1   Microclimate variability and long-term persistence of fragmented woodland

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8

9   Abstract

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

31

32   Keywords

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

34

35   1 Introduction

36   Global reductions in woodland size mean that fragmented populations play an increasingly
37   significant role in conservation (Haddad et al., 2015). Favourable microclimates in otherwise
38   inhospitable landscapes allowed the survival of climate relict tree populations and associated
39   biodiversity in the past, and are predicted to buffer populations against ongoing environmental
40   change (Hampe and Jump, 2011; Maclean et al., 2015). However, the timescales of modern

41 ecological studies are too brief to establish the extent to which microclimates can mitigate the
42 negative impacts of fragmentation through multiple climate shifts, including extinction debt and
43 local extinction-recolonization dynamics (Saunders et al., 1991; Vellend et al., 2006). Long timeseries
44 provide a powerful tool for understanding to what extent locally favourable conditions allow
45 populations to persist through multiple environmental changes. They offer insights into the origins
46 of modern conservation values in long-fragmented communities and their potential sensitivity to
47 future climatic fluctuations (Bhagwat et al., 2012).

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

66 1.1 Regional context and site description

67 In Scotland, woodland currently constitutes 18% of land cover, 22.5% of which is considered native
68 (Forestry Commission, 2014). This contrasts with the maximum extent of woodland cover around
69 5700 cal BP (calendar years before AD 1950), which has been estimated at 50-60% of the land area
70 (Tipping, 1994; Smout et al., 2005). Abrupt and widespread woodland contraction occurred across
71 northwest Scotland around 4400 cal BP, notably of pine. This is attributed primarily to climate
72 deterioration and resulted in the contraction of pine to near its current range (Fig. 1) (Bennett,
73 1995). For four millennia these woodland fragments have existed within a matrix of blanket peat and
74 heath, with small and dispersed areas of agriculture. The surviving climate relicts are highly valued
75 and form the basis for national and site-based woodland conservation and expansion goals.

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

87   ranges (Woodland Trust Scotland, 2015). A limited range of management interventions is advocated,
88   focused on reducing threats (e.g. thinning forestry plantation to remove exotic species and stimulate
89   native tree regeneration).

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

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

118   2 Methods

119   Field sampling, laboratory procedures and statistical methods are described for the Migdale analysis
120   site. Table 1 provides published references detailing the methods used at the four comparative sites.
121   A peat core was extracted from the edge of a valley mire at Migdale, adjacent to mature pinewoods.
122   Trees currently grow on the peat surface and woody material preserved in the stratigraphy indicates
123   that they have done so in the past. The full depth of peat was sampled using a closed-chamber
124   Russian peat corer to avoid contamination (Jowsey, 1966). To compare the palynological diversity of
125   modern and past assemblages, pollen was extracted from moss foliage that forms the current
126   ground cover in seventeen vegetation communities around the NNR (Table A1, Fig. A1). Sediment
127   stratigraphic description (Table A2) and pollen analysis follow standard techniques (Moore et al.,
128   1991). Pollen and spore nomenclature follow Bennett (1994), with the exception of *Sorbus*-type (e.g.
129   rowan) (Boyd and Dickson, 1987) and *Corylus avellana/Myrica gale* (hazel/bog myrtle) (Moore et al.,
130   1991). *P. sylvestris* stomata were identified on pollen slides following Sweeney (2004). The pollen
131   sum consists of a minimum of 500 land pollen grains, excluding aquatics and spores (total land
132   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

