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Microclimate variability and long-term persistence of fragmented woodland

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ABSTRACT

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

1. Introduction

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

Northern Scotland is an appropriate location to study interactions between microclimate and woodland resilience because it lies on the range edge for temperate woodland and extant woods are highly fragmented, thus exposing them to recruitment and dispersal stresses. Woods have been repeatedly exposed to climate stresses in the past (Tipping, 1994). This is particularly the case for *Pinus sylvestris* L. (Scots pine), which underwent multiple phases of population contraction and expansion in response to Holocene climate shifts (Willis et al., 1998). Favourable microclimates are also important for the adaptive capacity of species with a northerly biogeographical distribution: Scots pine is thought to have survived the last glaciation in northerly refugia, including the continental shelf off northwest Scotland, and its range is predicted to shift northeast in response to ongoing climate change (Bhagwat and Willis, 2008; Matias and Jump, 2012). Understanding the extent to which woods in this region were buffered against smaller

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amplitude climate shifts in the past can help evaluate current and future site potential to retain these populations in the event of more extreme future shifts by indicating whether they served as persistent or transient microclimate refugia (Keppel et al., 2012). Our investigation examines the effects of microclimatic heterogeneity on arboreal resilience in this region. We present new stand-scale pollen evidence for the effects of long-term fragmentation on community composition and diversity in a potentially favourable microclimate, and assess the role of microclimatic buffering on population persistence through a comparison of time series of tree abundance from five sites in contrasting settings across this region.

1.1. Regional context and site description

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

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

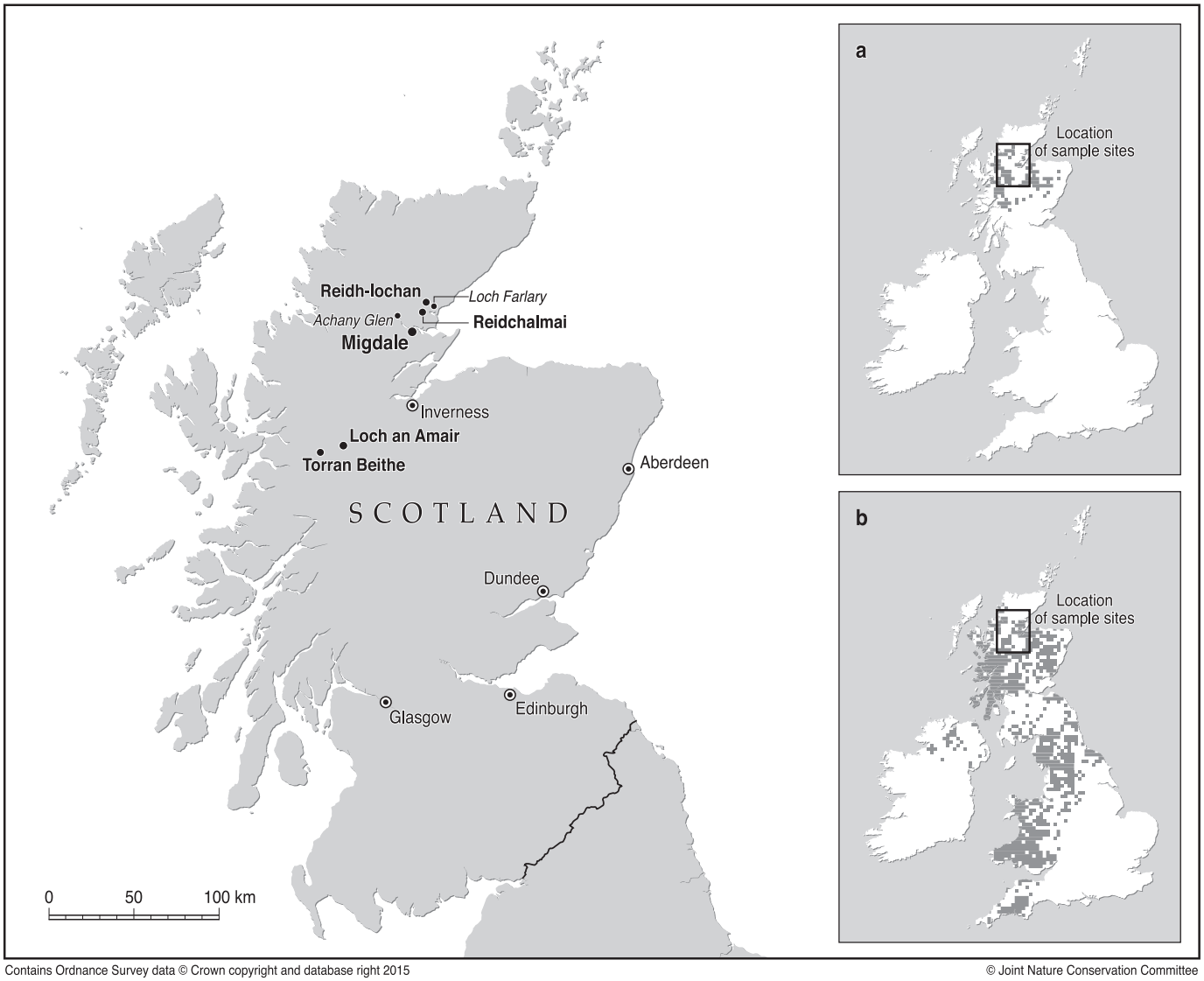

Fig. 1. Locations of study sites in northern Scotland, with other pollen studies mentioned in text and current range limits of (a) Caledonian pine forest and (b) old sessile oak woods with *Ilex* and *Blechnum* in UK (not mapped in Republic of Ireland).
(Source: JNCC).