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The relative importance of biotic and abiotic processes for structuring plant communities through time

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Summary

1. The question of the relative importance of biotic interactions versus abiotic drivers for structuring plant communities is highly debated but largely unresolved. Here, we investigate the relative importance of mean July air temperature, nitrogen (N) availability and direct plant interactions in determining the millennial-scale population dynamics through the Holocene (10 700–5200 cal. years BP) for four temperate tree taxa in the Scottish Highlands.
2. A variety of dynamic population models were fitted to our palaeoecological time-series data to determine the mechanism(s) by which each driver affected the population biomass dynamics of *Betula* (birch), *Pinus* (pine), *Alnus* (alder) and *Quercus* (oak). Akaike information criterion weights identified the best model(s) for describing the relationship between each population and driver. The relative importance of these drivers was then assessed by the ability of each model to predict the observed population biomass dynamics. We also measured the change in goodness-of-fit of each model over time.
3. We found that models of intra- and interspecific plant interactions described the plant population dynamics better than temperature- or N-dependent population growth models over the 5000-year study period. The best-fitting models were constant over time for pine, alder and oak. However, the plant–N availability and plant–temperature models provided a progressively better fit to the birch data when temperatures rose and N availability declined, suggesting increasing importance of these abiotic factors coincident with changing conditions.
4. *Synthesis.* Multiple mechanistic models were applied to palaeoecological data to infer the most likely processes driving millennial-scale plant biomass dynamics in a woodland ecosystem. Direct plant interactions provided a better explanation for population biomass dynamics than growing season temperature or N availability over the full study period. The relative importance of all drivers we assessed here varied by species and – in the case of birch – over time in response to warming and reduced N availability.

Key-words: climate change, competition, determinants of plant community diversity and structure, drivers of change, facilitation, native pine woodland, palaeoecology, population and community dynamics, stable isotopes of nitrogen

Introduction

Plants are known to compete for light, nutrients and water. Interactions between (and within) plant species may control the abundance and diversity of plants within a community over short (Clark *et al.* 2011) and long (Blois *et al.* 2014) time scales and are expected to play an important role in mediating plant community responses to global climate change (Suttle, Thomsen & Power 2007; Williams, Blois & Shuman 2011). However, the extent to which these plant–plant interactions structure plant communities under a changing climate is as yet unclear (Agrawal *et al.* 2007). This knowledge gap limits the ability of predictive models to generate plausible community-scale responses to future changes.

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A variety of modelling-based approaches exist that can provide biologically realistic predictions of plant community dynamics given a pre-determined response by the component species (or groups of functionally similar species) to specific environmental changes. For example, ecophysiological models achieve this by simulating the processes that operate at the individual plant level (e.g. photosynthesis, nutrient uptake and direct plant interactions), their change over time with respect to extrinsic forcing factors (e.g. climate) and determining how these lead to changes in the relative abundance of each species (or functional group) within the community (e.g. SORTIE, Pacala *et al.* 1996 or LPJ-GUESS, Smith, Prentice & Sykes 2001). These spatially explicit, individual- or plant functional type-based models use existing knowledge of the physiology of plant species as a proxy for population-scale responses to environmental drivers (e.g. climate, competition, nutrients) and use these pre-determined response parameters to simulate expected changes in community composition given alternative environmental change scenarios.

Incorporating the effects of direct plant interactions into such models has been hindered by the fact that the outcomes of plant–plant interactions are highly context dependent (Miller 1994; Armas & Pugnaire 2005; Gross *et al.* 2009), which can lead to unique forms (i.e. competition or facilitation), intensity (i.e. the absolute changes in growth rate of individuals or populations) and importance (relative to the other factors driving population changes) of plant interactions in different environments (Bertness & Callaway 1994; Callaway *et al.* 2002; Brooker & Kikividze 2008). Furthermore, positive and negative interactions can occur simultaneously within the same system (Callaway 1995). Thus, efforts to develop generalized rules about the impact of plant interactions on population dynamics and community structure (Brooker 2006) are aimed at identifying consistent patterns in plant interaction outcomes across environmental gradients (Bertness & Callaway 1994; Michalet *et al.* 2006; Maestre *et al.* 2009) and understanding the context in which plant–plant interactions play the dominant role in structuring community composition (Lortie *et al.* 2004; Brooker 2006; Suttle, Thomsen & Power 2007; Gross *et al.* 2009). Key knowledge gaps that remain include the relative importance of plant interactions as compared to abiotic drivers (e.g. climate), how the importance varies between species (Soliveres, Torices & Maestre 2012) and over time (Clark *et al.* 2011) and how species-specific responses scale up to changes in community composition (Callaway & Walker 1997; Brooker 2006; Agrawal *et al.* 2007; Freckleton, Watkinson & Rees 2009).

There are a variety of mechanisms by which plant species interact; however, the outcomes typically involve a change in the abundance of individuals of one plant species in response to changes in the abundance of individuals of the same (intraspecific) or other (interspecific) species. The primary mechanisms of plant competition include exclusion of individuals due to interference (i.e. occupation of sites, Connell & Slatyer 1977) or resource exploitation (i.e. reduction of nutrients, Tilman 1990). In contrast, facilitation can occur when one plant provides protection to other plants from climatic or resource stress (Butterfield 2009). Each of these mechanisms reflects the *intensity* of the interaction, defined here as the changes in population-scale biomass as a result of direct interactions between plants (Grace 1991; Brooker & Kikividze 2008; Freckleton, Watkinson & Rees 2009). The *importance* of plant–plant interactions is measured in terms of the impact on population biomass dynamics relative to other factors such as climate, nutrients and disturbances (Brooker *et al.* 2005; Brooker & Kikividze 2008).

Measuring the importance of plant–plant interactions requires long-term data that reflects the time scale over which abiotic processes (i.e. climate and nutrient fluxes) vary and competitive displacement occurs on landscapes (i.e. decades to millennia, Bardgett *et al.* 2005; Walker & Wardle 2014). These time scales are beyond the limit of modern observations or experiments; therefore, palaeoecological reconstructions of plant population and community dynamics are increasingly being used to investigate the dynamical nature of plant interactions (Virah-Sawmy, Bonsall & Willis 2009; Jeffers *et al.* 2011) and related processes (Green 1983; Miller *et al.* 2008; Willis *et al.* 2010; Birks 2012). High-resolution, fossil pollen time-series data have previously been used to quantify the form and intensity of plant interactions (Bennett 1986) and how these interactions may have varied under different environmental conditions (Jeffers *et al.* 2011). Yet, while previous palaeoecological research has provided a qualitative indication of periods of time in the past when the importance of plant interactions may have changed relative to other factors (Fuller 1997), this has not, to our knowledge, been demonstrated empirically.

It is possible to assess the importance of abiotic and biotic processes for plant population dynamics by the application of statistical modelling to palaeoecological data. This approach allows inferences to be made about population responses to selected processes from analysis of high temporal resolution, multi-proxy data (Jeffers, Bonsall & Willis 2011; Jeffers *et al.* 2011, 2012). We used this mechanistic modelling approach here to investigate the population-scale responses of four native woodland tree taxa in the Scottish Highlands to millennial-scale changes in mean July air temperature, nitrogen (N) availability and direct plant interactions with intra- and interspecific taxa during the early to mid-Holocene (10 700–5200 cal. years BP). We then estimated the relative importance of each of these processes in terms of the ability of the models representing each process to predict the observed population biomass dynamics, and how this changed over time. The population-scale responses to our selected abiotic and biotic processes were then used to consider the most likely drivers of community succession at our study site.

Materials and methods

SITE DESCRIPTION AND PALAEOECOLOGICAL DATA

We conducted new palaeoecological analyses on a sediment core taken from Dubh-Lochan, a small lake in the Great Glen region of the Scottish Highlands (4°26′7″W, 57°17′26″N), for which a full

Holocene fossil pollen sequence has previously been reported (Froyd 2005). New records reported here for the first time include chironomid-inferred mean July air temperature and sedimentary $\delta^{15}N$ dynamics. The time period included in this analysis spans 10 700 cal. years BP (the start of the sequence) to 5200 cal. years BP, which ends just prior to evidence of human impact at the site (Froyd 2006). The analyses of all palaeoecological proxy reconstructions were conducted at the same sampling depths throughout the sediment core to capture concurrent changes in each of the variables (n = 36 observations), which is required for our modelling approach. Five radiocarbon dates that were originally reported in Froyd (2005) were recalibrated in BCal (Buck, Christen & James 1999) using the IntCal09 (Reimer *et al.* 2009) calibration curve. The dates were interpolated in *p*simpoll (Bennett 2005) using a linear age-depth model (Appendix S1 in Supporting Information).

Fossil pollen accumulation rates (PAR) were used as a proxy of above-ground plant population biomass dynamics (Seppä *et al.* 2009) and these data were first reported in (Froyd 2002, 2005). As our aim is to investigate the factors driving successional changes in the woodland community, we have focused our analysis on four tree taxa that dominated the community during the early Holocene period (see Appendix S2 for full community dynamics). The first tree taxon to become established in this community was *Betula* sp. (birch), followed by *Pinus sylvestris* (Scots pine), *Alnus glutinosa* (European alder) and *Quercus* sp. (oak). The *Betula* pollen reported here is presumed to reflect the biomass of tree birch (i.e. *Betula pendula* or *B. pubescens*), the predominant birch taxa in the Scottish Highlands throughout the post-glacial period (Walker 1975). The two oak species extant in Britain during the post-glacial period include *Quercus petraea* and *Q. robur* (Bennett 1986). Life-history traits and ecological tolerances to stress are reported in Table 1 (note that where multiple species may have been present, we present the range of possible attributes).

