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The Charcoal Record of Small Spruce (Picea abies) -Swamps in Southeastern Norway: A Study of Local Fire History and Fine Scale Spatial Variation

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Abstract

The local fire history of a Norway spruce (*Picea abies*) forest with a high present-day biodiversity has been investigated to explore the spatiotemporal fire dynamics of a delimited part of Trillemarka Nature Reserve in southeastern Norway. The fire history of the nearby pine forest has previously been studied in detail revealing numerous fires the last 600 years. This study investigated if the adjacent spruce forest has burnt after spruce established and became abundant in the area, and if this changed the local fire regime. In addition, the fine scale spatial variation of the charcoal records was analyzed. Visible charcoal bands with macroscopic charcoal particles (>0,5 mm) were extracted from peat sequences from 12 closed-canopy spruce-swamps and three open Scots pine (*Pinus sylvestris*) dominated mires. Six peat sequences were extracted at each site, plus an additional sequence at eight sites for pollen analysis and ^{14}C dating.

In total, 249 charcoal bands with macroscopic charcoal were identified illuminating the local fire history covering the last 3000 years in most sites. All sites contained charcoal, but the number of bands and amount of charcoal particles varied greatly between and within sites. Overall, 24 % of the sequences did not contain any macroscopic charcoal, which demonstrates the extensive fine scale spatial variation of charcoal in the peat. The average number of charcoal bands per sequence was 2,2 ± SD 2,2 and the average number of macroscopic charcoal particles per sequence was 231 ± SD 210. The amount of charcoal particles increased with the length of the sequence and were mostly found in the lower end of the sequences. Based on pollen analysis it was concluded that spruce established around 900-1100 AD, and 66 % of the spruce dominated sites contained charcoal bands after spruce establishment, which gave an average of 2,2 local fire events in each site. Thus, most of the spruce dominated sites have burnt at some point, although with major spatial variation. In one part of the spruce forest, fire activity seemingly ceased after spruce establishment, whereas the fire frequency increased or remained stable in other parts. The high fire frequency in some sites the last millennia could possibly be attributed to anthropogenic activities. More charcoal bands were found in the spruce dominated sites than the pine dominated sites during the same period, suggesting higher probability of detecting local fires events in the peat of the small spruce-swamp hollows than the pine-mires.

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1 Introduction

The importance of forest fires as a disturbance agent in boreal forest ecosystems have been established for a long time (Bonan & Shugart, 1989; Amiro et al., 2001). Forest fire exhibit several ecological functions such as enhanced tree seedling regeneration and growth (Wardle et al., 1998), nutrient availability (Kong et al., 2018), production of pyrogenic carbon for long-term storage (Ohlson et al., 2009; Santín et al., 2016), and creation of habitats for pioneer species such as herbs and grasses (Purdie & Slatyer, 1976), and different pyrophile species (Kouki et al., 2012). These functions are important for diversity and long-term stability in the forest ecosystem (Zackrisson, 1977).

During the Holocene (the last 11 500 years) the global fire activity have varied considerably in time and space (Power et al., 2008). The fire regime is controlled by complex interactions between climatic variation, vegetation composition, anthropogenic activities, fuel properties and sources of ignition (Marlon et al., 2006; Colombaroli et al., 2007; Ohlson et al., 2011). Climate is often regarded as the primary natural regulator of the fire regime (Marlon et al., 2006), but the forest tree species composition have the potential to overshadow direct effects of climate change on fire regimes in boreal forests (Brubaker et al., 2009). The establishment of Norway spruce (*Picea abies*) forest in Fennoscandia altered the fire regime and caused a significant decrease, often a cessation, in local fire activity (Tryterud, 2003; Ohlson et al., 2011).

It has been assumed that most of the boreal forest has been impacted and shaped by reoccurring wildfires to a large extent (Zackrisson, 1977; Bonan & Shugart, 1989). The natural forest fire return intervals in Fennoscandian boreal forests have been estimated to be between 50 and 200-300 years (Zackrisson, 1977; Niklasson & Granström, 2000; Rolstad et al., 2017). These wildfires are often low-intensity ground fires compared to the high intensity stand-replacing fires of North America (Wooster & Zhang, 2004). However, Ohlson et al. (2009) found that the amount of historically burnt forest ground reached an average of 50 percent on a broad geographical scale. Fire-free systems could thus be less rare than previously thought (Tryterud, 2003; Ohlson et al., 2011), which imply true long-term continuity in some spruce dominated forests systems (Hörnberg et al., 1995; Ohlson &

Tryterud, 1999), which in turn are of importance for forest biodiversity (Ohlson et al., 1997; Hörnberg et al., 1998).

Spruce is a fire-sensitive species which will struggle to persist in forests with high fire frequency (Zackrisson, 1977; Sannikov & Goldammer, 1996), unlike Scots pine (*Pinus sylvestris*) which is adapted to fire-prone environments (Linder et al., 1997). Thus, it could be expected that fire has a less prominent role in spruce dominated forest compared to fire-prone dry pine forest (Ohlson et al., 2011). After a large wildfire in eastern Fennoscandia, Wallenius et al. (2004) found that moist depressions, swamps, and the plots of more fertile spruce forest mostly remained intact while the surrounding forest burned.

Forest completely dominated by spruce is a late Holocene phenomenon in Fennoscandia (Tallantire, 1972). The cause of the rapid spruce colonization of Fennoscandia is still not fully understood, although climate change is widely attributed as the catalyzing mechanism (Giesecke & Bennett, 2004; Miller et al., 2008). Spruce immigrated into Fennoscandia from east and spread westward (Tallantire, 1972). Most of the spruce forest colonization of Norway occurred between 0 and 1000 AD (Hafsten, 1992). Nonetheless, small outpost populations of spruce were widespread throughout Fennoscandia up to several millennia before the main invasion event (Giesecke & Bennett, 2004; Giesecke, 2005). 11.000 year old macrofossils of spruce have been documented from the Southern Scandes Mountains suggesting a glacial refugia on the exposed continental shelf during the end of the Last Glacial Period (Kullman, 2001; Kullman, 2002). Ancient DNA data suggests that spruce may even have been present at Andøya in Northern Norway during the Last Glacial Maximum over 20 000 years ago (Alsos et al., 2020).

Anthropogenic activities have significantly altered the fire regime and forest structure of Fennoscandian boreal forests during the last centuries/millennia (Östlund et al., 1997; Niklasson & Granström, 2000; Rolstad et al., 2017). Humans burned areas regularly to improve grazing and cultivation conditions (Östlund et al., 1997). The anthropogenic fire regime produced wildfires at a higher frequency than a natural fire regime, which resulted in smaller fires with short fire return intervals and increased the annually burnt area (Niklasson & Granström, 2000; Storaunet et al., 2013). Anthropogenic fires became common in the Fennoscandian outskirt from around the 15th century and continued until the mid-19th century (Niklasson & Granström, 2000; Wallenius et al., 2004). The anthropogenic fires gradually ceased as timber production increased in economic importance (Östlund et al., 1997), which catalyzed a period of effective fire suppression that has lasted until today (Zackrisson, 1977; Wallenius, 2011). In present Fennoscandian boreal forest fire is almost absent, except wildfire burns that are effectively wiped out, and some prescribed burnings in certain areas for conservation and forestry purposes (Zackrisson, 1977; Östlund et al., 1997; Niklasson & Granström, 2004; Lindberg et al., 2020).

1.1 Aim

The fire history of the last 600 years is examined in detail in the pine dominated parts of the study area through dendrochronological analysis of fire scars in old pine stumps (Storaunet et al., 2013; Rolstad et al., 2017). The studies revealed a fire-prone environment with relatively few fires covering large areas until the beginning of the 17th century, when a period of anthropogenic fire regimes began with frequent small fires, which ended in the beginning of the 19th century, and forest fires have been almost absent since. The fire history of the pine dominated parts of the study area is also previously studied through charcoal analysis of peat and soil (Kasin et al., 2013).

However, the fire history of the spruce dominated forest in the study area is poorly known due to a lack of old fire-scarred pines in this area. The forest is a biodiversity hotspot for wood-inhabiting fungi and other species associated with old-growth forest (Hofton, 2011; Hoch, 2020). The aim of the study was to increase the knowledge of the forest fire history in the areas with current spruce domination and to investigate if the immigration of spruce altered the local fire regime. Together with this the historical development in the local vegetational composition was examined at fine spatial scales to explore changes through time and illuminate possible causes for the rather rapid colonization of spruce in the area.

Peat contains stratigraphic sequences of pollen and charcoal particles, and peat from twelve closed-canopy spruce-swamps and three open mires partly covered by pine, was the main source of data in this study. Closed-canopy forest hollows have a source area of pollen and larger particles of at most a few hundred meters, which reveals the history of the local vegetational composition and fire history at a stand-scale in high spatial resolution over several millennia (Jacobson & Bradshaw, 1981; Bradshaw, 1988; Parshall & Calcote, 2001), while still capturing the essential features of the regional vegetation history (Lindbladh et al., 2000). The open mires have a larger pollen source area than the closed-canopy swamps representing more of the regional composition (Sugita et al., 1999).

The fire history of the sites was investigated through charcoal bands in the peat stratigraphy. The identification of charcoal bands is a time effective method to investigate the presence of macroscopic charcoal (particles >0,5 mm) (Ohlson et al., 2006), which have proved to be a reliable indicator of local fire events (Clark et al., 1998; Ohlson & Tryterud, 2000). A high number of sites and sampling-points within each site provides high resolution information of the peat charcoal record and fire history within the study area (Pitkänen et al., 2001).

2 Materials and Methods

2.1 Study area

The study was conducted at Heimseteråsen in Trillemarka-Rollagsfjell Nature Reserve in Viken (previously Buskerud) County. The area is situated in the mid-boreal vegetation zone (Moen, 1998) and is dominated by old-growth forest of spruce and pine with some larger and smaller areas of peatland and swamp-forest in between. More than 50 threatened or near threatened species from the Norwegian Red List are observed within the study area (Henriksen & Hilmo, 2015; Hoch, 2020; Norwegian Biodiversity Information Centre, 2021). The geology of the area consists of north-south extended ridges of Precambrian acidic rock, mostly gneisses (NGU, 2021). Richer moraine material exists in the east-facing slopes where the spruce dominates (Storaunet et al., 2013). The average annual temperature in the period 1990-2020 was 4-5 °C and the average precipitation in the same period was 800-1000 mm. The average temperature in January was between -4 and -5 °C, while the average temperature of July was 14-15 °C. The area is covered by a thick cover of snow (usually over 50 cm) from December to April (Norwegian Climate Service Centre, 2021).

The nature type in the study area, based on the Nature Types of Norway (NiN) (Bratli et al., 2019) classification system, was *Vaccinium myrtillus* forest (T4-C1) in the spruce dominated slopes, *Calluna vulgaris-Vaccinium* forest (T4-C5) in the transition areas between spruce and pine dominated areas, and *Calluna vulgaris* forest (T4-C9) in the exposed parts of the pine dominated area. Parts of "the Heimseteråsen slope" consisted of the richer forest type T4-C2 ("moderately rich herb forest"). The most common tree species were spruce and pine. Hairy birch (*Betula pubescens*) and aspen (*Populus tremula*) were regular features, while rowan (*Sorbus aucuparia*), goat willow (*Salix caprea*), and grey alder (*Alnus incana*) had only minor occurrences. Nomenclature for plant names follows Lids and Lids (2005).

Despite its old-growth forest properties the study area has had an extensive anthropogenic impact over the last centuries with several summer dairy farms (see map in Rolstad et al., 2017). Slash-and-burn cultivation and burning to improve grazing conditions were common in the area from the 17th century until the start of the 19th century (Storaunet et al., 2013; Rolstad et al., 2017). After the mid-19th century there have been very few forest fires in the area due to fire suppression (Storaunet et al., 2013). Selective and high-grading cutting have been conducted in the area until around 1940 AD. From 1920 until 1978 AD several minor patches were clear-cut and replanted with spruce within the study area (Hoch, 2020).

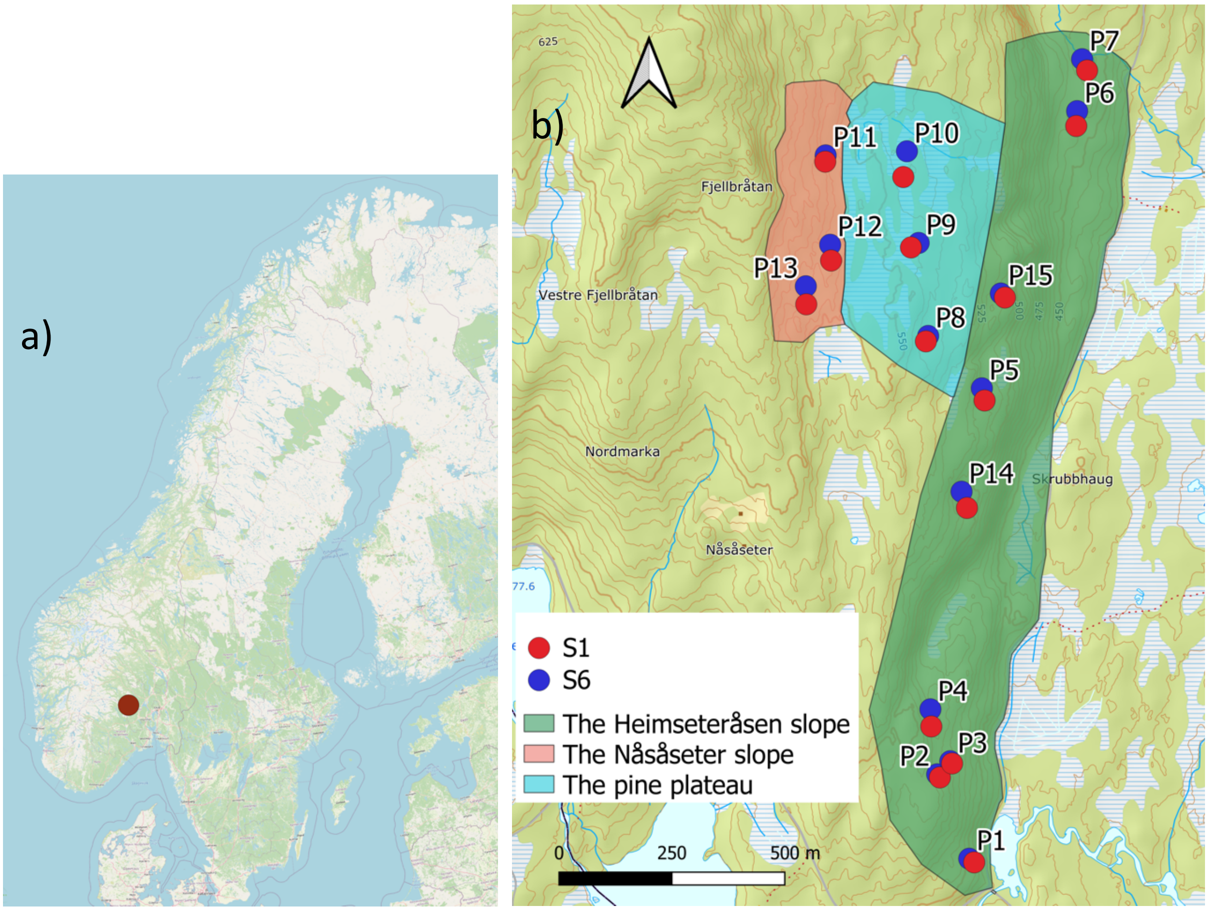


Figure 1: a) Location of the study area (red dot) within Scandinavia. Background map copyrighted OpenStreetMap and available from www.openstreetmap.org. b) Map of the study area dived into three sub-areas, showing the position of all the investigated sites. Red dot symbols the southernmost sampling point, blue dot the northernmost, see Figure 2. The contour line distance is 5 m. Background map copyrighted Norgeskart and available from www.norgeskart.no.

The study area was divided into three sub-areas based on forest composition and disposition within the study area (Figure 1). Sites P1-P7, and P14 and P15, were located in a spruce dominated, rather steep slope (up to 35°) facing east-southeast. This part of the study area is referred to as "the Heimseteråsen slope" throughout the thesis. The slope contain some of the most developed old-growth properties of the area with exceptionally high biodiversity of wood-decaying fungi (Hoch, 2020). The sites were located between 448 and 512 meters above sea level. The peatlands examined in this slope were small, shallow, and rather well-defined closed-canopy spruce-swamp hollows with varying tree-cover. The size of the hollows varied from 18x7 m (P1) to 29x26 m (P14). The sites P5, P6, P7 and P14 had some trample damages and traces of grazing, probably from moose and cattle. P6 had a small decline in height towards south and P7 had a rather large brook in the north end which could have contributed to long-distance material into the peat profile. P5 differed from the other sites in this area and had more in common with the sites P8-P10.

Sites P8-P10 were located in a pine dominated plateau above “the Heimseteråsen slope”. This part of the study area is referred to as “the pine plateau” throughout the thesis. The area was characterized by sparse tree-cover and quite large areas of poor minerotrophic peatland. The area was probably subjected to selective cutting until recently, but still contain viable populations of certain old-growth demanding species such as the lichen *Letharia vulpina*. The sites were located between 536 and 544 meters above sea level, on deep, partly pine covered mires with low biodiversity. The size varied from 47x27 m (P8) to 38x60 m (P9), but the edge was often not well-defined.

Site P11-P13 were located in the spruce dominated slope above “the pine plateau”, an area situated close to the old summer dairy farm Nåsåseter which is now inactive. This part of the study area is referred to as “the Nåsåseter slope” throughout the thesis. The area has certain old-growth spruce forest properties, although the forest is younger and the biodiversity less rich than that of “the Heimseteråsen slope”. Still, the quite demanding wood-inhabiting polypore *Postia guttulata* was observed. The sites were located between 557 and 561 meters above sea level, and the examined peatlands was similar to the ones examined in “the Heimseteråsen slope”. The name of the nearby mountaintop “Fjellbråten” suggests that this area has previously been “slash-and-burn” cultivated.

Several variables were registered at each site, such as the percentage abundance of different tree species within a radius of about 70 m from the site, and the abundance of *Vaccinium myrtillus,* ferns, grasses, and *Sphagnum* mosses. NiN nature type (Bratli et al., 2019) was registered for each site, revealing sites with pine dominance and P5 belonged to the poorest class of minerotrophic peatland (V1-C1 and C5), while the sites with spruce dominance except P5 belonged to the intermediate version of the latter (V1-C6). A short list of vascular plant species present at each site was also registered, see Appendix F.

2.2 Sampling of peat sequences and charcoal analysis

Six sampling points were selected in each site according to specific criteria: the sampling points were placed along two transects, one in the north end and one in the south end of the peatland. The two transect were placed in varying distance from each other in relation to the size of the different peatlands (Table 1). The sampling points were called S1, S2, and so on (Figure 2). S1 was placed in the southernmost part of the peatland at the first spot toward north where the depth of the peat layer was measured to be more than 50 cm. S2 was placed one meter north of S1 and S3 was placed two meters north of S2. S6 was placed in the north end after the same criteria as S1 while S5 and S4 were placed as S2 and S3, respectively, southward instead of northward. The peat sampled in this fashion are referred to as the original peat sequences throughout the thesis.

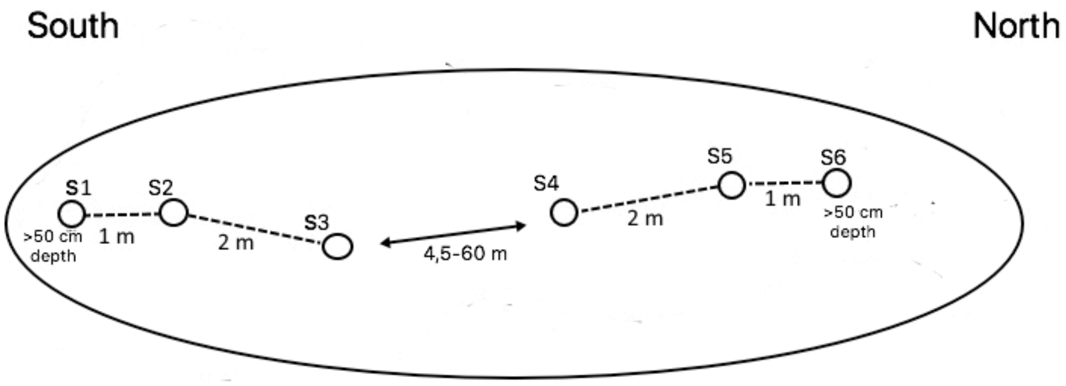


Figure 2: Draft of placement of sampling points for the original peat sequences within each site, and the variation in distance between S3 and S4.

The fieldwork was carried out in September, October, and November 2020. All peat sequences were collected using a Russian peat corer (Jowsey, 1966) as 50 cm long sequences with 5 cm diameter from the surface down to the mineral soil or bedrock. The peat sequences were immediately examined for bands of charcoal, as oxidation of peat makes the bands less visible after a short time (Ohlson et al., 2006; Halsall et al., 2018). Charcoal bands were identified as darker layers in the peat stratigraphy or where pieces of charcoal were visible on the surface of the sequence. The depth below the surface and the width of the layer were registered for each charcoal band. The charcoal bands were collected for laboratory analysis by cutting out a 1 cm thick slice of peat using a sharp knife, with the charcoal band in the middle, and stored in a small plastic zip lock bag. The depth from the surface and down to the transition from peat to mineral soil or rock was measured.

