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Holocene fire history of forest vegetation in central Europe based on soil and sedimentary charcoal

Holocenní dynamika požárů lesní vegetace v pískovcových oblastech založená na studiu uhlíků v půdních profilech

Doctoral thesis

Supervisor: Doc. RNDr. Petr Kuneš, Ph.D.

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Prohlášení

Prohlašuji, že jsem závěrečnou práci zpracoval samostatně a že jsem uvedl všechny použité informační zdroje a literaturu. Tato práce ani její podstatná část nebyla předložena k získání jiného nebo stejného akademického titulu.

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List of original publications

This thesis is based on the following papers. The contributions of the author are as follows.

Martin Adámek, **Přemysl Bobek**, Věra Hadincová, Jan Wild, Martin Kopecký (2015): Forest fires within a temperate landscape: A decadal and millennial perspective from a sandstone region in Central Europe. *Forest Ecology and Management* 336:81–90.

- Fire history data based on soil charcoal: PB 50 %
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- Charcoal data collection and fire hisrory reconstruction: PB 100 %
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Abstrakt

Požár je fundamentálním ekologickým faktorem, který přímo formuje mnoho terestrických ekosystémů na Zemi. Předkládaná práce se snaží poskytnout ucelený pohled na požárovou dynamiku v kontextu podmínek střední Evropy v průběhu posledních 12 000 let. Dřívější požárová aktivita byla zkoumána pomocí analýzy uhlíků obsažených v terestrických a lakustrinních sedimentárních sekvencích a zuhelnatělých rostlinných tkání deponovaných v půdách. Díky velkému počtu lokalit bylo možné dosáhnout rekonstrukce požárové aktivity na více prostorových úrovních – od lokálního až po krajinné měřítko. První část práce se zabývá identifikací hlavních faktorů, které podmiňují současný výskyt požárů, a na základě zjištěného vztahu hledá vazbu na distribuci požárů v krajině v průběhu mladšího holocénu. Podařilo se ukázat, že výskyt požárů je v současnosti řízen především abiotickými faktory odvozenými od charakteru reliéfu, jako je vyšší přísun sluneční energie na svazích a zvýšená členitost terénu. Naproti tomu antropogenní faktory vykazovaly nízkou míru vlivu. Vzhledem k tomu, že faktory determinující aktuální výskyt požárů jsou v průběhu holocénu stabilní, lze předpokládat, že existují stanoviště, která mají predispozici pro dlouhodobě zvýšenou požárovou aktivitu. Opakované požárové disturbance tak na těchto stanovištích zřejmě významně přispěly k udržení vegetace borů, která díky tomu odolala konkurenčnímu tlaku listnatých dřevin v průběhu klimatického optima holocénu.

Druhá část práce se zaměřuje na holocenní dynamiku požárů a vegetační vývoj v dílčí oblasti severočeské pískovcové krajiny. Ukázalo se, že požárová aktivita do značné míry koresponduje s dlouhodobým trendem změn klimatu, avšak v průběhu mladšího holocénu je navíc zásadně ovlivněna i způsobem antropogenního využívání krajiny. Nejvýraznější nárůst frekvence požárů byl identifikován v průběhu pozdní doby bronzové a během doby železné, což pravděpodobně souvisí s přímým využitím pískovcové oblasti lidmi. Lokální pylový záznam dokládá možné krátkodobé využití žárového zemědělství praktikovaného v období lužické kultury a následnou orientaci subsistenční strategie zdejší lidské populace na lesní pastvu hospodářských zvířat. Extenzivní antropogenní využití pískovcové krajiny v době bronzové spojené s opakovaným vypalováním lesa tak pravděpodobně způsobilo, nebo alespoň významně urychlilo degradaci zdejšího přírodního prostředí.

Dalším krokem k ucelenému pohledu na požárovou historii oblasti střední Evropy bylo využití uhlíků obsažených v půdních profilech temperátního horského lesa, které byly rozsáhle radiokarbonově datovány, a propojení těchto dat s pylovým a uhlíkovým záznamem z rašeliniště. Tento přístup umožnil odhadnout minimální frekvenci požárů na velmi jemné prostorové škále v průběhu celého postglaciálního období a zhodnotit možný vliv požárů na dlouhodobý vývoj půd. Výsledky ukázaly, že změna dominantní jehličnaté vegetace z období časného holocénu na vegetační typy s převahou listnáčů vyvolala zásadní pokles četnosti výskytu požárů v průběhu středního a mladšího holocénu. Požárové disturbance také ovlivňovaly průběh podzolizačního procesu a podílely se na formování vysokého stupně půdní diverzity zkoumané oblasti.

Závěrečná část práce se pokouší o syntézu všech získaných údajů o holocenním výskytu požárů na území ČR. Na základě změn koncentrací uhlíků v sedimentárních profilech mnoha rašelinišť byly odvozeny společné trendy požárové aktivity v dílčích regionech. Ty byly srovnávány s dlouhodobými změnami vegetace detekovanými pomocí pylové analýzy. Z výsledků vyplývá, že vysoká požárová aktivita charakteristická pro období časného a středního holocénu byla zásadně utlumena v důsledku šíření lesní vegetace s dominancí buku lesního. Tento obecný pokles požárových disturbancí byl kompenzován až zvýšeným antropogenním vlivem, který způsobil nárůst požárové aktivity v mladším holocénu. Z toho lze odvodit závěr, že požárová dynamika v lesních ekosystémech střední Evropy je řízena především lokálními faktory, jako je druhové složení vegetace a míra antropogenního vlivu.

Abstract

Fire is a fundamental environmental factor that directly shapes many terrestrial ecosystems on Earth. The present thesis attempts to provide a comprehensive overview of the fire dynamics in Central Europe over the course of the last 12,000 years. Based on extensive analyses of charcoal particles deposited in terrestrial and lacustrine sedimentary sequences and carbonized plant tissues deposited in soils, I was able to track past fire dynamics across a range of spatial scales – from the forest stand scale to the landscape scale. First, we described relationships between drivers of recent fire occurrence and proposed linkages to the spatial pattern of Late-Holocene biomass burning. We found factors related to relief characteristics, such as increased thermal flux or terrain roughness, to be important determinants of fire occurrence within the present-day landscape. Contrary to all expectations, anthropogenic drivers seem to have a weak influence at present. Because relief-based factors have been stable throughout the Holocene, it seems probable that habitats of certain types are more predisposed to increased burning. We hypothesized that recurrent fire disturbances may contribute to the long-term maintenance of Pinus sylvestris-dominated forests, which withstood the competitive pressure of broadleaf vegetation during the Holocene climatic optimum.

Based on multi-proxy evidence I reconstructed the fire history of and vegetation development within a sandstone landscape in northern Czechia. I found that the general pattern of fire activity corresponds to broad climatic trends but that it also reflects changes in human land-use practices during the Late Holocene. A major shift in the fire regime occurred during the Late Bronze Age and Iron Age, when the frequency of fires increased markedly as a probable consequence of landscape exploitation by humans. The pollen record suggests the possible practising of short-term slash-and-burn cultivation by people of the Lusatian culture and subsequent pastoral activity. Accordingly, a profound environmental transformation of sandstone landscapes during the Bronze Age was triggered or at least accelerated by widespread anthropogenic burning.

The next step towards a comprehensive overview of the fire history of temperate Central Europe was to employ a spatially-precise soil charcoal record, extensively dated using ^{14}C and combined with pollen and sedimentary charcoal. This approach allowed me to estimate stand-scale fire frequencies within a temperate mountain forest and to assess linkages between fires and soil development. I showed that biotic change from needle-leaf dominated Early Holocene forests to broadleaf vegetation induced a substantial decrease of fire activity. In addition, fire likely influenced the process of podzolization and partly contributed to the high degree of soil diversity in the region.

Finally, a synthesising effort was made to collected datasets on fire occurrence. Regional trends in biomass burning were identified by means of compositing multiple-site charcoal records. These were compared with long-term shifts in vegetation inferred from pollen data. I found that the elevated fire activity during the Early and Middle Holocene declined sharply as a response to a regional spread of Fagus sylvatica-dominated forest communities. Conversely, human activity resulted in an increase in biomass burning during the Late Holocene. This suggests that bottom-up controls such as vegetation composition and human activities are important determinants of fire activity in Central European forest ecosystems.

Chapter 1: General introduction

1.1 Fire in the Earth system

Fire is an important environmental factor influencing the behaviour of many terrestrial ecosystems on Earth. Its effects on global biogeochemical cycles (Dunnette et al., 2014; Leys et al., 2016a), biodiversity (Pausas and Ribeiro, 2017), soil properties (Certini, 2005) and the functioning of soils are to a large extent tied to changes in human communities. Combustion of plant biomass is an important source of atmospheric carbon dioxide emissions, which have the potential to affect the climate on the planetary level (Ruddiman, 2003). However, the burning of biomass also produces varying amounts of inert forms of carbon that accumulate in the soil environment. Soils then become a long-term pool of carbon, which, conversely, contributes to the reduction of the greenhouse gas carbon dioxide in the atmosphere (Czimczik et al., 2007). The fossil record of fire activity in the form of carbonized parts of plants provides information about the occurrence of wildfires far into Earth's history when the concentration of oxygen in the atmosphere reached 13 %, which permits the combustion of organic matter (Scott et al., 2006). At the same time it proves that fire was an integral part of natural processes in Earth's biosphere long before the arrival of man. At the shorter time scale of the Quaternary we can observe how the occurrence of fires oscillates hand in hand with global changes of the climate in connection with the alteration of glacial and interglacial periods (Daniau et al., 2010a; Fischer et al., 2015b). Warm periods were characterized by greater ecosystem productivity, which, besides elevated temperatures, was manifested by increased fire activity. Conversely, the cold conditions of glacial periods were associated with significant reductions in the amount organic matter and fire activity was limited by its availability (Daniau et al., 2010a; Pausas et al., 2013). Fire has therefore long been an inseparable component of Earth's biosphere and has induced pronounced evolutionary effects on organisms having to adapt to this phenomenon (Keeley et al., 2011). As a result, many plant species exhibit morphological adaptations to high temperatures, such as a thick insulating layer of bark in the genus *Pinus* or so-called serotinous cones releasing diaspores only under the influence of increased temperatures. However, not only individual organisms, but also whole communities, adapted to fires (Keeley et al., 2005). The existence of some communities is to a large extent even dependent on regular fire disturbances. In tropical regions there are vast expanses of savannas where cyclic fire-related disturbances block successional development towards forest communities and, in the long term, maintain the ecosystem in an alternative stable state (Bond et al., 2004; Shanahan et al., 2016). Wildfires are an important factor also in the dynamics of boreal forests, where they are the main disturbance factor influencing the species composition and age structure of forest communities (Zackrisson, 1977; Payette, 1992; Bergeron et al., 2001). In addition, wildfires significantly reduce the amount of humus present in upper soil layers, which fundamentally influences carbon sequestration and mobilizes nutrients bound to organic matter (Zackrisson et al., 1996). Other biomes, such as temperate grasslands and Mediterranean scrublands, also exhibit a heightened proneness to the occurrence of wildfires, and fire significantly affects their functioning and fundamentally determines their areal extent (Bond et al., 2004; Pausas, 2006; Vanniere et al., 2011). From the perspective of fire-prone ecosystems, the occurrence of fire in the conditions of the temperate part of Europe may appear to be a secondary factor with limited influence on the functioning of ecosystems on the continent (Leuschner et al., 2017). Over the last decades, however, there has been a growing body of evidence that fire has been an important factor in the development of post-glacial vegetation also in this climatic region. The present thesis attempts to supplement the current state of knowledge about the significance of fire as a factor influencing the biota of Central Europe.

1.2 Proxies of past biomass burning

Wildfires are a complex phenomenon involving interactions between the atmosphere, vegetation, relief and mankind. To attain a thorough understanding of the mutual relationships between these factors, it does not suffice to study their interactions at short time scales of years or decades, but it is necessary to analyse their interplay in the long term, in which all aspects of this environmental factor can sufficiently manifest themselves. The most effective tools for this are provided by palaeoecology, which allows to compare long-term changes of plant communities, climatic changes and human impact with proxies of wildfire history. Paradoxically, even though the area of Central Europe is covered by a dense network of palaeoecologically surveyed sites, high-quality records of Holocene fire activity in the region are exceedingly scarce (Marlon et al., 2013). The present thesis attempts to fill this knowledge gap by collecting a range of proxy evidence of past fire occurrence.

Products of the burning of biomass include a diverse array of carbon-rich materials forming a continuum between thermally partly modified plant matter and almost pure graphite (Preston et al., 2006). Compounds directly produced by the burning of materials as well as those resulting from structural changes induced by released heat can be considered direct indicators of fire (Conedera et al., 2009). However, high temperatures also affect properties of compounds that are not directly involved in the process of combustion, and these they may carry signal about the occurrence of this phenomenon. Direct indicators of fire include, most importantly, carbonized plant remains, which are summarily referred to as ‘charcoal’ (Scott, 2010). However, they also include a diverse array of organic compounds, of which one very often utilized group of indicators comprises the monosaccharide anhydrides levoglucosan, galactosan and monosan (Kirchgeorg et al., 2014; Zennaro et al., 2014). Fire also alters the magnetic properties of compounds, especially of ferrous minerals in upper soil layers, which are transformed by high temperatures into ferromagnetic compounds sustaining a permanent magnetic field (Oldfield et al., 2007).

It is possible to detect past fire events by the analysis of multiple types of markers, which raises the issue of mutual comparability of results. In the work leading to this thesis I focused on carbonized plant tissues contained in terrestrial and lacustrine sediments and soil profiles, which constitute direct proof of the occurrence of fire. Charcoal particles are abundant in these sedimentary environments, which enables the reconstruction of fire activity both over the course of the Holocene and in older periods of the Quaternary. One important aspect of anthracological research, because charcoal particles are the most frequently used proxy for reconstructing past fire regimes, is the possibility to compare results with those pertaining to other records in the area of the European continent. Carbonized plant tissues, moreover, convey further information, making it possible to more closely specify the circumstances of fire events, mainly the taxonomic identity of the original plant matter. Imperfect combustion of plant tissues causes the transformation of anatomical structures composed of lignin and cellulose into a graphitic form of carbon, which to a large extent retains its original arrangement and conserves features allowing to classify objects taxonomically. Thanks to this it is possible to infer the species composition of biomass affected by fire.

When research interest is focused on several past decades, the most appropriate approach is to utilize dendrochronological records, which offer exceptional annual precision and usually also high spatial accuracy (Niklasson et al., 2000; Heyerdahl et al., 2001). Meristematic cells are able to overgrow injuries caused to trunk tissues by high temperatures during fires, thus developing so-called 'fire scars'. By compiling numerous fire scar records within a forest stand, it is possible to reveal its fire disturbance history. The applicability of this approach is, however, confined to areas where long-lived tree species occur and fire-free intervals are not longer than the life-span of the trees present. Because forests in Central Europe are intensively managed and logging is carried out at the desired age (mean 115 years – Ministry of Agriculture of the Czech Republic, 2018), this heavily limits the temporal coverage that can be reached in this region. Moreover, tree-ring series typically cover several past centuries, making it difficult to filter out the effects of increasing human population on fire dynamics. This may raise the question to what extent is our tree ring-based knowledge about natural fire regimes affected by human influence (Niklasson et al., 2010; Hörnberg et al., 2018). Despite these shortcomings, dendrochronology has been successfully applied also in situations where tree trunks have been preserved *in-situ* within a sedimentary sequence. For example, a low-severity fire regime has been reconstructed in a *Pinus sylvestris*-dominated swamp forest at the locality Rynholec in Central Bohemia during the Early Holocene (Šamonil et al., 2018). Other example comes from the Reichwalde site in Lower Saxony, which has provided an extensive record of fire disturbances affecting pine-birch forest during the Allerød Interstadial (Friedrich et al., 2002). All the studies mentioned above have demonstrated very clearly the enormous potential of dendrochronology, as they not only allow to precisely reconstruct past fire frequencies, but also make it possible to even asses individual tree mortality due to fire events.

Proxies of past fire occurrence may come from other than natural archives, specifically from human created records such as written documents, remote sensing data or historical photographs. These sources often excel in spatial precision and may provide additional valuable information that can be used for inferring fire characteristics such as extent, intensity or type. Unfortunately, such data are usually available only for a few decades or are difficult to obtain for wider geographic areas, which makes them unsuitable for addressing long-term fire dynamics across different spatial scales.

However, in the context of Czech forestry, a unique body of data about the incidence of fires has been collected at the stand-scale level for the entire forested area of the country. Forest managers were obliged to record every fire event that had occurred within their area of operation. These written records provide a great opportunity for disentangling the drivers of recent fire occurrence within forests of various types in the Central European temperate zone.

1.3 Reconstructing fire regimes in the Holocene

The methods used for reconstructing past fire occurrence vary depending on the archive under study, the proxy used to detect fires and the desired temporal length and resolution (Conedera et al., 2009). Therefore, the suite of techniques that are currently available comes from various scientific disciplines, making it difficult to directly compare results. On the other hand, applying complementary approaches may substantially contribute to a better understanding of the complex phenomenon of fire. In this thesis I focused on direct evidence of fire – charcoal deposited in peat, lake sediments and soils.

1.3.1 Charcoal analysis of lake sediments and peat bogs

Charred organic matter is produced by incomplete combustion of terrestrial biomass caused by insufficient oxygen supply during pyrolysis. Once the main compounds of plant tissues, lignin and cellulose, are thermally altered, they are converted to a continuum of products ranging from highly polyaromatic to graphitic carbon (Schmidt et al., 2000). Some of these forms are resistant to biological and chemical degradation, thus forming a long-term pool of recalcitrant organic carbon in soils and sediments (Pessenda et al., 2001). This fact is one of the basic assumptions made in studies that have utilized charcoal abundances to reconstruct past fire activity (Conedera et al., 2009). It has been shown that various sedimentary environments supports long-term sequestration of charcoal, thus enabling to reveal direct evidence of fire occurrence (Daniau et al., 2010a; Marlon et al., 2013; Wolf et al., 2014). Nevertheless, there is also emerging evidence that charcoal may be less resistant than has been commonly assumed, particularly as a result of physical degradation on exposed surfaces (Zimmerman, 2010; Knicker, 2011; Singh et al., 2012). Accordingly, dispersal that occurs after a fire event allows charcoal particles to be deposited in lacustrine sediments or peat bogs, thus forming stratigraphically ordered charcoal records, which are less susceptible to degradation (Ohlson et al., 2013). Analysing charcoal content in such sedimentary archives is a highly reliable method of reconstructing long-term fire dynamics which has been widely used in palaeoecology (Whitlock et al., 2001). The main advantage of this approach is that enables to address much longer time scales than dendrochronology and is virtually limited only by the sedimentary archive available. This makes the method particularly suitable for analysing climate-fire relationships, biome-scale fire disturbance histories or anthropogenic-induced changes in fire regime. Laboratory methods for charcoal-based fire history reconstructions evolved rapidly during the last few decades, gaining importance in palaeoecological research. However, charcoal particles occurring in sedimentary samples attracted the attention of scientists much earlier, particularly within the framework of pollen analysis. Empirical as well as theoretical studies have shown that smaller particles disperse over longer distances than larger particles, so focusing on specific size classes can be used to differentiate between source area of charcoal. This finding has led to a general consensus that particles > ≈ 100 μm in diameter (often referred to as 'macrocharcoal' or 'thin-section charcoal', see Whitlock and Larsen, 2001) likely represent local fire events whereas particles < ≈ 100 μm in diameter ('microcharcoal';'pollen slide charcoal') were produced by fires in a wider geographic area. Nevertheless, defining the exact spatial representation of each size class is hampered by complex processes affecting charcoal production and transport. Clark (1988) developed a simple probabilistic model of atmospheric charcoal transport predicting the lateral distribution of particles as a function of injection height, wind speed, and particle size and density. He concluded that small charcoal particles 5–80 μm in size, which are usually counted on pollen slides, get dispersed to substantially more distant locations than macrocharcoal (50–10,000 μm). This theoretical suggestion was later supported by several empirical studies attempting to demonstrate a distance-dependent drop in charcoal abundances following modern fires (Tinner et al., 1998; Gardner et al., 2001; Lynch et al., 2004). However, a continent-scale calibration study relating recent charcoal deposition into lakes and remotely-sensed fire data (Adolf et al., 2018) demonstrated that regional fires (e.g. > 40 km) can substantially contribute to the macrocharcoal record (> 100 μm), casting doubt on the reliability of local fire event reconstructions. Accordingly, focusing on larger charcoal particles (i.e. > 600 μm) may benefit the detection of local fires (Adolf et al., 2018). Nevertheless, even large charcoal particles can be lifted by convection plumes during high-intensity fires and transported several kilometres away (Pisaric, 2002; Tinner et al., 2006a).

Macroscopic charcoal studies employ a high-resolution continuous sampling approach with usual increment length of 1 or 0.5 cm. This ensures that each change in charcoal abundance can be identified along the length of a sedimentary core, making it possible to detect individual fire episodes or several fires clustered in a single peak (referred to as a 'fire event'). Because temporal resolution varies over the magnitude of tens to hundreds of years, depending on the sediment accumulation rate, it is essential to carefully select the sampling site according to the information sought. Macroscopic charcoal analysis has been widely applied to lacustrine sediments, which typically enables to achieve a precision of ≈20 years in one centimetre (Goring et al., 2012). Nevertheless, the petrographic thin-section method has been used for charcoal quantification in varved sediment records, allowing to work even at annual resolution (Clark, 1988a). High-resolution sampling has also been applied to terrestrial sequences, particularly raised peat bogs and mires, which generally provide satisfactory temporal resolution of 20–30 years. The fundamental division between lacustrine and palustrine depositional environments has important consequences for taphonomic processes and the resulting interpretation of charcoal records (Remy et al., 2018). Each lake record integrates charcoal particles coming from both within and outside the watershed, allowing these archives to register fires that have occurred up several tens of kilometres from the lakeshore (Whitlock et al., 1996; Gardner et al., 2001; Duffin et al., 2008; Oris et al., 2014; Adolf et al., 2018; Vachula et al., 2018). Moreover, hydrological characteristics such as catchment area relative to lake size or the presence of inlet streams heavily influencing the transport of charcoal into the sedimentary basin (Meyer et al., 1995). Landform features such as steep slopes surrounding a lake basin may also increase the input of reworked charcoal from soils through surface run-off (Shakesby, 2011; Sass et al., 2012). Therefore, the term 'secondary charcoal' was introduced to distinguish particles deposited during non-fire years as a result of erosion or sediment mixing (Whitlock et al., 2001). Conversely, the term 'primary charcoal' denotes particles which enter the sedimentary basin immediately after the actual fire event. Depending on the rates of processes that deliver charcoal to the lake, resulting charcoal assemblages includes both sources, necessitating the development of analytical tools for differentiating between them. In the case of peat bogs, however, taphonomic processes delivering charcoal to the bog surface are substantially less complex than those in lakes (Innes et al., 2004). These sites have a smaller source area of charcoal, and redeposition of older particles embedded in soils surrounding the peatlands is limited (Blackford, 2000).

Statistical assessments of macrocharcoal series datasets are well established and follow two complementary approaches (Whitlock et al., 2001; Power et al., 2008). Choosing a proper technique depends on whether the research interest is focused on inferring local fire events or rather revealing trends in biomass burning at a regional to continental scale. When the aim is to reconstruct the local fire history at a single site, a suite of tools for analysing such time-series data are readily available (Higuera et al., 2009, 2010). The main effort is to decompose the fire signal into two components, background and peak, each representing different sources (and processes) of charcoal that contributed to each particular charcoal accumulation value in the record (Long et al., 1998). Within this theoretical concept, centennial-scale changes in charcoal accumulation are attributed to regional charcoal production, transport, sedimentation, post-deposition processes and sampling. These processes are modelled by a curve-fitting method such as locally weighted regression using a reasonable wide smoothing window which typically varies between 100 and 1,000 years. The second step is to remove the background trend from the charcoal series to obtain residuals. Thirdly, a threshold is applied to the residual series to distinguish between peaks related to local fire events and random variability (Gavin et al., 2006). Statistically significant peaks exceeding this threshold are then considered evidence of local fire events and can be used to calculate basic fire history statistics such as fire frequency and the fire return interval.

If the main research focus is on revealing broad-scale patterns of palaeofire activity, compositing multiple charcoal records to built a common trend is a frequently used approach (Power et al., 2008). It relies on the assumption that the total biomass burned in a particular region and time period is proportional to the amount of charcoal deposited in the sedimentary environment (Marlon et al., 2006). Because the quantity of charcoal is measured in different ways and site characteristic vary across different sedimentary archives, charcoal influx series have to be standardized to enable inter-site comparison. This is usually done by (1) rescaling values using a min–max transformation, (2) homogenizing variance of individual records by a Box-Cox transformation, and (3) rescaling values to Z-scores to ensure comparability between datasets (Power et al., 2008). Prior to this calculation, each charcoal series is resampled to a common temporal resolution (median) to account for the disproportionate influence of high-resolution records. Once data are standardized they are smoothed using LOWESS (locally weighted scatterplot smoothing) based on an appropriate width of the time window (> 200 years). The resulting composite charcoal curve makes it possible to identify shared trends in fire history in a given geographic area or during the time period of interest. A validation study which evaluated the correlation between observational fire records (annual area burned) and a charcoal-inferred fire history (composite charcoal) showed good correspondence (Kelly et al., 2013). Thus, centennial-scale trends in composite charcoal curves reflect relative changes in the biomass burned in a particular region (Higuera et al., 2011).

1.3.2 Charcoal in soils

Charcoal is ubiquitous in soils across various ecosystems, indicating the widespread occurrence of fire in the disturbance history of most of the world's biomes (Gavin et al., 2003a; Titiz et al., 2007; de Lafontaine et al., 2011a; Ohlson et al., 2011; Novák et al., 2014; Robin et al., 2014, 2018). Macroscopic charcoal in soils has extensively been used to determine *in situ* fire histories because the spatial dispersion of large charcoal particles (> 2 mm) is limited (Ohlson et al., 2000), the persistence of charred organic matter is high and charcoal material is especially suitable for radiocarbon dating. Each wildfire leaves a substantial amount of charred organic matter on the soil surface, which is eventually transported to sedimentary basins by water erosion but is partly incorporated into the soil profile by different kinds of bioturbation processes (Meysman et al., 2006; Šamonil et al., 2015). As a consequence of soil mixing and Earth's gravity, charcoal tends to migrate downwards through the soil column and thus potentially form raw age stratification. However, the age-depth relationship is frequently disrupted by the influence of tree uprooting, which represents a major perturbation in soil development. Consequently, charcoal particles were found to be poorly stratified or non-stratified in soils (Carcaillet, 2001), hampering the establishment of precise chronological control. This obvious weakness may partly be overcome by applying an extensive radiocarbon dating strategy, markedly increasing the cost of the method. This can be justified in areas where other preferable palaeoarchives (e.g. lake sediments and peat deposits) are lacking or a stand-scale fire record is desired. Nevertheless, one major strength of this palaeofire record is the possibility to achieve high spatial resolution and dense sampling coverage that is hardly acquirable by other approaches (Ohlson et al., 2000). Charcoal particles are extracted from soil samples by flotation and wet sieving (Carcaillet et al., 1996). This allows to obtain particles that are taxonomically identifiable based on anatomical features of wood (Schweingruber, 1990). Determining taxa and tree ring curvature may also help reduce the effect of 'inbuilt age', which adds significant uncertainty to radiocarbon age determination (Gavin, 2006). Charcoal samples from branches or short-living species are preferable for ^{14}C dating. Stand-scale fire frequency can be estimated with a sufficiently large dataset of ^{14}C dates of single charcoal particles (de Lafontaine et al., 2011a, 2011b; Robin et al., 2014).

1.4 Anthropogenic drivers of prehistoric fire regimes

Intentional use of fire by early hominids can be traced back over 1,500,000 years into the Early Pleistocene (James et al., 1989), yet this earliest evidence is not free of controversy. Archaeological evidence from Europe suggests that fire became a part of human technological knowledge much later, from ~300,000 to 400,000 years BP, which contradicts the general assumption of inevitable use of fire during the initial spread of humans into climatically colder northern latitudes (Roebroeks et al., 2011). Marine microcharcoal records have revealed that the colonization of Europe by Upper Palaeolithic humans (40–10 kyr cal BP) did not induce any change in natural fire regime at subcontinental scale, which would be expected if extensive fire management had been applied by humans (Daniau et al., 2010b). On the other hand, anthropogenic burning has been proposed as an important driver which may have substantially reduced the cover of forests during the Last glacial Maximum, ca 21,000 cal BP (Kaplan et al., 2016). Hunter-gatherer societies undoubtedly utilized fire in various ways¸including for cooking, heating, processing of materials; besides the domestic use, however, fire was also used for managing ecosystems to improve the availability of resources (Ferguson, 1979; Simmons et al., 1987; Pausas et al., 2009; Selsing, 2016). The ecological effects of fire on vegetation were deliberately used to increase the total quantity of food resources that could be obtained from particular ecosystems (Mellars, 1976). Early successional stages induced by fire disturbances substantially improve the amount and quality of forage available to browsing and grazing animals. Newly burned areas attract game animals and make their occurrence more predictable compared to their scattered distribution in unburnt landscapes. Therefore, subsistence strategies relying on controlled use of fire benefits from decreased uncertainty, which is otherwise associated with the unpredictable pattern of lightning-ignited fires. There are other reasons to burn vegetation such as to increase mobility and visibility which in turn improves the exploitative efficiency of human groups (Mellars, 1976) or to enhance yields of edible plants (Zvelebil, 1994; Mason, 2000; Bishop et al., 2013; Divišová et al., 2015). There is also an ongoing debate on whether Mesolithic people intentionally spread or even cultivated (sensu ‘Mesolithic agriculture’) certain plant species such as *Corylus avellana* or wild grasses (Zvelebil, 1994; Behre, 2007; Tinner et al., 2007; Kuneš et al., 2008b; Regnell, 2012). Such practices are believed to had involved the deliberate use of fire to open woodland canopies and create a mosaic of regeneration phases that stimulated the production of hazelnuts, berries and fruits (Bishop et al., 2013; Innes et al., 2013). In this context, it has been suggested that Mesolithic hunter-gatherers actively managed the structure of plant communities and thus systematically constructed their human niche (Smith, 2011; Scherjon et al., 2015; Boivin et al., 2016; Power et al., 2018). Nevertheless, observed patterns in palaeoecological records can alternatively be interpreted as opportunistic exploitation of forest clearings which were, however, created by various natural disturbances (Brown, 1997). Disentangling the influence of Mesolithic hunter-gatherers on fire regimes is challenging because of the complexity of interactions driving fire activity. Diverging trends in charcoal composite records from lowlands of Central European suggest that Mesolithic societies possibly significantly altered fire regimes at regional scales even in low population densities (Dietze et al., 2018). Notwithstanding, the climate has been repeatedly identified as a driving force of increased fire activity during the Early Holocene (Feurdean et al., 2012; Molinari et al., 2013; Carter et al., 2018b; Kuosmanen et al., 2018), thus admitting only a partial contribution of human-induced fires to this general trend.

Since the beginning of Neolithic, a period which is marked by early findings of the Linear Pottery Culture (Linearbandkeramik, ca 7,500–7,300 cal BP) in Central Europe, fire became an important component of agricultural practices (Turner et al., 2010). The first farmers had to clear the land to establish their settlements and fields, which they largely did using fire. However, the extent of such burning depended on various natural and socio-economic factors such as the type of vegetation cover prevalent in the landscape they settled in, the agro-technology applied in cereal cultivation and the size of their population. Moreover, the environmental context of such anthropogenic activities is unclear, as there has been a century-long discussion as to whether the Central European lowlands were covered by a natural grassland or were already forested at the time of the onset of agriculture (Gradmann, 1906, 1933; Lang, 1994; Vera, 2002; Kreuz, 2008; Pokorný et al., 2015). Therefore, the impact of Neolithic human societies on fire regimes is difficult to quantify from the fossil record. Two contrasting hypotheses of crop husbandry during the Neolithic have been suggested during the past two decades. The first hypothesis is referred to as shifting cultivation or slash-and-burn and assumes short-term cultivation of land which was abandoned after one to two years to allow natural regeneration of the vegetation cover (Rösch, 1993, 2013). Fire was used not only to clear woodlands by burning felled trees (Iversen, 1956), but primarily as tool for the mineralization of soil organic matter and releasing nutrients, making them instantaneously available for plant growth. The second hypothesis proposed permanent cultivation of intensively managed plots (termed 'garden cultivation'(Bogaard, 2005; Bogaard, 2002; Jacomet et al., 2016a, 2016b) in which weeds were controlled by weeding and soil fertility was increased by additional input of nutrients by manuring (Bogaard et al., 2007, 2013). Although there is a general consensus that Neolithic agrarian practices tended to be directed towards small-scale intensive cultivation, it is indisputable that fire was used for initial woodland clearing and occasionally as part of slash-and-burn agriculture, which was practised especially on poor soils (Jacomet et al., 2016). Charcoal records from the lowlands of Western and Southern Europe suggest a decrease of the total biomass burned which was simultaneous with the spread of Neolithic farming and, at the same time, a gradual increase in fire frequency that occurred after 7,000 cal BP (Vannière et al., 2016). This pattern in the charcoal record may have resulted from frequent anthropogenic burning related to the slash-and-burn strategy of early farmers (Tinner et al., 2005; Vannière et al., 2016), but a connection with other human activities such as pastoralism is also plausible. Available microcharcoal records from lowlands of Bohemia do not indicate any distinct increase of burning during the Early and Late Neolithic, although intensive settlement activity in the vicinity is documented by extensive archaeological evidence (Bešta et al., 2015; Pokorný et al., 2015). Accordingly, trends in charcoal influx from regions inhabited by Meolithic farmers show an ambiguous correspondence with human activity, pointing towards a variable but important cultural influence on the use of fire (Rius et al., 2009; Feurdean et al., 2013a; Molinari et al., 2013; Dietze et al., 2018).

A large number of European charcoal records evidence a progressive increase in fire activity in the Late Holocene (Tinner et al., 2005; Power et al., 2008; Rius et al., 2009; Feurdean et al., 2013a; Molinari et al., 2013; Vannière et al., 2016; Dietze et al., 2018). Moreover, a similar pattern of increasing fire activity on the Northern Hemisphere has also been reported from the Greenland ice core record, where a maximum concentration of the fire biomarker levoglucosan occurred around 2,500 cal BP (Zennaro et al., 2015). This trend was mostly explained by the rapid growth of the human population during the Bronze Age and Iron Age resulting in large-scale deforestation by fire (Power et al., 2008; Feurdean et al., 2012; Vannière et al., 2016). However, this process was spatially heterogeneous and dependent on specific land-use practices developed in particular regions. For instance, an increasing charcoal influx was concurrent with a major spread of arable farming in the Eastern Baltic region during the Bronze Age (Dietze et al., 2018). By contrast, many lowland areas of Western Europe exhibit rather below- average charcoal influx values that follow a decreasing trend despite a rise in fire frequency (Vannière et al., 2016). This may indicate differentiation in anthropogenic burning practices between regions with a long-term agrarian history and newly settled areas. The most striking example of a pervasive anthropogenic influence on the fire regime is the establishment of high-elevation pastoralism in the Alps. This subsistence strategy had utilized fire as a tool for lowering the timberline in order to extend alpine grasslands and to prevent tree regeneration on pastures. Such practices are distinguishable in the charcoal and pollen records at least from the Aeneolithic and they continued with some local disruptions until the Late Middle Ages (Roepke et al., 2013; Schwörer et al., 2014; Dietre et al., 2017; Pini et al., 2017). The environmental impact of increased fire disturbances was pronounced and led to extensive soil erosion (Sass et al., 2012), a decline of coniferous species including *Pinus cembra* (Dietre et al., 2017) and an expansion of fire-promoted species such as *Alnus viridis* (Gobet et al., 2003). Pollen evidence coupled with micro- and macro charcoal records from the Eastern and Southern Carpathians also suggests that burning activity at high elevations was likely related to seasonal pastoralism (Feurdean et al., 2009, 2012; Haliuc et al., 2016). Surprisingly, a distinct increase in fire frequency during the Late Bronze and Iron Age has also been reported from low-elevation mountain ranges in Central Europe, where natural alpine grasslands are not developed or cover only very limited areas (Robin et al., 2014; Carter et al., 2018b). This highlights the possibility that deliberate burning was applied also together with other anthropogenic activities such as mining or maintenance of prehistoric trading roads through densely forested mountain areas.

A prominent feature of numerous charcoal records from Western and Central Europe is a marked decrease in fire activity centred around the Roman Age and Migration Period followed by a substantial peak in the Early to High Middle Ages (Vannière et al., 2016; Dietze et al., 2018). This can be explained by socio-economic changes and a population decline induced by the fall of the Western

Roman Empire. However, another plausible explanation of little fire activity is the climatic cooling and precipitation increase which occurred between ~250 and 550 AD (Buntgen et al., 2011).

1.5 Long-term fire ecology of temperate forest ecosystems

Fire is a highly diverse process with regard to size, intensity, timing or duration, which makes its environmental influence span various magnitudes, from devastating crown fire events, which remove almost the entire plant cover, to low-intensity surface fires burning primarily the forest understorey. Therefore, the principal goal of fire ecology is to describe relevant components of fire activity and to reveal relationships to external driving forces. The fundamental concept lending a basis for addressing these questions is termed 'fire regime'. It is characterized by a particular combination of fire intensity, frequency, type and season of burning (Gill, 1975). When viewed over a longer time period, repeated patterns of fire characteristics occur at single points in the landscape, making possible to map the distribution of fire regimes across space (Morgan et al., 2001). At a global scale, functionally similar fire regimes can be amalgamated to broad categories termed 'pyromes' that can be considered analogous to biomes (Archibald et al., 2013). Fire regimes are driven by changes in climate, vegetation and human activity, but key biophysical factors, including biomass available for burning, atmospheric conditions enabling combustion and ignition triggers must coincide for fire to occur (Krawchuk et al., 2011). At small spatial scales and in short time periods, fire is limited by the distribution, moisture content and composition of fuels whereas at regional scales and over longer time periods, fire regimes are shaped by the vegetation and climate (Whitlock et al., 2010). At a global scale, it has been suggested that fire activity is related to productivity gradients, following a unimodal relationship (Krawchuk et al., 2011; Pausas et al., 2013). This intermediate fire–productivity hypothesis attributes different loads of the main fire drivers (drought and fuels) to the occurrence of fires occurrence along a productivity gradient. In high-productive and moist ecosystems, such as tropical forests, fire activity is driven by the frequency of droughts. In arid and low-productive ecosystems, by contrast, the availability of fuels effectively limits the occurrence of fire (Pausas et al., 2013). Seen from a millennial timescale, such climate-fuel-fire feedback also applies to changes in fire activity during Quaternary climatic oscillations, being low in cold glacial stages and progressively increasing throughout biomass-rich warm interglacials (Daniau et al., 2010a). Climate is a crucial driver shaping fire regimes at centennial to millennial time scales (Kappenberg et al., 2019). Climatic variation is largely controlled by long-term changes in solar irradiation, which in turn influence atmospheric circulation patterns, storm tracks and the frequency of lightning strikes or length and seasonality of the droughts. It has been repeatedly shown that climate-driven changes dominated charcoal records throughout the Holocene (Power et al., 2008; Ali et al., 2012; Daniau et al., 2012), even though local conditions such as topography, vegetation or human influence can amplify or override the direct influence of the climate (Vannière et al., 2011). For instance, higher summer insolation in the Early Holocene promoted biomass burning in Central Europe (Feurdean et al., 2012; Carter et al., 2018b) through higher-than-present temperatures and decreased precipitation. Direct fire-climate linkages are, however, were modulated to a great extent by the vegetation itself. Although the potential spatial distribution and species assembly of plant communities are ultimately determined by long-term climatic conditions, vegetation variability along local environmental gradients substantially contributes to heterogeneous patterns of fuels and flammability across space and time (Higuera et al., 2009). Such bottom-up control may result in divergent fire regimes even within the same climatic domain. This is of particular importance for *Pinus sylvestris*-dominated forest types, which are maintained by recurrent fire disturbances throughout most of the Holocene (Novák et al., 2012; Adámek et al., 2016). In this case, the elevated litter flammability and fire-resistant traits of this conifer tree favoured the frequent occurrence of fires which in turn caused increased mortality of strong competitors such as *Fagus sylvatica*, thus preventing its expansion. Divergent fire regimes may also arise from differences in plant traits of key species in the ecosystem. The most striking example is the mismatch between wildfires in boreal North America end Eurasia. Even though these areas have comparable climates, they differ substantially in the prevailing types of fire. High-intensity crown fires are frequent in North America whereas low-intensity surface fires are more common in Eurasia (Wooster et al., 2004; de Groot et al., 2013). It has been suggested that the evolutionary pathways of dominant trees were different and resulted in divergent adaptations to fire (Rogers et al., 2015), thus inducing profound differences in fire regimes. Black spruce (*Picea mariana*) has fire-promoting traits such as a ladder canopy structure and is widespread in boreal forest communities in North America, where it facilitates numerous crown fires. By contrast, thick-bark conifers such as Scots pine (*Pinus sylvestris*) are predominant in Eurasia and are better morphologically equipped to protect their cambium against damage by high temperatures. Moreover, large areas of Siberia are covered by forests dominated by Siberian larch (*Larix sibirica*) or other species of the genus *Larix* which suppresses fire by a high moisture content in its needles. Therefore, species-level traits are capable of inducing substantial shifts in fire regimes that are independent of the climate.

