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Long-time record of fire and open canopy in a high biodiversity forest in southeast Sweden

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Abstract

We studied a ca 200 ha large forest site that holds an exceptionally large number of red-listed saproxylic beetles. We conducted pollen, charcoal and dendroecological analyses to reveal the long-term stand-level history of the site. We also investigated which of the red-listed saproxylic beetles recorded at the site are probably dependent on forest fires or structures that are created by fires. Pollen from *Pinus* and *Betula* dominate the pollen diagram, and the pollen record shows that the canopy is more closed today than ever during the last 2500 years. Large amounts of charcoal fragments were found throughout the core except during three shorter periods, one of which is the latest ca 200 years. The dendroecological investigation revealed 11 different fires, the earliest dated to AD 1586 and the last dated to AD 1868. Of the 105 red-listed saproxylic beetles recorded at the site, at least 12 are associated with open forests with *Pinus sylvestris* or *Birch* spp. trees. We conclude that the fires, as recorded both by the charcoal and dendroecological analysis, kept the site largely open in the past, and this is likely one important explanation for the high conservation value of the site today. Other important factors could be that the site is rich in boulders, the relatively warm summer climate in the region, that *Picea abies* has not been planted in the surroundings until recently, and finally the presence of many old trees. The study supports the theory that fire could have been an important factor for keeping some forest types open before the large human impact on the northwestern European forests started.

Keywords: Charcoal analysis; Dendroecology; Forest conservation; Forest history; Pollen analysis; Saproxylic beetles

1. Introduction

Many forest types depend on recurrent natural disturbances, e.g. fire, grazing by large herbivores, storms or high water levels. It is evident that "free development" is unsuitable for forest reserves where the previous land-use kept the forest open, or where the natural disturbance regime is altered. "Free development" in these cases has created dense forests that are problematic for many of the species that were meant to be protected (e.g. Niklasson and Drakenberg, 2001). The degree of canopy openness is an important question in forest conservation in Europe (Vera, 2000; Nilsson et al., 2001; Svenning, 2002). This is particularly true for northern Europe, where the summers are relatively cool and where many species, e.g. saproxylic (wood dependent) beetles, depend on open conditions (Gärdenfors and Baranowski, 1992; Nilsson, 1992; Ranius and Jansson, 2000; Martikainen, 2000; Nilsson et al., 2001), and in the Fennoscandinavian countries a high proportion of the saproxylic beetles are red-listed (Gärdenfors, 2000; Rassi et al., 2001).

Hornsö-Allgunnen is one of the most important areas in Sweden for this species group (Nilsson, 2001), and so far 218 red-listed saproxylic species have been recorded here (Nilsson and Huggert, 2001). The reasons for this high diversity, by far the highest known for any area in Sweden (Nilsson, 2001), are largely unclear. For instance, the stand structures or amount of dead wood are not strikingly different compared to forests in neighbouring areas. In this paper we study one site in the Hornsö-Allgunnen area in detail, Skärsgölarna (Fig. 1). This ca 200 ha large site holds the largest number of red-listed saproxylic beetles in the area: at

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Fig. 1. The studied site: Skärsgölarna, with a burned *Pinus sylvestris* stump from the AD 1868 fire.

present more than 105 red-listed species have been found (Nilsson and Huggert, 2001). The site is mainly covered by mixed forests dominated by *Pinus sylvestris* (Scots pine) and *Betula* spp. (birch). Due to its inconspicuous appearance the site has been overlooked by the conservation authorities, and it is not yet protected, and not even assigned as one of Sweden's estimated 40,000 woodland key habitats (habitats on forest land that host, or are expected to host, red-listed species). However, recently it has been considered for protection by the conservation authorities.

Two large fires took place in the Hornsö-Allgunnen area in AD 1811 and 1868, according to historical documents (Gustafsson, 2000). These and the finding of several burned, old *P. sylvestris* stumps at Skärsgölarna made us suspect that fire previously has been a common disturbance factor. We started with pollen, charcoal and dendroecological analyses to reveal the long-term, stand-level forest and fire history of the site with a particular interest in reconstructing past openness and fire frequency. We continued with an analysis to determine which of the red-listed saproxylic beetles recorded at the site depend on forest fires, or depend on structures that are created by fires. We wanted to test whether knowledge of the history could give insight into the reason for the high biodiversity and could serve as a background for the future management of the site and area. Our hypothesis was that the forest on the site has been open and fire influenced, not only during the latest centuries, which the historical documents and stump findings indicate, but also during previous periods.

2. Material and methods

2.1. The study area

The Hornsö-Allgunnen area (57° 01′ N; 16° 07′ E) is located in southeast Sweden (Fig. 2), a region that is characterised by relatively warm and dry summers. The yearly precipitation is 550 mm and the mean January and July temperature are −2 °C and 18 °C respectively (Raab and Vedin, 1995). The bedrock consists of Småland-Värmland granite covered by moraine (Fredén, 1994), and very rich in boulders. The area lies within the boreonemoral, also called the hemiboreal, zone of southern Sweden (Ahti et al., 1968). It is a 600 km wide transition between the boreal and temperate zones that consists of tree species from both zones, coniferous species [e.g. *Picea abies* (Norway spruce) and *P. sylvestris*] from the boreal zone and deciduous species [e.g. *Quercus* spp. (oak) and *Fagus sylvatica* (beech)] from the temperate zone.