Using the data collected in the original peat sequences, eight sites were selected for further examination with pollen analysis and radiocarbon dating. At these eight sites one additional peat sequence was collected in close proximity to the sampling point with the highest amount of charcoal bands high in the profile. Charcoal bands in these sequences were identified and registered as previously described. The surface vegetation and topmost 10 cm of peat were collected in plastic zip lock bags before the peat sequences were extracted. The full peat sequences from surface to mineral soil were then wrapped in plastic foil and stored in plastic tubes which had been cut in half lengthwise, which again was wrapped in aluminium foil. This minimized the risk of damaging the stratigraphy during transport and pollution during storage (Kasin et al., 2013). These peat sequences are referred to as the PolDat sequences throughout the thesis as to not confuse them with the original peat sequences. The PolDat sequences were kept cool, but not frozen, before and between examinations in the laboratory.

The charcoal bands collected in the field and the charcoal bands of the PolDat sequences were individually examined for presence and amounts of macroscopic charcoal in the laboratory. Here, the samples were gently washed through a sieve of 0,5 mm, and were then diluted in water in a petri-dish to be searched for macroscopic charcoal under a stereo microscope (Hörnberg et al., 1995). The amount of charcoal particles in each sample was estimated and roughly sorted into four size classes: 0,5-1 mm, 1-3 mm, 3-10 mm, and above 10 mm. This resulted in an approximate number for the total amount of macroscopic charcoal particles in one centimetre of the peat sequence, 6,92 cm^3. Only black, often silver-shining, and opaque particles with broken angular ends and somewhat crispy texture were classified as charcoal.

Collected charcoal bands without macroscopic charcoal were included in the charcoal diagrams (Figure 3) as the bands observed in the field have a high probability of containing high concentrations of microscopic charcoal and can therefore indicate presence of regional fire activity (Kasin et al., 2013). Charcoal bands without macroscopic charcoal were not included in other figures and statistical analyses. Charcoal diagrams were created in R (R Core Team, 2021) with the package tidyverse (Wickham et al., 2019).

2.3 Pollen analysis and local establishment of spruce

Samples were extracted as 1 cm^3 peat from the PolDat sequences. The samples were prepared for pollen analysis at the University of Bergen following the standard method described in Fægri and Iversen (1989). This process removes all minerogenic and organic material from the samples by exposing them to strong acids (HCl, HF, A_2O/H_2SO_4) and base (KOH). After this treatment only the outer walls of the pollen grains, microscopic charcoal and a few other small organic components were left. The outer walls of the pollen grain have a unique structure used for species/genera determination. Tablets with known concentrations of *Lycopodium* spores were added to each sample to permit estimations of pollen concentrations (Stockmarr, 1971). The samples were stained with fuchsin and mounted in glycerine on microscope slides. The mounted sample was searched at 400x magnification, unless the pollen concentration was low, then 100x magnification was used.

The pollen analysis was conducted following the standard method described in Fægri and Iversen (1989). At least 300 arboreal pollen were counted in each sample (Hörnberg et al., 1995; Kasin et al., 2013). All identifiable pollen grains were determined to either species, genera, or family depending on the taxa following identification keys in Fægri and Iversen (1989). Microscopic charcoal particles were counted and separated into two size classes, over and under 6 μm. The relative abundance of microscopic charcoal was calculated by dividing the counted amount of microscopic charcoal by the counted amount of added *Lycopodium* spores. Stratigraphic pollen diagrams were created in R (R Core Team, 2021) with the packages tidyverse (Wickham et al., 2019) and patchwork (Pedersen, 2020).

Taxa of temperate deciduous trees, i.e. species with a requirement of mean temperature above 11 ^{o}C in the four summer months June, July, August, and September (Moen, 1998), were placed in a group called “deciduous trees”. In this study it included pollen from *Corylus, Quercus, Tilia, Ulmus, Fagus,* and *Fraxinus.*

Taxa from the pollen analysis which could indicate human activity were placed in a section called “open land species”. The selection of taxa to this group was based on Behre (1981) with supplements of lay and pastureland species from the NiN system (Halvorsen et al., 2016) and descriptions in Flora Nordica (Jonsell, 2001) and the Norwegian Flora (Lids & Lids, 2005). This included nitrophile taxa such as *Artemisia, Rumex*, Chenopodiaceae, and *Urtica*, and cultivated plants such as Cannabaceae, which are strong anthropogenic indicators in such a oligotrophic environment (Behre, 1981). Other included taxa thrive in meadows and other open habitats, such as *Campanula*, Asteraceae (*Lactucoideae*), *Ranunculus, Trifolium,* and Caryophyllaceae. Several species within the taxa included also grow in open forests on rich soils, i.e., the group could to some degree be affected by climatic factors as well as anthropogenic activities. This is the reason the group is called “open land species” instead of “anthropogenic species”. See Appendix C for complete list of the included taxa.

In this study the threshold of local spruce establishment was determined to be at 2 % spruce pollen of total tree (arboreal) pollen sum as this threshold has been used by several similar studies (e.g. Hörnberg et al., 1995; Ohlson & Tryterud, 1999; Ohlson et al., 2006; Kasin et al., 2013) based on the results of Hafsten (1992). Depth and time of spruce establishment at the different sites was extrapolated by calculating an exponential curve through the interval where spruce could have established, as this is a more probable development than a linear curve.

2.4 Radiocarbon dating and age-depth models

Samples for radiocarbon (^{14}C) dating were extracted from the PolDat sequences. Samples were obtained at the lower part of the peat sequence and in 1-6 other sections of different depth, depending on the site. The selected peat samples were cleared for charcoal and recent plant material such as roots and rhizomes, and thereafter dried in a drying cabinet. The remaining material of each sample weighted about 300-1000 mg, and were stored in separate small zip lock bags.

Samples were sent to Laboratory of Mass Spectrometry (Vilnius Radiocarbon) at the Centre for Physical Sciences and Technology (FTMC) in Lithuania, who conducted acceleration mass spectrometry (AMS) radiocarbon dating. The obtained radiocarbon age was calibrated to calendar years by the lab personnel using the program OxCal v.4.4.2 (Bronk Ramsey, 2020) with IntCal20 atmospheric curve (Reimer et al., 2020).

The age-depth models were created with the software R (R Core Team, 2021) using the package Bchron (Haslett & Parnell, 2008) for Figure 4 and the package tidypaleo (Dunnington, 2021) for Figure 3 and 5. All extrapolated ages were extracted with the Bchron package. Bchron can overestimate the uncertainties resulting in high standard deviations for extrapolated ages (Trachsel & Telford, 2017). All ages are presented as calibrated ages BC/AD, except for Figure 4 which presents calibrated ages BP.

2.5 Statistics

The peat sequences were sampled in a nested block design of samples within sites within type of forest. A variance components analysis was performed to determine what part of the hierarchy had the greatest effect on the variation. The variance component analysis was calculated using R (R Core Team, 2021) with the package VCA (Schuetzenmeister & Dufey, 2020). The number of charcoal particles in each sequence were logarithmically transformed before the analysis to achieve an approximate normal distribution.

ANOVA and linear mixed-model regression analyses were carried out to test if the numbers of charcoal bands and particles in the different sites were significantly different from each other, and to test if the length of the sequences, distance to the edge of the peatland, and dominant tree species surrounding the site had significant effect on the variance in charcoal particles. The R software (R Core Team, 2021), with the package nlme (Pinheiro et al., 2021) and the same log-transformed values as above, were used for the analyses.

3 Results

3.1 Within and between sites variation in the charcoal record

In total 267 charcoal bands were identified in the 90 original peat sequences collected from all fifteen sites. Additionally, 59 charcoal layers were identified from the eight PolDat sequences. Of these charcoal bands 200 contained macroscopic charcoal in the original peat sequences while 49 charcoal bands contained macroscopic charcoal in the PolDat sequences. This means 75 % of charcoal bands identified in the field in the original sequences contained macroscopic charcoal, while 83 % of identified charcoal bands contained macroscopic charcoal in the PolDat sequences. Mean depth of the original peat sequences was 79 ± SD 29 cm while it was 73 ± SD 15 cm for the PolDat sequences. The sequences S3 and S4 were generally longer than S1 and S6 as the former were collected further away from the edge of the peatland (Figure 2).

Table 1: Site specific characteristics and general information of the six original peat sequences sampled from each of the investigated sites.

Site	Elevation (m.a.s.l.)	Amount of spruce in the surrounding area	Size, length x width (m)	Distance S3-S4 (m)	Mean peat depth (cm)	Min peat depth (cm)	Max peat depth (cm)
P1	448	80 %	18x7	9	51,7	50	55
P2	481	96 %	16x11	9	68,8	50	100
P3	474	94 %	13x11	4,5	67,7	53	93
P4	480	80 %	30x10	22	80,7	66	90
P5	509	60 %	46x12	38	81,7	52	118
P6	457	92 %	25x11	16	59,3	50	75
P7	455	75 %	18x16	10	68,7	60	80
P8	537	15 %	47x27	38	82,3	50	124
P9	545	2 %	38x60	31	107,0	69	140
P10	544	1 %	67x28	60	117,3	74	207
P11	562	93 %	20x7	13	60,2	50	71
P12	560	85 %	49x12	40	88,2	70	127
P13	559	92 %	47x15	40	90,5	63	175
P14	501	93 %	29x26	20	79,5	57	109
P15	512	83 %	27x11	19	85,7	60	120

Of the 90 original peat sequences 68 of them contained macroscopic charcoal, while 22 of the sequences did not contain any macroscopic charcoal. This means 24 % of the original peat sequences did not contain macroscopic charcoal. P13 stands out in this context with macroscopic charcoal in only one of the six sequences. All PolDat sequences contained macroscopic charcoal. The PolDat sequences contained more macroscopic charcoal bands and particles than the original peat sequences because the PolDat sequences were collected close to the original peat sequence having the most charcoal bands at the respective site.

The number of charcoal bands and their vertical positions in the peat profiles were highly variable both within and between sites (Figure 3). The mean number of charcoal bands with macroscopic charcoal was 2,2 ± SD 2,2 bands in the original peat sequences, while it was 7,0 ± SD 2,4 bands in the PolDat sequences. The site with the highest number of charcoal bands with macroscopic charcoal was P10 with 30 bands (Table 2), while P13 had fewest with only one band. P10 and P1 had the most and least charcoal particles per peat sequence, respectively, both as mean and maximum values (Table 2). For all the original peat sequences the mean number of charcoal particles per sequence was 231 ± SD 210, while the mean was 620 ± SD 185 particles for the PolDat sequences.

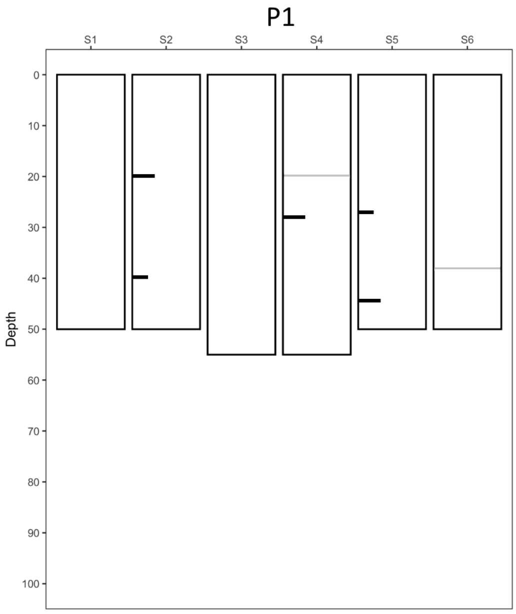
There was no correspondence between the number of charcoal bands and the present-day abundance of spruce adjacent to the sites, while it was a weak negative correlation between charcoal particle number and present-day spruce abundance (R= -0,39). However, there was not significantly more charcoal particles found in the pine dominated sites (p = 0,062, ANOVA). There were no significant differences between the sites in “the Heimseteråsen slope”, “the pine plateau” and “the Nåsåseter slope” (see Materials and Methods for definitions) regarding both numbers of charcoal bands and charcoal particles (p = 0,63 and p = 0,53, respectively, ANOVA).

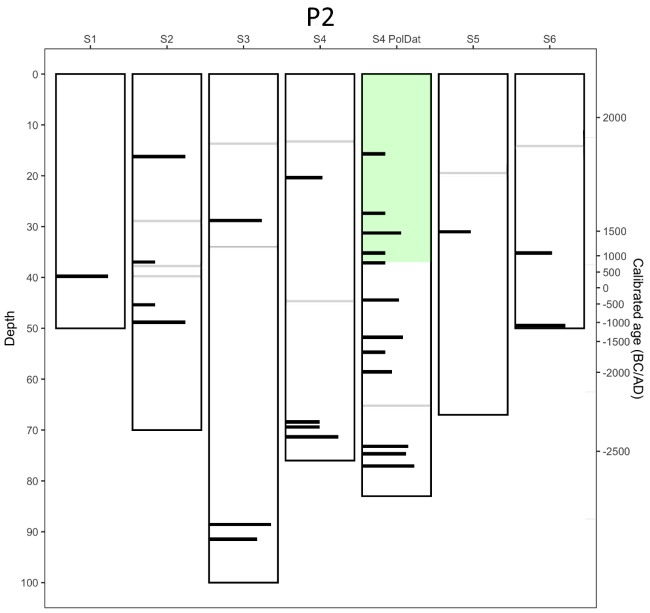
There were significant differences between the sites both in relation to number of charcoal bands (p = 0,0039, ANOVA) and charcoal particles (p = 6,85e-05, ANOVA). A linear mixed-effects model disclosed that the length of the sequence had significant effect on the number of charcoal particles (p = 0,035, ANOVA), while the distance from the sampling point to the edge of the peatland had no significant effect on the number of charcoal particles (p = 0,37, ANOVA)

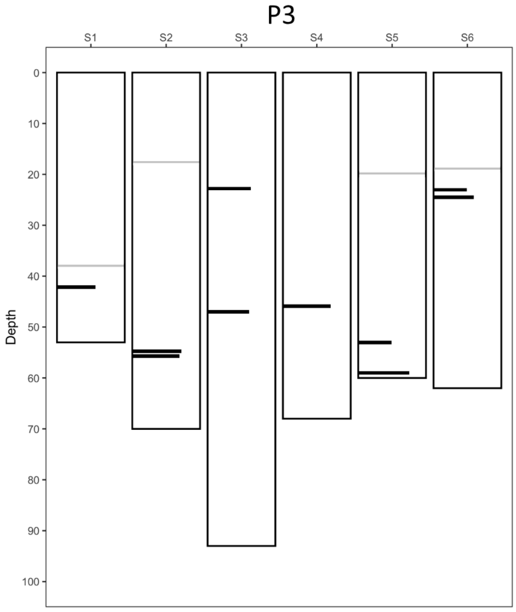
According to a variance component analysis of the original peat sequences the domination of spruce versus pine accounted for 2,9 % of the overall variance in number of charcoal particles found, while the between site variation accounted for 30,5 % of the overall variance in charcoal particles. The residual variation was 66,5 %. A major part of this was within-site variation when considering the standard deviations for the mean numbers of macroscopic charcoal particles per site (Table 2).

Table 2: Quality and quantity of the charcoal bands found in the six original peat sequences sampled from all the investigated sites. The number of charcoal particles originates from all charcoal bands within one peat sequence.

Site	Charcoal bands with macroscopic charcoal (no.)				Charcoal particles (no.)				Percent bands without macroscopic charcoal
	Total	Mean ± SD	Min	Max	Total	Mean ± SD	Min	Max	
P1	4	0,7 ± 1,0	0	2	25	4,2 ± 6,6	0	15	50,0 %
P2	15	2,5 ± 1,4	1	4	1755	292,5 ± 274,1	25	820	37,5 %
P3	10	1,7 ± 0,5	1	2	1080	180,0 ± 101,2	50	300	28,6 %
P4	18	3,0 ± 2,8	0	7	980	163,3 ± 138,7	0	330	14,3 %
P5	10	1,7 ± 1,8	0	5	1270	211,7 ± 207,4	0	510	0,0 %
P6	11	1,8 ± 1,5	0	4	930	155,0 ± 148,6	0	380	0,0 %
P7	5	0,8 ± 1,2	0	3	305	50,8 ± 86,3	0	215	44,4 %
P8	7	1,2 ± 0,8	0	2	1010	168,3 ± 145,0	0	350	0,0 %
P9	13	2,2 ± 2,6	0	7	1490	248,3 ± 295,5	0	760	0,0 %
P10	30	5,0 ± 1,5	4	8	2780	463,3 ± 270,2	220	950	3,2 %
P11	22	3,7 ± 2,3	1	8	1695	282,5 ± 204,2	145	690	33,3 %
P12	16	2,7 ± 3,4	0	9	1113	185,5 ± 238,2	0	600	20,0 %
P13	1	0,2 ± 0,4	0	1	30	5,0 ± 12,2	0	30	87,5 %
P14	19	3,2 ± 2,7	0	6	1370	228,3 ± 193,4	0	450	34,5 %
P15	19	3,2 ± 2,1	1	7	1840	306,7 ± 221,3	10	540	0,0 %


P1
S1
S2
S3
S4
S5
S6
Depth
0
10
20
30
40
50
60
70
80
90
100


P2
S1
S2
S3
S4
S4 PolDat
S5
S6
Depth
0
10
20
30
40
50
60
70
80
90
100
Calibrated age (BC/AD)
2000
1500
1000
500
0
-500
-1000
-1500
-2000
-2500


P3
S1
S2
S3
S4
S5
S6
Depth
0
10
20
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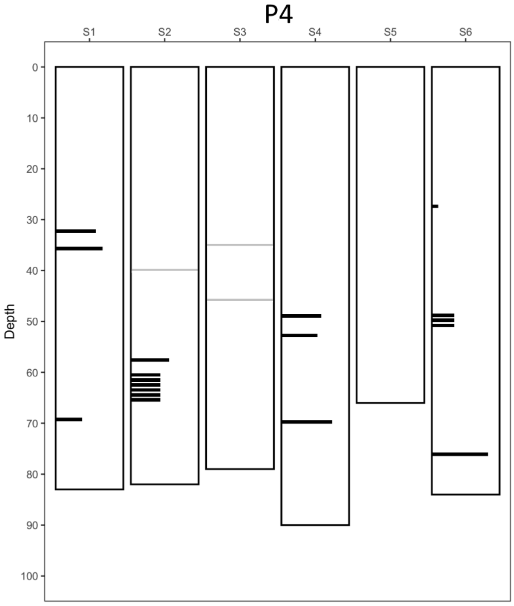
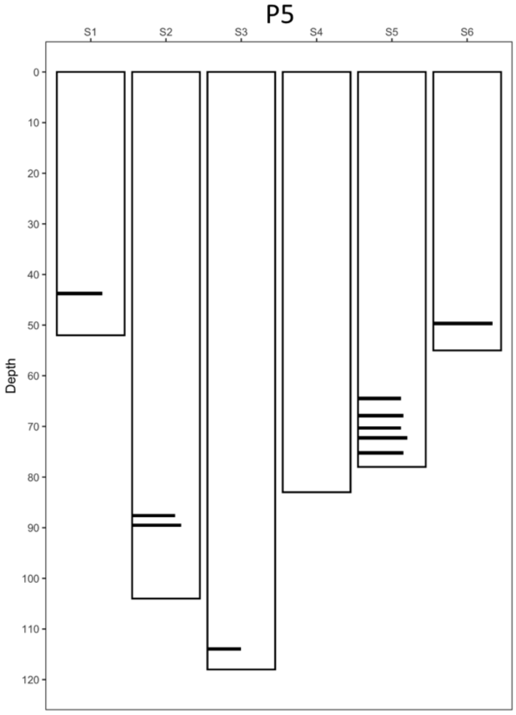
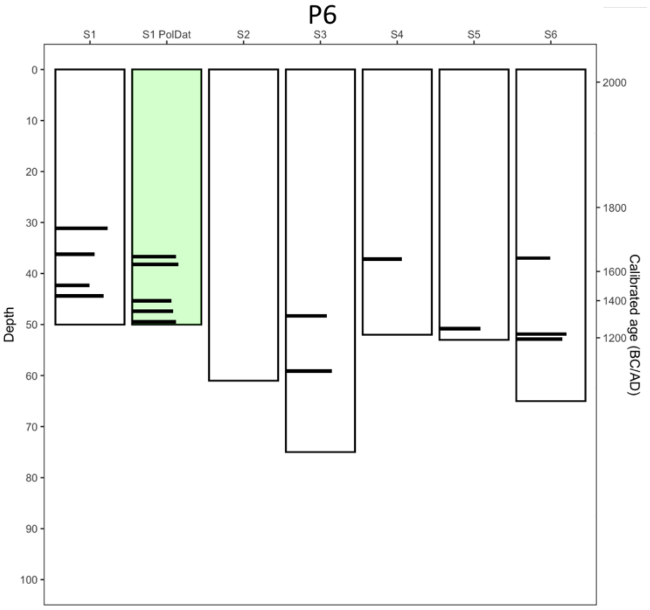
40
50
60
70
80
90
100