Perhaps the most illustrative fire-vegetation feedback has been documented in Fennoscandia, where a Late-Holocene expansion of *Picea abies* substantially altered the fire regime at a subcontinental scale. Ohlson et al. (2011) found a significant reduction in charcoal concentrations in soil profiles following the local establishment of spruce. Once this species with a dense canopy became an important constituent of the tree layer, it has altered local microclimate towards increasingly moist understorey conditions which in turn decreased the forest's susceptibility to ignition. This process resulted in a general reduction of fire activity across the boreal landscape and a diversification of fire regimes by decreasing fire frequencies, which was the most pronounced in moist sites located in recessed surface positions (Ohlson et al., 2006, 2011; Hörnberg et al., 2014). A similar landscape-scale inhibiting effect of spruce was identified in the Carpathians, where fire activity declined at the transition from *Pinus*-dominated to *Picea abies*-dominated forests in the Early Holocene (Feurdean et al., 2017a). On the other hand, some studies have reported that the frequency of fires did not change significantly after the expansion of spruce, but increasing peak magnitudes in lake charcoal records indicate a shift in the amount of fuels consumed by fire (Brown et al., 2014).

This may suggest that vegetation change affected key wildfire characteristics such fire type and severity. Regardless of whether the frequency of fires changed equally across various habitat types, it has been clearly shown that biotic change is able to alter important features of fire regimes independently of the climate.

Another example of fire-vegetation interactions is the substantial mitigation of burning activity in response to the expansion of broadleaf tree taxa in conifer-dominated forest communities (Girardin et al., 2013; Blarquez et al., 2015). A higher proportion of broadleaf trees may efficiently suppress fire activity in recent boreal forests by shortening the fire season to the period before foliage starts to spread out (Girardin et al., 2015). Such biotic effects were reported from the hemiboreal zone of Northern Europe where an increased quantity of temperate trees resulted in low fire activity during the Holocene Thermal Optimum, which is contradictory to the warm and dry climatic conditions occurring during this period (Feurdean et al., 2017b). Analogically, a similar effect may be expected to occured during the mid-Holocene spread of beech (*Fagus sylvatica*) in Central European highlands. These areas were largely occupied by boreal-like coniferous forests since the rapid reforestation in the Early Holocene (Abraham et al., 2016). The drivers of beech expansion and mechanisms of initial species establishment in forest communities have been frequently debated among vegetation scientists and palaeoecologists (see Tinner et al., 2006b). It seems that the climate exerts the main influence on the population growth of beech, but various bottom-up controls such as fire disturbances and human impact may have facilitated its spreading (Björkman et al., 1996; Bradshaw et al., 2005). Paradoxically, the rising proportion of broadleaf trees negatively affected fire activity, which started to diminish. Moreover, such compositional change in vegetation had far-reaching impact on forest disturbance regimes, which began to be dominated by gap dynamics processes.

1.6 Research questions and structure of the dissertation

This thesis aims to address the lack of knowledge about the history of fire disturbances in Central European temperate forests. To explore complex interactions between fires, the climate, vegetation and humans, I collected extensive datasets on different proxies of fire occurrence. I then compared them with other palaeoecological data including sequences of pollen, spores and fungal residues. This dissertation consists of a general introduction to the wildfire research and four chapters in the form of scientific articles. Each chapter includes a detailed description of the methodology used, a discussion of the respective results and a conclusions section. Formatting styles may differ between chapters to suit the submission requirements of the target peer-reviewed journal. A brief summary of all the research outputs is provided in the conclusions section of the entire dissertation. The research presented had the following aims:

- to identify environmental and anthropogenic factors which determine the recent and historical occurrence of fire in the Central European landscape;
- to assess the role of fire disturbances and human impact in the environmental transformation of Northern Bohemian sandstone;
- to reveal changes in Holocene fire frequency in temperate mountain forests based on spatially precise charcoal and pollen data; and
- to evaluate the effects of biotic changes on Holocene biomass burning within regions differing in the timing of the expansion of broadleaf forests.

Chapter 2:
Forest fires within a temperate landscape: A decadal and millennial perspective from a sandstone region in Central Europe

1.7 Abstract

In Europe, fire is considered an integral part of forest dynamics only in the Mediterranean and in Fenno-Scandinavia. In Central Europe, the ecological role of fire is largely neglected and deemed unimportant. To fill this knowledge gap, we studied ancient and recent fires in temperate coniferous forests of a sandstone landscape. We used palaeoecological and contemporary forestry data to reveal wildfire events in the present-day landscape and in the distant past. Using linear regression and the ENFA method, we identified the factors influencing fire occurrences in the landscape on two time scales. Analyses of soil charcoal concentrations correspond with contemporary forestry data. The main driving factors affecting the incidence of fires were topographic features, namely the heat load index and presence of rocks. Additional important factors were forest composition features, especially the abundance of Pinus sylvestris. Even though the landscape is populated and attractive to tourists, present-day anthropogenic factors, surprisingly, have only marginal effects. Fires have been occurring in similar fire-prone habitats at least since the Subatlantic period, regardless of whether they were caused by humans or lightning. Our results therefore show that fire affects long-term forest vegetation development also in temperate forests of Central Europe. This has far reaching consequences for forest management because, contrary to prevailing beliefs, fire must be considered a natural driver of forest vegetation patterns even in this temperate region.

1.8 Introduction

Wildfires are an important disturbance factor influencing forest ecosystems. They have a strong impact on both biotic and abiotic conditions. Fire eliminates sensitive species in favour of species that are able to survive or easily regenerate in burned places (Agee, 1998; Lloret et al., 2005). They alter the local light and thermal regime as well as physical, chemical and biological qualities of the soil (Certini, 2005). The occurrence of wildfires depends on complex interactions among the climate, topographic characteristics, vegetation structure and composition and the presence of natural or anthropogenic ignition triggers. Forest fires are more frequent during dry climatic periods, on convex relief forms and on south facing slopes (Angelstam, 1998). The frequency of wildfires decreases with increasing humidity, for example, towards the poles, higher elevations and a regions with a more oceanic climate (Angelstam, 1998; Skre et al., 1998). The most common natural cause of wildfires is lightning (Tinner et al., 1999; Goldammer et al., 2000; Niklasson et al., 2000). Generally, a gradual increase in biomass burning during the Holocene has been detected on the continental scale in Europe (Carcaillet et al., 2002; Power et al., 2008). It has been proposed that climate warming following deglaciation is responsible for this trend (Marlon et al., 2012). However, recent studies from the Alps (Stahli et al., 2006), Pyrenees (Rius et al., 2011) and the Pannonian Basin (Feurdean et al., 2013a) have shown substantial regional variation indicating a predominant role of anthropogenic drivers acting during the mid- and late Holocene (Molinari et al., 2013).

Wildfires in Europe are associated mainly with the Mediterranean region and the Boreal forest zone. In these areas, fire is considered to be the main forest vegetation disturbance factor (Engelmark, 1993; Skre et al., 1998; Pausas et al., 1999), and its ecological role and history are well studied there (Niklasson et al., 2010). In northern Eurasia, fires are often associated with forests of Scots pine (*Pinus sylvestris*). This coniferous tree species often occurs in drier conditions and produces resiny, easily inflammable litter. At the same time, Scots pine possesses several physiological and morphological adaptations to fire, for example, thick bark, a deep root system and an ability to quickly regenerate after fire in places with mineral soil (Agee, 1998). Regular fires can maintain pine stands also in places where other tree species would otherwise prevail due to site conditions (Engelmark, 1987; Angelstam, 1998; Gromtsev, 2002). Natural fire disturbances are thought to be of such importance that emulating them has been considered a legitimate forest management practice (Bergeron et al., 2002; Kuuluvainen, 2002).

The situation in Central Europe, where the most prevalent natural forests are composed of temperate broadleaf species, is entirely different. The ecological role of fire has traditionally been neglected (Clark et al., 1989; Ellenberg, 1996), and forest fires are regarded as purely adverse results of human activity. But even in temperate Central Europe, fire can play an important ecological role, at least in some forest types, where it shapes their stand structure, dynamics and species composition (Tinner et al., 2005; Niklasson et al., 2010). A comparable situation exists in North America where the perception of the importance of fire in temperate deciduous forests is increasing, but still remains to be disputable. On the other hand, no one doubts, for example, the fire-driven dynamics of the Pine Barrens, a temperate pine forests on sandy soils in north eastern USA (Abrams, 1992; Hoss et al., 2008). In Central Europe, there is evidence that wildfires normally occur in natural Scots pine-dominated forests in sandstone areas, which are considered a geographically disjunct analogy to boreal coniferous forests of northern Europe (Novák et al., 2012). There is also evidence that wildfires occurred throughout the Holocene period (i.e. the last 10000 years). Charred plant material has been found in sedimentary peat bog records (Pokorný et al., 2005; Abraham, 2006) and in sand sediments under rocks (Sádlo et al., 2007). However, the spatial and temporal dynamics of forest fires, and the environmental factors responsible for their occurrence over millennia had so far not been studied in the area.

Changes in the temporal distribution of fire events on the millennial scale are usually inferred from the sedimentary charcoal record in lakes or peat-bogs (Rius et al., 2011). This approach can reveal the frequency of fires in ancient times; however, the spatial distribution of ancient fires remains uncertain. On the contrary, spatially explicit fire histories can be derived from fire scar chronologies, which usually span only the last several centuries, however (Niklasson et al., 2010). In any case, well preserved traces of fire in the tree-ring record are rather infrequent and fragmentary in Central Europe due to the rarity of old scared trees caused by intensive forestry. Another possible reason is the prevalence of low-severity fires, which usually do not leave scars on mature pine trees (Piha et al., 2013).

The goal of this study was to determine the role of environmental factors affecting the frequency and distribution of forest fires on two temporal scales. We traced the occurrence of wildfires over the last three decades and in the last millennium combining two complementary approaches – the study of historical forest management records and assessment of charcoal content in the topmost layer of forest soil. Comparing fire patterns on two different time scales, but using similar environmental correlates, strengthens the inferences about processes controlling the distribution of forest fires in the landscape. Specifically, we aimed to reveal:

1/ Whether the region under study has a continuous long-term fire history;

2/ Whether the spatial distribution of wildfires is driven by the same environmental factors over decades as over millennia; and

3/ Whether the spatial distribution of wildfires in the landscape is driven more by anthropogenic or natural factors.

We also discuss the implications of our findings for forest management practice in protected natural areas of Central Europe.

1.9 Materials and methods

1.9.1 Study area

We worked in the Bohemian Switzerland National Park (BSNP), situated in the NW region of the Czech Republic (Figure 1). It is part of a larger landscape territory – the Elbe Sandstones, which also include the Saxon Switzerland National Park in Germany. The BSNP was established in 2000 and covers an area of 79 km^2. Elevations vary from 116 to 619 m a.s.l. The bedrock is composed of quartzose sandstone rocks of Cretaceous origin with occasional outcrops of Tertiary volcanic bodies. The terrain is very rugged, with cliffs, pillars, rock walls, arches, gorges, canyons and several conic volcanic hills. The depth of some gorges exceeds 200 m. Such landscape heterogeneity results in great variation in habitat conditions within a relatively small area, for example, frequent alternation of moist shady gorges with steep slopes and dry insolated rock tops (Figure 1).

The main part of the BSNP is covered by forest. The natural vegetation is an acidophilous beech and mixed spruce-fir-beech forest (*Luzulo–Fagetum*). Other forest communities occur in special habitats – Norway spruce (*Picea abies*) stands in narrow gorges with climatic inversion, acidic Scots pine and oak-pine forests (*Dicrano–Pinetum*; *Vaccinio vitis-idaeae–Quercetum*) on sandstone rock tops, and herb-rich beech forest (*Melico–Fagetum*) on several volcanic hills (Mikuláš et al., 2007).

Figure 1. Common topography of the BSNP landscape (Pravčický důl valley).

The contemporary forest is dominated mainly by spruce and pine plantations; natural vegetation remains mainly in inaccessible terrain (rock tops, gorges, hill slopes, etc.). The approximate present BSNP forest composition is: 71 % Norway spruce (*Picea abies*); 16 % Scots pine (*Pinus sylvestris*); 6 % European beech (*Fagus sylvatica*); 3 % European larch (Larix decidua), which is not native in this region; 2 % invasive White pine (*Pinus strobus*) and 1 % silver birch (*Betula pendula*). The abundance of other occurring species, for example, sessile oak (*Quercus petraea*), European ash (*Fraxinus excelsior*) and black alder (*Alnus glutinosa*), etc., is less than 1 %.

The earliest traces of human presence in the region date to the Mesolithic age (9500–5500 BC), when hunters and gatherers settled rock shelters (Svoboda, 2003). There is weak evidence that humans occupied the area during the Neolith and Bronze Age. Since that time, there is no evidence of any important human presence up until the early Middle Ages (Jenč et al., 2003).

Compared to the rest of the Czech Republic, forest fires are markedly more frequent in this area (Jankovská, 2006b). References about local forest fires are found in historical records (Belisová, 2006) and also in present mass media. Nowadays, all fires are suppressed by the fire brigade, although the very jagged terrain hinders early detection of fires and makes them difficult to extinguish.

Actual forest management in the BSNP is focused on active transformation of even-aged spruce plantations into a forest with natural tree species composition. Forest typology maps (Randuška, 1982) based on a concept similar to that of potential natural vegetation (Tüxen, 1956) are used as a benchmark for natural forest composition. Non-native species are removed, *Picea abies*, which is nowadays very abundant, is suppressed, and *Fagus sylvatica* and *Abies alba*, currently rare, are supported and planted. Natural *Pinus sylvestris* stands are proposed to occur only on dry rock cliffs with shallow soils.

1.9.2 Ancient forest fires

1.9.2.1 Charcoal spatial pattern

To detect the spatial distribution of ancient fires, we selected a pilot area of 4 × 2 km situated within the core zone of the BSNP (Figure 2, inset graph), where we assessed the spatial pattern of charcoal concentration in the topmost soil layer (0–20 cm). We consider this area to be representative of the rest of the protected sandstone landscape because it covers the common altitudinal gradient and has a typical relief configuration.

Charcoal can be retransported by various processes, including water erosion or wind dispersion, resulting in homogenization of spatial signal. The selection of proper sampling sites and charcoal size fraction can minimize the effect of post-depositional processes (Clark, 1995). We therefore selected sampling sites only in flat areas and on gentle slopes. Based on the digital elevation model, we identified places with an inclination not exceeding the arbitrarily chosen angle of 6° and occurring outside the accumulation area at the bottoms of valleys. Finally, we randomly selected 61 sampling sites within the pilot area where soil trenches were dug down to the topmost part of the mineral B-horizon (average depth 6.5 cm, SD=5.6), where the highest charcoal content could be expected. To eliminate intra-site heterogeneity in soil charcoal concentration (Touflan et al., 2009), we collected 100 cm^{-3} soil samples from four subsamples taken in the corners of the trench (approx. 1 m^2 plot). The final spatial distribution of sampling sites mainly covered flat ridges and larger plateaus at various heights above the valleys. The minimum distance between two nearest sites was 4 m, the maximum distance was 1136 m, and the mean distance was 165 m.

We determined the charcoal content of the soil samples by a modified method proposed by Winkler (1985) based on chemical quantification of carbonized residues of organic matter in the upper soil layer. Dried soil samples (12 hrs at 60°C) were weighed, and organic matter mixed with charcoal was separated from the mineral part by flotation. The floating fraction was captured on a 125 μm sieve. This dried sample was homogenized in a grinding mortar, and decomposable organic matter was subsequently removed by digestion with concentrated hot nitric acid (68 % HNO_3, 30 min, 90°C). Sample residue captured on ashless filter paper was dried and weighed. To completely oxidize pyrogenic carbon, each sample was placed in a furnace at 550°C for the 2 hour. The final inorganic residue was weighed again, and the difference represented charcoal mass. The resulting concentration of charcoal was expressed as the proportion of charcoal pieces greater than 125 μm to the dried weight of the soil sample.

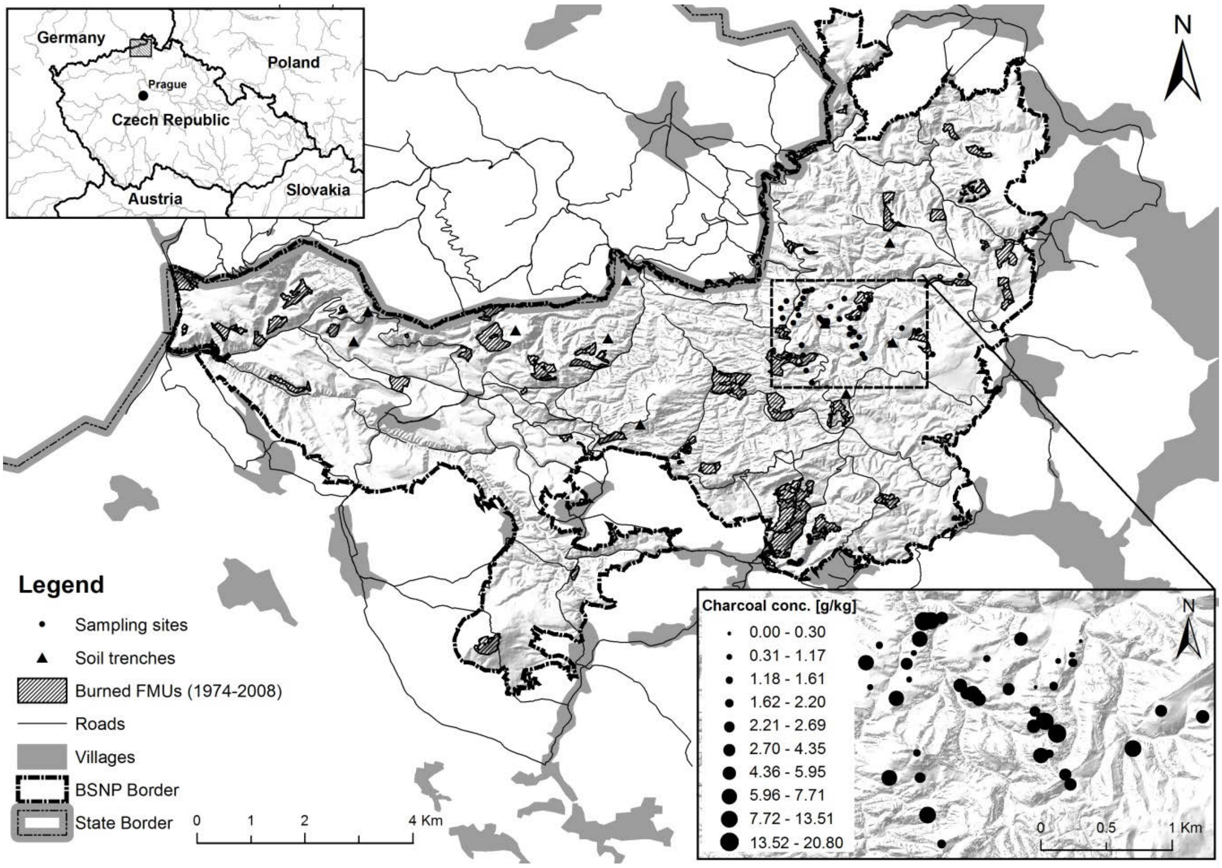

Figure 2. Map of the study area with soil charcoal sampling sites and fire-affected Forestry Management Units (FMUs). The map section shows the distribution of soil charcoal sampling sites within the pilot area. Dots size corresponds to charcoal concentrations in the upper 20 cm of soil. Triangles represent soil trenches from which samples for radiocarbon dating were taken.

1.9.2.2 Radiocarbon dating

We had 14 samples radiocarbon dated to build a time frame of charcoal formation. The samples for radiocarbon dating were taken from ten trenches within a larger area inside the BSNP (app. 10 × 5 km) to minimize the risk of multiple dating of single fire events and to capture the landscape scale variability in fire occurrence. The raw time scale of charcoal assemblage age within the sampled soil layer (down to 20 cm depth) was based on absolute radiocarbon dating. However, the age-depth relationship in the soil profile could have been distorted due to bioturbation or tree uprooting (Carcaillet, 2001). We therefore only take into account the most frequent age range. The exact probe location was chosen on the flat surface without any trace of former tree uprooting.

Samples (10–15 l each) were taken from the uppermost part of the mineral B-horizon (down to 20 cm) in each trench. Four trenches were sampled at two depth levels to obtain a more detailed insight into the fine soil stratigraphy. The dried soil samples were processed by flotation and wet sieving. Charcoals larger than 5 mm were hand-picked under a stereomicroscope to extract fragments suitable for radiocarbon dating carried out at the University of Salento. The calibrated age of 13 charcoals (one sample of modern age was excluded) were calculated using OxCal 4.1 (Ramsey, 2009) and IntCal09 (Reimer et al., 2009). To establish a “minimal insight“ (Robin et al., 2013a) into the frequency of fires in the study area, we attempted to distinguish single fire episodes. We thus plotted cumulative probability curves of calibrated radiocarbon dates (Figure 3) to explore the possible temporal overlaps of fire events.

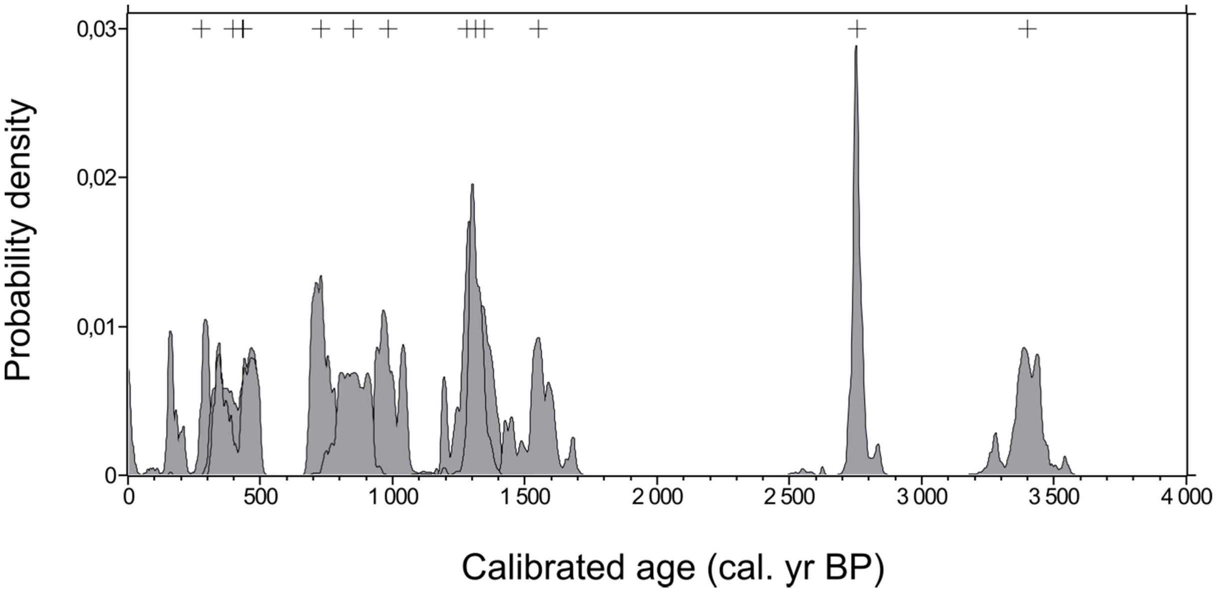

Figure 3. Distribution of the cumulated probability of calibrated ^{14}C dates (n=13, one modern sample excluded) of charcoal fragments extracted from soil profiles located across the whole BSNP area. The crosses denote the median probability of the 2 σ calibration interval.

1.9.3 Recent forest fires

We used archival forest fire records for the period 1974–2008 provided by the administration of the national park (2000–2008) and by two local forestry administrations – in Děčín (1992–2000, 1/3 of the current NP area) and in Rumburk (1974–2000, 2/3 of the current NP area). From these records, we extracted the date of the fire, the code of the affected forestry management unit (FMU), the size of the burned area and the cause of fire. The FMU code (stated in 96 % of records) enabled us to localize most fire events in the map using archival and current forestry maps with the accuracy of FMUs. The FMU area varied from 0.015 to 25.7 ha, with the mean value of 1.7 ha and the median value of 0.75 ha, which provides relatively rough fire localization. The other possibility was to precisely localize sites of fires by surveying the field, but we were unable to detect all recorded fires, probably because of their small areas, low fire intensity that left no visible traces after several decades, former forestry management, etc. We therefore preferred to analyse a less precise but larger dataset of fires localized with the precision of the FMU area (Figure 2).

Digitized FMUs were classified into two categories: A) Burned FMUs and B) Other FMUs. Burned units were FMUs affected by fire between 1974 and 2008 (96 FMUs in total). Other units were all FMUs with no fire detection within the given time period with the exception of FMUs intersecting the 50 m buffer zone around burned units (3277 FMUs in total). Burned FMUs were digitized from scanned forestry maps of ages relevant to the wildfire dates. Other FMU polygons came from the vector FMU map of 2001.

1.9.4 Fire incidence correlates

To identify the agents of fire incidence, we tested three groups of factors (Table 1) chosen according to the current knowledge of wildfire occurrence: A) Topographic factors, B) Forest canopy composition, and C) Anthropogenic factors. For each factor, a continuous layer covering the entire study area was created using GIS software.

A) Topographic factors were calculated using SAGA GIS (SAGA Development Team 2007,) from a detailed digital elevation model (DEM) generated by the LiDAR technology (TU Dresden Institut für Photogrammetrie und Fernerkundung (IPF), 2005). To reduce local variation, we resampled the original 1 m LiDAR DEM to a 5 m DEM through multilevel B-spline interpolation (Lee et al., 1997). We then calculated the following topographic factors from the resampled DEM: 1) Height above the valley that corresponds to the elevation of the site above the neighbouring valley bottom; 2) Heat load index (Boehner et al., 2009) indicating the thermal influx computed from slope and aspect with a maximum on SW and a minimum on NE slopes; 3) Rock height; and 4) Rockiness, a measure of rock abundance in the FMU. The vector layer of rocks used to compute factors 3–4 was created from a raster layer of slopes by arbitrarily considering slopes steeper than 55° as rocks. Rock height was computed as the difference between the minimum and the maximum elevation of each particular rock polygon. The Rockiness factor was computed as the sum of the areas of all rock polygons in the FMUs divided by the total FMU area. Factors 1–3 were used as the maximum value for each FMU polygon. Particular FMU shapes broadly reflect the relief, but in many FMU polygons, abiotic conditions vary immensely (e.g. FMUs along the slope profile from the valley bottom to rock tops). As the highest factor values are supposed to indicate the most favourable conditions for fire ignition, we operated with the maximum values of environmental factors (relief and distances).

B) The forest canopy composition factors were inferred from current and archival forestry management plans (FMP). The factors were abundances of particular tree species in FMUs measured in wood supply units (m^3/ha) and stand age in decades. We included abundances of tree species occurring in more than 5 % of FMUs: *Picea abies, Fagus sylvatica, Pinus sylvestris, Pinus strobus, Betula pendula* and *Larix decidua*. The archival FMP was used to find out the tree species composition of Burned FMUs in the time immediately before fire events. The FMP from the 2001 was used for the Other FMUs.

C) Anthropogenic factors were represented by each FMU's distance from the nearest village and the nearest road (in the sense of all asphalt roads inside and outside the BSNP area and marked tourist paths). The distance was measured from the nearest edge of the FMU polygon. GIS layers representing the road network and villages were vectorized from raster maps (1:10000). The current FMP was provided by the BSNP administration.

Table 1. List of environmental variables used in analyses.

Variable code	Analysis	Variable description	Min	Max	SD
Heat load	ancient	Max. heat load value within 30 m radius around sampling site [unitless]	−0.1	0.7	0.2
Heat load	recent	Max. heat load value within the FMU* [unitless]	−0.5	0.9	0.2
Height_valley	ancient	Height above the valley bottom at the sampling site [m]	0.5	19.1	4.1
Height_valley	recent	Max. height above the valley bottom within the FMU [m]	2.1	327.9	35.5
Rockiness	ancient	Total area of the rocks surface within 30 m radius around sampling site [m^2]	0	722.3	166.9
Rockiness	recent	Total area of the rock surface within the FMU related to its area [m^2/100 m^2]	0	41.2	5.5
Rock height	ancient	Max. height of the rock wall within a 30 m radius around the sampling site [m]	0	56	14.6
Rock height	recent	Max. height of the rock wall within the FMU [m]	0	126.1	22.1
Age	recent	Stand age of the FMU [decades]	0	17	4.3
Bet_pen	recent	Abundance (wood stock) of *Betula pendula* within the FMU related to its area [m^3/ha]	0	97	8.5
Fag_syl	recent	Abundance (wood stock) of *Fagus sylvatica* within the FMU related to its area [m^3/ha]	0	626	47.2
Lar_dec	recent	Abundance (wood stock) of *Larix decidua* within the FMU related to its area [m^3/ha]	0	290	20.7
Pic_abi	recent	Abundance (wood stock) of *Picea abies* within the FMU related to its area [m^3/ha]	0	564	139.8
Pin_str	recent	Abundance (wood stock) of *Pinus strobus* within the FMU related to its area [m^3/ha]	0	272	19.0
Pin_syl	recent	Abundance (wood stock) of *Pinus sylvestris* within the FMU related to its area [m^3/ha]	0	357	59.0
Roads	recent	Distance from the edge of the FMU to the nearest road or tourist path [m]	0	1060	179.3
Villages	recent	Distance from the edge of the FMU to the nearest village [m]	0	3517	846.4

* FMU = Forestry Management Unit

1.9.5 Data analysis of ancient fires

To analyse the relationship between charcoal concentrations and fire-driving factors, we used linear models with Pearson's correlation coefficient as a measure of the strength of linear relationships among variables. The following topographic predictor variables were used in the model: Rock height, Height above the valley, Rockiness and Heat load index. These predictor variables are the same as in the analyses of recent fires and were selected because they are stable over time. It was thus possible to draw a comparison between drivers of ancient and recent fires. Taking into account the possibility of restricted charcoal dispersion during fire events (Ohlson et al., 2000) and subsequent post-fire downfall of charred stumps, we used maximum values for derived topographic factors and the sum of all rocks for Rockiness within the radius of 30 m around each sampling site to approximate the spatial scale on which wildfires operate. Charcoal concentrations (n=61) were transformed prior to the regression analysis using a common logarithm. To investigate which factors significantly explain charcoal concentration, we used multiple linear regression and forward selection of variables as implemented in STATISTICA 8.0 (Hill et al., 2007).

1.9.6 Data analysis of recent fires

Relationships between the environment and presence-absence data on the occurrence of an observed phenomenon are traditionally computed by regression models or their generalized forms (GLM, GAM) that define the probability of the phenomenon's occurrence along a gradient of an environmental factor (Guisan et al., 2000, 2002). An essential condition for successful model calibration is a high-quality presence and absence dataset. The occurrence of wildfires is well documented by presence data, but to prove that a concrete locality was not affected by fire in the studied period is impossible without a detailed field survey. Moreover, the dataset available to us is limited by a relative short time period covered by the archival forestry record. We therefore cannot exclude the possibility that wildfires occurred in any of the FMUs before this period.

Special techniques for assessing relationships between the environment and the occurrence of phenomena that consider only presence data have been developed to deal with such cases (Elith et al., 2006; Phillips et al., 2006; Tsoar et al., 2007). For our purpose, we used the ENFA (Ecological Niche Factor Analysis) method developed by Hirzel et al. (2002), which is more focused on probable causal relationships between particular factors and a certain phenomenon than merely on predicting its occurrence. The ENFA is based on an ecological niche of a species (wildfires in our analyses) defined as an n-dimensional space composed of particular environmental factors. The niche position in the space is described using two measures: marginality and specialization. Marginality is in our case the difference between the mean of whole area factor values (all FMUs) and the mean of wildfire presence factor values (Burned FMUs). Higher absolute values of marginality imply higher differences between factor values of localities with fire occurrence and those for the whole study area. Factors with higher absolute marginality values have stronger effects on the incidence of wildfires. A positive number shows a shift towards higher mean factor values in the plots with a localized fire; the negative sign indicates an indirect proportional effect. Specialization is computed as the ratio of the standard deviation of factor values for the whole area to those in places with wildfire presence. Higher specialization values indicate narrower species niches, i.e. more restricted distribution of the habitat within the available environment. The analysis resembles principal component analysis (PCA). The marginality axis is extracted as the first axis, followed by several uncorrelated specialization axes until the number of initial variables is exhausted (Hirzel et al., 2002; Basille et al., 2008).

To cope with the different areas of FMUs, which could account for the observed fire incidence, but was beyond our interest, we subsampled the total number of 3277 Other FMUs according to their area, resulting in a subsample of 1000 units which have the same probability distribution function of FMU area as a set of 96 Burned FMUs. This sample set constitutes the landscape matrix used in the ENFA. This analysis was performed using the Adehabitat package (Calenge, 2006) for R (R Development Core Team, 2013). We tested the significance of the marginality values of particular factors by a randomization test of 1000 repetitions to distinguish the factors whose marginality values cannot be exceeded by a random distribution of presences (to be significant at least in 95 % cases). Spatially defined information was processed using ArcGIS software, version 9.2 (ESRI, 2007).

Results

1.9.7 Ancient fire events

Charred material larger than 125 μm was present in all 61 soil samples analysed within the pilot area. However, the abundance of charcoal in the topmost 20 cm of the soil profile varied considerably from 0.0006 g.kg^{-1} to 20.7964 g.kg^{-1} (mean 4.68, SD=4.37). Low charcoal concentrations under 1 g.kg^{-1} made up only 13 % of the whole dataset, suggesting ubiquitous occurrence of charcoals in forest soils of the sandstone area. We also found substantial variation of charcoal concentration between proximate sites, indicating a non-uniform distribution of charcoals following fire events. Since we performed homogenization of sub-samples within 1 m^2, we were unable to assess small-scale variability. However, the maximum difference between the nearest sampling sites was 3.1 g.kg^{-1}.

The regression Model 1 including all proposed topographic predictors was statistically significant; however, only because the Heat load index factor had a significant effect (Table 2). In the stepwise forward selection procedure, only the Heat load index contributed significantly to the model's explanatory power, and thus remained in the minimal adequate regression model (Model 2). Other environmental factors included in the analysis did not improve the model fit significantly. The positive estimated slope for the Heat load index indicates that charcoal concentrations in soil increase with increasing Heat load index, i.e. with high exposition to solar radiation (southwest-facing slope orientation).

The radiocarbon dating of 14 charcoal samples performed to assemble a time frame of charred matter formation revealed that 70 % of forest fires occurred during the last millennium. We also obtained much older (3399 cal. yrs BP) and recent (276 cal. yrs BP) dates within the investigated topmost soil layer (Table 3). Thus, the measurements of charcoal concentration within this soil layer represent an outcome of fire activity at a given site throughout the Subatlantic period (2500 cal. yrs BP - present). The spatial distribution of dates shows no apparent pattern with respect to the environmental gradients. The ranges of calibration intervals (2 σ) formed three major clusters during the Middle Ages and Early Modern Period and two non-overlapping fire events in the Bronze Age (Figure 3).

Table 2. Multiple regression results. Model 1: Linear regression of charcoal concentration in the topmost soil layer as a dependent variable and topographic parameters as independent variables, R= 0.41; R^2= 0.167; F(4.56)=2.8047; p<0.03415 ; Model 2: Stepwise linear regression with forward selection of variables, R= 0.40; R^2= 0.164; F(2.58)=5.6724; p<0.00562

		Model 1					**Model 2**		
Variables	***β***	**SE *β***	***t***	***p*-value**	**Step**	***β***	**SE *β***	***t***	***p*-value**
Intercept			5.894	0.000				6.762	0.000
Heat load	0.561	0.205	2.737	0.008	1	0.503	0.160	3.136	0.003
Rockiness	-0.018	0.256	-0.070	0.945					
Rock height	-0.078	0.273	-0.284	0.777					
Height_valley	-0.164	0.169	-0.970	0.336					

Table 3. ^{14}C ages of charcoal fragments extracted from the topmost 20 cm of soil profiles distributed across the whole BSNP area. Calibrated ages include the median probability of the calibration probability distribution and 2 σ range.

Site	Lab code	Depth (cm)	^{14}C age (BP)	Calibrated age (cal yrs BP ± 2 σ)
Ponova louka	LTL8214A	0–6	Modern	
Pravčický důl-hrana	LTL8206A	3–10	236 ± 45	276 (1–452)
Jedlina	LTL8211A	9–12	340 ± 45	396 (307–493)
Zadní Jetřichovice	LTL12356A	8–10	370 ± 35	431 (316–503)
Pryskyřičný důl	LTL8208A	4–8	368 ± 30	434 (316–502)
Piket	LTL12353A	10–15	818 ± 35	728 (680–788)
Pravčický důl-ústí	LTL12357A	7–13	938 ± 45	851 (746–931)
Jedlina	LTL8212A	15–20	1074 ± 40	984 (927–1060)
Česká silnice	LTL12347A	11–15	1351 ± 45	1281 (1182–1341)
Mlýny	LTL12358A	2–10	1399 ± 40	1313 (1271–1376)
Mlýny	LTL8202A	15–20	1449 ± 45	1345 (1285–1472)
Ponova louka	LTL8215A	6–20	1650 ± 45	1552 (1413–1692)
Pryskyřičný důl	LTL8209A	10–16	2626 ± 40	2755 (2716–2844)
Eustach	LTL8203A	12–16	3174 ± 50	3399 (3249–3553)

1.9.8 Recent fire events

In the period of 1974–2008, 71 fire events affected 96 FMUs within the territory of the BSNP (Figure 2). Some of the FMUs were affected by fire repeatedly over the course of the study. The real number of fires was probably higher because some of the fire records were impossible to localize (the FMU code was not stated) and due to a hiatus in the archival data from the W part of the BSNP in the period of 1974–1992.

The average fire frequency in the BSNP was two fires per year. The mean, median and mode size of the burned area was 0.75 ha, 0.08 ha and 0.01 ha, respectively. The largest fire was 17.92 ha. The causes of most fires were unknown or unstated (83 %), 10 % were caused by open fires (foresters, tourists) and 4 % by cigarettes and 3 % by lightning.

Using ENFA, we indicated the factors responsible for the wildfire distribution in the BSNP. These factors have a significant marginality value in the randomization test (Table 4). Fire incidence was primarily influenced by the factors Rockiness and Heat load index, followed by Height over the valley and Rock height. The factors with the least but still significant effects were Scots pine abundance and Stand age (Table 4 and Figure 4). Factors representing the abundance of other tree species were deemed insignificant by the randomization test of marginality. The influence of anthropogenic factors is of marginal significance. The ENFA did not show any noticeable trends in specialization (Figure 5). The highest values of specialization are related to Rockiness and Rock height. This can be interpreted as a partial limitation of wildfire occurrence on FMUs with rocks.

Table 4. *Marginality* values of environmental variables and their correlations with the *specialization* axes of the ENFA (Spe1, Spe2). The factors are sorted in descending order of *marginality* values and tested for *marginality* significance by a randomization test (p-value). Factors with significant *marginality* ($p < 0.05$) are highlighted in **bold.**

Variables	*Marginality*	p-value	Spe1	Spe2
Rockiness	0.563	**0.001**	0.557	0.121
Heat load	0.531	**0.001**	−0.159	0.552
Height_valley	0.435	**0.001**	0.203	−0.198
Rock height	0.431	**0.001**	−0.770	−0.494
Pin_syl	0.347	**0.001**	−0.024	−0.168
Age	0.272	**0.006**	0.063	0.279
Villages	−0.192	0.058	−0.061	0.076
Roads	−0.192	0.052	−0.076	−0.053
Pin_str	0.146	0.150	−0.049	0.023
Lar_dec	−0.145	0.124	0.036	0.471
Bet_pen	−0.105	0.246	0.066	−0.025
Fag_syl	0.096	0.324	0.041	0.015
Pic_abi	−0.059	0.550	0.079	0.243

In summary, the results indicate that wildfires are more frequent at the following sites (in descending order of importance): 1) rocky and elevated places (typically rock tops); 2) more insolated places (S, SW slopes); 3) stands with higher Scots pine abundance; 4) older forest stands; and 5) areas close to villages, roads, tourist paths and other places of human activity (with marginal effect).

