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Keywords	Paleoecology; climate change; conservation; woodland; fragmentation; Scotland
Taxonomy	Environmental History, Woodland, Climate Change Adaptation, Conservation Ecology, Community Ecology
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Microclimate variability and long-term persistence of fragmented woodland

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Abstract

Favourable microclimates are predicted to buffer fragmented populations against the effects of environmental change, but ecological timeseries are often too short to establish the extent to which such microsites facilitate population persistence through multiple climate shifts. We investigate the effects of microclimatic heterogeneity on woodland resilience through millennial climate and disturbance shifts near northwest European woodland range limits. We use palaeoecological data from northern Scotland to study the effects of fragmentation on community composition and diversity in a potentially favourable microclimate, and compare palynological timeseries of tree abundance from five sites to assess the effects of favourable (low-lying sheltered) versus more marginal (higher altitude) settings on population persistence and stability. The sheltered site shows persistence of tree cover through Holocene climatic and anthropogenic shifts, including climatically-driven regional woodland contraction around 4400 cal BP (calendar years before present), when surviving woods became compositionally differentiated into upland pine and low-lying deciduous communities. A favourable microclimate can thus buffer woodlands against environmental shifts and increase continuity of canopy cover, but it does not generate stable communities. Compositional reorganisation is an essential stress response mechanism and should be accommodated by conservation managers. The replacement of deciduous taxa by *Pinus sylvestris* after 1060 cal BP represents the decoupling of pine distribution from climate drivers by management intervention. As a result, current microrefugial woodland composition reflects late Holocene human intervention. Alternative models of community composition and behaviour from palaeoecology provide a stronger foundation for managing microsite communities than relict woods in contrasting environmental settings.

Keywords

Paleoecology; climate change; conservation; woodland; fragmentation; Scotland

1 Introduction

Global reductions in woodland size mean that fragmented populations play an increasingly significant role in conservation (Haddad et al., 2015). Favourable microclimates in otherwise inhospitable landscapes allowed the survival of climate relict tree populations and associated biodiversity in the past, and are predicted to buffer populations against ongoing environmental change (Hampe and Jump, 2011; Maclean et al., 2015). However, the timescales of modern ecological studies are too brief to establish the extent to which microclimates can mitigate the negative impacts of fragmentation through multiple climate shifts, including extinction debt and local extinction-recolonization dynamics (Saunders et al., 1991; Vellend et al., 2006). Long timeseries provide a powerful tool for understanding to what extent locally favourable conditions allow populations to persist through multiple environmental changes. They offer insights into the origins of modern conservation values in long-fragmented communities and their potential sensitivity to future climatic fluctuations (Bhagwat et al., 2012).

Northern Scotland is an appropriate location to study interactions between microclimate and woodland resilience because it lies on the range edge for temperate woodland and extant woods are highly fragmented, thus exposing them to recruitment and dispersal stresses. Woods have been repeatedly exposed to climate stresses in the past (Tipping, 1994). This is particularly the case for *Pinus sylvestris* L. (Scots pine), which underwent multiple phases of population contraction and expansion in response to Holocene climate shifts (Willis et al., 1998). Favourable microclimates are also important for the adaptive capacity of species with a northerly biogeographical distribution: Scots pine is thought to have survived the last glaciation in northerly refugia, including the continental shelf off northwest Scotland, and its range is predicted to shift northeast in response to ongoing climate change (Bhagwat and Willis, 2008; Matias and Jump, 2012). Understanding the extent to which woods in this region were buffered against smaller amplitude climate shifts in the past can help evaluate current and future site potential to retain these populations in the event of more extreme future shifts by indicating whether they served as persistent or transient microclimate refugia (Keppel et al., 2012). Our investigation examines the effects of microclimatic heterogeneity on arboreal resilience in this region. We present new stand-scale pollen evidence for the effects of long-term fragmentation on community composition and diversity in a potentially favourable microclimate, and assess the role of microclimatic buffering on population persistence through a comparison of time series of tree abundance from five sites in contrasting settings across this region.

1.1 Regional context and site description

In Scotland, woodland currently constitutes 18% of land cover, 22.5% of which is considered native (Forestry Commission, 2014). This contrasts with the maximum extent of woodland cover around 5700 cal BP (calendar years before AD 1950), which has been estimated at 50-60% of the land area (Tipping, 1994; Smout et al., 2005). Abrupt and widespread woodland contraction occurred across northwest Scotland around 4400 cal BP, notably of pine. This is attributed primarily to climate deterioration and resulted in the contraction of pine to near its current range (Fig. 1) (Bennett, 1995). For four millennia these woodland fragments have existed within a matrix of blanket peat and heath, with small and dispersed areas of agriculture. The surviving climate relicts are highly valued and form the basis for national and site-based woodland conservation and expansion goals.

These high conservation value fragments include the present study site, Ledmore and Migdale National Nature Reserve (NNR) (Fig. 1). It comprises a range of habitats including *Quercus* (oak) and *Betula* (birch) woodland, semi-natural *P. sylvestris* woods, open dwarf shrub heath and mire communities (see Supplementary material: Table A1). These include 95 ha ‘old’ sessile oakwoods at their northerly limits in Britain, characterised by an acidophilous heath understorey more commonly associated with pinewoods. The 144 ha pinewood on which our study focuses includes ‘ancient pinewood indicator’ species of orchids, lichens and invertebrates which suggest long-established pine communities (Woodland Trust Scotland, 2015). The 6.9 km^2 site is topographically diverse, rising from sea level to 228 m OD. Management goals include conserving the distinctive biodiversity mosaic and the ancient woodlands, improving natural regeneration and expanding native woodland cover to form a regional network that increases resilience to climate change impacts on species ranges (Woodland Trust Scotland, 2015). A limited range of management interventions is advocated, focused on reducing threats (e.g. thinning forestry plantation to remove exotic species and stimulate native tree regeneration).

The biogeographical position and composition of the site raise numerous uncertainties about community resilience and appropriate models for management. Maclean et al. (2014) suggest that landscapes with high refugial potential, notably biophysical heterogeneity, support more stable and qualitatively different plant assemblages from those in surrounding regions with lower topographic and climatic heterogeneity. We hypothesise that the comparatively sheltered, east-facing aspect of the study site, and local edaphic and topoclimatic heterogeneity enabled woodland persistence through the Holocene, in contrast with more homogeneous and exposed conditions in adjacent river valleys and upland plateaux. Within this proposed microclimate refugium, the continuity of particular species and origins of current communities are unclear. The NNR lies on the northern edge of current native woodland distribution and equidistant between westerly regions which underwent extensive woodland contraction and easterly woods which show greater continuity of cover. Furthermore, local pine communities suggest affinities with upland woods, while the presence of oak suggests affinities with woods on the Highland fringe (Tipping, 1994), and it is unclear which context provides an appropriate model for assessing and predicting community behaviour.

To examine these questions and understand the significance of microclimatic conditions for woodland resilience, the vegetation history from Migdale pinewood is compared with palaeoecological data from two contrasting sites in neighbouring catchments (upland Reidh-lochan and low-lying Reidchalmai), and two sites selected to represent the dominant regional upland trends: pinewood continuity (Loch an Amair) and mid-Holocene woodland contraction (Torran Beithe). The comparatively small diameter of these five sites (Table 1) means that they are sensitive to pollen input and thus vegetation dynamics within 50 to a few hundred metres around each site (Jacobson and Bradshaw, 1981). When discussing individual sites, we thus use the term ‘microclimate’ to refer to vegetation and environmental variability on a sub-landscape scale, at which topographic factors can create suitable conditions for localised tree populations and woodland communities to survive potentially unfavourable regional climatic regimes (sensu Dobrowski, 2011). Modern climate data for the sites is limited since the weather station network is sparse in the Highlands, but interpolated data allow us to identify broad rainfall and oceanicity contrasts and temperature similarities between the sites (Table 1) (Averis et al. 2004).

2 Methods

Field sampling, laboratory procedures and statistical methods are described for the Migdale analysis site. Table 1 provides published references detailing the methods used at the four comparative sites. A peat core was extracted from the edge of a valley mire at Migdale, adjacent to mature pinewoods. Trees currently grow on the peat surface and woody material preserved in the stratigraphy indicates that they have done so in the past. The full depth of peat was sampled using a closed-chamber Russian peat corer to avoid contamination (Jowsey, 1966). To compare the palynological diversity of modern and past assemblages, pollen was extracted from moss foliage that forms the current ground cover in seventeen vegetation communities around the NNR (Table A1, Fig. A1). Sediment stratigraphic description (Table A2) and pollen analysis follow standard techniques (Moore et al., 1991). Pollen and spore nomenclature follow Bennett (1994), with the exception of *Sorbus*-type (e.g. rowan) (Boyd and Dickson, 1987) and *Corylus avellana/Myrica gale* (hazel/bog myrtle) (Moore et al., 1991). *P. sylvestris* stomata were identified on pollen slides following Sweeney (2004). The pollen sum consists of a minimum of 500 land pollen grains, excluding aquatics and spores (total land pollen: TLP), although total counts for 18 of the 79 samples were lower due to low pollen concentrations (minimum 322 TLP). Values are expressed as a percentage of TLP (for land pollen) or TLP + taxon/group (for spores). Microscopic charcoal fragments >10 μm were tallied on pollen slides. Selected percentage data for pollen and spores, and influx data for pollen, pine stomata and charcoal are presented (Fig. 2-3). Local pollen assemblage zones that group assemblages of similar composition were defined using CONISS (Grimm, 1987). To compare Migdale with the four other sites, percentage pollen data are shown for three main arboreal taxa (*Betula*, *Pinus*, *Quercus*) to examine changes in their relative abundance, while *Pinus* stomata and pollen influx data provide proxies for local growth and vegetative population biomass dynamics, respectively (Fig. 3) (Parshall, 1999; Seppä et al., 2009).