The pollen and charcoal site is a wetland, ca 50×30 m, forested with mainly *Betula pubescens* individuals. The core was taken ca 8 m from the upland and not more than ca 20 m from the closest burned *P. sylvestris* stump (seen on Fig. 1). The many boulders are conspicuous in the surrounding upland that is dominated by *P. sylvestris* and *B. pendula* trees of different sizes. The ground vegetation in the wetland is dominated by mosses such as *Sphagnum* spp., *Dicranum* spp. and *Pleurozium schreberi*, and by dwarf shrubs such as *Vaccinium myrtillus*, *Ledum palustre* and some *Vaccinium*

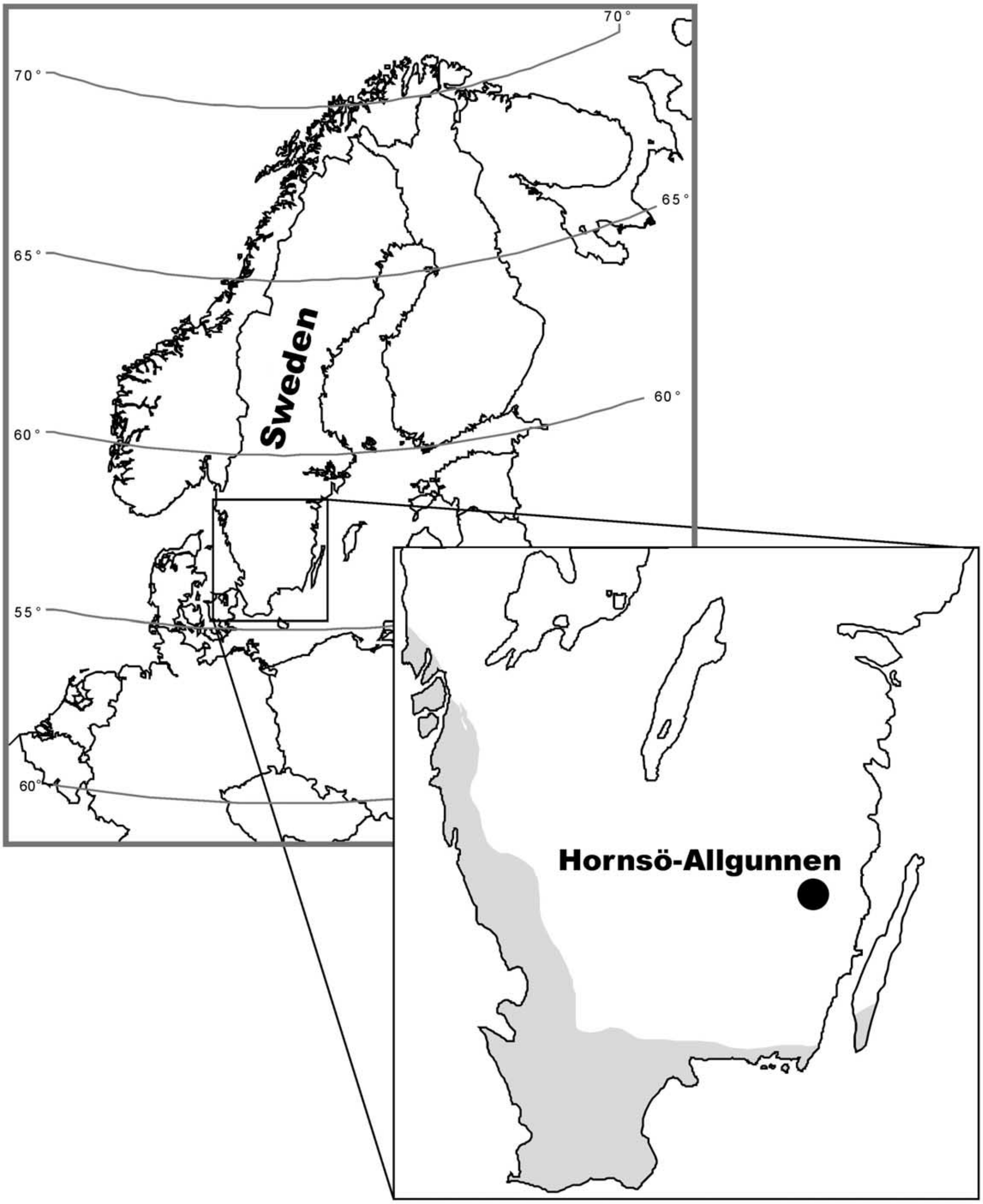

Fig. 2. The location of the study area. The shaded part of the map represents the temperate vegetation zone (nemoral zone) and the non-shaded part is the hemiboreal zone.

uliginosum. The ground vegetation in the upland is sparse but with some *V. myrtillus, Calluna vulgaris* and *Vaccinium vitis-idaea*.

The Hornsö-Allgunnen area consists primarily of Hornsö Kronopark, a 9180 ha forest estate that is owned by the state forest company Sveaskog. The soils and forest productivity are low, partly due to the acid moraine and partly because of the abundance of large boulders. The site at Skärsgölarna is located in a part of the Hornsö Kronopark that formerly was an ''allmänning''—a common land that at least since the Middle Ages until the 19th century was used by the local farmers as well as the State. The size of the ''allmänning'' varied over the years (between 670 and 938 ha) and it was used primarily for grazing by domestic animals and as a source for firewood and timber. The State became the exclusive owner of the ''allmänning'' in 1866 and, according to historical documents, the forest was heavily exploited at that time, not only as a result of harvest of wood and grazing, but also because of fires that covered large areas. From 1866 and onward the area has been managed primarily for timber production. From 1894 to 1999 the standing stock of wood has almost tripled from, from 40 to 111 m^3/ha (Gustafsson, 2000). In spite of the low value of standing stock in 1894 only 4% of the area was classified as non-forested land at that time; a small figure compared to many other areas in southern Sweden. According to the historical records the tree species composition in the ‘‘allmänning’’ was rather stable from 1795 until 1915 (Gustafsson, 2000). The forest during that period was dominated by *P. sylvestris* (ca. 70% of standing stock), and with a smaller proportion of northern deciduous species such as *Betula* spp., *Populus tremula* (aspen), *Alnus glutinosa* (alder) (ca. 20% together), and by the southern deciduous species *Quercus* spp. and *F. sylvatica* (ca. 5% together). *P. abies* made up ca. 2% of the growing stock during that period—a small proportion compared to other areas of southern Sweden at that time. *P. abies* increased after 1915 in the former ‘‘allmänning’’ and represented ca 10% of the standing stock in 1999. During the same period the northern deciduous species (*Betula* sp., *Populus tremula, Alnus glutinosa*) have decreased to about 15%; all other species have about the same figures as in the beginning of the 20th century. Even if *P. abies* has increased, is it still a less common tree species in the former ‘‘allmänning’’ compared to the region (Province of Kalmar) in general, where ca. 45% of the standing stock is *P. abies*.

Timber production is the primary goal for today’s management of the Hornsö Kronopark with some restrictions due to recent inventories and discovery of threatened fauna. Some larger reserves are planned and deciduous trees are temporarily protected until the discussions concerning the future status of the area are settled.

