Anthropocene 24 (2018) 14–29

Contents lists available at ScienceDirect

Anthropocene

journal homepage: www.elsevier.com/locate/ancene

Anthropogenic use of fire led to degraded scots pine-lichen forest in northern Sweden

G. Hörnberg[a,b,*], T. Josefsson[a,b], T.H. DeLuca[a,c], P.E. Higuera[d], L. Liedgren[a], L. Östlund[a,b], I. Bergman[a]

[a] The Institute for Sub-arctic Landscape Research, Silvermuseet, Torget, SE-938 31 Arjeplog, Sweden
[b] Department of Forest Ecology and Management, SLU, SE-901 83 Umeå, Sweden
[c] W.A. Franke College of Forestry & Conservation, University of Montana, 32 Campus Drive, Missoula, MT 59812, USA
[d] Department of Ecosystem and Conservation Sciences, University of Montana, Missoula, MT 59812, USA

ARTICLE INFO

Article history:
Received 28 March 2018
Received in revised form 15 October 2018
Accepted 15 October 2018
Available online 19 October 2018

Keywords:
Fire history
Northern Sweden
Long-term land-use
Reindeer herding
Pine–lichen forest

ABSTRACT

Northern pine-lichen forests are generally regarded as natural ecosystems that, in the past, were repeatedly affected by wild fires. This paper presents and tests a new hypothesis that reindeer herders used recurrent fires to promote and sustain reindeer lichen-dominated ground vegetation, in order to maintain good winter-grazing grounds in Scots pine forests. We investigated vegetation and fire history in three pine-lichen forests along the Luleälven River in northernmost Sweden. Methods included analyses of pollen, spores, charcoal and soil nutrient capital, coupled with investigation of written historical sources and previous studies. Results suggest that recurrent, intermediate-interval fires started sometime between the 2nd and 8th centuries CE, i.e. at the same time that reindeer became semi-domesticated in this region. Such fires continued until the 18th century, when introduction of active fire suppression reduced the occurrence of fire in the landscape. Repeated burning over this long period eventually depleted the soil-nutrient capital, especially nitrogen and phosphorous, thereby severely reducing productivity. In the early 20th century, foresters described such forests as degraded. Results of this study add a new dimension to understanding the genesis and history of many pine-lichen forests. They challenge the notion that reindeer herders have been reluctant, in the past, to use fire. Further studies are needed to evaluate whether a similar history can be ascribed to pine-lichen forests in other parts of northern Fennoscandia.

1. Introduction

1.1. Pine–lichen forests in northern Fennoscandia

Scots pine (*Pinus sylvestris*) ecosystems with understories dominated by ground lichens (mostly *Cladonia* species (spp.)) are a common forest type in northern boreal landscapes on dry – mesic land, especially on sediment soils along rivers. These forests provide high quality timber for forestry and are key winter-grazing grounds for reindeer (*Rangifer tarandus tarandus*) herding communities. Historically, this forest type is strongly associated with recurrent low intensity ground fires (*ca.* 50 year fire-return interval) (Engelmark, 1987; Högbom, 1934; Zackrisson, 1977), and is considered a natural ecosystem driven by natural disturbances (Engelmark and Hytterborn, 1999). However, growing evidence indicates that long-term anthropogenic activity has played an important role in shaping northern forest landscapes, even in areas with low historic population densities (Johnson and Miyanishi, 2012), including northernmost Sweden (Berg et al., 2011; Josefsson et al., 2017, 2009; Östlund et al., 2004).

In the two northernmost counties of Sweden, ground lichen-rich pine forests (i.e. with >50% cover of reindeer lichens) cover *ca.* 235 000 ha of the productive forest land (Sandström et al., 2016). The term “reindeer lichen” refers to a group of ground-dwelling lichens including *Cladonia* spp., (*see* Ahti and DePriest, 2001). These pine–lichen forests have been included in the Swedish Forest Surveys since the 1920s (SOU, 1932). However, over the last 70 years the extent of pine–lichen forests has decreased by 75% (Sandström et al., 2016); possibly a combination of forest management, active fire suppression (Berg et al., 2008; Sandström et al., 2016), and intensive reindeer grazing and trampling (Köster et al., 2015; Väre et al., 1996, 1995). A similar decrease has been observed in northern Finland (Oksanen and Ahti, 1982).

* Corresponding author.
E-mail address: greger.hornberg@silvermuseet.se (G. Hörnberg).

https://doi.org/10.1016/j.ancene.2018.10.002

Recent studies of fire history in remote pine-dominated forests in northernmost Fennoscandia suggest that natural fire-return intervals have been as long as 280 to over 400 years (Carcaillet et al., 2007; Wallenius et al., 2010). In contrast, some older studies (*e.g.* Engelmark, 1987; Zackrisson, 1977) have reported much shorter fire-return intervals (<120 years). A critical evaluation of these studies indicates that sampling in areas with a long history of human land use may have influenced the results. These findings have awakened interest in human impact on past fire regimes and the possibility that this may have been more significant than has previously been acknowledged (Wallenius, 2011). Further, during the last two thousand years, climate has gradually become cooler and wetter (Grudd et al., 2002; Mayewski et al., 2004). At the same time, the impact of fire has increased, as indicated by a general rise in charcoal contents in boreal palaeoecological data sets (Bradshaw et al., 1997; Carcaillet et al., 2007; Korsman and Segerström, 1998; Rosén et al., 2001). In addition, studies of Norway spruce (*Picea abies*) forests with abundant reindeer lichens, located close to the Scandinavian Mountain Range where the impact of fires has been extremely low (Granström, 1993), indicate that their genesis was a result of long-term anthropogenic fires (Deluca et al., 2013; Hörnberg et al., 1999). These contradicting perspectives raise questions regarding the origin of ground-lichen rich forests, and of pine–lichen forests located on sediment soils along the major rivers. Such forests have traditionally been used by herders as reindeer grazing grounds during wintertime.

Our hypothesis is that many pine–lichen forests in northernmost Sweden are a legacy of long-term land use. Such "domesticated" landscapes are now diminishing as a result of changed land-use patterns, including the discontinuation of burning as a management tool. We examine the following questions: 1) Was there a change in fire pattern and vegetation composition of pine–lichen forests during the first millennium CE (*Common Era*) when domestication of reindeer developed? 2) Is there any indication that the forests were used for grazing during this time? 3) What is the soil nutrient status of these forests today?

We evaluate our hypothesis through examination of vegetation and fire history in three pine–lichen forests located along the Luleälven River in northernmost Sweden. The methods include pollen, spore, charcoal and soil nutrient analyses. Historical documents were also examined to determine shifts in land use. We discuss our results in relation to previous palaeoecological and dendrochronological studies at and nearby our study sites, in order to shed new light on pine–lichen forest dynamics, including disturbance history and long-term land use in northern boreal forests. All ages below are given in Common Era (CE – generally not specified in the text) beginning with CE 1. The preceding era is referred to as Before Common Era (BCE – always specified in the text).

1.2. Present knowledge of pine–lichen forests and fire history

During the 1900s foresters debated low productivity "degraded pine-lichen forests" in northernmost Sweden (Ebeling, 1972; Romell and Malmström, 1945; Wretlind, 1934). Their pre-1900 distribution is unknown but presumably it was extensive (see Sjörs, 1965). Their low productivity has been explained as an effect of nitrogen (N) deficiency in the humus and underlying soil due to intense or recurrent natural fires and, to selective logging during the late 19th century (Ebeling, 1978; Häggström, 1981; Lundmark and Huss-Danell, 1981). Studies of pine forests performed in the interior of northernmost Sweden from the 1970s and 1980s indicate a mean fire return interval of 80–120 years; however, in pine–lichen forests, it has varied between 46 and 52 years (Engelmark, 1987; Zackrisson, 1977). More recent studies suggests a "natural" fire history before 1650, consisting of large fires and a median fire interval of *ca.* 80 years, and a pattern of anthropogenic fires after 1650, with small fires and a median fire interval of *ca.* 50 years – the latter as a result of slash-and-burn clearance around new settlements, and burning to improve forest grazing conditions in Sweden (Niklasson and Granström, 2000), Norway (Rolstad et al., 2017; Storaunet et al., 2013), Finland (Lehtonen et al., 1996) and Western Russia (Lehtonen and Kolström, 2000). During the 1700s, restrictions on burning forest for grazing were introduced in northernmost Sweden (Enequist, 1937), and in the late 1800s these forests became economically important for the timber industry (Östlund, 1995), resulting in active fire suppression (Zackrisson, 1977). Consequently, both natural and deliberate fires were important factors affecting vegetation dynamics and succession in these boreal forests until the late 1800s.

Post-fire vegetation in dry pine–lichen forests is characterized by several successional stages: an early stage 20–40 years after fire when the ground vegetation is dominated by various *Cladonia* spp., followed by a second stage when *Cladonia stellaris* becomes more dominant after another 30–40 years and in the absence of grazing (Morneau and Payette, 1989; Väre et al., 1995). In the absence of fire, lichens are subsequently replaced by mosses and dwarf-shrubs at an even later stage (Haapasaari, 1988). Thus, fires enhance the distribution of reindeer lichen and improve winter-grazing opportunities for reindeer herds (Eriksson and Moen, 2008).

Pine–lichen forests have been important winter-grazing grounds for reindeer since their domestication during the first millennium CE (Aronsson, 1991; Bergman et al., 2013). Up to 80% of reindeer forage may be lichens during the winter (Heggberget et al., 2002). The historical use of these forests has been disputed. In court transcripts from the 1700s there are examples of land-use disputes in which reindeer herders accused farmers of careless forest burning that destroyed the lichen cover, and in historical records there are descriptions of reindeer herders being reluctant to do burnings (Bylund, 1956; Laestadius, 1833). Based on these historical records, a general consensus has evolved that reindeer herders have been averse to including fire in their land-use practices, in contrast to farmers who used fire repeatedly (Granström and Niklasson, 2008).

2. Material and methods

2.1. Study area and description of study sites

The study area was selected based on the following characteristics: (1) presence of dry pine–lichen forests along a major river that are, or have been, important winter-grazing areas for reindeer; (2) access to information from historical records; (3) presence of biological archives; and (4) availability of previous studies on vegetation or fire history. Three boreal pine–lichen forests, located along a 60 km stretch of the Luleälven River in northernmost Sweden, were selected: Heden (65°49'26''N, 21°34'29''E, 35 m a.s.l.), Harads (66°08'41''N, 20°53'23''E, 60–80 m a.s.l.) and Edefors (66°13'25''N, 20°50'13''E, 70–80 m a.s.l), (Fig. 1a–d). This region is under the influence of post-glacial land upheaval; Heden emerged from the sea around 4000 years ago, whilst Harads and Edefors emerged between 7000 and 6000 years ago (Lindén et al., 2006; Ågren and Svensson, 2007). The studied forests are located on fluvial sand sediments on granite bedrock (www.sgu.se). The vegetation is characterized by Scots pine ($\geq$ 65% of the basal area), and by abundant reindeer lichen species, ericaceous species (*Vaccinium* spp., *Calluna vulgaris* and *Empetrum nigrum* ssp. *hermaphroditum*), and feathermosses (*Pleurozium schreberi* and *Hylocomium splendens*). Nomenclature for vascular plants follows Mossberg and Stenberg (2003).

Heden village is located on the south side of the Luleälven River, and southwest of the town of Boden (Fig. 1b). The pine–lichen forest (*ca.* 40 ha) from which the soil samples were collected is located east of the village. A small mire (<0.2 ha) located 300 m northwest of the forest was used for peat sampling. Finds of archaeological settlements from the 1500s have been discovered close to the village (www.fmis.raa.se). Heden is mentioned in cadastral records from 1543 (Enequist, 1937). Geometric documents from 1718 (Fig. 2a), show that the mire was surrounded by a forest described as "stone-rich sand with small trees" (www.lantmateriet.se). The regional vegetation history has been studied by Segerström (1990), who performed analysis of fossil pollen derived from Lake Fisktjärn located 3 km south of Heden.

Harads is a large pine–lichen forest located 5 km northwest of the village Harads, situated on the north side of the river at 60 to 80 m a.s.l. (Fig. 1c). A fire chronology was established by Zackrisson (1981) for part of the forest that was described as "burned coniferous forest" on delineation documents from 1862 (www.lantmateriet.se). This part of the forest was described as exhibiting "low productivity" during the 1980s (Lundmark and Huss-Danell, 1981; Huss-Danell and Lundmark, 1988). Our soil samples were collected from this part of the forest, and there is a small swamp forest (<0.4 ha) immediately adjacent to the soil sampling site, which was used for peat sampling. Archaeological finds such as settlement remains are present on the slope (www.fmis.raa.se). The Harads village is mentioned in cadastral records for 1543 (Enequist, 1937). In historical documents from 1707 (Fig. 2b), the area was described as "forest land including mostly spruce, pine and birch forest good for timber" (www.lantmateriet.se).

Edefors is a large pine–lichen forest located on the west side of the river 1 km west of the former Laxede Rapids (now a Hydropower Plant, Fig. 1d). Soil samples were taken on an eastern slope adjacent to a small swamp forest (<0.2 ha) from which peat samples were collected. In the valley bottom there is an open mire (0.4 ha) and to the west there is a mixed coniferous forest. Archaeological finds include hearths, cooking pits and pitfall systems (www.fmis.raa.se). The Edefors Rapids functioned as a meeting point for a long time (Wallerström, 1981), but no settlement was established until the 1600s (Enequist, 1937). Delineation maps from 1862 show a rectangular area described as a "meadow, mire provides hay" (www.lantmateriet.se); this area overlaps the swamp forest that we used for peat sampling (Fig. 2c). The swamp forest is located *ca.* 1 km north and south of Lake Strömbackatjärnen and Lake Kroktjärnen, respectively, from which Segerström (1990) collected sediments and conducted pollen analyses. A fire chronology was established for the area during the 1970s (Zackrisson, unpublished, referred to in Segerström, 1990).

2.2. Peat sampling, radiocarbon dating and soil collection

Peat cores and soil samples were collected in October 2014 (Heden) and July 2015 (Harads and Edefors). rUsing a Russian peat core (Jowsey, 1966), peat cores were collected from small closed-canopy sites that had restricted source areas for pollen, such that most of the pollen that accumulated was of local origin (Bradshaw, 2007; Sugita, 2007).

