



Long-term processes at Almeberget Nature Reserve: a 'hotspot' forest of high conservation interest

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Titel: Long-term processes at Almeberget Nature Reserve: a 'hotspot' forest of high conservation interest Rapportnummer: 2020:1 ISRN: LSTY-N-M--2020/01--SE Författare: Gina E. Hannon Bild förstasida: Foto - Mikael Stenström, bild över Sällstorpssjön, mellan kullarna Sjöberget och Almeberget i Almebergets naturreservat i Hallands län.

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Sammanfattning på svenska

Vegetationens utveckling i Almebergets naturreservat under de senaste 13 500 åren

- en studie som indikerar behov av kursändring inom restaurering av ädellövskog

Att lämna skog i naturreservat för fri utveckling är en ofta tillämpad strategi för bevarande och restaurering, men detta kan underskatta betydelsen av störningsdynamik för det långsiktiga bevarandet och utvecklingen av skogens biologiska mångfald. Den här studiens huvudsakliga syfte har varit att undersöka de långsiktiga påverkansfaktorerna av biologiska mångfaldsvärden i en nordeuropeisk blandskog; Almebergets naturreservat i sydvästra Sverige.

Med hjälp av pollen- och kolanalyser från sediment från en sjö och en liten myr, har den historiska vegetationsdynamiken rekonstruerats. Analyserna visar på obruten trädkontinuitet under de senaste cirka 13 500 åren. Banbrytande analyser av forntida DNA som extraherats från sjösedimenten, gav stöd för och tillförde vissa taxonomiska detaljer till pollenanalysresultaten. Pollenprov från sjön avslöjar att *tall, björk, viden, asp* och *havtorn* var först att kolonisera en halvöppen stäppmiljö efter att inlandsisen dragit sig tillbaka från området. Stäppen utvecklades till en skog med *tall, björk, hassel, al, alm* och *asp*, påverkad av frekventa bränder. Lövträd blev mer betydelsefulla när brandfrekvensen minskade och *ek, ask och lind* expanderade. Närvaron av brand ökade igen under bronsåldern, förmodligen förknippat med en viss mänsklig aktivitet och nyttjande av skogen. Nu registrerades även det första pollenkornet från *bok*. Bränder fortsatte genom järnåldern, men bevis för detta i form av kolfragment är frånvarande under en period som ofta kallas "Late Iron Age Lull", under sen järnålder. Skogen expanderade sedan åter, med successioner innehållande *en*, senare med en förändrad sammansättning från *blandlöv* till *bokdominerad* skog. Detta sammanfaller med de första registreringarna av pollen från *gran*. Storskaliga planteringsprogram med *gran* och *tall* på landskapsnivå sedan början av 1900-talet, tillsammans med effektiv brandbekämpning, har varit avgörande för den nutida skogliga sammansättningen.

I studien har även en uppskattning gjorts av variationen i mångfald av rödlistade skalbaggar associerade med den dominerande trädslagssammansättningen. Under tidig Holocen (9500 – 6500 år före nutid) var skogen variationsrik i sin struktur och byggdes upp av många olika trädslag. Bränder med låg intensitet förekom frekvent. Den här tidsperioden är potentiellt förknippad med den största mångfalden av rödlistade insektsarter.

Skogskontinuitet och de fragmenterade restpopulationerna av gamla lövträd i den idag *bokdominerade* skogen, har troligtvis varit avgörande för att bevara den nuvarande artrika och sällsynta epifytiska floran, vedlevande svampar och ryggradslösa djur. Störningshändelser har präglat skogens långsiktiga dynamik. Eftersom många av dessa skogsfragment kan bli mer sårbara med framtida klimatförändringar, kan <u>trädmångfald med</u> <u>viss störning</u> bli avgörande för framtida överlevnad av hotade arter knutna till ädellövskog.

Nyckelord: skogens biologiska mångfald, brand, skogskontinuitet, vedlevande arter, långtidsperspektiv, hemiboreal skog, pollen, mänsklig påverkan, forntida DNA.

English abstract

Non-intervention in forest reserves is a tried and tested approach to conservation and restoration, but this may underestimate the importance of disturbance dynamics for the long-term maintenance of important components of forest biodiversity. Here, the major purpose is to examine the long-term controls on the biodiversity values of a north European mixed forest, Almeberget forest reserve, in south-west Sweden. Vegetation dynamics reconstructed from lake sediments and a small hollow within a marsh complex, using pollen and charcoal analyses, have shown evidence for unbroken continuity of tree taxa over the last c.13 500 years. Pioneering analysis of ancient DNA extracted from the lake sediment supported and added some taxonomic detail to the pollen analytical results. The 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 some 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. Large scale planting programmes with Picea and Pinus since the beginning of the 1900s, together with fire reduction, have been significant recent features.

Disturbance events have been characterized, and the changing diversity of redlisted beetles associated with the dominant tree species estimated. 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.

Key words: Forest Hotspot, Fire, Forest Continuity, Saproxylic Species, Long Time Scales, Hemiboreal Forest, Pollen, Human Impact, Ancient DNA.

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1. Introduction

Forest is the natural vegetation cover for most of Europe, yet in many countries, forest cover has become rare. A widespread biotic homogenization has taken place 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 (Seppä et al. 2009; Lindbladh et al. 2014). 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 protection of forest habitats that offer a range of woody substrates of varied age and condition is one of the top priorities of Natura (2000). These habitats are often rich in red-listed species of insects, bryophytes, lichens and fungi of the 'saproxylic complex' (Speight, 1989) which can be used as indicators of habitat worthy of protection (Nitare and Norén, 1992; Gustafsson et al. 1999; Berg et al. 2002; Fritz, 2011). Protection of such forest reserves typically involves non-intervention within core areas and encouragement of a variety of suitable substrates such as dead wood, coarse woody debris in the form of both stumps and old tree trunks in surrounding buffer zones to facilitate the spread of red-listed and other forest species (Halme et al. 2013). It is an implicit assumption in most forest conservation projects, that the core forest habitat has a long history of little or no human intervention of the type that has led either to prolonged breaks in forest continuity, to sustained browsing pressure from domestic animals, or to an increased frequency of burning (Esseen et al. 1997; Ratcliffe, 1977).

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; Bradshaw et al. 2015). 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, and provide guidelines to tackle the influence of future climate change? While non-intervention in core areas and establishment of surrounding buffer zones is a tried and tested approach to forest conservation and restoration, there has been a tendency to underestimate the long-term resilience of certain red-listed species of the insects, fungi, lichens and bryophytes to various types of disturbance (Willis et al. 2010) and therefore overestimate the importance of long-term absence of human impact on forests for conservation value (Bradshaw et al. 2015). For example, Segerström et al. (1994) using pollen data found that a northern Swedish boreal forest that had been cleared by human activities between AD 1500 and 1700 was today indistinguishable in overall species content from unmanaged primary forest. This is important as setting standards too high for the fragments of forest to protect, limits the number of potential forest conservation objects in the heavily exploited landscapes of north-western Europe.

Palaeoecological investigations can provide relevant information about longterm 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, the establishment of *Fagus sylvatica* and dynamics of southern Scandinavian forest that could be partially resolved by a complete Holocene record from this region (Bradshaw et al. 2010; Molinari et al. 2013; Clear et al. 2014; Bradshaw et al. 2015).

In this report, the long-term vegetation and disturbance history in the forested *Fagus* environment at Almeberget Nature Reserve is examined using palaeoecolgical archives. Here, in the foothills of the southern Swedish highlands, in the province of Halland, south-west Sweden (Figure 1), is where the building of nature reserves has been designed to facilitate the restoration of natural forest values over large areas (Bengtsson, 1999). Such inland *Fagus sylvatica* forests, detailed on maps from the 1600s, are in Sweden taken to mean 'Old Forest' with long continuity (Fritz, 2009). The maps show that the 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. Little is known about the forests that pre-date the maps. Pollen analyses from sedimentary archives are very useful in this respect as they help to link the contemporary environmental status with that of the past. Almeberget is an important 'hotspot' for biodiversity of saproxylic species, rich epiphytes and wood inhabiting fungi (Fritz, 2009). It is now included in the Natura 2000 network of protected areas, set up to promote and protect Europe's most valuable habitats due to the rich and endangered red-listed taxa present on the old trees (Figure 2) (Fritz, 2009).



Figure 1: Almeberget Nature Reserve, southern Swedish highlands, Halland.