To improve chronological comparability, age models were produced for all five sites using the Intcal13 calibration curve and classical age-depth modelling techniques (CLAM) (Blaauw, 2010; Reimer et al., 2013). The Migdale chronology was constructed from twelve AMS radiocarbon dates (Table A3), with time-depth curves at the other four sites constructed from 6-10 radiocarbon dates (Table 1). Calendar ages (cal BP) are used throughout, where 0 cal BP = AD 1950.

Migdale data were analysed using principal components analysis (PCA) and rarefaction. The ordination displays changes in assemblage composition and stability through time. Surface pollen samples were included as passive samples in the fossil PCA to compare present and past assemblage composition (Fig. 4a). Gradient length in an initial detrended correspondence analysis was <2 SD, indicating that linear response models are appropriate. Only taxa with a value of ≥2 % in at least one sample were included to avoid rare types biasing the analysis. Data were recalculated to a sum of 100% and square-root transformed prior to analysis to stabilise variance. Ordinations were carried out in Canoco 4.5 (Ter Braak and Smilauer, 2002). Rarefaction analysis provides a robust measure of palynological richness (Birks et al., 2016). This was applied to all TLP pollen taxa and implemented in psimpoll 3.0 (Bennett, 1998) based on a rarefied sum of 300 TLP (Fig. 4b).

In the absence of a comprehensive Holocene palaeoclimate synthesis for Scotland, major shifts in temperature and/or moisture identified in northern Britain and north-west Europe are summarised in Fig. 3 to assess the effect of climate change on woodland dynamics (Anderson et al., 1998; Barber and Langdon 2007; Barber et al., 2013; Charman et al., 2006; Charman 2010; Seppä et al., 2009; Tipping et al., 2012). This draws on a range of palaeoclimate proxies, primarily humification, testate amoebae, chironomids, plant macrofossils and tree-ring widths.

3 Results and interpretation

3.1 Chronology

The age-depth models underpinning the chronology for each site are presented in Fig. A2. At all sites, the radiocarbon dates produced a conformable sequence, with no indications of sediment reworking or prolonged hiatuses in sediment accumulation. The age-depth plots indicate that sedimentation rates changed through time, likely as a result of a range of bathymetric, catchment and climatic factors that influence sediment accumulation. These changes are not discussed in any detail since our focus is on vegetation dynamics.

3.2 Migdale stand-scale succession and dynamics

Over the last 7790 years cal BP five phases of vegetation compositional stability and transition are identified from the pollen zonation (Fig. 2) and PCA analyses (Fig. 4a), as summarised in Table 2. Limited overlap between PCA phases indicates significant shifts in woodland composition, punctuated by periods of community stability. In brief, the local community was dominated by *Betula* and *Pinus* (7790-6000 cal BP), *Alnus* (alder) (6000-4400 cal BP), *Betula* (4400-600 cal BP), and then *Pinus* and *Betula* (600-0 cal BP, AD 2001). Palynological richness fluctuates largely below mean Holocene values until c. 4360 cal BP (Fig. 4b). Sustained higher palynological richness from c. 2290-670 cal BP coincides with higher pollen abundance for ruderal taxa. Richness values decline strongly to the present, as *Pinus* becomes the dominant pollen producer. Rarefaction values for surface samples overlap with subfossil values prior to c. 4360 cal BP (zone MIG1) and since 610 cal BP (zone MIG3), but, with one exception, are consistently below intervening values.

3.3 Regional range dynamics

Inter-sample variability in pollen diagrams, particularly at small sampling sites, is a product of taphonomy and vegetation dynamics immediately around the sampling site (e.g. stand-scale shifts in species distribution or abundance) with smaller contributions from regional pollen production (Bradshaw, 2013). To understand climatic influences on tree regeneration across a heterogeneous landscape, we focus on sustained trends as the basis for comparison, rather than finer-resolution variability likely to relate to gap-phase dynamics. Following rapid post-glacial climate amelioration after c. 11 700 cal BP, similar early Holocene woodland succession patterns are evident at Reidchalmai, Loch an Amair and Torran Beithe, where *Betula* expansion was followed by an increase in *Pinus* (Fig. 3). As pine pollen is widely dispersed, macrofossil and stomatal evidence is needed to securely differentiate local growth from regional pollen influx (Froyd, 2005). *Pinus* stomata are recorded at Loch an Amair from c. 9900 cal BP, with corresponding pine pollen abundance of only 1%, indicating small local populations which are difficult to identify from pollen data alone. There are insufficient sites with stomatal analyses to assess whether small populations were common before observed regional increases in pine pollen. Using 20-25% pollen as a conservative limit for inferring local growth (Bennett, 1984, 1995), pine populations were established by c. 8500 cal BP at Reidh-lochan and c. 7700 cal BP at Reidchalmai. After c. 7500 cal BP, pine percentages at Migdale are higher than neighbouring catchments and comparable with values at the regional sites until c. 6000 cal BP. Although stomata are absent from the sedimentary sequence, this could suggest pine growth at Migdale.

With the exception of Loch an Amair, *Pinus* abundance falls below ~20% by c. 6300-6000 cal BP, coinciding with percentage and influx increases in deciduous taxa, particularly *Alnus* and *Quercus*. *Alnus* values are highest at Migdale, indicating localised or dispersed growth at the other sites (Bennett and Birks, 1990; Froyd & Bennett, 2006; Tipping & McCulloch, 2003). *Quercus* values reach the 2% TLP level thought to indicate local growth by c. 8000 cal BP (Huntley and Birks, 1983). Although similar values are not recorded at Migdale until c. 5700 cal BP, only at this site do values exceed 10%, which suggests that oak was a significant vegetation component at c. 4900-4770 cal BP (Huntley and Birks, 1983). This overlaps with increased pine representation at Migdale, Reidchalmai and Torran Beithe from c. 5100-4100 cal BP. Sustained reductions in *Pinus* are recorded at all sites except Loch an Amair from c. 4600-4100 cal BP, although pine stomata persist at some sites after c. 4100 cal BP, suggesting that small populations remained around sites with (Torran Beithe) and without (Reidh-lochan) a pronounced pine decline until c. 3200-2600 cal BP.

Two mid-late Holocene features differentiate Migdale from the other sites: (1) the marked rise in *Betula* values after c. 4400 cal BP contrasts with relative continuity of pine at Loch an Amair and birch at Reidchalmai, and (2) the strong rise in influx and percentage *Pinus* values from c. 1180 cal BP is absent from the other sites. The increase in pine influx at Reidchalmai from c. 1340 cal BP likely reflects complex fluvial inputs and is not a species-specific response (Tipping and McCulloch, 2003).

4 Discussion

4.1 Microclimate effects on woodland biogeography, turnover and resilience

We identify three inter-related factors that influenced woodland persistence: regional climate gradients, landscape-scale topographic and altitudinal factors, and microclimate heterogeneity (that is, variability within each pollen catchment). While woodland dynamics were shaped by time-transgressive changes associated with postglacial population colonisation and succession, and regional synchronisation due to climate change, the outcomes were spatially variable as a result of finer-scale topoclimatic heterogeneity. *Pinus* was an early canopy dominant or co-dominant across the Highlands, but variations in pollen abundance over time and among sites indicate climatic and local constraints on population distribution. The pine population appears to have been discontinuous around Migdale, with low representation in upland and valley settings (Reidh-lochan, Reidchalmai), a persistent early decline at Reidh-lochan from c. 7200 cal BP, and higher values at Migdale and in nearby upland sites at Loch Farlary and Achany Glen (Fig. 1) (Smith, 1996; Tipping et al., 2008b). On a national scale, pine became increasingly restricted to upland habitats from c. 8200 cal BP (Bennett, 1984), but even here it is likely to have faced constraints. Independent peat stratigraphic and radiocarbon data indicate the spread of blanket peat before 6000 cal BP and pollen data show the spread of birch, both of which are likely to have constrained pine growth, particularly near northern range edges (Carlisle and Brown, 1968; Gallego-Sala et al., 2016; Tipping, 2008). Although the rate of spread and pollen abundance of *Quercus* declined as it reached its northern climatic and altitudinal limits, higher pollen frequencies around the Highland fringes suggest that populations were established in sheltered, lower-lying locations (Tipping, 1994). This restricted the realised niche of pine in sheltered valleys at Migdale, Reidchalmai and Achany Glen from c. 6000 cal BP (Smith, 1996).

