

Integrating fire-scar, charcoal and fungal spore data to study fire-events in the boreal forest of northern Europe

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Abstract

Fire is a major disturbance agent in the boreal forest, influencing many current and future ecosystem conditions and services. Surprisingly few studies have attempted to improve the accuracy of fire-event reconstructions even though the estimates of the occurrence of past fires may be biased, influencing the reliability of the models employing those data (e.g. C stock, cycle). This study aimed to demonstrate how three types of fire proxies – fire-scars from tree rings, sedimentary charcoal and, for the first time in this context, fungal spores of *Neurospora* – can be integrated to achieve a better

understanding of past fire dynamics. By studying charcoal and *Neurospora* from sediment cores from forest hollows, and the fire scars from tree rings in their surroundings in the southern Fennoscandian and western Russian boreal forest we produced composite fire-event data sets and fire-event frequencies, and estimated fire return intervals. Our estimates show that the fire return interval varied between 126–237 years during the last 11 thousand years. The highest fire frequency during the 18th–19th century can be associated with the anthropogenic influence. Importantly, statistical tests revealed a positive relationship between other fire event indicators and *Neurospora* occurrence allowing us to pinpoint past fire-events at times when the sedimentary charcoal was absent, but *Neurospora* were abundant. We demonstrated how fire proxies with different temporal resolution can be linked, providing potential improvements in the reliability of fire history reconstructions from multiple proxies.

Keywords: forest hollow, *Neurospora*, non-pollen palynomorphs, tree rings, Finland, Russia

Introduction

Forest fires are a key disturbance in boreal forests, and characteristics of fire regimes are among the most important factors explaining the variation in forest and landscape structure and species composition (Aakala et al., 2018). Climate change is predicted to strongly influence fire occurrence in forest ecosystems in the future (Girardin et al., 2009; Khabarov et al., 2016). Boreal forests contain approximately one-third of the global forest area and one-third of terrestrial carbon stocks, and hence changes in fire activity will have a substantial impact on global carbon emissions (Flannigan, 2015). Fire regime changes can have additional impacts because high-intensity crown and low-intensity surface fires result in different net effects on climate as a consequence of their contrasting impacts on terrestrial albedo (Rogers et al., 2015). Given the current and future societal importance of forest fires

and their long-term influence on many ecological processes, it is necessary to improve our understanding of fire occurrence over long time scales.

Documentary records can provide detailed information on fires and their occurrence over large areas, but their temporal coverage in the boreal zone is limited to 100–150 years at best (Wallenius, 2011). However, there are several ways of acquiring information about past fire activity from biological archives, such as tree rings or organic sediments. These archives differ in their resolution and their temporal coverage. Tree-ring-based reconstructions of past fire activity employ either information on the age structures of trees or stands that initiated after fire (Bergeron et al., 2004), the presence of fire scars on trees that were damaged but survived the fires (Wallenius et al. 2010, Aakala 2018), or both (Lankia et al., 2012). While of high temporal resolution, tree-ring-based fire history reconstructions in the boreal forest rarely cover more than a few centuries (Wallenius et al., 2010). Low-intensity fires may not always leave fire scars, potentially causing bias in fire regime reconstructions concerning surface fires (Dieterich and Swetnam, 1984).

Charcoal particles that are formed during incomplete combustion of biomass in forest fires and become deposited within organic sediments are another widely applied proxy in fire reconstructions (e.g. Dietze et al., 2018). Every forest fire has a unique combination of fuels and temperatures that define the intensity and severity of the fire and produce a range of different charcoal forms (Feurdean et al., 2017; Keeley, 2009; Marcisz et al., 2017; Ohlson, 2012; Zackrisson, 1977). Although there is no consensus on how resistant soil charcoal particles are to fragmentation over millennia in different biogeographical settings, and the dispersal of airborne charcoal particles is somewhat difficult to assess, it is clear that charcoal provide evidence on fire occurrence in the past (de Lafontaine and Asselin, 2011; Ohlson, 2012; Oris et al., 2014; Patterson et al., 1987). Compared to fire-scars, the temporal resolution of sedimentary charcoal is relatively poor, due to the uncertainty associated with the dating methods and natural sedimentation processes. Additionally, evidence indicates that charcoal can be absent from the sediments during times of known forest fires (Ohlson,

2012; Ohlson and Tryterud, 2000), which leads to problems in evaluating the fire occurrence or characteristics based on the charcoal record alone.

Several authors have attempted to correlate different fire proxies such as fire-scars and sedimentary charcoal for obtaining a more complete picture of the long-term fire occurrence (Brossier et al., 2014; Higuera et al., 2005; Remy et al., 2018), but only a few of them have been successful. Higuera et al. (2005) studied the calibration of fire scars and sedimentary charcoal from a small forest hollow (<0.1 ha wet depression in the forest) and concluded that the fire detection from sedimentary charcoal depends strongly on fire severity and that the fine-scale spatial patterns of lower-severity burns play an essential role in determining the charcoal signal of these events. An additional differences between these two proxies stems from differences in their origins: sedimentary charcoal is produced during medium to high-intensity fires at temperatures between 280 and 500 °C (Whitlock and Larsen, 2001), whereas the formation of fire scars requires that some of the trees survive and are hence usually formed after low-intensity (surface) fires (Gill, 1974). Characterization of the fire regime and its changes is thus dependent on the fire intensity, and the methods applied, and integration of different proxies to a more reliable composite data set would significantly increase our understanding of the long-term fire history of the boreal forest.

Traces for the presence of pyrophilous fungal species (i.e., species whose growth depends on fire) could potentially serve as another proxy for wildfire events. The formation of “blossoms” on charred wood after a fire is well-known characteristic of some species of moulds. These include *Neurospora* spp., which is a mould known to grow on charred tree and shrub bark after a fire and thus could potentially serve as another fire proxy (Jacobson et al., 2004, 2006; Kuo et al., 2014; Luque et al., 2012). Ascospores of *Neurospora* remain dormant until exposed to moist heat above 65° C, i.e. temperatures that in the boreal forests only occur during fires (Perkins et al., 1975). After a fire ascospores of the *Neurospora* germinate and form characteristic “orange bloom” on the black, charred tree trunks.

Here, we use composite data sets to estimate fire-event frequencies and return intervals over the Holocene in the boreal forest of northern Europe. In comparison with earlier studies that have employed two proxies (fire-scars and sedimentary charcoal; e.g., Higuera et al., 2005; Remy et al., 2018), we take one step further, and use three independent fire-event indicating proxies: fire-scars, sedimentary charcoal and *Neurospora* from small forest hollows. We specifically select small forest hollows under a closed tree canopy to reveal local fire-events. Studied time includes both periods of natural conditions and anthropogenic impacts on fire-event dynamics in the European boreal forest. We propose an approach for linking fire-scar and sedimentary fire proxies that is applicable to other similar studies.

Material and methods

Study area

The study sites are located in the boreal forest of Fennoscandia and the taiga forest in north-western Russia (Fig. 1). All study sites are small forest hollows within closed-canopy forest stands. Polttiais hollow (unofficial name; 1x1 m; N62°16'33", E36°45'3") is located in the Vodlozersky National Park in western Russia and is surrounded mainly by stands of Scots pine (*Pinus sylvestris*) and birch (*Betula* sp.). Mean annual temperature is 3.4°C (17.6°C in July, and -9.9°C in February), and the annual precipitation sum 660 mm (mean data 1981–2010, from the nearest city Vytegra; Peterson and Vose, 1997). Naava hollow (unofficial name; 15x20 m; N61°14'29", E25°3'22") and Kämmekkä hollow (unofficial name; 10x20 m; N61°14'33", E25°3'19") are located 90 m from each other in southern Finland. Both Kämmekkä and Naava hollow are surrounded by spruce dominated forest, situated within a protected area of old-growth forest. The forest cover consists mainly of old-growth mixed stands of Norway spruce (*Picea abies*) and deciduous species such as birch, aspen (*Populus tremula*) and alder (*Alnus glutinosa* and *Alnus incana*), and occasional large individuals of Scots pine.

The mean annual temperature is around 4 °C (16.5 °C in July, and -7 °C in February), and the mean annual precipitation is 645 mm (Pirinen et al., 2012).