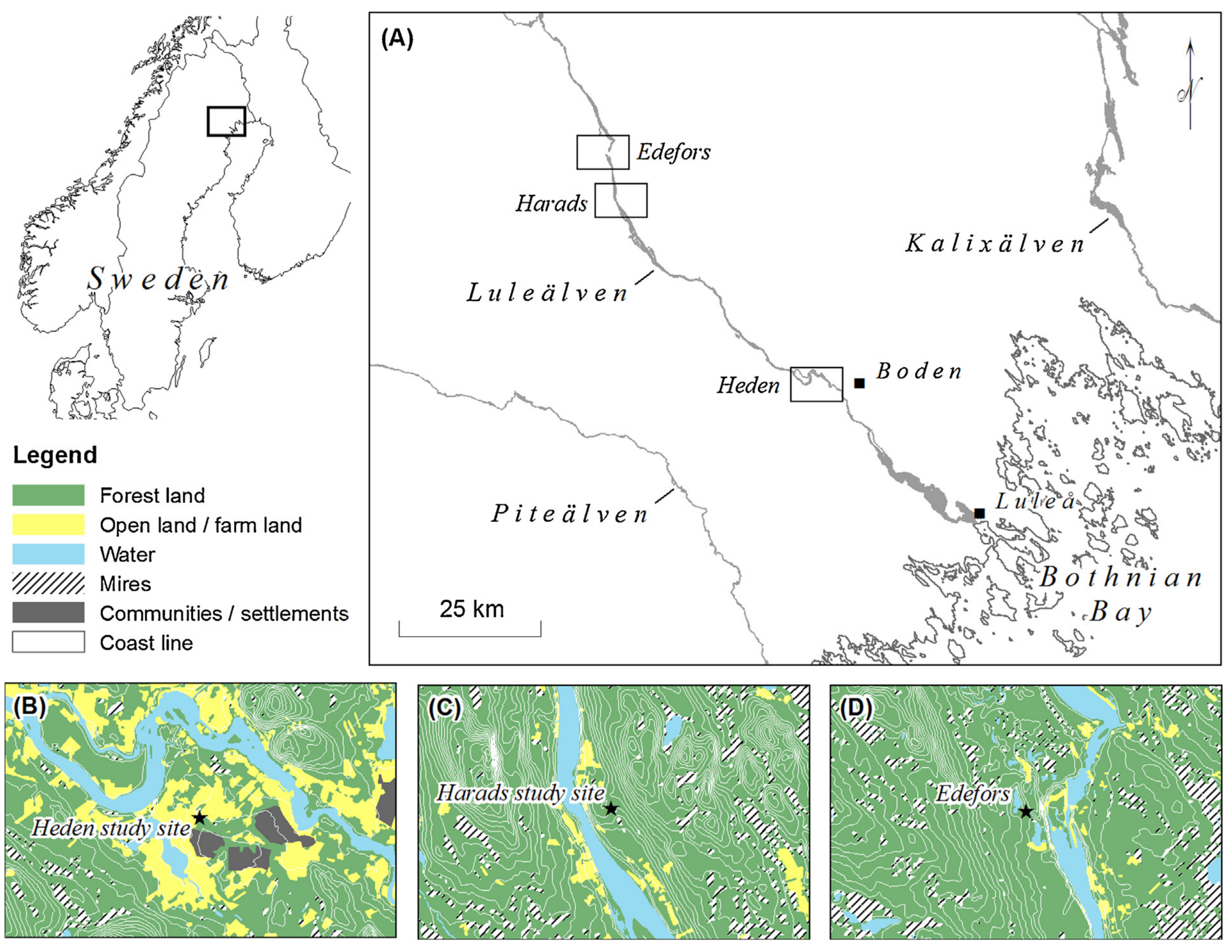

Fig. 1. Map of Fennoscandia with the study area indicated by a rectangle. Overview map with the locations of the three study sites (rectangles), place names and major rivers mentioned in the text (A). Detailed maps with the exact positions (stars) of the study sites Heden (B) 65°49'26''N, 21°34'29''E, Harads (C) 66°08'41''N, 20°53'23''E, and Edefors (D) 66°13'25''N, 20°50'13''E, as well as major features of the physical geography with the 10 m contour. Scale of detailed maps is 1:200 000.

In Heden, peat samples were collected from a mire (70 x 20 m, 32 m.a.s.l.), (Fig. 1b). The peat depth was 183 cm but the topmost part was waterlogged, so five overlapping cores were collected in total covering depths between 50 and 200 cm including visible lithological units that were used to match the cores. In Harads, peat samples were taken close to the northern edge of the swamp forest (60 x 60 m, 67 m a.s.l.), (Fig. 1c). The peat depth was 50 cm and two cores covering the entire depth were collected. In Edefors, peat samples were collected from a swamp forest (20 x 90 m, 78 m a.s.l.) located east of a mire in the pine–lichen forest (Fig. 1d). The peat depth was 110 cm and three cores covering the whole peat depth were collected.

For accelerator mass spectrometry (AMS) dating, mainly *Sphagnum* fragments were selected to give reliable AMS dates (Nilsson et al., 2001). In total, 17 samples were sent to Beta Analytic in London, U.K., for analysis (Table 1). The dates were calibrated using the IntCal 13.14C calibration curve (Reimer et al., 2013). Age–depth models were constructed using the non-Bayesian Clam model package (Blaauw, 2010) in the statistical software package (R Development Core Team, 2013). Dates are expressed as calibrated age BCE/CE according to "best fit" age, with maximum and minimum ages (2σ) given in brackets, in the linear age–depth model (see Blaauw, 2010 for details).

Soil samples were collected using a 5 cm diameter core at 10 sampling points spaced 20 m apart along a 200 m long linear transect. The depth of humus was measured and the full humus layer was collected within the 5 cm diameter core. Mineral soil samples (0–5 cm depth) were collected directly below the humus layer at each sampling point. Samples were dried at 70 °C, weighed to assess bulk density, and the whole sample was homogenized by sieving through a 2 mm mesh brass sieve. Subsamples of the homogenized soil were ground with a ball mill, passed through a 76 µm sieve and stored dry prior to analysis.

Fig. 2. Excerpts of historical maps on which the sampling sites are marked with stars indicating the Heden village and "Håmans mire" in 1718 (A), the Harads forest in 1707 (B), and the Edefors forest and a square described as "meadow, mire, provides hay" in 1862 (C). Source: www.lantmateriet.se.

2.3. Pollen, spore and charcoal analysis

In Heden, two parallel sets of samples (1 cm^3 each) were excised from the depth range 70–183 cm: 40 samples for pollen, spore and microscopic charcoal analysis, and 113 samples at contiguous levels for macroscopic charcoal analysis. The same procedure was used for samples from Harads, where 32 and 35 samples, respectively, from 15 to 50 cm, and Edefors where 32 and 65 samples from 25 to 90 cm were extracted. Samples used for pollen, spore and microscopic charcoal analysis were mixed with water, *Lycopodium* tablets were added (Batch 177745, Lund, Sweden) for accumulation rate calculations (Stockmarr, 1971), the samples were subjected to acetolysis according to Moore et al. (1991), and mounted in saffranine-stained glycerine. Pollen and spores were examined and a minimum of 500 terrestrial pollen grains was counted at each level. Pollen percentages were calculated based on the total sum of terrestrial pollen, and spore percentages were calculated based on the total sum of pollen and spores. For pollen identification, keys in Moore et al. (1991) were used. The pollen grains were grouped into 'anthropochores and apophytes' and used as indicators of anthropogenic activities (Josefsson et al., 2009). Pollen types (other than anthropochores and apophytes) that only occurred once and at one level were omitted from the diagrams. Four spore-types (*Sporormiella*, *Sordaria*, *Podospora* and *Delitschia*) associated with coprophilous fungi and one spore-type (*Gelasinospora*) associated with burned wood, were identified (Haas, 2010; van Geel et al., 2003; van Geel and Aptroot, 2006). Microscopic charcoal particles >50 μm were recorded and are presented as percentages of the total sum of pollen and spores. Accumulation rates ($cm^{-2} year^{-1}$) for pollen (PAR) from *Pinus*, *Picea*, *Betula* and anthropochores and apophytes, microscopic charcoal particles and spores from coprophilous fungi were then calculated. Pollen diagrams were constructed using the programs TILIA and TILIA GRAPH (Grimm, 1991, 2004) and pollen assemblage zones (PAZ) were established based on calculations undertaken in CONISS.

Macroscopic charcoal particles (>0.1 mm) were recorded under a stereomicroscope with x15-40 magnification (Segerström et al., 2008). Local fire events were inferred from peaks in macroscopic charcoal accumulation rates, as identified using the decomposition approach in the *CharAnalysis* program (Higuera et al., 2010) available online at www.github.com/phiguera/CharAnalysis. We used identical parameters in *CharAnalysis* for each record. Specifically, each record was interpolated to its median sample resolution, and 500-year background trends in charcoal accumulation rates were estimated with a lowess smoother that was robust to outliers. Background trends were subtracted from the interpolated series to obtain a residual ("peak") charcoal series. For each record, a global threshold value was determined using the 99th percentile of a Gaussian mixture model, fitted to the peak charcoal series and considered to represent natural and analytical noise. We also compared results using this threshold to alternative thresholds based on the 95th and 99.9th percentile values. Finally, any samples that were identified by these methods as peaks were screened using the minimum-count test (with $p = 0.05$), to guard against identifying "peaks" associated with non-significant changes in charcoal counts (Higuera et al., 2010).

Table 1
AMS-dating results and calibrated ages of the peat cores from Heden, Harads and Edefors. *Date omitted from the age–depth model, percent Modern Carbon (pMC).

Site	Depth (cm)	Lab no	^{14}C age (BP)	Cal age (2σ)	Material
Heden	70	Beta396265	100.5 ± 0.3*	pMC	Mosses
	75	Beta450427	240 ± 30	CE 1640-1950	Mosses, seeds
	85	Beta444085	1290 ± 30	CE 660-770	Mosses, seeds
	105	Beta396266	1570 ± 30	CE 435-535	Mosses, seeds
	118	Beta420700	1380 ± 30*	CE 620-670	Mosses, leaves
	130	Beta396267	1810 ± 30	CE 255-315	Mosses, leaves, seeds
	183	Beta369268	2540 ± 30	800-760 BCE	Mosses, leaves, seeds
Harads	27	Beta444086	104,1 ± 0,3*	pMC	Mosses, seeds
	32	Beta444087	100 ± 30	CE 1680-1950	Mosses, seeds
	35	Beta420703	1690 ± 30	CE 255-415	Wood, bark
	44	Beta450428	1850 ± 30	CE 70-240	Mosses
	50	Beta42704	2050 ± 30	165 BCE- CE 20	Charcoal, mosses
Edefors	26	Beta444088	104,5 ± 0,3*	pMC	Mosses, seeds
	34	Beta450429	180 ± 30	CE 1655-1950	Mosses
	55	Beta444089	410 ± 30	CE 1435-1615	Mosses
	70	Beta420698	1870 ± 30	CE 70-230	Mosses, needles
	120	Beta420699	3460 ± 30	1880-1690 BCE	Mosses, needles

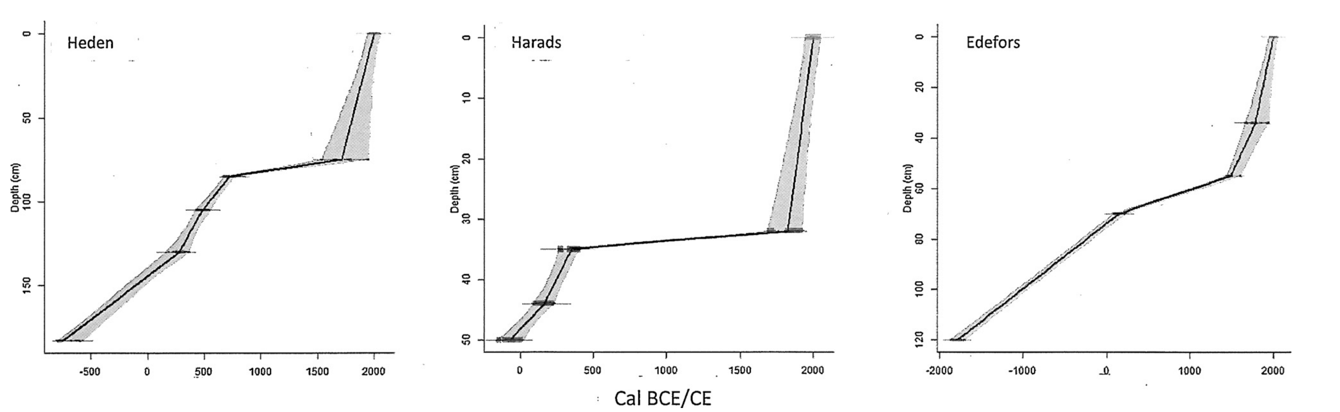

Fig. 3. Age–depth models (BCE/CE) for peat stratigraphies at Heden, Harads and Edefors. Shaded areas show the 95% confidence intervals of the linear models (Blaauw, 2010).

2.4. Soil nutrient analysis

Soil bulk density was determined by dividing total sample weight by the volume of the individual soil cores. Humus samples and surface mineral soil samples were measured for total carbon (C) and nitrogen (N) using a dry combustion analyzer (Leco True Spec). Total phosphorus (P) and calcium (Ca) were determined using a handheld X-ray fluorescence analyzer (Handheld XRF Spectrometer) after pulverizing the soil samples. Citric acid extractable P was assessed by placing 1.0 g dry soil into 10 ml of 0.1 M citric acid. The suspension was shaken for 1 h and filtered through Whatman 42 filter paper. The citric acid extract was then analyzed for orthophosphate using the Malachite green method (DeLuca et al., 2015), to evaluate P available to plants.

3. Results

3.1. Chronologies and peat accumulation

Radiocarbon dates and age–depth models for each site are presented in Table 1 and in Fig. 3. Three top levels were too recent to be dated, and one date, Heden 118 cm, was considered too young and was not included in the age–depth model. In Heden, Harads and Edefors peat started to accumulate around 750 BCE, 70 BCE and 1790 BCE (Table 1), respectively, and peat accumulation rates varied in the ranges 4–100, 6–490, and 6–90 years cm^{-1}, where slow rates indicate missing material, *i.e.* from c. 720–1715, 350–1825, and 140–490 (Fig. 3). Slow peat accumulation rates also mean that the calculated accumulation rates are low during these periods.