P4
S1
S2
S3
S4
S5
S6
Depth
0
10
20
30
40
50
60
70
80
90
100

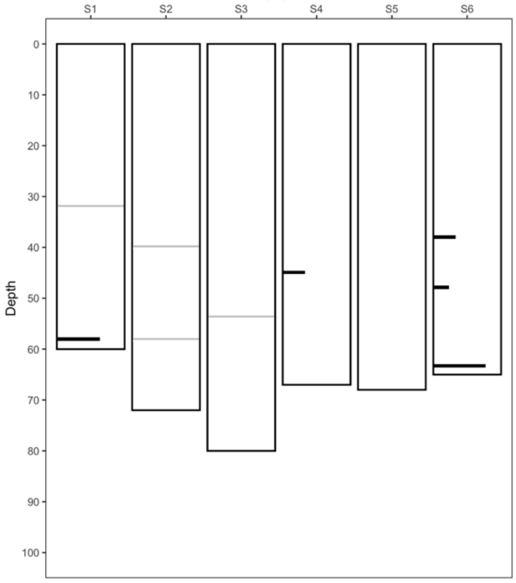
P5


S1
S2
S3
S4
S5
S6
Depth
0
10
20
30
40
50
60
70
80
90
100
110
120

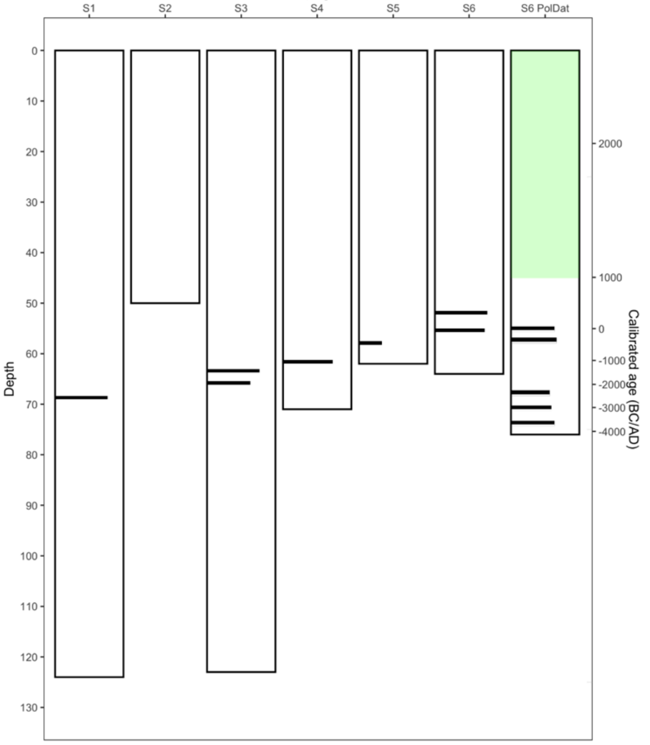
P6


S1
S1 PolDat
S2
S3
S4
S5
S6
Depth
0
10
20
30
40
50
60
70
80
90
100
Calibrated age (BC/AD)
2000
1800
1600
1400
1200

P7


S1
S2
S3
S4
S5
S6
Depth
0
10
20
30
40
50
60
70
80
90
100

P8


S1
S2
S3
S4
S5
S6
S6 PolDat
Depth
0
10
20
30
40
50
60
70
80
90
100
110
120
130
Calibrated age (BC/AD)
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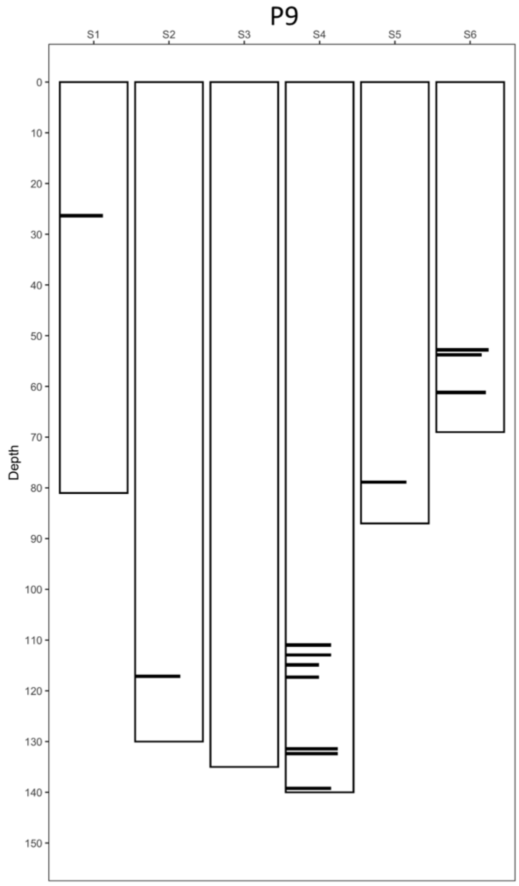
1000
0
-1000
-2000
-3000
-4000


P9
S1
S2
S3
S4
S5
S6
Depth
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10
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30
40
50
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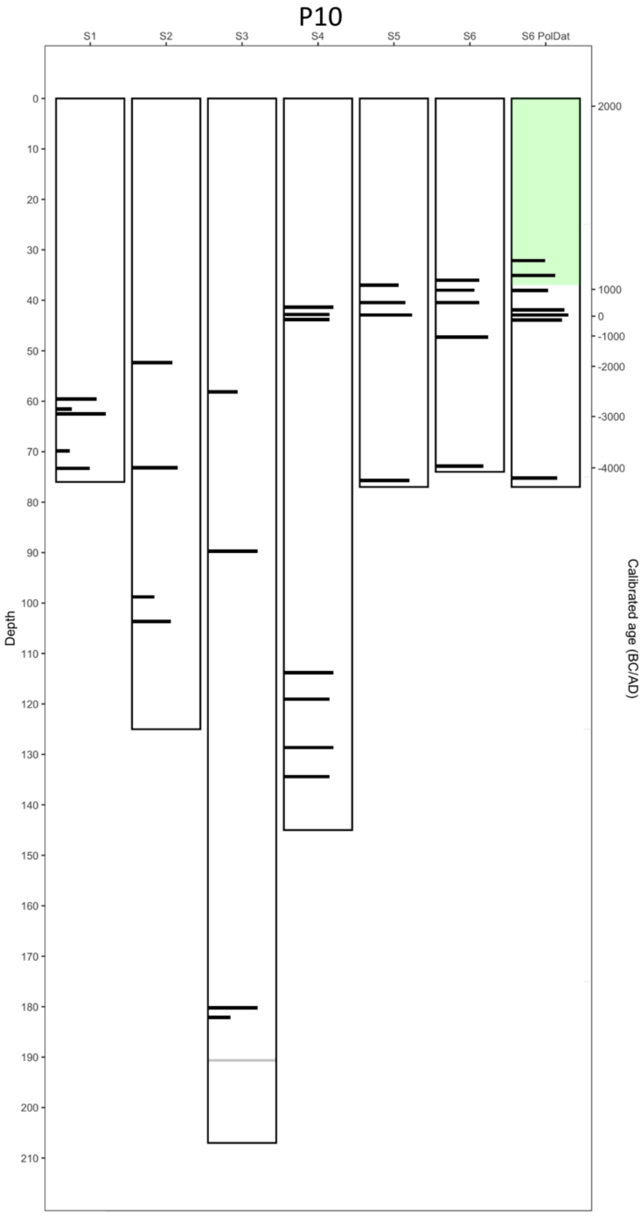
80
90
100
110
120
130
140
150


P10
S1
S2
S3
S4
S5
S6
S6 PolDat
Depth
0
10
20
30
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60
70
80
90
100
110
120
130
140
150
160
170
180
190
200
210
Calibrated age (BC/AD)
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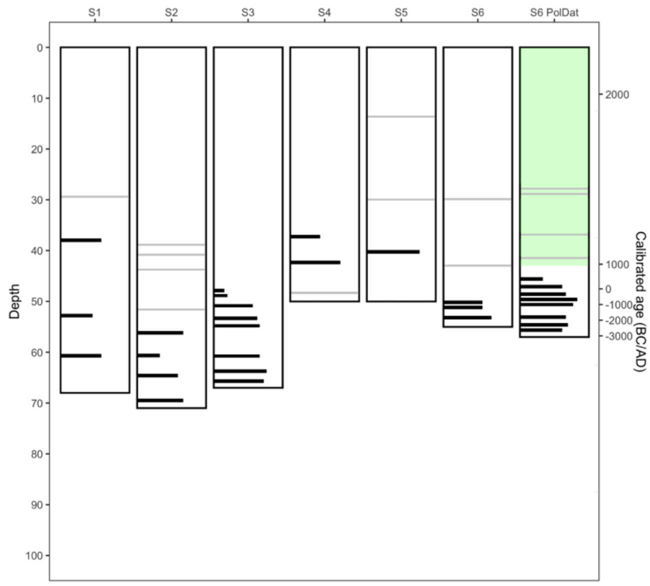
1000
0
-1000
-2000
-3000
-4000


P11
S1
S2
S3
S4
S5
S6
S6 PolDat
Depth
0
10
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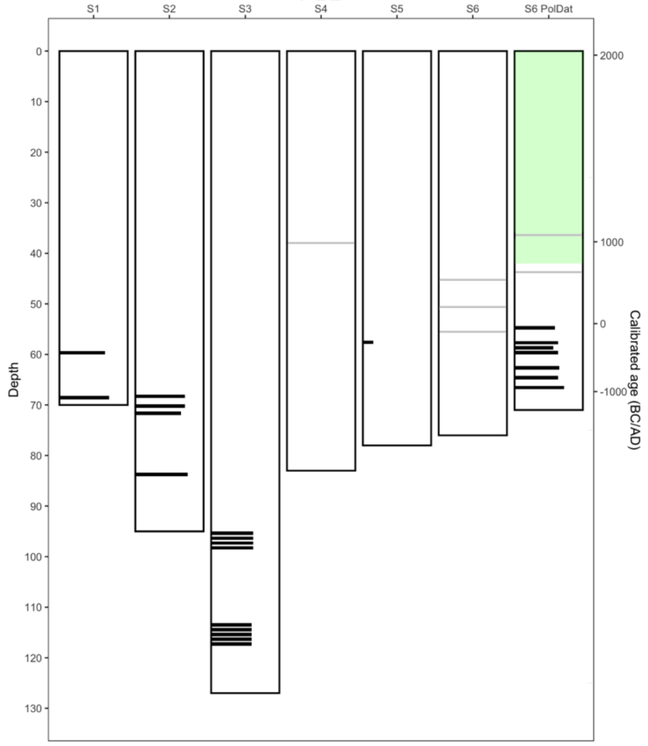
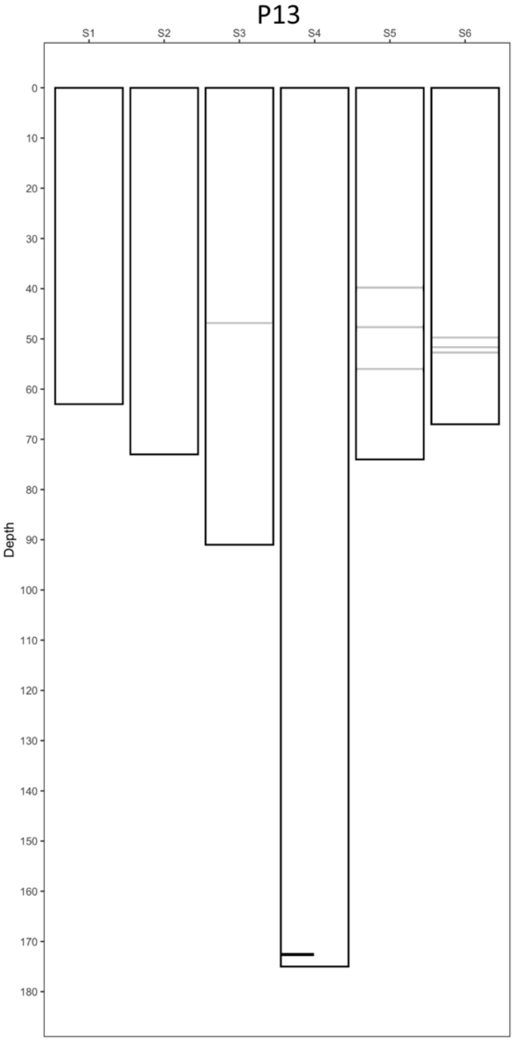
30
40
50
60
70
80
90
100
Calibrated age (BC/AD)
2000
1000
0
-1000
-2000
-3000


P12
S1
S2
S3
S4
S5
S6
S6 PolDat
Depth
0
10
20
30
40
50
60
70
80
90
100
110
120
130
Calibrated age (BC/AD)
2000
1000
0
-1000


P13
S1
S2
S3
S4
S5
S6
Depth
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30
40
50
60
70
80
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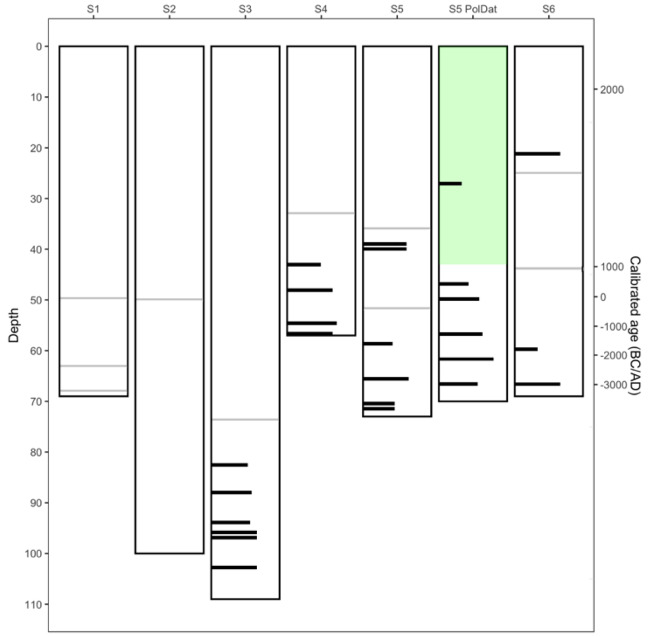
120
130
140
150
160
170
180


P14
S1
S2
S3
S4
S5
S5 PolDat
S6
Depth
0
10
20
30
40
50
60
70
80
90
100
110
Calibrated age (BC/AD)
2000
1000
0
-1000
-2000
-3000

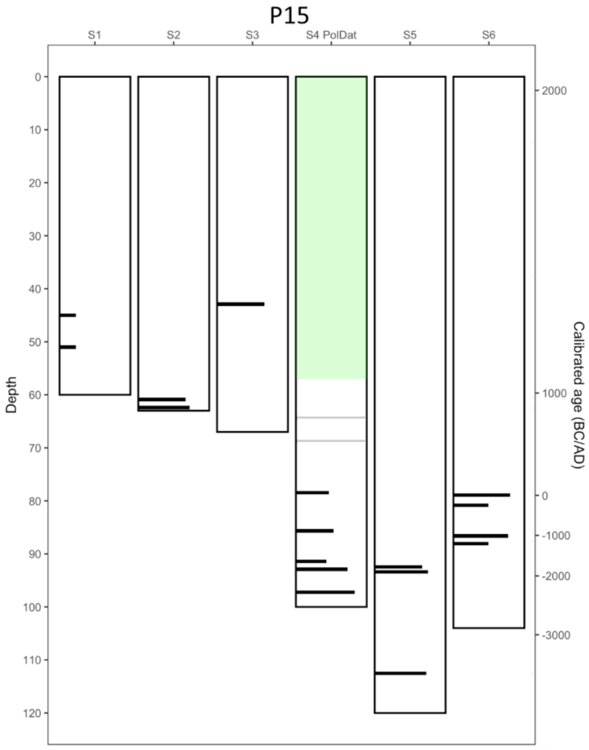


Figure 3: Charcoal diagrams from the investigated sites. Black horizontal bars indicate the presence and amount of macroscopic charcoal particles (>0,5 mm) in a 1 cm thick slice of the peat sequence on a logarithmic scale from 0 to 10^3. Grey bands indicate charcoal observations in the field which did not contain macroscopic charcoal. Only PolDat sequences were used for pollen analysis and ^{14}C dating (see Materials and Methods). The green area indicates the interval where spruce has been present at the site (spruce pollen percentage >2%). The calibrated ages BC/AD on the right y axis is only representative for the PolDat sequence and is an age-depth model created from the site specific ^{14}C dates.

3.2 Long-term forest history and vegetation change

The oldest ^{14}C dates in this study came from the sites P8 and P10 and dated back to ca. 4000 BC (Table 3). The time span covered by all sites with ^{14}C ages was from approximately 1250 BC to present, except for site P6 which was considerably younger covering only around 1240 AD to present. Information of all radiocarbon dates in this study is presented in Table 3. The samples collected in the upper parts of the sequences in site P2, P8, P11, and P14 turned out to contain high percentages of modern carbon, and were thereby dated to post 1950 AD. According to the age-depth models (Figure 4) the peat accumulation was highly variable between sites in the lower parts of the sequence. From 40-50 cm depth to the top of the sequence, covering the last millennia, the peat accumulation was rather similar for all sites, except P6 and P15, which had higher accumulation.

Table 3: ^{14}C dating of peat samples. High peak ages represent the area with the highest density of the calibration curve, i.e., the most probable age of the sample.

Site	Lab. ref.	Depth	Radiocarbon age BP	cal. age BC/AD 95 % conf.	cal. age high peak
P2	FTMC-OB80-1	15	-773 ± SD 26	1957-2000 AD	1998 AD
	FTMC-OB80-2	31	835 ± SD 26	1168-1256 AD	1221 AD
	FTMC-HT41-2	33	480 ± SD 27	1410-1453 AD	1435 AD
	FTMC-DO57-3	35	411 ± SD 28	1433-1620 AD	1458 AD
	FTMC-DO57-2	46	2497 ± SD 28	776-521 BC	630 BC
	FTMC-HT41-1	56	3592 ± SD 28	2031-1882 BC	1940 BC
	FTMC-DO57-1	71	3837 ± SD 30	2454-2155 BC	2280 BC
P6	FTMC-OB80-3	36	167 ± SD 26	1662-2000 AD	1727 AD
	FTMC-HT41-3	50	790 ± SD 28	1219-1278 AD	1236 AD
P8	FTMC-DO57-4	35	-1850 ± SD 27	1959-1982 AD	1982 AD
	FTMC-OB80-4	58	2215 ± SD 26	380-197 BC	293 BC
	FTMC-HT41-4	76	5312 ± SD 31	4249-4046 BC	4127 BC
P10	FTMC-OB80-5	32	272 ± SD 26	1520-1795 AD	1623 AD
	FTMC-DO57-5	40	1309 ± SD 28	657-775 AD	760 AD
	FTMC-DO57-6	50	3430 ± SD 29	1875-1627 BC	1690 BC
	FTMC-HT41-5	77	5573 ± SD 31	4456-4347 BC	4390 BC
P11	FTMC-DO57-7	30	-1 ± SD 28	1699-1957 AD	1955 AD
	FTMC-OB80-6	45	1203 ± SD 27	706-892 AD	872 AD
	FTMC-HT41-6	57	4410 ± SD 31	3316-2916 BC	3070 BC
P12	FTMC-DO57-8	45	1233 ± SD 28	681-884 AD	805 AD
	FTMC-OB80-7	58	2258 ± SD 27	394-207 BC	370 BC
	FTMC-HT41-7	71	2996 ± SD 30	1380-1122 BC	1250 BC
P14	FTMC-OB80-8	27	-179 ± SD 26	1955-1956 AD	1956 AD
	FTMC-DO57-9	42	851 ± SD 28	1157-1265 AD	1220 AD
	FTMC-OB80-9	47	1633 ± SD 27	382-539 AD	421 AD
	FTMC-HT41-8	70	4771 ± SD 30	3639-3386 BC	3578 BC
P15	FTMC-HT41-9	40	98 ± SD 29	1685-1928 AD	1714 AD
	FTMC-DO57-10	60	1084 ± SD 28	892-1021 AD	990 AD
	FTMC-OB80-10	79	2037 ± SD 26	146-60 BC	5 BC
	FTMC-HT41-10	100	4180 ± SD 30	2887-2636 BC	2770 BC