2.2. Field and laboratory methods

2.2.1. Pollen and charcoal analyses

The sediment in the wetland was sampled with a Wardenaar corer (Wardenaar, 1987) and was stored at +3 °C. The 1 m long monolith consisted of uniformly coloured detritus peat up to ca. 10 cm from the surface, from 10 cm to the top it consisted of coarse detritus peat with some wood. The core was cut into samples, ca 5 mm thick. Small sub-samples (0.4–1.14 cm^3) were taken from the centre of these samples, the volume being measured by water displacement. The pollen samples were prepared for analysis in a standard manner (Berglund and Ralska-Jasiewiczowa, 1986). Microscope slides were prepared from the residues and scored for pollen. In total 44 levels were studied, and a minimum of 400 pollen grains were counted at all levels except one, where 300 grains were counted. Additional levels were chosen from the upper part of the profile (100–70 cm every tenth cm; 70–45 cm every fifth cm; 45–25 every 2.5 cm; 25–0 cm every cm), to allow a more detailed comparison between the different palaeoecological record. Sub-samples (0.4–1.3 cm^3) for the charcoal analysis were dissolved in NaOH (10%), sieved through meshes with a net size of 2, 1, 0.5 and 0.25 mm. The charcoal fragments from the different residuals were counted with the help of a magnifier. Every cm (in some cases 0.5 cm) throughout the core were checked for charcoal fragments, i.e. all levels that were counted for pollen plus an additional 59 levels, in total 103 levels. All size classes were checked in all but 16 levels, where only fragments >0.5 mm were checked. These levels were 1, 10.5, 15.5, 20.5, 25.25, 30.25, 35.25, 40.25, 45.25, 50.25, 55.25, 60.25, 65.25, 70.25, 80.25, and 99.75 cm. Plant macrofossils and large charcoal fragments were submitted for AMS dating (Table 1).

2.2.2. Dendroecological analysis

We collected in total 13 wood samples from *P. sylvestris* individuals, 11 in Skärsgölarna and two in a clearcut located ca. 2 km from Skärsgölarna. Ten samples were either partial or full cross sections from snags and stumps. Some of the 10 samples did not have visible scars; the scars were completely overgrown and not visible from the outside. Today, scarred trees are very rare in southern Sweden. This is due to forestry operations that have removed damaged trees, including fire-scarred, over the last 100 years or so. Only three samples were taken from live trees (partial cross sections) with or without visible fire scars. The samples were brought to the laboratory, sanded and analysed under a binocular microscope at 3–50× magnifications. Samples were cross-dated by identifying local pointer years by the method proposed by Stokes and Smiley (1968) and Yamaguchi (1991). In many cases, documented dry summers coincided with narrow rings that were consistent in all trees, e.g. the summers of 1969, 1955 and 1914. After cross-dating the fire dates and scar position within the ring were recorded.

2.2.3. Insect sampling

Window traps (as shown in Nilsson and Baranowski, 1993) were mounted on 15 dead trees in the area, in 1999. These consisted of a window measuring 40×60 cm attached to the trunk, which had a container filled with glycol underneath for preservation of the catch. The tree species sampled were mainly *Betula* spp., but also four *P. tremula* individuals and one *P. sylvestris* individual. Hand collection on dead trees and flowers was also performed during spring and summer in 1998–2000, mainly in sunny and warm weather. The window traps were emptied at approximately 3–4 week intervals, and all insects from the traps were stored in 80% alcohol. The insects were then taken to the laboratory and later

Table 1
AMS radiocarbon dates from Skärsgölarna[a]

Laboratory number	Depth (cm)	Conventional ^{14}C BP	Calibrated ^{14}C age. Cal BC/AD ($\pm 2\sigma$)	Date used for chronology, Cal BC/AD	Basis
Ua-18088	6–7	*137±1 pM*	AD 1962–1977	AD 1970	*Betula* leafs and seeds
Ua-18089	10–11	230±65	AD 1480–1890	AD 1685	*Juniperus* leaf, *Salix* capsule
Ua-18197	15–16	560±70	AD 1280–1450	AD 1365	Charred Ericaceae and *Pinus* remains
Ua-18090	22–23	1200±65	AD 680–980	AD 830	Charred wood
Ua-18198	30–30.5	1860±70	AD 0–350	AD 175	Charred Ericaceae, *Juniperus*, and *Pinus* leafs
Ua-18091	40–40.5	2525±80	810–400 BC	405 BC	Charred Ericaceae and *Pinus* leafs
Ua-18092	80–80.5	1865±65	AD 0–340	AD 170	Ericaceae seeds, *Pinus* cone and bract

[a] Calibrations were made using OxCal 3.5. The date from 6 to 7 cm is calibrated with the aid of the varied levels of ^{14}C because of the atmospheric nuclear tests, where 137±1 pM corresponds to $\Delta 14C = 350 \pm 10$ o/oo (Levin and Kromer, 1997).

identified by Lars Huggert or Rickard Baranowski. For more detailed results consult Nilsson and Huggert (2001).

2.2.4. *Source and sampling areas*

The sampled basin is an isolated *Sphagnum*-covered wetland, today with a closed canopy of *B. pendula* and *P. sylvestris* individuals. The relevant pollen source area for this kind of site has been shown by theory and observation to be no more than a few hundred meters in radius (Sugita, 1994; Calcote, 1995; Jackson and Kearsley, 1998). The charcoal fragments are of local origin irrespective of the size of the wetland, at least for the fragments from the larger size classes (>0.5 mm; Ohlson and Tryderud, 2000). Given that the large majority of the investigated trees or stumps were located not more than ca 100 m from the pollen site, it is likely that the information obtained from tree-rings and deposited pollen reflects a similar spatial scale. The insects were trapped within 1 km from the cored basin. The *P. sylvestris* trees sampled for beetles are located in the same stand as the *P. sylvestris* stumps that were sampled in the dendroecological investigation.

3. Results

3.1. *Dating*

All radiocarbon datings except the one from 80 cm were used when making the chronology (Table 1 and Fig. 3). The smooth form of the age–depth curve when the dating from 80 cm was excluded justifies that decision (Fig. 3). It means, however, that the dating reliability below 40 cm is low, and therefore we chose to present the pollen and charcoal diagram from the entire core with a depth scale only (Figs. 4 and 5). We do not believe that the sediment below 40 cm is mixed because of several features in the diagram, e.g. the peak of small charcoal fragments just above 70 cm. However, a hiatus cannot be excluded. The diagram covering the top ca. 20 cm (Fig. 6), where the dating is much more reliable, is plotted against an age-scale. One must however bear in mind that calibration of radiocarbon dates to calendar year from the last ca. 400 year is imprecise—resulting in a margin of error of a hundred years or more during that period.