The median amount of time between observations was 150 years (min. = 100 years, max = 336 years), which is roughly equivalent to the maximum lifespan of *B. pendula*, *B. pubescens* and *A. glutinosa* and about 1/10th of the maximum lifespan of *P. sylvestris*, *Q. petraea* and *Q. robur* (Table 1). Therefore, our observations of above-ground plant biomass dynamics reflect long-term successional changes in the woodland community. Although the biomass of alder and oak increased long after the start of the series, the pollen evidence suggests the presence – albeit at low values – of all four taxa throughout the full record. While *Ulmus sp.* (elm) pollen was also present during the Holocene, the taxon was not included in this study because of its relatively low values (<5% of total pollen sum) (Appendix S2). *Corylus avellana* was not included because preliminary analyses indicated its population biomass dynamics were very similar to those of birch (Appendix S2) and thus would not contribute significantly unique information.

Mean July air temperatures (°C) were reconstructed from species assemblages of subfossil chironomid (non-biting midges) remains found in the lake sediments. This was achieved with a three-component WA-PLS transfer function based on a 153-lake modern Norwegian chironomid training set (Brooks & Birks 2000, 2001; Heiri, Brooks & Birks 2011).

Nitrogen availability was inferred from stable N isotope ($\delta^{15}N$) analysis of bulk lake sediments. Results are reported as ‰ relative to the IAEA reference standard of atmospheric N (i.e. 0‰). Sedimentary $\delta^{15}N$ values reliably record changes over time in the processes acting on N cycling within the lake catchment due to the strong biogeochemical links between terrestrial and lacustrine environments (McLauchlan *et al.* 2007, 2013; Wolfe *et al.* 2013). Increasing values of $\delta^{15}N$ (i.e. enrichment in ^{15}N) are interpreted as periods of rising terrestrial N availability because during these times, more N tends to be lost from the terrestrial environment through leaching and denitrification and these processes preferentially remove the lighter isotope (^{14}N), leaving the remaining terrestrial N pool enriched in ^{15}N (Houlton & Bai 2009).

Previous work has shown that sediment $\delta^{15}N$ values correlate well with changes in N availability to plants on the landscape as measured by $\delta^{15}N$ values of wood in living trees as well as concentrations of nitrate in streams flowing through the lake catchment (McLauchlan *et al.* 2007). A positive correlation between the direction and magnitude of change in terrestrial plant and sediment $\delta^{15}N$ values has also been demonstrated with stable isotope analysis of plant macrofossils and lake sediments aged between 7000 and 4500 cal. years BP (Wolfe *et al.* 2013). Readers are referred to the supporting information in McLauchlan *et al.* (2013) for further details regarding the interpretation of sedimentary $\delta^{15}N$ as a proxy of N availability. Stable isotope analysis was conducted at the Godwin Laboratory for Palaeoclimate Research in the Department of Earth Sciences at the University of Cambridge on a Costech Elemental Analyzer attached to a Thermo MAT 253 mass spectrometer in continuous flow mode (more details are available in Appendix S3).

MECHANISTIC MODELS OF POPULATION DYNAMICS

A model-fitting and model-selection approach was used to determine the most likely mechanism(s) underlying the observed changes in plant population biomass dynamics and concurrent changes in mean July air temperature, N availability or the biomass of interacting spe-

Table 1. Selected ecological attributes and tolerances of the study taxa

Attribute	Birch	Pine	Alder	Oak	Source
Maximum height (m)	20–25	48	33	40–45	Prentice & Helmisaari (1991)
Maximum growth rate (m year^{-1})	0.85–1.0	0.90	0.75	0.85	Prentice & Helmisaari (1991)
Maximum age (year)	300	900	150	1000	Prentice & Helmisaari (1991)
GDD_{min} > 5 °C	300–500	500	1000	1200–1500	Prentice & Helmisaari (1991)
GDD_{max} 5 °C	2100–2200	2400	4600	4000	Prentice & Helmisaari (1991)
N content (log N_{mass} as % dry mass)	0.279–0.441	0.121–0.224	0.549	0.27–0.458	Wright *et al.* (2004)
Leaf lifespan (year)	0.68	1.43–1.46	NA	0.78–0.83	Wright *et al.* (2004)
Index of low N tolerance (1–9)	4	2	6	4	Hill *et al.* (1999)
Specific leaf area (mm mg^{-1})	16.1	5.6	21.3	14.9–15.7	Cornelissen (1996)
Average Seed weight (g)	0.00025–0.0003	0.006	0.002	2.34–3.38	Liu *et al.* (2008)
Index of shade tolerance	1.85–2.03	1.67	2.71	2.45–2.73	Niinemets & Valladares (2006)

cies (as described in Jeffers, Bonsall & Willis 2011; Jeffers *et al.* 2011, 2012). Our modelling approach is comparable to the regression-based methods described by Freckleton & Watkinson (2001) for inferring the intensity and importance of plant interactions from long-term plant census data. However, the approaches differ in that we fit dynamical population models to the data in order to estimate the relationship(s) between each driver and the biomass dynamics of each taxa. Our results provide insights into the effect of the drivers on key demographic parameters (e.g. instantaneous population growth rates, carrying capacity, mortality rates), which are essential for understanding the response of plant taxa to drivers of change over time (Clark *et al.* 2011).

To accomplish this, a suite of population dynamical models expressed as ordinary differential equations were fitted to the palaeoecological data, where each model represents one possible hypothesis (out of a suite of candidate hypotheses) about the relationships between the variables over time. Each model was fitted to the palaeoecological time-series data using maximum-likelihood estimation (Bonsall & Hastings 2004; Bonsall & Hassell 2005) and a model-selection approach (described below) was used to determine which model(s) or hypotheses were best supported by the data (Johnson & Omland 2004).

Ten alternative models of plant–N availability interactions (see Table 2) were included in the analysis. Increasing N availability was assumed to have either a *positive* effect on population growth (N-dependent population growth) by increasing the intrinsic population growth rate, or *no* effect (N-independent population growth). Within the set of N-dependent population growth models, the response function describing the effect of increasing N availability on population growth was either linear (i.e. a constant rate of population growth with increasing N availability) or saturating (i.e. a linear increase in population growth with increasing N availability until a threshold is reached, beyond which there is no further response to increasing N). In both the N-dependent and N-independent models, there was an alternative configuration that incorporated a positive feedback effect of decaying plant biomass on the supply of N. Each of these model variations was fitted to the time-series data with and without a function describing density-dependent controls on population growth. See Appendix S4 for all model equations.

Increasing temperature was assumed to operate on plant biomass dynamics by altering the intrinsic population growth rate. The effect of rising mean July air temperatures on population growth was described by two possible functions: saturating, where warming leads to exponential population growth until a maximum temperature is reached, beyond which further temperature increases have no effect on population growth; or exponential decay, where the positive effect of warming on population growth decreases exponentially to zero as temperature increases.

Plant–plant interactions were modelled by the Lotka–Volterra competition model (as in Jeffers *et al.* 2011). Here, the rate of change in the population biomass of one taxon is regulated by its carrying capacity (i.e. the density-dependent controls on population growth) and the biomass of other taxa. Interactions were modelled for pairs of taxa because the modelling approach is limited to evaluating the dynamics of only two variables at one time due to the short time series (n = 36) and the large computational requirements of the model-fitting method. The maximum-likelihood-estimated competition coefficients from the Lotka–Volterra model were allowed to take on positive or negative values. Positive values indicate competition (i.e. an increase in the biomass of one taxon leads to a reduced population growth rate in the other), and negative values indicate facilitation (i.e. an increase in the biomass of one taxon leads to an increase in the population growth rate of the other). These parameter values were used as a proxy for the magnitude (or intensity) of each interaction because they reflect the impact of each interaction on the biomass of the component taxa (Freckleton & Watkinson 2001). The estimated competition coefficients and carrying capacities were then used to predict the expected equilibrium outcome of the interactions and the relative stability of the interaction.

Table 2. Akaike information criterion weights (w_i) show the relative amount of evidence for each of the plant–N availability and plant–temperature models for each plant taxon

N availability models	Birch (w_i)	Pine (w_i)	Alder (w_i)	Oak (w_i)
N-dependent population growth (%)				
Linear uptake	30	66	0	0
Linear uptake with density dependence	11	22	0	0
Saturating uptake	11	2	0	0
Saturating uptake with density dependence	4	1	0	0
N-dependent population growth with feedback effect on N availability (%)				
Linear uptake + feedback	11	3	0	0
Linear uptake + feedback with density dependence	4	1	0	0
Saturating uptake + feedback	4	1	0	0
Saturating uptake + feedback with density dependence	2	0	0	0
N-independent plant population growth (%)				
Logistic density dependence	11	2	0	0
Exponentially decaying density dependence	11	2	100	100
Temperature models (%)				
Saturating response	0	6	0	0
Exponentially decreasing response	100	94	100	100

The stability of each interaction was determined by the maximum-likelihood-estimated carrying capacity of each taxon in the pairwise interaction relative to the product of the other taxon's carrying capacity and the absolute value of the estimated competition coefficient. A competitive interaction (−/−) was deemed as stable coexistence if these inequalities held true: $K_x > K_y|\alpha|$ and $K_y > K_x|\beta|$ (where K_x and K_y are the carrying capacities of taxa x and y, respectively, α is the effect of competition with taxa y on x and β is the effect of competition with taxa x on y). In the case of stable coexistence, this means that the respective carrying capacities of both taxa are large enough for each to persist at low biomass levels even when the biomass of the other is near its own carrying capacity. In other words, the effects of intraspecific interactions on each taxon's population growth outweigh the effects of interspecific interactions. When these inequalities do not hold, the result is either competitive exclusion (i.e. when $K_x > K_y|\alpha|$ but $K_y \le K_x|\beta|$ or vice versa) or unstable equilibrium (i.e. when $K_x \le K_y|\alpha|$ and $K_y \le K_x|\beta|$).