Sediment sampling

Fieldwork was conducted in August-October 2015. We extracted a 125 cm long core from Kämmeekkä hollow, a 127 cm long core from Naava hollow and a 143 cm long core from Polttiais hollow, using a Russian peat sampler. We examined the cores in the field for visible charcoal layers, placed them in PVC semi-tubes, and wrapped in plastic. After fieldwork, the samples were stored in a cold room (air temperature of 4–5° C) for further analysis.

Sediment dating and age-depth models

All cores were dated using accelerator mass spectrometry ^{14}C dating (^{14}C AMS), in Poznań, Poland (Table 1). All ^{14}C dates were calibrated using the IntCal13 calibration dataset (Reimer et al., 2013) with a two σ (95.4%) confidence level, and the age-depth models of each sequence were developed using Bacon 2.2 package (Blaauw and Christen, 2011), in the R environment (R Core Team, 2014). In addition, we used a biostratigraphic correlation to define the lowermost age of Kämmeekkä hollow, based on Naava hollow and *Picea* expansion in southern Finland (Table 1; Supplementary material 1; Seppä et al., 2009a; Stivrins et al., 2017).

Sediment analyses

We analysed consecutive 1-cm samples for sedimentary charcoal and non-pollen palynomorphs from Kämmeekkä, Naava and Polttiais hollows. We extracted a record of sedimentary charcoal and

categorized them according to size: 1) microscopic charcoal (20–150 μm), 2) macroscopic charcoal (>150 μm –1 mm), and 3) large charcoal pieces (>1 mm).

Microscopic charcoal was counted from the pollen slides. These particles are in the range from 20–150 μm , but commonly 20–80 μm in size due to pollen preparation method which involves centrifuge usage that can break larger charcoal fragments into smaller pieces. We prepared each sample (volume 1 cm^3 , thickness 1 cm), using common pollen preparation procedures (HCl 10%, KOH 10%, acetolysis 3 min, mounted in glycerol; Berglund and Ralska-Jasiewiczowa, 1986). We added known quantities of *Lycopodium* spores to each sample to allow calculation of charcoal concentrations (Stockmarr, 1971), and counted microscopic charcoal particles according to Finsinger et al. (2008).

Macroscopic charcoal analysis was used to estimate the concentration of charcoal pieces >150 μm in size in each sample. For this, we treated each sediment sample (volume 1 cm^3 , thickness 1 cm) with dilute NaOCl to promote sediment bleaching and disaggregation before sieving at 150 μm . The sediment residue was added to 20 ml distilled water and decanted to a petri dish for charcoal analysis. Charcoal was identified as brittle, black crystalline particles with angular broken edges using a stereomicroscope at 30–60x magnification, (Swain, 1973).

Large charcoal pieces >1 mm in size were recorded during plant macrofossil analysis, which followed the procedure described by Gałka et al. (2017). Sediment samples (volume 3 cm^3) were wet-sieved and analysed using a Nikon SMZ800 stereoscopic microscope at magnifications of 10–200 and a transmitted light microscope.

Finally, we identified and counted the *Neurospora* (HdV-55c in size 22–28x15–18 μm ; with a grooved surface with longitudinal ribs; Miola, 2012; Shear and Dodge, 1927; van Geel, 1978) and *Gelasinospora* (HdV-1, HdV-2, HdV-528 in size ca 22–33x14–20 μm ; with a pitted wall; Dowding, 1933; van Geel, 1972, 1978) ascospores from the pollen slides. Based on molecular methods

Gelasinospora and *Neurospora* species were treated as a synonym of *Neurospora* genus within the order *Sordariales* (Dettman et al., 2001; García et al., 2004). Hence, identified spores of *Gelasinospora* and *Neurospora* were merged and treated as *Neurospora* spp. Fungal spores were counted alongside pollen analysis and we stop counting them when at least 500 pollen grains were identified.

Fire dates from scarred trees

We sampled fire scars at the Polttiais hollow site in August 2015, at the same time when sediment samples were taken. For this, we searched the vicinity of Polttiais hollow for fire-scarred trees, at approx. 100 m radius around the hollow, but so that we remained in the same stand in which the hollow was located. When encountered, we extracted a partial stem disk that contained the tip of the fire scar for dating the year of fire. In the lab, samples were dried and sanded to fine grit (600). We visually cross-dated the year of fire under a microscope, using marker rings (Yamaguchi, 1991) from samples obtained from live trees in the same stand.

For the Naava and Kämmeikkä hollow, we used the fire dates from Tuominen (1990). Based on this data, fires occurred in 1773, 1827, 1857, and 1886. Fires have been absent from the stand since 1886. These fire dates were originally obtained from tree ring samples from 18 fire scarred pines in the study stand, by inspecting the changes in tree growth rates typically associated with surface fires as described by Mikola (1950).

Data analyses

We used CharAnalysis (Higuera et al., 2009), to identify fire events from the sedimentary charcoal record. This analysis is based on the charcoal peak screening process (Gavin et al., 2006), in which a

threshold value is used to separate the background charcoal deposition (noise) from the occurrence of peaks that are indicative of actual fire events. CharAnalysis was originally designed for the analysis of lake sediments, and hence we adjusted the procedure for using it for small forest hollow data (see Supplementary material 2). CharAnalysis was used for screening the macroscopic and microscopic charcoal, whereas the observations of *Neurospora* and large charcoal pieces were treated as a dichotomous fire indicator.

For assessing the usefulness of *Neurospora* as a fire indicator, we tested its connection with other fire indicators (fire scars, macro- and microcharcoal) using a permutation test. In the test, we used the number of samples (slices), where *Neurospora* and other indicators were observed, as our test statistic. As the slicing of the sediment core may cause different indicators to be in separate slices even if they indicate the same fire-event, *Neurospora* and another indicators were considered to match if they were in the same or in the neighboring samples. We assigned the fire scar-based fire events into a sediment sample whose dating appears to match it the best. In the permutations, *Neurospora* observations were randomly assigned to sediment samples while keeping sequential *Neurospora* observations in sequent slices. The p -value was obtained as the proportion of random permutations where the number of matches were at least as high as observed. We conducted the test separately for each sequence and by pooling the area-wise test statistics together. Furthermore, we examined whether the existence of charcoal or fire scar in a sample increased the probability of observing *Neurospora*. This was estimated as the risk ratio RR :

$$RR = \frac{c}{N}, \text{ where}$$

c is proportion of slices with *Neurospora* among a sample with charcoal in the same or neighboring sample, and N is the proportion of slices with *Neurospora* among samples without another fire indicator in the same or neighboring sample.

Risk ratio above one indicates that *Neurospora* was observed more often when another fire indicator is present than when another fire indicator was absent. The confidence intervals of the risk ratio were calculated using the function *riskratio* in package *fmsb* of R software.

While combining the three separate fire indicators into a composite indicator, a sample was considered as a “fire sample” if at least one proxy indicated a fire. Using CharAnalysis, we then estimated fire frequencies, as well as the mean and median fire return (mFRI) intervals. Usually (and as implemented in the CharAnalysis software), the confidence intervals for the mFRI are obtained, using bootstrapping. However, as these intervals omit the effect of timing uncertainty which is available from the Bayesian age-depth model, we augmented the computation of confidence intervals by considering both the sampling distribution of the mFRI and the timing uncertainty. To quantify and compare these two sources of uncertainty, we also report the uncertainty intervals obtained only considering the timing uncertainty and the bootstrap intervals without the timing uncertainty.

While computing the time-varying fire frequency, CharAnalysis sums the total number of fires within a 1000-yr period and smooths the obtained series with a Lowess smoother. Preliminary analyses showed that Naava, Kämmeikkä and Polttiais sediment sequences all had higher sedimentation rate towards the present day. The topmost section of sediment sequence was formed mainly of moss peat matrix that was less decomposed and not suppressed as subsequent lowermost sediment layers (similarly to bogs). As a result, the sampling density was considerably higher during the last 200 years (sediment is less compacted at the top – higher temporal resolution than for lowermost sediment), and we therefore binned the samples into 120-year bins that correspond to the smallest of the 95% quantiles of the sampling resolution over the period. We show the timing uncertainty also in the fire frequency estimates in the form of highest posterior density intervals.

