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The reconstruction of past forest dynamics over the last 13,500 years in SW Sweden

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Abstract

Evidence for unbroken continuity of tree taxa over the last *c.* 13,500 years is presented from a biodiversity 'hotspot' nature reserve in south-west Sweden. Forest composition, continuity, fire and disturbance events are reconstructed using palaeoecological methods. A lake record reveals that *Pinus sylvestris, Betula* spp., *Salix* spp., *Populus tremula* and *Hippophae rhamnoides* were the initial trees scattered in a semi-open, steppe environment. This developed into forest with *Pinus, Betula, Corylus, Alnus, Ulmus* and *Populus* with evidence for frequent fires. Deciduous trees became more significant as fires became less frequent and *Quercus, Fraxinus* and *Tilia* expanded. Fire frequencies increased again in the Bronze Age probably associated with anthropogenic use of the forest, and the first *Fagus sylvatica* pollen was recorded. Burning continued through the Iron Age, but charcoal is briefly absent for a period often referred to as the 'Late Iron Age Lull'. The forest re-expanded with successions involving *Juniperus*, but with an altered composition from the earlier mixed deciduous community, to one dominated by *Fagus*. This is coincident with the first pollen records for *Picea abies*. The early Holocene mixed forest with frequent low-intensity fires is potentially associated with the greatest diversity of red-listed insect species. Forest continuity and the fragmented reservoir populations of old deciduous trees in the *Fagus*-dominated forest today are likely to have been critical in preserving the present-day, species-rich, rare epiphytic flora, wood-inhabiting fungi and invertebrate communities. As many of these forest fragments may become more vulnerable with future climate change, tree diversity with some disturbance may become essential for survival of the endangered saproxylic species.

Keywords

biodiversity hotspot, fire, forest, long timescales, pollen, Scandinavia

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Introduction

A widespread biotic homogenization of forests has taken place in Europe during recent centuries, particularly affecting local tree diversity. One example of such homogenization is the 'borealisation' of southern Scandinavia, which has been driven by both natural forces, such as climate change, and cultural forces, including commercial forestry operations (Lindbladh et al., 2014; Seppä et al., 2009). The replacement of diverse deciduous forests by monocultures of *Picea abies* is associated with the local loss of many species of insect, bryophyte and lichen that are dependent on *Quercus, Tilia, Populus, Alnus* and other trees (Jonsell et al., 1998). The late-Holocene spread of *Fagus sylvatica* through northern Europe has also resulted in a reduced tree diversity throughout large areas of forest in Germany, Denmark and southern Sweden, and this change in forest composition has been driven by combinations of natural and anthropogenic factors (Bradshaw et al., 2010; Giesecke et al., 2011). These major forest changes pose a challenge to nature conservation. If tree diversity is a valid target for management of biodiversity, what type of forest composition should be encouraged and which management tools are appropriate? For restoration purposes, managers would like to know how the present forest composition has developed from earlier conditions and what likely future compositions may develop (Higgs et al., 2014). If current composition differs from the past, how, why and at what rates have these changes occurred? Do past conditions indicate appropriate forest compositions for the future that would maximize diversity and minimize the legacy of anthropogenic modifications? These questions can be addressed through the reconstruction of past forest dynamics using palaeoecological techniques, yet have only rarely been approached in this way (Willis et al., 2010). Palaeoecological investigations can provide relevant information about long-term changes in species diversity, forest continuity, types and frequency of disturbance and the extent of human impact (Bradshaw et al., 2015). There is still debate and uncertainty about the influence of anthropogenic activities and the role of fire on past forest composition and dynamics of southern Scandinavian forest that could be partially resolved by a complete Holocene record from this region (Bradshaw et al., 2010, 2015; Clear et al., 2014; Molinari et al., 2013). All this information is of value in planning successful forest conservation measures (Dietl et al., 2015).

In this paper, we investigate the long-term history of a forested landscape in south-west Sweden (Figure 1). Here, the building of nature reserves has been designed to facilitate the restoration of

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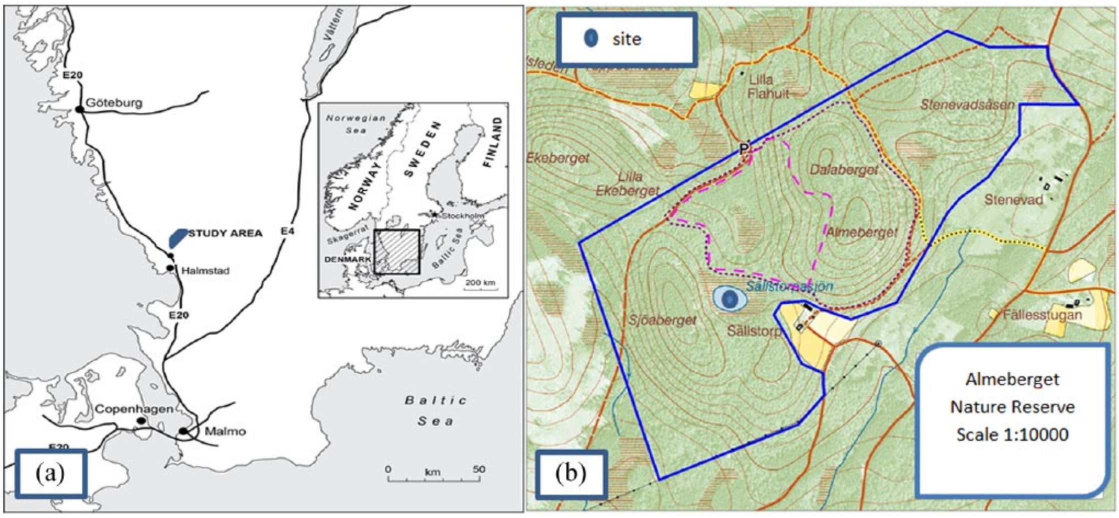