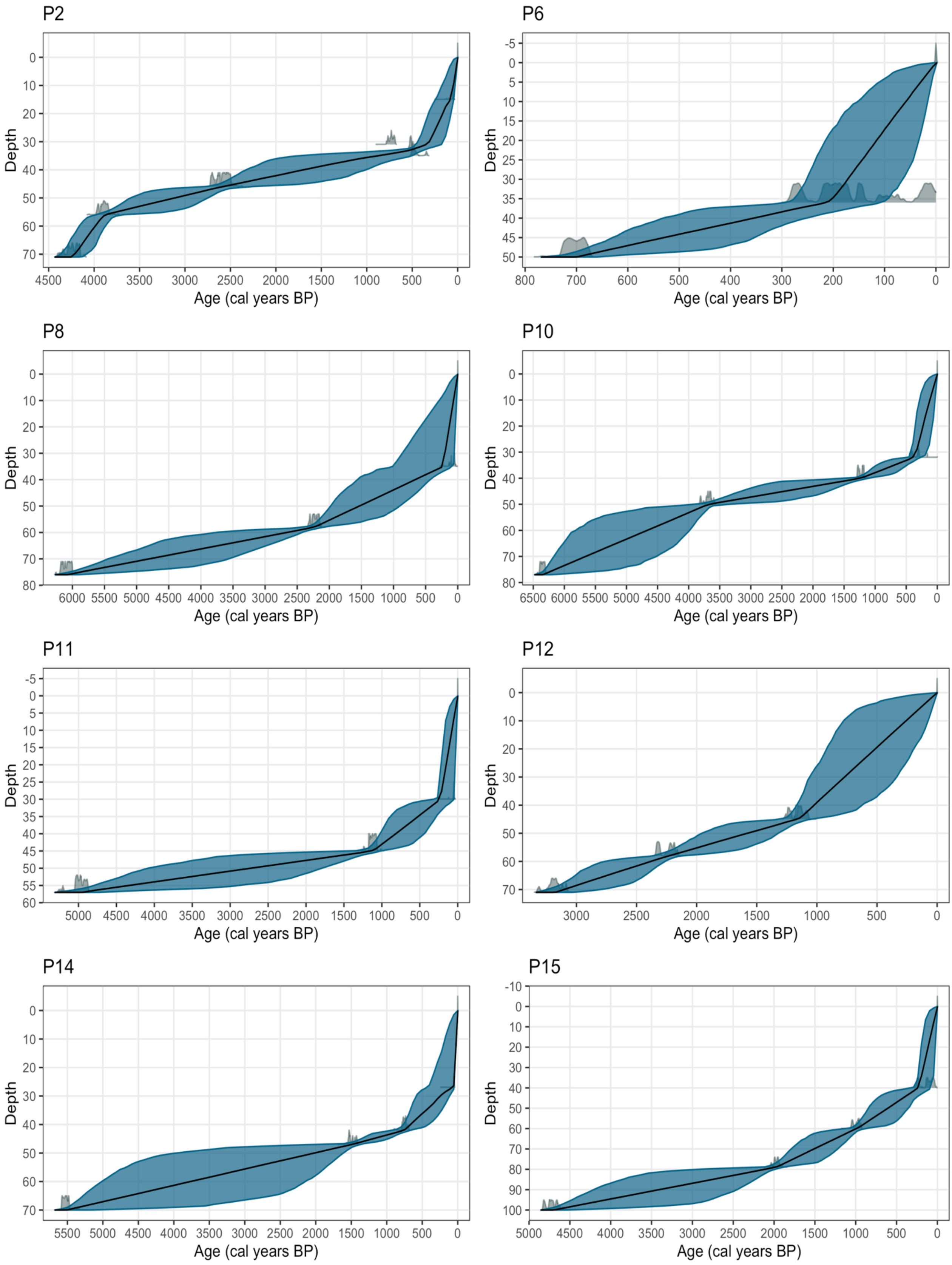


Figure 4: Age-depth models from the eight PolDat sequences. The blue area represents the 95 % confidence interval of the mean. The gray bars represent the calibration curve of the radiocarbon ages. Note different scales on both vertical- and horizontal axes.

Spruce pollen percentages exceeded 2 % of the total arboreal pollen sum in the study area between 900 and 1100 AD (Table 4). The threshold occurred at 40 ± 5 cm depth in all sites, except for site P15 where it occurred at 57 cm. Spruce pollen percentages were already above 2 % in the oldest part of the P6 sequence at 50 cm. After reaching the 2 % threshold, spruce pollen percentages quickly rose to above 10 % in most sites (Figure 5). Spruce pollen were detected in several of the oldest pollen samples long before the broadscale establishment, e.g., in P14 at 70 cm dated to 3578 BC ± SD 63 with 2,5 % spruce pollen and P12 at 71 cm dated to 1250 BC ± SD 64 with 1,7 % spruce pollen.

Table 4: General information about the PolDat peat sequences and spruce (*Picea abies*) establishment, along with numbers of charcoal bands per one thousand years before and after the establishment of spruce in the PolDat sequence at the different sites. Spruce was already established in the oldest part of the P6 sequence.

Site	Depth (cm)	Age at maximum depth**	Depth of spruce establishment (cm)	Time of spruce establishment**	Charcoal bands pre and post spruce establishment per 1000 yr***	
					Pre	Post
P2	83	2802 BC ± SD 495*	37 ± SD 3	651 AD ± SD 340*	2,03	3,65
P6	50	1236 AD ± SD 15	*NA*	*NA*	*NA*	3,9
P8	76	4127 BC ± SD 51	45 ± SD 5,25	830 AD ± 246*	1,01	0
P10	77	4390 BC ± SD 27	37 ± SD 1,75	1054 AD ± 99*	0,92	2,06
P11	57	3070 BC ± SD 100	43 ± SD 1,25	968 AD ± SD 104*	1,98	0
P12	72	1250 BC ± SD 64	42 ± SD 1	898 AD ± SD 130*	3,26	0
P14	70	3578 BC ± SD 63	43 ± SD 1	1039 AD ± SD 73*	1,08	1,02
P15	100	2770 BC ± SD 63	57 ± SD 2,25	1094 AD ± SD 97*	1,29	0

* Ages obtained from extrapolation

**Age presented as cal. yr. BC/AD

*** Charcoal bands containing macroscopic charcoal

In the period just before and during the spruce establishment (approximately 500-1500 AD) most sites had a marked increase in birch pollen percentages and a decline in pine pollen percentages (Appendix A). This was especially visible in site P12, P14, and P15. The birch pollen percentages decreased with rising percentages of spruce pollen in several sites.

In the youngest pollen samples from site P6, P11, and P14 (approximately 1600-1700 AD) spruce pollen percentages had a marked decline compared to the spruce pollen peak (approximately 1200-1500 AD) of the sites. The decline was from 46 % to 22 % in P11, from 28 % to 4 % in P14, and from 10 % to 6 % in P6.

“Deciduous trees”, i.e., temperate deciduous tree taxa, had a continuous decline in pollen percentages throughout the investigated time period (Figure 5). Most sites had the highest percentages of “deciduous” pollen in the oldest pollen samples. The two highest percentages of “deciduous trees” were attained from site P2 with 15,1 % in 2280 BC ± SD 74,7, and 10 % in 630 BC ± SD 63,7. In both these samples *Tilia* and *Corylus* dominated the “deciduous” pollen group. In most sites the high peak of “deciduous trees” was from 4000 BC to 2000 BC. Around the time of spruce establishment all sites experienced an increased decline in “deciduous” pollen percentages, and the percentages kept low or declining in every pollen sample after spruce establishment. All pollen samples contained pollen from “deciduous” taxa. This includes the youngest samples e.g., P11 28 cm from 1769 AD ± SD 67, and P14 30 cm from 1672 AD ± SD 116 with 1,4 % and 0,8 % “deciduous” pollen, respectively.

In the “open land species” pollen group (see Materials and Methods for definitions) there were no obvious trends as in the “deciduous trees” pollen record. Highest pollen percentages from “open land species” was found at the bottom of the P6 PolDat sequence with 10,2 % which was dated to 1236 AD ± SD 15. The sites P2, P12, P14 and P15 experienced their highest levels of “open land species” after the establishment of spruce, while P11 had the highest percentages long before in 3070 BC ± SD 100. P8 and P10 never had above inconsiderable percentages of “open land species”. Poaceae and “open land species” show the same trends to a large extent. Generally, the time period of most “open land species” and Poaceae pollen were from around 1000 AD until the end of the investigated pollen record, around 1700 AD.

Fern spore percentages had different developments through time at the different sites. High fern percentages indicate wet and cool conditions (Bjune et al., 2009). The sites P11 and P12 had a marked reduction in fern spore percentages after spruce establishment (Figure 5).

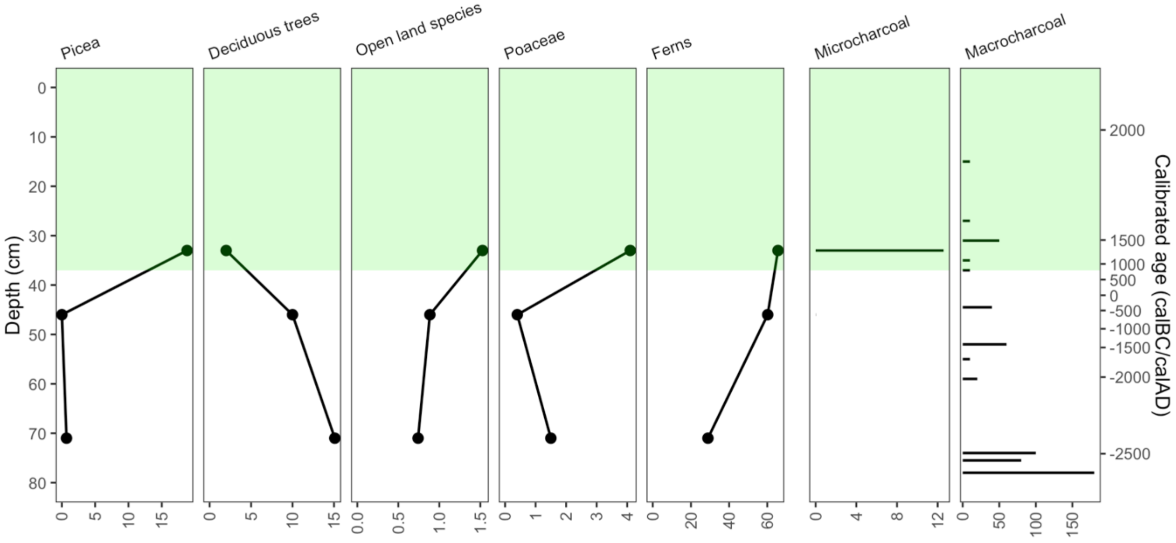
3.3 Post-spruce establishment fire activity

In total 53 charcoal bands were found in the part of the sequences covering post-spruce establishment, with a conservative inclusion of charcoal bands from sequences without ^{14}C dates, assuming an approximately similar peat accumulation the last millennia. These charcoal bands were assumed to represent 29 separate fire events (Appendix E). 26 of these fire events were in spruce dominated sites. The number of fire events varied greatly between sites with six fire events in P2 and P6, four in P14, three in P4, two in P1, P3, P10 and P11, and one in P7 and P9. The sites P5, P8, P12, and P13 had no fire events after spruce establishment, while P15 had one fire event which could be from after spruce establishment, but it was excluded due to too high uncertainty. Thus, it has been at least one local fire event after spruce establishment in 66 % of the spruce dominated sites, the same percentage as in the pine dominated sites. The spruce dominated sites had on average 2,2 fire events after spruce establishment, while the pine dominated sites had on average one fire event in the same period. The sites with the highest detected fire activity after spruce establishment was P2, P6, and P14.

There were considerable differences between the two spruce dominated parts of the study area in detected fire activity after spruce establishment. There were detected local fire events in all sites except P5 in “the Heimseteråsen slope” after spruce established, while local fire events were detected only in P11 in “the Nåsåseter slope” in this time period. The average number of fire events per site after spruce establishment was 2,67 and 0,67 in “the Heimseteråsen slope” and “the Nåsåseter slope”, respectively.

When the PolDat sequences were divided into sections of one thousand years the frequency of charcoal bands increased after spruce establishment in site P2 and P10 (Table 4), while the frequency declined in site P8, P11, P12, and P15, and remained unchanged in site P14. The increase was highest in P2 while the decline was highest in P12. The frequency of charcoal bands after spruce establishment was highest in P6 with 3,9 bands per 1000 years.

P2


Picea
Deciduous trees
Open land species
Poaceae
Ferns
Microcharcoal
Macrocharcoal
Depth (cm)
0
10
20
30
40
50
60
70
80
Calibrated age (calBC/calAD)
2000
1500
1000
500
0
-500
-1000
-1500
-2000
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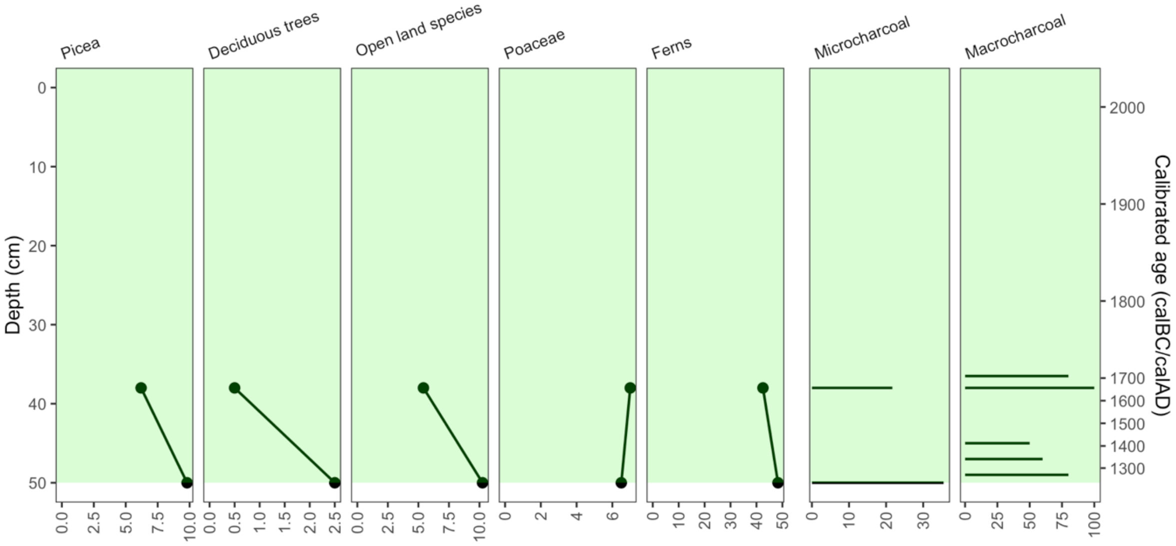
0 4 8 12
0 50 100 150

P6


Picea
Deciduous trees
Open land species
Poaceae
Ferns
Microcharcoal
Macrocharcoal
Depth (cm)
0
10
20
30
40
50
Calibrated age (calBC/calAD)
2000
1900
1800
1700
1600
1500
1400
1300
0.0 2.5 5.0 7.5 10.0
0.0 0.5 1.0 1.5 2.0 2.5
0.0 2.5 5.0 7.5 10.0
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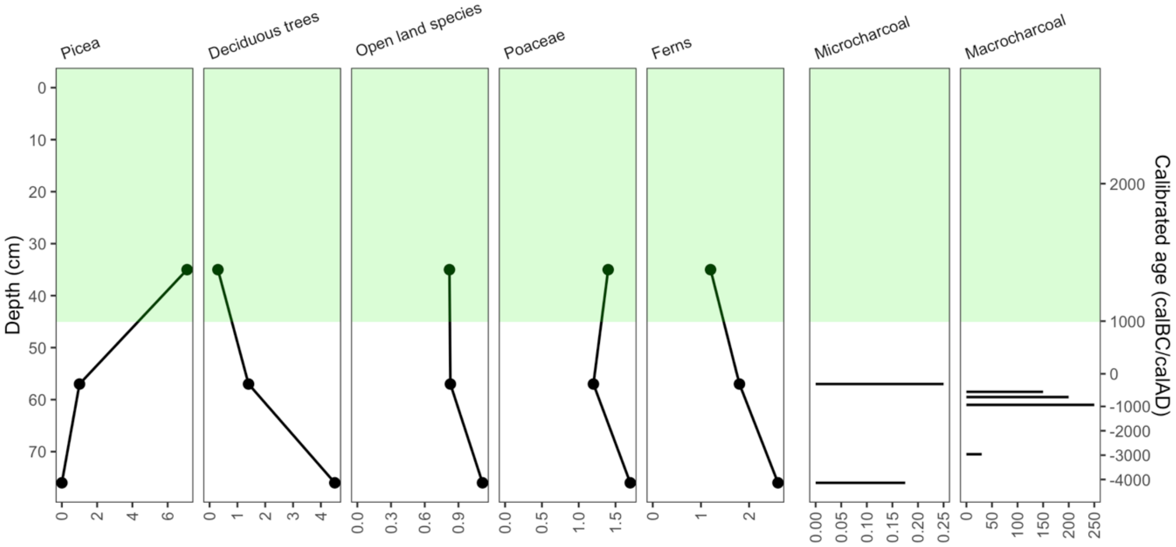
0 10 20 30
0 25 50 75 100

P8


Picea
Deciduous trees
Open land species
Poaceae
Ferns
Microcharcoal
Macrocharcoal
Depth (cm)
0
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20
30
40
50
60
70
Calibrated age (calBC/calAD)
2000
1000
0
-1000
-2000
-3000
-4000
0 2 4 6
0 1 2 3 4
0.0 0.3 0.6 0.9
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0 1 2
0.00 0.05 0.10 0.15 0.20 0.25
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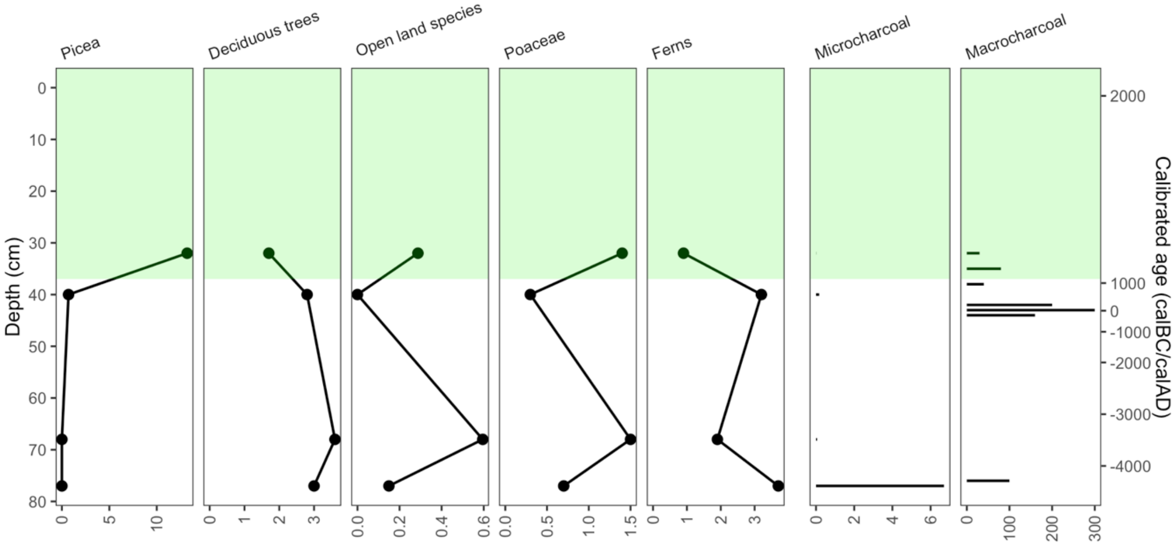
P10