Figure 2: Endangered red-listed taxa (Fritz, 2009) on older *Fagus* stumps, surrounded by mixed age, younger *Fagus* stands.



Figure 3: Sällstorpssjön, between the hills of Sjöaberget and Almeberget.



Figure 4: Small Hollow in marsh below Sällstorpssjön.

Sedimentary pollen assemblages, charcoal influx and concentrations of mineral elements over the last c.13700 years from two sites are examined from the reserve: a small lake and a neighboring small forest hollow (Figures 3, 4 and 5). A continuous vegetational record such as these, are limited from this part of the Scandinavian Peninsula. A pilot study to explore the potential of ancient DNA preserved in temperate lake sediments was undertaken to develop interactions between molecular genetics and palaeoecology. Long-term disturbance history and composition dynamics, particularly the successional history of the important 'Keystone' species, such as *Fagus sylvatica*, upon which much of the present-day biodiversity status is based (Fritz, 2011), is examined in this report. Tree immigration and colonization are tracked in the early Holocene (11 700-8000 cal. BP), together with forest development, disturbance history, environmental change, anthropogenic use of the forest and arrival of the late immigrants Carpinus betulus, Fagus and Picea abies. Bradshaw et al. (2015) discussed the relative importance of forest continuity and disturbance dynamics as controls on current biodiversity in northwest 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 examine the long-term balance between forest continuity and dynamic processes in a currently protected area and propose appropriate management measures (Brunet et al. 2010).

2. Study setting, sites, present vegetation, field and laboratory methods

2.1. Study setting

The 70-ha forest reserve at Almeberget is in the temperate vegetation zone of south-west Sweden (Ahti el 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 5).



Figure 5: Location map showing the position of Almeberget Nature Reserve in south-west Sweden. The positions of the pollen sites are marked as blue dots. Skötselkarta 2 © Lantmäteriet, 2006. Ur GSD Fastighetskartan, 106-2004/188-N

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* (Figure 6) appear as large, slow growing individuals (Fritz and Malmqvist, 2014). They date from the late 1790's 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 (Table 1).



Figure 6: Pertusaria velata (Fritz, pers comm. 2012)

Table 1: Description of land in hectares (source Länsstyrelsen, 2011).

Land cover	ha
Broadleaves	48.3
Deciduous (alder) swamp woods	6.1
Coniferous swamp	1.5
Spruce	11.0
Clear-felled areas	2.2
Mire	0.2
Water	0.5
Other	0.2
Total	70.0

2.2. Fieldwork

Sällstorpssjön (56°51'1.75"N, 12°53'32.75"E) is a small kettle hole lake nestling between the hills of Sjöaberget and Almeberget (Figures 3 and 5). There are no inflows to this closed lake basin. The small hollow ($c.20 \times 40m$), is part of a marsh to the north-east of the lake and at a lower elevation (Figure 4 and 5). The bedrock is largely Pre-Cambrian granite (Fredén, 1995). Both sites are 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, annual average 1975-90) and moderate temperatures (mean January and July temperatures are from -2.4°C to 15.4°C (Syren, 1995).

A vegetation survey was carried out to establish all major trees, shrubs and herbs around Sällstorpssjön (Table 2). The wetter area immediately around the lake consists of mixed forest (Figure 7) while the upland slopes are drier and dominated by *Fagus* (Figure 8) or planted conifers. A survey was also made within a 150 m radius from the small hollow (Table 3). Six transects, each 150 m in length, were surveyed for numbers of trees of diameter larger than 10 cm at breast height at 50 m intervals (Figure 9), and numbers of trees were recorded around the coring point (Table 4). A large range of species were recorded, with *Pinus* and *Alnus* dominating. The *Picea* plantations crossing transects U4, U5 and U6 explain the large numbers of *Picea* seen throughout these transects.



Figure 7: Mixed forest around the lake.



Figure 8: Dry upland slopes dominated by Fagus sylvatica.

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	<i>Galium</i> 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
Vaccinum myrtillus	Carex lasiocarpa
Erica tetralix	Scheuzeria palustris
	Luzula sylvatica
	Deschampsia flexuosa
	Veronica officinalis
	Brassica sp.
	Rhynchospora alba
	Athyrium filix-femina
	Gymnocarpium dryopteris
	Caltha palustris

Table 2: Main trees, shrubs, herbs and ferns recorded around the lake, July 2011.



Figure 9: Transects of the forest in the marsh, carried out at 50 m intervals (U1 – U6), and by the coring site (S1- S2). The position of the pollen site is marked with a red cross (Williams, 2012).

Transect	Trees	0-50m	50-100	100-150	total
U1	Fagus	14	16	24	54
	Pinus	1	0	3	4
	Picea	1	0	1	2
	Betula	1	0	0	1
U2	Fagus	15	12	9	36
	Pinus	0	4	0	4
	Picea	0	1	5	6
	Betula	0	1	6	7
U3	Fagus	16	13	15	44
	Pinus	0	3	2	5
	Alnus	0	0	3	3
	Quercus	0	0	1	1
U4	Picea	68	22	0	22
	Fagus	1	7	17	25
U5	Fagus	1	11	10	22
	Pinus	4	0	0	4
	Picea	39	20	0	59
	Betula	2	0	0	2
U6	Fagus	1	5	10	16
	Pinus	1	0	1	2
	Picea	33	10	1	44
	Alnus	1	0	0	1

Table 3: Major trees in the marsh within 150 m of the site.

Transect	Trees	Number
S 1	Picea	9
	Betula	8
	Alnus	8
	Pinus	20
	Fagus	2
S2	Picea	4
	Betula	4
	Alnus	14
	Pinus	7

Table 4: Number of trees by the coring site along transects S1 and S2, July 2011.

The lake sediment was collected through the ice using a 10 cm Russian corer, in the winter of 2009 (Figure 10) and kept in refrigerated conditions (4° C) until March 2010, when it was subsampled and frozen at -20°C for ancient DNA (aDNA) analysis. The sediment/water interface was at 450 cm below the ice. The small hollow is in the deepest part of a long, continuous marsh at the bottom of the valley below the lake (Figure 5, Figure 11) and was sampled using an 8 cm Russian corer in the summer of 2011. The marsh is fed by a tributary running from Sällstorpssjön. All cores were wrapped in plastic, stored in half drain pipes for transport and kept in refrigerated conditions (4° C).



Figure 10: Ice coring at Sällstorpssjön, using a 10 cm Russian corer, February 2009. Simon Bystedt, Őrjan Fritz, Richard Bradshaw.



Figure 11: The small hollow was sampled using an 8 cm Russian corer in the summer of 2011. Karin Hernborg, Richard Bradshaw, Hannah Williams, Chiara Molinari.



Figure 12: Sällstorpssjön basal sediments.



Figure 13: Visible charcoal bands in the small hollow sediments.

2.3. Laboratory Methods

Six thin sediment samples from the lake and three from the marsh were sent to the AMS dating facility at Lund University for analysis. All radiocarbon dates were calibrated using CLAM software (Blaauw, 2010) (Table 5) (Figures 14 and 15). Total concentrations of atmospherically deposited lead (Pb) and other geochemical elements were determined using the Bruker S2 Ranger X-ray Fluorescence Spectrometry (XRF) spectrometer (University of Liverpool) (Williams, 2012). Samples were taken at 5-10 cm intervals from the lake, freeze dried at -55°C, and then ground into a powder. Calibrations were made by comparing massattenuation corrected peak heights with known concentrations for a set of reference materials (Boyle, 2000) and computer software generated the concentration values for each element (Figure 16). Peak values for Pb were correlated with dated values from nearby sites (Bindler et al. 2011). The age-depth relationships (Figures 14 and 15) were drawn up using both radiocarbon and Pb dates (Table 5). The chronology is presented as calibrated years before present (cal. BP), where BP refers to 1950 AD.

Pollen samples of 1 cm³ were prepared using standard techniques between 4 and 10 cm throughout the sediment profiles (Berglund & Ralska-Jasiewiczowa, 1986; Moore et al. 1991). *Lycopodium* tablets were added to allow pollen concentration and influx calculations. Slides were counted at a magnification of x400 and the pollen diagrams were drawn up as a percentage of the sum of terrestrial pollen, excluding aquatics and spores. The pollen diagrams were divided into periods where major changes in vegetation could be seen (Figures 17, 18 and 19). Samples for percentage loss on ignition were burned at 450°C for four and a half hours and results presented on the pollen diagrams (Figures 17 and 19).