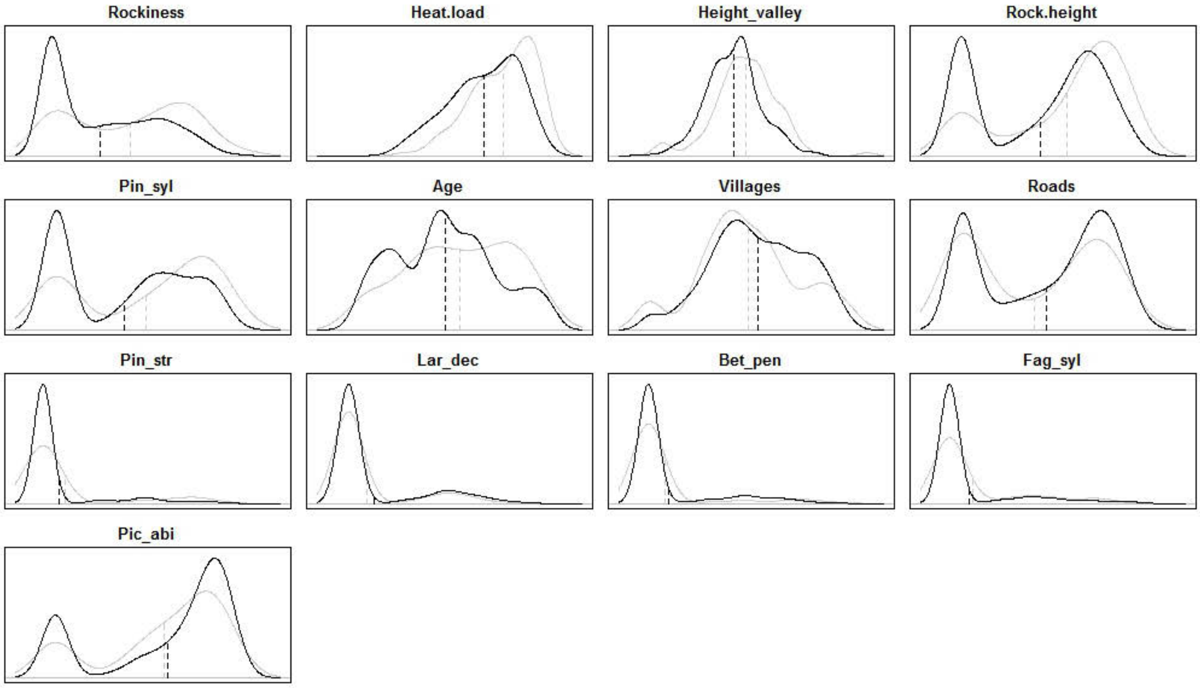

Figure 4. Graphic output of ENFA. Kernel density estimates (smoothed histograms) of values of particular environmental variables. The grey line represents factor values of FMUs affected by wildfires; the black line represents values of all FMUs.

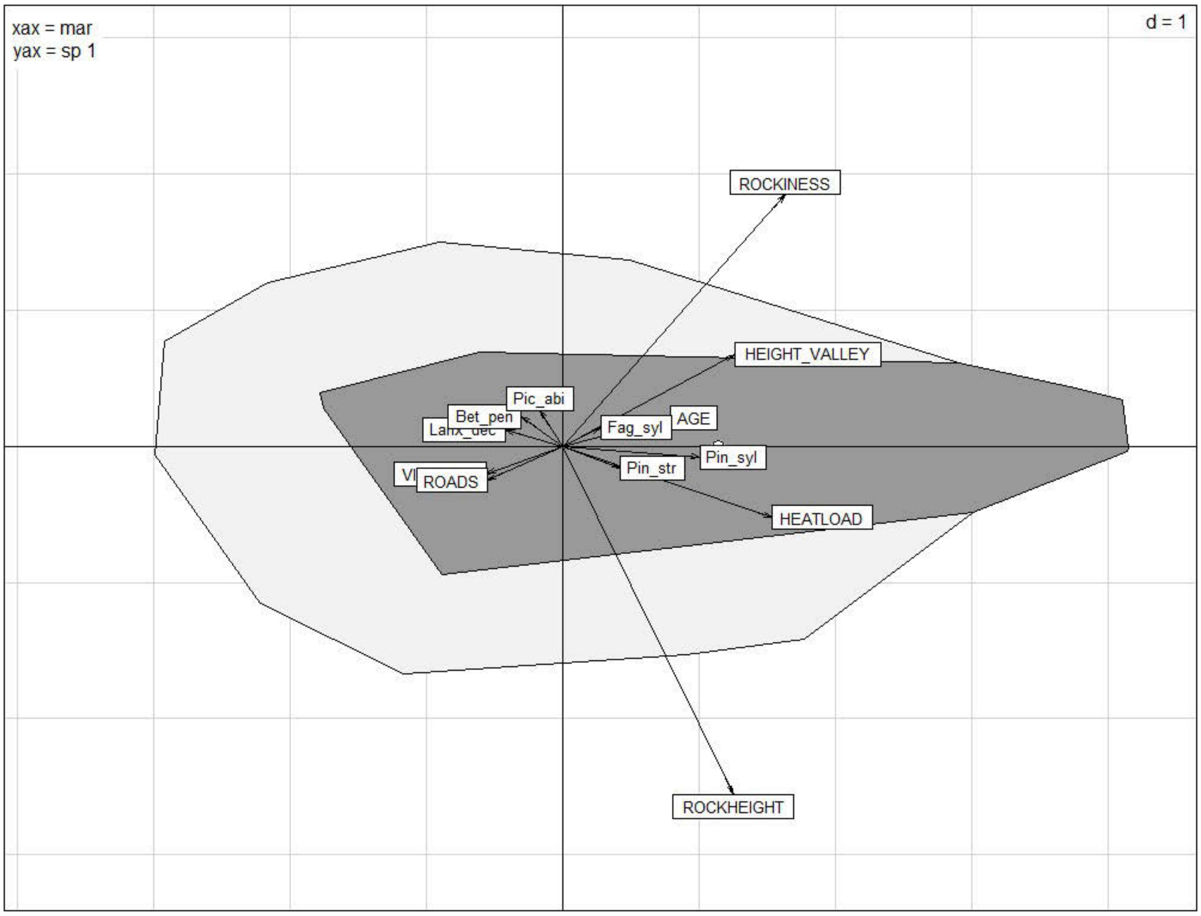

Figure 5. Graphic output of ENFA. Biplot of the ENFA formed by the marginality axis (X axis) and the first specialization axis (Y axis). The light and dark areas correspond to the minimal convex polygon enclosing the projections of all and burned FMUs, respectively. The white dot G corresponds to the centroid of burned FMUs. The arrows are projections of environmental variables.

1.10 Discussion

1.10.1 Topographic determinants of fire distribution

The results of our two approaches describing the spatial pattern of forest fires on the time scale of the last 34 years and the scale of the last two millennia are comparable. The distribution of wildfires in the present-day BSNP landscape is largely explained by topographic factors. Biotic variables including vegetation composition and stand age have weaker control over the occurrence of wildfires. Long-term fire occurrence inferred from charcoal content in mineral soil varies with the Heat load index. Sandstone landscape landforms thus determine a mosaic of fire-prone sites with higher fire occurrence probability. The overriding effect of Rockiness is probably connected with convex relief forms, shallow sandy soils and reduced canopy density, which increases the irradiation of the soil surface. A higher rate of evaporation at such sites results in a local decrease of humidity and the formation of fire-prone conditions. The significant effect of the Heat load index (i.e. site-specific thermal regime), thus also explains part of the variability connected with moisture distribution at the landscape level. Other parameters with marginal albeit significant effects could also be related to the thermal regime, for example, position along the valley slope profile or height of rocks. However, their positive effect also determines the elevated position of fire-prone areas above the surrounding landscape, thus increasing the probability of lighting strike, which is the most common natural trigger of wildfires (Gromtsev, 2002).

Since we consider topographic characteristics to be constant over the given time period, we also used them as explanatory variables of ancient wildfire distribution. We assume a simple process driven by gravity during which charcoal mass left on the surface by a forest fire is gradually incorporated into mineral soil and moves downwards through the profile (Preston et al., 2006). Subsequent fire events can partly consume charcoal in organic soil layers but simultaneously adds charcoal material, thus increasing its concentration. The total amount of charcoal in mineral soil therefore corresponds to the number of fires which had occurred at a given place. We found that soil charcoal content as a proxy for former fire incidence significantly increases with the increasing Heat load index within a 30 m radius around the sampling site. Our model, however, explained only part of the observed variability (16 %), thus implying the role of other factors not included in the model. These missing parameters are related to former vegetation cover and past anthropogenic activity – data on which it is impossible to obtain at stand-scale resolution. It is, however, more probable that the low proportion of observed variation comes down to the chosen methodological approach, which focused on a priori selected sites with a minimal risk of redeposition of charcoal (i.e. less than 6° slopes and places outside bottoms of valleys) due to fluvial transport. This selection reduced the total variability of topography-based factors pertaining to steeper slopes and relative vertical elevation (i.e. Heat load and Height above the valley) in the charcoal analyses. Within the context of our sandstone landscape, we suppose that fire spreads from optimal conditions until it reaches a barrier such as an edge of a plateau. We therefore searched for maximum values of the Heat load index inside the 30 m radius around our sampled plots, which represents the minimum distance of charcoal dispersion due to falling burned trees. The relationship could moreover be affected by post-depositional processes generated during the fire event such as small-scale ($<1 m^2$) heterogeneous charcoal distribution. This variability has also been reported by other authors (Touflan et al., 2009), who related it to the distribution of coarse woody debris on the surface prior to fire events. We partly eliminated this problem by using a sub-sampling strategy from several pits to get an average value of charcoal concentration.

1.10.2 Biotic determinants of fire distribution

Forest canopy composition and anthropogenic factors were tested in relation to present-day fire occurrence only. According to the ENFA results, the vegetation factors influencing the incidence of fires are only the abundance of Scots pine (*Pinus sylvestris*) and stand age, both with a positive effect. These results correspond to findings from northern Eurasia, where fires are often associated with Scots pine forests. Scots pine occurs often in dryer habitats, and its abundant resiny litter accumulated in developed older forests is easily inflammable (Ellenberg, 2009). At the same time, it is supposed to be one of the most fire-adapted tree species of the region, and the existence of certain Scots pine formations can be conditioned in the region by regular fires (see Engelmark, 1987; Agee, 1998; Angelstam, 1998; Gromtsev, 2002; Angelstam et al., 2004). Higher stand age may increase the probability of fire due to accumulation of organic litter and reduced canopy density (Angelstam et al., 2004). Based on an interpretation of pollen analyses (Pokorný et al., 2005; Abraham, 2006), the natural occurrence of Scots pine in the BSNP landscape was always restricted to sandstone rock tops with shallow soil. However, its present-day distribution is much broader and includes slopes and larger plateaus with deeper soil. We thus suppose that the occurrence of Scots pine influences the incidence of fires also in other relief types apart from rock tops.

The anthropogenic influence was approximated as the distance from the nearest road and village. These factors have a marginal effect on fire occurrence compared to the relief and vegetation. This indicates the dominance of natural factors over factors associated with human presence in the landscape as a trigger of fire incidence. Although forest management statistics provide strong evidence for the prevalence of human-lit forest fires in the BSNP area, it is obvious that this ignition trigger is only one presumption from a complex group of preconditions necessary for a fire to break out.

1.10.3 Local versus landscape drivers

As summarized above, our results indicate a positive effect of the variable landscape surface on fire occurrence. This does not correspond with the situation in regions with frequent fires (MFI < 39 yrs), where the variability of the landscape surface is negatively correlated with fire frequency (Stambaugh et al., 2008). If a landscape is predominantly flat, barriers limiting the spread of fire are infrequent, and the distribution of fuel is continuous. Fires should be more frequent under these conditions than in a variable landscape (Stambaugh et al., 2008). However, in regions climatically less favourable for the occurrence of wildfires, fire-prone conditions occur more frequently on convex landforms than in the flat surrounding landscape (Angelstam, 1998).

This also means that factors operating at the stand scale are more responsible for variation in forest fire incidence than landscape-scale drivers (i.e. the climate) (Iniguez et al., 2008). We suggest that in climatic regions without pronounced drought periods, bottom-up processes are responsible for wildfire occurrence. The specific environmental features of the BSNP sandstone landscape, such as sharp gradients in soil moisture content and numerous fire spread barriers, result in a small-scale pattern of plots affected by fire. The size of most present-day fires does not exceed 0.1 ha, although they are difficult to locate and put out in the rugged landscape. Moreover, our results from radiocarbon dating of soil charcoal do not provide any evidence of large-scale (>100 ha) fire events. The calibration ranges of all fourteen ^{14}C dates collected within the whole BSNP area are clustered in several groups, which could indicate a possibility of synchronous fire events during certain time intervals (Figure 3). However, the sampling sites are separated by long distances (max distance between soil trenches ~10 km) and numerous barriers to the spread of fire. Based on the available evidence, we find the concept of a larger number of singular events to be more likely.

1.10.4 Fire frequency

Because our radiocarbon dates are distributed over an extensive area and the number of analyses is low, we were unable to calculate any parameter describing fire frequency. On the other hand, the dates indicate a marked increase in fire occurrence after the beginning of the Early Middle Ages (approx. 500 AD). This could constitute evidence for logging or pastoral activity within areas not permanently settled based on available archaeological and historical data (Jenč et al., 2003). During the subsequent High Medieval colonization, human pressure, including establishing of settlements, was concentrated in the surrounding regions. We can reasonably expect an interaction between human activity and other factors influencing the fire regime, resulting in a change of fire frequency. Such a positive effect on wildfire occurrence as a consequence of human activity has been detected in the palaeoecological record all across Europe (Rius et al., 2011). However, the spatial pattern of the most fire-prone areas is driven mainly by non-anthropogenic factors such as relief characteristics, fuel distribution and vegetation type. Moreover, fire disturbances also occurred during the Middle and Early Holocene, as we know from ^{14}C dating of charcoal extracted from deeper soil layers and microcharcoal (>125 μm) deposited in peat-bogs (Bobek, 2013). We therefore hypothesize that the topography-driven distribution of fires has a long-term influence on the sandstone landscape.

1.10.5 Fire as a natural driver in the temperate zone

Our results could significantly alter the current attitudes towards wildfires in Central Europe. Our findings concerning the incidence of wildfires in the BSNP landscape are in accordance with information from regions where wildfires are considered a natural part of forest dynamics. The correspondence between the results of two different methodical approaches and the weak effect of anthropogenic factors indicate that wildfires occurred in similar places at least during the Subatlantic period (from about 2500 years ago to the present day), although fires had probably been less frequent in periods without noticeable human activity. Vegetation occurring on rock tops and plateaus (typically *Pinus sylvestris* stands) has been influenced by human- or lightning-lit fires for centuries. Considering how well *P. sylvestris* and its understorey species are adapted to fire, we assume that the natural occurrence of Scots pine forests in the BSNP landscape partly depends on wildfire activity. This especially concerns Scots pine stands on deeper soils, where other tree species like beech or oak are presumed to form climax forests.

1.10.6 Implications for forest management

For a long time, wildfires have not been considered to be an important natural disturbance factor in Central Europe. Forest managers and conservationists therefore have not taken them into account. The present management practice in the area under study and similar protected areas is mostly driven by the concept of potential natural vegetation (Tüxen, 1956) or similar forestry typology (Randuška, 1982). This concept, which is based solely on remnants of what is thought to be natural vegetation in equilibrium with the recent climate and soil, does not take into account any disturbance event because it is, by definition, static (see Carrión et al. (2009) and the follow-up discussion). This has an impact, for example, on *Pinus sylvestris* stands in elevated positions characterized by more favourable soil conditions, where pine prevails thanks to the influence of wildfires. Current management policies consider these pine stands as being far from the natural state. They are thus supposed to be replaced by stands with presumed natural tree composition. Our study, however, strongly supports the idea that contemporary Central European forest restoration should accept non-equilibrium states as regular aims of natural conservation. Fire is a natural and important agent forming such states in at least part of this region.

1.11 Acknowledgments

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Chapter 3:
Human-induced changes in fire regime and subsequent alteration of the sandstone landscape of Northern Bohemia (Czech Republic)

1.12 Abstract

Multiproxy palaeoecological evidence from a sandstone region in northern Czech Republic was collected to explore the impact of fire disturbances on the decline of the broadleaved forests during the Late Bronze Age (3250–3050 cal. BP). It has been hypothesized that human-accelerated soil leaching affected the nutrient availability in the sandstone area, thus promoting the expansion of oligotrophic-adapted plant communities in the late-Holocene. Little is known about the mechanisms which induced such large-scale vegetation transformation. We sought to determine which driving forces were involved using independent proxy records – soil and sedimentary charcoal, pollen and fungal spores. Local fire history was derived from the variation in charcoal accumulation rates (CHAR) preserved in Eustach peatbog. The fire frequency (FF) estimation over the past ~7500 years revealed distinct phases of increased burning between 3100 and 2120 cal. BP (3.0 fires 1000 yr^{-1}) and 1400–600 cal. BP (4.3 fires 1000 yr^{-1}). Rapid compositional changes in the pollen assemblage were documented during the Late Bronze Age period, suggesting vegetation responded to increased fire disturbances. The human influence on the fire regime is implied by the short-term increase in cereal pollen concurrent with a major fire event, indicating possible use of slash-and- burn cultivation by Late Bronze societies. This type of human subsistence strategy practised in the sandstone landscape further evolved to pastoralism as suggested by continuous presence of coprophilous fungi Sporormiella and Sordaria, which occurred since the Hallstatt/La Tène period (2750–1950 cal. BP). Our study documents, for the first time, the intentional, human-caused biomass burning from densely forested areas of Northern Bohemian sandstone region. Our results imply that increased rate of fire disturbances contributed to the Late Bronze Age transformation of broadleaved forests to oligotrophic forest communities of late-Holocene.

1.13 Introduction

Holocene vegetation history of sandstone regions from northern Bohemia, Czech Republic has been shaped by various factors including climate change, soil development, species migration legacies, and human impact (e.g. (Ložek, 1998; Pokorný et al., 2005; Kuneš et al., 2008b; Novák et al., 2012, 2015). However, all these processes are widely modulated by the unique feature of this landscape; extraordinarily variable topography formed as a consequence of sandstone bedrock erosion

(Turkington et al., 2005; Young et al., 2009; Bruthans et al., 2014). The resulting landforms are responsible for most of the spatio-temporal vegetation patterns observed across various environmental gradients (Stein et al., 2014), thus making interpretations of Holocene development highly challenging from the region. This also applies for the recent fire dynamics, which is strongly related to relief characteristics (Adámek et al., 2015). As a consequence, multi-trajectory vegetation development has been postulated by previous paleoecological studies (Bobek, 2013; Novák et al., 2015) which have attempted to bring together multiple lines of evidence, including pollen, macrofossils, soil and archaeological charcoal. Based on these proxies, the reconstructions from the Czech sandstone regions suggest that vegetation could behave in two contrasting modes: progressively changing, or persistently stable, even at the spatial scale of neighbouring forest stands. However, particular ecological mechanisms responsible for such divergent ecosystem response remains poorly understood. So far, the most accepted ecological mechanism suggests that sandy soil degradation leads to the substantial loss of Ca^{2+} and Mg^{2+} cations, resulting in the formation of oligotrophic-adapted species-poor plant communities in the Czech sandstone area (Pokorný et al., 2005). Such gradual soil impoverishment seems to be an integral part of the Quaternary climatic cycles, as proposed by Andersen (Andersen, 1969; see also Birks and Birks, 2004; Kuneš et al., 2011). Although the process itself is naturally-driven by various external factors, such as precipitation changes or disturbance frequency, the rate of soil degradation could also be accelerated by increased anthropogenic impact. Such human-forced changes could lead to widespread landscape-scale vegetation transformations far exceeding the naturally-driven processes.

One of the most striking examples of such vegetation change induced by soil depletion occurred during the Late and Final Bronze Age (c. 3000 cal. BP) in the central part of the sandstone region in northern Czech Republic. This event (called 'Late Bronze Age environmental collapse' (Ložek, 1997, 1998)) has originally been recognized as the sudden decline in species rich snail faunas, and subsequent expansion of species poor oligotrophic snail communities, which are characteristic for present-day Pinus sylvestris-dominated forests. It has been suggested that human-induced woodland clearance and grazing pressure, coupled with late-Holocene climatic instability was responsible for speeding up the process of soil leaching and irreversible ecosystem changes (Pokorný, 2005; Pokorný et al., 2005). However, pollen and microcharcoal data used in previous studies do not allow for joint assessment of various driving forces, particularly local fire disturbance history and grazing activity, which are often found to be responsible for pronounced changes in vegetation composition, especially in mountain areas (Feurdean et al., 2013b; Roepke et al., 2013). Furthermore, commonly used secondary anthropogenic pollen indicators (Behre, 1981; Brun, 2010), such as *Urtica, Cirsium, Rumex acetosa*-type have limited applicability within the densely wooded sandstone landscape, because these plant species are frequently found also within present-day early successional forest stages (Adámek et al., 2016). Therefore, independent proxy, like coprophilous fungal spores, is urgently needed to quantify the effect of grazing in the area. There is also a growing body of evidence that fire has been involved in landscape-scale vegetation transformations during the Late Bronze Age, as indicated by radiocarbon-dated fire events from charcoal embedded in soil (Novák et al., 2012). Also numerous findings of charcoal-rich layers in peat sequences (Bobek, 2013) suggest widespread occurrence of forest fires in the Czech sandstone areas in the past. Consequently, a great amount of biomass had been repeatedly transformed into the volatile compounds through burning, mobilizing nutrients and making them vulnerable to leaching out of the ecosystem cycling (Leys et al., 2016b). The occurrence of fire events coupled with subsequent nutrient loss and increased erosional processes could have accelerated degradation of sandy soils in the past.

This study aimed to address the effect of fire disturbances and grazing on the Late Bronze Age vegetation transformation within a small portion (c. 79 km^2) of the sandstone region in northern Czech Republic. We have collected a comprehensive fire history record based on changes in charcoal accumulation rates (CHAR) and spatially extensive soil charcoal dating and identification. This is the first opportunity that estimates fire frequency from the sandstone region of northern Bohemia since the beginning of middle-Holocene. Moreover, spatially precise charcoal data derived from soil enabled us to investigate fire history and forest composition at the stand scale. Simultaneous analysis of pollen and fungal spores from a small forest hollow allowed us to determine local changes in vegetation composition in relation to grazing activity, fires, and human impact. By conducting this study we aim to improve existing understanding of fire history of temperate forest ecosystems during the Holocene, which until recently was a limited scientific interest in Central Europe (Niklasson et al., 2010; Feurdean et al., 2013a; Robin et al., 2013b, 2013a; Tinner et al., 2015). Specifically we focus on (1) assessing the role of fire disturbances during the Late Bronze Age environmental decline in the sandstone region, and (2) validating presumed grazing activity in the area using independent evidence.

1.14 Regional setting

Our study area is located inside the Bohemian Switzerland National Park (hereafter BS area), which is situated at the margin of the Northern Bohemian sandstone region (Figure 1). The landscape is formed by Cretaceous sandstone bedrock, which later eroded into enormously diverse geomorphological features consisting of a network of deep gorges separated by rocky ridges (hereinafter referred to as “sandstone landscape” (Härtel et al., 2007)). Moreover, the Tertiary volcanic activity induced penetration of basaltic rocks through sedimentary deposits resulting in the formation of isolated hills. The altitudinal gradient ranges from 115 to 556 m a.s.l. Soils that developed on sandstone bedrock are mainly dystric cambisols or acidic sandy podosols. However, remnants of glacial wind-blown deposits are relatively common on the plateaus, creating more favourable luvisols. The study area belongs to the temperate oceanic climate (Cfb according Köppen) with yearly precipitation of 700 mm year^{-1}, and a mean annual temperature of 8 °C (Tolasz, 2007). The area is situated in the mid-altitudinal zone of beech (*Fagus sylvatica*), and mixed beech-fir (*Fagus sylvatica–Abies alba*) forest (Plíva, 1991). Nevertheless, enormous habitat diversity allows for coexistence of open-canopy pine (*Pinus sylvestris*) forests on rocky plateaus, and mountain-like spruce (*Picea abies*) stands in cold valley bottoms. The recent vegetation composition is heavily affected by management practices, which have transformed large areas into spruce plantations. Nowadays, forest fires occur more frequently within the Northern Bohemian sandstone region in comparison with other parts of Czech Republic (Kula et al., 2013; Adámek et al., 2016).

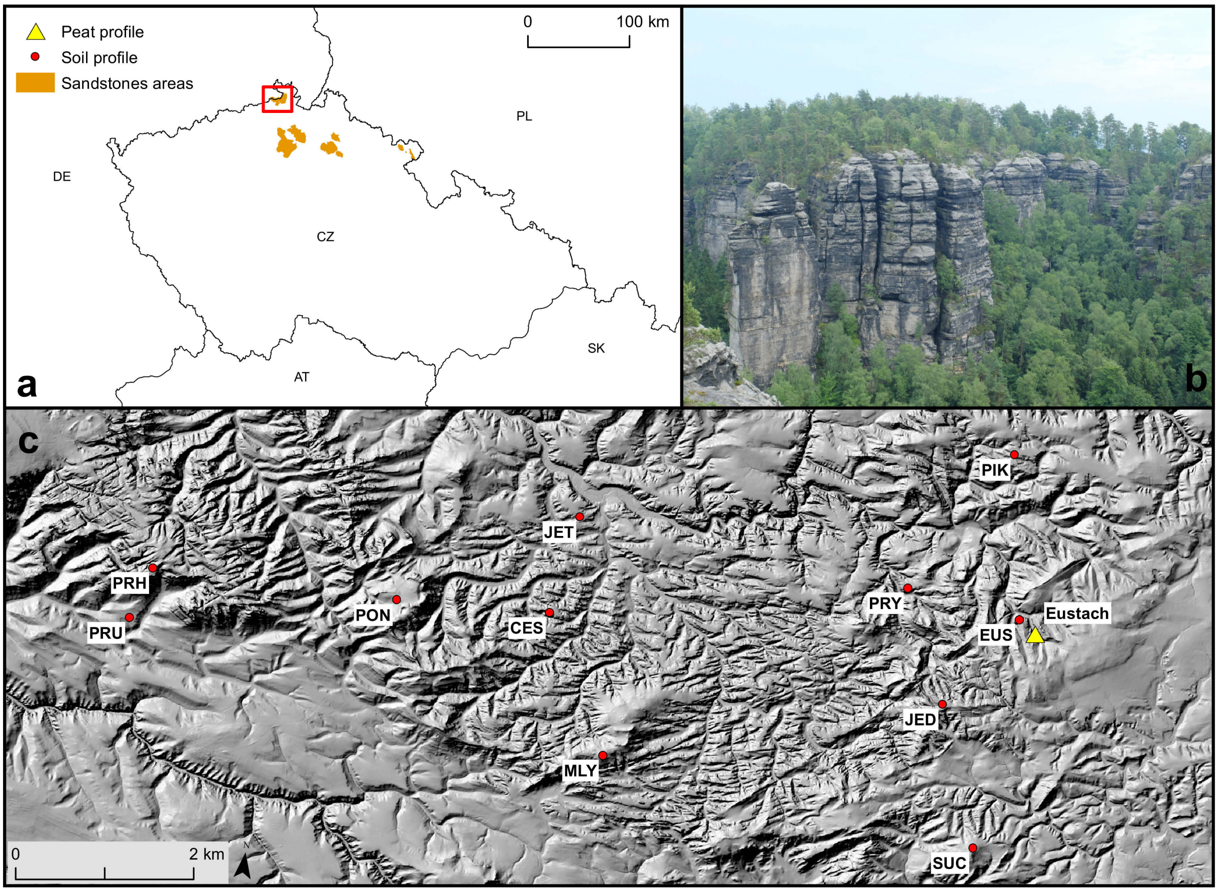

Figure 1. Location of the Bohemian Switzerland National Park (BS area) (a) in relation to the other protected sandstone regions of the Northern Bohemian sandstone area. An example location (b) of soil profile (site PRH) on exposed plateau showing typical position of sampling sites with respect to landscape geomorphology. (c) Shaded relief map indicating spatial distribution of the soil profiles and the Eustach peat core.

Human presence has been recorded since the Mesolithic by numerous archaeological excavations of rock shelters (Svoboda, 2003; Šída et al., 2011, 2014). Repeated findings of fireplaces, hazel (*Corylus avellana*) nutshells and stone tools provide evidence about hunter and gatherer occupation in the sandstone landscape. The area was most likely not affected by the Neolithic agricultural societies. Traces of Bronze-Age human occupation are still missing in archaeological record coming from the studied area, however, several findings have been made in the neighbouring area of Lusatian Mountains (Kozáková et al., 2015) and České Středohoří (Jenč et al., 2013). The same situation applies to the early Iron Age, which is represented here by the occasional findings of artefacts. From the beginning of the late Iron Age until the Early Middle Ages there is a substantial hiatus in archaeological evidence, indicating human abandonment of the area. However, the situation rapidly changed with respect to medieval colonization activities culminating during the High Medieval.

1.15 Material and methods

1.15.1 Chronologies

Chronologies were based on accelerator mass spectrometry (AMS) radiocarbon dating (CEDAD, University of Salento) and alpha spectrometry measurements of ^{210}Pb activity (Czech Geological Survey) in the topmost peat layers. For ^{210}Pb dating, bulk peat samples were extracted in regular 2 cm increments from core depths 0–36 cm. Sample age was estimated using a constant-rate-of-supply model adapted from Binford (1990). Terrestrial plant macroremains were used for ^{14}C dating whenever possible. However, due to scarcity of suitable plant material within a peat profile, one sample of bulk sediment had to be used. Charred wood particles extracted from soil profiles were selected for ^{14}C dating according to their weight and taxonomic identification. Sampling strategy aimed to date each soil layer whenever suitable fragment was present. All radiocarbon measurements were calibrated based on the IntCal13 curve (Reimer et al., 2013) provided by OxCal v4.2.24 (Ramsey, 2009) and reported as the median date before present (cal. BP) within the 2σ interval. Age-depth modelling was performed in Clam 2.2 R package (Blaauw, 2010) using a cubic spline interpolation between all ^{14}C and ^{210}Pb dated layers. The confidence envelope was produced for sedimentation model on the basis of Monte-Carlo permutation repeated 1000 times.

1.15.2 Pollen, micro-charcoal analysis and fungal spores

A small mire (Eustach site, 50°53′26.4″ N 14° 25′42.33″E) located at the bottom of a sandstone valley was selected for the study site. The peat profile was extracted using a U-shaped corer (5 cm diameter, 1 m length). Samples for pollen analysis were taken in 5 cm intervals, however high-resolution sampling was applied to the expected fire horizons determined by lithographic description in the field, thus resulting in 53 pollen samples analysed in total. Peat samples of 1 cm³ volume were prepared for pollen analysis according to standard methods (Berglund et al., 2003). A *Lycopodium* marker (Stockmarr, 1971) was added to each sample prior to the treatment and soaked in 10 % HCl solution to remove carbonates. The material was then carefully passed through a 500 μm sieve with aid of deionized water. Acetolysis was followed in a boiling water-bath for 10 minutes. Final samples for pollen analysis were mounted in glycerine for storing. A minimum number of 200 pollen grains or 50 *Lycopodium* markers were counted in each sample. Pollen types were determined to the highest taxonomic resolution using the reference collection at the Institute of Botany (CAS, Průhonice), pollen atlases (Reille, 1992, 1995, 1998), and pollen keys (Punt 1976-2003) (Beug, 2004). Algal remains were determined using special keys (Jankovská et al., 1982; Komárek et al., 2001). Non-pollen Palynomorphs (NPP) were determined according to available publications (van Geel, 1978; Pals et al., 1980; van Geel et al., 1983, 1986; Van Geel et al., 1989) and follow the terminology reviewed by Miola (Miola, 2012). Fossil stomata were identified according to C. A. Sweeney (Sweeney, 2004). Charcoal counting on pollen slides (microcharcoal) was performed in three size classes (largest axis: 10–50 μm, 50–100 μm and ≥ 100 μm), focusing exclusively on completely black, opaque fragments with angular shape (Clark, 1988a). Microscopic charcoal particles were counted until the whole area of single pollen slide was inspected. The results of pollen analyses (selected taxa) and non-pollen palynomorphs are presented as a percentage diagrams plotted on time. All percentage values were calculated proportionally to the total terrestrial pollen sum of arboreal (AP) and nonarboreal (NAP) pollen types where aquatic plants, ferns and NPPs were excluded. Microcharcoal content is expressed as a number of particles of respective size class per one slide. Stratigraphic diagrams were plotted in *Tilia v.1.7.16* (Grimm, 2011). Pollen zones were delimited using optimal splitting by sum of squares technique implemented in Psimpoll v. 4.27 (Bennett, 2009).

1.15.3 Quantitative analyses of pollen data

We used Detrended Canonical Correspondence Analysis (DCCA) (Hill et al., 1980) to quantify compositional turnover of chronologically ordered pollen percentage data (Birks, 2007). The DCCA results are scaled in ordination space as standard deviations units (SD), thus enabling direct assessment of compositional change between samples. The length of the first ordination axis gives a total dissimilarity (gradient) of the pollen sequence. A half-change in species composition is reached at 1 SD, however a full turnover between neighbouring assemblages appears at 4 SD. Analysis was performed in CANOCO v.5 (ter Braak et al., 2012) with pollen percentages standardized using a square-root transformation and detrended by segments. Rare species down-weighting was not applied. Calculations were constrained by sample age estimate according to the age-depth model to take into account stratigraphical nature of the pollen sequence. An alternative approach to assess the speed of compositional changes is based on quantifying the inter-sample dissimilarity per equal time unit (Jacobson et al., 1986). This method is critically dependent on reliable age estimation, which is used to standardise dissimilarity and may give false results during the ^{14}C plateau (Lotter et al., 1992). Our age-depth model includes dates laying outside major radiocarbon plateaus (Guilderson, 2005), which we consider to be suitable. An Index value was calculated by the squared chord distance (i.e. Euclidean distance of square-rooted pollen percentage data) between two adjacent pollen assemblages divided by its time span and expressed as dissimilarity change per year. Interpolation and resampling to equal time interval prior to a dissimilarity calculation was not applied. The direct effect of fire history and grazing pressure on vegetation composition has been assessed using redundancy analysis (RDA) (Legendre et al., 2012). In order to employ an appropriate response model (linear vs. unimodal) we examined length of gradient using Detrended Correspondence Analysis (DCA). Since we observed minor changes in species composition along main gradient (less than 3 SD) we preferentially applied linear techniques. We used fire frequency estimates (number of fires per 1000 years based on CHAR analysis, see below) as a proxy for local fire history. Moreover, total influx of coprophilous fungal spores (*Sporormiella, Sordaria, Podospora, Delitschia*) were used to quantify presence of browsing animals (Baker et al., 2013). The number of spores counted were converted into concentration values based on the *Lycopodium* marker added to the sample and counted in the pollen slide. Fungal spore influx was calculated by dividing these values by sediment accumulation rate. An estimated sample age has been used as a co-variable to partial out the variance originating from temporal trend. The significance of the first constrained axis has been tested using unrestricted Monte Carlo permutation test (999 permutations).

1.15.4 Soil charcoal sampling

The macroscopic fragments of charred wood (>0.5 mm) buried in soils are valuable markers of *in situ* fire occurrence (Carcaillet, 1998; Ohlson et al., 2000). As these particle are limited in aerial transport by their size they do disperse only several tens of meters around the burned sites (Clark, 1988b). They are also taxonomically identifiable according to wood anatomy, so reconstruction of past vegetation composition can be achieved. Eleven sampling locations within the BS area covering the main types of site conditions (i.e. rocky ridges, elevated basaltic hills, large plateaus), were selected (for site abbreviation see Figure 1c). Charcoal samples were excavated from soil trenches dug down to the parent material. We did not take samples from slopes steeper than 5°, or the valley bottoms in order to minimize input of allochtonous charcoal particles via soil erosion. Precise trench location was conducted on the basis of micro-topographical features reconnaissance in the field, which allowed to avoid pit-and-mound relief caused by tree uprooting. Soil samples of volumes between 8 and12 litres were taken in non-continuous fashion with respect to visible soil layering. Profiles exhibiting texture and colour inhomogeneity within soil horizons were excluded from sampling due to possible mixed stratigraphy. The soil samples were then dried in the laboratory (60°C for 24 hrs) in order to improve charcoal flotation capability. Charred wood particles were extracted using a water flotation technique (Carcaillet et al., 1996) followed by wet sieving with a 200 μm mesh size. Subsequent hand-sorting of the fraction greater than 2 mm under a stereomicroscope resulted in charcoal assemblages suitable for taxonomical identification. All recovered charcoal particles were analysed, however, several charcoal-rich samples were randomly sub-sampled to reduce the total sum. Taxonomical analysis was performed under a reflected light microscope (Jenatech 50–500×) by observing three anatomical planes (transversal, tangential, radial) created with the aid of razor. The determination was based on presence of anatomical features, which were compared to wood anatomy atlases (Wheeler et al., 1989; Schweingruber, 1990, 2011; Benkova et al., 2004; Richter et al., 2004), and charcoal reference collection material. Identification was generally feasible to the genus level, however several anatomically well-defined taxa were determined to the species level. Distinguishing between genera *Vaccinium* and *Calluna* on small charcoal pieces was not always possible, so we aggregate the anatomical group Ericaceae, which includes *Calluna vulgaris, Vaccinium vitis-idaea, Vaccinium myrtillus* and *Vaccinium uliginosum*.

1.15.5 Charcoal accumulation rates and fire event detection

Macroscopic charcoal (typical size 125–250 μm) records from lake and peat bog sedimentary sequences can be used to infer local fire history (Whitlock et al., 2001). It has been theoretically demonstrated that this approach is reliable to detect fires on the spatial scale ranging between 0,5-1 km (Gavin et al., 2003b; Higuera et al., 2007). The charcoal series from small sedimentary basins (i.e. forest hollows) tends to consistently record high-severity fires, while low-severity fires are less well represented (Higuera et al., 2005). Therefore, the resulting fire frequency reconstruction originating in such depositional context should be regarded as a conservative estimate. We contiguously sampled the peat core into 1 cm resolution, and a sample size of 2 cm^3. The aim was to reveal local fire activity, so we extracted charcoal particles greater than 125 μm (Whitlock et al., 1996). Peat samples were gently disaggregated using 10 % KOH for 12 hrs and washed through a 125 μm sieve. The procedure resulted in a coarse fraction consisting mainly of plant tissues which was then bleached using 3 % hydrogen peroxide to increase contrast between black charcoal and non-charred organic material. However, time-consuming hand cleaning had to be applied in order to remove larger plant debris making charcoal counting easier. We applied a semi-automated charcoal quantification method executed on uniformly dispersed particles in a thin water layer inside Petri-dishes. Sample images were captured using a high-resolution scanning device, and particle counting was processed by ImageJ (Schneider et al., 2012) capabilities. An obtained series of charcoal concentrations (pieces cm^{-3}) were converted into charcoal accumulation rate ($CHAR_{raw}$, pieces cm^{-2} $year^{-1}$) by multiplying by sediment accumulation rate (cm $year^{-1}$) inferred from the age-depth model. We adopted a widely used method for fire history reconstructions based on Charcoal Accumulation Rate (CHAR) in lake and peat sequences (Clark, 1988b; Higuera et al., 2010). To derive a local fire events, we employed a peak detection procedure implemented in CharAnalysis 0.9 software (Higuera et al., 2009) (available at http://phiguera.github.io/CharAnalysis). The charcoal series was resampled into constant time intervals ($CHAR_{int}$) corresponding to the median sample resolution of 32 years. The CHAR time series was decomposed into a peak component ($CHAR_{peak}$), and a background component ($CHAR_{back}$). The $CHAR_{peak}$ represents the sudden increase of charcoal input into the sedimentary record, which can be attributed to a local fire event. On the other hand, a slowly varying $CHAR_{back}$ represents changes caused by regional shifts in fire activity, or sediment mixing within the basin. The optimal sampling interval to detect a local fire followed a criterion of 0.12 times the known mFRI for the studied ecosystem (Higuera et al., 2007), which equals 60 years per sample when assuming 500 years FRI reported from Central Europe (Robin et al., 2014). We modelled $CHAR_{back}$ using a robust locally weighted regression (LOWESS) within a 1000-year window. We applied non-transform-residual model ($CHAR_{peak}=CHAR_{int} - CHAR_{back}$) to remove a background trend from $CHAR_{int}$ series resulting in high-frequency residual $CHAR_{peak}$ (Higuera et al., 2010). This procedure did not include any variance-stabilising methods (i.e. data transformation) and assumes that charcoal peaks are created via additive processes (i.e. charcoal input per fire is constant). The distinction between fire-related charcoal peaks ($CHAR_{fire}$) and random noise ($CHAR_{noise}$) was based on locally fitted Gaussian mixture model to 1000 year window (Gavin et al., 2006; Higuera et al., 2009). Charcoal peaks exceeding 99th percentile of the modelled noise distribution were considered as a local fire event. We assessed a separation of $CHAR_{fire}$ and $CHAR_{noise}$ populations using signal-to-noise index (SNI), which compares variability inherent to both distributions (Kelly et al., 2011). In order to test a reliability of each peak, $CHAR_{fire}$ series was screened with the minimum-count test to account for statistically insignificant variation in charcoal counts (Higuera et al., 2010). Fire history was expressed as the number of fire events per 1000 years (i.e., Fire Frequency (FF), fires 1000 year^{-1}) span which was smoothed afterwards using LOWESS filter.

1.16 Results

1.16.1 Peat profile chronology and sample resolution

The Eustach peat profile continuously covers the last 7532 years. A sedimentary age-depth model (Figure 2) was developed using 18 ^{210}Pb dates, and four AMS ^{14}C dates, respectively (Table 1). However, one radiocarbon date was excluded from the model, as it yielded an unexpectedly old date. This was probably caused by selecting reworked material originated from a *Picea abies* trunk embedded in the peat sequence. The uppermost core section (0-75 cm) revealed rapid accumulation of unconsolidated *Sphagnum* peat at the mean rate of 0.196 cm year^{-1}. The following part (76-154 cm) is characterised by a gradual transition to woody peat and a decrease mean in sedimentation rate to 0.023 cm year^{-1}, giving the median time resolution of 43 year cm^{-1} (Figure 2). The bottom core section (155–200 cm) consisted of well-humified dark peat, which decreased in median resolution to 75 year cm^{-1}. Because of the absence of any sand or clay layers, we can reasonably assume continuous sedimentation without any major erosional events.