173   Over the last 7790 years cal BP five phases of vegetation compositional stability and transition are
174   identified from the pollen zonation (Fig. 2) and PCA analyses (Fig. 4a), as summarised in Table 2.
175   Limited overlap between PCA phases indicates significant shifts in woodland composition,
176   punctuated by periods of community stability. In brief, the local community was dominated by
177   *Betula* and *Pinus* (7790-6000 cal BP), *Alnus* (alder) (6000-4400 cal BP), *Betula* (4400-600 cal BP), and
178   then *Pinus* and *Betula* (600-0 cal BP, AD 2001). Palynological richness fluctuates largely below mean
179   Holocene values until c. 4360 cal BP (Fig. 4b). Sustained higher palynological richness from c. 2290-
180   670 cal BP coincides with higher pollen abundance for ruderal taxa. Richness values decline strongly
181   to the present, as *Pinus* becomes the dominant pollen producer. Rarefaction values for surface
182   samples overlap with subfossil values prior to c. 4360 cal BP (zone MIG1) and since 610 cal BP (zone
183   MIG3), but, with one exception, are consistently below intervening values.

184   3.3 Regional range dynamics

185   Inter-sample variability in pollen diagrams, particularly at small sampling sites, is a product of
186   taphonomy and vegetation dynamics immediately around the sampling site (e.g. stand-scale shifts in
187   species distribution or abundance) with smaller contributions from regional pollen production
188   (Bradshaw, 2013). To understand climatic influences on tree regeneration across a heterogeneous
189   landscape, we focus on sustained trends as the basis for comparison, rather than finer-resolution
190   variability likely to relate to gap-phase dynamics. Following rapid post-glacial climate amelioration
191   after c. 11 700 cal BP, similar early Holocene woodland succession patterns are evident at
192   Reidchalmai, Loch an Amair and Torran Beithe, where *Betula* expansion was followed by an increase
193   in *Pinus* (Fig. 3). As pine pollen is widely dispersed, macrofossil and stomatal evidence is needed to
194   securely differentiate local growth from regional pollen influx (Froyd, 2005). *Pinus* stomata are
195   recorded at Loch an Amair from c. 9900 cal BP, with corresponding pine pollen abundance of only
196   1%, indicating small local populations which are difficult to identify from pollen data alone. There are
197   insufficient sites with stomatal analyses to assess whether small populations were common before
198   observed regional increases in pine pollen. Using 20-25% pollen as a conservative limit for inferring
199   local growth (Bennett, 1984, 1995), pine populations were established by c. 8500 cal BP at Reidh-
200   lochan and c. 7700 cal BP at Reidchalmai. After c. 7500 cal BP, pine percentages at Migdale are
201   higher than neighbouring catchments and comparable with values at the regional sites until c. 6000
202   cal BP. Although stomata are absent from the sedimentary sequence, this could suggest pine growth
203   at Migdale.
204
205   With the exception of Loch an Amair, *Pinus* abundance falls below ~20% by c. 6300-6000 cal BP,
206   coinciding with percentage and influx increases in deciduous taxa, particularly *Alnus* and *Quercus*.
207   *Alnus* values are highest at Migdale, indicating localised or dispersed growth at the other sites
208   (Bennett and Birks, 1990; Froyd & Bennett, 2006; Tipping & McCulloch, 2003). *Quercus* values reach
209   the 2% TLP level thought to indicate local growth by c. 8000 cal BP (Huntley and Birks, 1983).
210   Although similar values are not recorded at Migdale until c. 5700 cal BP, only at this site do values
211   exceed 10%, which suggests that oak was a significant vegetation component at c. 4900-4770 cal BP
212   (Huntley and Birks, 1983). This overlaps with increased pine representation at Migdale, Reidchalmai
213   and Torran Beithe from c. 5100-4100 cal BP. Sustained reductions in *Pinus* are recorded at all sites
214   except Loch an Amair from c. 4600-4100 cal BP, although pine stomata persist at some sites after c.
215   4100 cal BP, suggesting that small populations remained around sites with (Torran Beithe) and
216   without (Reidh-lochan) a pronounced pine decline until c. 3200-2600 cal BP.
217
218   Two mid-late Holocene features differentiate Migdale from the other sites: (1) the marked rise in
219   *Betula* values after c. 4400 cal BP contrasts with relative continuity of pine at Loch an Amair and