As indicated above, a positive or facilitative interaction was indicated by a positive value in the maximum-likelihood-estimated competition coefficient, which means that increasing biomass of one taxa leads to population growth in the other (i.e. the opposite effect of competition). Conversely, declining population biomass of the facilitating taxa would dampen the population growth of the beneficiary taxa. An unstable interaction would occur when the positive effect of the interaction on the beneficiary outweighs its own intraspecific controls on population growth (i.e. $K_x < K_y|\alpha|$ and/or $K_y < K_x|\beta|$ as above).

The Lotka–Volterra equations provide a simple model of plant interactions, which is most suitable for describing the direct interactions between taxa in data sets of our sample size ($n = 36$) since the Lotka–Volterra model describes the interaction between two species with only a few model parameters ($\Theta = 6$). Meta-population models of plant interactions incorporate immigration and emigration from the populations (e.g. Tilman 1994), but these require the use of proportion data (not absolute abundance – here the above-ground biomass of each population). We therefore did not use a meta-population approach to model plant–plant interactions as it would preclude us from comparing the impacts of plant–plant interactions on population dynamics with the effects of the other ecosystem processes, which are modelled with biomass data. Furthermore, while it is likely that the intensity of the plant interactions varied over time, this would be best analysed through applying the model to subsets of the data (as in Jeffers *et al.* 2011), requiring a much larger sample size than can be obtained from the sedimentary sequence.

The modelling approach we describe here provides a new method for evaluating the relative importance of a range of processes acting on the observed plant population dynamics for which we have local, independent records at concurrent points in time from a single study site. Thus, while other biotic and abiotic factors may have affected the population dynamics in this Highland community, here we restrict our consideration to those for which we had independent environmental proxy data reconstructed directly from the Duch-Lochan sediment core. The modelling approach requires that data are available at the same time periods throughout the series. Therefore, external data (e.g. CO_2 or insolation) were not included but would be of interest for future study. Fire activity data were available, but previous work has already shown that burning was negligible around Dubh-Lochan during this period (Froyd 2002, 2006). While we did not have an independent proxy for precipitation changes from the Dubh-Lochan sediment core, data on known pluvial (i.e. periods of high rainfall) events were available from previous work (Dubois & Ferguson 1985) and so we used this information qualitatively to inform our interpretation of the modelling results. The dates of these events, which were originally reported in uncalibrated ^{14}C years, were calibrated in BCal using the IntCal09 curve so that their timing would be comparable with our reconstructed ecosystem dynamics.

MODEL-FITTING AND MODEL-SELECTION

Model-fitting involved integrating the population dynamics models (described above) over variable time steps using a standard numerical integration approach. Maximum-likelihood estimation and a downhill optimization algorithm (Press *et al.* 1992) were used to find the set of model parameters that yielded the smallest difference between the model-generated and observed biomass data over the entire time series. For the plant–N and plant–plant interaction models, a Gaussian likelihood function was used. However, since the mean July air temperatures were reconstructed indirectly through subfossil chironomid assemblages, we used a structured Gaussian likelihood function to fit the plant–temperature dynamics models (Jeffers *et al.* 2012). This involved estimating an additional parameter that represented the additional variance associated with using an indirect proxy (see Appendix S4 for the likelihood functions).

Model-selection approaches (Burnham & Anderson 2002) determine which model(s) provide the best-fit to the data. Here, we used the Akaike information criterion (AIC), which penalizes more complex models. The AIC scores were converted into AIC weights, which provides a normalized measure of the goodness-of-fit of each model to the plant and covariate dynamics within each data set (e.g. plant biomass and N availability), but cannot be used to compare the goodness-of-fit between different data sets (Burnham & Anderson 2002). Therefore, a further step was required to compare the ability of each of the models reflecting unique processes (e.g. plant–N versus plant–plant interaction models) to predict the observed biomass dynamics of each tree taxa. This involved using the AIC-inferred best model for each ecosystem process to generate predicted values of the plant biomass data using a one-step-ahead prediction routine. Root-mean-square error (RMSE) values were then calculated from the model-predicted and observed plant population dynamics data; the lowest RMSE value indicated the driver (or population) that had the greatest effect on the biomass dynamics of each population. We use this as our measure of relative importance of each process we study here. To determine whether the relative importance of each driver changed over time, we calculated a moving average RMSE score over intervals of about 500 years ($\bar{x} = 511$, range = 433–594 years). Confidence intervals for the maximum-likelihood estimates (MLE) of the model parameters from the best-fitting models were calculated from the likelihood profiles (Morgan 1999).

Results

TIME-SERIES DATA

Mean July air temperatures (Fig. 1), as inferred from a transfer function analysis of subfossil chironomid remains in the Dubh-Lochan lake sediments, varied between 13.5 and 15.5 °C (mean = 14.4 °C, standard deviation = 0.67 °C) during the early Holocene period (i.e. from 10 700 to 8600 cal. years BP); this is similar to modern July air temperatures for this region of Scotland (www.metoffice.gov.uk). After 8600 cal. years BP, mean July air temperatures increased from 13.5 to 17 °C over an 1800-year period and then cycled between 15 and 17 °C until about 5700 cal. years BP. This hypsithermal interval ended around 5700 cal. years BP, when mean July air temperatures fell back to early Holocene levels (13.5–14 °C). While we did not have an independent proxy of changes in precipitation from Dubh-Lochan, there is evidence that major pluvial events occurred in the Cairngorm Mountain region around 8300–8000 and 7300–6900 cal. years BP (adapted from Dubois & Ferguson 1985). These events are indicated by the grey-shaded regions in Fig. 1.

Nitrogen availability (as inferred from the values of sedimentary δ^{15}N) was at its peak value around 10 700 cal. years BP and then declined progressively over the following 3000 years. It reached a minimum value around 7300 cal. years BP, after which the trend in δ^{15}N abruptly shifted to increasing enrichment before stabilizing around 0‰ (relative to atmospheric N) for the rest of the time series. While the sedimentary δ^{15}N results could have been affected by diagenetic processes occurring within the lake after deposition, there is no *a priori* reason for us to suspect that this has occurred. Enrichment of δ^{15}N from the diagenetic loss of ^{14}N in older sediments are typically indicated by decreasing δ^{15}N values down-core (Talbot 2001) yet our sediments display the opposite trend (i.e. $\delta^{15}N$ is lower in younger sediments than in older sediments). However, even when phytoplankton resynthesize N molecules within the lake, the fractionation effect on $\delta^{15}N$ this tends to be relatively low and the sedimentary $\delta^{15}N$ generally retains the signal of allocthonous material (i.e. that of N molecules derived from the lake catchment) (Enders *et al.* 2008). See Appendix S3 for all geochemistry data.

Birch was the first tree taxa to become established in the woodland after 10 700 cal. years BP (see Appendix S2 for pollen percentage diagram). Birch PAR (our proxy for above-ground biomass of each tree population) decreased after 9000 cal. years BP, which coincided with a rise in pine PAR. Pine biomass was relatively high until 7300 cal. years BP after which there was a 2000 year long decline in pine population biomass. The change from increasing to decreasing pine biomass was concurrent with a rapid rise in alder biomass from low values at 7300 cal. years BP to peak values by 7050 cal. years BP. These changes in the biomass of each taxon within the community were coincident with the second major pluvial event (7300–6900 cal. years BP) and a shift to increasing N availability (after 7300 cal. years BP) on the landscape. Oak biomass began to rise shortly after alder expansion and rising N availability.

MODELLED RESPONSES TO ABIOTIC DRIVERS

The AIC weights (w_i) indicate the relative amount of support (%) for each model describing plant–N availability and plant–temperature dynamics (Table 2). The AIC-inferred best plant–N model for birch and pine was N-dependent population growth described by a linear N-uptake function. For oak and alder, the best-fitting plant–N model was that of N-independent population growth where population growth was only controlled by intraspecific competition (described by an exponentially decaying density-dependent factor). The maximum-likelihood-estimated parameters of the N-dependent