Results

Sediment chronology

Age-depth modelling of all three sediment sequences reveal overall superposition sedimentation. Few samples were excluded from the age-depth models as they indicated outliers (Table 1). Because plant remains for AMS ^{14}C dating were not available throughout the sediment sequences, several bulk peat samples were dated. A bulk sample consists of a mixture of terrestrial plant remains and tend to be slightly older than the date of plant macrofossil. These differences may arise due to a composition of the bulk sample (e.g. roots, fungi, humic acids), trampling of animals or change in peat decomposition rate (see for example Valiranta et al., 2014). Hence, establishing a chronology of small forest hollow is somewhat challenging as possible hiatus, and non-linear sedimentation may occur.

The chronology for the basal section of Kammekka hollow was established based on the rise of spruce (*Picea*) pollen values, as the AMS ^{14}C date of wood was an outlier (too young age). According to the Naava hollow pollen data (Stivrins et al., 2017), and general knowledge of spruce migration into Finland (Seppa et al., 2009a), the appearance of spruce 4800 years ago was used as a biostratigraphic marker. Considering the proximity of Naava hollow, we adjusted the basal age of Kammekka hollow according to this biostratigraphic marker. An example of circumstances that result in younger-than-expected wood remains is the fall of a tree branch that penetrates into an older sediment section. Except for this younger piece of wood, we found no signs of significant disturbance in sediment or the pollen spectra (Stivrins et al., 2017).

Tree-ring and sedimentary data on fire events

The tree-ring record from the stand surrounding Polttiais hollow indicated four fires: 1654, 1734, 1914 and 1949. While the number of fires from tree rings was the same for both Finnish and Russian sites, their spread in time was very different. The record from Tuominen (1990) showing fires for Naava and Kammekka hollows in 1773, 1827, 1857, and 1886.

All sediment sequences contained charcoal (microscopic to large charcoal pieces) which were further analysed individually and combined into a composite dataset (Figure 3). Interestingly, we observed several samples with macrocharcoal pieces in size of >1 mm but no significant microcharcoal (20–150 μm) values and *vice versa*.

The connection between Neurospora and other fire indicators

Neurospora abundance in samples was low and did not exceed eight spores per sample. In Kämmeikkä hollow, nine out of eleven, Polttiais hollow six out of seven and in Naava hollow 18 out of 19 *Neurospora* observations were in the same or neighboring slice with another fire indicator. The permutation test yielded *p*-values 0.16 for Kämmeikkä, 0.21 for Polttiais and 0.09 for Naava, whereas the *p*-value for pooled data was 0.01. Hence, even though the connection was not significant in separately analysed sequences, a statistically significant connection was found when all the sequences were pooled together.

The risk ratios for Kämmeikkä hollow was 3.5 (95% confidence interval (CI) 0.8–15.5), for Polttiais hollow 3.4 (CI 0.4–27.7) and Naava hollow 5.3 (CI 0.7–38.2) and when combining all the areas, the risk ratio was 4.3 (CI 1.5–11.8). All the risk ratios were well above one (3.4–5.3), but the confidence intervals were wide, and above one only for the pooled data.

Composite data for fire-event reconstructions

We used the composite of fire proxies (Figure 3) to compute the fire return intervals (FRI) (Table 2). The median FRIs were smaller than the mean FRIs indicating a skewed distribution of FRIs. In addition, it appeared that the uncertainty related to the sampling distribution of median or mean FRIs was more prominent than the uncertainty related to the timing.

The composite fire record from Polttiais hollow in western Russia showed that the fire frequency was lower 11–8 ka years ago but increased 8–4 ka years ago (Figure 4). Fire frequency slightly decreased 4–2 ka years ago but increased substantially over the last 1000 years. In Finland, the fire return interval was lower in Kämmeekkä hollow from 6.5 to 4 ka years ago and increased from two to seven fires per 1000 years in a period from 4 to 1.5 ka years ago. Fire frequency decreased from 1.5 ka to 600 years ago followed by an abrupt rise up to nine fires per 1000 years towards the present day. Naava hollow had on average four to five fire events per 1000 years 7.5 to 4 ka years ago, with a slight decrease 3–2 ka years ago and distinct increase in fire frequency afterwards, particularly over the last 600 years. A common feature in all fire reconstructions was the abrupt increase in fire frequency over the last 1000 to 500 years.

Discussion

Proxies of fire

Prior to further exploration of the results and their interpretation, it is necessary to discuss the validity and strength of proxies used in fire reconstructions. In palaeoecology, sedimentary charcoal has been used in numerous publications, but to a lesser extent as a compilation of different size categories. Empirical studies show that larger charcoal particles ($>150\text{ }\mu\text{m}$) fall out relatively close to its emission source ($<100\text{ m}$), and smaller particles ($20\text{--}150\text{ }\mu\text{m}$) can be windblown from a broader region ($>100\text{ m}$) (Clark and Patterson, 1997; Conedera et al., 2009; Whitlock and Larsen, 2001). Recently, Adolf et al. (2018) provided the first European-scale geospatial training set relating the charcoal signal in surface lake sediments to fire parameters recorded by moderate satellite resolution imaging spectroradiometer sensors. According to these findings, the source area for both microscopic and macroscopic charcoal particles is very similar and can regionally be 40 km in diameter. However, these results were obtained from somewhat open European vegetation conditions and lakes. In the

current study, only small (< 0.1 ha) forest hollows from densely forested conditions were analysed with a closed forest canopy. It is difficult to assess the source area of the smallest charcoal particles as they can spread over long distance in the air, but considering that for pollen, the source area in forest hollow usually is limited to 100 m (Overballe-Petersen and Bradshaw, 2011), it seems likely that also the sedimentary charcoal from such depository might reflect local fire events. Small-scale variability in fire occurrence can be seen from our results where two nearby hollows Naava and Kämmeikkä (located 90 m apart) did not record the same fire events. Nevertheless, as noted by Remy et al. (2018) and Pitkänen et al. (2001), fire events detected from terrestrial sedimentary environments are more spatially and temporally precise and robust than those detected from lake sediments.

The spatial and temporal precision of the fire record is not an issue for fire scar-based reconstructions. Trees record fires at specific locations and, when cross-dated, at an annual resolution. However, compared to the sediments, the time span of the tree-ring-based fire record is in most cases more limited rarely dating back more than the last several centuries (but see Wallenius et al., 2010). This time limitation is generally due to the short life span of the tree species, and the disappearance of fire scars with advancing decomposition following tree death. In addition, also fire scar-based reconstructions may suffer from imperfect detection, depending on the fire regime. In high-intensity fires all trees may be killed, leaving no fire scar record. In such instances, fires can still be deduced from tree age structures (Dansereau and Bergeron, 1993), but this information gradually disappears as post-fire age cohorts die. On the other hand, low-intensity fires may pass through a forest without leaving a scar (Piha et al., 2013), as large fire-adapted trees can sustain low-intensity fires without being damaged. In such a case, fires could locally produce charcoal and/or raise temperatures enough to induce growth of pyrolytic fungi (such as the *Neurospora* spp.), producing evidence of fire that is visible only in the sediment data.

In the field of non-pollen palynomorphs, ascospores of *Neurospora* (HdV-55c; with longitudinal ribs) and *Gelasinospora* (HdV-1, HdV-2, HdV-528; pitted spores) are usually counted

separately. However, genetic data suggest, that these two genera of Sordariaceae family should be united (Dettman et al., 2001; García et al., 2004). In a palaeoecological context, ascospores of *Gelasinospora* found in sediments have been associated with fires when found in sediment layers containing charcoal (Dietre et al., 2017; Kuhry, 1985, 1997; van Geel, 1978), or during dry conditions (van Geel, 1972). Shumilovskikh et al. (2015) demonstrated correspondence of *Gelasinospora* to charred layers and dry phases of *Sphagnum* peat bog development. Some studies, however, indicate that *Gelasinospora* species can be coprophilous as well as carbonicolous and lignicolous (Lundqvist, 1972; Krug, 2004). Likewise, *Neurospora* (HdV-55c) ascospores in palaeoecology are associated with fires, as they have been found in charred sediment layers (van Geel, 1978). The palaeoecological context of these ascospores usually refer to bog sediment sequences and thus far have not been used as a forest fire proxy.