3.2. Pollen, spore and charcoal composition

The pollen diagrams of Heden, Harads and Edefors were divided into three, four and five local pollen assemblage zones (LPAZ; Figs. 4–6). Major shifts in pollen, spore and microscopic charcoal percentages, including maximum and minimum accumulation rates and CHAR peaks, are thoroughly described in the Appendix. Minimum and maximum influx values for microscopic charcoal particles varied between 0 and 2275.7 particles cm^{-2} $year^{-1}$. Charcoal accumulation rates varied among records, with mean (median) values of 0.83 (0.39), 0.66 (0.21), and 0.47 (2.73), for, Heden, Harads, and Edefors, respectively (Fig. 7); in contrast,

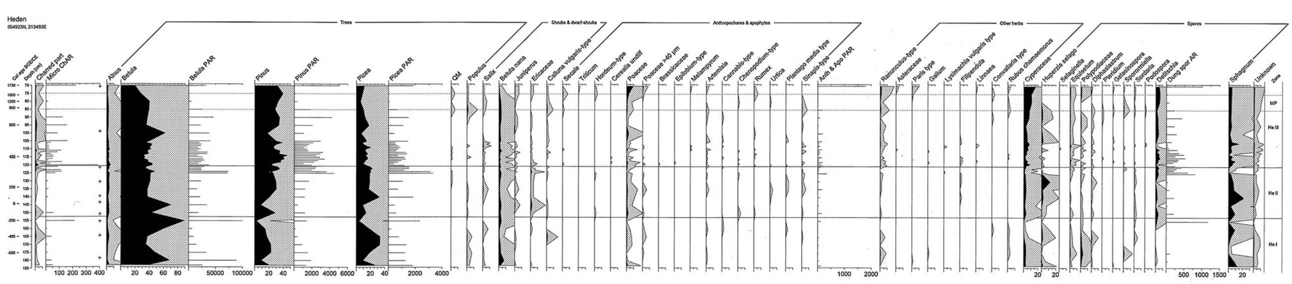

Fig. 4. Pollen percentage diagram for Heden divided into three local pollen assemblage zones (He I-III) based on CONISS. MP = missing peat material. From left to right: interpolated calibrated ages (BCE/CE), depths (cm); microscopic charcoal (>50 μm), microscopic charcoal accumulation rates (MiChAR; n cm^{-2} $year^{-1}$); plus sign (+) indicates peak in CHAR (see Fig. 7); pollen and spore types as percentages (black shading) and at x10 (grey shading); pollen accumulation rates (PAR; pollen cm^{-2} $year^{-1}$); and accumulation rates for dung-dwelling fungi (DSpAR; n cm^{-2} $year^{-1}$). Aquatic pollen and herb pollen only recorded once and at one level have been omitted.

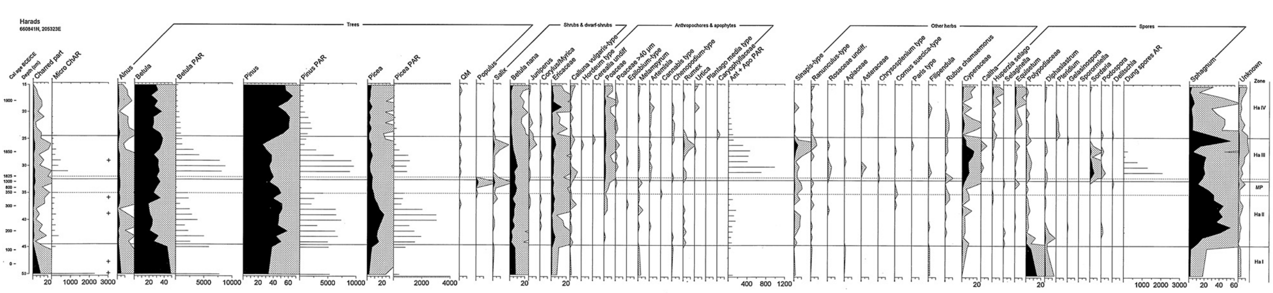

Fig. 5. Pollen percentage diagram for Harads divided into four local pollen assemblage zones (Ha I-IV) based on CONISS. See Fig. 4 for explanations.

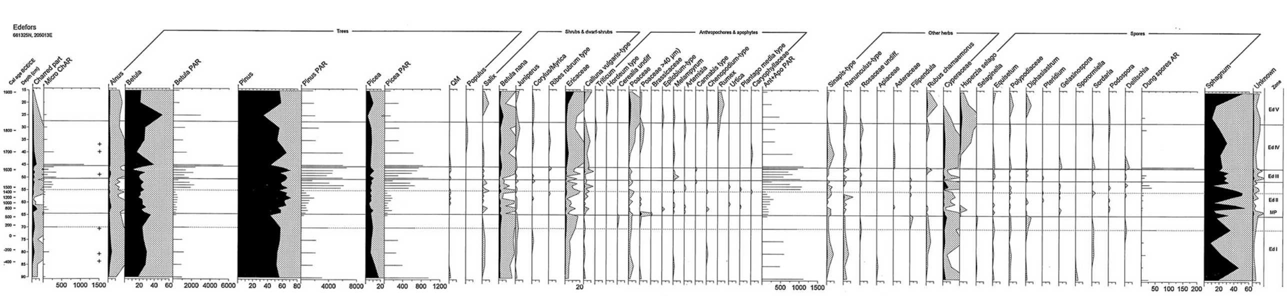

Fig. 6. Pollen percentage diagram for Edefors divided into four local pollen assemblage zones (Ed I–V) based on CONISS. See Fig. 4 for explanations.

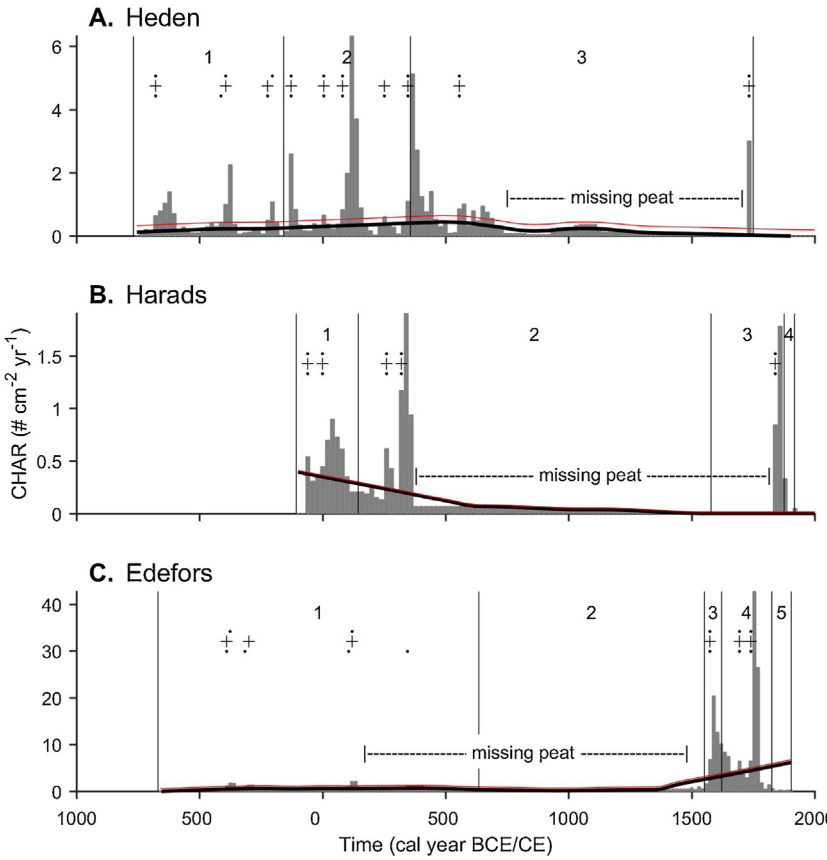

Fig. 7. Macroscopic charcoal peak analysis results for (A) Heden, (B) Harads, and (C) Edefors. Interpolated charcoal accumulation rates are plotted as grey bars, with 500-yr background trends (thick black line) and the threshold values used to separate peak from non-peak values (thin red line). Black "+" symbols indicate charcoal peaks interpreted as local fire events, with "•" symbols indicating charcoal peaks identified on the basis of alternative threshold values (higher, above the "+" and lower below the "+" symbols). Pollen assemblage zones are indicated by black vertical lines and numerical values. Finally, sections of missing peat, which are not interpreted for fire history, are indicated by a horizontal dashed line.

median sample resolution among sites was more consistent, with 19, 20, and 15 year sample^{-1}, respectively. Each record also had a global signal-to-noise index value well above 3 (i.e., 12, 9, and 4, respectively), the minimum value, suggesting suitability for charcoal peak analysis (Kelly et al., 2011). Peak analysis identified a total of 10, 5, and 6, peaks at Heden, Harads, and Edefors, respectively, and peak identification was generally robust with respect to the two alternative threshold values (i.e., 95th and 99.9th percentile thresholds; Fig. 7). Excluding periods of missing peat from each record and accounting for only complete return intervals, estimated fire return intervals did not differ significantly between the sites, with mean (standard deviation) values of 154 (70), 127 (115), and 169 (105) years, for Heden, Harads, and Edefors, respectively. Peak magnitude was generally consistent among peaks within each record, with the exception of pollen zone 1 at Edefors, which had notably lower peak magnitudes relative to the rest of that record (Fig. 7).

3.3. Soil nutrient capital

Total C and N in humus and mineral soils are shown in Fig. 8. Soil nutrient values and total C in mineral soils from the three pine–lichen forests showed little difference between the three sites; however, both total C and total N in humus were notably low at Harads and notably high at Heden. Total P, total C and citrate extractable P in the surface mineral soil and total P in the humus layer are shown in Fig. 9. The quantities of total P and C in the surface mineral soil showed little variation between sites while citrate extractable P (plant available) and total P in humus varied, with high values recorded at Edefors (Fig. 9).

4. Discussion

4.1. Vegetation and fire history

We combined data from several sources to decipher a complex relationship between vegetation changes, anthropogenic influences and fire dynamics. Our interpretations of vegetation history focus on the forests surrounding the sampling sites and are based on the presence of pollen types associated with coniferous forest, grazing and dung-associated spores, charcoal accumulation rates and peaks (Appendix A; Figs. 4–7), information derived from historical documents (www.lantmateriet.se; www.fmis.raa.se) and from previous scientific studies (Segerström, 1990; Zackrisson, 1981).

4.1.1. Heden

4.1.1.1. LPAZ He I: Deciduous-rich forest, low impact of fire and grazing 750–160 BCE (183-152.5 cm). Around 750 BCE the Heden mire was surrounded by a deciduous-rich coniferous forest, indicated by the presence of pine, spruce, birch and aspen (*Populus tremula*) pollen (Fig. 4). Pollen from grasses (Poaceae), dwarf birch, juniper (*Juniperus commune*) and heather (*Calluna vulgaris*), apophytes

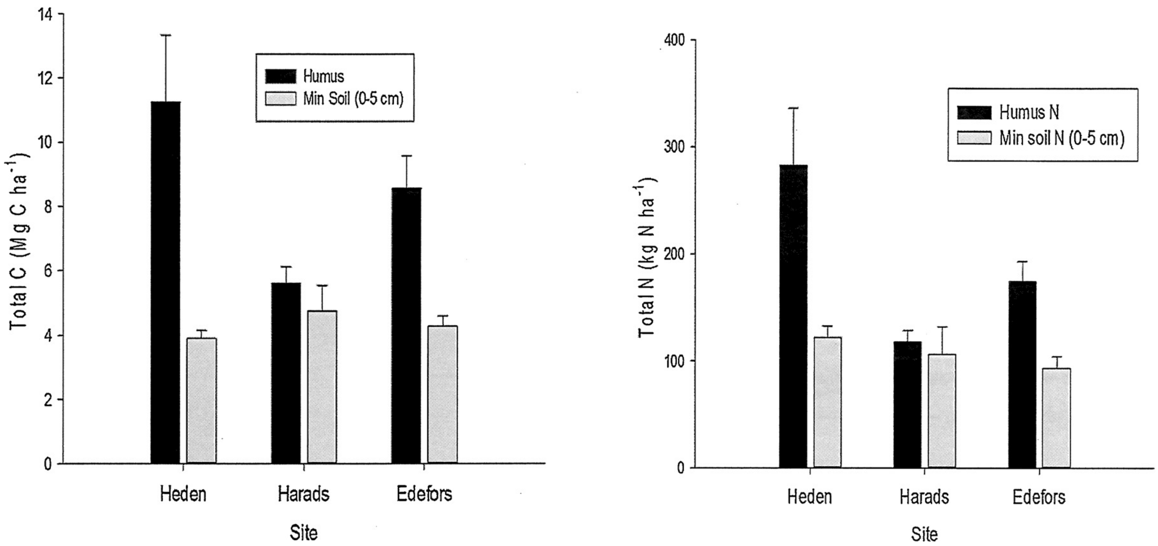

Fig. 8. Total C (Mg ha^{-1}), and total N (kg ha^{-1}) in the humus layer and surface mineral soil (0–5 cm), at Heden, Harads and Edefors in north-eastern Sweden.