Numerous studies note a correspondence between reductions in pine representation and shifts to wetter climatic conditions, based on independent reconstructions of lake levels and peatland watertables (Anderson et al., 1998; Bridge et al., 1990). Regeneration in marginalised pine populations thus appears to have been synchronised at a regional scale by climate change, but the mechanism of population regulation varied. In the uplands, wetter conditions may have reduced pine regeneration, indicated by declining pollen and macrofossil abundances c. 6500-6000 cal BP (Bridge et al., 1990). At lower altitudes, wetter climate may have contributed to a rise in water-tables which allowed *Alnus* to outcompete *Pinus* in valley mires like Migdale (Bennett and Birks, 1990). This combination of climatic, recruitment and competition effects led to extinction-recolonization dynamics in pine. This is particularly evident during the mid-Holocene, when macrofossil evidence indicates that pine expanded its range northward around 5400-4200 cal BP in response to lower peatland water-tables (Gear and Huntley, 1991). Stomatal evidence for renewed growth at Reidh-lochan and Loch Farlary (Tipping et al., 2008b) contrasts with a weak pollen influx response and absence of stomata at Migdale (Fig. 3). This suggests that pine colonised drier upland peat surfaces, but gained little advantage in valleys where peat was limited and pine remained subject to competitive exclusion by deciduous taxa and possibly by human impacts.

Anthropogenic disturbance may have selectively advantaged deciduous taxa in sheltered settings. Migdale is differentiated from the other sites after c. 5700 cal BP by late expansion and unusually high representation of *Quercus* compared with adjacent valleys and regional trends (Fig. 3). Neolithic farming and selective management is considered causal, inferred from a temporary rise in Poaceae and the occurrence of cereal type and *Rumex* (dock) pollen, with similar disturbance recorded in nearby valleys at Reidchalmai and Achany Glen from c. 5600 cal BP (Smith, 1996). Increased light penetration and managed browsing may have allowed oak to replace shorter-lived deciduous trees and shrubs, although disturbance was probably low intensity since woodland cover was maintained. Drier/warmer climatic conditions during this period could have increased the rate of oak growth in this favourable microclimate setting.

Stronger inter-site contrasts emerge during the mid-Holocene, with extensive loss of upland pinewoods and fragmentary woodland survival in upland and low-lying catchments (Fig. 3). Climate deterioration, particularly increased wetness, is considered to be a key driver of pine dieback at a regional scale, but the spatial differentiation of relict tree cover into upland pine (Loch an Amair) and broadleaved valley woods (Migdale, Reidchalmai) indicates the need for more complex explanatory mechanisms than rising water tables alone, particularly in low-lying areas with limited peat cover (Bennett, 1995). Steeper slopes, unsuited to blanket peat expansion, and a less oceanic climate may explain *Pinus* survival around Loch an Amair and in the northeast, respectively (Froyd and Bennett, 2006; Tipping, 1994). At Migdale, potential drivers of the transition from alder to birch-dominated woods around 4430 cal BP include poorly understood aspects of climate change like seasonality, which may have created conditions suited to birch growth, rather than persistently humid conditions that previously favoured alder (McVean, 1956). Climate deterioration may also have altered competition outcomes, contributing to reduced recruitment and competitive ability in oak and allowing birch to replace it, as occurs now near oak range limits (Atkinson, 1992; Jeffers et al., 2015). Locally increased anthropogenic disturbance from c. 4800 cal BP could have favoured birch over alder (Barthelmes et al., 2010). At all sites in this study where woodland survived the mid-Holocene ‘collapse’, regeneration persisted through subsequent anthropogenic activity. This suggests modest or managed disturbance, and that woodland regeneration was not near a critical threshold (cf. Scheffer et al., 2012).

The current mosaic of pine- and oakwoods and open communities that differentiates Ledmore and Migdale NNR from other ‘ancient’ woodland fragments emerged during the last c. 1000 years. Pine re-expansion takes place in the context of regionally low pine abundance across the northwest. It is not possible to disprove the survival of some individuals at Migdale throughout the Holocene, but low pine pollen values (<7%) at Reidchalmai and Reidh-lochan suggest that there were no sizeable populations at or around Migdale from c. 4170-1180 cal BP, particularly after c. 3330-2600 cal BP when stomata disappear from upland pine decline sites. The replacement of deciduous taxa, apart from birch, by pine after 1060 cal BP and a decline in herbaceous diversity at c. 620 cal BP are interpreted as indicators of silvicultural management, with deliberate selection for pine, probably by planting (Mills and Crone, 2012). Pine abundance had increased further by the nineteenth century, indicated by the presence of fossil fuel-derived spheroidal carbonaceous particles (SCPs) (Rose and Appleby, 2005). This corresponds with local and regional evidence of intensive timber management (Bangor-Jones, 2002; Rydval et al., 2015). This shift represents the decoupling of pine dynamics from climate fluctuations that previously governed local and regional population fluxes and stand composition.

4.2 Microclimate buffering and management implications for *Pinus sylvestris*

Migdale represents a rare example of continuous deciduous-coniferous woodland cover from the early Holocene through to the present, possibly owing to comparative shelter from westerly climate systems. This provided a favourable microclimate which allowed woods to withstand multiple climate and disturbance shifts. Uneven topography and varied drainage also may have made the site less suited to farming, which remains a feature of the wider valley floor at Reidchalmai. This is good news for conservation. Although canopy cover was maintained as a result of favourable growing conditions and limited farming, community composition was far from stable. In terms of management, woodland resilience therefore depends on allowing composition to adapt to changing conditions and on appropriate ecological models for anticipating change. Community replacement and reassembly in the last c. 1000 years has created floristic affinities between Migdale and long-established pinewoods, overriding earlier similarity with deciduous fragments in similar low-lying valleys. Pinewood communities thus provide an inappropriate model for anticipating change at this site. Challenging existing ecological models and allowing adaptive ecological responses introduces uncertainties that may conflict with conservation targets, like the desire to conserve the distinctive biodiversity of these woodlands (Hiers et al., 2016; Woodland Trust Scotland, 2015). In view of the uncertainties surrounding climate change, long-term evidence emphasises the importance of shifting conservation and management focus from compositional stability to functional viability.

While the microclimate at Migdale buffered woodlands against environmental change and mature trees around the site demonstrate that conditions are suitable for pine growth, the ecological history of this site suggests that continued community change is highly likely and, over the longer term, local pine populations are probably transient. The transition to pine dominance from c. 1060 cal BP has resulted in a prolonged decline in diversity and the existing pine-dominated stand may still be in a state of flux, characterised by high levels of compositional change more typical of the early Holocene (Fig. 4) (Froyd and Bennett, 2006; Seddon et al., 2015; Tipping et al., 2006). Predicted future milder climatic conditions may allow broadleaved species like birch, oak and rowan to expand, thus replaying the successional replacement of pine seen at all except marginal, peat-dominated sites over the course of the Holocene. Birch is also likely to increase due to more wind disturbance (Ray, 2008); this is a potential outcome of recent storm damage to pines around Loch Migdale. Scattered pines occur on blanket peat in higher areas of the NNR and sheltered valleys like Migdale may continue to act as seed sources for tree colonisation in adjacent upland areas if environmental conditions, deer numbers and cultural preferences allow.

In terms of diversity baselines, current palynological richness across the NNR is low relative to values during Iron Age and Dark Age settlement periods (c. 2290-670 cal BP) and comparable with the early Holocene range of variability (Fig. 4b). High diversity during the woodland grazing period indicates the potential benefits of small-scale, low intensity intervention. It also suggests that the current strategy of thinning planted woods to stimulate natural regeneration could benefit diversity in longer-established stands. Both the early and late Holocene periods of lower diversity correspond with unstable, possibly transitional, assemblages. This emphasises the need for managers to anticipate and manage for change. Surface sample ordination scores indicate high spatial diversity across the NNR (Fig. 4a) and, using space-for-time substitution, this suggests that maintaining spatial heterogeneity across the site, which is one of the current management goals, can help support a dynamic mosaic.

The relatively recent origins of the pinewood raise questions about the diagnostic value of the ‘ancient pinewood indicators’ present at the site (Whittet and Ellis, 2013). It appears that continuous canopy cover, rather than the persistence of pine per se, helped maintain distinctive understorey diversity by ensuring the availability of humid, shaded microclimates within the NNR (Bradshaw et al., 2015). While debate continues over the biodiversity and ecosystem service benefits of planted versus native coniferous woodland (Quine and Humphrey, 2010), these findings support existing evidence that semi-native woods of uncertain origin and planted ancient woodland sites are useful in conservation (Roche et al., 2015). Therefore, maintaining distinctive biodiversity seems compatible with accommodating change in canopy dominants, as long as woodland cover is maintained and community reorganisation is expected and accepted as an essential attribute of resilience.