Most field collections of *Neurospora* species contain isolates from tropical and subtropical regions, originating from either prescribed or natural fires. In general, natural populations of *Neurospora* often occur where fires are an essential part of the ecosystem (Perkins et al., 1975). The ascospores do not germinate under ambient temperatures, but they do germinate after being exposed to moist heat at 65–70° C for a few minutes. Therefore, for comparatively long time *Neurospora* spp. were thought to belong only to moist tropical and subtropical regions, but more recent literature has made it clear that particular species are common primary colonizers of trees and shrubs after the forest fires also in North America and Europe (Jacobson et al., 2006; Luque et al., 2012). In particular, Kuo et al. (2014) showed that *Neurospora* spp. can grow as a symbiont (endophyte) within Scots pine, rapidly shifting to a parasitic or saprophytic lifestyle following a fire. Moreover, *Neurospora* spp. ascospores were not detectable in the soil after wildfire in samples taken after wildfire from Indonesia and Finland, rather *Neurospora* spp. survive the wildfire within the tree trunk (Kuo et al., 2014).

Typical “orange bloom” developing on the charred tree trunks consists mainly of conidia containing conidium spores – micro and macro conidiospores with a typical size of 3 µm × 4 µm and

5 μm \times 9 μm respectively (Lee, 2012; Maheswari et al., 1999). In contrast to the ascospores, increased heat is not necessary for conidiospores to develop (Maheswari et al., 1999). In our samples, none of the particles detected corresponded to a size characteristic to the conidium spores, only ascospores with their characteristic surface morphology (ribbed or pitted) and size 20–30 μm . All in all, the use of *Neurospora* spp. as a fire proxy requires a completion of a full life cycle, starting with germination of ascospore initiated by heat, continued by the formation and development of perithecium, and culminating in the maturation of new asci that produce significant amounts of ascospores.

Compared to the use of charcoal as a fire proxy, *Neurospora* spp. has the additional advantage that it can potentially be used to constrain the season of fire occurrence. The minimum temperature for *Neurospora* spp. development from the germinated ascospores is 4°C (Dix and Webster, 1995). In laboratory settings, the development of perithecium, generation of asci and spore maturation has taken approximately one month. It is likely that in a forest setting this process takes an even longer time (Lee, 2012). Therefore, hypothetically, if a wildfire has occurred in the boreal forest during late autumn/winter time, it is most likely that no *Neurospora* spp. perithecium will develop even if the heat treatment from a wildfire was present, leaving no trace from such late season fires. Hence, findings of *Neurospora* spp. indicate fires occurring during spring/summer.

Fire-events in the Northern European boreal forest

For the period for which we had data for fire proxies, *Neurospora* was linked with the two other, well-known proxies. Based on this relationship and the autecology of this fungus (i.e., its dependence on high temperatures), we suggest that integrating these different proxies complements the fire record and helps to improve our understanding of fire occurrence in the boreal forest. The fire history reconstructions developed here indicated that, on average, the fire occurred every 126 to 237 years (median 52 to 137 years) in these studied forests (Table 2).

Analyzed separately, the mean and median fire return intervals in the Polttiais hollow in western Russia were 237 and 137 years over the last 11 ka years. For the Finnish sites, the mean fire return intervals were 126–143. These long-term estimates of fire return interval are within the range for modern boreal forest fire intervals of 50–200 years (Bonan and Shugart, 1989), but shorter than many previous long-term fire history reconstructions from these regions indicate (Pitkänen et al., 2002). For example, Kuosmanen et al. (2014) used microscopic charcoal particles to study the effect of local fire on the forest in western Russia (in the same region as Polttiais hollow; Fig.1) and suggested relatively few fire events, or even an absence of local fires during the Holocene (last ca 12 ka years), depending on the site. In a similar study, Clear et al. (2013) used macroscopic charcoal data from the small forest hollow to study the fire frequency variability in Vesijako, Finland. The mean fire frequency was estimated as 430 years in semi-natural conditions (5–2 ka years ago), 180 years during anthropogenic influence (2 ka to 750 years ago) and no fires over the last 750 years (Clear et al., 2013). In fire-scar based reconstruction, Wallenius et al. (2007) estimated a 50-year fire interval for the 17th and 18th century for the region, before the cessation of fires in the mid-19th century.

Variability of the fire return interval can be partly explained by the substantial changes in climate over the entire Holocene, and changes in human impact especially in the more recent past. During the 11.7–8.2 ka years ago, air temperatures were lower than present in western Russia and Finland (Kuosmanen et al., 2016). The warmest period appeared within the 8.2–4.2 ka years ago and during the last 4.2 ka years temperatures decreased gradually (Seppä et al., 2009b). However, while analyses on fire-climate relationships often rely on temperature reconstructions as the primary driver of the forest dynamics (Kuosmanen et al., 2016), the use of recently accomplished precipitation reconstructions have shown that concomitant decreases in precipitation may induce increased fire occurrence during colder time periods in the European boreal forest (Aakala et al., 2018). This makes explaining changes in fire frequency as a function of climate variability less straightforward.

A much stronger signal in the fire record was the increased fire frequency in the last ca 1000 years that is likely linked to increased human activities. While the timing and the intensity of changes in human activities have differed between the study regions, both have been subjected to similar fire-conducive human impact in the past (Tikkanen and Chernyakova, 2014; Wallenius, 2011). These have included slash-and-burn agriculture which has been an active use of fire to alter the landscape, but also probably unintentionally from other human activities such as fire spread from hunters' campfires. Huttunen (1980) notes that the Evo region, where Naava and Kämmeikkä hollows are located, comprises only 1–2% arable land and slash and burn cultivation with the clearing of forest for agricultural purposes was carried out rarely, whereas around 20 km towards the south at Lammi, the land becomes more fertile and as such more suitable for cultivation. In line with this, Stivrins et al. (2017) showed that the first crop pollen indicating agricultural practices appeared only 400 years ago at Naava and Kämmeikkä hollow, while in other areas of Finland, an intensification of slash and burn activity can be seen in the charcoal records after 1000 cal yr BP due to the expansion of cultivation and establishment of more permanent settlements (Alenius et al., 2013; Lagerås, 1996; Taavitsainen et al., 1998).

Earlier studies have demonstrated that using various charcoal size categories with a combination of fire-scar data may aid in gaining more comprehensive information about the occurrence of forest fires. However, we suggest that including *Neurospora* as a complementary proxy for fire reconstructions can further improve our understanding of fire occurrence. An additional advantage of *Neurospora* is that the germination and spread of their spores occurs over more extended time (e.g. days to weeks) compared to charcoal production during a fire event and are hence less dependent on short-term weather (particularly wind) conditions, increasing the probability of detection from sediments. Using multiple types of evidence for tracking past fires still needs more experimental studies to understand the strengths and weaknesses of these different fire proxies.

Conclusions

In this study, we presented a novel approach for past fire event reconstruction. We utilized three types of independent fire proxies – fire scar, charcoal and fungal spore of *Neurospora* spp. – to create a composite data set that was statistically analysed and used to reconstruct fire events in two study areas in the boreal forest. While each proxy has its strengths and weaknesses that require further research, our findings suggest that adding an additional complementary proxy (here: the spores of *Neurospora* spp.) complements the fire record, suggesting that fire reconstructions based on a single proxy technique may provide underestimates about past fire activity.

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Figure 1. Location of studied sites in Fennoscandia and western Russia (A): 1 – Naava hollow (B); 2- Kämmeikkä hollow (C); 3 – Polttiais hollow (D). We compared our findings to nearby sites studied earlier: 4 – Sudenpesä (Clear et al., 2015); 5 – Vesijako (Clear et al., 2013); 6 – Kukka hollow, 7 – Larix hollow, 8 – Mosquito hollow and 9 – Olga hollow (Kuosmanen et al., 2014).

Figure 2. Bacon age-depth models for (A) Polttiais hollow, (B) Naava hollow and (C) Kämmeikkä hollow. The calibrated ^{14}C AMS dates are shown in transparent blue, and the age-depth model is shown in grey (darker greys indicate more likely calendar ages; grey stippled lines show 95% confidence intervals). The red curve is the posterior mean chronology. The laboratory numbers for the ^{14}C AMS dates are also shown (see Table 1). Biostratigraphic marker of *Picea* pollen values according to Naava hollow data and southern Finland *Picea* pollen-stratigraphical patterns (Supplementary material 1).

Figure 3. Fire proxies in Polttiais (A), Naava (B) and Kämmeikkä (C) hollow, as a function of depth. Fire proxies are represented by quadrats – microscopic charcoal (20–150 μm), stars – macroscopic charcoal (150 μm –1 mm), diamonds – large charcoal pieces (>1 mm), asterisk – fire scar (assigned into a sediment sample whose age appears to match it the best) and filled circles – *Neurospora*.