1.16.2 Soil charcoal data and age

We have collected 11 soil profiles distributed within 79 km^2 of the BS area. In total, c. 500 litres of soil were sampled and processed by flotation and wet sieving which resulted in 37 charcoal assemblages from different soil horizons. The anatomical identification was successful for 3024 charcoal fragments belonging to 12 taxa at the species or genera level (Figure 3). The overall species composition of the charcoal assemblages were dominated mainly by *Pinus* spp. (64 %) (consider that *Pinus sylvestris* prevails, however this could potentially include other native species *P. mugo* and *P. rotundata*, which are not present within the area at present) followed by *Quercus* spp. (9 %) (includes species *Q. robur, Q. petraea, Q. pubescens*) and *Fagus sylvatica* (7 %). A minor proportion of the charcoal spectra was formed by other tree or shrub taxa like *Picea abies* (5 %), *Abies alba* (4 %), *Calluna vulgaris* (4 %), respectively. The charcoal spectra with *Pinus* spp. proportion exceeding 50 % of total sum were frequently accompanied by acidophillous understorey shrub *Calluna vulgaris* and *Vaccinium* spp (expressed as the summary of the Ericaceae group). Other light-demanding tree taxa

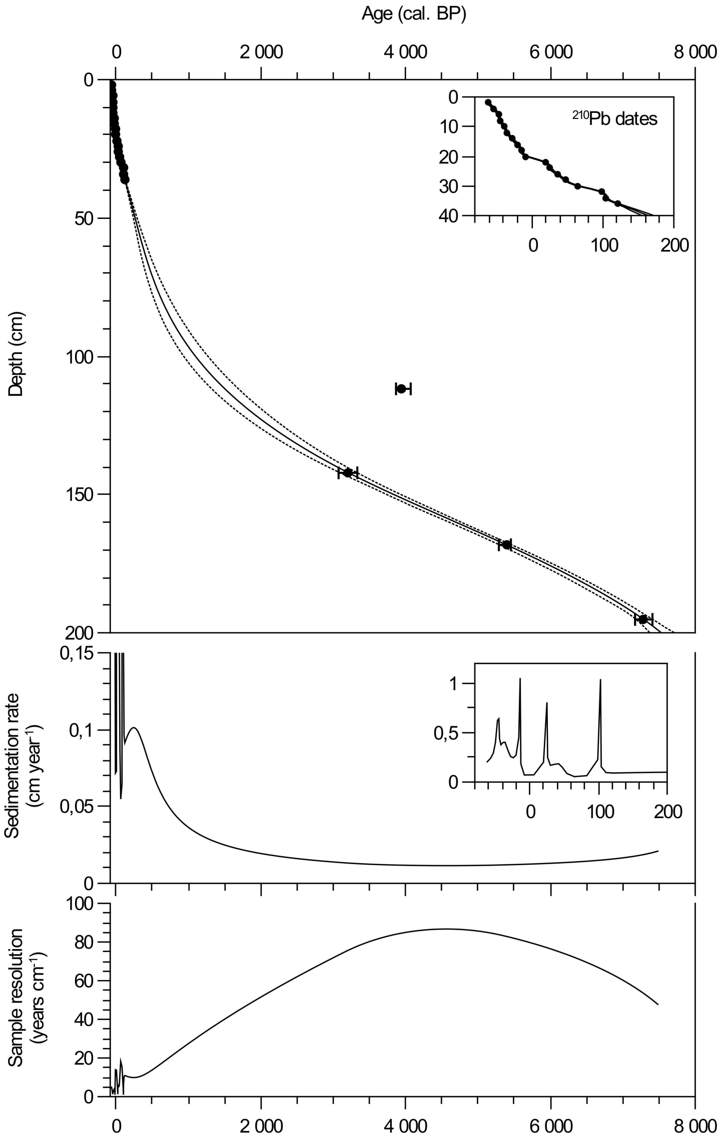

Figure 2. Age–depth model for the Eustach peatbog based on ^{210}Pb and ^{14}C dating. Calculations were performed in Clam 2.2 (Blaauw, 2010) using a cubic spline interpolation between dated layers. 95 % Confidence interval (dashed lines) were constructed based on Monte Carlo permutation test (n = 1000). One outlying date was excluded from the model.

characteristic for early successional stages are not frequent (<1 %), except for *Betula* spp. (2 %). The main differences in site species composition were driven by higher abundance of deciduous trees *Fagus sylvatica* and *Quercus* spp. Such charcoal spectra have occurred more frequently at the sites located on basaltic bedrock or near alluvium of Křinice River (sites MLY, JET, SUC, PON). The quantity of *Fagus sylvatica* increased up to 10 % at such sites and rare findings of nutrient-demanding taxa like *Fraxinus* spp., *Acer* spp. and *Tilia* spp. were also recorded. Radiocarbon dating of 27 charcoal particles extracted from soil horizons shows wide range of dates covering the whole Holocene (Figure 3 and Table 1). The oldest *Pinus sylvestris* charcoal preserved in the soil profile revealed a date of 11 151 cal. BP showing the presence of this tree within the sandstone area at the Pleistocene/Holocene transition. Based on radiocarbon dating, several fire episodes has been detected during the Middle Holocene, however the majority of ^{14}C dates belongs to the Early/High Middle Ages.

Table 1. Table of AMS radiocarbon dates from 11 soil profiles and Eustach peatbog. Individual charcoal particles were dated in soil horizons. Calibration range is shown at 2σ (95,4 % probability).

Lab code	Site	Context	Depth (cm)	Material dated	Conv. age (yr BP)	Error (±)	Upper calib. range (2σ)	Lower calib. range (2σ)	Median age (cal BP)
LTL12358A	Mlýny	soil horizon	2-10	Quercus charcoal	1399	40	1379	1270	1313
LTL8202A	Mlýny	soil horizon	15-20	Quercus charcoal	1449	45	1476	1285	1344
LTL8203A	Eustach	soil horizon	12-16	Pinus charcoal	3174	50	3555	3249	3399
LTL8204A	Eustach	soil horizon	19-30	Pinus charcoal	6625	45	7575	7437	7513
LTL12357A	Pravčický důl-ústí	soil horizon	7-13	Pinus charcoal	938	45	932	746	851
LTL8205A	Pravčický důl-ústí	soil horizon	21-30	Picea charcoal	4546	45	5435	5046	5167
LTL8206A	Pravčický důl - hrana	soil horizon	3-10	Larix charcoal	236	45	437	0	275
LTL8207A	Pravčický důl - hrana	soil horizon	14-26	Pinus charcoal	350	45	496	311	400
LTL8208A	Pryskyřičný důl	soil horizon	4-8	Pinus charcoal	368	30	503	316	433
LTL8209A	Pryskyřičný důl	soil horizon	10-16	Pinus charcoal	2626	40	2845	2716	2755
LTL8210A	Pryskyřičný důl	soil horizon	19-26	Picea charcoal	7132	50	8029	7848	7959
LTL8211A	Jedlina	soil horizon	9-12	Pinus charcoal	340	45	494	307	395
LTL8212A	Jedlina	soil horizon	15-20	Pinus charcoal	1074	40	1061	927	983
LTL8213A	Jedlina	soil horizon	23-30	Quercus charcoal	6356	50	7418	7175	7293
LTL8214A	Ponova louka	soil horizon	0-6	Fagus charcoal	after 1950 AD				
LTL8215A	Ponova louka	soil horizon	6-10	Fagus charcoal	1650	45	1693	1413	1552
LTL8216A	Ponova louka	soil horizon	37-50	Fagus charcoal	1667	45	1701	1417	1574
LTL12347A	Česká silnice	soil horizon	11-15	Pinus charcoal	1351	45	1342	1182	1280
LTL12348A	Česká silnice	soil horizon	28-34	Quercus charcoal	178	45	302	0	173
LTL12349A	Česká silnice	soil horizon	34-51	Pinus charcoal	9727	65	11254	10793	11151
LTL12350A	Suchý vrch	soil horizon	40-50	Pinus charcoal	961	45	960	782	859
LTL12351A	Piket	soil horizon	60-75	Pinus charcoal	5844	45	6776	6509	6660
LTL12352A	Piket	soil horizon	32-49	Pinus charcoal	9528	55	11099	10664	10868
LTL12353A	Piket	soil horizon	10-15	Pinus charcoal	818	35	789	680	727
LTL12354A	Zadní Jetřichovice	soil horizon	39-50	Quercus charcoal	617	45	665	541	601
LTL12355A	Zadní Jetřichovice	soil horizon	25-36	Fagus charcoal	4225	45	4864	4616	4745
LTL12356A	Zadní Jetřichovice	soil horizon	8-10	Quercus charcoal	370	35	505	315	431
LTL13405A	Eustach peatbog	peat profile	195	Picea needle	6344	45	7170	7415	7279
LTL13406A	Eustach peatbog	peat profile	142	bulk peat	3010	35	3076	3337	3200
DeA-6116	Eustach peatbog	peat profile	112	Picea wood	3630	26	3865	4071	3940
DeA-6117	Eustach peatbog	peat profile	168	Poaceae tissue	3870	45	4418	4155	4301

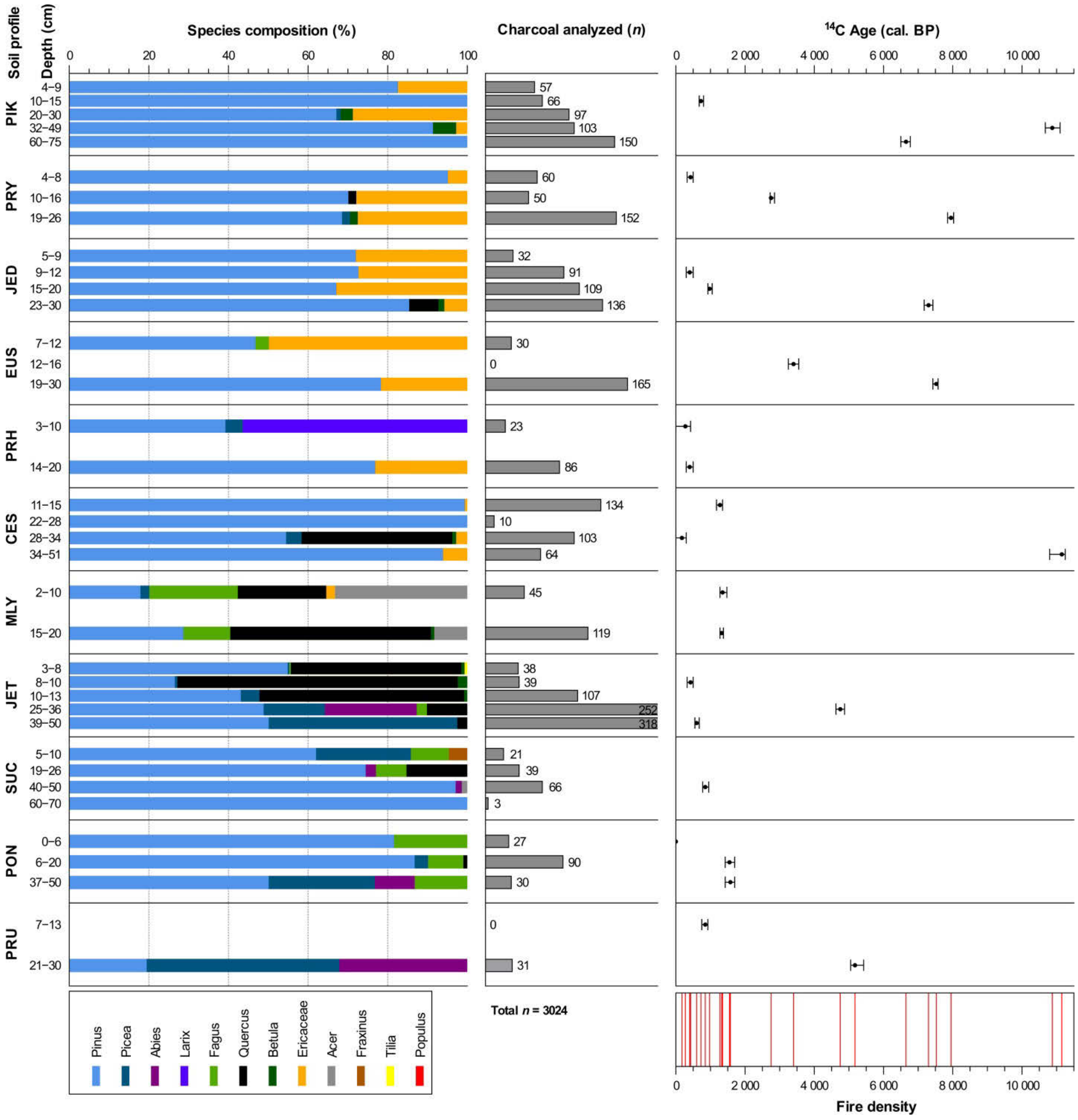

Figure 3. The taxonomic composition of charcoal assemblages acquired from 11 soil profiles which were placed within the BS area.

1.16.3 Vegetation development inferred from the Eustach profile

The Eustach peat profile records both the vegetation and fungal spores changes from the BS sandstone area since the onset of the Middle Holocene (Figure 4 and 5). Considering the small size of the mire and the valley-bottom location within the sandstone landscape, observed vegetation changes mirror local dynamics in plant communities. The pollen diagram is divided into the six Local Pollen Assemblage Zones (LPAZ).

In LPAZ EU 1 (7532–6207 cal. BP) circumjacent valley floor habitats were overgrown by mixed oak forests, as suggested by the high pollen percentages of *Quercus, Ulmus, Fraxinus* and *Tilia*. Basal sections show maximum values of *Corylu*s (40 %), which demonstrate its important admixture

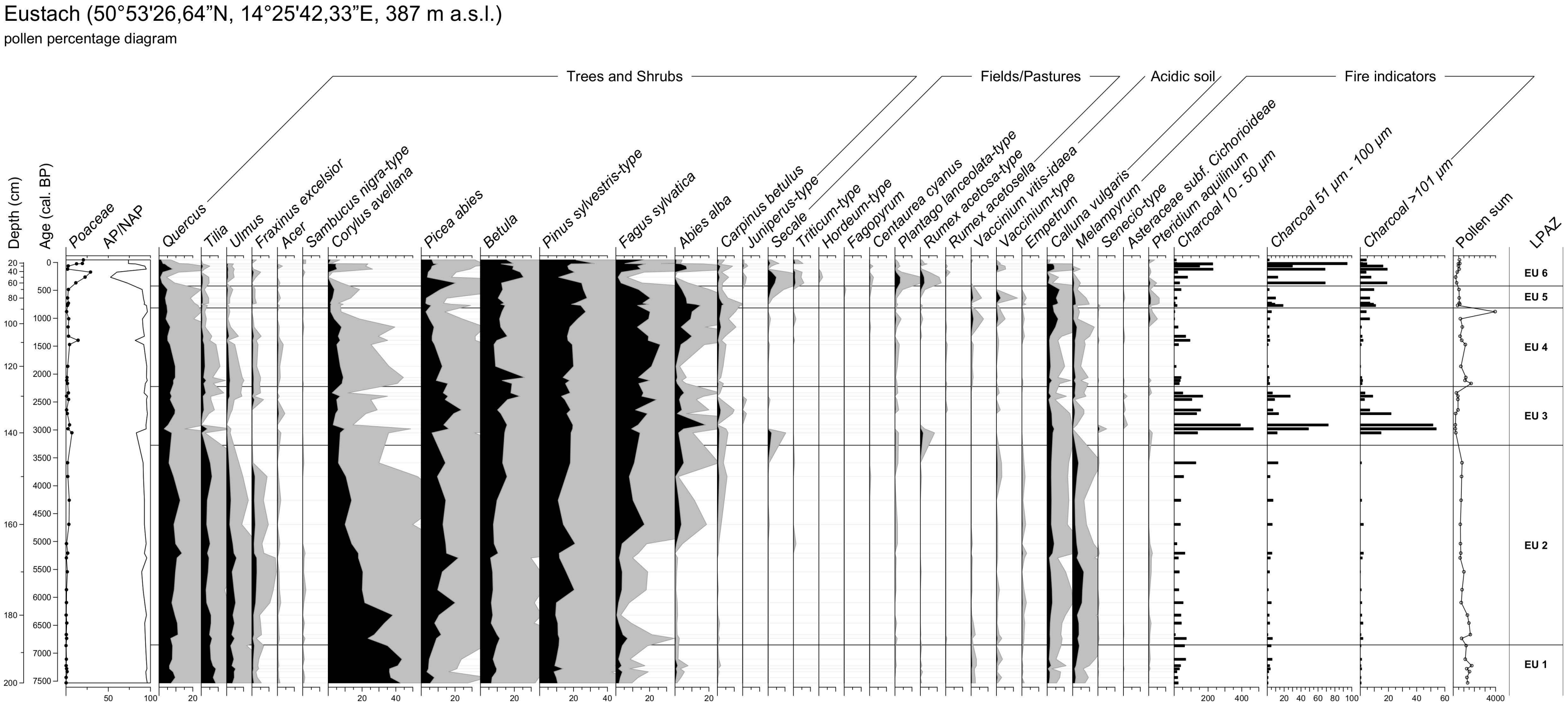

Figure 4. Simplified pollen percentage diagram of the Eustach peatbog based on the total pollen sum of all terrestrial taxa excluding wetland pollen taxa. Charcoal values are given as a proportion to total pollen sum. Local pollen assemblage zones (LPAZs) are delimited according to optimal splitting by sum of squares.

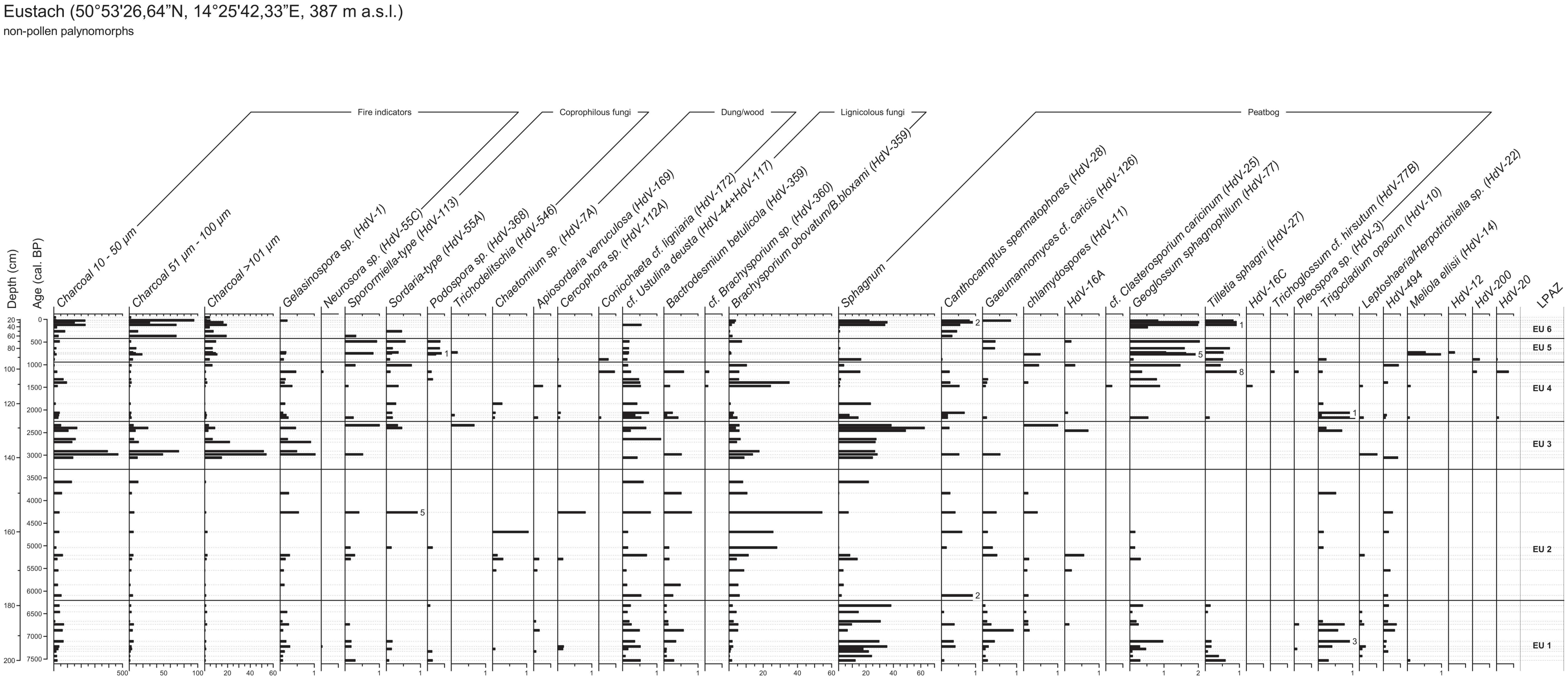

Figure 5. Simplified non-pollen palynomorph (NPP) percentage diagram of the Eustach peatbog. Percentage values are proportional to total pollen sum.

in forest vegetation. The limited spatial extent of coniferous forests is indicated by low *Pinus sylvestris* values (10 %), and the occurrence of *Vaccinium*-type, *Calluna vulgaris* and *Vaccinium vitis-idea* pollen. *Pinus sylvestris* stands were located on dry sandstone plateaus and ridges probably since the early Holocene. *Picea* stomata indicate its local occurrence on waterlogged sites during the initial stage of the peat layer formation. Sporadic finds of *Rumex acetosa*-type (including species *R. acetosella*) pollen suggest the occurrence of early successional stages (Figure 4). Fire events are indicated by microcharcoal and spores of *Gelasinospora* and *Neurospora* (Figure 5).

During LPAZ EU 2 (6207–3313 cal. BP) a gradual change of forest vegetation towards coniferous types was observed. *Picea* expanded outside of the waterlogged sites, as indicated by pieces of *Picea* charcoal from the soil layer on the plateau (site JET). This occurrence could be attributed to spruce's ability to colonize disturbed sites (Engelmark, 1993). Also, *Pinus sylvestris* pollen increased suggesting the spread of oligothrophic communities on poor sandy soils. *Quercus* pollen suggests the population sustained ongoing changes in a stable state, however, *Corylus* pollen decreased during this zone. This process of hazel retreat was accelerated during the rapid expansion of *Fagus sylvatica* and *Abies alba*, as the light-demanding hazel could not sustain the competitive pressure of beech. Low pollen percentages of both the secondary anthropogenic indicator *Plantago lanceolata*, and the single find of *Triticum*-type probably reflect human occupation located outside BS area. Short-term increases of coprophilous fungal spores (*Podospora sp., Sporormiella*-type, *Sordaria*-type) represents grazing by animals.

LPAZ EU 3 (3313–2252 cal. BP) is characterised by an abrupt increase of microcharcoal, and the retreat of broad-leaved trees such as *Tilia, Ulmus* and *Fraxinus*. A pronounced increase in fire activity is also documented by the abundant findings of fire demanding fungus *Gelasinospora* sp. The delayed expansion of the pioneering tree, *Betula*, suggests the presence of early successional forest stages. The same applies for the peaks in *Abies alba* and *Picea abies*, which are able to easily colonize disturbed soils affected by fire or abandoned agricultural land(Engelmark, 1993; Volařík et al., 2013). Also, the presence of herb species *Senecio*-type*, Asteraceae* subfam. *Cichorioideae* and fern *Pteridium aquilinum* supports the gap occurrence within the tree canopy. The marked increase in *Secale cereale* and *Rumex acetosa*-type was related to samples with elevated microcharcoal content. . A continuous presence of dung fungus *Sordaria*-type, *Sporormiella*-type, as well as the presence of *Juniperus communis* pollen confirms grazing by animals in the surrounding area.

In LPAZ EU 4 (2252–945 cal. BP) forest recovery following the previous disturbance phase has occurred. *Fagus sylvatica* further expanded reaching maximum pollen percentage values. The formation of extensive beech-fir forest is documented by the increase in *Abies alba* pollen. The human impact substantially decreased, as reported by rare findings of cerealpollen.

LPAZ EU 5 (945–423 cal. BP) shows an expansion of poor pine-dominated forests with *Calluna vulgaris*, *Vaccinium*-type, *Vaccinium vitis-ideae* undergrowth. Microcharcoal size classes 51-100 μm and >100 μm are moderately abundant indicating biomass burning in the wider area.

LPAZ EU 6 (423–(-62) cal. BP) denotes High Medieval colonization activity in the surroundings of the BS sandstone area. Medieval farming is represented by *Fagopyrum* together with abundant *Secale cereale*, *Triticum*-type and *Hordeum*-type pollen. Microcharcoal input could be partly attributed to the presence of kiln sites in the vicinity.

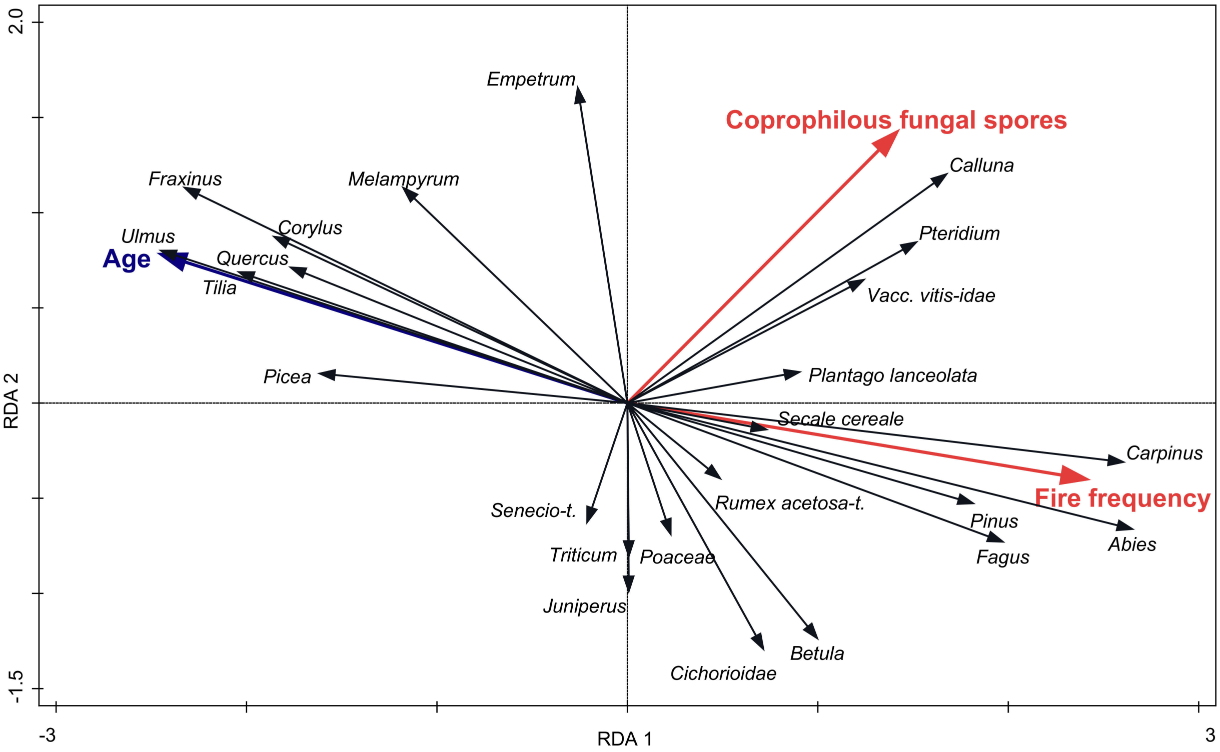

Figure 6. Redundancy analysis (RDA) ordination triplot of pollen record from Eustach peatbog. Explanatory variables (coprophilous fungal spores, FF) and co-variable (age) expressed as arrows. Only selected taxa are shown. The total variance in pollen composition explained by ordination axes equals 8.9 %.

1.16.4 Quantitative assessment of vegetation changes

In order to quantify compositional turnover throughout the whole pollen record, we used DCCA ordination constrained by sample age (included in Figure 7). The first canonical axis accounts for 13.1 % of the total variability. The differences in sample scores on the first axis show a period of great compositional change during the Middle and Late Bronze Age, which coincided with an increase in fire frequency. The total change over this period accounts for 0.7 SD, indicating exchange of nearly half of the available species pool. When compositional change induced by modern forestry practices is neglected (~ last 250 years), Middle to Late Bronze Age species turnover represents the most significant plant community transformation during the last seven millennia.

When including both fire frequency and influx of selected coprophilous fungi in RDA analysis as explanatory variables, first two ordination axes accounts for 8.9 % of the total variability. The analysis is statistically significant as assessed by Monte Carlo permutation test (pseudo-F=2.4, p=0.002). RDA revealed a close association of pollen taxa *Calluna vulgaris, Vaccinium vitis-idaea, Plantago lanceolata*-type and *Pteridium aquilinum* spores with increasing influx of coprophilous fungi

(Figure 6). Furthermore, several tree taxa (*Pinus, Fagus, Abies, Carpinus*) were assigned to the periods of higher fire frequency. A minor correlation to fire has been observed for *Secale cereale*, *Betula, Asteraceae* subfam. *Cichorioideae, Rumex acetosa*-type.

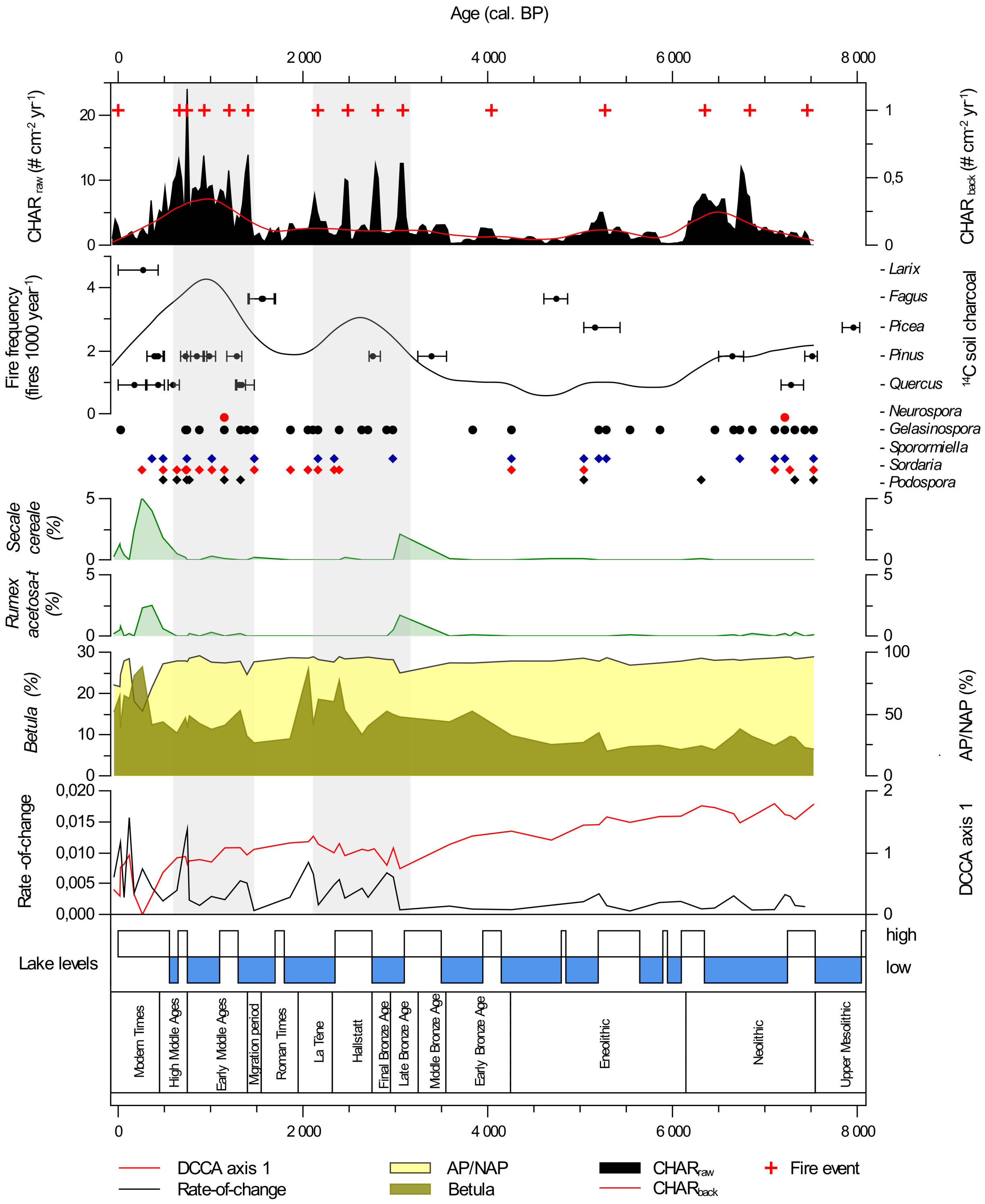

Figure 7. Summary diagram linking diverse fossil evidence from the Eustach peat profile, and soil charcoal recovered within the sandstone area. (1) Charcoal accumulation rates (CHARraw) with estimated background charcoal deposition (CHARback), crosses denote a timing of a fire event; (2) dating and taxonomical identification of selected soil charcoal (early-Holocene dates are not shown), calibration 2σ range given by IntCal13, median calendar age is denoted by dots; (3) presence of fungal spores (Neurospora and Gelasinospora) indicating fire occurrence; (4) FF (fires 1000 yr^{-1}, solid line); (5)

presence of dung fungal spores (Sporormiella, Sordaria and Podospora) linked to large herbivore activity (Baker et al., 2013); (6) percentage of Betula pollen, vegetation openness expressed as AP/NAP ratio; (7) compositional change revealed by DCCA ordination (units in SD) and rate-of-change analysis (units in chord distance dissimilarity per 1 year); (8) Mid-Europe lake-level fluctuation (Magny, 2004); (9) archaeological periods for Bohemia (Kuna et al., 2014).

1.16.5 Charcoal accumulation rates and fire history reconstruction

Charcoal concentration in peat samples range from 3 pieces cm^{-3} up to 919 pieces cm^{-3}. When considering changes in sedimentation rate, charcoal accumulation rates (CHAR$_{raw}$) vary between 0.233 pieces cm^{-2} year^{-1} and 24.06 pieces cm^{-2} year^{-1} (Figure 7). An observed median time between continuous charcoal samples was 32 years (mean=39, SD=29, range=1–87). This value was used for the interpolation of the CHAR$_{raw}$ series. Low CHAR$_{raw}$ occurred from the basal part of the record to 6868 cal. BP. Thereafter, a pronounced increase in CHAR$_{raw}$ values resulted in two charcoal peaks between 6 838 and 6 238 cal. BP, afterwards it decreased to the mean value of 1.571 pieces cm^{-2} year^{-1} lasting for three millennia. A calculated fire frequency peaked at 2.2 fires 1000 year^{-1} during the period 7528-6148 cal. BP, than dropped to the lowest recorded value 0.6 fires 1000 year^{-1} between 6148-3118 cal. BP. Significant changes occurred during the Bronze/Iron Age period between 3118 to 2098 cal. BP when several distinctive peaks indicate instantaneous charcoal input into the sedimentary basin. This period is characterised by rapid increase in fire frequency up to 3.0 fires 1000 year^{-1}. CHAR$_{raw}$ decreased again to low values during the period between 2098 –1468 cal. BP, which corresponds to minimum of 1.9 fires 1000 year^{-1}. Since the Early/High Medieval Times (1408-628 cal. BP) CHAR$_{raw}$ suddenly increased and peaked at 24.06 pieces cm^{-3}. The fire frequency reconstruction showed the maximum value of 4.3 fires 1000 year^{-1}. A gradual decrease in CHAR$_{raw}$ and fire frequency denotes the youngest part of the record (628-0 cal. BP). Altogether, the decomposition of charcoal series revealed 15 fire events (Figure 7). Mean signal-to-noise index (SNI=4.9, not shown) was constantly above the threshold (SNI>3) recommended by empirical studies (Kelly et al., 2011) which indicated sufficient separation of charcoal peak component from inherent noise of the series.

1.17 Discussion

1.17.1 Early Holocene fire disturbance regime

Soil charcoal data revealed at least two fire disturbance episodes at the beginning of the Holocene. These fires primarily affected *Pinus sylvestris* stands, because charcoal of this species prevailed within soil assemblages. An understorey dwarf-shrub belonging to the Ericaceae family has also been found, indicating poor acidic soils, while *Betula* sp. further suggest post-disturbance successional phases or presence of mixed pine-birch woodlands. However, pedoanthracological results should be interpreted with caution because of biases introduced by soil mixing processes, which could result in an unclear age chronology (Carcaillet, 2001; Šamonil et al., 2013b). A combination of multiple-site sampling approach, and extensive radiocarbon dating could partly overcome such limitations. Thus, negative evidence of other tree taxa within the soil layers containing the early Holocene charcoal lead to the conclusion that *Pinus sylvestris*-dominated forests grew on the sandstone plateaus during the early Holocene. This is consistent with anthracological analysis carried out on charcoal from archaeological layers buried under rock shelters, which also show the prevalence of Scots pine (Novák et al., 2015). Since there is a lack of sedimentary charcoal within the BS area dating back to the early Holocene period, fire frequency could not be reconstructed. However, a general increase in biomass burning has been observed across Central Europe, suggesting climate change as the main driving force (Marlon et al., 2013). Regional lake records (Hošek et al., 2014) document climatic warming at the transition from the Younger Dryas to the Early Holocene, which was followed by rapid afforestation. Such a re-colonization process may have led an increase in biomass accumulation, which would have created an essential prerequisite for fire activity. Therefore, fire disturbances may have influenced the postglacial forest re-establishment in Central Europe, and should be integrated in forest dynamics.

Since the Northern Bohemian sandstone landscapes have been widely occupied by Mesolithic hunters-gatherer communities (Svoboda, 2003), there is a possibility that fire has been used by humans (Innes et al., 2013). Intentional burning aimed to stimulate early successional phases within closed-canopy woodlands was part of the subsistence strategy of the Mesolithic people (Zvelebil, 1994), although its long-term effect on forest ecosystems seems to be weak and hardly detectable in pollen records (Kuneš et al., 2008b). It has also been hypothesized that Mesolithic communities may have promoted *Corylus avellana* for dietary reasons (Kuneš et al., 2008b; Regnell, 2012). Frequent findings of carbonized nutshells and hazel wood within Mesolithic archaeological sites around the entire area of the Northern Bohemia sandstone region (Opravil, 2003; Šída et al., 2011; Novák et al., 2015) supports this hypothesis. Whereas its intentional spreading by humans is questionable (Huntley, 1993), hazel benefits from increased fire frequency (Clark et al., 1989), as it has an ability to resprout easily from the stem basis, which facilitates the rapid regeneration after a fire disturbance (Delarze et al., 1992). A common coincidence of high proportions of hazel pollen, and elevated charcoal concentrations evokes a positive mutual relationship (Finsinger et al., 2006). Higher charcoal values found in the basal layers of the Eustach peatbog resemble such a pattern of high hazel pollen and charcoal concentrations. However, there are two problematic points within our record. First, the charcoal accumulation rates revealed fire frequency of two fires per millenium which is insufficiently low to maintain early successional forest stages at the broader spatial scale. In the case of deliberate human biomass burning, we have to assume low population density or extensive migration between camp sites in order to explain infrequent fire occurrence. Low fire frequency at the Upper Mesolithic/Neolithic transition could also be attributed to the gradual retreat of hunter-gatherer societies, which is consistent with diminishing traces of Mesolithic inhabitation around 7500 cal. BP (Šída et al., 2011). Second, we did not find any trace of *Corylus avellana* from the soil charcoal assemblages investigated throughout the region (sites CES, PRH, EUS, PIK, PRY, JED). This contradicts its ubiquitous presence in our pollen record (up to 40 %). Fires that burned in *Corylus avellana* dominated bushes most likely would have burned the entire stand due to its dense stem structure, thus leaving vast quantities of charcoal on the soil surface. The overall absence of *Corylus* *avellana* charcoal during the Early-and Mid-Holocene on plateaus leads to the conclusion that vegetation must have had distinct spatial structure which could not be captured by our soil sampling design. Thus, forest stands with strong admixture of *Corylus avellana* were probably limited to the steep slopes along the ravine hillside (i.e. sites not sampled here due to input of allochtonous soil material).