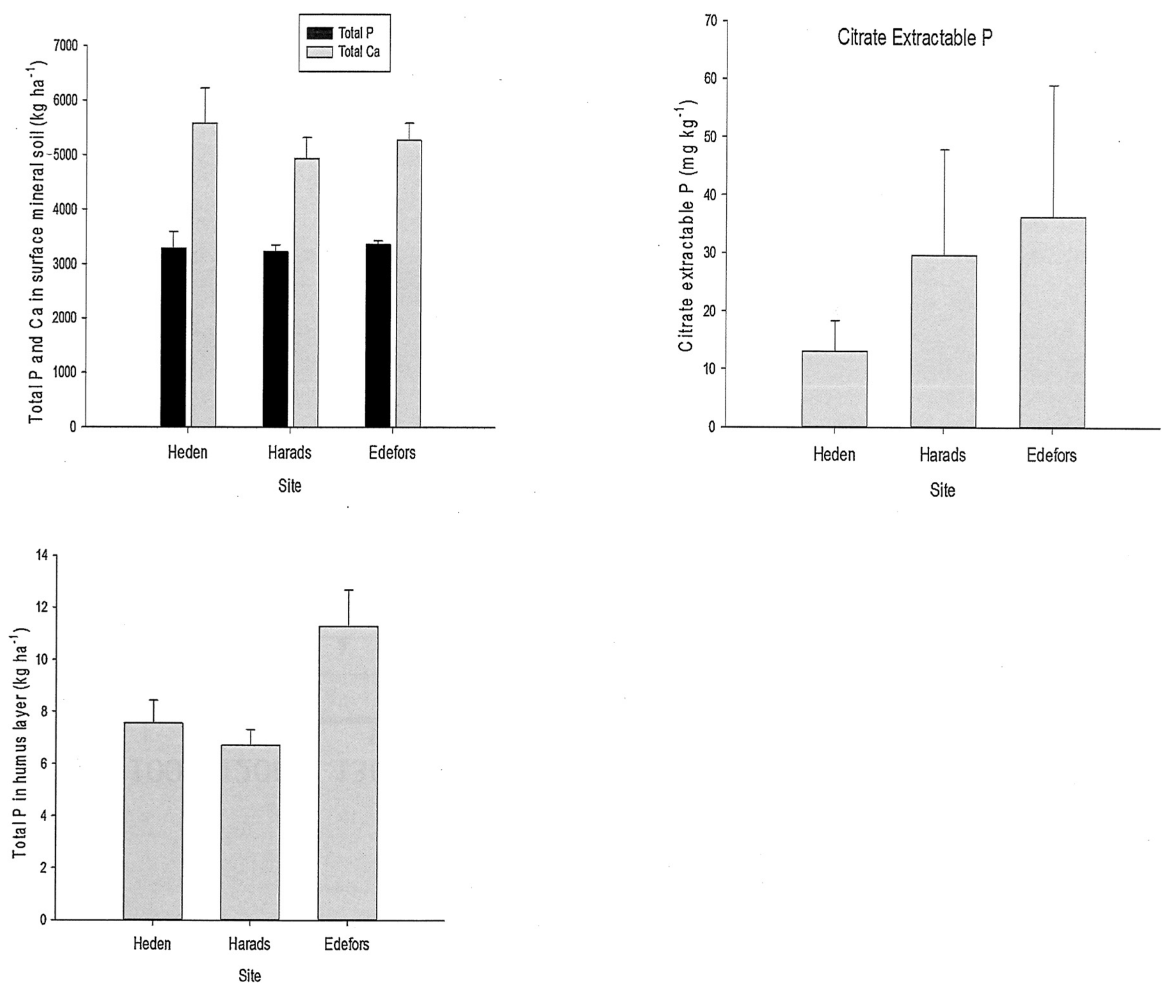

Fig. 9. (single column). Total P and total Ca in surface mineral soil (kg ha^{-1}), citrate extractable P (mg kg^{-1}) in the surface mineral soil (0–5 cm), and total P in humus (kg ha^{-1}), at Heden, Harads and Edefors in north-eastern Sweden.

and coprophilous fungi spores suggest that the local area provided good grazing grounds (Cugny et al., 2010; Hicks, 1988). Grazing and cultivation have also been documented prior to the BCE/CE transition (hereafter BCE/CE) on other land-uplift meadows around the Bothnian Bay (Engelmark, 1976; Wallin and Segerström, 1994). The presence of heather, a species that grows together with reindeer lichens in fire-prone pine forests (Engelmark, 1987; Zackrisson, 1977), microscopic charcoal around 700 and 400 BCE, and peaks in CHARs around 680 and 390 BCE indicate fire events (Figs. 4 and 7). Increased accumulation rates of microscopic charcoal and one CHAR peak at the end of the zone, together with an increase in birch and a decrease in conifers indicate local fire events around 220 BCE. At the same time, Lake Fisktjärn became isolated (Segerström, 1990), and that could explain the increase in PAR of birch as more land became forested due to land-uplift. Nevertheless, we suggest that fire and grazing affected the local area from around 200 BCE.

4.1.1.2. LPAZ He II: Mixed coniferous forest, impact of fire and grazing 160 BCE–360 CE (152.5-120.5 cm). Increased PAR for pine and spruce, continuous presence of dwarf shrub pollen and fir clubmoss (*Huperzia selago*) spores indicate a shift to a mixed coniferous forest (Fig. 4). An increase in apophyte pollen types, together with continuous records of spores from coprophilous fungi indicate local grazing throughout this period. Peaks in CHARs around 130 BCE, BCE/CE, 80, 250 and 350 CE indicate clear impacts of fire (Fig. 7). The scattered occurrences of *Hordeum*-type pollen are probably sand ryegrass (*Leymus arenarius*), a wild grass typically found on sandy shores in Fennoscandia. At the end of the zone, increased accumulation rates of microscopic charcoal indicate a change in local fire pattern that may have been caused by increased lightning ignitions, or by human-induced fires with the aim to improve grazing. In addition, higher PAR of apophytes and increased accumulation rates of coprophilous fungi indicate a heavier grazing impact.

4.1.1.3. LPAZ He III: Pine forest, recurrent fires, grazing and cultivation 360–1730 (120.5-70 cm). High PAR for pine and birch together with decreasing PAR for spruce, continuous presence of dwarf shrub pollen and overall intermediate PAR of apophytes indicate a transformation into a pine-dominated forest (Fig. 4). Around 380 and 430, microscopic charcoal accumulation rates are high, indicating local fire. CHARs peak again around 560 (Fig. 7), and microscopic charcoal rates are high at 480, 540 and 660. These records coincide with the first signs of human impact on forest vegetation at Lake Fisktjärn (Segerström, 1990). Apophytes are recorded continuously at intermediate PAR, and cereal pollen are recorded from *ca.* 380, coinciding with an increase in charcoal particles, indicating that fire was used to create cultivation land. Forest fires in the surrounding areas occurred regularly throughout this period. However, the missing peat and slow peat accumulation affected the peat stratigraphy from 720 to 1715 (Fig. 3), which makes interpretation of vegetation changes and fire impact difficult. Indirectly, it indicates that the impact of local fire was considerable and that peat was burnt; however, no distinct charcoal layers are recorded in the stratigraphy. *Gelasinospora* spores do occur repeatedly throughout this period, supporting the suggestion that there were frequent fires (Dietre et al., 2017), until *ca.* 1730 when CHARs, microscopic charcoal accumulation rates and apophyte PAR (including cereals) peak. Further, spores from coprophilous fungi are recorded continuously. This suggest that the impact of fire was substantial and that the area close to the sampling site was used as pasture (*cf.* Cugny et al., 2010).

4.1.2. Harads

4.1.2.1. LPAZ Ha I: Pine–birch forest, low impact of fire 70 BCE–145 CE (50-44.5 cm). Around 70 BCE, peat started to accumulate and the pollen record indicates that the surrounding forest was dominated by pine and birch, and the forest floor by dwarf-shrubs. The charcoal particles at the bottom of the peat profile probably originate from fires since the time the land emerged from the sea. The impact of fires during LPAZ Ha I was limited given the overall low CHAR accumulation rates, the low peak magnitudes and a single additional peak in CHARs around BCE/CE (Fig. 7). Apophyte pollen indicates modest levels of grazing, probably by wild ungulates.

4.1.2.2. LPAZ Ha II: Mixed coniferous forest, increased impact of fire and grazing 145–1580 (44.5-32.5 cm). LPAZ Ha II marks a change to a pine-dominated forest with spruce on mesic sites. The pollen record indicates that ericaceous species and heather dominated the forest floor, but with a gradual increase in grasses. Increased pollen of apophytes indicate grazing in the local area (Hicks, 1988; Josefsson et al., 2009). Micro- and macroscopic charcoal particles are recorded at low accumulation rates throughout the first part of the zone, indicating limited influence of local fire. However, around 260 a peak in CHARs indicates local burning that affected the surrounding forest, and led to a decrease in spruce, while birch, aspen, willow (*Salix*) and grasses increased. Peat was consumed by fires from 350 to 1825, which explains the low accumulation rates (see Figs. 3 and 5). Presumably, the notable accumulation of macroscopic charcoal seen in the CHAR peak around 320 (Fig. 7) is the result of numerous fires. The fire chronology established by Zackrisson (1981) shows that 18 fires occurred in the local area from 1081 to 1888, with a mean fire return interval of 47 years (Fig. 10). Based on micro- and macroscopic charcoal accumulation rates, recurrent fires may have started *ca.* 320, and definitely from the 11th century according to the fire chronology. Only a few spores from coprophilous fungi are recorded. Presumably a result of short ranged dispersal ability of spores (Kamerling et al., 2017), and that grazing mainly occurred in the surrounding pine forest during winter by reindeer.

4.1.2.3. LPAZ Ha III: Pine–birch forest, recurrent fires and intensive grazing 1580–1865 (32.5-24.5 cm). Missing material in the peat profile makes interpretations of vegetation change and fire history difficult until 1825. Higher pollen percentages of birch and willow indicate that the swamp forest was characterized by a deciduous-rich pine forest with dwarf-shrubs, grasses and herbs. Consistent microscopic charcoal accumulation rates and a CHAR peak around 1840 indicate recurrent fires, but they are also an effect of increased peat accumulation rates from around 1830 (Fig. 3 and 7). High pollen percentages and PAR of apophytes together with high percentages and accumulation rates of spores from coprophilous fungi show that local grazing was intensive (Blackford and Innes, 2006). Repeated burnings of the forest are reflected in the short fire return intervals up until 1715 when, according to the fire chronology, three consecutive fires affected the area (Fig. 10).

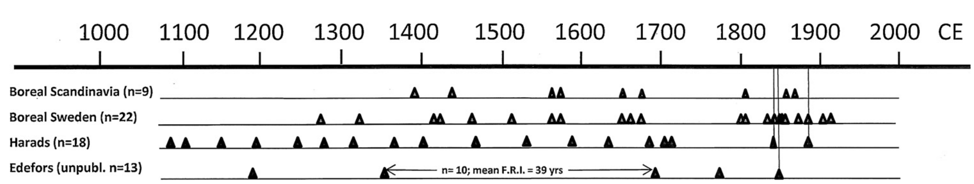

Fig. 10. Large fire years (CE) in boreal Scandinavia (Drobyshev et al., 2014), in boreal Sweden (Drobyshev et al., 2015), and local fire years recorded in Harads (Zackrisson, 1981) and in Edefors (Zackrisson unpublished, referred to in Segerström, 1990). No detailed data are available for the Edefors chronology between 1342 and 1691 except for the mean fire return interval (F.R.I). Vertical lines indicate coinciding fire years in Boreal Sweden, Harads and Edefors; 1847, 1852 and 1888.

Presumably, these fires were initiated at more mesic sites prior to cultivation or to improve summer grazing for domesticated animals, and in accordance with the general change in fire pattern after 1650 suggested by Niklasson and Granström (2000). Microscopic charcoal particles co-occur with pollen from fireweed (*Epilobium*-type) and cereals recorded at the end of the zone.

4.1.2.4. LPAZ Ha IV: Pine forest, fire suppression and grazing 1865–1920 (24.5-15 cm). Pollen percentages show that pine dominated the tree layer – a result of the many recurrent fires that occurred during the previous zones. Seemingly, spruce only managed to survive in wetter parts. The lack of charcoal marks the end of the recurrent fire period and the start of fire suppression, following the last local fire in 1888 (Fig. 10). The subsequent fire-free period is characterized by apophyte pollen and spores from coprophilous fungi which together indicate continued grazing.

4.1.3. Edefors

4.1.3.1. LPAZ Ed I: Mixed coniferous forest, low impact of fire and grazing 630 BCE – 635 CE (90-64.5 cm). At the start birch and spruce dominated the swamp forest that was affected by groundwater outflow contributing to a good nutrient status reflected in the high PAR values for apophytes (mainly grasses). The surrounding forest was dominated by pine with scattered occurrences of spruce, birch and dwarf-shrubs. Low continuous records of spores from coprophilous fungi, suggest continuous grazing. Fires occurred in the area but the impact was initially low as indicated by low charcoal accumulation rates, except for CHAR peaks around 390, 300 BCE and 120 CE, which indicate local fires. However, peat accumulation was slow from 140 CE (Fig. 3), so it is possible that the CHAR peak around 120 (Fig. 7) contains macroscopic charcoal particles from numerous consecutive fires. Interestingly, juniper, PAR for apophytes and accumulation rates for coprophilous fungi peak simultaneously, suggesting land use, initially for grazing and from around 590 even for cultivation as indicated by unidentified cereal pollen (cf. Josefsson et al., 2014). Segerström (1990) also found unidentified Cerealia pollen not far from our study site pre-dating BCE/CE, and recorded an increase in apophytes from around 500–600 representing the introduction of animal grazing, or small-scale cultivation. Thus, the impact of grazing in Edefors, recorded from 140, could have included domesticated animals in the mesic depression near the mire and not in the surrounding forest.

4.1.3.2. LPAZ Ed II: Pine forest, recurrent fires and grazing 635–1550 (64.5-50.5 cm). An increase of heather and a decrease of ericaceous species indicate that the surrounding forest was dominated by pine while spruce and birch were confined to mesic sites. At the start of this zone, large grasses, Brassicaceae, mugwort (*Artemisia vulgaris*), cow wheat (*Melampyrum*), willow and juniper are present. Then, several apophyte pollen types are recorded. Despite a slow peat accumulation rate until 1490 (Fig. 3), microscopic charcoal accumulation rates vary continuously from 680 to 1480, with a temporarily peak around 770 (Fig. 6). No CHAR peak was recorded during this period, but the microscopic charcoal occurrences together with repeated records of spores from coprophilous fungi, *Gelasinospora* spores, and apophyte pollen including fireweed indicate fire and grazing. Around 1500 accumulation rates for trees and apophyte pollen, coprophilous fungi spores and charcoal particles increase, possibly an effect of increased peat accumulation rates (Fig. 3). In addition, the first documented farms in the Edefors area were established during the early 16th century (Enequist, 1937). Based on microscopic charcoal accumulation rates, it seems likely that fires were deliberately initiated in the surrounding pine forest from 1500, but probably as early as 770. This is partly supported by the unpublished fire chronology from the Edefors area by Zackrisson (referred to in Segerström, 1990), that recorded one fire event in 1191 followed by a period between 1342 and 1691 during which there were ten fires with a mean fire return interval of 39 years (Fig. 10).

4.1.3.3. LPAZ Ed III: Pine forest, recurrent fires and grazing CE 1550–1625 (50.5-45.5 cm). PARs indicate that pine continued to dominate the surrounding forest. Initially dwarf-shrubs increased and heather decreased, suggesting that the forest floor entered a late successional stage with more ericaceous species. PARs for apophytes are high, but fewer pollen grains are recorded compared to the previous zone, and heather increases at the top of this zone. Spores from coprophilous fungi are also present, and microscopic and macroscopic charcoal accumulation rates are high (Fig. 6), indicating grazing and local fire with a peak in CHARs around 1575 (Fig. 7). This fits well with the Edefors fire chronology, indicating frequent fires during this period (Fig. 10).