5.0 Conclusions

Palaeoecological evidence from a currently diverse woodland in a sheltered valley on the northern range limits for pine and oak in Scotland demonstrates that communities within favourable microclimate locations show greater continuity of canopy cover and resilience to climate change than upland catchments, but have undergone significant compositional turnover. The suggestion that microclimate variability arising from biophysical heterogeneity promotes more stable plant communities (Keppel et al., 2012; Maclean et al., 2014) is, therefore, only supported if stability is measured in terms of the continuity of woodland cover; it is not true for composition. Continuity of cover allowed ‘ancient’ woodland indicator taxa to persist despite changes in canopy composition. Favourable microclimatic conditions and topographic variability conferred low suitability for agriculture and buffered tree populations against climatic shifts. However, prior to late Holocene silvicultural intervention, sheltered conditions mitigated against the survival of pine, which may have been out-competed by deciduous taxa. This highlights the need for more data and alternative models of community composition and behaviour to inform ecological understanding and management of microrefugia communities. Further work is also needed to characterise and map the distribution of favourable long-term microclimates at a landscape-scale in order to understand how they influence ecological responses to changing climate and land-use mosaics over long timescales (Valencia et al., 2016). This will enable palaeoecology to contribute more directly to predictive ecology and climate change conservation strategies by helping to evaluate the likely effectiveness of protected areas under changing climate regimes (Hannah et al., 2002; Lindbladh et al., 2013).

6.0 Acknowledgements

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7.0 References

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Table 1. Location, current vegetation and comparative characteristics for all study sites

Site	Description
Migdale pinewood, Ledmore & Migdale NNR	**Main study site** **Location**: 4°15'22" W 57°53'14" N, 40 m OD **Sampling site**: valley mire edge **Current vegetation**: *Betula* with mire understorey and *P. sylvestris* and *Quercus* within 100 m **Current climate**: <14 °C July mean temperature but immediately N of 14-15 °C limit, on boundary between <750 mm and 750-1000 mm annual rainfall, comparable index of oceanicity (mean wet days/monthly mean temperature range) to Reidchalmai, Reidh-lochan and Loch an Amair (Averis et al., 2004) **Chronology**: 12 AMS ^{14}C dates
Reidchalmai, east Sutherland	**Comparison**: neighbouring low altitude, valley floor catchment with deciduous woodland **Location**: 4°9'1" W 58°0'12" N, 90 m OD **Sampling site**: small infilled lake basin, 80-90 m diameter **Current vegetation:** improved pastoral grassland within heather moorland with *Betula*-dominated woods to south **Current climate**: <14 °C July mean temperature, 750-1000 mm annual rainfall, comparable index of oceanicity to Migdale and Reidh-lochan **Chronology**: 10 AMS ^{14}C dates **Sources**: Tipping & McCulloch 2003, Tipping et al. 2008b
Reidh-lochan, east Sutherland	**Comparison**: neighbouring upland catchment, treeless **Location**: 4°07'26" W 58°02'13" N, 160 m OD **Sampling site**: small lake, c.100 m diameter **Current vegetation**: extensive blanket mire, agriculture to the east **Current climate**: as Reidchalmai **Chronology**: 6 bulk ^{14}C dates **Sources**: Froyd 2001, Froyd & Bennett 2006
Loch an Amair, East Glen Affric	**Comparison**: example of upland pinewood continuity **Location**: 4°53'25" W 57°17'20" N, 315 m OD **Sampling site**: small lake, c.100 m diameter **Current vegetation**: non-native *Pinus contorta* plantation with *P. sylvestris* woodland to north **Current climate**: <14 °C July mean temperature but immediately N of 14-15 °C limit, >1500 mm annual rainfall, comparable index of oceanicity to Migdale, Reidchalmai and Reidh-lochan **Chronology**: 7 bulk ^{14}C dates **Sources**: Froyd 2001, Froyd & Bennett 2006
Torran Beithe, West Glen Affric	**Comparison**: example of upland pinewood contraction **Location**: 5°6'2" W 57° 14'29" N, 265 m OD **Sampling site**: peat-filled bedrock basin, c.56 m surface diameter **Current vegetation**: blanket mire **Current climate**: <14 °C July mean temperature, >1500 mm annual rainfall, higher index of oceanicity than the other four sites **Chronology**: 9 AMS ^{14}C dates **Sources**: Davies 1999, Tipping et al. 2006

Table 2. Summary of Migdale stand dynamics based on pollen assemblage zones and ordination (PCA) phases. See Fig for ordination plot

Pollen assemblage zone and age	Palynological characteristics	C
MIG3: 610-0 cal BP (AD 2001)	Renewed expansion of *Betula*, marked rise in *Pinus*, very low values for *Quercus*, *Alnus* and *Corylus*, *Myrica*, *Calluna* and fern values decline, and herbaceous pollen abundance and diversity is reduced. Low charcoal values. Spheroidal carbonaceous particles indicative of fossil fuel burning post-c. AD 1850 occur from 12 cm; extrapolated date of 310 cal BP (AD 1640) using ^{14}C-derived chronology appears too old, likely due to lower decomposition and compaction in upper sediments above youngest radiocarbon date	P *P* sp tr
MIG2b: 2230-610 cal BP	Differentiated from zone MIG2a by lower arboreal pollen sums and increased abundance of mire taxa (*Calluna*, *Myrica*, *Sphagnum* and *Erica*). Higher *Pinus* percentage and influx values, especially from 1090 cal BP. More abundant disturbance indicators and cereal type pollen (*P. lanceolata*, *Potentilla*-type, Asteraceae and *Rumex*). Charcoal values rise. More minerogenic peat with fine sand and silt at c. 2120-1790 cal BP	W zo in p
MIG2a: 4430-2230 cal BP	Shift to *Betula* dominance with reductions in the other arboreal taxa, particularly *Pinus* and *Alnus*. *Sorbus* and *Salix* are the main exceptions. *Myrica gale*-type is more abundant, along with *Hordeum* group, *Plantago lanceolata*, *Potentilla*-type and other herbaceous pollen types. Reduced frequencies for *Pteridium* and Pteropsida spores	P q
MIG1b: 5940-4430 cal BP	High *Alnus* percentage and influx values, peaking around 5130-5050 cal BP, with secondary peaks at c. 5580 cal BP and 4750-4650 cal BP. High total pollen influx and more rapid peat accumulation. Subsequent alder reduction corresponds with increases in *Betula*, *Pinus* and *Corylus* (5580-5160 cal BP), then *Quercus* and Poaceae (5020-4770 cal BP). Maximum *Quercus* abundance from 5020-4700 cal BP. Short-lived percentage and influx increased in *Pinus* values from c. 4840-4600 cal BP. *Hordeum* group pollen is recorded more frequently from 4800 cal BP	O st
MIG1a: 7790-5940 cal BP	High but erratic values for *P. sylvestris* and *Betula*, rising *Alnus* frequencies, increased in *Quercus* relative and influx values late in zone, *Salix* and *Calluna* values decline. High representation for Pteropsida and *Pteridium aquilinum* spores. Peak charcoal values	P cl sc