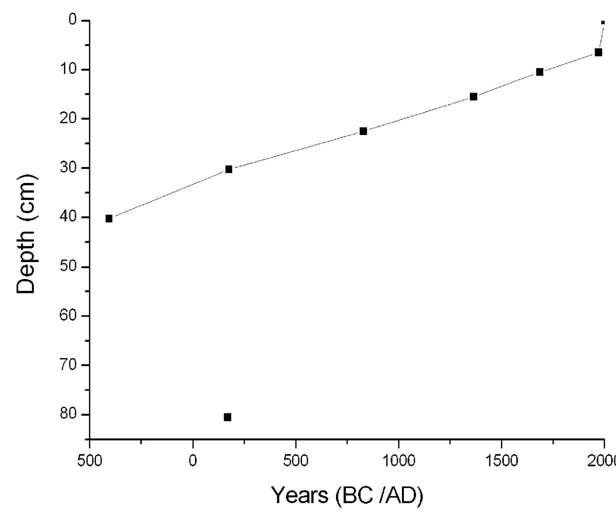

Fig. 3. Depth/age relationship based on the radiocarbon dates for the profile from Skärsgölarna.

3.2. *Pollen and charcoal*

The different size classes in the charcoal analyses show large conformity during the whole sequence (Fig. 5), even between the smallest (0.25–0.5 mm) and the largest (>2 mm) size class at all levels but one. A large influx (2004 fragments/ml) of the smallest fragments at 67 cm is not accompanied by the larger size classes, particularly by the largest size class where no fragments at all were found at those levels. This probably reflects a large influx of small fragments at this level derived from a more remote, but probably extensive, fire (Ohlson and Tryderud, 2000).

3.2.1. *98–40 cm (prior to 400 BC)*

The diagram below 60 cm is dominated (as in the rest of the core) by pollen from *Pinus* and *Betula* (Fig. 4).

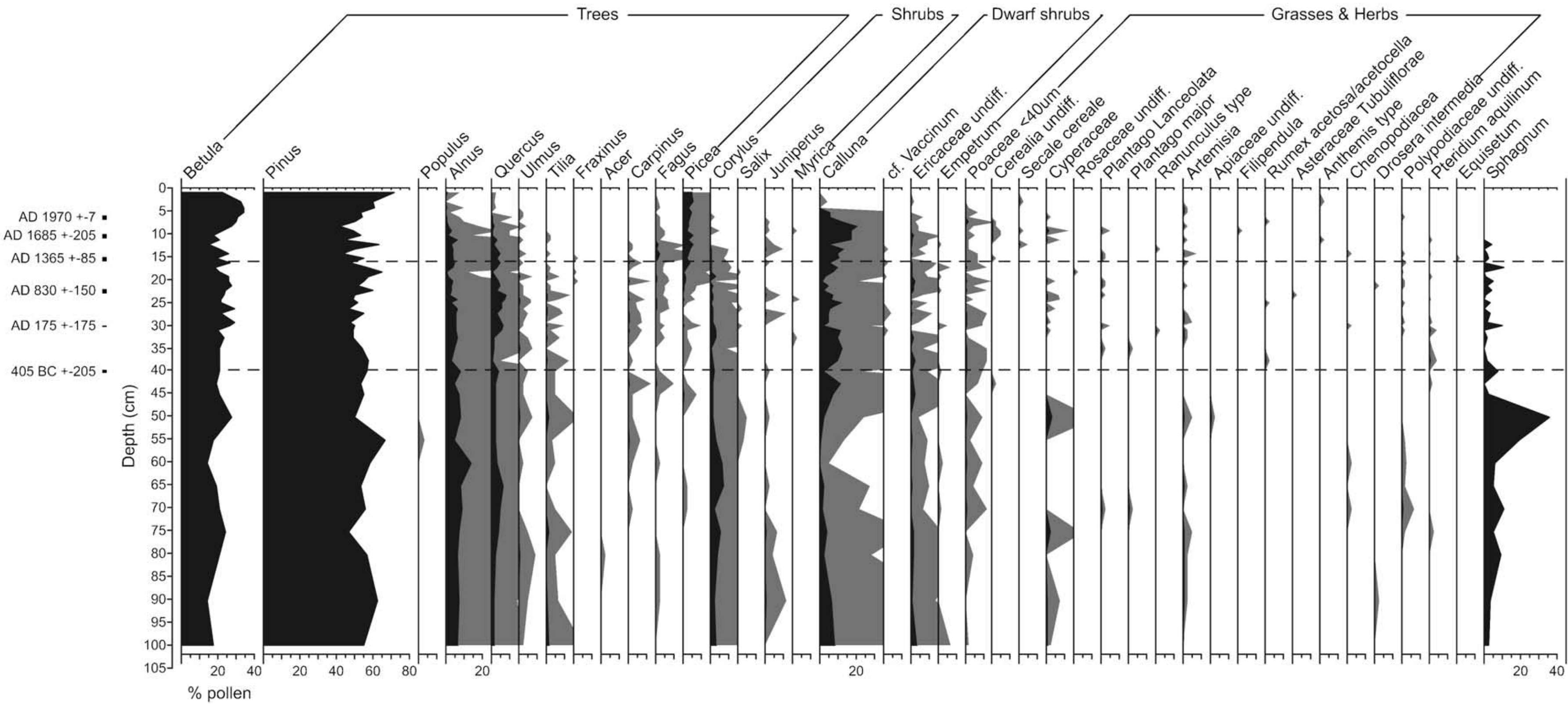

Fig. 4. Percentage pollen diagram from Skärsgölarna. The shaded portion of the graphs is a 10× exaggeration of the true value. The calculation sum comprises all seed plants (division Spermatophyta).