Contiguous 2 cm³ samples were extracted for charcoal analysis, measured out using water displacement, into test tubes of distilled water. Charcoal pieces larger than 250 microns were counted, and the area (area/cm²/year) for each unit was estimated using image analysis techniques developed by Mooney & Black (2003) and converted into influx values using the age depth relationship (Hannon et al. 2018)(Figure 20). As values were generally very low, charcoal area influx is exaggerated by a factor of 100 on the pollen diagrams. A statistical analysis of the charcoal data from Sällstorpssjön was carried out using the CHAR programme (Higuera et al. 2007) to determine "background" and "peak" charcoal values with peak magnitude values identifying locally important fire events (Hannon et al. 2018)(Figure 20). The raw charcoal accumulation rates (CHAR, units/cm²/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-yr 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 *c*.1 km from the site (Higuera et al. 2007). Fire history was also described by quantifying the variation of fire return intervals (FRI, years between two consecutive fire events) and fire frequency over time, smoothed using a locally-weighted regression with a 1000-year window (Figure 20). These numerical treatments were carried out using the CharAnalysis program (Version 1.1, available online at http:

//phiguera.github.io/CharAnalysis/).

In March 2010, 22 samples were analysed for aDNA content. There were two independent extractions for each sample using the Sergey Bulat protocol (Bulat et al. 2000). The extracts that proved positive for aDNA were amplified using the polymerase chain reaction (PCR) technique with primers and tags according to Sønsterbø et al. (2010). The amplifications were then used for FLX sequencing and the results were blasted to match the aDNA sequences to a reference library of DNA from taxonomically identified sources (Sønstebø et al. 2010).

3. Results and interpretation

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

The basal lake sediments (Figure 12) date from c.13500 cal. BP. The most recent regional deglaciation estimates for southern Sweden based on cosmogenic nuclide surface exposure dating are between 17 and 16 000 cal. BP (Anjar et al. 2013) with southwest Sweden ice free between c.18-16 000 cal. BP (Lundqvist & Wohlfarth, 2001). 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 6; Figure 18). This is a similar picture to other parts of southern Sweden at this time (Berglund, 1979; Björck & Möller 1987). PAR (Pollen Accumulation Rate) data can help interpret the vegetation structure and quantitative tree volume (m^3/ha) in semi-open landscapes such as this (Seppä & Hicks, 2006; Seppä et al. 2009; Mazier et al. 2012). The threshold PAR value for the presence/absence of *Pinus* in the immediate vicinity is 500 grains/cm²/year based on modern day tree-line pollen traps (Seppä & Hicks, 2006). *Pinus* (PAR) values of between 500 and 1700 grains/cm²/year at this site suggest local presence of *Pinus* (Figure 17). Indicator taxa such as *Hippophae rhamnoides* (sea buckthorn), associated with minimum mean July temperatures of 11°C and pollen of Filipendula and Juniperus (Figures 17 and 18) associated with temperatures of near 10°C (Isarin & Bohncke, 1999), suggest a certain degree of warmth. Pollen of Typha and *Potamogeton* recorded in the lake sediments support this conclusion (Hu & Brubaker, 1996).

Table 5: Radiocarbon dates calibrated into calendar years BP using Clam software (Blaauw, 2010).

Sällstorpssjön

	Depth (cm)	¹⁴ C years BP	Cal. yr BP	Probability
Lead Date	510-511		950 <u>+</u> 3	
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	10648-11105	91.6%
LuS 9185	995-996	11655 ± 65	13334-13707	95.0%

Almeberget small Hollow

	Depth (cm)	¹⁴ C years BP	Cal. yr BP	Probability
Lead Date	11-12		150 <u>+</u> 3	
LuS 9662	46-47	880 ± 45	724-915	92.8 %
LuS 9663	78-79	1520 ± 50	1326-1522	93.7 %
LuS 9664	94-95	1780 ± 50	1568-1821	95.0 %



Figure 14: Age depth relationship, Sällstorpssjön (Hannon et al. 2018).



Figure 15: Age-depth relationship, Almeberget hollow, adapted from Williams (2012).



Figure 16: The geochemical signal from the lake sedimentary record. Selected elements are exaggerated by a factor of 10 for clarity.

Table 6: Summary of palaeoecological dynamics.

Time Periods		Palaeoecological evidence
<i>c</i> . 13 500 -12 700 cal. BP		Light-demanding taxa <i>Juniperus, Hippophae,</i> <i>Empetrum</i> , Ericaceae, Poaceae, Cyperaceae, <i>Artemisia</i> and Chenopodiaceae on possibly unstable soils, with <i>Pinus, Betula, Populus</i> and <i>Salix</i> .
<i>c</i> . 12 700 - 11 700 cal. BP	Palaeolithic 12 000 – 9 600 BC	A decline in <i>Pinus</i> and increase in herbaceous taxa, particularly Poaceae. Organic sediment content decreases and total pollen concentration falls from 605,698 to just over 40,000 pollen/cm ³ . This is one of the few sites in Fennoscandia with a sedimentary charcoal record at this time (Clear et al. 2014).
<i>c</i> . 11 700 - 8500 cal. BP	Mesolithic 9 600 – 4 000 BC	Tree pollen expands stepwise with Holocene warming together with a threefold increase in % organic sediment content. Fire adapted <i>Pinus</i> has its highest values. <i>Ulmus</i> and <i>Alnus</i> values increase. The disturbance-adapted <i>Populus</i> remains an important forest component. There is a continuous charcoal record.
<i>c</i> . 8500 - 6700 cal BP		<i>Quercus, Fraxinus</i> and <i>Tilia</i> increase. Tree pollen diversity is high, comprising both temperate and boreal species. Low or discontinuous records of most herbaceous types and fern spores.
<i>c</i> . 6700 - 4000 cal. BP	Neolithic 4 000 – 1 800 BC	A wide variety of deciduous trees with <i>Quercus, Ulmus, Tilia</i> and <i>Fraxinus</i> as the main dominants and <i>Alnus, Betula, Salix, Sorbus</i> and <i>Frangula. Populus</i> only occasionally present. <i>Pinus</i> has declined to low frequencies. <i>Carpinus betulus</i> pollen first recorded.
<i>c</i> . 4000 - 2500 cal. BP	Bronze Age 1 800 – 500 BC	<i>Fagus</i> first recorded. Values for <i>Carpinus</i> increase and <i>Corylus</i> decrease towards the end of the period. Cultural indicators include continuous <i>Plantago lanceolata</i> , <i>Artemisia, Filipendula</i> and a single cereal grain <i>c</i> . 3600 cal. BP.
<i>c</i> . 2500 - 1400 cal. BP	Iron Age 500 BC – AD 1100	Decrease in <i>Corylus</i> and decrease in <i>Ulmus</i> and <i>Alnus</i> frequencies. Increase in <i>Betula</i> and Polypodiaceae spores. First major increase in <i>Fagus</i> and the initial pollen evidence for <i>Picea</i> .
<i>c</i> . 1400 - 500 cal. BP	Mediaeval 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.

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

The interstadial ends abruptly with a return to 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) and is reflected at this site by decline in pollen of *Pinus* and an increase in herbs (Figures 17 and 18). 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). The contrast between the first vegetation recorded at the site and that during the following cold episode (c.12 700 - 11 700 cal. BP) is immediately discernible (Table 6; Figures 17 and 18). The trees recede, the organic sediment content halves, suggesting more solifluction to the lake, total pollen concentration falls from 605 698 to just over 40 000 pollen/cm³ (Figure 17) and the landscape is likely to have become more open. Pinus and Betula PAR values, Juniperus, Empetrum, Ericaceae and Poaceae pollen frequencies all decrease. Populus trees may have disappeared from the area, whereas Betula and Salix pollen remain constant, although this may be due to increased representation by dwarf varieties. Pollen from coldtolerant light-demanding plants, including Dryas octopetala and Saxifraga oppositifolia increase, and drought-tolerant species persist (Figure 18), suggesting that cold, arid conditions prevailed. Other late-glacial sites in the area record similar features (Berglund 1979; Berglund et al. 1994) and have suggested local persistence of tree Betula during this cold episode, although the low absolute values (influx) recorded for *Betula* (418 grains/cm²/ year) would argue against this and any pollen recorded might be long distance transport. Charcoal fragments, widely interpreted in the sedimentary record as a proxy for fire (Power et al. 2008) are recorded close to the start of the Holocene (Figures 17 and 18). This is one of the few sites
in Fennoscandia with a sedimentary charcoal record at this time (Clear et al. 2014). An increase in biomass burning may have been driven by an increase in fuel availability.