220 birch at Reidchalmai, and (2) the strong rise in influx and percentage *Pinus* values from c. 1180 cal BP
221 is absent from the other sites. The increase in pine influx at Reidchalmai from c. 1340 cal BP likely
222 reflects complex fluvial inputs and is not a species-specific response (Tipping and McCulloch, 2003).
223
224 4 Discussion

225 4.1 Microclimate effects on woodland biogeography, turnover and resilience

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

247 Numerous studies note a correspondence between reductions in pine representation and shifts to
248 wetter climatic conditions, based on independent reconstructions of lake levels and peatland
249 watertables (Anderson et al., 1998; Bridge et al., 1990). Regeneration in marginalised pine
250 populations thus appears to have been synchronised at a regional scale by climate change, but the
251 mechanism of population regulation varied. In the uplands, wetter conditions may have reduced
252 pine regeneration, indicated by declining pollen and macrofossil abundances c. 6500-6000 cal BP
253 (Bridge et al., 1990). At lower altitudes, wetter climate may have contributed to a rise in water-
254 tables which allowed *Alnus* to outcompete *Pinus* in valley mires like Migdale (Bennett and Birks,
255 1990). This combination of climatic, recruitment and competition effects led to extinction-
256 recolonization dynamics in pine. This is particularly evident during the mid-Holocene, when
257 macrofossil evidence indicates that pine expanded its range northward around 5400-4200 cal BP in
258 response to lower peatland water-tables (Gear and Huntley, 1991). Stomatal evidence for renewed
259 growth at Reidh-lochan and Loch Farlary (Tipping et al., 2008b) contrasts with a weak pollen influx
260 response and absence of stomata at Migdale (Fig. 3). This suggests that pine colonised drier upland
261 peat surfaces, but gained little advantage in valleys where peat was limited and pine remained
262 subject to competitive exclusion by deciduous taxa and possibly by human impacts.

263 Anthropogenic disturbance may have selectively advantaged deciduous taxa in sheltered settings.
264 Migdale is differentiated from the other sites after c. 5700 cal BP by late expansion and unusually
265 high representation of *Quercus* compared with adjacent valleys and regional trends (Fig. 3). Neolithic

266   farming and selective management is considered causal, inferred from a temporary rise in Poaceae
267   and the occurrence of cereal type and *Rumex* (dock) pollen, with similar disturbance recorded in
268   nearby valleys at Reidchalmai and Achany Glen from c. 5600 cal BP (Smith, 1996). Increased light
269   penetration and managed browsing may have allowed oak to replace shorter-lived deciduous trees
270   and shrubs, although disturbance was probably low intensity since woodland cover was maintained.
271   Drier/warmer climatic conditions during this period could have increased the rate of oak growth in
272   this favourable microclimate setting.

273   Stronger inter-site contrasts emerge during the mid-Holocene, with extensive loss of upland
274   pinewoods and fragmentary woodland survival in upland and low-lying catchments (Fig. 3). Climate
275   deterioration, particularly increased wetness, is considered to be a key driver of pine dieback at a
276   regional scale, but the spatial differentiation of relict tree cover into upland pine (Loch an Amair) and
277   broadleaved valley woods (Migdale, Reidchalmai) indicates the need for more complex explanatory
278   mechanisms than rising water tables alone, particularly in low-lying areas with limited peat cover
279   (Bennett, 1995). Steeper slopes, unsuited to blanket peat expansion, and a less oceanic climate may
280   explain *Pinus* survival around Loch an Amair and in the northeast, respectively (Froyd and Bennett,
281   2006; Tipping, 1994). At Migdale, potential drivers of the transition from alder to birch-dominated
282   woods around 4430 cal BP include poorly understood aspects of climate change like seasonality,
283   which may have created conditions suited to birch growth, rather than persistently humid conditions
284   that previously favoured alder (McVean, 1956). Climate deterioration may also have altered
285   competition outcomes, contributing to reduced recruitment and competitive ability in oak and
286   allowing birch to replace it, as occurs now near oak range limits (Atkinson, 1992; Jeffers et al., 2015).
287   Locally increased anthropogenic disturbance from c. 4800 cal BP could have favoured birch over
288   alder (Barthelmes et al., 2010). At all sites in this study where woodland survived the mid-Holocene
289   'collapse', regeneration persisted through subsequent anthropogenic activity. This suggests modest
290   or managed disturbance, and that woodland regeneration was not near a critical threshold (cf.
291   Scheffer et al., 2012).