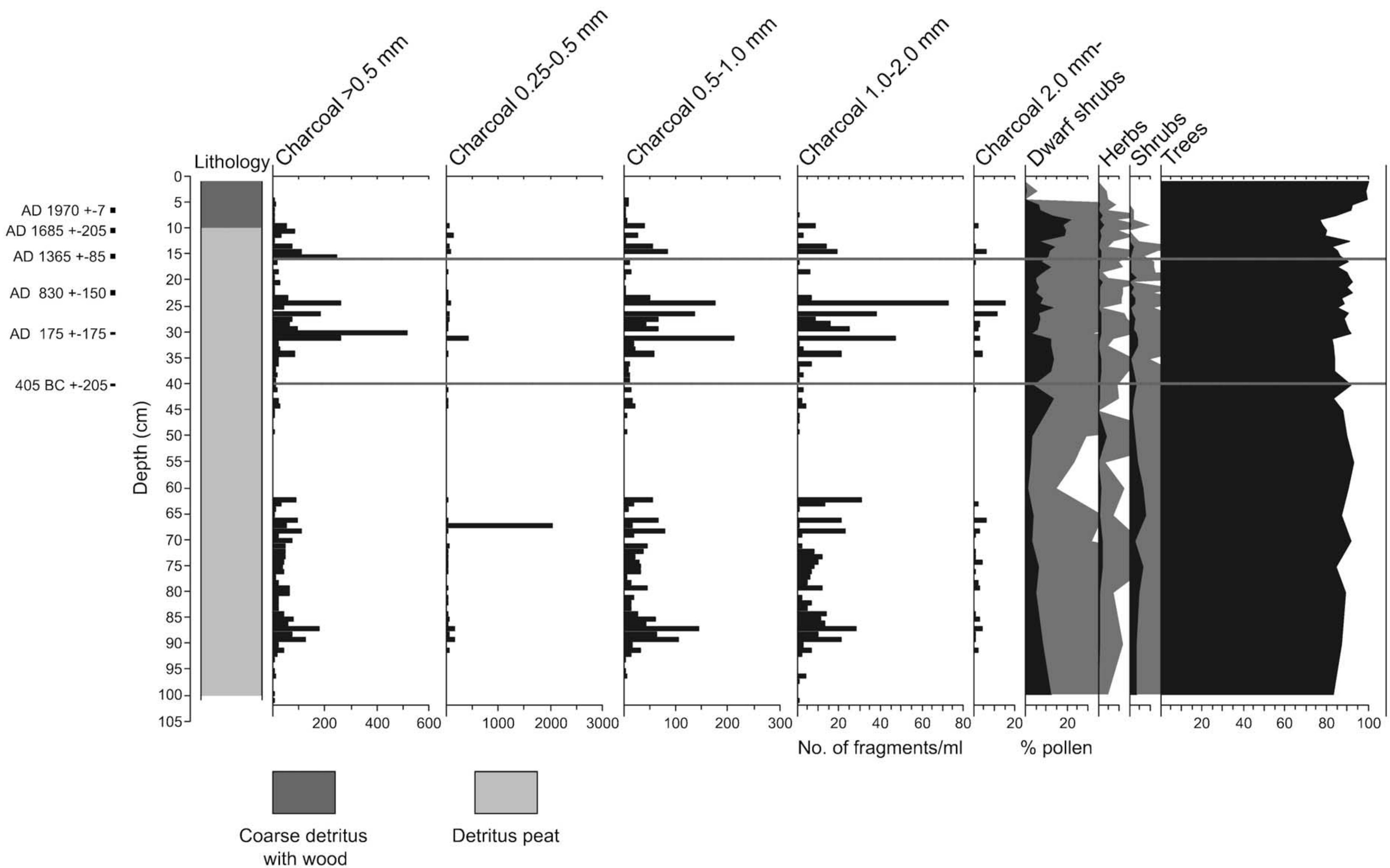

Fig. 5. Lithology, charcoal fragments of different size classes and pollen sums from Skärsgölarna. The shaded portion of the pollen graphs is a 10× exaggeration of the true value.