3.3 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 on Figures 17, 20a and 20b respectively. Charcoal accumulation rate is interpolated to constant 68-year time intervals (CHAR, black histograms). The charcoal peaks, which are the magnitude of detected fire events, with periods characterized by a signal-to-noise index (SNI) > 3.0 are shown as red crosses, whereas peaks that fail to pass the Poisson minimum-count criterion are displayed as grey dots. The background threshold CHAR (BCHAR, grey line) (Figure 20b) shows the de-trended CHAR data, with threshold values identifying noiserelated variability (positive and negative red lines) and the fire return interval (FRI) expressed as time since last fire (grey squares) and fire frequency (black line).

The first fire peak identified (Figure 20a), is close to what is the likely opening of the Holocene (Figure 17). The tree pollen response *c*.11 700 cal. BP appears to be stepwise 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 of *Artemisia*, Asteraceae, Poaceae and Chenopodiaceae were gradually replaced by shrubs and trees including *Juniperus*, *Betula*, *Pinus*, *Populus* and *Corylus* (Figure 17). 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 & Brubaker 1996), particularly megaspores of *Isoetes lacustris* (Figure 18), 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 & Birks, 2008). Other aquatic vascular plants recorded are *Potamogeton, Myriophyllum* and *Typha* which when compared with sites in Poland, central Germany, Belgium and France, suggest that temperatures rapidly approached 13°C (Isarin & Bohncke, 1999).

Boreal forest conditions develop with the expansion of Pinus, Betula, Corylus, Alnus, Ulmus and decreases in Salix, Juniperus, Ericaceae, Poaceae, Cyperaceae and Polypodiaceae (Figures 17 and 18) and repeated fire events (Figure 20). The fire-adapted Pinus has highest Holocene pollen frequencies here (Figure 17), while Populus and Betula, taxa which benefit from increased light following disturbance events, remain consistently present. This is associated with charcoal fragments registering frequent burning with peaks at $c.10\ 900,\ 9900$ and 8600 cal. BP (Figures 17 and 20). The high incidence of fire on the landscape might be attributable to a combination of a warmer more continental climate, with temperatures 2.5°C higher than at present, markedly dry conditions (Seppä et al. 2005) and the possibly more flammable nature of the ground vegetation. 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, an increase in representation by Arboreal Pollen and reduction in Non-Arboreal Pollen frequencies can be observed (Figure 17). Ulmus and Alnus pollen values increase prior to the expansion of Quercus, Fraxinus and Tilia c.8500 cal. BP. Frequent fires have been shown to disadvantage Quercus (Niklasson et al. 2002) which despite coming into the region just after $c.10\ 600\ cal.$ BP, shows a delayed response to expansion, increasing in pollen frequency as fire-adapted Pinus and charcoal influx decrease.

3.4 Hemiboreal forest with high tree diversity and frequent fires (8500 cal. BP).

Hemiboreal forest conditions follow, with high tree pollen diversity comprising both temperate and boreal species and constant low intensity burning (Figures 17 and 20). *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 17). The disturbance-adapted *Populus* is still an important forest component, and the total diversity of tree species is high, comprising both temperate and boreal species.



Figure 17: Pollen percentage diagram from Sällstorpssjön. The percentages are calculated on the sum of upland pollen. Charcoal is expressed as area cm²/year. Exaggeration of selected taxa is x 10.



Figure 18: Pollen percentage diagram from Sällstorpssjön. Aquatics and Polypodiaceae are calculated on the sum of upland pollen plus aquatics and upland pollen and Polypodiaceae respectively. Exaggeration of selected taxa is x 10.



Figure 19: Pollen percentage diagram from the small hollow calculated on the sum of upland pollen. Polypodiaceae are calculated on the sum of upland pollen and Polypodiaceae respectively. Exaggeration of selected taxa is x 10.

The present day dividing line between the temperate part of southern Scandinavia, (Scania, the coastal parts of Halland, southern Bohuslän and Blekinge (Sjörs, 1999)) and the mixed boreal/deciduous or 'hemiboreal' zone probably became established c.7000 cal. BP (Berglund et al. 2007) towards the end of this fire period. Hemiboreal 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 20a) 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 17). 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 21). The low values for most herbaceous pollen and fern spores (Figure 18) 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 20a) probably reflects the development of a temperate forest ecosystem with mixed, mainly deciduous pollen taxa recorded (Figure 17).



Figure 20: Reconstructed Palaeo Fire Peaks (a) and Fire Return Interval (b) from Sällstorpssjön (Hannon et al. 2018).



Sallstorp - RDA (moving Window)

Figure 21: Redundancy Analysis showing the changing percentage of vegetation variance attributable to charcoal at Sällstorpssjön (Hannon et al. 2018).

3.5 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 20a), yet the redundancy analysis (Figure 21) indicates that the influence of fire on vegetation dynamics was at its lowest values during this period (Figure 17). The forest became a temperate ecosystem and the canopy closes over and became dominated by a wide variety of deciduous trees with Quercus, Ulmus, *Tilia* and *Fraxinus* the main dominants, *Alnus* in wetter areas and a rich shrub understory with Betula, Salix, Sorbus and Frangula (Figure 17). Populus disappears from the record. Pinus pollen declines to low frequencies which are maintained until the planting programs of the 20th century. The first *Carpinus betulus* pollen is recorded. *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 & Pylvänäinen, 2002) and does not grow in the reserve today. A late immigrant to the forests of north-west Europe, and shade-tolerant like Fagus, it has a dense canopy which tends to restrict shrub or herb undergrowth. The continued very low and discontinuous nature of most herbaceous pollen and fern spores may be due to some natural gaps in the forest canopy (Figure 18). This probably reflects a temperate, rather dense forest ecosystem with low light conditions on the forest floor dominated mainly by deciduous pollen taxa. The first possible weak signs of human use of the forest are seen towards the end of this period indicated by a slight increase in the percentages of NAP and Polypodiaceae (Figures 17 and 18). The sediment element geochemistry (Figure 16) is characterized by low concentrations of elements associated with silicate rock minerals, and a high concentration of Si, probably reflecting biogenic silica from diatoms. Fagus sylvatica pollen is first recorded c.4000 cal. BP, and *Populus* reappears towards the end of this period, possibly colonizing the edges of open areas.

While *Fagus* immigration is frequently associated with disturbance (Bradshaw & Lindbladh, 2005), declining values for Corylus and increase in Carpinus is broadly synchronous within mid to high latitude forest ecosystems in Europe at this time (Giesecke et al. 2011) suggesting the temporal pattern of vegetation change c.4000 years ago 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 & 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; Olsson and Lemdahl, 2009). So, there might be an underlying climatic control to Fagus immigration and the shifting nature of the vegetation composition in addition to the first signs of possible anthropogenic activity in the forest in the form of burning. While Bronze Age activity had a large impact on forest structure and composition over south-west Sweden, canopy cover and old trees may have persisted longer in upland marginal sites with poor soils such as in this nature reserve, where any clearance must have been relatively small although grazing, indicated by pollen of *Rumex acetosa* and *Potentilla*-type, seems reasonably certain (Figure 18).

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

Fires increased in importance with high charcoal influx values *c*.3800 and 3660 cal. BP, a major peak *c*.3400 cal. BP and a further peak *c*.2900 cal. BP (Figure 20). Slight decreases in pollen of *Corylus, Alnus, Ulmus, Fraxinus* and increases in *Pinus, Populus, Betula, Tilia* and latterly *Sorbus* pollen, together with fire, could well reflect some clearance for slash and burn cultivation and improvement of grazing resources (Figure 17). Cultural indicators include continuous *Plantago lanceolata, Artemisia, Filipendula* and *Ranunculus* (Figure 18), although NAP pollen frequencies remain consistently low with total values of

between 6 and 8% until the end of the period. Forest cover appears to be high (Figure 17). A single cereal-type pollen grain is an isolated occurrence *c*.3600 cal. BP, and may only signify temporary cultivation, but it is coincident with the change in the pattern of charcoal deposition (Figure 18). An increase in *Calluna* and *Juniperus* pollen indicates possible grazing pressure. *Carpinus*, often associated with human impact in many parts of Europe and in southern Sweden on abandoned pastures (Bergendorff et al. 1979), shows an increase in pollen frequency, so there were probably some open glades on drier slopes. The element geochemistry (Figure 16) shows little difference from the preceding period.



