172_1, 173_1, 179_1, 180_1, 185_1, 186_1, 187_1, 188_1, 189_1, 194_1, 195_1, 198_1,
200_1, 201_1, 203_1, 204_1, 205_1, 206_1, 209_1, 212_1, 216_1, 217_1, 218_1, 220_1, 221_1, 223_1, 225_1, 227_1, 229_1, 231_1,
232_1, 233_1, 234_1, 235_1, 237_1, 239_1, 240_1, 241_1, 242_1, 244_1, 246_1, 252_1, 254_1, 255_1, 257_1, 258_1, 261_1, 263_1,
265_1, 266_1, 271_1, 273_1, 274_1, 276_1, 277_1, 281_1, 283_1, 284_1, 285_1, 287_1, 288_1, 289_1, 290_1, 291_1, 292_1, 293_1,
295_1, 296_1, 297_1, 298_1, 300_1, 302_1, 303_1, 304_1, 306_1, 307_1, 310_1, 312_1, 314_1, 315_1, 316_1, 317_1, 318_1, 319_1,
320_1, 321_1, 322_1, 323_1, 324_1, 325_1, 326_1, 330_1, 331_1, 332_1, 333_1, 334_1, 336_1, 337_1, 338_1, 340_1, 341_1, 343_1,
344_1, 346_1, 347_1, 351_1, 354_1, 356_1, 357_1, 359_1, 362_1, 364_1, 365_1, 367_1, 368_1, 369_1, 371_1, 372_1, 373_1, 375_1,
376_1, 378_1, 380_1, 382_1, 386_1, 390_1, 391_1, 392_1, 393_1, 394_1, 395_1, 398_1, 400_1, 402_1, 403_1, 404_1, 405_1, 408_1,
409_1, 410_1, 411_1, 412_1, 413_1, 414_1, 418_1, 419_1, 420_1, 421_1, 423_1, 424_1, 425_1, 429_1, 430_1, 432_1, 434_1, 436_1,
437_1, 438_1, 440_1, 442_1, 445_1, 446_1, 448_1, 449_1, 451_1, 452_1, 454_1, 455_1, 456_1, 458_1, 459_1, 460_1, 461_1, 462_1,
463_1, 464_1, 465_1, 467_1, 468_1, 469_1, 470_1, 472_1, 475_1, 476_1, 477_1, 478_1, 480_1, 482_1, 486_1, 487_1, 488_1, 489_1,
491_1, 494_1, 495_1, 499_1, 500_1, 502_1, 504_1, 506_1, 509_1, 510_1, 511_1, 513_1, 514_1, 516_1, 540_1, 544_1, 547_1, 548_1,
549_1, 550_1, 551_1, 552_1, 554_1, 555_1, 558_1, 559_1, 560_1, 563_1, 565_1, 566_1, 567_1, 569_1, 576_1, 577_1, 580_1, 581_1,
582_1, 583_1, 585_1, 586_1, 589_1, 590_1, 624_1, 625_1, 639_1,

The borderline negative group:  Number of objects = 38  comprising:

1, 8, 13, 16, 19, 75, 100, 116, 134, 137, 139, 140, 155, 213, 223, 270, 492, 528, 540, 571, 606, 13_1, 91_1, 138_1, 147_1, 151_1, 169_1,
172_1, 173_1, 180_1, 195_1, 198_1, 216_1, 221_1, 445_1, 509_1, 569_1, 624_1,

The misclassified negatives:  Number of objects = 25  comprising:

108, 109, 112, 127, 131, 138, 234, 235, 255, 293, 482, 551, 581, 582, 585, 586, 590, 187_1, 324_1, 336_1, 486_1, 540_1, 559_1, 585_1,
590_1,

The positive group: 3 Number of objects = 298  comprising:

3, 7, 9, 29, 30, 34, 36, 39, 40, 41, 43, 44, 45, 49, 51, 52, 53, 54, 55, 57, 58, 59, 61, 62, 63, 64, 65, 66, 67, 68, 69, 72, 76, 78, 81, 82, 83, 85,
88, 90, 95, 96, 99, 102, 105, 107, 111, 114, 119, 120, 121, 122, 124, 125, 129, 141, 142, 151, 153, 157, 159, 162, 166, 171, 172, 175, 176,
177, 178, 180, 183, 184, 192, 193, 196, 199, 208, 210, 211, 214, 216, 221, 224, 232, 262, 281, 282, 491, 498, 518, 520, 522, 531, 532,
533, 535, 536, 537, 538, 539, 541, 542, 554, 569, 570, 575, 595, 598, 600, 601, 602, 607, 608, 609, 611, 612, 613, 616, 617, 618, 619,
636, 637, 705, 706, 711, 712, 713, 714, 715, 716, 717, 718, 719, 720, 721, 722, 723, 724, 726, 727, 728, 729, 730, 731, 735, 1_1, 3_1,
7_1, 8_1, 9_1, 12_1, 16_1, 19_1, 21_1, 22_1, 24_1, 29_1, 30_1, 34_1, 36_1, 40_1, 44_1, 45_1, 49_1, 51_1, 52_1, 53_1, 54_1, 55_1,
57_1, 58_1, 59_1, 61_1, 62_1, 63_1, 64_1, 65_1, 66_1, 67_1, 68_1, 69_1, 72_1, 75_1, 76_1, 78_1, 81_1, 82_1, 83_1, 85_1, 88_1, 90_1,
95_1, 96_1, 99_1, 100_1, 102_1, 105_1, 107_1, 108_1, 109_1, 110_1, 111_1, 112_1, 113_1, 114_1, 115_1, 116_1, 117_1, 118_1, 119_1,
120_1, 121_1, 122_1, 124_1, 125_1, 127_1, 129_1, 131_1, 134_1, 137_1, 139_1, 140_1, 141_1, 142_1, 149_1, 150_1, 153_1, 155_1,
157_1, 159_1, 162_1, 163_1, 166_1, 171_1, 175_1, 176_1, 177_1, 178_1, 183_1, 184_1, 192_1, 193_1, 196_1, 199_1, 208_1, 210_1,
211_1, 213_1, 214_1, 224_1, 249_1, 262_1, 270_1, 282_1, 492_1, 498_1, 518_1, 520_1, 522_1, 524_1, 525_1, 526_1, 528_1, 529_1,
531_1, 532_1, 533_1, 535_1, 536_1, 537_1, 538_1, 539_1, 541_1, 542_1, 570_1, 571_1, 575_1, 595_1, 598_1, 600_1, 601_1, 602_1,
605_1, 606_1, 607_1, 608_1, 609_1, 611_1, 612_1, 613_1, 616_1, 617_1, 618_1, 619_1, 636_1, 637_1, 640_1,

The borderline positive group: Number of objects = 34  comprising:

9, 95, 111, 141, 151, 166, 177, 193, 232, 281, 282, 491, 531, 532, 533, 539, 542, 554, 569, 575, 601, 1_1, 12_1, 16_1, 100_1, 108_1,
177_1, 193_1, 213_1, 214_1, 249_1, 270_1, 526_1, 542_1,

The misclassified positive:Number of objects = 18  comprising:

3, 99, 142, 153, 180, 183, 208, 262, 541, 9_1, 44_1, 90_1, 134_1, 142_1, 159_1, 183_1, 262_1, 492_1,

Species preferring the negative group of quadrats

BAR_ALP 1 (175, 1) BET_NAN 1 (280, 1) CAS_HYP 1 (307, 61) DRY_OCT 1 (501, 107) JUN_BIG 1 (184, 20) LEO_AUT 1 (125, 1)
PED_OED 1 (431, 47) PHL_ALP 1 (115, 1) PIN_VUL 1 (206, 12) SAL_GLA 1 (274, 71) SAL_LAN 1 (139, 17) TRI_EUR 1 (208, 18)
TRI_SPI 1 (309, 22) VAC_MYR 1 (114, 3) BAR_ALP 2 (112, 0) BET_NAN 2 (230, 0) CAR_SPP 2 (211, 53) CAS_HYP 2 (205, 17)
DRY_OCT 2 (452, 43) PED_OED 2 (371, 15) PIN_VUL 2 (156, 9) SAL_GLA 2 (195, 29) TRI_EUR 2 (122, 0) TRI_SPI 2 (200, 2) BET_NAN
3 (204, 0) CAR_SPP 3 (174, 32) CAS_HYP 3 (152, 9) DRY_OCT 3 (411, 12) EUP_ALP 3 (112, 28) PED_OED 3 (303, 4) PIN_VUL 3 (119,
```

9) RUM_ASA 3 (287, 78) SAL_GLA 3 (133, 17) TRI_SPI 3 (153, 1) BET_NAN 4 (142, 0) CAR_SPP 4 (120, 10) DRY_OCT 4 (331, 1) PED_OED 4 (172, 0) RUM_ASA 4 (158, 28) DRY_OCT 5 (287, 0) RUM_ALA 5 (219, 55) DRY_OCT 6 (247, 0) RUM_ALA 6 (177, 35) DRY_OCT 7 (166, 0) RUM_ALA 7 (127, 26)

Species biased towards the positive group of quadrats

ARE_SPP 1 (17, 62) CER_CER 1 (15, 164) DES_ALP 1 (12, 90) NAR_STR 1 (54, 210) PHY_CAE 1 (92, 246) PYR_SPP 1 (45, 71) SAL_RET 1 (1, 91) SAX_OPP 1 (15, 84) TOF_PUS 1 (58, 153) CER_CER 2 (5, 97) NAR_STR 2 (11, 123) PHY_CAE 2 (42, 172) TOF_PUS 2 (21, 90) CER_CER 3 (1, 62) NAR_STR 3 (2, 96) PHY_CAE 3 (22, 112)

Species with no quadrat preference

CAR_SPP 1 (291, 99) EUP_ALP 1 (252, 126) LUZ_ARC 1 (77, 82) RUM_ASA 1 (422, 186) RUM_ALA 1 (449, 234) EUP_ALP 2 (149, 56) RUM_ASA 2 (340, 109) RUM_ALA 2 (386, 171) RUM_ALA 3 (345, 148) RUM_ALA 4 (263, 78)

END OF LEVEL 1

TWINSPAN QUADRAT CLASSIFICATION LEVEL 1

QUADRAT DIVISION 2 Number of quadrates in cluster = 540
eigenvalue = 0.3056 number of iterations = 3
Indicators and their sign
RUM_ALA [+];
DRY_OCT [-];
BET_NAN [-];
TRI_SPI [-];
SAL_GLA [-];
The maximum indicator score for the negative group = -1
The minimum indicator score for the positive group = 0
Negative group: 4 Number of objects = 385 comprising:

21, 22, 108, 113, 116, 117, 118, 135, 137, 138, 143, 147, 150, 155, 158, 160, 163, 165, 167, 168, 169, 173, 186, 189, 195, 203, 205, 209, 212, 217, 223, 229, 231, 237, 239, 240, 241, 242, 244, 246, 249, 254, 257, 258, 261, 263, 265, 266, 270, 271, 273, 274, 276, 277, 283, 284, 287, 288, 289, 290, 291, 292, 295, 296, 297, 298, 300, 302, 303, 304, 306, 307, 310, 312, 314, 315, 316, 317, 318, 321, 325, 330, 331, 333, 334, 337, 338, 340, 341, 343, 344, 346, 347, 351, 354, 356, 357, 359, 362, 364, 365, 367, 368, 369, 371, 372, 373, 375, 376, 378, 380, 382, 386, 390, 391, 392, 393, 394, 395, 398, 400, 402, 403, 404, 405, 408, 409, 410, 411, 412, 413, 414, 418, 419, 420, 421, 423, 424, 425, 429, 430, 432, 434, 436, 437, 438, 440, 442, 445, 446, 448, 449, 451, 452, 454, 455, 456, 458, 459, 460, 461, 462, 463, 464, 465, 467, 468, 469, 470, 472, 475, 476, 477, 478, 480, 487, 488, 489, 494, 499, 500, 504, 506, 509, 510, 511, 513, 514, 516, 524, 525, 526, 529, 544, 549, 550, 563, 567, 571, 577, 580, 605, 606, 625, 639, 135_1, 145_1, 147_1, 151_1, 154_1, 158_1, 160_1, 165_1, 167_1, 168_1, 169_1, 173_1, 189_1, 195_1, 203_1, 209_1, 217_1, 223_1, 229_1, 239_1, 240_1, 242_1, 244_1, 246_1, 254_1, 255_1, 257_1, 258_1, 261_1, 263_1, 265_1, 266_1, 271_1, 273_1, 274_1, 276_1, 277_1, 281_1, 284_1, 285_1, 287_1, 288_1, 289_1, 290_1, 291_1, 292_1, 295_1, 296_1, 297_1, 298_1, 300_1, 302_1, 303_1, 304_1, 306_1, 307_1, 310_1, 312_1, 314_1, 315_1, 316_1, 317_1, 318_1, 321_1, 325_1, 330_1, 331_1, 333_1, 337_1, 338_1, 340_1, 341_1, 343_1, 344_1, 346_1, 347_1, 351_1, 354_1, 356_1, 357_1, 359_1, 362_1, 364_1, 365_1, 367_1, 368_1, 369_1, 371_1, 372_1, 373_1, 375_1, 376_1, 378_1, 380_1, 382_1, 386_1, 390_1, 391_1, 392_1, 393_1, 394_1, 395_1, 398_1, 400_1, 402_1, 403_1, 404_1, 405_1, 408_1, 409_1, 410_1, 411_1, 412_1, 413_1, 414_1, 418_1, 419_1, 420_1, 421_1, 423_1, 424_1, 425_1, 429_1, 430_1, 432_1, 434_1, 436_1, 437_1, 438_1, 440_1, 442_1, 445_1, 446_1, 448_1, 449_1, 451_1, 452_1, 454_1, 455_1, 456_1, 458_1, 459_1, 460_1, 461_1, 462_1, 463_1, 464_1, 465_1, 467_1, 468_1, 469_1, 470_1, 472_1, 475_1, 476_1, 477_1, 478_1, 480_1, 482_1, 487_1, 488_1, 489_1, 491_1, 494_1, 500_1, 504_1, 506_1, 509_1, 510_1, 511_1, 514_1, 516_1, 544_1, 549_1, 550_1, 563_1, 567_1, 577_1, 580_1, 625_1,

The borderline negative group: Number of objects = 30 comprising:

113, 116, 137, 138, 155, 167, 189, 223, 237, 241, 254, 331, 334, 425, 487, 499, 571, 606, 147_1, 173_1, 189_1, 195_1, 254_1, 255_1, 281_1, 351_1, 445_1, 487_1, 567_1, 580_1,

The misclassified negatives: Number of objects = 10 comprising:

22, 160, 186, 205, 276, 376, 446, 529, 160_1, 223_1,

The positive group: 5 Number of objects = 155 comprising:

1, 8, 12, 13, 16, 19, 75, 91, 92, 93, 97, 100, 109, 110, 112, 115, 127, 131, 134, 139, 140, 145, 149, 154, 179, 185, 187, 188, 194, 198, 200, 201, 204, 206, 213, 218, 220, 225, 227, 233, 234, 235, 252, 255, 285, 293, 319, 320, 322, 323, 324, 326, 332, 336, 482, 486, 492, 495, 502, 528, 540, 547, 548, 551, 552, 555, 558, 559, 560, 565, 566, 576, 581, 582, 583, 585, 586, 589, 590, 624, 13_1, 91_1, 92_1, 93_1, 97_1, 138_1, 143_1, 172_1, 179_1, 180_1, 185_1, 186_1, 187_1, 188_1, 194_1, 198_1, 200_1, 201_1, 204_1, 205_1, 206_1, 212_1, 216_1, 218_1, 220_1, 221_1, 225_1, 227_1, 231_1, 232_1, 233_1, 234_1, 235_1, 237_1, 241_1, 252_1, 283_1, 293_1, 319_1, 320_1, 322_1, 323_1, 324_1, 326_1, 332_1, 334_1, 336_1, 486_1, 495_1, 499_1, 502_1, 513_1, 540_1, 547_1, 548_1, 551_1, 552_1, 554_1, 555_1, 558_1, 559_1, 560_1, 565_1, 566_1, 569_1, 576_1, 581_1, 582_1, 583_1, 585_1, 586_1, 589_1, 590_1, 624_1, 639_1,

The borderline positive group: Number of objects = 31 comprising:

75, 92, 110, 112, 131, 149, 154, 201, 204, 285, 319, 320, 492, 528, 92_1, 138_1, 143_1, 172_1, 179_1, 186_1, 204_1, 205_1, 212_1, 220_1, 227_1, 231_1, 283_1, 319_1, 495_1, 513_1, 639_1,

The misclassified positive:Number of objects = 19 comprising:

140, 188, 322, 332, 336, 482, 555, 566, 237_1, 252_1, 293_1, 322_1, 323_1, 326_1, 332_1, 334_1, 336_1, 499_1, 551_1,

Species preferring the negative group of quadrats

ARC_spp 1 (94, 7) BAR_ALP 1 (152, 23) BET_NAN 1 (267, 13) LEO_AUT 1 (122, 3) PHL_ALP 1 (112, 3) SAL_GLA 1 (240, 34) SAL_LAN 1 (122, 17) TRI_SPI 1 (284, 25) VAC_MYR 1 (103, 11) BAR_ALP 2 (96, 16) BET_NAN 2 (226, 4) SAL_GLA 2 (172, 23) TRI_SPI 2 (189, 11) VAC_MYR 2 (80, 7) BET_NAN 3 (201, 3) DRY_OCT 3 (359, 52) SAL_GLA 3 (117, 16) TRI_SPI 3 (148, 5) BET_NAN 4 (142, 0) DRY_OCT 4 (312, 19) PED_OED 4 (151, 21) BET_NAN 5 (107, 0) DRY_OCT 5 (277, 10) PED_OED 5 (92, 14) BET_NAN 6 (79, 0)

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DRY_OCT 6 (242, 5) DRY_OCT 7 (164, 2) DRY_OCT 8 (108, 0)

Species biased towards the positive group of quadrats

GNA_NOR 1 (17, 53) GNA_SUP 1 (42, 47) JUN_COM 1 (37, 36) LOI_PRO 1 (31, 48) LUZ_ARC 1 (35, 42) PHY_CAE 1 (42, 50)
PYR_SPP 1 (11, 34) SAX_STE 1 (7, 44) GNA_NOR 2 (3, 35) PIN_VUL 3 (65, 54) CAR_SPP 4 (63, 57) RUM_ALA 4 (119, 144) CAR_SPP
5 (49, 46) RUM_ALA 5 (80, 139) CAR_SPP 6 (36, 37) RUM_ALA 6 (51, 126) RUM_ALA 7 (26, 101) RUM_ALA 8 (12, 65)

Species with no quadrat preference

ANT_ODO 1 (56, 37) CAR_SPP 1 (197, 94) CAS_HYP 1 (210, 97) DRY_OCT 1 (383, 118) EUP_ALP 1 (165, 87) JUN_BIG 1 (145, 39)
PED_OED 1 (325, 106) PIN_VUL 1 (131, 75) RUM_ASA 1 (338, 84) RUM_ALA 1 (295, 154) TRI_EUR 1 (169, 39) V._ULI 1 (54, 42)
CAR_SPP 2 (133, 78) CAS_HYP 2 (134, 71) DRY_OCT 2 (372, 80) EUP_ALP 2 (94, 55) PED_OED 2 (289, 82) PIN_VUL 2 (95, 61)
RUM_ASA 2 (278, 62) RUM_ALA 2 (234, 152) TRI_EUR 2 (99, 23) CAR_SPP 3 (102, 72) CAS_HYP 3 (99, 53) EUP_ALP 3 (69, 43)
PED_OED 3 (250, 53) RUM_ASA 3 (237, 50) RUM_ALA 3 (196, 149) RUM_ASA 4 (126, 32)


QUADRAT DIVISION 3  Number of quadrates in cluster = 298
eigenvalue = 0.2722  number of iterations = 3
Indicators and their sign
RUM_ALA [-];
SAL_RET [+];
PYR_SPP [-];
CAS_HYP [-];
RUM_ASA [-];
The maximum indicator score for the negative group = -1
The minimum indicator score for the positive group = 0
Negative group: 6 Number of objects = 161  comprising:

3, 7, 9, 29, 30, 49, 53, 54, 58, 59, 61, 62, 64, 65, 66, 67, 69, 76, 78, 81, 82, 88, 90, 95, 96, 99, 102, 107, 111, 114, 119, 124, 129, 141, 142,
151, 153, 157, 159, 162, 166, 171, 172, 175, 176, 177, 178, 180, 183, 184, 192, 193, 196, 199, 208, 210, 211, 214, 216, 221, 224, 232,
262, 281, 282, 491, 498, 518, 520, 531, 532, 533, 535, 536, 538, 539, 541, 542, 554, 569, 575, 595, 598, 600, 601, 602, 607, 608, 609,
611, 612, 619, 636, 729, 1_1, 3_1, 7_1, 8_1, 9_1, 12_1, 16_1, 19_1, 21_1, 22_1, 30_1, 88_1, 90_1, 95_1, 96_1, 99_1, 100_1, 102_1,
107_1, 108_1, 109_1, 110_1, 118_1, 127_1, 131_1, 134_1, 149_1, 153_1, 155_1, 157_1, 159_1, 162_1, 163_1, 166_1, 171_1, 175_1,
176_1, 177_1, 178_1, 183_1, 184_1, 192_1, 193_1, 196_1, 199_1, 210_1, 211_1, 213_1, 214_1, 224_1, 249_1, 262_1, 270_1, 282_1,
492_1, 498_1, 524_1, 525_1, 526_1, 528_1, 529_1, 531_1, 541_1, 542_1, 571_1, 575_1, 598_1,

The borderline negative group:  Number of objects = 19  comprising:

49, 59, 62, 64, 67, 142, 611, 729, 7_1, 22_1, 30_1, 109_1, 110_1, 118_1, 127_1, 149_1, 162_1, 171_1, 541_1,

The misclassified negatives:  Number of objects = 12  comprising:

65, 262, 518, 595, 175_1, 262_1, 492_1, 524_1, 528_1, 531_1, 575_1, 598_1,

The positive group: 7 Number of objects = 137  comprising:

34, 36, 39, 40, 41, 43, 44, 45, 51, 52, 55, 57, 63, 68, 72, 83, 85, 105, 120, 121, 122, 125, 522, 537, 570, 613, 616, 617, 618, 637, 705, 706,
711, 712, 713, 714, 715, 716, 717, 718, 719, 720, 721, 722, 723, 724, 726, 727, 728, 730, 731, 735, 24_1, 29_1, 34_1, 36_1, 40_1, 44_1,
45_1, 49_1, 51_1, 52_1, 53_1, 54_1, 55_1, 57_1, 58_1, 59_1, 61_1, 62_1, 63_1, 64_1, 65_1, 66_1, 67_1, 68_1, 69_1, 72_1, 75_1, 76_1,
78_1, 81_1, 82_1, 83_1, 85_1, 105_1, 111_1, 112_1, 113_1, 114_1, 115_1, 116_1, 117_1, 119_1, 120_1, 121_1, 122_1, 124_1, 125_1,
129_1, 137_1, 139_1, 140_1, 141_1, 142_1, 150_1, 208_1, 518_1, 520_1, 522_1, 532_1, 533_1, 535_1, 536_1, 537_1, 538_1, 539_1,
570_1, 595_1, 600_1, 601_1, 602_1, 605_1, 606_1, 607_1, 608_1, 609_1, 611_1, 612_1, 613_1, 616_1, 617_1, 618_1, 619_1, 636_1,
637_1, 640_1,

The borderline positive group: Number of objects = 12  comprising:

63, 72, 85, 616, 717, 24_1, 52_1, 105_1, 533_1, 535_1, 539_1, 605_1,

The misclassified positive:Number of objects = 14  comprising:

36, 40, 68, 83, 105, 120, 125, 69_1, 81_1, 111_1, 112_1, 129_1, 139_1, 640_1,

Species preferring the negative group of quadrats

CAR_BEL 1 (38, 10) CAR_SPP 1 (72, 27) CAS_HYP 1 (56, 5) DRY_OCT 1 (78, 29) LOI_PRO 1 (44, 14) PED_OED 1 (45, 2) PYR_SPP 1
(67, 4) SAL_GLA 1 (57, 14) V._ULI 1 (39, 14) CAR_SPP 2 (47, 6) DRY_OCT 2 (36, 7) PYR_SPP 2 (41, 0) RUM_ASA 2 (90, 19) RUM_ALA
2 (140, 31) RUM_ASA 3 (72, 6) RUM_ALA 3 (129, 19) RUM_ALA 4 (73, 5) RUM_ALA 5 (53, 2) RUM_ALA 6 (35, 0)

Species biased towards the positive group of quadrats

ARA_ALP 1 (7, 29) CAR_PET 1 (18, 41) SAL_RET 1 (14, 77) SAX_CES 1 (10, 36) CER_CER 2 (32, 65) DES_ALP 2 (19, 36) SAL_RET 2
(3, 29) CER_CER 3 (15, 47)

Species with no quadrat preference

ARE_SPP 1 (33, 29) CER_CER 1 (74, 90) DES_ALP 1 (37, 53) EUP_ALP 1 (72, 54) LUZ_ARC 1 (55, 27) NAR_STR 1 (123, 87)
PHY_CAE 1 (123, 123) RUM_ASA 1 (115, 71) RUM_ALA 1 (154, 80) SAX_OPP 1 (43, 41) TOF_PUS 1 (79, 74) EUP_ALP 2 (33, 23)
NAR_STR 2 (81, 42) PHY_CAE 2 (84, 88) TOF_PUS 2 (46, 44) NAR_STR 3 (64, 32) PHY_CAE 3 (48, 64) TOF_PUS 3 (22, 28)

  END OF LEVEL 2

TWINSPAN QUADRAT CLASSIFICATION LEVEL 2
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QUADRAT DIVISION 4  Number of quadrates in cluster = 385
eigenvalue = 0.2682  number of iterations = 4
Indicators and their sign
VAC_MYR [-];
CAR_SPP [-];
BET_NAN [-];
OXY_DIG [-];
EUP_ALP [-];
The maximum indicator score for the negative group = -3
The minimum indicator score for the positive group = -2
Negative group: 8 Number of objects = 95  comprising:

229, 231, 237, 239, 240, 241, 242, 244, 246, 287, 303, 310, 318, 325, 330, 331, 333, 334, 337, 340, 341, 344, 347, 351, 354, 356, 357,
359, 362, 364, 365, 367, 368, 369, 371, 372, 373, 375, 386, 419, 423, 425, 436, 437, 438, 442, 475, 477, 478, 480, 500, 567, 625, 229_1,
239_1, 240_1, 242_1, 244_1, 246_1, 325_1, 330_1, 333_1, 337_1, 340_1, 341_1, 344_1, 347_1, 351_1, 354_1, 356_1, 359_1, 362_1,
364_1, 365_1, 367_1, 368_1, 369_1, 371_1, 372_1, 373_1, 375_1, 376_1, 386_1, 390_1, 419_1, 437_1, 438_1, 442_1, 477_1, 478_1,
480_1, 500_1, 563_1, 567_1, 625_1,

The borderline negative group:  Number of objects = 9  comprising:

231, 241, 303, 310, 331, 357, 362, 372, 563_1,

The misclassified negatives:  Number of objects = 8  comprising:

318, 368, 423, 229_1, 368_1, 438_1, 477_1, 567_1,

The positive group: 9 Number of objects = 290  comprising:

21, 22, 108, 113, 116, 117, 118, 135, 137, 138, 143, 147, 150, 155, 158, 160, 163, 165, 167, 168, 169, 173, 186, 189, 195, 203, 205, 209,
212, 217, 223, 249, 254, 257, 258, 261, 263, 265, 266, 270, 271, 273, 274, 276, 277, 283, 284, 288, 289, 290, 291, 292, 295, 296, 297,
298, 300, 302, 304, 306, 307, 312, 314, 315, 316, 317, 321, 338, 343, 346, 376, 378, 380, 382, 390, 391, 392, 393, 394, 395, 398, 400,
402, 403, 404, 405, 408, 409, 410, 411, 412, 413, 414, 418, 420, 421, 424, 429, 430, 432, 434, 440, 445, 446, 448, 449, 451, 452, 454,
455, 456, 458, 459, 460, 461, 462, 463, 464, 465, 467, 468, 469, 470, 472, 476, 487, 488, 489, 494, 499, 504, 506, 509, 510, 511, 513,
514, 516, 524, 525, 526, 529, 544, 549, 550, 563, 571, 577, 580, 605, 606, 639, 135_1, 145_1, 147_1, 151_1, 154_1, 158_1, 160_1,
165_1, 167_1, 168_1, 169_1, 173_1, 189_1, 195_1, 203_1, 209_1, 217_1, 223_1, 254_1, 255_1, 257_1, 258_1, 261_1, 263_1, 265_1,
266_1, 271_1, 273_1, 274_1, 276_1, 277_1, 281_1, 284_1, 285_1, 287_1, 288_1, 289_1, 290_1, 291_1, 292_1, 295_1, 296_1, 297_1,
298_1, 300_1, 302_1, 303_1, 304_1, 306_1, 307_1, 310_1, 312_1, 314_1, 315_1, 316_1, 317_1, 318_1, 321_1, 331_1, 338_1, 343_1,
346_1, 357_1, 378_1, 380_1, 382_1, 391_1, 392_1, 393_1, 394_1, 395_1, 398_1, 400_1, 402_1, 403_1, 404_1, 405_1, 408_1, 409_1,
410_1, 411_1, 412_1, 413_1, 414_1, 418_1, 420_1, 421_1, 423_1, 424_1, 425_1, 429_1, 430_1, 432_1, 434_1, 436_1, 440_1, 445_1,
446_1, 448_1, 449_1, 451_1, 452_1, 454_1, 455_1, 456_1, 458_1, 459_1, 460_1, 461_1, 462_1, 463_1, 464_1, 465_1, 467_1, 468_1,
469_1, 470_1, 472_1, 475_1, 476_1, 482_1, 487_1, 488_1, 489_1, 491_1, 494_1, 504_1, 506_1, 509_1, 510_1, 511_1, 514_1, 516_1,
544_1, 549_1, 550_1, 577_1, 580_1,

The borderline positive group: Number of objects = 11  comprising:

390, 413, 414, 418, 445, 487, 499, 303_1, 318_1, 413_1, 475_1,

The misclassified positive:Number of objects = 5  comprising:

291, 302, 421, 331_1, 423_1,

Species preferring the negative group of quadrats

ANT_ODO 1 (29, 27) CAR_SPP 1 (88, 109) EUP_ALP 1 (78, 87) GNA_SUP 1 (28, 14) JUN_TRI 1 (21, 15) JUN_COM 1 (26, 11)
OXY_DIG 1 (62, 9) SIL_ACA 1 (37, 15) VAC_MYR 1 (76, 27) ANT_ODO 2 (21, 11) CAR_SPP 2 (81, 52) EUP_ALP 2 (62, 32) OXY_DIG 2
(46, 5) SIL_ACA 2 (26, 7) TRI_EUR 2 (50, 49) TRI_SPI 2 (75, 114) VAC_MYR 2 (69, 11) BET_NAN 3 (84, 117) CAR_SPP 3 (71, 31)
EUP_ALP 3 (51, 18) OXY_DIG 3 (34, 3) SIL_ACA 3 (20, 3) TRI_EUR 3 (40, 29) TRI_SPI 3 (67, 81) VAC_MYR 3 (63, 7) BET_NAN 4 (78,
64) CAR_SPP 4 (55, 8) EUP_ALP 4 (36, 4) TRI_EUR 4 (27, 9) TRI_SPI 4 (47, 24) VAC_MYR 4 (57, 1) BET_NAN 5 (66, 41) CAR_SPP 5
(46, 3) EUP_ALP 5 (29, 1) TRI_EUR 5 (24, 5) TRI_SPI 5 (40, 12) VAC_MYR 5 (44, 0) BET_NAN 6 (54, 25) CAR_SPP 6 (35, 1) EUP_ALP
6 (21, 1) TRI_EUR 6 (23, 3) TRI_SPI 6 (26, 5) VAC_MYR 6 (25, 0) BET_NAN 7 (33, 10) BET_NAN 8 (21, 5)

Species biased towards the positive group of quadrats

CAS_HYP 1 (17, 193) SAL_GLA 1 (25, 215) SAL_LAN 1 (17, 105) CAS_HYP 2 (5, 129) SAL_GLA 2 (17, 155) SAL_LAN 2 (9, 66)
CAS_HYP 3 (4, 95) SAL_GLA 3 (8, 109) PED_OED 4 (16, 135) PED_OED 5 (7, 85)

Species with no quadrat preference

ARC_spp 1 (28, 66) BAR_ALP 1 (38, 114) BET_NAN 1 (88, 179) DRY_OCT 1 (95, 288) JUN_BIG 1 (37, 108) LEO_AUT 1 (34, 88)
PED_OED 1 (68, 257) PHL_ALP 1 (16, 96) PIN_VUL 1 (50, 81) RUM_ASA 1 (64, 274) RUM_ALA 1 (50, 245) TRI_EUR 1 (61, 108)
TRI_SPI 1 (84, 200) BAR_ALP 2 (25, 71) BET_NAN 2 (85, 141) DRY_OCT 2 (94, 278) LEO_AUT 2 (20, 50) PED_OED 2 (54, 235)
PIN_VUL 2 (35, 60) RUM_ASA 2 (48, 230) RUM_ALA 2 (42, 192) BAR_ALP 3 (20, 53) DRY_OCT 3 (91, 268) PED_OED 3 (41, 209)
PIN_VUL 3 (23, 42) RUM_ASA 3 (40, 197) RUM_ALA 3 (38, 158) DRY_OCT 4 (81, 231) RUM_ASA 4 (28, 98) RUM_ALA 4 (26, 93)
DRY_OCT 5 (76, 201) RUM_ALA 5 (24, 56) DRY_OCT 6 (71, 171) DRY_OCT 7 (57, 107) DRY_OCT 8 (40, 68)
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QUADRAT DIVISION 5  Number of quadrates in cluster = 155
eigenvalue = 0.2747  number of iterations = 3
Indicators and their sign
RUM_ALA [+];
PIN_VUL [+];
CAR_SPP [+];
SAX_STE [+];
The maximum indicator score for the negative group = 1
The minimum indicator score for the positive group = 2
```

Negative group: 10 Number of objects = 94 comprising:

1, 8, 12, 13, 16, 19, 75, 91, 92, 93, 97, 100, 109, 110, 112, 115, 127, 131, 134, 139, 140, 145, 149, 154, 179, 185, 187, 194, 198, 200, 201, 204, 206, 213, 218, 220, 235, 285, 319, 320, 323, 492, 495, 528, 540, 547, 548, 560, 586, 624, 13_1, 91_1, 92_1, 93_1, 97_1, 138_1, 143_1, 172_1, 179_1, 180_1, 185_1, 186_1, 187_1, 188_1, 194_1, 198_1, 200_1, 201_1, 204_1, 205_1, 206_1, 212_1, 216_1, 218_1, 220_1, 221_1, 252_1, 283_1, 293_1, 319_1, 320_1, 495_1, 513_1, 540_1, 547_1, 548_1, 551_1, 554_1, 560_1, 566_1, 569_1, 586_1, 624_1, 639_1,

The borderline negative group: Number of objects = 6 comprising:

323, 547, 218_1, 252_1, 551_1, 554_1,

The misclassified negatives: Number of objects = 5 comprising:

235, 540, 540_1, 566_1, 624_1,

The positive group: 11 Number of objects = 61 comprising:

188, 225, 227, 233, 234, 252, 255, 293, 322, 324, 326, 332, 336, 482, 486, 502, 551, 552, 555, 558, 559, 565, 566, 576, 581, 582, 583, 585, 589, 590, 225_1, 227_1, 231_1, 232_1, 233_1, 234_1, 235_1, 237_1, 241_1, 322_1, 323_1, 324_1, 326_1, 332_1, 334_1, 336_1, 486_1, 499_1, 502_1, 552_1, 555_1, 558_1, 559_1, 565_1, 576_1, 581_1, 582_1, 583_1, 585_1, 589_1, 590_1,

The borderline positive group: Number of objects = 6 comprising:

188, 233, 551, 566, 233_1, 241_1,

The misclassified positive:Number of objects = 4 comprising:

252, 255, 482, 589,

Species preferring the negative group of quadrats

LUZ_ARC 1 (35, 7) NAR_STR 1 (24, 6) PYR_SPP 1 (26, 8) RUM_ASA 1 (68, 16) TOF_PUS 1 (25, 6) LUZ_ARC 2 (20, 0) RUM_ASA 2 (50, 12) RUM_ASA 3 (41, 9)

Species biased towards the positive group of quadrats

ANT_ODO 1 (8, 29) BAR_ALP 1 (6, 17) CAR_SPP 1 (40, 54) GER_SYL 1 (4, 13) GNA_NOR 1 (17, 36) GNA_SUP 1 (13, 34) JUN_COM 1 (11, 25) PED_LAP 1 (3, 13) PIN_VUL 1 (24, 51) RAN_PYG 1 (0, 16) SAX_RIV 1 (1, 13) SAX_STE 1 (8, 36) SIL_ACA 1 (1, 17) TRI_EUR 1 (11, 28) TRI_SPI 1 (5, 20) V._ULI 1 (18, 24) ANT_ODO 2 (2, 23) BAR_ALP 2 (3, 13) CAR_SPP 2 (25, 53) EUP_ALP 2 (16, 39) GNA_NOR 2 (9, 26) GNA_SUP 2 (4, 22) JUN_COM 2 (1, 17) PHY_CAE 2 (10, 18) PIN_VUL 2 (14, 47) SAX_STE 2 (2, 26) TRI_EUR 2 (5, 18) V._ULI 2 (10, 16) ANT_ODO 3 (0, 20) CAR_SPP 3 (20, 52) EUP_ALP 3 (10, 33) GNA_NOR 3 (4, 23) GNA_SUP 3 (1, 16) JUN_COM 3 (1, 15) PHY_CAE 3 (4, 14) PIN_VUL 3 (13, 41) SAX_STE 3 (0, 20) TRI_EUR 3 (1, 15) CAR_SPP 4 (10, 47) EUP_ALP 4 (6, 20) PIN_VUL 4 (6, 23) CAR_SPP 5 (4, 42) EUP_ALP 5 (2, 15) PIN_VUL 5 (5, 14) CAR_SPP 6 (2, 35) EUP_ALP 6 (2, 14) CAR_SPP 7 (1, 22) CAR_SPP 8 (0, 16) RUM_ALA 8 (14, 51) RUM_ALA 9 (0, 22)

Species with no quadrat preference

CAS_HYP 1 (64, 33) DRY_OCT 1 (73, 45) EUP_ALP 1 (39, 48) JUN_BIG 1 (23, 16) LOI_PRO 1 (33, 15) LYCO_ANN 1 (14, 15) PED_OED 1 (69, 37) PHY_CAE 1 (24, 26) RUM_ALA 1 (93, 61) SAL_GLA 1 (25, 9) CAS_HYP 2 (48, 23) DRY_OCT 2 (47, 33) LOI_PRO 2 (20, 7) PED_OED 2 (51, 31) RUM_ALA 2 (91, 61) CAS_HYP 3 (35, 18) DRY_OCT 3 (29, 23) PED_OED 3 (31, 22) RUM_ALA 3 (88, 61) RUM_ASA 4 (24, 8) RUM_ALA 4 (84, 60) RUM_ALA 5 (80, 59) RUM_ALA 6 (69, 57) RUM_ALA 7 (47, 54)

QUADRAT DIVISION 6 Number of quadrates in cluster = 161
eigenvalue = 0.2129 number of iterations = 4
Indicators and their sign
PYR_SPP [+];
RUM_ASA [-];
DRY_OCT [-];
CER_CER [-];
The maximum indicator score for the negative group = 0
The minimum indicator score for the positive group = 1
Negative group: 12 Number of objects = 124 comprising:

29, 30, 49, 53, 58, 59, 61, 62, 64, 65, 66, 67, 69, 76, 78, 81, 82, 107, 111, 114, 119, 124, 129, 141, 142, 151, 153, 157, 159, 162, 166, 171, 172, 177, 178, 180, 184, 192, 196, 199, 208, 210, 211, 216, 232, 262, 281, 282, 491, 498, 518, 520, 531, 532, 533, 535, 536, 538, 539, 541, 542, 554, 575, 595, 598, 600, 601, 602, 607, 608, 609, 611, 612, 619, 636, 729, 7_1, 19_1, 22_1, 30_1, 95_1, 107_1, 108_1, 109_1, 110_1, 118_1, 127_1, 131_1, 134_1, 149_1, 153_1, 155_1, 157_1, 159_1, 162_1, 163_1, 166_1, 171_1, 175_1, 177_1, 178_1, 184_1, 192_1, 196_1, 199_1, 210_1, 211_1, 213_1, 249_1, 262_1, 270_1, 282_1, 492_1, 524_1, 525_1, 526_1, 528_1, 529_1, 531_1, 541_1, 542_1, 571_1, 575_1, 598_1,

The borderline negative group: Number of objects = 10 comprising:

29, 30, 69, 180, 196, 216, 498, 575, 30_1, 196_1,

The misclassified negatives: Number of objects = 1 comprising:

7_1,

The positive group: 13 Number of objects = 37 comprising:

3, 7, 9, 54, 88, 90, 95, 96, 99, 102, 175, 176, 183, 193, 214, 221, 224, 569, 1_1, 3_1, 8_1, 9_1, 12_1, 16_1, 21_1, 88_1, 90_1, 96_1, 99_1, 100_1, 102_1, 176_1, 183_1, 193_1, 214_1, 224_1, 498_1, The borderline positive group: Number of objects = 4 comprising:

7, 175, 569, 102_1,

The misclassified positive:Number of objects = 8 comprising:

90, 96, 214, 21_1, 90_1, 100_1, 214_1, 498_1,

Species preferring the negative group of quadrats

ARE_SPP 1 (29, 4) CER_CER 1 (72, 2) DES_ALP 1 (34, 3) DRY_OCT 1 (74, 4) GNA_NOR 1 (29, 2) LUZ_ARC 1 (48, 7) RUM_ASA 1 (108, 7) SAL_GLA 1 (56, 1) SAX_OPP 1 (43, 0) V._ULI 1 (38, 1) CAR_SPP 2 (41, 6) CER_CER 2 (32, 0) DRY_OCT 2 (36, 0) EUP_ALP 2 (31, 2) RUM_ASA 2 (86, 4) CAR_SPP 3 (27, 3) PHY_CAE 3 (45, 3) RUM_ASA 3 (70, 2) RUM_ASA 4 (28, 0)

Species biased towards the positive group of quadrats

CAS_HYP 1 (33, 23) LOI_PRO 1 (24, 20) PYR_SPP 1 (32, 35) CAS_HYP 2 (5, 9) LOI_PRO 2 (7, 11) PYR_SPP 2 (19, 22) LOI_PRO 3 (3, 10) PYR_SPP 3 (9, 11)

Species with no quadrat preference

CAR_BEL 1 (27, 11) CAR_SPP 1 (58, 14) EUP_ALP 1 (62, 10) NAR_STR 1 (94, 29) PED_OED 1 (31, 14) PHY_CAE 1 (101, 22) RUM_ALA 1 (117, 37) TOF_PUS 1 (62, 17) NAR_STR 2 (61, 20) PHY_CAE 2 (72, 12) RUM_ALA 2 (107, 33) TOF_PUS 2 (33, 13) NAR_STR 3 (49, 15) RUM_ALA 3 (96, 33) RUM_ALA 4 (55, 18) RUM_ALA 5 (41, 12) RUM_ALA 6 (25, 10) RUM_ALA 7 (17, 9)

QUADRAT DIVISION 7 Number of quadrates in cluster = 137
eigenvalue = 0.2715 number of iterations = 4
Indicators and their sign
DES_ALP [+];
NAR_STR [+];
CER_CER [+];
TOF_PUS [-];
SAX_OPP [+];
The maximum indicator score for the negative group = 1
The minimum indicator score for the positive group = 2
Negative group: 14 Number of objects = 90 comprising:

40, 41, 44, 45, 51, 52, 57, 63, 72, 120, 537, 613, 618, 711, 712, 713, 715, 717, 718, 721, 722, 723, 726, 735, 29_1, 34_1, 36_1, 40_1, 44_1, 45_1, 49_1, 51_1, 52_1, 53_1, 54_1, 55_1, 57_1, 58_1, 59_1, 61_1, 62_1, 63_1, 64_1, 65_1, 66_1, 67_1, 68_1, 69_1, 72_1, 75_1, 76_1, 78_1, 105_1, 113_1, 114_1, 116_1, 117_1, 120_1, 121_1, 124_1, 125_1, 137_1, 139_1, 141_1, 142_1, 150_1, 208_1, 518_1, 520_1, 532_1, 533_1, 535_1, 536_1, 537_1, 538_1, 539_1, 595_1, 601_1, 605_1, 606_1, 607_1, 608_1, 609_1, 611_1, 612_1, 613_1, 616_1, 617_1, 618_1, 619_1,

The borderline negative group: Number of objects = 7 comprising:

29_1, 52_1, 105_1, 121_1, 125_1, 612_1, 619_1,

The misclassified negatives: Number of objects = 1 comprising:

718,

The positive group: 15 Number of objects = 47 comprising:

34, 36, 39, 43, 55, 68, 83, 85, 105, 121, 122, 125, 522, 570, 616, 617, 637, 705, 706, 714, 716, 719, 720, 724, 727, 728, 730, 731, 24_1, 81_1, 82_1, 83_1, 85_1, 111_1, 112_1, 115_1, 119_1, 122_1, 129_1, 140_1, 522_1, 570_1, 600_1, 602_1, 636_1, 637_1, 640_1,

The borderline positive group: Number of objects = 5 comprising:

55, 714, 727, 728, 730,

The misclassified positive:Number of objects = 6 comprising:

39, 122, 24_1, 115_1, 119_1, 640_1,

Species preferring the negative group of quadrats

CAR_PET 1 (34, 7) CER_ALP 1 (19, 2) TOF_PUS 1 (65, 9) SAL_RET 2 (24, 5) TOF_PUS 2 (40, 4) TOF_PUS 3 (24, 4)

Species biased towards the positive group of quadrats

DES_ALP 1 (19, 34) SAX_NIV 1 (3, 10) SAX_OPP 1 (13, 28) CER_CER 2 (26, 39) DES_ALP 2 (4, 32) NAR_STR 2 (11, 31) RUM_ASA 2 (7, 12) SAX_OPP 2 (2, 21) CER_CER 3 (20, 27) DES_ALP 3 (2, 23) NAR_STR 3 (5, 27) RUM_ALA 3 (9, 10) SAX_OPP 3 (1, 11) DES_ALP 4 (1, 11) NAR_STR 4 (1, 14)

Species with no quadrat preference

ARA_ALP 1 (18, 11) ARE_SPP 1 (19, 10) CAR_SPP 1 (14, 13) CER_CER 1 (48, 42) DRY_OCT 1 (22, 7) EUP_ALP 1 (41, 13) LUZ_ARC 1 (17, 10) NAR_STR 1 (47, 40) PHY_CAE 1 (84, 39) RUM_ASA 1 (43, 28) RUM_ALA 1 (55, 25) SAL_RET 1 (58, 19) SAX_CES 1 (25, 11) PHY_CAE 2 (59, 29) RUM_ALA 2 (18, 13) PHY_CAE 3 (44, 20)

END OF LEVEL 3

TWINSPAN QUADRAT CLASSIFICATION LEVEL 3

THIRTY YEARS OF PRIMARY SUCCESSION ON THE STORBREEN GLACIER FORELAND, JOTUNHEIM, NORWAY:

SPECIES POPULATIONS, COMMUNITY DYNAMICS AND ENVIRONMENTAL INFLUENCES

VOLUME II

MARGARET ANN NICHOLLS, B.Sc

Thesis submitted for the PhD degree

University of Wales, Swansea

2005

VOLUME II

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S51 *Trientalis europea*

S52 *Viola palustris*

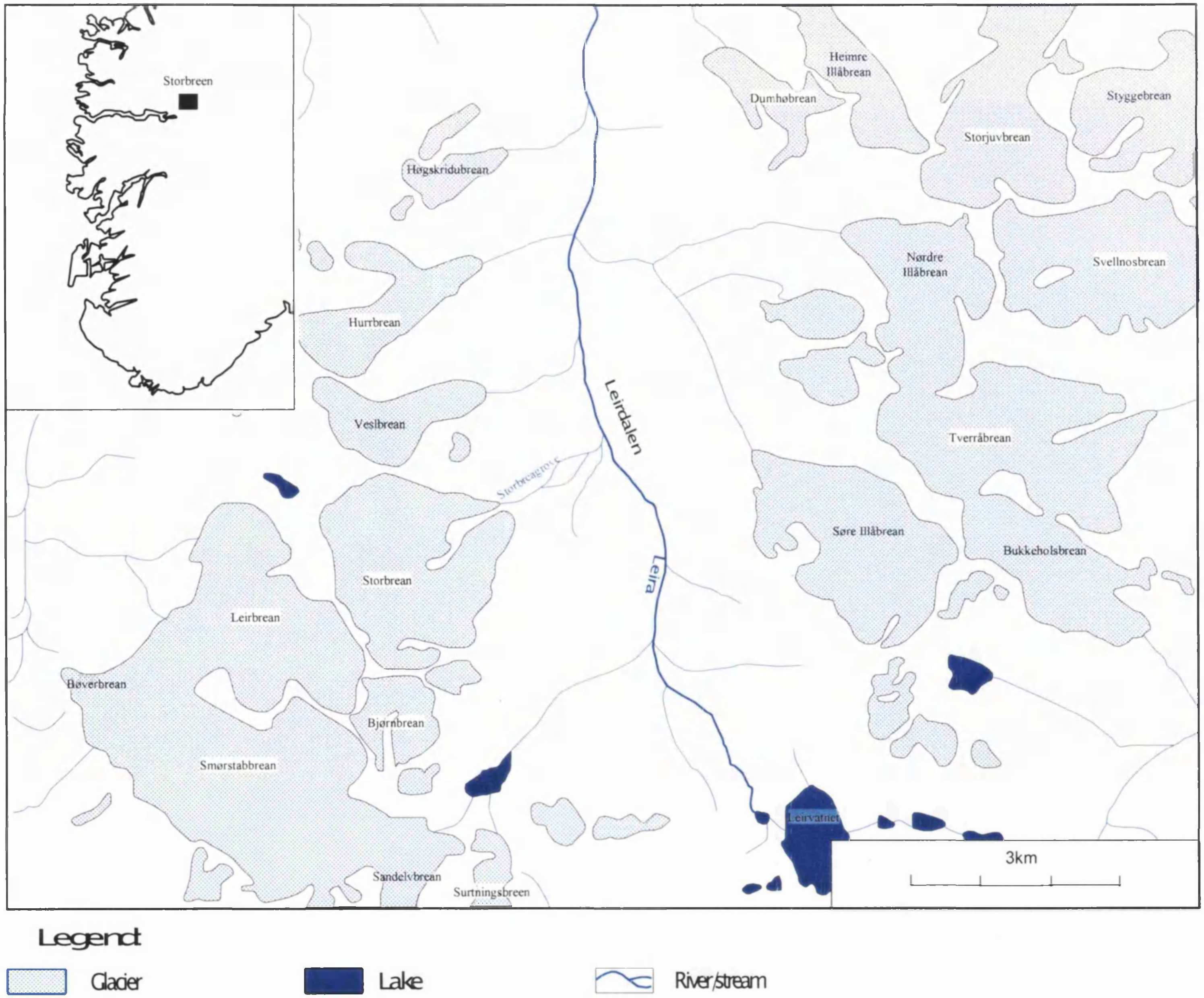


Figure 1.1: Location of study area
(from the 1997 Storbreen glacier map Norges Vassdrags-og Energidirektorat, NVE)

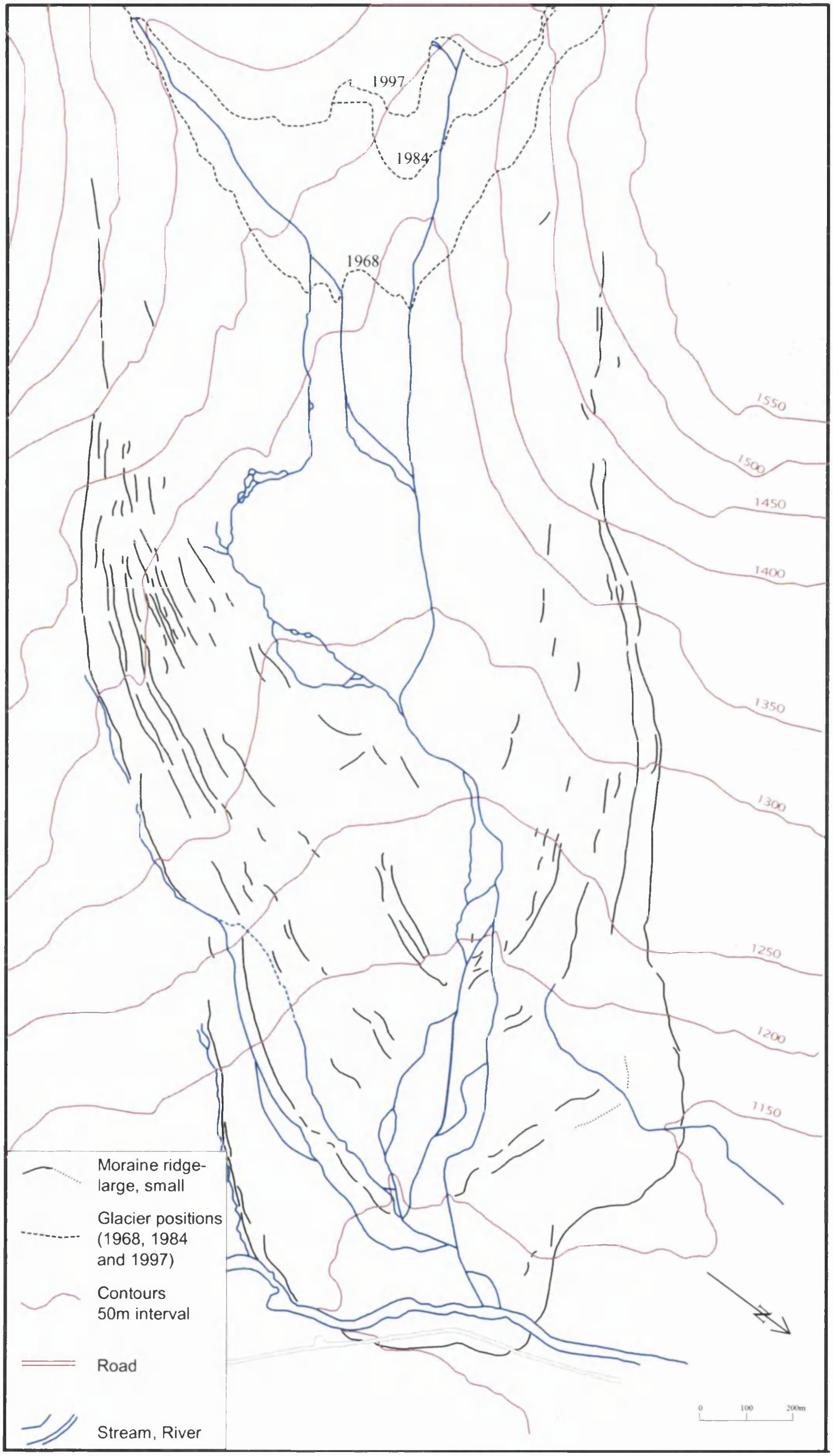


Figure 1.2: Storbreen glacier foreland
Based on the 1997 Storbreen glacier map (Norges Vassdrags-og Energidirektorat, NVE)

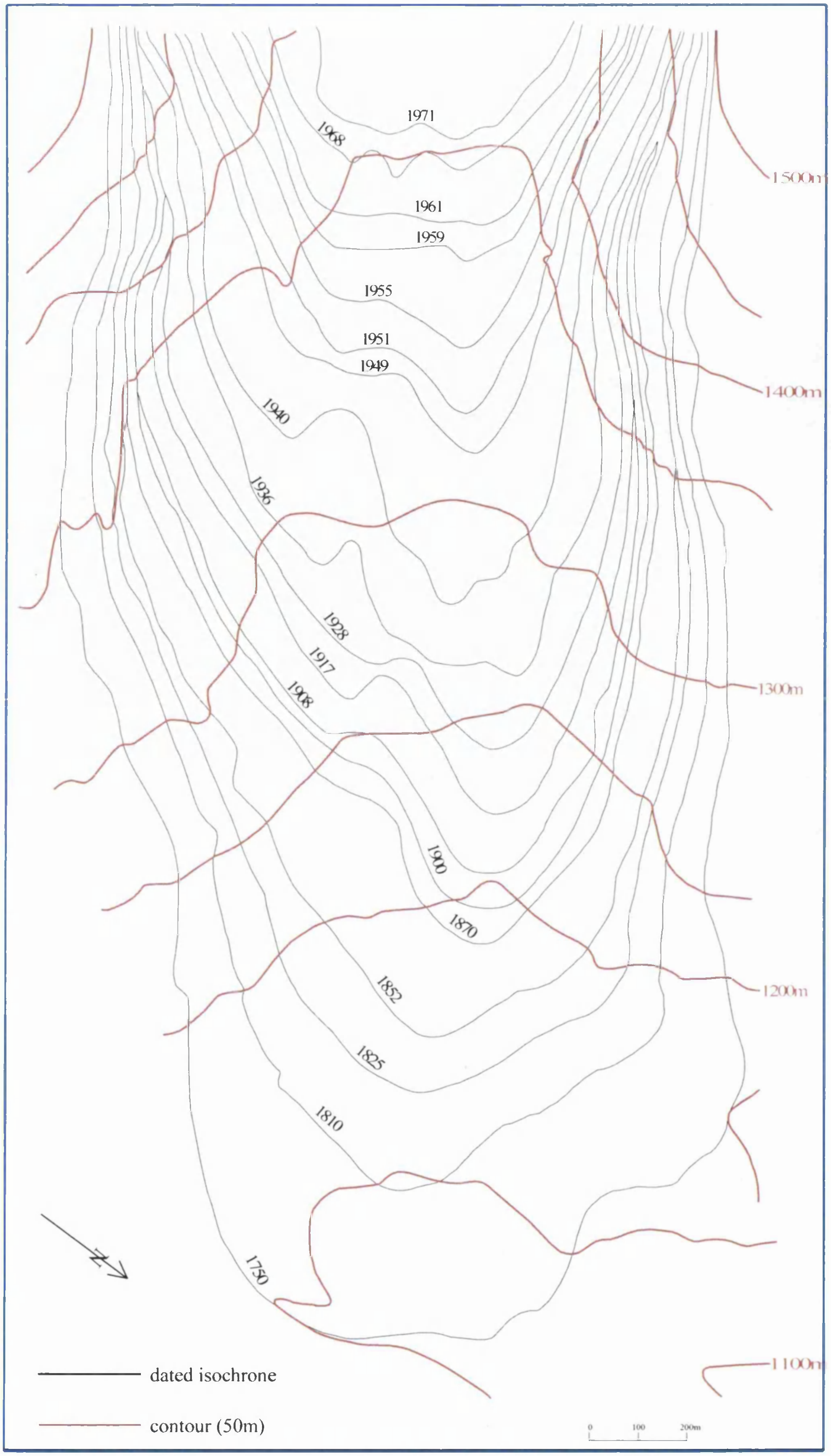
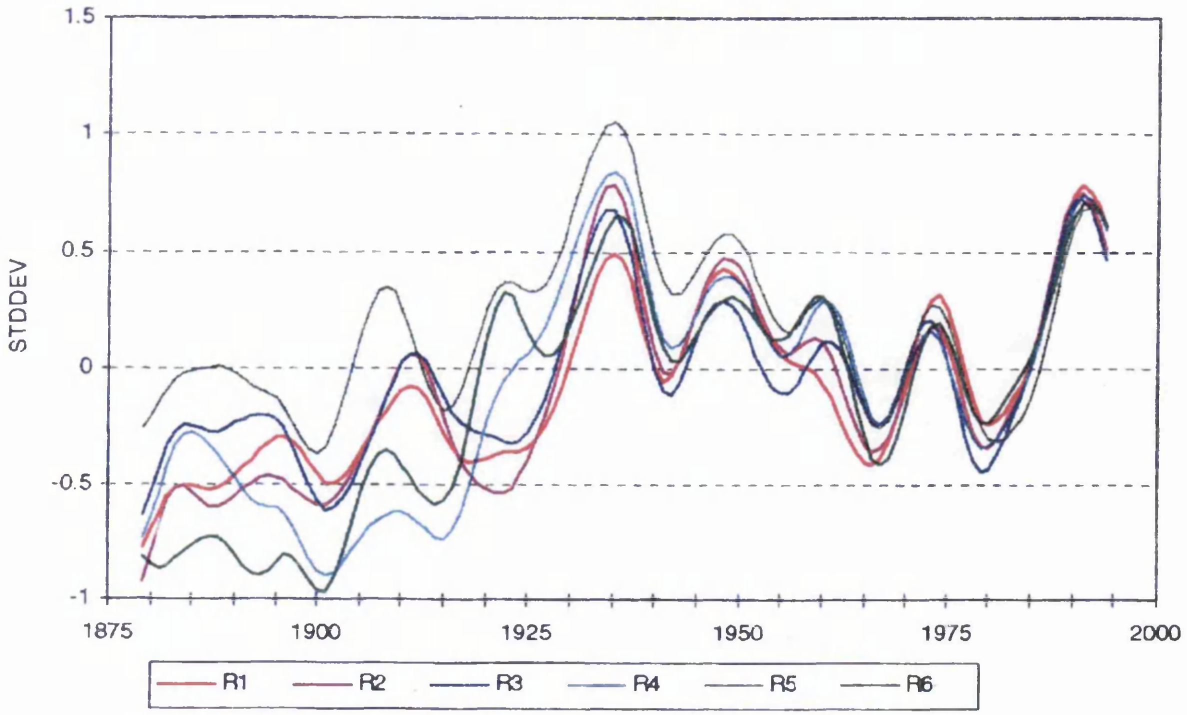
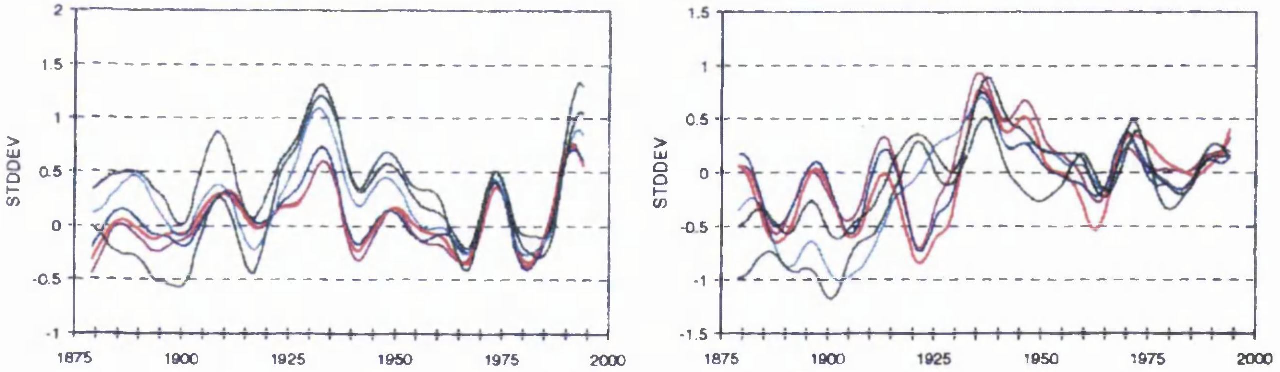


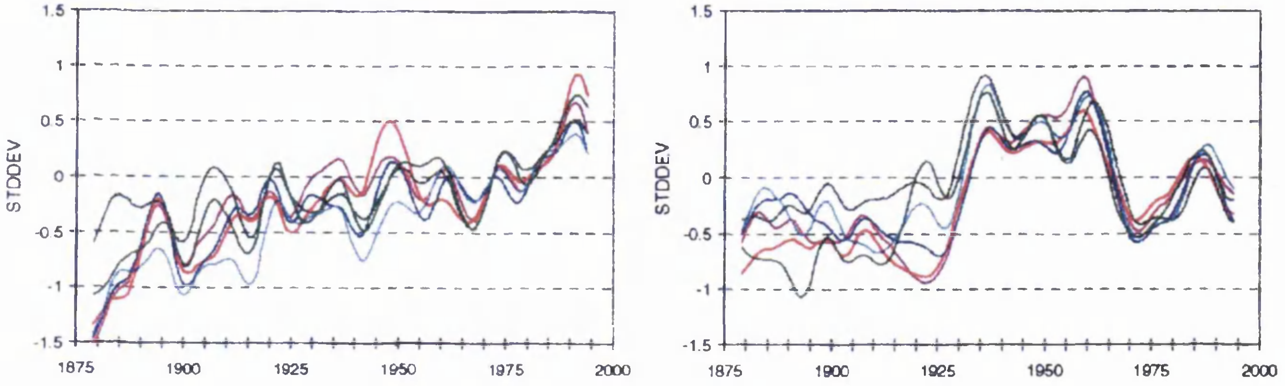
Figure 1.3: Areal chronology at Storbreen (from Matthews, 1992 Figure 5.28) Dating determined by historical sources for isochrones of 100 years or later, and lichenometry for earlier dates (see section 3.2.1).

a)




b) winter

d) summer


c) spring

e) autumn

Figure 1.4: Time series of annual and seasonal mean temperatures for regions in Norway from 1876 to 1997
R1 South east; R2 south west; R3 central; R4 north west; R5 northern inland; and R6 north east.
(From Hanssen-Bauer and Nordli, 1998)

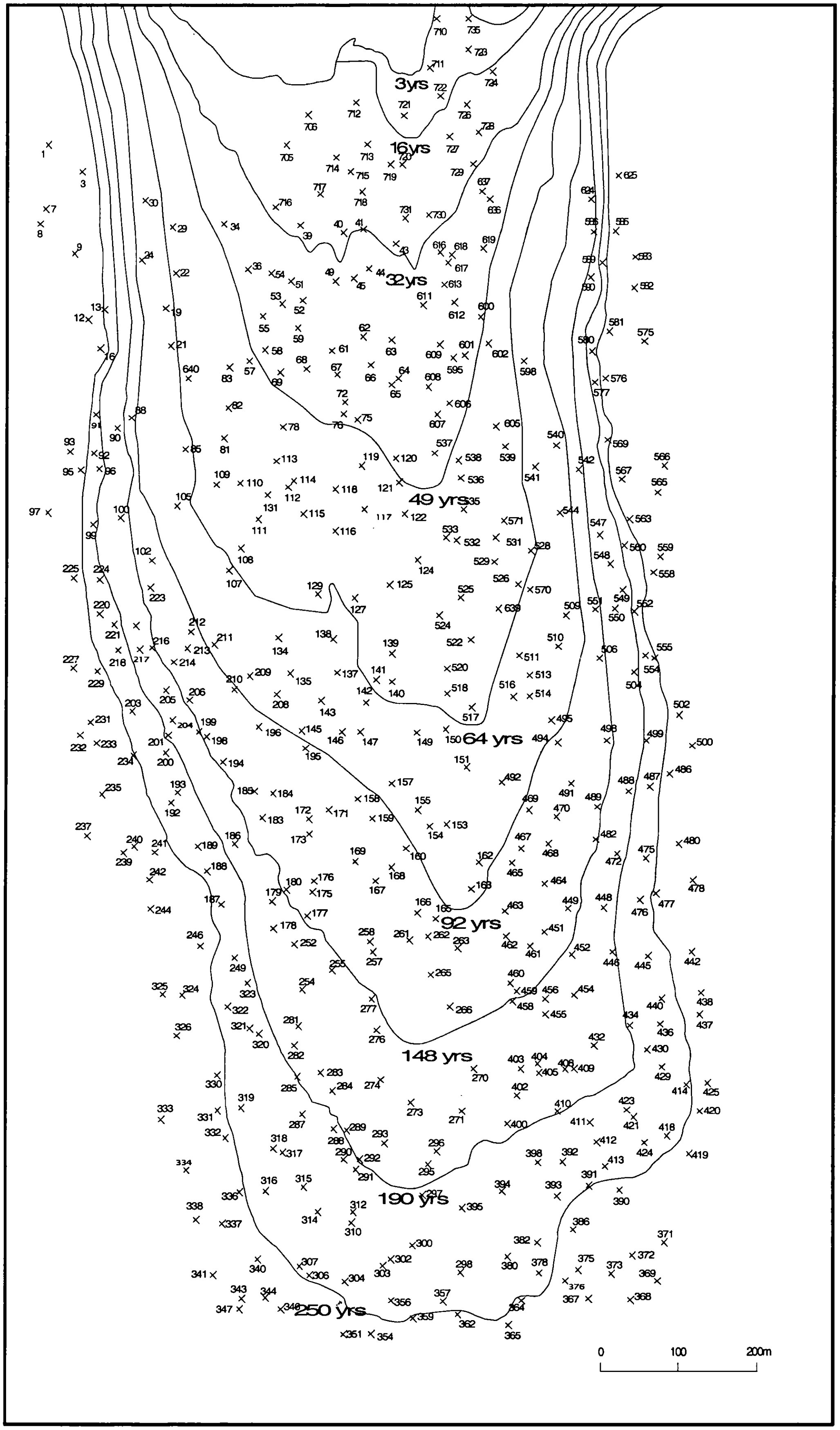


Figure 3.3: 1970-71 sites selected for inclusion in the 2000-01 survey and new sites established in 2000-01:
new sites are numbered from 700.

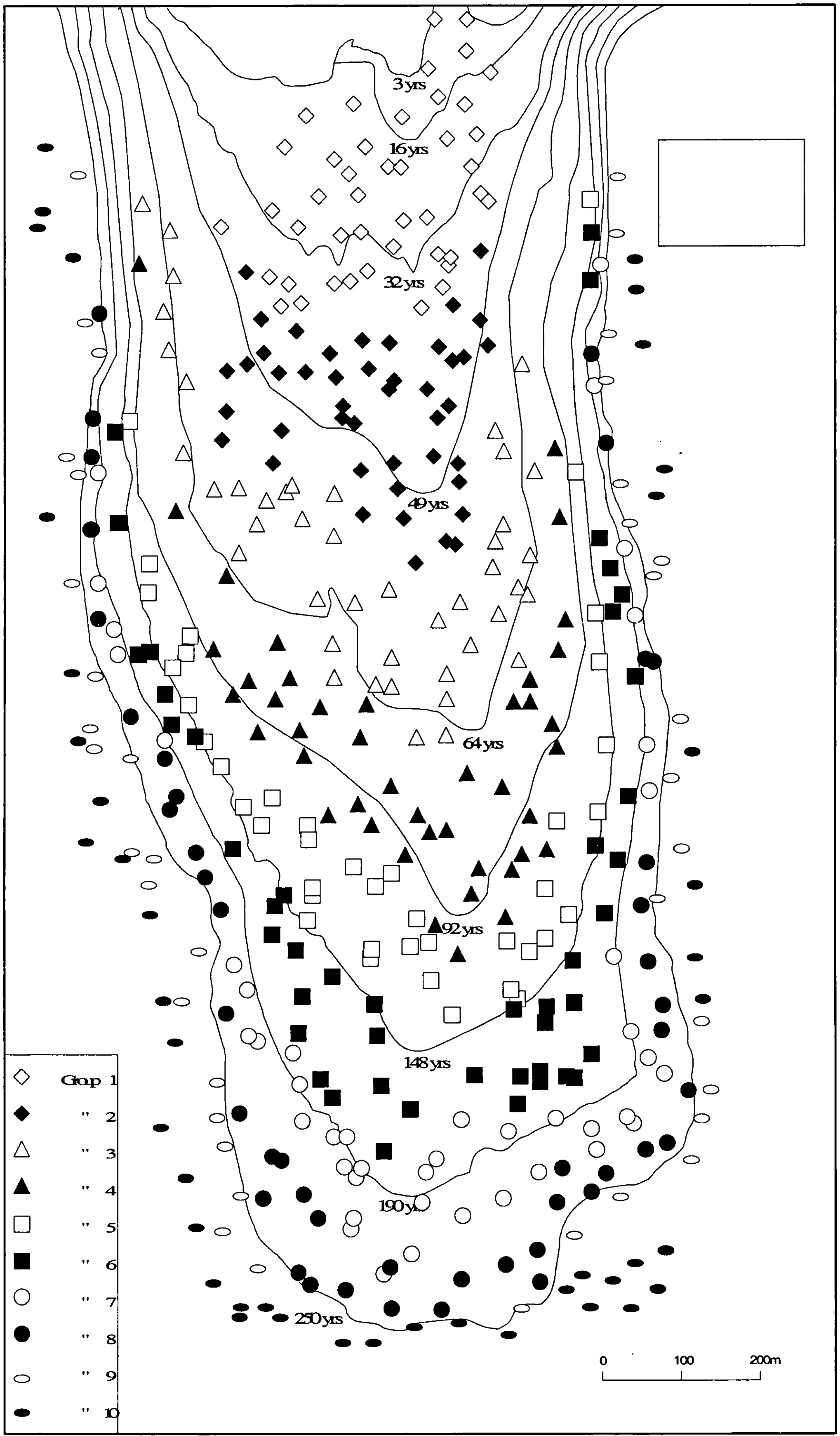


Figure 4.1: Spatial distribution of age groups
Dating on isochrones is that applying in 2000
(see Table 4.4 for age range of sites included in each group).