Picea
Deciduous trees
Open land species
Poaceae
Ferns
Microcharcoal
Macrocharcoal
Depth (cm)
0
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20
30
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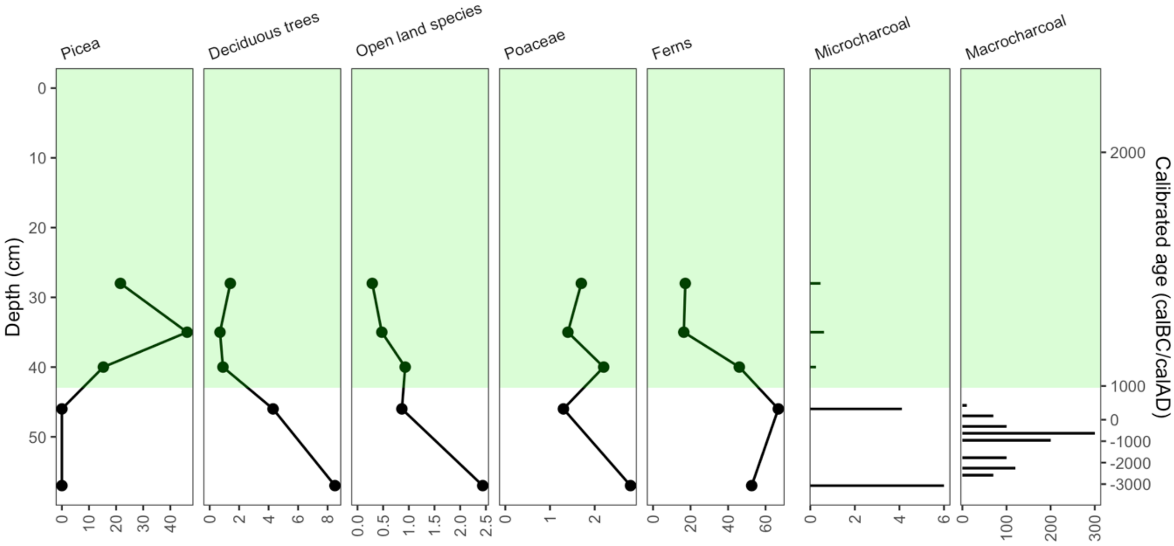
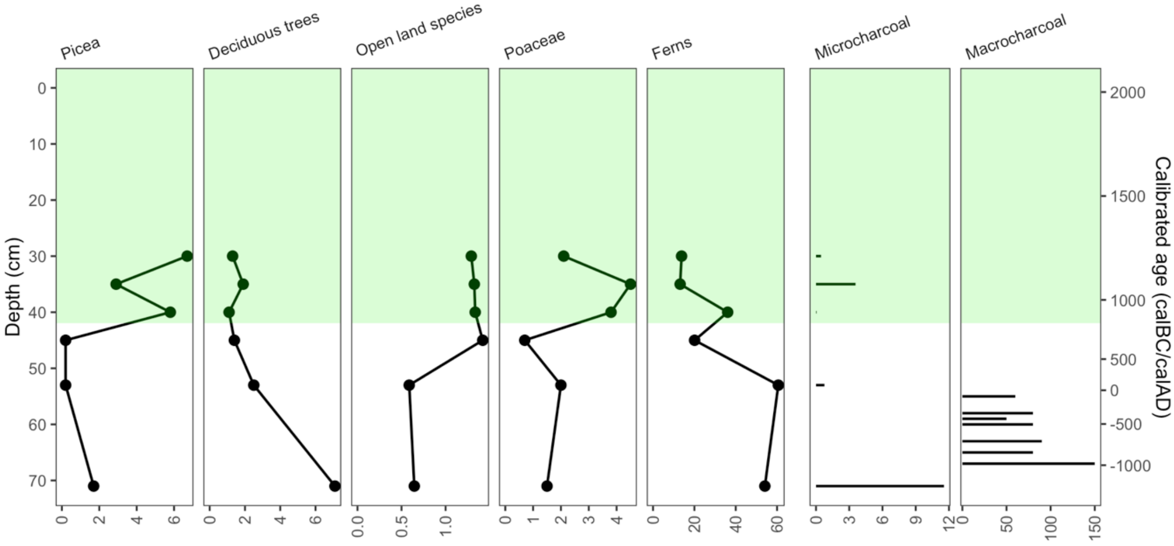
50
60
70
80
0
5
10
0
1
2
3
0.0
0.2
0.4
0.6
0.0
0.5
1.0
1.5
0
1
2
3
0
2
4
6
0
100
200
300
Calibrated age (calBC/calAD)
2000
1000
0
-1000
-2000
-3000
-4000

P11


Picea
Deciduous trees
Open land species
Poaceae
Ferns
Microcharcoal
Macrocharcoal
Depth (cm)
0
10
20
30
40
50
0
10
20
30
40
0
2
4
6
8
0.0
0.5
1.0
1.5
2.0
2.5
0
1
2
0
20
40
60
0
2
4
6
0
100
200
300
Calibrated age (calBC/calAD)
2000
1000
0
-1000
-2000
-3000

P12


Picea
Deciduous trees
Open land species
Poaceae
Ferns
Microcharcoal
Macrocharcoal
Depth (cm)
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150
Calibrated age (calBC/calAD)
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500
0
-500
-1000

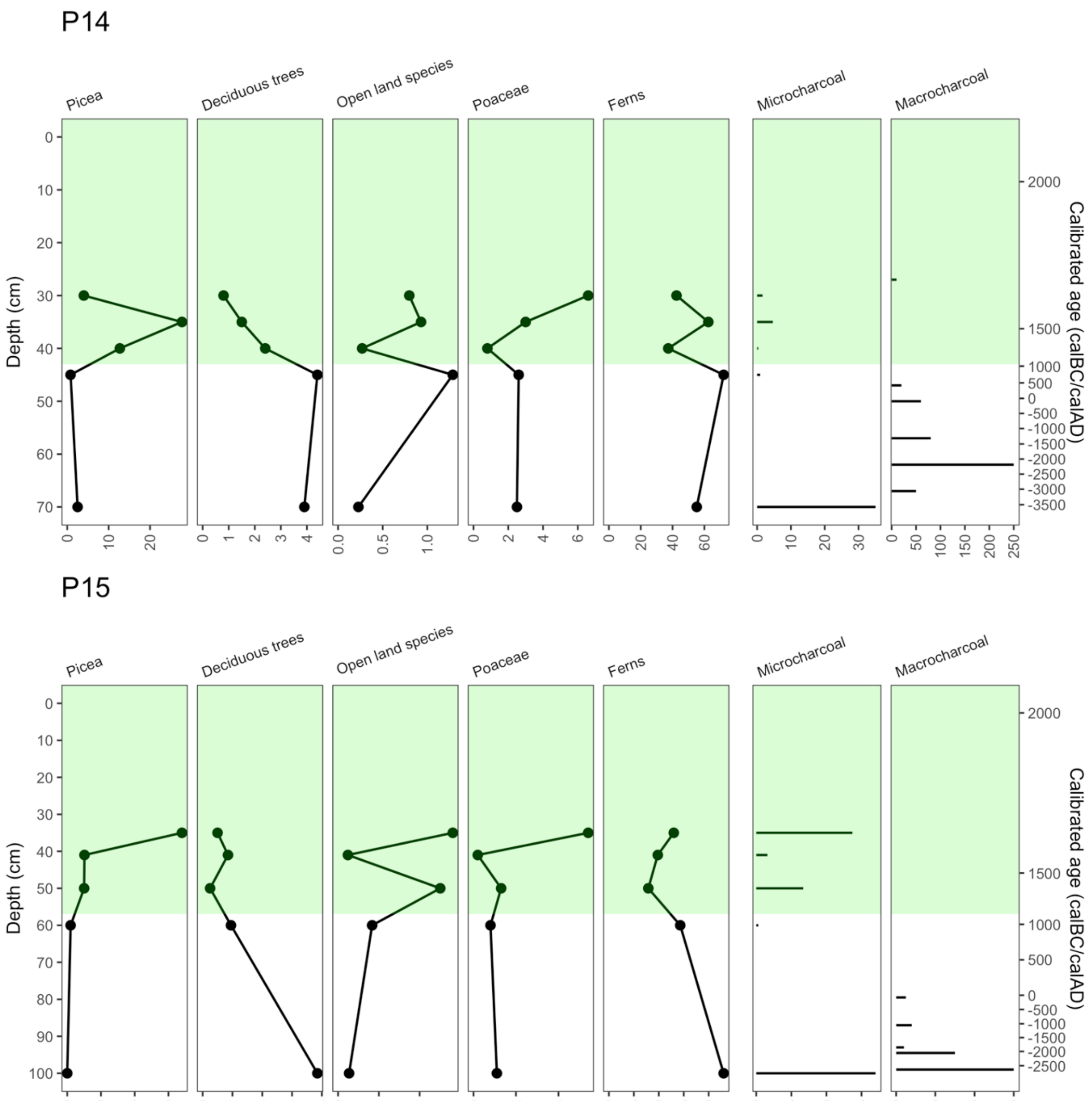

Figure 5: Pollen percentage diagrams of selected taxa and charcoal diagrams from the eight PolDat sequences. See Materials and Methods for description of the species groups “deciduous trees” and “open land species”. The green area represent the interval of spruce pollen percentages >2 %. Microcharcoal relative abundance derives from division of the microscopic charcoal amount by the amount of added *Lycopodium* spores. Macrocharcoal numbers represent the number of macroscopic charcoal particles (>0,5 mm) found in 1 cm of peat sequence. The whole sequence was searched for macroscopic charcoal, while microscopic charcoal was only searched for in the pollen samples. Note that the scale of the x-axis is controlled by the max values and thereby changes with each subplot. The y-axis varies between the sites, see Table 4 for exact depth and age. Age is presented as calibrated ages BC/AD. Pollen percentages were calculated from total pollen sum, subtracted ferns and *Sphagnum,* for all taxa, except ferns which is calculated from the total pollen sum including ferns and *Sphagnum*.

4 Discussion

4.1 Spatial variation in the charcoal record

The macroscopic charcoal record had considerable spatial variation both within sites and between sites. This major variation concerned both the number of identified charcoal bands and the number of macroscopic charcoal particles in each band (Figure 3). This means the fires and the area burnt were highly variable across fine spatial lines both at a local and landscape scale, leaving highly variable mosaics of burnt and unburnt areas. These findings are in line with other studies which confirms that the macroscopic charcoal record are highly variable in boreal peatlands (see e.g. Ohlson et al., 2006; Kasin et al., 2013).

The within site variation seemingly account for a major part of the overall variance in the deposition of macroscopic charcoal particles (Table 2), while the between site variation accounts for 30 % of the variation. One reason for relatively low between site variation could be the high number of charcoal particles found in the lower end of the sequences in most sites (Figure 3). This charcoal accumulation could origin from warmer climatic periods with higher fire frequencies (Kasin et al., 2013), although the age of the lower part of the sequences were highly variable between the sites (Figure 4). The high within site variation testament the extent of the fine scale spatial variation found in all the peatlands investigated.

Macroscopic charcoal particles in the peat profile are indisputable evidence of occurrence of local fires (Whitlock & Millspaugh, 1996; Clark et al., 1998; Ohlson & Tryterud, 2000). The extent of the sampling in this study provides indications that the whole study area has burnt throughout most of the investigated time span of over 3000 years, but in a varying degree, as some sites have burnt more often than others. Kasin et al. (2013), who conducted their study in pine dominated peatlands close to the areas sampled in this study, found most of the charcoal to originate from warm and dry climatic periods, although the charcoal accumulation rate was higher or similar during colder and wetter climatic periods.

No macroscopic charcoal was found in 24 % of the original peat sequences. Ohlson et al. (2006) concluded that fire had played a rather subordinate role in their investigated sites based on the absence of macroscopic charcoal in 16 % of the extracted peat sequences (n=247) and the high proportion of the remaining sequences only containing one or a few charcoal bands. The results of Ohlson et al. (2006) were quite similar to those of the present study, suggesting fire could have been a disturbance factor of less importance in several of the investigated swamp hollows. This is a contrast to the general assumption of fire being a principal disturbance agent of boreal forests (Zackrisson, 1977). However, it is important to note that the investigated swamps have high moisture levels and lower flammability than the surrounding forest on mineral soil and have consequently probably burnt less.

Ohlson et al. (2006) concluded that swamp-forest sites have idiosyncratic fires histories, which could be the case in this study as well, because closely situated sites often had completely different charcoal records. Site P13 for instance separates from the other sites in having only one, probably old, macroscopic charcoal band, which also raise questions of possibilities for small long-term fire free refugia within the study area.

It was expected that the dry pine dominated parts of the study area would have burnt more often than the more fertile and mesic spruce dominated areas (Wallenius et al., 2004). However, there was no statistical difference between the pine and spruce dominated sites in the number of charcoal bands. As the sites P8 and P10 represented the oldest sites in the study, there were fewer charcoal bands per 1000 years in the pine dominated sites than many of the spruce dominated sites. However, there was a weak negative correlation between the number of charcoal particles and the abundance of spruce adjacent to the site, indicating that many of the fires in the pine dominated areas probably burned at a higher intensity than in the areas of present spruce dominance.

Absence of macroscopic charcoal must be carefully interpreted as it is not unambiguous evidence of absence of local fire events. Low intensity ground fires do not necessarily produce macroscopic charcoal, only microscopic charcoal particles (Pitkänen et al., 1999; Higuera et al., 2005). The production of charcoal particles are dependent upon the access of woody fuel (Clark et al., 1998), meaning burning of other materials, e.g., peat and herbs/grass, will not produce considerable amounts of macroscopic charcoal particles. On the other hand, macroscopic charcoal particles can be transported over long distances by air after major fire events (Tinner et al., 2006). Several of the charcoal bands in this study contained few macroscopic charcoal particles, often of small sizes, and it can be questioned to what extent these bands represent local fires.

The mechanisms behind the small-scale spatial variation in the charcoal record are complex and intertwined. Experimental forest fires have revealed that the macroscopic charcoal were highly unevenly distributed within the burnt area, even with burnt areas without macroscopic charcoal depositions (Clark et al., 1998; Ohlson & Tryterud, 2000). The prevalence of low-intensity fires in boreal Fennoscandia (Zackrisson, 1977) usually results in the burning of only a small proportion of the peatlands due to an irregular advance of the wildfire across the peat surface. The variation within such a patchy burn can partially be explained by micro-topography of the peat surface regulated by moisture levels and vegetational composition (Ohlson et al., 2006). Most importantly, the presence, distribution, and abundance of woody vegetation and debris within the peatland will decide the extent of the local fires and formation of charcoal bands, as the woody material will be the primary fuel of the fire and the main source for production of macroscopic charcoal particles (Clark et al., 1998; Pitkänen et al., 2003b; Kasin et al., 2013). Hydrology too, has a decisive role in the ability of a peat basin to form visible charcoal bands (Pitkänen et al., 2003b) and Ohlson et al. (2006) concluded that differences in hydrological conditions were an important explanation for the within and between site variation in macroscopic charcoal depositions. Lastly, charcoal bands, or parts of them can disappear from the peat record due to decomposition of charcoal particles through oxidative degradation (Ascough et al., 2011), consumption by subsequent fires (Pitkänen & Turunen, 1999), and incorporation of charcoal bands due to decomposition of peat (Pitkänen et al., 2002).

Some relocation of macroscopic charcoal will occur after a fire event due to down-slope transportation by water (Ohlson et al., 2013) which is probably most prominent during yearly spring flood/snowmelt events. Post-fire transportation of charcoal particles can continue for several years after a fire (Whitlock & Millspaugh, 1996). The larger the particle, the higher probability of origin from an *in situ* fire (Clark, 1988), and quite many charcoal bands in this study contained charcoal particles >10 mm. However, it is reasonable to assume that the charcoal bands represent local fires in the nearby forest on mineral soil rather than strictly *in situ* fires on the peatland surface as most sites were situated in wet swamp-hollows located in steep slopes, making them exposed for wash-down transportation and accumulation of charcoal particles. Occurrence of mineral bands of sand/silt in some of the peat sequences support this view. The relocation of charcoal particles by water transportation could also possibly affect the small-scale spatial variation in the charcoal record due to accumulation of particles in depressions and removal of particles from augmentations in the micro-topography of the peat surface.

The extraction of the peat sequences in this study has been inspired by the “basin approach” (Pitkänen et al., 2001) which aims at reconstructing Holocene fire history through several sampling points across short transects in small peatlands. The results of e.g. Pitkänen et al. (2002) and Pitkänen et al. (2003a) show that this is a promising method of fire history reconstruction. Fire history reconstruction from presence of macroscopic charcoal have in many studies been based on a single peat sequence which is suggested to be representative for the whole site (Hörnberg et al., 1995; Ohlson & Tryterud, 1999; Magnan et al., 2012). This method is insufficient to detect small scale spatial patterns and reconstruct reliable long-term fire histories (Ohlson et al., 2006). Several sampling points are necessary to avoid rough and highly conservative estimates of the fire activity (Pitkänen & Turunen, 1999).

The sampling method in this study enabled the detection of some of the spatial variation of charcoal deposits across fine spatial scales in a gradient from the edge toward the centre of the peatlands. The chance of detecting more recent fires through charcoal bands in the peat record increases towards the margin of the mire (Pitkänen et al., 2001), as local forest fires have a higher probability of scaring the margin rather than burning the entire peat surface (Pitkänen et al., 2002). In this study there were no statistical differences in charcoal bands and particles in relation to the distance to the edge of the peatland. However, there were significant differences in both charcoal bands and particles in relation to the length of the peat sequence, meaning more charcoal was found in the longer sequences. The longest peat sequences were generally found furthest away from the edge, towards the centre of the peatlands, but the bands found in these sequences were often restricted to the lower parts of the sequence and not representing recent fires. This might be due to peatland expansion, meaning the deep parts of the peatland were closer to the peatland edge in the past. In all sites except P1, P2 and P8 the charcoal bands located highest in the peat sequences were found in either S1 or S6 (Figure 3), i.e., one of the sequences closest to the margin of the peatland (Figure 2). These results strengthen the view that multiple sampling points close to the edge of the peatland is the most reliable method of detecting recent fires in small, forested peatlands.

It is difficult to determine which of the charcoal bands from the different peat sequences represents the same fire events due to natural variation in peat accumulation rates which is common in boreal peatlands (Økland & Ohlson, 1998). The onset of peat genesis is a site-specific event resulting in major variation in peat age between sites (Weckström et al., 2010). However, the age-depth models (Figure 4) displayed rather similar trends in peat accumulation between sites during the last millennia, i.e., the topmost 40-50 cm of the sequences. It was attempted to determine which charcoal bands from different sequences within a site represented the same fire events for this period (Appendix E), resulting in most detected fire events being represented in more than one sequence. It should be noted that the ^{14}C dates (Table 3) could be affected by downward transportation of younger carbon from e.g., roots, rhizomes, and mycelia or by water inflow. This can lead to increased amounts of modern carbon in the peat which results in too young radiocarbon ages (Tolonen et al., 1992). This was most likely the case for the samples P2 at 15 cm depth, P8 at 35 cm depth, P11 at 30 cm, and P14 at 27 cm depth. Age-depth relationships in surface peat are known to be highly variable, and peat close to a peatland surface can be surprisingly old, see Økland and Ohlson (1998).

As macroscopic charcoal indicates local fires, presence of microscopic charcoal indicates a fire prone environment on a regional scale (Patterson et al., 1987) because microscopic charcoal can be transported in large amounts over long distances, thereby leaving traces of regional fire activity. Microscopic charcoal can be present throughout the whole peat sequence (Innes et al., 2004) in regions of high fire activity. Most of the pollen samples in this study contained traces of microscopic charcoal (Figure 5) which indicates a fire prone environment throughout the investigated time span.

It is important to note that the number of independent charcoal bands gives a minimum number of local fires. A key question in this context is to what extent a local fire is recorded in a given peat stratigraphy. Comparisons of charcoal bands with closely situated tree-ring records of fires (fire scars) (Higuera et al., 2005; Kasin et al., 2013) have shown that few of the fires found as fire scars produced charcoal bands in nearby located soil/peat archives.

The number of fires found through dendrochronology is also a minimum number of *in situ* fires, ergo it is safe to assume that quite many local fires were not represented in the peat charcoal records. Storaunet et al. (2013) found fire scars from several fires after 1400 AD within 75 m of P5, P8, P9, P10, P12, P14, and P15 (Figure D1). Yet, only a few of these were detected in the peat charcoal record as charcoal bands (Appendix E).

Higuera et al. (2005) argued that fire intensity had major effect on the probability of detecting a local fire event in sediments, and that high intensity fires were often accurately presented in the charcoal record, while many moderate to low intensity fires were missed. Most fires detected in the study area through dendrochronology were low intensity fires covering small areas (Storaunet et al., 2013) while two fires in 1499 AD and 1575 AD burnt over large areas (Rolstad et al., 2017), and were probably of relatively high intensity. These two fires were most likely detected as charcoal bands, possibly in several sites (Appendix E). The 1499 AD fire could be represented by the charcoal bands at depths of 37-35 cm in site P2, P10, P11, and P14, and 45 cm in P6, while the 1575 AD fire could be represented in P2 at 27 cm, P6 at 38 cm, and P10 at 32 cm. Note that there are high uncertainties in these interpretations.

Human land use might partially explain the discrepancies between the peat charcoal record and the tree-ring records of fires (Kasin et al., 2013). Prior to 1625 AD the fire regime of the study area was predominantly climate-driven with little influence of human activity, characterized by few, but often large fires (Rolstad et al., 2017). After 1625 AD the fire regime was primarily anthropogenic (Storaunet et al., 2013), and the high frequency fire regime and other anthropogenic activities may have strongly reduced the accessibility of wooded fuel, and consequently the ability of the fires to produce charcoal and charcoal bands. In 1667 it was reported in the land register that the farms of the area only had timber for fencing and firewood (Mørch, 1954; as cited in Storaunet et al., 2013).

The percentage of charcoal bands identified in the field without macroscopic charcoal was higher in this study (25 % in the original peat sequences and 17 % in the PolDat sequences) than in other similar studies (Ohlson et al., 2006; Ohlson et al., 2017). This result can be partially explained by the unusual dark peat present at several of the small closed-canopy spruce-swamp sites. Layers of dark peat could be confused with charcoal bands. In the pine dominated sites with paler peat there were very few misidentified charcoal bands demonstrating this was mainly a problem in the spruce-swamps.