Figure 22: Clearance cairns within woodland in Almeberget Nature Reserve.

Many Bronze Age pollen records in south-western Sweden and Denmark (Andersen, 1997; Odgaard & Rasmussen, 2000; Hannon et al. 2008; Sköld et al. 2010; Brown et al. 2011) show this time period to be one of marked cultural impact, with deforestation and extensive vegetation alteration. At Yttra Berg, a site further north, rich in clearance cairns and stone walls, at a similar elevation but 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 this 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, charcoal fragments were recovered from the base of many burial mounds (Hannon et al. 2008), and episodic burning affected many decorated Bronze Age rock carvings (Brown et al. 2011). The tumbled down cairns visible in the reserve today (Figure 22) are thought to possibly date from the Bronze Age (Länsstyrelsen, 2006). 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.

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

A decline in the mixed deciduous pollen communities (*Corylus*, *Ulmus* and *Alnus*) and an increase in *Betula* and Polypodiaceae spores can be observed during the Iron Age (Figures 17, 18 and 19), coincides with the first major increase in *Fagus* pollen suggesting a reduction in anthropogenic use of the forest and a consequent increase in forest cover. High sediment organic matter (LOI = c.80%) (Figure 17), and Br (c.80 ppm) (Figure

16), are consistent with the development of a marginal floating layer of peat that developed at this lake, most likely during the latter part of the Holocene. The very high concentration of S (*c*.40 mg/g) may indicate leaching of sulphate from catchment peat, while the very high concentration of Ca (*c*.50 mg/g) suggests that catchment soils contain calcium carbonate of possible glacial and marine origins. 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 20a) with a decline in fire incidence (Figure 20b) 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. Just under 2000 years ago, the marsh in which the small hollow is located began to form, possibly as a result of water-logging (Figure 5).

Reduced anthropogenic use of the forest in the late Iron Age is implied by the gap in the fire record between c.1400 and 800 cal. BP (Figures 17, 19 and 20). A peak in Polypodiaceae (Figure18 and 19) is followed by successions involving *Juniperus, Salix, Betula* and increasing numbers of *Fagus*. The geochemical signal (Figure 16) does not show evidence for mineral soil erosion, suggesting that no land clearance occurred in the hydrological catchment to the lake. The Ca concentration reaches its maximum value in this time (c.90 mg/g – equivalent to c.20 wt% calcium carbonate).

3.8. Fagus dominated Forest (1400 cal. BP).

A change in forest dominance (Figure 17) can be seen in the rapid rise of *Fagus* and the first records for *Picea*, a late Holocene tree immigrant in this part of southern Sweden (Giesecke & Bennett, 2004). Quercus, Betula, Ulmus, Fraxinus, Corylus, Sorbus and *Frangula* pollen values fall. The organic content of the lake sediment decreases (Figure 17) suggesting erosion of some mineral material into the lake basin, and elements such as Zr rise steadily, suggesting progressively increasing disturbance of the catchment soil from c.1500 to 1000 cal. BP (Figure 16). There is a slight increase in herbaceous pollen from 7% to 9%, consisting mainly of Poaceae, Rumex acetosa, Lamiaceae, Galium-type and Rosaceae with a decrease in Polypodiaceae spores, Plantago lanceolata, Artemisia and Filipendula pollen (Figure 18). Downscaling from the lake record, the small wet hollow shows how these changes are reflected at the scale of forest stand (1 ha) (Figure 19). Forest dominants Tilia, Quercus, Alnus, Ulmus and Corylus are replaced by a stepwise increase in Fagus c.1350 cal. BP, as Polypodiaceae spores decline. Poaceae and Cyperaceae values are initially low, but then increase together with weeds (*Rumex acetosa, Galium*-type, *Filipendula* and *Artemisia*), many of which can be associated with pasture and/or grazing (Gaillard et al. 1992). A single Hordeum-type pollen is recovered c.1500 years ago, but the continuous record begins c.1000 years ago.

3.9. Grazing, some cultivation, slash and burn activities (600 cal. BP).

Although charcoal influx values are generally low in the small hollow record, there is an increase between *c*.600 and *c*.200 cal. BP (Figure 19). The decline of the mixed temperate forest is seen in the near disappearance of *Carpinus, Ulmus, Fraxinus, Tilia, Corylus, Sorbus* and latterly *Quercus. Fagus* pollen values remain stable together with *Betula, Alnus* and *Pinus. Secale cereale* is recorded in addition to *Hordeum*-type pollen. Some evidence for former cultivation ridges (Figure 23) can be seen on one small south-facing slope in the reserve today.



Figure 23: Former cultivation ridges in the reserve.

Quantitative summer-temperature reconstructions from Fennoscandia show a colder period between *c*.650 - 750 cal. BP (Bjune et al. 2009), corresponding roughly with the Little Ice Age, the onset of which is dated to *c*.650-750 cal. BP in northern Europe (Lamb, 1997; Grove, 2001). Temperature reconstructions based on Scandinavian tree ring measurements also show a long cold period beginning *c*.750 cal. BP (Grudd, 2008), so successions involving *Juniperus* and Ericeaceae *c*.200-300 years ago (Figure 19) could be because of cultural abandonment driven by a climatic deterioration. Some large *Juniperus* can still be seen in the reserve today on steep slopes or rocky faces. *Quercus* can be observed on rocky slopes, and other residual remnants of the former mixed temperate forest are mainly around the lake where the forest structure is more diverse (Table 2), and on rocky slopes which are inaccessible to grazing animals (Figure 24).



Figure 24: Mixed woodland on steep slopes inaccessible to grazing animals persists in the reserve today.

The marked increase in *Pinus* and *Picea* pollen values reflect the tree planting forestry programmes of the 19th and 20th centuries (Figure 19). 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 & Granström, 2000) and might have further facilitated the rise to dominance of the fire-sensitive *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 of opening of the Holocene to a minimum value of less than 10% by 5000 cal. BP. This value increased during the late Holocene to almost 15% by the end of the record (Figure 21).

3.10 Ancient DNA recovered from the sediments of Sällstorpssjön

The 22 sediment samples analysed for ancient DNA (aDNA) ranged in age from 600 cal. BP to 12 800 cal. BP. aDNA was successfully isolated from the youngest 8 samples covering the last 4000 years. A successful isolation entailed the identification on agarose gels of polymerase chain reaction (PCR) amplification products of the expected size for DNA from two independent PCRs. Two independent PCRs yielded aDNA from the sample from 6280 cal. BP, while just one of two PCRs yielded aDNA from samples aged 5400 and 7985 cal. BP. The other 11 samples yielded no aDNA. Ancient DNA from 6 of the 11 samples from which aDNA was isolated were sequenced and matched with a modern DNA reference library. The number of individual aDNA sequences assigned to plant taxa were are shown in Table 7.

Recovery of aDNA from 11 of 22 samples is a good return for this technique. Most taxa were identified in the youngest sample and the number of positive identifications fell through time, with no aDNA recovered from sediment older than *c*.8000 cal. BP. The results shown here are consistent with the pollen diagrams for the taxa identified from aDNA (Figures 17 and 18). aDNA potentially has a greater taxonomic resolution than pollen morphology. Although less taxa were recorded using aDNA, there was greater taxonomic resolution for e.g. *Alnus*, *Betula* and Poaceae. aDNA analysis is a fast-developing technique, but the identifications presented here are among the first systematic studies to have been carried out.

Table 7. Plant taxa identified from aDNA fragments.

Age cal. yr BP	Plant taxa identified from aDNA fragments
636	Alnus glutinosa (2), Alnus incana (2), Betula pendula (3), Betula pubescens
	(11), Carpinus (5), Corylus (1), Fagus (13), Quercus (3), Sambucus (4),
	Anagallis (2), Antennaria (2), Cicuta (1), Lysimachia (4), Umbelliferae (1)
1 800	Alnus glutinosa (1), Alnus incana (1), Betula pubescens (6), Quercus (2),
	Sorbus (1), Tilia (2), Crataegus (1), Rosaceae (1)
2 700	Betula pubescens (2), Carpinus (1), Quercus (4), Sorbus (3), Crataegus (1),
	Frangula (5), Aegopodium (1), Angelica (1), Umbelliferae (1)
3 000	Alnus glutinosa (5), Alnus incana (18), Betula pendula (1), Betula
	pubescens (6), Pinus (13), Sorbus (9), Tilia (3), Crataegus (2), Allium (1),
	Brassicaceae (1)
4 000	Alnus glutinosa (2), Alnus incana (3), Betula pendula (1), Betula pubescens
	(38), Pinus (1), Sorbus (4), Arrhenatherum elatius (5), Festuca (7), Lolium
	(2), Poa (6)
6 280	Alnus incana (1), Betula pendula (2), Betula pubescens (7), Carpinus (1)

4. Consequences of long-time scales for conservation and restoration

The vegetational history of southwest 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 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 (Figures 17, 19 and 20). 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 diversity change through time is apparent (Figure 25). Red-listed insects gradually increase in diversity from the Late-Glacial until the period 9500-6500 cal. BP when the forest had its most diverse tree flora but was not as closed in structure as during the following period (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 favored trees with greater numbers of associated red-listed insects. Subsequently, increasing human impact was associated with continuous loss of tree and red-listed insect diversity (Figure 25).