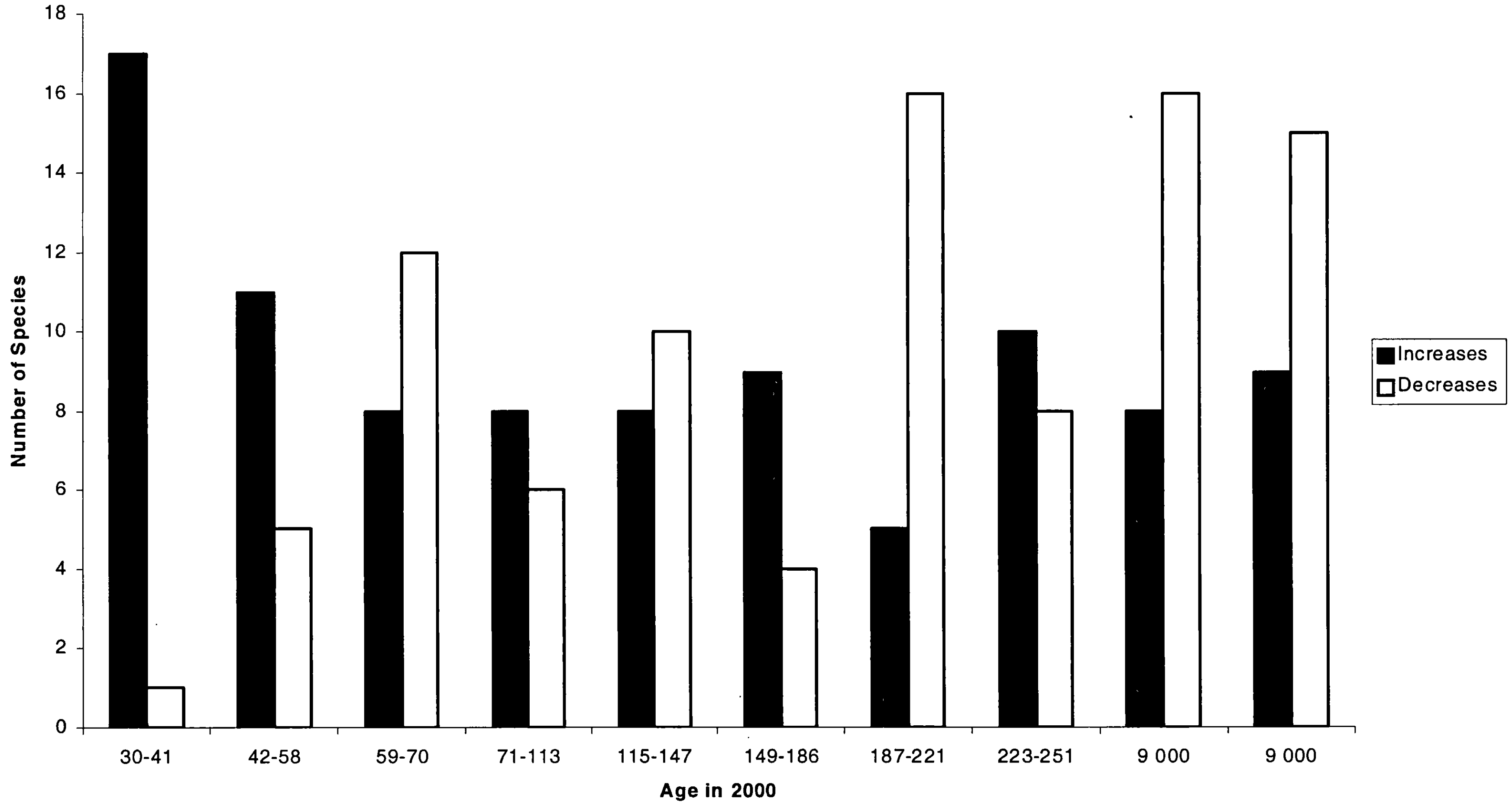


Figure 4.2: The number of species showing major changes in frequency summed by age group
The two groups aged 9000 years correspond to groups 9 and 10 (see section 4.3.1)

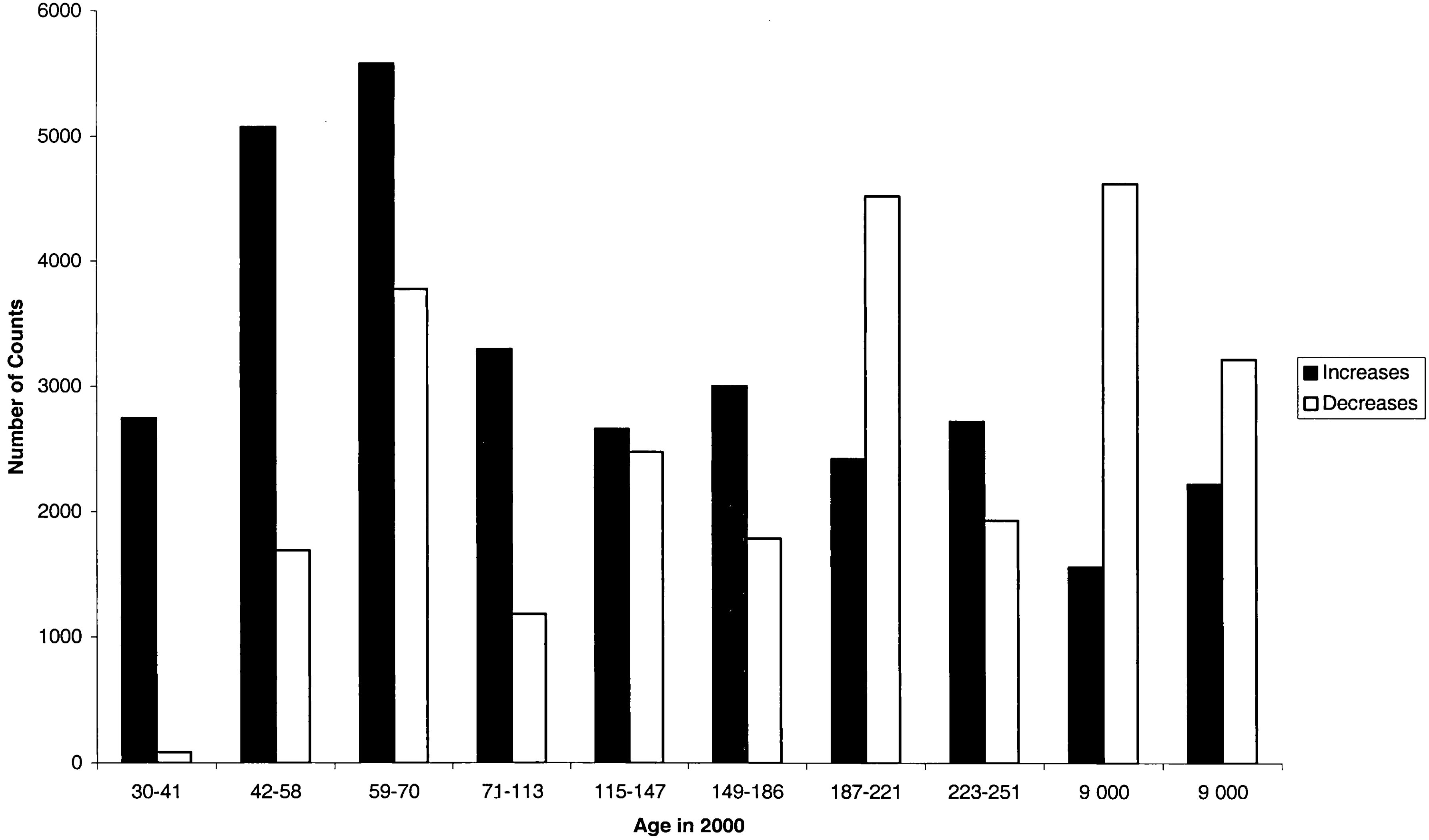
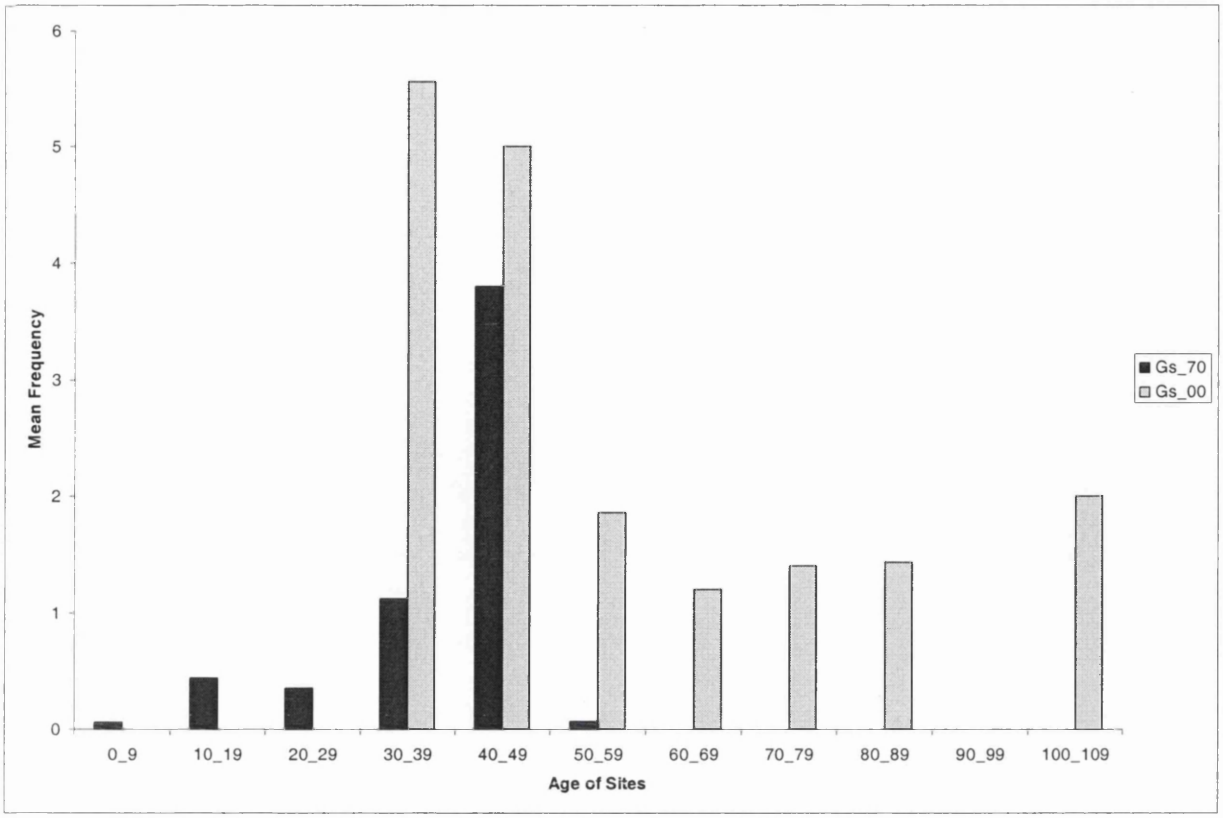


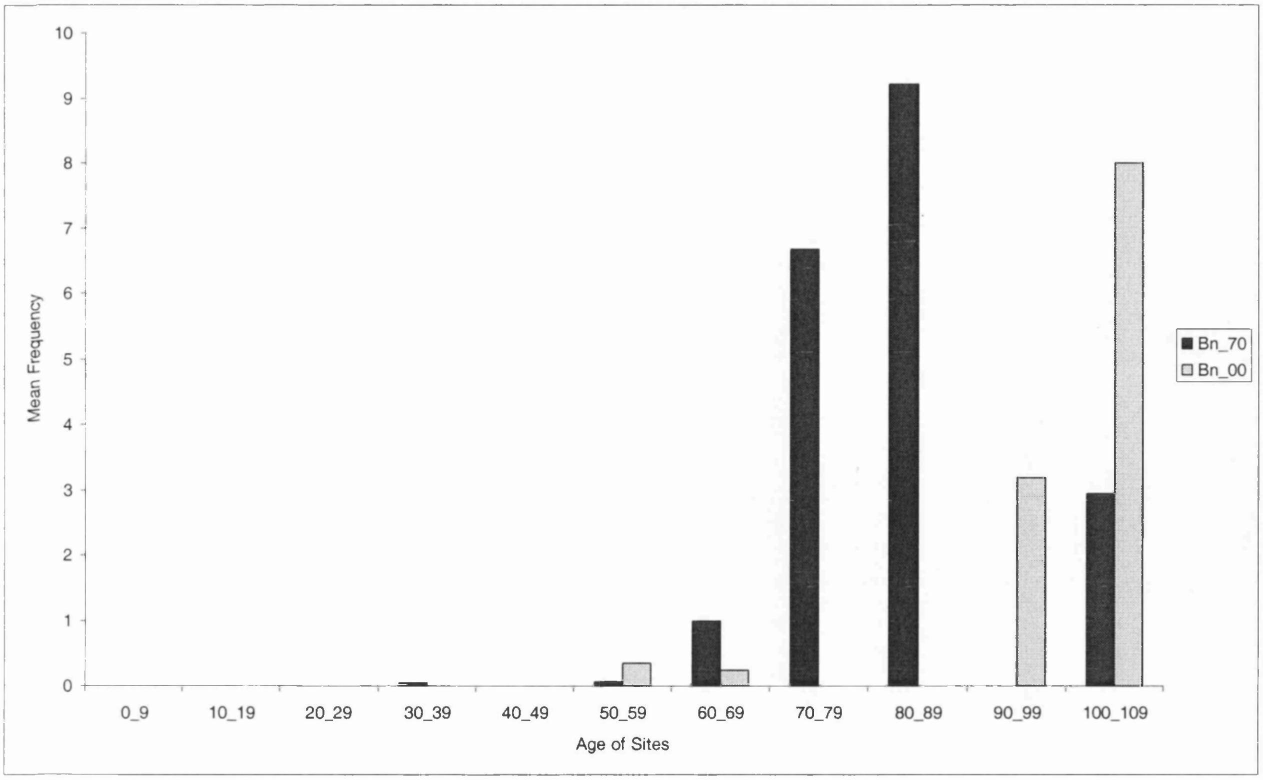
Figure 4.3: Changes in individual species frequency 1970 to 2000, summed by age group
(The two groups aged 9000 correspond to groups 9 and 10, see section 4.3.1.)



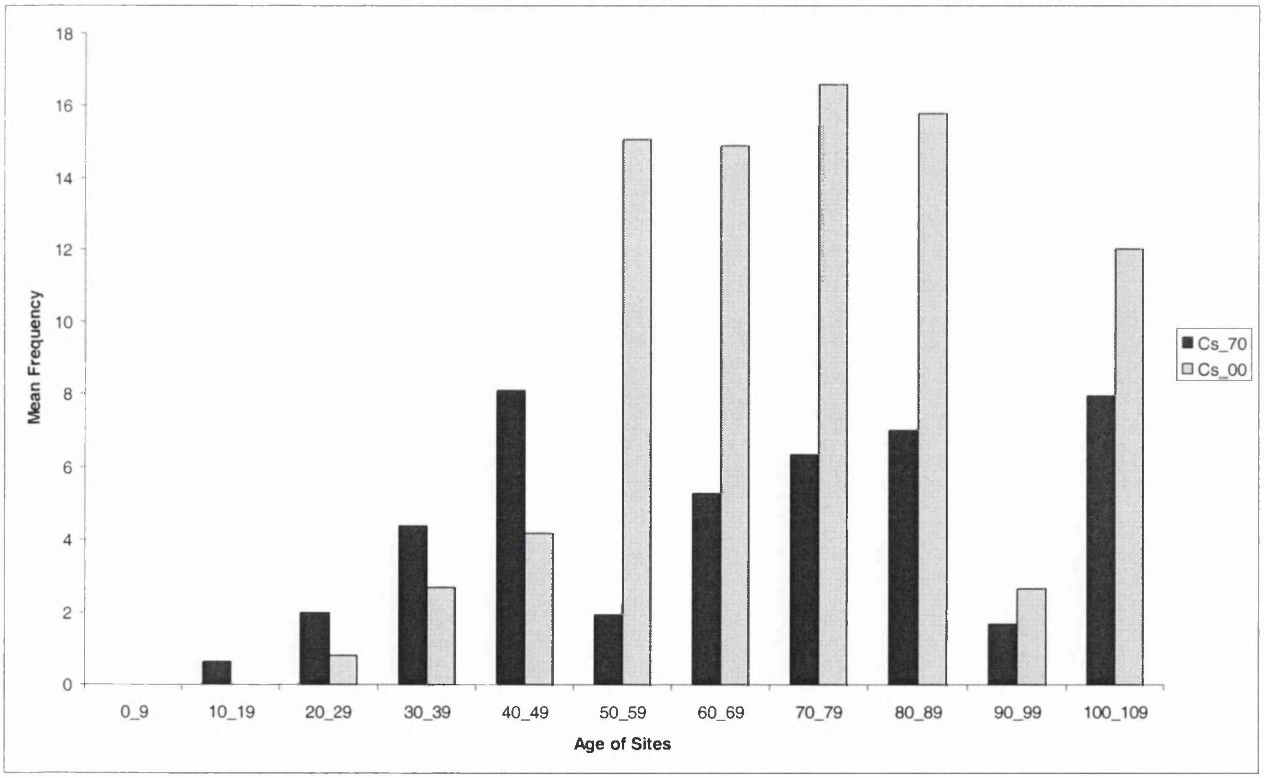
a) *Gnaphalium supinum*

Figure 4.4: Comparisons of frequencies on young terrain between 1970 and 2000
a) *Gnaphalium supinum*; b) *Betula nana*; c) *Carex* spp.; d) *Empetrum hermaphroditum*
and e) *Salix glauca*

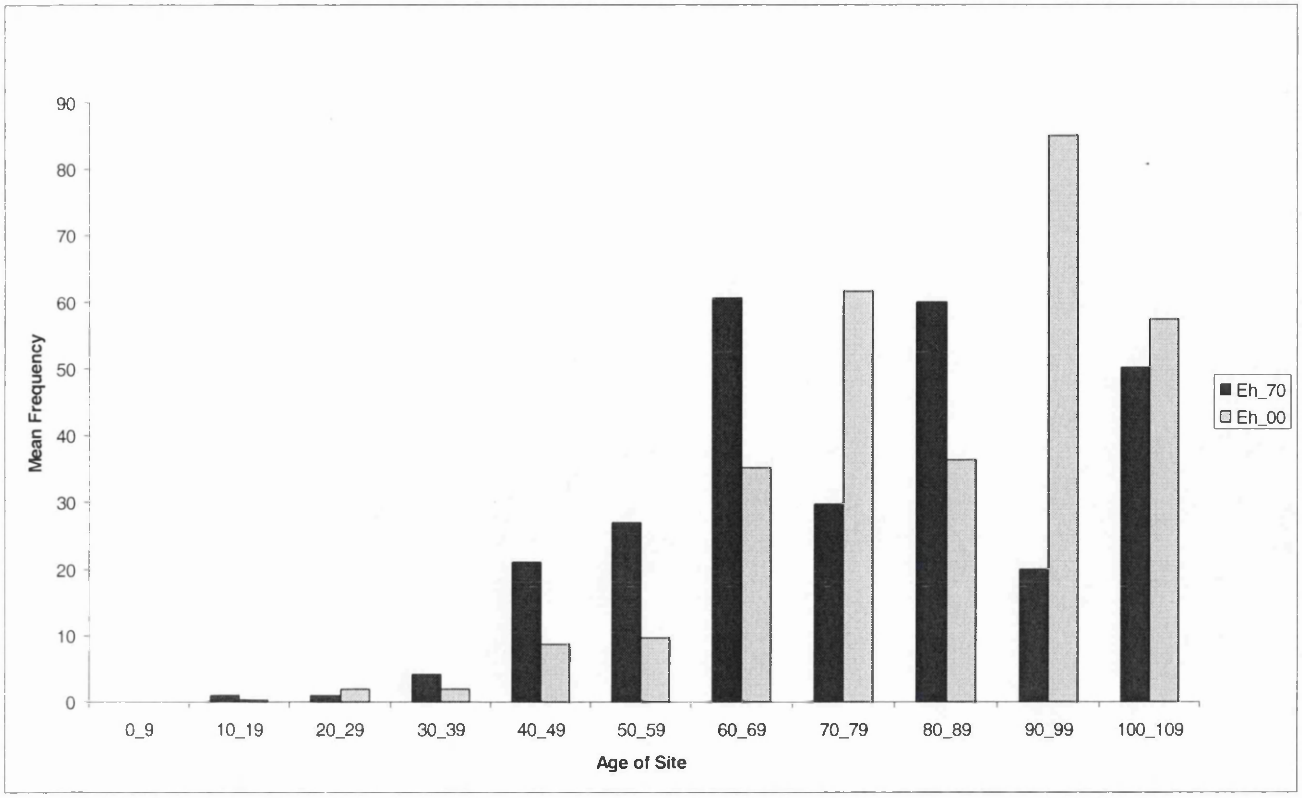
(The graphs show mean frequency in 10 year age bands for the youngest sites in each dataset
and include the 24 new sites established in 2000)



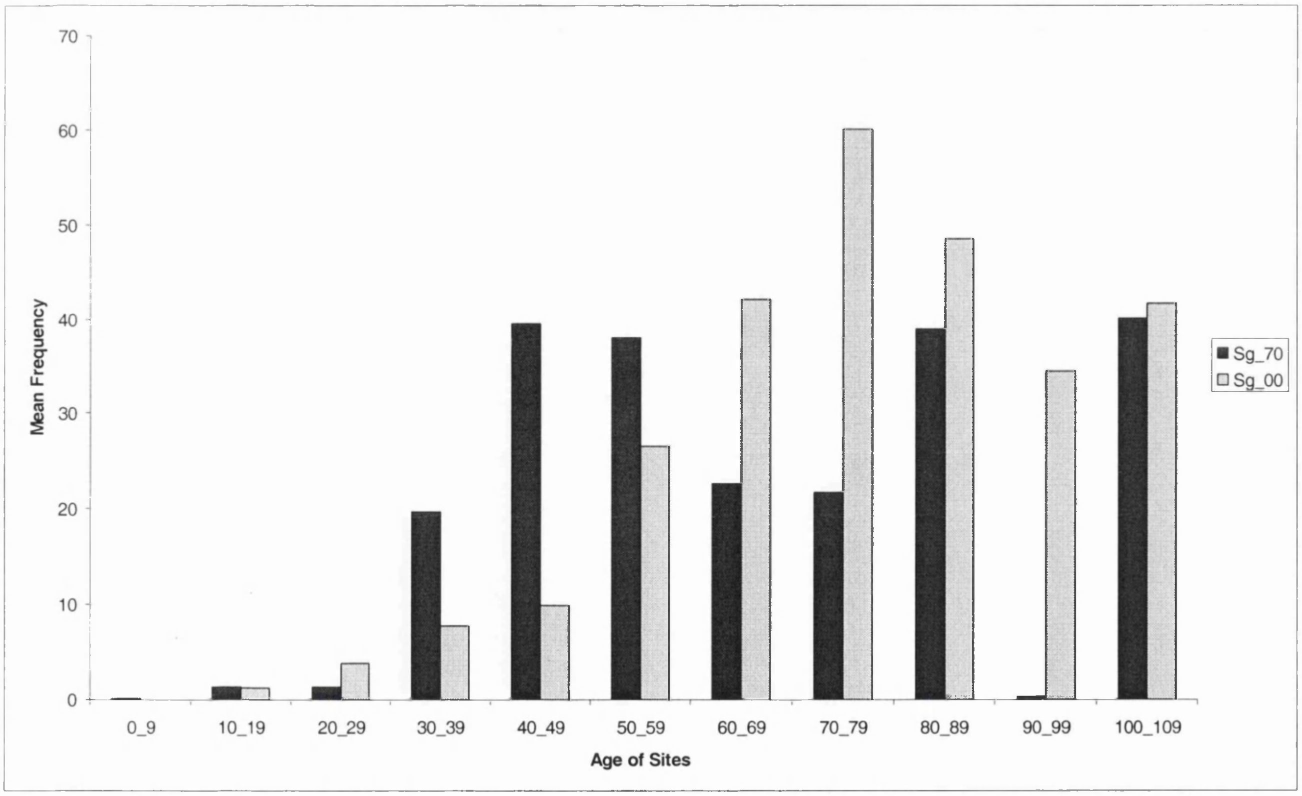
b) *Betula nana*



c) *Carex spp.*



d) *Empetrum hermaphroditum*



e) *Salix glauca*

Figure 4.5 *Arctostaphylos* spp.: A, frequency in 1970; B, change in frequency 1970-2000; C, frequency in 2000

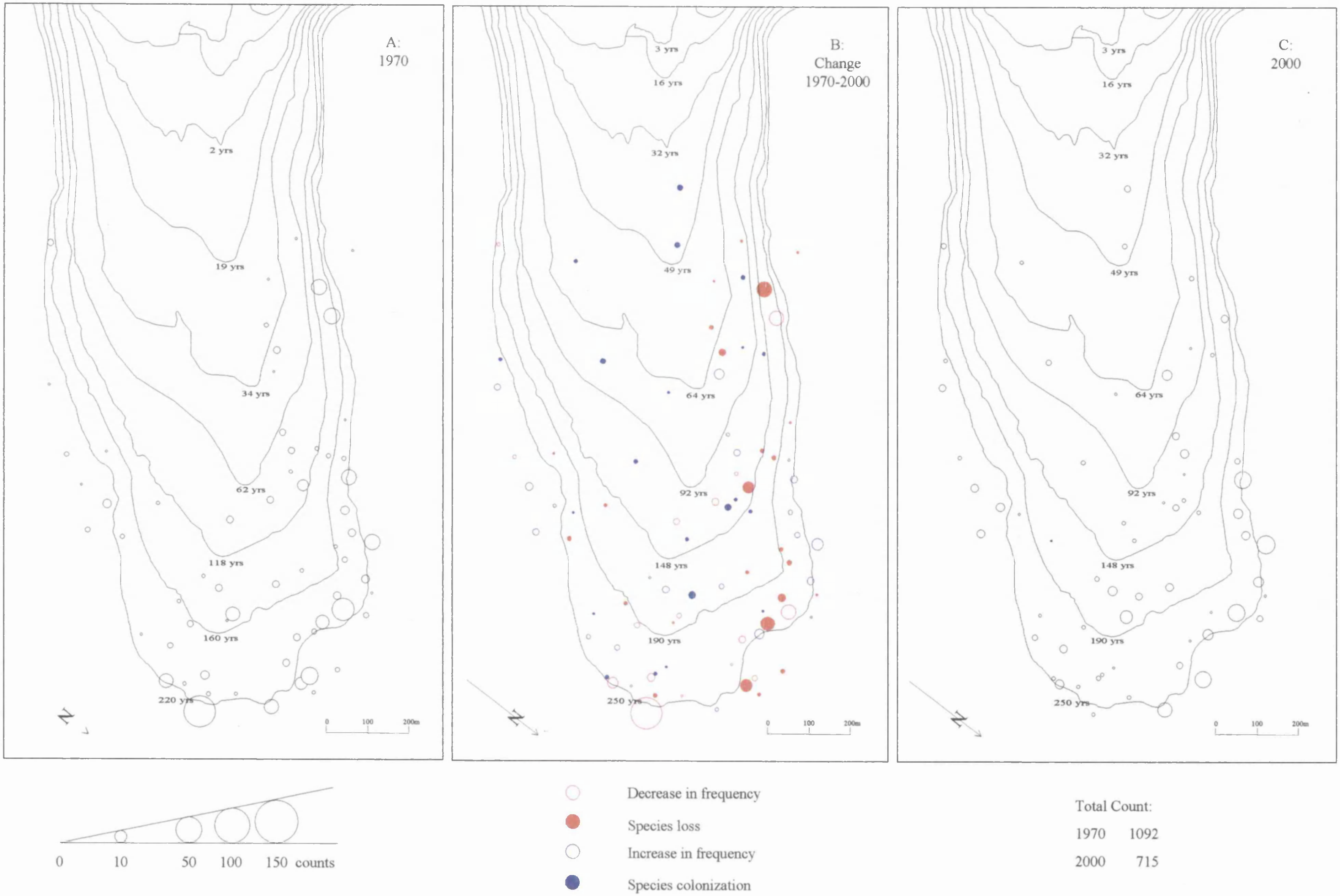


Figure 4.6 *Betula nana*: A, frequency in 1970; B, change in frequency 1970-2000; C, frequency in 2000

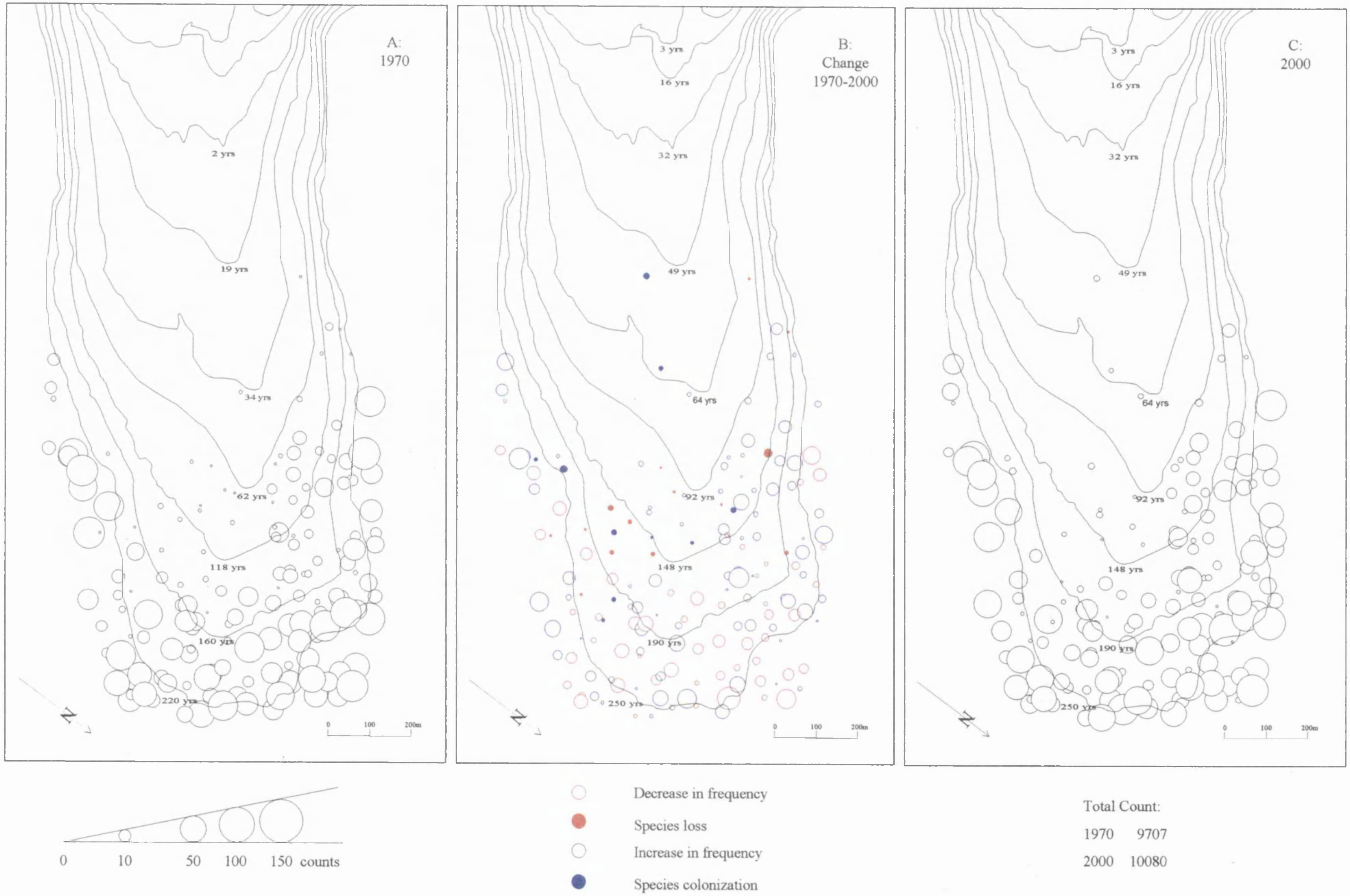


Figure 4.7 *Betula pubescens* ssp *carpatica*: A, frequency in 1970; B, change in frequency 1970-2000; C, frequency in 2000

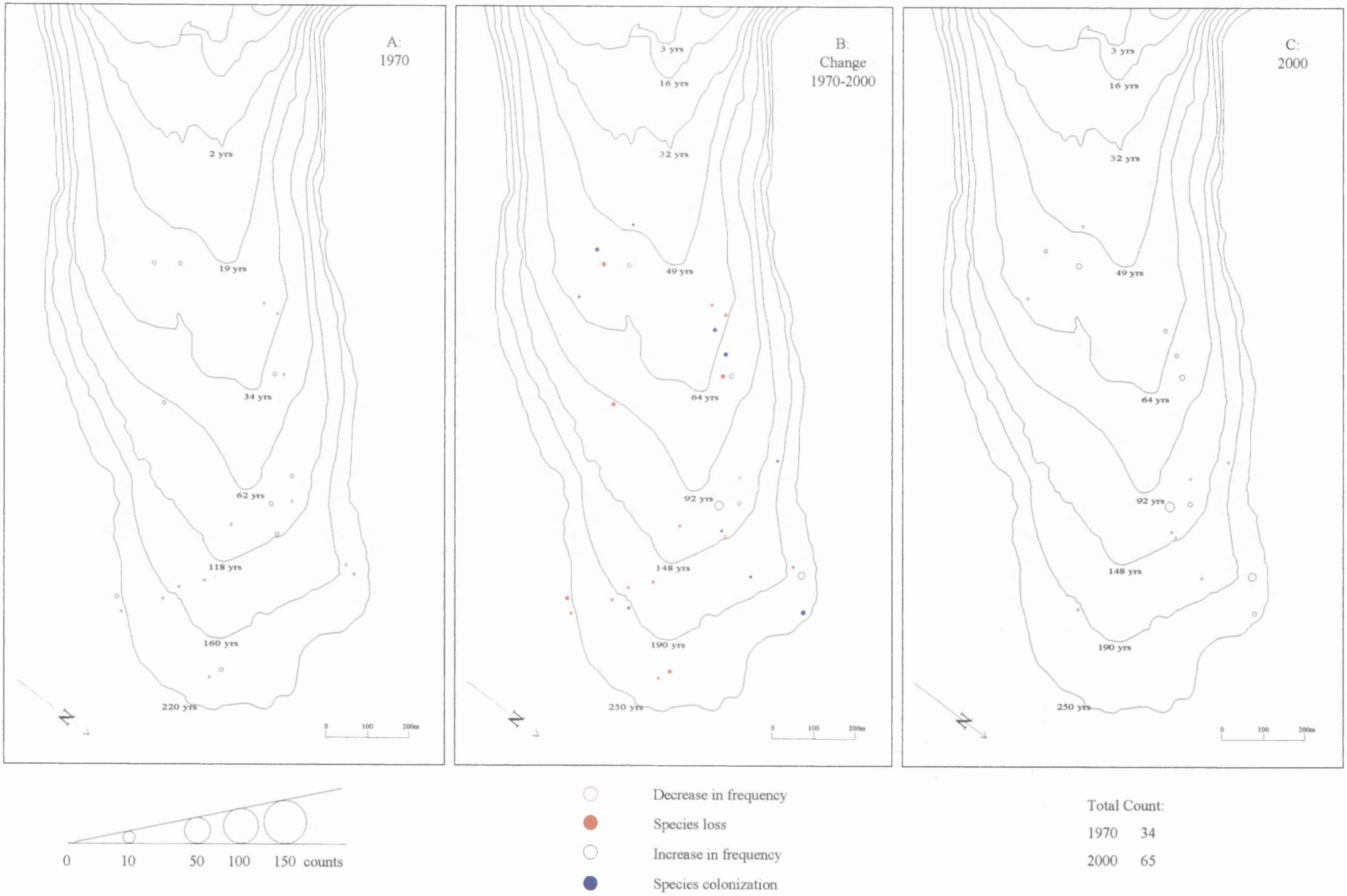


Figure 4.8 *Cassiope hypnoides*: A, frequency in 1970; B, change in frequency 1970-2000; C, frequency in 2000

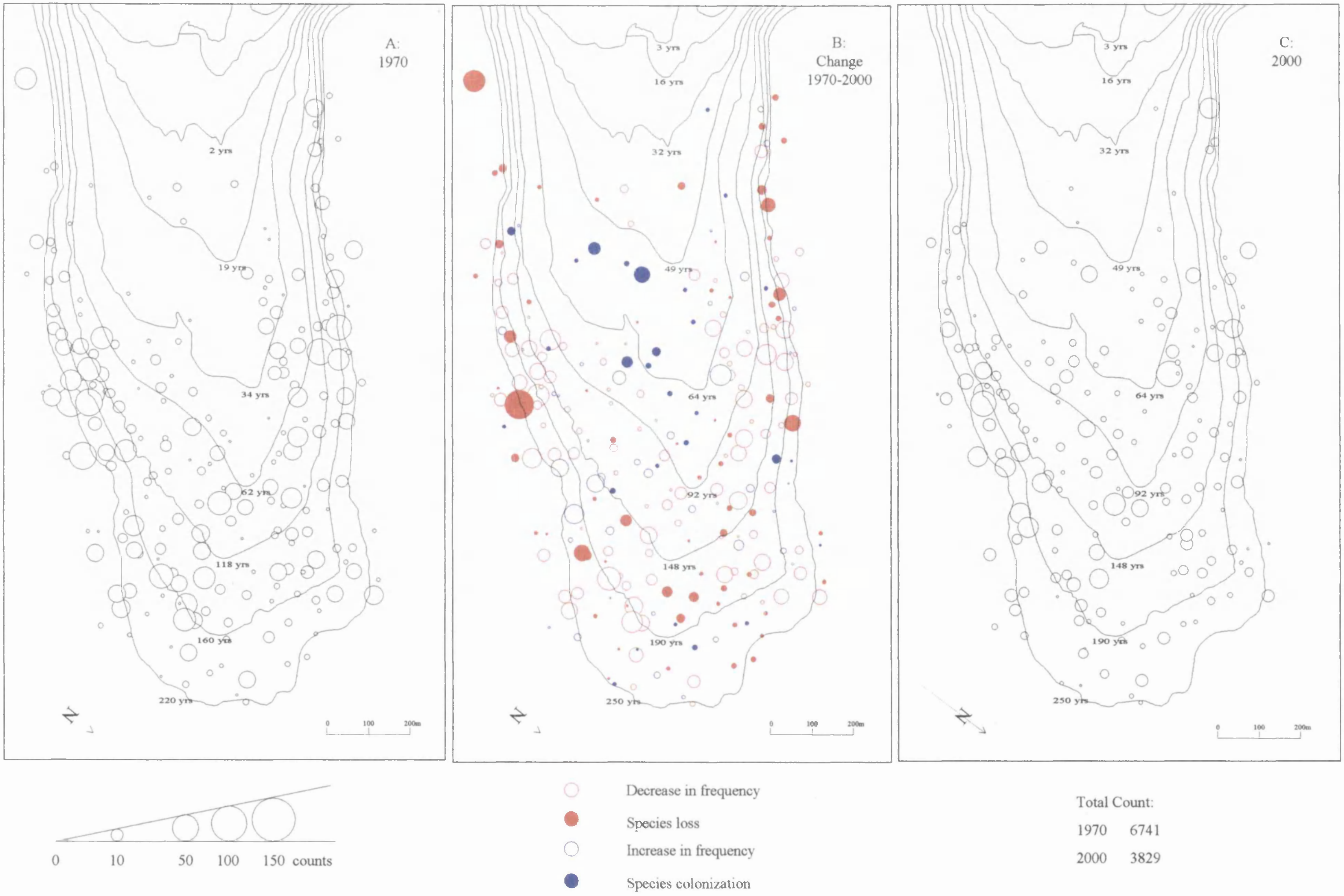


Figure 4.9 *Empetrum hermaphroditum*: A, frequency in 1970; B, change in frequency 1970-2000; C, frequency in 2000

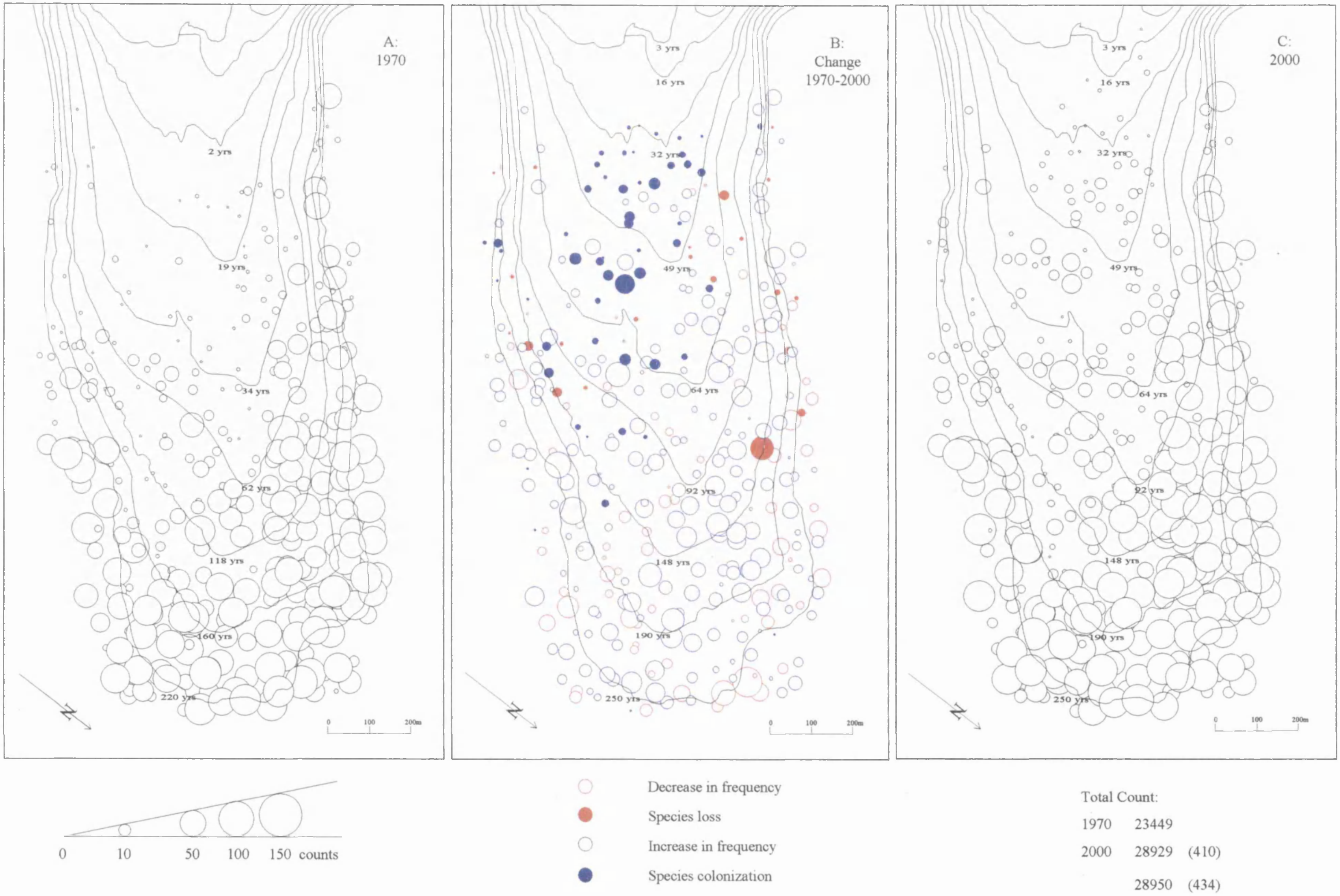


Figure 4.10 *Juniperus communis*: A, frequency in 1970; B, change in frequency 1970-2000; C, frequency in 2000

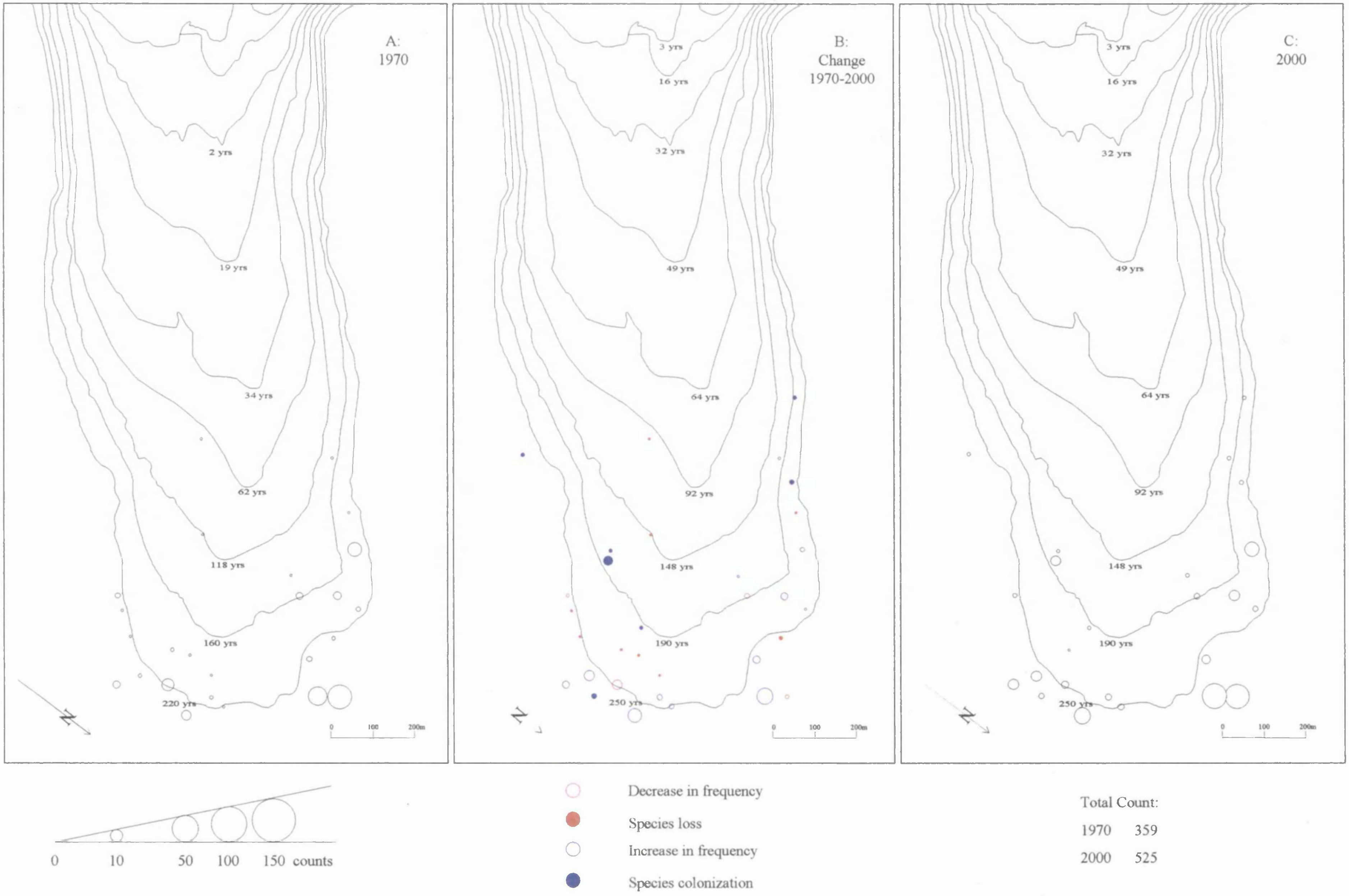


Figure 4.11 *Loiseleuria procumbens*: A, frequency in 1970; B, change in frequency 1970-2000; C, frequency in 2000

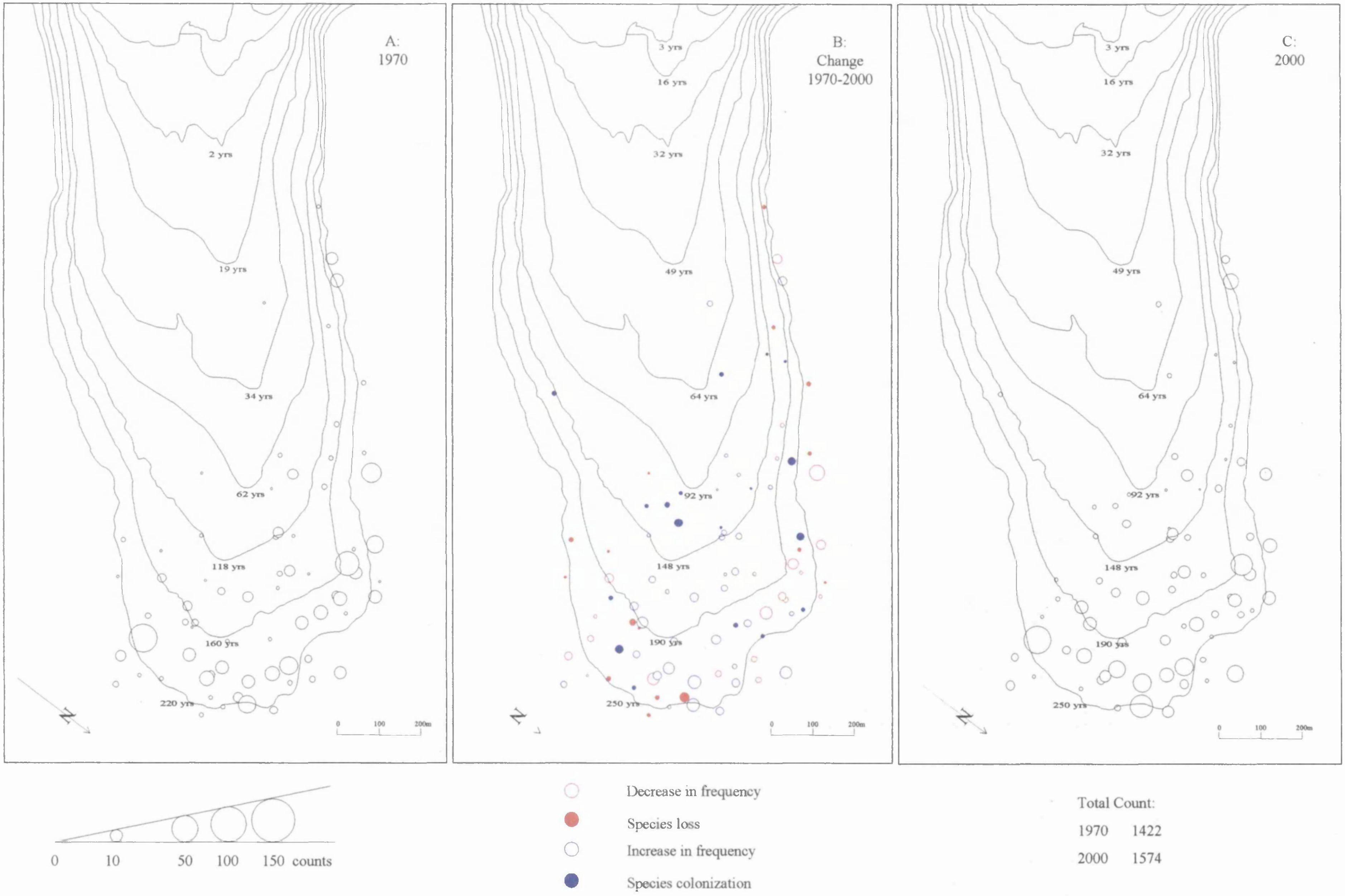


Figure 4.12 *Phyllodoce caerulea*: A, frequency in 1970; B, change in frequency 1970-2000; C, frequency in 2000

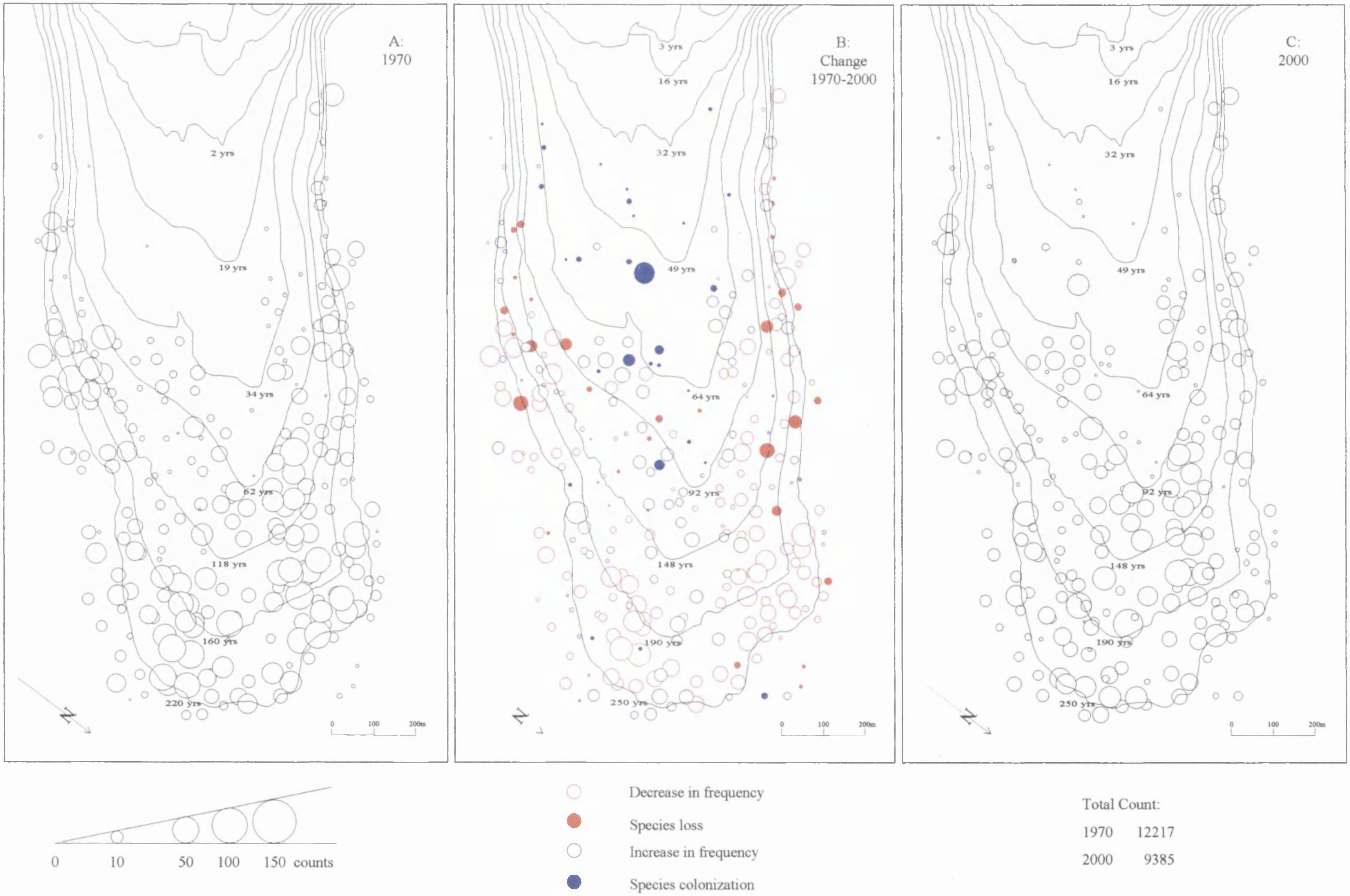


Figure 4.13 *Salix glauca*: A, frequency in 1970; B, change in frequency 1970-2000; C, frequency in 2000

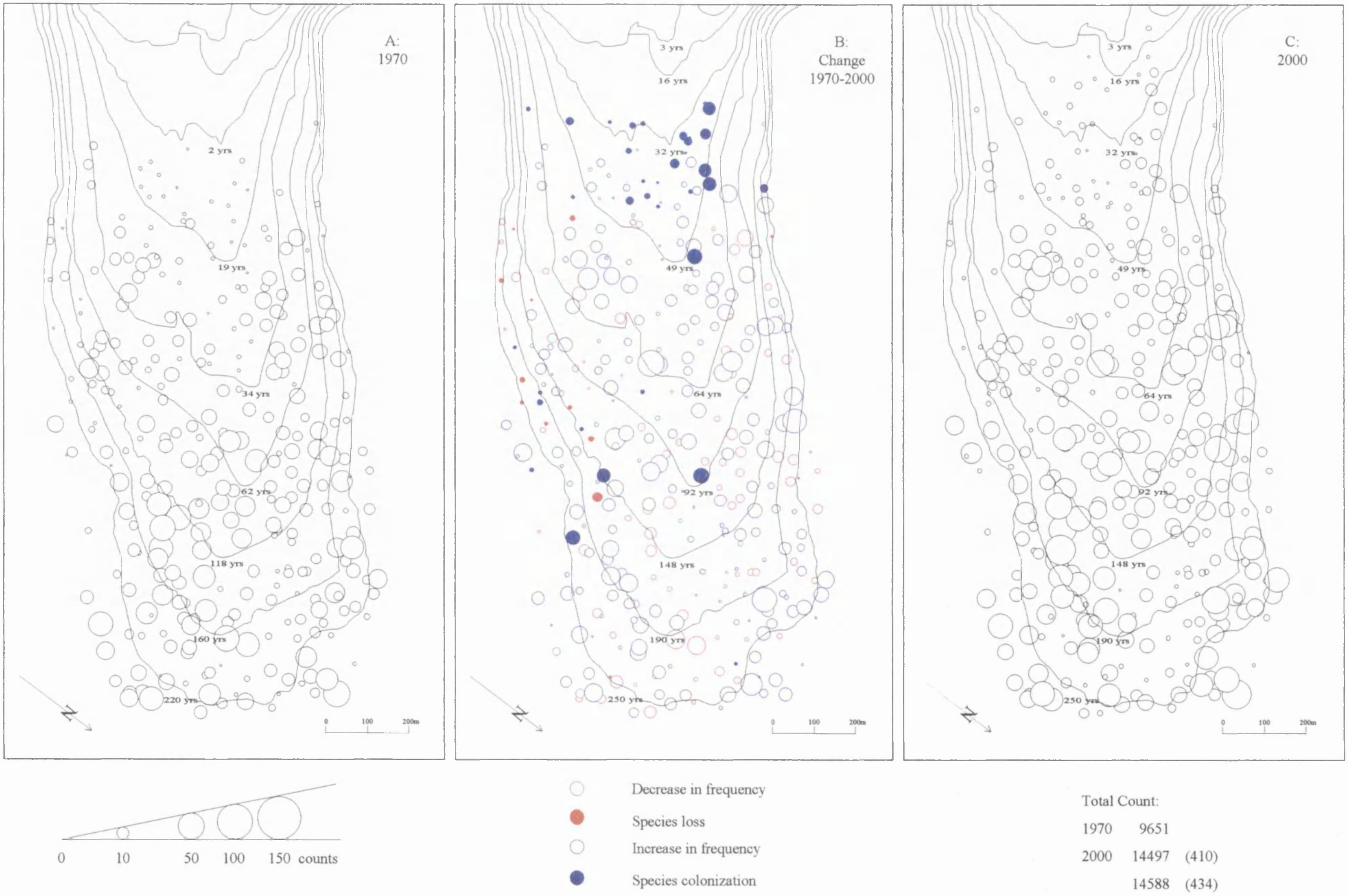


Figure 4.14 *Salix herbacea*: A, frequency in 1970; B, change in frequency 1970-2000; C, frequency in 2000

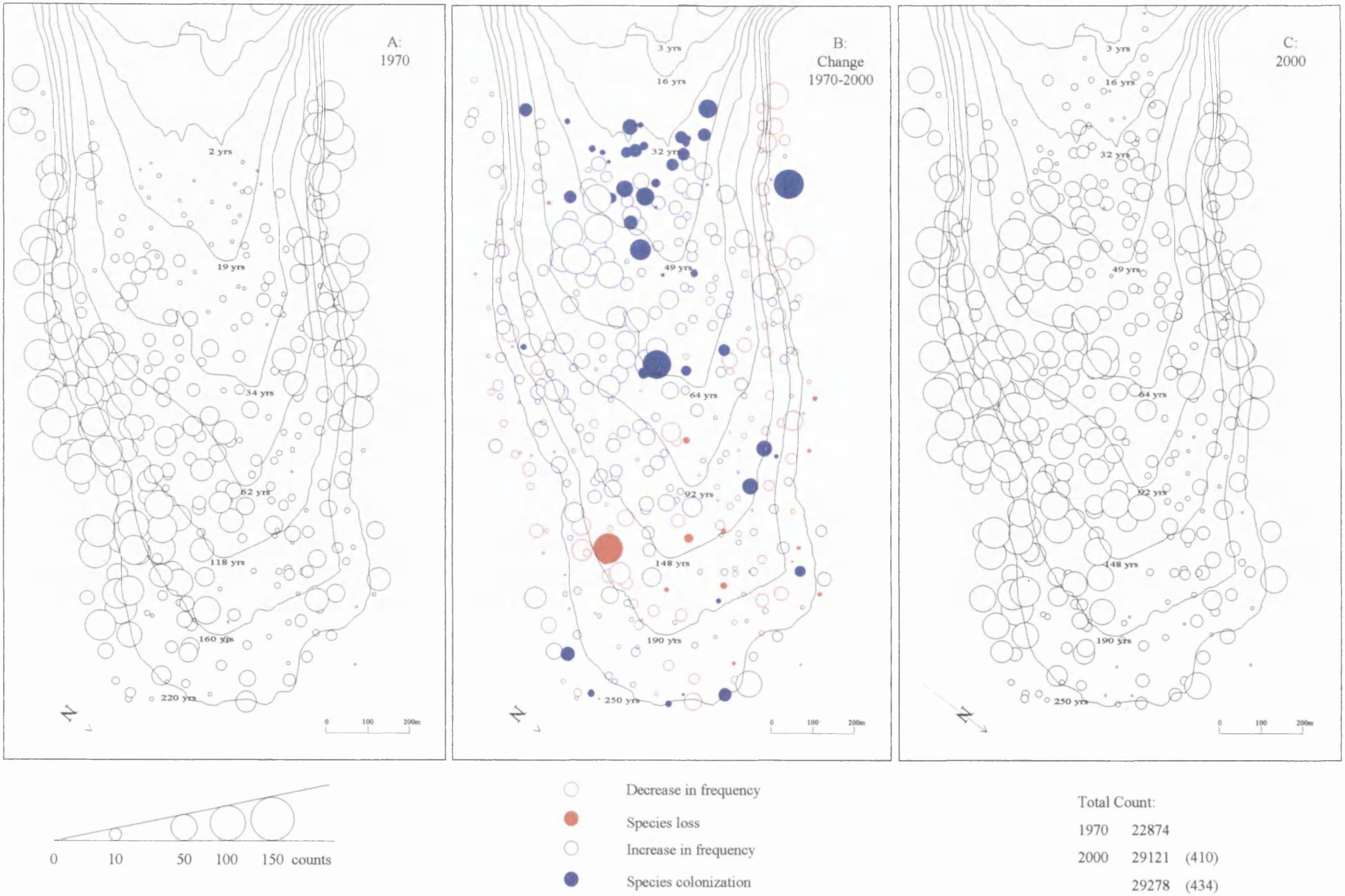


Figure 4.15 *Salix lanata*: A, frequency in 1970; B, change in frequency 1970-2000; C, frequency in 2000

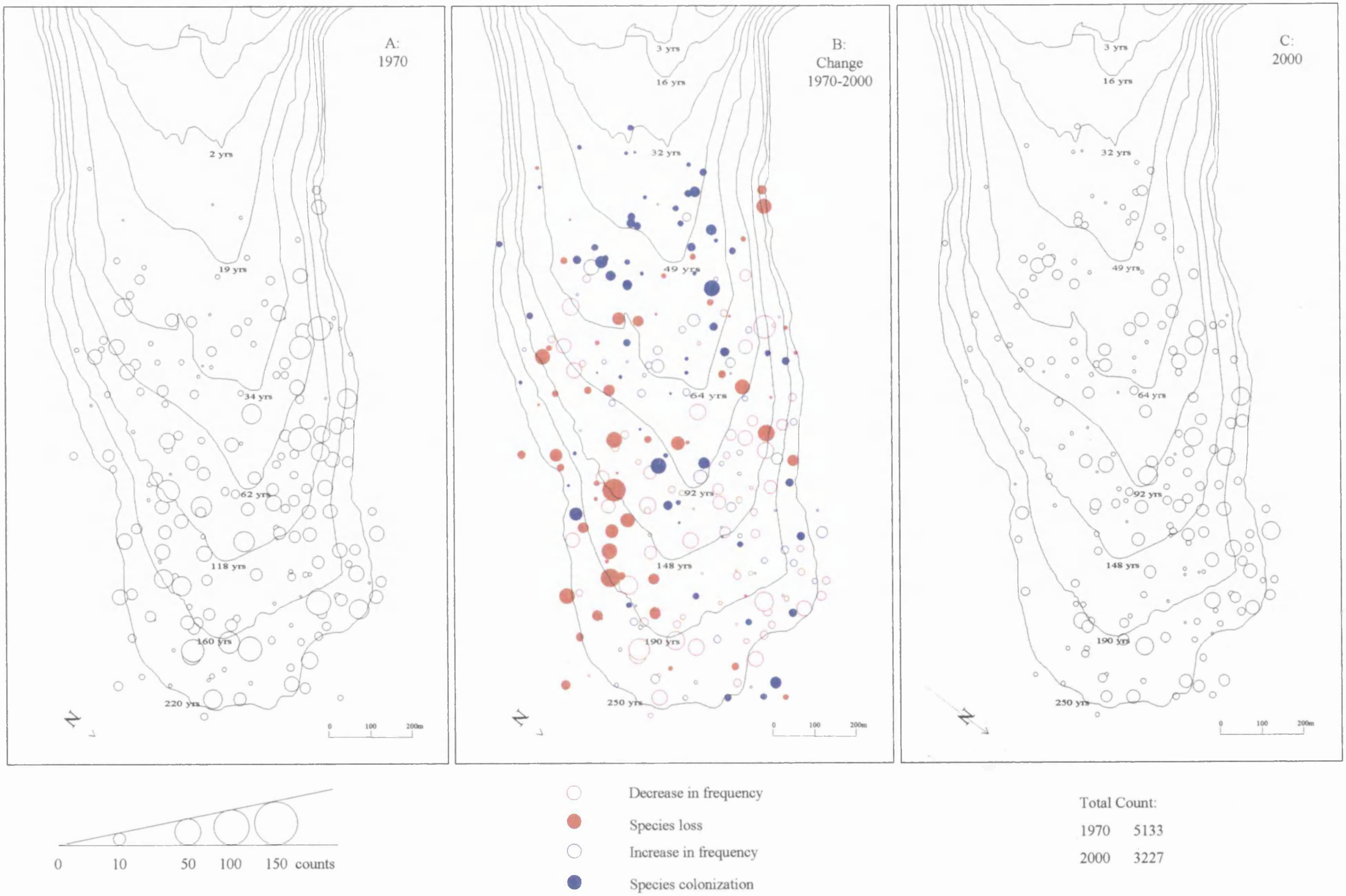


Figure 4.16 *Salix myrsinites*: A, frequency in 1970; B, change in frequency 1970-2000; C, frequency in 2000

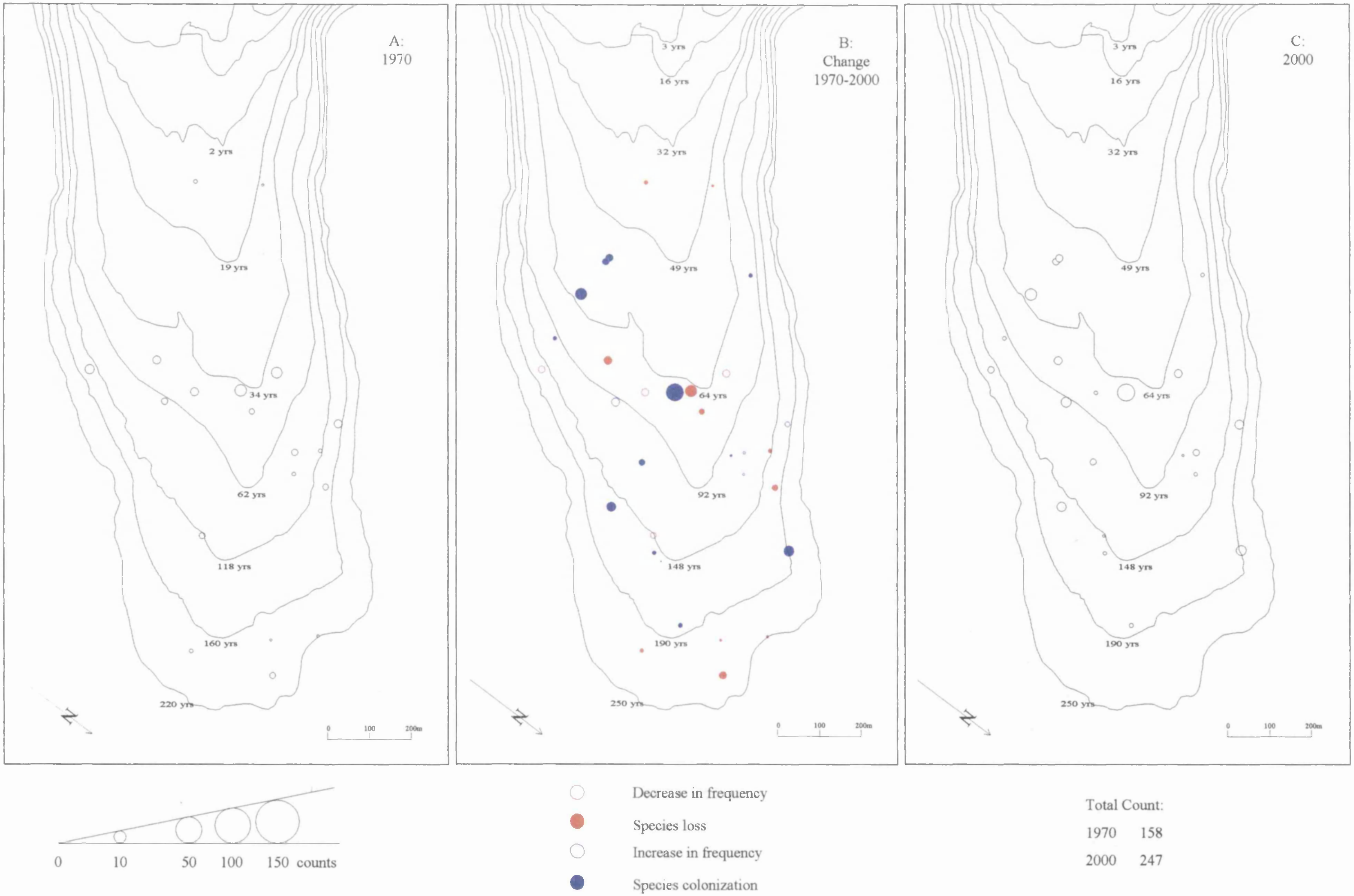


Figure 4.17 *Salix phylicifolia*: A, frequency in 1970; B, change in frequency 1970-2000; C, frequency in 2000

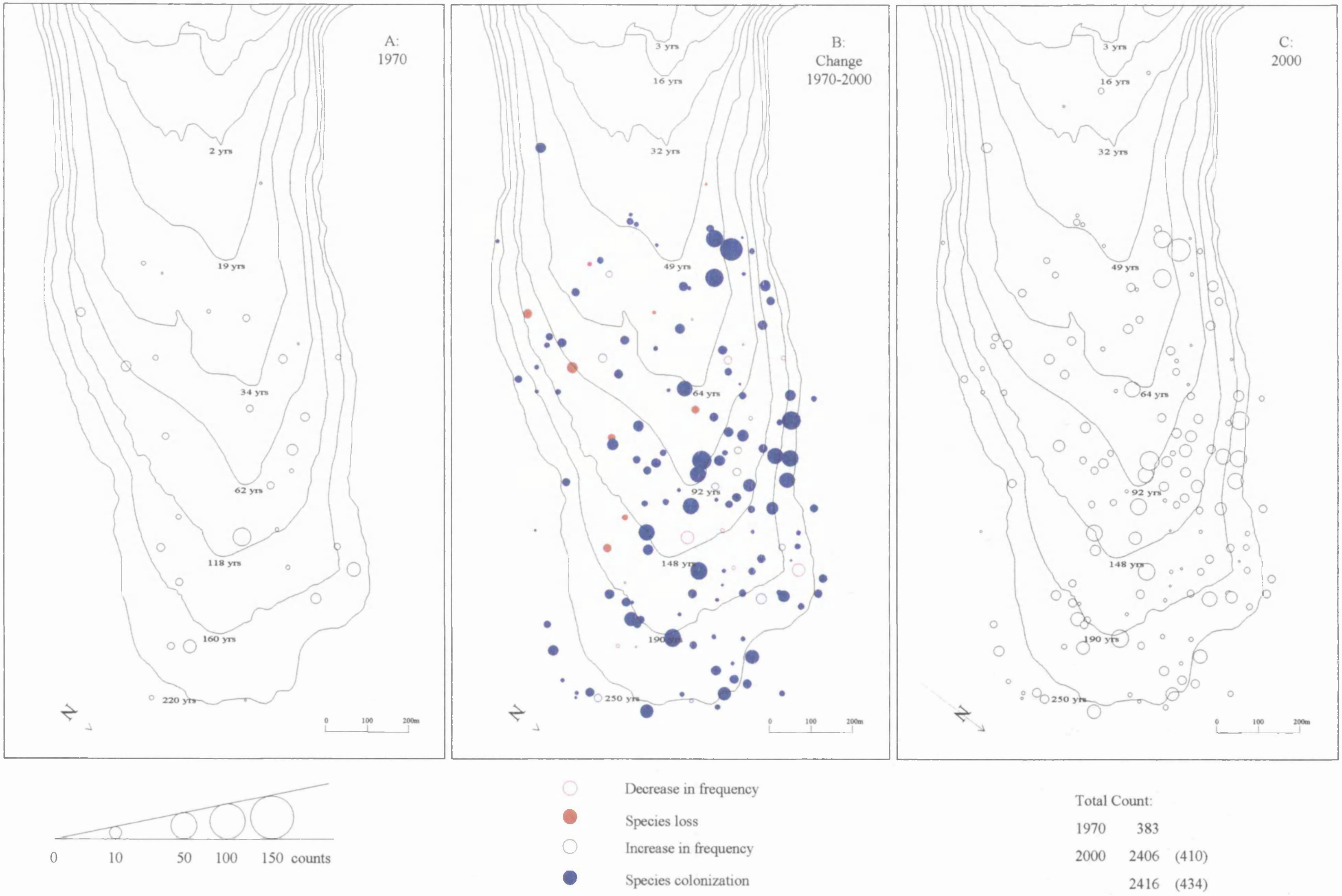


Figure 4.18 *Vaccinium myrtillus*: A, frequency in 1970; B, change in frequency 1970-2000; C, frequency in 2000