The dark peat also raises questions weather some charcoal bands could be missed due to less visibility. Ten samples of 4-5 cm dark peat, which was assessed not to contain charcoal in the field, were collected and analysed. Three of the samples contained macroscopic charcoal, ranging from 10 to 25 particles per cm, mostly in the sizes of 0,5-1 mm. Although a small sample, this is a higher proportion of macroscopic charcoal found in peat without charcoal bands than reported in other studies (Meen, 1998; Ohlson et al., 2006). It is possible analysis of the whole peat sequence for macroscopic charcoal presence would improve the result in sites with very dark peat.

4.2 Establishment of spruce and change in fire regime

Spruce established with high certainty throughout the study area in the time span 900-1100 AD due to the synchronous rise of the spruce pollen curve (>2 %) at all sites (Table 4). Spruce was probably established within most of its current distribution already in 1000 AD. Hafsten (1992) dated the establishment of spruce at three sites 15-25 km from the study area to be 635-1200 AD. Kasin et al. (2013) dated spruce establishment at two sites within the study area to be 1426 AD and 1349 AD, and two sites less than 1 km from the study area to be 676 AD and 0 AD. The old ages of spruce establishment found by Kasin et al. (2013) could be caused by early local establishment or long-distance transportation.

Spruce pollen are heavy and drop quickly to the ground (Bjune et al., 2009), but can also be distributed over long distances in low amounts (Bjune, 2014). Spruce pollen presence in closed-canopy sites have a high probability of indicating local presence due to the restricted pollen source area (Bradshaw, 1988). Giesecke and Bennett (2004) argued that a 1 % threshold of total terrestrial pollen is a robust and conservative indication of local or regional presence of spruce in areas below the treeline. Such a small percentage does not necessarily mean the local presence of spruce is more than a few trees or a small population within a short distance (Segerström & von Stedingk, 2003; Giesecke, 2005). From where 1 % spruce pollen is detected in a peat sequence until where 10 % spruce pollen is observed there could be a long time period, up to several thousand years (Giesecke & Bennett, 2004), but usually just a few hundred years at Norwegian and Swedish locations (Hafsten, 1992; Giesecke & Bennett, 2004).

Spruce pollen was present in 56 % of the pollen samples from before the time of broadscale spruce establishment. Most of these samples had less than 1 % spruce pollen, while some had higher percentages such as P14 at 70 cm dated to 3580 BC ± SD 63 with 2,5 % spruce pollen and P12 at 71 cm dated to 1250 BC ± SD 64 with 1,7 % spruce pollen. When the majority of the pre-spruce establishment pollen samples contained spruce pollen, it is likely that spruce had a local presence in the area before the broadscale spruce establishment, maybe for more than 5000 years due to the high percentage of spruce pollen found in site P14 at 70 cm. Bjune et al. (2009) found, at a site 70 km from the study area of the present study, occasional spruce pollen from ca. 7000 BC until the initial spruce establishment at 500 AD and concluded it was possible spruce had been present at the site for a considerable time.

Spruce established throughout the study area around 1000 AD and quickly increased in abundance at most sites over the next centuries (Figure 5). Spruce expansion is widely attributed to the gradual late-Holocene climate cooling (Tallantire, 1972; Seppä et al., 2009b), although this remains equivocal (Miller et al., 2008). However, disturbances are considered to be the main control of local stand establishment and the reason for rapid local dominance (Björkman & Bradshaw, 1996; Lindbladh et al., 2000; Hörnberg et al., 2012; Ohlson et al., 2017). Important disturbances include forest fire and human activities such as livestock grazing, hay-mowing and tree cutting (Bradshaw & Hannon, 1992; Segerström & Emanuelsson, 2002; Ohlson et al., 2011). Although, there are examples of spruce establishment in dense and intact forests where the native forest put up no or weak resistance to the colonization (Seppä et al., 2009a).

In the present study there were no synchronous fire events detected at the timing of the spruce establishment. Site P2 had a minor charcoal band at the depth of spruce establishment, but no other sites had charcoal bands closely linked to the time of spruce establishment. However, in the time just before and during the spruce establishment, approximately 500-1500 AD, the relative pollen percentage of birch increased, while pine percentages declined (Appendix A), and this occurred in most sites with current spruce-swamps. High birch abundance is an indicator of post-disturbance succession (Bradshaw & Lindbladh, 2005). In southern Sweden spruce was demonstrated to preferably invade successional birch forest during the main establishing event (Bradshaw & Lindbladh, 2005). The successional birch forests had become increasingly widespread in the region prior to the invasion due to human activity (Lindbladh et al., 2000). The pattern observed in southern Sweden was notably similar to the pattern observed in the present study and occurred almost simultaneously. However, the birch abundance of the study area can't with certainty be attributed to human activity as there is a possibility that the successional birch forest was a result of natural forest fires, although few charcoal bands was detected in the intervals of high birch pollen percentages. These results suggests spruce colonized a disturbed environment in the study area. Altogether, the invasion of spruce was probably a natural process which was favored and accelerated by anthropogenic activities, as concluded by Molinari et al. (2005) and Bjune et al. (2009) in a similar area of southeastern Norway.

Due to the knowledge that forest fire activity has been generally low in Fennoscandian spruce forests (Tryterud, 2003; Ohlson et al., 2011), and especially low in spruce-swamps (Hörnberg et al., 1995; Pitkänen et al., 2003b; Ohlson et al., 2006), it was expected to find few charcoal bands in the part of the sequences covering the time after spruce establishment in the spruce dominated sites. 26 separate fire events were identified in the spruce dominated sites after spruce establishment (Appendix E), assuming a rather similar peat accumulation the last millennia, with an average of 2,2 fire events per site. The pine dominated sites had three detected fire events after spruce establishment with an average of one per site, although based on fewer observations. More of the local fire activity has probably been preserved in the peat in the spruce dominated areas than in the pine dominated areas, possibly explained by down-slope transportation of charcoal by water after fire events with subsequent accumulation, and higher availability of wooded fuel for charcoal production. However, if this was a prominent cause of charcoal band formation, it could be expected to find more recent charcoal bands in "the Nåsåseter slope", because the name of the mountain above these sites is "Fjellbråten" meaning area/mountain cleared by burning (Helleland & Schmidt, 2021).

Most of the spruce dominated parts of the study area have burnt after spruce establishment, although with varying frequency. The importance of fire as a disturbance agent in the spruce-swamps was difficult to determine, but most likely has fire had a subordinate role, as most of the sites had a low fire frequency after spruce establishment. The exceptions are P2, P6, and P14, and partly P3 and P4. The three former sites had higher detected fire frequencies than similar studies in spruce-swamps (Ohlson et al., 1997; Pitkänen et al., 2003b; Ohlson et al., 2006), with approximately 200 years in P2, 150 years in P6, and 350 years in P14. These sites are all situated in a humid environment with slightly more fertile soils than the rest of the study area. These features should have reduced the flammability and fire activity (Wallenius et al., 2004). This raises the question of possible human influence as these areas would produce the most productive pastures in the vicinity. This applies especially to P6 which was placed next to an old summer dairy farm, and results from the pollen analysis suggest there has been human activity at the site for the whole duration covered by the peat sequence (Figure 5).

Ohlson et al. (2011) found that the establishment of spruce significantly reduced the forest fire activity throughout Fennoscandia, thus changing the pre-existing disturbance dynamics of the boreal forests. Spruce create a denser and more humid forest, which contribute to reduced ignition probability and flammability (Ohlson et al., 2011). Thus, it would be expected to find fewer charcoal bands after spruce establishment than prior. The number of charcoal bands per 1000 years in the PolDat sequence (Table 4) increased after spruce establishment in site P2 while it declined in P11, P12 and P15, and remained stable in P14. The cessation of charcoal bands after spruce establishment in site P11 and P12 was the most noticeable change, and the pattern was similar in all sequences in these two sites (Figure 3). The increased fire activity in P2 could possibly be attributed to anthropogenic activity. Altogether, the change in fire regime after spruce establishment were different in the two spruce dominated parts of the study area. In “the Nåsåseter slope” fire activity possibly ceased after spruce established, while the fire activity remained mostly stable or increased in “the Heimseteråsen slope”. Although, it should be noted that spruce has probably not been as abundant in the spruce dominated sites in the time span covered by the pollen analysis as the current situation, due to the rather low spruce pollen percentages (Appendix A), even when controlled for relative pollen representation (Prentice et al., 1987).

Further research is needed to fully understand the underlying mechanisms controlling the fire regime of the study area. A promising method to expand our comprehension of the subject is species identification of charcoal to determine the composition of the available fuel for the fire. Ohlson et al. (2017) found that the charcoal which originated post spruce establishment in a spruce forest mainly consisted of pine, suggesting pine was still dominant at the time of the fires. This could be case in the present study as well.

4.3 Changes in vegetational composition and anthropogenic activity

Temperate deciduous tree species have decreased in abundance from the boreal zone of Fennoscandia during the late Holocene and have disappeared completely in many regions. The reduction has largely been attributed to climate change (Miller et al., 2008; Bjune et al., 2009), but anthropogenic influence (Lindbladh et al., 2000; Segerström & Emanuelsson, 2002) and competitive exclusions by spruce (Seppä et al., 2009a) have also been suggested as reasons for the decline. Although limited resolution of the pollen diagrams in the present study (Figure 5) the results suggests that the decline of temperate deciduous trees was caused by climate change due to synchroneity in the decrease and continuous decline through the whole investigated time span. The highest pollen percentages of temperate deciduous trees were found in the oldest pollen samples from most sites. The highest percentages were found in P2, underpinning the notion that this site has historically had a more favorable microclimate and richer forest soil than the other sites in this study, see Halvorsen et al. (2016). At the time of local spruce establishment, the rate of decline of temperate deciduous trees increased. It is possible anthropogenic activities pushed the final decline/disappearance of temperate deciduous trees after spruce establishment, although this development could also have been caused by increased competition from spruce. Increased climatic stress during the “Little Ice Age” could have further contributed to the final decline/disappearance of temperate tree taxa from the study area (Bradshaw et al., 2000; Bjune et al., 2009). Temperate deciduous trees were never abundant in the study area during the investigated time span, and today there exists only a few scattered individuals in the surrounding district.

The study area has been affected by anthropogenic activities for several centuries. There are historical sources of five summer dairy farms in and around the study area in the 19th century (Mørch, 1954; as cited in Storaunet et al., 2013). Most of these were abandoned around 1850 and the only one with remains of buildings is the one called Nåsåseter (see Figure 1) west of the study area, not far away from the sites of “the Nåsåseter slope”. Two of the summer dairy farms were located right next to the site P6. One summer dairy farm was situated southeast of the study area, quite close to site P1, P2, P3, and P4. In summer dairy farms hay was usually grown in small meadows, occasionally with cereals and other crops, while the livestock, mostly cattle, grazed in the surrounding forest (Segerström & Emanuelsson, 2002).

The group “open land species” in the pollen diagram (Figure 5) include species and taxa which are favored by different cultural activities (see Materials and Methods). The amount and changes in the “open land species” pollen percentages have probably been mostly affected by site specific events, both natural and anthropocentric. In most sites Poaceae (grass pollen) shows the same trends as the “open land species” which supports the assumption that “open land species” indicate human activity (Segerström & Emanuelsson, 2002). The percentage of “open land species” was generally low in all samples, and it should be noted that pollen analyses aiming at revealing previous anthropogenic activities usually have a greater pollen sum in each sample than in this study (generally around 1000 pollen grains, see e.g., Bjune et al. (2009)). This is because most species indicating human activities are insect pollinated with subsequent low pollen production and poor pollen dispersal abilities (Behre, 1981).

Generally, the pollen analyses indicated that the vegetational composition of the field layer has been relatively little affected by human activities, suggesting the land-use in the study area was mostly of low intensity during the investigated time period. The exception was P6, which contained high percentages of “open land species” in both pollen samples. The oldest pollen sample, from 1236 AD ± SD 15, contained 10,2 % “open land species”, indicating the summer dairy farm situated right next to P6 already was in use and active in the 13th century, before the Black Death (1348-1350 AD). It is possible the summer dairy farm was abandoned during the Black Death and not inaugurated again until the 16th–17th century, which would explain the pattern of anthropogenic fire activity found by Storaunet et al. (2013).

Fern spore percentages were considerably reduced in site P11 and P12 after spruce establishment (Figure 5), which suggests something changed in the local microclimate in “the Nåsåseter slope”. Due to ferns’ preference of wet and cool conditions (Bjune et al., 2009) one explanation is that the forest was cleared or partly cleared in this area, resulting in drier conditions. Ericaceae also increased in P11 and P12 at the same time (Appendix C) suggesting a more open environment (Segerström & Emanuelsson, 2002). A sparse, or absent tree layer could further explain the lack of younger charcoal bands in these sites.

There were not found any pollen grains of cereals in any of the sites, thus there was not found evidence for the presence of slash-and-burn cultivation in the study area which has been suggested as an important part of the anthropogenic fire regime (Storaunet et al., 2013). However, absence of cereal pollen grains could easily occur even with cultivation nearby due to the poor dispersal of cereal pollen (Behre, 1981) and low resolution of the pollen analysis.

5 Conclusion

This study provided further affirmation to existing knowledge regarding the extent of the small-scale spatial variation in the macroscopic charcoal record in boreal peatlands. High within site variation supports the assumption that the peat surface is burnt highly irregularly during a fire event, leaving large parts unburnt. Other explanations for the extensive small-scale variation in the charcoal record is down-slope transportation of charcoal by water, especially during the snowmelt/spring floods, with accumulation of the charcoal in the swamp-hollows, and subsequent distribution of particles across the micro-topography of the peat surface.

All investigated sites have burnt at some point in time, but with highly varying frequency. The study strengthens the hypothesis that the most reliant way of detecting recent fires in peat charcoal records is through multiple sampling close to the edge of the peatland. However, it is important to note that many local low intensity fires were probably not detected in the peat charcoal record.

Pollen data suggests that spruce has possibly been locally present in the study area for up to 5000 years. The broadscale spruce establishment occurred around 900-1100 AD in a disturbed environment with successional birch and pine forest. Most of the sites have burnt after the spruce establishment, although with varying frequency. The fire frequency ceased in some sites and increased or remained stable in others. High fire frequency after spruce establishment in some sites could possibly be attributed to anthropogenic activities. The apparent fire cessation after spruce establishment in one part of the study area could possibly be attributed to spruce influence, although it is possible the area had a reduced tree cover during this period.

Human activities were most likely present in the study area before the Black Death. However, the composition of the field layer vegetation indicated only marginal impact from cultural activities during the investigated time period, suggesting rather low intensity land-use.

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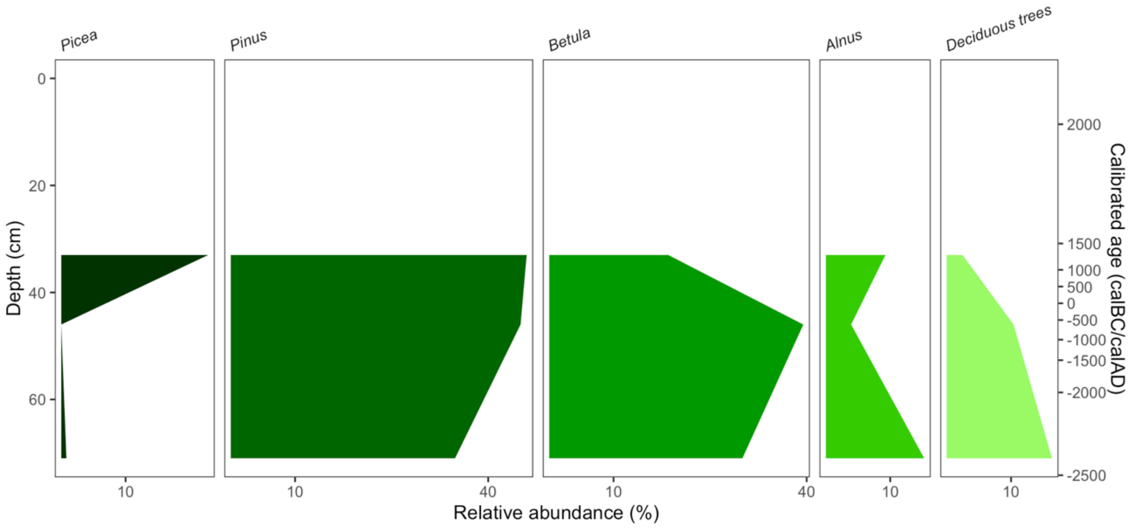
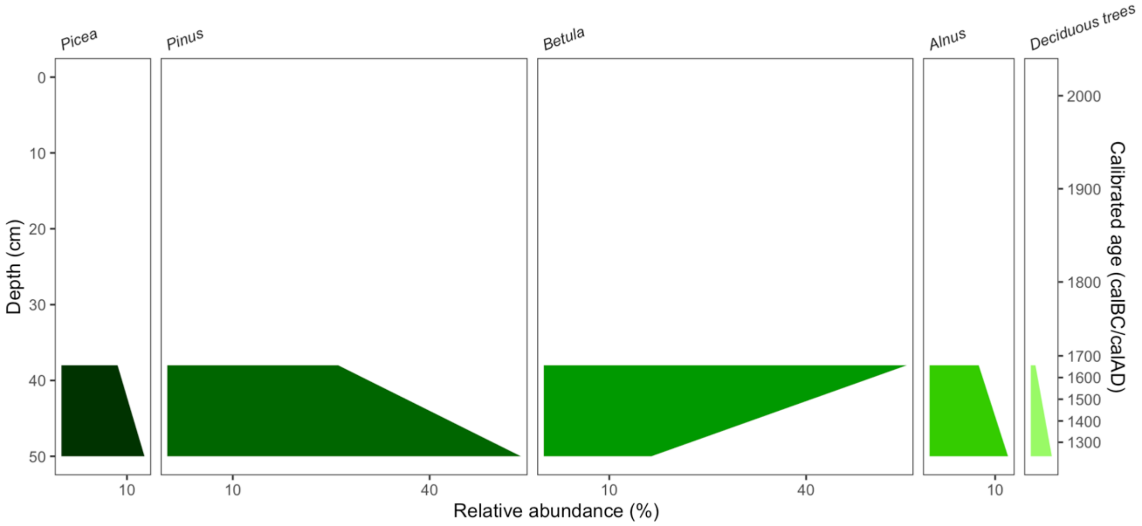
Appendix A Arboreal pollen diagrams