1.17.2 Diverse vegetation structure of the Mid-Holocene sandstone landscape

During the transition from the Upper Mesolithic to the Early Neolithic (LPAZ EU1, 7532-6207 cal. BP), charcoal influx was low, indicating little local fire activity. When comparing to sedimentary charcoal records from temperate Europe the inferred fire frequency of 2.2 fires 1000 year^{-1} is two times lower than what others have reported from the north Alpine foreland (Clark et al., 1989). Nevertheless, a corresponding fire frequency (~ 2 fires 1000 year^{-1}) has been detected within Mid-Holocene broadleaved forests in the foothills of the Pyrenees (Rius et al., 2009). The overall temperature during the Mid-Holocene warmed by ~1–2,5°C from the mean of the past 200 years (Renssen et al., 2009), which should stimulate vegetation burning (Daniau et al., 2012). Moreover, considering current microclimate variability which is highly modified by the landform characteristics (Wild et al., 2013), an increase in temperatures would lead to changes in the distribution of soil moisture, resulting in pronounced periods of drought on sun-exposed sites. This topography-driven mechanism could amplify the precipitation changes during the mid-Holocene, when several low lake-level phases indicate the occurrence of dryer climatic conditions (Magny, 2004). As a result, higher temperatures, along with more pronounced droughts would have created favourable conditions for fire activity (Gavin et al., 2003a; Kane et al., 2015). However, we have observed low level of fire frequency during the mid-Holocene implying other driving forces than climate. Changes in vegetation composition could possibly explain the decline in fire frequency, as the biomass changed to a temperate deciduous forest (i.e. 'Quercetum mixtum') during the Holocene thermal maximum (c. 8000–5000 cal. BP), which may have reduced the susceptibility to fire activity. While there is a general consensus about the widespread occurrence of temperate deciduous forests in the Central European lowlands (Firbas, 1949; Kalis et al., 2003; Jamrichová et al., 2014; Novák et al., 2017b), prevalence on poor sandy soils within mid-altitudes regions (200-500 m a.s.l.) is questionable (Szabó et al., 2016). We detected rather low pollen percentages of temperate deciduous taxa, such as *Quercus*, *Tilia, Ulmus,* and *Fraxinus,* in the Eustach record. This can be explained by the reduced spatial extent of such communities as a result of poor soil conditions on slopes. Nevertheless, there is also indirect evidence for the occurrence of deciduous oak forests, as demonstrated by the high abundance of *Ustulina deutsa* (HdV-44 and HdV-117), a parasitic fungi on various broad-leaved trees excluding *Corylus avellana* (van Geel et al., 1988). Since this fungus is especially common on *Fagus sylvatica*, it may also indicate beech forest in the vicinity (van Geel et al., 2013). This is consistent with finding of beech pollen and charcoal dated to this period. Moreover, our soil charcoal record revealed only minor occurrence of broad-leaved taxa, thus implying a rather limited spatial extent of such vegetation type. Additionally, soil charcoal data contradict to extensive coverage of closed-canopy deciduous forests, because of the high proportion of light-demanding *Pinus sylvestris*. This suggests that seedling recruitment of *Pinus sylvestris* preferably takes place under high light conditions (Adámek et al., 2016). Moreover, a continuous pollen curve of the heliophilous dwarf shrub *Empetrum* confirms the persistence of open heath-like habitats, as this species hardly survives light depletion under the canopy of broad-leaved trees (Svenning, 2002). Also, a pollen threshold value of local presence for *Picea* (1 %) and *Pinus* (10 %) (Lisitsyna et al., 2011) has been far more exceeded which implies a considerable admixture of conifers in forest community, or distinct vegetation pattern. On the other hand, pollen composition resembling oak-dominated deciduous forests has been discovered in other parts of the BS sandstone area (Pokorný et al., 2005), thus suggesting possible local occurrence of this vegetation type. All the above mentioned evidence points to the Mid-Holocene coexistence of light demanding vegetation types (e.g. *Pinus sylvestris*) and broad-leaved forests formed by *Quercus*, and later on during the Subboreal by *Fagus*. Since the fire occurrence was low during this period, vegetation structure was controlled by the heterogeneity in site conditions, rather than fire frequency.

1.17.3 Hidden Late Bronze Age land-use in sandstone areas

An important environmental change has occurred during the Late Bronze Age, which is indicated by increased compositional changes in plant communities. Species turnover and rate-of change analysis of pollen data exhibit substantial vegetation transformation exceeding the magnitude Mid-Holocene values (Figure 7). Because rate-of-change calculations depend on a precise chronology (Lotter et al., 1992), a simultaneous response of multivariate DCCA method can provide a more robust estimate of compositional shifts in community assembly. The overall trend shows a rapid retreat of broad-leaved taxa like *Tilia, Ulmus*, *Fraxinus, Corylus*, and lagged expansion of *Picea, Abies* and *Betula*. Concurrent with this change are numerous independent evidences that document an increase in biomass burning. Firstly, the charcoal accumulation rates showed large fluctuations which indicate a series of local fire episodes. The estimated fire frequency increased to 3 fires 1000 year^{-1}. Further, fire-related fungal spores emerged, such as *Gelasinospora*, an ascospore fungus that is often found within charcoal-rich layers (van Geel, 1978; van Geel et al., 2006; Innes et al., 2013). Moreover, we found *Pinus sylvestris* charcoal particles in the soil profile EUS, located on a rock plateau <100 meters away from the Eustach peat core, with an age that corresponds to the beginning of the Late Bronze Age (Figure 3). Woodland communities were subjected to moderate canopy opening due to fire disturbance as arboreal pollen values decreased to 85 %. The abrupt increase in charcoal influx was followed by a short-term occurrence of *Secale cereale* and *Rumex acetosa*-type pollen suggesting cereal cultivation. All above-mentioned indices suggest a linkage between fire occurrence and human activity in the sandstone area during the Late Bronze Age. A variety of agro-pastoral practices involved fire for human subsistence, as demonstrated by the simultaneity of clearance phase and cereal pollen occurrence in relation to slash-and-burn cultivation (Pitkänen et al., 1999). The spread of human settlements into less favourable regions outside of the lowlands is known for the Bronze Age period

(Dreslerová et al., 2013b), which makes such agricultural practices even more probable within the BS area. However, an overall absence of permanent settlements in a 16 km radius of the study site dating back to the Late Bronze Age and Hallstatt/La Tène period (Archaeological Database of Bohemia maintained by Institute of Archaeology, Prague) does not support such agricultural activity. Thus, the character of human landscape utilisation must have been based on short-term exploitation events, without establishing a permanent settlement. This agrees with the requirements of slash-and-burn cultivation, which requires extensive forested areas in order to permit frequent shifts of burned/sown sites (Rösch, 2013). Long-term cultivation experiments from mixed-deciduous forests in Germany (Rösch et al., 2002; Ehrmann et al., 2014) proved this technique as a reliable tool for food production in a densely forested landscape, even on poor soils. The short-term effectiveness of this agricultural practice is illustrated by the higher crop yields during the first year after burning in comparison to the medieval three-field crop rotation system (Ehrmann et al., 2014), even without need of additional manure. Nutrients are primarily released from burned topsoil organic matter, which temporarily increases soil fertility. However, the speed of subsequent soil organic matter build-up is a factor limiting the frequency of slash-and-burn cycles. This is consistent with short-term occurrence of *Secale cereale* in our pollen record. In this regard, there was no need for weed suppression on burned sites because of their absence in the soil seed bank. Thus, common field weeds were substituted by native forest species making the detection of cultivated plots using pollen indicators difficult (Behre, 1981). This is in accordance with the Eustach pollen record which does not show any distinct increase in secondary anthropogenic indicators, except for *Rumex acetosa*-type. Even though this pollen type is routinely used for indication of man-made habitats, recent observation of secondary forest succession on burned sites suggests that Rumex species are also frequent within pioneering plant communities following fire disturbance (Adámek et al., 2016). Furthermore, it must be mentioned that intentional use of *Secale cereale* as a crop during the Bronze Age is rather questionable (Behre, 1992). Individual archeobotanical finds of *Secale cereal*e grains dated back to the Early Bronze Age are not considered as a reliable evidence (Hajnalová, 1990), and the beginning of intentional cultivation started during the La Tène period in the Czech Republic (Dreslerová et al., 2013a). However, also other pollen records originated from uninhabited forested regions show sporadic occurrence of *Secale cereale* throughout the Bronze Age (Kozáková et al., 2015) indicating that human agro-pastoral activity, likely associated with slash-and-burn practices, was probably more common within these areas. This could partly be explained by the previous status of *Secale cereale* which grew among other crop as a weed and has been recorded due to high pollen productivity. Nevertheless, the synchronous increase of *Secale cereale* and fire frequency indirectly supports the use of slash-and-burn for cereal cultivation within a BS area. This fire-based subsistence strategy further developed since the beginning of La Tène period when hay making was introduced to provide winter feed (Hejcman et al., 2013). Since meadows were probably incorporated into non-forested areas surrounding villages, distant parts of the landscape become more attractive for pastoralism. Such change is visible in our fungal spores record as the frequent occurrence of both *Sporormiella*-type and *Sordaria*-type, a coprophilous taxa, indicate local presence of herbivores (Davis et al., 2006; Baker et al., 2013). The BS sandstone landscape has probably been favourable for grazing due to ongoing fire activity. The presence of early successional forest stages since the Hallststt period is in agreement with the recorded increase in *Betula* pollen which is able to readily colonize burned sites. During the Roman Times and Migration Period, such pastoral utilisation of the landscape was interrupted as the evidence for grazing and biomass burning diminished.

1.17.4 Disentangling fire influence on the vegetation change

The originally proposed “Late Bronze Age environmental collapse” (Ložek, 1998) revealed unprecedented landscape-scale vegetation transformation within the Czech lowland sandstone regions, and outlined possible linkages to human influence on this change. Subsequent research, however, demonstrated that the environmental collapse event was a part of a climatically-driven soil acidification process during the interglacial cycle, which were locally accelerated by human impact (Pokorný et al., 2005). Our data provide clear evidence that fire was involved in this vegetation transformation, but had also been influencing vegetation dynamics in the BS area long before this event occurred. Soil charcoal indicates that fires continuously maintained *Pinus sylvestris*-dominated communities during the maximal expansion of mid-Holocene broadleaved forests. Because of decreased fire frequency during that time, however, it must have acted synergically with poor soil conditions in order to sustain such forest type. Therefore, the climatic control over the fire regime seems to be the major factor operating during the early to mid-Holocene period which is consistent with observations from other part of Central Europe (Robin et al., 2013a). Since the Late Bronze age, fire regime has undergone a change to a predominantly human-driven process, as indicated by the simultaneous occurrence of cereal pollen and various fire proxies, such as charcoal accumulation rates and *Gelasinospora*. We attributed this change to the expansion of Late Bronze Age human societies (i.e. Lusatian culture) which practised slash-and-burn agriculture in the forested landscape. The increased fire frequency probably disrupted effective nutrient cycling within ecosystem pathways, and may have triggered the soil leaching process. While we did not observe an abrupt change in the dominant tree species in the pollen data, distinct compositional changes in plant communities was identified using a DCCA and rate-of-change analysis, which illustrated immediate effect of fire disturbances on speciescomposition. This differs from findings reported from densely settled lowland sandstone areas of Central Czech Republic where human intervention using fire and grazing induced rapid expansion of *Pinus sylvestris* stands (Pokorný, 2005). Therefore, the magnitude of Late Bronze Age environmental change differed between particular sandstone regions and seemed to be less pronounced in mid-altitude areas where oligotrophic forest types were already established since the early Holocene.

1.18 Conclusions

Our reconstruction of fire regime provided new insight into vegetation dynamics within the sandstone landscape of the Northern Czech Republic. The fire proxies revealed a continuous record of fire disturbances spanning the entire Holocene period. The general pattern of fire frequency corresponds to climate trends, but reflects also changes in human land-use practices during the late Holocene. Radiocarbon dating of soil charcoal demonstrated that fire occurred early during postglacial forest expansion as a function of biomass accumulation. Possible influence of Mesolithic societies on the fire regime has been discussed, with special regards to intentional spreading of *Corylus avellana* for dietary purposes. We did not find any soil charcoal evidence for using the fire as a tool within human subsistence strategy, however, high pollen proportion of *Corylus avellana* in Upper Mesolithic section of Eustach peatbog confirmed its important role in the vegetation. Fire frequency decreased during the Holocene climatic optimum as a consequence of spreading of less flammable broad-leaved forests. However, patches of *Pinus sylvestris*-dominated forests maintained by both, recurrent fire disturbances and nutrient-poor soils, continuously persisted throughout bottle-neck of shade-giving mid-Holocene vegetation types. The major shift in fire regime occurred during the Late Bronze Age and Iron Age, when human activities increased fire frequency as a consequence of landscape exploitation. Our pollen data suggest the possible use of slash-and-burn practices may have been linked to short-term cereal cultivation by people of the Lusatian culture. The subsequent increase in coprophilous fungal spores since the Hallstatt/La Tène period further indicated the development of human land-use strategy to the pastoralism. This late Holocene transition to the human-driven fire regimewas followed by fluctuation in species composition which had a rather gradual character. Accordingly, we confirmed the anthropogenic origin of “Late Bronze Age environmental collapse” (Ložek, 1998) within a Bohemian Switzerland sandstone area. Furthermore, we conclude that observed vegetation transformation was triggered by fire disturbances related to slash-and-burn cultivation.

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Chapter 4:
Biotic controls on Holocene fire frequency in a temperate mountain forest, Czech Republic

1.21 Abstract

Mountain spruce-beech-fir mixed forests are an important type of vegetation at higher elevations in the temperate zone of Europe. We aimed to determine how fire disturbances have affected the long-term vegetation dynamics and to assess their contribution to soil formation. We detected fire episodes using a soil charcoal record extensively dated based on ^{14}C and combined with pollen and macrocharcoal records from a local peat bog. Altitudinal shifts of the timberline during the Younger Dryas/Holocene transition seem to be responsible for an abrupt occurrence of fire at 11,200 cal a BP. The minimum fire frequency estimation based on dated soil charcoal particles showed variation during the early to mid Holocene in response to climatic changes. A marked decrease of fire frequency since 6200 cal a BP is attributed to the transformation of vegetation from *Picea abies*-dominated forests into mixed *Fagus sylvatica-Abies alba* stands. Once *Fagus sylvatica* established, a dense canopy a profound alternation of the disturbance regime occurred, leading to the exclusion of fire, and has indirectly accelerated the process of podzolization. Thus, the synergistic effects of biotic change are capable of amplifying a climatic impulse, illustrating the important influence of bottom-up controls on fire regimes and soil development.

1.22 Introduction

Forest ecosystems in the mountains of Central Europe experienced profound changes in species composition following the immigration of major tree taxa in the postglacial period, which are considered to have been predominantly driven by top-down processes such as climate change (Feurdean et al., 2014). Alternations in keystone species affected various ecosystem properties, for instance vegetation structure and species diversity, but also soil chemistry and microclimates. Such a change in predominant taxa is also capable of substantially impacting the dynamics of disturbances and is frequently species-specific (e.g. bark beetle – Müller et al., 2008; Fischer et al., 2015). Recent studies from temperate Europe have revealed that the Late Glacial and Holocene succession of vegetation was significantly affected by fire disturbances (Robin et al., 2014; Vannière et al., 2016; Carter et al., 2018b) and that some ecosystems have even been predominantly driven by fire (Novák et al., 2012; Adámek et al., 2015). Global-scale retrospective syntheses show distinct co-variation in fire activity with changes related to glacial-interglacial climatic cycle, implying a strong relationship between temperature and biomass burning (Daniau et al., 2010a). On the Quaternary time-scale, climatically favourable warm periods, such as the Holocene, are characterized by a general increase in biomass burning driven by higher fuel accumulation resulting from increased vegetation productivity (Pausas et al., 2013). Warming also enhances fire-prone weather conditions, leading to prolonged dry seasons and thus increasing the probability of fire occurrence due to lightning or human-caused ignitions (Milad et al., 2011; de Rigo et al., 2017). Accordingly, the climate acts on fire activity directly through the modulation of moisture content and lightning strike frequency. On the other hand, bottom-up processes operating at the local scale, such as forest structure and species composition of the tree layer, interfere with such direct climate control in various ways, yet they are capable of superimposing a general trend in fire activity. These biotic drivers further diversify regional fire regimes, making them heterogeneous even across the uniform climatic space. This is naturally reflected in the formation of multiple successional (e.g. Abrams et al. 1985) and pedogenetical (e.g. Schaetzl, 1994) pathways, resulting in a high spatial variability of vegetation and pedocomplexity on the landscape scale (e.g. Schaetzl et al., 2018). So far, the mechanisms of the formation of these complex spatial patterns (e.g Šamonil et al., 2014) and their role in ecosystem dynamics have not been sufficiently described. Distinguishing between the relative importance of particular drivers may lead to a better understanding of the influence of fire on ecosystem functioning and improve predictions of forest disturbance dynamics with respect to ongoing climate change.

Although general trends in the development of postglacial vegetation in the Hercynian mountain ranges of Central Europe are relatively well known (Svobodová et al., 2001, 2002; Engel et al., 2010; Dudová et al., 2014; Vočadlová et al., 2015), little attention has been paid to the effect of fire disturbances (Carter et al., 2018b). Nevertheless, the early- to mid-Holocene (11,700 cal a BP; 8,200 cal a BP; Walker et al., (2012)) stand dynamics of conifer-dominated forests have partly been shaped by fire disturbances because these forests closely resemble boreal forests in terms of species composition, structure and dynamics (Chytrý, 2012; Novák et al., 2012; Robin et al., 2014; Bobek et al., 2018b). Unfortunately, the sparse charcoal evidence from this region has caused difficulties in assessing the impact of fires. When comparing the influences of fire on vegetation development within other European mountain areas, various, even contradictory, effects have been reported. For example, sedimentary charcoal sequences from the Carpathians indicate that *Picea abies* (spruce) has been favoured by periodic low/moderate severity fires at intervals of ~250 years (Feurdean et al., 2017a). On the contrary, fire frequency markedly decreased during the late Holocene expansion of *Picea abies* throughout Fennoscandia (Ohlson et al., 2011), although climatic warming promoted suitable conditions for burning (Brown et al., 2014). Another important tree taxon, *Fagus sylvatica* (beech), seemed to be favoured by fire during the initial phase of stand establishment (Bradshaw et al., 2005; Ohlson et al., 2017) whereas its predominance in later successional stages eliminate fires from forest disturbance dynamics (Feurdean et al., 2017a). Such evidence points to the important modulating effects of species composition on fire regimes and possible links to soil evolutionary pathways (fires influence podzolization, see Schaetzl 1994).

The soil charcoal record can provide spatially explicit information about past fire occurrences because charcoal formation is inherently connected to in-situ biomass burning. Moreover, macroscopic charcoal particles (>200 µm) stored within a forest soil enable the tracing of changes in vegetation composition and fire frequencies over millennial time scales. Although the soil environment is not a truly chronologically stratified palaeoarchive, since soil mixing processes (e.g. tree uprooting, bioturbation) distort the age-depth relationship, this limitation may be partly overcome by employing accelerator mass spectrometry (AMS) and radiocarbon dating of numerous charcoal particles. The major benefit of this approach is the opportunity to study fire history at smaller scales than the stand scale (<1 ha), which is practically unachievable using other palaeoecological techniques. Here, we collected an extensive dataset of radiocarbon-dated charcoal particles that were sampled from mineral soils of an old-growth beech-fir forest located in a low Central European mountain range. In addition to this, we analysed sediments from an adjacent peat bog by means of high resolution pollen analysis and continuous macrocharcoal (>125 µm) counting. The objectives were: (1) to uncover the stand-scale fire history during the Holocene; (2) to estimate the frequency of fires based on the soil charcoal record; (3) to assess the effect of change in key tree taxa on fire activity; and (4) to trace the possible influence of fire on soil formation processes.

1.23 Material and methods

1.23.1 Study site

Our research was carried out in the Žofínský Primeval Forest (hereinafter Žofín) in the Novohradské mountains (Figure 1), which is the fourth oldest forest reserve in Europe, established in 1838 (Welzholz et al., 2007). The annual average temperature is 4.3 °C and annual average rainfall is 704 mm (Tolasz, 2007). The study site is situated along an altitudinal gradient ranging between 735 and 830 m a.s.l. on porphyritic and biotite granite. Šamonil et al. (2011) found high local soil diversity and variability within the site. Podzols and Cambisols predominate on terrestrial areas and hydromorphic areas are occupied mainly by Gleysols and Histosols (soil taxonomy according to Michéli et al. (2007)). The complex spatial pattern of soils has been at least partly driven by fine-scale disturbances such as tree uprooting, breakage by wind and bark beetle outbreaks (Šamonil et al., 2014). Plant communities can be mostly classified in the *Galio odorati–Fagetum, Mercuriali perennis–Fagetum, Calamagrostio villosae–Fagetum,* and *Luzulo–Fagetum* associations. Spring-area plant communities can be classified into the association *Equiseto–Piceetum* (Boublík et al., 2009). Such waterlogged sites are characterized by an accumulation of organic matter, thus allowing the preservation of sedimentary pollen and charcoal records.

1.23.2 Soil charcoal sampling and processing

We excavated and sampled four main terrestrial soil types (Albic Podzols, Entic Podzols, Dystric Cambisols, Haplic Cambisols) occurring within the study area using two replicate trenches (Figure 1). Sites to be used for charcoal sampling were subjected to several selection criteria: (1) Profiles

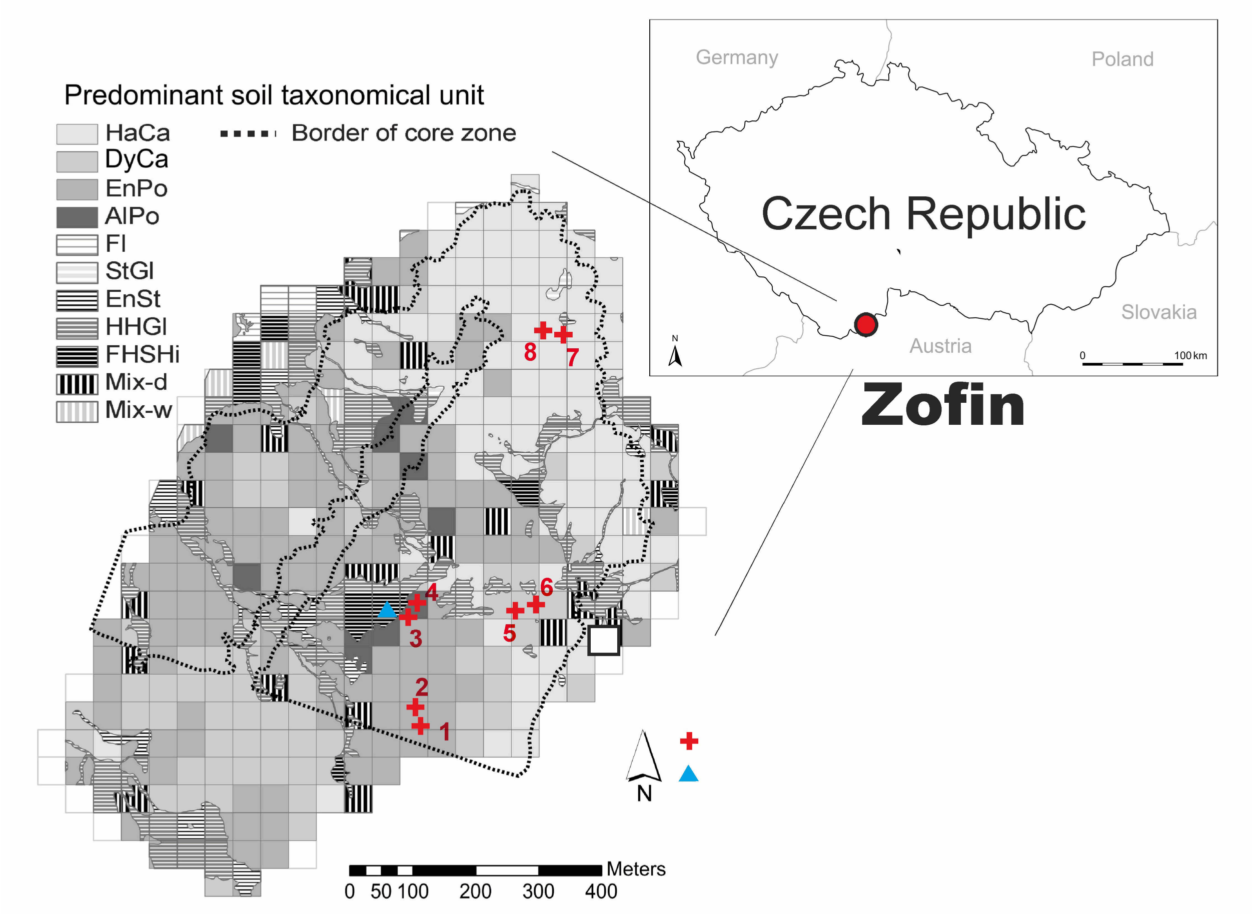

Figure 1. Location of the study area. Žofínský Prales Reserve is located in the Novohradské Mts in the Czech Republic. A map of the predominant soil taxonomical units (STU) according to the World Reference Base for Soil Resources is shown. We considered an STU to be predominant when it occurred in at least three soil profiles per plot (in total five profiles were evaluated at each square plot – see details in Šamonil et al. 2014); on the other hand, the occurrence of three STUs within a single plot was considered to be a mixture; haCa – Haplic Cambisols, DyCa – Dystric Cambisols, EnPo – Entic Podzols, AlPo – Albic Podzols, Fl – Fluvisols, StGl – Stagnic Gleysols, EnSt – Endogleyic Stagnosols, HHGl – Histic or Haplic Gleysols, FHSHi – Fibric or Hemic or Sapric Histosols, Mix-d – mixed terrestrial soils (dry), Mix-w – mixed (semi)-hydromorphic soils (wet). The dotted line shows the border between the historically human affected and unaffected zones. Pedoanthracological data originated from eight soil profiles (crosses), and the pollen profile originated from a central peat bog (triangle).

belonging to one soil unit were situated 20–30 m apart, which was within the range of spatial autocorrelation of the main soil properties, which depending on the soil property was about 50–150 m (Šamonil et al., 2011). Between soil units the profiles were mutually independent in terms of soil properties and were located at a distances 180–400 m apart (Figure 1). (2) We avoided slopes steeper than 10° in order to reduce the input of reworked charcoal particles via slope processes. (3) Trenches were located outside of pit-and-mound micro-topographical features caused by tree uprooting. Soil trenches 1.0-m wide and 1.7-2.2-m depth were excavated down to the bedrockand were described in detail in terms of soil morphology (Schoeneberger et al., 1998) and soil taxonomy (Michéli, 2007). Charcoal samples were taken from all present soil horizons which were distinguishable after visual inspection. Organic horizons were removed prior to sampling. The common sampling depths of 0-10 cm (A soil horizon), 10-20 cm, 20-40 cm, 40-60 cm and 60-110 cm were used in all profiles, however, an exact sample position was slightly modified according to the actual soil horizon transitions. Soil sample volumes of about 6–10 liters were collected from each layer. Charred wood particles were extracted from dry samples using a water flotation technique (Carcaillet et al., 1996) followed by wet sieving with 200 μm mesh size. Taxonomical identification was performed under a reflected light microscope (50–500×) by observing transversal, tangential and radial anatomical planes. Identifications followed wood anatomy atlases (Benkova et al., 2004; Schweingruber, 2011) and charcoal reference collection material. Differentiation of *Pinus sylvestris* (Scots pine) and *Pinus mugo* (dwarf pine) is not feasible on the basis of wood anatomy (Schweingruber, 2011). Since these species potentially formed the vegetation cover around the timberline during the Late Glacial/Holocene transition, we reported them together as *Pinus sylvestris/mugo*.

1.23.3 Pollen profile sampling and processing

Based on a previous pedo-morphological description of 1765 soil profiles in Žofín (Šamonil et al., 2011), we selected a small topographic depression infilled by peat deposits of various depths. This peat bog is situated in a canopy gap of the *Picea abies*-dominated forest. A sediment sequence was extracted using a U-shaped corer 100 cm in length and 5 cm in diameter (Eijkelkamp Soil & Water, Giesbeek, the Netherlands). The profile for pollen and macrocharcoal (>125 μm) analysis was sub-sampled in laboratory at 1 cm increments (volume of 1 ml) and samples were processed by standard palynological techniques (Faegri et al., 1989). Samples containing mineral material were pre-treated with cold concentrated HF for 24 hours and then processed by KOH and acetolysis. At least 500 terrestrial pollen grains were identified using standard key and pollen atlases (Beug, 2004; Punt, 1976-2003; Reille, 1992), for the determination of non-pollen palynomorphs, van Geel et al. (1980) was used. Percentages of pollen data were calculated based on the total pollen sum of terrestrial pollen (TS) with the exclusion of pollen from (semi)-aquatic plants, spores and non-pollen palynomorphs. A pollen percentage diagram was created in Tilia v. 1.7.16 (Grimm, 2011). The delimitation of pollen zones boundaries was based on stratigraphically constrained cluster analysis (CONISS) with a square root transformation of percentage data (Grimm, 1987). We then constructed a synthetic diagram comparing the soil charcoal and local pollen records from the peat bog in Žofín to a regional vegetation development recorded in the paleolake Švarcenberk, located 53 km away in the lowland area of the Třeboň basin (Pokorný, 2002). In order to assess linkages between climatic change and fire regime, a comparison with independent paleoclimatic proxies from the wider region of Central Europe were used. This included lake level fluctuations (Magny, 2004) and cold/humid phases (Haas et al., 1998) identified in the Swiss Plateau and the Alps. In addition, the variation in oxygen isotopic ratio ($\delta^{18}O$) from the Ammersee, southern Germany, (von Grafenstein, 1999) were plotted against our local records.

1.23.4 Chronologies

In order to determine the ages of in situ fire events, single charcoal particles extracted from soil layers were radiocarbon-dated. The selection of charcoal fragments to be dated was based on the dry weight of the particles (> 10 mg), botanical identification (focusing on dominant tree taxa) and an equal distribution among the eight soil trenches. In our sampling design we also assessed the vertical distribution of the charcoal particles by dating at least one charcoal per layer. A total of 40 charcoal fragments were dated by the AMS radiocarbon method at the CEDAD Laboratory, Italy, and Isotoptech, Hungary, after standard acid-alkali-acid pretreatments necessary to remove humic and fulvic acids. All radiocarbon measurements were calibrated via the IntCal13 curve (Reimer et al., 2013) provided by OxCal v4.2.24 (Ramsey, 2009) and reported in years before present (hereafter cal a BP). The radiocarbon age of a charcoal fragment corresponds to the time when the wood that yielded charcoal was produced, and not to the actual age of a fire event. This ”inbuilt-age” error is in addition to the radiometric error (Gavin, 2006), but was not considered in further analyses. Chronological constrains of the peat bog sequence were provided by four radiocarbon dates (Czech Radiocarbon Laboratory) of terrestrial macroremains or bulk sediment. An age-depth model (see Supplementary Figure S3 in Appendix 1) was constructed using the Clam 2.2 package (Blaauw, 2010) in the statistical software R (R Development Core Team, 2013) by fitting smoothing spline (smoothing parameter of 0.3, 1000 iterations).

1.23.5 Estimation of the minimum fire frequency based on soil charcoal

We adopted the method of “minimum fire frequency” (hereafter minFF) proposed by Robin and Nelle (2014), which is based on grouping a set of available soil charcoal radiocarbon dates into temporally associated clusters representing a single fire event. This approach clearly depends on the number of available radiocarbon measurements; however, we assessed the issue of the expected number of fire events regarding our sampling effort by constructing an accumulation curve (Payette et al., 2012). The approximation of missed fires is based on a rarefaction analysis and subsequent extrapolation method implemented in EstimateS software (Colwell et al., 2012). The number of local fire events in the Žofín area was inferred by a pairwise chi-square test between all radiocarbon dates within a dataset (Ramsey et al., 2009). This test compares the significance of the 2σ range of two radiocarbon dates in order to verify their contemporaneity related to the respective positions along the calibration curve. In cases where two dates were statistically significantly different (at 95 % level of confidence), we considered each as a single fire event. On the other hand, when the test failed to find a significant difference, we assumed those charcoal pieces resulted from the same local fire event. Afterwards, such two or more statistically-identical radiocarbon dates were merged in order to produce a composite calibration interval (using the R_combine function in Oxcal software), which represents the probable time span when the fire event occurred. When a radiocarbon date was assigned into two separate groups, its calibration intervals were added to each of them. The exact timing of the fire event along the composite calibration interval was arbitrary set to median value. The minFF was then calculated using a running total (500 years window) on the inferred time series of fire events. The resulting minFF was fitted by smoothing spline, allowing the general trend to be better visualized.

1.24 Results

1.24.1 Age and taxonomic composition of the soil charcoal

We analysed altogether eight soil profiles in the Žofín area covering the main soil types using at least two replicate soil trenches (Figure 1). In total, c. 500 litres of soil were sampled and processed by flotation and wet sieving, which resulted in 40 charcoal assemblages originating from different soil horizons. The anatomical identification was successful for 1551 charcoal fragments belonging to 9 taxa at the species or genus level. The charcoal counts were pooled across all eight soil trenches and the overall taxonomic composition was shown as the sum per topsoil (0-16 cm) and subsoil (20-100 cm) horizons (Figure 2). The species composition of the topsoil was dominated mainly by *Abies alba* (fir) (53.8 %), followed by *Fagus sylvatica* (35.4 %). A minor proportion of the charcoal spectra was formed by other tree taxa, namely *Acer* ssp. (0.7 %), *Picea abies* (8.3 %) and *Pinus sylvestris/mugo* (1.4 %). Subsoil horizons contained especially *Picea abies* (67.3 %) and *Pinus sylvestris/mugo* (29.7 %), followed by Abies *alba* (1.5 %) and *Fagus sylvatica* (0.4 %). *Pinus sylvestris/mugo* is considered to be *Pinus sylvestris*; however, the group potentially includes the other native species *P. mugo* and *P. rotundata*, which are not currently present in the area. Other light-demanding tree taxa characteristic for early successional stages were infrequent: *Betula* spp. (0.4 %) and *Populus* spp. (0.1 %). Acidophilic dwarf-shrubs of the coniferous forest understorey were sparse as well, represented by Ericaceae (0.3 %).

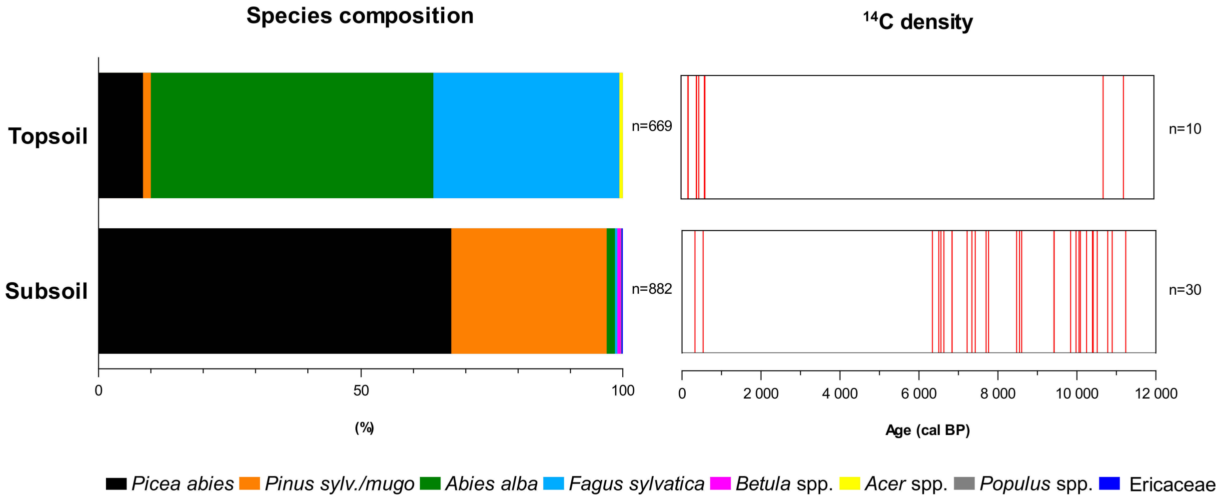

Figure 2. Summary plot of charcoal taxonomic identification from eight soil trenches (left panel). Particular soil layers were merged to a topsoil (0–16 cm) and a subsoil (20–100 cm) to visualize contrasting species composition. The density of radiocarbon dates is given as lines denoting the median age.

Radiocarbon dating of 40 charcoal particles extracted from soil samples showed a wide range of dates covering the entire Holocene period (Figure 3, Supplementary Table S1 in Appendix 1). Nevertheless, radiocarbon dates were clustered into two distinct time intervals separated by a c. 5700 year long fire-free period. The older phase, spanning from the beginning of the Holocene up to 6,300 cal a BP, was characterized by the prevalence of conifers in the charcoal spectra. A subsequent subdivision was made based on taxonomic composition. The oldest fire episode preserved in the soil charcoal record had a median age of 11,200 cal a BP, and demonstrated the presence of *Pinus sylvestris/mugo* within this mountain area at the Pleistocene-Holocene transition (c. 11,700 cal a BP; Walker et al., (2009)). In fact, this oldest phase consisted exclusively of *Pinus sylvestris/mugo*, but since 9,970 cal a BP an admixture of *Picea abies* indicates its immigration into the area. A major expansion of *Picea abies* occurred after 9,400 cal a BP, when *Pinus sylvestris/mugo* charcoal disappeared. There was only a minor proportion of ^{14}C dates belonging to the Early/High Middle Ages, which probably originated from anthropogenic burning.

1.24.2 Pollen and macrocharcoal record of the peat bog

Based on the results of cluster analysis, the pollen diagram was divided into four main phases reflecting changes in the vegetation cover (Figure 4). Over the entire record there was a significant pollen representation of *Picea* (varying between 50-80 % of TS), implying a substantial contribution by *in-situ* growing trees. This is also demonstrated by abundant occurrences of stomata and *Picea* needles found in the sediment core. The pollen influx from local *Picea* stand could have overshadowed the pollen input from regional trees, and therefore when describing the pollen record both the regional and local occurrence of *Picea* needs to be considered.

The first phase (Phase 1; 110-91.5 cm; 7,800-6,300 cal a BP) showed a domination of *Picea* in the close vicinity of the study site, also evidenced by the presence of stomata. This phase was characterized by higher amounts of pollen from *Pinus* and deciduous trees such as *Corylus*, and to a lesser extent *Tilia* and *Ulmus*. The distinct fluctuations in *Abies* pollen occurrence and absence of stomata or needles indicates initial population establishment. The regional presence of scattered *Fagus* trees could be inferred from continuous but low pollen percentage.

The pronounced change in forest vegetation occurred at ca. 6,300 cal a BP (Phase 2; 91.5–49.5 cm; 6,300–2,400 cal a BP) and was characterized by a rapid increase in the pollen of *Abies* followed by the delayed expansion of *Fagus*. This compositional change towards fir-beech forest is synchronous with the retreat of other deciduous trees, mainly *Corylus* and *Tilia*. Also *Picea* responded to this marked change by gradual lowering of pollen percentage, which indicates reduction in its abundance in vegetation, especially in mesic sites surrounding the bog. The occurrence of *Abies* stomata and needles demonstrates the presence of individuals growing directly on peat substrate.

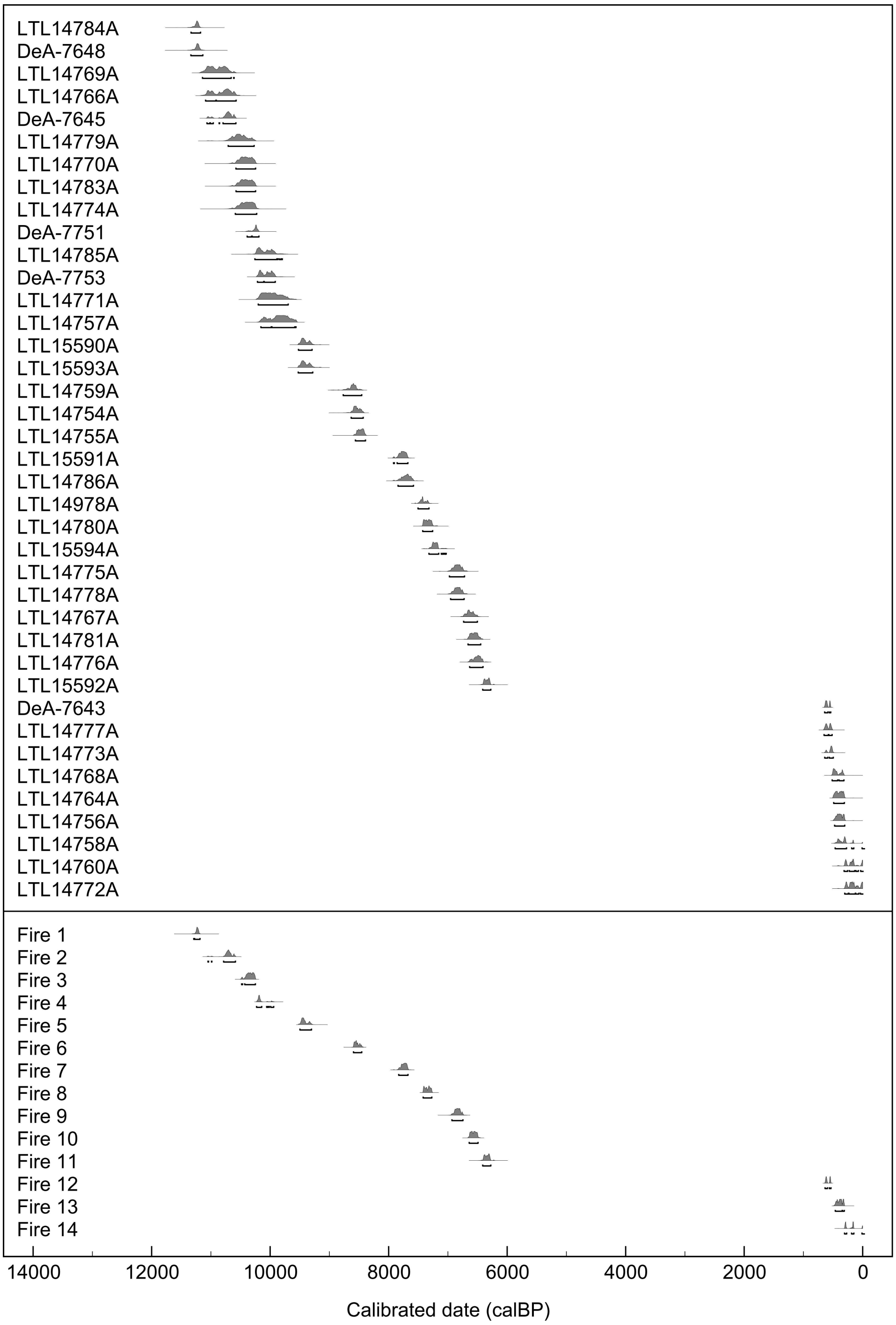

Figure 3. The calibration interval with probability distribution (Intcal13 curve, 2 σ range) of soil charcoal radiocarbon data from Žofín (upper panel). The lower panel shows the merged probability distribution of significantly differing groups of dates determined by a pairwise chi-square test. Image generated by OxCal v4.2.24.