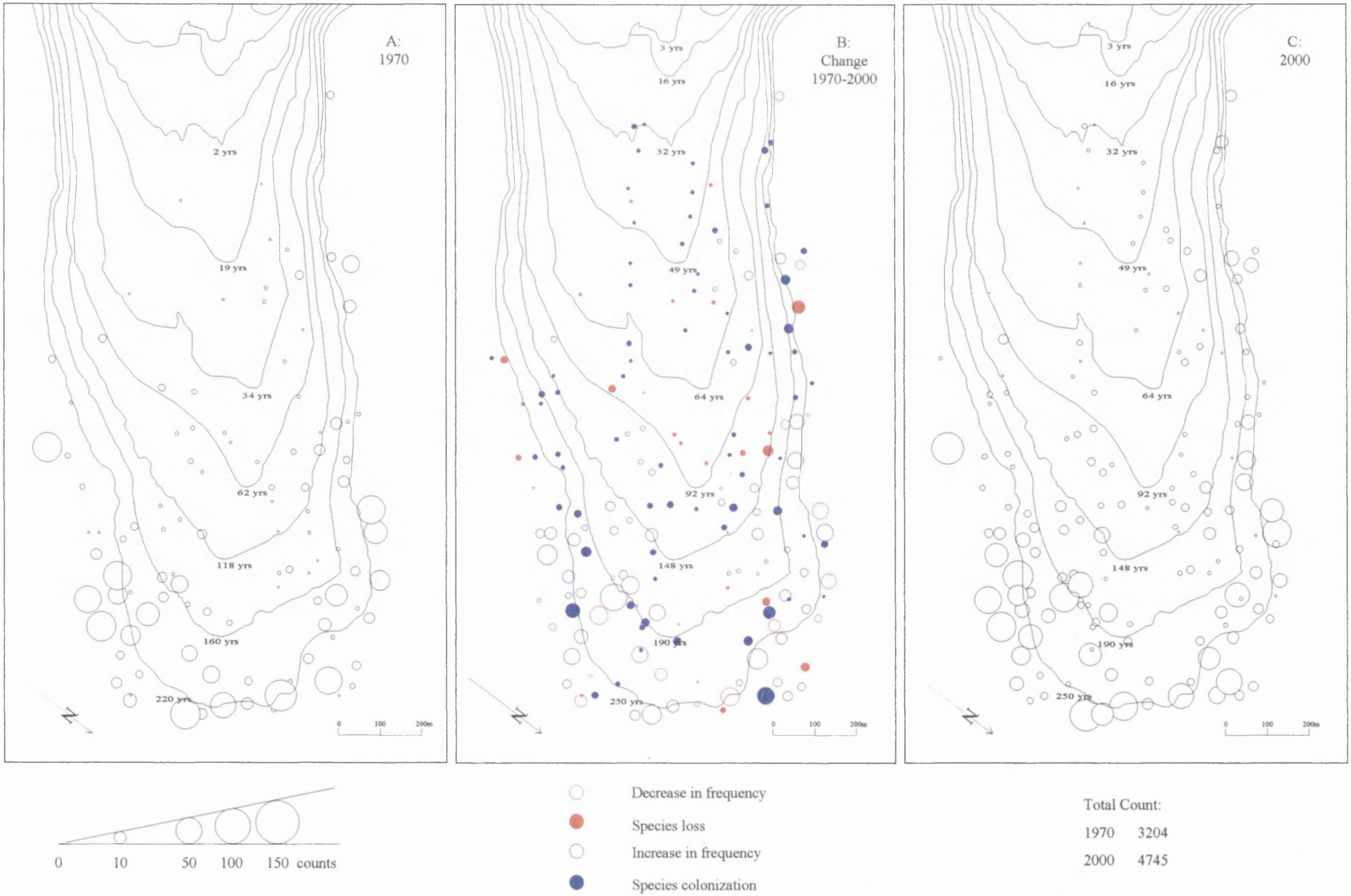


Figure 4.19 *Vaccinium uliginosum*: A, frequency in 1970; B, change in frequency 1970-2000; C, frequency in 2000

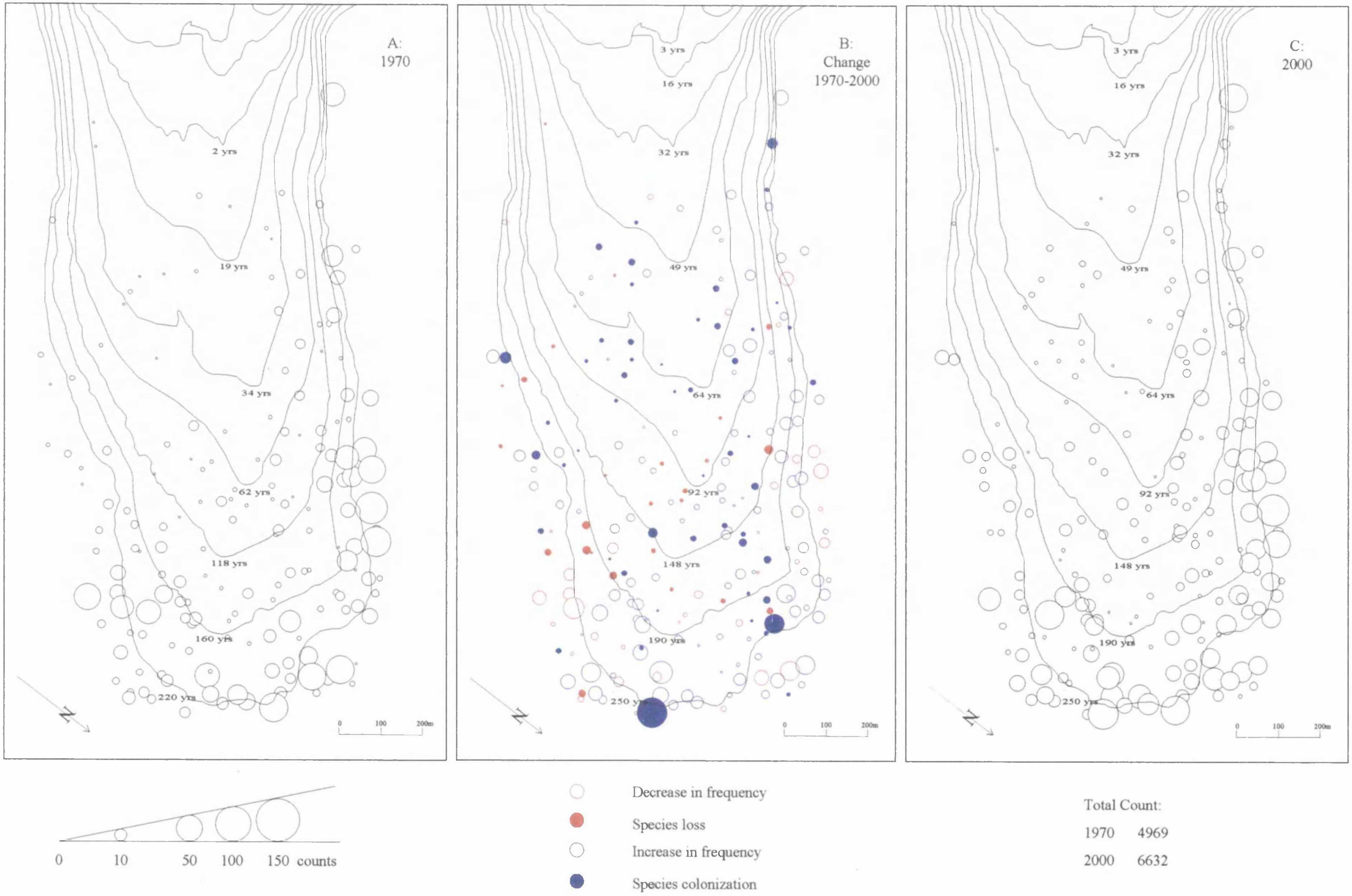


Figure 4.20 *Vaccinium vitis-idaea*: A, frequency in 1970; B, change in frequency 1970-2000; C, frequency in 2000

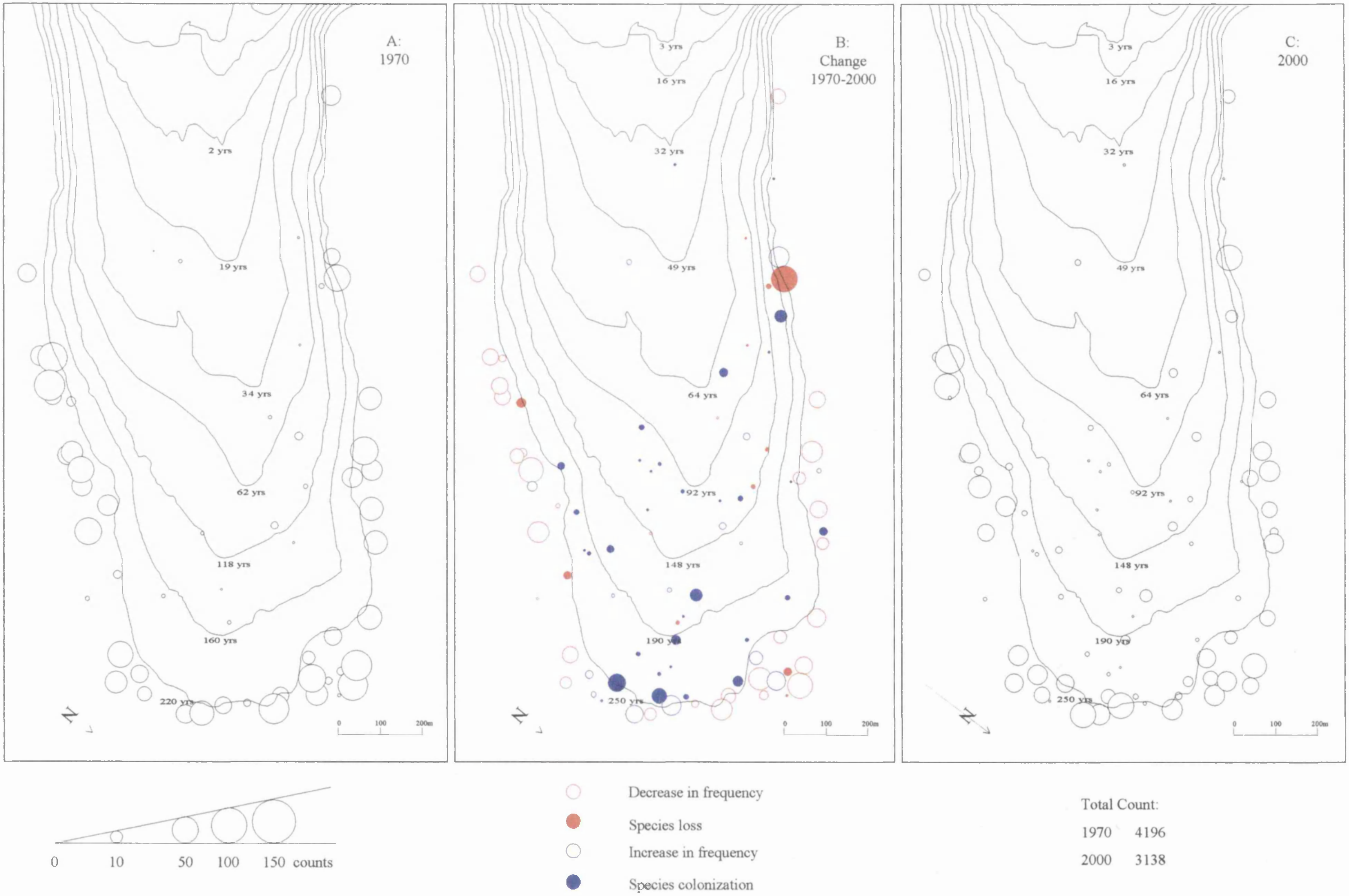


Figure 4.21 *Arabis alpina*: A, frequency in 1970; B, change in frequency 1970-2000; C, frequency in 2000

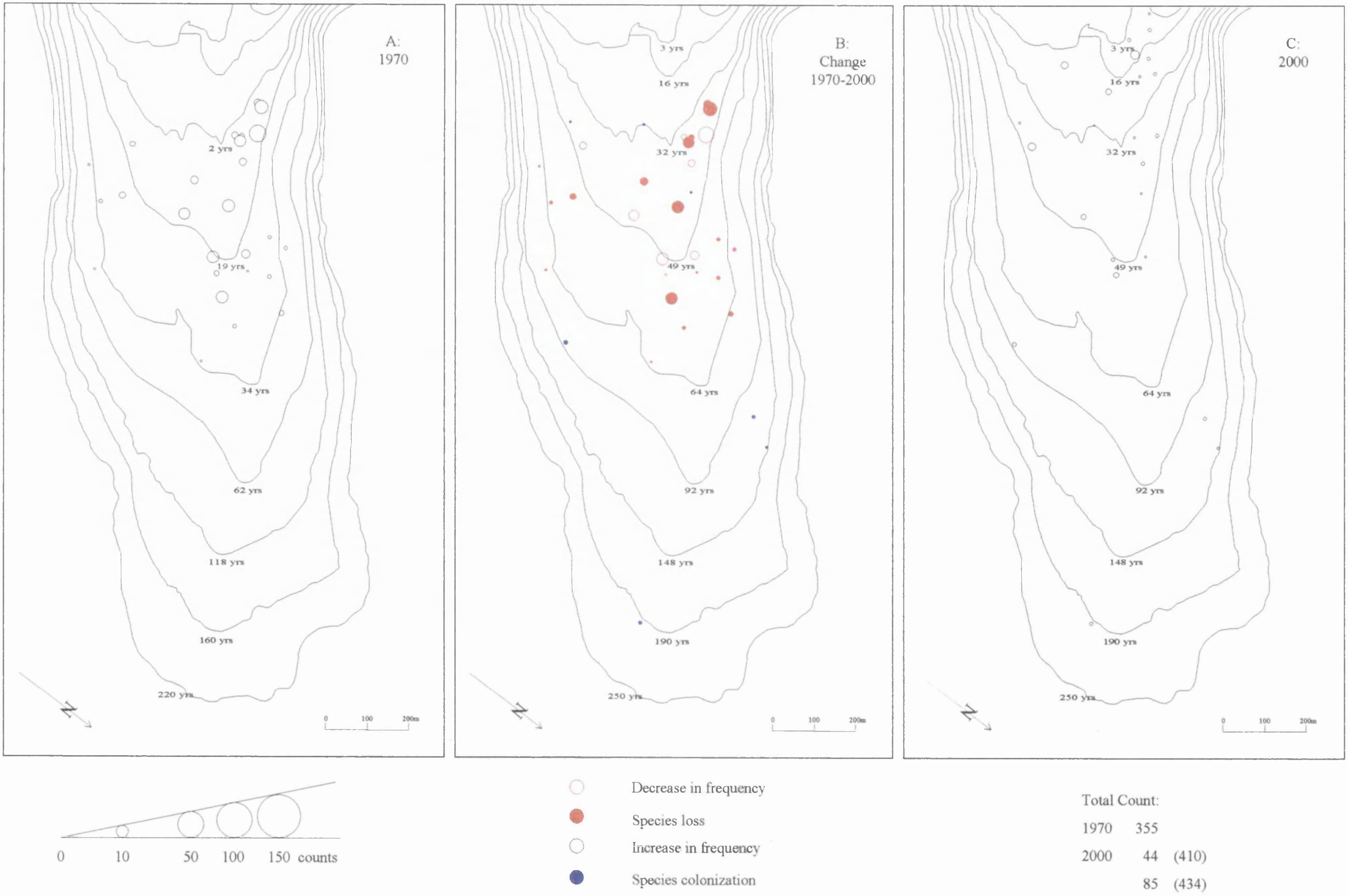


Figure 4.22 *Arenaria* spp.: A, frequency in 1970; B, change in frequency 1970-2000; C, frequency in 2000

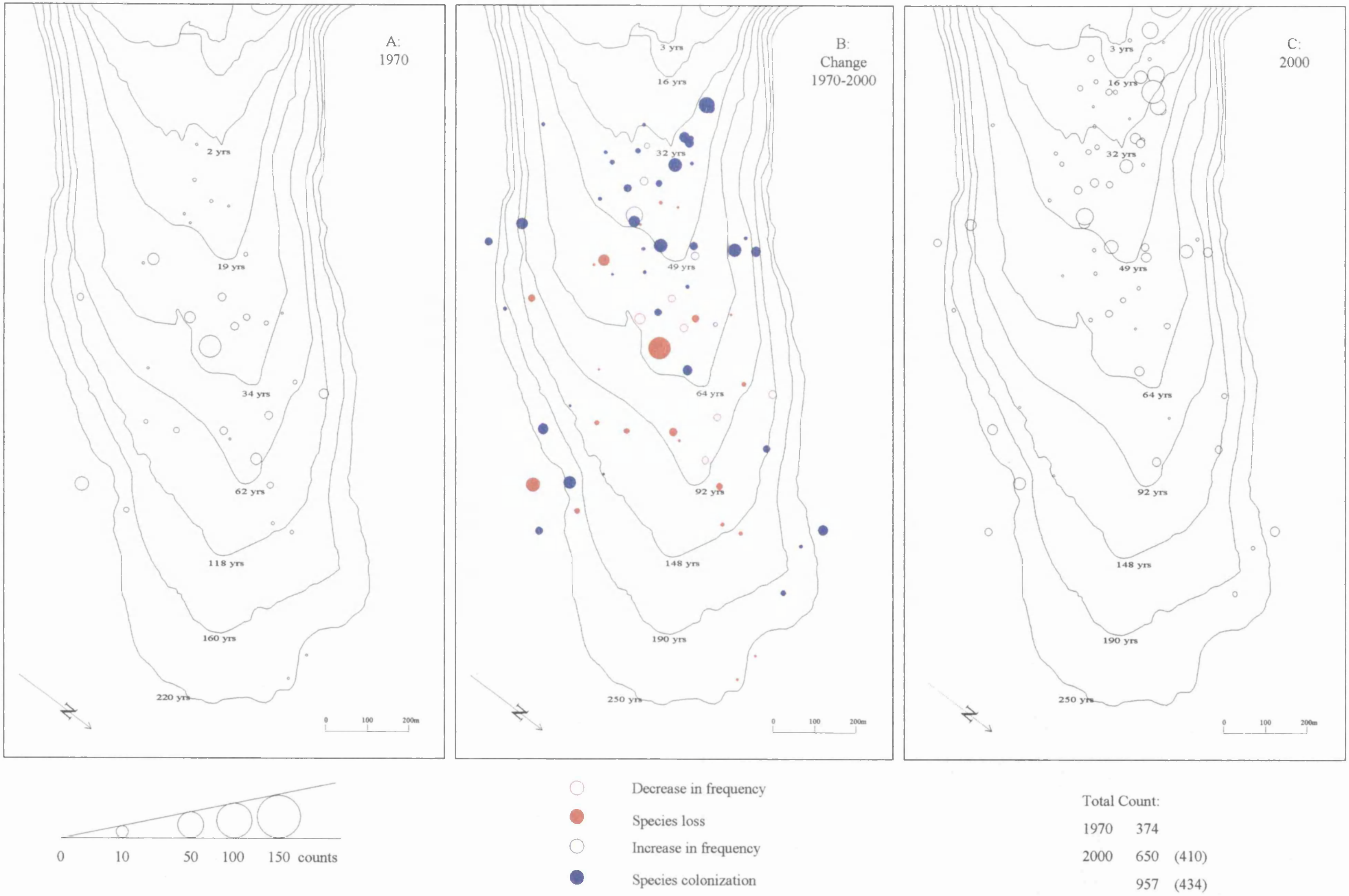


Figure 4.23 *Cerastium alpinum*: A, frequency in 1970; B, change in frequency 1970-2000; C, frequency in 2000

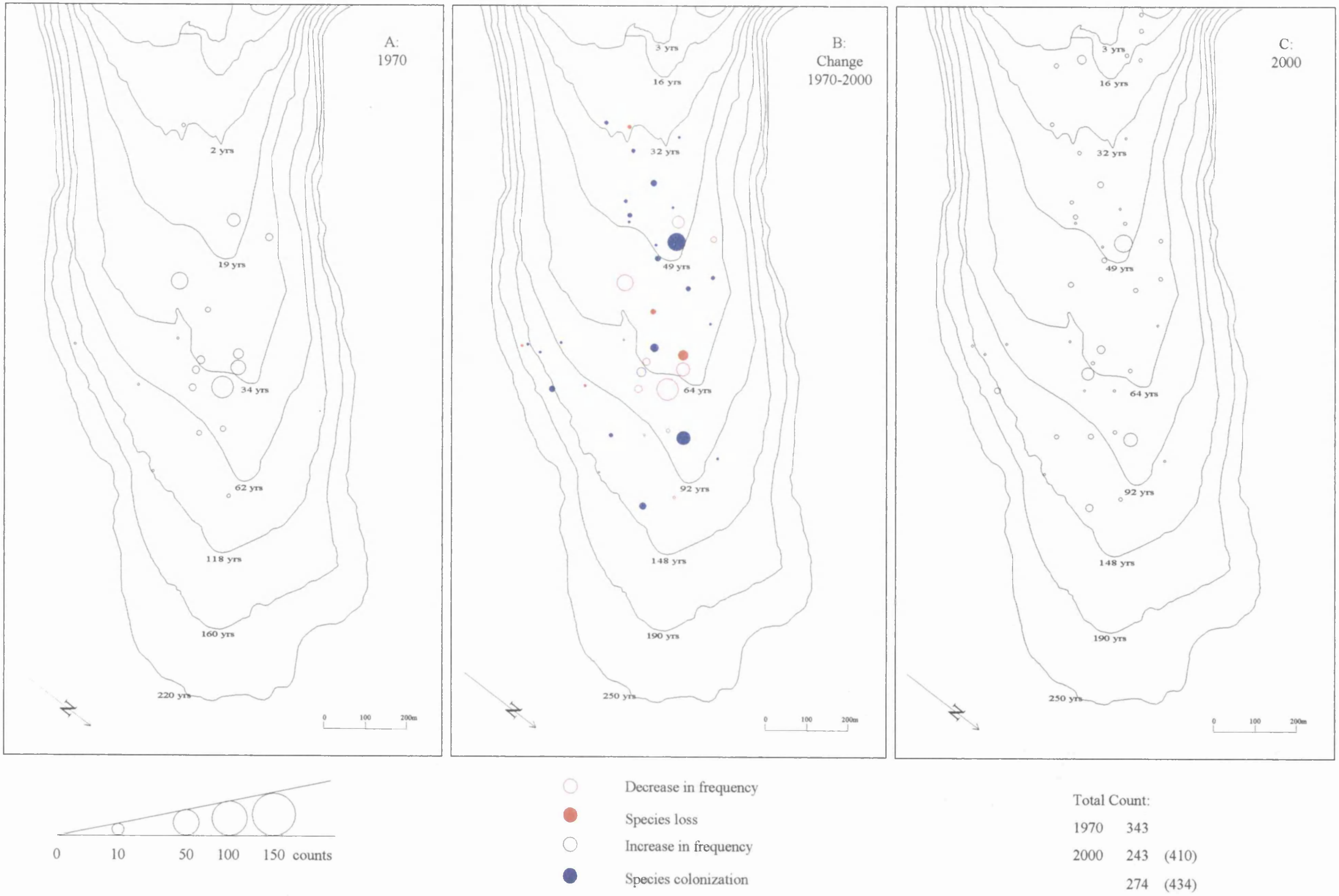


Figure 4.24 *Cerastium cerastoides*: A, frequency in 1970; B, change in frequency 1970-2000; C, frequency in 2000

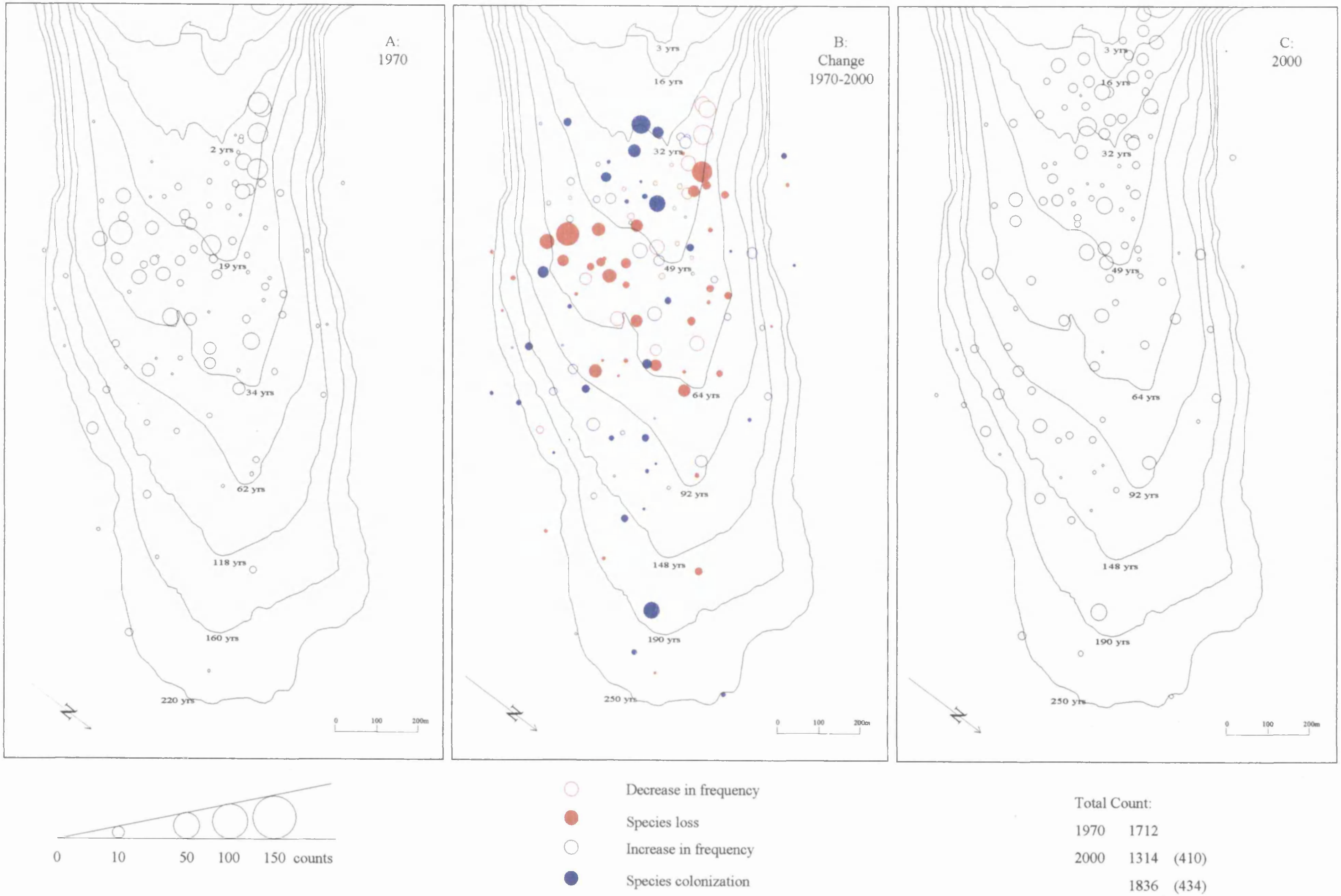


Figure 4.25 *Deschampsia cespitosa* ssp. *alpina*: A, frequency in 1970; B, change in frequency 1970-2000; C, frequency in 2000

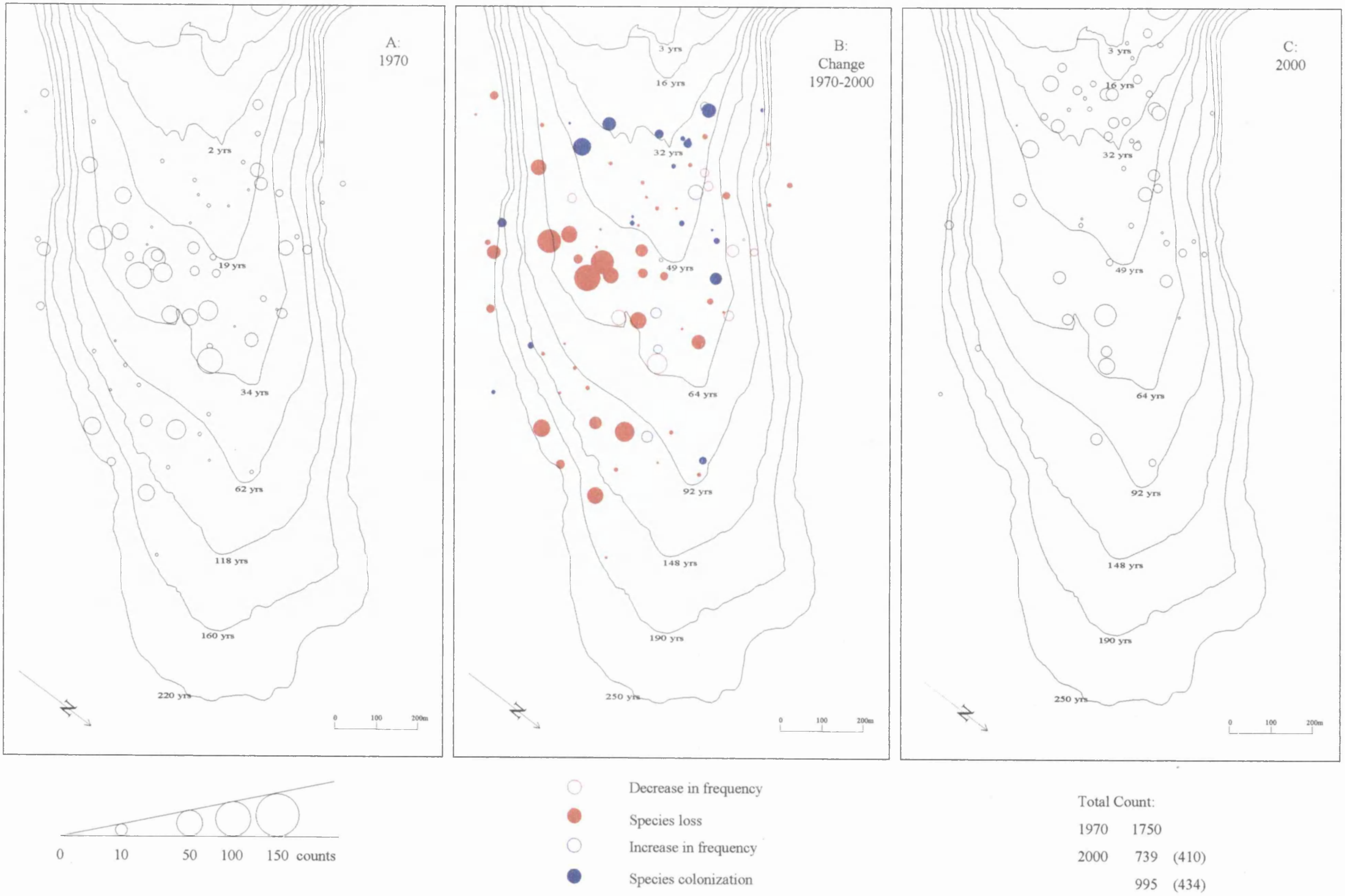


Figure 4.26 *Oxyria digyna*: A, frequency in 1970; B, change in frequency 1970-2000; C, frequency in 2000

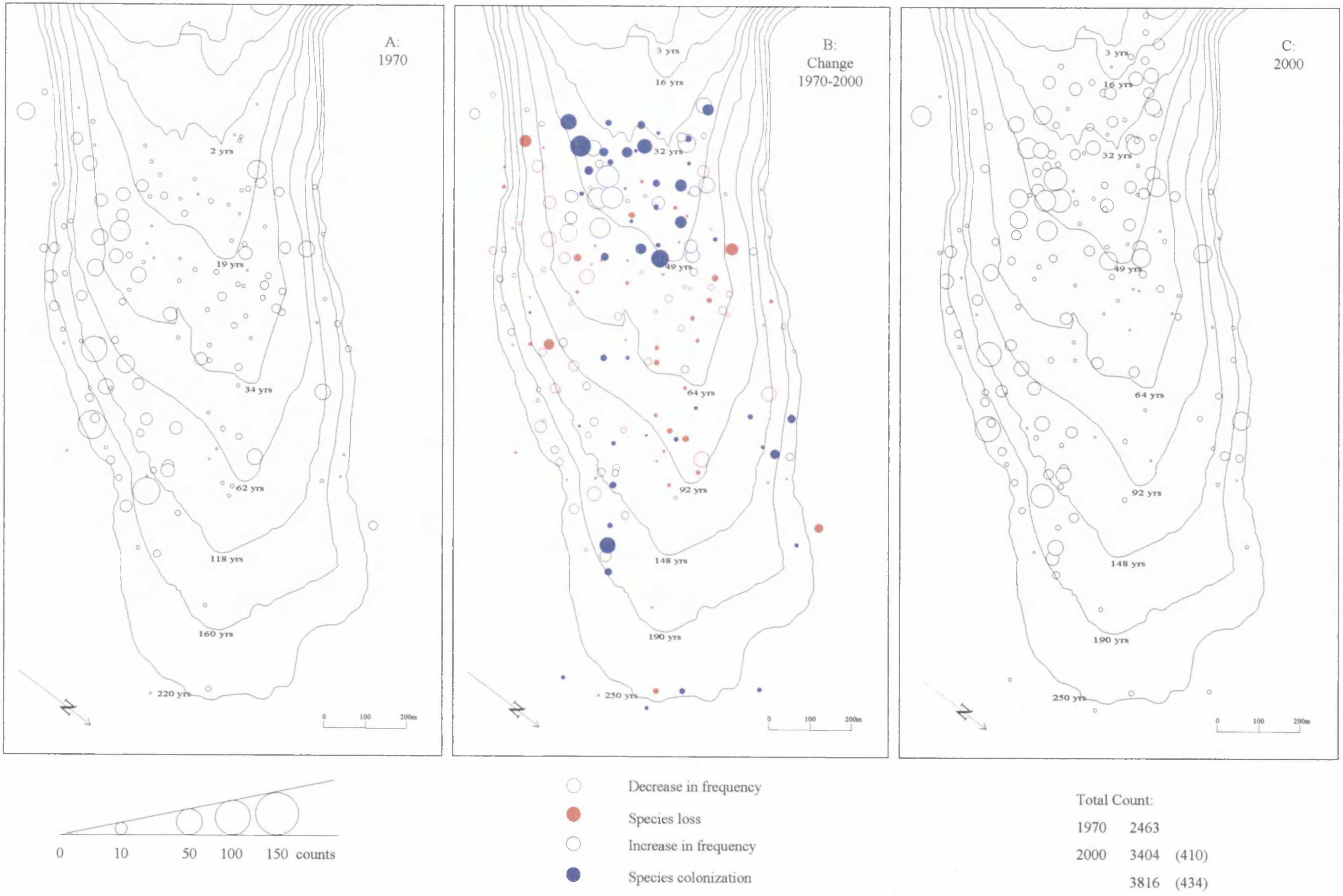


Figure 4.27 *Poa* spp: A, frequency in 1970; B, change in frequency 1970-2000; C, frequency in 2000

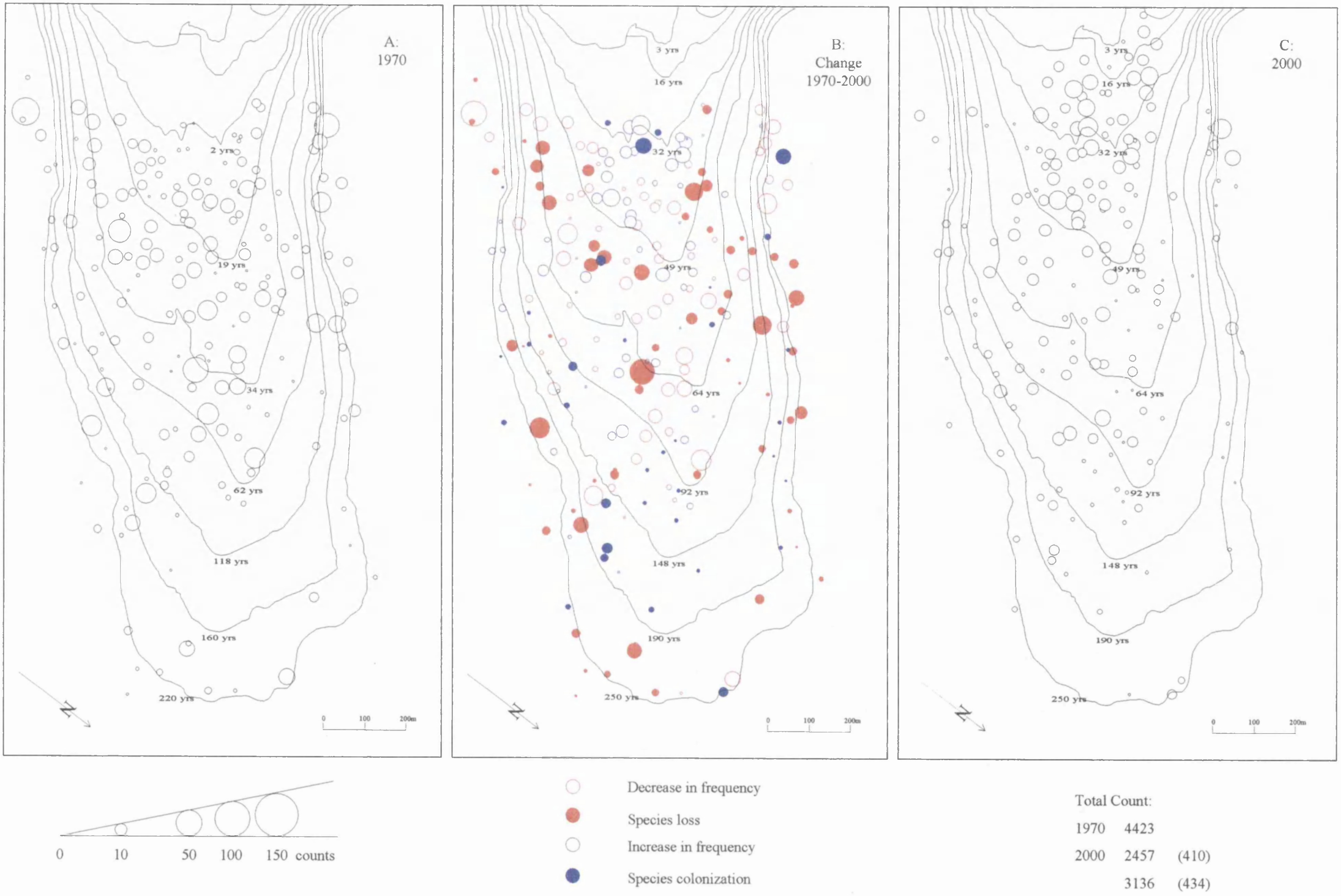


Figure 4.28 *Ranunculus glacialis*: A, frequency in 1970; B, change in frequency 1970-2000; C, frequency in 2000

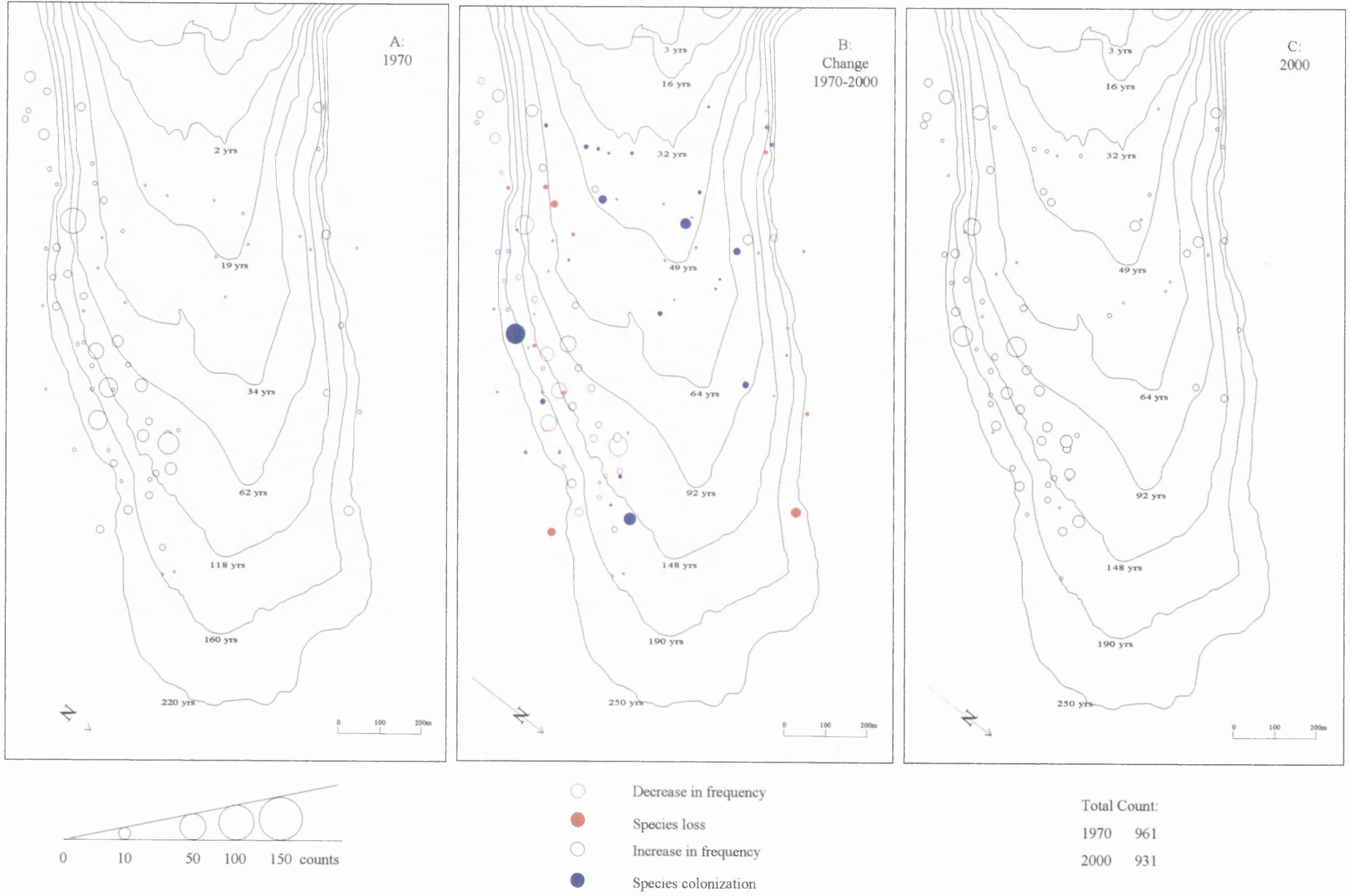


Figure 4.29 *Saxifraga cespitosa*: A, frequency in 1970; B, change in frequency 1970-2000; C, frequency in 2000

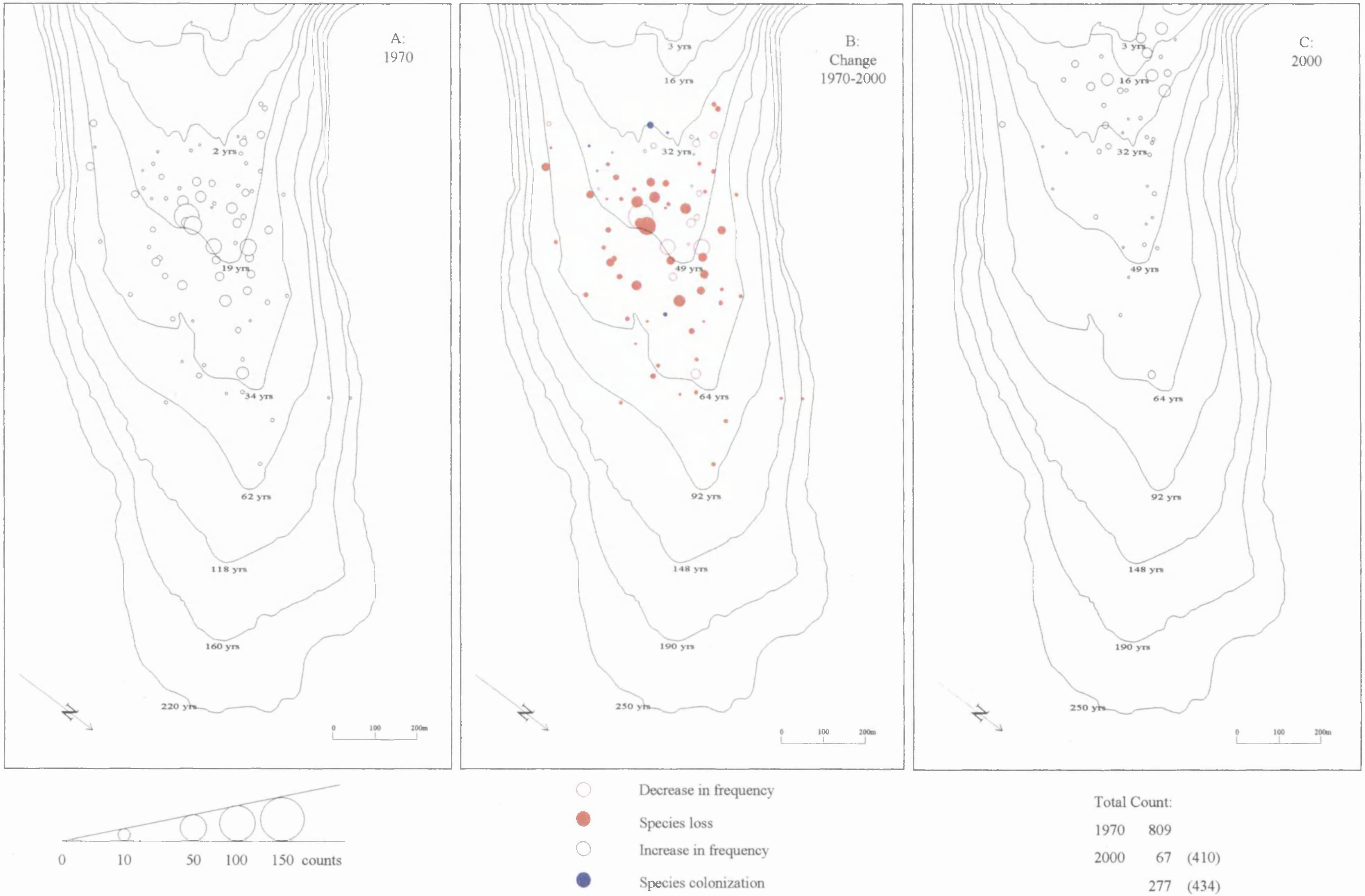


Figure 4.30 *Saxifraga oppositifolia*: A, frequency in 1970; B, change in frequency 1970-2000; C, frequency in 2000

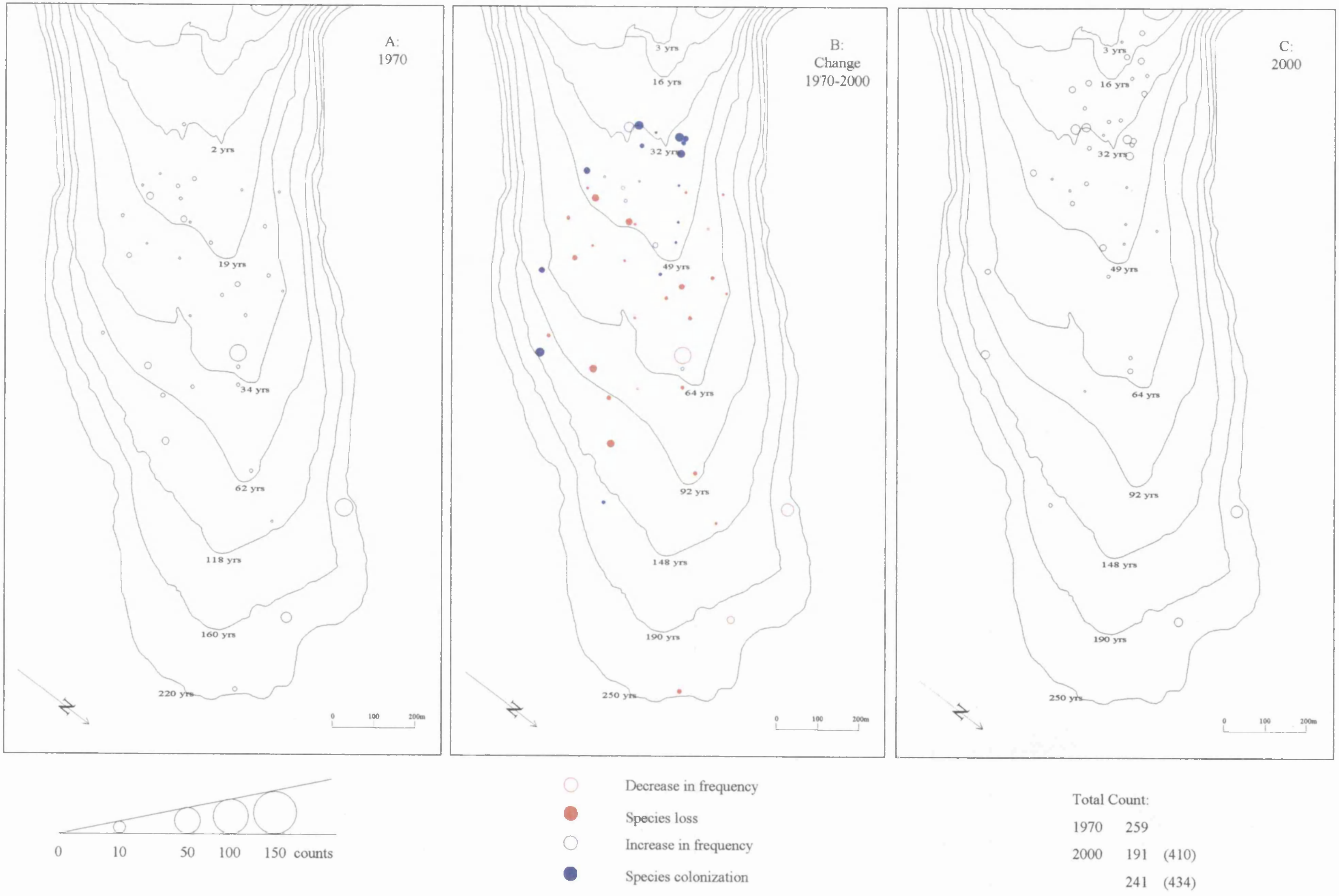


Figure 4.31 *Trisetum spicatum*: A, frequency in 1970; B, change in frequency 1970-2000; C, frequency in 2000

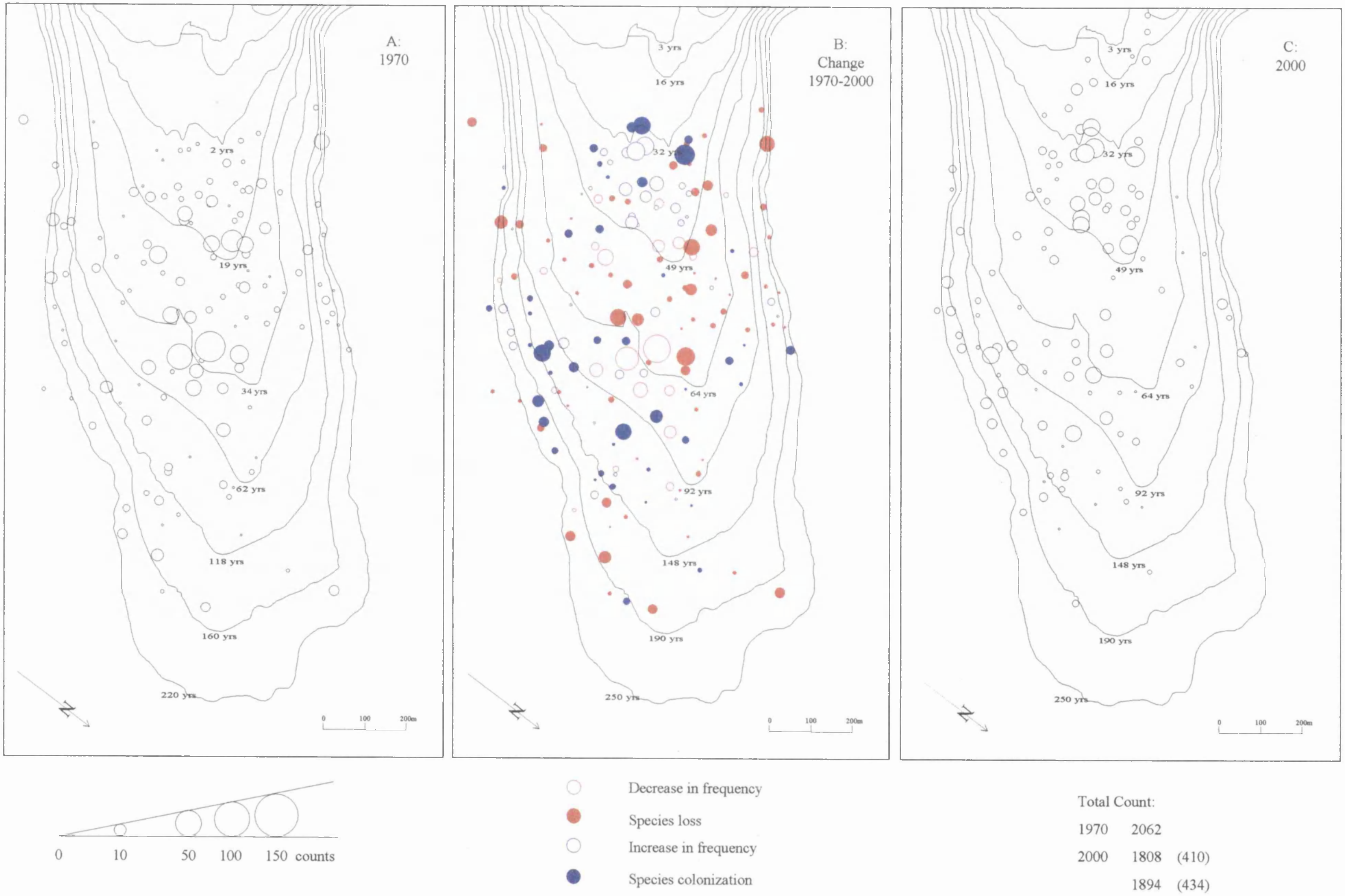


Figure 4.32 *Anthoxanthum odoratum*: A, frequency in 1970; B, change in frequency 1970-2000; C, frequency in 2000

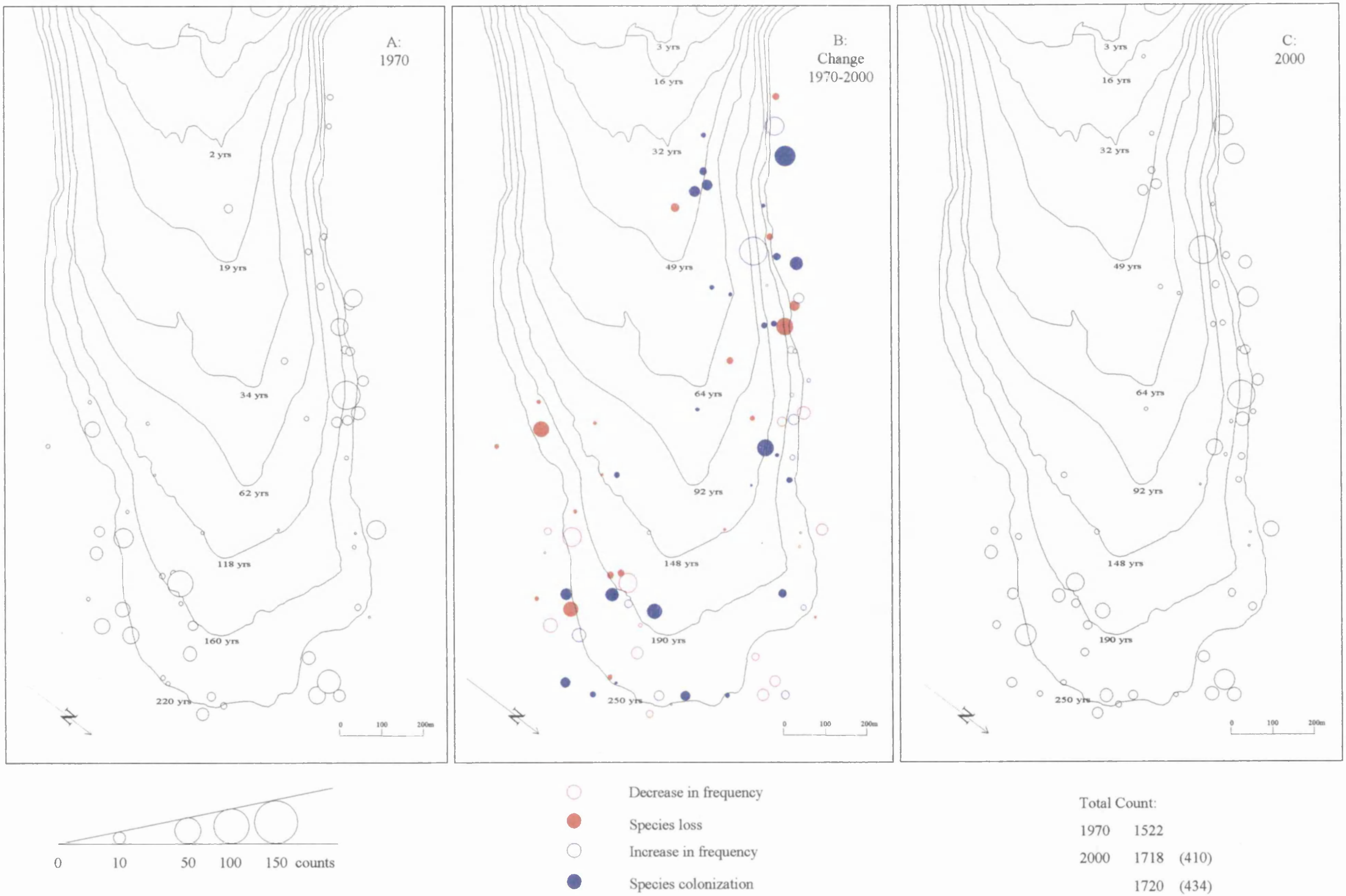


Figure 4.33 *Carex* spp.: A, frequency in 1970; B, change in frequency 1970-2000; C, frequency in 2000

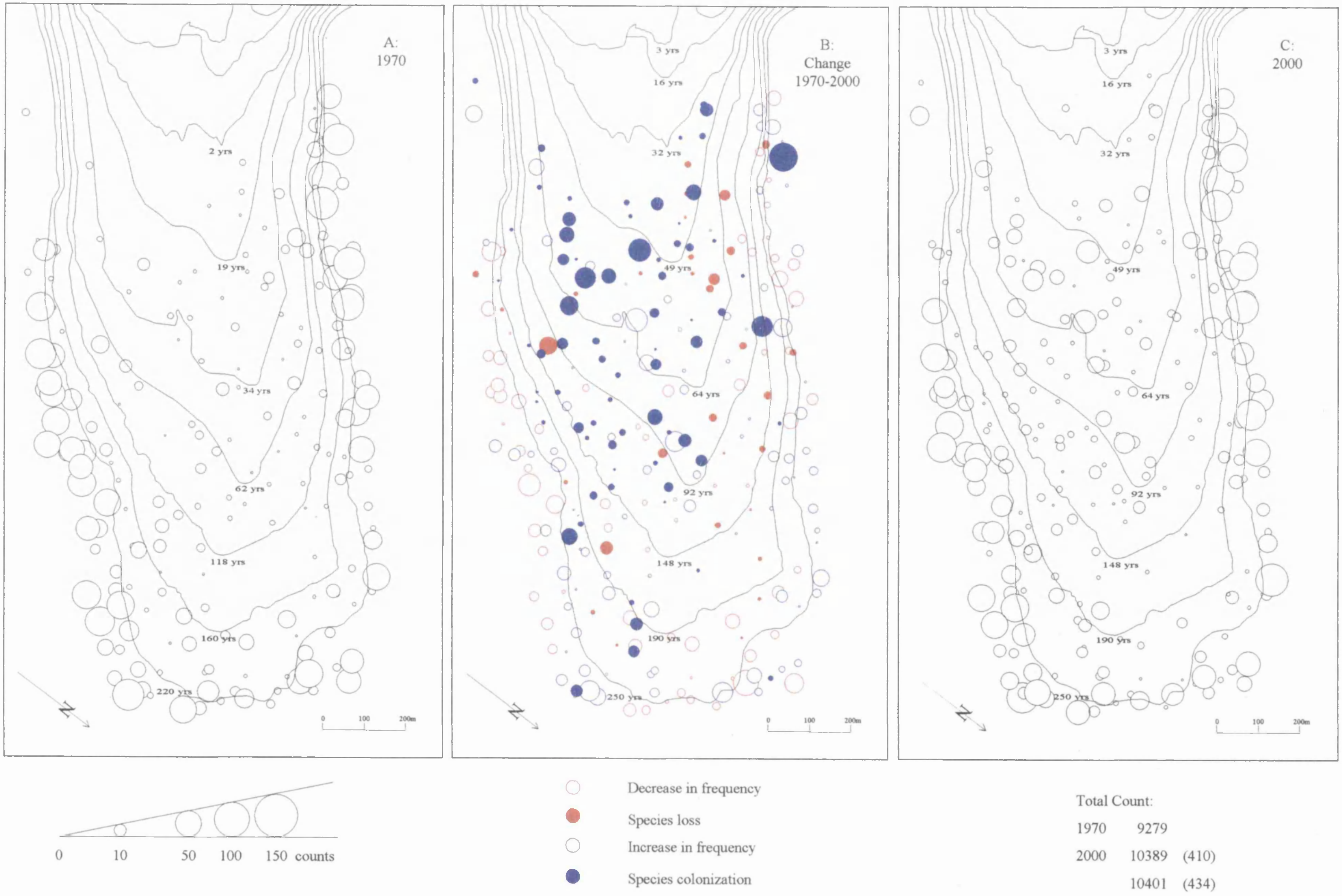


Figure 4.34 *Deschampsia cespitosa*: A, frequency in 1970; B, change in frequency 1970-2000; C, frequency in 2000

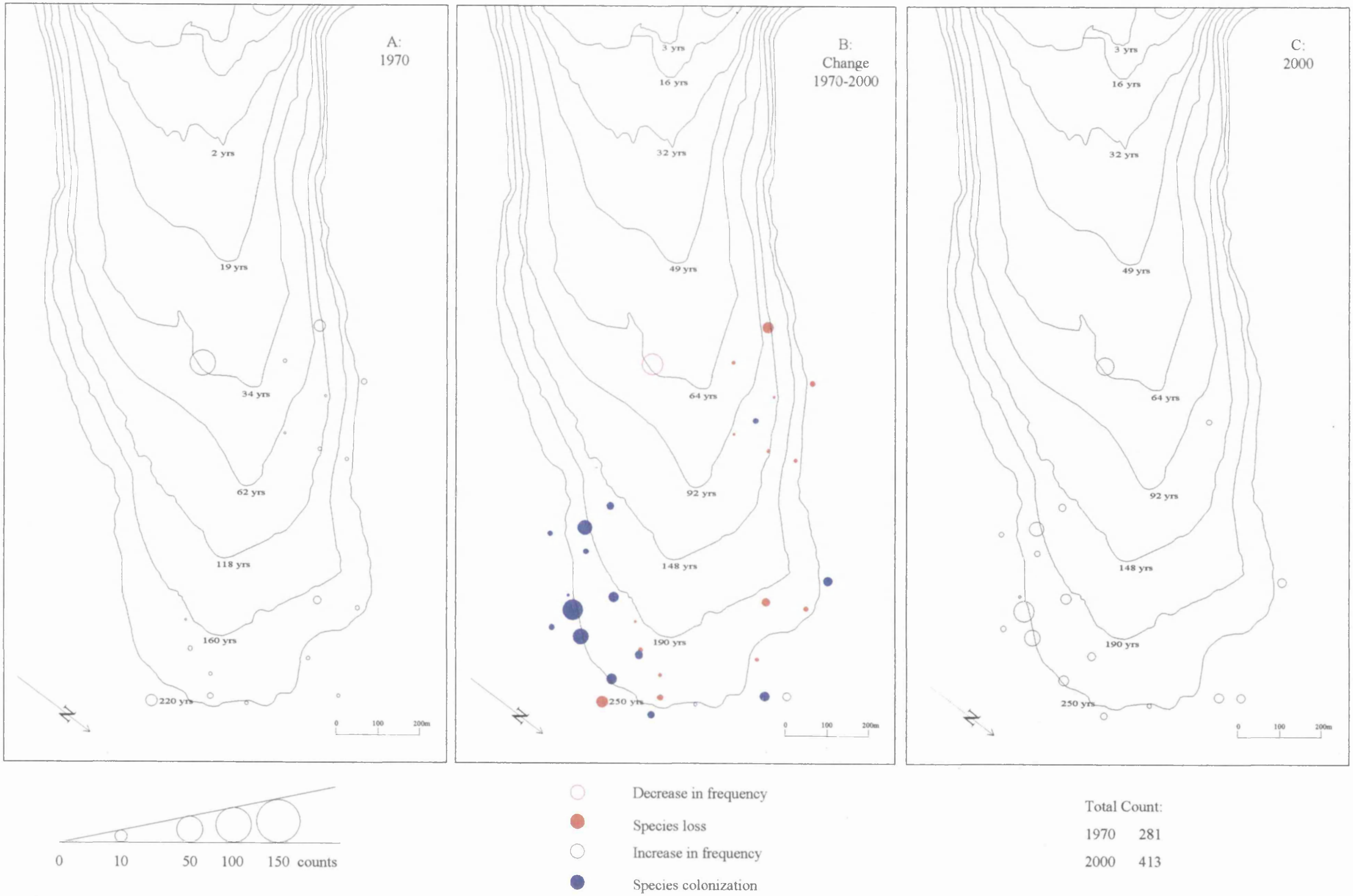


Figure 4.35 *Eriophorum angustifolium*: A, frequency in 1970; B, change in frequency 1970-2000; C, frequency in 2000

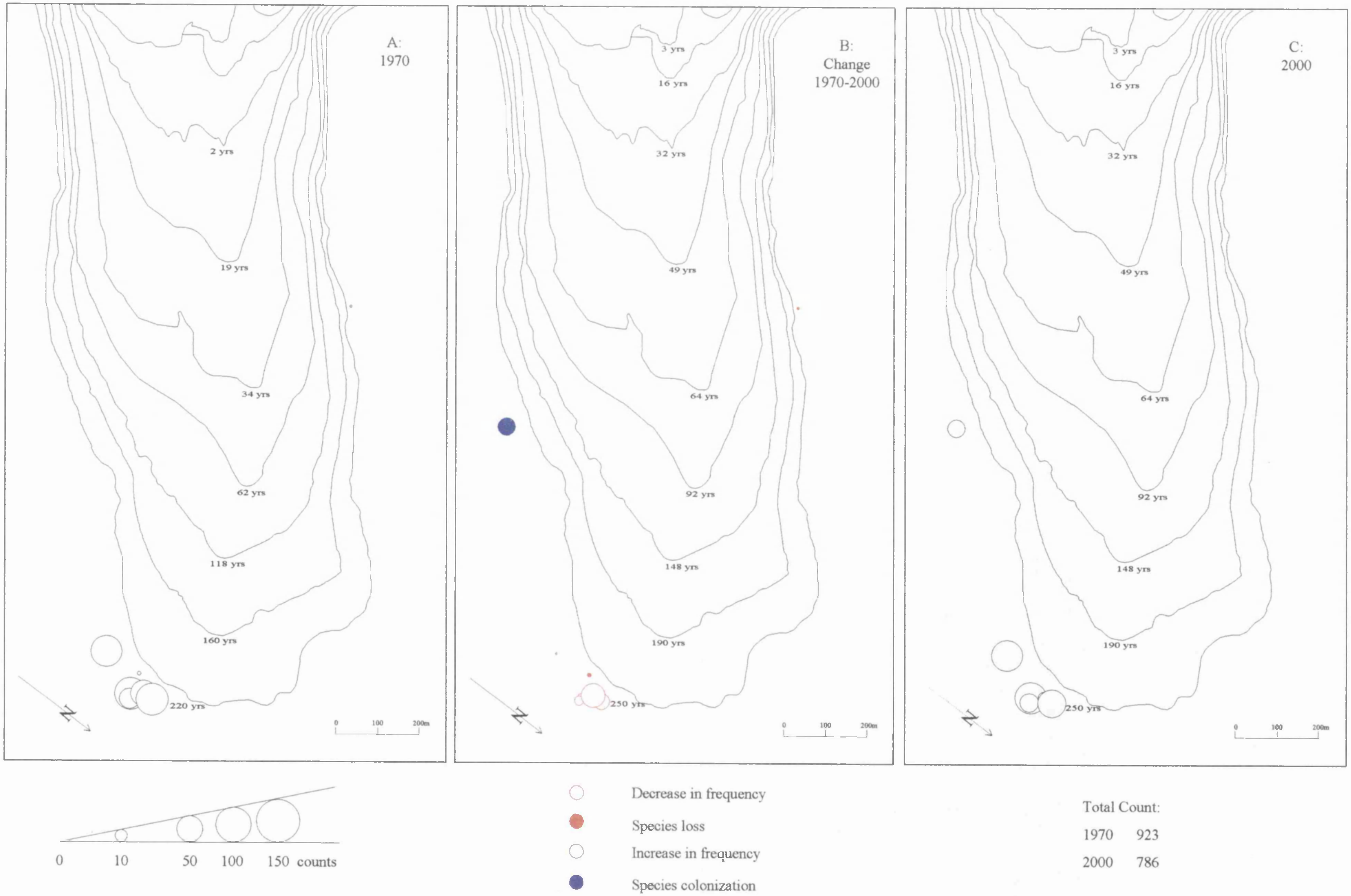


Figure 4.36 *Festuca* spp.: A, frequency in 1970; B, change in frequency 1970-2000; C, frequency in 2000

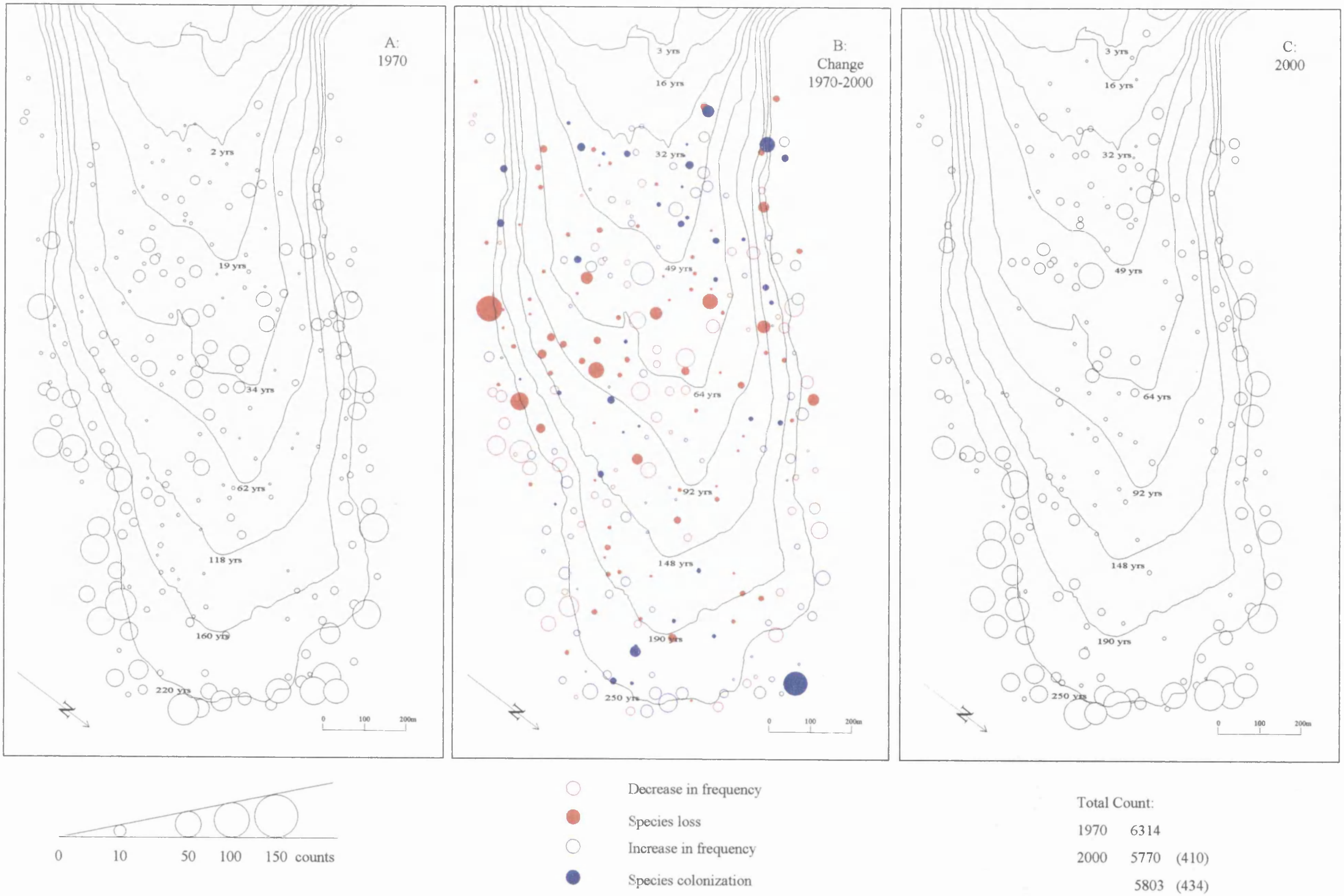


Figure 4.37 *Juncus trifidus*: A, frequency in 1970; B, change in frequency 1970-2000; C, frequency in 2000