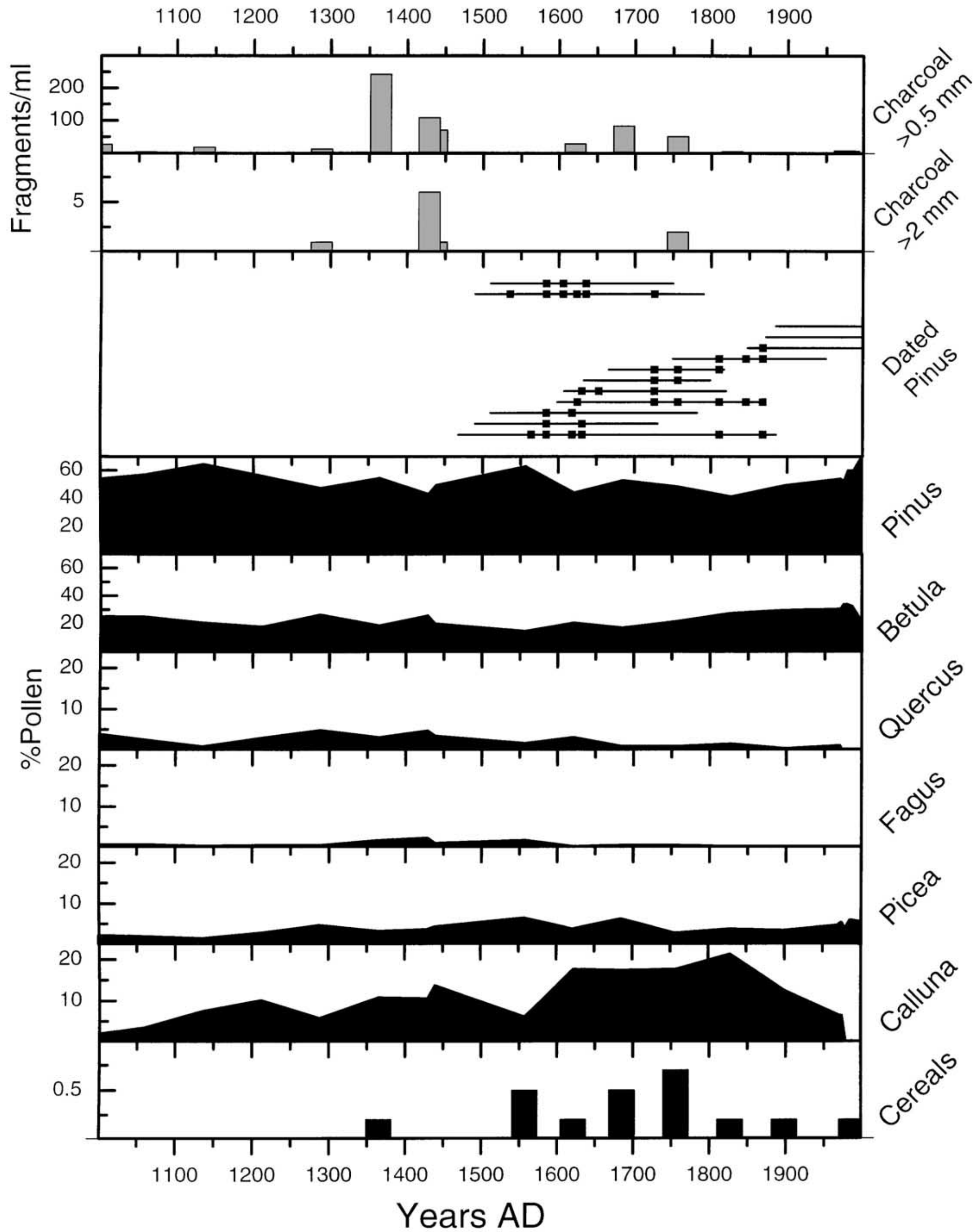

Fig. 6. Diagram showing charcoal fragments (>0.5 and 2 mm), pollen percentages for selected taxa and tree-ring analysed trees. Each horizontal line represents one *Pinus sylvestris* tree. The top two trees are from the clearcut 2 km from Skärsgölarna; the lower 11 from Skärsgölarna. A black square on the line represents date of fire according to the dendroecological analysis.

Together they make up almost 80% of total pollen. These species are prominent pollen producers and dispersers (the latter for *Pinus* in particular; Erdtman 1969), and their actual presence around the site must be corrected downwards. But even so, they probably represented a majority of the surrounding trees. *Alnus* was also a common tree-species at that time, probably growing in the surrounding wetland. *Tilia* (lime) is represented in the pollen diagram at low percentages, with the highest values at the bottom of the profile. *Tilia* is insect-pollinated; even a small relative presence in the diagram suggests that it was rather common in the vicinity. The continuous occurrence of *Quercus*, *Corylus* (hazel) and, in particular, *Calluna* (heather) and *Juniperus* (juniper), in the diagram during the period suggest that the forest was relatively open. The two latter may also indicate that the area was grazed (Behre, 1981).

A continuous record of charcoal is found up to 60 cm (Fig. 5), where it is interrupted by a period of moister conditions in the wetland, as indicated by an increased occurrence of spores from *Sphagnum* and pollen from Cyperaceae and *Salix* (willow), all characteristic of wetter conditions. Fires occurring in the upland during this period, however, cannot be excluded. The pollen percentage of *Calluna* decreased during the wetter period.

Two *Plantago* grains at 70 cm and a single cereal grain at 42 cm was found, but apart from these there were few indications of agriculture in the area up to 400 BC.

3.2.2. 40–16 cm (400 BC – AD 1350)

The charcoal record is resumed at 40 cm (ca. 400 BC), accompanied by an increase in *Calluna* pollen percentages. Apart from a gradual decline in the percentages of *Tilia* there are only small changes in the pollen diagram until around AD 1000, when *Picea* (a late immigrant to the region) becomes noticeable. The relatively few charcoal fragments found from the period AD 750–1350 could reflect a decrease in the number of fires at the site, which perhaps promoted the local increase of *Picea*. *Pinus* and *Betula* were still the dominating tree species at the site. A somewhat larger amount of pollen from anthropogenic indicators (Behre, 1981) was found from this period, for instance a few pollen grains from *Plantago lanceolata* and *Pteridium aquilinum*, but the human influence at the site was probably still low.

3.2.3. AD 1350–(16 cm)

The peak in number of charcoal fragments at AD 1350 was perhaps the beginning of an increased human activity in the area (Figs. 4–6). The cereal pollen grains found in the diagram occurred, with only one exception, from this period onward (Fig. 6). Pollen from *Calluna* became increasingly common, especially during the 17–19th centuries, probably reflecting that the site was kept more open due to cultural activities such as cultivation of cereals and grazing. *Fagus* never became common in the region (Björse et al., 1998; Valdemardotter, 2001), but the increase in *Fagus* pollen percentage at this site, although small, corresponding to with the charcoal peaks during the 14th and 15th centuries, follows a pattern of initial establishment related to fires, that can be seen in many studies from Scandinavia (Björkman and Bradshaw, 1996; Karlsson, 1996; Hannon et al., 2000; Bradshaw and Lindbladh, unpublished; Niklasson et al., 2002). The pollen percentages of both *Quercus* and *Alnus* decreased continuously during the period, to less then 1% in the top part of the profile. *Picea* pollen became increasingly common during the period and reached ca 5% at the site around AD 1500. The timing of the *Picea* immigration to this site corresponds with other local pollen analyses in the region (Lindbladh et al., 2000; Bradshaw and Lindbladh, unpublished).

The three uppermost samples, representing the last decades, show that the forest became increasingly dense at that time as the percentage of pollen from trees reached 99–100% in these samples. Every pollen grain deposited into the wetland in the uppermost sample came from trees; not a single non-arboreal pollen (NAP) grain was found. *Pinus* and *Betula* were still the dominating tree species at the site with their highest pollen percentages in the two top samples of the profile, 71 and 22% respectively.

The final larger influx of charcoal particles occurred during the 18th century (Figs. 5 and 6).

3.3. Dendroecology

Eleven different fires were dated in Skärsgölarna (Fig. 6, lower 11 trees). These were: AD 1564, 1584, 1618, 1625, 1631, 1653, 1726, 1757, 1811, 1846, and 1868. The earliest fire recorded was dated to AD 1564. This stump had originated before 1468 and had six fire scars. The last fire, in 1868, was dated in one live tree and three dead. According to a contemporary newspaper article this fire occurred in August 1868 (Calmarposten: August 26, 1868). A total of 420 ha or 2/3 of the "allmänning" was affected, including the site at Skärsgölarna (Gustafsson, 2000). A large part of today's older stands, a mix of *P. sylvestris, Betula* spp. and *P. tremula,* regenerated after this fire.