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

307   4.2 Microclimate buffering and management implications for *Pinus sylvestris*

308   Migdale represents a rare example of continuous deciduous-coniferous woodland cover from the
309   early Holocene through to the present, possibly owing to comparative shelter from westerly climate
310   systems. This provided a favourable microclimate which allowed woods to withstand multiple
311   climate and disturbance shifts. Uneven topography and varied drainage also may have made the site

312 less suited to farming, which remains a feature of the wider valley floor at Reidchalmai. This is good
313 news for conservation. Although canopy cover was maintained as a result of favourable growing
314 conditions and limited farming, community composition was far from stable. In terms of
315 management, woodland resilience therefore depends on allowing composition to adapt to changing
316 conditions and on appropriate ecological models for anticipating change. Community replacement
317 and reassembly in the last c. 1000 years has created floristic affinities between Migdale and long-
318 established pinewoods, overriding earlier similarity with deciduous fragments in similar low-lying
319 valleys. Pinewood communities thus provide an inappropriate model for anticipating change at this
320 site. Challenging existing ecological models and allowing adaptive ecological responses introduces
321 uncertainties that may conflict with conservation targets, like the desire to conserve the distinctive
322 biodiversity of these woodlands (Hiers et al., 2016; Woodland Trust Scotland, 2015). In view of the
323 uncertainties surrounding climate change, long-term evidence emphasises the importance of shifting
324 conservation and management focus from compositional stability to functional viability.

325 While the microclimate at Migdale buffered woodlands against environmental change and mature
326 trees around the site demonstrate that conditions are suitable for pine growth, the ecological history
327 of this site suggests that continued community change is highly likely and, over the longer term, local
328 pine populations are probably transient. The transition to pine dominance from c. 1060 cal BP has
329 resulted in a prolonged decline in diversity and the existing pine-dominated stand may still be in a
330 state of flux, characterised by high levels of compositional change more typical of the early Holocene
331 (Fig. 4) (Froyd and Bennett, 2006; Seddon et al., 2015; Tipping et al., 2006). Predicted future milder
332 climatic conditions may allow broadleaved species like birch, oak and rowan to expand, thus
333 replaying the successional replacement of pine seen at all except marginal, peat-dominated sites
334 over the course of the Holocene. Birch is also likely to increase due to more wind disturbance (Ray,
335 2008); this is a potential outcome of recent storm damage to pines around Loch Migdale. Scattered
336 pines occur on blanket peat in higher areas of the NNR and sheltered valleys like Migdale may
337 continue to act as seed sources for tree colonisation in adjacent upland areas if environmental
338 conditions, deer numbers and cultural preferences allow.

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

350 The relatively recent origins of the pinewood raise questions about the diagnostic value of the
351 'ancient pinewood indicators' present at the site (Whittet and Ellis, 2013). It appears that continuous
352 canopy cover, rather than the persistence of pine per se, helped maintain distinctive understorey
353 diversity by ensuring the availability of humid, shaded microclimates within the NNR (Bradshaw et
354 al., 2015). While debate continues over the biodiversity and ecosystem service benefits of planted
355 versus native coniferous woodland (Quine and Humphrey, 2010), these findings support existing
356 evidence that semi-native woods of uncertain origin and planted ancient woodland sites are useful
357 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