Figure 4. Fire frequency for Polttiais (A), Naava (B) and Kämmeikkä (C), hollow. Dots at the top of boxes indicate the sampling density, a higher row of crosses – the inferred fires and the lower row of crosses – the fires in 120-year bins. Black curve – the posterior mean of the fire frequency and gray band – the 95% highest density interval. Horizontal axis - time in years before present. Vertical axis - fire frequency

Table 1. ^{14}C Accelerator mass spectrometry and biostratigraphic dates used in age-depth models of Polttiais, Naava and Kämmeikkä hollows.

Table 2. The mean and median fire return intervals with three different sources of uncertainty.

Timing: posterior mean of the mean or median fire return interval along with the credibility interval computed from the Bacon chronologies. Bootstrap: the mean and median of the fire return intervals using the mean chronology along with the bootstrap-based confidence interval. Both: The posterior mean of the mean (median) fire return interval along with the uncertainty limits that considers the timing uncertainty and the uncertainty from the estimation of the sampling distribution of the mean (median).

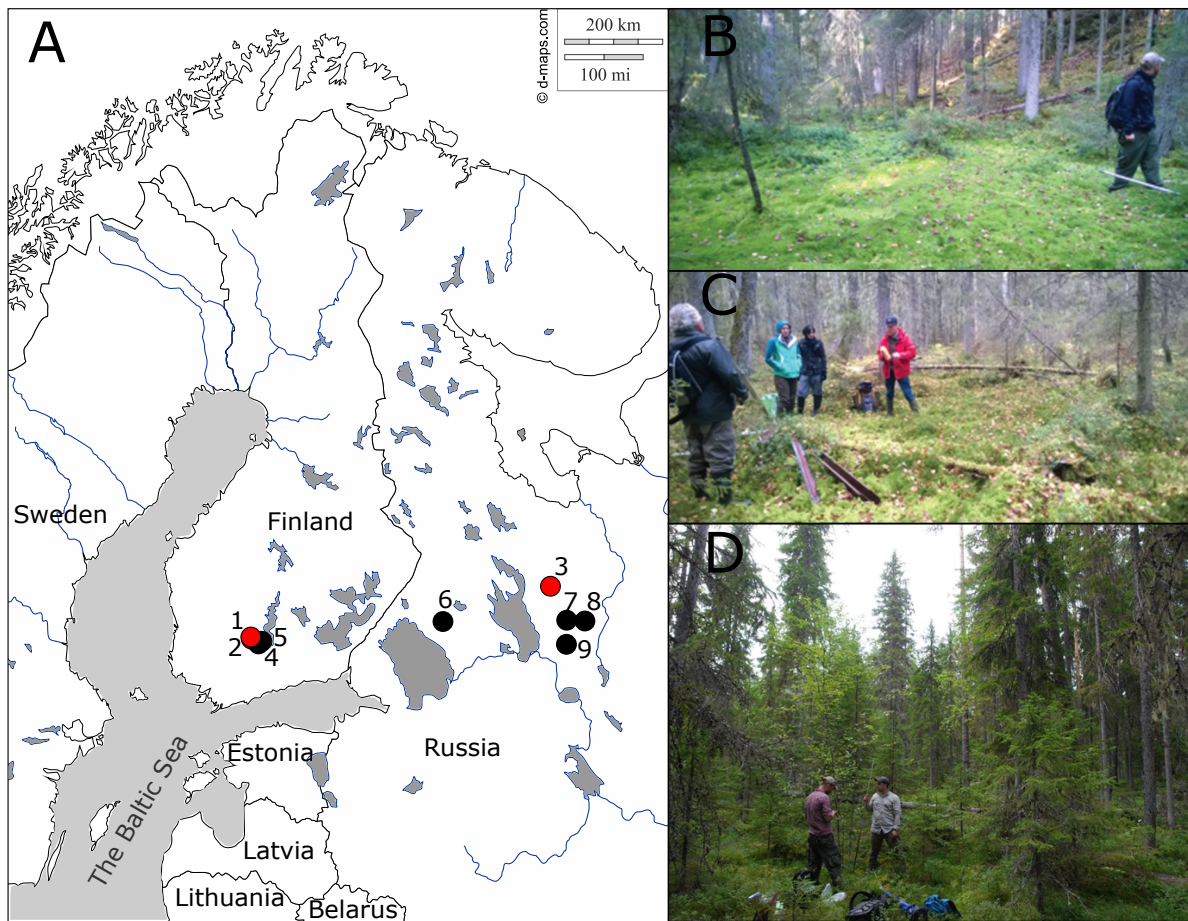


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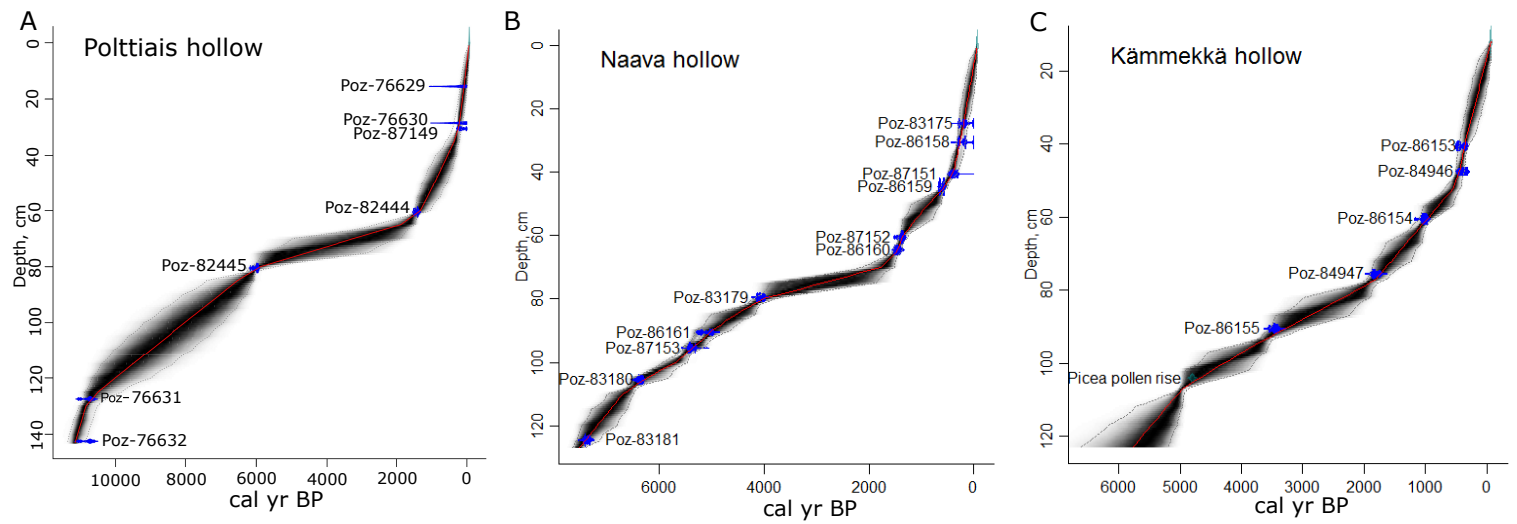