Figure 25: The number of red-listed saproxylic insects (red) associated with specific dominant and sub-dominant tree species (blue) at Almeberget nature reserve.

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 between 6500-9500 cal. BP when *Quercus, Corylus, Alnus, Tilia, Fraxinus, Ulmus* and *Sorbus* were the major forest trees with a fire regime of frequent but low intensity burning (Figures 17 and 20). Much surviving biological value in the reserve is linked to lichens which can switch tree hosts more easily than other species groups (Fritz et al. 2009; Ellis, 2012). 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 this *Fagus* dominated nature reserve. Their reduced importance is most likely due to management history rather than significant changes in climate (Björse & Bradshaw, 1998).

5. Conclusions

The record of human-natural interactions with the environment goes back much further than we often believe. The further back in time, the 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, disturbance has exerted a considerable impact on forest composition and structure, both regionally and at stand level, and has facilitated the expansion of the late Holocene immigrant *Fagus* (Bradshaw & Lindbladh, 2005). Suppression of fire, as is documented in southern Sweden over the last 200 years (Bradshaw et al. 2010), along with the national planting programs of the 20^{th} century, have assisted *Fagus* and *Picea* to obtain canopy dominance.

Nature reserve planning is often species driven, based on which red-listed species live on the major stand dominants today (Fritz, 2009). However, the evidence from the paleoecological record shows that many forests have undergone structural and compositional changes in stand dominants through time (Björse & Bradshaw, 1998). A dynamic equilibrium has existed, where there has been no single climax or single reference point, but a range of variability within which there are systems that have been driven by changing combinations of natural and mild anthropogenic disturbance. Semi-open steppe vegetation *c*.13 500 years ago, developed into boreal forest with *Pinus, Betula, Corylus, Alnus, Ulmus, Populus* and frequent fires followed by further diversification after *c*.9500 cal. BP. Deciduous trees, including *Quercus, Fraxinus* and *Tilia*, became more significant as fires became less frequent or intense. Fire frequencies increased in the Bronze Age influenced by anthropogenic use of the forest, and the first *Fagus sylvatica* pollen was recorded. Burning continued through the Iron Age but charcoal was 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*. Evidence for regular but mild local burning alongside local, small-scale cultivation *c*.600 to 200 years ago preceded large scale planting programmes with *Picea* and *Pinus* since the beginning of the 1900s and fire suppression. The early Holocene mixed forest with frequent low intensity fires was associated with highest diversity of red-listed species in the past. 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. Low levels of disturbance from fire have favoured tree diversity and the long-term survival of endangered saproxylic species.

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' can claim to have unbroken continuity throughout the Holocene, albeit with constantly changing structure and composition and minimal anthropogenic activity. A similar conclusion was reached by Lindbladh et al. (2008) and Bradshaw et al. (2015) based on data from small hollows 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 (Figure 26), 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 utilised coastal environments, or nearby sites such as Yttra Berg (Sköld et al.

2010). The relatively low intensity anthropogenic disturbance that Almeberget reserve has had in the past, may well be a feature critical to maintain its biodiversity in the future.



Figure 26: Older Fagus trees encrusted with diverse epiphytic mosses and lichens in the reserve today.

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References

Ahti, T., Hamet-Ahti, L. and Jalas, J. 1968. Vegetation zones and their sections in northwestern Europe. *Annales Botanici Fennici* 5: 169-211.

Andersen, S.T. 1997. Pollen analyses from early Bronze Age barrows in Thy. *Journal of Danish Archaeology* 13: 7–17.

Anjar, J., Larsen, N. K., Håkansson, L., Möller, P., Linge, H., Fabel, D. and Xu, S. 2013. A ¹⁰Be-based reconstruction of the last deglaciation in southern Sweden. *Boreas* 43: 132–148.

Bengtsson, S. 1999. Biskopstorp – skogstyper, ekologi och skötsel. Meddelande 1999, 20, Länsstyrelsen, Halland, 118 pp. Berg, Å., Gärdenfors, U., Hallingbäck, T. and Norén, M. 2002. Habitat preferences of redlisted fungi and bryophytes in woodland key habitats in southern Sweden – analyses of data from a national survey. *Biodiversity and Conservation* 11: 1479-1503.

Bergendorff, C., Larsson, A. and Nihlgård, B. 1979. Sydliga Lövskogsbestand i Sverige. -Statens Naturvardsverk. Rapport. SNV PM 1278, Solna, 68 pp.

Berglund, B.E. 1979. The deglaciation of southern Sweden 13,500-10,000 B.P. *Boreas* 8: 89–118.

Berglund, B.E. and Ralska-Jasiewiczowa, M. 1986. Pollen analysis and pollen diagrams. Handbook of Holocene palaeoecology and palaeohydrology. In B.E. Berglund, (Ed.), pp. 455–484. John Wiley & Sons, Chichester.

Berglund, B.E., Gaillard, M.-J., Björkman, L. and Persson, T. 2007. Long-term changes in floristic diversity in Southern Sweden: palynological richness, vegetation dynamics and land-use. *Vegetation History and Archaeobotany* 17, 573–84.

Berglund, M. 1995. Late Weichselian shore displacement in Halland, southwestern Sweden: relative sea-level changes and their glacio-isostatic implications. *Boreas* 24: 324-344.

Berglund M., Eriksson, J. A. and Fernlund, J.M.R. 1994. The Late Weichselian in Halland, southwestern Sweden: a pollen-analytical study. *Geologiska Föreningens i Stockholm Förhandlingar* 116: 215-230.

Bindler, R., Segerström, U., Pettersson-Jensen, I.M., Berg, A., Hansson, S., Holmström, H., Olsson, K. and Renberg, I. 2011. Early medieval origins of iron mining and settlement in central Sweden: multiproxy analysis of sediment and peat records from the Norberg mining district. *Journal of Archaeological Science* 38: 291-300.

Birks H.J.B. and Birks, H.H. 2008. Biological responses to rapid climate change at the Younger Dryas-Holocene transition at Kråkenes, western Norway. *The Holocene* 18: 19-30.

Bjune, A.E., Seppä, H. and Birks, H. J. B. 2009. Quantitative summer-temperature reconstructions for the last 2000 years based on pollen-stratigraphical data from northern Fennoscandia. *Journal of Paleolimnology* 41: 43–56.

Björse, G. and Bradshaw, R.H.W. 1998. 2000 years of forest dynamics in southern Sweden: suggestions for forest management. *Forest Ecology and Management* 104: 15-26.

Björck, S. and Möller, P. 1987. Late Weichselian environmental history in southeastern Sweden during the deglaciation of the Scandinavian ice sheet. *Quaternary Research* 28: 1–37.

Boyle, J.F. 2000. Rapid elemental analysis of sediment samples by isotope source XRF. *Journal of Paleolimnology* 23: 13–221.

Blaauw, M. 2010. Methods and code for 'classical' age-modelling of radiocarbon sequences. *Quaternary Geochronology* 5: 512-518.

Bradshaw, R.H.W. and Lindbladh, M. 2005. Regional spread and stand-scale establishment of *Fagus sylvatica* and *Picea abies* in Scandinavia. *Ecology* 86: 1679-1686.

Bradshaw, R.H.W., Lindbladh, M. and Hannon, G.E. 2010. The role of fire in southern Scandinavian forests during the late Holocene. *International Journal of Wildland Fire* 19: 1040–1049.

Bradshaw, R.H.W., Jones, C. S., Edwards, S. J. and Hannon, G. E. 2015. Forest continuity and conservation value in Western Europe. *The Holocene* 25: 194-202.