Two large dead *P. sylvestris* trees at the clearcut 2 km from Skärsgölarna experienced six fires from 1536 to 1726 (Fig. 6, top two trees), these were AD 1536, 1584, 1606, 1624, 1636, 1726. Two of these fires were also dated in trees in Skärsgölarna (1584 and 1726). The fires dating from these two sites indicate that the fire regime for the last ca 450 years has been a mix of smaller and larger fires, with some fires capable of spreading over several kilometres. Such large fires could thus have covered several hundred hectares, while fires only recorded in one site may have been much smaller, perhaps a few hectares.

3.4. Saproxylic beetles

Out of the 105 red-listed saproxylic beetles that have been found at the site since 1975, at least 12 are connected to open, sun-exposed forests with *P. sylvestris* or *Birch* spp. trees (Table 2). Also, many of the other red-listed species caught in the area are associated with these tree species but are more generalists in terms of habitat selections. Most of the red-listed species found depend on deciduous trees, especially *Betula* spp. and *P. tremula*, but this may reflect the dominance of traps on these two species. However, several of the red-listed

Table 2
Red-listed saproxylic beetles found in the Skärsgölarna area that are dependent on open forests, mainly with *Pinus sylvestris* or *Betula* spp.[a]

Species and red-list category	Associated tree species	Important substrates
EN—Endangered		
Dircaea australis	*Betula* spp., *Populus tremula*, etc.	White-rotten deciduous wood
Strangalia attenuata	*Betula* spp., *Alnus glutinosa, Quercus* spp.	Deciduous wood and forest glades with flowers
VU—Vulnerable		
Tragosoma depsarium	*Pinus sylvestris*	Old sun-exposed logs
Nothorhina punctata	*Pinus sylvestris*	Old living, sun-exposed trees
Leptura pubescens	*Pinus sylvestris*	Wood of large diameters
NT—Near Threatened		
Platysoma minus	*Betula* spp.	Sun-exposed logs and high stumps
Denticollis borealis	*Betula* spp.	Sun-exposed high stumps
Ampedus cinnaberinus	*Betula* spp., *Quercus* spp.	White-rotten, sun-exposed deciduous wood
Dicerca moesta	*Pinus sylvestris*	Sun-exposed dead parts of living trees
Buprestis octoguttata	*Pinus sylvestris*	Dead roots and stems in open conditions
Corticeus bicolour	*Betula* spp.	Dead trees in open conditions
Necydalis major	*Betula* spp., *Populus tremula*, *Alnus glutinosa*.	Sun-exposed high stumps

[a] Data concerning red-list category from Gärdenfors (2000), tree species and substrate preferences from Palm (1959), Nilsson and Huggert (2001),

species depend on recently dead or dying branches of oak (Nilsson and Huggert, 2001).

4. Discussion

4.1. Forest fires

Results from this study provide evidence that forest fire historically has been a common feature in south-eastern Sweden. The fire history of southern Sweden is still rather unexplored but recent charcoal and dendroecological studies (Lindbladh et al., 2000; Niklasson and Drakenberg, 2001; Niklasson et al., 2002) have confirmed considerably higher fire frequency in south-eastern Sweden compared to southwestern Sweden, as predicted by Granström's (1993) study based on density of lightning ignitions. Compared to other studied sites in southern Sweden, Skärsgölarna has a much later ending of frequent fires (1868), about one century after Norra Kvill National Park (1770: Niklasson and Drakenberg, 2001) and Siggaboda Forest Reserve (1752: Niklasson et al., 2002). We believe that this is an important factor behind the survival of the present threatened fauna, since many of them depend on a sunny and warm microclimate. The reason for the late fire cessation at Skärsgölarna is unclear, but the land ownership situation was probably a contributing factor. The ''allmänning'' was a common land used for extensive grazing and slash-and-burn cultivation until 1866 according to historical data (and further confirmed by the findings of cereal pollen in the pollen analysis, Fig. 6). Historical documents from southern Sweden (Larsson, 1989) offer several anecdotal examples of accidentally ignited forest fires in connection with slash-and-burn cultivation, but quantitative data is lacking. It is further known that fire was deliberately used to improve grazing conditions during times before forestry became important. However, this has seldom been documented since burning of forests has been strongly regulated by law over the last 300 years (Granström, 1995; Eliasson, 2002). Even if the area under study is small, the high number of fires recorded in the dendroecological analysis points toward an elevated number of ignitions compared to the natural level. It is therefore likely that humans caused many of these fires, as the last fire in the area, shown by historical records to be ignited by humans (Gustafsson, 2000). In line with this assumption, as recorded both by the historical documents and the dendroecological data, the fires ended shortly after the state forests became the main owner of the ''allmänning'' in 1866, and forestry became the dominating land-use in the area. We believe that the cessation of fire ignition by people is a more important reason for the end of forest fires in the area, than improved fire extinguishing technology and increased fire suppression activities.

4.2. The former openness of the site

The openness of forests is a key question for the conservation of many threatened forest species (Vera, 2000; Nilsson et al., 2001; Svenning, 2002), and for threatened saproxylic beetles in particular (Gärdenfors and Baranowski, 1992; Jonsell et al., 1998; Ranius and Jansson 2000; Martikainen, 2000). Therefore, it is important to identify areas with a continual openness and retained high biodiversity. Skärsgölarna is today relatively open compared to south Swedish standards, but the pollen diagram shows that it presently is more closed than ever before during the more than 2500 year record covered in the diagram (Fig. 4). Not a single pollen grain from field- or shrub-layer (NAP) species was found in the top sample in the profile, and less than 1% from the last decades, a situation that should be compared to the high influx of *Calluna* pollen (an indicator for open conditions) during the 15th to the 19th century where this dwarf shrub reached as much as 20% of all pollen (Fig. 6). These centuries were characterised by a large degree of human activity that probably kept the site open, as evident for instance from the influx of cereals, but the canopy of the site was probably largely open before this period also. We believe that frequent and continuous fires (as recorded by the charcoal and dendroecology records) kept the site relatively open during the major part of the time period covered by the study, and our hypothesis is therefore supported. These fires were probably a prerequisite for the long-time recorded dominance of *Pinus*, *Betula* and *Calluna*, and for the occurrence of *Quercus* and *Corylus*, and also for the almost total absence of all shade-tolerant tree species. Many *Pinus* trees can survive mild to moderate fires, whereas *Betula* is a prominent pioneer species after fires. *Calluna* is known to re-sprout vigorously after moderate fires. Both *Quercus* and *Corylus* have difficulties in regenerating in closed forests. Our findings support the conclusion by Nilsson et al. (2001) and Svenning (2002) that fire could have been an important factor for keeping some northwest European forest types open, and an important agent for maintaining the populations of *P. sylvestris* and *Quercus* spp. before the large human impact on the northwestern European forests started. However, during the later part of the diagram (from 400 BC and onwards), grazing cannot be excluded as a contributing factor to the openness, as indicated by the high percentages of *Calluna*, a strong indicator for grazing (Behre, 1981), in the diagram (Fig. 6).