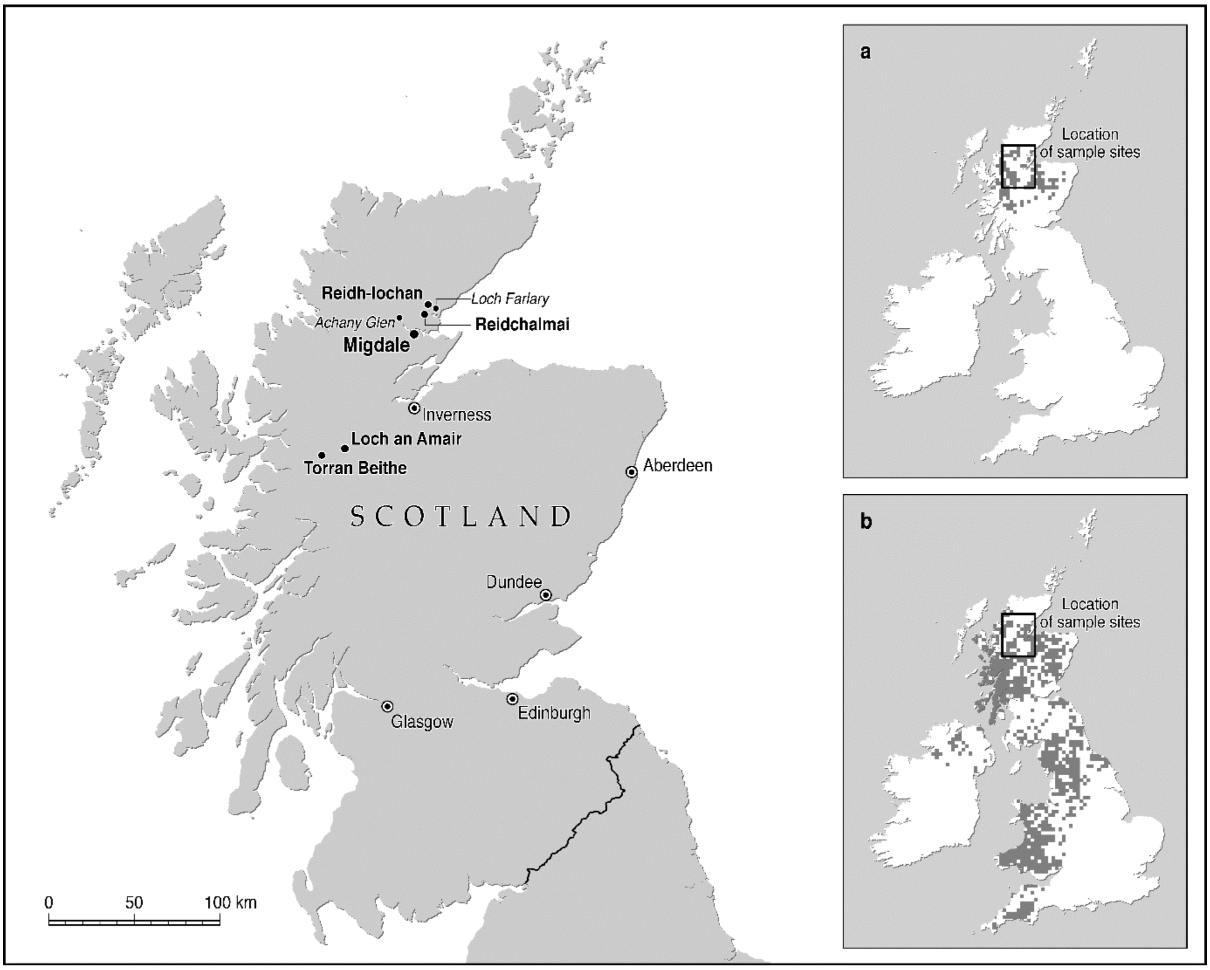

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Figure 1. Locations of study sites in northern Scotland, with other pollen studies mentioned in text and current range limits of (a) Caledonian pine forest and (b) old sessile oak woods with *Ilex* and *Blechnum* in UK (not mapped in Republic of Ireland) (source: JNCC)

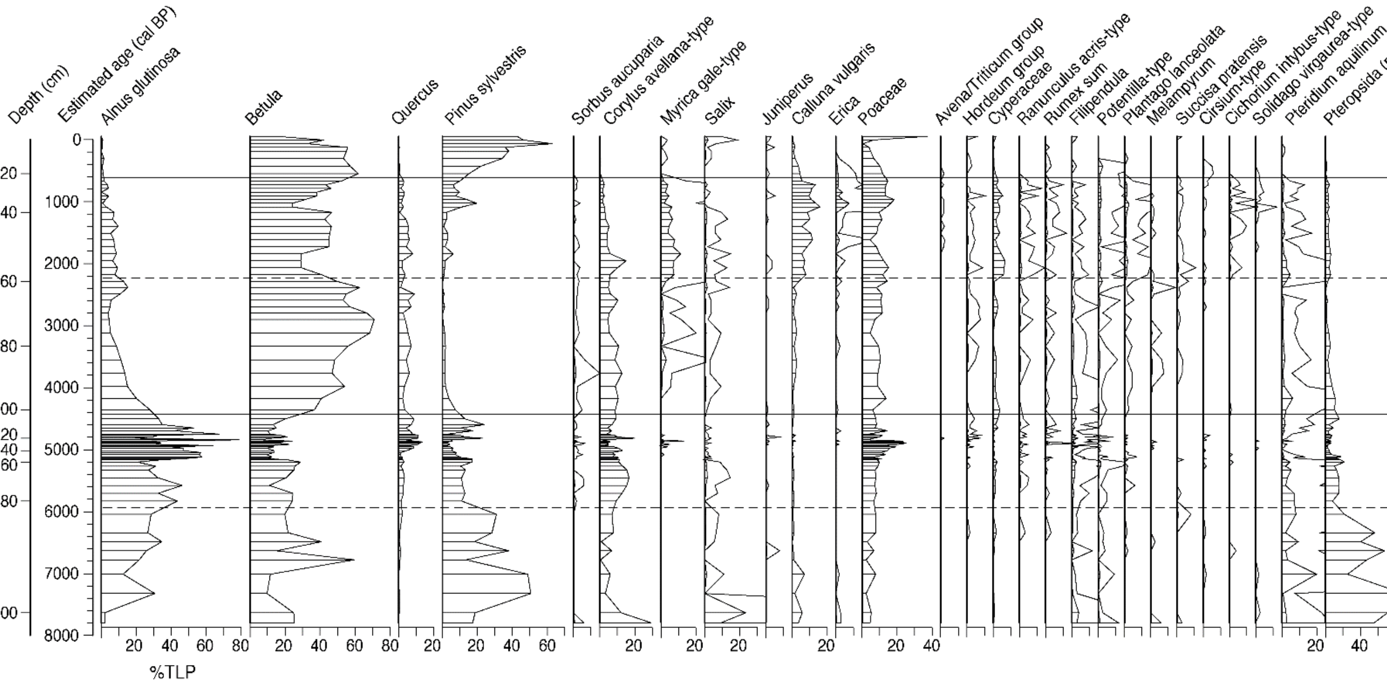

Figure 2. Selected percentage pollen and spore data from Migdale, with influx data for charcoal and spheroidal carbo exaggeration curve x10

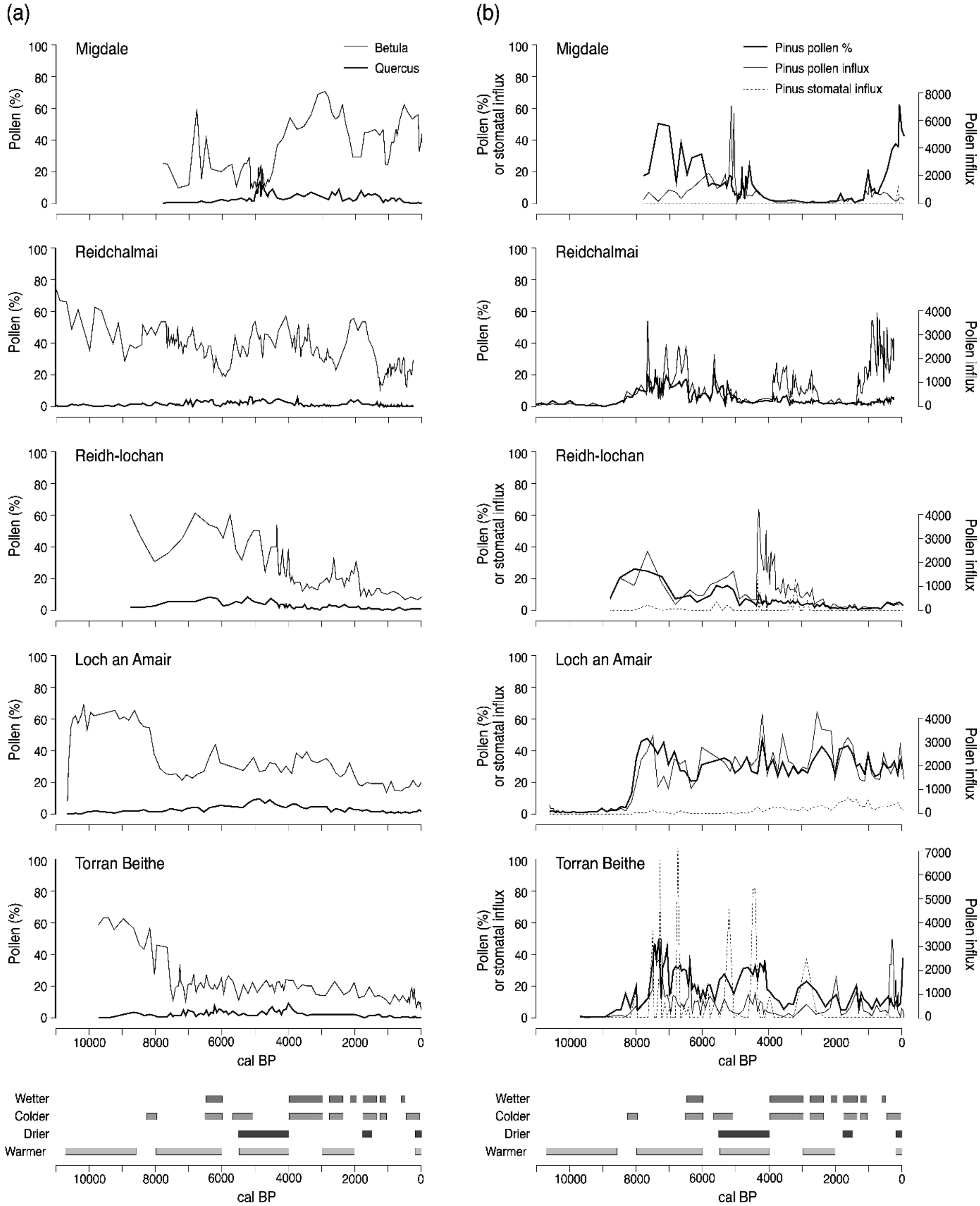

Figure 3. Comparison of data from Migdale, Reidchalmai, Reidh-lochan, Loch an Amair and Torran Beithe, showing (a) percentage data (%TLP) for *Betula* and *Quercus* and (b) percentage (%TLP) and influx (pollen grains or stomata cm^{-2} yr^{-1}) data for *Pinus* pollen and stomata (stomata unavailable for Reidchalmai), with a qualitative summary of the main climate shifts (see text for references)