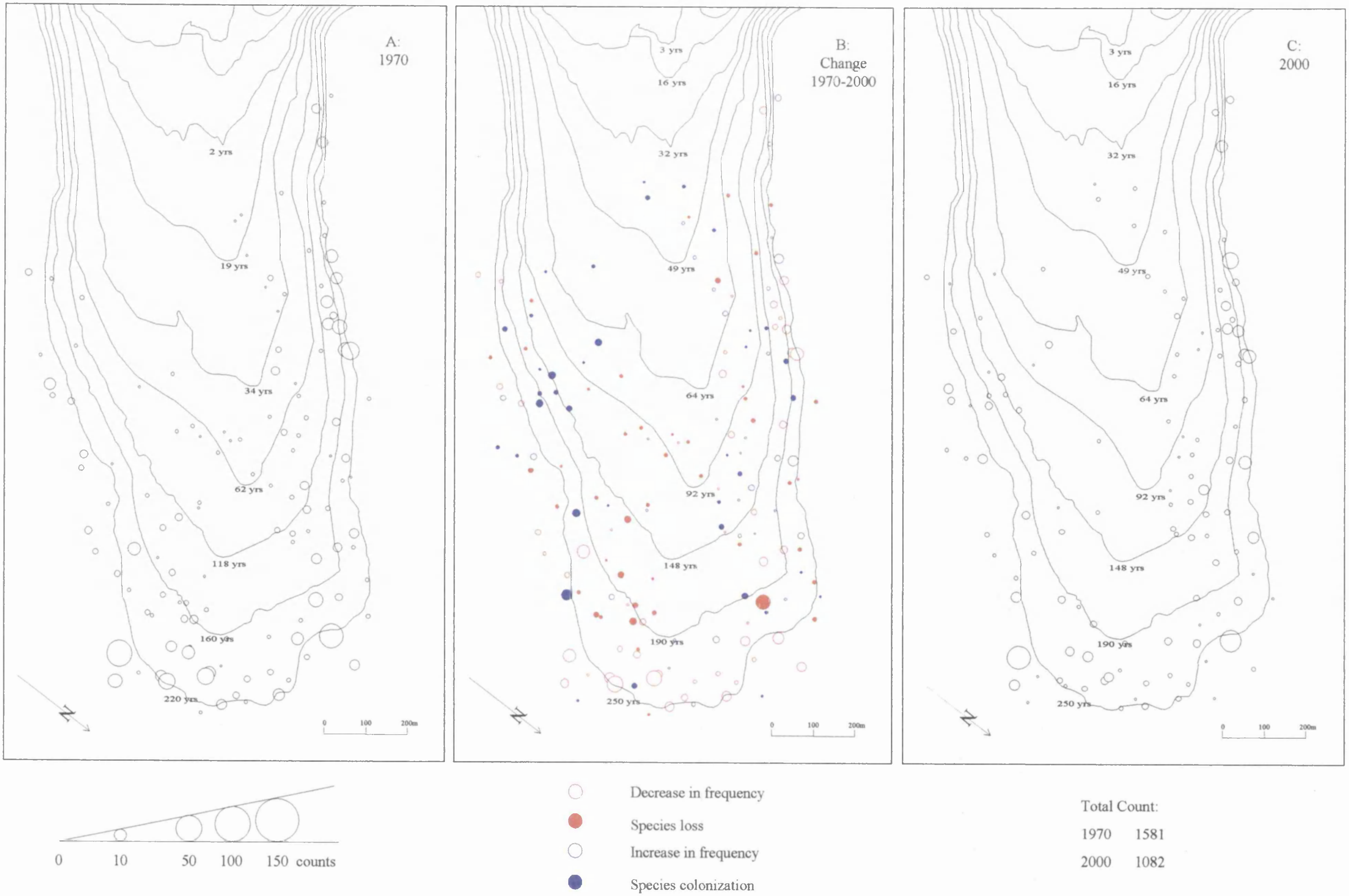


Figure 4.38 *Luzula arcuata*: A, frequency in 1970; B, change in frequency 1970-2000; C, frequency in 2000

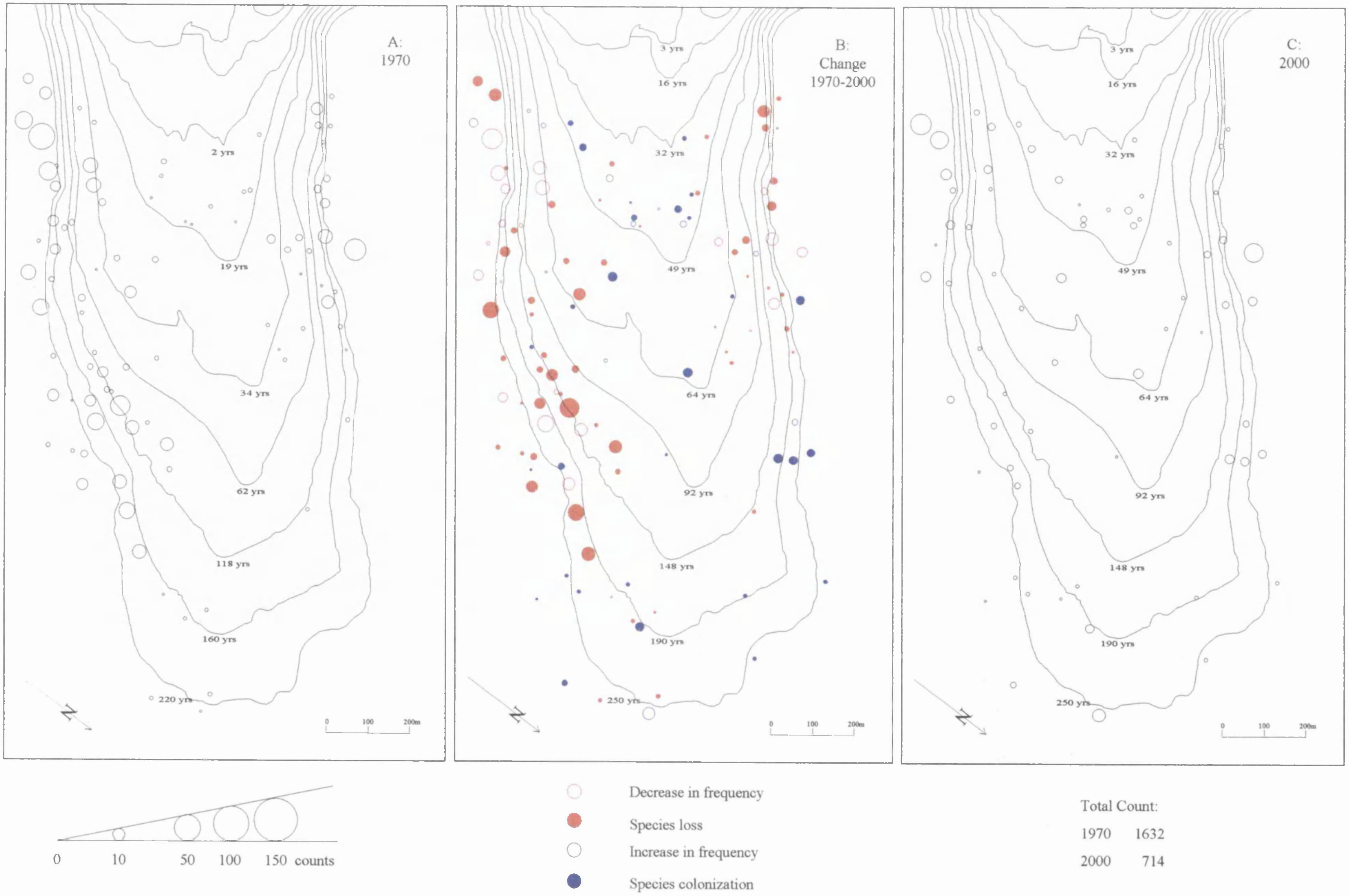


Figure 4.39 *Luzula spicata*: A, frequency in 1970; B change in frequency 1970-2000; C, frequency in 2000

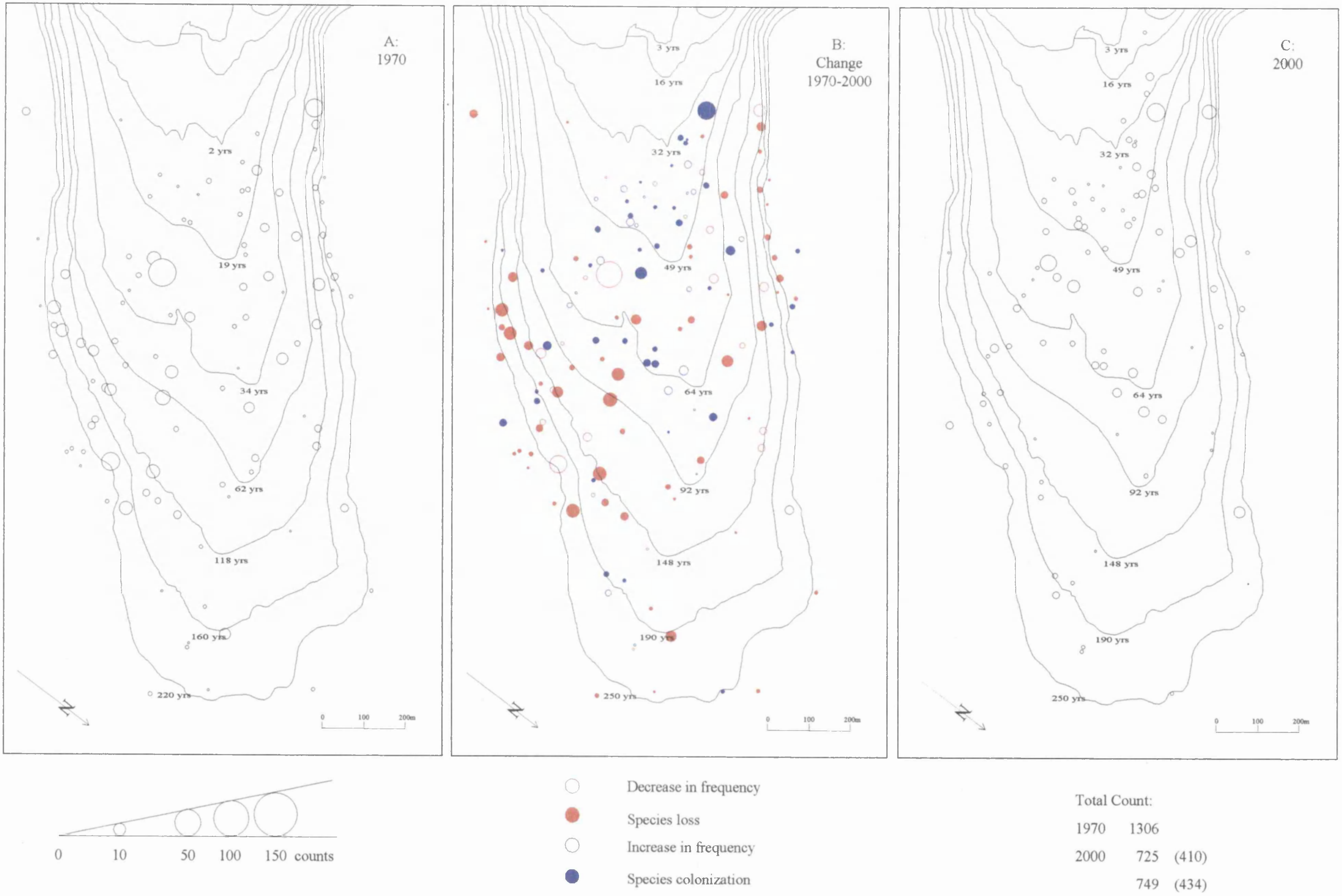


Figure 4.40 *Huperzia selago*: A, frequency in 1970; B, change in frequency 1970-2000; C, frequency in 2000

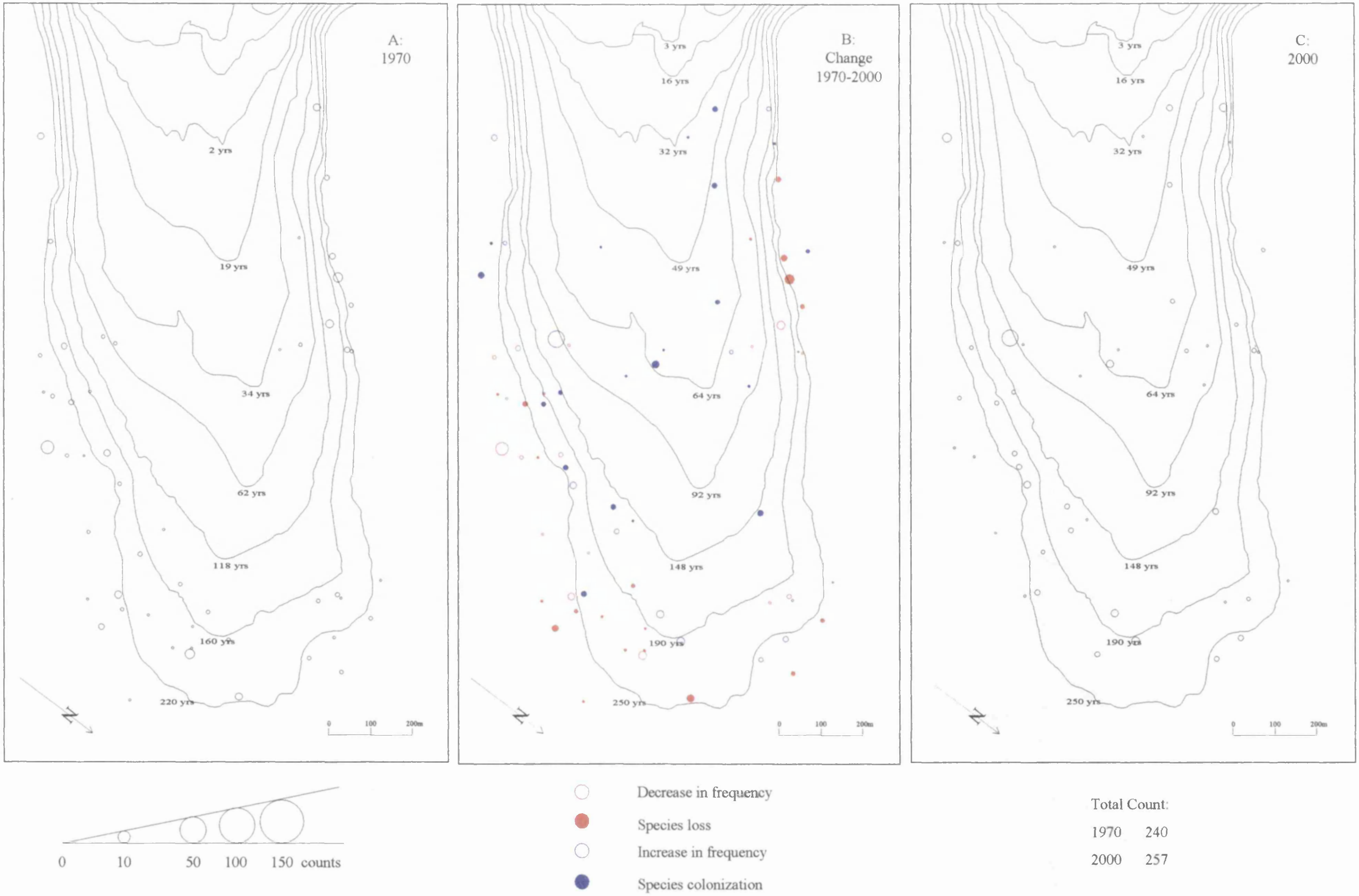


Figure 4.41 *Phleum alpinum*: A, frequency in 1970; B, change in frequency 1970-2000; C, frequency in 2000

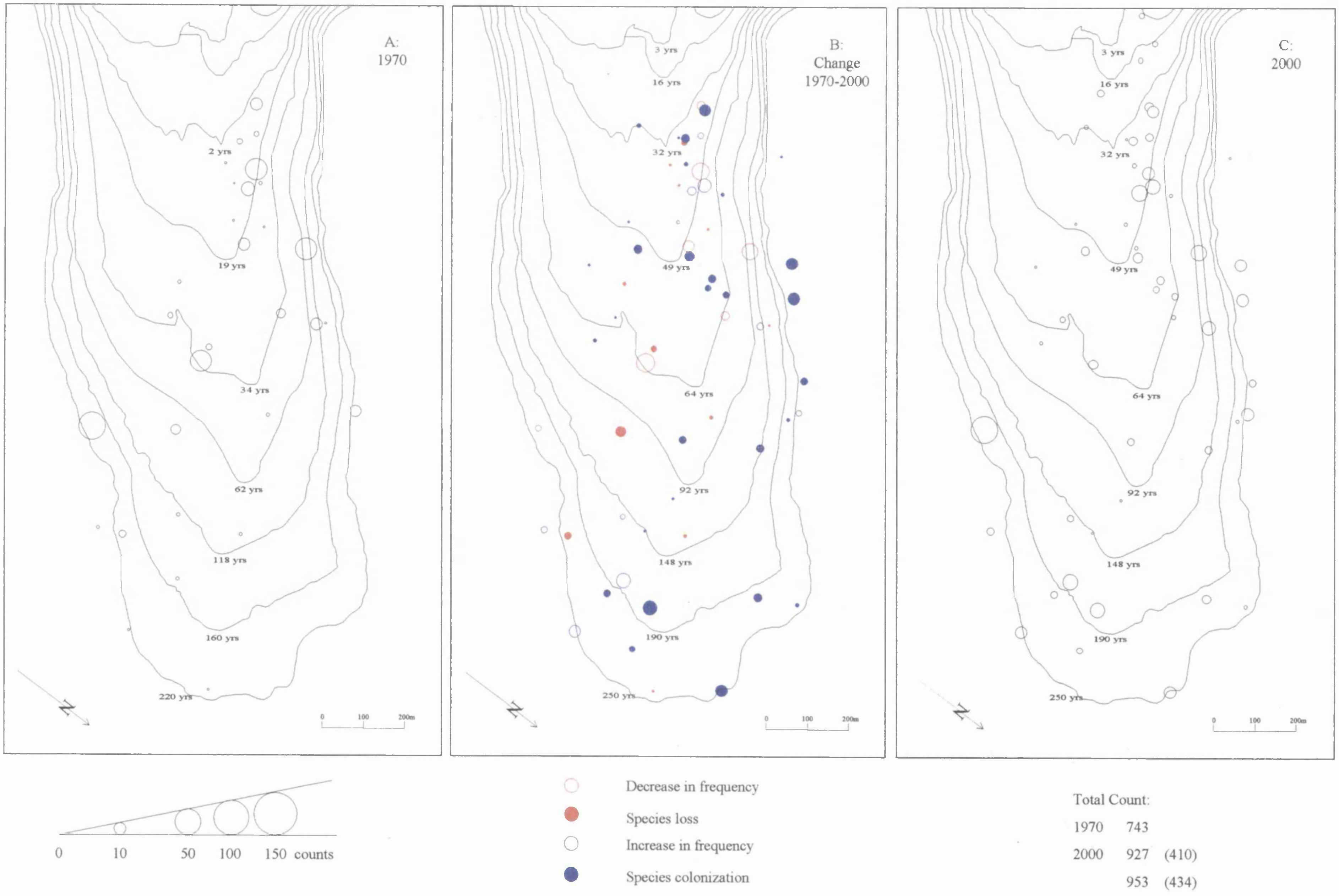


Figure 4.42 *Antennaria alpina*: A, frequency in 1970; B, change in frequency 1970-2000; C, frequency in 2000

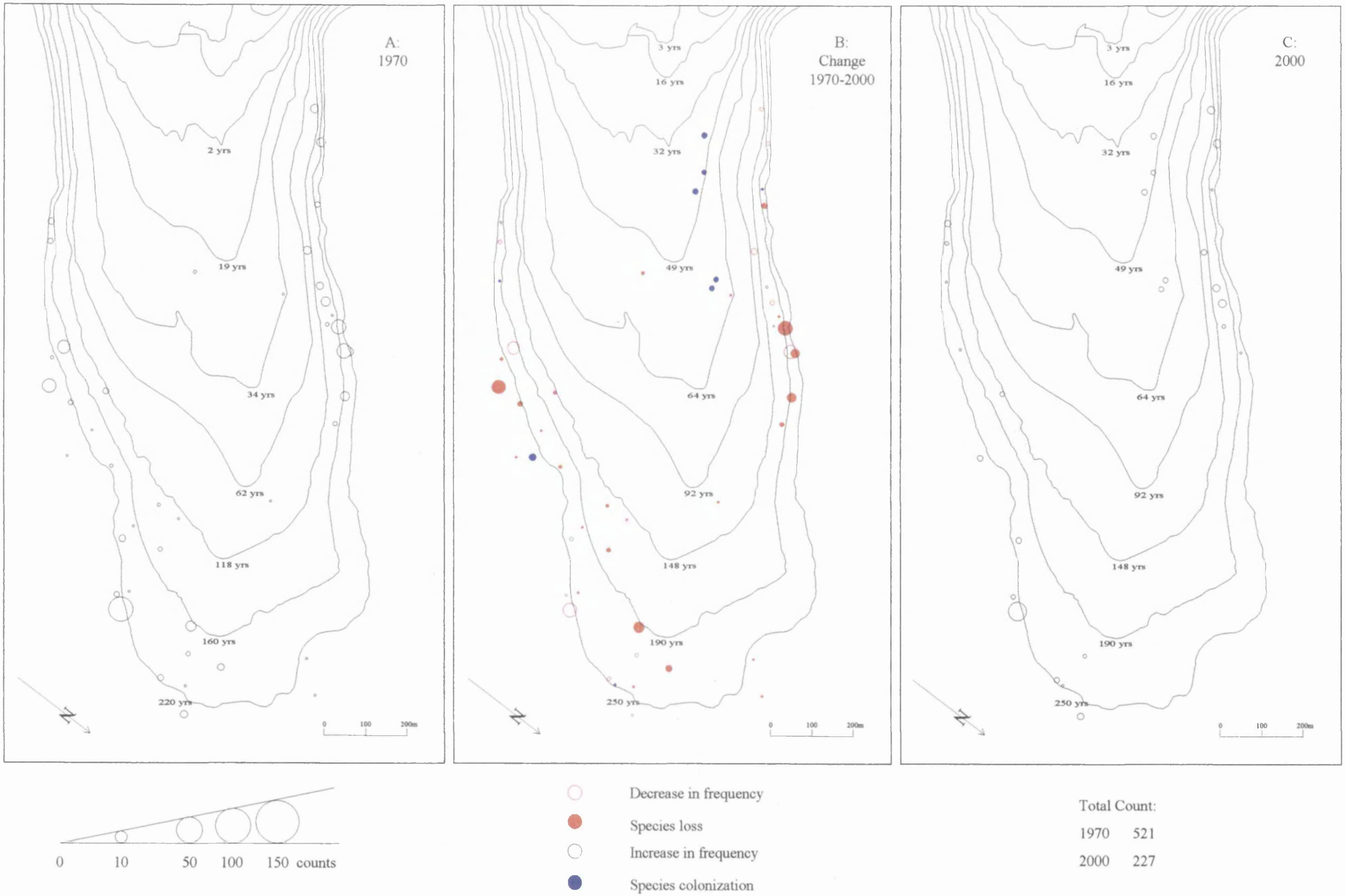


Figure 4.43 *Bartsia alpina*: A, frequency in 1970; B, change in frequency 1970-2000; C, frequency in 2000

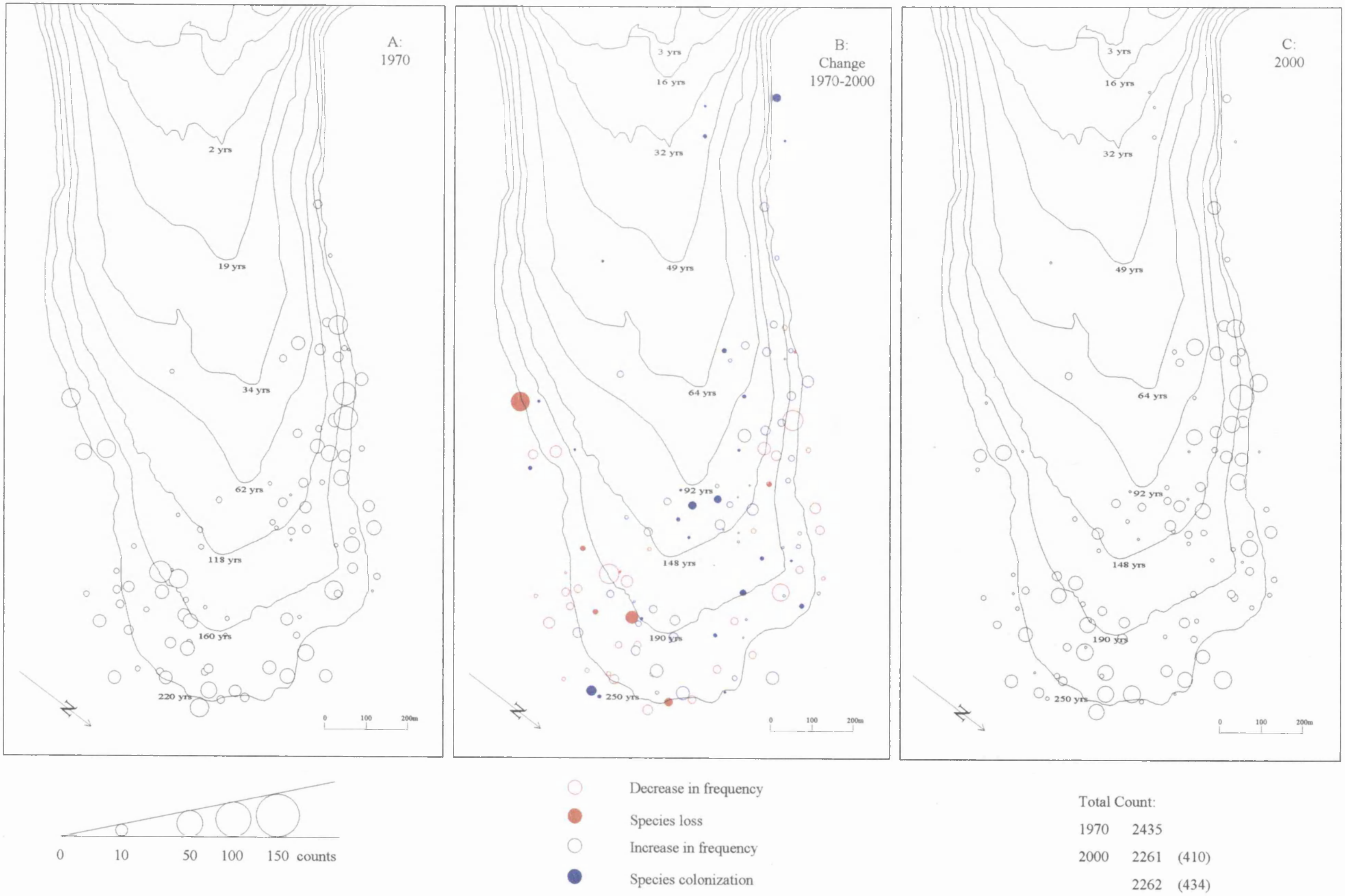


Figure 4.44 *Cardamine bellidifolia*: A, frequency in 1970; B, change in frequency 1970-2000; C, frequency in 2000

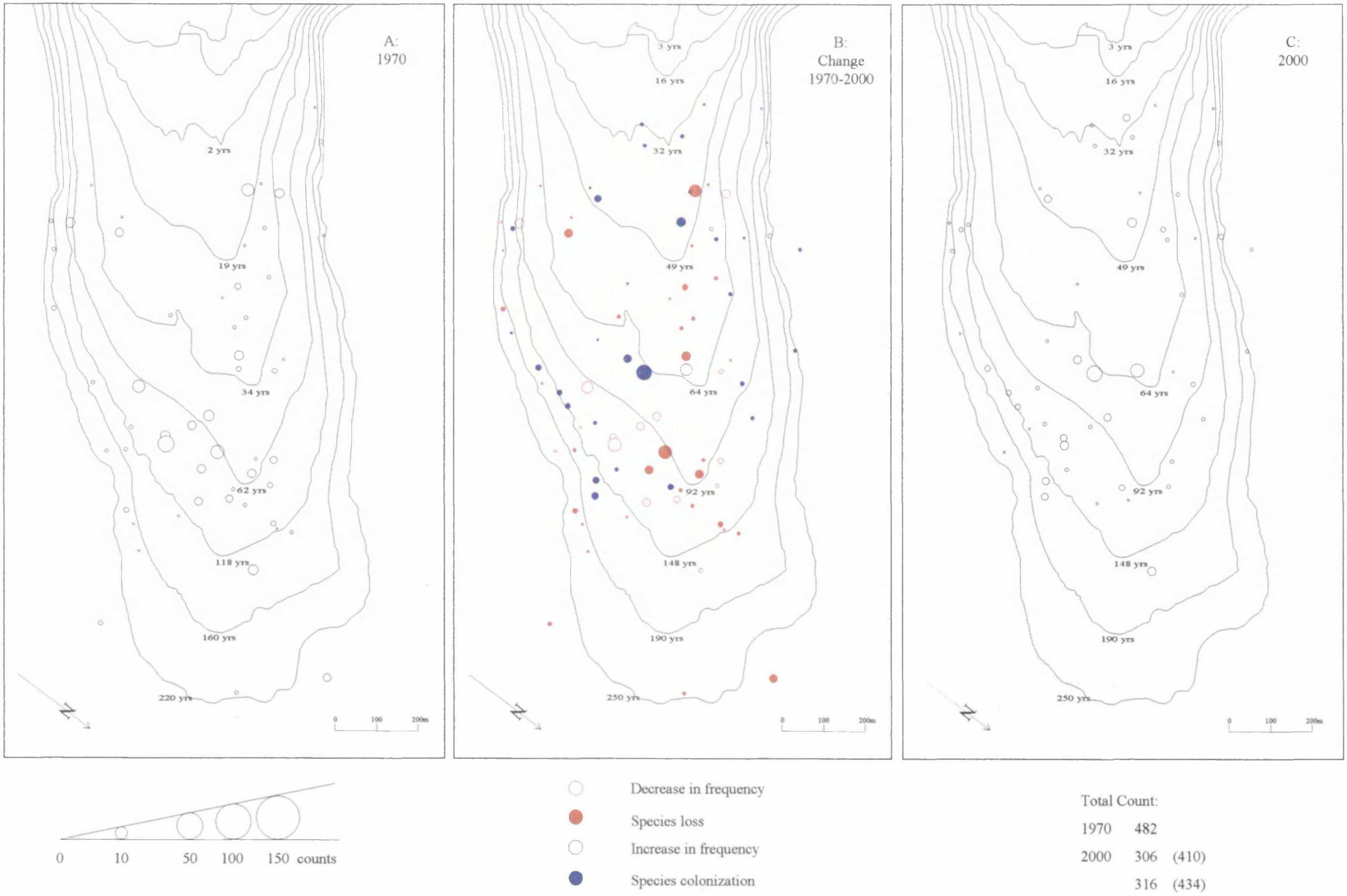


Figure 4.45 *Cardaminopsis petraea*: A, frequency in 1970; B, change in frequency 1970-2000; C, frequency in 2000

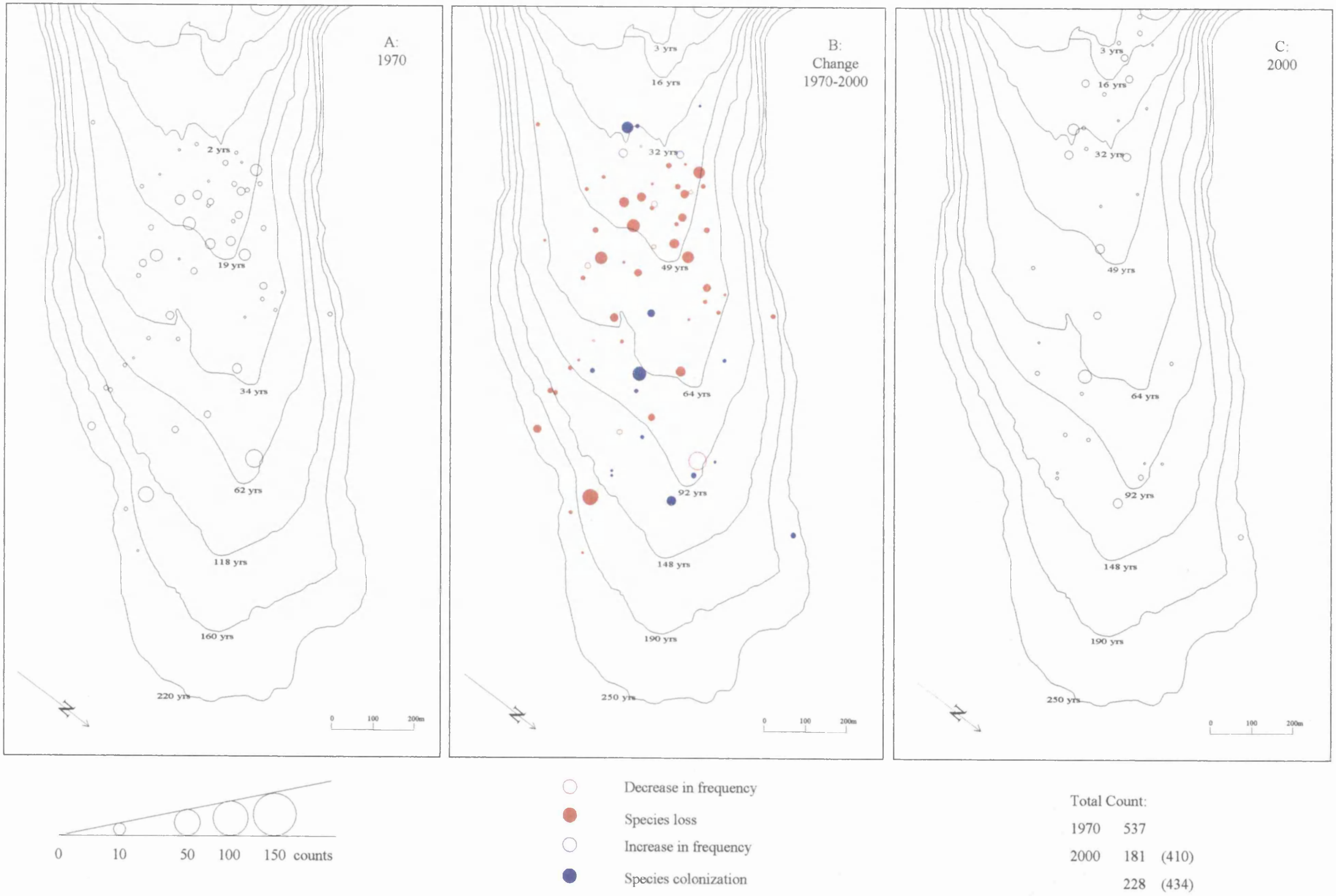


Figure 4.46 *Gnaphalium supinum*: A, frequency in 1970; B, change in frequency 1970-2000; C, frequency in 2000

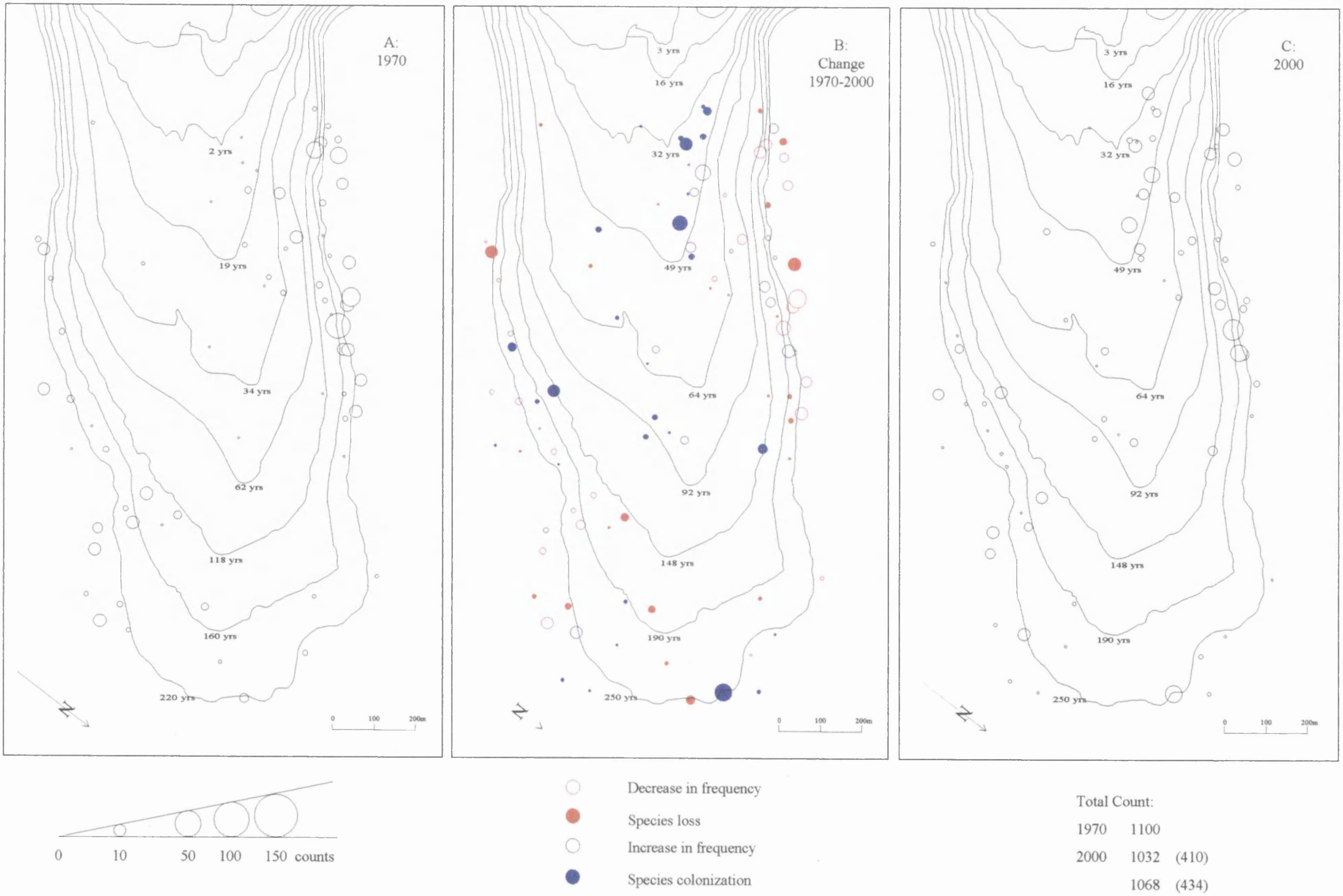


Figure 4.47 *Hieracium alpinum*: A, frequency in 1970; B, change in frequency 1970-2000; C, frequency in 2000

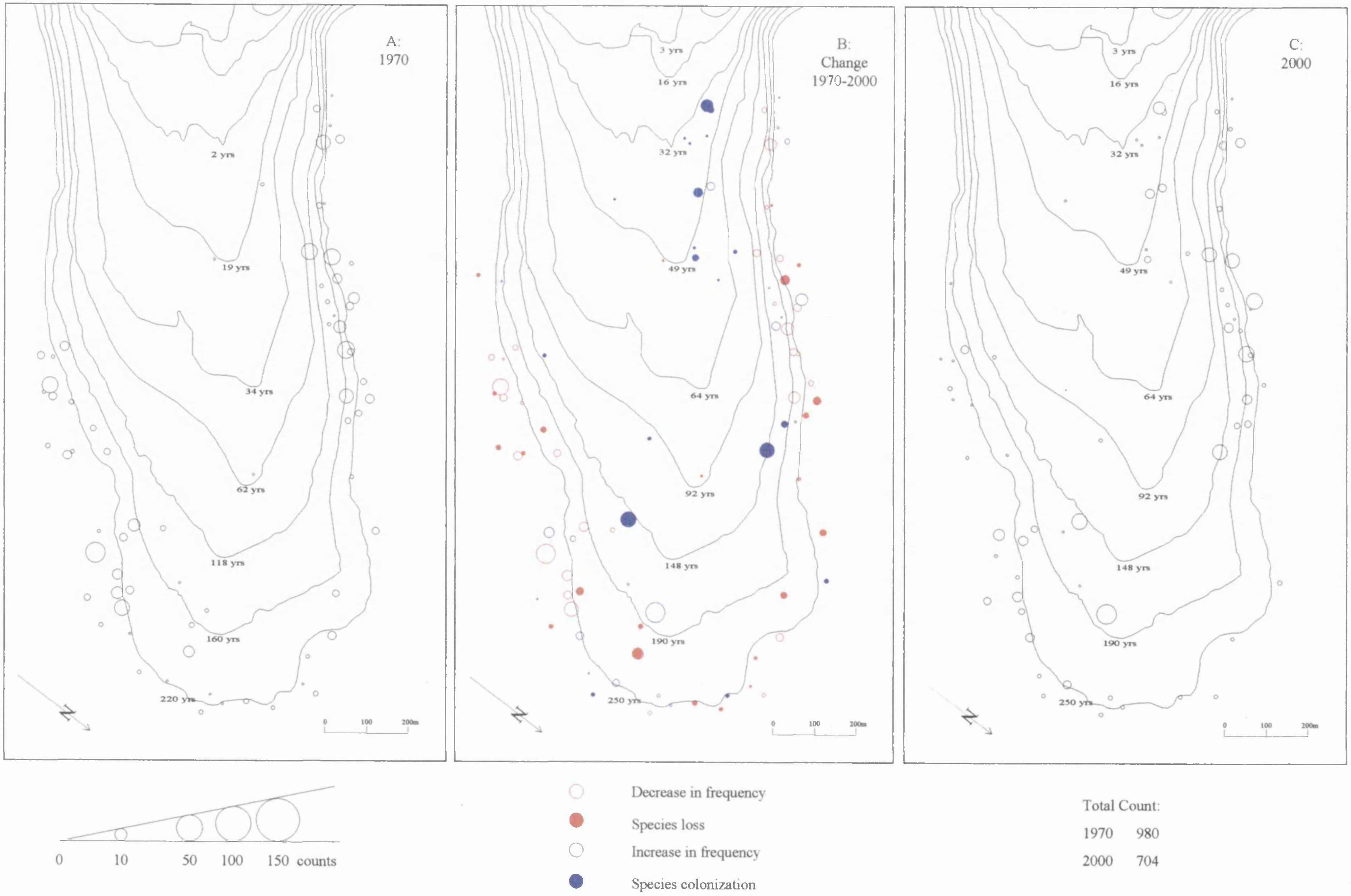


Figure 4.48 *Leontodon autumnalis*: A, frequency in 1970; B, change in frequency 1970-2000; C, frequency in 2000

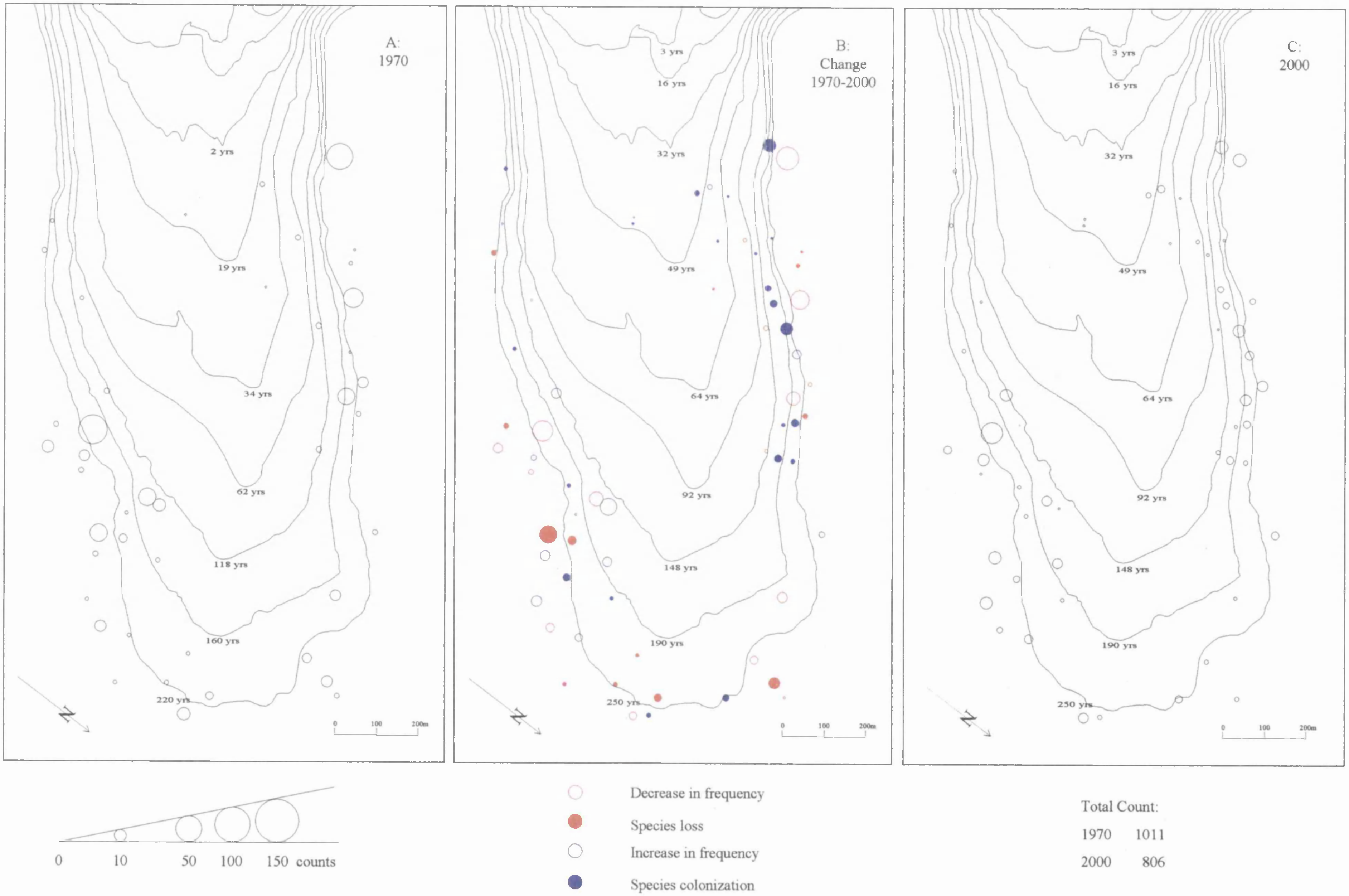


Figure 4.49 *Pedicularis lapponica*: A, frequency in 1970; B, change in frequency 1970-2000; C, frequency in 2000

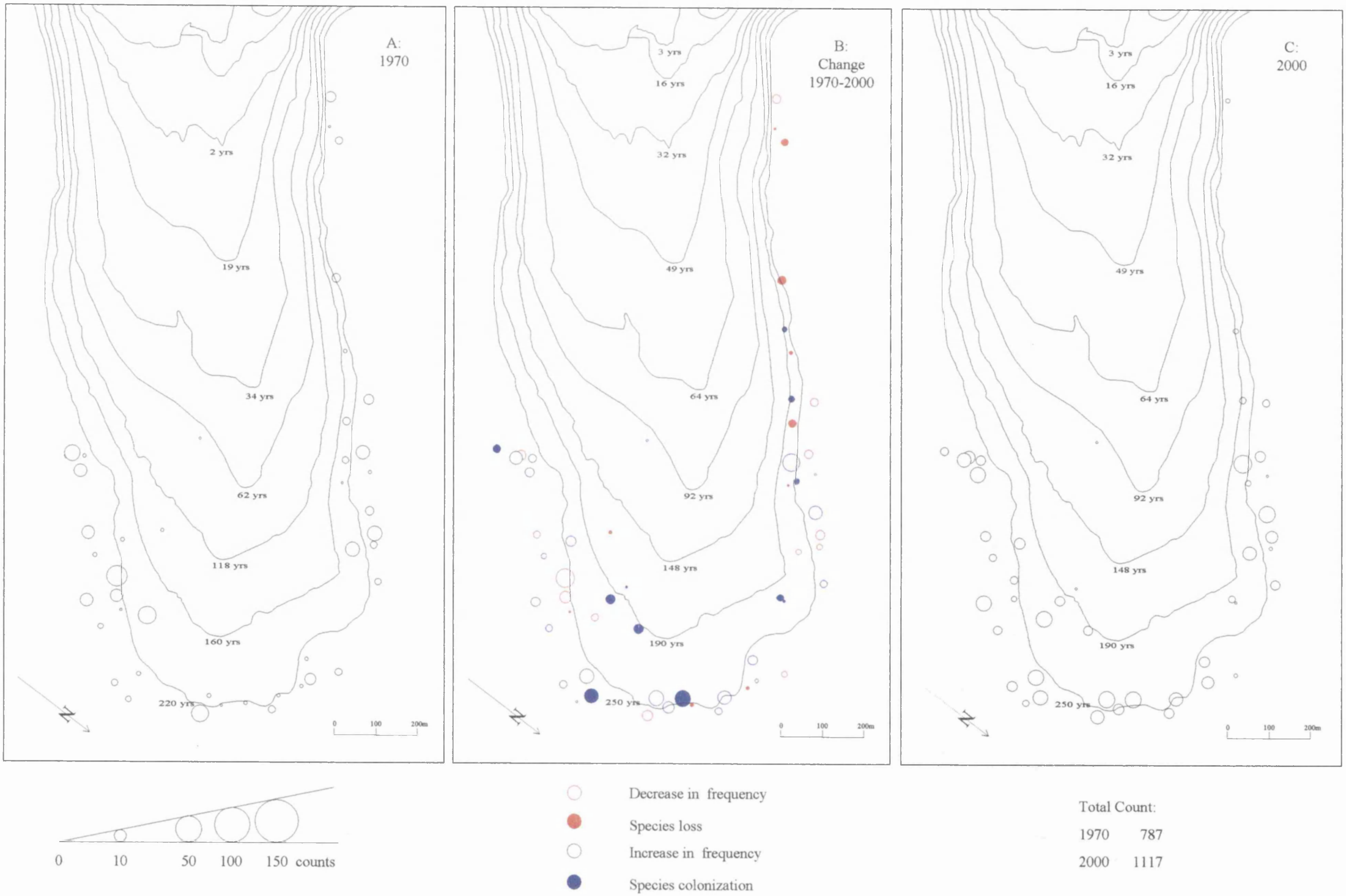


Figure 4.50 *Pinguicula vulgaris*: A, frequency in 1970; B, change in frequency 1970-2000; C, frequency in 2000.

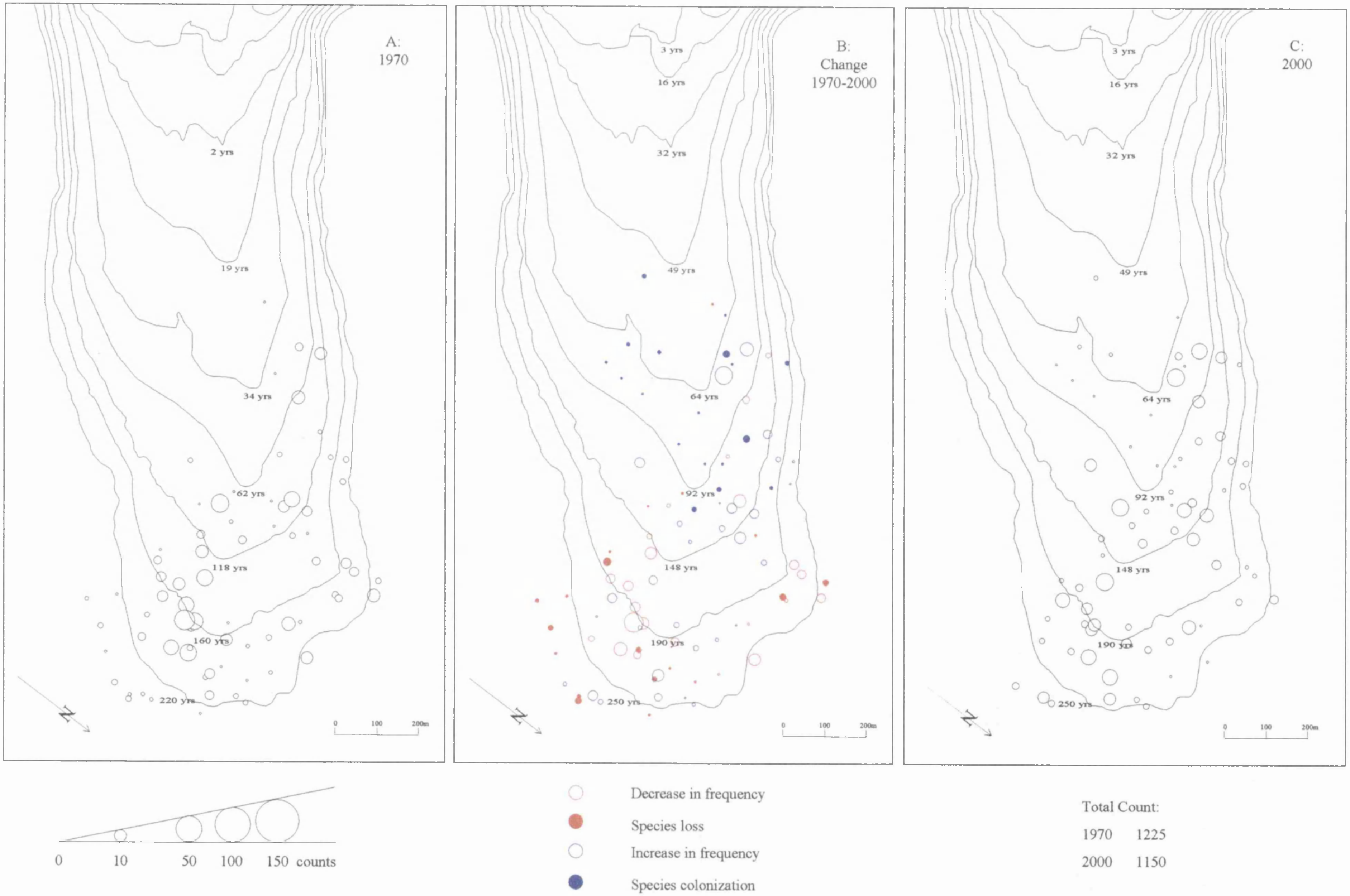


Figure 4.51 *Polygonum viviparum*: A, frequency in 1970; B, change in frequency 1970-2000; C, frequency in 2000.

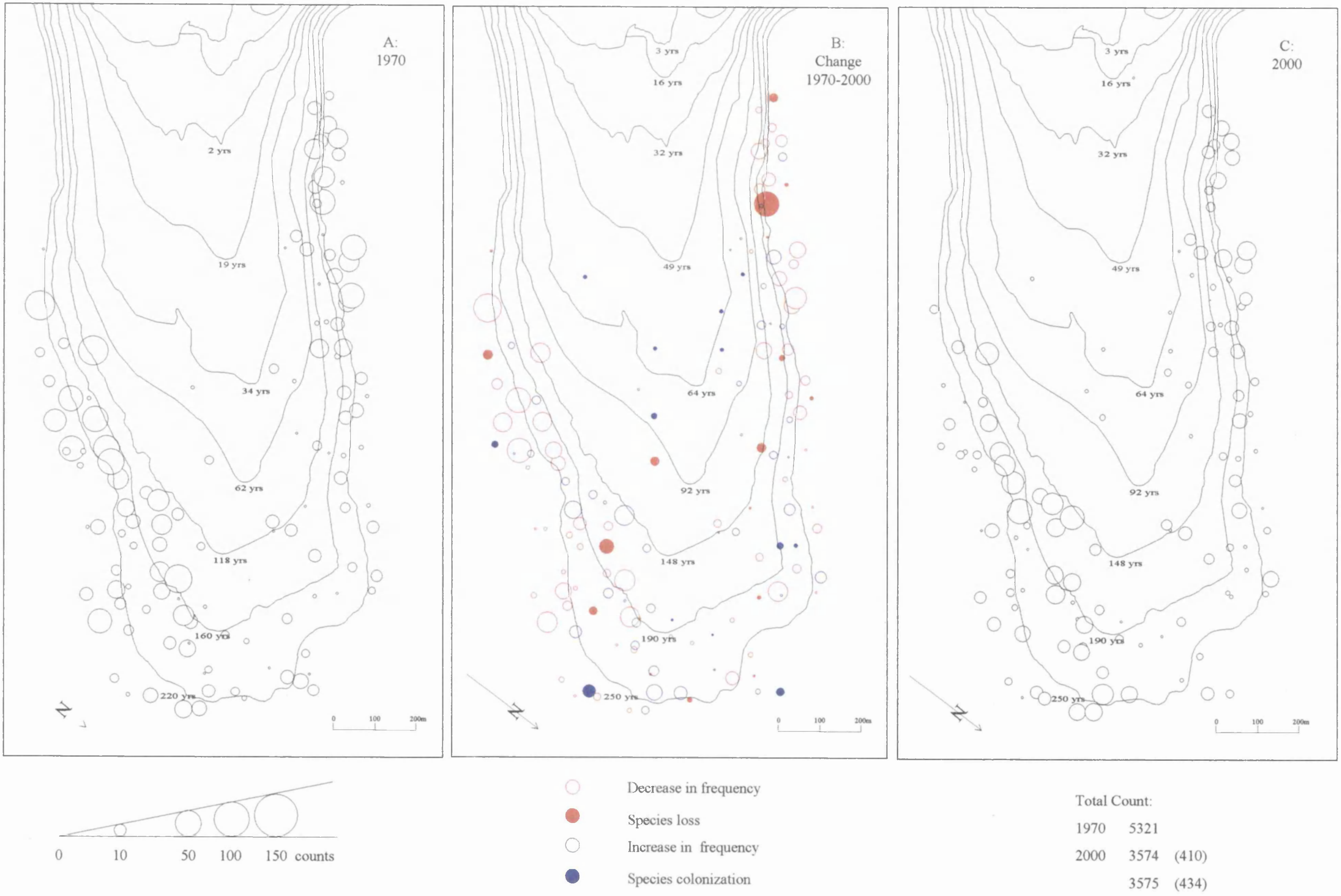


Figure 4.52 *Pyrola* spp.: A, frequency in 1970; B, change in frequency 1970-2000; C, frequency in 2000.

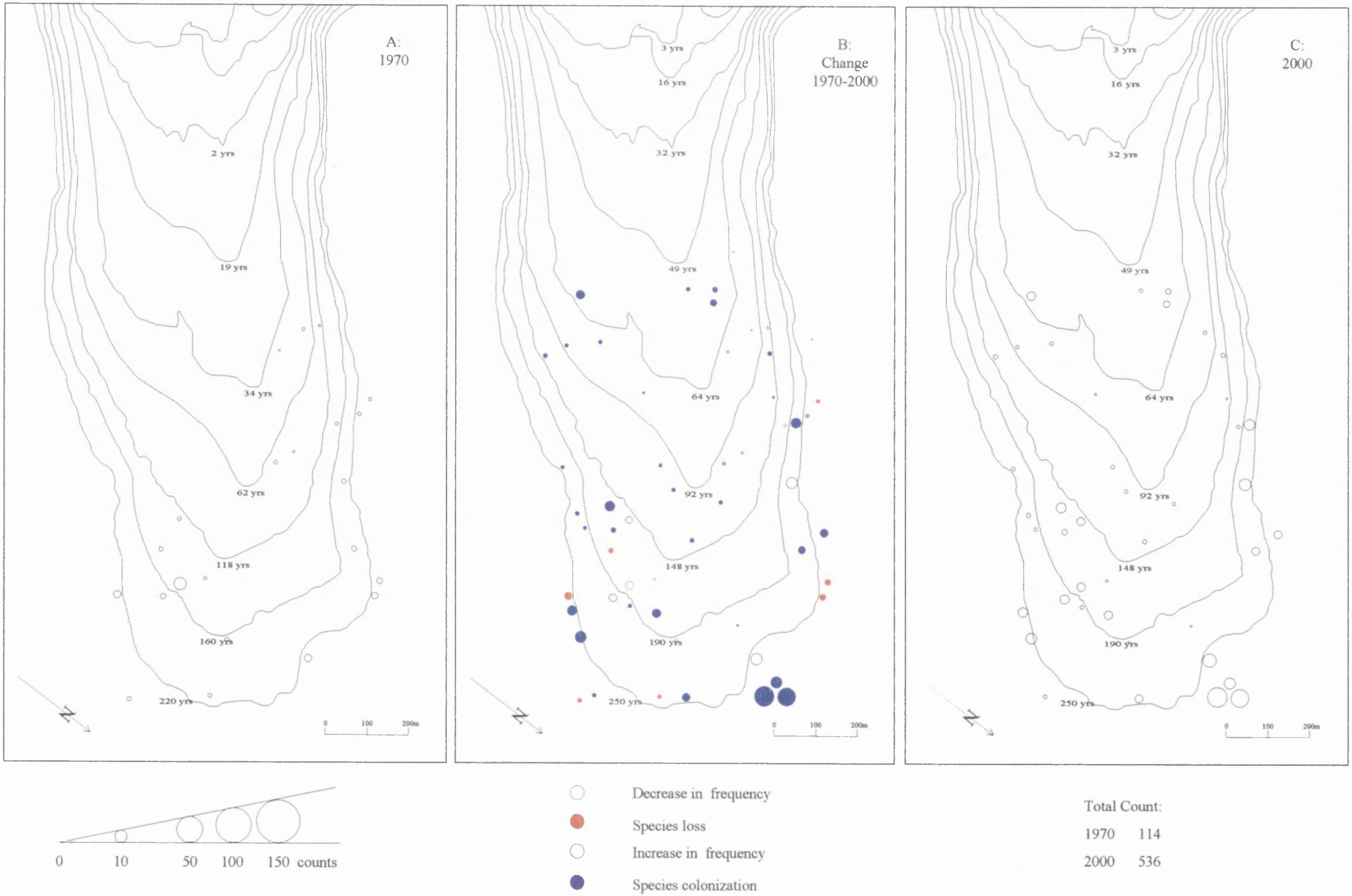


Figure 4.53 *Saxifraga stellaris*: A, frequency in 1970; B, change in frequency 1970-2000; C, frequency in 2000

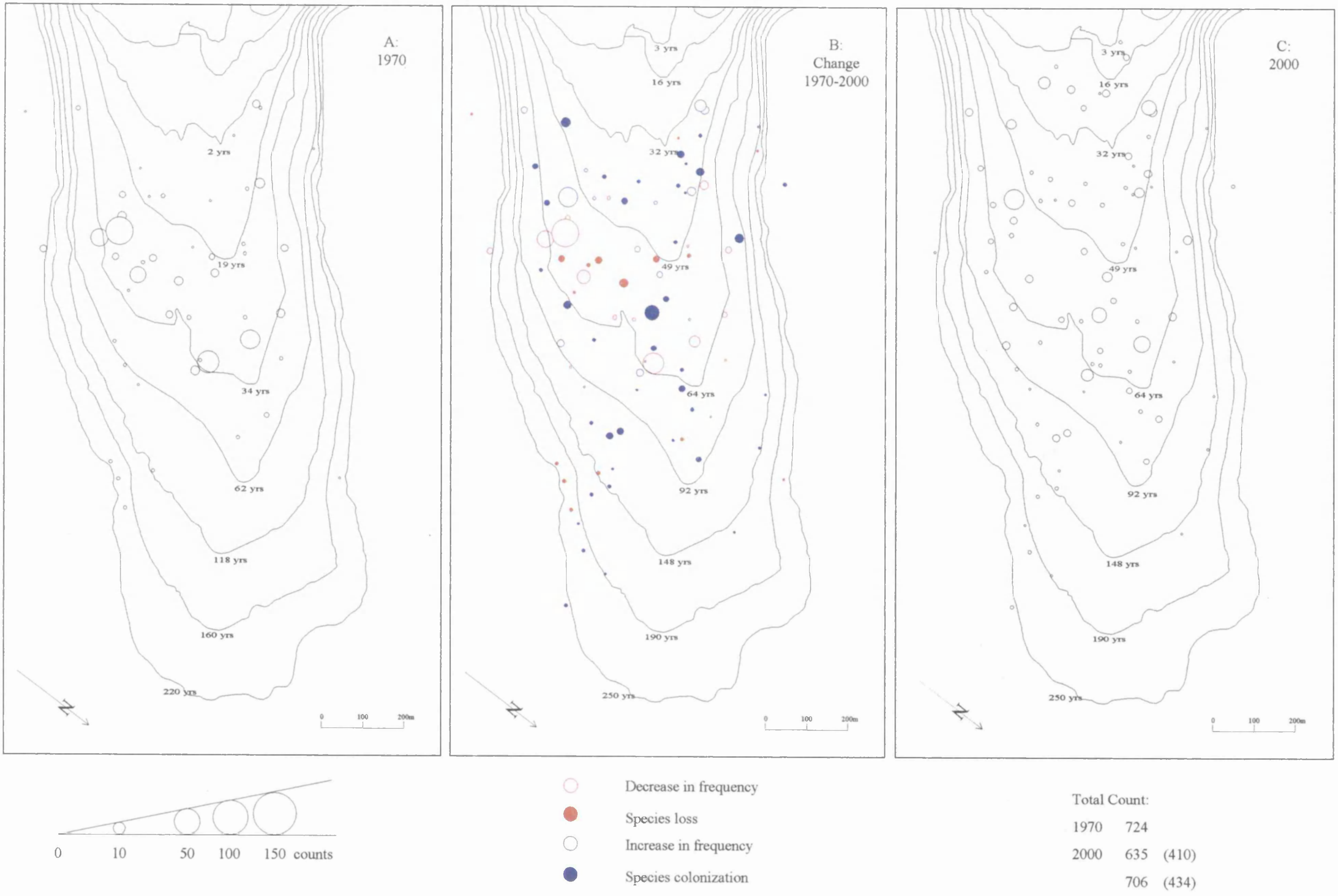


Figure 4.54 *Sibbaldia procumbens*: A, frequency in 1970; B, change in frequency 1970-2000; C, frequency in 2000

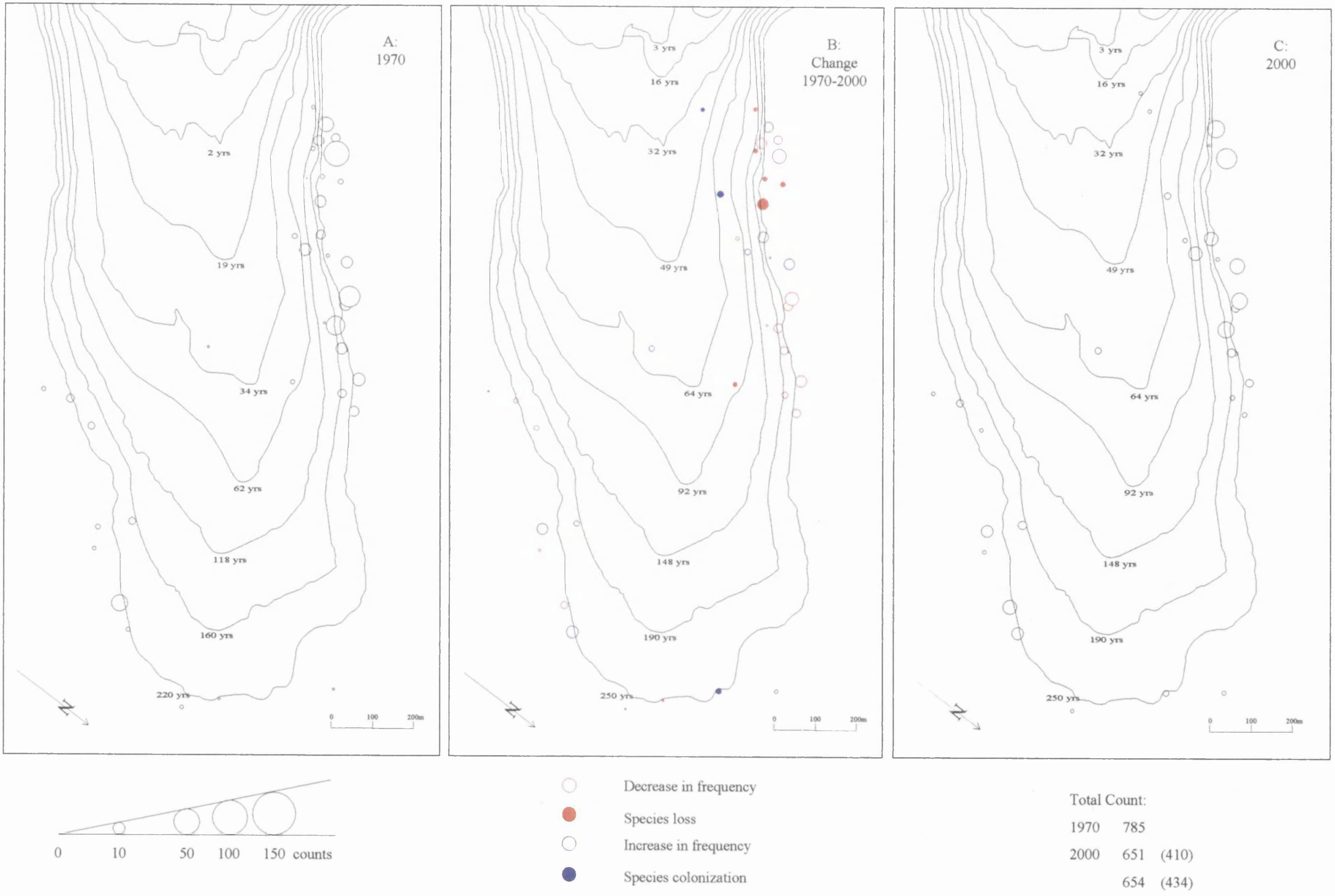


Figure 4.55 *Solidago virgaurea*: A, frequency in 1970; B, change in frequency 1970-2000; C, frequency in 2000

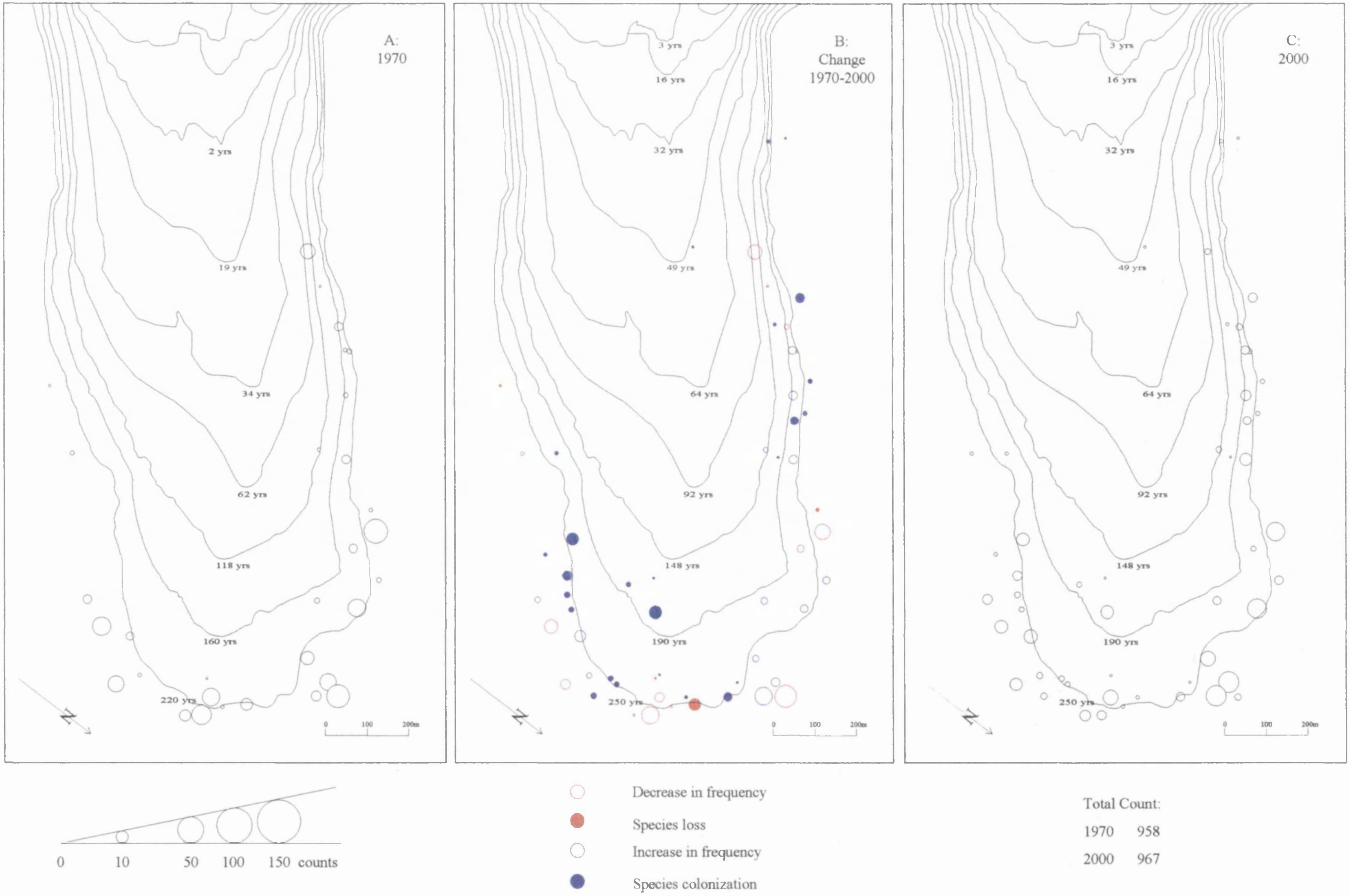


Figure 4.56 *Tofieldia pusilla*: A, frequency in 1970; B, change in frequency 1970-2000; C, frequency in 2000