7.0 References

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562

563 **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

564

565 Table 2. Summary of Migdale stand dynamics based on pollen assemblage zones and ordination (PCA) phases. See Fig. 2 for selected pollen data and Fig. 4a
566 for ordination plot

| Pollen assemblage zone and age	Palynological characteristics	Corresponding PCA phase
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	Phase 5 (430-0 cal BP): shift towards *Pinus* with *Betula* and away from species scores for other deciduous trees, heath and herb taxa
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	Weaker correspondence between zones and phases: zone MIG2b includes part of PCA phase 3 and all of phase 4 (1090-550 cal BP)
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	Phase 3: shift in sample scores to new quasi-equilibrium (3990-1180 cal BP)
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	Overlaps with phase 2 quasi-stable state (5830-4360 cal BP)
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	Phase 1 (7790-6050 cal BP): characterised by variable sample scores

567
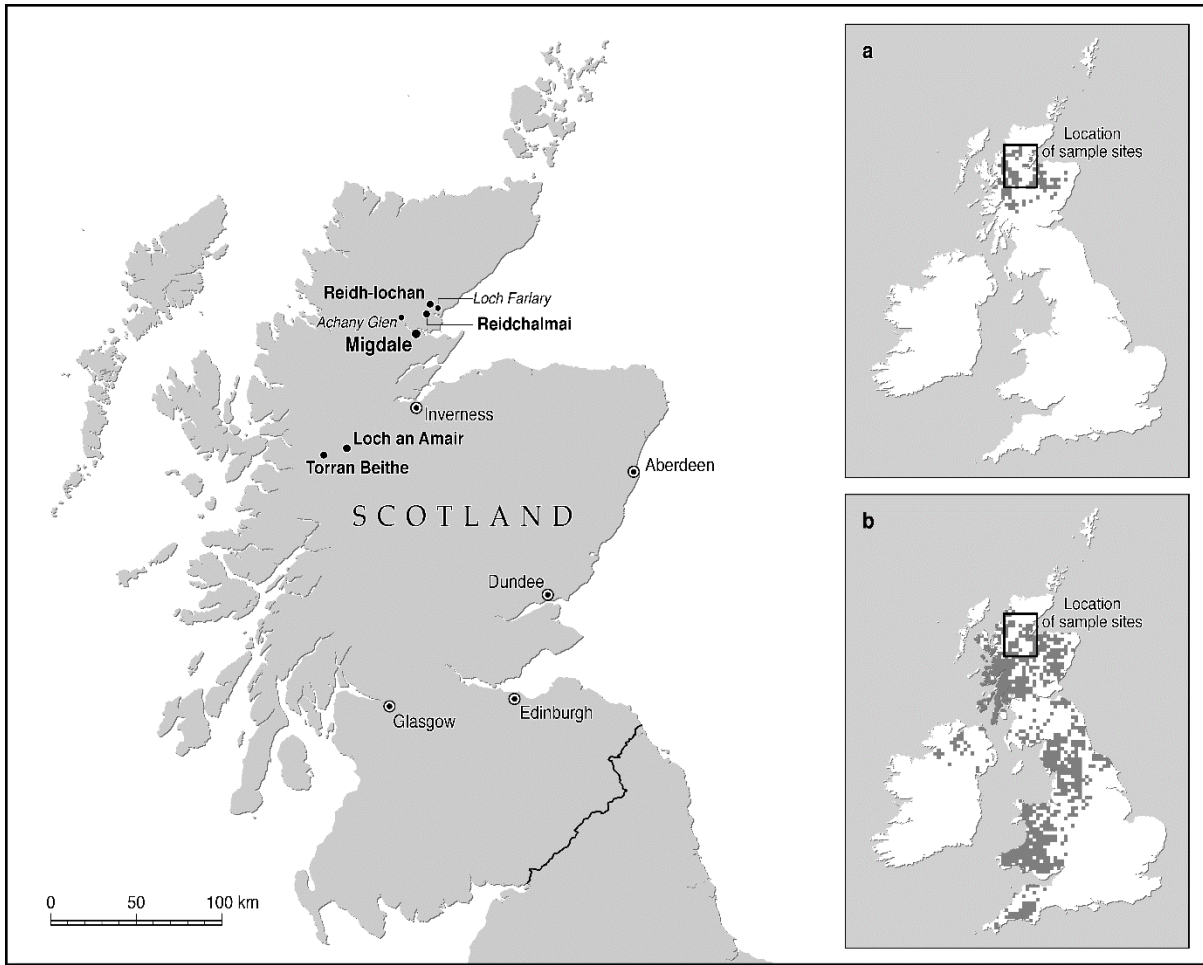
Figure 1. Locations of study sites in northern Scotland, with other pollen studies mentioned in text and current range limits of (a) Caledonian pine forest and (b) old sessile oak woods with *Ilex* and *Blechnum* in UK (not mapped in Republic of Ireland) (source: JNCC)
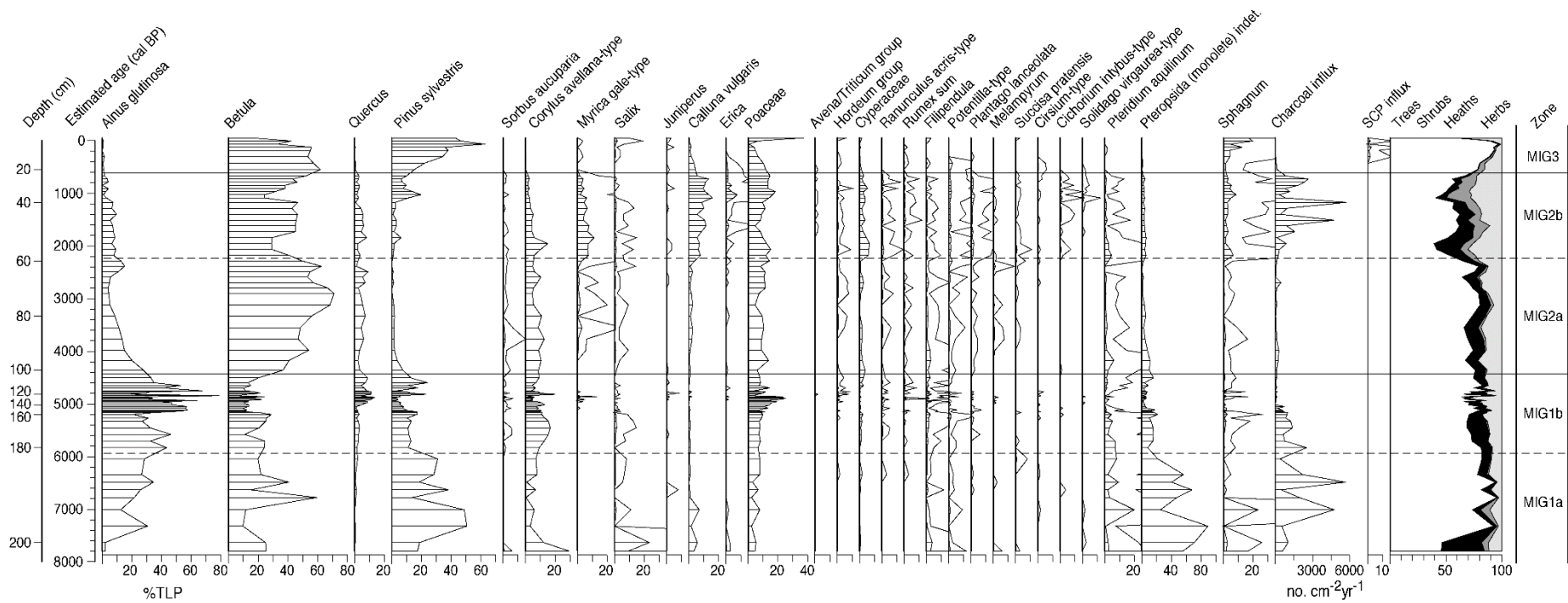
573