Figure 1. Location map showing (a) the position of Almeberget Nature Reserve in south-west Sweden and (b) the location of the lake within the reserve.

natural forest values over large areas (Bengtsson, 1999). Such forests, detailed on maps from the 1600s (Fritz, 2009), are in Sweden taken to mean 'Old Forest' with long continuity. The maps show that this forest reserve used to be part of a much larger *Fagus* forest, after which there was a sharp decline in areal extent over the following centuries. We present sedimentary pollen assemblages and charcoal influx over the last 13,500 years from a small lake (Figure 1). Continuous late-Glacial and full Holocene vegetational records are limited from this part of the Scandinavian Peninsula. Bradshaw et al. (2015) discussed the relative importance of forest continuity and disturbance dynamics as controls on current biodiversity in north-west Europe and concluded that dynamic processes were of greater significance. Our major purpose is to test the hypothesis that the perceived natural value of rich epiphytes, wood-inhabiting fungi and invertebrate communities so valued today is associated with long-term forest continuity and minor anthropogenic impact over long timescales. We therefore examine the long-term balance between forest continuity and dynamic processes in a currently protected area.

Materials and methods

Study setting

The 70 ha forest reserve at Almeberget is in the temperate vegetation zone of south-west Sweden (Ahti et al., 1968), in low hills (85–150 m a.s.l.) at the edge of the southern Swedish highlands. It is approximately 15 km north-east of the town of Halmstad (Figure 1).

The forest reserve today is dominated by *Fagus*, but there are some mature *Pinus sylvestris* (pine), *Quercus robur* (oak) and *Sorbus aucuparia* (rowan). Younger areas of *Alnus* spp. (alder), *Pinus* and *Betula* spp. (birch) can be found in the valleys, while *Salix* spp. (willow) and *Populus tremula* (aspen) are less common. The oldest *Fagus* trees, which act as hosts for many of the present-day red-listed species (Fritz, 2009; Lindström, 2012) including the extremely rare and endangered *Pertusaria velata* (Fritz and Malmqvist, 2014), appear as large, slow-growing individuals. They date from the late 1790s and into the early 1800s, and there is abundant coarse woody debris on the forest floor in the form of both stumps and trunks. The forest is allowed to develop without direct intervention. Peripheral forests consist of younger, thinned *Fagus* enclaves alongside forest plantations (mainly *Picea*), which are being gradually dismantled and naturally regenerating *Picea* is being removed.

Sällstorpssjön (56°51′1.75″N, 12°53′32.75″E) is a kettle hole lake *c.* 0.5 ha in size in a bowl-shaped basin (Figure 1b). The bedrock is largely pre-Cambrian granite. The site is above the highest marine limit, which in this part of Sweden is *c.* 65 m a.s.l. (Berglund, 1995). The region can be considered to have a maritime climate with high rainfall (*c.* 1000 mm p.a. average 1975–1990) and moderate temperatures (mean January and July temperatures are from −2.4°C to 15.4°C; Syren, 1995).

Fieldwork

The lake sediment was cored through the ice with a 10-cm Russian corer. The sediment/water interface was at 450 cm below the ice. The wetter area immediately around the lake was surveyed and consisted mainly of mixed forest (Table 1), while the upland slopes were drier and dominated by *Fagus* or planted conifers. There are no inflows to the lake (Figure 1b).

Laboratory methods

Six thin sediment samples were sent to the AMS dating facility at Lund University for analysis. All radiocarbon dates were calibrated to a calendar year timescale (cal. BP), where BP refers to 1950. Total concentration of atmospherically deposited lead (Pb) was determined using the Bruker S2 Ranger X-ray Fluorescence Spectrometry (XRF) spectrometer (University of Liverpool). Samples were taken at 5 to 10 cm intervals, freeze-dried at −55°C and then ground into a powder. Peak values for Pb were correlated with dated values from nearby sites (Bindler et al., 2011). An age–depth relationship (Figure 2) was drawn up with both radiocarbon and Pb dates (Table 2), using CLAM software (Blaauw, 2010).

Pollen samples of 1 cm^3 were prepared using standard techniques (Berglund and Ralska-Jasiewiczowa, 1986) with a sampling interval of either 4 or 10 cm throughout the sediment profile. *Lycopodium* tablets were added to allow pollen concentration and influx calculations. Slides were counted at a magnification of 400× and the pollen diagrams were drawn up as a percentage of the sum of terrestrial pollen, excluding aquatics and spores (Figures 3 and 4). The pollen diagrams were divided into periods where major changes in vegetation could be seen. Samples for percentage loss on ignition were burned at 450°C for 4.5 h.

Contiguous 2 cm^3 samples were extracted for charcoal analysis, measured out using water displacement, into test tubes of distilled water. Charcoal pieces larger than 250 µm were counted, and

Table 1. Species recorded around the lake.

Trees and shrubs	Herbs and ferns
Fagus sylvatica	*Rubus chamaemorus*
Quercus robur	*Plantago major*
Betula pendula	*Molinia caerulea*
Pinus sylvestris	*Agrostis canina*
Picea abies	*Hypericum maculatum*
Alnus glutinosa	*Galium sp.*
Sorbus aucuparia	*Scutellaria sp.*
Frangula alnus	*Eriophorum angustifolium*
Salix aurita	*Eriophorum vaginatum*
Juniperus communis	*Juncus effusus*
Calluna vulgaris	*Carex panicea*
Vaccinium oxycoccus	*Carex rostrata*
Vaccinium myrtillus	*Carex lasiocarpa*
Erica tetralix	*Scheuzeria palustris*
	Luzula sylvatica
	Deschampsia flexuosa
	Veronica officinalis
	Brassica sp.
	Rhynchospora alba
	Athyrium filix-femina
	Gymnocarpium dryopteris
	Caltha palustris