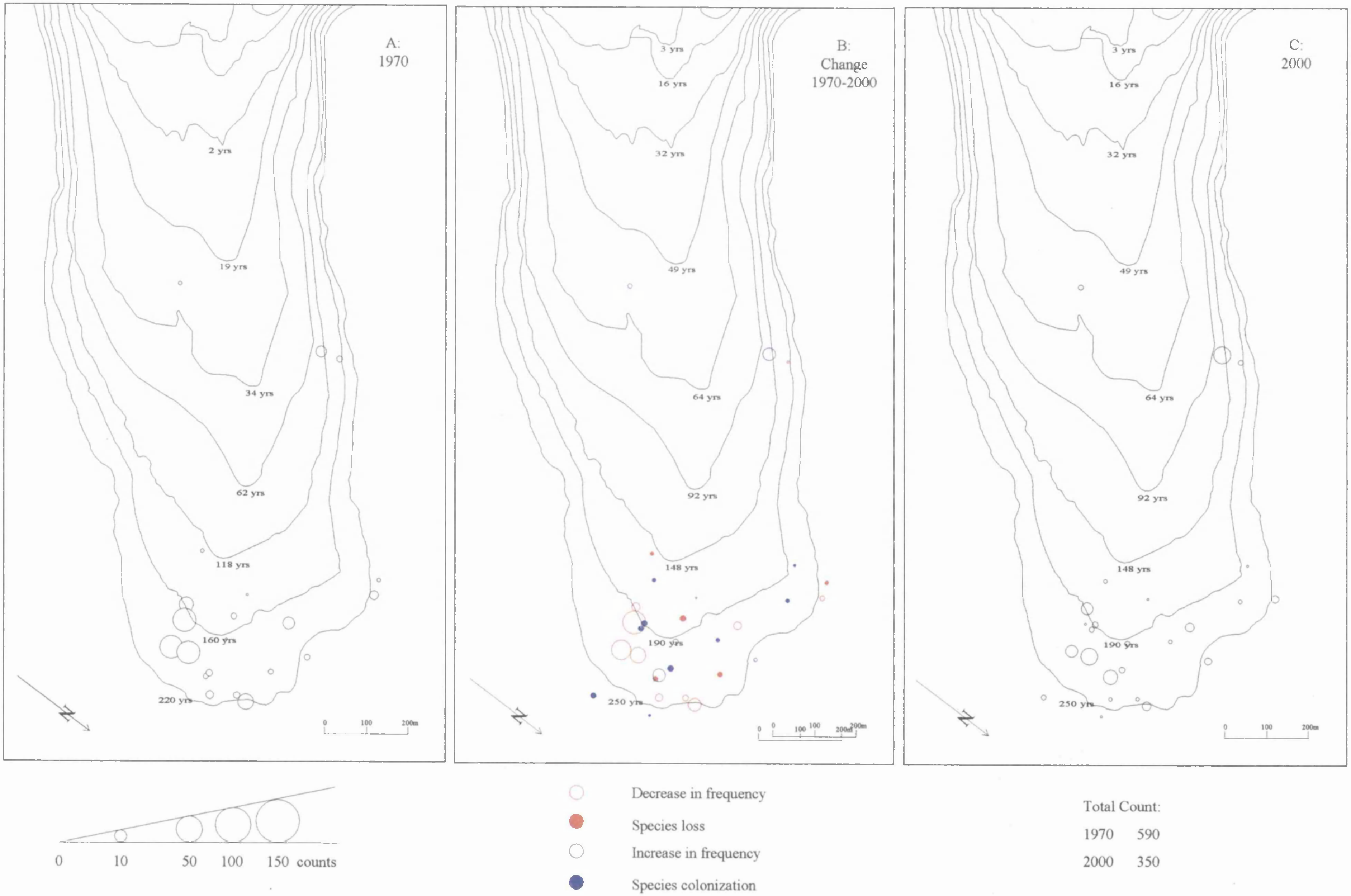
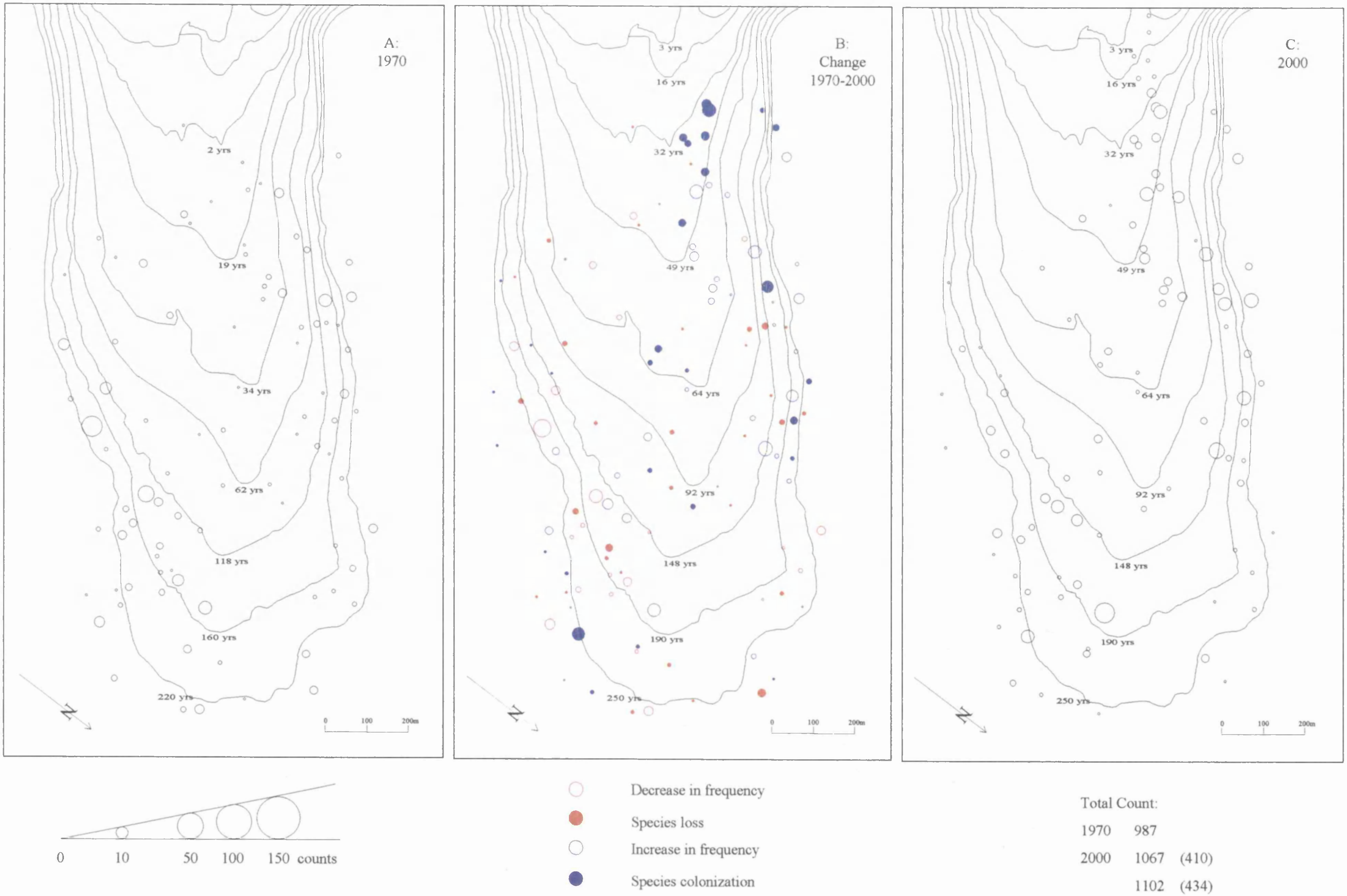


Figure 4.57 *Veronica alpina*: A, frequency in 1970; B, change in frequency 1970-2000; C, frequency in 2000



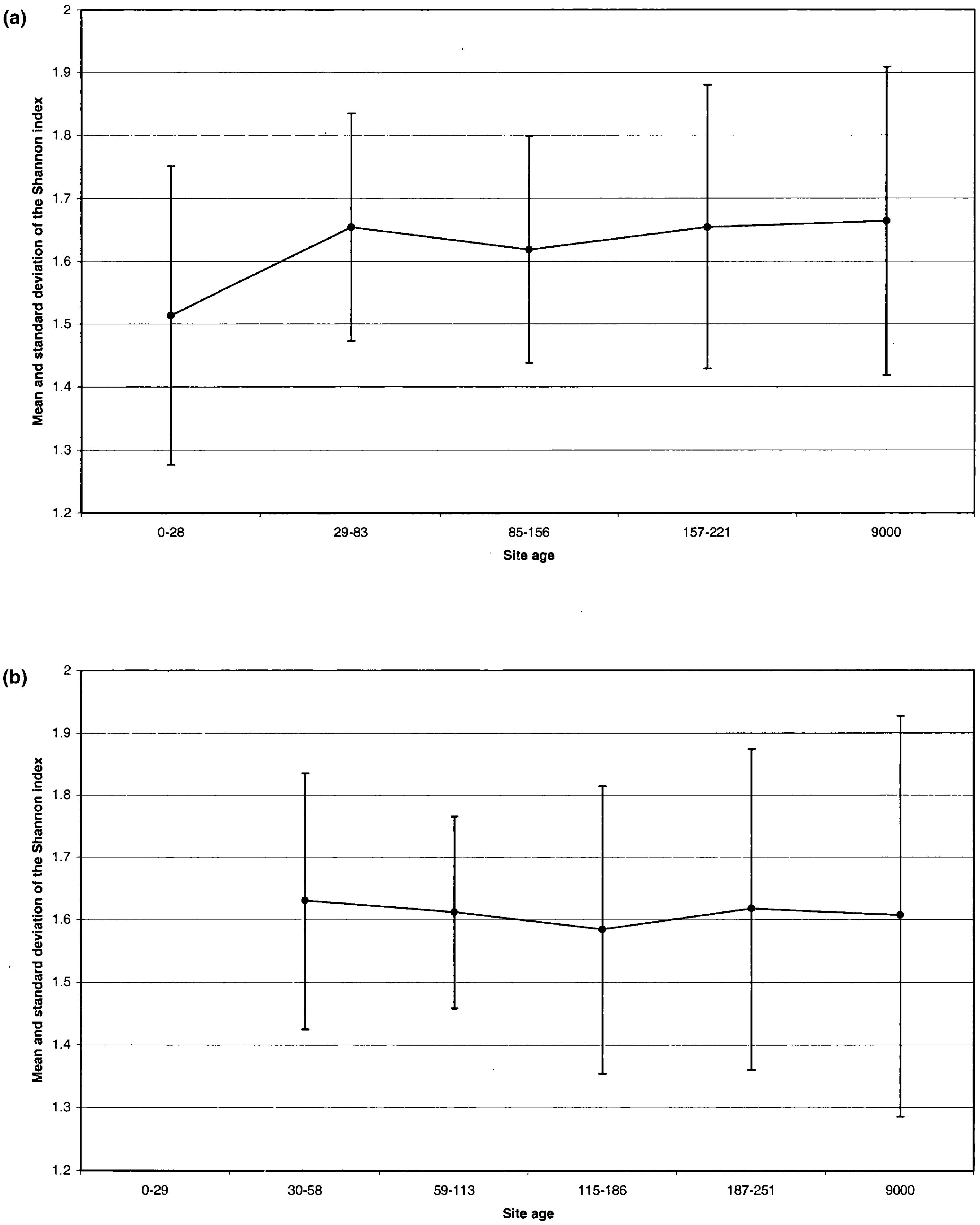


Figure 5.1: Comparison of the mean and standard deviation of the Shannon index in (a) 1970 and (b) 2000

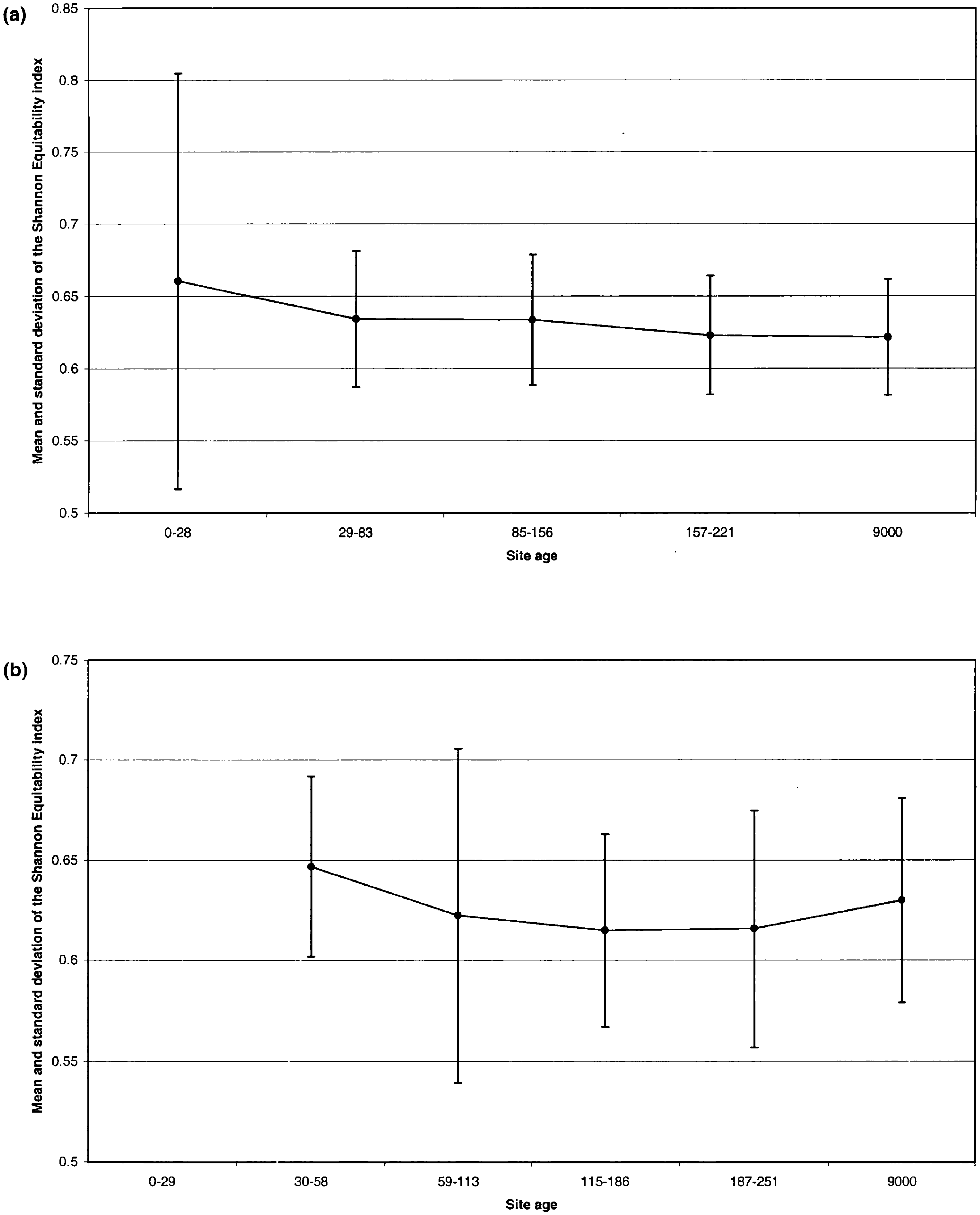


Figure 5.2: Comparison of the mean and standard deviation of the Shannon Equitability index in (a) 1970 and (b) 2000

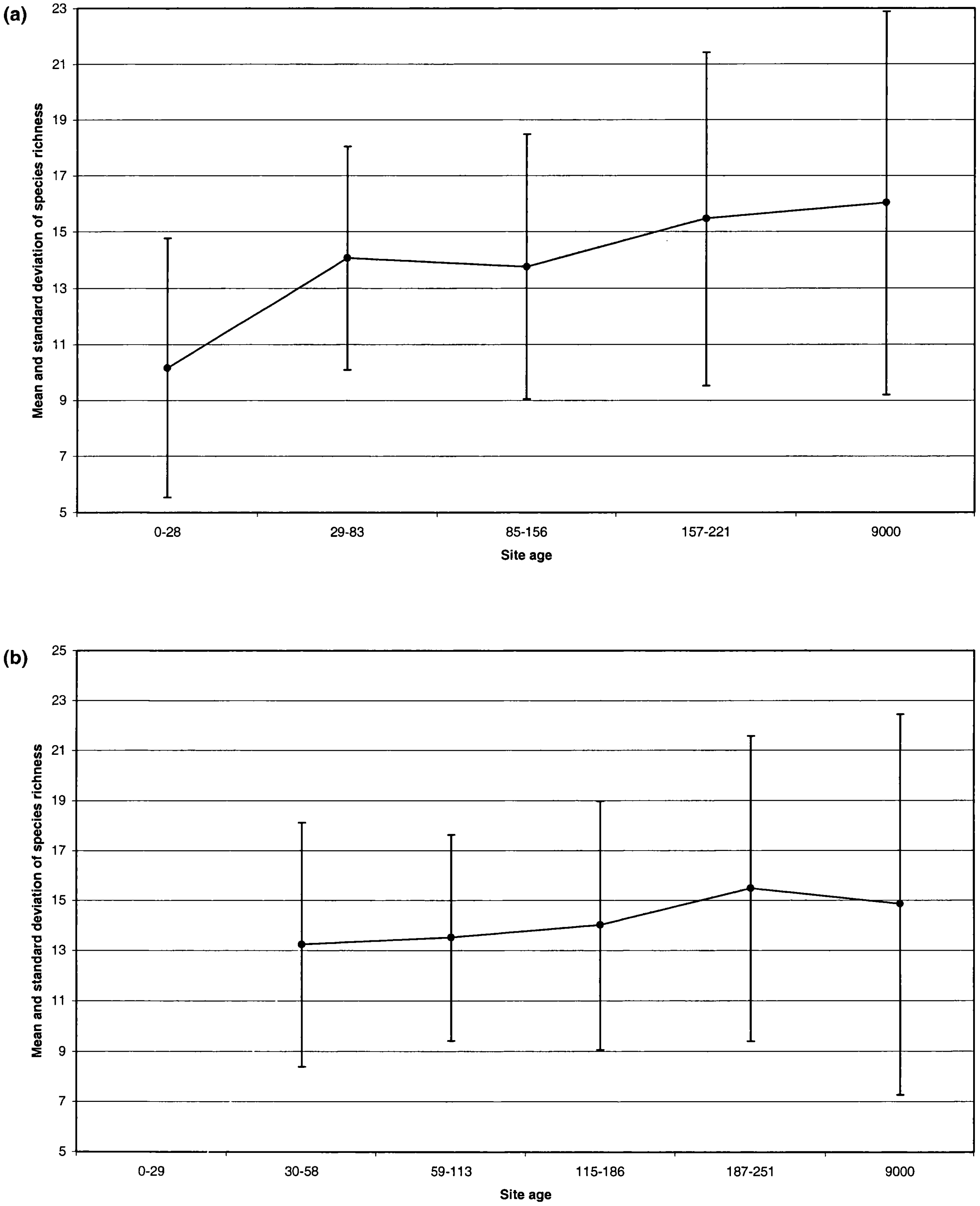


Figure 5.3: Comparison of the mean and standard deviation of species richness in (a) 1970 and (b) 2000

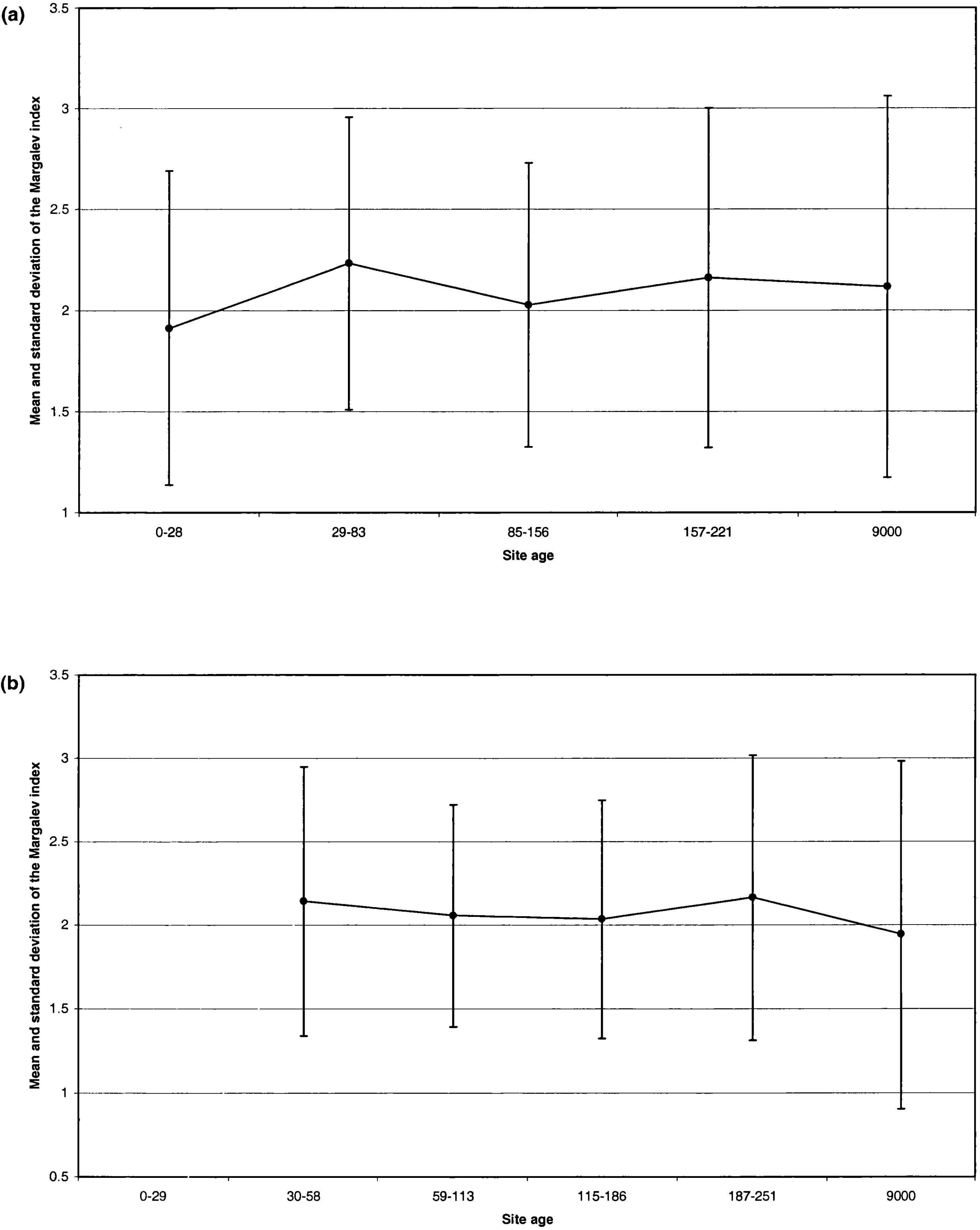


Figure 5.4: Comparison of the mean and standard deviation of the Margalev index in (a) 1970 and (b) 2000

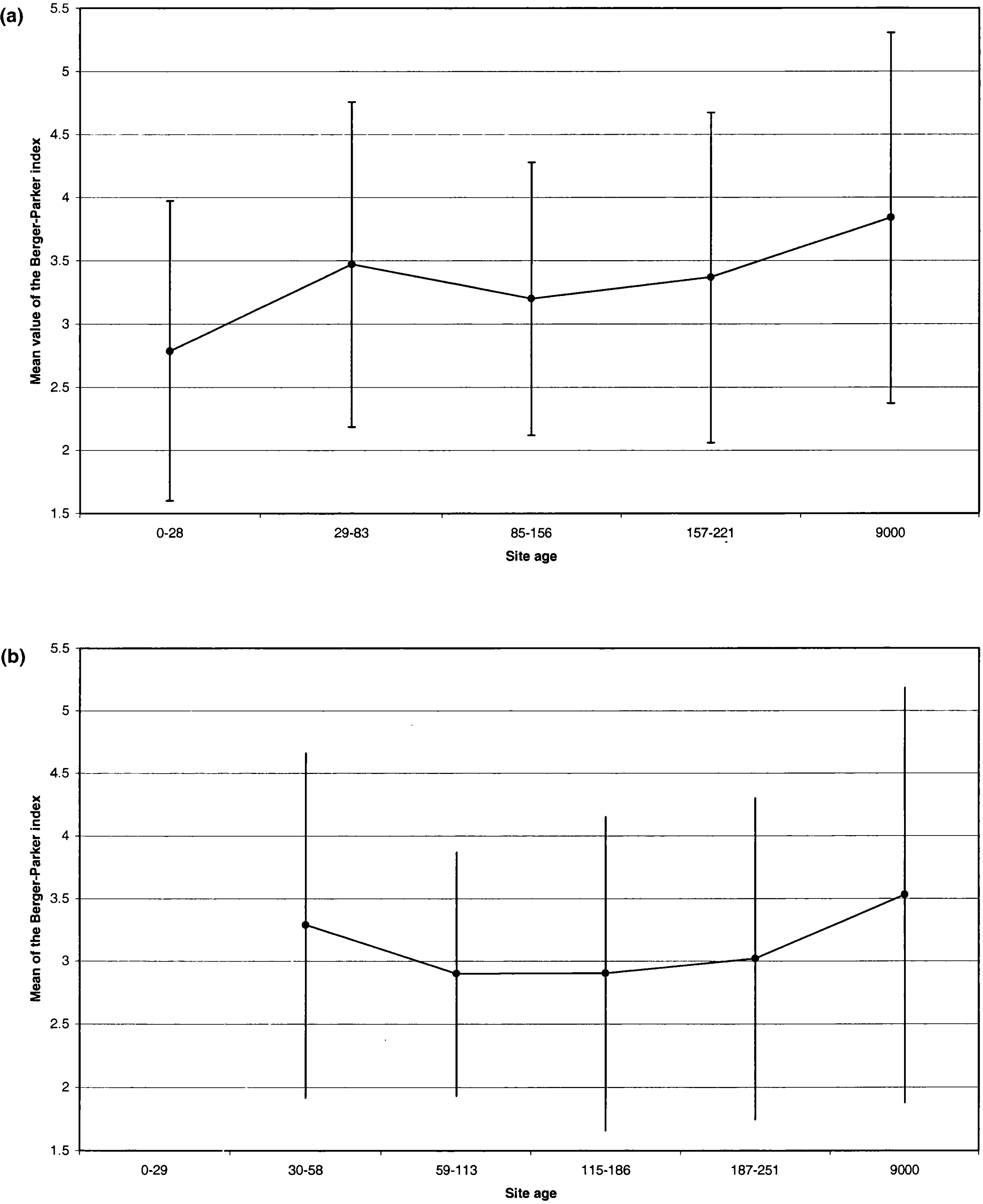


Figure 5.5: Comparison of the mean and standard deviation of the Berger-Parker index in (a) 1970 and (b) 2000

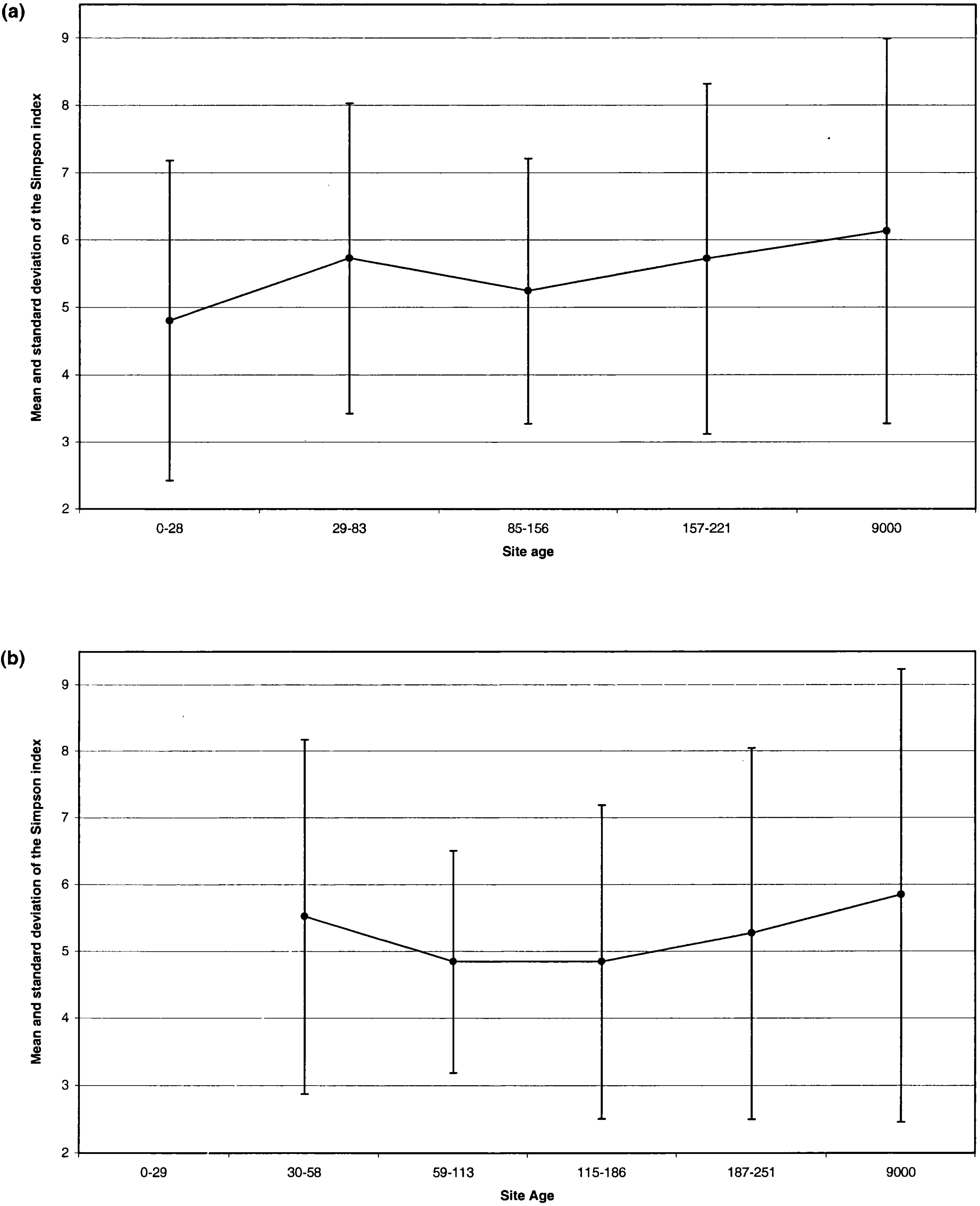


Figure 5.6: Comparison of the mean and standard deviation of the Simpson index in (a) 1970 and (b) 2000

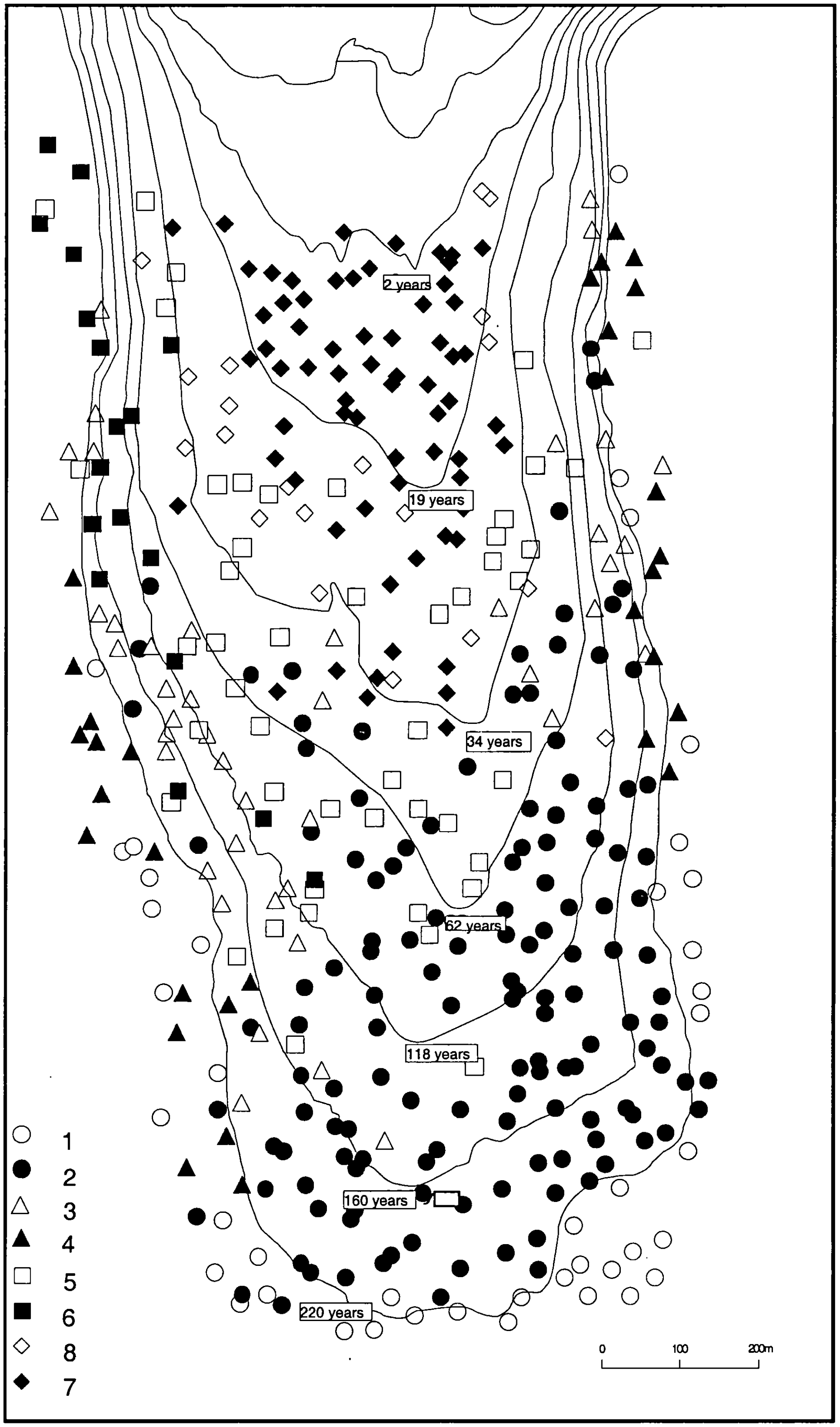


Figure 5.7: The location of sites comprising the TWINSPAN groups in 1970

The identity of the groups is as follows: 1: Mature, species-rich heath; 2: Immature, species-poor heath; 3: Late pioneer/heath intermediate; 4: Mature snowbed; 5: Early pioneer/heath intermediate; 6: Late pioneer/snowbed intermediary; 7: Early pioneer; and 8: Late pioneer
For a further discussion of the species composition, see section 5.3

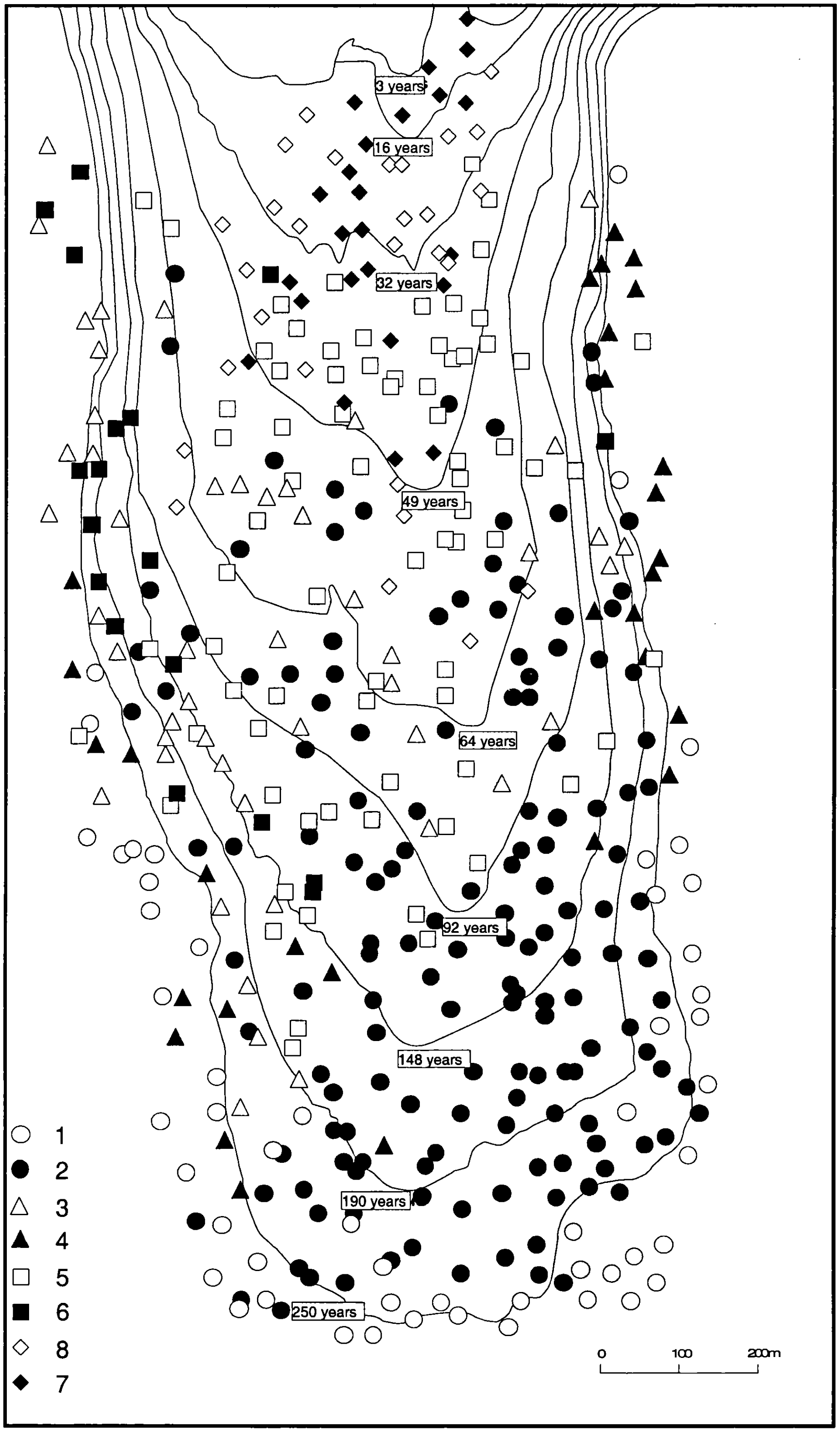


Figure 5.8: The location of sites comprising the TWINSPAN groups in 2000

The identity of the groups is as follows: 1: Mature, species-rich heath; 2: Immature, species-poor heath; 3: Late pioneer/heath intermediate; 4: Mature snowbed; 5: Early pioneer/heath intermediate; 6: Late pioneer/snowbed intermediary; 8: Late pioneer and 7: Early pioneer

For a further discussion of the species composition, see section 5.3

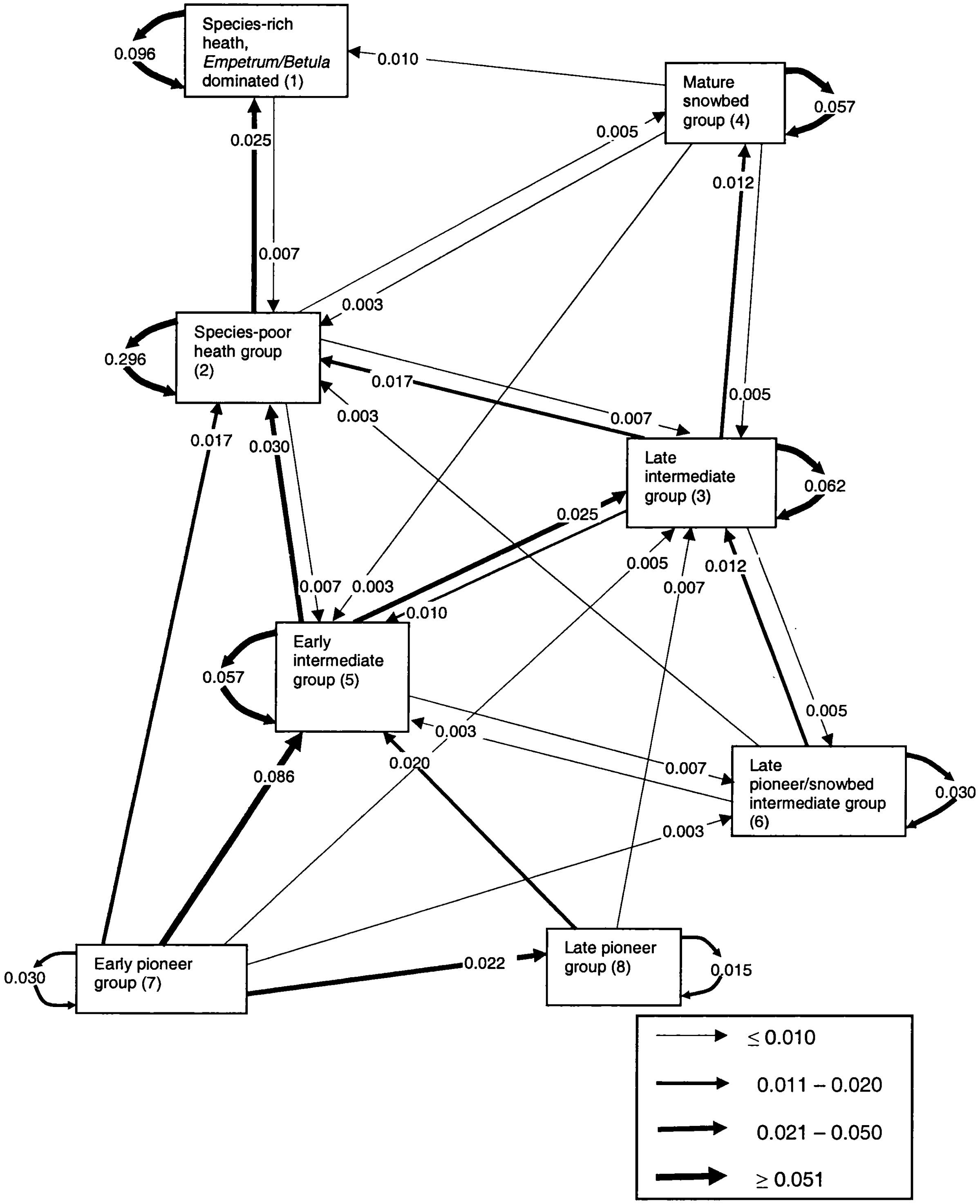


Figure 5.9: Transition probabilities between TWINSPAN classification groups
The assemblage types are those identified from the TWINSPAN site classification in section 5.3. The numbers on the arrows refer to the probability of that transition occurring between 1970 and 2000.
Solid arrows indicate transitions that are progressive or retrogressive, curved arrows show the probability of a site remaining in the same compositional group.

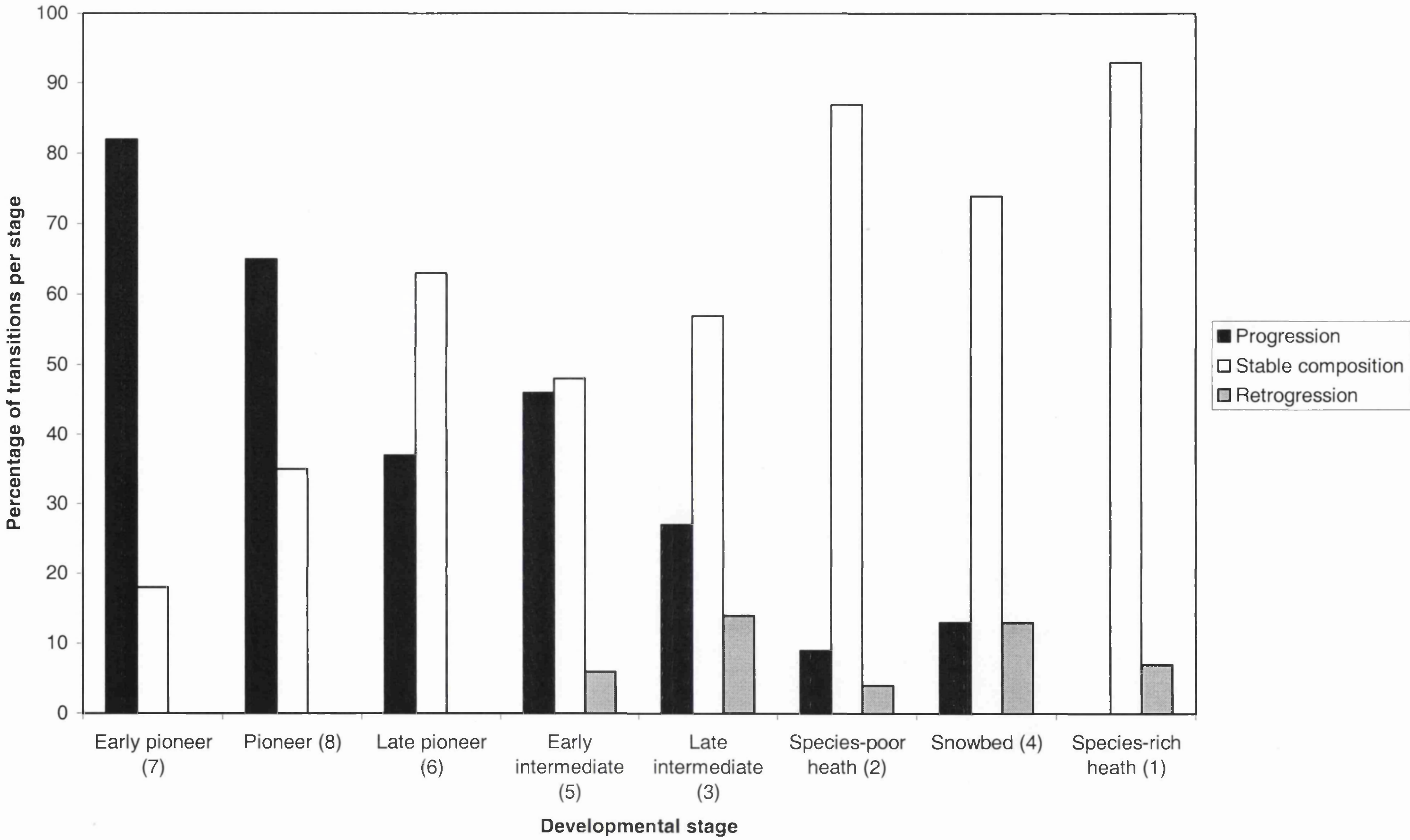


Figure 5.10: The relative importance of progression, stability, and retrogression between 1970 and 2000 within the developmental stages identified by the TWINSPAN classification.

The relative contributions of each category are calculated as a percentage of the total number of transitions occurring from that stage (see section 5.7).

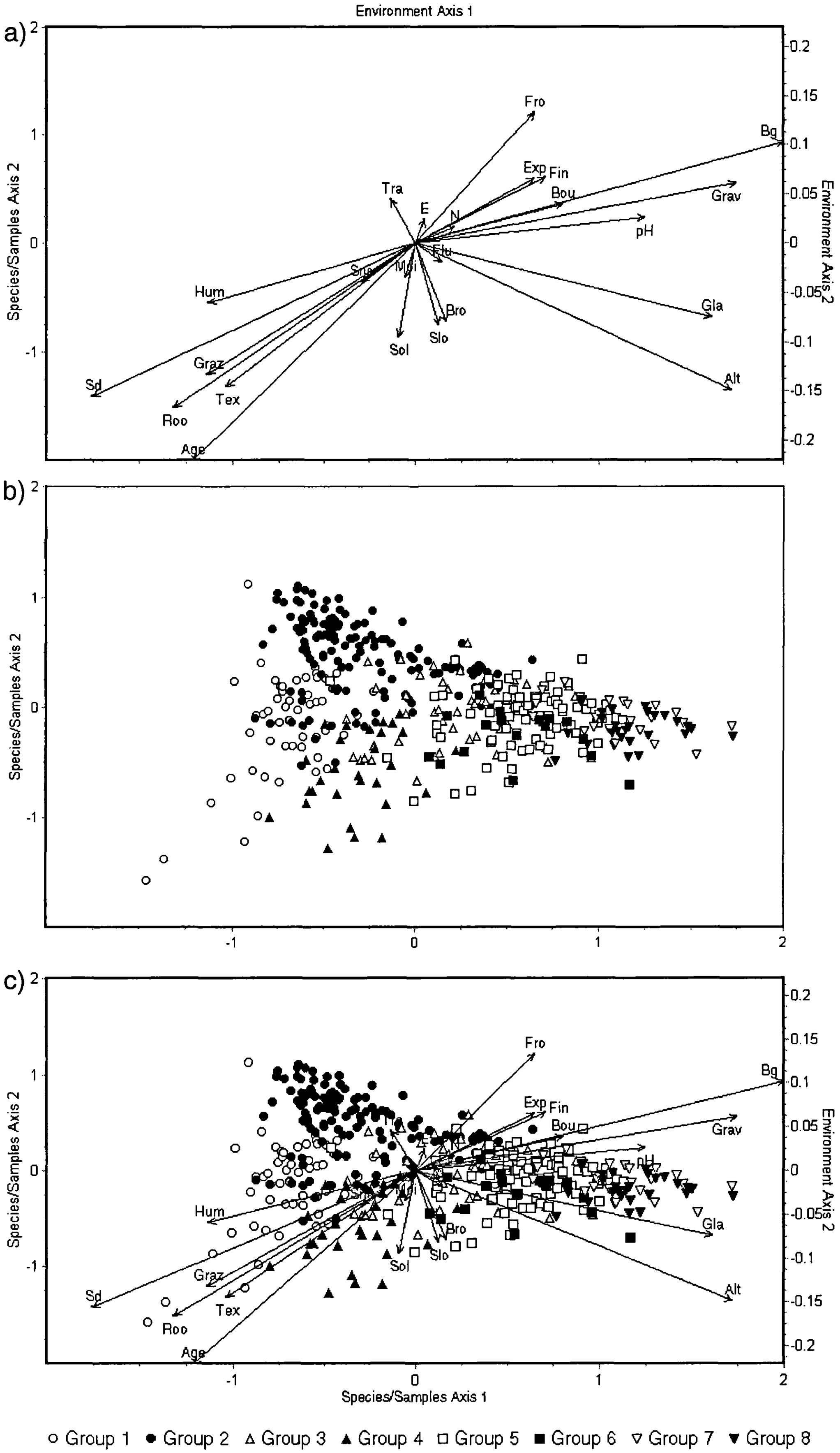


Figure 6.1: Canonical Correspondence Analysis biplots for all sites; a: environmental vectors; b: site positions (from TWINSPAN Classification); c: a) superimposed on b)

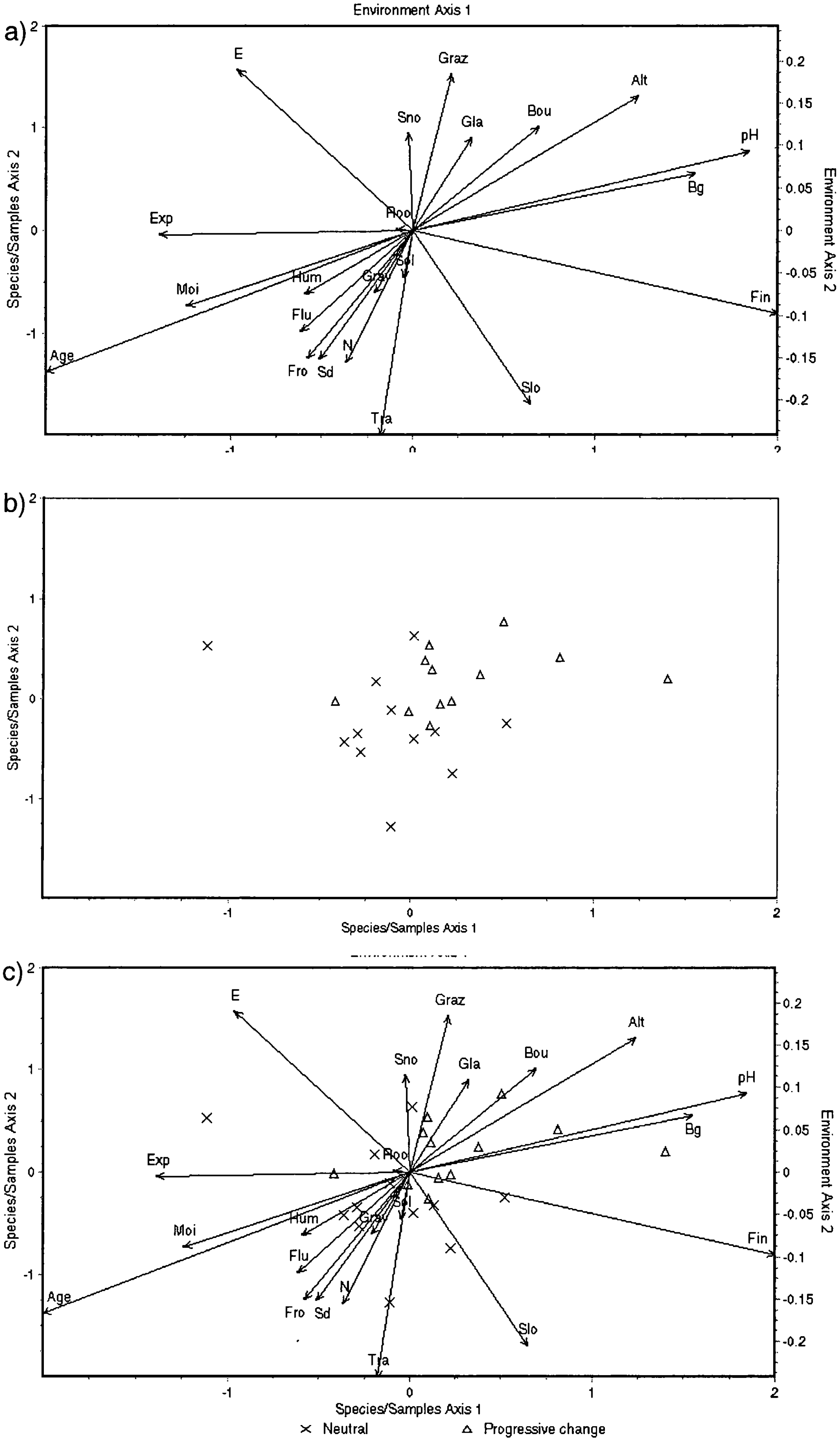


Figure 6.2: Canonical Correspondence Analysis Biplots Group 7; a: environmental vectors; b: site positions (from TWINSPAN classification); c: a) superimposed on b)

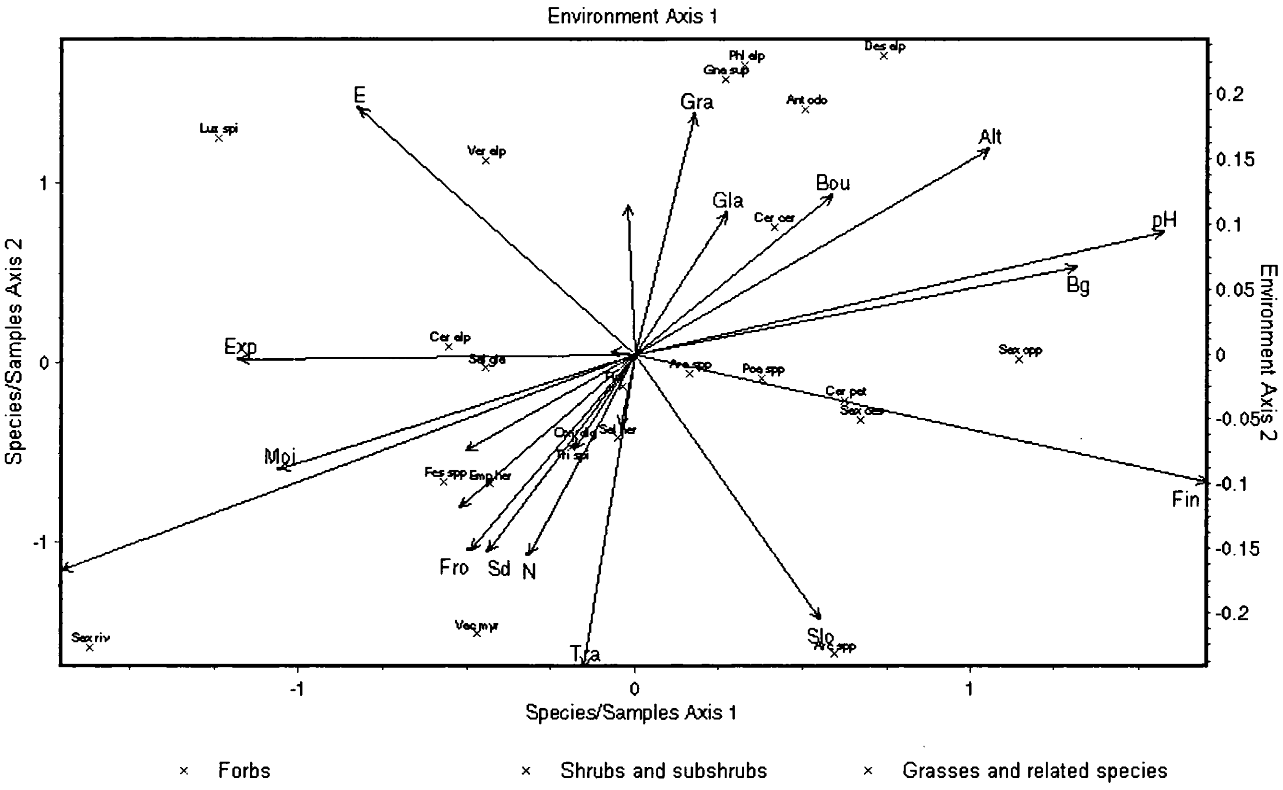


Figure 6.3: Early pioneer group 7 species ordination plot
a list of abbreviations and full species names are given in Appendix 1

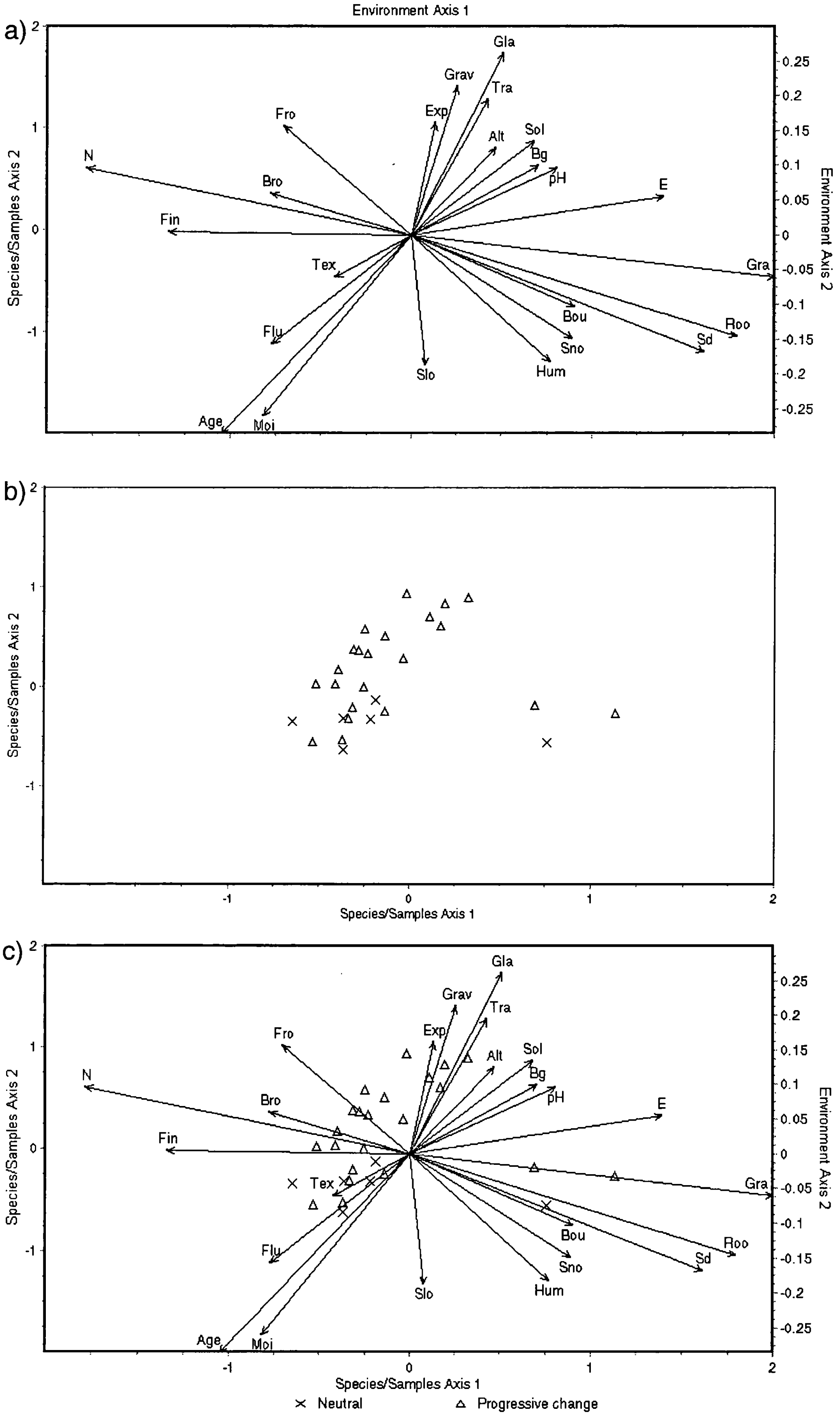


Figure 6.4: Canonical Correspondence Analysis Biplots Group 8; a: environmental vectors; b: site positions (from TWINSPAN classification); c: a) superimposed on b)

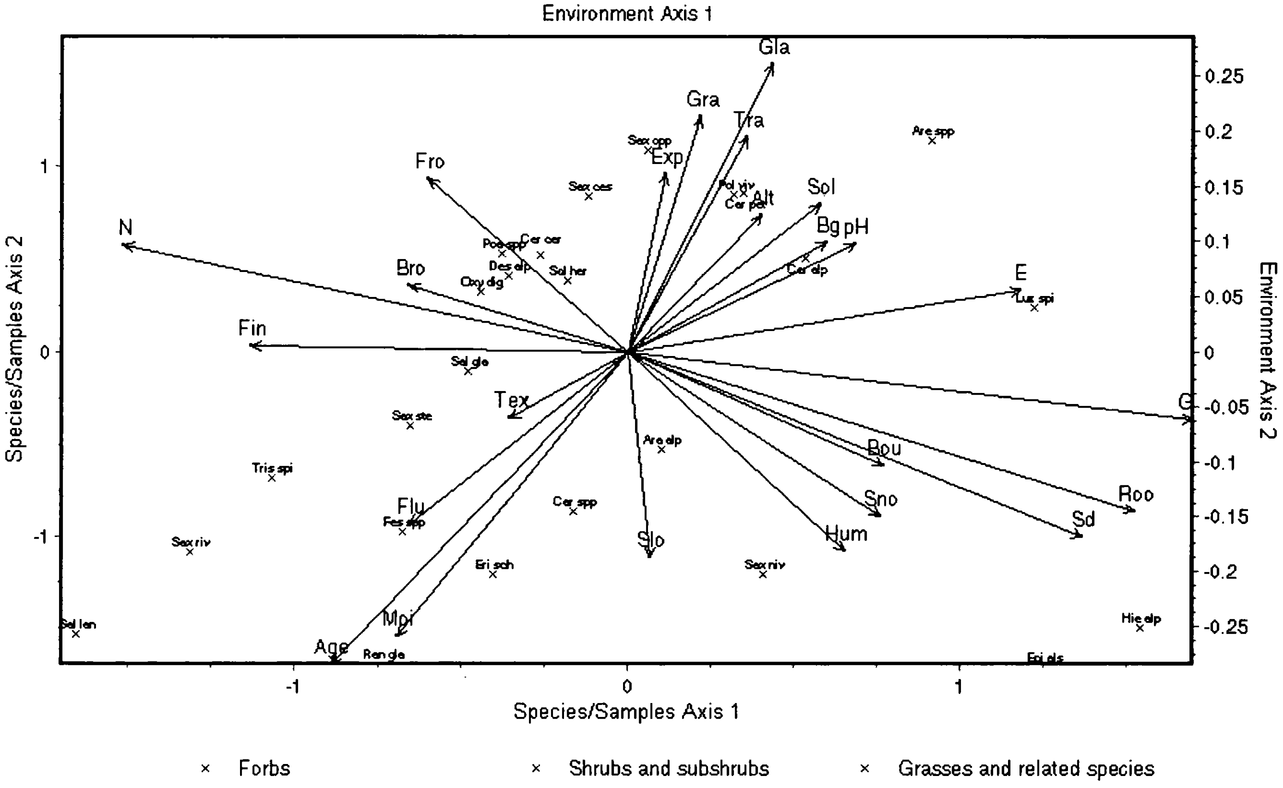


Figure 6.5: Late pioneer group 8 species ordination
a list of abbreviations and full species names is given in Appendix 1

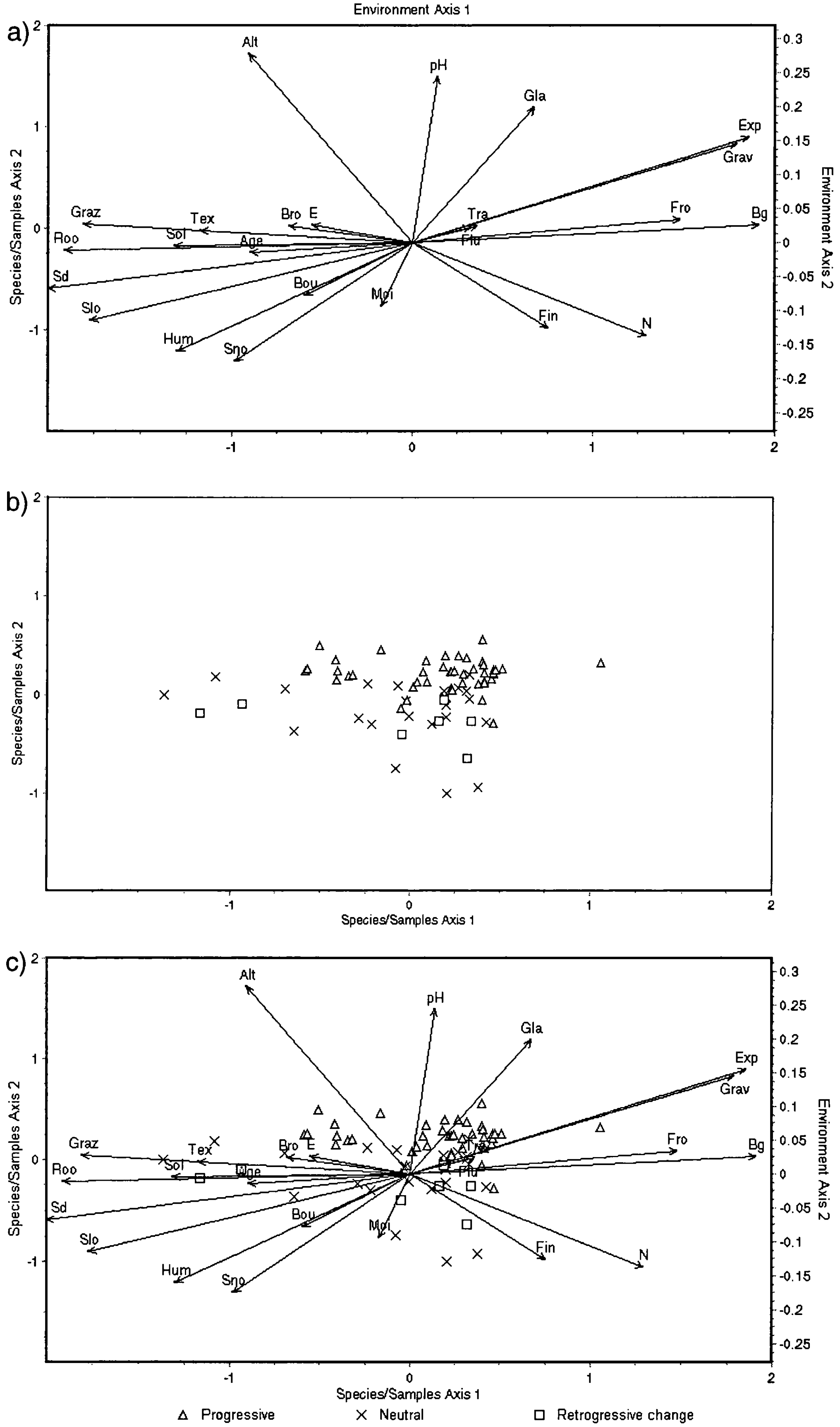


Figure 6.6: Canonical Correspondence Analysis Biplots, Group 5; a: environmental vectors; b: site positions (from TWINSPAN classification); c: a) superimposed on b)

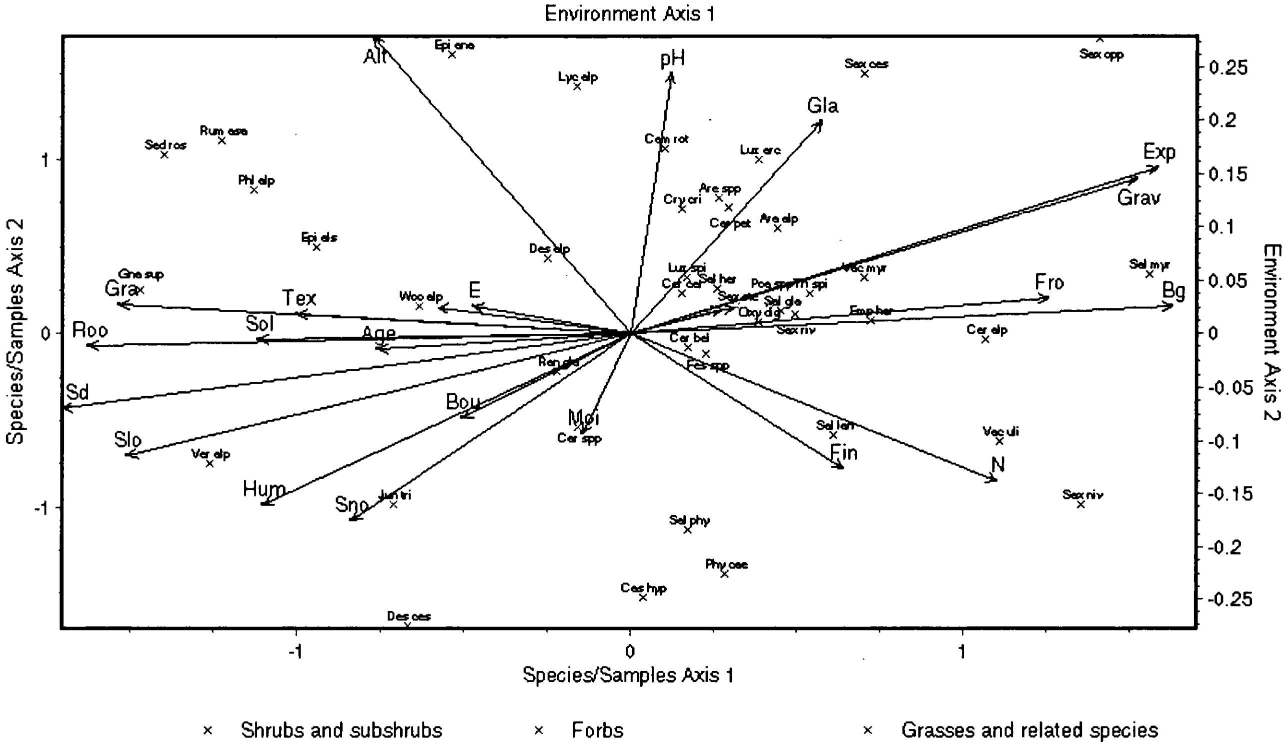


Figure 6.7 The early intermediate group 5 species ordination

a list of abbreviations and full species names is given in Appendix 1

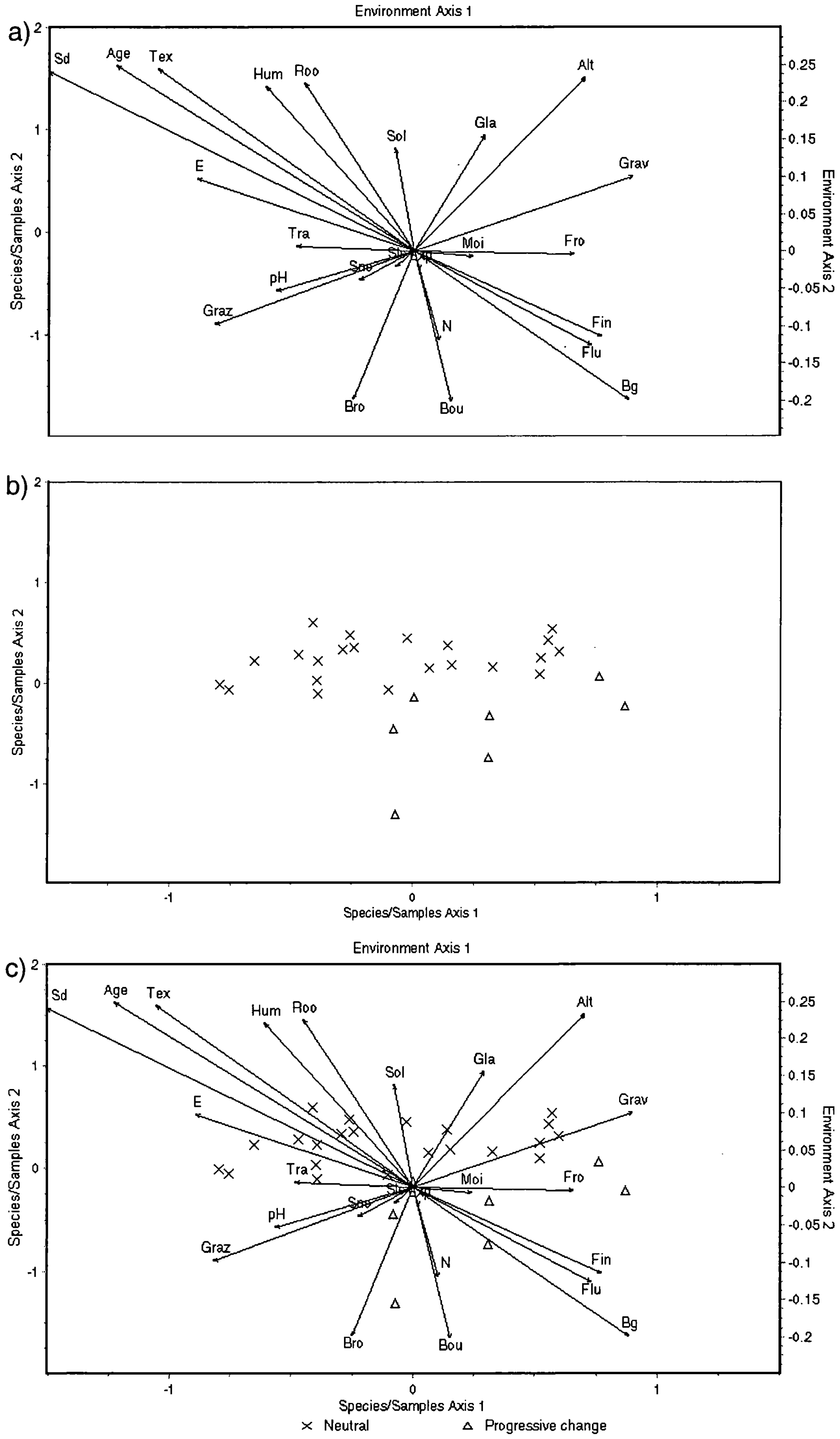


Figure 6.8: Canonical Correspondence Analysis Biplots, Group 4; a: environmental vectors; b: site positions (from TWINSPAN classification); c: a) superimposed on b)