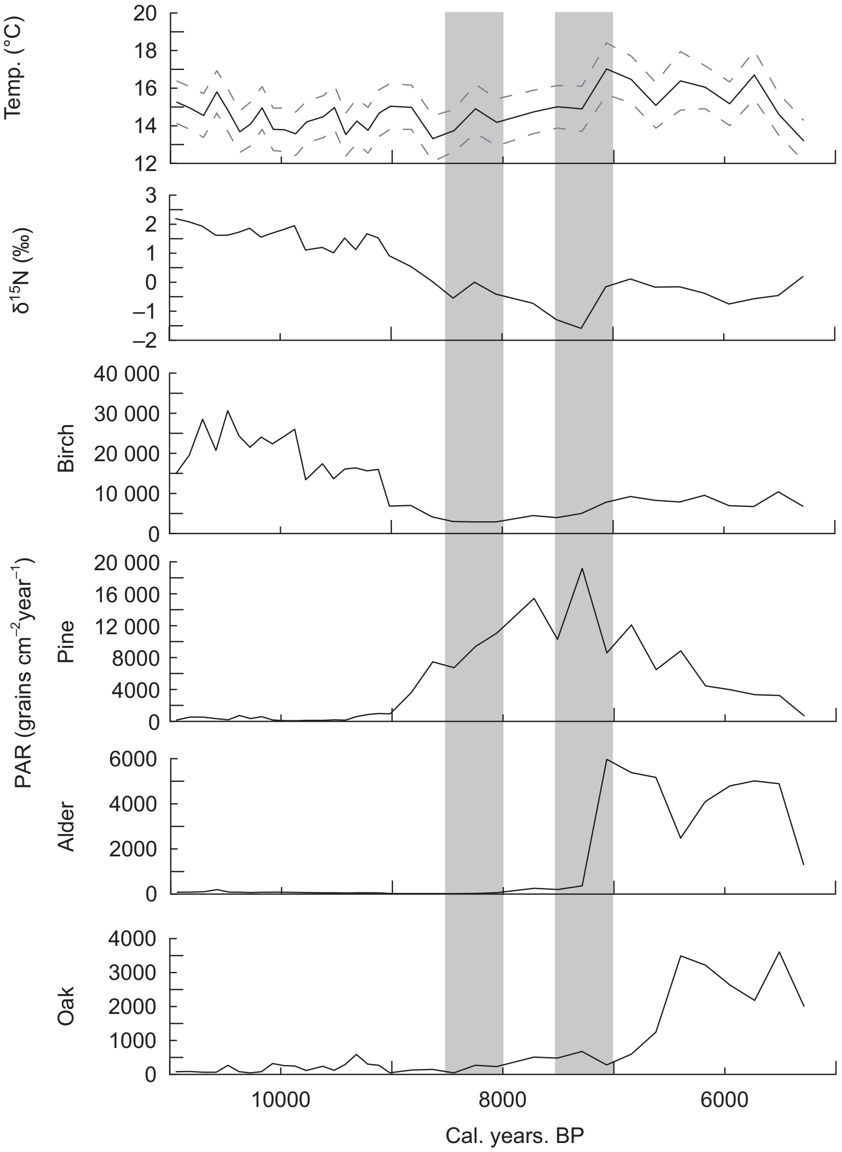

Fig. 1. Early to mid-Holocene ecosystem dynamics at Dubh-Lochan Scotland. Mean July air temperatures were inferred from the species assemblages of subfossil chironomid remains (estimated errors shown as dashes). Ecosystem-scale nitrogen (N) availability was reconstructed from stable isotope analysis of N ($\delta^{15}N$, measured as ‰ relative to atmospheric N) of bulk lake sediments. Birch, pine, alder and oak population biomass dynamics were reconstructed from their pollen accumulation rates (PAR). Pluvial events have previously been identified for the periods around 8314–8026 and 7256–6974 cal. years BP (adapted from Dubois & Ferguson 1985), which are indicated by the grey-shaded regions.

population growth rates for pine and birch are plotted across the range of observed sedimentary $\delta^{15}N$ values (note only the positive values of $\delta^{15}N$ were plotted to aid interpretation). These plots allow for a comparison across the two populations in terms of their model-estimated N-dependent population growth rates (Fig. 2); this shows that for any increase in N availability, there would be a larger rate of biomass increase in pine than birch.

The AIC-inferred best-fitting plant–temperature model demonstrated unanimous support for the exponentially decreasing population growth model for all taxa (Table 2). This model describes a positive population growth response to warmer mean July air temperatures until a threshold value of temperature was reached; beyond this point, the effect of additional warming is negligible. The maximum-likelihood-estimated temperature-dependent intrinsic population growth rate parameter in this model was infinitesimally small for all four taxa.

MODELLED PLANT INTERACTION OUTCOMES

The maximum-likelihood-estimated parameters for the pairwise Lotka–Volterra models provide evidence for the occurrence of both competitive (−/−) and facilitative (+/+, +/−) interactions between the taxon pairs over the full time series (Table 3). Positive interactions were indicated by the model-estimated interaction coefficient for half of the taxon pairs and these were spread almost evenly across all taxa (i.e. there is evidence of positive interactions involving each of the study taxa). Many of the model-inferred interaction outcomes were designated as unstable (i.e. the interspecific interactions had a greater impact than intraspecific interactions on the population growth of the taxa in the pairwise interaction). The model-estimated effect of interspecific interactions for each population (relative to intraspecific interactions) varied with respect to the taxa involved (Table 3 and see Appendix S4 for the estimated model parameters).

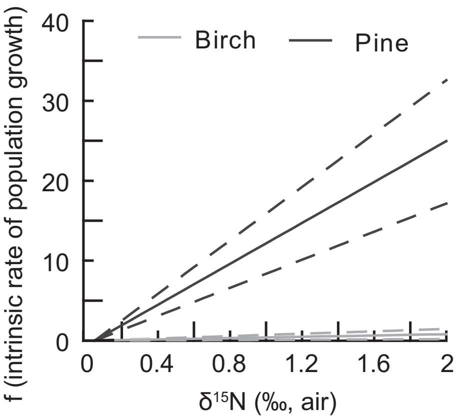

Fig. 2. Model-inferred use of available nitrogen (N) by pine and birch. Maximum-likelihood-estimated parameters (and their 95% confidence intervals) of the plant–N model with the highest Akaike information criterion weight were used to demonstrate the differences in the N-dependent population growth rates of birch and pine. This reflects the N-dependent intrinsic rate of plant population growth (*ra*N) in grains cm^{-2} year^{-1}.

IMPORTANCE OF DRIVERS FOR POPULATION DYNAMICS

Root-mean-squared errors measure the difference between the predicted and observed values of population biomass for each of the best-fitting models of plant–N, plant–temperature and plant–plant interactions. The lowest RMSE values indicate which driver(s) best predicted the population dynamics of each taxon over the entire time series (Table 4). Direct plant–plant interactions were the best predictor for all of the taxa except alder. Alder dynamics were best described by two models with similar RMSE values: the N-independent population growth model (where population growth was moderated only by a density-dependent process described by the logistic equation, see Appendix S4), and the model describing direct alder–oak interactions.

There were similarities between the RMSE values of the drivers for some of the taxa. This suggests that the individual drivers may have had an interacting effect on the taxa. There were two instances of this: (i) there was little difference between the RMSE of the Lotka–Volterra model describing competition with birch for pine, alder and oak with the RMSE values of the plant–temperature models for these three taxa; and (ii) the RMSE of the Lotka–Volterra model describing direct interactions between oak and alder (i.e. mutualism, as indicated by the maximum-likelihood-estimated model parameters) was the exact same value as the RMSE of the oak–N interaction model for describing oak biomass dynamics.

CHANGES IN IMPORTANCE OF DRIVERS OVER TIME

The moving window RMSE values show that the most important drivers – defined here as the model yielding the lowest RMSE value out of all models applied to the full time series for each taxon – remained consistent over time for all of the taxa except for birch (Fig. 3). There was a clear decrease in RMSE for the plant–N availability and plant–temperature models for describing birch dynamics between 8600 and 6800 cal. years BP (Fig. 3); the increase in the goodness-of-fit of these two models is concurrent with increasing mean July air temperatures and decreasing N availability (Fig. 1).

The similarities in RMSE values described above (Importance of drivers for population dynamics) remained roughly constant through time when RMSE was calculated on a moving average across the time series (Fig. 3). Specifically, the goodness-of-fit of the Lotka–Volterra model of competition with birch for describing pine, alder and oak population dynamics changed consistently through time with the moving average RMSE value of the plant–temperature model for each taxon. Similarly, the correspondence between the RMSE value of the oak–alder mutualism model and the plant–N model for describing oak dynamics remained constant across the full time series. While the RMSE values for the plant–N

Table 3. Estimated plant interactions, the relative effects of intra- versus interspecific interactions at equilibrium and the predicted outcomes of interactions between each taxon pair based on the maximum-likelihood-estimated parameters from the Lotka–Volterra competition model

Taxa pair	Interaction*	Intra- > Inter-specific? Taxon 1	Intra- > Inter-specific? Taxon 2	Predicted outcome
Pine–Birch	−/−	Yes	Yes	Stable competition
Pine–Alder	−/−	No	No	Unstable equilibrium
Birch–Alder	−/+	No	No	Unstable facilitation of birch
Pine–Oak	+/+	Yes	No	Unstable mutualism
Oak–Birch	−/−	No	Yes	Competitive exclusion of oak
Oak–Alder	+/+	Yes	No	Unstable mutualism

*The sign for the interaction describes the effect of the first taxa on the second (e.g. −/+ means that species *x* has a negative effect on species *y*, and species *y* has a positive effect on species *x*).

Table 4. Root-mean-square error values show the goodness-of-fit of each modelled interaction as measured over the entire time series

Driver	Goodness-of-fit for Birch	Pine	Alder	Oak
Birch	–	3584	2287	1241
Pine	7727*	–	944	974
Alder	7853	4580	–	15*
Oak	7903	430*	1565	–
Nitrogen availability	15 541	6321	20*	18*
Mean July air temp.	10 711	3957	2257	1241

*Indicates the lowest RMSE score.

and plant–temperature models for describing birch population dynamics over the full time series were not similar, the dynamics of the moving average RMSE values across time followed similar trajectories throughout the record and the values became (and remained) nearly identical after 8600 cal. years BP (Fig. 3).

There was more change in the moving average RMSE values for the models that were ranked as secondary and above (i.e. when RMSE was calculated on the full time series) than the moving average RMSE values for models which had the lowest RMSE values when calculated over the full time series (i.e. the primary drivers). Within this, the relative abilities of each model to predict the biomass data (i.e. relative rankings of drivers) remained consistent through time for pine and alder and mirrored the rankings that were established from the RMSE calculations as measured over the full time series (i.e. in Table 4). In contrast, the moving average RMSE values for oak show that the relative abilities of the non-primary models to predict the biomass data shifted over time (Fig. 3). Interestingly, the goodness-of-fit of these secondary to quinary-ranked models tended to deviate for all taxa at different points in time after 9000 cal. years BP (Fig. 3). This was most apparent for pine, alder and oak, where all models provided a good fit to the observed biomass data in the first millennia (or two) of the record, when the biomass of each population was low, then beyond this point the non-primary ranked models provide a poor fit to the data.