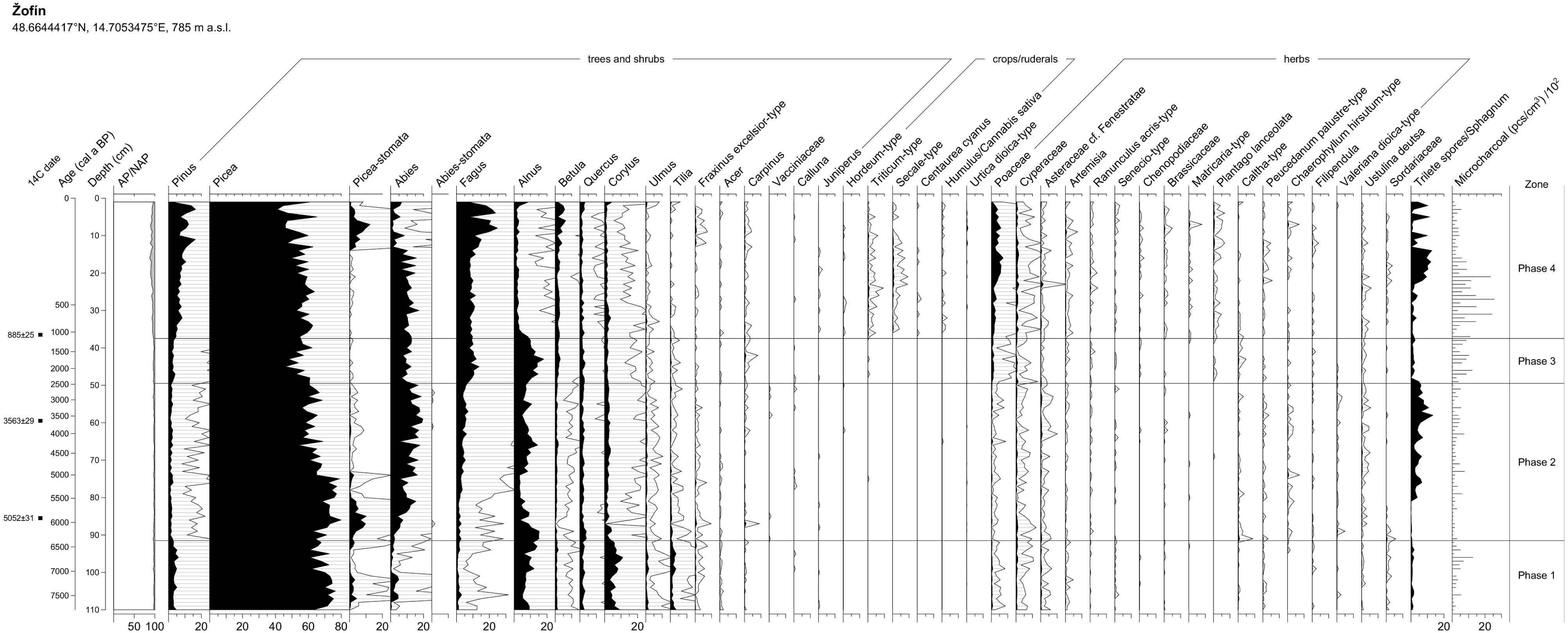

Figure 4. Pollen percentage diagram from the Žofín peat bog with time scale depicted in calibrated years BP. Abundances of spores and stomata are relative to total pollen sum. Microcharcoal content is given as a concentration (pcs·cm^{-3}). Grey curves are magnified 10×. Zones are delimited according to CONISS.

The forest vegetation composition remained stable up to ca. 2,400 cal a BP (Phase 3; 49.5–37.5 cm; 2,400–1,100 cal a BP), when *Fagus* further expanded into the landscape. The amount of *Picea* and *Abies* slightly declined, there was also a decline in *Picea* stomata, and the stomata of *Abies* disappeared. This could be attributed to a decline in *Picea* and *Abies* growing on peat bog, probably due to an expansion of *Alnus* stands.

The final change in vegetation cover occurred at ca. 1,100 cal a BP (Phase 4; 37.5–0 cm; 1-100 cal a BP–recent) and was connected with an increase in human activity, reflected by the continuous occurrence of crop pollen (*Triticum* t., *Secale* t.) as well as indicators of pastures (*Plantago lanceolata* t.) There was also a visible increase in herbaceous pollen types, suggesting a gradual opening of the landscape due to increasing human pressure.

Macroscopic charcoal accumulation rates (CHAR) indicated several periods of increased deposition of charred material on the surface of the peat bog (Figure 6). In particular, high charcoal peaks occurred between 7,600–3,900 cal a BP and 350 cal a BP up to recent times. The intermediate period is characterized by constantly low charcoal influx indicating sharply diminished fire activity at the peat bog surface.

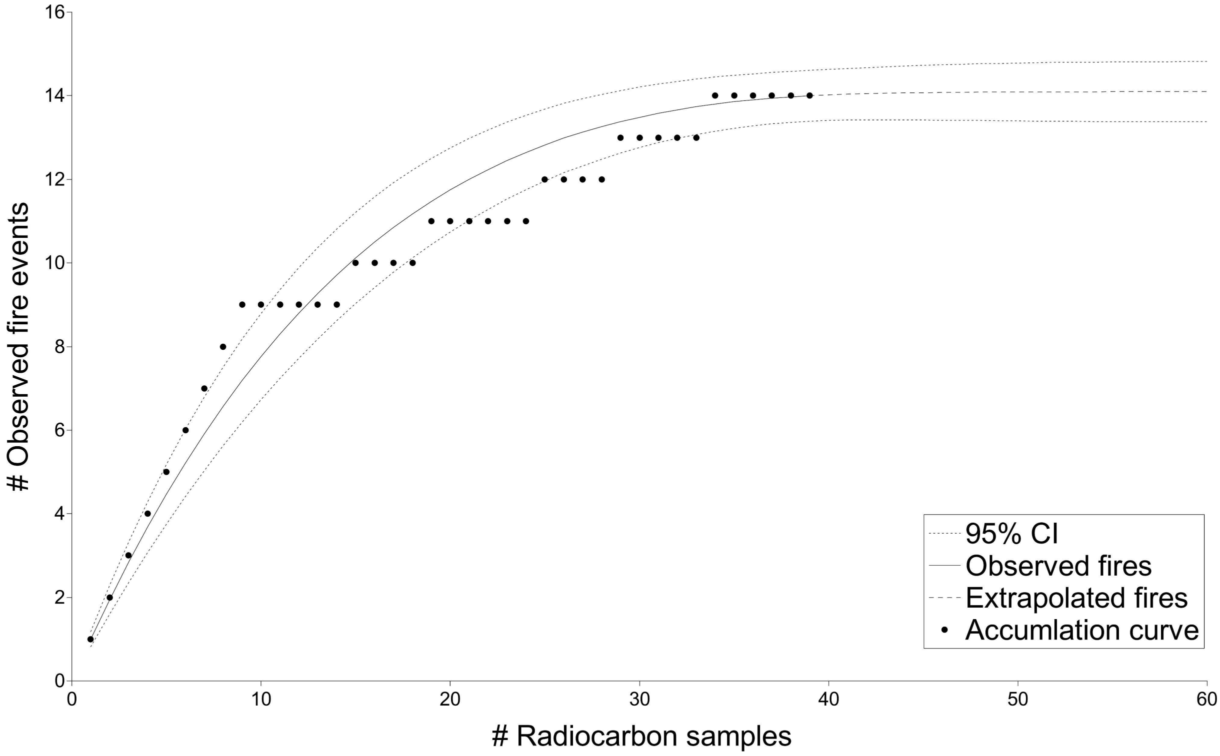

Figure 5. Rarefaction of the observed number of fire events (solid black line) as a function of sampling effort (n=40). The extrapolation curve (dashed line) provides the expected number of fire events to be found by increasing the number of radiocarbon dates. The dotted lines indicates the 95 % confidence interval for both curves. The accumulation curve of observed fire events is shown by dots.

1.24.3 Stand-scale minimum fire frequency

Using the pairwise chi-square test among the 40 dated soil charcoal particles, we detected 14 local fire events after the Late Glacial period (Figure 3). According to the rarefaction analysis and subsequent extrapolation, we likely recorded most of the Holocene fire events at Žofín (Figure 5). The early Holocene fire regime (11,200-9,300 cal a BP) showed a minimum fire frequency of 1 to 2 fires per 500 years, burning exclusively in pine-dominated forests. A pronounced decline in minFF occurred between 9,300–8,800 cal a BP and 8,400–7,900 cal a BP, when no fire event was detected. The period spanning 8,800–6,200 cal a BP was characterized by the formation of a mountain *Picea abies* forest, which experienced an increase in minFF ranging between 0 and 2 fires per 500 years. There was then a marked decline in minFF between 6,200 and 600 cal a BP (Figure 6), characterized by the complete absence of any fires on sites outside the peat bog. Fires became more frequent at the end of late Holocene, reaching minFF 3 fires per 500 years.

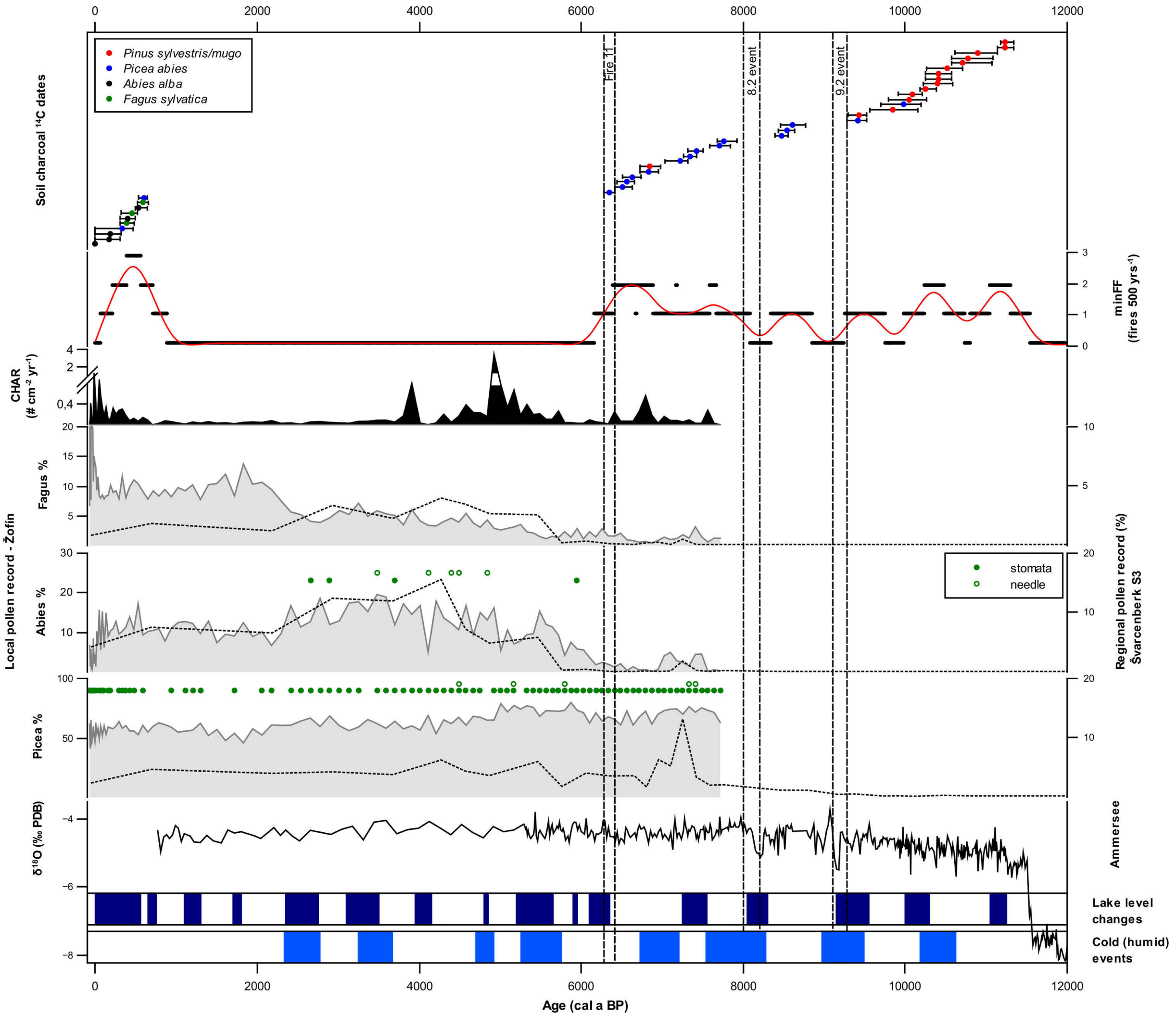

Figure 6. Synthetic diagram linking the local fire history and pollen record (Žofín peat bog, this study) to the regional vegetation development preserved in lake Švarcenberg . Synchronization of biotic proxies with climate reconstructions from Central and Western Europe illustrates possible driving forces on the fire regime. The topmost panel shows calibrated ^{14}C dates of soil charcoal (Intcal13 curve, 2 σ range, median age marked with a dot). The estimated minimum fire frequency

(minFF) is expressed as the sum of fire events within a 500 year window (dots) that is fitted with smoothing spline (curve) to visualize the general trend. Deposition of macroscopic charcoal (>125 µm) into the Žofín peat bog. The local pollen record showing percentage values of main trees that are based on the pollen sum of all terrestrial taxa (grey). The presence of stomata and needles is indicated by the symbols shown. Oxygen-isotope record ($\delta^{18}O$) inferred from benthic ostracodes from the Ammersee . Higher lake levels in the Jura mountains and cold/humid events in the Alps and the Swiss Plateau denote phases of climate deterioration in areas surrounding Central Europe.

1.25 Discussion

1.25.1 The occurrence of fire in the early Holocene tracked the altitudinal forest expansion

The pollen records and tree macroremains findings from the southern Czech Republic indicates rapid afforestation along an altitudinal gradient during the Late Glacial-Early Holocene transition, represented in its initial phase by an expansion of pine-birch dominated woodland communities (Vočadlová et al., 2015; Carter et al., 2018b). A park-like taiga occupied lowland areas of the Třeboň basin (~400 m.a.s.l.) at least since the Allerød (13,350-12,680 cal a BP; Litt et al., (2001)) climate amelioration; however, the forest cover was partly reduced by the subsequent Younger Dryas climatic cooling (Pokorný et al., 2010). By contrast, mountain zones ~1,000 m a.s.l. were covered by alpine herbaceous tundra or cool steppe with patches of shrubland and scattered trees during the Late Glacial (Jankovská, 2006a; Vočadlová et al., 2015). The Žofín area is located in a lower-elevation mountain range (~750 m a.s.l.), suggesting a transitional status between these two vegetation formations at the beginning of the Holocene. Given that fire activity is limited by the available biomass, we might expect a low charcoal production and delivery into the soil environment when unproductive vegetation types burn, such as herb tundra or cold steppe. Highly variable fire regimes with mean fire return intervals from 150–6,500 years have been reported from the tundra biome (Hu et al., 2015), implying a spatially heterogeneous charcoal formation, especially when millennial-scale fires occurred only rarely. Therefore, infrequent low intensity fires would be difficult to detect using a soil charcoal record. Because we also lacked a macrocharcoal record from the peat profile, we cannot fully exclude the possibility of unrecorded Late Glacial fire events affecting the herbaceous vegetation. Nevertheless, the observed abrupt increase in the occurrence of fire after 11,200 cal a BP was more likely linked to the local establishment of a dense cover of coniferous trees or shrubs. This is corroborated by the oldest radiocarbon-dated soil charcoal particle discovered at Žofín belonging to *Pinus sylvestris/mugo*. However, it was not possible to distinguish between *Pinus sylvestris* or *Pinus mugo* charcoal, leaving open the possibility that dwarf pine prevailed in the vegetation cover. During the period 11,200–9,500 cal a BP, fire regularly occured with an estimated minFF of 1–2 fires per 500 years. This frequency could not suppress the early Holocene expansion of *Pinus sylvestris* or *Pinus mugo* in herb communities, as both species are highly resistant to fire (Leys et al., 2014). A possible implication for the spatial structure of the early Holocene vegetation could be made on the basis of a single fire event detected simultaneously in multiple soil trenches (fire events 1,2,3; see Figure 3).

This would indicate spatial connectivity in fuels that originated from a high tree or shrub stand density, allowing fire to spread within a landscape. Such an observed charcoal pattern could not be generated through topsoil erosional processes as these sampling sites are located on different slopes. Moreover, early Holocene climatic reconstructions from Central Europe have shown reduced annual precipitation and warm summer temperatures (Litt et al., 2009; Kuneš et al., 2015; Houfková et al., 2017), which may have resulted in prolonged drought periods promoting fires. Thus, we hypothesize that closed-canopy tree or shrub vegetation consisted of *Pinus sylvestris* or *Pinus mugo* had formed no earlier than 11,200 cal a BP in the Žofín area at the expense of herbaceous communities. The observed timing of the tree or shrub expansion is consistent with the timberline upshift reported from other low mountain ranges such as the Giant Mountains (Treml et al., 2008). Similar results were also reported from the Harz Mountains, where soil charcoal data indicate the presence of pine-dominated open woodland at the Younger Dryas/Holocene transition (Robin et al., 2013a). All these records point to a major shift in fire disturbance dynamics accompanying the early Holocene afforestation of mountain areas. Such an increase in biomass burning is a widespread process, as indicated by regional patterns in fire regimes observed across southern Europe, the Alps and the Carpathians (Morales-Molino et al., 2014; Vannière et al., 2016; Florescu et al., 2018). This suggests that low biomass burning prior to the establishment of forests reflects a limited fuel availability that suppressed the emergence and spreading of fire. As the altitudinal position of the timberline is largely controlled by summer temperatures and the length of the growing season (Körner, 1998), the occurrence of fire during the early Holocene was indirectly driven by the climate through changes in biomass abundance.

1.25.2 Fires within coniferous forests

Picea abies started to invade pine-dominated forests between c. 9,000–10,000 cal a BP, as shown by the mixed composition of soil charcoal assemblages (Figure 6). This relatively early macrofossil evidence (charcoal dated 9,978 cal a BP) is consistent with the onset of the major expansion phase identified in the adjacent Bohemian Forest (Stalling, 1987; Svobodová et al., 2001; Jankovská, 2006a; Carter et al., 2018a) (see Supplementary Figure S1 in Appendix 1).. The timing of this process could be attributed to the nearby location of a refugial area which was proposed to have existed at the southern margin of the Bohemian Massif (Willis et al., 2004; Tollefsrud et al., 2008) or the proximate position on the northward migration route from the eastern Alps (Svobodová et al., 2001; Ravazzi, 2002). The major phase of *Picea abies* dominance on well-drained soils took place between 8,600-6,300 cal a BP, and was associated with the variable minFF ranging from 0 to 2 fires per 500 years. Nevertheless, such a biotic change did not alter the fire regime considerably when compared to the preceding early Holocene pine-dominated period that experienced the same range in minFF. This may indicate that the expansion of *Picea abies* did not necessarily lead to a substantial decline in fire activity as has been reported from Scandinavian boreal forests (Ohlson et al., 2011). The cause for the short-term reduction in minFF could probably be attributed to the Early Holocene climatic anomalies, as indicated by pronounced fire-free periods 7,900-8,400 cal a BP and 8,800-9,200 cal a BP, which coincided with higher lake levels (Magny, 2004), oxygen-isotope decline (von Grafenstein, 1999) and cold/humid events recorded in the Alps (Haas et al., 1998). A period of increased humidity during the 8,200 cal a BP cooling event has been proposed for mid-European zone (Magny et al., 2003), which could have inhibited fire activity independently of biotic changes in coniferous vegetation. The observed centennial-scale minFF is consistent with fire frequency reported from coniferous forests in the Eastern Carpathians where *Picea abies* successfully persisted under low to moderate severity fires recurring in 200-300 year intervals (Feurdean et al., 2017a). Although spruce is a fire-intolerant tree species characterized by a low ability to survive fire ditsurbances (Adámek et al., 2016), its well-established population is highly resilient due to vigorous post-fire regeneration (Adámek et al., 2016). Accordingly, fire disturbance should be considered as an integral part of the long-term forest dynamics of current *Picea abies*-dominated forests within mountain areas of Central Europe.

1.25.3 Biotic controls on the fire disturbance frequency

Several fire history reconstructions have shown that changes of the dominant tree species within the vegetation cover can trigger substantial changes in the fire regime. For example, the late Holocene expansion of *Picea abies* significantly reduced the fire activity in boreal forests of Fennoscandia, especially in moist habitat types occurring in concave landforms (Ohlson et al., 2011; Clear et al., 2014). Vegetation change is able to largely modulate the climate-fire relationship by introducing species with different flammability (Rogers et al., 2015). This amplifies the impact of the climate when fire-prone species act synergistically with climate warming. However, negative feedback may also arise when the vegetation change alters the probability of fire in the opposite way, by affecting moisture conditions and the quality of fuels. Our soil charcoal data provides robust evidence of a long-term exclusion of fire due to a vegetation change towards a relatively non-flammable mixed deciduous forest (Figure 6). According to the radiocarbon-dated charcoal record, fire disappeared from the Žofín area after ~ 6,200 cal a BP, when the last signs of fire were found in the soil. No other fire event was detected at mesic sites during the period 6,200–600 cal a BP. Such a major decline in fire activity coincides with the spread of mixed fir-beech forests in well-drained sites that surround the peat bog (Figure 4). This forest type outcompeted previously established *Picea abies*-dominated stands in all mesic habitat types except hydromorphic soils, where the spruce population remained stable throughout the middle and late Holocene (Figure 4; see high pollen percentage and stomata). However, an independent fire record using the influx of macroscopic charcoal particles (i.e. >125 μm) obtained from the peat bog showed increased values even after the general disappearance of fires in the area. These charcoal peaks probably represent several fire episodes that were restricted exclusively to the bog spruce forest and did not spread into the surrounding mixed fir-beech stands. This highlights the important biotic control on biomass burning via the alteration of fuel types and moisture content, which could effectively suppress the spread of fire within contrasting vegetation types.

The timing of the local beech expansion in Žofín area corresponds to the pollen record from the Švarcenberk paleolake, where a major *Fagus* expansion occurred ~5,500 cal a BP (Pokorný et al., 2010). In a neighbouring mountain area of the Bohemian Forest, an increase in the beech population took place earlier between 7,000-5,600 cal a BP (Svobodová et al., 2001, 2002; Carter et al., 2018a)(see Supplementary Figure S2 in Appendix 1). The Holocene migration history of *Fagus sylvatica* at the continental scale was likely driven by climatic forces, especially by periods of cool and precipitation-rich conditions, resulting in stepwise population growth (Tinner et al., 2006b). However, fire disturbances related to human activity has also been proposed to have facilitated *Fagus sylvatica* expansion at the regional or local scales (Küster, 1997; Bradshaw et al., 2005). Even though beech is a fire-sensitive species lacking ecological adaptations to fire (Tinner et al., 2000), such a type of forest disturbance creates gaps with favourable understorey conditions for seedling recruitment, thus allowing invasion into formerly established forest stands (Björkman et al., 1996). Our soil charcoal data suggest that the local establishment of beech on mesic sites may have been facilitated by fire disturbance. Nevertheless, further population increase was made possible by reduction of fire activity in the Žofín area. It is difficult to determine whether this process has also been influenced by changes in human activity. As the Žofín area is situated in a low mountain range unsuitable for agriculture and far from the southern Bohemian Basins that were sparsely inhabited by Neolithic cultures (Beneš et al., 2007; Dreslerová, 2012), human influence on the fire regime can likely be disregarded. The absence of human activity in the surroundings is also supported by the scarcity of anthropogenic indicators in the pollen record. Therefore, landscape-scale expansion of beech stands reflects intrinsic population processes driven by the climate, whereas stand-scale establishment seems to be mediated by fire disturbances.

1.25.4 The role of fire disturbances in the formation of pedodiversity

Long-term dynamics of plant communities and past fire regime can be linked to current soil diversity (Šamonil et al., 2014), soil variability (Šamonil et al., 2011) and the recent disturbance regime (Šamonil et al., 2013b, 2013a). Integration of past disturbance data with soils can help us to better understand the driving mechanisms of the exceptional pedocompexity found at Žofín, which has yet to be sufficiently explained (see Šamonil et al., 2014). The early Holocene predominance of pine as well as the subsequent predominance of spruce at Žofín undoubtedly drove the podsolization of terrestrial soils on granite (Michéli, 2007). The high acidification potential of both woody species has been well known for decades (Němec, 1940; Błońska et al., 2016), and other pedogenetical pathways are unlikely. Our local pollen analysis revealed that concave topography forms were gradually occupied by hydromorphic soils like Gleysols and Histosols, where glejization and ulmification predominate. At the beginning of the Holocene, soils on terrestrial sites were most likely in the stage of Entic Podzols, not Albic Podzols. Nowadays, Albic Podzols occur only sparsely at Žofín, close to hydromorphic sites (Šamonil et al., 2011), and retrograde pedogenesis from Albic to Entic Podzols has not been demonstrated (cf. Barrett and Schaetzl, 1998; Šamonil et al., 2015). The formation of Entic Podzols during the early Holocene seems to be adequate to the length of time since the Würm glaciation (see a review of Podzol ages by Sauer et al., 2007) as well as the mineral strength of granite. For example, according to Barrett and Schaetzl (1992, 1993), differentiation of a soil profile to eluvial E and illivial Bhs soil horizons requires 4–10 thousands of years even on extremely poor sandy outwash. Moreover, at Žofín, podzolization was likely hindered by frequent fire events. Fires generally mineralize the forest floor, which therefore cannot be a source of fulvic acids in the podzolization process (Lundström et al., 2000; Buurman et al., 2005). The loss of organic acid complexation with amorphous sesquioxides blocks the differentiation of pedon to eluvial and illuvial horizons, and holds the soil close to the initial developmental stage (Schaetzl, 1994; Schaetzl et al., 2015). These soils blocked in pedogenesis can be classified as Regosols, Arenosols (Michéli, 2007) or Entisols.

The increase in beech changed not only the fire regime at Žofín, but also influenced pedogenetical trajectories and pedodiversity. On the one hand, beech restricted podzolization in terrestrial areas because of the fast decomposition of more nutrient-rich leaves (even the possibility of regressive pedogenesis from Entic Podzols to Dystric Cambisols cannot be ruled out). On the other hand, beech indirectly intensified podzolization close to peat bogs. These areas were occupied by *Picea abies* throughout the Holocene, and spruce was also competitive in adjacent anhydromorphic areas. Acidification and complexation due to decomposed spruce (and fir) needles slowly gave rise to the current Albic Podzols near peat bogs. Moreover, podzolization following the neighboring beech expansion was not hindered by fires and included significant humusosesquioxide translocation and precipitation. Finally, we can conclude that the current exceptional local pedodiversity at Žofín (Šamonil et al., 2011, 2014) at least partly resulted from the gradual exclusion of conifers to peat bogs by the beech expansion and the related changing disturbance regime and soil pedogenetical trajectories. The idea of widespread Holocene polygenesis of soils is consistent with the “dynamic pedogenesis” of Johnson et al., (1990) as well as the theory of deterministic chaos in soils and landscape evolution (Phillips, 2006). The expected future predominance of beech could cause a decrease of the pedodiversity in Žofín, i.e. a regressive development of spatial pedocomplexity. Elucidating such pedogenetical pathways would require additional research focused on changes in soil chemistry and physics due to changing disturbance regimes and vegetation composition.

The idea described above of an interconnection between pedodiversity and disturbance regime also sheds new light on strategies of woody species and ecosystem engineering (e.g. (Wilby, 2002; Verboom et al., 2006; Corenblit et al., 2011). The various biomechanical and biochemical effects of trees on soils (e.g. Šamonil et al. Under review) are probably rather the result of evolutionary-based species behavior, and not sophisticated strategies on how to succeed in competition. The same behavior of a tree species (e.g. soil acidification by decomposed *Picea abies* needles) can lead to different results depending on environmental conditions and even on the presence of other tree species. Whereas frequent fires hold acidified soils in the relatively nutrient-rich initial stage of pedogenesis, the decrease of fire frequency due to beech expansion causes rapid podzolization. Both results can be positive or negative for new *Picea abies* regeneration.

1.26 Conclusions

This study analyses the postglacial fire history in a temperate mountain forest in Central Europe. More frequent fire disturbances were related to coniferous forests dominated by *Pinus sylvestris/mugo* during the period 11,200–9,300 cal a BP and the subsequent expansion phase of *Picea abies* between 9,300–6,200 cal a BP. The fire disturbance dynamics closely resembled those of boreal forests, with fire occurring with a frequency of 1 to 2 fires per 500 years during the early to mid Holocene. By contrast, from 6,200 to 600 cal a BP, fire completely disappeared from mesic sites. This marked decrease was likely a response to climatic cooling around 5,300–5,600 cal a BP, which triggered an expansion of less-flammable mixed deciduous forests consisting of *Fagus sylvatica* and *Abies alba*. This suggests that climatic factors acted synergistically with biotic change, resulting in a modulation of the local fire regime. These results highlight the importance of fire disturbances for forest communities in Central Europe, especially for coniferous forests.

1.27 Acknowledgement

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Chapter 5:
Divergent fire history trajectories in Central European temperate forests revealed a pronounced influence of broadleaved trees on fire dynamics

1.28 Abstract

Fire occurrence is driven by a complex interplay between vegetation, climatic, landform and human factors making it challenging to separate the individual effect of each variable. Here we present a reconstruction of the Holocene biomass burning history of two regions located in the Central European temperate zone that differ in the timing of the Middle Holocene expansion of broadleaf-dominated forest communities. This allowed us to investigate the effect of biotic changes on past fire activity. Multiple-site charcoal accumulation records were used to estimate regional-scale trends in biomass burning and to compare them with major trajectories of vegetation development. Extensive ^{14}C-dated soil charcoal records collected within both regions were amalgamated using a cumulative probability function to identify a stand-scale proxy of past fire occurrence. Our results suggest that rising vegetation productivity driven by rapid Early Holocene climate amelioration enhanced biomass burning. The increased fire activity during this period was driven by both a drier- and warmer-than-present climate and easily flammable fuels produced by conifer-dominated vegetation. We identified an inhibiting effect of the concomitant *Fagus sylvatica* expansion on levels of biomass burning that occurred asynchronously between our mountain and mid-elevation sandstone regions 6500 cal yr BP and 4900 cal yr BP, respectively. The amount of compositional change in plant communities was more related to the transformation of major vegetation types than to fluctuations in fire activity levels. The divergent timing of the fire decline in response to the *Fagus sylvatica* expansion implies biotic control over biomass burning that is independent of a direct climatic influence.

1.29 Introduction

The temperate deciduous forests of Central Europe have evolved from Late Glacial and Early Holocene boreal coniferous communities, implying both pronounced changes in species composition and transformations of disturbance regimes. Long-term biotic rebuilding of forest communities has ultimately been driven by climate change, recolonization pathways from Last Glacial Maximum refugia, competition between keystone species or their interactions with soils (Normand et al., 2011). Notwithstanding, various exogenous disturbance agents, including fire, are able to trigger alternative development trajectories (Johnstone et al., 2006; Whitlock et al., 2010; McWethy et al., 2013; Paritsis et al., 2014). Fire is the principal disturbance agent in boreal forest ecosystems, where it exerts a large influence on ecosystem functioning and structure by inducing successional cycles (Flannigan et al., 2000; Niklasson et al., 2000). By contrast, its importance in the dynamics of temperate deciduous forests is substantially diminished by the high foliar moisture content of broadleaved trees, the absence of flammable resins in their wood and the damp under-canopy environment they create, which decreases combustibility of broadleaved biomass. Accordingly, fire can act as a tipping factor during transitions between contrasting forest ecosystems by maintaining alternative steady states potentially diverging from the climatically induced trend of Holocene vegetation development (Bergeron et al., 2004; Paritsis et al., 2014). Whether these alternative trajectories are followed depends on a complex interplay of fire, vegetation and climate factors, which are difficult to disentangle without observing long-term palaeorecords. Recent studies have shown that functional traits of broadleaved taxa influence the fire regime to such an extent that they can counterbalance the enhancing effect of a warmer climate on fire activity (Feurdean et al., 2017b). Conversely, positive feedback has been reported from *Pinus sylvestris*-dominated forests in Central Europe, which exhibit millennial-scale resilience to recurrent fire disturbances (Novák et al., 2012; Adámek et al., 2015; Bobek et al., 2018b). A continental-scale synthesis of sedimentary charcoal records from Europe documented an increasing trend in fire activity at the onset of the Holocene that coincided with gradually increasing availability of biomass due to the rapid spread of forest vegetation at the time (Power et al., 2008; Marlon et al., 2013; Vannière et al., 2016). Thus, a climatically induced rise in vegetation productivity increased fuel loads, which had in turn limited the incidence of fire throughout the Late Glacial period (Power et al., 2008; Daniau et al., 2010a). The Early Holocene climate was characterized by more fire-conductive weather conditions caused by higher-than-present temperatures (Renssen et al., 2009) and decreased moisture availability, which together prolonged drought periods. Moreover, the frequent occurrence of needleleaf trees significantly contributed to the increased flammability of vegetation. A marked decline in fire activity occurred since 8000–7000 cal yr BP in Western and eastern Central Europe, followed by a period of highly differentiated fire regimes (Feurdean et al., 2012; Vannière et al., 2016). The reduction in the amount of burnt biomass in the Middle Holocene was attributed to a decline in summer insolation, which caused moister and cooler summers (Feurdean et al., 2012; Molinari et al., 2013). Nevertheless, the direct influence of the climate must have interfered with the progressive vegetation transformation into broadleaved forests, which likely had an additional inhibiting effect on fire incidence. Disentangling the particular roles of climatic and biotic drivers is essential for the understanding of past fire dynamics and making robust predictions of ecosystem behaviour under the changing climate in the future.

Mountainous areas of eastern Central Europe underwent a biome-scale transformation from Early Holocene conifer-dominated forests composed predominantly of *Picea abies* to Middle and Late Holocene deciduous forests characterized by their prominent constituent *Fagus sylvatica*. This process was inevitably accompanied by substantial species exchange which in turn had a negative feedback effect on fire activity through the decreased flammability of broadleaved vegetation (Girardin et al., 2013). A similar vegetation transformation into *Fagus sylvatica*-dominated forest communities occurred also within the mid-elevation zone of Central Europe; however, this process was delayed compared to mountainous regions. We investigated the impact of the conversion of key ecosystem species on past fire dynamics. We hypothesized that if the climate was the primary driver of fire activity, a synchronous pattern in biomass burning is likely to be observed at the sub-continental scale. The observed divergence from this pattern suggests that the pervasive influence of the climate can be balanced out by other drivers, including vegetation itself. Two independent biomass burning proxies were developed using the sedimentary charcoal record in stratigraphic profiles and a cumulative probability density function obtained by combining radiocarbon dates for soil charcoal. Long-term trajectories of vegetation change and the timing of the major expansion of forest trees were inferred from pollen records collected alongside sedimentary charcoal as well as from the Czech Quaternary Palynological Database (PALYCZ).

1.30 Material and methods

1.30.1 Study area

We focused on the temperate ecoregion of eastern Central Europe, which is to this day underexplored in terms of fire history reconstructions. The sampling sites are distributed in the lowlands of the Bohemian Cretaceous Basin and uplands of the Bohemian Massif (Figure 1). The sites were divided into two groups according to environmental conditions and landscape characteristics and are further referred to as the mountain sub-region and the sandstone sub-region (Table 1). They differ in their position along an elevation gradient on which sandstone sites are located in uplands (mean 363 m a.s.l. SD=76) whereas mountain sites are situated predominantly in highlands (793 m a.s.l. SD=33). The term 'sandstones' also refers to the major bedrock type supporting the development of specific landforms (see Migoń et al., 2017). Furthermore, the defined sub-regions differ in their Holocene vegetation development and human occupation history. The sandstone sites are located at the borders of the prehistoric settlement zones of Central Bohemia and Upper Saxony, and thus have been subjected to long-term human influence (Demján et al., 2016). By contrast, mountain sites were much less affected by human activity, which is traceable only since the Bronze Age and its intensity increased only since the High Medieval period (Kozáková et al., 2015).

1.30.2 Continuous charcoal series

We compiled 14 macro-charcoal influx series (CHAR, >125 μm, charcoal counts cm^{-2} yr^{-1}) that were extracted from several depositional environments, including raised peat bogs, alluvial fens and lake sediments distributed in the territory of Czech Republic, eastern Central Europe (Figure 1). A summary of the laboratory procedures used, sample volumes and measurement units is presented in Table 1. Sedimentary sequences were drilled between 2010 and 2016; however, several of the sites were subjected to a previous investigation in the early 90s and the original cores were stored in an archive in dry state. These sites were re-analysed using charcoal analysis and the time-control was improved by additional ^{14}C dating. Macro-charcoal extraction was carried out on sedimentary samples 1-4 cm^3 in volume taken from the core at 1–2 cm intervals. At several depths the cores could not be sampled due to the presence of compact wood or an insufficient volume of sediment caused by previous macroremains extraction. During the pretreatment stage, organic matter was disaggregated with the aid of a 10 % NaCl solution and subsequently bleached by sodium hypochloride (NaOCl). Samples were gently wet sieved through a 125 µm mesh and non-charred organic material was manually removed from the coarse fraction under a stereomicroscope at 6.3–60× magnification to facilitate counting. The charcoal particles were quantified by visual counting or using a custom-built image analysis system (http://www.microspock.cz/).

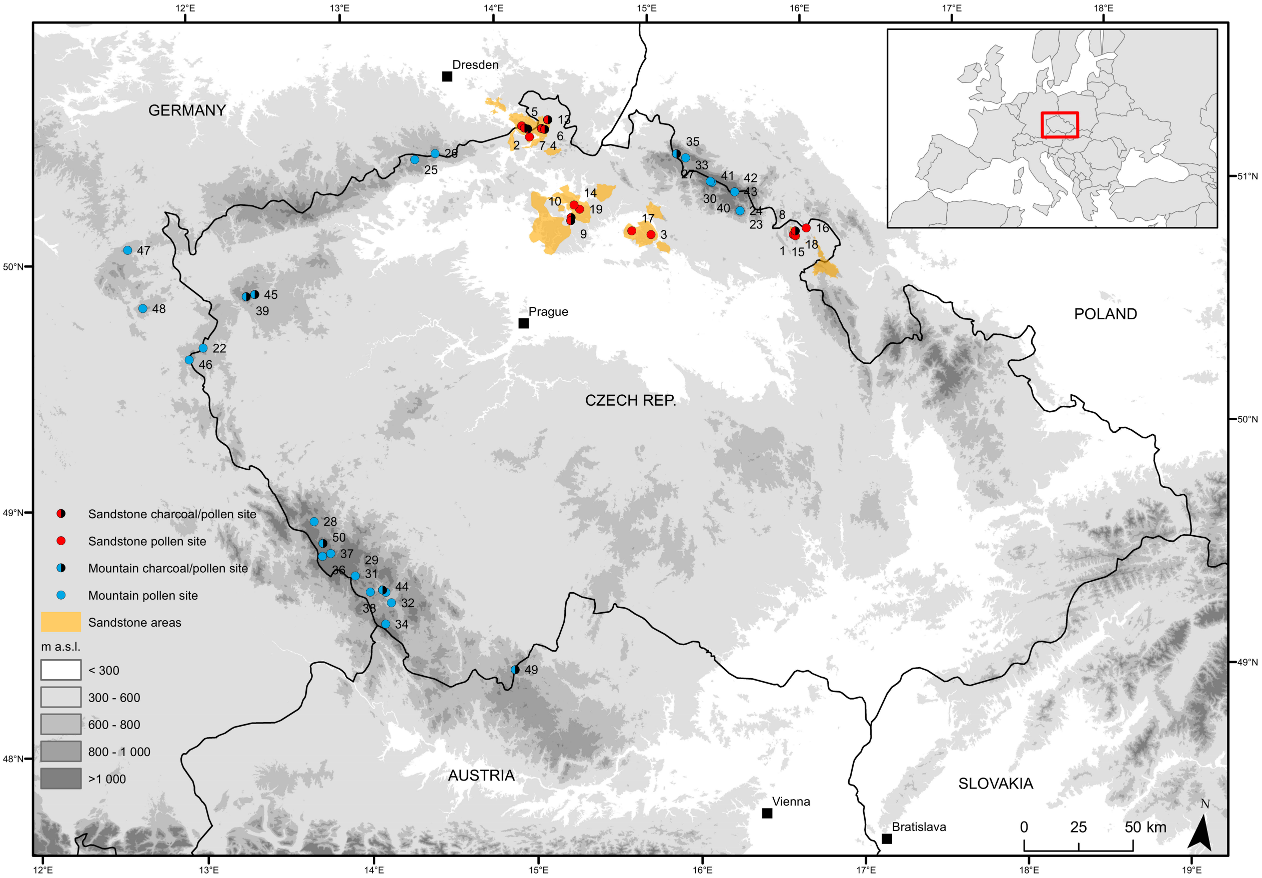

Figure 1. Geographic distribution of charcoal and pollen records considered for the analysis. Sites are grouped to sandstone and mountain sub-regions (see map legend) according to elevation and bedrock type. Sedimentary macro-charcoal sequences (CHAR) are marked in black symbol. Yellow filling bounds nature protected areas within sandstone landscape.