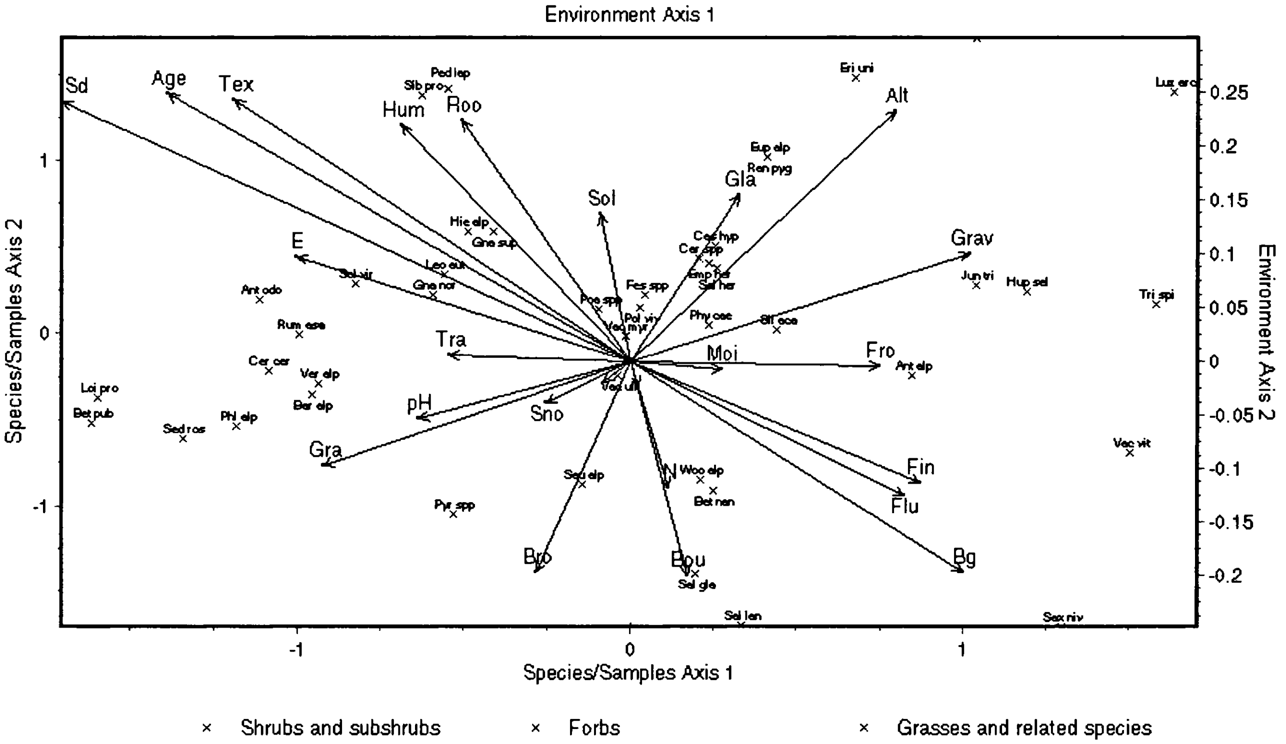


Figure 6.9 The mature snowbed group 4 species ordination

a list of abbreviations and full species names is given in Appendix 1

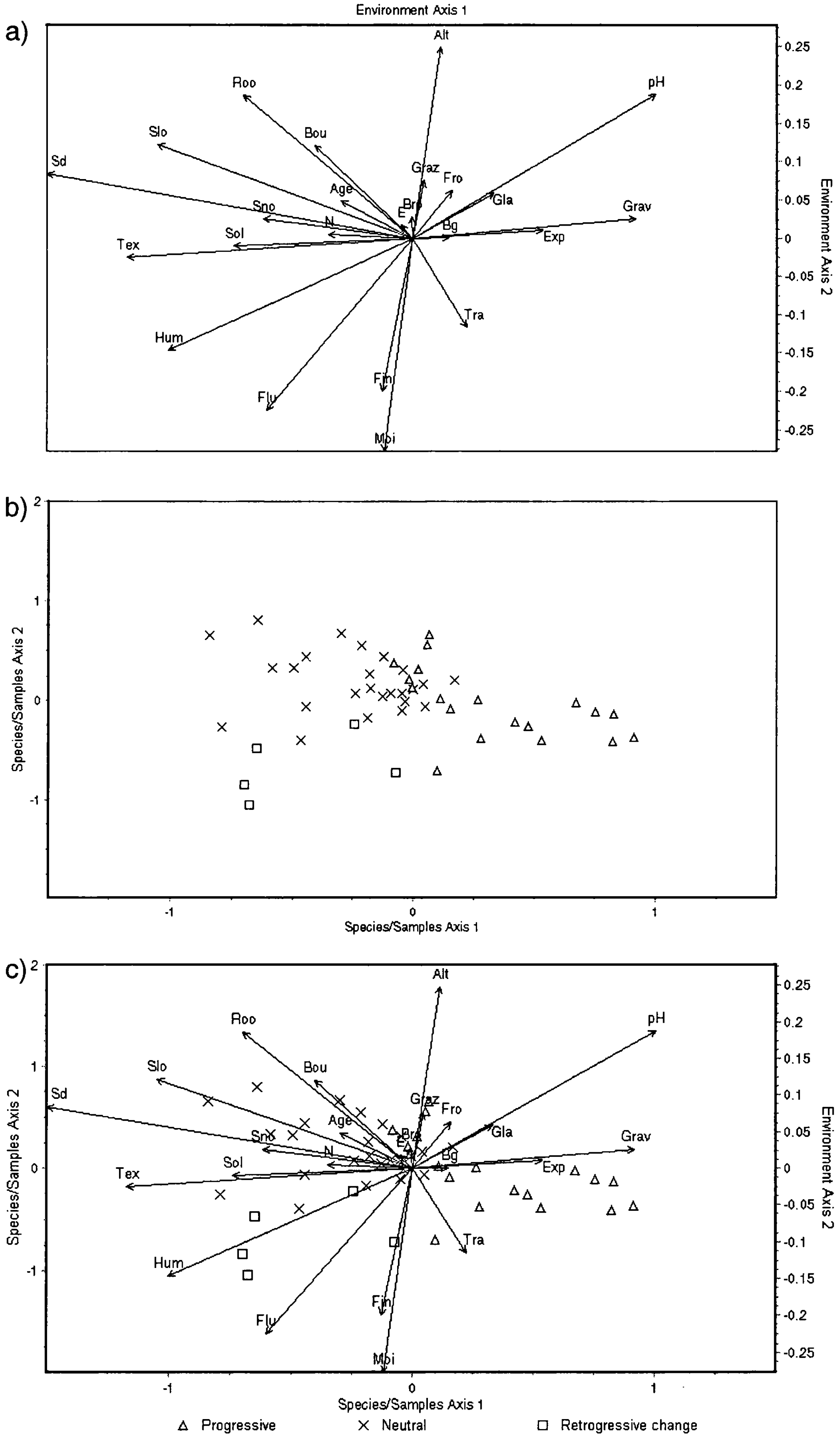


Figure 6.10: Canonical Correspondence Analysis Biplots, Group 3; a: environmental vectors; b: site positions (from TWINSPAN classification); c: a) superimposed on b)

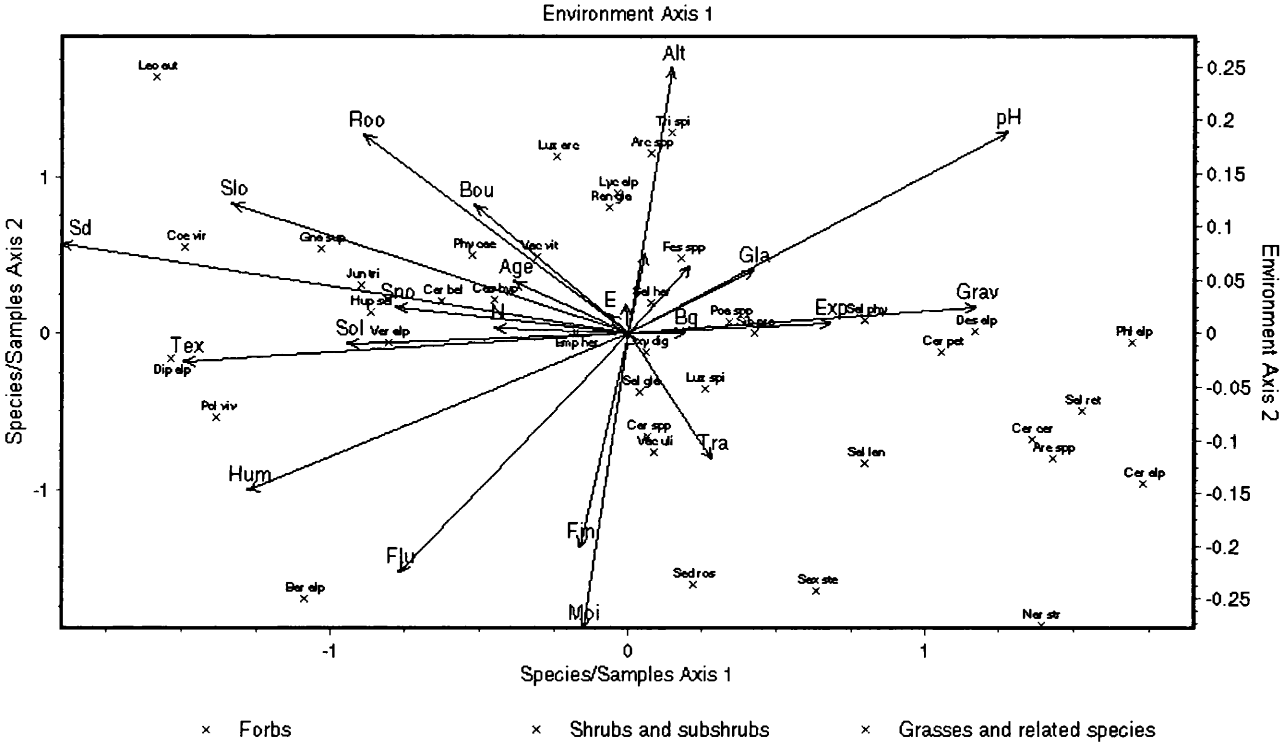


Figure 6.11 Late intermediate group 3 species ordination
a list of abbreviations and full species names is given in Appendix 1

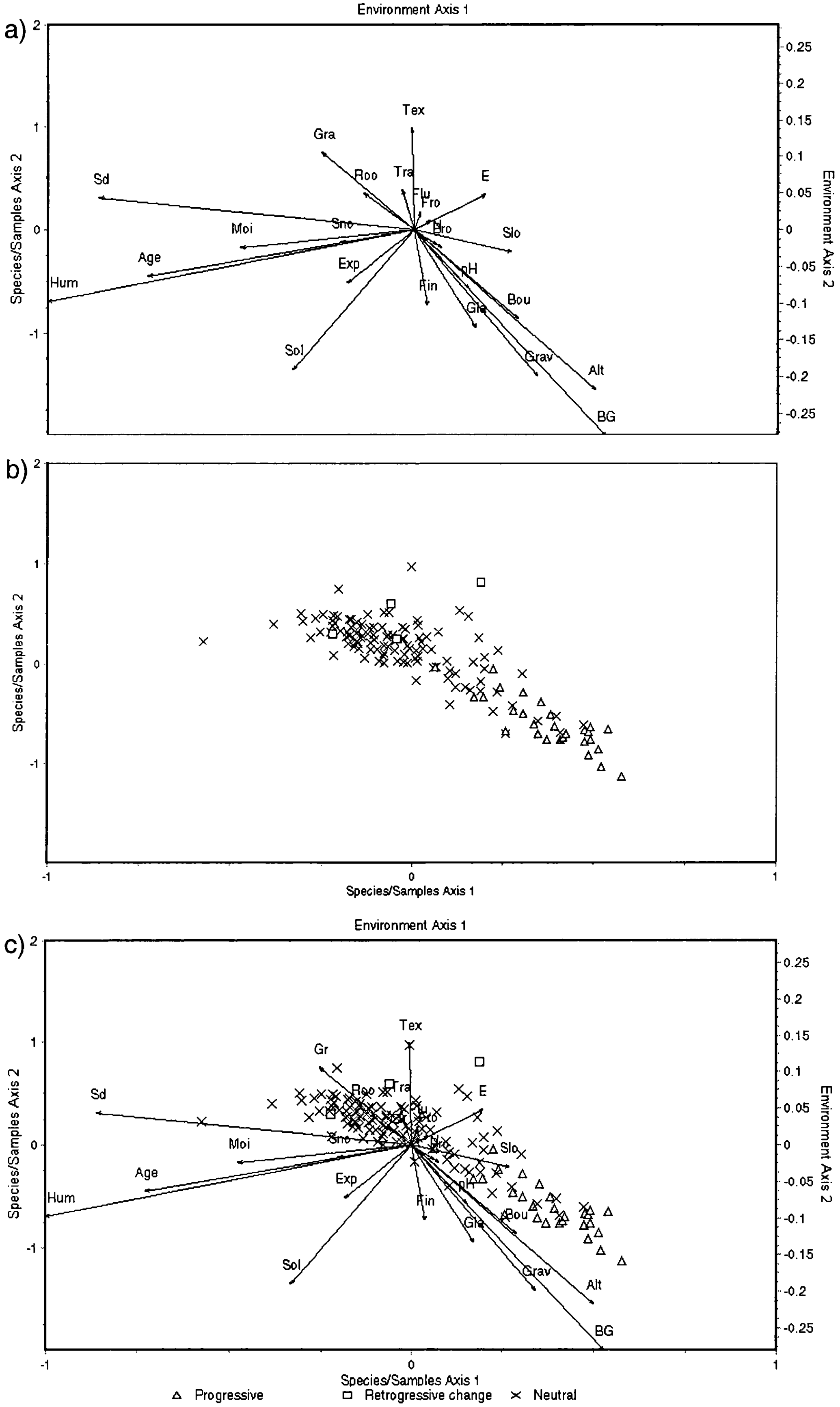


Figure 6.12: Canonical Correspondence Analysis Biplots, Group 2; a: environmental vectors; b: site positions (from TWINSPAN classification); c: a) superimposed on b)

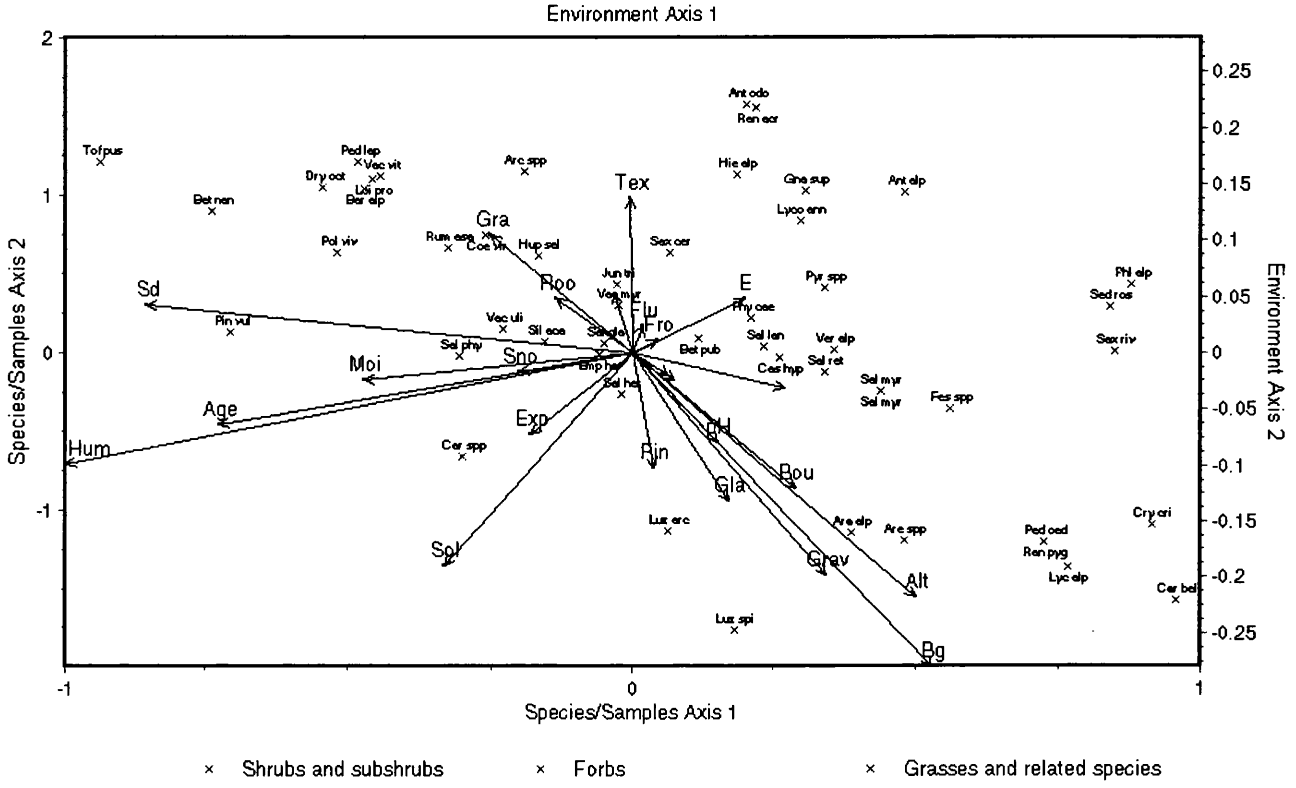


Figure 6.13 Species-poor heath group 2 species ordination
a list of abbreviations and full species names is given in Appendix 1

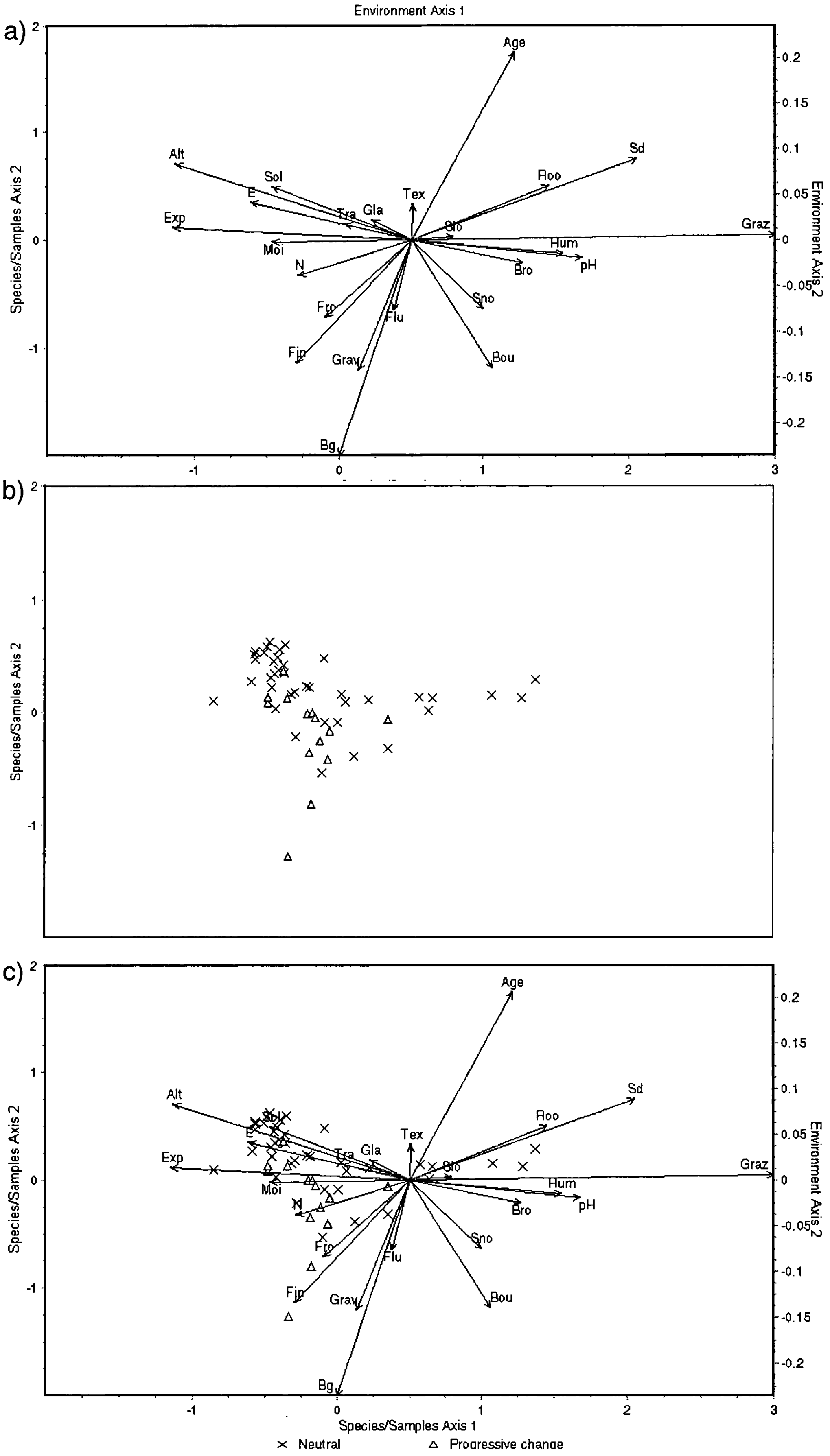


Figure 6.14: Canonical Correspondence Analysis biplot, Group 1; a: environmental vectors; b: site positions(from TWINSPAN Classification); c: a) superimposed on b)

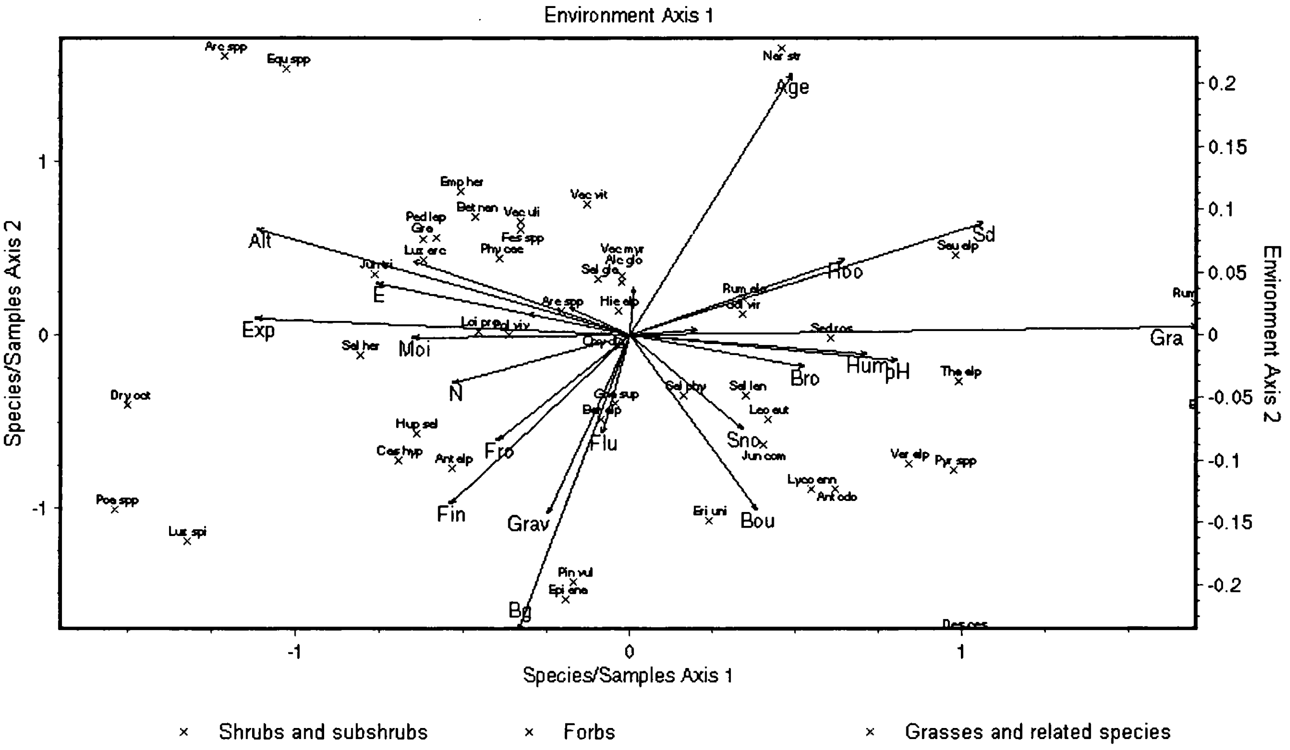


Figure 6.15 Species-rich heath group 1 species ordination
a list of abbreviations and full species names is given in Appendix 1

Figure S1 *Calluna vulgaris*: A, frequency 1970; B, change in frequency 1970-2000; C, frequency in 2000

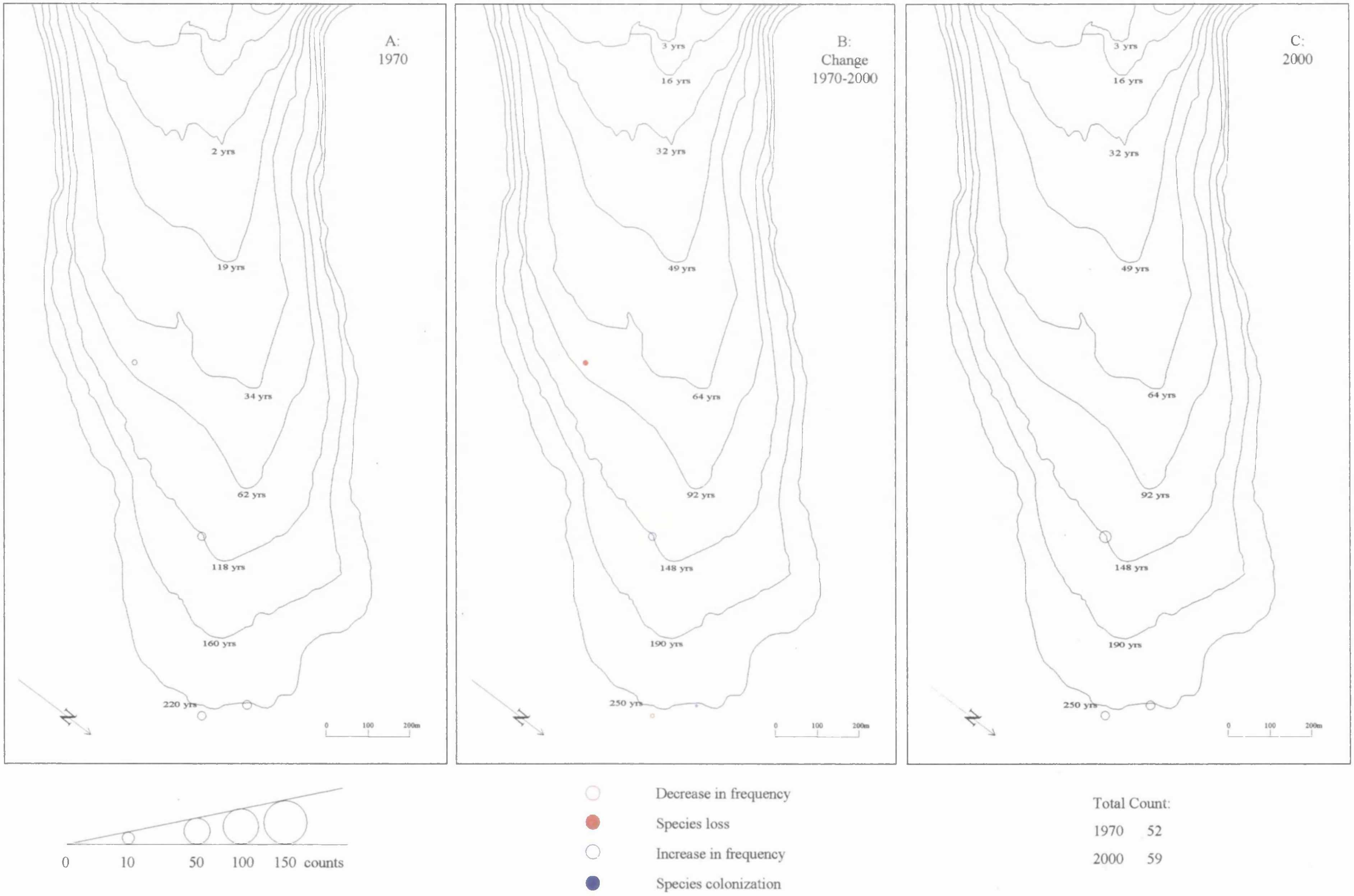


Figure S2 *Salix reticulata*: A, frequency in 1970; B, change in frequency 1970-2000; C, frequency in 2000

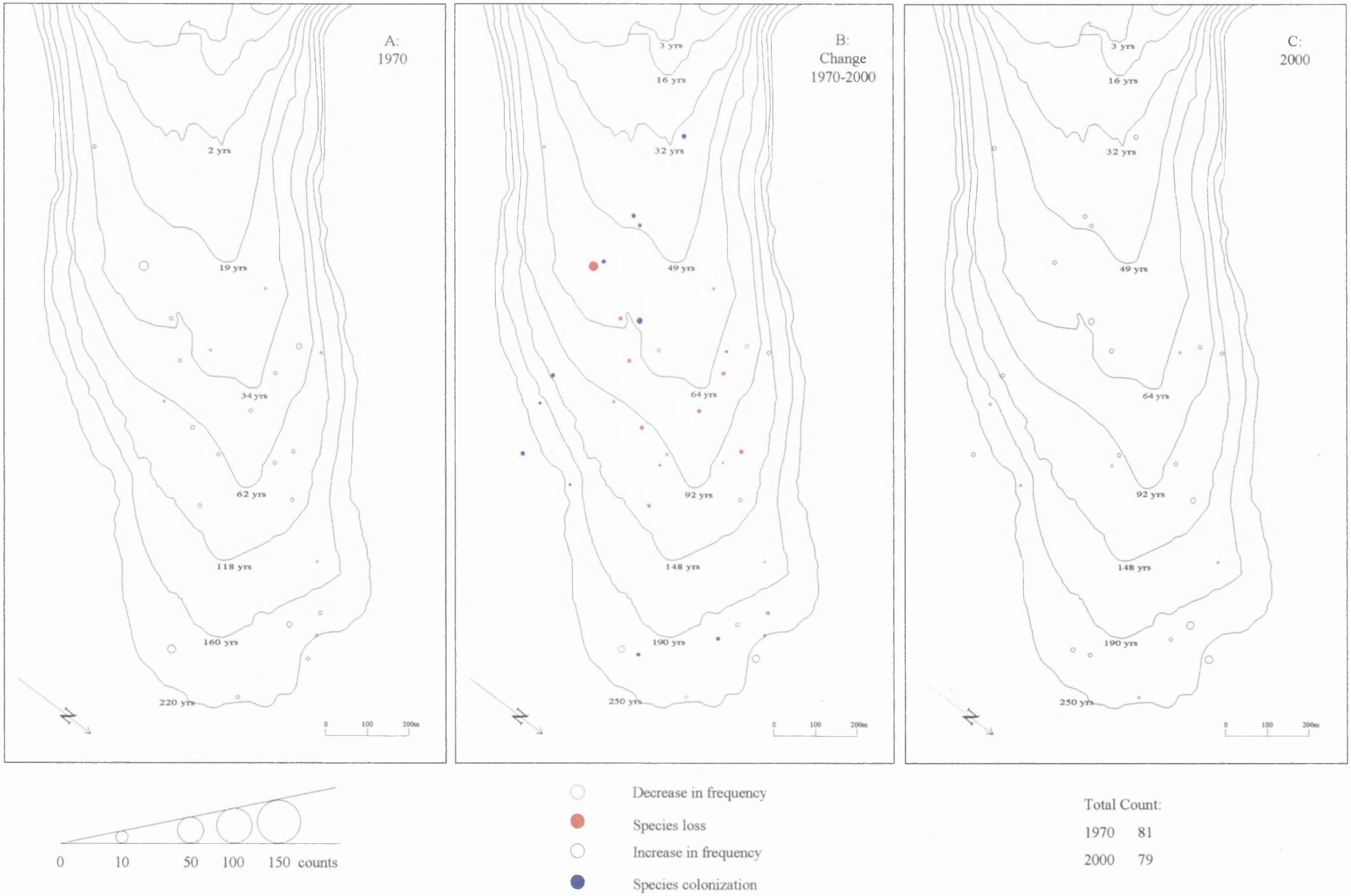


Figure S3 *Adiantum capillus-veneris*: A, frequency in 1970; B, change in frequency 1970-2000

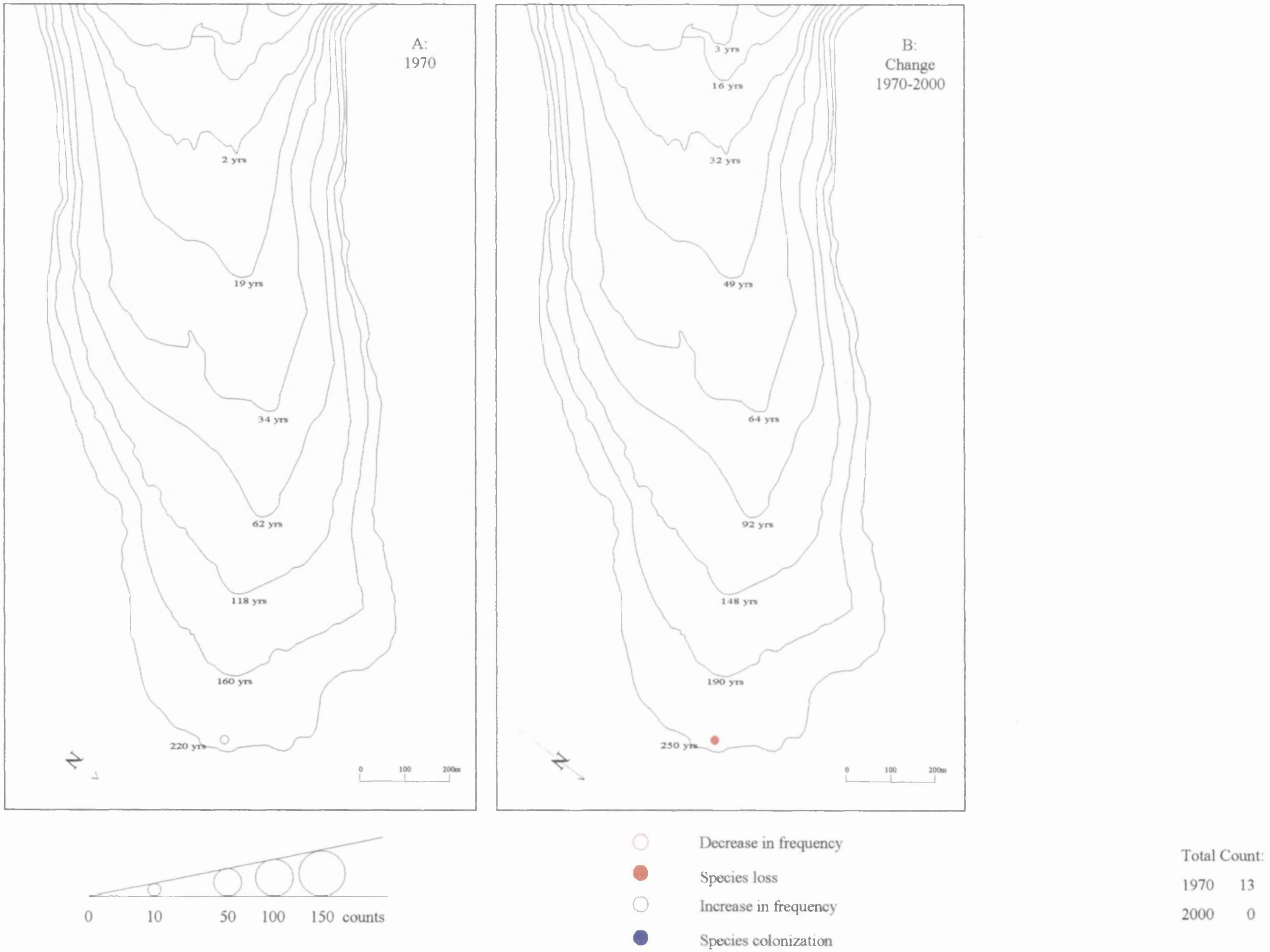
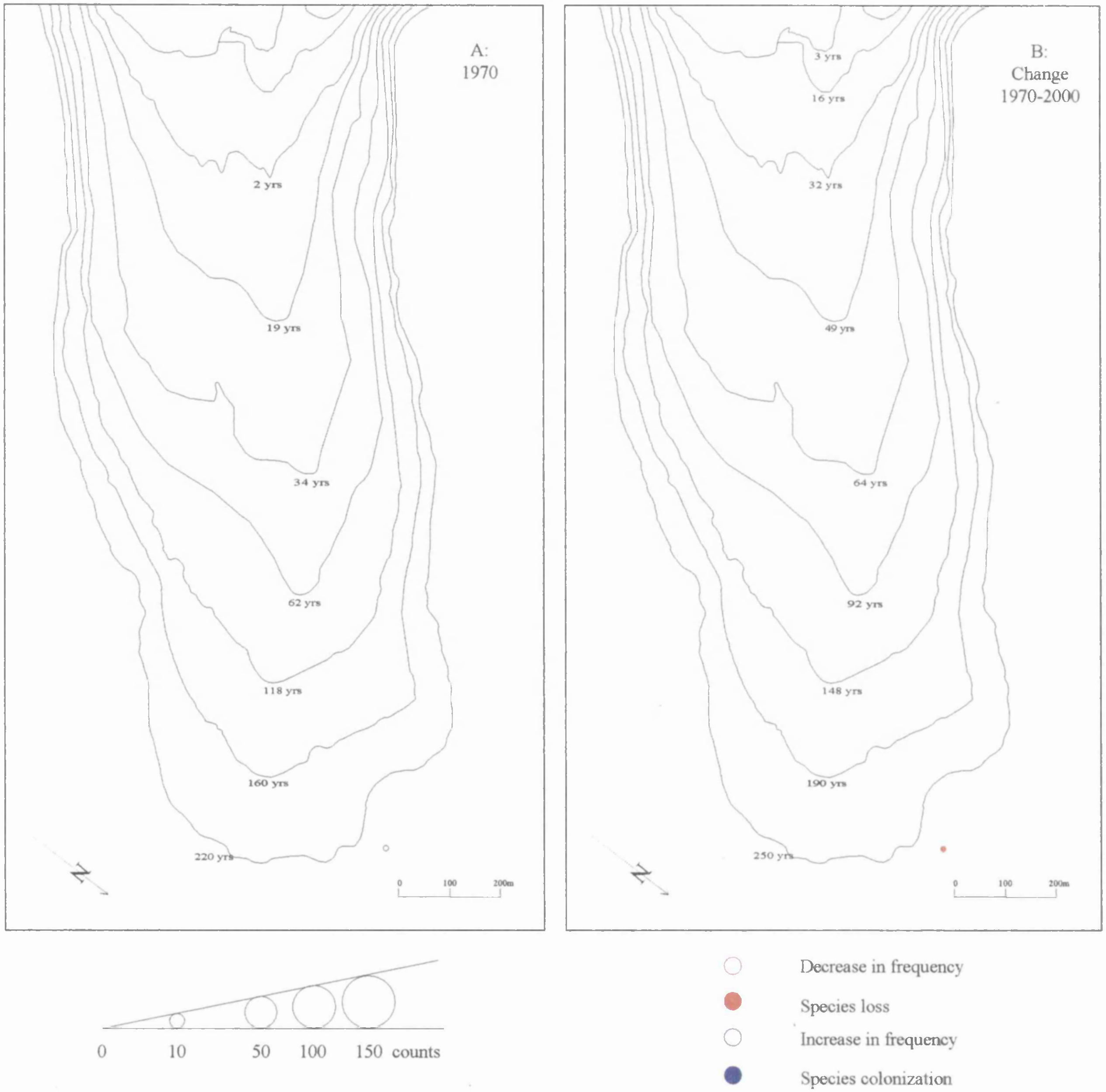


Figure S4 *Botrychium lunaria*: A, frequency in 1970; B, change in frequency 1970-2000



Total Count:

1970	4
2000	0

Figure S5 *Cryptogramma crispa*: A, frequency in 1970; B, change in frequency 1970-2000; C, frequency in 2000

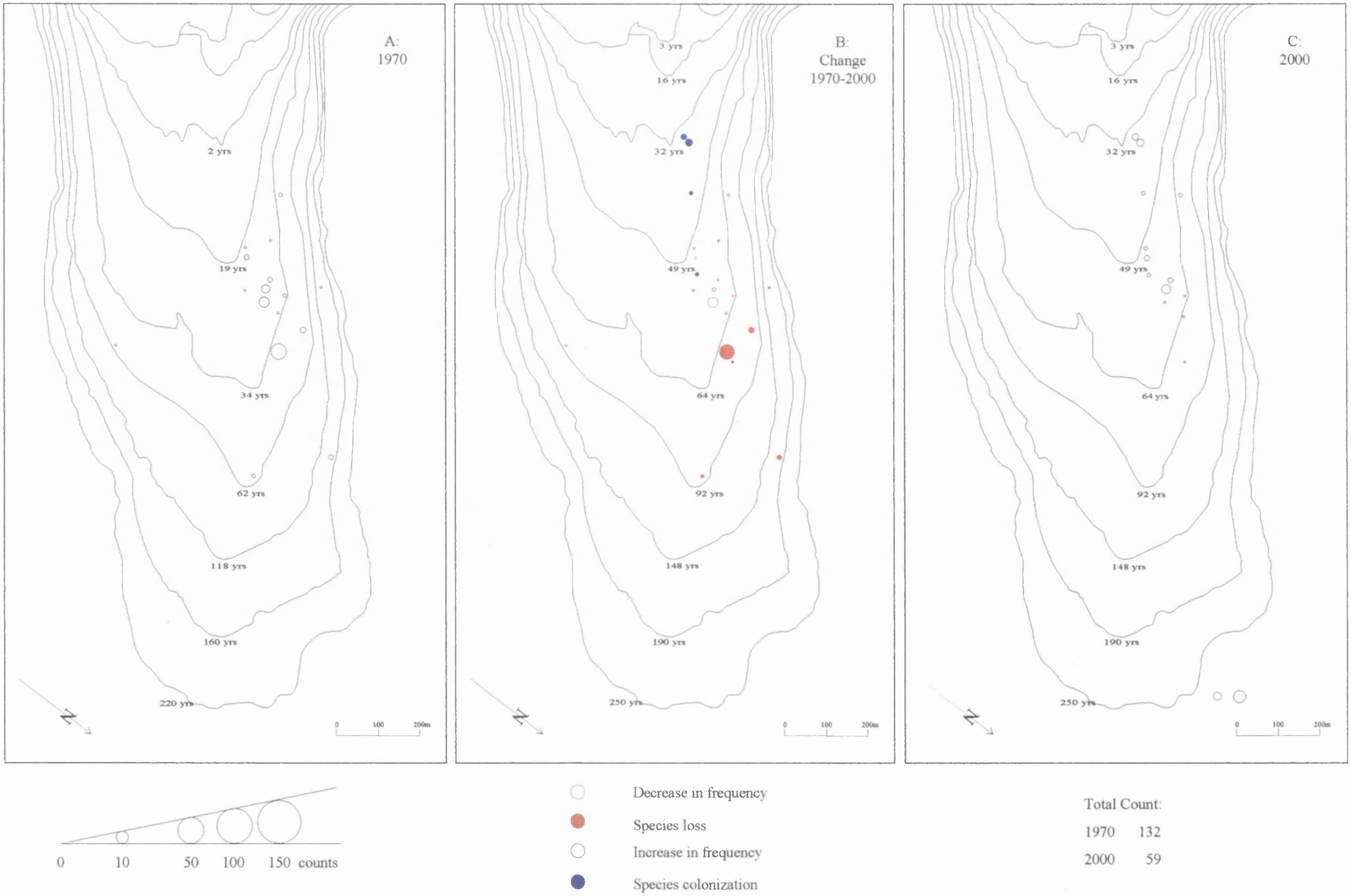


Figure S6 *Cystopteris fragilis*: A, frequency in 1970; B, change in frequency 1970-2000; C, frequency in 2000

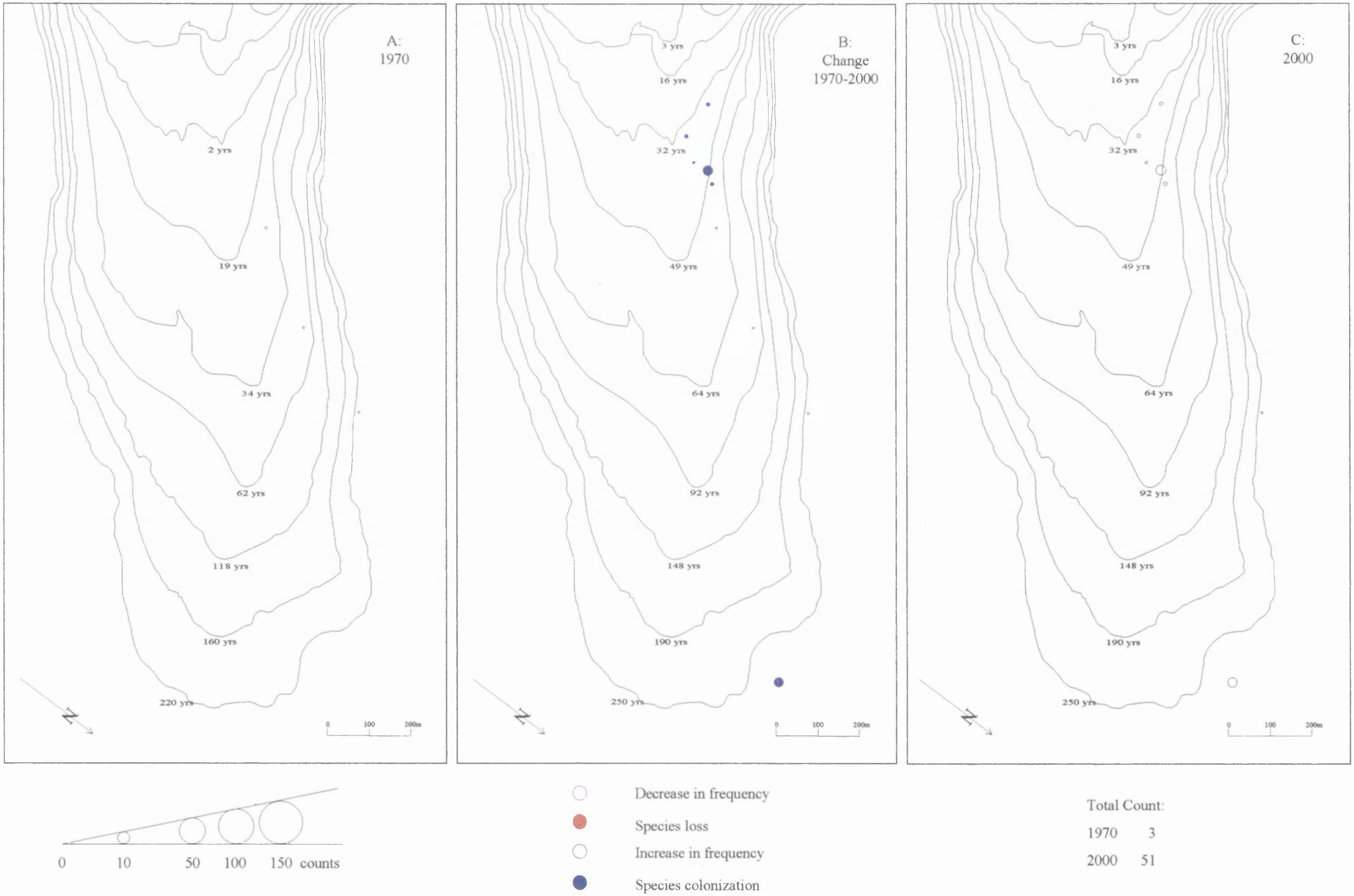
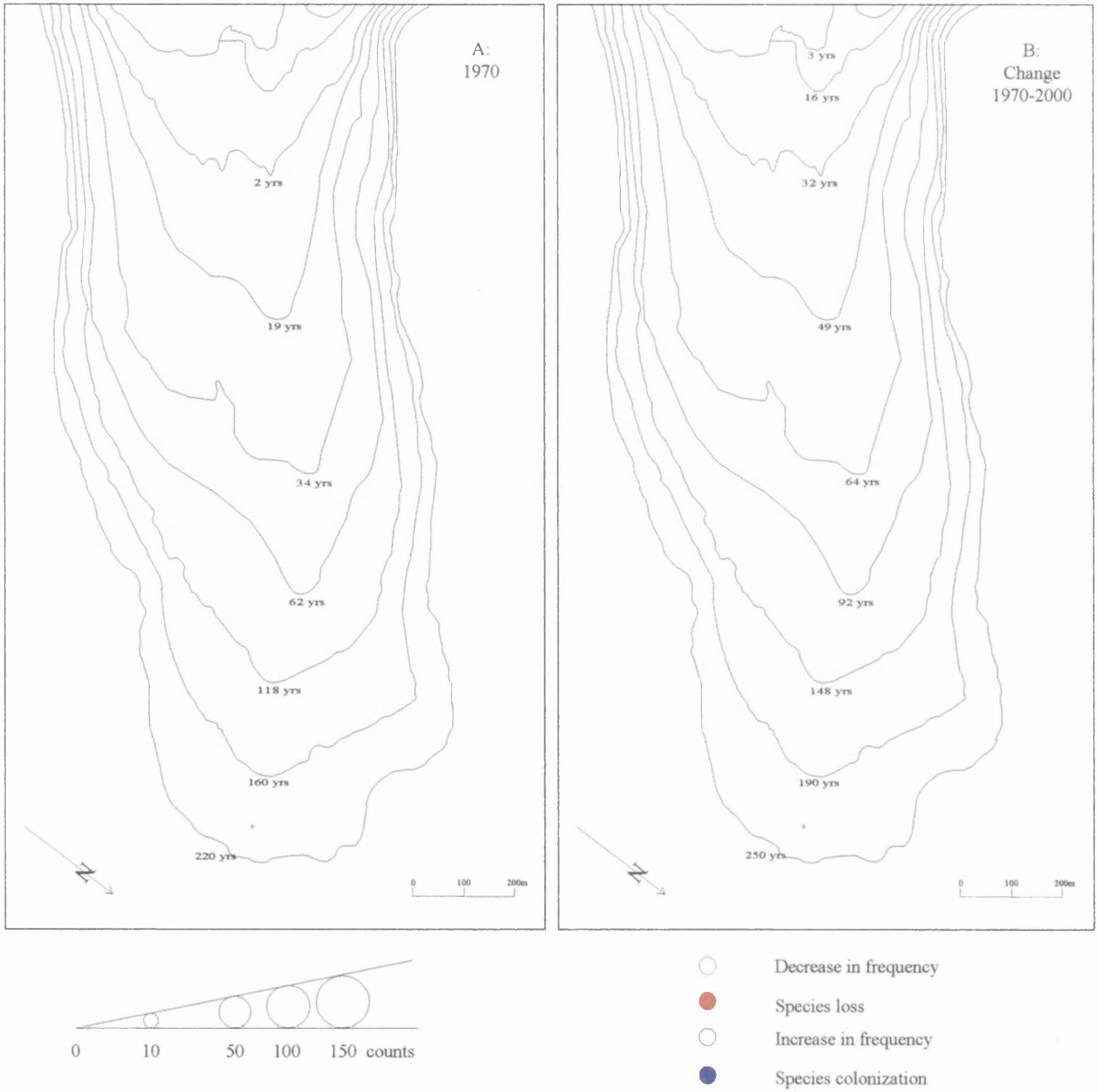


Figure S7 *Deschampsia flexuosa*: A, frequency in 1970; B, change in frequency 1970-2000

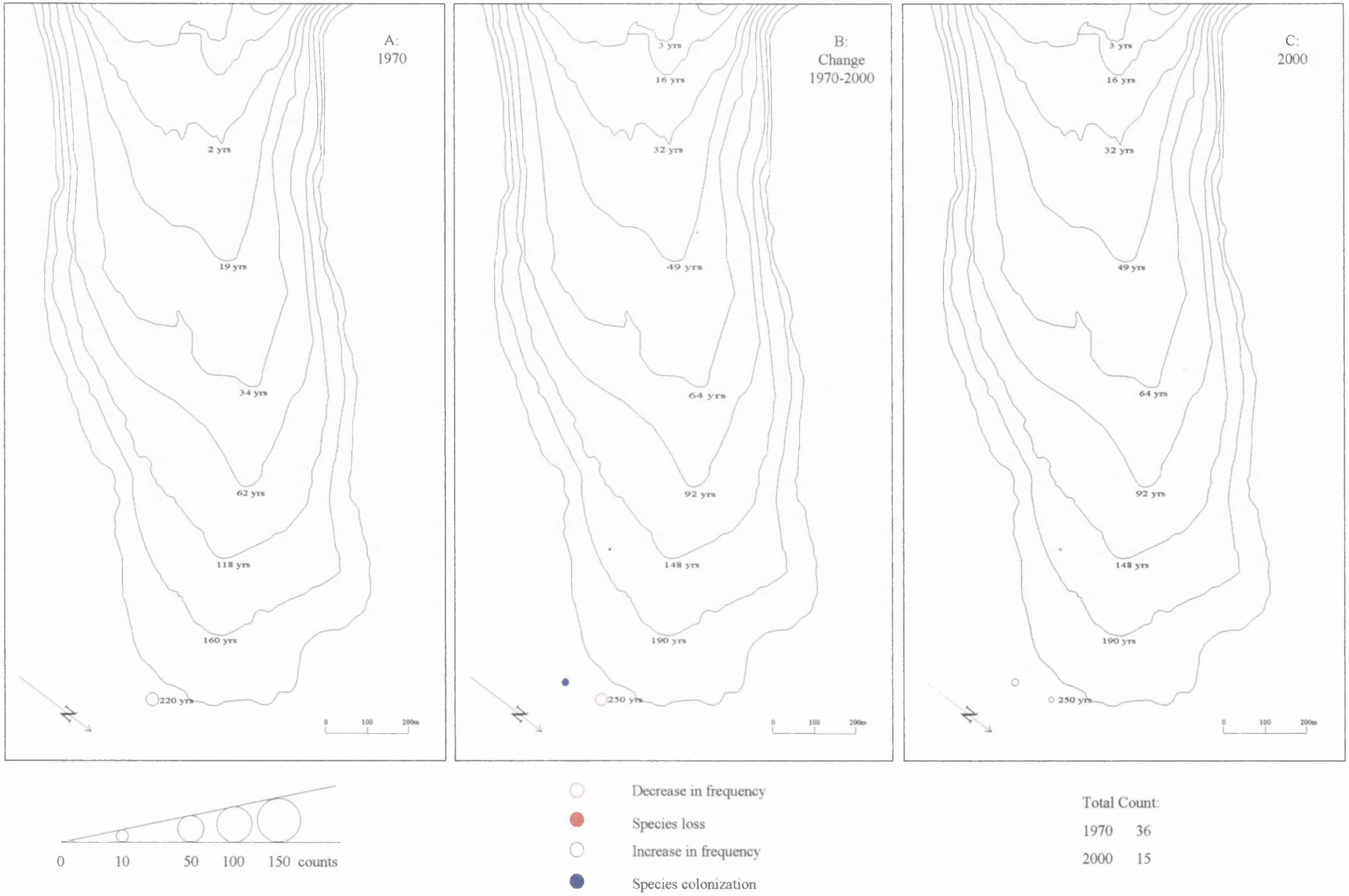


Total Count:

1970 1

2000 0

Figure S8 *Equisetum* spp.: A, frequency in 1970; B, change in frequency 1970-2000; C, frequency in 2000



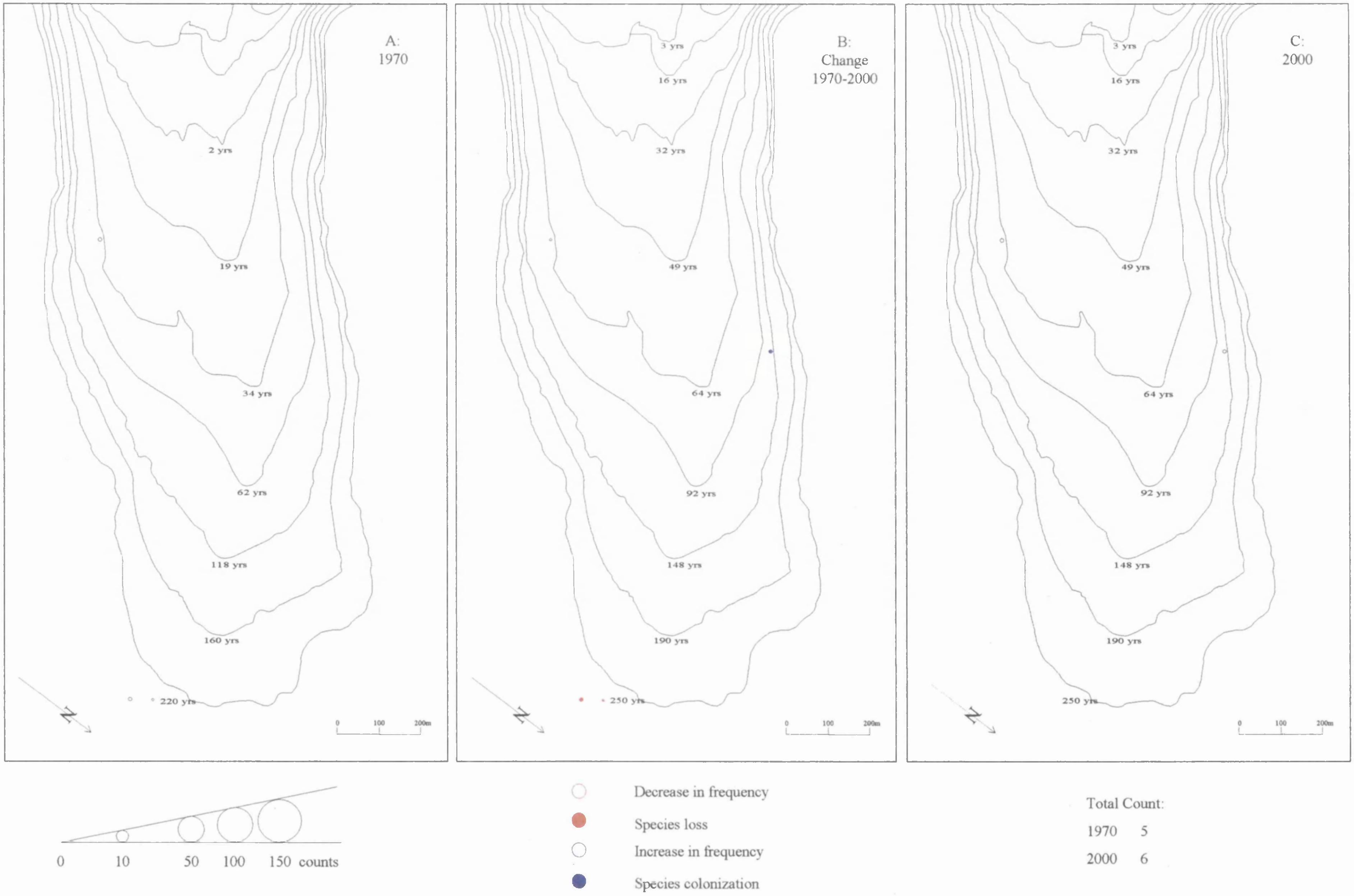


Figure S9 *Eriophorum scheuchzeri*: A, frequency in 1970; B, change in frequency 1970-2000; C, frequency in 2000

Figure S10 *Juncus biglumis*: A, change in frequency 1970-2000; B, frequency in 2000

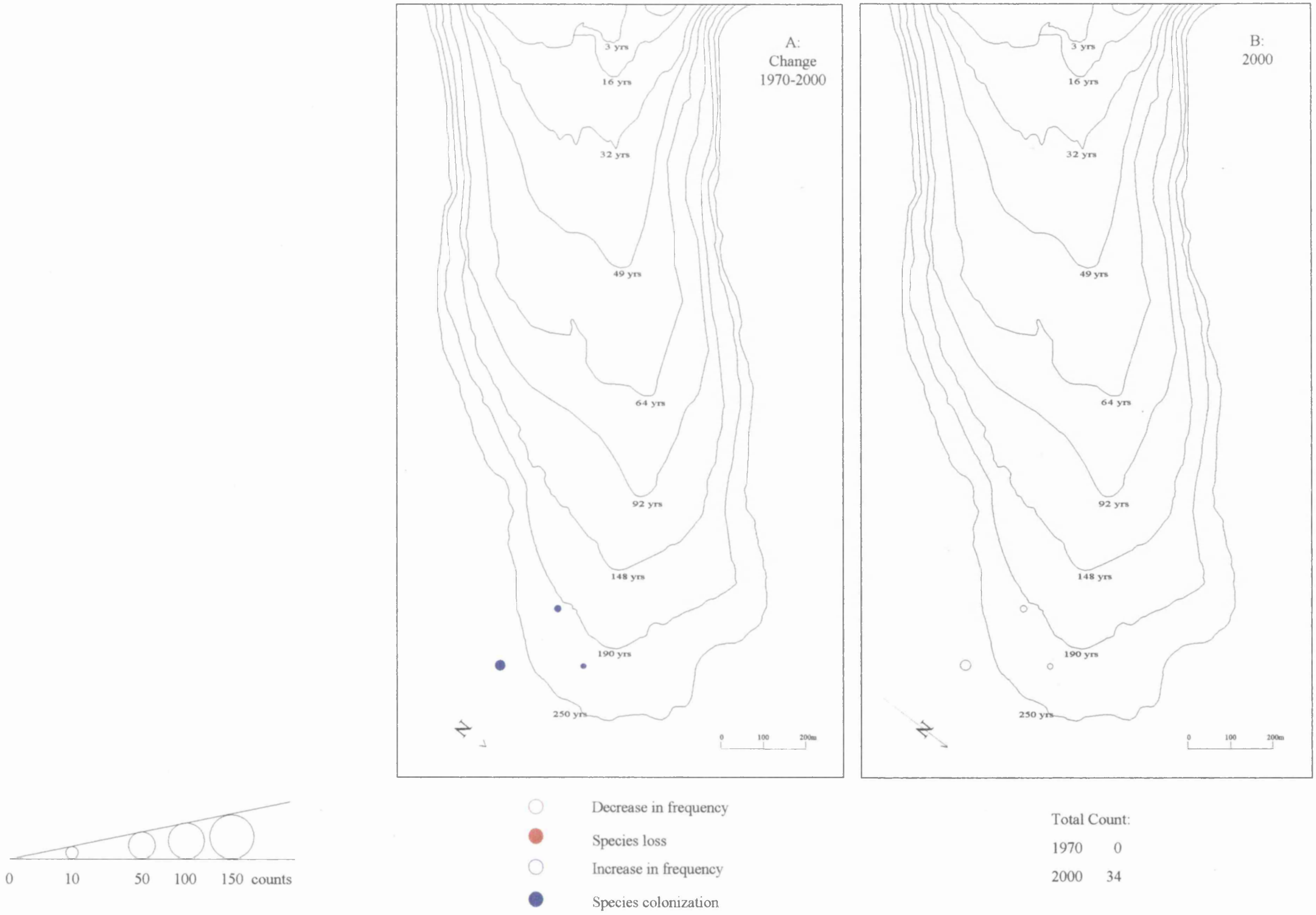


Figure S11 *Diphasiastrum alpinum*: A, frequency in 1970; B, change in frequency 1970-2000; C, frequency in 2000

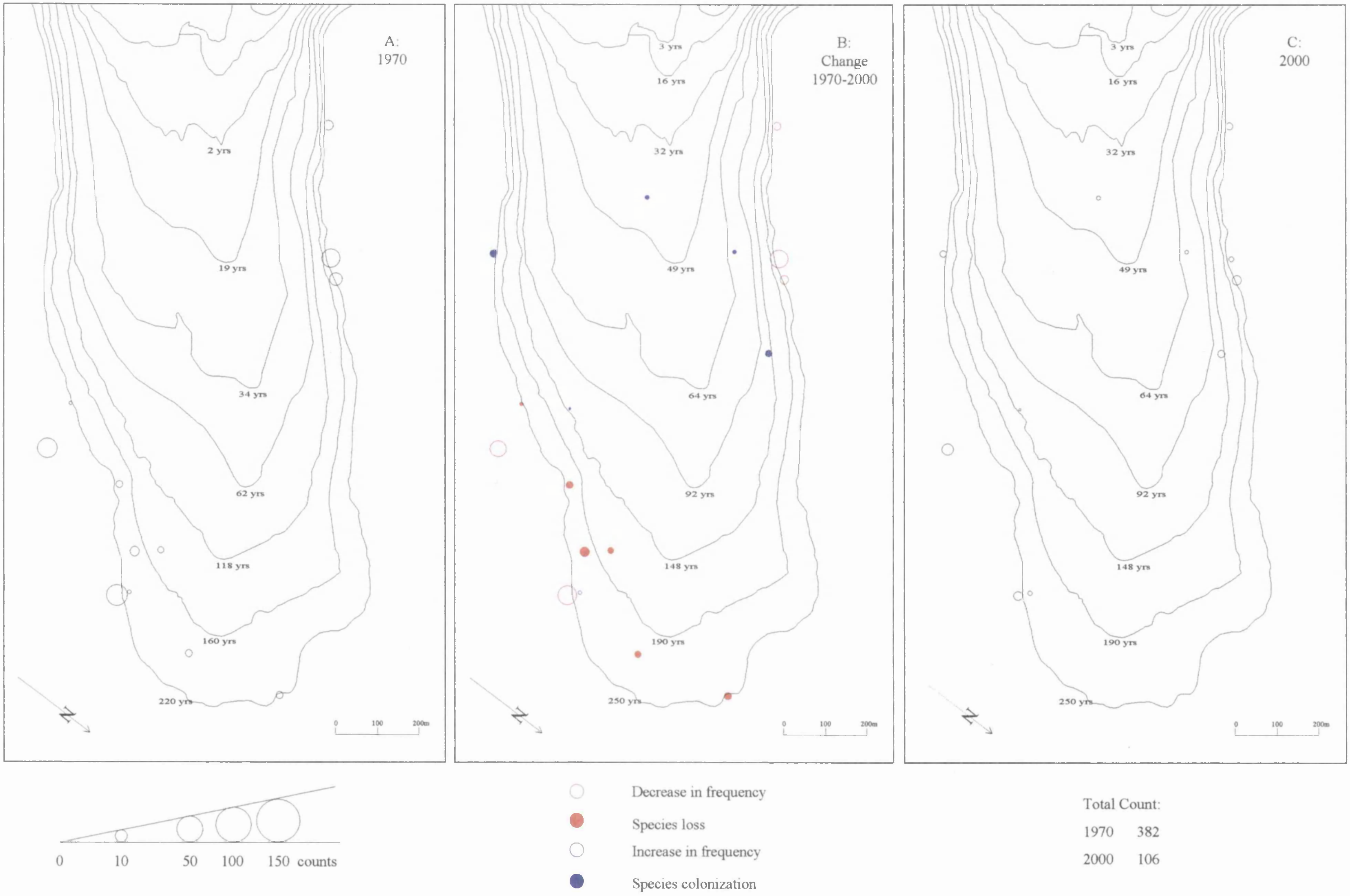


Figure S12 *Lycopodium annotinum*: A, frequency in 1970; B, change in frequency 1970-2000; C, frequency in 2000

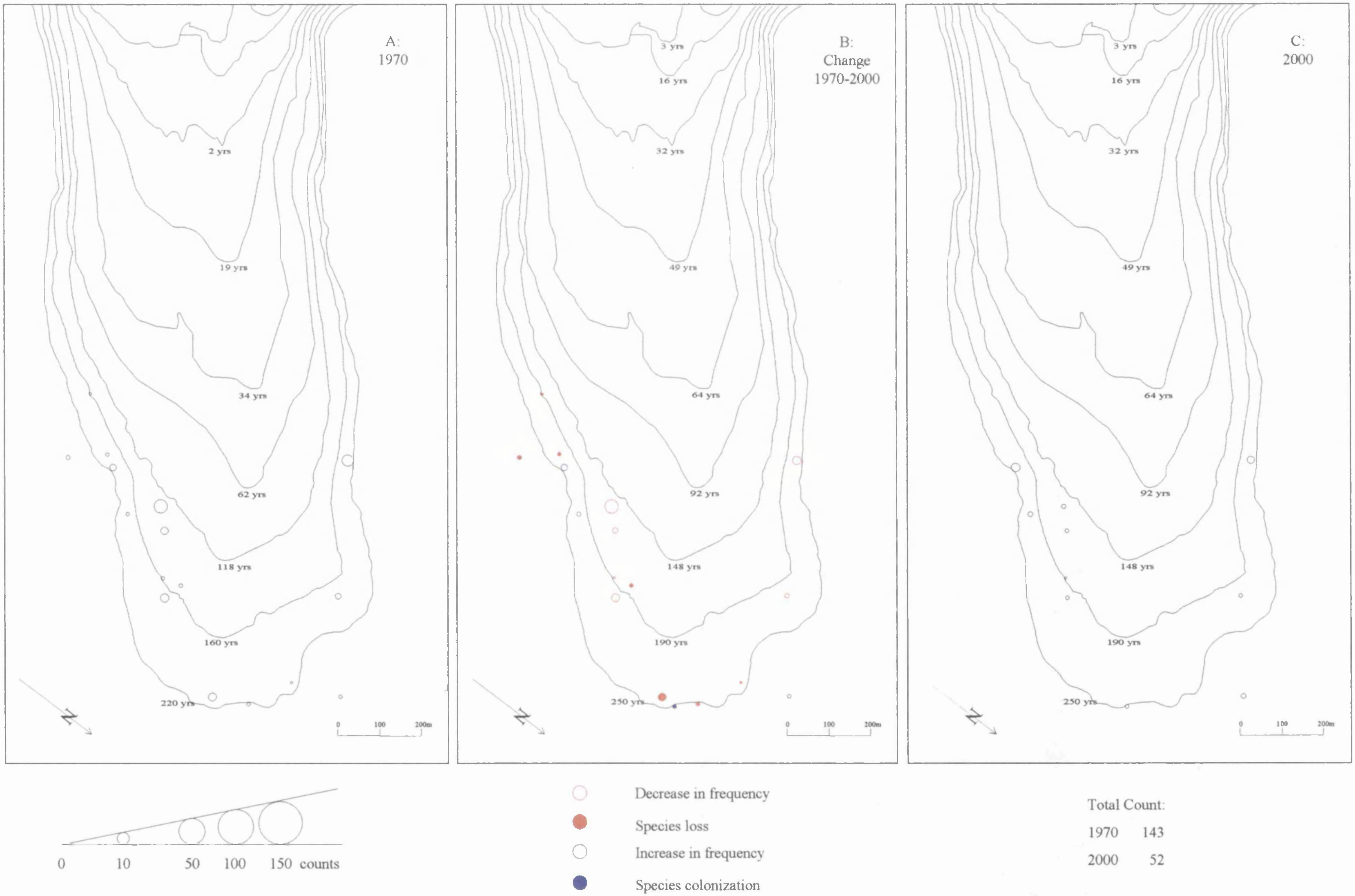


Figure S13 *Nardus stricta*: A, change in frequency 1970-2000: B, frequency in 2000

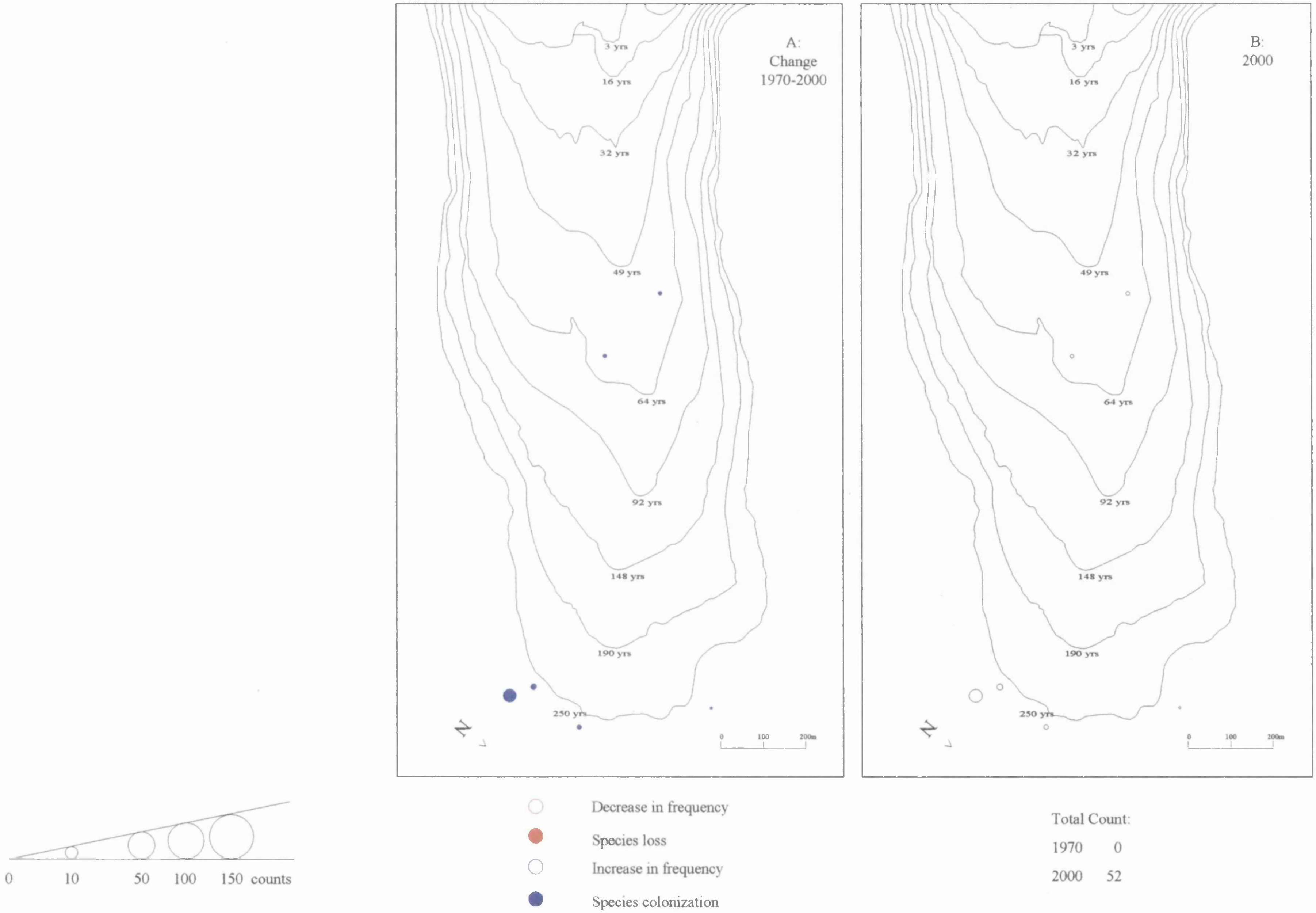


Figure S14 *Woodsia alpina*: A, frequency in 1970; B, change in frequency 1970-2000; C, frequency in 2000