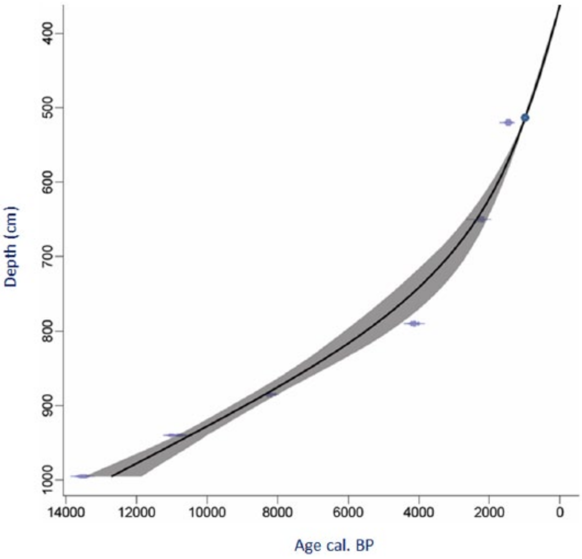

Figure 2. Age–depth relationship for sediments from Sällstorpssjön.

the area (area/cm^2/year) for each unit was estimated using image analysis techniques developed by Mooney and Black (2003) and converted into influx values using the age–depth relationship (Figures 2 and 3). A statistical analysis of the charcoal data was carried out using the charcoal accumulation rate (CHAR) program (Higuera et al., 2007) to determine ‘background’ and ‘peak’ charcoal values with peak magnitude values identifying locally important fire events (Figure 5). The raw charcoal data (units/cm^2/year) were first interpolated to 68-year time steps, a value that corresponds approximately to the median temporal resolution of the entire record (Higuera et al., 2011) to reduce biases in the ability to detect fire events due to variable sample resolution within the record. The resulting interpolated data were then decomposed into background (BCHAR) and peak components with a locally weighted regression robust to outliers, using a 1000-year window. BCHAR was removed by subtraction to obtain a residual series of ‘peak’ events. A Gaussian mixture model was then used to separate the high-frequency component within each overlapping 1000-year portion of the record into ‘noise’ and ‘peaks’, the peak component being the 99th percentile of the noise component. In this way, an individual threshold was calculated for each sample. While the noise component reflects natural and analytical effects (e.g. sediment mixing, sampling), charcoal peaks, shown as red crosses, are assumed to reflect the occurrence of local fire events that are likely to be related to the occurrence of one or more local fires occurring within ca. 1 km from the site (Higuera et al., 2007). Fire history was also described by quantifying the variation of fire return intervals (FRIs, years between two consecutive fire events) and fire frequency over time, smoothed using a locally weighted regression with a 1000-year window (Figure 5). These numerical treatments were carried out using the CharAnalysis program (Version 1.1, available online at http://phiguera.github.io/CharAnalysis/). The changing proportion of the vegetation variance through time explained by the charcoal data was calculated using Redundancy Analysis (RDA; Thöle et al., 2016; Figure 6).

Results and interpretation

Initial vegetation, scattered trees in a semi-open landscape (13,500 cal. BP)

The vegetation reconstruction from the oldest part of this record suggests that light-demanding taxa such as *Juniperus, Empetrum*/Ericaceae, Poaceae, Cyperaceae, *Artemisia* and Chenopodiaceae were growing on possibly unstable soils, interspersed with scattered trees of *Pinus, Betula, Populus* and *Salix* (Table 3; Figures 3 and 4). This is a similar picture to other parts of southern Sweden at this time (Berglund, 1979; Björck and Möller, 1987). The threshold PAR value for the presence/absence of *Pinus* in the immediate vicinity is 500 grains/cm^2/year based on modern-day tree-line pollen traps (Seppä and Hicks, 2006). *Pinus* (PAR) values of between 500 and 1700 grains/cm^2/year at this site suggest local presence of *Pinus* (Figure 3). Indicator taxa such as *Hippophae rhamnoides* (sea buckthorn), associated with minimum mean July temperatures of 11°C (Figure 3), and pollen of *Filipendula* and *Juniperus* (Figures 3 and 4), associated with temperatures of near 10°C (Isarin and Bohncke, 1999), suggest a certain degree of warmth.

Cold steppe conditions dominated by herbs and shrubs (12,700 cal. BP)

A brief period of colder and drier conditions on a European scale between approximately 12,700 and 11,700 cal. BP (Rasmussen et al., 2006) is reflected at this site by decline in pollen of *Pinus* and an increase in herbs (Figures 3 and 4). Glacier activity increased in western Norway (Nesje, 2009), a cold precipitation period with increased snow-bed communities is reported on land (Seppä et al., 2002) and the ice sheet on the Scandinavian Peninsula re-advanced (Anjar et al., 2013). Pollen-based temperature reconstructions from the Norwegian Barents Sea Coast suggest dry conditions, such as can be observed in modern arctic deserts (Seppä et al., 2008). At this site, the organic sediment content decreases, total pollen concentration falls from 605,698 to just over 40,000 pollen/cm^3 (Figure 3) and the landscape is likely to have become more open.

Fire-adapted boreal forest (11,700 cal. BP)

The palaeofire reconstruction over the last *c.* 13,500 years using the macro area/volume charcoal count data, and the results from the CHAR analysis, can be seen in Figures 3 and 5, respectively. The first fire peak identified (Figure 5a) is close to what is the likely Younger *Dryas*/Holocene transition. The tree pollen response at the beginning of the Holocene *c.* 11,700 cal. BP appears to be stepwise (Figure 3) and may be driven by either climatic warming or immigration of the tree species to the region (Giesecke et al., 2011). The previously more open communities

Table 2. Radiocarbon and Pb dates calibrated into calendar years BP using CLAM software (Blaauw, 2010).