Discussion

IMPORTANCE OF PLANT–PLANT INTERACTIONS

Our model of direct plant–plant interactions was able to predict the observed population biomass for all four study taxa better than any of the 10 plant–N models and four plant–temperature models employed here to describe millennial-scale population dynamics around Dubh-Lochan (Table 4). While the plant–N model provided the best-fit to the observed alder biomass dynamics, this model described alder impacts on N availability (not vice versa) and involved intraspecific, density-dependent controls on alder population growth.

The estimated parameters of our plant–plant interaction models identified the occurrence of both positive and negative interactions occurring between the four study taxa. These results suggest that all of the taxa benefited from facilitation (i.e. where increasing biomass of the interacting taxon leads to an increase in the population growth rate of the target taxon) by at least one other taxon and all but birch were predicted to have a facilitative effect on another taxon (Fig. 4). However, there is no consistent pattern in the form of model-inferred interaction effect (+ or −) across the study taxa; instead, we found that the model-predicted outcomes varied with respect to the taxa involved (Fig. 4).

The stability of each interaction was determined by the relationship between the maximum-likelihood-estimated competition coefficients and carrying capacity in the parameterized Lotka–Volterra models for each taxon pair. This interpretation is based on the mathematically derived conditions required for the stable equilibrial coexistence of two interacting species (Tilman 2007). A taxon's *response* to an interaction was defined as stable if the effect of the interspecific interaction on population growth was smaller than the intraspecific effects. We found that the stability of each interaction depended on the identity of the interacting taxa (Fig. 4). Each of the taxa was predicted to have at least one unstable response to an interaction.

We also classified the pairwise interactions in terms of the rank importance of the interaction for explaining the population dynamics of the responding taxa (i.e. based on the RMSE value as calculated on the full time series). There was clear asymmetry in the model-inferred importance of each interaction for the taxa in each pair (i.e. the estimated relative importance of the interaction tended to be greater for one taxon than for the other). Despite the overall prevalence of predictions of unstable responses to interactions, our model results suggest that the most important interactions for each taxon (as indicated by RMSE scores and relative ranking in Fig. 4) were predicted to be stable.

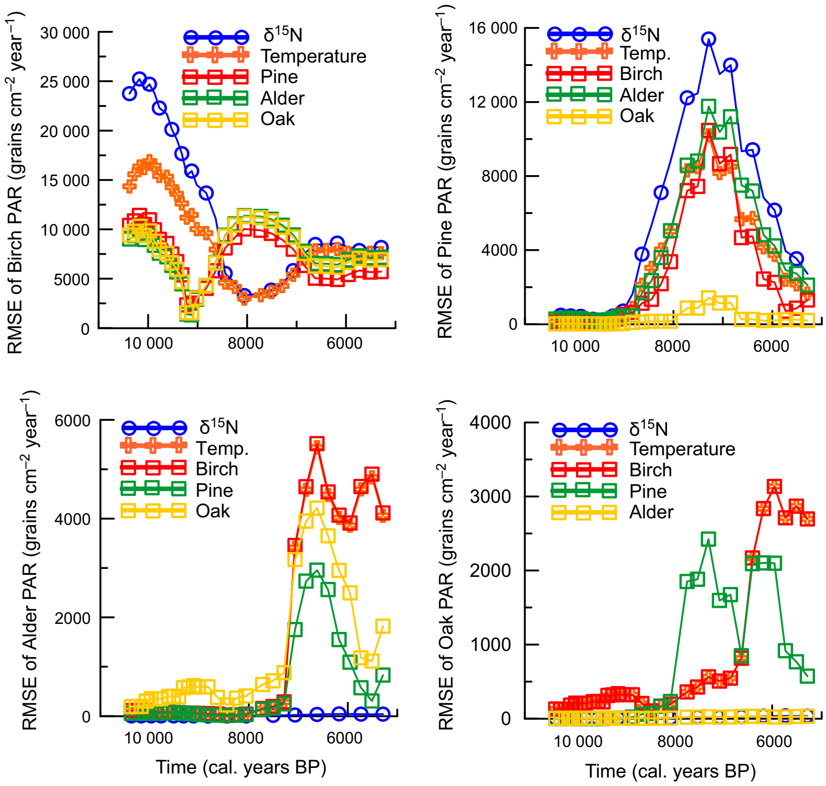

Fig. 3. Moving window root-mean-square error values of each model for describing the biomass dynamics of each population in terms of their pollen accumulation rates (PAR). The best-fitting model for each driver was indicated by Akaike information criterion weights and this model was used to predict the population dynamics of each taxa. A moving average value of root-mean-square errors was calculated for each set of predicted biomass dynamics. The mean period between calculations was about 500 years. Low values indicate a good fit between the parameterized model and the PAR data.

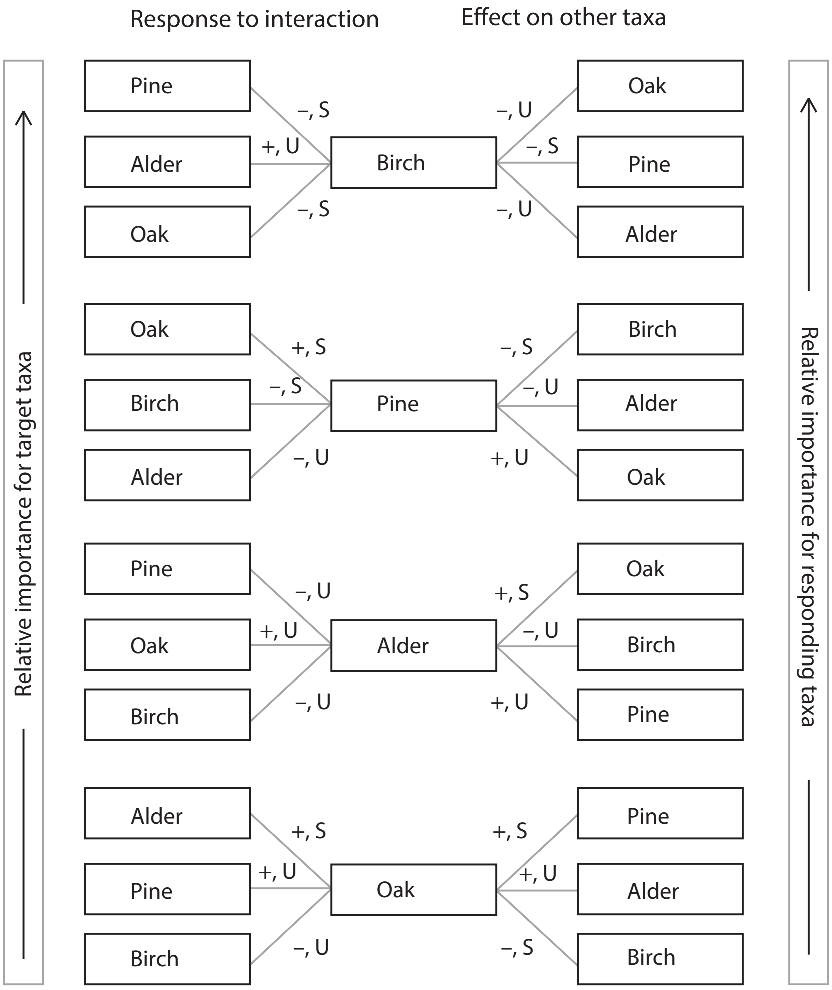

Fig. 4. The response of each taxon to interactions and its effect on the other taxa through direct interactions. The sign of each interaction reflects whether the interacting taxa had a positive or negative effect on its population growth and this effect was either stable (S, where its density-dependent controls exceeded the effect of the interspecific impacts) or unstable (U, where the interspecific impacts exceeded its density-dependent effects). The taxa driving (left hand column) and responding to (right column) its changes in population biomass are ranked in terms of the importance of the interaction to the target taxa (middle column) and the importance of the interaction on the responding taxa. In this regard, importance is indicated by the relative ranking of the interaction for each taxon based on the root-mean-square error values of the interaction model. One exception is the effect of pine on alder and oak, which was equally important to these responding taxa.

Overall, we found that the identity of the interacting species played an important role in determining the outcome of the plant–plant interaction models since the estimated form, intensity and importance of each interaction varied between each of the pairs (Fig. 4). This is consistent with findings from neo-ecological research, which suggest that predicting the effects of interactions on population dynamics requires knowledge of the species involved (Symstad *et al.* 1998; Gómez-Aparicio 2009; Soliveres *et al.* 2011). Furthermore, our model-based results support previous recommendations that niche-based species distribution models should incorporate the impacts of biotic drivers (Craine & McLauchlan 2004; Wisz *et al.* 2013), including both positive and negative plant–plant interactions, particularly when growing season temperatures fall within the ecological tolerances of the study taxa (Miller *et al.* 2008).

STABILITY THROUGH TIME IN IMPORTANCE OF PRIMARY DRIVERS

In most instances, the model-inferred primary driver of population dynamics remained constant through time (Fig. 3). Given that the RMSE results favour the plant–plant interaction model over the plant–N and plant–temperature models, we thus tentatively conclude that direct plant interactions were an important driver of population dynamics in this community for the entire 5000-year study period. However, we do acknowledge that there are other biotic and abiotic factors which were not considered here that could have had important, but unmeasured, effects on the population dynamics of our study taxa (e.g. precipitation).