Brown, A.D., Bradley, R.J., Goldhahn, J. and Nord, J. 2011. The environmental context of a prehistoric rock carving on the Bjäre peninsula, Scania, southern Sweden. *Journal of Archaeological Science* 38: 746-752.

Brunet, J. 1997. Plant colonization in heterogeneous landscapes: an 80-year perspective on restoration of broadleaved forest vegetation. *Journal of Applied Ecology* 44: 563-572.

Brunet, J., Fritz, Ö. and Richnau, G. 2010. Biodiversity in European beech forests – a review with recommendations for sustainable forest management. *Ecological Bulletins* 53: 77-94.

Bulat, S.A. Lübeck, M., Alekhina, I.A., Jensen, D.F., Knudsen, I.M.B. and Lübeck, P.S. 2000.
Identification of a Universally Primed-PCR-Derived Sequence-Characterized Amplified
Region Marker for an Antagonistic Strain of *Clonostachys rosea* and Development of a
Strain-Specific PCR Detection Assay. *Applied and Environmental Microbiology* 66, 4758-4763.

Clear, J.L., Molinari, C. and Bradshaw, R.H.W. 2014. Holocene fire in Fennoscandia and Denmark. *International Journal of Wildland Fire* 23: 781-789.

Čtvrtlikova M., Znachor P. and Vrba J. 2014. The effect of temperature on the phenology of germination of *Isoëtes lacustris*. *Preslia* 86: 279–292.

de Jong, R., Björck, S., Björkman, L. and Clemmensen, L. B. 2006. Storminess variation during the last 6500 years as reconstructed from an ombrotrophic peat bog in Halland, southwest Sweden. *Journal of Quaternary Science* 21: 905–919.

Digerfeldt, G. and Håkansson, H. 1993. The Holocene palaeolimnology of Lake Sämbosjön, Southwestern Sweden. *Journal of Paleolimnology* 8: 189-210.

Ellis, C.J. 2012. Lichen epiphyte diversity: A species, community and trait-based review. Perspectives in Plant Ecology, *Evolution and Systematics* 14: 131-152.

Esseen, P.-A., Ehnström, B., Ericsson, L. and Sjöberg, K. 1997. Boreal Forests. *Ecological Bulletins* 46: 16-47.

Fredén, C. 1995. Geology. National atlas of Sweden, Almqvist and Wiksell International, Stockholm, 208 pp.

Fritz, Ö. 2009. Ecology and conservation of bryophytes and lichens on *Fagus sylvatica*. Acta Universitatis Agriculturae Sueciae. Doctoral thesis. Sveriges Lantbruksuniversitet.10, 158 pp.

Fritz, Ö. 2011. Lunglav minskar och bokfjädermossa ökar i Hallands bokskogar. *Svensk Botaniskt Tidskrift* 105: 163-177.

Fritz, Ö. and Malmqvist, A. 2014. Uppföljning av bokporlav Pertusaria velata i Hallands län och på Hallands Väderö 2013-2014. Länsstyrelsen i Hallands län Meddelande 2014 (7), 48 pp.

Gaillard, M.-J., Birks, H.J.B., Emanuelsson, U. and Berglund, B.E. 1992. Modern pollen/land-use relationships as an aid in the reconstruction of past land-uses and cultural landscapes: an example from south Sweden. *Vegetation History and Archaeobotany* 1: 3–17.

Giesecke, T. and Bennett, K.D. 2004. The Holocene spread of *Picea abies* (L.) Karst. in Fennoscandia and adjacent areas. *Journal of Biogeography* 31: 1523-1548.

Giesecke, T., Bennett, K.D., Birks, H.J.B., Bjune, A.E., Bozilova, E., Feurdean, A., Finsinger,
W., Froyd, C., Pokorný, P., Rösch, M., Seppä, H., Tonkov., S., Valsecchi, V. and Wolthers, S.
2011. The pace of Holocene vegetation change - testing for synchronous developments. *Quaternary Science Reviews* 30: 2805-2814.

Grove, J.M. 2001. The initiation of the "Little Ice Age" in regions around the North Atlantic. *Climate Change* 48: 53–82.

Grudd, H. 2008. Torneträsk tree-ring width and density AD 500-2004: a test of climatic sensitivity and a new 1500- year reconstruction of north Fennoscandian summers. *Climate Dynamics* 31: 843–857.

Gustafsson, L., De Jong, J. and Norén, M. 1999. Evaluation of Swedish woodland key habitats using red-listed bryophytes and lichens. *Biological Conservation* 8: 1101-1114.

Gustavsson, G., Lemdahl, G. and Gaillard, M.-J. 2009. Abrupt forest ecosystem change in SW Sweden during the late Holocene. *The Holocene* 19: 691–702.

Hallanaro, E.-L. and Pylvänäinen, M. (Eds.) 2002. Nature in Northern Europe - Biodiversity in a changing Environment. Nord 2001, 13. Nordic Council of Ministers, Copenhagen.

Halme, P., Allen, K.A., Auniņš, A., Bradshaw, R.H.W., Brūmelis, G., Čada, V., Clear, J.L.,

Eriksson, A-M., Hannon, G., Hyvärinen, E., Ikauniece, S., Iršėnaitė, R., Jonsson, BG.,

Junninen, K., Kareksela, S., Komonen, A., Kotiaho, J.S., Kouki, J., Kuuluvainen, T.,

Mazziotta, A., Mönkkönen, M., Nyholm, K., Oldén, A., Shorohova, E., Strange, N.,

Toivanen, T., Vanha-Majamaa, I., Wallenius, T., Ylisirniö, A-L. and Zin, E. 2013. Challenges of ecological restoration: Lessons from forests in northern Europe. *Biological Conservation* 167: 248-256.

Hannon, G.E., Bradshaw, R.H.W., Nord, J. and Gustafsson, M. 2008. The Bronze Age landscape of the Bjäre peninsula, southern Sweden, and its relationship to burial mounds. *Journal of Archaeological Science* 35: 623-632. Hannon, G.E., Halsall, K.M., Molinari, C., Boyle, J. and Bradshaw, R.H.W. 2018. The reconstruction of past forest dynamics over the last 13,500 years in SW Sweden. *The Holocene* 28 (11): 1791-1800.

Hammarlund, D., Björck, S., Buchardt, B., Israelson, C. and Thomsen, C.T. 2003. Rapid hydrological changes during the Holocene revealed by stable isotope records of lacustrine carbonates from Lake Igelsjön, southern Sweden. *Quaternary Science Reviews* 22: 353-370.

Higgs, E., Falk, D.A., Guerrini, A. et al. 2014. The changing role of history in restoration ecology. *Frontiers in Ecology and the Environment* 12: 499-506.

Higuera, P.E., Peters, M.E., Brubaker, L.B et al. 2007. Understanding the origin and analysis of sediment-charcoal records with a simulation model. *Quaternary Science Reviews* 26: 1790-1809.

Higuera, P.E., Whitlock, C. and Gage, J.A. 2011. Linking tree-ring and sediment-charcoal records to reconstruct fire occurrence and area burned in subalpine forests of Yellowstone National Park, USA. *The Holocene* 21: 327-341.

Hu, F.S. and Brubaker, L.B. 1996. Boreal Ecosystem Development in the Northwestern Alaska Range since 11,000 yr B.P. *Quaternary Research* 45: 188–201.

Isarin, R. F. B. and Bohncke S.J. P. 1999. Mean July Temperatures during the Younger Dryas in Northwestern and Central Europe as Inferred from Climate Indicator Plant Species. *Quaternary Research* 51: 158–173.

Jonsell M., Weslien J. and Ehnström B. 1998. Substrate requirements of red-listed saproxylic invertebrates in Sweden. *Biodiversity and Conservation* 7: 749–764.

Kuosmanen, N., Marquer, L., Tallavaara, M. et al. 2018. The role of climate, forest fires and human population size in Holocene vegetation dynamics in Fennoscandia. *Journal of Vegetation Science* 29: 382-392.

Lamb, H.H. 1997 Climate, history and the modern world. Routledge, London, 445pp.

Lindbladh, M., Niklasson, M., Karlsson, M. et al. 2008. Close anthropogenic control of Fagus sylvatica establishment and expansion in a Swedish protected landscape - Implications for forest history and conservation. *Journal of Biogeography* 35: 682-697.

Lindbladh, M., Axelsson, A-L., Hultberg, T. 2014. From broadleaves to spruce - The borealization of southern Sweden. *Scandinavian Journal of Forest Research* 29: 686-696.