	Depth (cm)	^{14}C yr BP	Cal. BP	Probability
Pb date	510–511		950	
LuS 9025	520–521	1570 ± 50	1353–1552	95.0%
LuS 9026	650–651	2235 ± 50	2144–2344	95.0%
LuS 9027	790–791	3765 ± 50	3978–4293	94.9%
LuS 9028	885–886	7380 ± 60	8044–8339	95.0%
LuS 9029	940–941	9520 ± 50	10,648–11,105	91.6%
LuS 9185	995–996	11,655 ± 65	13,334–13,707	95.0%

were gradually replaced by shrubs and trees, including *Juniperus, Betula, Pinus* and *Populus*. The organic sediment content shows a threefold increase (between *c.* 11,700 and 9700 cal. BP), suggesting catchment stabilization. Evidence for early Holocene climatic warming is indicated by the aquatic plant record (Hu et al., 1996), particularly megaspores of *Isoetes lacustris* (Figure 4), where rapid population increases suggest nutrient-rich conditions and rising summer temperatures. At the present day, the minimum temperature necessary for germination success of *Isoetes lacustris*, common in oligotrophic lakes, has been shown to be 12°C (Čtvrtlikova et al., 2014) for 119 days during summer months. Flowering and fruiting of water plants in early Holocene lakes is known from many localities where there is sudden input of base-rich water from rejuvenated soils (Birks and Birks, 2008). Other aquatic vascular plants recorded are *Potamogeton, Myriophyllum* and *Typha* (Figure 4), which, when compared with sites in Poland, central Germany, Belgium and France, suggest that temperatures rapidly approached 13°C (Isarin and Bohncke, 1999).

Hemi-boreal forest with high tree diversity and frequent fires (8500 cal. BP)

Hemi-boreal forest conditions follow, with high tree pollen diversity comprising both temperate and boreal species (Figure 3), and repeated fire events (Figure 5). *Ulmus* and *Alnus* pollen values increase prior to the expansion of *Quercus, Fraxinus* and *Tilia. Corylus* pollen frequency is temporarily reduced, a phenomenon known from many pollen sites in Europe at this time (Giesecke et al., 2011), but quickly returns to close to its former values (Figure 3). The disturbance-adapted *Populus* is an important forest component, possibly due to frequent fires keeping some areas open. Hemi-boreal forest sites show considerably higher charcoal influx values than temperate forest in southern Scandinavia today (Bradshaw et al., 2010). The repeated occurrence of fires (Figure 5a) could be attributable to a combination of a warmer more continental climate, with temperatures 2.5°C higher than at present and markedly dry conditions as described in the literature (Seppä et al., 2005). With climatic conditions and fuel availability more favourable for wildfires, this period is one where 56% of sites from southern Norway, southern and central Sweden and southern Finland show an increase in charcoal abundance compared with the pre-10,000 cal. BP sedimentary records (Clear et al., 2014). A steep increase in sediment organic matter, increase in representation by Arboreal Pollen (AP) and reduction in Non-Arboreal Pollen (NAP) frequencies can also be observed (Figure 3). Frequent fires have been shown to disadvantage *Quercus* (Niklasson et al., 2002), which, despite being recorded just after *c.* 10,600 cal. BP, only increases in pollen frequency as fire-adapted *Pinus* and charcoal influx values decrease (Figure 3). The importance of fire as a driver of vegetation change at this time is emphasized by the peak value of over 20% vegetation variance that can be explained by the charcoal data (Figure 6).

The low values for most herbaceous pollen and fern spores (Figures 3 and 4) after *c.* 8500 cal. BP suggest low light conditions on the forest floor and a rather dense forest structure dominated by a wide variety of deciduous trees and shrubs. The gap in fire peaks (Figure 5a) probably reflects the development of a temperate forest ecosystem with mixed, mainly deciduous pollen taxa recorded (Figure 3). The present-day dividing line between the temperate part of southern Scandinavia and the mixed boreal–deciduous or 'hemi-boreal' zone became established by *c.* 7000 cal. BP (Berglund et al., 2007).

Closed temperate mixed forest dominated by deciduous trees (6700 cal. BP)

The CHAR analysis suggests that fires once again became significant with peak events recorded between *c.* 6700 and 3000 cal. BP (Figure 5a), yet the RDA indicates that the influence of fire on vegetation dynamics was at its lowest values during this period (Figure 6). The first *Carpinus betulus* pollen is recorded *c.* 6000 cal. BP (Figure 3). *Carpinus* is not a common tree in Sweden today and generally does not form pure stands but grows with other deciduous trees, particularly *Quercus* and *Fagus* (Brunet, 1997). It is confined to the southern part of the country (Hallanaro and Pylvänäinen, 2002) and does not grow in the reserve today. *Carnipus* is a shade-tolerant late immigrant to the forests of northwest Europe. It forms a dense canopy which tends to restrict shrub or herb undergrowth.

Frequent intense fires and human use of the forest (4000 cal. BP)

Some indication of limited clearance, possibly from slash-and-burn cultivation, is coincident with a slight increase in *Calluna* pollen (Figure 4), an indication of grazing pressure, *c.* 4000 cal. BP. Cultural indicators include continuous *Plantago lanceolata, Artemisia, Filipendula* and *Ranunculus* (Figure 4). A single cereal-type pollen grain *c.* 3600 cal. BP is coincident with the change in the pattern of charcoal deposition (Figures 3 and 4) and increasing values of the vegetation variance that can be attributed to fire (Figure 6). *Fagus* pollen is first recorded *c.* 4000 cal. BP at the same time as values for *Carpinus*, which is often associated with abandoned pastures in southern Sweden (Bergendorff et al., 1979), increase and *Corylus* decrease (Figure 3). A few tumbled down stone cairns close to the lake may well date from this time although they have not been examined in detail by archaeologists (Karin Hernborg, personal communication, June 2012).