4.1.3.4. LPAZ Ed IV: Pine forest, decreasing impact of fire and grazing 1625–1825 (45.5-27.5 cm). A decrease in pine and spruce PAR, and stable PAR of birch, characterize the tree layer conditions during LPAZ Ed IV. In the surrounding forest, dwarf-shrubs initially became more dominant while apophyte PAR decreased, indicating that the ground vegetation transitioned into a late successional stage with ericaceous species. High microscopic charcoal percentages, initially high microscopic charcoal accumulation rates and CHAR peaks around 1695 and 1740 (in agreement with fire years 1691 and 1765 in the local chronology, Fig. 10), indicate recurrent fires. High charcoal accumulation rate is accompanied by presence of *Gelasinospora* spores and high accumulation rates of spores from coprophilous fungi, indicating intensive grazing. Then follows a period characterized by a decrease in ericaceous species, including heather, an increase in grasses, and the presence of mugwort and sorrel (*Rumex*). Also, wheat (*Triticum*) is recorded in the upper level of LPAZ Ed IV. Presumably, the area was used for summer grazing, and for some small-scale shifting cultivation around 1770 (see Hörnberg et al., 2015).

4.1.3.5. LPAZ Ed V: Pine forest, grazing, and cultivation 1825–1905 (27.5-15 cm). Birch PAR increases initially, while pine and spruce PAR both decrease substantially, suggesting that the surroundings were recovering from a disturbance that promoted birch. The pollen record shows that willow, grass and sorrel increased, several apophyte pollen types were present, as was barley (*Hordeum*-type). These records indicate that the depression continued to be used as pasture during the 19th century (Fig. 2c; www.lantmateriet.se). After the 1852 fire in the Edefors chronology (Fig. 10), the impact of fire disappears, as indicated by the lack of CHAR peaks and the last microscopic charcoal accumulation value around the 1880s (Figs. 6 and 7). Towards the end of the zone, pollen from spruce and willow and apophytes decreases, whilst pine, ericaceous species and spores from peat moss (*Sphagnum* spp.) increase, suggesting that the impact of local grazing was reduced, and that post-fire late succession vegetation increased in the surrounding forest.

4.2. Long-term fire history in pine–lichen forests

The local fire history and disturbance patterns at our three study sites can be summarized as follows. At Heden, the first nine recorded local fires had estimated fire return intervals that varied between 80 and 290 years, with a mean of >150 years (Figs. 4 and 7). From the early 8th century it is difficult to evaluate the fire pattern. Presumably, the impact of local fires increased, as indicated by missing peat material, and continued until *ca.* 1730.

At Harads, four fires occurred irregularly with an estimated mean fire return interval of >125 years (minimum and maximum intervals varied between 60 and 260 years) until *ca*. 320 CE (Fig. 7). The fire pattern probably changed into recurrent local fire events from 350, lasting until the late 1800s (Figs. 5 and 7). According to the Zackrisson (1981) fire chronology, a total of 18 local fires occurred between 1081 and 1888 (Fig. 10). After 1888 there are no indications of local fires at Harads. At Edefors, three local fire events can be traced back to *ca*. 390 and 300 BCE, and 120 CE (Fig. 6), indicating variable fire return intervals. Then there is a period of over 1400 years when local fire events are difficult to interpret because of missing peat, microscopic charcoal was recorded at low rates and no CHAR peaks were documented (Figs. 6 and 7). Subsequently, microscopic charcoal accumulation rates and CHAR peaks indicate recurring local fires around 1575, 1695 and 1740, and no fires thereafter (Figs. 6 and 7).. The fire chronology from Edefors supports our interpretation as it indicates one fire event in 1191 that was followed by ten fires between 1342 and 1691, and two final fires in 1765 and 1852, of which only the most recent fire does not correspond to our findings (Fig. 10).

The changes in fire pattern recorded do not coincide with any major shift in regional climate during the last 2000 years, like the Medieval Warming of 950–1250 or during Little Ice Age of 1450–1850 (Grudd et al., 2002; Mayewski et al., 2004). Several CHAR peaks nearly coincide; around the BCE/CE transition and 250–260 CE at Heden and Harads, and *ca*. 390 BCE and 1730–1740 CE at Heden and Edefors (Fig. 7). However, the local fire chronology at Harads and the available information from the Edefors chronology do not coincide with the regional fire history in northern Sweden (Fig. 10). Extensive studies of fire chronologies from boreal Scandinavia (Drobyshev et al., 2015, 2014) have identified 25 years with increased forest fire activity related to climate, from 1270 to 1960. Only two of these large fire years coincide with the fire years recorded in Harads (1847 and 1888) and one in Edefors (1852) (Fig. 10), suggesting that these fires were the result of natural causes. This also implies that the other fires recorded in Harads and Edefors did not follow this general pattern. Accordingly, the recurring local fires from the 2nd and 4th centuries (Edefors and Harads), and from the 8th century (Heden) were possibly initiated by humans. If so, the initiation of recurrent fires at the study sites clearly precedes the shift from “natural” to “anthropogenic” fire regimes during the mid-1600s suggested by Niklasson and Granström (2000). The age–depth models (Fig. 3) show that peat was burnt at the Heden, Harads and Edefors sites from *ca*. 720, 350 and 140, respectively, which makes it difficult to assess the fire history and the vegetation development accurately. However, there is no evident loss of peat before those dates, and less peat seems to have been lost in Edefors where a change in fire pattern was indicated by a CHAR peak around 140 and by an increase in the microscopic charcoal record from *ca*. 770 (Fig. 6), suggesting early onset and then a possible increasing use of fire in this area. To summarize, the similarity in the pollen and charcoal records during the periods of missing peat material, from the 2nd, 4th and 8th until the 17th century (Figs. 4–7), suggests that the fire return intervals at all three sites were similar to the ones documented in the Harads and Edefors fire chronologies (Fig. 10).

4.3. Recurrent fires, nutrient capital and succession

A combined look at fire history, soil properties and historical human occupation of the region helps our understanding of how and why the degraded pine-lichen forests may have developed. Two thousand years ago, fire return intervals were variable and long in pine forests on till soils, >300 years as suggested by Wallenius et al. (2010) and Carcaillet et al. (2007), and >125-250 years in pine forests on sediment soils as shown in this study. The forests were characterized by conifers and birch in the tree layer, and by dwarf-shrubs, herbs and mosses on the forest floor. In boreal forests, cyanobacteria living in association with feather mosses fix N_2 (convert gaseous N_2 to NH_4^+) and provide the ecosystem with up to 4.5 kg N ha^{-1} and year^{-1} (DeLuca et al., 2002; Zackrisson et al., 2009), and the rate of N_2 fixing activity increases with increasing age of the stand (Zackrisson et al., 2004). Given the fact that recurrent fires remove ecosystem N during heating above 120 °C as a result of volatilization (Neary et al., 1999) and given the lack of woody or herbaceous N_2 fixing plants in this region, N_2 fixation in feathermosses provides a key source of N accumulation in boreal forests where it is a limiting factor (DeLuca et al., 2002; DeLuca and Zackrisson, 2007). Extended fire return intervals and succession cycles create the prerequisites for N_2 fixation, given the high N demand in trees growing on nutrient poor sediment soils and coarser till (Wardle et al., 2003). Over time, litter and humus produce well-developed E (eluviated) and Bs (spodic, podzolic) horizons typical of secondary pine–lichen forest. The slow-growing pine–lichen forest that characterizes the study sites today is in stark contrast to forest types that are commonly found in the region. We believe that the development of such degenerated pine–lichen forests is the result of dramatic changes in the fire regime caused by humans during the last 1800 years that are still reflected in their humus and soil nutrient capital.

The amount of total C and N in the humus in the three pine–lichen forests (Fig. 8) was notably high in comparison to the quantities recorded in the fire-maintained spruce–lichen forests located further north and west and studied by DeLuca et al. (2013), but still low in relation to the amounts recorded in the reference areas used by Huss-Danell and Lundmark (1988) and by DeLuca et al. (2013) (Table 2). In Harads, the amount of total C and N in humus and mineral soil were at levels well in excess of that recorded at the same area thirty years earlier (Table 2) when the site was classified as exhibiting “low productivity”. The citrate extractable P levels (Fig. 9) equaled those dwarf shrub-heath in the uplands of Wales and Scotland (DeLuca et al., 2015). Presumably, the frequently recurring fires, starting sometime between the 2nd and 8th centuries, caused an accrued loss of nutrients through repeated combustion of the humus layer, loss of feathermoss cover (including loss of N build up through N_2-fixing cyanobacteria) and by leaching, so that the nutrient content in the humus and soil slowly declined (Table 2). Over time, this promoted a pine-dominated forest with scattered birch trees and a thin vegetation layer covering the forest floor, mainly dominated by dwarf-shrubs such as heather but also reindeer lichens. This general development is supported by our vegetation analyses. If we presume that these fires were initiated by people, one intriguing question emerges: For what purpose did they burn the pine forest?

Table 2
Total C and total N in humus and mineral soil from the pine–lichen forests in Heden, Harads and Edefors (He-Ha-Ed), and from previous studies of forest soils on sandy sediments in Harads (Ha) and reference areas (Ref) (data derived from Huss-Danell and Lundmark, 1988), and spruce–lichen forests in Marrajåkkå, Marrajegge and Kartajauratj (Ma-Ma-Ka) and reference areas (Ref) west of Porjus, northern Sweden (data derived from DeLuca et al., 2013).

	He-Ha-Ed (this study)	Ha (1988)	Ref (1988)	Ma-Ma-Ka (2013)	Ref (2013)
Total C (Mg ha^{-1})					
Humus	5.6-11.3	4.7	40-50	1-2	25-40
Mineral Soil	3.9-4.8	3.9	4-10	13-17	15-17
Total N (kg ha^{-1})					
Humus	118-282	79	500-600	25-45	510-870
Mineral Soil	94-122	64	100-200	780-890	730-840

4.4. An alternative explanation for burning

To answer why people were burning these forests we start by looking at the fire chronology from Harads (Fig. 10). From 1081 to 1687 the fire return interval varied between 26 and 73 years, with a mean interval of 47 years. In the late 17th century, there was a clear shift in fire return interval with three consecutive fires between 1687 and 1715 – a fire pattern typical of slash-and-burn clearance and using fire to improve livestock grazing by farmers (Granström and Niklasson, 2008; Lehtonen et al., 1996; Storaunet et al., 2013). After 1715 only two more fires, in 1847 and 1888, affected the forest at Harads and these were probably natural large-scale fires as indicated by the regional fire chronology established by Drobyshev et al. (2015) (Fig. 10). A similar pattern was found in the Edefors chronology, with a mean fire interval of 52 years between 1191 and 1765, and the most recent fire in 1852 being synchronous with the regional fire chronology (Fig. 10).

Frequent records of spores that derive from coprophilous fungi during periods with recurrent local fires, in addition to the presence of various types of apophyte pollen show that grazing has occurred on or close to the sampling sites (*cf.* Dietre et al., 2017). While the general interpretation of such finds includes fire practices to enhance the conditions for livestock grazing or cultivation (Granström and Niklasson, 2008), we introduce an additional explanation: *recurrent fires aimed at creating lichen-dominated ground vegetation to improve winter-grazing conditions for reindeer*. Pine heaths with plenty of reindeer lichens and pendant tree lichens constitute a critical resource area for reindeer herders and must have been carefully managed. A fire return interval of 40–80 years fits well with a practice suitable to promote and maintain lichen-dominated vegetation in pine forests. Accordingly, we suggest that the repeated fires recorded at the study sites from the 2nd up until the 17th century was induced by reindeer herders to maintain good winter-grazing grounds (Fig. 7), whereas the fires with very short intervals from 1687 to 1715 were initiated by newly settled farmers to improve livestock grazing conditions and for cultivation (Fig. 10).

In order to promote lichen-dominated vegetation within a few decades and with the pine stand still intact, the fires must have been of low-intensity – just enough to burn dwarf-shrubs and the moss layer but without harming the trees and the pendant tree lichens. We suggest that this fire practice erased the feathermosses and the N_2-fixing cyanobacteria living on them, thus slowly reducing the overall nutrient capital in humus and soil. In the early 1900s, the legacy of this long-term land use was still clearly visible resulting in the “pine–lichen forest degradation” discussion that concerned foresters at that time (*e.g.* Ebeling, 1972; Romell and Malmström, 1945; Wretlind, 1934). Today, 130–290 years after the last fires, the studied forests are grazed by reindeer to some extent, the dwarf-shrub layer is now recovering, the cover of lichen decreasing, and the feathermoss–cyanobacteria complex restoring and slowly improving the N capital (Fig. 8, Table 2).. Hence, the effects of the early use of fire are slowly diminishing. This change in forest floor vegetation towards a late successional stage is clearly visible in the National forest surveys of northernmost Sweden (Sandström et al., 2016).

4.5. Reindeer herding subsistence and past use of fire

The shift in fire history and patterns at the three study sites during the first millennium occurred during a time when the domestication of reindeer gained momentum in northern Fennoscandia (Aronsson, 1991; Bergman et al., 2013; Hedman et al., 2015). Although very little is known about reindeer herding this far back, it is known that Sami and other groups, kept reindeer as part of a multifaceted way of living (Bjørklund, 2013). Because most sediment soils are located along rivers (www.sgu.se) and it was convenient to migrate with the herds on the ice during wintertime, the pine–lichen forests along frozen waterways were especially attractive winter-grazing grounds. We suggest that deliberate burnings were introduced in order to secure access to good winter-grazing grounds. After fire, the area had to “rest” for up to 20 years so that the reindeer lichens could re-establish, and then be used for winter grazing. Ground lichens are, however, sensitive to trampling so intensive grazing accelerates the succession of the ground vegetation (Väre et al., 1996). Therefore the same area could not be used for too long before mosses and dwarf-shrubs begun to dominate. Consequently, fire was deliberately induced to promote and sustain reindeer lichen-dominated ground vegetation at different successional stages dispersed across the landscape, and resulting in a fire return interval of around 40–80 years in pine–lichen forests along rivers.

The deliberate fires must have been ignited early in the season as soon as dwarf-shrubs and mosses had dried. Presumably, these fires only affected the pine heaths since forests on mesic till sites would have been still too wet to carry fire. Farmers, especially from the 1600s (Niklasson and Granström, 2000), burned their mesic areas more frequent (every 10–20 years) and such areas dry up later in early summer (Lehtonen et al., 1996; Zackrisson, 1977). These later season fires could easily spread to pine–lichen forests, which then could be very dry. Because these two kinds of intentional burnings were separated in both time and space, these differences may explain controversies in old court protocols between reindeer herders and farmers during the 16–1700 s regarding use of fire (Bylund, 1956; Granström and Niklasson, 2008; Laestadius, 1833).

Burning of pine–lichen forests has passed unremarked over time because knowledge of past land use has mainly been transferred orally among reindeer herders and has gradually been lost. Further, the written historical records mainly originate from the 16th century onwards and were recorded by officials who were unfamiliar with boreal forest lifestyle and reindeer herding. Our results suggest that reindeer herders at that time had a profound knowledge of fire dynamics and vegetation succession stages stretching over several decades and were able to create specific resources that they could use, just like people have done in other parts of the world (*e.g.* Butsic et al., 2015; Fowler and Welch, 2015).