The one exception to this finding of stable importance of drivers through time was birch, where the relative importance of each factor did vary over the study period (Fig. 3). In the early Holocene period, when birch biomass was high (Fig. 1), the lowest moving average RMSE values were provided by the Lotka–Volterra models of competition with pine, alder and oak (Fig. 3). Referring back to the maximum-likelihood-estimated parameters for these competition models, which indicate greater intraspecific (versus interspecific) controls on birch biomass dynamics, we can infer that density-dependent processes were driving this result (i.e. more so than interactions with the other taxa, which had very low biomass values prior to 9000 cal. years BP).

Around 9000 cal. years BP, there was a shift in the goodness-of-fit of all models such that the plant–temperature and plant–N models provided the best-fit to the birch biomass dynamics data for the period until 7000 cal. years BP. This shift was coincident with a period of increasing mean July air temperature and decreasing N availability (Fig. 1). These factors would have had opposing effects on birch population growth, such that declining N availability could have dampened the positive growth response of birch to climatic warming. While the ecological attributes of birch do not indicate strong intolerance of low N availability under stable conditions (Table 1), an experimental study has shown that soil warming around *B. pubescens* leads to increased root N uptake, higher plant N concentrations, increased leaf productivity and ultimately to higher growth rates (Karlsson & Nordell 1996). Thus, we can tentatively interpret the concurrent increase in importance of N availability and climate warming for birch biomass dynamics (Fig. 3) as indicative of increasing N limitation of its growth response to warming. By 6800 cal. years BP, when mean July air temperatures stopped increasing, terrestrial N availability stopped decreasing, and the biomass of oak and alder were at peak values (for the study period), all models were equally capable of predicting the observed birch dynamics (Fig. 3). The result for birch is in keeping with the observation by Gross *et al.* (2009) that the importance of interactions can depend on the availability of limiting resources. It was surprising to find that time-varying responses to drivers of population change were only indicated for one of the four study taxa.

The pine, alder and oak populations demonstrated a high level of conservatism in their model-inferred response to direct plant interactions, N availability and growing season temperatures. This result suggests a potentially high degree of resilience within the *primary* processes driving population dynamics despite the occurrence of multiple environmental changes.

SHIFTS IN THE RELATIVE IMPORTANCE OF NON-PRIMARY DRIVERS

When multiple drivers act simultaneously upon terrestrial ecosystems, the resulting changes in ecosystem structure and composition are not simply an additive effect of the response to each individual driver (Brown *et al.* 2001). Instead, interactions between drivers and higher order effects of multiple drivers can lead to unanticipated changes in ecosystem structure and composition (Tylianakis, Tscharntke & Lewis 2007; Tylianakis *et al.* 2008). Here, we found that all four populations had a high level of variation in the moving average RMSE values (i.e. importance) among the non-primary processes driving plant population dynamics (Fig. 3).

For pine and alder, while the model-inferred importance of each driver changed significantly through time, the *relative* rankings of the non-primary drivers remained constant (i.e. their importance changed in parallel through time). Interestingly, the goodness-of-fit of these models declined (Fig. 3) as their respective population biomass values increased through time (Fig. 1). When each taxon reached their peak biomass levels (Fig. 1), the goodness-of-fit of these models was at its lowest level (as indicated by the highest level of error in the model prediction, Fig. 3). This result can be interpreted as evidence, albeit indirect, for latent density-dependent processes acting on the population dynamics of pine and alder.

There is thus valuable information contained within the secondary to quinary-ranked models for understanding the full suite of processes underlying population responses to multiple environmental changes. The modelling methodology we employed here allows for inferences to be drawn from multiple models of population dynamics and has great potential for predicting changes in plant communities given simultaneous effects of multiple plant interactions and environmental changes (Kawai & Tokeshi 2007; Tylianakis *et al.* 2008).

PLANT INTERACTIONS INDIRECTLY RELATED TO ABIOTIC DRIVERS

The regulatory role of plant–plant interactions in determining the composition of plant communities has previously been shown to mediate the direct responses by plant populations to external drivers (e.g. water availability, Suttle, Thomsen & Power 2007). At Dubh-Lochan, there were two instances in which the moving average RMSE values of the parameterized Lotka–Volterra models changed concurrently through time with the values obtained from the models describing abiotic controls on population dynamics.

Firstly, the model-inferred importance of direct interactions with birch for describing the population dynamics of pine, alder and oak were found to change through time roughly in concert with their model-inferred importance of rising mean July air temperatures (Fig. 3). This suggests that competition with birch had the potential to mediate the response of pine, alder and oak to climate warming; however, the relatively poor goodness-of-fit of the birch competition models for describing the population dynamics of these taxa indicates that this process was not a significant driver of the observed plant community changes at Dubh-Lochan during the early Holocene period.

The second instance involves the similarity in the goodness-of-fit of the alder–oak interaction model (indicating facilitation of oak by alder, Table 3) and the oak–N availability model across time (Fig. 3). This can be interpreted as evidence that the oak–alder interaction mediated the model-inferred response by oak to changing N availability. Alder trees have a symbiotic relationship with a N-fixing bacteria (*Frankia alni*), which converts inert N_2 gas from the atmosphere into ammonium that can be readily utilized by plants. Alder establishment in plant communities is often associated with significant increases in the availability of N in surrounding soils (Walker & Chapin 1986). This effect can lead to ecosystem-scale increases in N availability, as was found with alder expansion in south-western Alaska during the Holocene period (Hu, Finney & Brubaker 2001).

The timing of alder expansion around Dubh-Lochan was also concurrent with an abrupt shift to rising N availability (Fig. 1). Did facilitation of oak by alder mediate the negative effects of declining N availability on subsequent oak population growth? Model-inferred facilitation of oak population growth by alder was closely coupled through time with the modelled effect of changing N availability on oak population dynamics (Fig. 3), which suggests a strong link between these processes. However, as the estimated importance of these drivers did not vary over time, it is not clear from the available evidence how the long-term decline in N availability affected the actual interaction between these taxa.

MECHANISMS UNDERLYING COMMUNITY SUCCESSION

The successional changes in the woodland community at Dubh-Lochan demonstrate a similar pattern to other temperate sites across much of NW Europe in the early post-glacial period. Here, we present model-based evidence that plant–plant interactions (both inter- and intraspecific) were more important for structuring the plant community at Dubh-Lochan than mean July air temperature and N availability over the entire early Holocene period (Fig. 5). This is an important and unexpected result. However, this result alone does not explain the full complexity of the plant community dynamics observed over five millennia at this study site. To make inferences about the likely causes of community succession at Dubh-Lochan during the early Holocene, we need to integrate all of the information derived from our modelling results (Fig. 5).

Firstly, the replacement of birch with pine in the early post-glacial period has been previously attributed to the relative longevity of pine trees (Table 1), which reduces the availability of forest gaps in which birch seedlings are able to grow (Bennett 1984). Changing N availability and mean July air temperatures may have also contributed to the transition from birch to pine dominance (Fig. 5), given the increasing model-estimated importance of these drivers for birch

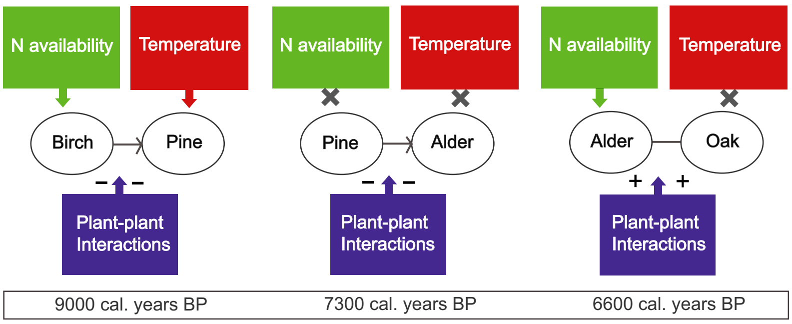

Fig. 5. Conceptual diagram representing the model-inferred effects of nitrogen (N) availability, changes in mean July air temperature and plant–plant interactions on the transitions between the dominant taxa in the community. The form of the predominant plant–plant interaction is either competition (−/−) or mutualism (+/+). The time bar reflects the point in time around which each transition occurred. Arrows indicate where there was model-based evidence for an effect while X's indicate a lack of evidence for an effect.

population dynamics at this transition time (ca. 9000 cal. years BP, Fig. 3).

Secondly, the subsequent pine decline in Scotland has been a subject of research for more than three decades. Competitive displacement of pine by alder was suggested by Bennett & Birks (1990) as a likely explanation for the rapid transition in community dominance between these two taxa observed across the region. We found no evidence to suggest that mean July air temperature or terrestrial N availability explains the observed outcome of reduced pine biomass concurrent with rising alder biomass. Of the drivers considered here, direct competition provided the best explanation for this transition; however, we must acknowledge that our study did not explicitly test for the role of precipitation changes on tree population dynamics, which has been suggested by others as a strong contributor to the early evidence of pine decline in Scotland (Dubois & Ferguson 1985; Tipping *et al.* 2008).

Lastly, there is some evidence (albeit inconclusive) for a role of terrestrial N availability in mediating the facilitative interaction between oak and alder in the mid-Holocene and the subsequent oak population expansion around Dubh-Lochan. This conclusion is supported by experimental evidence that N_2 fixed within *A. glutinosa* trees is transferred to non-N_2 fixing tree species including *B. pendula* when grown together (Millett *et al.* 2012). Given the relatively low tolerance of oak to low N availability (Table 1), it is reasonable to accept that that the presence of N-fixing alder could have enabled the rapid expansion of oak in the mid-Holocene.

Conclusion

Here, we demonstrate an empirical approach for deriving from palaeoecological data the relative importance of biotic and abiotic factors controlling population and community dynamics, and how this varies through time.