While *Fagus* immigration is frequently associated with disturbance (Bradshaw and Lindbladh, 2005), declining *Corylus* pollen frequencies and increase in *Carpinus* are broadly synchronous within mid- to high-latitude forest ecosystems in Europe *c.* 4000 years ago (Giesecke et al., 2011). This suggests that the temporal pattern of vegetation change might be a partial response to climatic change. Many proxy records from the eastern seaboard of northern Europe show increasingly cold, moist and unstable climate at this time (Seppä et al., 2005). In Sweden, this can be associated with an increase in regionally reconstructed lake levels (Digerfeldt and Håkansson, 1993), a rise in groundwater (Hammarlund et al., 2003) and inferred hydrological changes in local bogs in Halland (De Jong et al., 2006; Gustavsson et al., 2009).

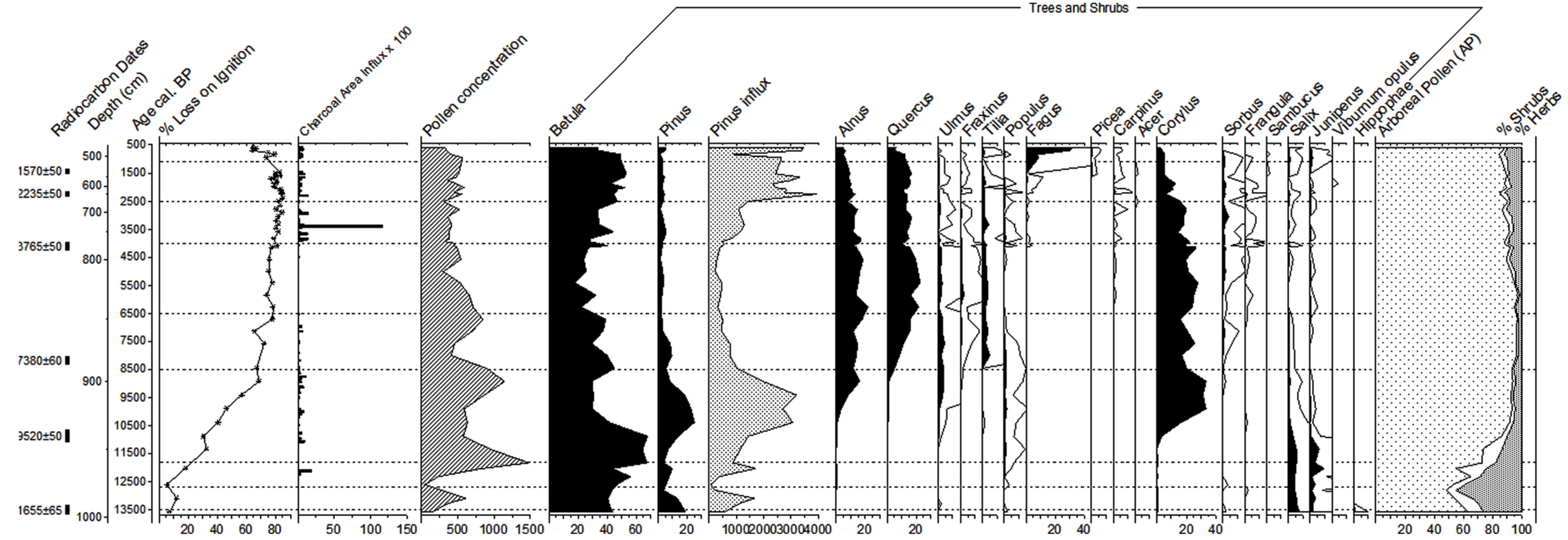

Figure 3. Pollen percentage diagram from Sällstorpssjön showing trees, shrubs and the AP/NAP relationship. The percentages are calculated on the sum of terrestrial pollen. Loss on ignition is the percentage weight loss of organics at 450°C. Exaggeration of selected taxa is ×10.