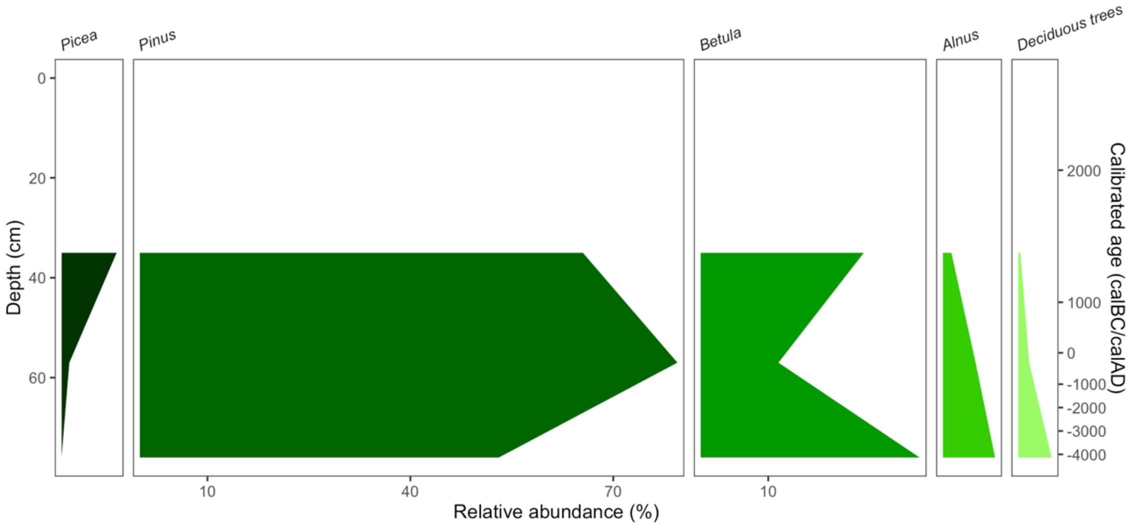
P2



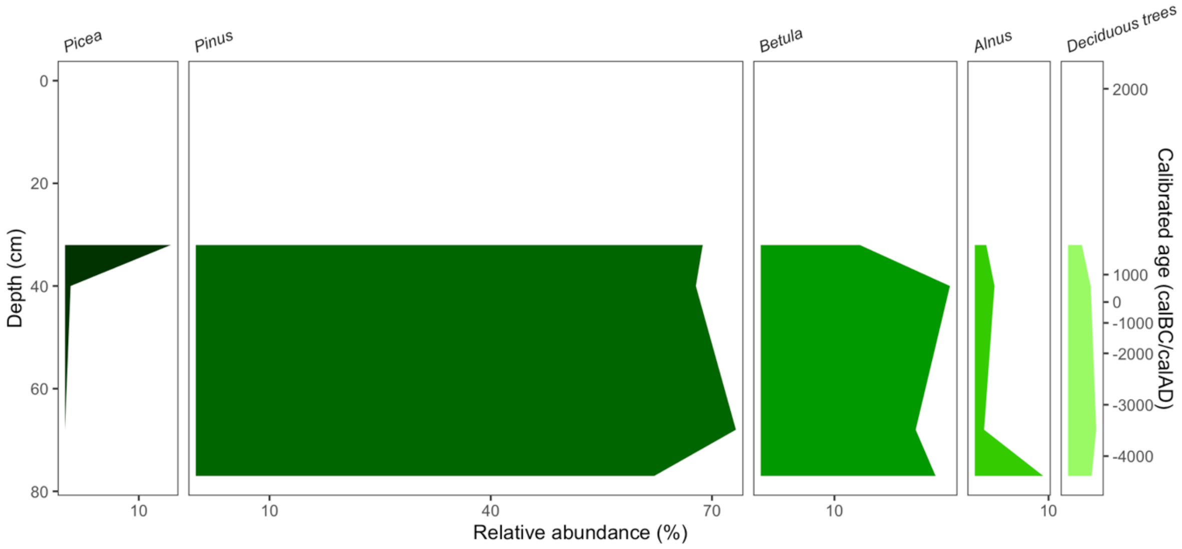
P6



P8

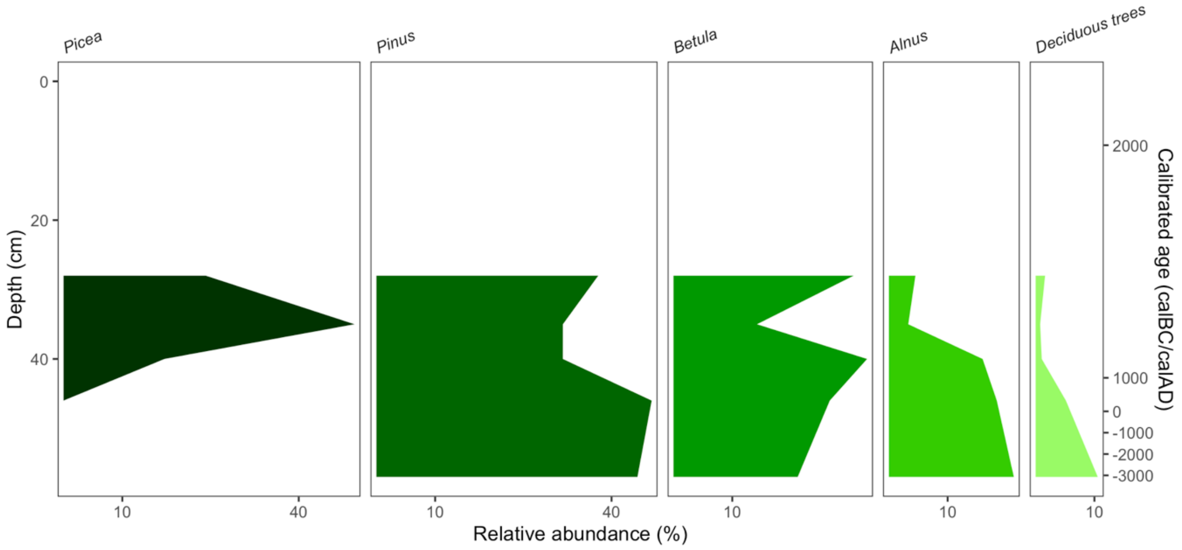


P10



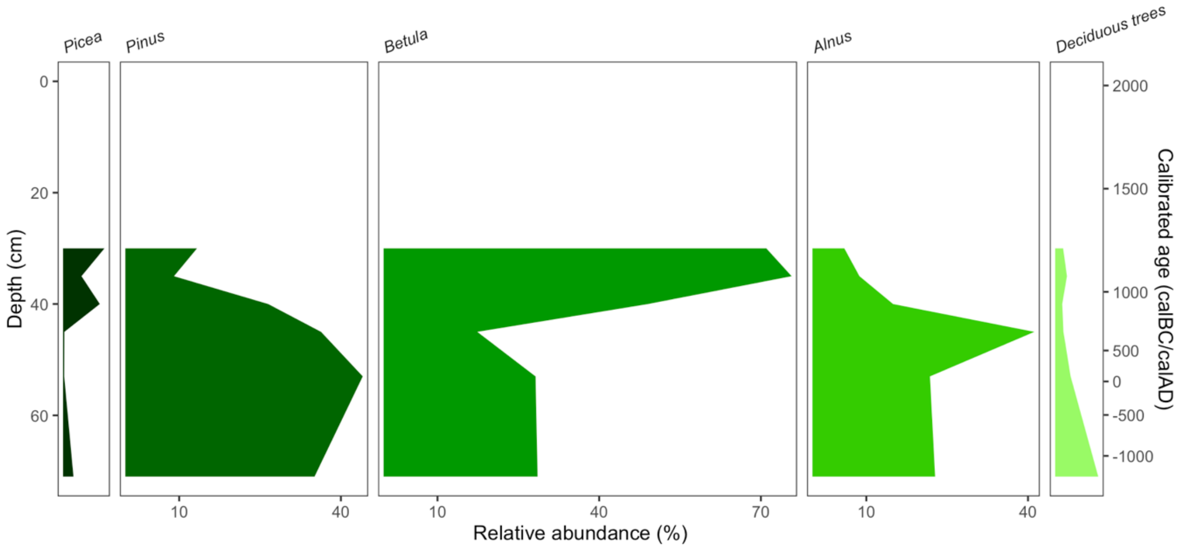
Picea
Pinus
Betula
Alnus
Deciduous trees
Depth (cm)
0
20
40
60
80
10
10
40
70
10
10
Relative abundance (%)
Calibrated age (calBC/calAD)
2000
1000
0
-1000
-2000
-3000
-4000

P11



Picea
Pinus
Betula
Alnus
Deciduous trees
Depth (cm)
0
20
40
10
40
10
40
10
10
10
Relative abundance (%)
Calibrated age (calBC/calAD)
2000
1000
0
-1000
-2000
-3000

P12



Picea
Pinus
Betula
Alnus
Deciduous trees
Depth (cm)
0
20
40
60
10
40
10
40
70
10
40
Relative abundance (%)
Calibrated age (calBC/calAD)
2000
1500
1000
500
0
-500
-1000

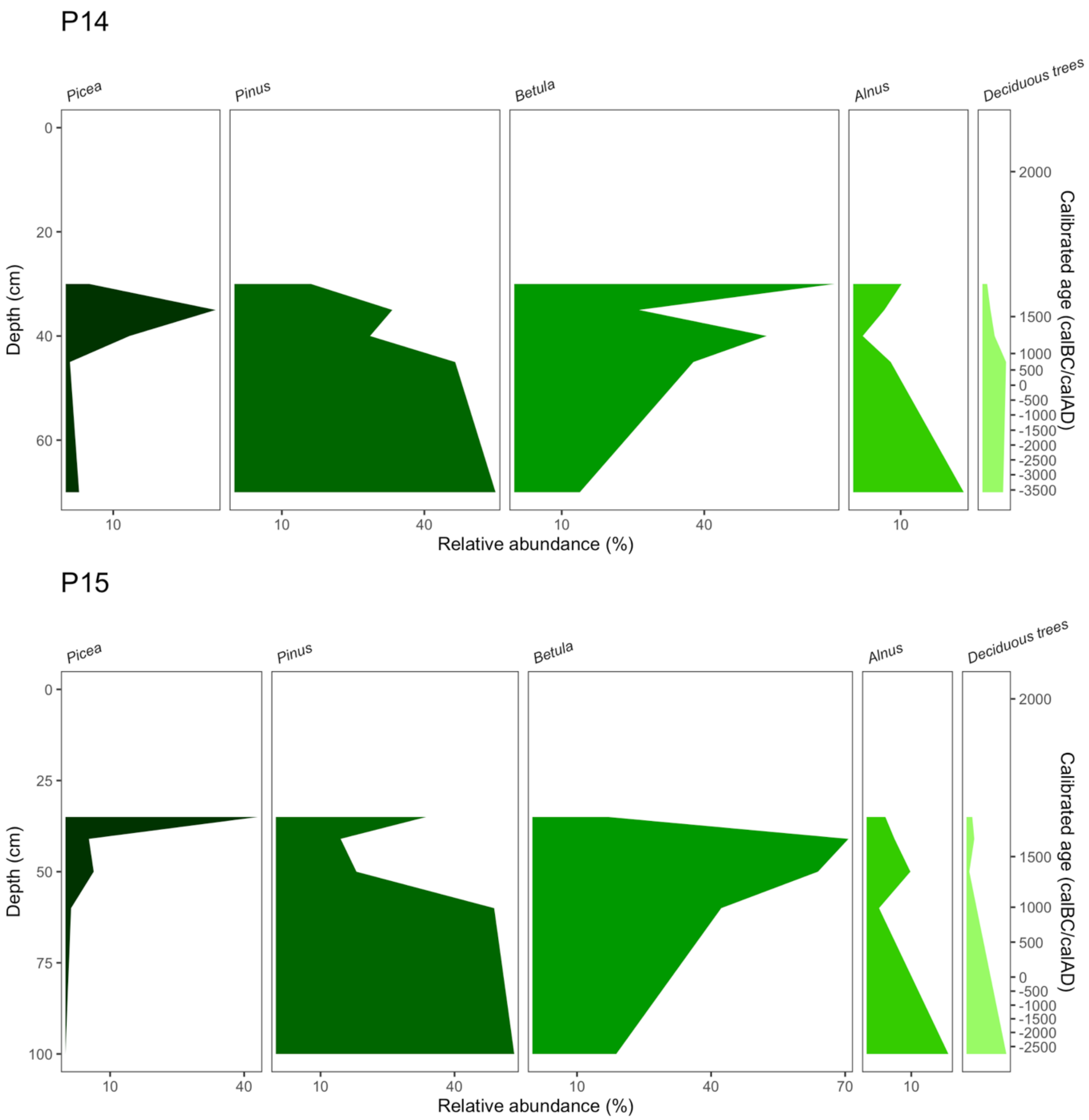


Figure A1: Relative abundance (%) pollen diagram of arboreal pollen from the eight PolDat sequences. See Materials and Methods for taxa included in "Deciduous trees". Pollen percentages was calculated from total arboreal pollen, excluding non-arboreal pollen. Age is given as calibrated years BC/AD.

Appendix B Pictures of the sites

P1

P2

P3

P4

P5

P6

P7

P8

P9

P10

P11

P12

P13

P14

P15

Appendix C Tables of pollen counts

Table C1: The complete counts from all analyzed pollen samples including all observed taxa. Green cells are taxa included in the group “deciduous trees”. Red cells are taxa included in the group “open land species”. “Sum pollen” are all counted microfossils except ferns, *Sphagnum* and added *Lycopodium*. “Total inc. ferns & Sphagnum” are all counted microfossils except added *Lycopodium*.

P2

Depth	**33**	**46**	**71**
Picea	74	0	3
Pinus	149	195	130
Betula	60	171	112
Alnus	30	17	57
Sorbus	3	6	7
Salix	0	0	1
Populus tremula	0	0	1
Prunus padus	0	0	1
Corylus	3	25	38
Quercus	5	2	1
Tilia	0	17	21
Ulmus	0	0	1
Fraxinus excelsior	0	1	0
Poaceae	16	2	6
Cyperaceae	2	1	0
Solidago-type	7	4	0
Composita chic.	4	1	0
Artemisa	2	0	0
Caryophyllaceae	0	0	1
Apiaceae	0	3	1
Brassicaceae	0	0	1
Ericaceae	14	3	1
Myrica gale	0	1	1
Rosaceae	16	0	3
Potentilla	0	0	3
Geranium	0	1	0
Melampyrum	0	0	10
Lycopodium annotinum	8	2	5
Ferns	759	726	252
Sphagnum	5	27	214
Charcoal>60 µm	123	0	0
Charcoal<60 µm	569	1	0
Lycopodium (added)	55	35	34
Sum pollen	393	452	405
Total inc. ferns & Sphagnum	1157	1205	871

P6

Depth	**38**	**50**
Picea	24	71
Pinus	73	302
Betula	155	92
Alnus	21	67
Sorbus	2	7
Salix	3	3
Corylus	1	6
Quercus	1	7
Ulmus	0	5
Poaceae	27	47
Cyperaceae	9	16
Solidago-type	3	12
Composita chic.	6	28
Artemisa	1	2
Campanula	0	1
Caryophyllaceae	2	4
Chenopodiaceae	0	3
Ranunculus	6	34
Rumex	5	2
Apiaceae	1	0
Ericaceae	20	6
Juniperus	4	0
Epilobium	2	2
Rosaceae	9	2
Rubus chamaemorus	9	0
Potentilla	0	2
Hupertzia	0	1
Lycopodium annotinum	3	0
Polypodium vulgare	1	0
Ferns	300	678
Sphagnum	18	4
Charcoal>60 µm	2150	119
Charcoal<60 µm	7250	840
Lycopodium (added)	433	27
Sum pollen	388	722
Total inc. ferns & Sphagnum	706	1404

P8

Depth	**35**	**57**	**76**
Picea	26	5	0
Pinus	209	345	172
Betula	77	50	105
Alnus	4	21	25
Sorbus	0	2	3
Salix	2	4	3
Corylus	0	3	10
Quercus	1	1	0
Tilia	0	2	3
Ulmus	0	1	3
Poaceae	5	6	6
Cyperaceae	7	2	8
Solidago-type	0	1	0
Composita chic.	1	0	0
Artemisa	0	1	4
Campanula	0	1	0
Ranunculus	0	1	0
Rumex	2	1	0
Ericaceae	14	17	4
Juniperus	1	0	0
Rosaceae	1	4	0
Potentilla	1	0	0
Melampyrum	13	0	0
Lycopodium annotinum	2	12	0
Polypodium vulgare	0	1	0
Ferns	7	9	12
Sphagnum	200	13	90
Tilletia (Fungi)	0	2	13
Charcoal>60 µm	0	0	0
Charcoal<60 µm	0	9	10
Lycopodium (added)	510	36	57
Sum pollen	366	483	359
Total inc. ferns & Sphagnum	573	505	461

P10

Depth	**32**	**40**	**68**	**77**
Picea	46	2	0	0
Pinus	220	177	230	388
Betula	43	67	66	148
Alnus	5	7	4	58
Sorbus	0	0	1	6
Salix	0	0	1	4
Corylus	3	3	8	8
Quercus	3	3	1	4
Tilia	0	1	3	4
Ulmus	0	0	0	4
Fagus	0	1	0	0
Poaceae	5	1	5	5
Cyperaceae	4	3	0	4
Solidago-type	1	0	0	0
Artemisa	0	0	1	0
Campanula	0	0	1	1
Cannabaceae	1	0	0	0
Ericaceae	12	16	11	30
Juniperus	0	0	0	1
Epilobium	0	0	0	1
Rubus chamaemorus	0	1	2	1
Melampyrum	2	5	0	0
Caltha	1	0	0	0
Diphasiastrum	1	0	0	0
Lycopodium annotinum	1	0	0	2
Ferns	5	17	7	27
Sphagnum	202	233	35	30
Tilletia (Fungi)	0	0	2	0
Charcoal>60 µm	0	0	0	38
Charcoal<60 µm	4	4	8	96
Lycopodium (added)	335	23	121	20
Sum pollen	348	287	336	669
Total inc. ferns & Sphagnum	555	537	378	726

P11

Depth	**28**	**35**	**40**	**46**	**57**
Picea	75	195	99	0	0
Pinus	117	125	183	273	353
Betula	95	56	190	155	168
Alnus	14	13	92	107	169
Sorbus	4	1	6	13	19
Salix	0	1	1	5	2
Corylus	2	1	1	12	59
Quercus	0	1	1	14	14
Tilia	0	0	0	2	7
Ulmus	3	0	4	2	4
Fagus	0	1	0	0	0
Poaceae	6	6	14	9	28
Cyperaceae	4	3	5	9	5
Solidago-type	1	1	12	13	14
Composita chic.	0	0	0	4	21
Artemisa	0	0	1	1	0
Campanula	0	0	0	0	2
Urtica dioica	0	0	0	1	0
Chenopodiaceae	0	0	1	0	0
Ranunculus	1	2	2	0	1
Rumex	0	0	2	0	0
Ericaceae	14	9	5	5	12
Juniperus	1	1	0	0	0
Rosaceae	3	0	9	40	62
Rubus chamaemorus	2	2	2	1	0
Epilobium	0	1	0	1	0
Myriophyllum	0	0	2	0	0
Selaginella	0	0	0	1	0
Hupertzia	0	0	0	1	0
Lycopodium annotinum	5	3	14	25	31
Ferns	73	83	553	1404	1097
Sphagnum	4	1	4	5	5
Tilletia (fugi)	0	0	0	0	13
Charcoal>60 µm	4	7	3	14	43
Charcoal<60 µm	76	17	10	23	143
Lycopodium (added)	174	39	51	9	31
Sum pollen	347	422	646	694	984
Total inc. ferns & Sphagnum	424	506	1203	2103	2086

P12

Depth	**30**	**35**	**40**	**45**	**53**	**71**
Picea	26	11	26	1	1	8
Pinus	45	29	101	142	200	145
Betula	240	243	187	68	128	118
Alnus	20	28	57	161	99	94
Sorbus	0	3	5	10	13	15
Salix	2	0	0	1	0	0
Corylus	4	4	3	3	7	15
Quercus	0	1	0	0	4	7
Tilia	1	0	0	0	1	0
Ulmus	0	2	2	2	1	11
Fraxinus excelsior	0	0	0	1	0	0
Poaceae	8	17	17	3	10	7
Cyperaceae	5	5	9	0	6	15
Solidago-type	0	1	3	5	6	5
Composita chic.	0	0	0	1	1	3
Artemisa	1	1	1	2	1	0
Caryophyllaceae	0	0	0	1	0	0
Chenopodiaceae	0	2	0	0	1	0
Ranunculus	0	1	3	1	0	0
Rumex	4	1	2	0	0	0
Trollius europaeus	0	0	0	1	0	0
Ericaceae	14	19	3	1	6	4
Juniperus	11	3	2	0	0	0
Epilobium	0	0	2	0	0	0
Rosaceae	1	5	9	0	15	15
Rubus chamaemorus	1	1	0	1	1	0
Potentilla	2	0	0	0	0	3
Melampyrum	0	0	0	1	0	0
Lycopodium annotinum	0	0	17	13	10	0
Ferns	62	57	255	106	793	557
Sphagnum	1	0	2	0	5	7
Tilletia (Fungi)	2	0	0	0	0	0
Charcoal>60 µm	5	31	0	0	5	57
Charcoal<60 µm	64	223	2	0	18	1133
Lycopodium (added)	147	71	38	23	30	103
Sum pollen	387	377	449	422	511	465
Total inc. ferns & Sphagnum	450	434	706	528	1309	1029