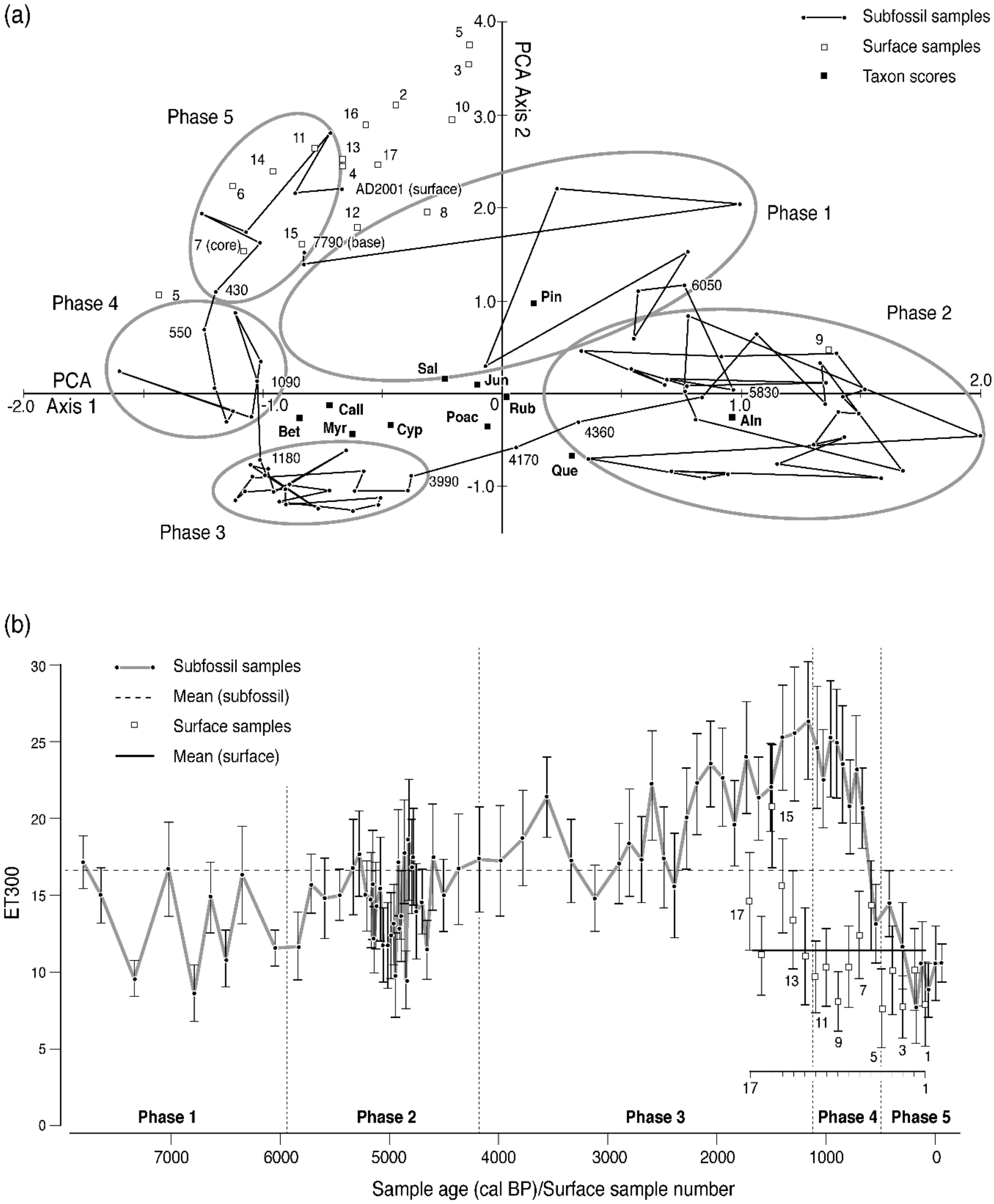

Figure 4. (a) Principal components analysis and (b) palynological richness data for Migdale with 95% confidence intervals, both showing five main communities (phases). Surface samples (1-17) passively ordinated on PCA and plotted against fossil rarefaction values. Taxon abbreviations: Aln – *Alnus*, Bet – *Betula*, Call – *Calluna vulgaris*, Cyp – Cyperaceae, Myr – *Myrica gale*-type, Pin – *Pinus sylvestyris*, Poac – Poaceae, Que – *Quercus*, Rub – Rubiaceae. The first and second principal components (eigenvalues) account for 51.1% and 26.6% of the variance, respectively


(a)
(b)
Migdale
Betula
Quercus
Pinus pollen %
Pinus pollen influx
Pinus stomatal influx
Reidchalmai
Reidh-lochan
Loch an Amair
Torran Beithe
Pollen (%)
Pollen (%) or stomatal influx
Pollen influx
100
80
60
40
20
0
8000
6000
4000
2000
0
10000
8000
6000
4000
2000
0
cal BP
Wetter
Colder
Drier
Warmer

Table A2. Sediment description of peat core from Migdale

Depth (cm)	**Description**
0-10	Unhumified, elastic, yellow *Sphagnum* peat with possible *Betula* seeds; Tb4 Dh+
10-17	*Sphagnum* peat, increasingly less humified up the sequence; Tb3/4 Sh1
17-21	*Sphagnum* peat, gradual upper boundary to less humified peat; Tb3 Sh1 Th+
21-36	Gradual lower boundary to darker, more amorphous peat, with monocotyledon leaves, roots and some mineral matter; Ag+ Ga+ Gs+ Dl+ Dh1 Tb+ Th1 Sh2
36-51	Slightly sticky, minerogenic peat; Ag+/1 Ga1 Gs+ Dh1 Th+ Sh1
51-57	Inwash band in peat; Ag+ Ga1/2 Gs+ Dl1 Dh1 Th1 Sh1
57-81	Slightly lighter brown, crumbly herbaceous peat with mineral component; Ag+ Ga1 Gs+ Dl+/1 Dh2 Th1 Sh1
81-110	More amorphous peat with less herbaceous material and higher mineral content; Ag+ Ga+/1 Dl+ Dh1 Th1 Sh1/2
110-131	Gradual change to more elastic herbaceous peat with slight mineral matter; Ag+ Ga+ Dl+/1 Dh1/2 Th1 Sh1
131-150	Gradual upper boundary to quite crumbly herbaceous peat with wood fragments and twigs, less amorphous with no mineral matter, wood decreasing up profile; Dl1 Dh1 Th1 Sh1
150-170	Less wood, slightly less amorphous than below with rare coarse sand (to 2 mm) and mineral matter, with fine roots; Ag+ Ga+ Gs+ Dh1 Th1 Sh2
170-188	More amorphous and woody, including large fragments, especially at 182-185 cm; Dl1Dh1Th+Sh2
188-198	Dark/black herbaceous peat with abundant monocot leaf fragments, possible *Phragmites* at 192-193 cm, and small wood fragments; Dl+ Dh2 Sh2
198-201	Amorphous peat with monocot leaf fragments and wood, slight mineral component near base but no visible stratigraphic change from underlying sediment; Gs+ Dl+/1 Dh2 Sh2
201-202	Dark/black amorphous peat with plant fragments and silt at very base; Ag+/1 Dh2 Sh2

Table A3. AMS radiocarbon ages for bulk sediment samples from Migdale: calibrated age represents median probability derived from Intcal13, rounded to the nearest 10 years

Laboratory code	Depth (cm)	^{14}C age (BP)	Cal. BP age	Δ^{13}C (‰)
SUERC-1950	39-38.5	1189 ± 25	1120	-28.8
Beta-170445	58.5-59	2220 ± 40	2230	-28.1
SUERC-1948	71-70.5	2761 ± 24	2850	-28.9
SUERC-1947	92-91.5	3654 ± 29	3970	-29.3
SUERC-1946	102-101.5	3971 ± 29	4450	-28.9
SUERC-1944	114-113.5	4209 ± 27	4740	-28.8
SUERC-1943	122-121.5	4262 ± 30	4840	-30.0
SUERC-1942	140-139.5	4432 ± 31	5020	-29.0
SUERC-1941	159-158.5	4497 ± 29	5170	-29.0
SUERC-1937	182-181.5	5148 ± 30	5910	-28.6
SUERC-1936	195-194.5	6014 ± 33	6860	-28.2
Beta-162640	201.5-200.5	7040 ± 60	7870	-28.5