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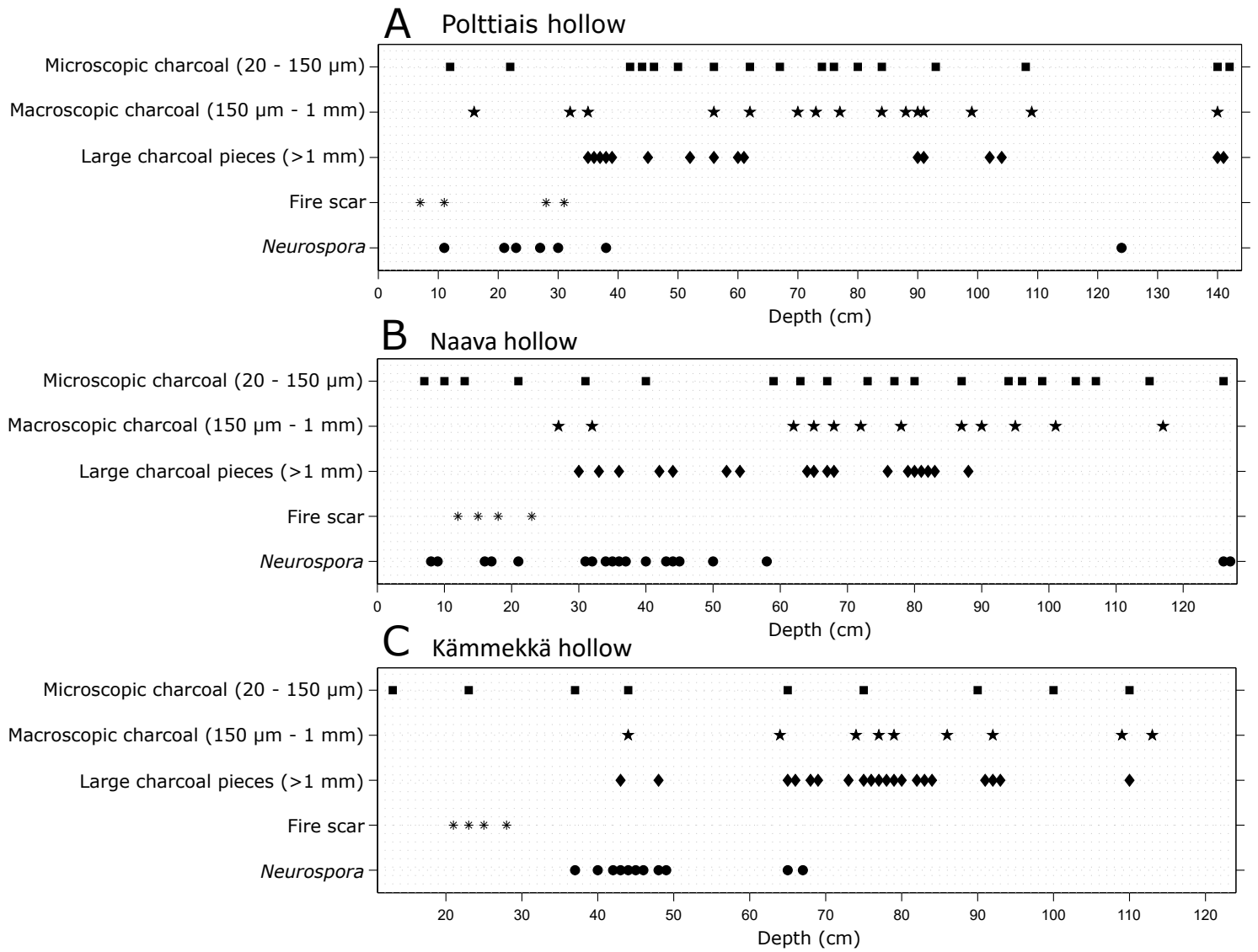


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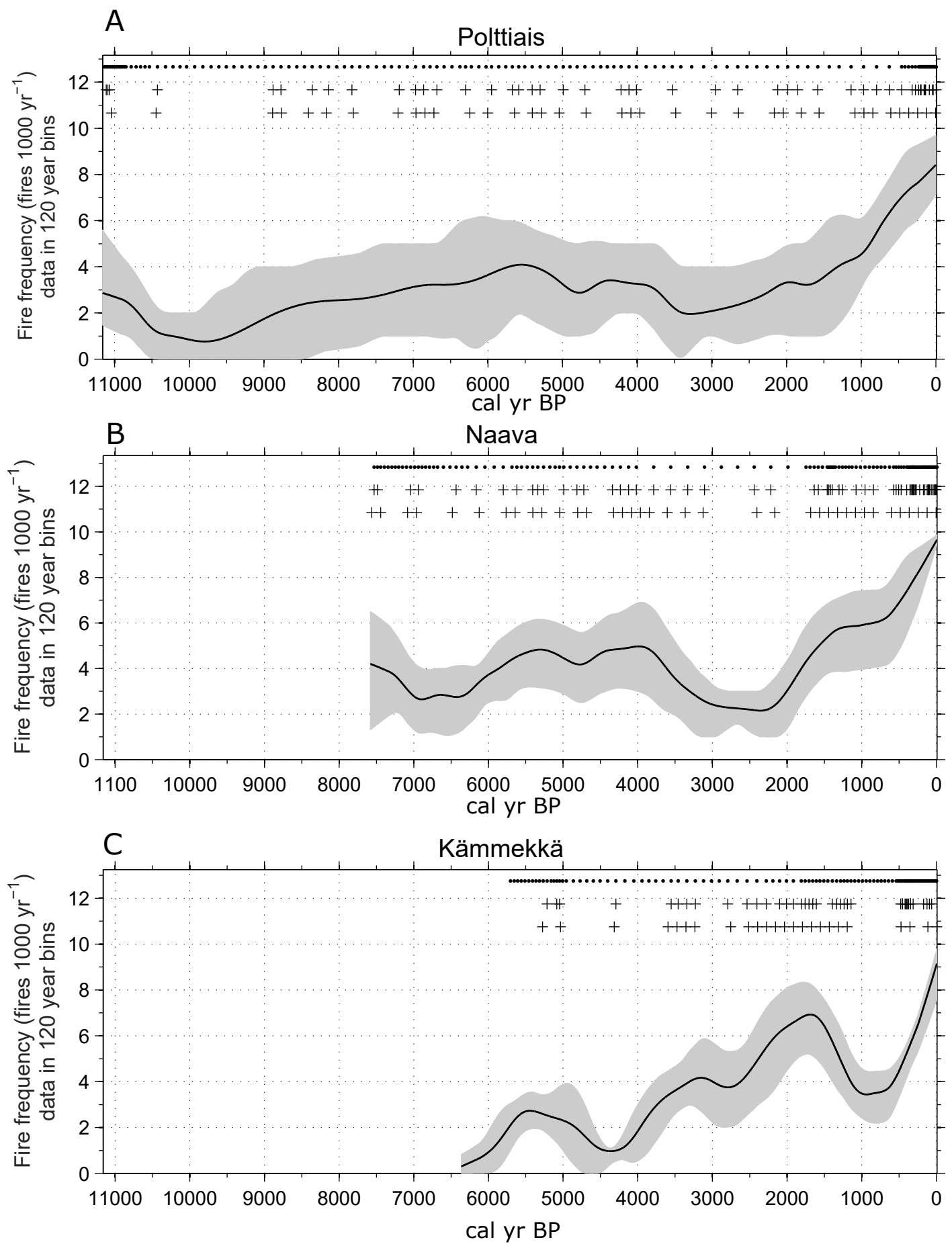


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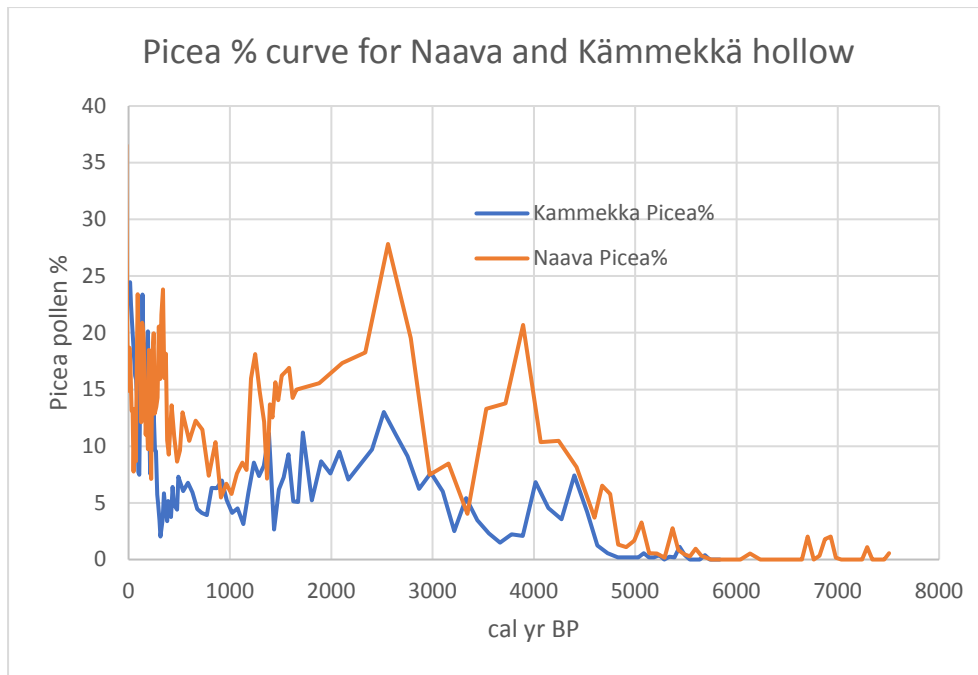
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Site	Depth, cm	Laboratory number	Age, ^{14}C	Cal yr BP, 95% ranges	Material dated/notes
Polttiais hollow	15–16	Poz-76629	125.07±0.37 pMC	75–115	Two seeds of <i>Picea abies</i> , one stem of <i>Polytrichum</i> sp.
Polttiais hollow	28–29	Poz-76630	122.33±0.37 pMC	70–120	Stems of <i>Polytrichum</i> sp. and <i>Sphagnum</i> sp.
Polttiais hollow	30–31	Poz-87149	155±30	155–285	bulk, peat
Polttiais hollow	40–41	Poz-82443	3743±35	3985–4230	bulk, peat; Not used in the model because of an outlier
Polttiais hollow	60–61	Poz-82444	1530±30	1350–1525	bulk, peat
Polttiais hollow	80–81	Poz-82445	5240±35	5920–6180	bulk, peat
Polttiais hollow	100–101	Poz-87150	3185±35	3350–3480	bulk, peat; Not used in the model because of an outlier
Polttiais hollow	127–128	Poz-76631	9480±50	10580–11070	<i>Sphagnum teres</i> stems
Polttiais hollow	142–143	Poz-76632	9480±60	10573–11080	Three fruits + two fragm. of fruit scales of <i>Betula</i> sec. Alba, one fruit scales of <i>Populus</i> sp.
Naava hollow	24–25	Poz-83175	190±30	-5–300	Plant remains
Naava hollow	30–31	Poz-86158	210±30	-5–305	Bulk, peat