574   Figure 2. Selected percentage pollen and spore data from Migdale, with influx data for charcoal and spheroidal carbonaceous particles (SCPs). Clear
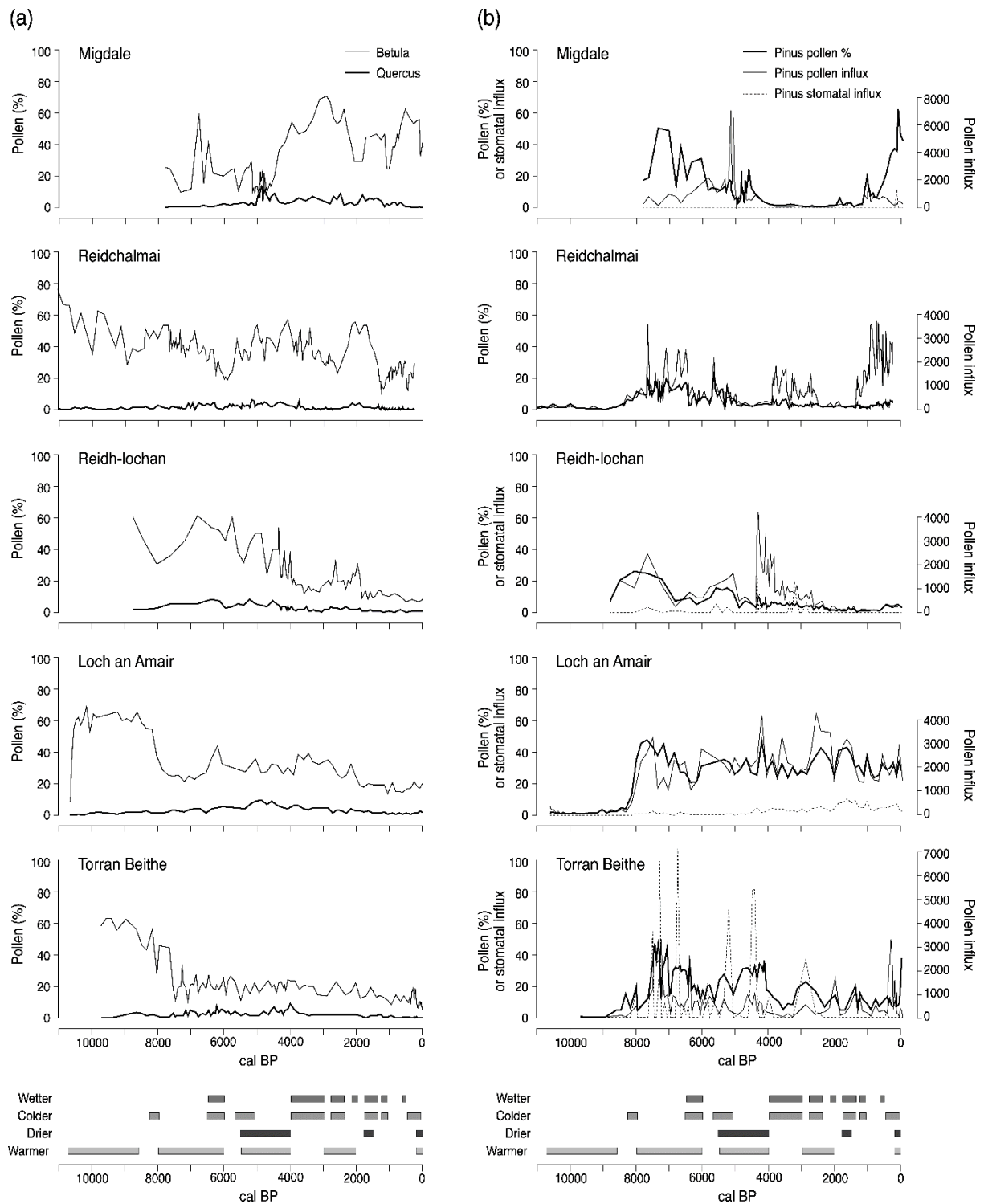575   exaggeration curve x10