4.6. Methodological considerations

The strength of our study is the joint interpretation of pollen, spore, charcoal and soil nutrient data that have been combined with information from historical sources, and two fire chronologies. This information gives a general picture of *what may* have happened at the study sites, and radiocarbon dates give us an idea of *when* the changes occurred. However, we cannot separate natural and man-made fires with these methods, and we cannot say much about their geographical distribution (but see Niklasson and Granström, 2000). It is also difficult to identify fire events by analyzing charcoal in peat profiles (Higuera et al., 2005; Kasin et al., 2017; Ohlson et al., 2006). Normally it is difficult to separate local and regional fires based on microscopic charcoal, but the identification of macroscopic charcoal particles in a separate non-destructive way allows more robust interpretations of local fire events (Ohlson and Tryterud, 2000; Segerström et al., 2008), and *CharAnalysis* makes it possible to separate fire-related CHAR peaks from background noise. Hence, long fire return intervals (>125–250 years) were identified at the study sites before the 2nd, 4th and 8th centuries. Subsequently, peaks in CHAR, increases in microscopic charcoal particles, and the short fire return intervals in the fire chronologies clearly indicate increased fire impact, especially when they co-occur with vegetation changes (Hörnberg et al., 2012; Ohlson and Tryterud, 2000). The problem with peat lost in the stratigraphy due to fire could be tackled with complementary studies of charcoal in small lake sediments (e.g. Davis et al., 2016).

5. Conclusions

Based on our results we suggest that many pine–lichen forests, that were a common landscape feature in northernmost Fennoscandia until the early 1900s, were the result of a long-term use of fire to remove mosses and dwarf-shrubs to promote ground-lichens in winter-grazing grounds for semi-domesticated reindeer. This land use started during the first millennium CE, it shortened the fire return interval from >125–250 years to around 40–80 years, and continued until fire suppression was introduced in the 1700s. The recurrent fires eventually depleted soil nutrients, especially N and P, which reduced overall ecosystem productivity, but favored ground lichens. Consequently, land use in many pine–lichen forests (previously considered unimportant for people and mainly influenced by natural disturbances), may have been affected by deliberate burnings, grazing and trampling. This finding challenges the view of a natural fire return interval of *ca.* 50 years in pine–lichen forests and impose that boreal forests along major rivers in northern Sweden should be view upon as domesticated landscapes. The results are yet another example of the importance of disturbance history studies when interpreting ecosystem development, explaining their productivity and understanding their function.

Declaration of interest

None.

Acknowledgements

The language has been improved by Sees-editing in the UK. The study is a part of the "Recalling the Past"-research program financed by The Bank of Sweden Tercentenary Foundation [grant number M11-0361:1].

Appendix A. Major changes in vegetation composition in local pollen assemblage zones (PAZ) in Heden (He), Harads (Ha) and Edefors (Ed). Accumulation rates (AR) are given for pollen (PAR), dung spores (DSpAR), microscopic charcoal particles (MiChAR) as pollen-spores-particles/cm^2 and year. Macroscopic charcoal peak analysis (CHAR) indicate fire events

PAZ: depth (cm) Cal CE/BCE	Zone description
Heden	
He I: 183-152.5 750 – 160 BCE	Trees: *Alnus* <2%, *Betula* 68-35% then increase to 89% (PAR 630-10000), *Pinus* 23-9% then decline to 2% (PAR 1500-150), *Picea* 10-33% then decline to 3% (PAR 200-2300). Shrubs & dwarf-shrubs: *Betula nana* 1-7%, *Salix* recurrently <1%, *Juniperus* & Ericaceae sporadically <1%. Anthropochores & apophytes (PAR 130-15): Poaceae recurrently 0-2%, Poaceae>40 μm, *Artemisia* & *Cannabis*-type intermittently <1%, *Plantago media*-type sporadically <1%. Other herbs: Cyperaceae 1-3%, *Sinapis*-type, *Ranunculus* & *Rubus chamaemorus* intermittently <1%. Spores: *Sphagnum* 1-12% & Polypodiaceae 1-3%, dung spores sporadically <1% (DSpAR 0-1170). Microscopic charcoal continuously 2-1%, MiChAR 5-212 (212 = 205 BCE). CHAR peaks: 680, 390 and 220 BCE.
He II: 152.5-120.5 160 BCE – 340 CE	Trees: *Alnus* 1-3%, *Betula* 70% then decline to 48-34% and increase (PAR 1500-7300), increase in *Pinus* 8-35% (PAR 440-4400) & in *Picea* 9-23% (PAR 1800-3300). Shrubs & dwarf-shrubs: *Betula nana* 1-3%, Ericaceae 1-2%, *Salix* & *Juniperus* recurrently <1%. Anthropochores & apophytes (PAR 23-340): Poaceae 1-2%, *Hordeum*-type (150 cm, 110 BCE; 125 cm, CE 320), Poaceae>40 μm, *Artemisia*, *Chenopodium*-type, *Plantago media*-type recurrently <1%, *Rumex* sporadically <1%. Other herbs: Cyperaceae 1-3%, *Sinapis*-type, *Ranunculus*, Rosaceae undiff. & *Filipendula* recurrently <1%. Spores: *Sphagnum* 9-1%, *Huperzia selago* 1-11% & Polypodiaceae 1-3% recurrently, dung spores continuously 1-4% (DSpAR 27-810). Microscopic charcoal recurrently 1-2%, MiChAR 0-115 (115 = CE 330). CHAR peaks: 130 BCE, BCE/CE, 80, 250 and 350 CE.
He III: 120.5-70 340 – 1730 CE	Trees: *Alnus* 2-5%, *Betula* 44-31% then decline to 19% (PAR 145-4500), *Pinus* fluctuating 37-17% (PAR 4210-200), *Picea* fluctuating 20-6% (PAR 1800-45). Shrubs & dwarf-shrubs: *Betula nana* 1-4%, *Salix*, *Juniperus*, Ericaceae & *Calluna* recurrently <1%. Anthropochores & apophytes (PAR 10-1770): Poaceae continuously 1-3% then increase to 9% (70 cm), *Secale* (119 cm, CE 370; 110 cm, CE 445; 85 cm, CE 720; 75 cm, CE 1715), Poaceae >40 μm, *Artemisia*, *Cannabis*-type, Chenopodiaceae & *Rumex* recurrently <1%, *Cerealia* (118 cm, CE 380; 115 cm, CE 400), *Hordeum*-type (75 cm, CE 1715; 70 cm, CE 1735), *Triticum* (70 cm, CE 1735), Brassicaceae, *Epilobium*, *Urtica* & *Plantago media*-type sporadically <1%. Other herbs: Cyperaceae continuously 2-8% then increase to 10-16%, *Ranunculus* continuously <2%, *Sinapis*-type & Rosaceae undiff. recurrently <1%. Spores: *Sphagnum* 2-9% (14% at 106 cm), *Equisetum* continuously <1%, Polypodiaceae & *Diphasiastrum* recurrently <1%, dung spores continuously <1% (DSpAR 8-1010), *Gelasinospora* intermittently <1%. Microscopic charcoal 4% (120 cm, CE 360) then continuously 1-2%, MiChAR 3-385 (385 = CE 360). CHAR peaks: 560 and 1730 CE.
Harads	
Ha I: 50-44.5 70 BCE – 145 CE	Trees: *Alnus* 5-2%, *Betula* 49-44% (PAR 7700-5900), *Pinus* 34-38% (PAR 5100-5300), *Picea* 2-6% (PAR 390-830). Shrubs & dwarf-shrubs: *Betula nana* 8%, Ericaceae <1%. Anthropochores & apophytes (PAR 90-45): *Melampyrum* continuously <1%, Chenopodium sporadically <1%. Other herbs: *Filipendula* continuously <1%, *Sinapis*-type, *Ranunculus*, Apiaceae & Cyperaceae sporadically <1%. Spores: Polypodiaceae continuously 15-7%, *Diphasiastrum* & *Sphagnum* continuously 1-2%. Microscopic charcoal continuously 10-2%, MiChAR 2280-200 (2280 = 70 BCE). CHAR peaks: 60 BCE and BCE/CE.
Ha II: 44.5-32.5 145 – 1580 CE	Trees: *Alnus* 1-3%, *Betula* 19-34% (PAR 4950-46), *Pinus* 58-35% (PAR 7300-47), *Picea* increase to 22% then decrease to 6% (PAR 3020-10), *Populus* sporadically 3% (33 cm). Shrubs & dwarf-shrubs: *Betula nana* 4-9%, Ericaceae 1-5%, *Calluna* & *Corylus*/*Myrica* recurrently <1%, Salix sporadically 2% (33 cm). Anthropochores & apophytes (PAR 160-3): Poaceae continuously 1-2% (from 38 cm, CE 290), *Melampyrum* & *Rumex* recurrently <1%, *Epilobium*, *Artemisia*, *Cannabis*-type & Chenopodiaceae sporadically <1%. Other herbs: Cyperaceae 1-6%, *Sinapis*-type, *Ranunculus, Hornungia*-type & *Rubus chamaemorus* recurrently <1%. Spores: *Sphagnum* 54-11%, Polypodiaceae & *Diphasiastrum* recurrently <1%, dung spores & *Gelasinospora* sporadically <1% (DSpAR 0-43). Microscopic charcoal continuously 1-3%, MiChAR 5-353 (353 = CE 185). CHAR peaks: 260 and 320 CE.
Ha III: 32.5-24.5 1580 – 1865 CE	Trees: *Alnus* 1-3%, *Betula* 25-38% (PAR 75-8100), *Pinus* decrease to 33-25% then increase to 38% (PAR 100-9500), *Picea* decrease to 7-2% (PAR 1120-18). Shrubs & dwarf-shrubs: *Betula nana* decrease to 7-3%, Ericaceae 2-6%, *Salix* & *Juniperus* recurrently 1-3%. Anthropochores & apophytes (PAR 7-980): Poaceae continuously 1-2%, Poaceae<40 μm, *Artemisia* & *Rumex* recurrently <1%, *Hordeum*-type (26 cm, CE 1855), *Cerealia* undiff. (25 cm, CE 1865), *Epilobium*, *Chenopodium* & *Urtica* sporadically <1%. Other herbs: *Sinapis*-type 1-2% with 5% peak at 26 cm, Cyperaceae increase to 2-15% then decline to 5%, *Ranunculus*, Rosaceae undiff & *Rubus chamaemorus* recurrently <1%. Spores: *Sphagnum* fluctuating 4-55%, *Equisetum*, Polypodiaceae & *Diphasiastrum* recurrently <1%, dung spores continuously 1-5% (DSpAR 3-2050), *Gelasinospora* sporadically 1%. Microscopic charcoal continuously 1-2%, MiChAR 6-840 (840 = CE 1830). CHAR peak: 1840 CE.
Ha IV: 24.5-15 1865 – 1920 CE	Trees: *Alnus* 2-1%, *Betula* 34-22% (PAR 850-215), *Pinus* 45-65% (PAR 2040-390), *Picea* 2-6% (PAR 180-25). Shrubs & dwarf-shrubs: *Betula nana* 1-4%, Ericaceae 1-3% with 13% peak at 19 cm, *Calluna* recurrently <1%. Anthropochores & apophytes

(*Continued*)

PAZ: depth (cm) Cal CE/BCE	Zone description
	(PAR 90-8): Poaceae 1-2%, Poaceae>40 μm, *Artemisia*, Chenopodium & *Urtica* recurrently <1%, *Melampyrum* & *Rumex* sporadically <1%. Other herbs: Cyperaceae 1-3%, Ranunculus <1%, *Sinapis*-type, Asteraceae & *Rubus chamaemorus* sporadically <1%. Spores: *Sphagnum* peak 30% (24 cm) then continuously 1-6%, *Huperzia* & *Equisetum* recurrently 1-2%, dung spores sporadically <1% (DSpAR 13-0). Microscopic charcoal continuous 1% then decline, MiChAR 12-0 (12 = 1900). No CHAR peak.
Edefors Ed I: 90-64.5 630 BCE – 635 CE	Trees: *Alnus* 1-5%, *Betula* 17-34% (PAR 1150-300), *Pinus* 57-43% (PAR 3900-370), *Picea* 18-7% (PAR 950-60). Shrubs & dwarf-shrubs: *Betula nana* & Ericaceae 1-4%, *Salix*, *Juniperus* & *Calluna* recurrently <1%. Anthropochores & apophytes (PAR 1110-125): Poaceae <1%, Cerealia undiff. (65 cm, CE 590), Poaceae>40 μm, *Melampyrum* & *Chenopodium*-type sporadically <1%. Other herbs: Cyperaceae 1-5%, *Sinapis*-type, *Ranunculus* & *Rubus chamaemorus* continuously <1%. Spores: *Sphagnum* 8-46%, *Equisetum*, Polypodiaceae & *Diphasiastrum* recurrently <1%, dung spores recurrently <1% (DSpAR 0-52). Microscopic charcoal continuously 1-3%, MiChAR 365-14 (365 = CE 140). CHAR peaks: 340 and 300 BCE, and 120 CE.
Ed II: 64.5-50.5 635 – 1550 CE	Trees: *Alnus* 1-4%, *Betula* 28-18% (PAR 200-2230), *Pinus* 55-74% (580-6090), *Picea* 10-5% (PAR 50-650). Shrubs & dwarf-shrubs: *Betula nana* 1-3%, Ericaceae 1-2%, *Salix*, *Juniperus* & *Calluna* recurrently <1%. Anthropochores & apophytes (PAR 90-1060): Poaceae, Poaceae>40 μm, *Melampyrum* & *Artemisia* recurrently <1%, *Epilobium*, *Cannabis*-type, *Chenopodium*, *Urtica*, *Plantago media*-type & Caryophyllaceae sporadically <1%. Other herbs: Cyperaceae 1-7%, *Ranunculus* recurrently <2%, *Sinapis*-type recurrently <1%,. Spores: *Sphagnum* 10-51%, *Equisetum*, Polypodiaceae & *Gelasinospora* recurrently <1%, dung spores recurrently <1% (DSpAR 0-36). Microscopic charcoal continuously 1-6%, MiChAR 3-252 (252 = CE 1515, 22-128 = CE 680-770). No CHAR peak.
Ed III: 50.5-45.5 1550 – 1625 CE	Trees: *Alnus* 2-3%, *Betula* decrease to 19-10% then increase to 22% (PAR 1160-2360), *Pinus* 65-70% then decline to 60% (PAR 3640-6510), *Picea* 10-6% (PAR 300-940). Shrubs & dwarf-shrubs: *Betula nana*, Ericaceae & *Calluna* 1-4%, *Salix* & *Juniperus* recurrently <1%. Anthropochores & apophytes (PAR 560-1020): Poaceae <1%, *Melampyrum* recurrently <1%, *Cannabis*-type sporadically <1%. Other herbs: Cyperaceae 1-2%, *Sinapis*-type, *Ranunculus*, Rosaceae undiff., *Filipendula* sporadically & *Rubus chamaemorus* <1%. Spores: *Sphagnum* 32-19%, *Equisetum*, Polypodiaceae & *Diphasiastrum* recurrently <1%, *Pteridium* sporadically <1%, dung spores sporadically <1% (DSpAR 0-15). Microscopic charcoal continuously 1-3%, MiChAR 105-333 (333 = CE 1560). CHAR peak: 1575 CE.
Ed IV: 45.5-27.5 1625 – 1825 CE	Trees: *Alnus* 2%, *Betula* decline to 16% then increase to 27% (PAR 5350-1010), *Pinus* increase to 65% then decline to 55% (PAR 5960-2040), *Picea* 6-7% (PAR 820-300). Shrubs & dwarf-shrubs: *Betula nana* & Ericaceae 4-1%, *Calluna* continuously <1%, *Salix*, *Juniperus*, *Corylus/Myrica* & *Ribes rubrum* sporadically <1%. Anthropochores & apophytes (PAR 1100-330): Poaceae <1%, *Triticum* (30 cm, CE 1810), Poaceae>40 μm, Melampyrum, Artemisia, Rumex & Caryophyllaceae sporadically <1%. Other herbs: Cyperaceae 2%, *Sinapis*-type, Rosaceae undiff. & Asteraceae recurrently <1%. Spores: *Sphagnum* 29-21%, *Huperzia* continuously <1% from 40 cm, *Equisetum*, Polypodiaceae, *Diphasiastrum* & *Gelasinospora* sporadically <1%, dung spores sporadically <1% (DSpAR 0-190). Microscopic charcoal decline 5-1%, MiChAR 1080-85 (1080 = CE 1630). CHAR peaks: 1695 and 1740 CE.
Ed V: 27.5-15 1825 – 1905 CE	Trees: *Alnus* 2%, *Betula* decline to 50-21% (PAR 2920-620), *Pinus* increase to 33-55% (PAR 1950-1630), *Picea* 2-4% (120-290). Shrubs & dwarf-shrubs: *Betula nana* 5-2%, Ericaceae increase to 1-11%, *Salix*, *Corylus/Myrica*, *Calluna* sporadically <1%. Anthropochores & apophytes (PAR 450-125): Poaceae & *Rumex* <1%, *Hordeum*-type (20 cm, CE 1875), *Epilobium*, *Melampyrum* & Chenopodiaceae sporadically <1%. Other herbs: *Sinapis*-type, *Ranunculus*, *Rubus chamaemorus* & Cyperaceae sporadically <1%. Spores: *Sphagnum* increase to 10-51%, *Huperzia selago* 2-1%, *Equisetum*, Polypodiaceae & *Diphasiastrum* sporadically <1%, dung spores sporadically <1% (DSpAR 11-0). Microscopic charcoal decline <1%, MiChAR 66-6 (66 = CE 1840). No CHAR peak.