Naava hollow	40–41	Poz-87151	315±30	300–465	Bulk, peat
Naava hollow	44–45	Poz-86159	655±30	560–670	Bulk, peat
Naava hollow	60–61	Poz-87152	1495±30	1310–1515	Bulk, peat
Naava hollow	64–65	Poz-86160	1560±30	1390–1530	Bulk, peat
Naava hollow	79–80	Poz-83179	3730±30	3980–4150	Plant remains
Naava hollow	90–91	Poz-86161	4445±30	4890–5280	Bulk, peat
Naava hollow	95–96	Poz-87153	4635±35	5305–5465	Bulk, peat
Naava hollow	105–106	Poz-83180	5600±40	6300–6450	Plant remains
Naava hollow	124–125	Poz-83181	6480±40	7315–7465	Plant remains
Kämmekkä hollow	40–41	Poz-86153	370±30	320–500	Bulk, peat
Kämmekkä hollow	47–48	Poz-84946	335±30	310–475	<i>Picea abies</i> needle + wood
Kämmekkä hollow	60–61	Poz-86154	1115±30	940–1170	Bulk, peat
Kämmekkä hollow	75–76	Poz-84947	1880±35	1725–1890	Charcoal
Kämmekkä hollow	90–91	Poz-86155	3240±35	3390–3560	Bulk, peat
Kämmekkä hollow	104			4800	Picea pollen rise
Kämmekkä hollow	123.5	Poz-84948	3820±35	4090–4400	Wood; excluded from the age-depth model due to outlier.

Table 2 The mean and median fire return intervals with three different sources of uncertainty. Timing: posterior mean of the mean or median fire return interval along with the credibility interval computed from the Bacon chronologies. Bootstrap: the mean and median of the fire return intervals using the mean chronology along with the bootstrap-based confidence interval. Both: The posterior mean of the mean (median) fire return interval along with the uncertainty limits that considers the timing uncertainty and the uncertainty from the estimation of the sampling distribution of the mean (median).

		Mean	Median
Polttiais	Timing	237 (231–244)	137 (91–181)
	Bootstrap	237 (167–312)	168 (106–267)
	Both	237 (139–373)	137 (45–262)
Naava	Timing	126 (123–129)	52 (34–71)
	Bootstrap	125 (91–170)	62 (34–105)
	Both	126 (78–183)	52 (21–128)
Kämmekkä	Timing	143 (130–161)	64 (41–94)
	Bootstrap	135 (84–194)	54 (47–114)
	Both	143 (72–259)	64 (25–135)



Supplementary material 1. *Picea* pollen (%) curve of Naava and Kämmeikkä hollow.

Supplementary Material 2

Using CharAnalysis for small hollow data

The macroscopic and microscopic charcoal records underwent statistical analysis using the program CharAnalysis, which is a set of diagnostic and analytical tools designed for analysing sediment-charcoal records when the goal is peak detection to reconstruct ‘local’ fire history (Higuera, 2009, CharAnalysis manual). CharAnalysis decomposed the record into low- and high-frequency components in order to determine significant fire episodes. First raw charcoal series was interpolated to equally spaced time intervals (using the age-depth model; Figure 2 in the article) in order to define the interpolated charcoal record C_{int} (particles $\text{cm}^{-2} \text{yr}^{-1}$). Brossier et al. (2014) have found that the median temporal resolution from the entire raw sequence (the default option in CharAnalysis) is too low for interpolation and therefore suggest that the optimal temporal resolution for the interpolation should be $<0.12\text{--}0.20$ times the mFFI (median fire free interval). For this purpose, we estimated the mFFI based on the fire scars observed in the three small hollows, resulting 5-year time steps for each hollow.

The non-log transformed C_{int} series was then smoothed with a Lowess smoother, robust to outliers, in order to define $C_{\text{background}}$ which is the low-frequency trend in C_{int} . We followed the guidelines of Brossier et al. (2014) and selected the smoothing window width to be the smallest width which resulted signal to noise index (SNI) >3 and the goodness of fit test values smaller than 0.1. This resulted us with the following smoothing window widths: Kämmekkä 800 yr, Naava 800 yr and Polttiais 1200 yr. We denote by C_{peak} the high-frequency component in C_{int} , obtained by subtracting $C_{\text{background}}$ from C_{int} . We used a local Gaussian mixture model for detecting possible fire-events from C_{peak} samples (Higuera, 2009, CharAnalysis manual). After this CharAnalysis performs a further “minimum count” screening where it removes those fire-events that appear to be insignificant. In the “minimum count” screening, CharAnalysis tests the fire-events one by one by assessing whether the interpolated charcoal accumulation rate (particles $\text{cm}^{-2}\text{yr}^{-1}$) in 75-year window before and after the event are from the same Poisson distribution. If an event passes the test, it is indicated as a significant fire-event.

If a group of possible fire-events occur in consecutive time points, CharAnalysis screens only the oldest event and if the test is passed, the significant fire-event is located in the oldest time point. Such a procedure works well when analyzing the lake charcoal sediment as their profiles are spiked with not many consecutive events. However, in the case of small hollows, we had many consecutive events and the oldest time point in the event group was not necessarily the

one with the highest charcoal accumulation rate. Hence, we adjusted the significant event to be the one with the largest accumulation rate in the group or the middlemost one in the case when no single value was clearly higher than the others. Furthermore, a larger window than 75 years may be needed if the time window from the oldest event to the newest event in a consecutive fire-event group is longer than 75 years, but this was not the case here.

The macroscopic and microscopic charcoal abundancies along with the significant events are shown in Figure 1–3. The figures show that without the adjustment the event locations for the significant peaks would be occasionally remarkably different.