576

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)
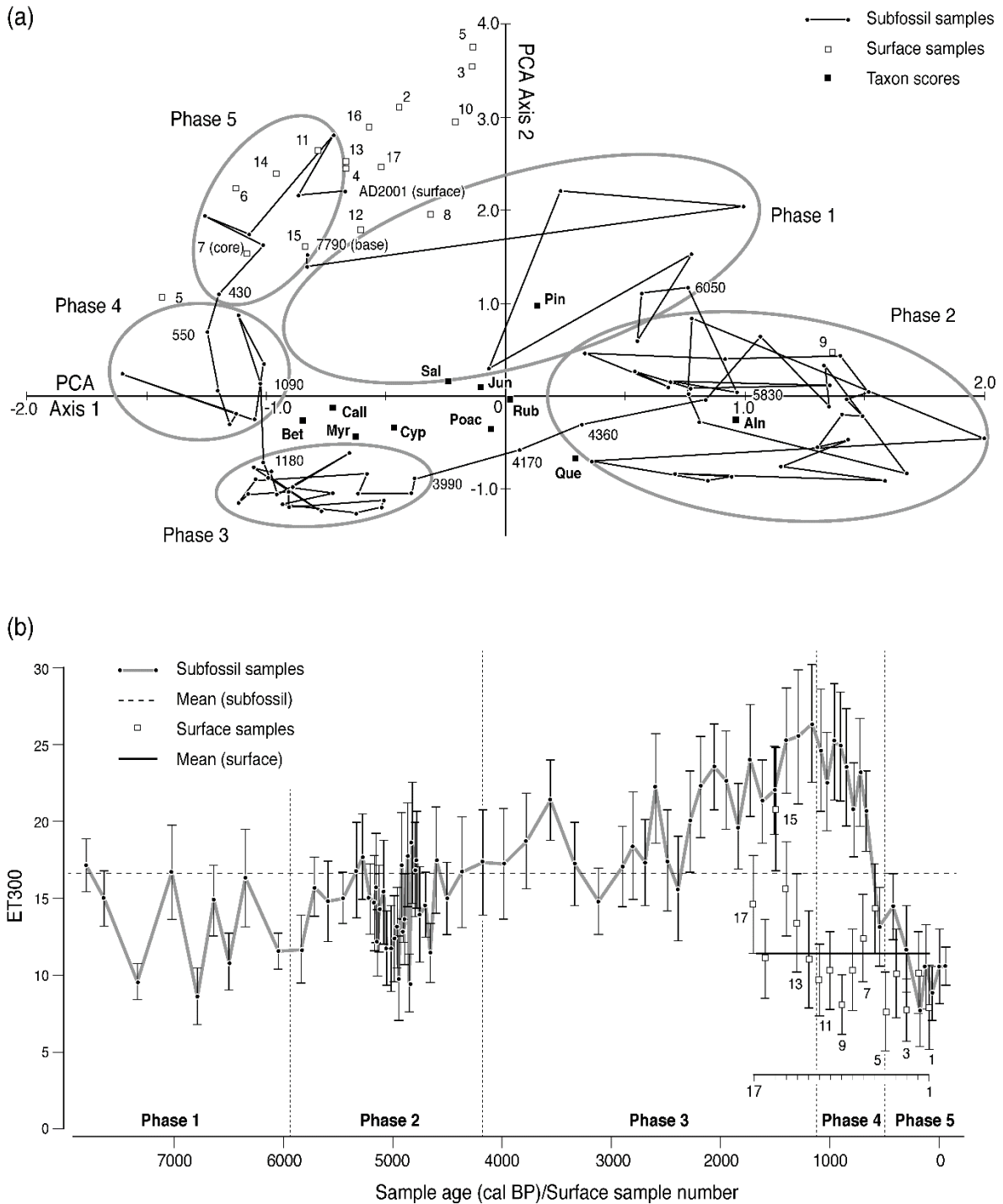
Figure 4. (a) Principal components analysis and (b) palynological richness data for Migdale with 95% confidence intervals, both showing five main communities (phases). Surface samples (1-17) passively ordinated on PCA and plotted against fossil rarefaction values. Taxon abbreviations: Aln – *Alnus*, 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