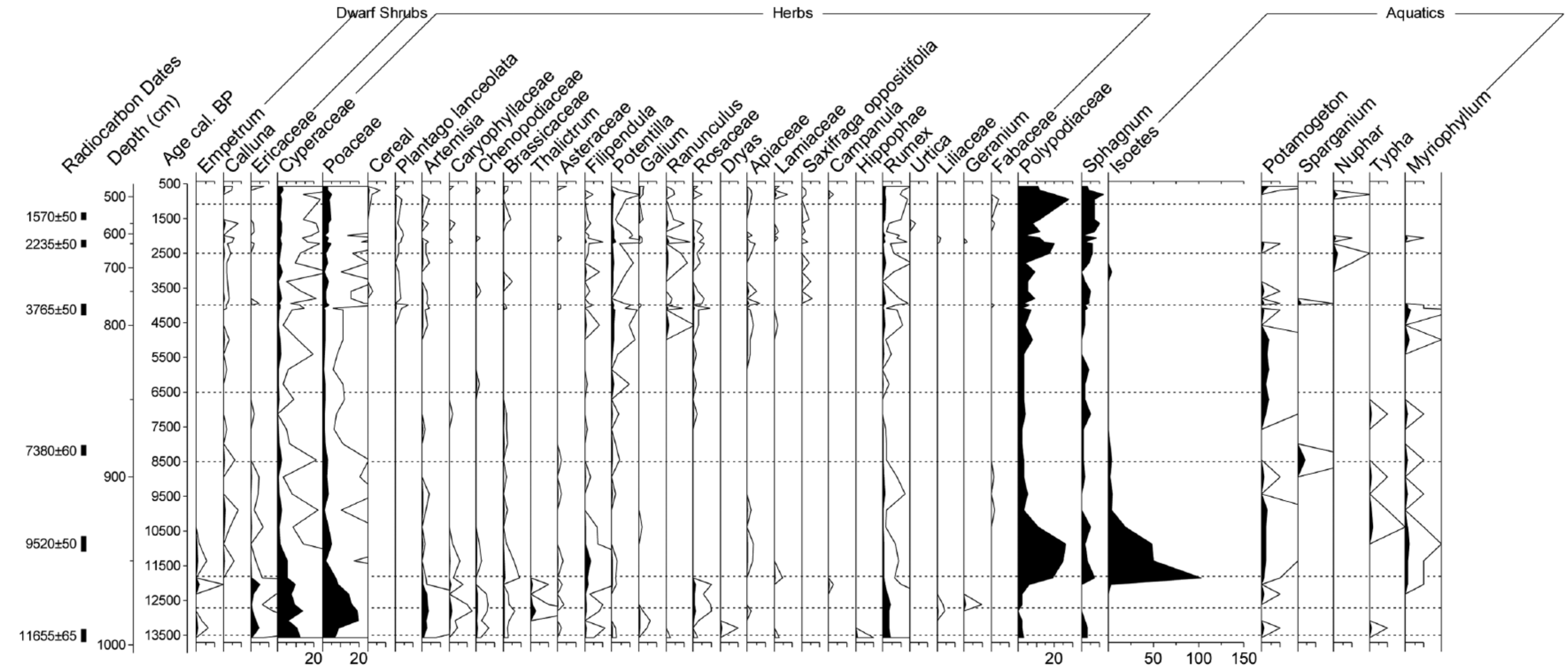

Figure 4. Pollen percentage diagram from Sällstorpssjön showing dwarf shrubs, herbs and aquatics. The herb percentages are calculated on the sum of terrestrial pollen. Aquatics and Polypodiaceae are calculated based on the sum of terrestrial pollen plus aquatics and terrestrial pollen plus Polypodiaceae, respectively. Exaggeration of selected taxa is ×10.

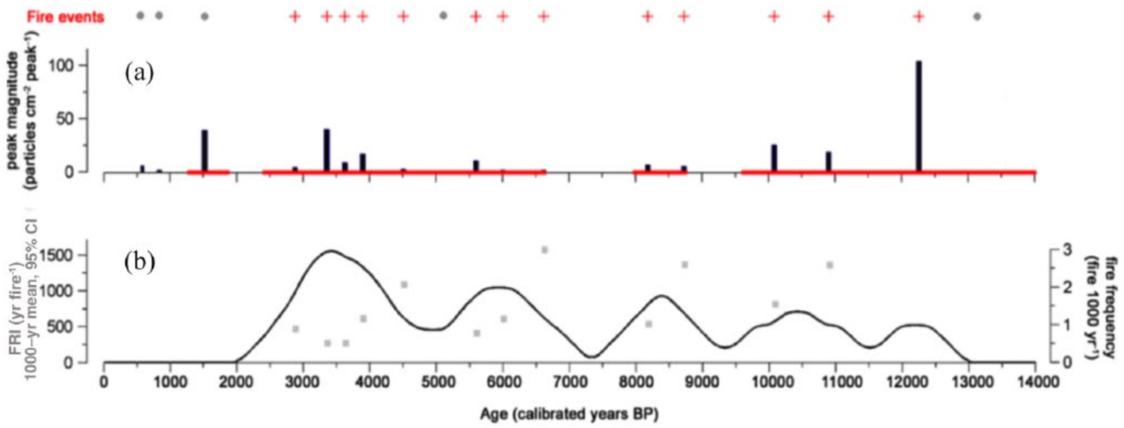

Figure 5. (a) Reconstructed palaeofire peaks and (b) fire return interval. No sediment younger than 500 cal. BP was recovered.

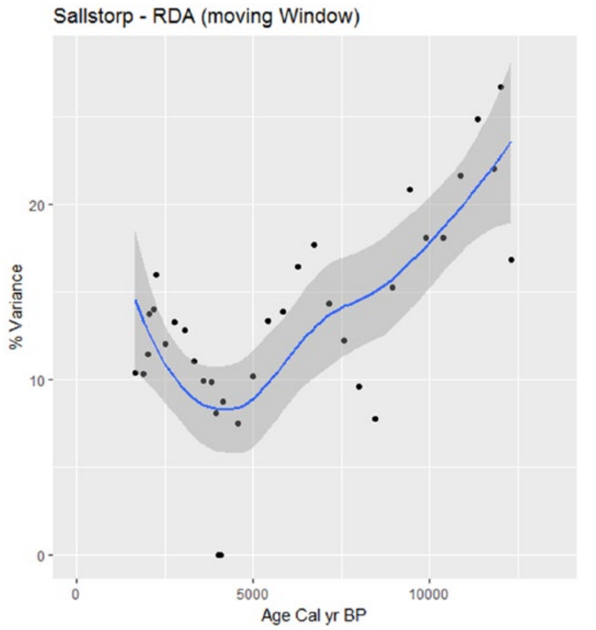

Figure 6. Redundancy Analysis showing the changing percentage of vegetation variance attributable to charcoal.

So, there might be underlying climatic control to the shifting nature of the vegetation composition in addition to the first weak signs of anthropogenic activity in the forest.