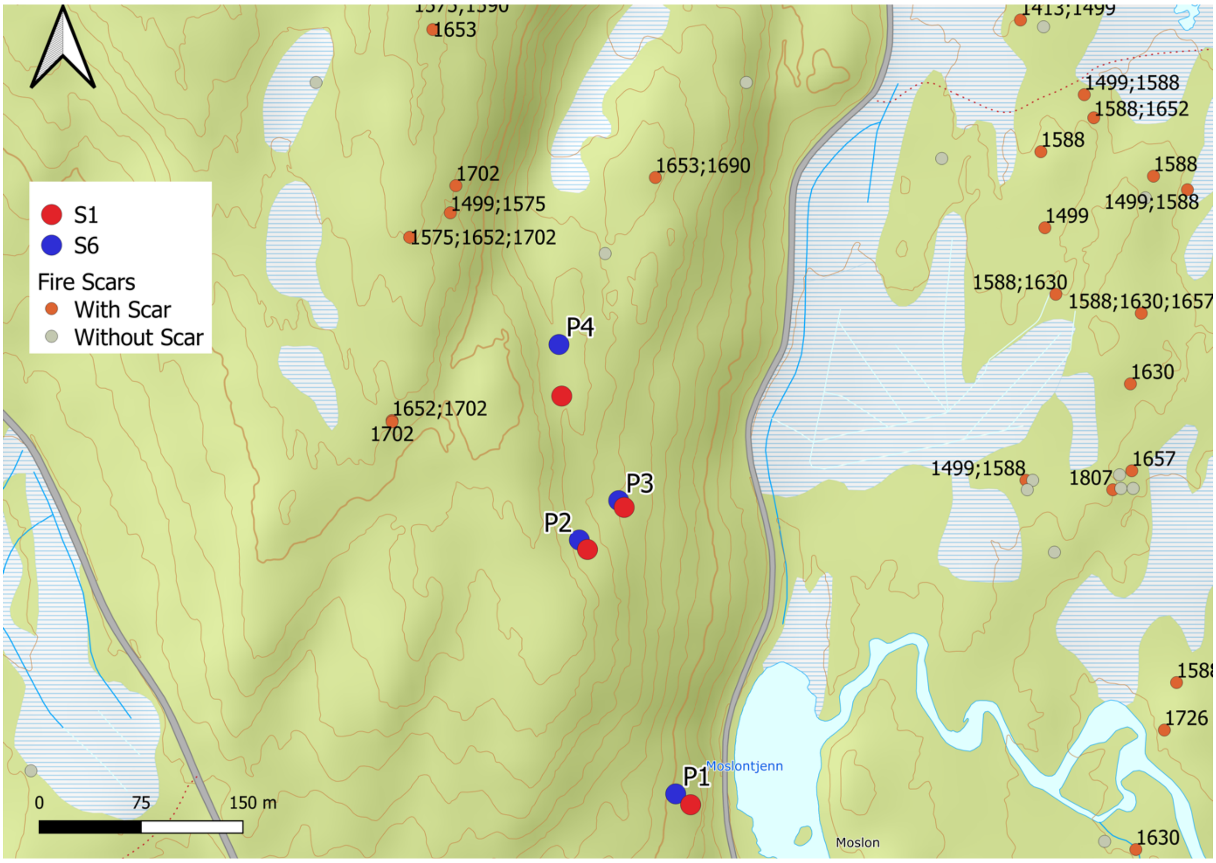
P14

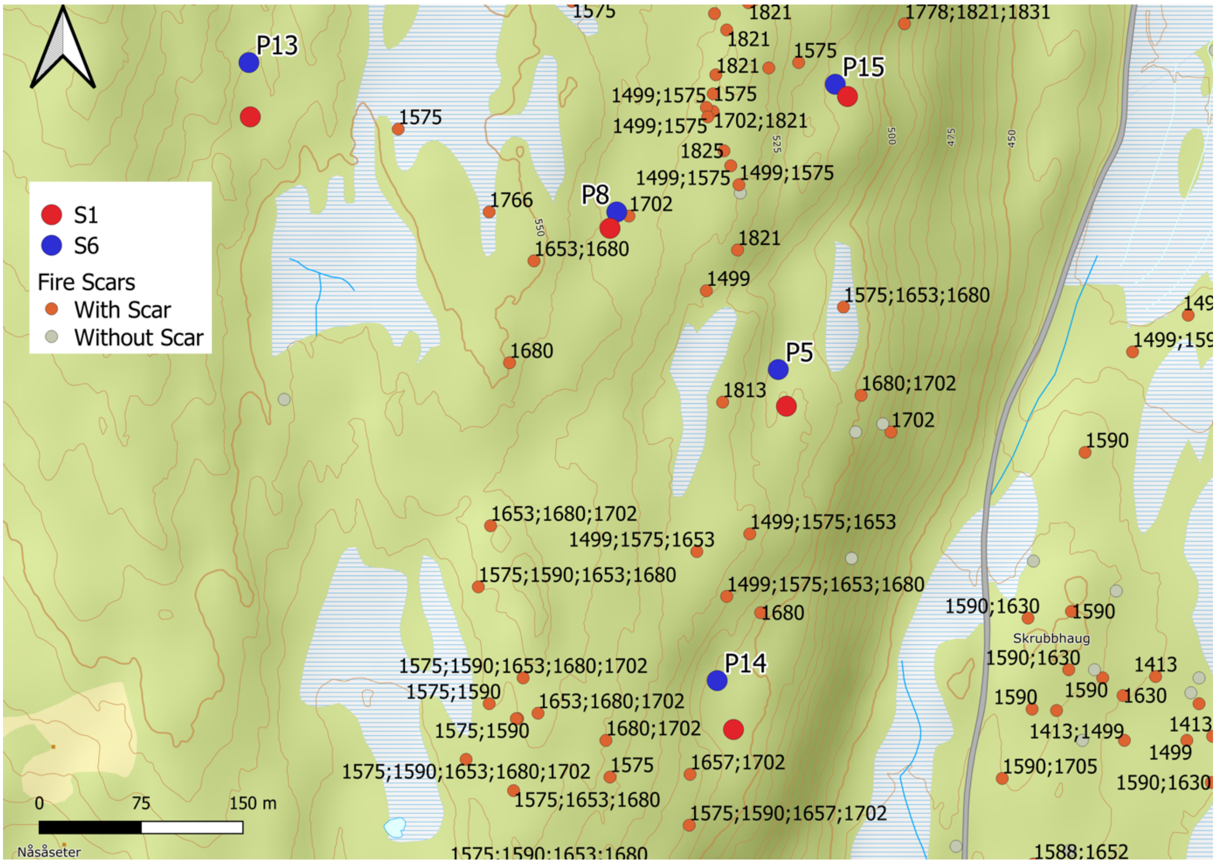
Depth	**30**	**35**	**40**	**45**	**70**
Picea	15	149	47	3	11
Pinus	49	157	100	159	215
Betula	205	124	186	129	54
Alnus	31	31	7	27	91
Sorbus	1	1	1	7	1
Salix	0	2	0	0	2
Corylus	2	4	8	5	13
Quercus	0	0	0	5	1
Tilia	0	1	0	0	1
Ulmus	1	3	1	7	2
Poaceae	25	16	3	10	11
Cyperaceae	3	9	0	7	20
Solidago-type	3	8	3	3	4
Composita chic.	0	1	0	1	1
Campanula	0	0	0	1	0
Ranunculus	1	3	1	3	0
Rumex	2	1	0	0	0
Ericaceae	20	3	3	6	3
Juniperus	1	3	0	0	0
Epilobium	0	4	0	0	0
Rosaceae	6	6	3	10	3
Rubus chamaemorus	5	3	2	2	0
Nymphaea	0	1	0	1	0
Hupertzia	0	2	0	1	0
Lycopodium annotinum	5	6	6	2	6
Polypodium vulgare	1	0	0	0	0
Ferns	282	904	221	1018	548
Sphagnum	6	4	1	5	6
Charcoal>60 µm	37	39	1	0	213
Charcoal<60 µm	184	217	4	25	2730
Lycopodium (added)	137	55	14	28	84
Sum pollen	376	538	371	389	439
Total inc. ferns & Sphagnum	664	1446	593	1412	993

P15

Depth	**35**	**41**	**50**	**60**	**100**
Picea	133	21	20	5	0
Pinus	104	58	57	193	341
Betula	53	283	202	167	120
Alnus	13	25	31	11	117
Sorbus	0	4	2	10	3
Salix	2	2	2	1	1
Corylus	2	5	2	7	36
Quercus	1	2	0	0	3
Tilia	0	0	0	1	16
Ulmus	1	0	0	0	2
Fraxinus excelsior	0	0	0	1	0
Poaceae	21	1	5	4	8
Cyperaceae	9	1	0	0	1
Solidago-type	2	0	1	1	3
Composita chic.	0	0	0	1	1
Artemisa	1	0	1	0	0
Caryophyllaceae	0	0	0	1	0
Chenopodiaceae	2	1	0	0	0
Ranunculus	3	0	9	2	0
Rumex	5	0	0	0	1
Ericaceae	18	9	39	2	4
Juniperus	6	0	1	0	0
Lonicera	0	0	0	1	0
Epilobium	0	0	3	0	0
Rosaceae	5	2	3	0	5
Rubus chamaemorus	3	0	2	0	0
Potentilla	0	0	0	0	1
Melampyrum	0	0	0	5	0
Thalictrum	0	0	0	1	0
Selaginella	0	0	0	0	1
Lycopodium annotinum	2	0	19	65	76
Ferns	60	45	35	80	233
Sphagnum	12	0	9	1	38
Tilletia (Fungi)	5	1	0	0	0
Charcoal>60 µm	12	5	70	0	4
Charcoal<60 µm	199	15	136	2	25
Lycopodium (added)	154	128	307	65	17
Sum pollen	391	415	399	479	740
Total inc. ferns & Sphagnum	463	460	443	560	1011

Appendix D Additional maps of the study area





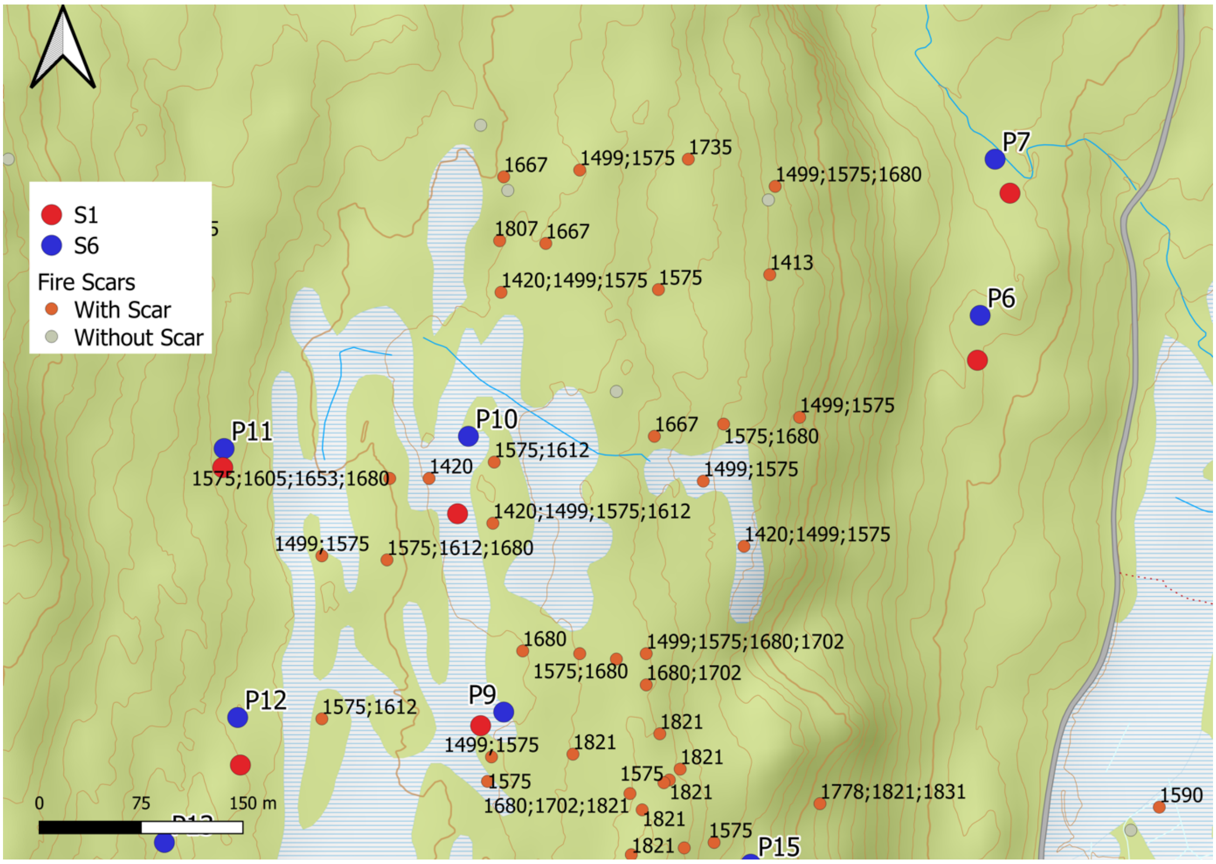


Figure D1: Maps of the investigated sites with ages of nearby cross-dated fire-scar samples from pine stumps (data from Storaunet et al., 2013; Storaunet, unpublished). Time of fires are showed as years AD. Background map copyrighted Norgeskart and available from www.norgeskart.no.

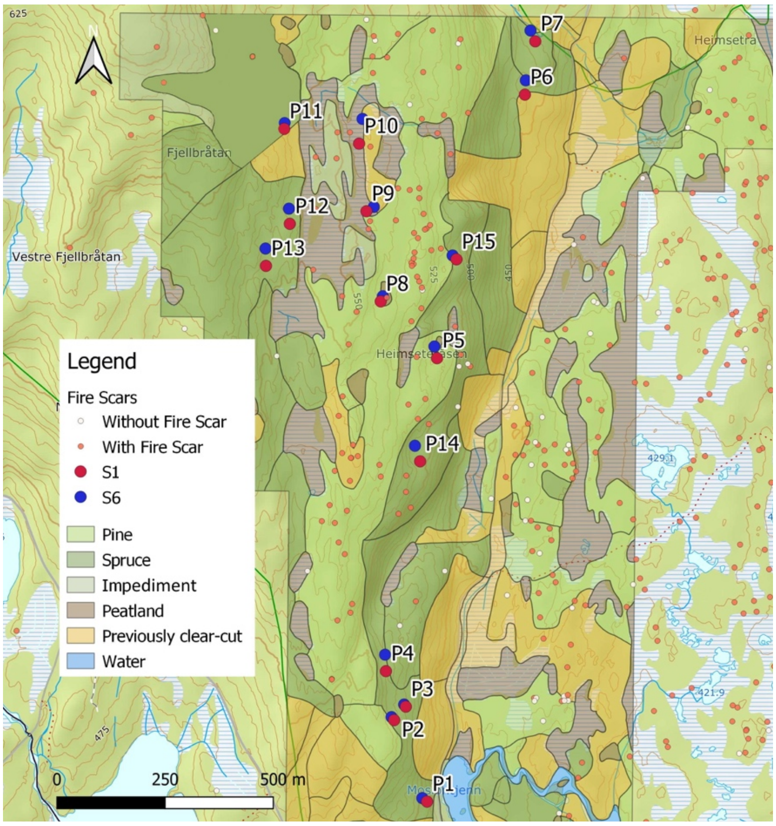


Figure D2: Map of the study area categorized after pine or spruce dominance, or if the area has been clear-cut sometime in the 20th century (data form Storaunet, unpublished). Impediment means unproductive forest in a forestry perspective. Background map copyrighted Norgeskart and available from www.norgeskart.no.

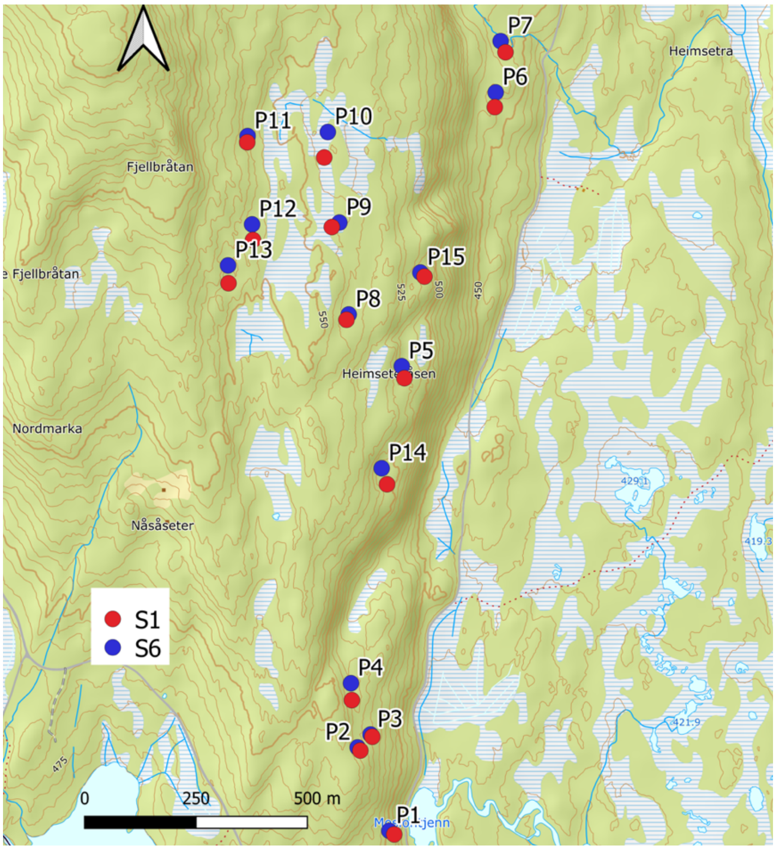


Figure D3: Map of the topography of the study area with all investigated sites. Background map copyrighted Norgeskart and available from www.norgeskart.no.

Appendix E Table of fires after spruce establishment

Table E1: All charcoal bands with macroscopic charcoal after the establishment of spruce in the investigated peat sequences. Conservative inclusions of charcoal bands from sites without pollen analysis and ^{14}C dating. Ages in red are extrapolated from a different sequence than the observed charcoal band and should consequently be interpreted with care. Fire scars AD are age AD of dendrochronological dated fire scars in old pine stumps found within 75 meters from the site (see Figure D1).

Site	Sequence(s)	Depth of charcoal band	Age of charcoal band AD	Fire scars AD within 75 m
P1	S2	20		
	S4/S5	28		
P2	PolDat/S2	15	1998 SD 10,7**	
	S4	20	1771 SD 67*	
	PolDat/S3	27	1686 SD 75*	
	PolDat/S5	31	1221 SD 24	
	PolDat/S6	35	1456 SD 47	
	PolDat/S2	37	655 SD 331*	
P3	S3/S6	19		
	S6	23		
P4	S6	27		
	S1	32		
	S1	35,5		
P5				1813
				1702
				1680
				1653
				1575
				1499
P6	S1	31	1768 SD 49,7*	
	PolDat/S1/S4/S6	36,5	1727 SD 84	
	PolDat	38	1650 SD 64*	
	PolDat/S1/S3/S6	45	1426 SD 57*	
	PolDat/S1/S5/S6	47	1360 SD 55*	
	PolDat	49	1236 SD 15	
P7	S6	38		
P8				1702
				1680
				1653
P9	S1	26		1821
				1680
				1575
				1499

P10	PolDat/S4/S5/S6	32	1623 SD 69	1680
	PolDat/S4/S5/S6	35	1258 SD 100*	1653
				1612
				1602
				1575
				1499
				1420
P11	S1/S4	37	1306 SD 126*	
	S4/S5	42	1032 SD 118*	
P12				1612
				1575
P13				
P14	S6	21	1844 SD 88*	1702
	PolDat	27	1956 SD 0,2**	1680
	S5	36	1448 SD 99*	1657
	S5	39	1333 SD 84*	1653
				1590
				1575
				1499
P15				1831
				1821
				1778
				1575

* Ages obtained from extrapolation

** ^{14}C datings with high percentage of modern carbon (pMC), probably due to downward transportation of younger carbon from plant roots etc. Age of fire probably older than depicted.

Appendix F Site specific vegetational characteristics

Table F1: Vegetational composition of the sites and adjacent forest. The numbers of *Picea, Pinus, Betula* and "Other trees" are percentage abundance within a radius of about 70 m from the site. "Other trees" consists of *Populus tremula, Sorbus aucuparia* and *Salix caprea*. Numbers of *Vaccinium myrtillus, Sphagnum*, Ferns and Poaceae are percentage coverage of the investigated peatland. The "selection of vascular plants" covers the most common species at the site. Nomenclature for plant names follows Lids and Lids (2005).

Site	*Picea*	*Pinus*	*Betula*	Other trees	*Vaccinium myrtillus*	*Sphagnum*	Ferns	Poaceae	Selection of vascular plants
P1	80	0	15	5	5	70	4	10	*Agrostis canina* *Trientalis europaea*
P2	96	0	2	2	5	65	7	10	*Calamagrostis phragmitoides* *Deschampsia cespitosa* *Pyrola sp.* *Viola palustris*
P3	94	0	5	1	5	80	5	20	*Calamagrostis phragmitoides* *Dactylorhiza maculata* *Deschampsia cespitosa* *Geranium sylvaticum* *Oxalis acetosella* *Pyrola sp.* *Trientalis europaea*
P4	80	0	12	8	2	90	3	60	*Calamagrostis phragmitoides* *Carex nigra* *Equisetum sylvaticum* *Eriophorum angustifolium*
P5	60	30	10	0	0	85	1	1	*Carex nigra* *Equisetum vaginatum* *Juncus filiformis* *Oxycoccus sp.*
P6	92	0	7	1	3	95	1	20	*Calamagrostis phragmitoides* *Dactylorhiza maculata* *Pyrola sp.* *Rubus saxatilis* *Trientalis europaea* *Viola riviniana*
P7	75	0	20	5	1	95	2	40	*Calamagrostis phragmitoides* *Carex echinate* *Carex pauciflora* *Dactylorhiza maculata*
P8	15	84	1	0	0	80	0	0	*Carex echinate* *Carex nigra* *Carex pauciflora* *Equisetum vaginatum* *Rubus chamaemorus*
P9	2	95	3	0	0	85	0	0	*Andromeda polifolia* *Equisetum vaginatum*
P10	1	95	4	0	0	85	0	0	*Andromeda polifolia* *Equisetum vaginatum* *Oxycoccus sp.*
P11	93	0	7	0	2	85	5	5	*Blechnum spicant* *Equisetum vaginatum* *Pteridium aquilinum* *Pyrola sp.*
P12	85	7	6	2	1	85	1	2	*Calamagrostis phragmitoides* *Carex nigra* *Equisetum vaginatum* *Rubus chamaemorus*

P13	92	1	7	0	2	80	0	6	*Calamagrostis phragmitoides* *Carex echinate* *Carex nigra* *Equisetum vaginatum* *Juncus filiformis*
P14	93	1	6	0	2	75	5	20	*Calamagrostis phragmitoides* *Juncus filiformis* *Luzula Pilosa* *Lycopodium annotinum* *Pteridium aquilinum*
P15	83	10	7	0	1	85	0	2	*Carex nigra* *Equisetum sylvaticum* *Equisetum vaginatum* *Potentilla erecta*

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