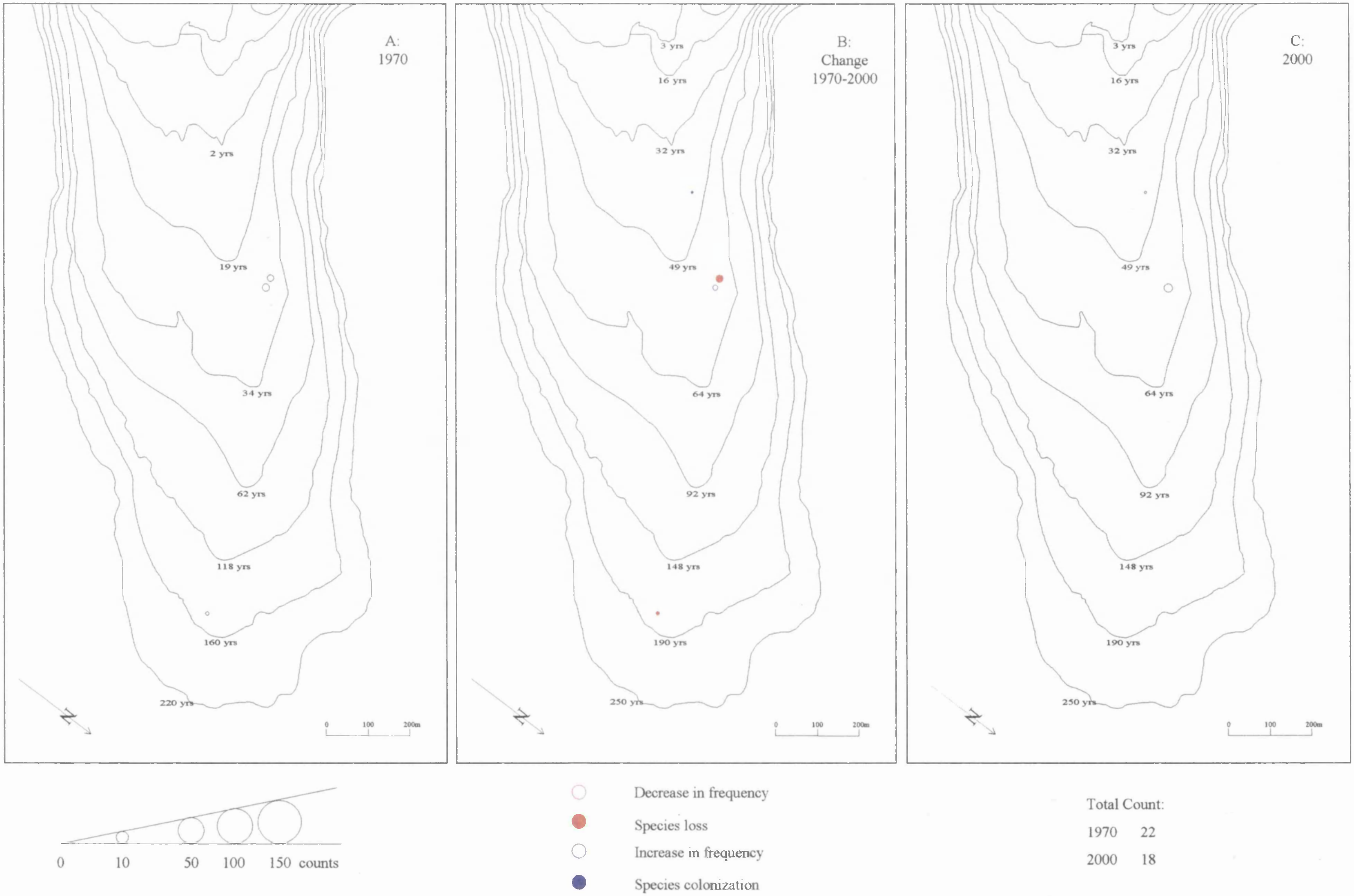


Figure S15 *Achillea millefolium*: A, frequency in 1970; B, change in frequency 1970-2000; C, frequency in 2000

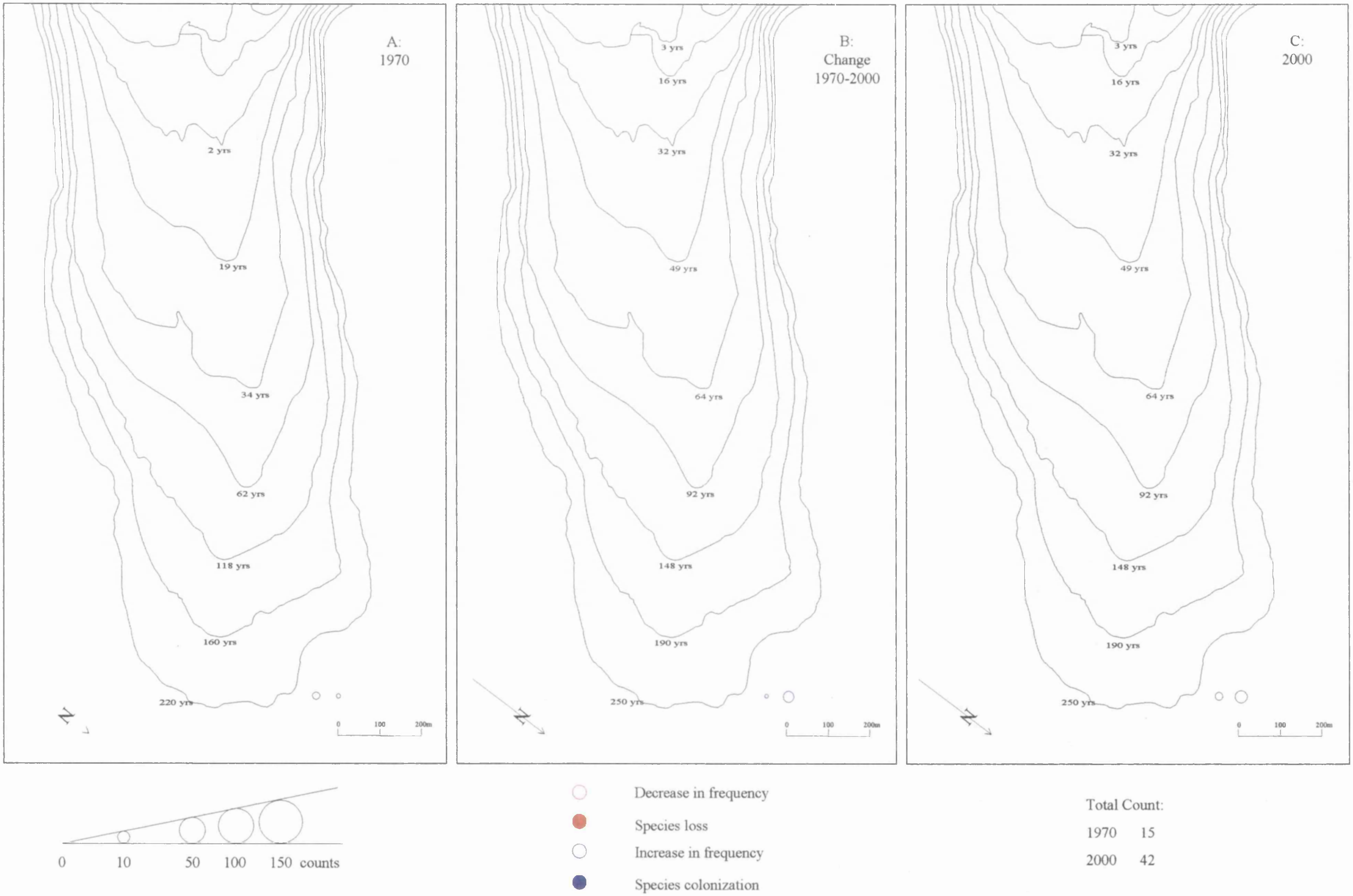


Figure S16 *Aconitum septrionale*: A, frequency in 1970; B, change in frequency 1970-2000; C, frequency in 2000

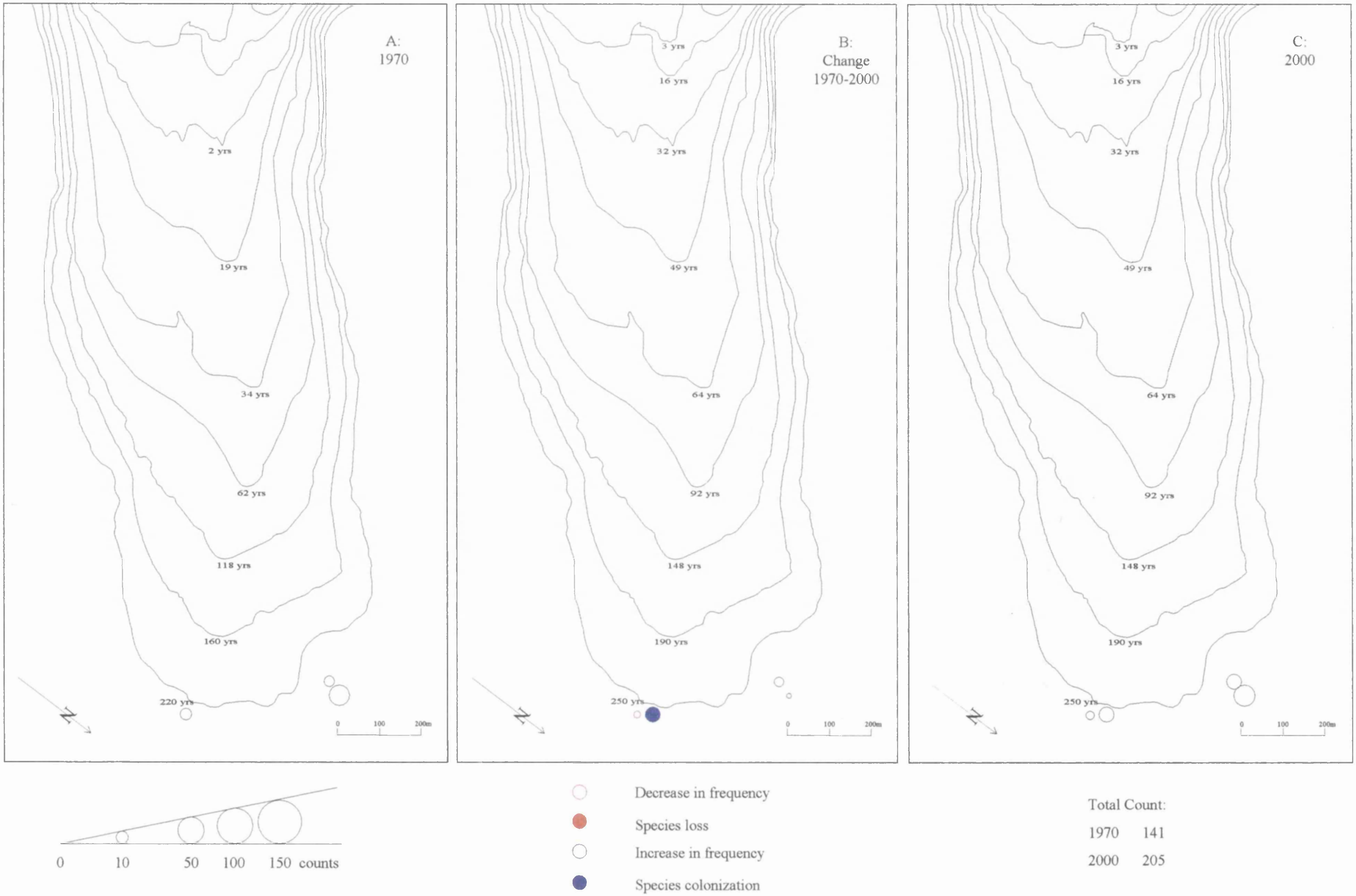
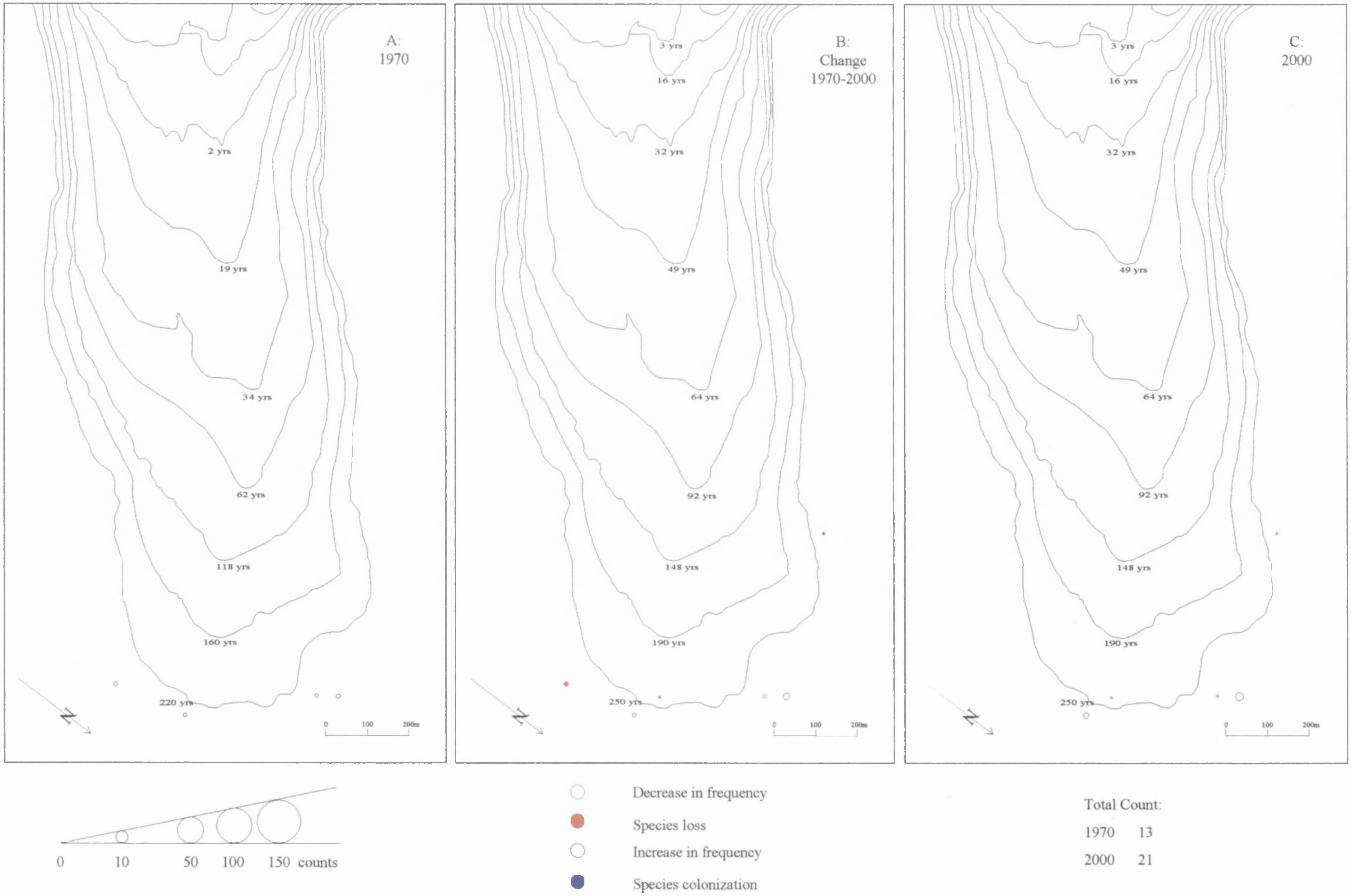


Figure S17 *Alchemilla alpina*: A, frequency in 1970; B, change in frequency 1970-2000; C, frequency in 2000



Total Count:
1970 13
2000 21

Figure S18 *Alchemilla glomerulans*: A, frequency in 1970; B, change in frequency 1970-2000; C, frequency in 2000

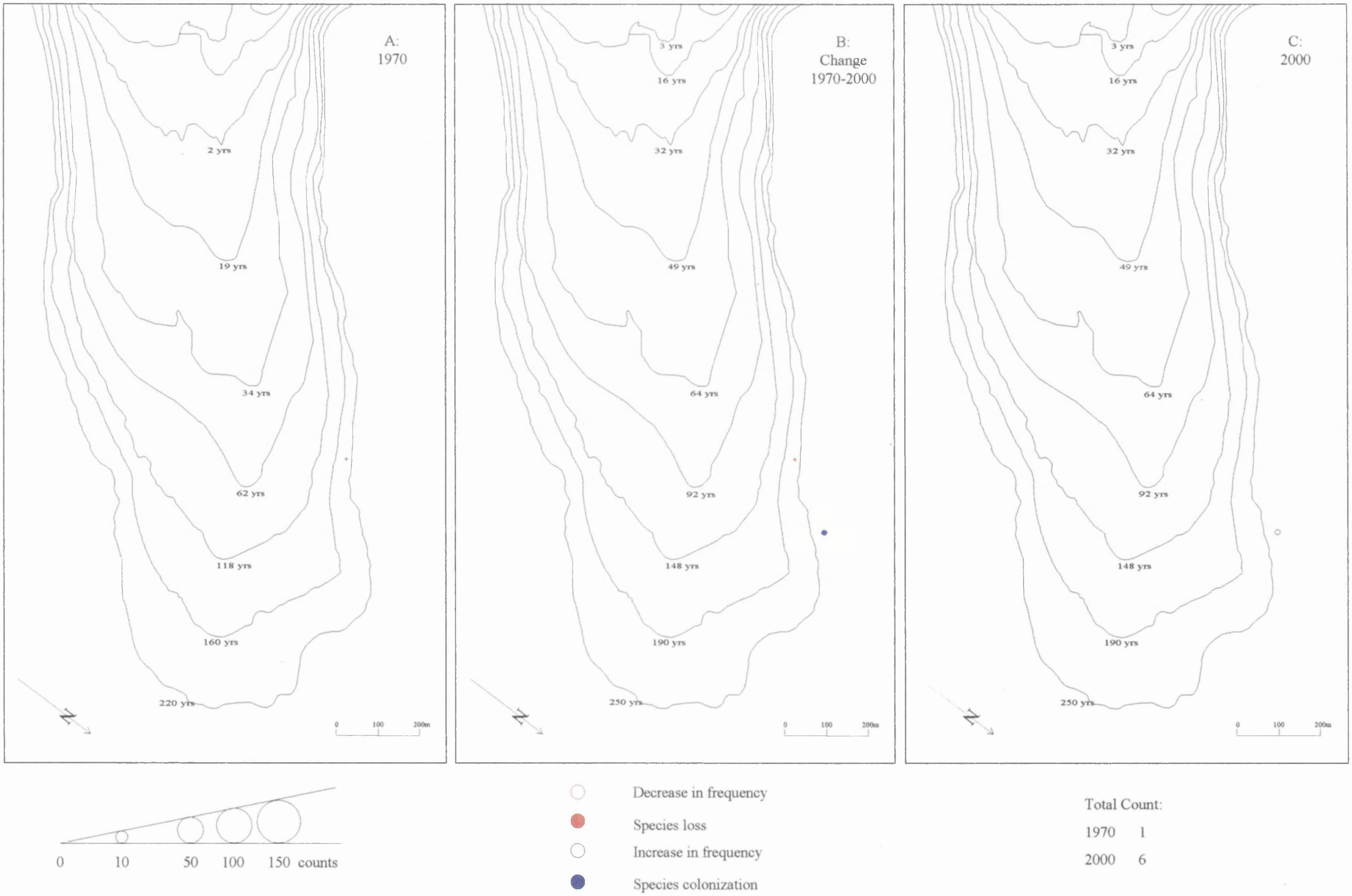


Figure S19 *Angelica archangelica*: A, frequency in 1970; B, change in frequency 1970-2000

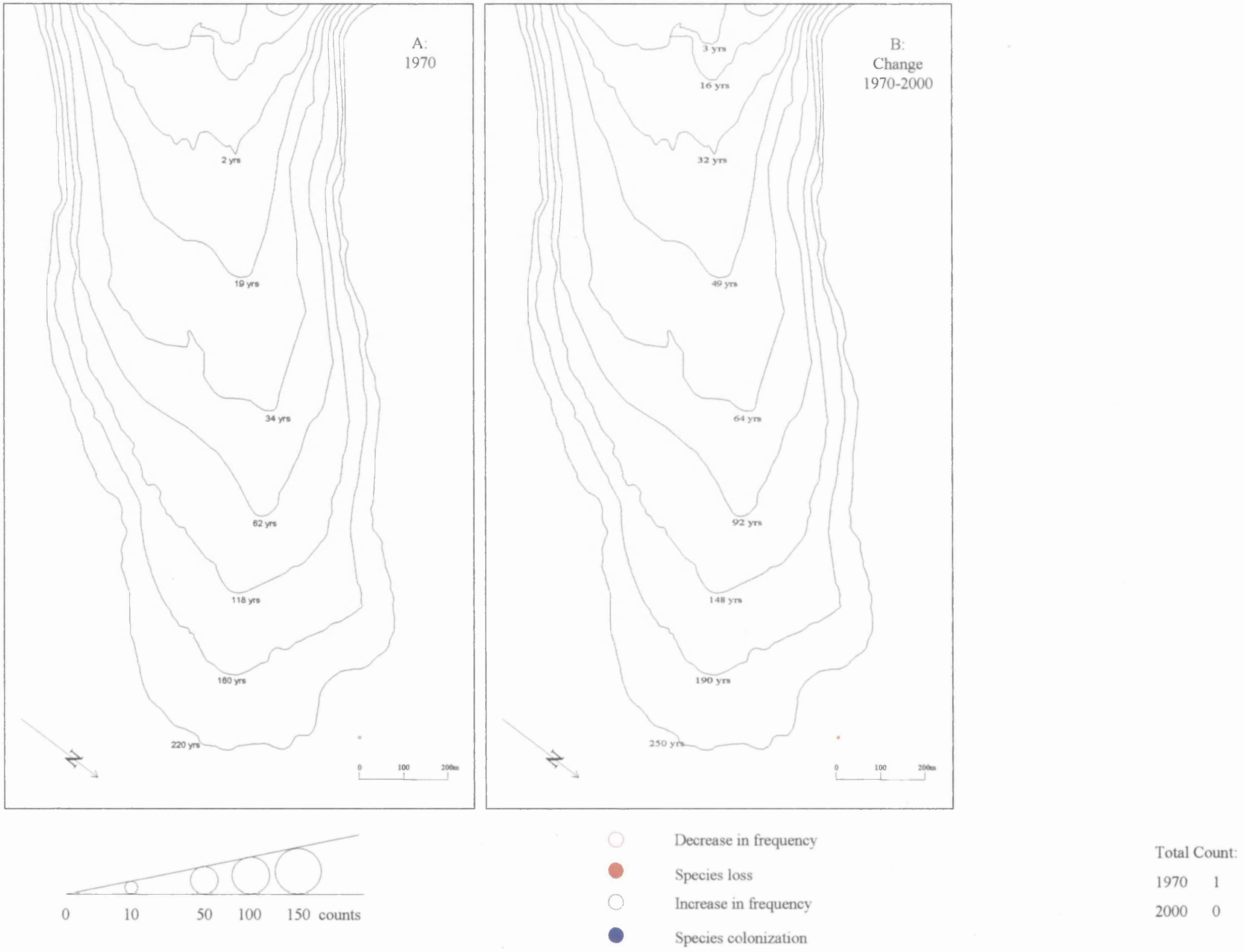


Figure S20 *Astragalus alpinus*: A, frequency in 1970; B, change in frequency 1970-2000; C, frequency in 2000

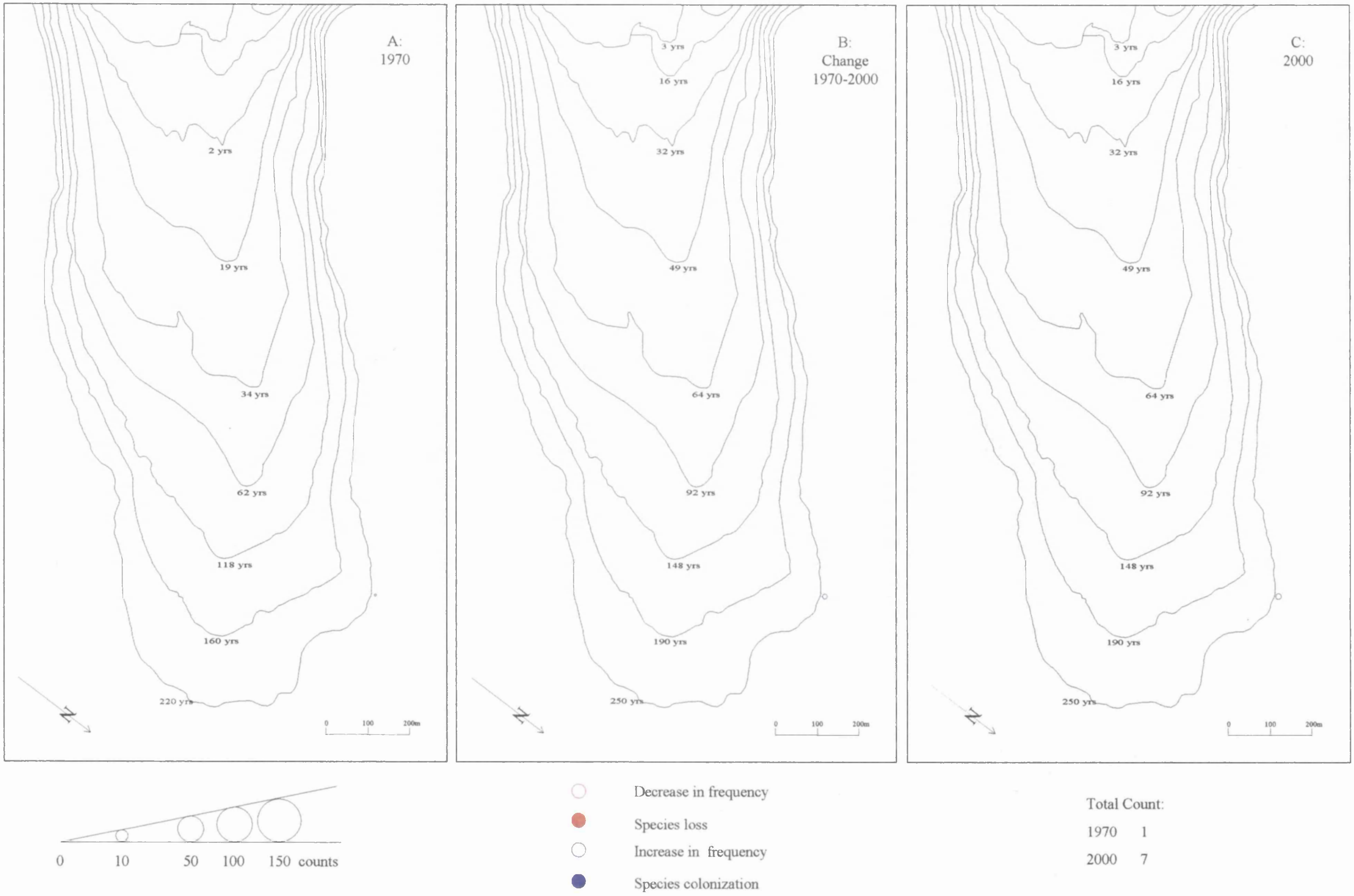


Figure S21 *Campanula rotundifolia*: A, frequency in 1970; B, change in frequency 1970-2000; C, frequency in 2000

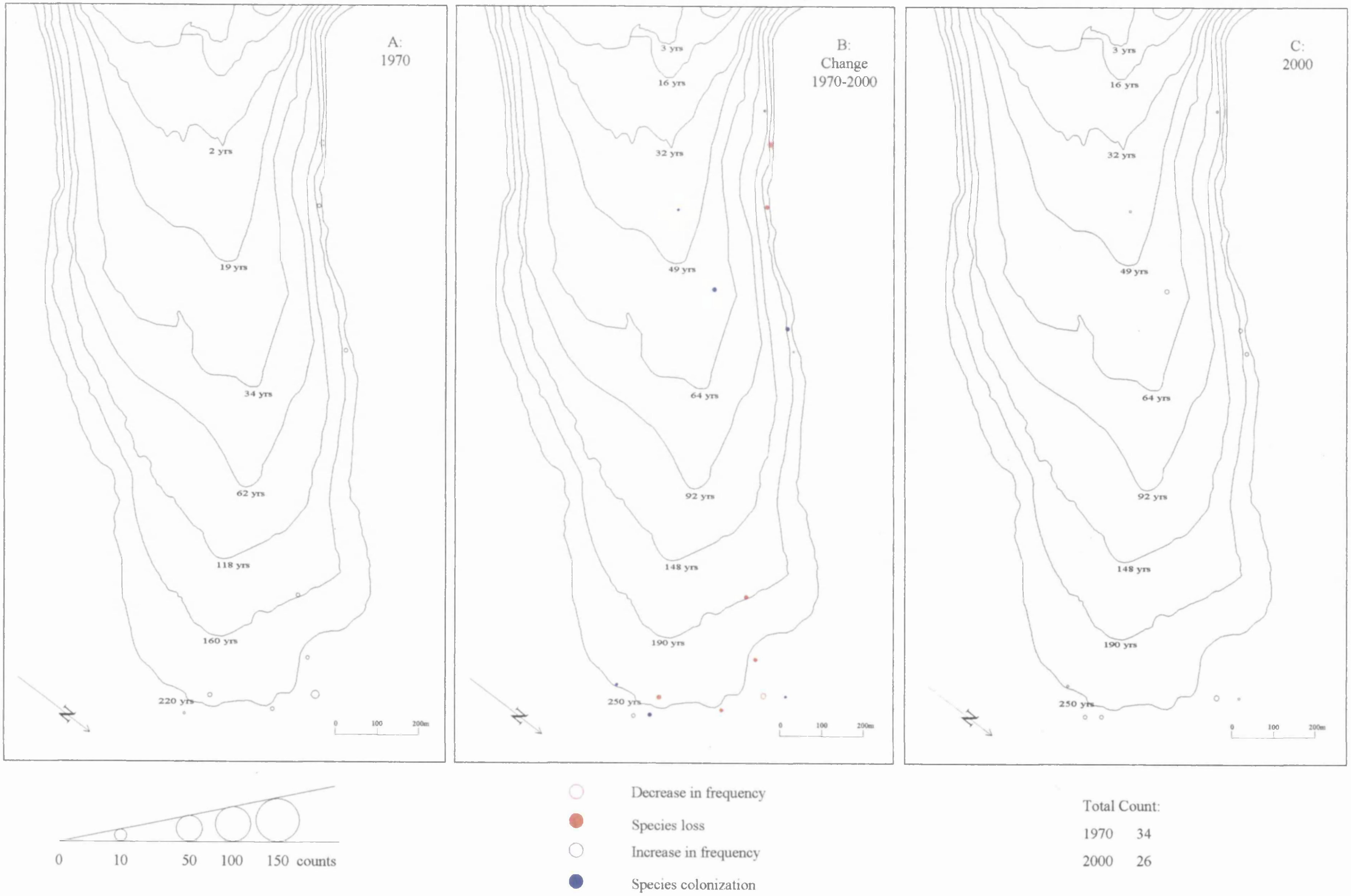


Figure S22 *Coeloglossum viride*: A, frequency in 1970; B, change in frequency 1970-2000; C, frequency in 2000

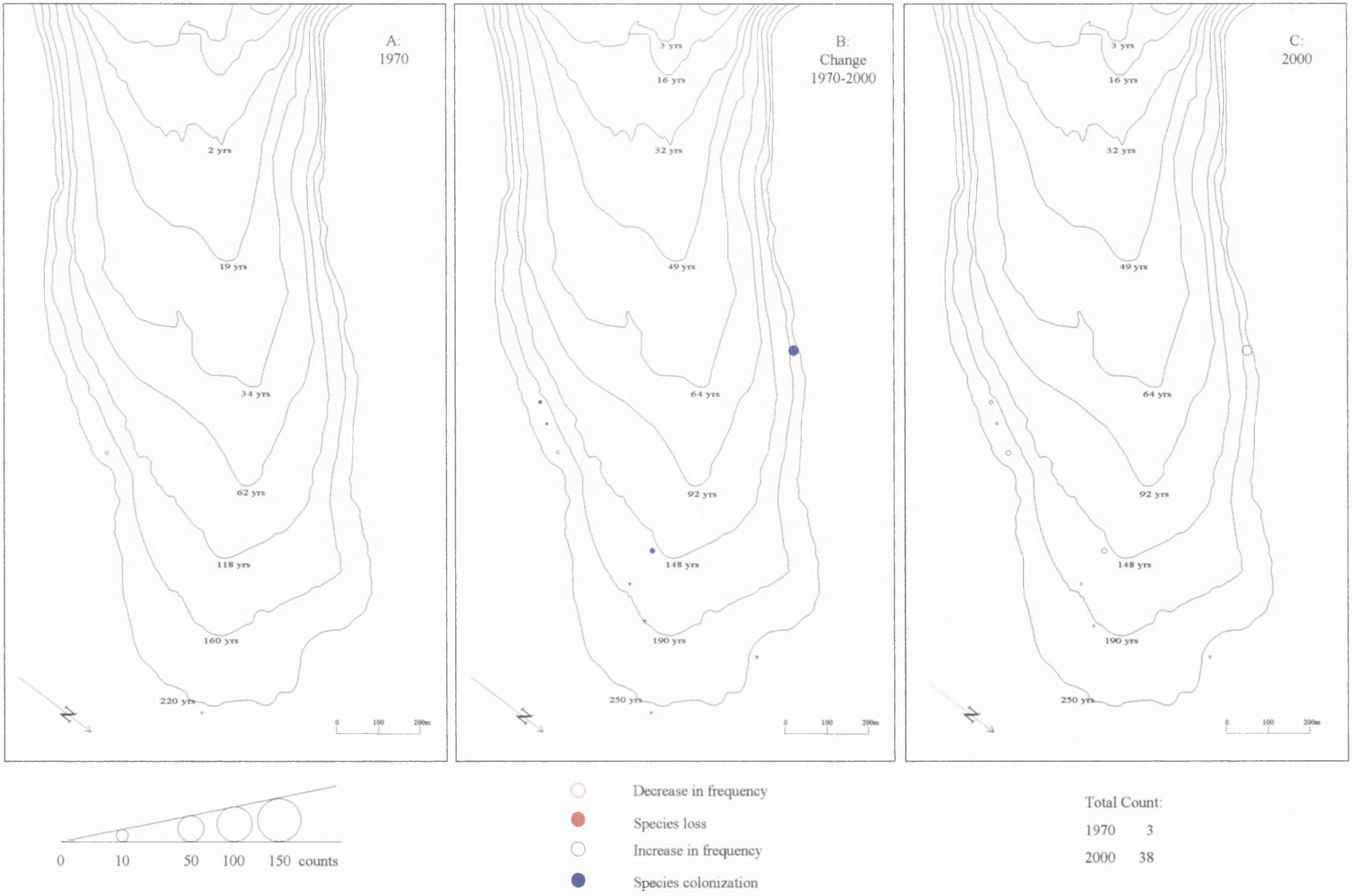


Figure S23 *Comarum palustre*: A, frequency in 1970; B, change in frequency 1970-2000; C, frequency in 2000

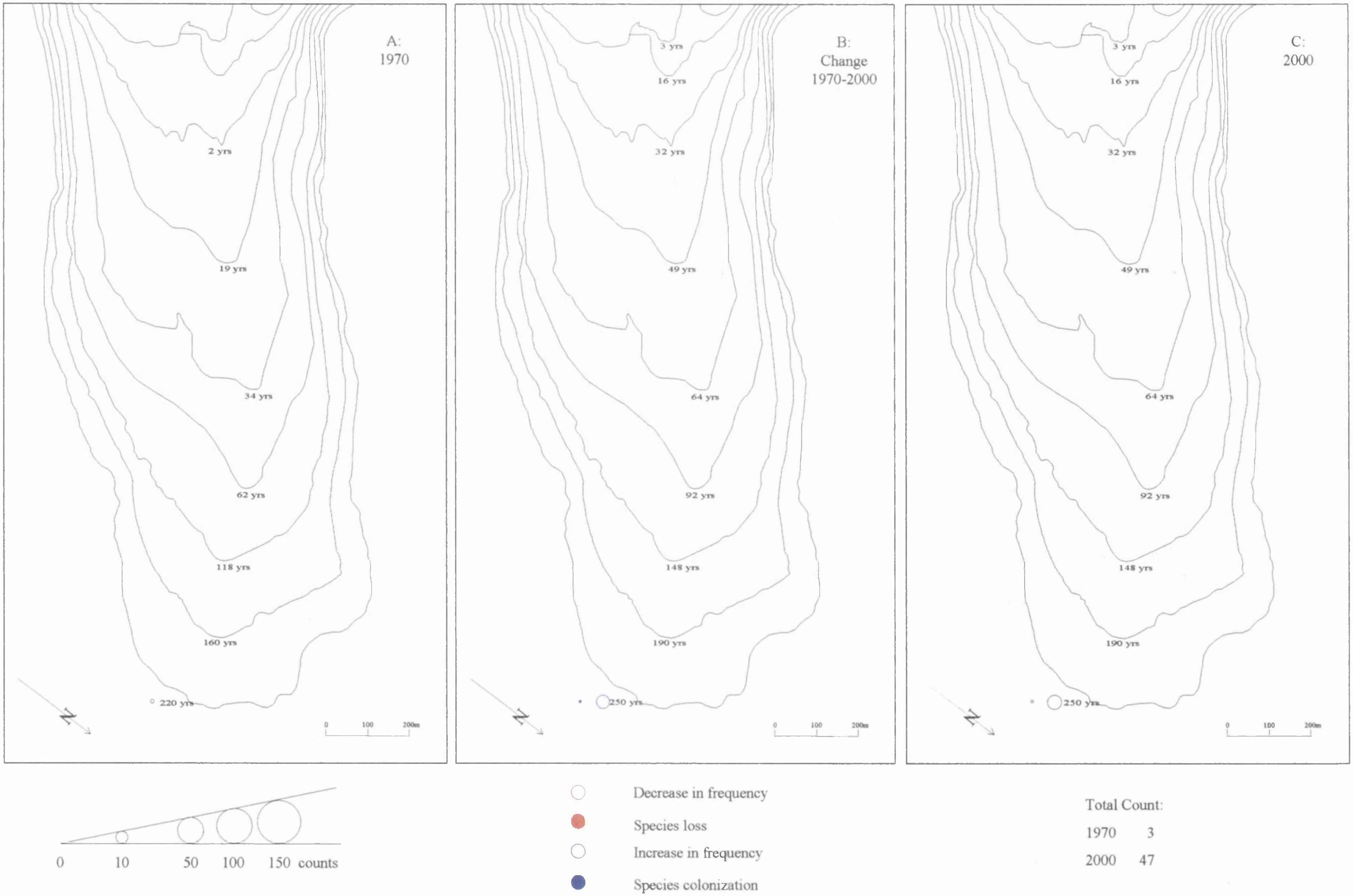


Figure S24 *Crepis paludosa*: A, change in frequency 1970-2000; B, frequency in 2000

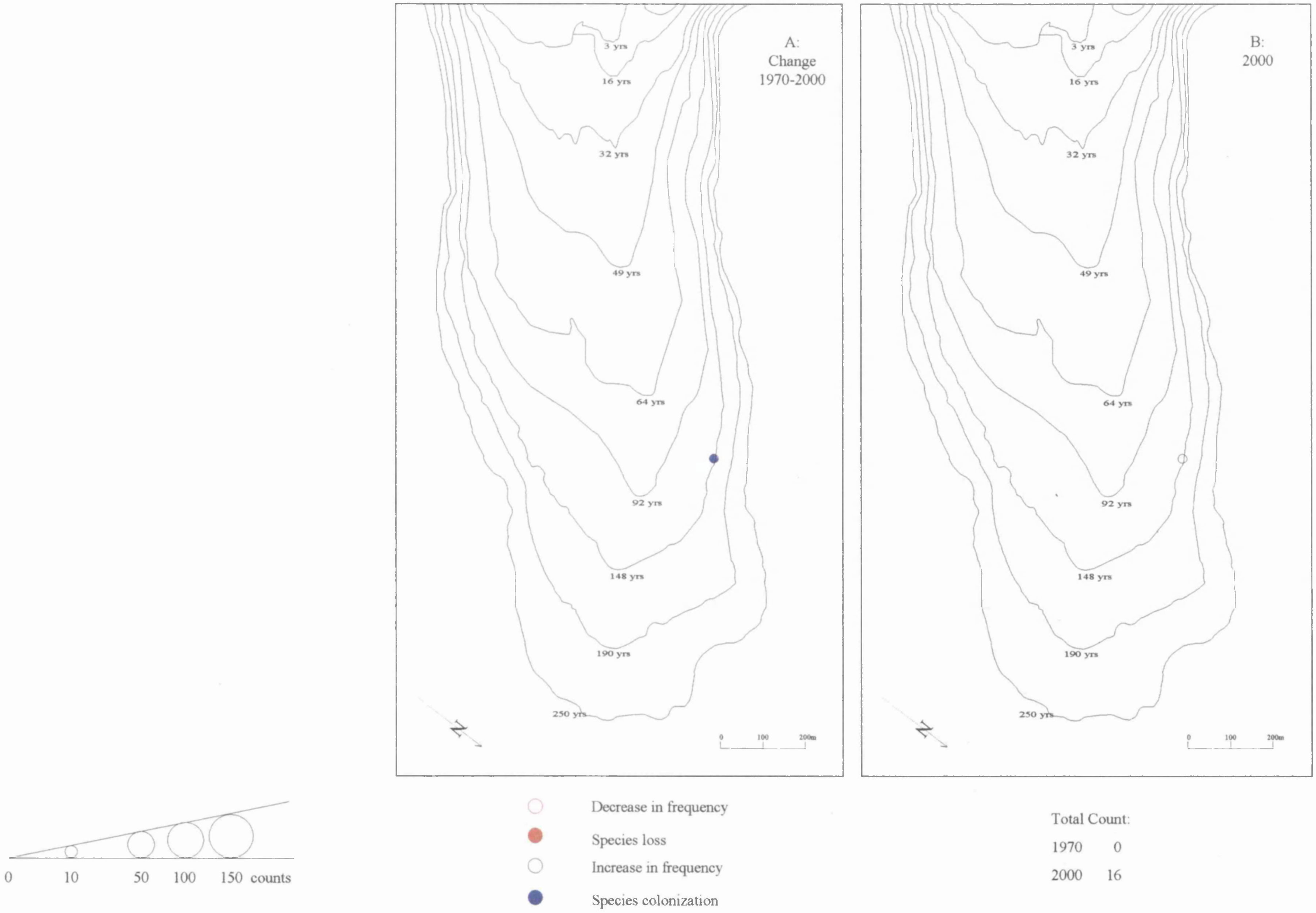


Figure S25 *Dryas octopetala*: A, frequency in 1970; B, change in frequency 1970-2000; C, frequency in 2000

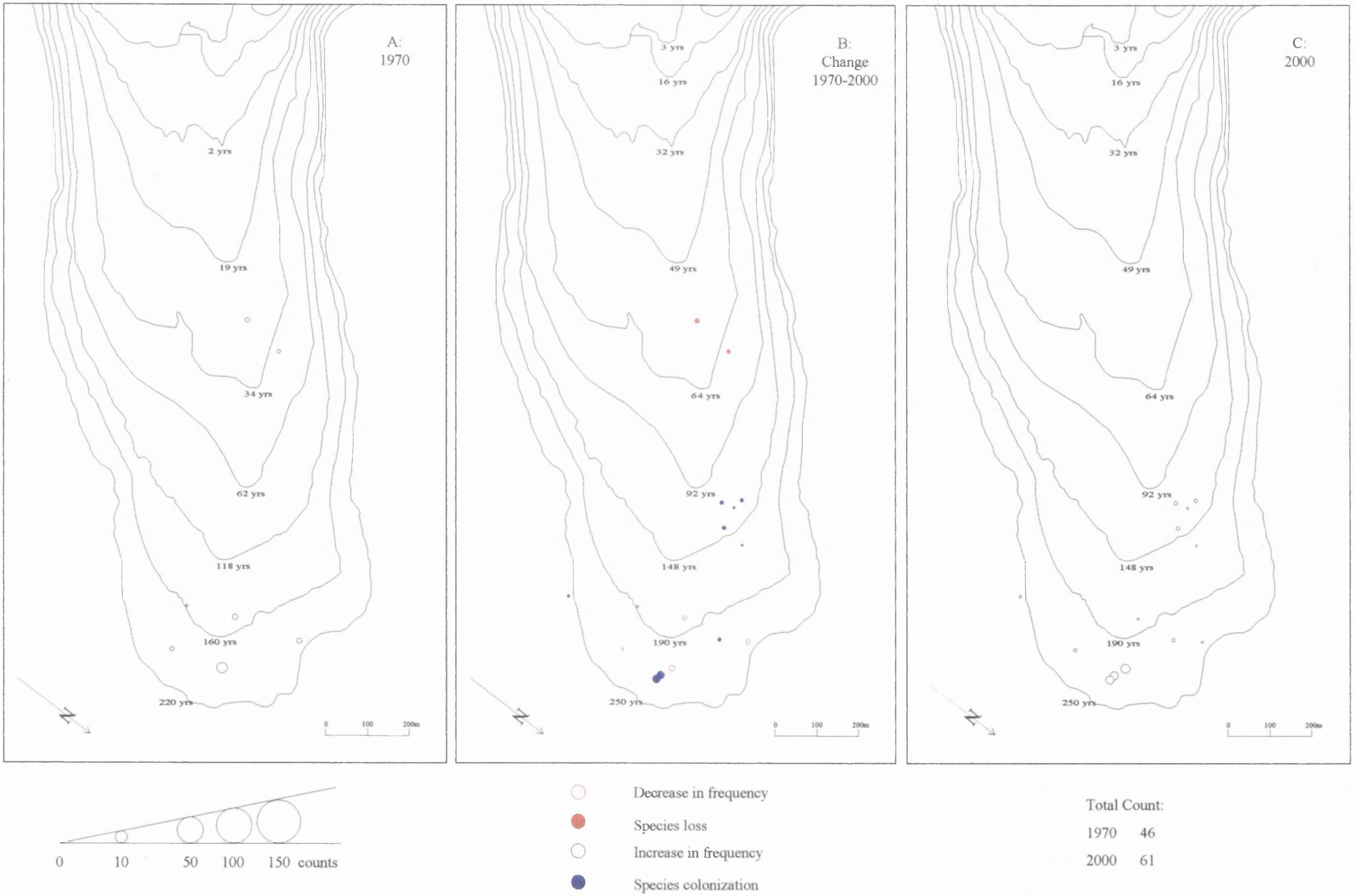


Figure S26 *Epilobium alsinifolium*: A, frequency in 1970; B, change in frequency 1970-2000; C, frequency in 2000

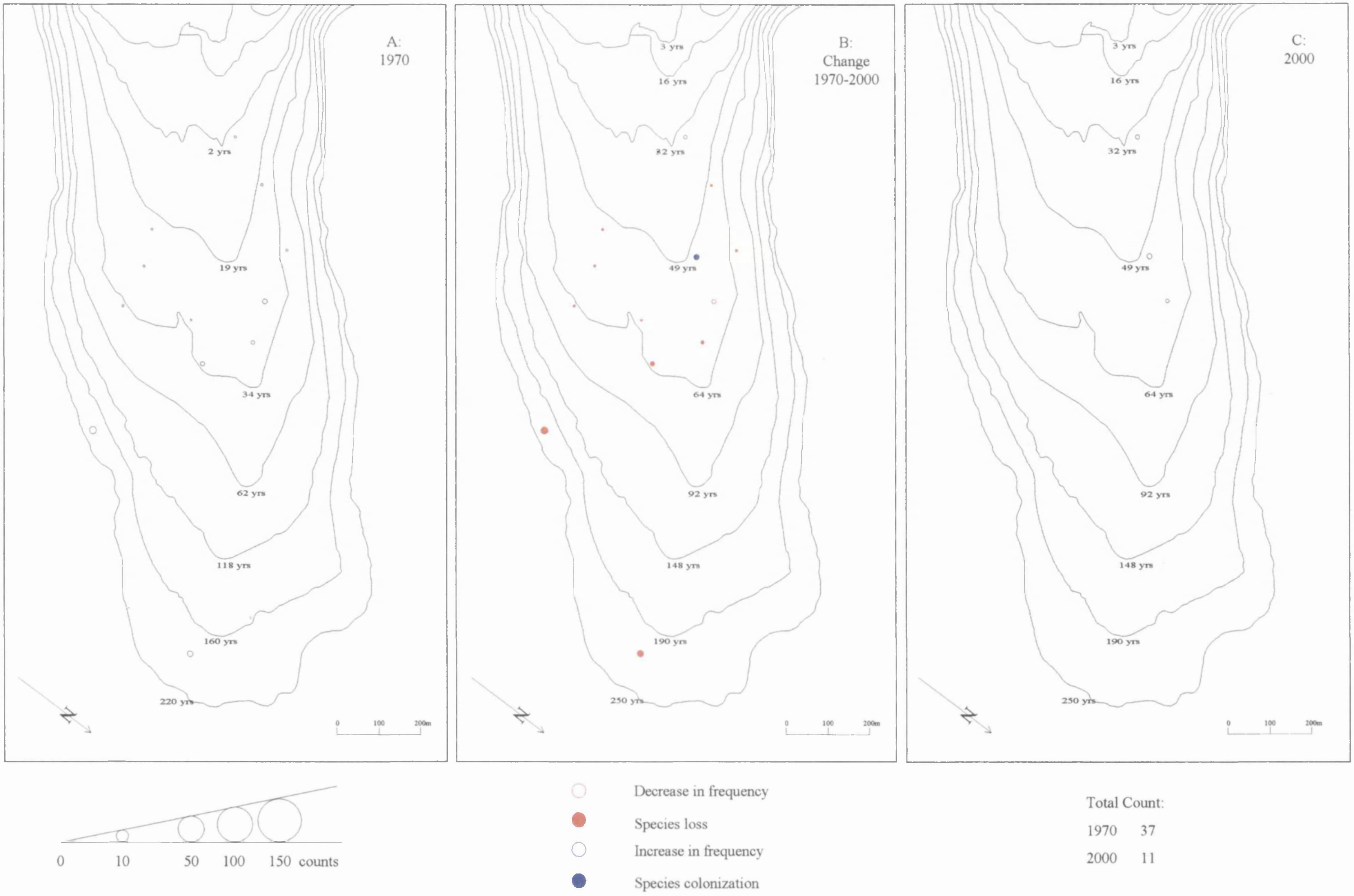


Figure S27 *Epilobium anagallidifolium*: A, frequency in 1970; B, change in frequency 1970-2000; C, frequency in 2000

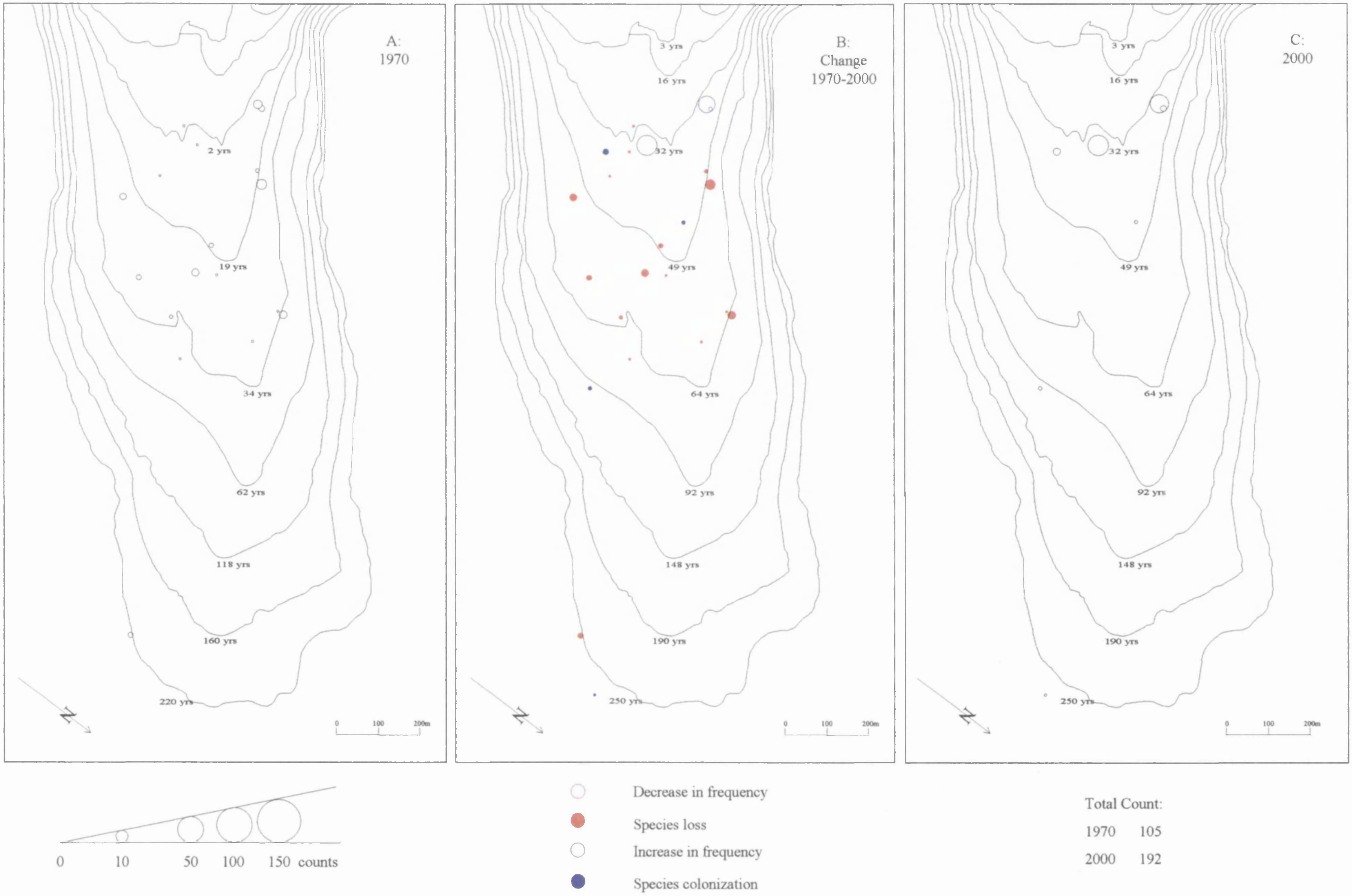
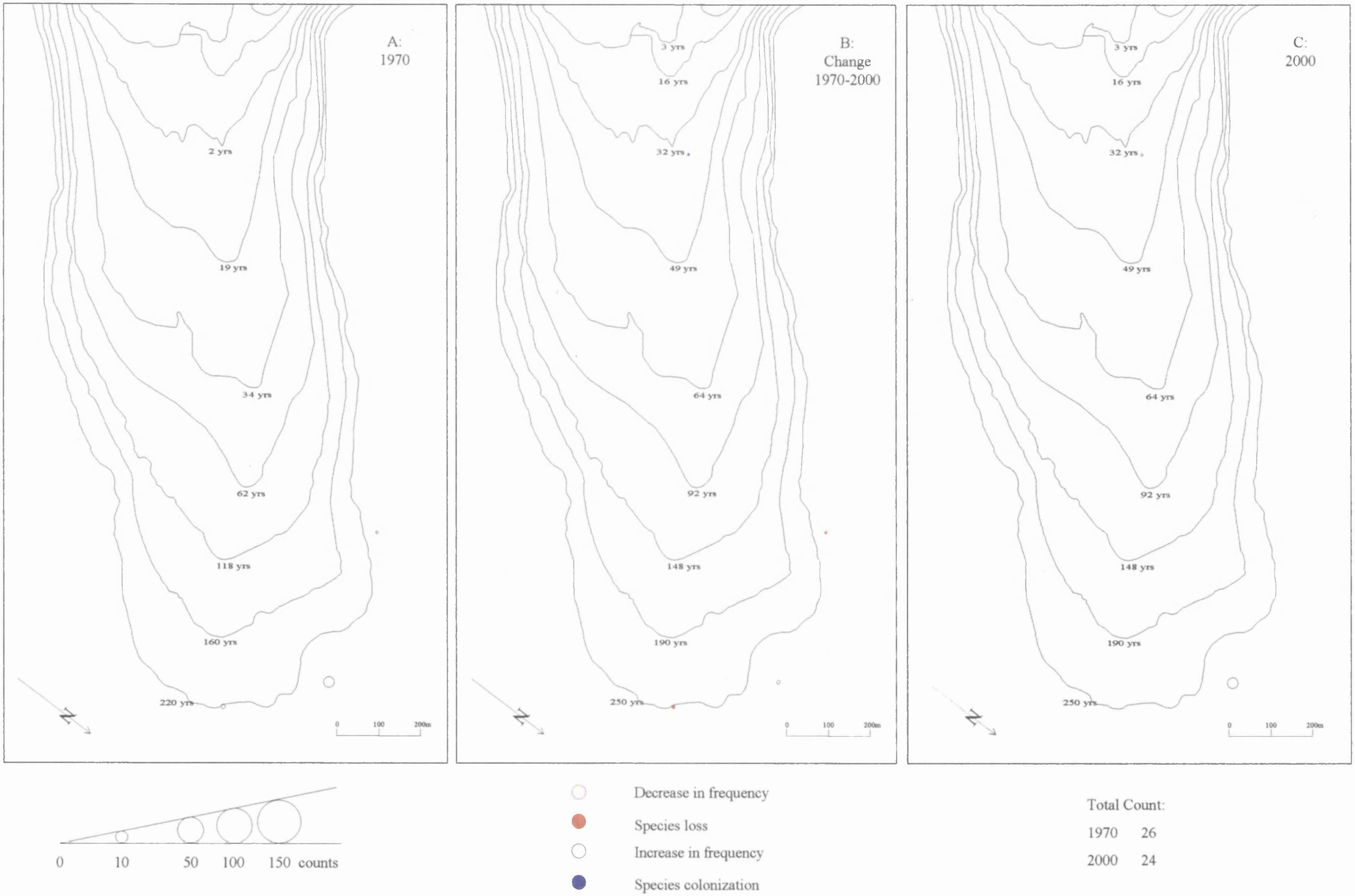


Figure S28 *Epilobium angustifolium*: A, frequency in 1970; B, change in frequency 1970-2000; C, frequency in 2000



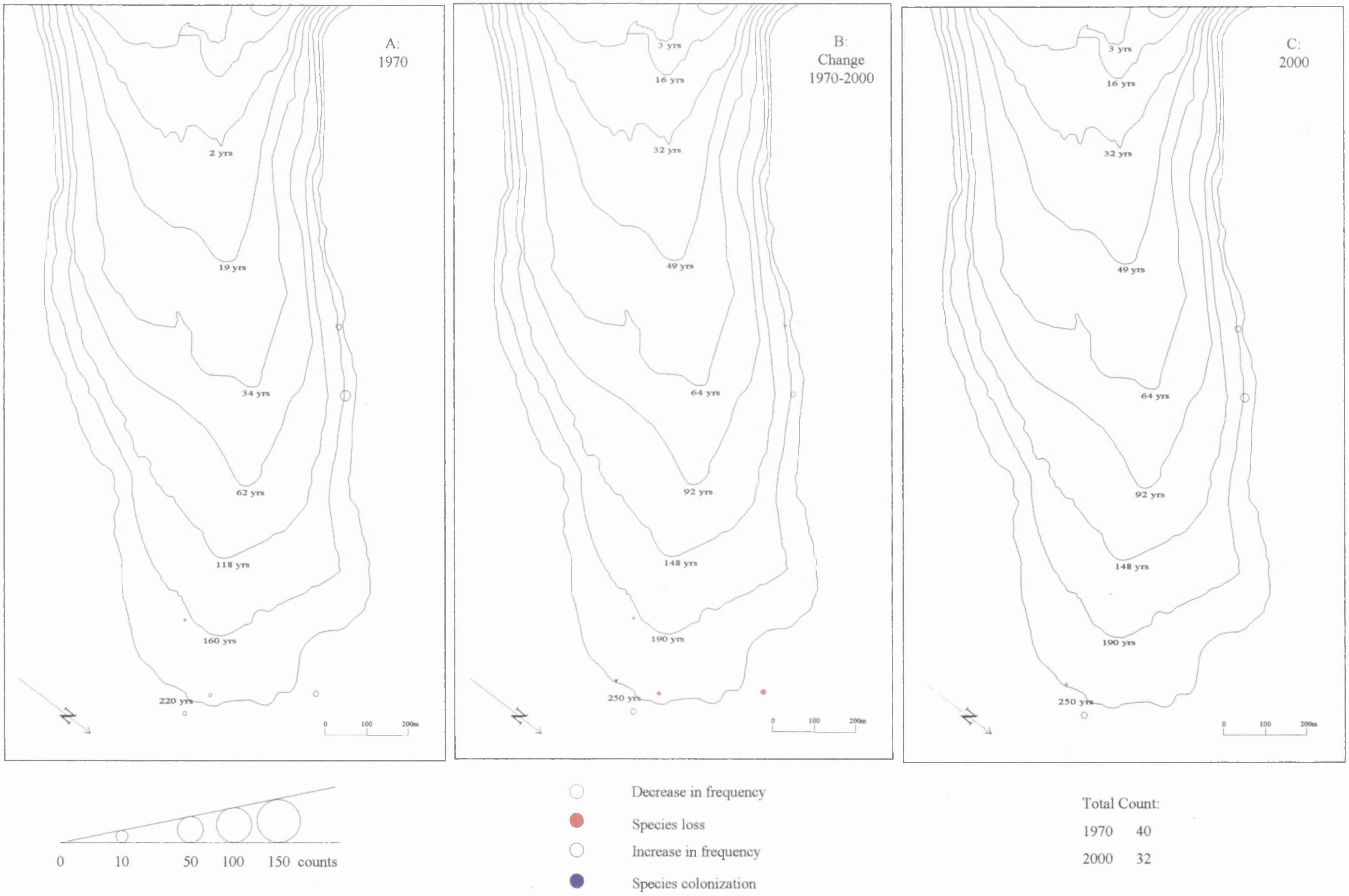


Figure S29 *Euphrasia alpina*: A, frequency in 1970; B, change in frequency 1970-2000; C, frequency in 2000

Figure S30 *Geranium sylvaticum*: A, frequency in 1970; B, change in frequency 1970-2000; C, frequency in 2000

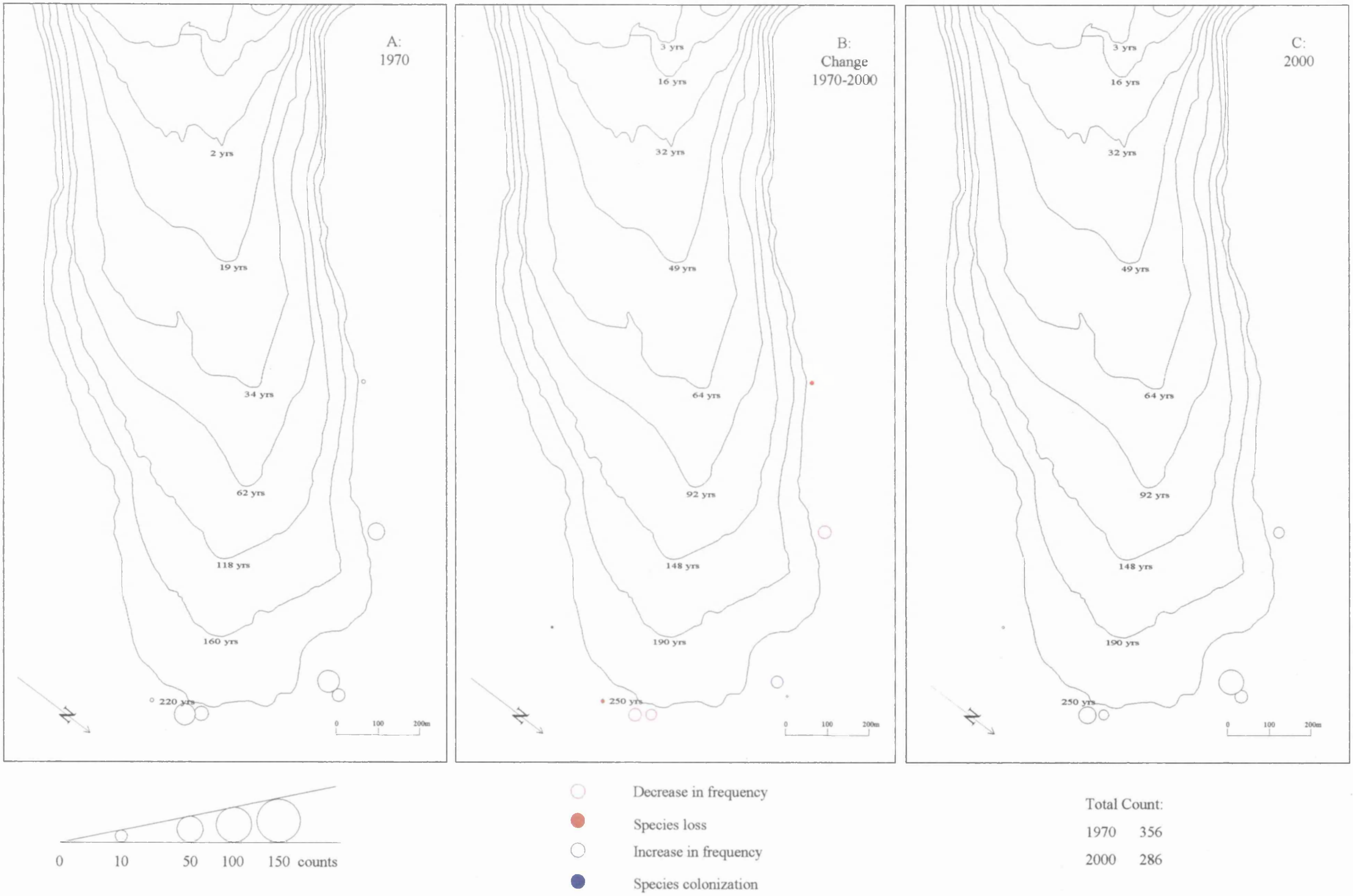


Figure S31 *Gnaphalium norvegicum*: A, frequency in 1970; B, change in frequency in 1970-2000; C, frequency in 2000

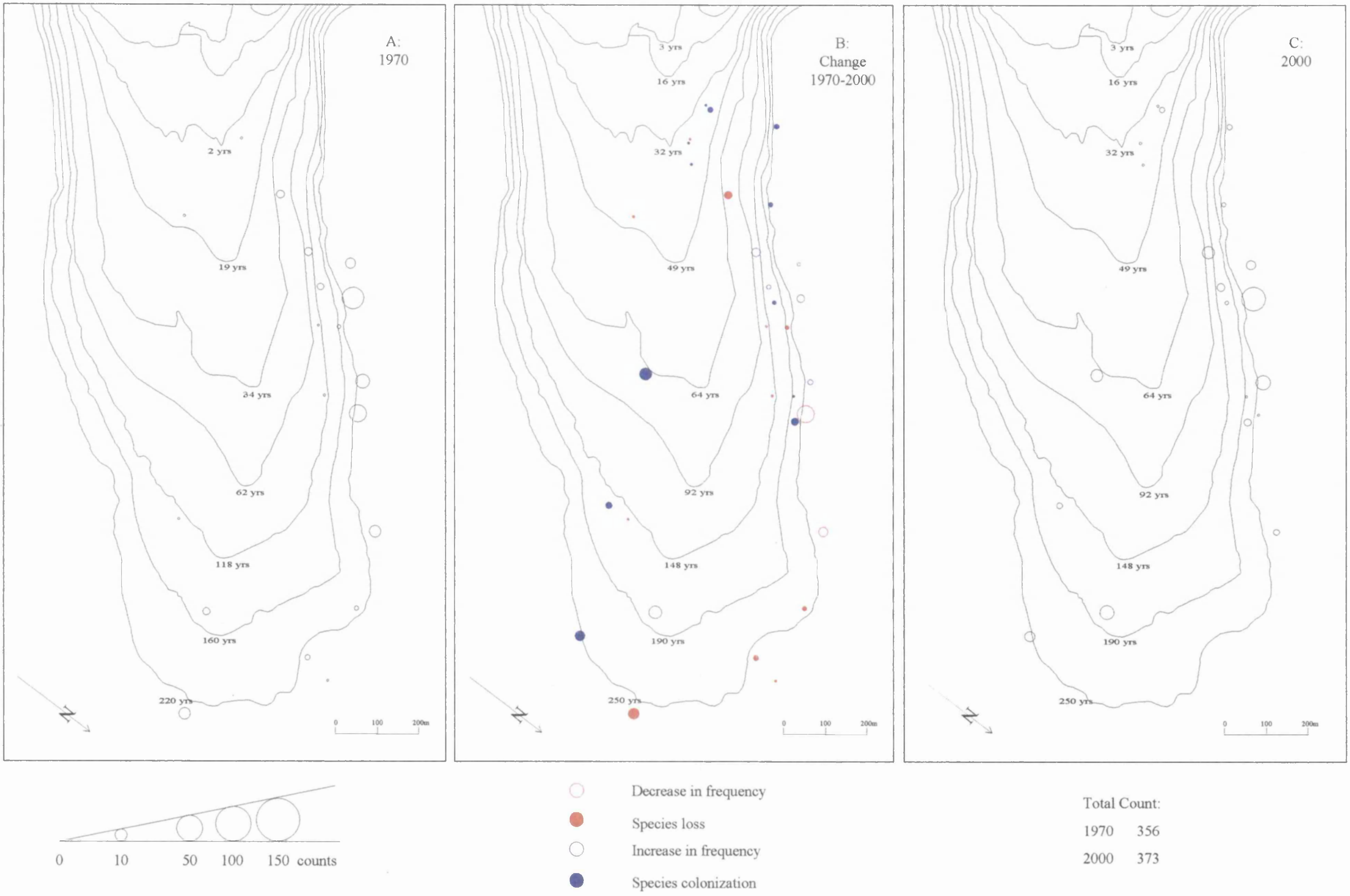


Figure S32 *Lychnis alpina*: A, frequency in 1970; B, change in frequency 1970-200; C, frequency in 2000

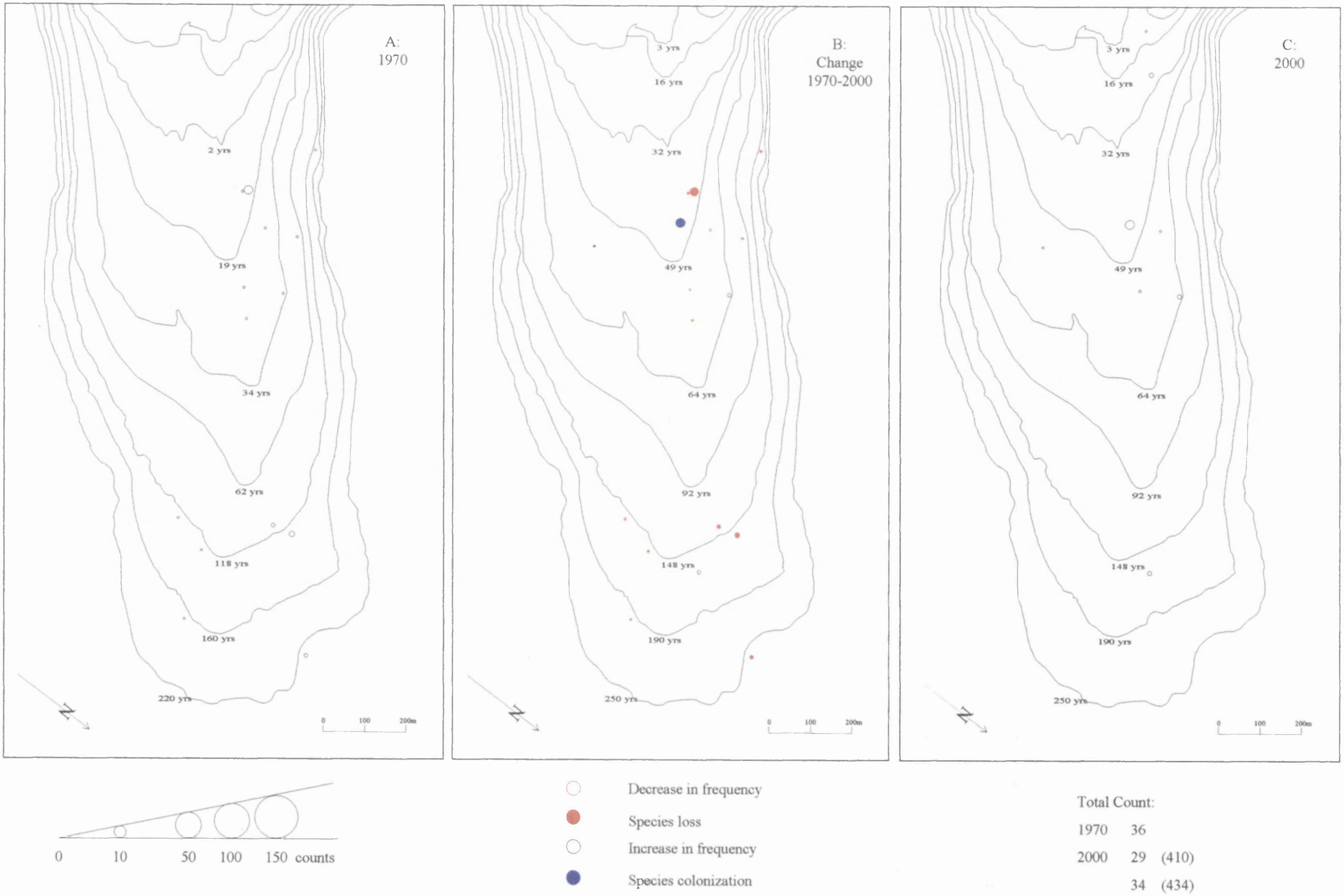


Figure S33 *Melampyrum pratense*: A, change in frequency 1970-2000; B, frequency in 2000

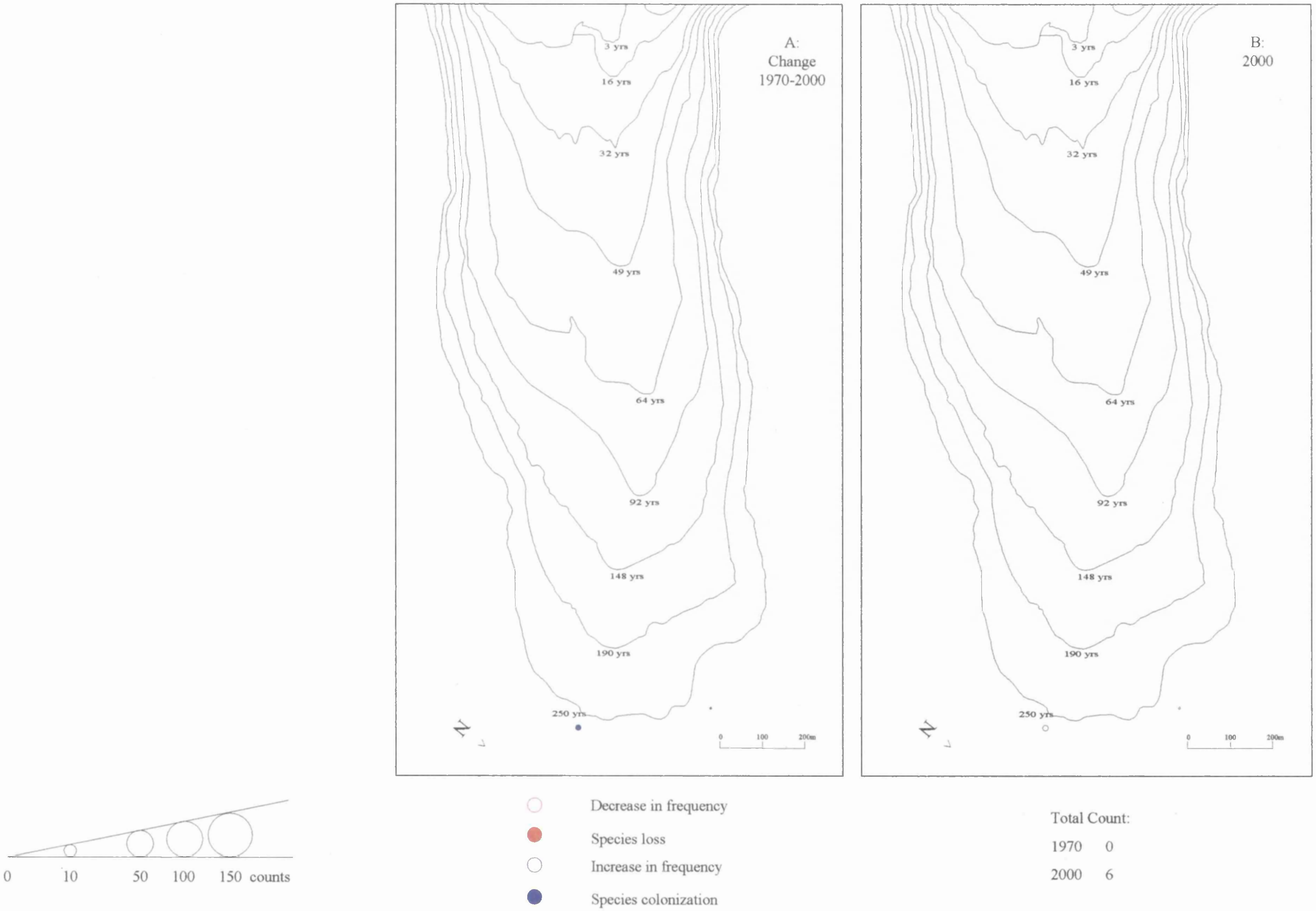
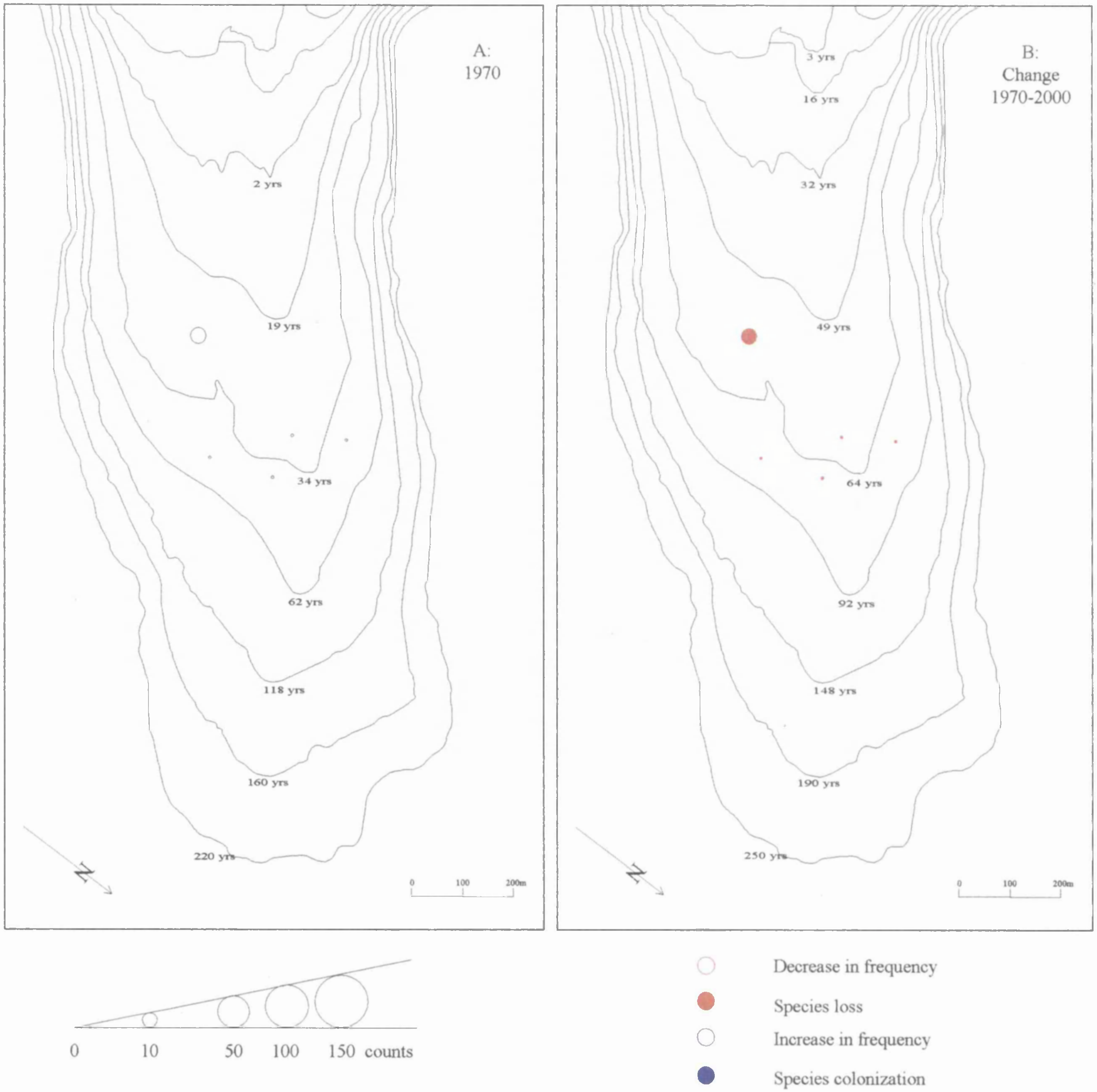


Figure S34 *Melandrium apetalum*: A, frequency in 1970; B, change in frequency 1970-2000



Total Count:

1970	40
2000	0

Figure S35 *Pedicularis oederi*: A, change in frequency 1970-2000; B, frequency in 2000.