References

Ågren, J., Svensson, R., 2007. Postglacial Land uplift model and system definition for the New Swedish height system RH 2000Reports in Geodesy and Geographical Information System. Lantmäteriet, Gävle. . Available at: https://www.lantmateriet.se/globalassets/kartor-och-geografisk-information/gps-och-matning/geodesi/rapporter_publikationer/rapporter/lmv-rapport_2007_4.pdf.

Ahti, T., DePriest, P.T., 2001. New combinations of Cladina epithets in Cladonia (Ascomycotina: cladoniaceae). Mycotaxon 78, 499–502.

Aronsson, K.-Å., 1991. Forest reindeer herding AD 1-1800. Archaeology and Environment 10. Umeå University, Umeå.

Berg, A., Östlund, L., Moen, J., Olofsson, J., 2008. A century of logging and forestry in a reindeer herding area in northern Sweden. For. Ecol. Manage. 256, 1009–1020. doi:http://dx.doi.org/10.1016/j.foreco.2008.06.003.

Berg, A., Josefsson, T., Östlund, L., 2011. Cutting of lichen trees: a survival strategy used before the 20th century in northern Sweden. Veg. Hist. Archaeobot. 20, 125–133. doi:http://dx.doi.org/10.1007/s00334-010-0275-x.

Bergman, I., Zackrisson, O., Liedgren, L., 2013. From herding to hunting: land use, ecosystem processes and social transformation among the Sámi AD 800-1500. Arctic Anthropol. 50, 25–39. doi:http://dx.doi.org/10.3368/aa.50.2.25.

Bjørklund, I., 2013. Domestication, reindeer husbandry and the development of Sámi pastoralism. Acta Boreal. 30, 174–189. doi:http://dx.doi.org/10.1080/08003831.2013.847676.

Blaauw, M., 2010. Methods and code for "classical" age-modelling of radiocarbon sequences. Quat. Geochronol. 5, 512–518. doi:http://dx.doi.org/10.1016/j.quageo.2010.01.002.

Blackford, J.J., Innes, J.B., 2006. Linking current environments and processes to fungal spore assemblages: surface NPM data from woodland environments. Rev. Palaeobot. Palynol. 141, 179–187. doi:http://dx.doi.org/10.1016/j.revpalbo.2006.03.010.

Bradshaw, R.H.W., Tolonen, K., Tolonen, M., 1997. Holocene records of fire from the boreal and temperate zones of Europe. In: Clark, J.S., Cachier, H., Goldammer, J. G., Stocks, B. (Eds.), Sediment Records of Biomass Burning and Global Change. NATO ASI Series, vol. 51. Springer Verlag, Berlin, pp. 347–365. doi:http://dx.doi.org/10.1007/978-3-642-59171-6_16.

Bradshaw, R.H.W., 2007. Stand-scale palynology. In: Elias, S. (Ed.), Encyclopedia of Quaternary Science. Elsevier Science Publishers B.V, Amsterdam, pp. 2535–2543.

Butsic, V., Kelly, M., Moritz, M., 2015. Land use and wildfire: a review of local interactions and teleconnections. Land 4, 140–156. doi:http://dx.doi.org/10.3390/land4010140.

Bylund, E., 1956. Koloniseringen av Pite lappmark t.o.m. 1867. Geographica 30, 1–447.

Carcaillet, C., Bergman, I., Delorme, S., Hörnberg, G., Zackrisson, O., 2007. Long-term fire frequency not linked to prehistoric occupations in northern Swedish boreal forest. Ecology 88, 465–477. doi:http://dx.doi.org/10.1890/0012-9658(2007)88[465:LFFNLT]2.0.CO;2.

Cugny, C., Mazier, F., Galop, D., 2010. Modern and fossil non-pollen palynomorphs from the Basque mountains (western Pyrenees, France): the use of coprophilous fungi to reconstruct pastoral activity. Veg. Hist. Archaeobot. 19, 391–408. doi:http://dx.doi.org/10.1007/s00334-010-0242-6.

Davis, E.L., Courtney Mustaphi, C.J., Gall, A., Pisaric, M.F.J., Vermaire, J.C., Moser, K.A., 2016. Determinants of fire activity during the last 3500 yr at a wildland–urban interface, Alberta, Canada. Quat. Res. 86, 247–259. doi:http://dx.doi.org/10.1016/j.yqres.2016.08.006.

DeLuca, T.H., Zackrisson, O., Nilsson, M.-C., Sellstedt, A., 2002. Quantifying nitrogen-fixation in feathermoss caprets of boreal forests. Lett. Nat. 419, 917–920. doi:http://dx.doi.org/10.1038/nature01051.

DeLuca, T.H., Zackrisson, O., 2007. Enhanced soil fertility under Juniperus communis in arctic ecosystems. Plant Soil 294, 147–155. doi:http://dx.doi.org/10.1007/s11104-007-9242-4.

Deluca, T.H., Zackrisson, O., Bergman, I., Hörnberg, G., 2013. Historical land use and resource depletion in spruce-Cladina forests of subarctic Sweden. Anthropocene 1, 14–22. doi:http://dx.doi.org/10.1016/j.ancene.2013.03.002.

DeLuca, T.H., Glanville, H.C., Harris, M., Emmett, B.A., Pingree, M.R.A., de Sosa, L.L., Morenà, C., Jones, D.L., 2015. A novel biologically-based approach to evaluating soil phosphorus availability across complex landscapes. Soil Biol. Biochem. 88, 110–119. doi:http://dx.doi.org/10.1016/j.soilbio.2015.05.016.

Dietre, B., Walser, C., Kofler, W., Kothieringer, K., Hajdas, I., Lambers, K., Reitmaier, T., Haas, J.N., 2017. Neolithic to Bronze Age (4850–3450 cal. BP) fire management of the Alpine Lower Engadine landscape (Switzerland) to establish pastures and cereal fields. Holocene 27, 181–196. doi:http://dx.doi.org/10.1177/0959683616658523.

Drobyshev, I., Granström, A., Linderholm, H.W., Hellberg, E., Bergeron, Y., Niklasson, M., 2014. Multi-century reconstruction of fire activity in northern European boreal forest suggests differences in regional fire regimes and their sensitivity to climate. J. Ecol. 102, 738–748. doi:http://dx.doi.org/10.1111/1365-2745.12235.

Drobyshev, I., Bergeron, Y., Linderholm, H.W., Granström, A., Niklasson, M., 2015. A 700-year record of large fire years in northern Scandinavia shows large variability and increased frequency during the 1800s. J. Quat. Sci. 30, 211–221. doi:http://dx.doi.org/10.1002/jqs.2765.

Ebeling, F., 1972. Norrländska skogsvårdsfrågor. Skogsstyrelsen, Stockholm.

Ebeling, F., 1978. Nordsvenska skogstyper. Sveriges Skogsvårdsförbunds Tidskrift, H4, .

Enequist, G., 1937. Nedre Luledalens byar. En kulturgeografisk studie. Geographica 4. Appelbergs Boktryckeri, Uppsala.

Engelmark, R., 1976. The Vegetational History of the Umeå Area During the Past 4000 Years. Palaeo-ecological Investigations in Coastal Västerbotten, N. Sweden. Early Norrland 9. Kunglig Vitterhets Historie och Antikvitets Akademien, Stockholm, pp. 75–111.

Engelmark, O., 1987. Fire history correlations to forest type and topography in northern Sweden. Ann. Bot. Fenn. 24, 317–324.

Engelmark, O., Hytterborn, H., 1999. Coniferous forests. Acta Phytogeogr. Suecica 84, 55–74.

Eriksson, Å., Moen, J., 2008. Effekter av skogsbruket på rennäringen – en litteraturstudie. Rapport 18. Skogsstyrelsens Förlag, Jönköping.

Fowler, C.T., Welch, J.R., 2015. Introduction: special issue on fire ecology and ethnobiology. J. Ethnobiol. 35, 1–3. doi:http://dx.doi.org/10.2993/0278-0771-35.1.1.

Granström, A., 1993. Spatial and temporal variation in lightning ignitions in Sweden. J. Veg. Sci. 4, 737–744. doi:http://dx.doi.org/10.2307/3235609.

Granström, A., Niklasson, M., 2008. Potentials and limitations for human control over historic fire regimes in the boreal forest. Philos. Trans. R. Soc. B Biol. Sci 363, 2353–2358. doi:http://dx.doi.org/10.1098/rstb.2007.2205.

Grimm, E.C., 1991. TILIA (v. 2.0. b.4). Springfield, IL: Research and Collection Center. Illinois State Museum.

Grimm, E.C., 2004. TILIA-GRAPH (v. 2.0.2). Springfield, IL: Research and Collection Center. Illinois State Museum.

Grudd, H., Briffa, K.R., Karlén, W., Bartholin, T.S., Jones, P.D., Kromer, B., 2002. A 7400-year tree-ring chronology in northern Swedish Lapland: natural climatic variability expressed on annual to millennial timescales. Holocene 12, 657–665. doi:http://dx.doi.org/10.1191/0959683602hl578rp.

Haapasaari, M., 1988. The oligotrophic heath vegetation in northern Fennoscandia and its zonation. Acta For. Fenn 135, 1–219.

Haas, J.N., 2010. Fresh insights into palaeoecological and palaeoclimatical value of quaternary non-pollen palynomorphs. Special issue. Veg. Hist. Archaeobot. 19 (5-6), 389–558.

Häggström, B., 1981. Skogsskötsel på tallhedar. Sv. Skogsvårdsförb. Tidskr 79 (3), 3–16.

Hedman, S.-D., Olsen, B., Vretemark, M., 2015. Hunters, herders and hearths: interpreting new results from hearth row sites in Pasvik, Arctic Norway. Rangifer 35, 1–24. doi:http://dx.doi.org/10.7557/2.35.1.3334.

Heggberget, T.M., Gaare, E., Ball, J.P., 2002. Reindeer (Rangifer tarandus) and climate change: importance of winter forage. Rangifer 22, 13–31. doi:http://dx.doi.org/10.7557/2.22.1.388.

Hicks, S., 1988. The representation of different farming practices inpollen diagrams from northern Finland. In: Birks, H.H., Birks, H.J.B., Kaland, P.E., Moe, D. (Eds.), The Cultural Landscape: Past, Present and Future. Cambridge University Press, Cambridge, pp. 189–207.

Higuera, P.E., Sprugel, D.G., Brubaker, L.B., 2005. Reconstructing fire regimes with charcoal from small-hollow sediments: a calibration with tree-ring records of fire. Holocene 15, 238–251. doi:http://dx.doi.org/10.1191/0959683605hl789rp.

Higuera, P.E., Gavin, D.G., Bartlein, P.J., Hallett, D.J., 2010. Peak detection in sediment-charcoal records: impacts of alternative data analysis methods on fire-history interpretations. Int. J. Wildl. Fire 19, 996–1014. doi:http://dx.doi.org/10.1071/WF09134.

Högbom, A.G., 1934. Om skogseldar förr och nu och deras roll i skogarnas utvecklingshistoria. Norrländskt handbibliotek XIII. Almqvist & Wiksell, Stockholm.

Hörnberg, G., Östlund, L., Zackrisson, O., Bergman, I., 1999. The genesis of two Picea-Cladonia forests in northern Sweden. J. Ecol. 87, 800–814. doi:http://dx.doi.org/10.1046/j.1365-2745.1999.00399.x.