Lindström, M. 2012. En studie av tvåvingar och skalbaggar i antropogena och ickeantropogena stamhåligheter i bok i två halländska skogsreservat 2012. Länsstyrelsen i Hallands län. Enheten för naturvård & miljöövervakning. Meddelande 11: 43 pp.

Lundqvist, J. and Wohlfarth, B. 2001. Timing and east-west correlation of south Swedish ice marginal lines during the Late Weichselian. *Quaternary Science Reviews* 20: 1127–1148.

Länsstyrelsen 2006. Länsstryelsen Halland, Skötselplan 1, Naturvård och miljöövervakning, Bilaga 1 (12).

Länsstyrelsen 2011. Almeberget: www. lansstyrelsen.se/Halland.

Mazier, F., Nielsen, A.B., Bröstrom, A., Sugita, S. and Hicks, S. 2012. Signals of tree volume and temperature in a high resolution record of pollen accumulation rates in northern Finland. *Journal of Quaternary Science* 27: 567-574.

Molinari, C., Lehsten, V., Bradshaw, R.H.W. et al. 2013. Exploring potential drivers of European biomass burning over the Holocene: A data-model analysis. *Global Ecology and Biogeography* 22: 1248-1260.

Mooney, S. D. and Black, M. 2003. A simple and fast method for calculating the area of macroscopic charcoal isolated from sediments. *Quaternary Australasia* 21: 18-21.

Moore, P.D., Webb, J.A. and Collinson, M.E. 1991. Pollen Analysis, second edition, Blackwell, Oxford, 216 pp.

Natura 2000. http://www.lansstyrelsen.se/halland/SiteCollectionDocuments/sv/djur-ochnatur/skyddad-natur/natura-2000/Almeberget.pdf.

Nesje, A. 2009. Latest Pleistocene and Holocene alpine glacier fluctuations in Scandinavia. *Quaternary Science Reviews* 28: 2119-2136.

Niklasson, M. and Granström, A. 2000. Numbers and sizes of fires: long-term spatially explicit fire history in a Swedish boreal landscape. *Ecology* 81: 1484–1499.

Niklasson, M., Lindbladh, M. and Björkman, L. 2002. A long-term record of *Quercus* decline, logging and fires in a southern Swedish *Fagus-Picea* forest. *Journal of Vegetation Science* 13: 765–774.

Nitare, J. and Norén, M. 1992. Nyckelbiotoper kartläggs i nytt projekt vid. Skogsstyrelsen. *Svensk Botanisk Tidskrift* 86: 219-226.

Odgaard B.V. and Rasmussen, P. 2000. Origin and temporal development of macro-scale vegetation patterns in the cultural landscape of Denmark. *Journal of Ecology* 88: 733-748.

Olsson, F. and Lemdahl, G. 2009. A continuous Holocene beetle record from the site Stavsåkra, southern Sweden: implications for the last 10 600 years of forest and land use history. *Journal of Quaternary Science* 24: 612–626.

Olsson, F., Gaillard, M.-J., Lemdahl, G., Greisman, A., Lanos, P., Marguerie, D., Marcoux, N., Skoglund, P. and Wäglind, J. 2010. A continuous record of fire covering the last 10,500 calendar years from southern Sweden-The role of climate and human activities. *Palaeogeography, Palaeoclimatology, Palaeoecology* 291: 128–141.

Power, M.J., Marlon, J., Ortiz, N., Bartlein, P., Harrison, S.P., Mayle, F.E., Ballouche, A.,

Bradshaw, R.H.W., Carcaillet, C., Cordova, C., Mooney, S., Moreno, P.I., Prentice, I.C.,

Thonicke, K., Tinner, W., Whitlock C., Zhang, Y., Zhao, Y., Ali, A.A., Anderson, R.S.R.,

Beer, R., Behling, H., Briles, C., Brown, K.J., Brunelle, A., Bush, M., Camill, P., Chu, G.Q.,

Clark, J., Colombaroli, D., Connor, S., Daniau, A.-L., Daniels, M., Dodson, J., Doughty, E.,

Edwards, M.E., Finsinger, W., Foster, D., Frechette, J., Gaillard, M.-J., Gavin, D.G., Gobet,

E., Haberle, S., Hallett, D.J., Higuera, P., Hope, G., Horn, S., Inoue, J., Kaltenrieder P.,

Kennedy, L., Kong, Z.C., Larsen, C., Long, C.J., Lynch, J., Lynch, E.A., McGlone, M.,

Meeks, S., Mensing, S., Meyer, G., Minckley, T., Mohr, J., Nelson, D.M., New, J., Newnham,

R., Noti, R., Oswald, W., Pierce, J., Richard, P.J.H., Rowe, C., Sanchez Goñi, M. F., Shuman,

B. N., Takahara, H., Toney, J., Turney, C., Urrego-Sanchez, D.H., Umbanhowar, C.,

Vandergoes, M., Vanniere, B., Vescovi, E., Walsh, M., Wang, X., Williams, N., Wilmshurst,

J. and Zhang, J.H. 2008. Changes in fire regimes since the last Glacial Maximum: an

assessment based on a global synthesis and analysis of charcoal data. *Climate Dynamics* 30: 887–907.

Rasmussen, S.O., Andersen, K.K., Svensson, A.M., Steffensen, J.P., Vinther, B.M.,

Clausen, H.B., Siggard-Andersen, M.-L., Johnsen, S.J., Larsen, L.B., Dahl-Jensen, D.,Bigler,
M., Röthlisberger, R., Fischer, H., Goto-Azuma, K., Hansson, M.E. and Ruth, U. 2006. A
new Greenland ice core chronology for the last glacial termination. *Journal of Geophysical Research-Atmospheres* 111: D06102.

Ratcliffe, D. (Ed.) 1977. A Nature Conservation Review. Volume 1. Cambridge University Press, 386 pp.

Segerström, U., Bradshaw, R.H.W., Hörnberg, G. and Bohlin, E. 1994. Disturbance history of a swamp forest refuge in northern Sweden. *Biological Conservation* 68: 189-196.

Seppä, H., Birks, H.H. and Birks, H.J.B. 2002. Rapid climatic changes during the Greenland stadial 1 (Younger Dryas) to early Holocene transition on the Norwegian Barents Sea coast. *Boreas* 31: 215–225.

Seppä, H., Hammarlund, D. and Antonsson, K. 2005. Low-frequency and high frequency changes in temperature and effective humidity during the Holocene in south-central Sweden: implications for atmospheric and oceanic forcings of climate. *Climate Dynamics* 25: 285-297.

Seppä, H. and Hicks, S. 2006. Integration of modern and past pollen accumulation rate (PAR) records across the arctic tree-line: a method for more precise vegetation reconstructions. *Quaternary Science Reviews* 25: 1501-1516.

Seppä, H., MacDonald, G.M., Birks, H.J.B., Gervais. B.R. and Snyder, J.A. 2008. Late-Quaternary summer temperature changes in the northern-European tree-line region. *Quaternary Research* 69: 404-412.

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

Sjörs, H. 1999. Swedish plant geography. The background: Geology, climate and zonation *Acta phytogeographica Suecica* 84: 5-14.

Sköld, E., Lagerås, P. and Berglund, B.E. 2010. Temporal cultural landscape dynamics in a marginal upland area: agricultural expansions and contractions inferred from palynological evidence at Yttra Berg, southern Sweden. *Vegetation History and Archaeobotany* 19: 121-136.

Speight, M.C.D. 1989. Saproxylic invertebrates and their conservation. Strasbourg, France: Council of Europe, 79 pp.

Syren, M. 1995. Climate, Lakes and Rivers. Stockholm.

Sønstebø, J.H., Gielly, L., Brysting, A.K., Elven, R., Edwards, M., Haile, J., Willerslev, E., Coissac, E., Rioux, D., Sannier, J., Taberlet, P. and Brochmann, C. 2010. *Molecular Ecology Resources* 10, 1009-1018.

Williams, H. 2012. The 2000 Year History of Almeberget Nature Reserve in SouthwesternSweden. Dissertation submitted as partial fulfilment of the degree BSc Geography.Department of Geography and Planning, School of Environmental Sciences, LiverpoolUniversity, UK. 73 pp.

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

Wohlfarth, B., Luoto, T.P., Muschitiello, F. et al. 2018. Climate and environment in southwest Sweden 15.5-11.3 cal. ka BP. *Boreas* 47: 687-710.



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