Our model results indicated that direct plant interactions between and among species provided a better explanation for the population dynamics of our four study taxa than growing season temperature or N availability in this native pine woodland community in the Scottish Highlands during the period from 10 700 to 5200 cal. years BP. However, the relative importance of all of our assessed drivers (plant–plant interactions, N availability and growing season temperatures) was found to vary by species and – in the case of birch – over time in response to increasing mean July air temperatures and reduced N availability. Thus, to generate preliminary conclusions about the controls on community succession, we had to rely on the full extent of our modelling results, not only the models that provided the best-fit to our observed population biomass data.

Therefore, by tracking the changes in importance of multiple drivers of population change through time, we were able to uncover key information regarding the potential roles of indirect interactions and environmental context in determining the outcomes of plant community succession. We argue that reliable predictions of future shifts in plant community structure given expected environmental changes can only be achieved by considering the full complexity of ecosystem responses to environmental change.

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Data accessibility

Fossil pollen accumulation rates: European Pollen Database. Chironomid-based mean July air temperature reconstruction: National Oceanic and Atmospheric Administration National Climatic Data Center. Stable isotope data: uploaded online in Appendix S3.

References

Agrawal, A.A., Ackerly, D.D., Adler, F., Arnold, A.E., Caceres, C., Doak, D.F. *et al.* (2007) Filling key gaps in population and community ecology. *Frontiers in Ecology and the Environment*, **5**, 145–152.

Armas, C. & Pugnaire, F.I. (2005) Plant interactions govern population dynamics in a semi-arid plant community. *Journal of Ecology*, **93**, 978–989.

Bardgett, R.D., Bowman, W.D., Kaufmann, R. & Schmidt, S.K. (2005) A temporal approach to linking aboveground and belowground ecology. *Trends in Ecology & Evolution*, **20**, 634–641.

Bennett, K.D. (1984) The postglacial history of *Pinus sylvestris* in the British Isles. *Quaternary Science Reviews*, **3**, 133–155.

Bennett, K.D. (1986) Competitive interactions among forest tree populations in Norfolk, England, during the last 10,000 years. *New Phytologist*, **103**, 603–620.

Bennett, K.D. (2005) Documentation for *p*simpoll 4.25 and *p*scomb 1.03: C programs for plotting pollen diagrams and analysing pollen data available at http://www.chrono.qub.ac.uk/psimpoll/psimpoll.html.

Bennett, K.D. & Birks, H.J.B. (1990) Postglacial history of alder (*Alnus glutinosa* (L) Gaertn) in the British Isles. *Journal of Quaternary Science*, **5**, 123–133.

Bertness, M.D. & Callaway, R. (1994) Positive interactions in communities. *Trends in Ecology & Evolution*, **9**, 191–193.

Birks, H.J.B. (2012) Ecological palaeoecology and conservation biology: controversies, challenges, and compromises. *International Journal of Biodiversity Science, Ecosystem Services & Management*, **8**, 292–304.

Blois, J.L., Gotelli, N.J., Behrensmeyer, A.K., Faith, J.T., Lyons, S.K., Williams, J.W. *et al.* (2014) A framework for evaluating the influence of climate, dispersal limitation, and biotic interactions using fossil pollen associations across the late Quaternary. *Ecography*, **37**, 1095–1108.

Bonsall, M.B. & Hassell, M.P. (2005) Understanding ecological concepts: the role of laboratory systems. *Advances in Ecological Research*, **37**, 1–36.

Bonsall, M.B. & Hastings, A. (2004) Demographic and environmental stochasticity in predator-prey metapopulation dynamics. *Journal of Animal Ecology*, **73**, 1043–1055.

Brooker, R.W. (2006) Plant-plant interactions and environmental change. *New Phytologist*, **171**, 271–284.

Brooker, R.W. & Kikividze, Z. (2008) Importance: an overlooked concept in plant interaction research. *Journal of Ecology*, **96**, 703–708.

Brooker, R., Kikvidze, Z., Pugnaire, F.I., Callaway, R.M., Choler, P., Lortie, C.J. & Michalet, R. (2005) The importance of importance. *Oikos*, **109**, 63–70.

Brooks, S.J. & Birks, H.J.B. (2000) Chironomid-inferred late-glacial air temperatures at Whitrig Bog, southeast Scotland. *Journal of Quaternary Science*, **15**, 759–764.

Brooks, S.J. & Birks, H.J.B. (2001) Chironomid-inferred air temperatures from Lateglacial and Holocene sites in north-west Europe: progress and problems. *Quaternary Science Reviews*, **20**, 1723–1741.

Brown, J.H., Whitham, T.G., Ernest, S.K.M. & Gehring, C.A. (2001) Complex species interactions and the dynamics of ecological systems: long-term experiments. *Science*, **293**, 643–650.

Buck, C.E., Christen, J.A. & James, G.N. (1999) BCal: an on-line Bayesian radiocarbon calibration tool. *Internet Archaeology*, **7**. http://intarch.ac.uk/journal/issue7/buck/

Burnham, K.P. & Anderson, D.R. (2002) *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*. Springer, New York, London.

Butterfield, B.J. (2009) Effects of facilitation on community stability and dynamics: synthesis and future directions. *Journal of Ecology*, **97**, 1192–1201.

Callaway, R.M. (1995) Positive interactions among plants. *Botanical Review*, **61**, 306–349.

Callaway, R.M. & Walker, L.R. (1997) Competition and facilitation: a synthetic approach to interactions in plant communities. *Ecology*, **78**, 1958–1965.

Callaway, R.M., Brooker, R.W., Choler, P., Kikvidze, Z., Lortie, C.J., Michalet, R. *et al.* (2002) Positive interactions among alpine plants increase with stress. *Nature*, **417**, 844–848.

Clark, J.S., Bell, D.M., Hersh, M.H. & Nichols, L. (2011) Climate change vulnerability of forest biodiversity: climate and competition tracking of demographic rates. *Global Change Biology*, **17**, 1834–1849.

Connell, J.H. & Slatyer, R.O. (1977) Mechanisms of succession in natural communities and their role in community stability and organization. *American Naturalist*, **111**, 1119–1144.

Cornelissen, J.H.C. (1996) An experimental comparison of leaf decomposition rates in a wide range of temperate plant species and types. *Journal of Ecology*, **84**, 573–582.

Craine, J.M. & McLauchlan, K.K. (2004) The influence of biotic drivers on North American palaeorecords: alternatives to climate. *Holocene*, **14**, 787–791.

Dubois, A.D. & Ferguson, D.K. (1985) The climatic history of pine in the Cairngorms based on radiocarbon dates and stable isotope analysis, with an account of the events leading up to its colonization. *Review of Palaeobotany and Palynology*, **46**, 55–80.

Enders, S.K., Pagani, M., Pantoja, S., Baron, J.S., Wolfe, A.P., Pedentchouk, N. & Nuñez, L. (2008) Compound-specific stable isotopes of organic compounds from lake sediments track recent environmental changes in an alpine ecosystem, Rocky Mountain National Park, Colorado. *Limnology and Oceanography*, **53**, 1468–1478.

Freckleton, R.P. & Watkinson, A.R. (2001) Nonmanipulative determination of plant community dynamics. *Trends in Ecology & Evolution*, **16**, 301–307.

Freckleton, R.P., Watkinson, A.R. & Rees, M. (2009) Measuring the importance of competition in plant communities. *Journal of Ecology*, **97**, 379–384.

Froyd, C.A. (2002) *Holocene Pine (Pinus sylvestris* L.) Forest Dynamics in the Scottish Highlands. University of Cambridge, Cambridge.

Froyd, C.A. (2005) Fossil stomata, reveal early pine presence in Scotland: implications for postglacial colonization analyses. *Ecology*, **86**, 579–586.

Froyd, C.A. (2006) Holocene fire in the Scottish Highlands: evidence from macroscopic charcoal records. *Holocene*, **16**, 235–249.

Fuller, J.L. (1997) Holocene forest dynamics in southern Ontario, Canada: fine-resolution pollen data. *Canadian Journal of Botany – Revue Canadienne De Botanique*, **75**, 1714–1727.

Gómez-Aparicio, L. (2009) The role of plant interactions in the restoration of degraded ecosystems: a meta-analysis across life-forms and ecosystems. *Journal of Ecology*, **97**, 1202–1214.

Grace, J.B. (1991) A clarification of the debate between Grime and Tilman. *Functional Ecology*, **5**, 583–587.

Green, D.G. (1983) The ecological interpretation of fine resolution pollen records. *New Phytologist*, **94**, 459–477.

Gross, N., Kunstler, G., Liancourt, P., de Bello, F., Suding, K.N. & Lavorel, S. (2009) Linking individual response to biotic interactions with community structure: a trait-based framework. *Functional Ecology*, **23**, 1167–1178.

Heiri, O., Brooks, S.J. & Birks, H.J.B. (2011) A 274-lake calibration data-set and inference model for chironomid-based summer air temperature reconstructions in Europe. *Quaternary Science Reviews*, **30**, 3445–3456.

Hill, M.O., Mountford, J.O., Roy, D.B. & Bunce, R.G.H. (1999) *ECOFACT 2a Technical Annex – Ellenberg's Indicator Values for British Plants*. Natural Environment Research Council, Norwich.

Houlton, B.Z. & Bai, E. (2009) Imprint of denitrifying bacteria on the global terrestrial biosphere. *Proceedings of the National Academy of Sciences*, **106**, 21713–21716.

Hu, F.S., Finney, B.P. & Brubaker, L.B. (2001) Effects of holocene *Alnus* expansion on aquatic productivity, nitrogen cycling, and soil development in southwestern Alaska. *Ecosystems*, **4**, 358–368.

Jeffers, E.S., Bonsall, M.B. & Willis, K.J. (2011) Stability in ecosystem functioning across a climatic threshold and contrasting forest regimes. *PLoS One*, **6**, e16134.