We calculated sedimentary macro-charcoal influx (CHAR, charcoal counts cm^{-2} yr^{-1}) by dividing the charcoal content in samples (particles cm^{-3}) by corresponding deposition time (yr cm^{-1}). Even though a common laboratory protocol was used, a standardizing procedure was needed to ensure reliable between-site comparison. Macro-charcoal influx data were transformed into Z-scores following the technique proposed by Power et al. (2008) and later adapted by (Blarquez et al., 2014) in the 'paleofire' R package. The basic rationale for this set of mathematical operations is to account for differences in site-specific depositional characteristics and the diverse analytical methods and units used for charcoal quantification, which can confound regional synthesis when left untreated. In order to detect common biomass burning trends within specific region, each CHAR series was pre-binned using non-overlapping 100-year bins to counterbalance the impact of high-resolution records. The resulting sequences were rescaled using ‘minimax’, followed by a Box-Cox transformation to homogenize intra-record variability and, finally, z-score-transformed at the base period of -65 to 12,000 cal yr BP. The zero z-score value corresponds to the mean charcoal influx of all transformed series at the scale of the whole Holocene period. A locally weighted scatter plot smoother (LOWESS) was then used to 1000-year windows in order to construct charcoal composite curves. Confidence intervals (95 %) were then calculated by 1000 bootstrap resampling with replacement of individual CHAR series.

According to modelling and empirical studies, charcoal particles larger than 100 µm are predominantly dispersed over limited distances (<500 m) from the burnt area, thus allowing ‘local’ fire signal to be derived from sedimentary charcoal sequences (Gavin et al., 2003b; Higuera et al., 2007). On the other hand, charcoal from more distant sources (40 km radius) also contributes to the macro-charcoal record, allowing to detect regional fire activity (Adolf et al., 2018). Moreover, the intensity of a fire influences its ability to emit charcoal particles into the atmosphere (Vachula et al., 2017), and more intense fires are likely to be recognizable at greater distances. On the contrary, soil charcoal fragments larger than 2 mm are poorly dispersed beyond fire area margins, thus providing high spatial resolution reaching the scale of individual trees. Based on charcoal trapping conducted during experimental burns, particles larger than 2 mm are predominantly deposited up to 1 m beyond the edge of the fire (Ohlson et al., 2000).

1.30.3 Soil charcoal record

Macroscopic charcoal particles embedded in soil and peat provide robust evidence of fire occurrence at a given site (Ohlson et al., 2000; Remy et al., 2018). They may also serve as excellent material for taxonomic identification and radiocarbon dating, making it possible to develop an independent proxy of fire activity and vegetation cover (Fregeau et al., 2015). We collected a set of 90 ^{14}C-dated soil charcoal samples from sites located within the mountain sub-region (n=51) and the sandstone (n=49) sub-region in order to detect individual fires. Charcoal particles were extracted from soil trenches that were placed on flat relief to decrease a chance of soil re-working via erosional processes (for the detailed methodology, see (Bobek et al., 2018b, 2018a). For each sub-region we calculated a cumulative probability function (CPF) of all available ^{14}C dates using the ‘SUM’ function in OxCal 4.3 (Ramsey, 2009). CPFs has been used as proxies for flooding activity (Macklin et al., 2005) or human population dynamics (Armit et al., 2014) and may be potentially used also to reveal past fire activity. Because of the limited number of ^{14}C data, we used CPFs to identify phases of fire activity without attempting to assess their magnitude.

Table 1. Description of sites, sampling strategy, extraction techniques and chronological control used in this study. The site numbering follows designation used in Fig 1.

Map ID	Site	Sub-region	Location (Lat.; Long.)	Elevation (m a.s.l.)	Sample volume (cm^3)	Sampling interval (cm)	Charcoal size	Number of samples	^{14}C dates	^{210}Pb dates	Median resolution (yrs)	Temporal coverage (cal yr BP)	Reference
2	Polomový důl	Sandstones	50,882869° N; 14,317496° E	313	2	1	>125 µm	134	2	0	12	-50 to 2183	this study
4	Eustach	Sandstones	50,890667° N; 14,428425° E	387	2	1	>125 µm	198	3	18	31	-62 to 7532	Bobek et al 2018a
6	Křepelčí důl	Sandstones	50,931874° N; 14,438233° E	357	2	1	>125 µm	200	3	0	77	-55 to 14061	this study
8	Velké ohbí	Sandstones	50,604057° N; 16,127125° E	528	4	1	>125 µm	321	15	0	22	670 to 10342	this study
9	Okna	Sandstones	50,532070° N; 14,675930° E	277	6.7	2	>125 µm	53	7	0	36	-63 to 12899	this study
10	Poselský rybník	Sandstones	50,544398° N; 14,675370° E	274	2	1	>125 µm	80	10	0	39	-62 to 11429	this study
11	Pravčický důl	Sandstones	50,884236° N; 14,296834° E	382	2	1	>125 µm	303	7	12	9	-63 to 2692	this study
13	Puklina	Sandstones	50,932394° N; 14,439768° E	386	2	1	>125 µm	82	3	0	80	-35 to 6657	this study
31	Malá niva	Mountains	48,913760° N; 13,816060° E	753	2	1	>125 µm	435	3	0	13	-40 to 6031	this study
35	Rašeliniště Jizery	Mountains	50,861706° N; 15,301881° E	843	4	1	>125 µm	330	7	0	17	-56 to 11323	this study
39	Tajga	Mountains	50,026100° N; 12,680355° E	817	2	1	>125 µm	563	8	0	19	-43 to 13956	this study
45	Vlček	Mountains	50,039798° N; 12,731939° E	769	2	1	>125 µm	330	7	0	32	-9 to 10873	this study
49	Žofínský prales	Mountains	48,664442° N; 14,705347° E	785	1	1	>125 µm	110	4	19	77	-68 to 7792	Bobek et al 2018b
50	Stará Jímka SJH	Mountains	49,068764°N; 13,402947°E	1129	1	1	>125 µm	316	9	0	28	-59 to 11066	this study

1.30.4 Pollen data collection

Pollen analysis was performed on selected samples obtained from the same sedimentary cores as those used for charcoal analysis. Samples of 1-2 ml volume were taken along the core at intervals of 2-10 cm and processed using standard laboratory treatments, including HCl, HF and acetolysis (Berglund et al., 2003). Pollen identification and nomenclature followed descriptions in atlases (Punt, 1976; Reille, 1992, 1995, 1998; Beug, 2004) and the reference collections at the Institute of Botany of the Czech Academy of Sciences and Charles University in Prague. A minimum of 200 grains of terrestrial pollen taxa were counted, but usually a pollen sum greater than 500 was reached. The percentage calculations are based on the pollen sum of trees, shrubs and upland herbs; wetland taxa, spores and various NPPs are excluded. Moreover, the pollen sequences stored in the Czech Quaternary Palynological Database (https://botany.natur.cuni.cz/palycz/) (Kuneš et al., 2009) were included in the analyses to detect regional vegetation trajectories (Table 2). Available sites were assigned to predefined two sub-regions. The nomenclature used for pollen analysis was adjusted according to PALYCZ database. LOWESS smoothing of pollen sequences was employed to visualise long-term vegetation trajectories. For this we adopted a compositing approach used for CHAR series (Blarquez et al., 2014) and modified it to be applicable to pollen percentages. Individual pollen sequences were pre-binned into non-overlapping 100-year bins and no further transformation was used. The 'LOWESS' smoother with a bandwidth of 1000 years was then applied to pooled pollen percentage values. Confidence intervals were generated by bootstrapping where individual pollen sequences (not samples) were sampled with replacement.

1.30.5 Chronological control

The age-depth models of our sedimentary charcoal records were based on ^{14}C samples and upper parts of selected cores (ca. 15-20 cm) were analysed for ^{210}Pb radioisotope activity (Table 1). The material dated included seeds of terrestrial plants, needles and charred wood fragments, but also bulk peat samples or non-differentiated plant tissues. The constant rate of supply (CRS) model was used to estimate the sample age (Binford, 1990) of ^{210}Pb measured depths. Radiocarbon ages were calibrated with the IntCal13 curve (Reimer et al., 2013) and age-depth models were constructed using Clam 2.2 (Blaauw, 2010) in R (R Development Core Team, 2013). The age-depth relationship was modelled by a smoothing spline (span 0.1 to 0.4) or linear interpolation. The best-fitting model was obtained by repeated random sampling (1000 iterations) of the ^{14}C date calibrated distribution followed by calculation of weighted means for every depth. The chronology for pollen profiles extracted from the PALYCZ database followed age-depth models provided by database providers. Single charcoal particles extracted from soils or peat cores were dated using Accelerated Mass Spectrometry and calibrated as described above. Additional soil charcoal dates available in the study area were searched in the literature and included in the analysis (Supplementary Table S1 in Appendix 2).

Table 2. Description of all pollen records used for estimation of regional vegetation trends. The site numbering follows designation used in Fig 1.

Map ID	Site	Depositional context	Sub-region	Temporal coverage (cal yr BP)	Location (Lat.; Long.)	Elevation (m a.s.l.)	Reference
1	Anenské údolí	Peat bog in a sandstone valley	sandstones	-49 to 9165	50,588729°N; 16,11745°E	663	(Pokorný et al., 2005)
2	Polomový důl	Peat bog in a sandstone valley	sandstones	56 to 2177	50,882869°N; 14,317496°E	313	this study
3	Čin-Čan-Tau	Holocene bog in the sandstone valley	sandstones	-63 to 15187	50,518113°N; 15,202707°E	264	(Svoboda et al., 2018)
4	Eustach	Mire at the bottom of sandstone valey	sandstones	-44 to 7532	50,890667°N; 14,428425°E	387	(Bobek et al., 2018b)
5	Jelení louže	Peat bog in a sandstone valley	sandstones	-55 to 6355	50,892609°N; 14,27661°E	438	(Pokorný et al., 2005)
6	Křepelčí důl	Peat bog in a sandstone valley	sandstones	23 to 14061	50,931874°N; 14,438233°E	357	this study
7	Nad Dolským mlýnem	Peat bog in a hollow at sandstone plateau	sandstones	53 to 10547	50,851782°N; 14,337259°E	288	(Abraham, 2006)
8	Velké ohbí	Peat bog in a sandstone valley	sandstones	772 to 10354	50,604057°N; 16,127125°E	528	this study
9	Okna	Wet meadows	sandstones	-33 to 12786	50,532070°N; 14,67593°E	277	(Pokorný et al., 2017)
10	Poselský rybník	Wet meadows	sandstones	-38 to 11429	50,544398°N; 14,67537°E	274	(Svoboda et al., 2018)
11	Pravčický důl	Peat bog in a sandstone valley	sandstones	-62 to 2675	50,884236°N; 14,296834°E	382	this study
12	Pryskyřičný důl	Peat bog in a sandstone valley	sandstones	-54 to 2752	50,893039°N; 14,406338°E	309	(Abraham et al., 2008)
13	Puklina	Peat bog on sandstone plateau	sandstones	223 to 6407	50,932394°N; 14,439768°E	386	this study
14	Skřítkův Hrnec	Waterlogged mire	sandstones	2203 to 4674	50,597963°N; 14,684241°E	347	Novák et al., 2015
15	Teplické údolí	Peat bog in a sandstone valley	sandstones	-50 to 8474	50,58494°N; 16,13153°E	695	Kuneš and Jankovská, 2000
16	Vernéřovice	Flat valley	sandstones	-25 to 12288	50,62165°N; 16,19577°E	488	Peichlová, 1979
17	Vlčí důl	Peat bog	sandstones	-66 to 12506	50,52288°N; 15,076528°E	296	Pokorný et al., 2017
18	Vlčí rokle	Peat bog in a sandstone valley	sandstones	-43 to 14497	50,6045°N; 16,128409°E	535	Kuneš and Jankovská, 2000
19	Voroněž	Peat bog	sandstones	1414 to 11363	50,583593°N; 14,72334°E	273	Novák et al., 2012
20	Bílé Labe A	Mountain raised bog	mountains	33 to 3068	50,735506°N; 15,706526°E	1431	Svobodová, 2004
21	Bílé Labe C	Mountain raised bog	mountains	-54 to 3713	50,735506°N; 15,706526°E	1431	Svobodová, 2004
22	Brentenlohe	Peat bog	mountains	-39 to 23315	49,787219°N; 12,4625°E	754	Knipping, 1989
23	Černá hora	Mountain ombrotrophic peat bog	mountains	-29 to 2212	50,660609°N; 15,75586°E	1193	Speranza et al., 2000
24	Černohorská rašelina	Mountain ombrotrophic peat bog	mountains	296 to 1861	50,660609°N; 15,75586°E	1193	Svobodová et al., 2002
25	Fláje - Kiefern	Mountain raised bog	mountains	-39 to 11662	50,691056°N; 13,619721°E	749	(Jankovská et al., 2007)
26	Georgenfelder Hochmoor	Peat bog	mountains	198 to 3524	50,728624°N; 13,74384°E	868	Stebich and Litt, 1997
27	Hala Izerska	Mountain raised bog	mountains	437 to 8579	50,850185°N; 15,363206°E	838	Skrzypek et al., 2009

Map ID	Site	Depositional context	Sub-region	Temporal coverage (cal yr BP)	Location (Lat.; Long.)	Elevation (m a.s.l.)	Reference
28	Hůrecká slať	Large ombrotrophic mire	mountains	456 to 13728	49,15222°N; 13,32755°E	871	Svobodová et al., 2002
29	Knížecí pláně	Transitional mire	mountains	-52 to 11858	48,955438°N; 13,634408°E	995	Svobodová et al., 2001
30	Labský důl	Mire in cirque basin	mountains	795 to 29380	50,762777°N; 15,552222°E	1034	Engel et al., 2010
31	Malá niva	Large ombrotrophic mire	mountains	-28 to 5801	48,913760°N; 13,81606°E	753	Svobodová et al., 2002
32	Mrtvý luh	Large ombrotrophic mire	mountains	-52 to 6347	48,866799°N; 13,88292°E	738	Svobodová et al., 2001
33	Pančavská louka	Mountain raised bog	mountains	-13 to 3736	50,76619°N; 15,54102°E	1329	A. Speranza et al., 2000
34	Plešné jezero	Glacial mountain lake	mountains	60 to 22311	48,776739°N; 13,86571°E	1085	Jankovská, 2006
35	Rašeliniště Jizery	Mountain raised bog	mountains	-56 to 11354	50,861706°N; 15,301881°E	843	this study
36	Rokytecká slať	Large ombrotrophic mire	mountains	-53 to 10947	49,0153°N; 13,4122°E	1098	(Svobodová et al., 2002)
37	Rybárenská slať	Large ombrotrophic mire	mountains	123 to 9411	49,031289°N; 13,46189°E	1012	(Svobodová et al., 2002)
38	Stráženská slať	Large ombrotrophic mire	mountains	590 to 10434	48,89887°N; 13,74226°E	802	(Svobodová et al., 2001)
39	Tajga	Mountain raised bog	mountains	-43 to 13791	50,026100°N; 12,680355°E	817	this study
40	Úpská rašelina	Mountain raised bog	mountains	-39 to 1787	50,735506°N; 15,706526°E	1431	(Speranza, 2000)
41	Úpské rašeliniště - Palza	Mountain raised bog	mountains	-54 to 5122	50,735506°N; 15,706526°E	1431	(Svobodová, 2004)
42	Úpské rašeliniště A	Mountain raised bog	mountains	-48 to 3466	50,735506°N; 15,706526°E	1431	(Svobodová, 2004)
43	Úpské rašeliniště B	Mountain raised bog	mountains	-53 to 2368	50,735506°N; 15,706526°E	1431	(Svobodová, 2002)
44	Velká niva-Volary	Large ombrotrophic mire	mountains	-51 to 12379	48,906601°N; 13,838808°E	750	(Svobodová et al., 2001)
45	Vlcek	Wet meadows	mountains	195 to 10873	50,039798°N; 12,731939°E	769	(Švarcová, 2012)
46	Weiherlohe	Peat bog	mountains	-21 to 11369	49,72972°N; 12,387499°E	694	(Knipping, 1989)
47	Weissenstadter Forst	Peat bog	mountains	-41 to 7352	50,133783°N; 11,881848°E	720	Knipping, 1989
48	Wolfslohe 1	Peat bog	mountains	-41 to 5397	49,907559°N; 12,04038°E	826	Hane, 1992
49	Žofínský prales	Small depression infilled by peat deposits	mountains	-68 to 7792	48,664442°N; 14,705347°E	785	Bobek et al., 2018a

Table 2 (Continued). Description of all pollen records used for estimation of regional vegetation trends. The site numbering follows designation used in Fig 1.

1.30.6 Numerical analyses

We attempted to quantify the amount of compositional change in plant communities using Detrended Canonical Correspondence Analysis (DCCA) performed on pooled pollen sequences from each sub-region. This multivariate analysis benefits from the stratigraphical nature of pollen data where the temporal order of samples is known and can be utilized as an external constraint on the first ordination axis. The resulting sample scores are directly scaled in standard deviation (SD) units of compositional change (i.e. palynological beta-diversity), which offers ecologically interpretable values in terms of the amount of species which have changed along the time gradient (Birks, 2007). Hence, the difference between any two sample scores on the first time-constrained axis expresses the magnitude of a particular change in the respective pollen record. A complete turnover in pollen assemblage (i.e. no pollen type in common) occurs in 4 SD units whereas a half-change is reached within 1-1.4 SD units (Legendre et al., 2012).

The individual pollen sequences were analysed using DCCA as implemented in CANOCO 5.0 (ter Braak et al., 2012). Percentage values were calculated based on the sum of all terrestrial pollen types prior to the analysis. The data were square-root-transformed in order to stabilize their variances and to suppress the influence of strong pollen producers. No down-weighting of rare species, detrending by segments and non-linear rescaling were applied during the analysis. The resulting scores on the first time-constrained ordination axis were stacked into a single dataset covering the base period of 12,000 cal yr BP to -65 cal yr BP. The analysis output is presented as the maximum compositional change during the 1000 year time-step interval along individual pollen sequences, allowing to summarize the variability and magnitude of species turnover over multiple records.

1.31 Results

1.31.1 Trends in regional biomass burning

In total, 3455 macro-charcoal samples were processed by a common laboratory protocol providing a multiple-site dataset covering the last 12,000 cal yr BP of biomass burning history. The general trends of charcoal deposition were based on six continuous sedimentary sequences within the mountain sub-region and eight profiles originated in the sandstone sub-region, respectively (Figure 2; Supplementary Figure 3 in Appendix 2).

Within the sandstone sub-region, the transition between the Late Glacial and Early Holocene (11,700 cal yr BP) was characterized by low biomass burning. The first distinct peak in fire activity occurred around 10,500 cal yr BP, followed by rapid a decline in the period between 10,000 and 9000 cal yr BP. A varying trend in fire signal from 9000 cal yr BP to 5000 cal yr BP indicates a period of oscillating fire activity with several local maxima at 8800, 6400 and 5100 cal yr BP. A pronounced drop in the level of biomass burning was recorded since 4900 cal yr BP and a subsequent period of suppressed fire occurrence lasted for the next 1300 years. The incidence of fire increased rapidly since 3600 cal yr BP, peaking at 3200 cal yr BP. Since then, a decreasing trend suggests a lowering in

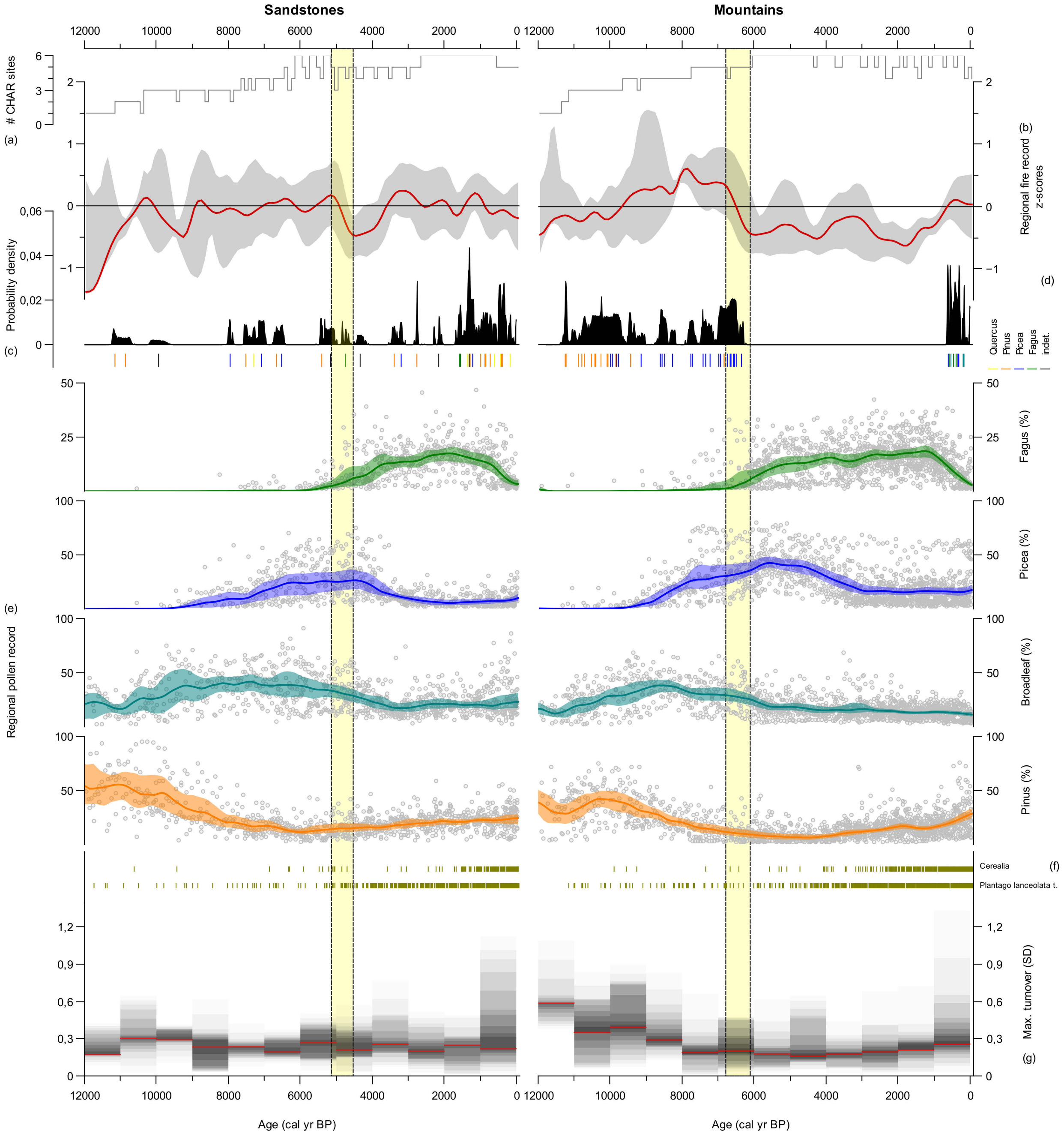

Figure 2. Regional fire activity, soil charcoal record, major vegetation changes and species turnover in two sub-regions of Central Europe. (a) number of individual charcoal series per 100-year bin used for calculating composite record; (b) regional-scale fire activity based on CHAR composites for sandstone and mountain areas (median and 95 % confidence interval); (c) fire occurrence based on probability density function of ^{14}C dates (n=90) of charcoal extracted from soil profiles distributed in particular sub-region (for description see Supplementary table S1, Bobek et al., 2018b, 2018a; Svoboda et al., 2017); (d) taxonomical identification of single ^{14}C dated charcoal particle from soil profiles (see Supplementary table S1); (e) regional vegetation dynamics derived from multiple-site pollen sequences (for site description see Supplementary table S1). Grey dots represent pollen percentage in single sample and lines indicate general trend based on LOESS smoothing (500 yr window, 95 % confidence interval is constructed from 1000 bootstrap resamplings). Broadleaf taxa includes pollen of *Quercus*, *Corylus avellana*, *Betula alba*-type, *Fraxinus excelsior*-type; (f) An occurrence of anthropogenic pollen indicators and other pollen types; (g) compositional turnover in pollen assemblages based on Detrended canonical correspondence analysis. The percentile histogram (shade gradient, median in red) depicts a distribution of maximum difference of scores on the age-constrained first DCCA axis (for single pollen sequence, scaled in standard deviation) within 1000-years window. Vertical bars denote a major decline in fire activity within particular sub-region.

biomass burning, which culminated at around 1600 cal yr BP. A medium level of burning has been recorded over the past two millennia with the exception of a marked maximum at 1100 cal yr BP.

The mountain records show limited fire activity at the onset of the Holocene period, which extended until 9600 cal yr BP. After this initial stage, biomass burning remained above-average level till 6800 cal yr BP. This rising trend was, however, highly variable among the sites, resulting in a broad confidence interval. A step-like increase in the charcoal composite curve occurred after 8300 cal yr BP, which is characterized by small between-site variation, indicating a synchronous response. A maximum level of fire activity occurred at 7900 cal yr BP, followed by substantial decrease between 6800 and 6000 cal yr BP. Middle to Late Holocene biomass burning declined to below-average values, interrupted by a moderate increase around 5100 and 3100 cal yr BP. The last millennium was characterized by sharp increase in fire activity.

1.31.2 Identifying major vegetation changes

A total of 2643 pollen samples were used to identify trends in abundance of key tree taxa within the sandstone (19 profiles) and the mountain sub-region (30 profiles). Despite the large variation in pollen percentage values, some common patterns were identified, allowing us to identify major shifts in forest composition over the Holocene period (Figure 2).

The Early Holocene vegetation in sandstone areas consisted *of Pinus*, *Betula* and an extensive admixture of other broadleaf trees and shrubs (mainly *Corylus avellana, Quercus*). *Picea abies* invaded these areas starting from 9300 cal yr BP, when the overall pollen proportion exceeded the 1 % threshold, indicating its regional presence. Since then, the gradual rise of the *Picea abies* compositional curve to 23 % indicates an expansion of the spruce population during the Middle Holocene. The species' presence was cross-validated by five ^{14}C-dated charcoals originated from soil trenches or directly from peat sequences. A pronounced decline was detected between 4500 cal yr BP and 3000 cal yr BP, when the overall pollen proportion dropped to 8 % and subsequently stabilized around 5 % at the end of the Late Holocene. *Fagus sylvatica* immigrated into the sandstone region as early as 8000 cal yr BP, which is evidenced by numerous findings of its pollen grains (<0.5 %) and radiocarbon-dated macroremains (Novák et al., 2017; Svoboda et al., 2018). However, its population did not expand until 5500 cal yr BP, when a sharp increase occurred. This process peaked around 2000 cal yr BP by reaching an overall pollen proportion of about 17 %. A subsequent slow decline during the Early Middle Ages was followed by a significant drop in the last five hundred years.

The history of key tree species in mountain areas holds evidence of a rapid expansion of *Picea abies* since 9500 cal yr BP, reaching values of around 27 % in the subsequent two millennia. Sporadic pollen grains occurring over the earlier stage of the Holocene do not constitute solid evidence about the species' presence; however, no later than 9978 cal yr BP the species grew in sheltered valleys in southern part of the Bohemian Massif (Bohemian Forest and the Gratzen Mts). This initial stage of forest development was characterized by a dominance of *Pinus*, as shown by high pollen proportions and confirmed by the soil charcoal record. The dominance of spruce peaked in the Middle Holocene ca

5500 cal yr BP, when it exceeded the composite pollen proportion of 40 %. Since then, it gradually declined to a constant value of 15% at 3000 cal yr BP and virtually has not oscillated up to the recent times. The migration history of *Fagus sylvatica* in the mountain area showed an initial period of discontinuous occurrence throughout the Early Holocene, which was followed by an unprecedented rise starting 6600 cal yr BP. Since then, beech maintained its abundance and took over the role of the key tree species in forest vegetation. However, its marked retreat has been recorded from the beginning of the Middle Ages. Anthropogenic indicators showed a rising trend starting ca 4000 cal yr BP and its pollen frequency has accelerated in the last thousand years.

1.31.3 Compositional turnover

The compositional turnover in pollen assemblages showed divergent pattern within both sub-regions (Figure 2g; Supplementary Figure 1 and Supplementary Figure 2 in Appendix 2). The greatest amount of species exchange was detected at the Younger Dryas/Early Holocene transition (time window 12,000-11,000 cal yr BP) and in the Early Holocene (10,000-8000 cal yr BP) at sites distributed in the mountain sub-region. By contrast, sites located in the sandstone sub-region exhibited only a slight increase during the Early (11,000-9000 cal yr BP), Middle (6000-5000 cal yr BP) and Late Holocene (1000-0 cal yr BP). In the remaining time windows, median value remained low indicating more gradual changes in vegetation composition.

1.32 Discussion

1.32.1 Fuel limitation and climatic influence on fire activity in the Early Holocene

The charcoal composite record covering the Younger Dryas/Preboreal transition (11,700 cal yr BP; Walker et al., 2012) indicates low biomass burning across the whole elevational range. Lower-than-average charcoal influxes suggest low-intensity or spatially constrained fires producing weak charcoal signal recorded in sedimentary sequences. Given the limited number of sites (n=2) extending back to the Late Glacial, over-generalization should be avoided when interpreting such a record. Nevertheless, suppressed fire activity, albeit following a rising trend, has been reported by multiple-site charcoal studies from Central Europe (Feurdean et al., 2013a; Marlon et al., 2013) or Fennoscandia (Clear et al., 2014), indicating the existence of factors limiting the emergence and spread of fires during this transitional period. This is also in agreement with available microcharcoal records from the study area, pointing to reduced biomass burning at the regional scale (Pokorný et al., 2010; Svoboda et al., 2018). The Early Holocene climate was likely more continental than today because of higher summer insolation (Berger et al., 1991) and reduced precipitation caused by weakened North Atlantic circulation (Houfková et al., 2017; Perşoiu et al., 2017). Accordingly, stronger continentality promotes periods of decreased effective moisture in summer, thus enhancing the proneness of combustible materials to burn (Marcisz et al., 2017). Moreover, biome-scale vegetation reorganization that tracked the rapid climatic warming-induced shifts in ecosystem productivity that have supported greater fuel built-up (Pausas et al., 2012). Biomass limitation was probably an important constraint on fire occurrence until the forest density reached a threshold enabling its effective spread. The Early Holocene forest cover in eastern Central Europe was discontinuous at higher elevations (>700 m a.s.l.), as illustrated by the REVEALS estimate of landscape openness, which reached 50 % in the Bohemian/Bavarian Forest (Carter et al., 2018a). On the other hand, land-cover reconstructions for the lowlands of Bohemia estimate that *Pine*-dominated forests occupied ~60-80 % of total area (Abrahám, 2016) and were accompanied by patches of steppe grasslands (Pokorný et al., 2015). Our pollen record consistently reflects this vegetation pattern, showing greater pollen percentages of *Pinus* within the mid-altitude sandstone region. Nevertheless, such a fuel threshold was passed immediately after the initial warming, as evidenced by the synchronous occurrence of oldest soil charcoal dated to ca 11,200 cal yr BP. This finding documents that increased fire activity was linked to the spread of forest vegetation during the rapid climatic amelioration in the Early Holocene.

1.32.2 Biotic turnover in response to fire activity

Indices of compositional changes in plant communities show that periods of increased biotic turnover differ in their timing between the two sub-regions (Figure 2g). The triggering factor at the beginning of the Holocene (window 12,000-11,000 cal yr BP) was apparently rapid climate warming, which enhanced shifts in the geographic distribution of many plant species across Europe and altered the rates of biotic changes (Finsinger et al., 2017; Stivrins et al., 2016). Fire disturbances were likely not an important driver in such vegetation dynamics, as a low charcoal influx and lack of soil charcoal indicates limited biomass burning. However, the much weaker response of sandstone plant communities, exhibiting rather minor biotic turnover, indicates that increasing temperatures did not induce as deep compositional changes within mid-altitude areas as in mountainous areas. We argue that the observed disparity between the two sub-regions can be attributed to differences in afforestation patterns, which were highly discontinuous within mountain areas during the Younger Dryas/Early Holocene (Abraham et al., 2016). The continental climate and a rugged relief supported the mosaic coexistence of light-demanding cold-steppe and shrub-tundra taxa along with scattered trees growing only in sheltered topographic positions, as corroborated by vegetation analogues from Siberia (Kuneš et al., 2008a; Janská et al., 2017; Chytrý et al., 2019). The afforestation pathway had a different character in sandstone areas, where a park-like taiga composed of *Pinus sylvestris* established earlier in the Late Glacial and survived the Younger Dryas cold spell (Pokorný et al., 2017). Low turnover rate thus suggest a rather gradual vegetation transformation in the sandstone sub-region compared to abrupt changes detected in the mountain sub-region.

An association between fire activity and rates of biotic turnover was generally weak throughout the Middle to Late Holocene, because periods of increased fire activity did not show any consistent pattern of higher compositional changes. This may indicate that fire disturbances did not induce substantial disparity between pre- and post-fire vegetation. The frequency or intensity of fire disturbances likely did not exceed the threshold of ecosystem resilience, as ecosystems recovered quickly into the pre-disturbance state. However, other drivers such as the expansion of key tree taxa apparently triggered greater compositional changes than fire disturbances, pointing to the assembling of novel plant communities. In addition, the last millennium exhibits large variation in turnover that is likely associated with differences in the magnitude of human influence.

1.32.3 Fire activity changes related to the *Picea abies* expansion

It is assumed that *Picea abies* colonized the area of eastern Central Europe from full-glacial refugia located between the southern margin of the Bohemian Massif and the eastern foreland of the Alps (Tollefsrud et al., 2008). Our multiple-site pollen record covering a region situated north of this likely refugial area suggests a near-synchronous trend in regional expansion that started ~9300 cal yr BP. However, an earlier presence of a small outpost populations in mountain regions is evidenced by the irregular occurrence of pollen percentages exceeding 1 % (Lisitsyna et al., 2011) and ^{14}C-dated charred wood remains in soils dated back to 9 900 cal yr BP (Figure 2, Supplementary Table S1 in Appendix 2). The Early Holocene spread of spruce in this area presumably mimics the species' migration history in Northern Europe (Giesecke et al., 2004) because it has started as a range expansion in low population densities followed by a delayed establishment of dense stands. This migration scenario may also be evidenced by the increased compositional turnover in pollen assemblages accompanying spruce establishment pointing to instantaneous competitive exclusion of preceding plant communities. Interestingly, the soil charcoal record suggests numerous fire events throughout this initial stage of the spruce expansion in the mountain sub-region. This may imply that fire contributed to the spread of *P. abies* throughout the Central European landscape during the Early Holocene. It has recently been demonstrated that fire facilitated the Middle Holocene expansion of *P. abies* in the north-western Alps by suppressing its competitors, namely *Abies alba* (Schwörer et al., 2015). Likewise, in Scandinavian boreal forests, spruce stand establishment could have been mediated by fires (Björkman et al., 1996; Molinari et al., 2005; Hörnberg et al., 2012; Ohlson et al., 2017). Although the continental-scale dynamics of *P. abies* are probably controlled by top-down drivers such as the climate, local tree establishment apparently benefited from fire disturbances which created patches of early successional vegetation that enabled for generative propagation.

Although the increased charcoal influx observed 9700-6500 cal yr BP in mountain areas of Bohemia are linked to phases of high *P. abies* abundance (Figure 2), this does not necessarily mean that spruce increased the frequency of fires. Norway spruce is a fire avoider lacking any trait that increases its chances of surviving the damage caused by high temperatures during a wildfire (e.g. thick bark). At the same time it has a ladder canopy structure and high resin content both in wood and needles. These morphological drawbacks make spruce susceptible to high-intensity crown fires that generate vast quantities of burning residues, including charcoal. Therefore, excessive charcoal deposition during periods of increased spruce abundance may reflect a shift in the fire regime from surface to more intense crown fires not necessarily accompanied by a rise in fire frequency. This can partly explain the contradictory findings from Fennoscandia that the Late Holocene expansion of *P. abies* substantially reduced the fire activity in boreal ecosystems (Ohlson et al., 2011). An analogous decline in biomass burning linked to the expansion of spruce has been reported from temperate mountain coniferous forests in the Carpathians (Feurdean et al., 2017a).

1.32.4 Widespread Mesolithic burning in the Early Holocene?

The environmental impacts of Mesolithic hunter-gatherers have been repeatedly recognized in palaeoecological records, suggesting the widespread use of fire as a tool for managing landscapes (Jacobi et al., 1976; Mellars, 1976; Simmons et al., 1987; Kuneš et al., 2008b). The deliberate use of fire enhanced vegetation diversification, which in turn significantly increased resource availability in the form of game animals and edible plants (Zvelebil, 1994; Divišová et al., 2015). In the area of Bohemia, Mesolithic occupation (12,000-7500 cal yr BP; Pokorný et al., 2017) has mostly been reported from the sandstone sub-region, where numerous stone artifacts were discovered in sedimentary sequences under rock shelters (Svoboda et al., 2007, 2018). By contrast, archaeological evidence from mountain areas has until recently been nearly non-existent and only the latest research suggest a sporadic human presence in the uplands of the Bohemian Forest (Eigner et al., 2017). Our charcoal composite records from these contrastingly inhabited areas indicate distinct divergence in biomass burning trends (Figure 2b), which, however, must be interpreted with caution because of a limited number of records. Interestingly, the observed trend in mean charcoal influx seems to contradict recent archaeological knowledge indicating higher fire activity in the mountain sub-region. Accordingly, how hunter-gatherers influenced the fire regime likely did not override the natural driving forces such as the climate, the types of fuel and the frequency of lightning, as we did not find any clear dependence on human presence. This is further confirmed by the fact that a major decline in the incidence of fires occurred no earlier than in the Neolithic. If hunter-gatherers were a driving force, we have to presume that the foraging subsistence strategy persisted within both sub-regions alongside Neolithic farming. Although archaeological evidence from the Baltic region indicates a long transitional period (Zvelebil, 2008), rapid cultural change took place in eastern Central Europe (Pavlů et al., 2013).

1.32.5 Identifying the drivers of the Middle Holocene fire decline

The observed pattern of fire activity in the Middle Holocene is characterized by a distinct phase of increased charcoal influx followed by a pronounced decline indicating an important change in the fire regime. Interestingly, this trend was regionally time-transgressive and occurred about 1500 years earlier in the mountain sub-region than in mid-elevation sandstone areas (see the vertical bands in Figure 2b). The divergent timing suggests that climate control was not the ultimate driver of this process, which should tend to be synchronous over a large spatial scale if climate change was its major trigger (Daniau et al., 2012). Decreased biomass burning after ca 6500 cal yr BP and 4900 cal. yr BP, respectively, thus likely reflects non-climatic factors, including vegetation change or human impact. Because we observed a small amount of anthropogenic pollen indicators (Figure 2f), possible changes in agro-pastoral practices do not seem to coincide with the aforesaid fire decline. Based on our comprehensive synthesis of pollen records, the establishment of *Fagus sylvatica*-dominated forest communities has been identified as being contemporaneous with diminishing fire activity (Figure 2e). This major vegetation restructuring took place asynchronously in the two elevational domains, suggesting that the regional population expansion of *F. sylvatica* was involved in the decrease in the incidence of fires. The continental-scale spread of *F. sylvatica* across Europe was a highly complex process and various environmental and biotic factors were involved (Tinner et al., 2006b). Beech undoubtedly occurred in populations of low density throughout the Central European landscape long before its mass expansion, which is evidenced by isolated pollen findings (Figure 2e) and radiocarbon-dated macroremains (Robin et al., 2016; Novák et al., 2017a; Svoboda et al., 2018). Although this tree species is considered fire-sensitive (Tinner et al., 2000), fire disturbances have been proposed as a triggers of local establishment of beech in hemiboreal forests of southern Fennoscandia (Bradshaw et al., 2005; Ohlson et al., 2017). Recently, Feurdean et al. (2017a) recognized that fire facilitated the initial spread of beech in the Carpathians. Post-fire vegetation stages may have been beneficial for its seedlings recruitment, thus enabling the species' intrusion into previously established forest communities. However, the rapid growth of these scattered populations was probably induced asynchronously between sandstone and mountain sub-regions by different phases of climatic deterioration (Wanner et al., 2011).