Hörnberg, G., Staland, H., Nordström, E.-M., Korsman, T., Segerström, U., 2012. Fire as an important factor for the genesis of boreal Picea abies swamp forests in Fennoscandia. Holocene 22, 203–214. doi:http://dx.doi.org/10.1177/0959683611414936.

Hörnberg, G., Josefsson, T., Bergman, I., Liedgren, L., Östlund, L., 2015. Indications of shifting cultivation west of the Lapland border: multifaceted land use in northernmost Sweden since AD 800. Holocene 25, 989–1001. doi:http://dx.doi.org/10.1177/0959683615574894.

Huss-Danell, K., Lundmark, J.-E., 1988. Growth of nitrogen-fixing Alnus incana and Lupinus spp., For restoration of degenerated forest soil in northern Sweden. Studia Forestalia Suecica 181, 1–20.

Johnson, E.A., Miyanishi, K., 2012. The boreal forest as a cultural landscape. Ann. N. Y. Acad. Sci. 1249, 151–165. doi:http://dx.doi.org/10.1111/j.1749-6632.2011.06312.x.

Josefsson, T., Hörnberg, G., Östlund, L., 2009. Long-term human impact and vegetation changes in a boreal forest reserve: implications for the use of protected areas as ecological references. Ecosystems 12, 1017–1036. doi:http://dx.doi.org/10.1007/s10021-009-9276-y.

Josefsson, T., Ramqvist, P.H., Hörnberg, G., 2014. The history of early cereal cultivation in northernmost Fennoscandia as indicated by palynological research. Veg. Hist. Archaeobot. doi:http://dx.doi.org/10.1007/s00334-014-0446-2.

Josefsson, T., Hörnberg, G., Liedgren, L., Bergman, I., 2017. Cereal cultivation from the Iron age to historical times: evidence from inland and coastal settlements in northernmost Fennoscandia. Veg. Hist. Archaeobot. 23, 821–840. doi:http://dx.doi.org/10.1007/s00334-016-0586-7.

Jowsey, P.C., 1966. An improved peat sampler. New Phytol. 65, 245–248. doi:http://dx.doi.org/10.1111/j.1469-8137.1966.tb06356.x.

Kamerling, I.M., Schofield, J.E., Edwards, K.J., Aronsson, K.Å., 2017. High-resolution palynology reveals the land use history of a Sami renvall in northern Sweden. Veg. Hist. Archaeobot. 26, 369–388. doi:http://dx.doi.org/10.1007/s00334-016-0596-5.

Kasin, I., Ellingsen, V.M., Asplund, J., Ohlson, M., 2017. Spatial and temporal dynamics of the soil charcoal pool in relation to fire history in a boreal forest landscape. Can. J. For. Res. 47, 28–35. doi:http://dx.doi.org/10.1139/cjfr-2016-0233.

Kelly, R.F., Higuera, P.E., Barrett, C.M., Hu, F.S., 2011. A signal-to-noise index to quantify the potential for peak detection in sediment-charcoal records. Quat. Res. 75, 11–17. doi:http://dx.doi.org/10.1016/j.yqres.2010.07.011.

Korsman, T., Segerström, U., 1998. Forest fire and lake-water acidity in a northern Swedish boreal area: holocene changes in lake-water quality at Makkassjon. J. Ecol. 86, 113–124. doi:http://dx.doi.org/10.1046/j.1365-2745.1998.00239.x.

Köster, K., Berninger, F., Köster, E., Pumpanen, J., 2015. Carbon Dynamics Influences of reindeer grazing on above- and below- ground biomass and soil carbon dynamics. Arctic Antarct. Alp. Res. 47, 495–503. doi:http://dx.doi.org/10.1657/AAAR0014-062.

Laestadius, P., 1833. Fortsättning af Journalen öfver missionsresor I Lappmarken innefattande åren 1828-1832. Gustaf Norström, Stockholm.

Lehtonen, H., Huttunen, P., Zetterberg, P., 1996. Influence of man on forest fire frequency in North Karelia, Finland, as evidenced by fire scars on Scots pines. Ann. Bot. Fenn. 33, 257–263. http://www.jstor.org/stable/23726304.

Lehtonen, H., Kolström, T., 2000. Forest fire history in Viena Karelia, Russia. Scand. J. For. Res. 15, 585–590. doi:http://dx.doi.org/10.1080/02827580050216833.

Lindén, M., Möller, P., Björck, S., Sandgren, P., 2006. Holocene shore displacement and deglaciation chronology in Norrbotten, Sweden. Boreas 35, 1–22. doi:http://dx.doi.org/10.1080/03009480500359160.

Lundmark, J.-E., Huss-Danell, K., 1981. Odlingsförsök med gråal och lupin på tallhedar I Norrbotten. Sv. Skogsvårdsförb. Tidskr 79 (3), 17–26.

Mayewski, P.A., Rohling, E.E., Stager, J.C., Karlén, W., Maasch, K.A., Meeker, L.D., Meyerson, E.A., Gasse, F., van Kreveld, S., Holmgren, K., Lee-Thorp, J., Rosqvist, G., Rack, F., Staubwasser, M., Schneider, R.R., Steig, E.J., 2004. Holocene climate variability. Quat. Res. 62, 243–255. doi:http://dx.doi.org/10.1016/j.yqres.2004.07.001.

Moore, P.D., Webb, J.A., Collinson, M.E., 1991. Pollen Analysis. Blackwell Scientific Publications, London.

Morneau, C., Payette, S., 1989. Postfire lichen-spruce woodland recovery at the limit of the boreal forest in northern Quebec. Can. J. Bot. 67, 2770–2782. doi:http://dx.doi.org/10.1139/b89-357.

Mossberg, B., Stenberg, L., 2003. Den nya nordiska floran. Wahlström & Widstrand, Stockholm.

Neary, D.G., Klopatek, C.C., DeBano, L.F., Ffolliott, P.F., 1999. Fire effects on belowground sustainability: a review and synthesis. For. Ecol. Manage. 122, 51–71. doi:http://dx.doi.org/10.1016/S0378-1127(99)00032-8.

Niklasson, M., Granström, A., 2000. Numbers and sizes of fires: long-term spatially explicit fire history in a Swedish boreal landscape. Ecology 81, 1484–1499. doi:http://dx.doi.org/10.1890/0012-9658(2000)081[1484:NASOFL]2.0.CO;2.

Nilsson, M., Klarqvist, M., Bohlin, E., Possnert, G., 2001. Variation in14C age of macrofossils and different fractions of minute peat samples dated by AMS. Holocene 11, 579–586. doi:http://dx.doi.org/10.1191/095968301680223521.

Ohlson, M., Tryterud, E., 2000. Interpretation of the charcoal record in forest soils: forest fires and their production and deposition of macroscopic charcoal. Holocene 10, 519–525. doi:http://dx.doi.org/10.1191/095968300667442551.

Ohlson, M., Korbøl, A., Økland, R.H., 2006. The macroscopic charcoal record in forested boreal peatlands in southeast Norway. Holocene 16, 731–741. doi:http://dx.doi.org/10.1191/0959683606hl955rp.

Oksanen, J., Ahti, T., 1982. Lichen-rich pine forests in Finland. Ann. Bot. Fenn. 21, 275–301. http://www.jstor.org/stable/23725858.

Östlund, L., 1995. Logging the virgin forest; Northern Sweden in the early-nineteenth century. For. Cons. Hist 39, 160–171. http://www.jstor.org/stable/3983957.

Östlund, L., Bergman, I., Zackrisson, 2004. Trees for food – a 3000 year record of subarctic plant use. Antiquity 78, 278–286. doi:http://dx.doi.org/10.1017/S0003598X00112943.

R Development Core Team, 2013. R: a Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna. www.r-project.org.

Reimer, P.J., Bard, E., Bayliss, A., Beck, J.W., Blackwell, P.G., Ramsey, C.B., Buck, C.E., Cheng, H., Edwards, R.L., Friedrich, M., Grootes, P.M., Guilderson, T.P., Haflidason, H., Hajdas, I., Hatté, C., Heaton, T.J., Hoffmann, D.L., Hogg, A.G., Hughen, K.A., Kaiser, K.F., Kromer, B., Manning, S.W., Niu, M., Reimer, R.W., Richards, D.A., Scott, E.M., Southon, J.R., Staff, R.A., Turney, C.S.M., van der Plicht, J., 2013. IntCal13 and Marine13 radiocarbon age calibration curves 0–50,000 years cal BP. Radiocarbon 55, 1869–1887. doi:http://dx.doi.org/10.2458/azu_js_rc.55.16947.

Rolstad, J., Blanck, Y.L., Storaunet, K.O., 2017. Fire history in a western Fennoscandian boreal forest as influenced by human land use and climate. Ecol. Monogr. 87, 219–245. doi:http://dx.doi.org/10.1002/ecm.1244.

Romell, L.-G., Malmström, C., 1945. Henrik Hesselmans tallhedsförsök åren 1922-42. [the ecology of lichen-pine forest experiments (1922-42) by the late Dr H Hesselman] in Swedish with English summary. Medd. Statens Skogsförsöksanst. Häfte 34 (11), 543–616.

Rosén, P., Segerström, U., Eriksson, L., Renberg, I., Birks, H.J.B., 2001. Holocene climatic change reconstructed from diatoms, chironomids, pollen and near-infrared spectroscopy at an alpine lake (Sjuodjijaure) in northern Sweden. Holocene 11, 551–562. doi:http://dx.doi.org/10.1191/095968301680223503.

Sandström, P., Cory, N., Svensson, J., Hedenås, H., Jougda, L., Borchert, N., 2016. On the decline of ground lichen forests in the Swedish boreal landscape: implications for reindeer husbandry and sustainable forest management. Ambio 45, 415–429. doi:http://dx.doi.org/10.1007/s13280-015-0759-0.
Segerström, U., 1990. The Post-Glacial History of Vegetation and Agriculture in the Luleälv River Valley. Archaeology and Environment 7. Umeå University, Umeå.
Segerström, U., Von Stedingk, H., Hörnberg, G., 2008. Long-term sustainability of a northern boreal deciduous swamp forest in northern Sweden: succession in the absence of fire. Holocene 18, 1113–1122. doi:http://dx.doi.org/10.1177/0959683608093539.
Sjörs, H., 1965. Forest regions. Acta Phytogeogr. Suecica 50, 48–63.
SOU, 1932. Uppskattning av Sveriges skogstillgångar verkställd åren 1923-29. Statens offentliga utredningar 1932: 26. Jordbruksdepartementet, Stockholm.
Stockmarr, J., 1971. Tablets with spores used in absolute pollen analysis. Pollen et Spores 13, 615–621.
Storaunet, K.O., Rolstad, J., Toeneiet, M., Blanck, Y., 2013. Strong anthropogenic signals in historic forest fire regime: a detailed spatiotemporal case study from south-central Norway. Can. J. For. Res. 43, 836–845. doi:http://dx.doi.org/10.1139/cjfr-2012-0462.
Sugita, S., 2007. Theory of quantitative reconstruction of vegetation II: all you need is LOVE. Holocene 17, 243–257. doi:http://dx.doi.org/10.1177/0959683607075838.
van Geel, B., Aptroot, A., 2006. Fossil ascomycetes in Quaternary deposits. Nowa Hedwigia 82, 313–329. doi:http://dx.doi.org/10.1127/0029-5035/2006/0082-0313.
van Geel, B., Buurman, J., Brinkkemper, O., Schelvis, J., Aptroot, A., van Reenen, G., Hakbijl, T., 2003. Environmental reconstruction of a Roman Period settlement site in Uitgeest (the Netherlands), with special reference to coprophilous fungi. J. Archaeol. Sci. 30, 873–883. doi:http://dx.doi.org/10.1016/S0305-4403(02)00265-0.
Väre, H., Rauni, O., Oksanen, J., 1995. Effects of reindeer grazing on understorey vegetation in dry *Pinus sylvestris* forests. J. Veg. Sci. 6, 523–530. doi:http://dx.doi.org/10.2307/3236351.
Väre, H., Ohtonen, R., Mikkola, K., 1996. The effect and extent of heavy grazing by reindeer in oligotrophic pine heaths in northeastern Fennoscandia. Ecography 19, 245–253. doi:http://dx.doi.org/10.1111/j.1600-0587.1996.tb01251.x.
Wallenius, T., Kauhanen, H., Herva, H., Pennanen, J., 2010. Long fire cycle in northern boreal Pinus forests in Finnish Lapland. Can. J. For. Res. 40, 2027–2035. doi:http://dx.doi.org/10.1139/x10-144.
Wallenius, T., 2011. Major decline in fires in coniferous forests - reconstructing the phenomenon and seeking for the cause. Silva Fenn. doi:http://dx.doi.org/10.14214/sf.36.
Wallerström, T., 1981. De kulturhistoriska intressena vid Edefors. Edefors socken. Västerbotten (Norrbottens län) - en översikt. Norrbottens Museum, Luleå.
Wallin, J.E., Segerström, U., 1994. Natural resources and agriculture during the Iron age in Ostrobothnia, western Finland, investigated by pollen analysis. Veg. Hist. Archaeobot. 3, 89–105. doi:http://dx.doi.org/10.1007/BF00189929.
Wardle, D.A., Hörnberg, G., Zackrisson, O., Kalela-Brundin, M., Coomes, D.A., 2003. Long-term effects of wildfire on ecosystem properties across an island area gradient. Science 300, 972–975. doi:http://dx.doi.org/10.1126/science.1082709.
Wretlind, J.E., 1934. Naturbetingelserna för de nordsvenska järn-podsolerade moränmarkernas tallhedar och mossrika samhällen. Norrl. Skogsvårdsf. Tidskr. 21, 331–394.
Zackrisson, O., 1977. Influence of forest fires on the North Swedish boreal forest. Oikos 29, 22–33. doi:http://dx.doi.org/10.2307/3543289.
Zackrisson, O., 1981. Naturresursutnyttjande i relation till skogsekosystemens tidigare dynamik och struktur i Lule Älvdal. In: Baudou, E., Nejati, M. (Eds.), Luleälvssymposiet 1-3 juni 1981. Skrifter från Luleälvsprojektet 1. Umeå Universitet, Umeå, pp. 121–130.
Zackrisson, A.O., Deluca, T.H., Nilsson, M., Sellstedt, A., Berglund, L.M., 2004. Nitrogen fixation increases with successional age in boreal forests. Ecology 85, 3327–3334. doi:http://dx.doi.org/10.1890/04-0461.
Zackrisson, O., Deluca, T.H., Gentili, F., Sellstedt, A., Jäderlund, A., 2009. Nitrogen fixation in mixed Hylocomium splendens moss communities. Oecologia 160, 309–319. doi:http://dx.doi.org/10.1007/s00442-009-1299-8.