Jeffers, E.S., Bonsall, M.B., Brooks, S.J. & Willis, K.J. (2011) Abrupt environmental changes drive shifts in tree-grass interaction outcomes. *Journal of Ecology*, **99**, 1063–1070.

Jeffers, E.S., Bonsall, M.B., Watson, J.E. & Willis, K.J. (2012) Climate change impacts on ecosystem functioning: evidence from an *Empetrum* heathland. *New Phytologist*, **193**, 150–164.

Johnson, J.B. & Omland, K.S. (2004) Model selection in ecology and evolution. *Trends in Ecology & Evolution*, **19**, 101–108.

Karlsson, P.S. & Nordell, K.O. (1996) Effects of soil temperature on the nitrogen economy and growth of mountain birch seedlings near its presumed low temperature distribution limit. *Ecoscience*, **3**, 183–189.

Kawai, T. & Tokeshi, M. (2007) Testing the facilitation-competition paradigm under the stress-gradient hypothesis: decoupling multiple stress factors. *Proceedings of the Royal Society B-Biological Sciences*, **274**, 2503–2508.

Lortie, C.J., Brooker, R.W., Choler, P., Kikvidze, Z., Michalet, R., Pugnaire, F.I. & Callaway, R.M. (2004) Rethinking plant community theory. *Oikos*, **107**, 433–438.

Maestre, F.T., Callaway, R.M., Valladares, F. & Lortie, C.J. (2009) Refining the stress-gradient hypothesis for competition and facilitation in plant communities. *Journal of Ecology*, **97**, 199–205.

McLauchlan, K.K., Craine, J.M., Oswald, W.W., Leavitt, P.R. & Likens, G.E. (2007) Changes in nitrogen cycling during the past century in a northern hardwood forest. *Proceedings of the National Academy of Sciences of the United States of America*, **104**, 7466–7470.

McLauchlan, K.K., Williams, J.J., Craine, J.M. & Jeffers, E.S. (2013) Changes in global nitrogen cycling during the Holocene epoch. *Nature*, **495**, 352–355.

Michalet, R., Brooker, R.W., Cavieres, L.A., Kikvidze, Z., Lortie, C.J., Pugnaire, F.I., Valiente-Banuet, A. & Callaway, R.M. (2006) Do biotic interactions shape both sides of the humped-back model of species richness in plant communities? *Ecology Letters*, **9**, 767–773.

Miller, T.E. (1994) Direct and indirect species interactions in an early old-field plant community. *American Naturalist*, **143**, 1007–1025.

Miller, P.A., Giesecke, T., Hickler, T., Bradshaw, R.H.W., Smith, B., Seppa, H., Valdes, P.J. & Sykes, M.T. (2008) Exploring climatic and biotic controls on Holocene vegetation change in Fennoscandia. *Journal of Ecology*, **96**, 247–259.

Millett, J., Godbold, D., Smith, A. & Grant, H. (2012) N_2 fixation and cycling in *Alnus glutinosa*, *Betula pendula* and *Fagus sylvatica* woodland exposed to free air CO_2 enrichment. *Oecologia*, **169**, 541–552.

Morgan, B.J.T. (1999) *Applied Stochastic Modelling*. Arnold, London.

Niinemets, U. & Valladares, F. (2006) Tolerance to shade, drought, and waterlogging of temperate Northern Hemisphere trees and shrubs. *Ecological Monographs*, **76**, 521–547.

Pacala, S.W., Canham, C.D., Saponara, J., Silander Jr, J.A., Kobe, R.K. & Ribbens, E. (1996) Forest models defined by field measurements: estimation, error analysis and dynamics. *Ecological Monographs*, **66**, 1–43.

Prentice, I.C. & Helmisaari, H. (1991) Silvics of North European trees – compilation, comparisons and implications for forest succession modelling. *Forest Ecology and Management*, **42**, 79–93.

Press, W.H., Teukolsky, S.A., Vetterling, W.T. & Flannery, B.P. (1992) *Numerical Recipes in C: the Art of Scientific Computer*. Cambridge University Press, Cambridge.

Reimer, P.J., Baillie, M.G.L., Bard, E., Bayliss, A., Beck, J.W., Blackwell, P.G. *et al.* (2009) IntCal09 and Marine09 radiocarbon age calibration curve. *Radiocarbon*, **51**, 1111–1150.

Royal Botanic Gardens Kew. (2015) *Seed Information Database (SID)*. Version 7.1. available at: http://data.kew.org/sid.

Seppä, H., Alenius, T., Muukkonen, P., Giesecke, T., Miller, P.A. & Ojala, A.E.K. (2009) Calibrated pollen accumulation rates as a basis for quantitative tree biomass reconstructions. *The Holocene*, **19**, 209–220.

Smith, B., Prentice, I.C. & Sykes, M.T. (2001) Representation of vegetation dynamics in the modelling of terrestrial ecosystems: comparing two contrasting approaches within European climate space. *Global Ecology and Biogeography*, **10**, 621–637.

Soliveres, S., Torices, R. & Maestre, F.T. (2012) Evolutionary relationships can be more important than abiotic conditions in predicting the outcome of plant–plant interactions. *Oikos*, **121**, 1638–1648.

Soliveres, S., Eldridge, D.J., Maestre, F.T., Bowker, M.A., Tighe, M. & Escudero, A. (2011) Microhabitat amelioration and reduced competition among understorey plants as drivers of facilitation across environmental gradients: towards a unifying framework. *Perspectives in Plant Ecology, Evolution and Systematics*, **13**, 247–258.

Suttle, K.B., Thomsen, M.A. & Power, M.E. (2007) Species interactions reverse grassland responses to changing climate. *Science*, **315**, 640–642.

Symstad, A.J., Tilman, D., Willson, J. & Knops, J.M.H. (1998) Species loss and ecosystem functioning: effects of species identity and community composition. *Oikos*, **81**, 389–397.

Talbot, M.R. (2001) Nitrogen istopes in palaeolimnology. *Tracking Environmental Change Using Lake Sediments*. Vol. 2 (eds W.M. Last & J.P. Smol), pp. 401–439. Kluwer Academic Publishers, Dordrecht; London.

Tilman, D. (1990) Mechanisms of plant competition for nutrients: the elements of a predictive theory of competition. *Perspectives on Plant Competition* (eds J.B. Grace & D. Tilman), pp. 117–141. Academic Press, San Diego; London.

Tilman, D. (1994) Competition and biodiversity in spatially structured habitats. *Ecology*, **75**, 2–16.

Tilman, D. (2007) Interspecific competition and multispecies coexistence. *Theoretical Ecology: Principles and Applications* (eds R.M. May & A.R. McLean), pp. 84–97. Oxford University Press, Oxford.

Tipping, R., Ashmore, P., Davies, A.L., Haggart, B.A., Moir, A., Newton, A., Sands, R., Skinner, T. & Tisdall, E. (2008) Prehistoric *Pinus* woodland dynamics in an upland landscape in northern Scotland: the roles of climate change and human impact. *Vegetation History and Archaeobotany*, **17**, 251–267.

Tylianakis, J.M., Tscharntke, T. & Lewis, O.T. (2007) Habitat modification alters the structure of tropical host–parasitoid food webs. *Nature*, **445**, 202–205.

Tylianakis, J.M., Didham, R.K., Bascompte, J. & Wardle, D.A. (2008) Global change and species interactions in terrestrial ecosystems. *Ecology Letters*, **11**, 1351–1363.

Virah-Sawmy, M., Bonsall, M.B. & Willis, K.J. (2009) 'Tales of Symphonia': extinction dynamics in response to past climate change in Madagascan rainforests. *Biology Letters*, **5**, 821–825.

Walker, M.J.C. (1975) Late glacial and early postglacial environmental history of the central Grampian Highlands, Scotland. *Journal of Biogeography*, **2**, 265–284.

Walker, L.R. & Chapin, F.S. (1986) Physiological controls over seedling growth in primary succession on an Alaskan floodplain. *Ecology*, **67**, 1508–1523.

Walker, L.R. & Wardle, D.A. (2014) Plant succession as an integrator of contrasting ecological time scales. *Trends in Ecology & Evolution*, **29**, 504–510.

Williams, J.W., Blois, J.L. & Shuman, B.N. (2011) Extrinsic and intrinsic forcing of abrupt ecological change: case studies from the late Quaternary. *Journal of Ecology*, **99**, 664–677.

Willis, K.J., Bailey, R.M., Bhagwat, S.A. & Birks, H.J.B. (2010) Biodiversity baselines, thresholds and resilience: testing predictions and assumptions using palaeoecological data. *Trends in Ecology & Evolution*, **25**, 583–591.

Wisz, M.S., Pottier, J., Kissling, W.D., Pellissier, L., Lenoir, J., Damgaard, C.F. *et al.* (2013) The role of biotic interactions in shaping distributions and realised assemblages of species: implications for species distribution modelling. *Biological Reviews*, **88**, 15–30.

Wolfe, A.P., Hobbs, W.O., Birks, H.H., Briner, J.P., Holmgren, S.U., Ingólfsson, Ó., Kaushal, S.S., Miller, G.H., Pagani, M., Saros, J.E. & Vinebrooke, R.D. (2013) Stratigraphic expressions of the Holocene-Anthropocene transition revealed in sediments from remote lakes. *Earth-Science Reviews*, **116**, 17–34.

Wright, I.J., Reich, P.B., Westoby, M., Ackerly, D.D., Baruch, Z., Bongers, F. *et al.* (2004) The worldwide leaf economics spectrum. *Nature*, **428**, 821–827.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Radiocarbon dating.

Appendix S2. Fossil pollen percentage diagram.

Appendix S3. Stable isotope and elemental data.

Appendix S4. Population dynamic models.