Many Bronze Age pollen records in south-western Sweden and Denmark (Hannon et al., 2008; Odgaard and Rasmussen, 2000; Sköld et al., 2010) show this time to be one of marked cultural impact, with deforestation and extensive vegetation alteration. At Yttra Berg, a site rich in clearance cairns and stone walls, at a similar elevation but further north and 27 km from the Halland coast, the forest is thought to have been initially used for herding or transhumance activities with micro-charcoal evidence suggesting clearance by fire to benefit grazing from *c.* 4000 cal. BP (Sköld et al., 2010). On the Bjäre peninsula, a short distance south, with a very high density of well-preserved burial mounds throughout the Bronze Age, forest cover is generally estimated to be as little as 20–40%, and the mounds were probably built to be visible in an open landscape (Hannon et al., 2008). It has been argued that there was a more intense use of the landscape at that time rather than in the Iron Age because of a coastal culture and fertile soils, although in some local settings deforestation may have taken place slightly later at *c.* 3500 cal. BP (Brown et al., 2011). The few macro-charcoal sites available show Bronze Age burning was taking place on the landscape, and charcoal fragments were recovered from the base of many burial mounds (Hannon et al., 2008). Episodic burning affected many decorated Bronze Age rock carvings (Brown et al., 2011). While Bronze Age activity had a large impact on forest structure and composition over much of south-west Sweden, canopy cover and old trees may have persisted longer in upland marginal sites with poor soils such as in Almeberget Nature Reserve.

Mixed deciduous forest and wetter conditions (2500 cal. BP)

A decline in the mixed deciduous pollen communities and an increase in *Betula* can be observed during the Iron Age (Figures 3 and 4), coincident with the first major increase in *Fagus* pollen suggesting a reduction in anthropogenic use of the forest. This time is characterized by a period of rapid environmental change and cooler wetter conditions seen in many proxy records (Olsson et al., 2010). Fire peak events cease to be significant (Figure 5a) with a decline in fire incidence (Figure 3), and climatic conditions may have become unfavourable for fire, especially in these upland marginal sites. There may have been some regeneration and closing over of small glades, which *Fagus* would have been in a good position to exploit.

The residual remnants of the former mixed temperate forest are mainly around the lake (Table 1) and on rocky slopes which are inaccessible to grazing game. The marked increase in *Pinus* and *Picea* pollen values reflect the tree planting forestry programmes of the 19th and 20th centuries (Bradshaw et al., 2015). Otherwise, the forest reserve is today dominated by *Fagus*. The lack of charcoal in the uppermost sediments is a likely reflection of general fire suppression in Scandinavia over the last 200 years (Niklasson and Granström, 2000) and might have further facilitated the rise to dominance by *Fagus*. The RDA showed that the changing percentage of the pollen assemblage variance explained by the charcoal data declined continuously from *c.* 25% at the opening of the Holocene to a minimum value of less than 10% by 5000 cal. yr BP. This value increased during the late Holocene to almost 15% by the end of the record (Figure 6).

Consequences of long timescales for conservation and restoration

The late-Glacial and Holocene vegetational history of south-west Sweden shows continuous change driven by climate, a dynamic fire regime and human impact. Climatic change was most influential during the late Glacial and the early Holocene, while human activities were the dominant drivers of forest

Table 3. Summary of palaeoecological dynamics in Almeberget Nature Reserve.

Time periods	Archaeological age	Palaeoecological evidence
13,500–12,700 cal. BP		Light-demanding taxa *Juniperus, Hippophae, Empetrum*, Ericaceae, Poaceae, Cyperaceae, *Artemisia* and Chenopodiaceae on possibly unstable soils, with *Pinus, Betula, Populus* and *Salix* (Figures 3 and 4).
12,700–11,700 cal. BP	Palaeolithic 12,000–9600 BC	A decline in *Pinus* and increase in herbaceous taxa, particularly Poaceae (Figure 4). Organic sediment content decreases and total pollen concentration falls from 605,698 to just over 40,000 pollen/cm^3 (Figure 3). This is one of the few sites in Fennoscandia with a sedimentary charcoal record at this time (Clear et al., 2014).
11,700–8500 cal. BP	Mesolithic 9600–4000 BC	Tree pollen expands stepwise with Holocene warming together with a threefold increase in the percentage of organic sediment content. Fire-adapted *Pinus* has its highest values. *Ulmus* and *Alnus* values increase. The disturbance-adapted *Populus* remains an important forest component. There is a continuous charcoal record.
8500–6700 cal. BP		*Quercus, Fraxinus* and *Tilia* increase. Tree pollen diversity is high, comprising both temperate and boreal species. Low or discontinuous records of most herbaceous types and fern spores (Figure 4).
6700–4000 cal. BP	Neolithic 4000–1800 BC	A wide variety of deciduous trees with *Quercus, Ulmus, Tilia* and *Fraxinus* as the main dominants together with *Alnus, Betula, Salix, Sorbus* and *Frangula*. *Populus* only occasionally present. *Pinus* has declined to low frequencies. *Carpinus betulus* pollen first recorded.
4000–2500 cal. BP	Bronze Age 1800–500 BC	*Fagus* first recorded. Values for *Carpinus* increase and *Corylus* decrease towards the end of the period. Cultural indicators include continuous *Plantago lanceolata, Artemisia, Filipendula* and a single cereal grain *c.* 3600 cal. BP.
2500–1400 cal. BP	Iron Age 500 BC–AD 1100	Decrease in *Corylus* and decrease in *Ulmus* and *Alnus* frequencies. Increase in *Betula* and Polypodiaceae spores. First major increase in *Fagus* and the initial pollen evidence for *Picea*.
1400–500 cal. BP	Medieval AD 1100–1500	Decline of mixed deciduous taxa and rise to dominance of *Fagus*. *Ulmus, Fraxinus, Corylus, Sorbus* and latterly *Quercus* decrease. Poaceae and Cyperaceae values maintained with *Rumex acetosa, Galium*-type, *Filipendula* and low cereal pollen values. A subsequent peak in Polypodiaceae spores is followed by successions involving *Juniperus* and *Salix* and increasing *Fagus* frequencies as cultivation is abandoned.