Another factor that probably contributed to the open conditions at the site, the last several hundred years in particular, is that *Picea* never became a dominant tree species. Modern forestry in southern Sweden with large-scale plantation of *P. abies* monocultures has in most areas created forests much denser than they were before. That development apparently did not occur in the "allmänning", probably mainly due to the dominance of poor soils and numerous boulders. The boulders can furthermore explain why overgrowing since the last fires in the 19th centuries has been a slow process at the site. The historical data and the pollen data stress that *P. abies* played a minor role in the "allmänning" (max. 10%) and at the site (max. ca. 5%) compared to most other areas in the region, also after the fires stopped in the 19th century. For instance, in Ebbegärde, another "kronopark" located not more than a couple of kilometres from Hornsö, *P. abies* reached almost 50% of the growing stock in the middle of the 20th century (Gustafsson, 2000). Even if the tree-cover at the studied site today is obviously denser than during the period with fires, it probably would have been much denser if *P.abies* had been established at the site.

4.3. Possible reasons behind the occurrence of the red-listed beetles

The continuous and long-term occurrence of fires and openness as recorded here is probably an important factor behind the presence of many of the red-listed beetles species at the site. It is evident that many forest organisms, in particular these beetles, will not be able to survive if the current fire-free, and increasingly dark, conditions continue. Several species connected to open forests have become extinct from the area due to forestry and this also includes species dependent on *P. sylvestris* and *Betula* spp. (Nilsson and Huggert, 2001). The species-specific reasons for the recorded extinctions in the area will be elucidated in detail in another paper (Nilsson et al., unpublished).

Another important factor behind the high conservation values found is probably the occurrence of old trees at the site during the last several hundred of years. In modern forestry *P. sylvestris* individuals are usually cut before they reach the age of 120 years. One living *P. sylvestris* tree growing at the site was dated to be more than 160 years old, and many of the dated, but today dead, trees reached high ages (>400 years), which implies that old trees also have been common in the past and that the fires were mainly of low intensity, not killing the largest trees. A couple of large living *P. sylvestris* individuals at the site are probably also very old, but they could not be cored due to hollow rot. They had experienced four or five fires, implying that their ages exceed 300 years. Several of the red-listed beetles found in Skärsgölarna depend on large, old *P. sylvestris* trees: *Nothorhina punctata* depends on old, sun-exposed, living *P. sylvestris* individuals; *Leptura pubescens* on dead *P. sylvestris* wood of large diameters; and *Tragosoma depsarium* on sun-exposed, *P. sylvestris* logs on the ground. *T. depsarium* has one of its few southern Swedish localities not more than 50 m from the pollen site and it is extremely sensitive to dense regrowth and dark conditions. Also, several of the beetles dependent mainly on *Betula* spp. at the site need large trees and there are some old *B. pendula* individuals at the site that probably regenerated after the fire in 1868.

As stated above, many of the red-listed species found in Skärsgölarna depend on an open mixed forest, but one has to keep in mind that this dependency probably does not occur at the stand scale, but rather at the landscape level. The relatively warm summer climate in this region of southern Sweden has been proposed as one important reason for the rich fauna (Nilsson and Huggert, 2001). Furthermore, important for the high biodiversity of saproxylic beetles in the Hornsö Kronopark could be the fact that more than 20% of the forest area is covered by old mixed deciduous forests, and a study of historical documents and maps revealed that this forest type also was present during the previous two centuries (Gustafsson, 2000; Nilsson and Huggert, 2001). Also the numerous large boulders in the area is a possible explanation for the high diversity. There are several examples of forests in southern Sweden with high conservational values, where these values coincide with frequent large boulders (Nilsson et al., 1995).

4.4. Forest history in the landscape

Although partly operating at different geographic scales, the historical data, the pollen data and the dendroecological data fit in most parts well together during the period when they overlap, i.e. the last 200 years (Fig. 6). In both the pollen and historical records, *Pinus* clearly dominates, followed by *Betula*, and with a noticeable, but much more rare, occurrence of *Picea*. The conditions at Skärsgölarna as revealed by the paleoecological data, probably represent a larger area than the site itself. The difference in the timing of the ending of fires in the dendroecological and charcoal data could perhaps reflect a difference in spatial sensitivity between the two methods. But as the sampled *P. sylvestris* stumps are located very close to the sediment sampling point (max. 30 m), it is more likely that it reflects the imprecision of the radiocarbon dating. The calibration of the radiocarbon date from 10 to 11 cm (a level with 83 charcoal fragments/ml) spans from AD 1480 to 1890. This means that this level may actually represent the 19th century, and if that were the case, the charcoal and dendrochronological data would fit more precisely.

5. Conclusions

We believe that the recorded long-term occurrence of fires and open conditions created by fire are important factors behind the high conservation values found at the site. Other important factors are that the site is rich in boulders, allowing for some patches to remain open and being difficult to exploit; the relatively warm summer climate; that *P. abies* has not been planted in the surrounding forests until recently; and finally that old trees have been relatively abundant. The pollen and charcoal record clearly shows that these conditions have been rather stable over a long time and did not start to change until the most recent decades.

The findings have several implications for the conservation of the site (and area):

1. Open forest conditions need to be restored in many formerly disturbed sites that are now regrowing.
2. Prescribed burns should be the most appropriate way to achieve open conditions at many sites, including the studied site, and at the same time a way to create substrates needed by many of the threatened beetles as well as other organism groups.

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