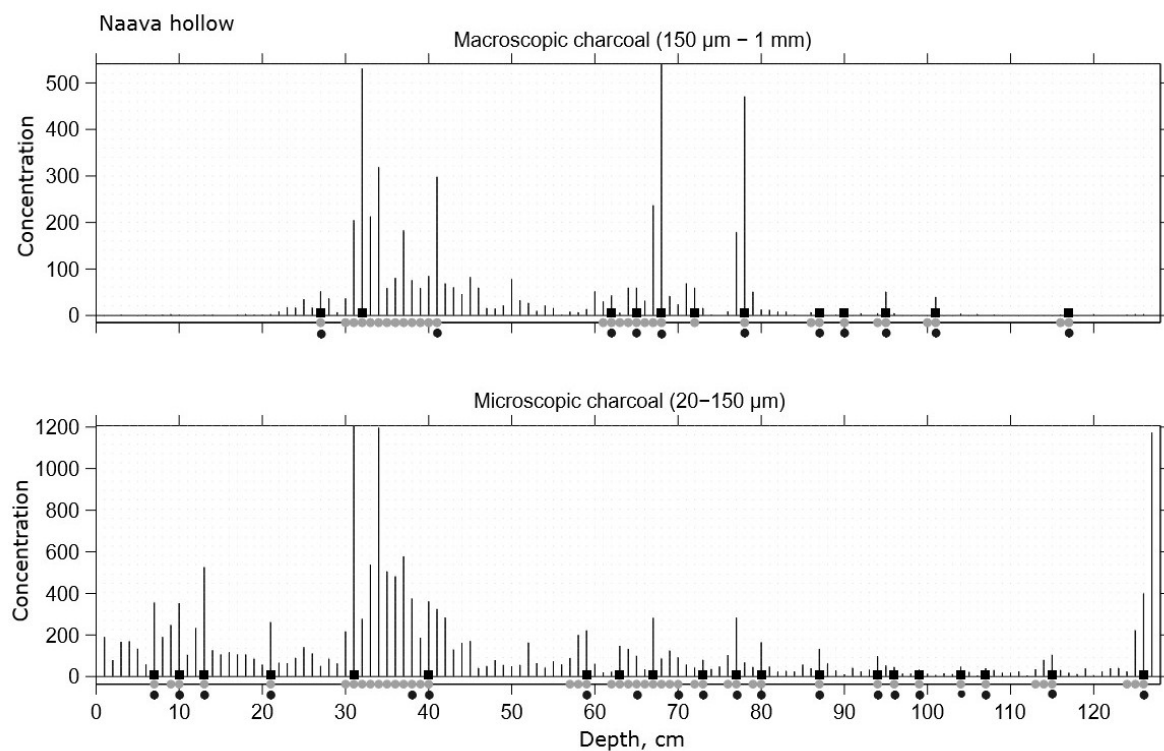


Figure 1. Macroscopic (upper panel) and microscopic (lower panel) charcoal abundancies for Naava hollow in the original sediment samples. Gray dots indicate the sample groups that are screened as significant. The black squares show the adjusted locations of detected events and black dots show the unadjusted locations of events (see text for further information). Note that the vertical axis has been cut from above for aiding the visualization.

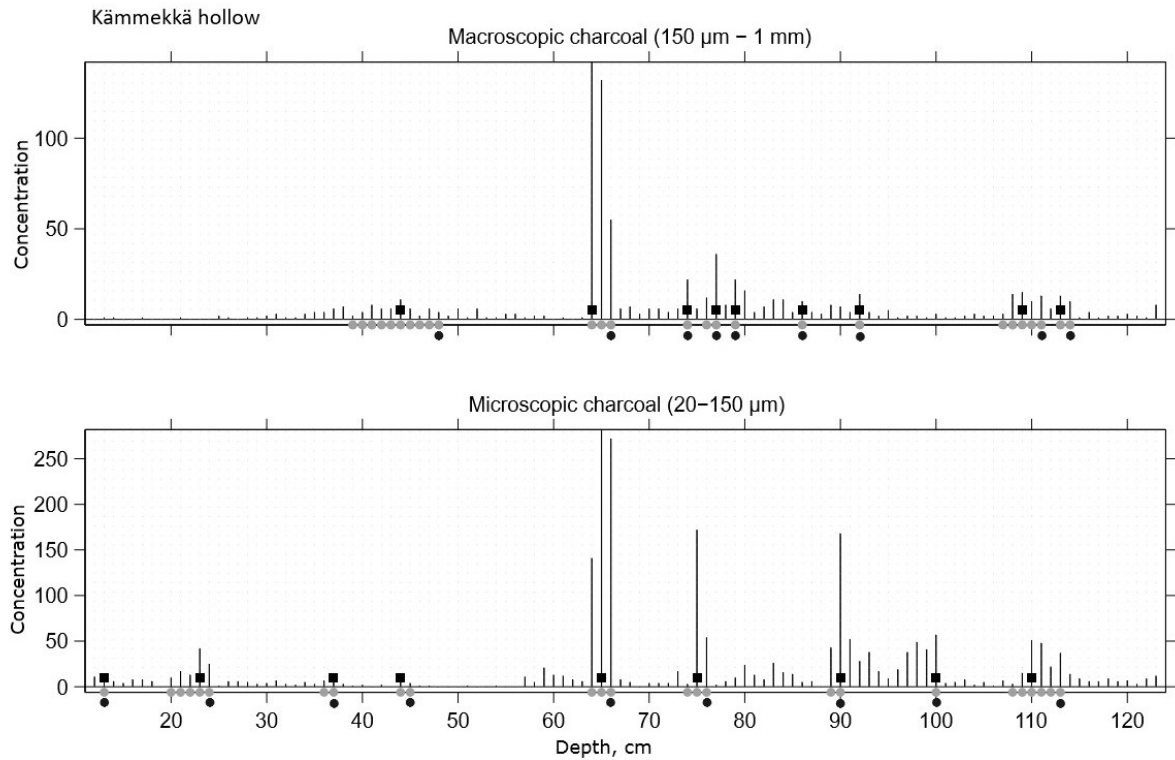


Figure 2. Macroscopic (upper panel) and microscopic (lower panel) charcoal abundances for Kämmeikkä hollow along with the identified events. See the caption of Figure 1 for further information.

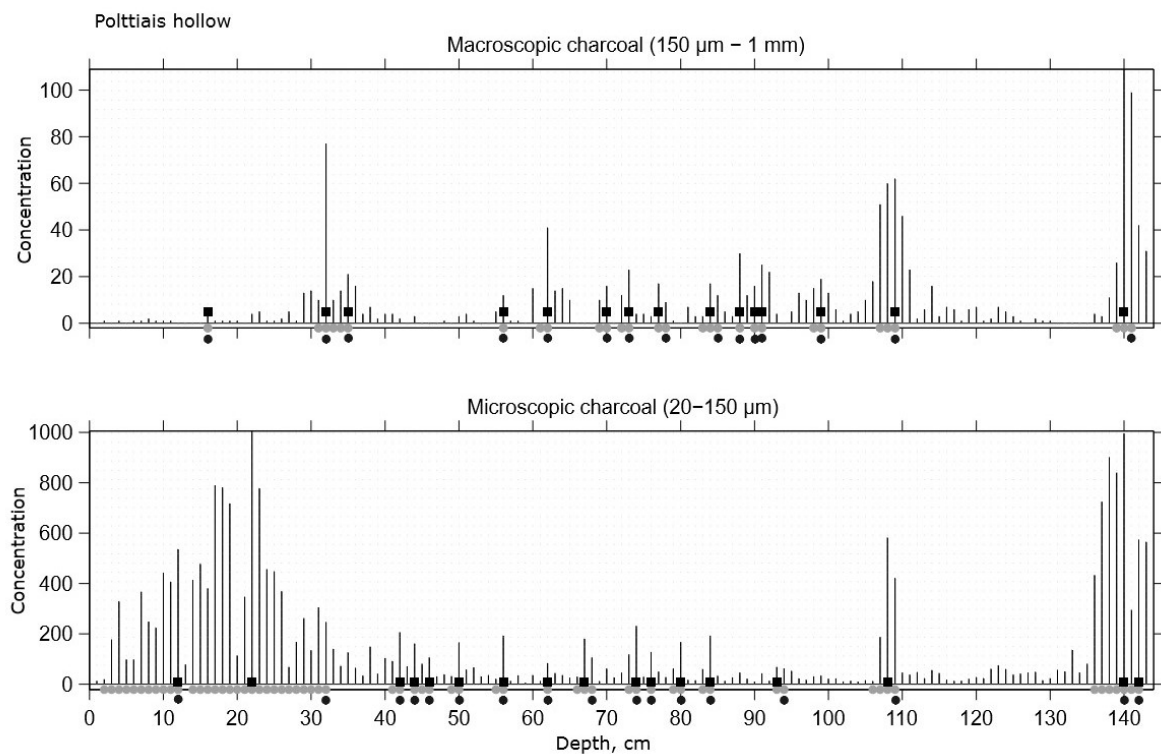


Figure 3. Macroscopic (upper panel) and microscopic (lower panel) charcoal abundances for Polttiaishollow along with the identified events. See the caption of Figure 1 for further information.