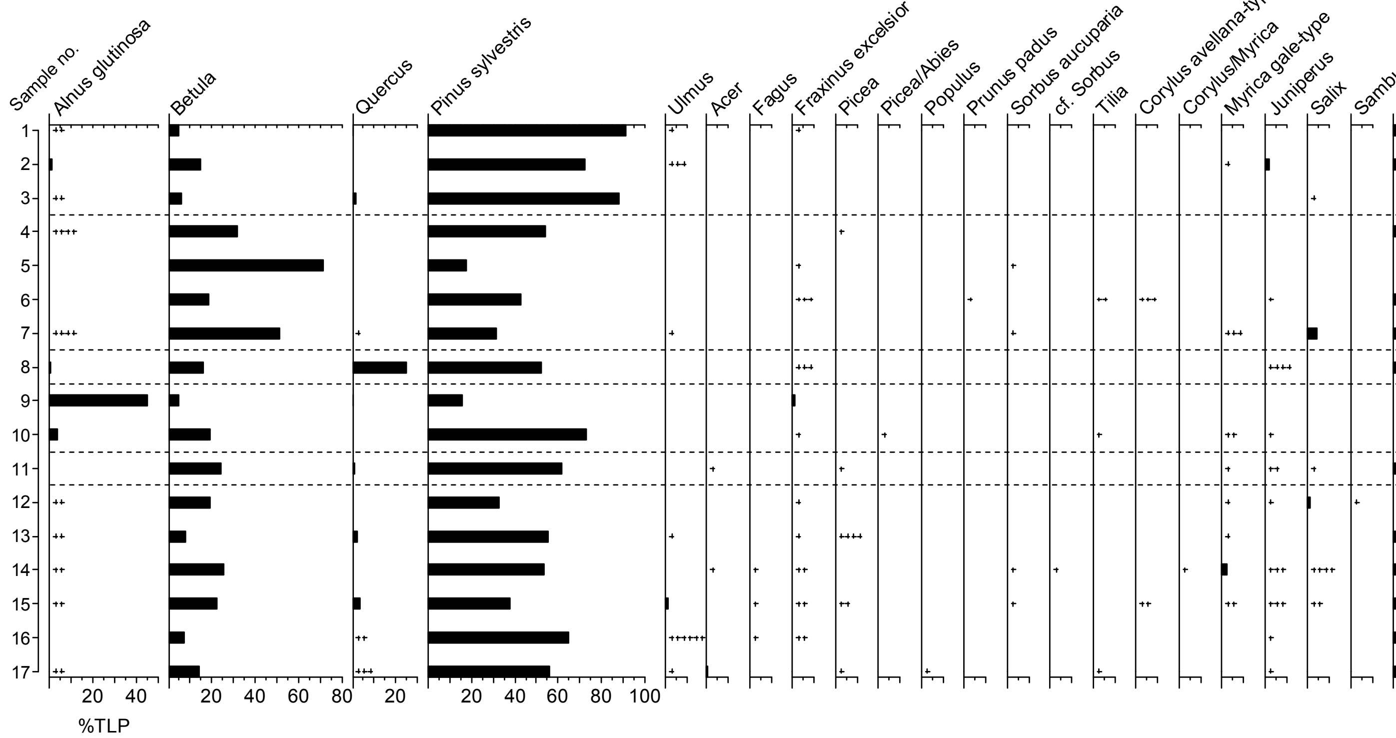

Figure A1. Surface pollen sample results from Ledmore and Midgale NNR. See Table A1 for information on vegetation
symbols refer to numbers of pollen grains where these are less than 2% of total land pollen (%TLP) and improve legib

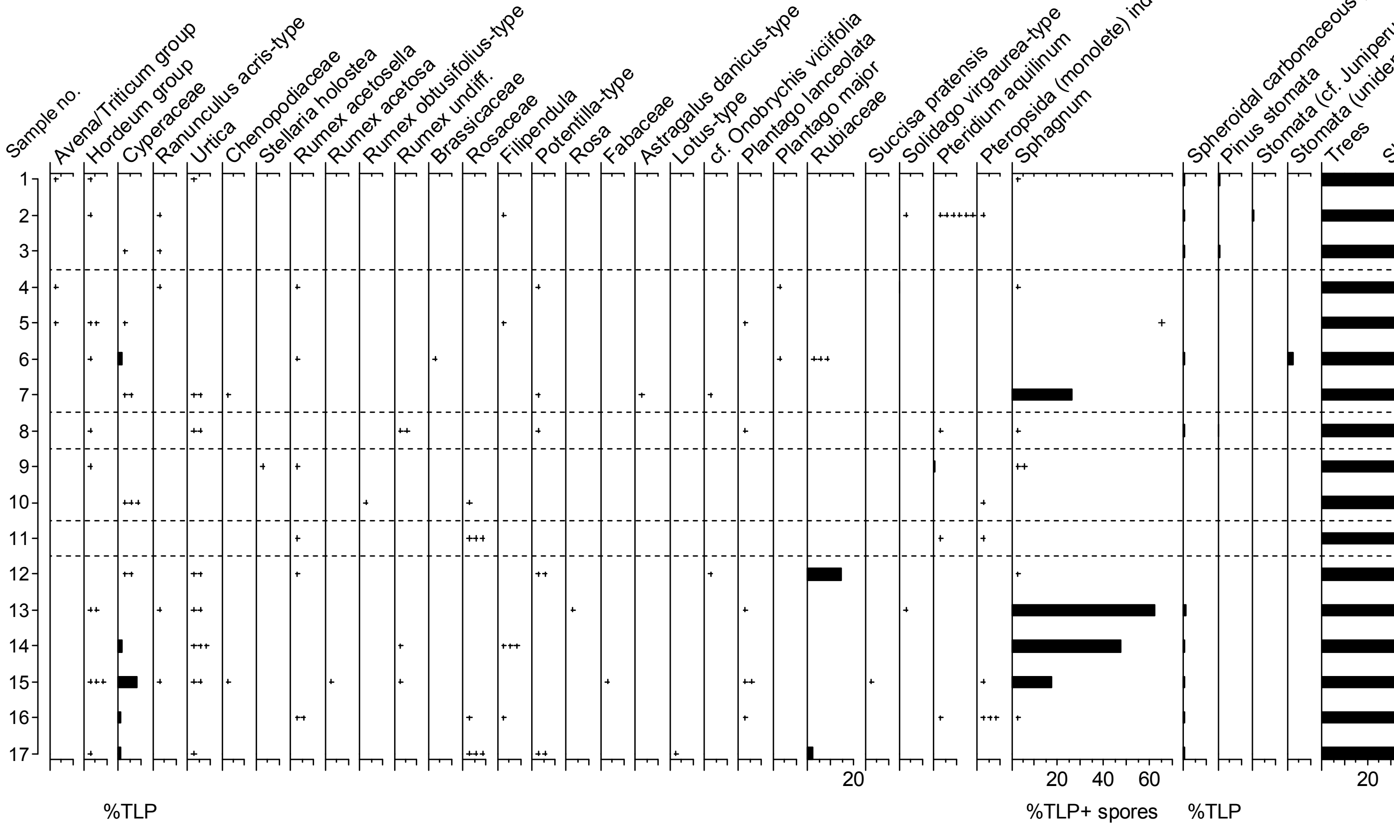

Fig A1 (continued)

Table A1. Surface pollen sites at Ledmore and Migdale National Nature Reserve

Four samples of mosses forming the ground cover were taken randomly from within a 2m x 2m quadrat at each sample site. These were sealed in plastic bags and stored at 4^{o}C in the laboratory prior to processing to extract pollen representing surrounding vegetation communities. Main canopy, shrub and dominant herb species were recorded within 100 m of each quadrat to identify the corresponding National Vegetation Classification (NVC) community (Rodwell, 1991a, b, 1992)