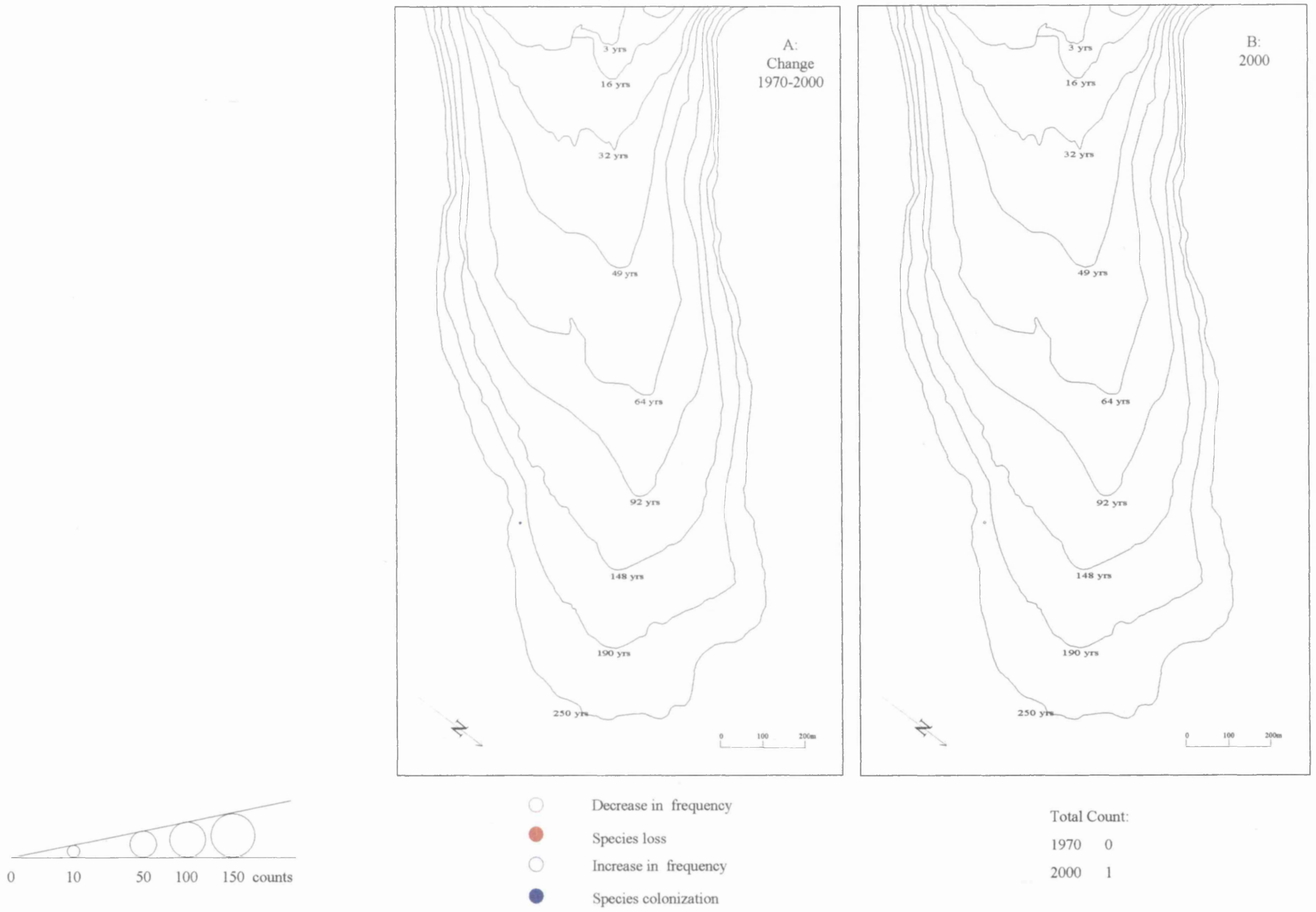


Figure S36 *Potentilla crantzii*: A, change in frequency 1970-2000; B, frequency in 2000.

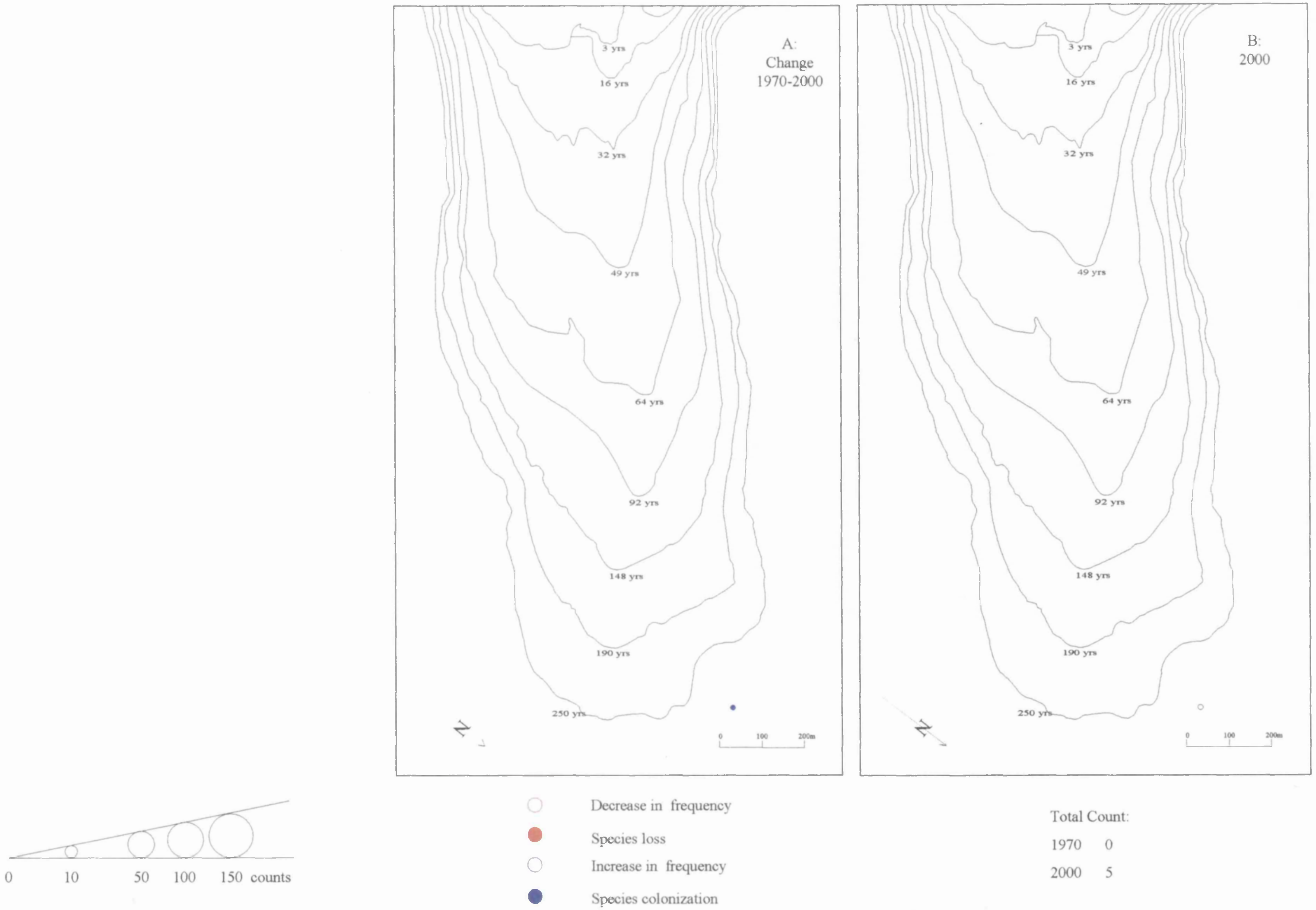


Figure S37 *Pulsatilla vernalis*: A, frequency in 1970; B, change in frequency 1970-2000; C, frequency in 2000.

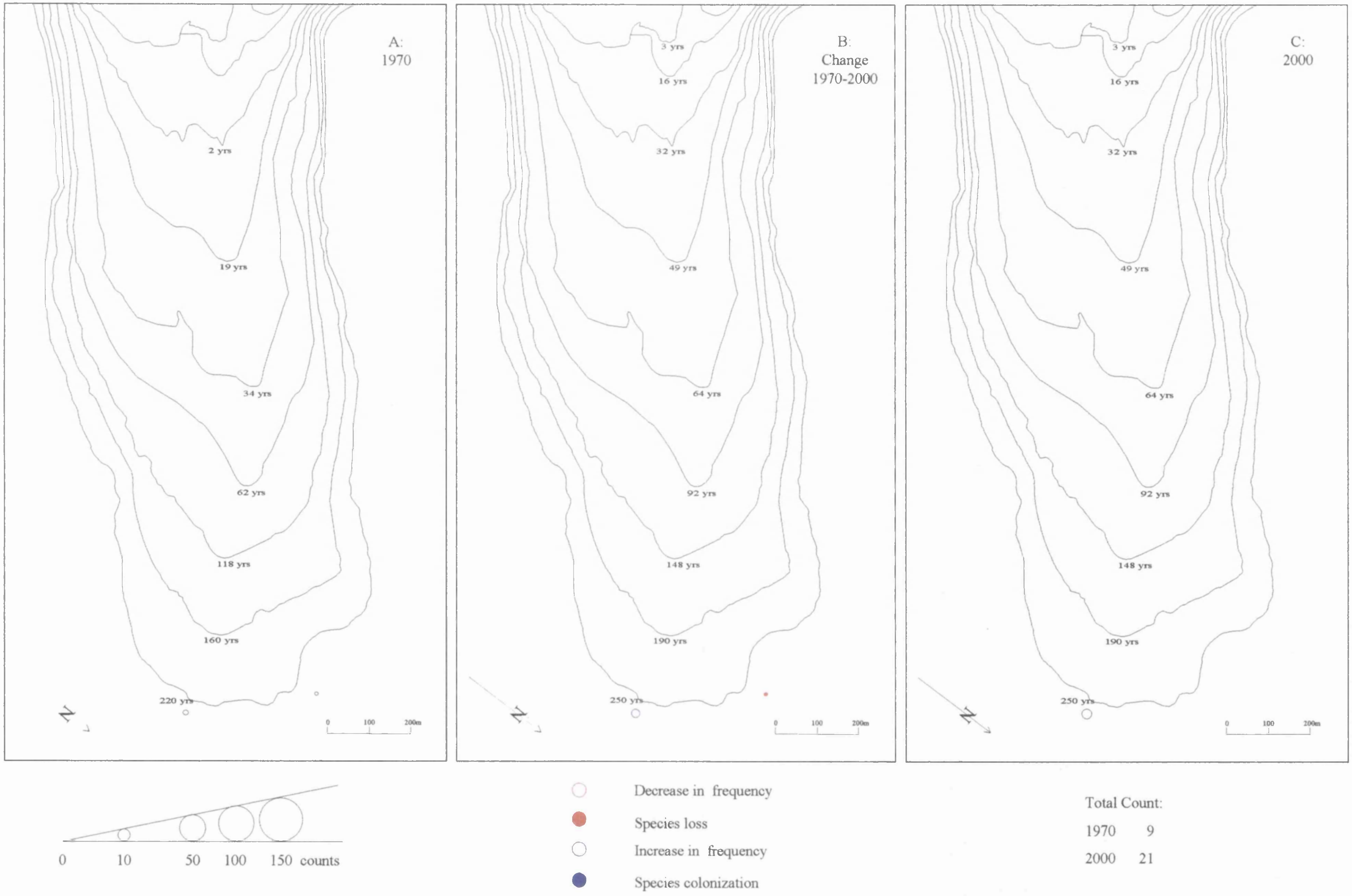


Figure S38 *Ranunculus acris*: A, frequency in 1970; B, change in frequency 1970-2000; C, frequency in 2000

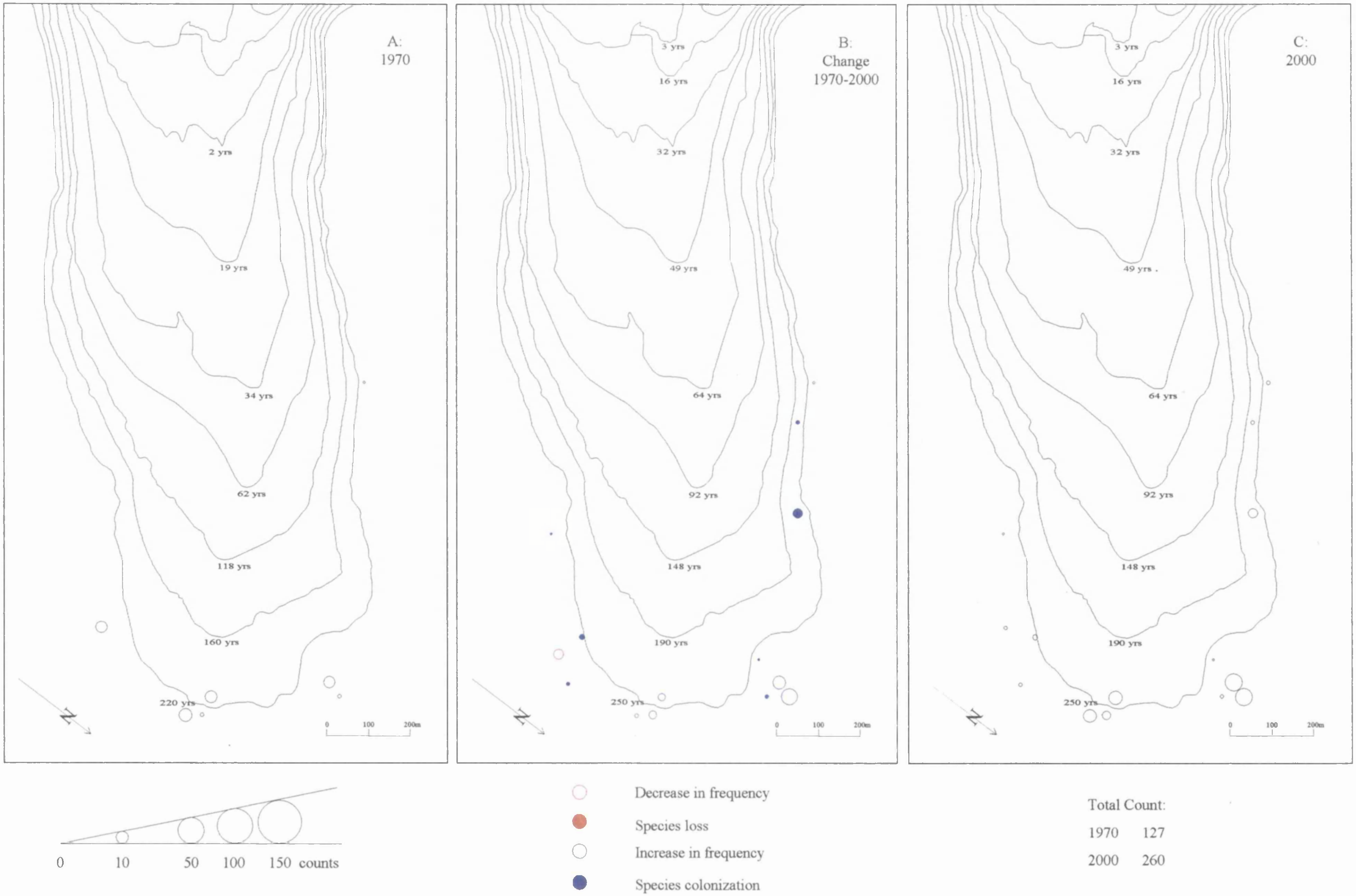


Figure S39 *Ranunculus pygmaeus*: A, frequency in 1970; B, change in frequency 1970-2000; C, frequency in 2000.

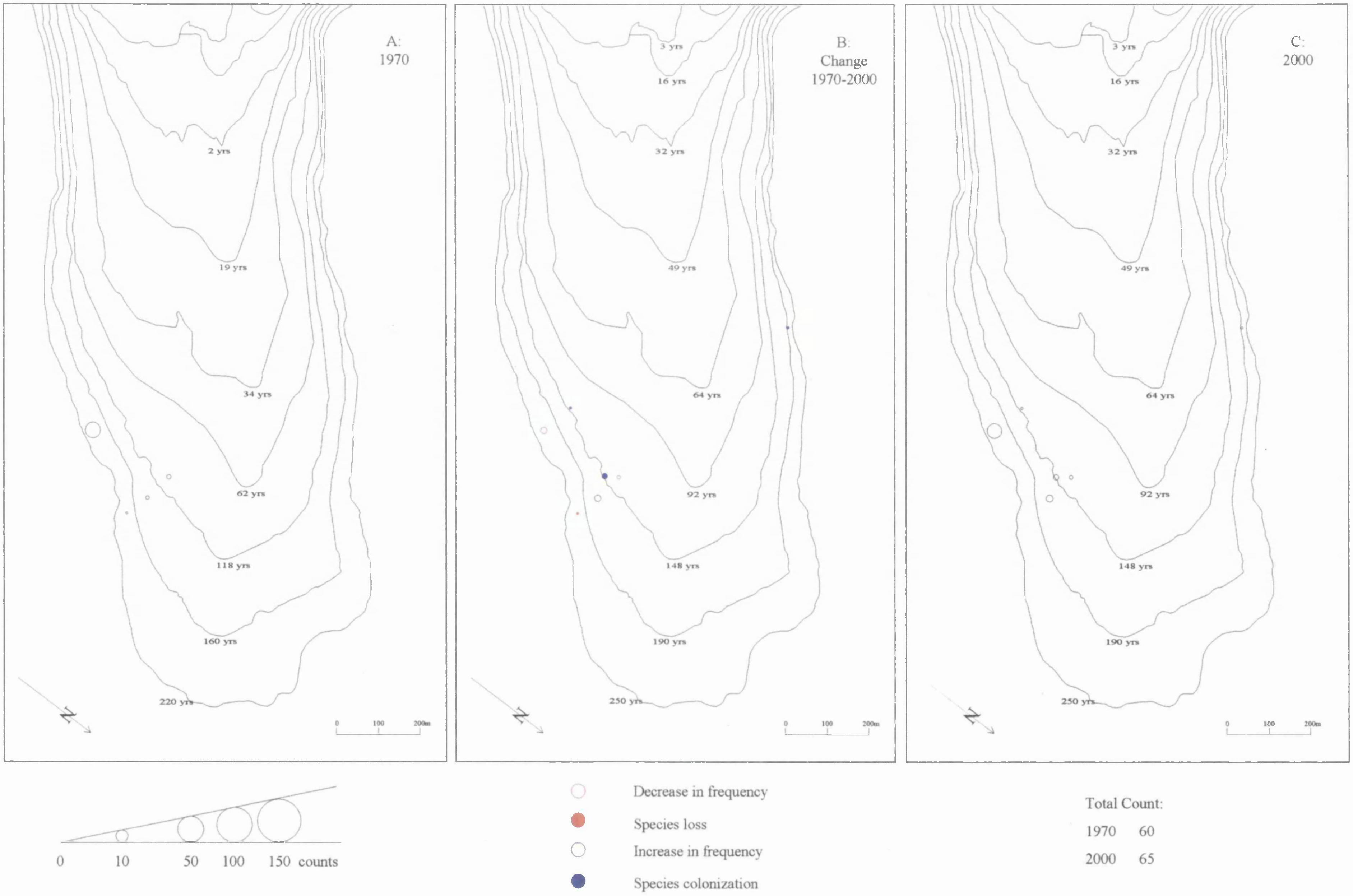


Figure S40 *Rubus arcticus*: A, frequency in 1970; B, change in frequency 1970-2000; C, frequency in 2000.

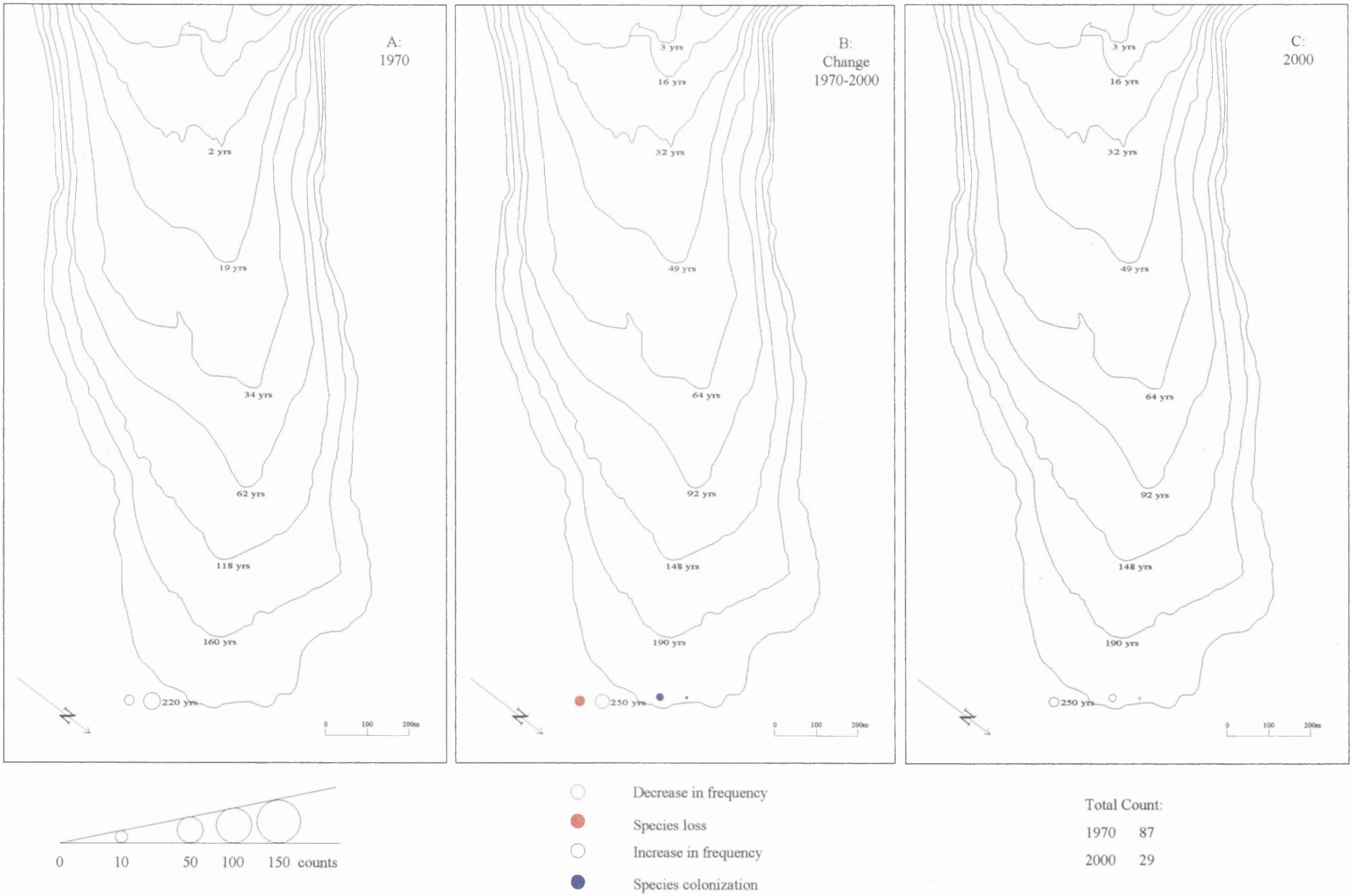


Figure S41 *Rumex acetosa*: A, frequency in 1970; B, change in frequency 1970-2000; C, frequency in 2000.

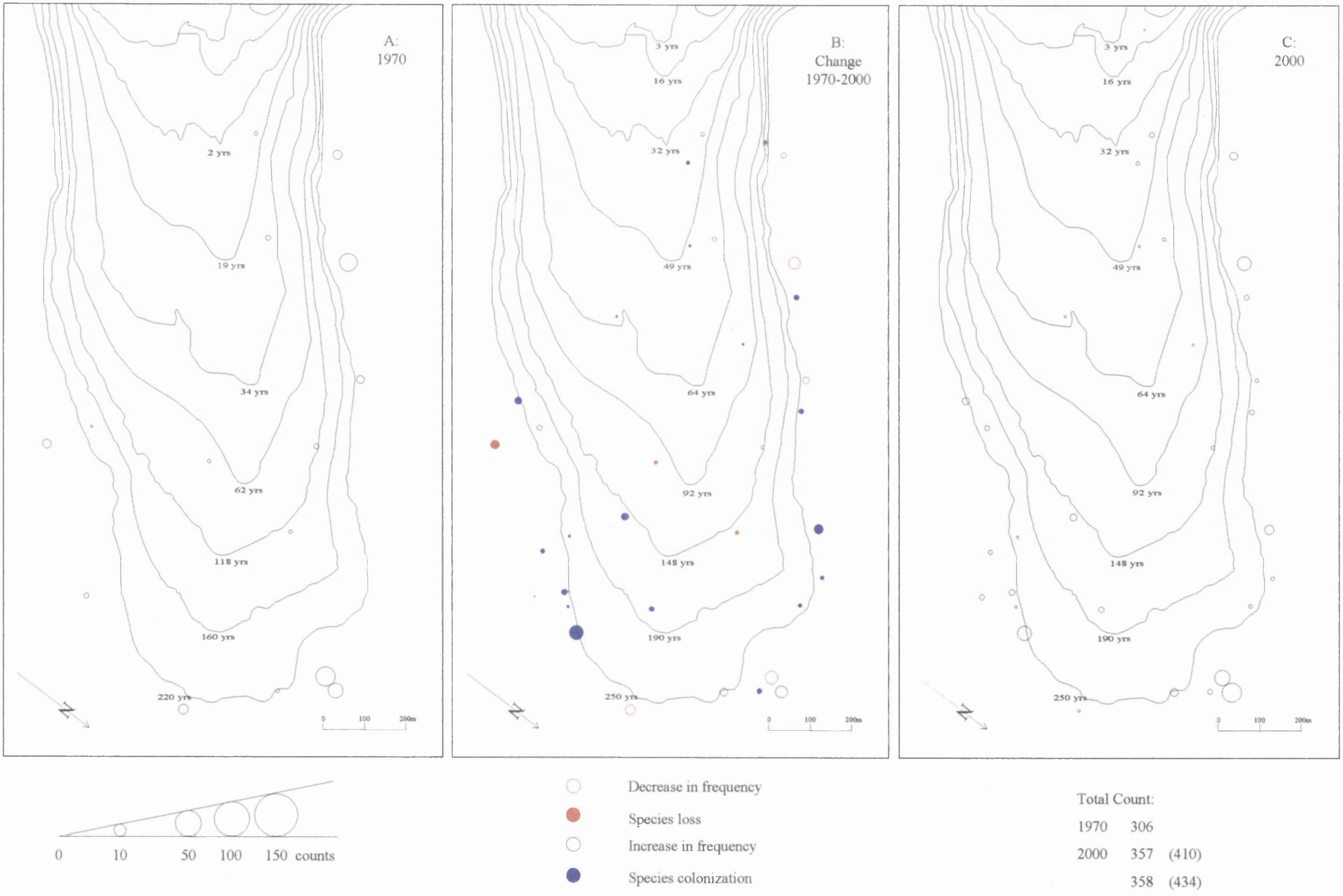


Figure S42 *Rumex acetosella*: A, change in frequency 1970-2000; B, frequency in 2000.

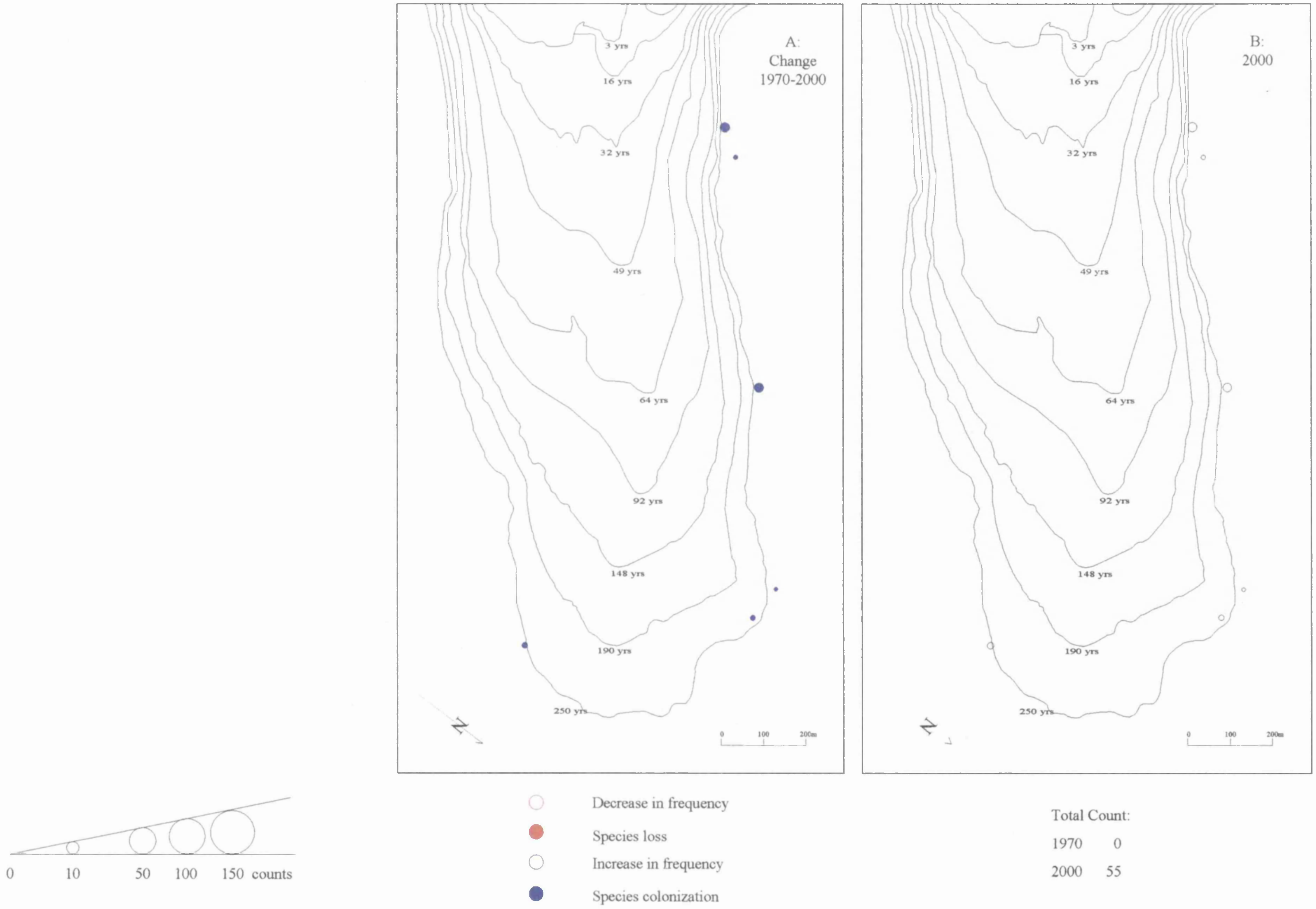


Figure S43 *Saussurea alpina*: A, frequency in 1970; B, change in frequency 1970-2000; C, frequency in 2000.

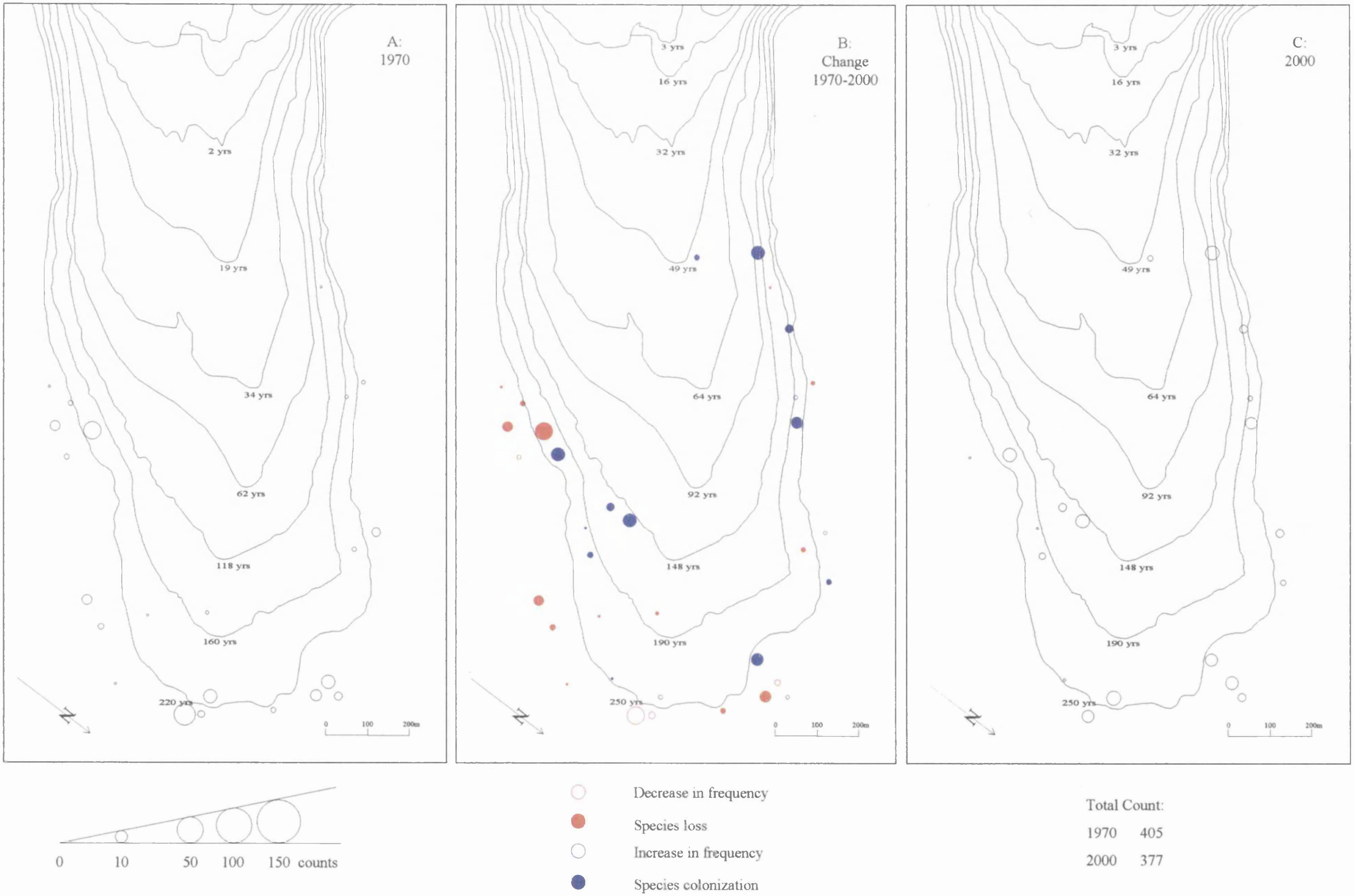
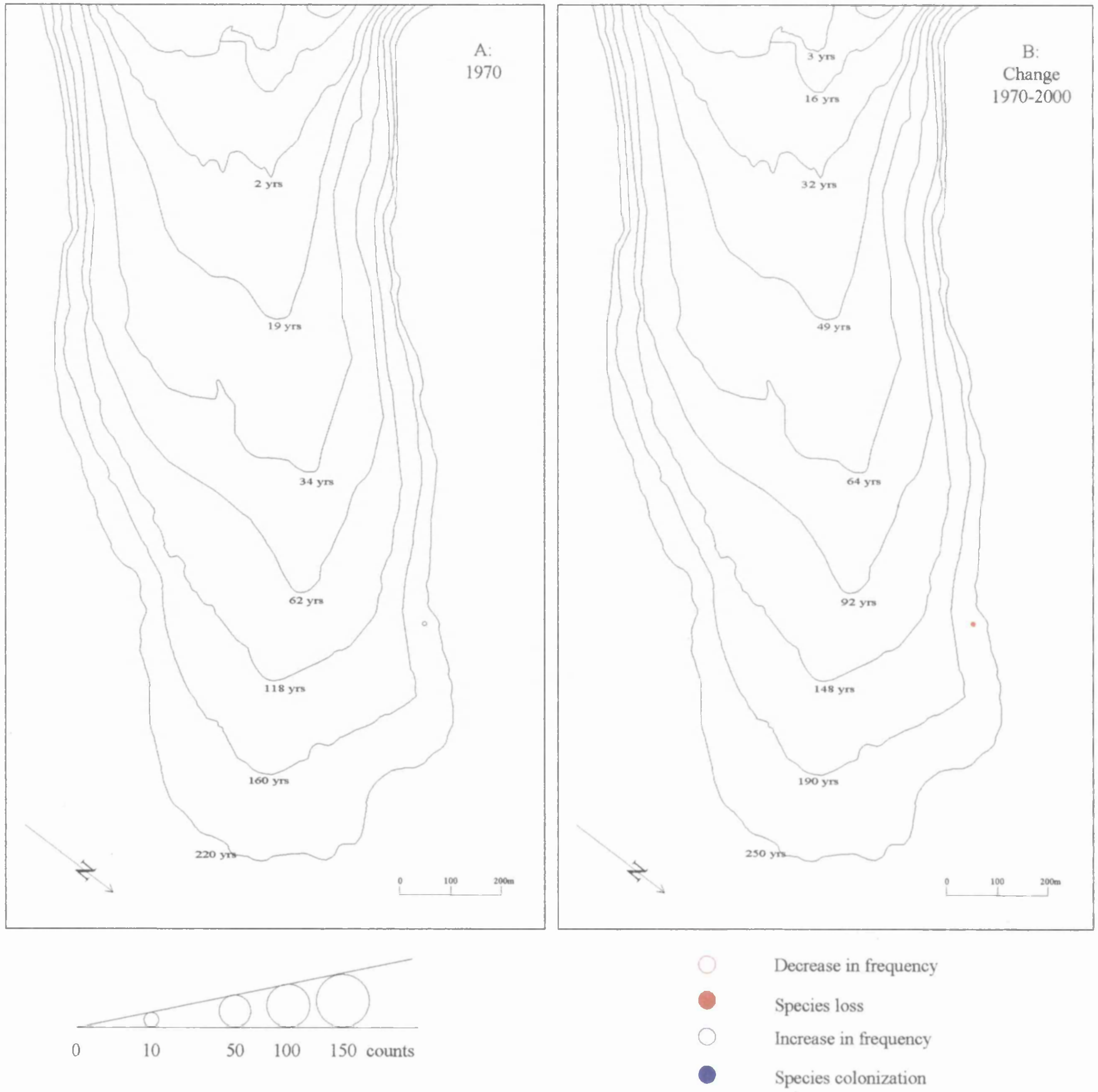


Figure S44 *Saxifraga cernua*: A, frequency in 1970; B, change in frequency 1970-2000.



Total Count:

1970	2
2000	0

Figure S45 *Saxifraga nivalis*: A, frequency in 1970; B, change in frequency 1970-2000; C, frequency in 2000

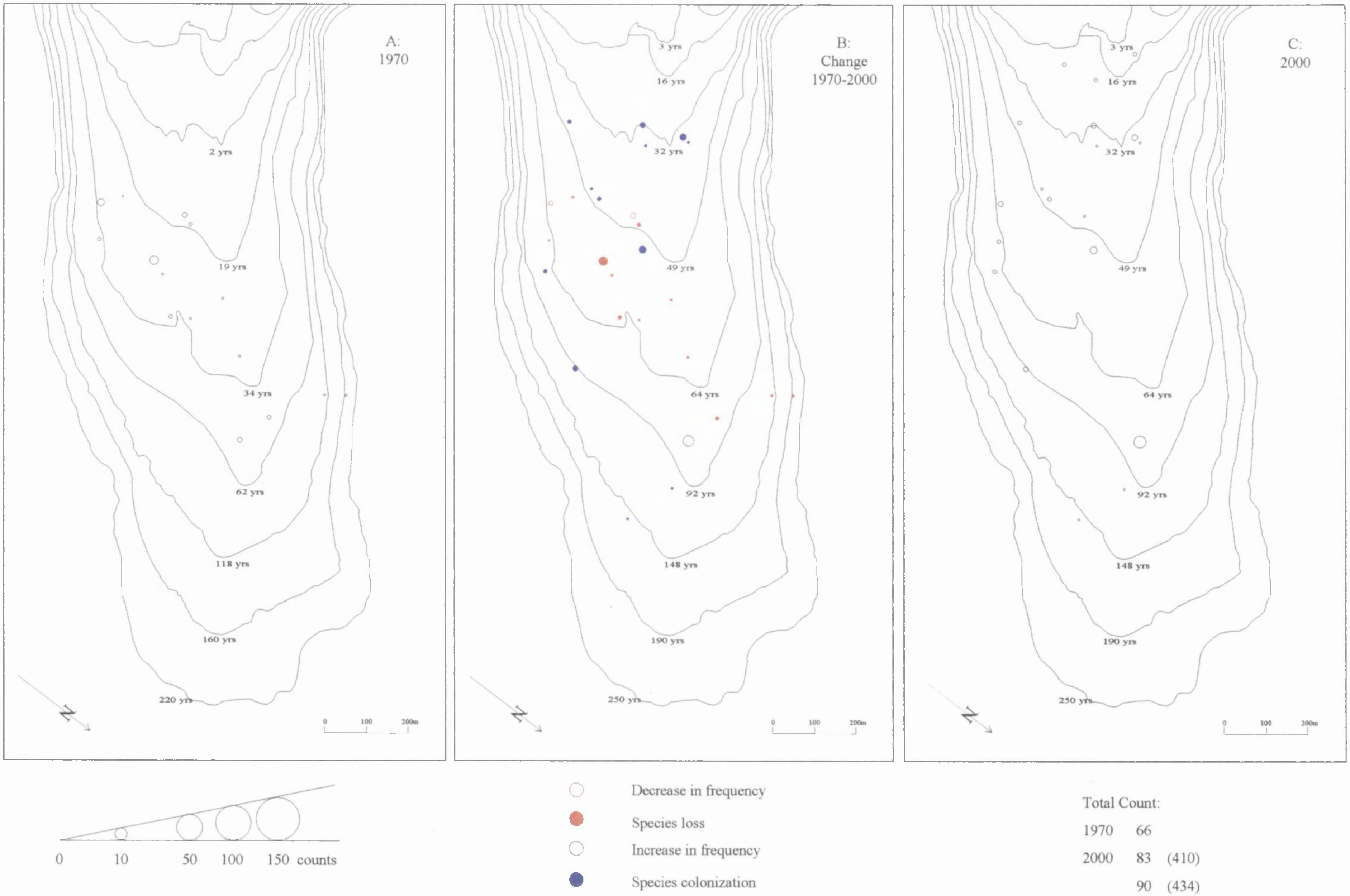


Figure S46 *Saxifraga rivularis*: A, frequency in 1970; B, change in frequency 1970-2000; C, frequency in 2000

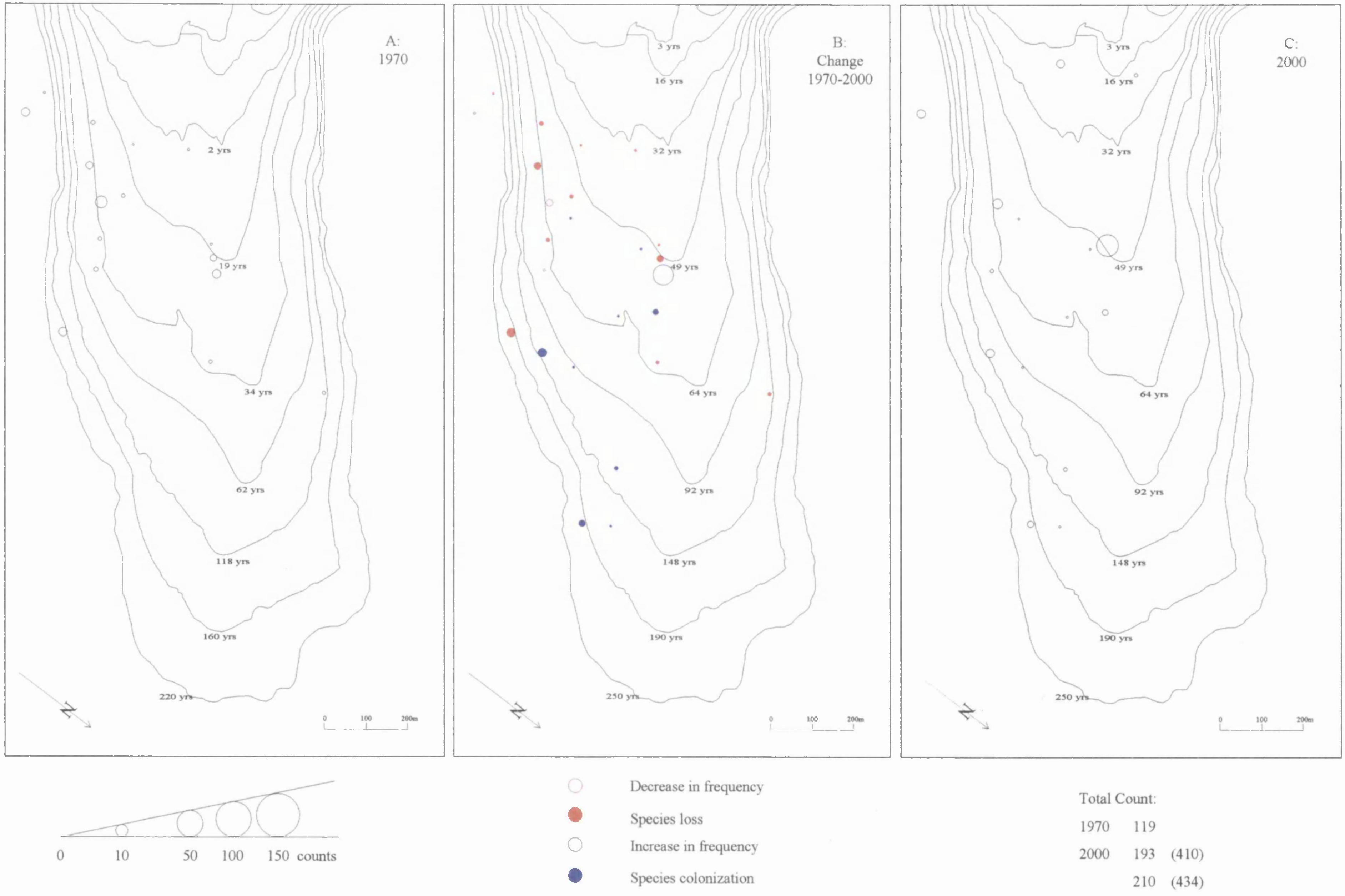


Figure S47 *Sedum rosea*: A, frequency in 1970; B, change in frequency 1970-2000; C, frequency in 2000

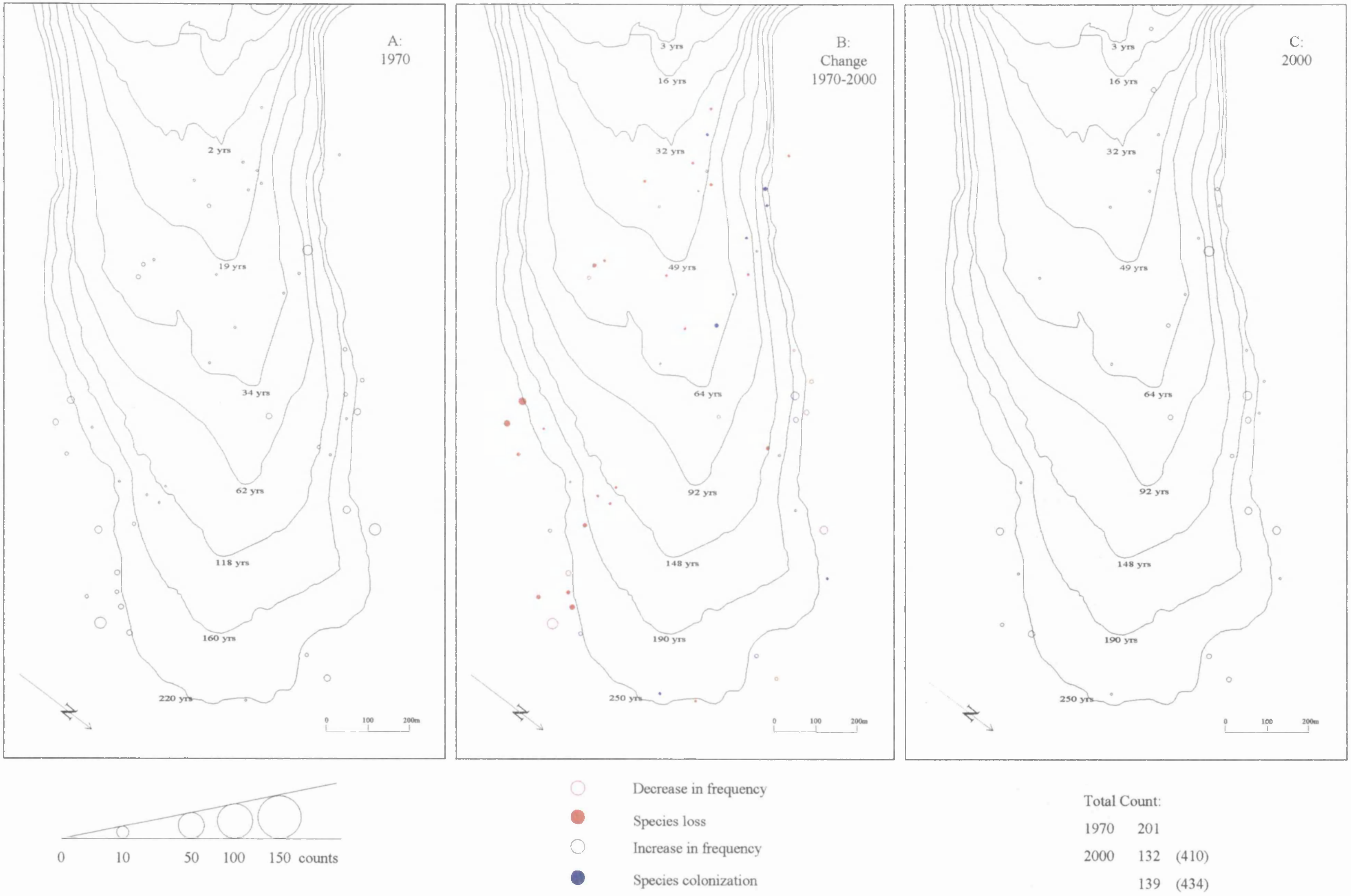


Figure S48 *Silene acaulis*: A, frequency in 1970; B, change in frequency 1970-2000; C, frequency in 2000

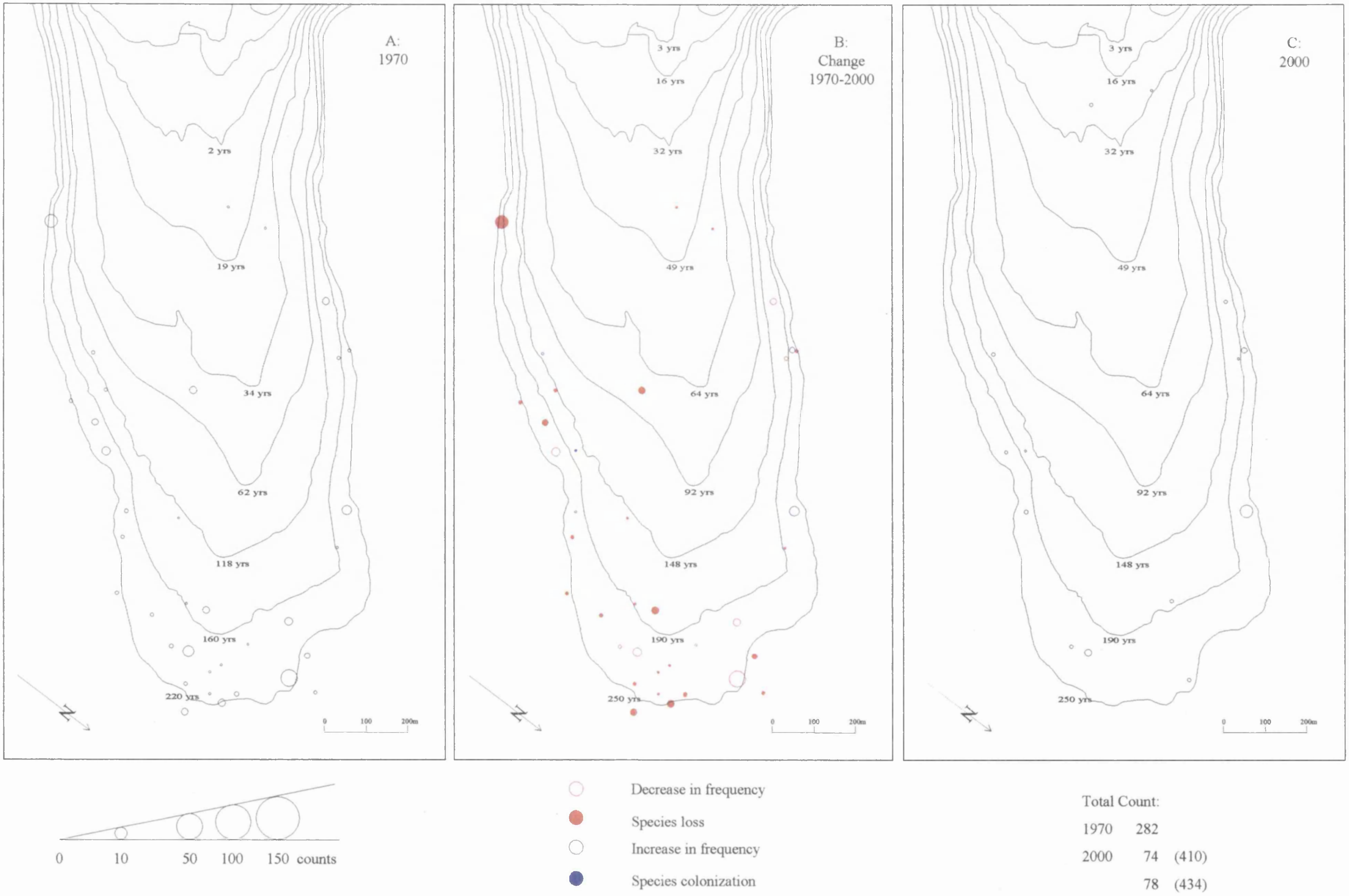


Figure S49 *Silene dioica*: A, change in frequency 1970-2000; B, frequency in 2000

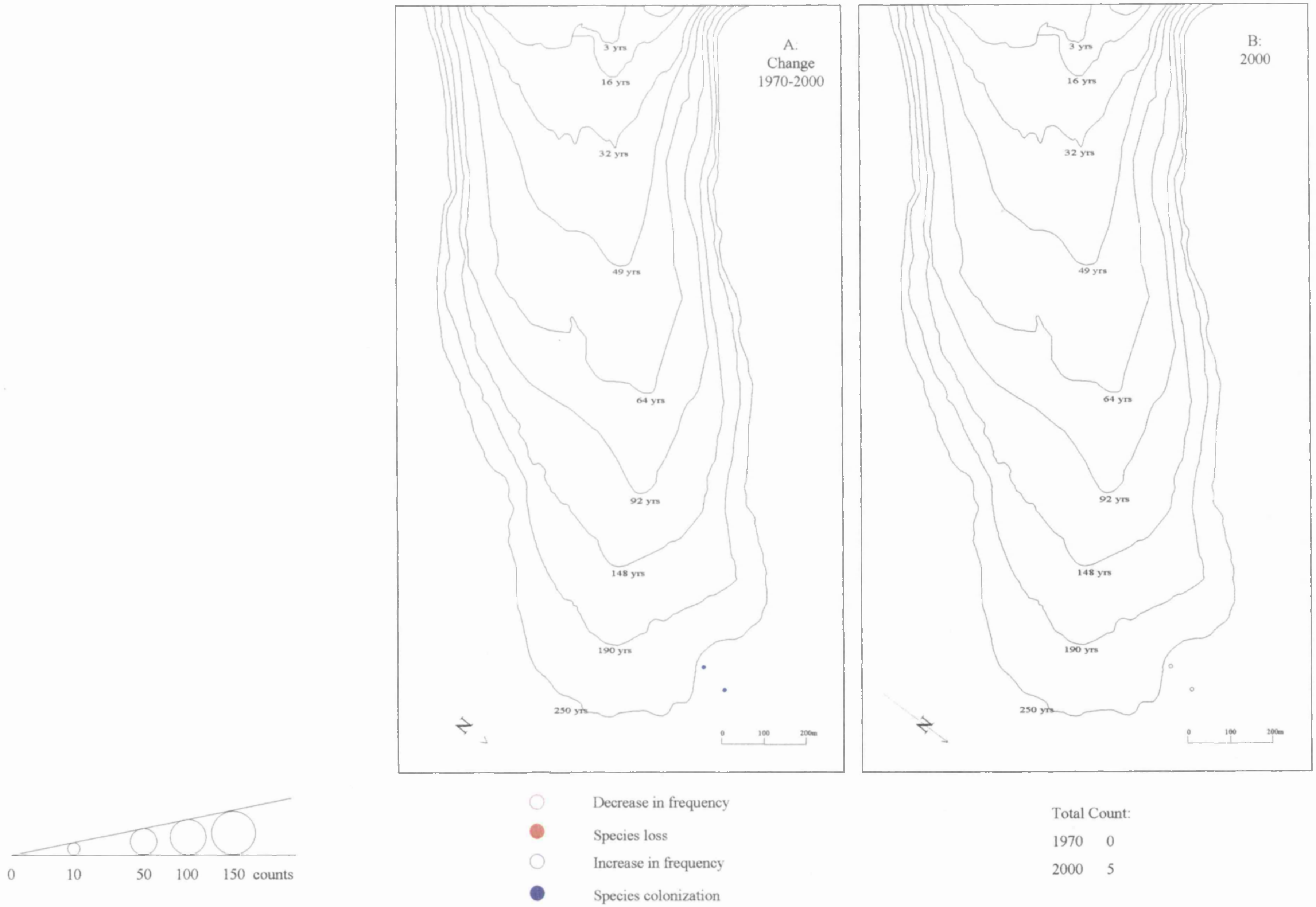


Figure S50 *Thalictrum alpinum*: A, frequency in 1970; B, change in frequency 1970-2000; C, frequency in 2000

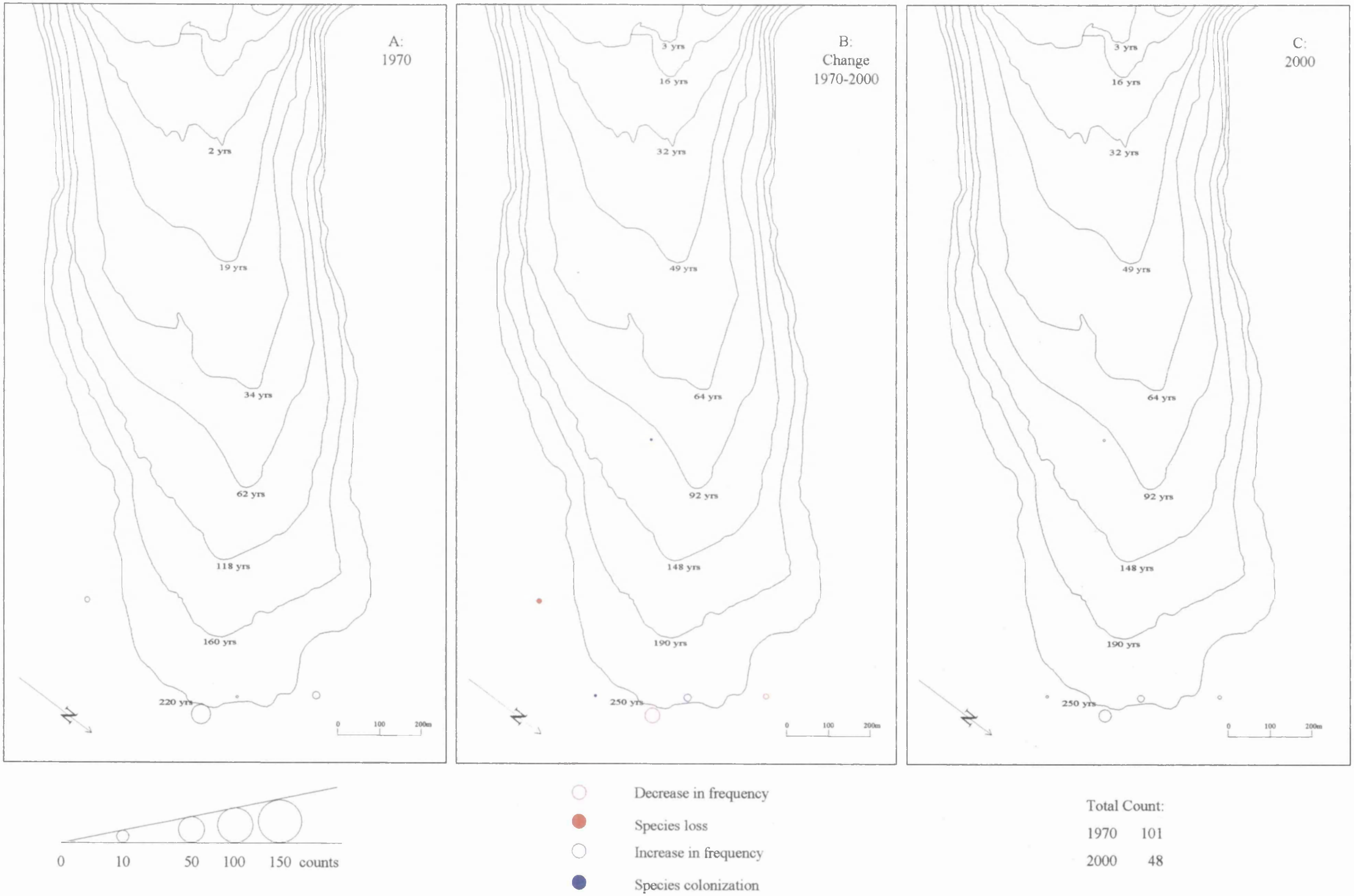


Figure S51 *Trientalis europaea*: A, frequency in 1970; B, change in frequency 1970-2000; C, frequency in 2000

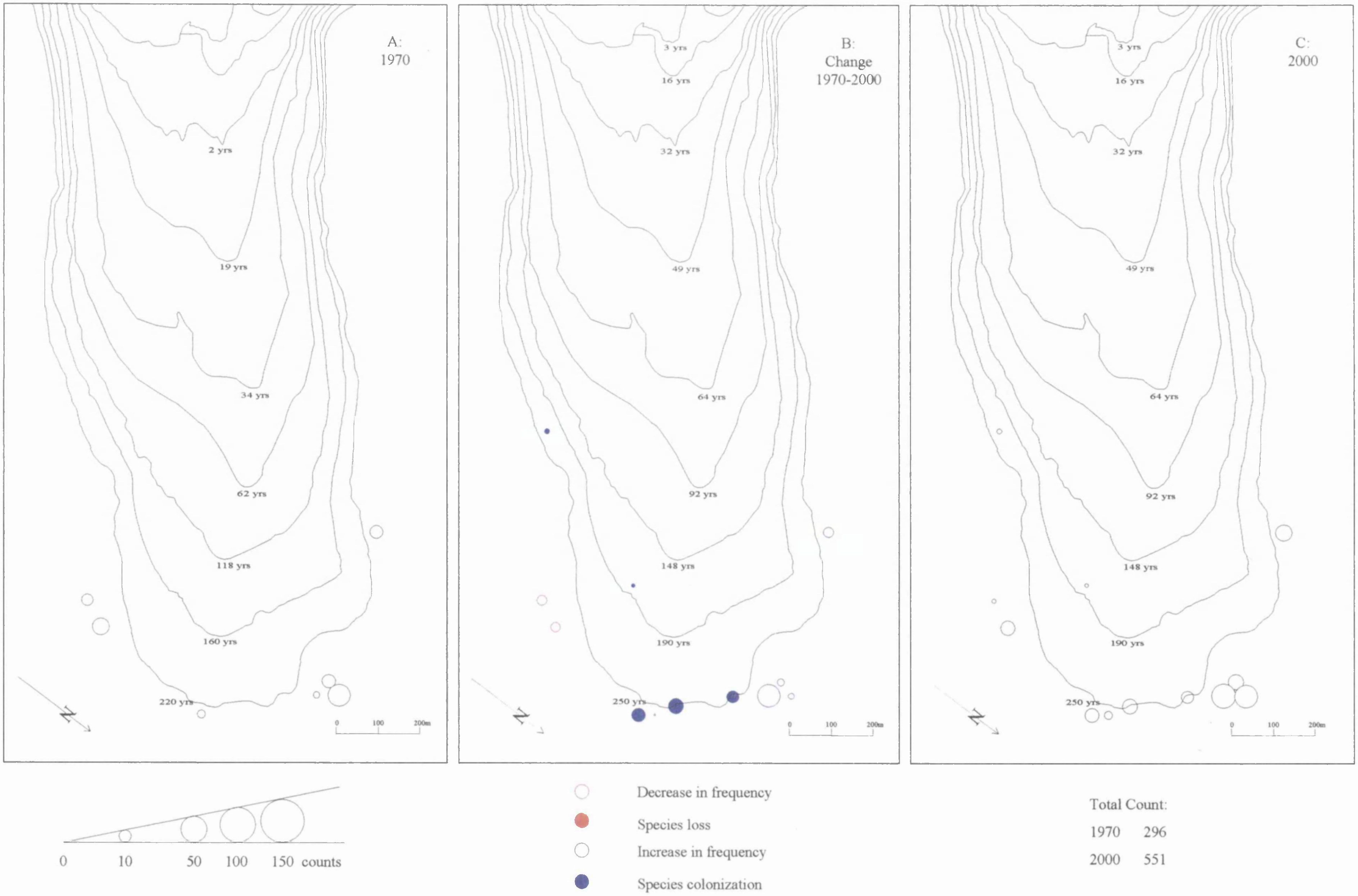


Figure S52 *Viola palustris*: A, frequency in 1970; B, change in frequency 1970-2000; C, frequency in 2000