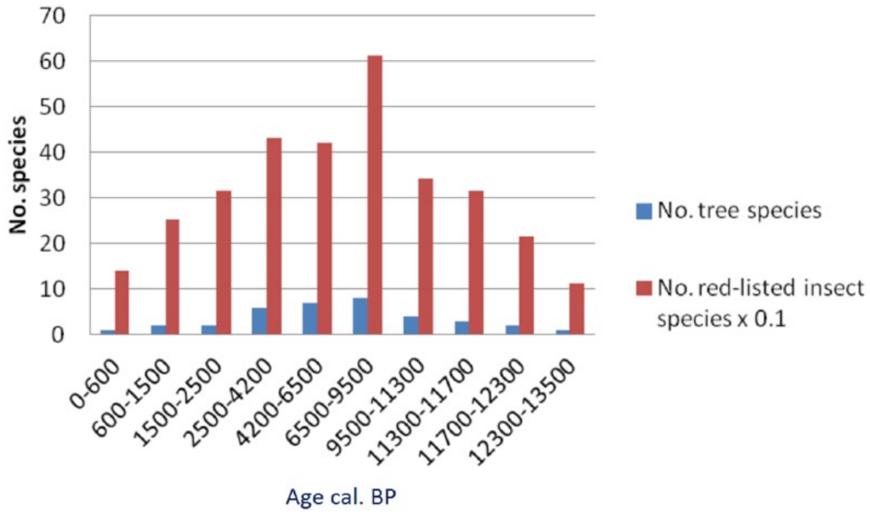

Figure 7. The number of red-listed saproxylic insects (red) associated with specific dominant and sub-dominant tree species (blue) at Almeberget Nature Reserve.

composition during the late Holocene (Kuosmanen et al., 2018; Wohlfarth et al., 2018). At Almeberget Nature Reserve, natural fire had its greatest influence during the early Holocene, then declined in importance as a driver of vegetation change until anthropogenic burning developed during the late Holocene (Figure 5). What were the consequences of these changes for forest biodiversity, particularly components of the saproxylic complex? The palaeoecological record of insects, bryophytes and lichens is poor, but a record of possible diversity change could be indicated by the current host specificity of these species, which has been established for 542 red-listed saproxylic insect species in Sweden (Jonsell et al., 1998). By matching the number of host-specific insects to the number of dominant/sub-dominant tree species occurring during different time periods, a clear pattern of potential diversity change through time is apparent (Figure 7). Red-listed insects gradually increase in diversity from the late Glacial until *c.* 9500–6500 cal. BP when the forest had its most diverse tree flora, but was not as closed in structure as during *c.* 6500–4200 cal. BP. The subsequent increase in human impact (4200–2500 cal. BP) initially had little effect on potential insect diversity. Indeed, the slight opening of the canopy through disturbance may have favoured trees with slightly greater numbers of associated red-listed insects. Subsequently, increasing human impact was associated with continuous loss of tree and red-listed insect diversity (Figure 7).

This analysis gives an indication as to when forest conditions might have been best suited for maximum diversity of red-listed species in the past. This was the period in the mid-Holocene, when *Quercus, Corylus, Alnus, Tilia, Fraxinus, Ulmus* and *Sorbus* were the major forest trees providing far more substrate diversity for the saproxylic species than is available at present (Figure 3). Much surviving biological value in the reserve is linked to lichens which can switch tree hosts more easily than other species groups (Ellis, 2012; Fritz et al., 2008). All these trees still grow in the region at present but in small populations, which are severely depleted in size, and some do not grow in the *Fagus*-dominated Nature Reserve. Their reduced importance is most likely due to management history rather than significant changes in climate (Björse and Bradshaw, 1998).

Conclusion

The record of human–nature interactions with the environment goes back much further than we often believe. A dynamic equilibrium exists where there is not a single climax or a single reference but a range of variability within which there are systems driven by dynamic combinations of natural and anthropogenic disturbance. During the early to mid-Holocene, more species-rich forest composition existed within the constraints imposed by climate in southern Sweden. Human use of the forest has resulted in significant shifts in canopy dominants, even in this Nature Reserve where anthropogenic influence has been low impact. When fire regimes have been periodically severe, the disturbance has exerted a considerable impact on forest composition and structure. Suppression of fire, as is documented in southern Sweden over the last 200 years (Bradshaw et al., 2010), along with the national planting programmes of the 20th century have assisted *Fagus* and *Picea* to obtain canopy dominance.

Nature reserve planning in Swedish forests is often species driven, based on which red-listed species live on the major stand dominants today (Fritz, 2009). The evidence from the paleoecological record shows that many forests have undergone structural and compositional changes (Björse and Bradshaw, 1998). Forests are not steady-state systems, so knowledge of the range of variability over long timescales is valuable for the future. Appropriate management goals might usefully combine preservation of existing diversity with restoration of former diversity, guided by the palaeoecological record. An appropriate restoration goal might be to encourage the spread of mixed deciduous trees and their associated fauna and flora. Diverse forest systems are more resilient to unanticipated impacts and reduce risk of biodiversity loss. This forest ‘hotspot’, in contrast to the surrounding landscape, can claim to have unbroken forest continuity throughout the Holocene, albeit with constantly changing structure and composition and some disturbance. A similar conclusion was reached by Lindbladh et al. (2008) and Bradshaw et al. (2015) based on data from four small hollows all located close to the study site. Taken together, these analyses support our initial hypothesis. The most likely reason for the rich epiphytes, wood-inhabiting fungi and invertebrate communities so valued today is that forest continuity has been maintained despite significant tree composition dynamics. There has been anthropogenic impact but less than that recorded from the more heavily utilized coastal environments or nearby sites such as Yttra Berg (Sköld et al., 2010). The relatively low-intensity anthropogenic disturbance that Almeberget Nature Reserve has had in the past may well be a feature critical to maintain its biodiversity in the future.

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