Sample	**Location and dominant vegetation within c.100 m**
1	Relatively even aged stand of *Pinus sylvestris* (4°16'19" W 57°53'7" N). Infrequent *Betula*, Sorbus aucuparia and *Quercus* within 100m. Shrub and ground flora dominated by ericoid shrubs, with some Vaccinium myrtillus. Relatively low diversity of herbaceous species. NVC: W18a
2	*P. sylvestris* dominated canopy, less even-aged stand and more open canopy than site 1 (4°16'3" W 57°53'3" N). *Betula*, *Populus*, *Alnus*, *Sorbus* and *Ilex* within 100m. Shrub layer dominated by ericoid shrubs, *V. myrtillus*, *V. vitis-idaea* and *Juniperus communis*. NVC: W18b
3	Higher up slope than site 7 (4°17'18" W 57°53'16" N). Relatively open *Pinus* canopy, with scattered *Betula* and *Sorbus*. *Juniperus*, *Calluna* and *V. myrtillus* dominant species in understory. *Quercus* within 100m downslope of sample site. NVC: W18b
4	Upslope from shore of Loch Migdale (4°16'20" W 57°53'3" N). *Betula* dominated, mainly young saplings, with one ‘granny’ pine within 10m of sample site. *Salix caprea*, *Sorbus*, *Populus* and *Quercus* within 100m. Ground flora dominated by grasses, sedges and Pteridium, with frequent bryophytes. *Calluna* and *V. myrtillus* scattered but infrequent. NVC: W4 but open canopy, therefore ground flora typical of U20b
5	Sample site above path and *Betula* stand with some *Populus*, occasional *Fraxinus*, *Sorbus* and *Salix* sp. (4°16'22" W 57°53'4" N). *Pinus* dominant within 100m. Ground flora mainly grasses, *Cerastium*, *Galium*, *Anemone nemorosa*, bryophytes and sedges, with infrequent *Pteridium*. NVC: W4b, but with ground flora more typical of U20a
6	On north slope above valley mire (4°14'28" W 57°53'21" N). *Betula* regeneration dominant with some *Pinus* regeneration. *Calluna* dominant shrub. NVC: H10a
7	**Peat core site** (4°15'22" W 57°53'14" N). *Betula* dominant mature tree immediately around site with some *S. caprea*. *Pinus*, *Sorbus* and *Quercus* growing within 100m. Shrub and herb layer dominated by *Myrica gale*, rare *Calluna*, grasses, sedges and *Sphagnum*. NVC: M19a
8	North side of Loch Migdale, on steep slope (4°17'23" W 57°53'14" N). Mature tree canopy of *Quercus* and *Pinus*, with scattered *Betula*, *Populus* and *Sorbus* within 100m. Shrub layer of *Juniperus*, *Ilex*, *V. myrtillus*, *Calluna* with some *V. vitis-idaea*. NVC: Varying between W17d and W18
9	*Alnus*-dominated stand at head of Loch Migdale (4°16'23" W 57°53'0" N), mostly mature trees. Isolated *Pinus* and stunted *Ilex*. *Fraxinus*, *Betula*, *Sorbus* and *Quercus* within 100 m. Ground flora mainly sedges and grasses with scattered *Calluna* and *V. myrtillus*. NVC: W7, but ground flora more closely resembles U20a
10	By Spinningdale Burn (4°15'17" W 57°53'4" N). *Alnus* immediately around sample site. *Pinus* woodland dominant within 100m. *Sorbus* and *Betula* present within 20m. Herb layer dominated by *Pteridium* and grass, with *V. myrtillus*. Low diversity of herbaceous species. NVC: U20a
11	Adjacent to road, within *Populus* stand, including scattered *Betula* and *Sorbus* (4°15'19" W 57°53'17" N). *Pinus* woodland within 100m. *V. myrtillus* and *Calluna* common, with grasses and bryophytes typical of drier conditions. NVC: W18b

12	Open glade by side of track (4°15'35" W 57°53'11" N). *Salix*, sapling *Betula*, *Rubus*, *Rosa*, *Ulex* and *Myrica*. Mature *Betula*, *Alnus* and *Pinus* within 100m. Ground flora dominated by grasses and mosses, with some *Pteridium* and reasonably diverse herbaceous taxa. NVC: U20b
13	Above/north of Ledmore oakwood (4°14'56" W 57°52'29" N). *Quercus* within 100m. Open heath with *Pinus* plantation within 100m. *Calluna* dominant with *Betula* and *Pinus* regeneration. NVC: H10a, H12a, M15b
14	Edge of valley mire (4°15'10" W 57°53'12" N). Scattered *Pinus* and *Betula* scrub regeneration. *Myrica*, *Salix*, *Calluna*, scattered *Juniperus*. Grasses, bryophytes and sedges dominant ground flora. NVC: M15a, M4, W4c
15	Recently burnt moorland, shallow blanket bog (4°13'53" W 57°53'11" N). *Betula* regeneration dominant, with *Pinus*. Ericoid shrubs with infrequent *V. myrtillus*. *Sphagnum* and sedges common in ground layer. NVC: H10a, M15b
16	Slope to south of valley mire (4°15'54" W 57°52'56" N). Open *Pteridium* dominated, with *Betula* regeneration and some *Pinus*. *Sorbus*, *Crataegus monogyna* and *Pinus* plantation within 100m. *V. myrtillus*, ericoid shrubs common, with grasses, bryophytes and reasonably diverse herbaceous layer. NVC: U20b
17	South valley side, above valley mire (4° 14' 52" W 57° 52' 59" N). *Pinus* and *Betula* regeneration dominate, but open canopy. Mature and degenerate *Calluna*, with grasses and herbaceous species including *Filipendula ulmaria*, *Prunella vulgaris* and *Primula*. Bryophytes common ground layer. *Juniperus* within 20m. NVC: H10a, W4c but scattered

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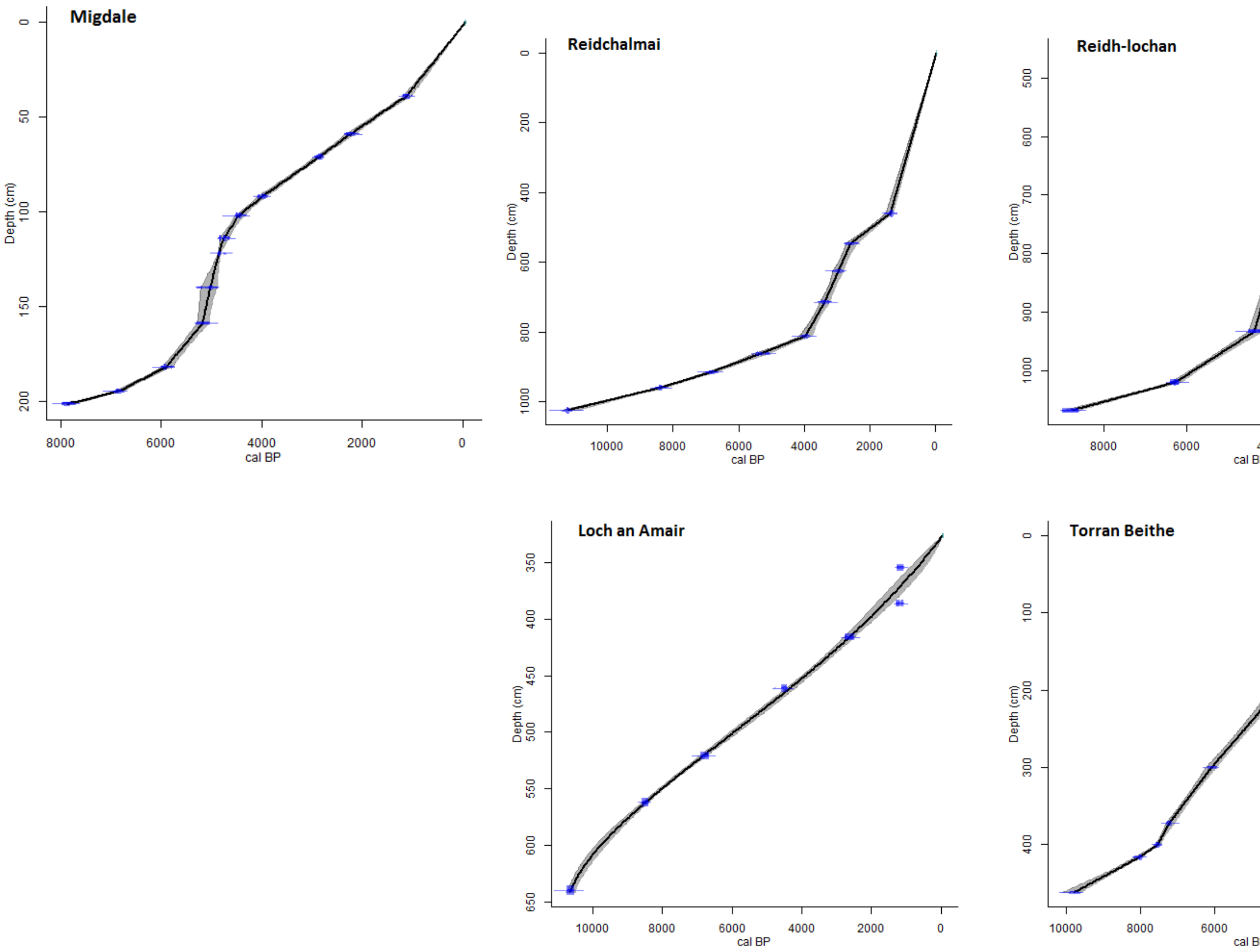

Figure A2. Age depth models for all study sites. Calculated using linear interpolation, except at Loch an Amair, where a fo
the best fit based on rapid accumulation between the two uppermost radiocarbon dates (Froyd & Bennett, 2006)