1.32.6 Human-driven fire regime in Late Holocene

Early and Middle Holocene fire regimes in Europe are generally thought to be driven by the climate (Feurdean et al., 2012; Marlon et al., 2013; Florescu et al., 2018; Kuosmanen et al., 2018), specifically as a result of increased summer insolation (Renssen et al., 2009). The underlying assumption is that if humans altered the climate-driven fire regimes, regional-scale differences in fire activity should emerge (Carcaillet et al., 2007). A study by Dietze et al. (2018) in the lowlands of Central European detected divergent burning trends between nearby regions, suggesting that humans may have significantly altered fire regimes. By contrast, Carcaillet et al. (2007) did not find any influence of prehistoric human societies during the Mesolithic and Neolithic in the northern Swedish boreal forest. We identified a pronounced increase in fire activity during the Late Bronze Age, peaking at ~3100 cal yr BP, that can be linked with human activity within the sandstone sub-region. It has been shown that slash-and-burn practices and pastoral fires contributed to the transformation of Middle Holocene broadleaved forests into Late Holocene oligothrophic forest communities that are widespread in these areas today (Bobek et al., 2018b) by accelerating gradual soil leaching (Ložek, 1998; Pokorný et al., 2005). By contrast, fires in the mountain sub-region were rare or virtually absent between 6000-700 cal yr BP, as evidenced by generally low rates of charcoal deposition and a pronounced gap in the soil charcoal record. Such divergence implies that a change to the human-driven fire regime occurred in mid-elevation areas during the Bronze Age (after 3600 cal yr BP). This is consistent with continental- (Molinari et al., 2013) and regional-scale (Rius et al., 2011; Florescu et al., 2018) trends in biomass burning that suggest a major human influence on the incidence of fires in the Late Holocene.

1.33 Conclusions

Our results suggest that rising vegetation productivity driven by rapid climate amelioration in the Early Holocene enhanced biomass burning. The increased fire activity during this period was driven, on the one hand, by a drier- and warmer-than-present climate, and on the other, by the presence of easily flammable biomass produced by conifer-dominated vegetation. We identified an inhibiting effect of the concomitant *Fagus sylvatica* expansion on levels of biomass burning that occurred asynchronously between mountainous and mid-elevation sandstone regions 6500 cal yr BP and 4900 cal yr BP, respectively. The replacement of coniferous tree taxa led to a pronounced decline in fire activity, evidencing their incidental role in the dynamics of temperate broadleaved forests. Compositional changes in plant communities were more related to the transformation of major vegetation types than to an increased frequency or intensity of fire disturbances. The divergent timing of the fire decline in response to the expansion of *Fagus sylvatica* implies biotic control over biomass burning independent of a direct climatic influence.

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Chapter 6: General conclusions

The results presented in this dissertation demonstrated the active role of fire in shaping postglacial forest development in Central Europe. The use of sedimentary and soil charcoal as a fire proxy has shown that fire disturbances have affected much of the vegetation during the entire Holocene, but the causes and ecological consequences vary between different ecosystems and time periods.

We have identified the environmental factors governing the occurrence of fire in today's landscape, specifically that fires have occurred most frequently in habitats with high thermal influx, exposed topography and a strong presence of Scots pine in the tree cover. By contrast, anthropogenic factors turned out to be secondary drivers of the occurrence of fires in the present landscape. Based on the quantity of charcoal accumulated in the topsoil, a record which integrates site-specific fire activity over millennial time scales, we were able to determine the pattern of fire distribution since the Bronze Age and compare it to the present situation derived from written records. We have found spatial consistency in the identification of fire-prone habitats, indicating that the character of the relief can, in the long term, condition the occurrence of fires and, consequently, induce changes in the composition of the vegetation to the benefit of fire-resistant woody species.

Further, it has been shown that fire can be a major driver of landscape-scale ecosystem transformations, which has been observed especially in the sandstone region of North Bohemia. I collected multiple lines of evidence showing that fires have in the area since the Early Holocene and that their frequency changed in response to climatic changes and the extent of anthropogenic influence. Repeated fire-induced disturbances could have, on the one hand, facilitated the long-term persistence of fire-resistant forest types even at the time of the maximum expansion of deciduous forests during the Holocene climatic optimum. On the other, however, anthropogenic changes to the fire regime, connected with the agricultural and pastoral use of these regions, substantially accelerated the degradation of the environment of sandstone areas.

The study also focused on mechanisms governing the occurrence of wildfires in montane forests of temperate regions. Fire activity increased hand in hand with the warming of the climate at the transition of the Younger Dryas and the Holocene, apparently as a consequence of more rapid accumulation of biomass induced by the spread of closed-canopy forests along the elevational gradient. The local frequency of wildfires, estimated by ^{14}C dating of soil charcoal, exhibited great variation during the Holocene in response to climatic changes coupled with the changes in vegetation. As a consequence of the transformation of the prevailing spruce forest vegetation into mixed forests dominated by *Fagus sylvatica* approximately 6,200 years ago, fire-induced disturbances got eliminated from successional forest dynamics. This shift in the disturbance regime also indirectly influenced the development of soils, in which the process of podzolization was accelerated. The study revealed that large-scale effects of climate changes in the fire regime can be substantially modified by shifts in the dominant woody species at local scale.

Finally, we synthesized available records of Holocene fire activity in two regions of Central Europe differing in the timing of the expansion of temperate deciduous forests dominated by beech to explore feedback loops between fire and vegetation. For each of the regions it has been shown that warming at the beginning of the Holocene was accompanied by an increase in fire activity, apparently as a consequence of drier and warmer climatic conditions and increased availability of easily combustible biomass of conifers. A transformation into mixed deciduous forests took place in montane and sandstone regions asynchronously, namely 6,500 cal BP and 4,900 cal BP ago. The switch of the dominant tree species to *Fagus sylvatica* led to a marked reduction in the occurrence of fires in montane regions. This process took place after a delay of approximately 1,500 years also in sandstone regions situated at lower elevations, where, however, this short-term decline in fire activity was replaced by their anthropically conditioned intensification in the Bronze Age. The different timing of the decrease in fire activity implies that the climatic influence on the occurrence of wildfires in Central Europe can be overridden by biotic factors such as vegetation species composition.

References

Abraham V. 2006. *Přirozená vegetace a její změny v důsledku kolonizace a lesnického hospodaření v Českém Švýcarsku [The natural vegetation of Bohemian Switzerland and its changes as an impact of habitation and forest management].* MSc. thesis, Charles University in Prague,

Abraham V, Kunes P, Petr L, et al. 2016. A pollen-based quantitative reconstruction of the Holocene vegetation updates a perspective on the natural vegetation in the Czech Republic and Slovakia. *Preslia* 88: 409–434.

Abraham V, Pokorný P. 2008. Vegetační změny v Českém Švýcarsku jako důsledek lesnického hospodaření - pokus o kvantitativní rekonstrukci [Vegetation changes in Czech Switzerland as a result of forestry management - an attempt at quantitative reconstruction on the basis of pollen ana. In *Bioarchaeology in the Czech Republic*. Beneš J, Pokorný P (eds). Jihočeská univerzita and Archeologický ústav AV ČR, Praha: 443–470.

Abrams MD. 1992. Fire and the Development of Oak Forests. *BioScience* 42: 346–353.

Adámek M, Bobek P, Hadincová V, et al. 2015. Forest fires within a temperate landscape: A decadal and millennial perspective from a sandstone region in Central Europe. *Forest Ecology and Management* 336: 81–90.

Adámek M, Hadincová V, Wild J. 2016. Long-term effect of wildfires on temperate Pinus sylvestris forests: Vegetation dynamics and ecosystem resilience. *Forest Ecology and Management* 380: 285–295.

Adolf C, Wunderle S, Colombaroli D, et al. 2018. The sedimentary and remote-sensing reflection of biomass burning in Europe. *Global Ecology and Biogeography* 27: 199–212.

Agee JK. 1998. Fire and pine ecosystems. In *Ecology and biogeography of Pinus*. Richardson DM (eds). Cambridge University Press: Cambridge; 193–218.

Ali AA, Blarquez O, Girardin MP, et al. 2012. Control of the multimillennial wildfire size in boreal North America by spring climatic conditions. *Proceedings of the National Academy of Sciences* 109: 20966–20970.

Andersen ST. 1969. Interglacial vegetation and soil development. *Medd. Dansk Geol. Foren.* 19: 90–101.

Angelstam P, Kuuluvainen T. 2004. Boreal forest disturbance regimes, successional dynamics and landscape structures – a European perspective. *Ecological Bulletins* 51: 117–136.

Angelstam PK. 1998. Maintaining and restoring biodiversity in European boreal forests by developing natural disturbance regimes. *Journal of Vegetation Science* 9: 593–602.

Archibald S, Lehmann CER, Gomez-Dans JL, et al. 2013. Defining pyromes and global syndromes of fire regimes. *Proceedings of the National Academy of Sciences* 110: 6442–6447.

Armit I, Swindles GT, Becker K, et al. 2014. Rapid climate change did not cause population collapse at the end of the European Bronze Age. *Proceedings of the National Academy of Sciences of the United States of America* 111: 17045–17049.

Baker AG, Bhagwat SA, Willis KJ. 2013. Do dung fungal spores make a good proxy for past distribution of large herbivores? *Quaternary Science Reviews* 62: 21–31.

Barrett LR, Schaetzl RJ. 1992. An examination of podzolization near Lake Michigan using chronofunctions. *Canadian Journal of Soil Science* 72: 527–541.

Barrett LR, Schaetzl RJ. 1993. Soil development and spatial variability on geomorphic surfaces of different age. *Physical Geography* 14: 39–55.

Barrett LR, Schaetzl RJ. 1998. Regressive pedogenesis following a century of deforestation: evidence for depodzolization. *Soil Science* 163: 482–497.

Basille M, Calenge C, Marboutin É, et al. 2008. Assessing habitat selection using multivariate statistics: Some refinements of the ecological-niche factor analysis. *Ecological Modelling* 211: 233–240.

Behre K-E. 1981. The Interpretation of Anthropogenic Indicators in Pollen Diagrams. *Pollen et Spores* XXIII: 225–245.

Behre KE. 1992. The history of rye cultivation in Europe. *Vegetation History and Archaeobotany* 1: 141–156.

Behre KE. 2007. Evidence for Mesolithic agriculture in and around central Europe? *Vegetation History and Archaeobotany* 16: 203–219.

Belisová N. 2006. Historické záznamy o požárech v Českém Švýcarsku. In *Minulosti Českého Švýcarska. Sborník příspěvků z historického semináře 2006*. Belisová N (eds). 118–136.

Beneš J, Chvojka O. 2007. Archeologie doby kamenné v jižních Čechách: současný stav bádání. In *Archeologie na pomezí*. Chvojka O, Krajíc R (eds). Jihočeské muzeum v Českých Budějovicích: České Budějovice; 9–28.

Benkova VE, Schweingruber FH. 2004. *An anatomy of Russian woods: an atlas for the identification of trees, shrubs, dwarf shrubs and woody lianas from Russia.* Haupt: Bern.

Bennett KD. 2009. Psimpoll and Pscomb Programs for Plotting and Analysis. .

Berger A, Loutre MF. 1991. Insolation values for the climate of the last 10 million years. *Quaternary Science Reviews* 10: 297–317.

Bergeron Y, Gauthier S, Flannigan M, et al. 2004. Fire regimes at the transition between mixed wood and confierous boreal forest in Northwestern Quebec. *Ecology* 85: 1916–1932.

Bergeron Y, Gauthier S, Kafka V, et al. 2001. Natural fire frequency for the eastern Canadian boreal forest: consequences for sustainable forestry. *Canadian Journal of Forest Research* 31: 384–391.

Bergeron Y, Leduc A, Harvey B, et al. 2002. Natural fire regime: a guide for sustainable management of the Canadian boreal forest. *Silva Fennica* 36: 81–95.

Berglund BE, Ralska-Jasiewiczowa M. 2003. *Handbook of the holocene palaeoecology and palaeohydrology.* Blackburn Press: Caldwell.

Bešta T, Novák J, Dreslerová D, et al. 2015. Mid-Holocene history of a central European lake: Lake Komořany, Czech Republic. *Boreas* 44: 563–574.

Beug HJ. 2004. *Leitfaden der Pollenbestimmung für Mitteleuropa und angrenzende Gebiete.* Verlag Dr. Friedrich Pfeil: München.

Binford M. 1990. Calculation and uncertainty analysis of 210Pb dates for PIRLA project lake sediment cores. *Journal of Paleolimnology* 3: .

Birks HJB. 2007. Estimating the amount of compositional change in late-Quaternary pollen-stratigraphical data. *Vegetation History and Archaeobotany* 16: 197–202.

Birks HJB, Birks HH. 2004. The Rise and Fall of Forests. *Science* 305: 484–485.

Bishop RR, Church M, Rowley-conwy PA. 2013. Seeds, fruits and nuts in the Scottish Mesolithic. *Proceedings of the Society of Antiquaries of Scotland* 143: 9–72.

Björkman L, Bradshaw R. 1996. The immigration of Fagus sylvatica L. and Picea abies (L.) Karst. into a natural forest stand in southern Sweden during the last 2000 years. *Journal of Biogeography* 23: 235–244.

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

Blackford JJ. 2000. Charcoal fragments in surface samples following a fire and the implications for interpretation of subfossil charcoal data. *Palaeogeography, Palaeoclimatology, Palaeoecology* 164: 33–42.

Blarquez O, Ali AA, Girardin MP, et al. 2015. Regional paleofire regimes affected by non-uniform climate, vegetation and human drivers. *Scientific Reports* 5: 13356.

Blarquez O, Vannière B, Marlon JR, et al. 2014. Computers & Geosciences paleofire : An R package to analyse sedimentary charcoal records from the Global Charcoal Database to reconstruct past biomass burning $. *Computers and Geosciences* 72: 255–261.

Błońska E, Lasota J, Gruba P. 2016. Effect of temperate forest tree species on soil dehydrogenase and urease activities in relation to other properties of soil derived from loess and glaciofluvial sand. *Ecological Research* 31: 655–664.

Bobek P. 2013. Langfristige Auswirkungen von Waldbränden auf die Wald- vegetation/Dlouhodobý vliv požárů na složení vegetace. In *Historische Waldentwicklung in der Sächsisch-Böhmischen Schweiz/Historický vývoj lesa v Českosaském Švýcarsku.* Seiler U, Wild J (eds). Rhombos-Verlag: Berlin; 5–26.

Bobek P, Šamonil P, Jamrichová E. 2018a. Biotic controls on Holocene fire frequency in a temperate mountain forest, Czech Republic. *Journal of Quaternary Science* 33: 892–904.

Bobek P, Svobodová HS, Werchan B, et al. 2018b. Human-induced changes in fire regime and subsequent alteration of the sandstone landscape of Northern Bohemia (Czech Republic). *The Holocene* 28: 427–443.

Boehner J, Antonic O. 2009. Land-surface parameters specific to topo-climatology. In *Geomorphometry: concepts, software, applications*. Hengl T, Reuter H. (eds). Elsevier: Amsterdam; 195–226.

Bogaard A. 2002. Questioning the relevance of shifting cultivation to Neolithic farming in the loess belt of Europe: Evidence from the Hambach Forest experiment. *Vegetation History and Archaeobotany* 11: 155–168.

Bogaard A. 2005. “Garden agriculture” and the nature of early farming in Europe and the Near East. *World Archaeology* 37: 177–196.

Bogaard A, Fraser R, Heaton THE, et al. 2013. Crop manuring and intensive land management by Europe’s first farmers. *Proceedings of the National Academy of Sciences* 110: 12589–12594.

Bogaard A, Heaton THE, Poulton P, et al. 2007. The impact of manuring on nitrogen isotope ratios in cereals: archaeological implications for reconstruction of diet and crop management practices. *Journal of Archaeological Science* 34: 335–343.

Boivin NL, Zeder MA, Fuller DQ, et al. 2016. Ecological consequences of human niche construction: Examining long-term anthropogenic shaping of global species distributions. *Proceedings of the National Academy of Sciences* 113: 6388–6396.

Bond WJ, Woodward FI, Midgley GF. 2004. The global distribution of ecosystems in a world without fire. *New Phytologist* 165: 525–538.

Boublík K, Lepší M, Lepší P. 2009. Vegetace Národní přírodní rezervace Žofínský prales v Novohradských horách. *Silva Gabreta* 15: 121–142.

ter Braak C, Šmilauer P. 2012. *Canoco Reference Manual and User’s Guide: Software for Ordination (version 5.0).* Microcomputer power, Itaca:

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

Brown KJ, Giesecke T. 2014. Holocene fire disturbance in the boreal forest of central Sweden. *Boreas* 43: 639–651.

Brown T. 1997. Clearances and Clearings: Deforestation in Mesolithic/Neolithic Britain. *Oxford Journal of Archaeology* 16: 133–146.

Brun C. 2010. Anthropogenic indicators in pollen diagrams in eastern France: a critical review. *Vegetation History and Archaeobotany* 20: 135–142.

Bruthans J, Soukup J, Vaculikova J, et al. 2014. Sandstone landforms shaped by negative feedback between stress and erosion. *Nature Geoscience* 7: 597–601.

Buntgen U, Tegel W, Nicolussi K, et al. 2011. 2500 Years of European Climate Variability and Human Susceptibility. *Science* 331: 578–582.

Buurman P, Jongmans AG. 2005. Podzolisation and soil organic matter dynamics. *Geoderma* 125: 71–83.

Calenge C. 2006. The package “adehabitat” for the R software: A tool for the analysis of space and habitat use by animals. *Ecological Modelling* 197: 516–519.

Carcaillet C. 1998. A spatially precise study of Holocene fire history, climate and human impact within the Maurienne valley, North French Alps. *Journal of Ecology* 86: 384–396.

Carcaillet C. 2001. Are Holocene wood-charcoal fragments stratified in alpine and subalpine soils? Evidence from the Alps based on AMS 14 C dates. *The Holocene* 11: 231–242.

Carcaillet C, Almquist H, Asnong H, et al. 2002. Holocene biomass burning and global dynamics of the carbon cycle. *Chemosphere* 49: 845–863.

Carcaillet C, Bergman I, Delorme S, et al. 2007. Long-Term Fire Frequency Not Linked to Prehistoric Occupations in Northern Swedish Boreal Forest. *Ecology* 88: 465–477.

Carcaillet C, Thinon M. 1996. Pedoanthracological contribution to the study of the evolution of the upper treeline in the Maurienne valley (North French Alps): methodology and preliminary data. *Review of Palaeobotany and Palynology* 91: 399–416.

Carrión JS, Fernández S. 2009. The survival of the “natural potential vegetation” concept (or the power of tradition). *Journal of Biogeography* 36: 2202–2203.

Carter VA, Chiverrell RC, Clear JL, et al. 2018a. Quantitative palynology informing conservation ecology in the

Bohemian/Bavarian Forests of Central Europe. *Frontiers in Plant Science* 8: .

Carter VA, Moravcová A, Chiverrell RC, et al. 2018b. Holocene-scale fire dynamics of central European temperate spruce-beech forests. *Quaternary Science Reviews* 191: 15–30.

Certini G. 2005. Effects of fire on properties of forest soils: a review. *Oecologia* 143: 1–10.

Chytrý M. 2012. Vegetation of the Czech Republic: diversity, ecology, history. *Preslia* 84: 427–504.

Chytrý M, Horsák M, Danihelka J, et al. 2019. A modern analogue of the Pleistocene steppe-tundra ecosystem in southern Siberia. *Boreas* 48: 36–56.

Clark J. 1995. Particle-Size Evidence for Source Areas of Charcoal Accumulation in Late Holocene Sediments of Eastern North American Lakes. *Quaternary Research* 43: 80–89.

Clark JS. 1988a. Stratigraphic charcoal analysis on petrographic thin sections: Application to fire history in northwestern Minnesota. *Quaternary Research* 30: 81–91.

Clark JS. 1988b. Particle motion and the theory of charcoal analysis: Source area, transport, deposition, and sampling. *Quaternary Research* 30: 67–80.

Clark JS, Merkt J, Muller H. 1989. Post-Glacial Fire, Vegetation, and Human History on the Northern Alpine Forelands, South-Western Germany. *The Journal of Ecology* 77: 897.

Clear JL, Molinari C, Bradshaw RHW. 2014. Holocene fire in Fennoscandia and Denmark. *International Journal of Wildland Fire* 23: 781–789.

Colwell RK, Chao A, Gotelli NJ, et al. 2012. Models and estimators linking individual-based and sample-based rarefaction, extrapolation and comparison of assemblages. *Journal of Plant Ecology* 5: 3–21.

Conedera M, Tinner W, Neff C, et al. 2009. Reconstructing past fire regimes: methods, applications, and relevance to fire management and conservation. *Quaternary Science Reviews* 28: 555–576.

Corenblit D, Baas ACW, Bornette G, et al. 2011. Feedbacks between geomorphology and biota controlling Earth surface processes and landforms: A review of foundation concepts and current understandings. *Earth-Science Reviews* 106: 307–331.

Czimczik CI, Masiello CA. 2007. Controls on black carbon storage in soils. *Global Biogeochemical Cycles* 21: 8.

Daniau A-L, Bartlein PJ, Harrison SP, et al. 2012. Predictability of biomass burning in response to climate changes. *Global Biogeochemical Cycles* 26: .

Daniau A-L, Harrison SP, Bartlein PJ. 2010a. Fire regimes during the Last Glacial. *Quaternary Science Reviews* 29: 2918–2930.

Daniau A, D'Errico F, Sánchez Goñi MF. 2010b. Testing the Hypothesis of Fire Use for Ecosystem Management by Neanderthal and Upper Palaeolithic Modern Human Populations. *PLoS ONE* 5: e9157.

Davis OK, Shafer DS. 2006. Sporormiella fungal spores, a palynological means of detecting herbivore density. *Palaeogeography, Palaeoclimatology, Palaeoecology* 237: 40–50.

Delarze R, Caldelari D, Hainard P. 1992. Effects of Fire on Forest Dynamics in Southern Switzerland Effects of fire on forest dynamics in southern Switzerland. *Journal of Vegetation Science* 3: 55–60.

Demján P, Dreslerová D. 2016. Modelling distribution of archaeological settlement evidence based on heterogeneous spatial and temporal data. *Journal of Archaeological Science* 69: 100–109.

Dietre B, Walser C, Kofler W, et al. 2017. Neolithic to Bronze Age (4850–3450 cal. BP) fire management of the Alpine Lower Engadine landscape (Switzerland) to establish pastures and cereal fields. *The Holocene* 27: 181–196.

Dietze E, Theuerkauf M, Bloom K, et al. 2018. Holocene fire activity during low-natural flammability periods reveals scale-dependent cultural human-fire relationships in Europe. *Quaternary Science Reviews* 201: 44–56.

Divišová M, Šída P. 2015. Plant use in the Mesolithic period . Archaeobotanical data from the Czech Republic in a European context – a review. *Interdisciplinaria Archaeologica Natural Sciences in Archaeology* VI: 95–106.

Dreslerová D. 2012. Human Response to Potential Robust Climate Change around 5500 cal BP in the Territory of Bohemia (the Czech Republic). *Interdisciplinaria Archaeologica Natural Sciences in Archaeology* 3: 43–55.

Dreslerová D, Kočár P. 2013a. Trends in cereal cultivation in the Czech Republic from the Neolithic to the Migration period (5500 B.C.-A.D. 580). *Vegetation History and Archaeobotany* 22: 257–268.

Dreslerová D, Kočár P, Chuman T, et al. 2013b. Variety in cereal cultivation in the Late Bronze and Early Iron Ages in relation to environmental conditions. *Journal of Archaeological Science* 40: 1988–2000.

Dudová L, Hájková P, Opravilová V, et al. 2014. Holocene history and environmental reconstruction of a Hercynian mire and surrounding mountain landscape based on multiple proxies. *Quaternary Research* 82: 107–120.

Duffin KII, Gillson L, Willis KJJ. 2008. Testing the sensitivity of charcoal as an indicator of fire events in savanna environments: quantitative predictions of fire proximity, area and intensity. *The Holocene* 18: 279–291.

Dunnette P V., Higuera PE, Mclauchlan KK, et al. 2014. Biogeochemical impacts of wildfires over four millennia in a Rocky Mountain subalpine watershed. *New Phytologist* 203: 900–912.

Ehrmann O, Biester H, Bogenrieder A, et al. 2014. Fifteen years of the Forchtenberg experiment-results and implications for the understanding of Neolithic land use. *Vegetation History and Archaeobotany* 23: 5–18.

Eigner J, Kapustka K, Parkman M, et al. 2017. Mezolitické osídlení Šumavy pohledem studia surovin kamenných artefaktů z lokalit Javoří Pila 1 a Nová Pec [Mesolithic occupation of the Bohemian Forest according to the study of raw materials for lithic production from the sites of Javoří Pila 1 and Nová. *Silva Gabreta* 23: 33–44.

Elith J, H. Graham C, P. Anderson R, et al. 2006. Novel methods improve prediction of species' distributions from occurrence data. *Ecography* 29: 129–151.

Ellenberg H. 1996. *Vegetation Mitteleuropas mit den Alpen in ökologischer, dynamischer und historischer Sicht.* Ulmer: Stuttgart.

Ellenberg H. 2009. *Vegetation Ecology of Central Europe.* Cambridge University Press: Cambridge.

Engel Z, Nývlt D, Křížek M, et al. 2010. Sedimentary evidence of landscape and climate history since the end of MIS 3 in the Krkonoše Mountains, Czech Republic. *Quaternary Science Reviews* 29: 913–927.

Engelmark O. 1987. Fire history correlations to forest type and topography in nothern Siberia. *Annales Botanici Fennici* 24: 317–324.

Engelmark O. 1993. Early Post-Fire Tree Regeneration in a Picea-Vaccinium Forest in Northern Sweden. *Journal of Vegetation Science* 4: 791–794.

ESRI. 2007. *ArcGIS Desktop: Release 9.2.* Environmental Systems Research Institute: Redlands, CA.

Faegri K, Iversen J. 1989. *Textbook of pollen analysis.* John Wiley & Sons: Chichester.

Ferguson TA. 1979. *Productivity and Predictability of Resource Yield: Aboriginal Controlled Burning in the Boreal Forest.* University of Alberta,

Feurdean A, Florescu G, Vannière B, et al. 2017a. Fire has been an important driver of forest dynamics in the Carpathian Mountains during the Holocene. *Forest Ecology and Management* 389: 15–26.

Feurdean A, Liakka J, Vannière B, et al. 2013a. 12,000-Years of fire regime drivers in the lowlands of Transylvania (Central-Eastern Europe): a data-model approach. *Quaternary Science Reviews* 81: 48–61.

Feurdean A, Parr CL, Tanţău I, et al. 2013b. Biodiversity variability across elevations in the Carpathians: Parallel change with landscape openness and land use. *The Holocene* 23: 869–881.

Feurdean A, Perşoiu A, Tanţău I, et al. 2014. Climate variability and associated vegetation response throughout Central and Eastern Europe (CEE) between 60 and 8 ka. *Quaternary Science Reviews* 106: 206–224.

Feurdean A, Spessa A, Magyari EK, et al. 2012. Trends in biomass burning in the Carpathian region over the last 15,000 years. *Quaternary Science Reviews* 45: 111–125.

Feurdean A, Veski S, Florescu G, et al. 2017b. Broadleaf deciduous forest counterbalanced the direct effect of climate on Holocene fire regime in hemiboreal/boreal region (NE Europe). *Quaternary Science Reviews* 169: 378–390.

Feurdean AN, Willis KJ, Astaloş C. 2009. Legacy of the past land-use changes and management on the "natural" upland forest composition in the Apuseni Natural Park, Romania. *Holocene* 19: 967–981.

Finsinger W, Giesecke T, Brewer S, et al. 2017. Emergence patterns of novelty in European vegetation assemblages over the past 15 000 years. *Ecology Letters* 20: 336–346.

Finsinger W, Tinner W, van der Knaap WO, et al. 2006. The expansion of hazel (Corylus avellana L.) in the southern Alps: a key for understanding its early Holocene history in Europe? *Quaternary Science Reviews* 25: 612–631.

Firbas F. 1949. *Spät- und nacheiszeitliche Waldgeschichte Mitteleuropas nördlich der Alpen, Erstrer Band: Allgemeine*

Waldgeschichte. Verlag von Gustav Fischer in Jena: Jena.

Fischer A, Fischer HS, Kopecký M, et al. 2015a. Small changes in species composition despite stand-replacing bark beetle outbreak in Picea abies mountain forests. *Canadian Journal of Forest Research* 45: 1164–1171.

Fischer H, Schüpbach S, Gfeller G, et al. 2015b. Millennial changes in North American wildfire and soil activity over the last glacial cycle. *Nature Geoscience* 8: 723–727.

Flannigan M., Stocks B., Wotton B. 2000. Climate change and forest fires. *Science of The Total Environment* 262: 221–229.

Florescu G, Vannière B, Feurdean A. 2018. Exploring the influence of local controls on fire activity using multiple charcoal records from northern Romanian Carpathians. *Quaternary International* 1–17.

Fregeau M, Payette S, Grondin P. 2015. Fire history of the central boreal forest in eastern North America reveals stability since the mid-Holocene. *The Holocene* 25: 1912–1922.

Friedrich M, Boeren I, Remmele S, et al. 2002. A Late-Glacial forest in the lignite mine of Reichwalde – An interdisciplinary project. In *TRACE – Tree Rings in Archaeology, Climatology and Ecology, Proceedings of the Dendrosymposium 2002*. Bonn/Jülich; 90–91.

Gardner JJ, Whitlock C. 2001. Charcoal accumulation following a recent fire in the Cascade Range, northwestern USA, and its relevance for fire-history studies. *Holocene* 11: 541–549.

Gavin D. 2006. Estimation of inbuilt age in radiocarbon ages of soil charcoal for fire history studies. *Radiocarbon* 43: 27–44.

Gavin DG, Brubaker LB, Lertzman KP. 2003a. Holocene fire history of a coastal temperate rain forest based on soil charcoal radiocarbon dates. *Ecology* 84: 186–201.

Gavin DG, Brubaker LB, Lertzman KP. 2003b. An 1800-year record of the spatial and temporal distribution of fire from the west coast of Vancouver Island, Canada. *Canadian Journal of Forest Research* 33: 573–586.

Gavin DG, Hu FS, Lertzman K, et al. 2006. Weak climatic control of stand-scale fire history during the late holocene. *Ecology* 87: 1722–32.

van Geel B. 1978. A palaeoecological study of holocene peat bog sections in Germany and The Netherlands, based on the analysis of pollen, spores and macro- and microscopic remains of fungi, algae, cormophytes and animals. *Review of Palaeobotany and Palynology* 25: 1–120.

van Geel B, Andersen ST. 1988. Fossil ascopores of the parasitic fungus Ustulina deusta in Eemian deposits in Denmark. *Review of Palaeobotany and Palynology* 56: 89–93.

van Geel B, Aptroot A. 2006. Fossil ascomycetes in Quaternary deposits. *Nova Hedwigia* 82: 313–329.

van Geel B, Bohncke SJP, Dee H. 1980. A palaeoecological study of an upper late glacial and holocene sequence from “de borchert”, The Netherlands. *Review of Palaeobotany and Palynology* 31: 367–448.

van Geel B, Bos JM, Pals JP. 1983. Archaeological and palaeoecological aspects of a medieval house terp in a reclaimed raiseg bog area in North Holland. *Ber. Rijksd. Oudheidkd. Bodemonderz* 33: 419–444.

Van Geel B, Coope GR, Van Der Hammen T. 1989. Palaeoecology and stratigraphy of the lateglacial type section at Usselo (the Netherlands). *Review of Palaeobotany and Palynology* 60: 25–129.

van Geel B, Engels S, Martin-Puertas C, et al. 2013. Ascospores of the parasitic fungus Kretzschmaria deusta as rainstorm indicators during a late Holocene beech-forest phase around lake Meerfelder Maar, Germany. *Journal of Paleolimnology* 50: 33–40.

van Geel B, Klink AG, Pals JP, et al. 1986. An Upper Eemian lake deposit from Twente, eastern Netherlands. *Review of Palaeobotany and Palynology* 47: 31–61.

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

Gill AM. 1975. Fire and The Australian Flora: A Review. *Australian Forestry* 38: 4–25.

Girardin MP, Ali AA, Carcaillet C, et al. 2013. Vegetation limits the impact of a warm climate on boreal wildfires. *New Phytologist* 199: 1001–1011.

Girardin MP, Terrier A. 2015. Mitigating risks of future wildfires by management of the forest composition: an analysis of the offsetting potential through boreal Canada. *Climatic Change* 130: 587–601.

Gobet E, Tinner W, Hochuli PA, et al. 2003. Middle to Late Holocene vegetation history of the Upper Engadine (Swiss

Alps): the role of man and fire. *Vegetation History and Archaeobotany* 12: 143–163.

Goldammer JG, Page H. 2000. *Fire History of Central Europe : Implications for Prescribed Burning in Landscape Management and Nature Conservation.* Global Fire Monitoring Center (GFMC), Fire Ecology Research Group:

Goring S, Williams JW, Blois JL, et al. 2012. Deposition times in the northeastern United States during the Holocene: Establishing valid priors for Bayesian age models. *Quaternary Science Reviews* 48: 54–60.

Gradmann R. 1906. Beziehungen zwischen Pflanzengeographie und Siedlungsgeschichte. *Geographische Zeitschrift* 12: 305–325.

Gradmann R. 1933. Die steppenheidetheorie. *Geographische Zeitschrift* 39: 265–278.

von Grafenstein U. 1999. A Mid-European Decadal Isotope-Climate Record from 15,500 to 5000 Years B.P. *Science* 284: 1654–1657.

Grimm EC. 1987. CONISS: a FORTRAN 77 program for stratigraphically constrained cluster analysis by the method of incremental sum of squares. *Computers & Geosciences* 13: 13–35.

Grimm EC. 2011. *Tilia software 1.7.16.* Illinois State Museum, Research and Collection Center: Springfield.

Gromtsev A. 2002. Natural Disturbance Dynamics in the Boreal Forests of European Russia : a Review. *Silva Fennica* 36: 41–55.

de Groot WJ, Cantin AS, Flannigan MD, et al. 2013. A comparison of Canadian and Russian boreal forest fire regimes. *Forest Ecology and Management* 294: 23–34.

Guilderson TP. 2005. The Boon and Bane of Radiocarbon Dating. *Science* 307: 362–364.

Guisan A, Edwards TC, Hastie T. 2002. Generalized linear and generalized additive models in studies of species distributions: setting the scene. *Ecological Modelling* 157: 89–100.

Guisan A, Zimmermann NE. 2000. Predictive habitat distribution models in ecology. *Ecological Modelling* 135: 147–186.

Haas JN, Richoz I, Tinner W, et al. 1998. Synchronous Holocene climatic oscillations recorded on the Swiss Plateau and at timberline in the Alps. *The Holocene* 8: 301–309.

Hajnalová M. 1990. *Geschichte des an archgobotanischen Funden dokumentierten Anbaues mancher Getreidearten in der Slowakei.* Nitra,

Haliuc A, Hutchinson SM, Florescu G, et al. 2016. The role of fire in landscape dynamics: An example of two sediment records from the Rodna Mountains, northern Romanian Carpathians. *Catena* 137: 432–440.

Hane J. 1992. *Untersuchungen zur spät- und postglazialen Vegetationsgeschichte im nordöstlichen Bayern.* Bayerisches Vogtland, Fichtelgebirge, Steinwald:

Härtel H, Cílek V, Herben T, et al. 2007. *Sandstone landscapes.* Academia: Praha.

Hejcman M, Hejcmanová P, Pavlů V, et al. 2013. Origin and history of grasslands in Central Europe - a review. *Grass and Forage Science* 68: 345–363.

Heyerdahl EK, Brubaker LB, Agee JK. 2001. Spatial Controls of Historical Fire Regimes: A Multiscale Example from the Interior West, USA. *Ecology* 82: 660–678.

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

Higuera PE, Brubaker LB, Anderson PM, et al. 2009. Vegetation mediated the impacts of postglacial climate change on fire regimes in the south-central Brooks Range, Alaska. *Ecological Monographs* 79: 201–219.

Higuera PE, Gavin DG, Bartlein PJ, et al. 2010. Peak detection in sediment–charcoal records: impacts of alternative data analysis methods on fire-history interpretations. *International Journal of Wildland Fire* 19: 996.

Higuera PE, Sprugel DG, Brubaker LB. 2005. Reconstructing fire regimes with charcoal from small-hollow sediments: a calibration with tree-ring records of fire. *Holocene* 15: 238–251.

Higuera PE, Whitlock C, Gage JA. 2011. Linking tree-ring and sediment-charcoal records to reconstruct fire occurrence and area burned in subalpine forests of yellowstone National Park, USA. *Holocene* 21: 327–341.

Hill MO, Gauch HG. 1980. Detrended correspondence analysis: An improved ordination technique. *Vegetatio* 42: 47–58.

Hill T, Lewicki P. 2007. *STATISTICS: Methods and Applications.* StatSoft: Tulsa.

Hirzel AH, Hausser J, Chessel D, et al. 2002. Ecological-Niche Factor Analysis: How to Compute Habitat-Suitability Maps without Absence Data? *Ecology* 83: 2027.

Hörnberg G, Josefsson T, DeLuca TH, et al. 2018. Anthropogenic use of fire led to degraded Scots pine-lichen forest in northern Sweden. *Anthropocene* .

Hörnberg G, Ohlson M, Zackrisson O. 2014. Stand dynamics, regeneration patterns and long-term continuity in boreal old-growth Picea abies swamp-forests. *Journal of Vegetation Science* 6: 291–298.

Hörnberg G, Staland H, Nordström E-M, et al. 2012. Fire as an important factor for the genesis of boreal Picea abies swamp forests in Fennoscandia. *The Holocene* 22: 203–214.

Hošek J, Pokorný P, Kubov V, et al. 2014. Late glacial climatic and environmental changes in eastern-central Europe: Correlation of multiple biotic and abiotic proxies from the Lake Švarcenberk, Czech Republic. *Palaeogeography, Palaeoclimatology, Palaeoecology* 396: 155–172.

Hoss JA, Lafon CW, Grissino-Mayer HD, et al. 2008. Fire History of a Temperate Forest with an Endemic Fire-Dependent Herb. *Physical Geography* 29: 424–441.

Houfková P, Bešta T, Bernardová A, et al. 2017. Holocene climatic events linked to environmental changes at Lake Komořany Basin, Czech Republic. *The Holocene* 27: 1132–1145.

Hu FS, Higuera PE, Duffy P, et al. 2015. Arctic tundra fires: natural variability and responses to climate change. *Frontiers in Ecology and the Environment* 13: 369–377.

Huntley B. 1993. Rapid early-Holocene migration and high abundance of hazel (Corylus avellana L.): alternative hypotheses. In *Climate Change and Human Impact on the Landscape*. Springer Netherlands: Dordrecht; 205–215.

Iniguez JM, Swetnam TW, Yool SR. 2008. Topography affected landscape fire history patterns in southern Arizona, USA. *Forest Ecology and Management* 256: 295–303.

Innes JB, Blackford JJ, Rowley-Conwy P a. 2013. Late Mesolithic and early Neolithic forest disturbance: a high resolution palaeoecological test of human impact hypotheses. *Quaternary Science Reviews* 77: 80–100.

Innes JB, Blackford JJ, Simmons IG. 2004. Testing the integrity of fine spatial resolution palaeoecological records: microcharcoal data from near-duplicate peat profiles from the North York Moors, UK. *Palaeogeography, Palaeoclimatology, Palaeoecology* 214: 295–307.

Iversen J. 1956. Forest Clearance in the Stone Age. *Scientific American* 194: 36–41.

Jacobi RM, Tallis JH, Mellars PA. 1976. The Southern Pennine Mesolithic and the ecological record. *Journal of Archaeological Science* 3: 307–320.

Jacobson GL, Grimm EC. 1986. A Numerical Analysis of Holocene Forest and Prairie Vegetation in Central Minnesota. *Ecology* 67: 958.

Jacomet S, Ebersbach R, Akeret Ö, et al. 2016. On-site data cast doubts on the hypothesis of shifting cultivation in the late Neolithic (c. 4300–2400 cal. BC): Landscape management as an alternative paradigm. *The Holocene* 26: 1858–1874.

James SR, Dennell RW, Gilbert AS, et al. 1989. Hominid Use of Fire in the Lower and Middle Pleistocene: A Review of the Evidence. *Current Anthropology* 30: 1–26.

Jamrichová E, Potůčkova A, Horsák M, et al. 2014. Early occurrence of temperate oak-dominated forest in the northern part of the Little Hungarian Plain, SW Slovakia. *The Holocene* 24: 1810–1824.

Jankovská V. 2006a. Late Glacial and Holocene history of Plešné Lake and its surrounding landscape based on pollen and palaeoalgological analyses. *Biologia* 61: S371–S385.

Jankovská V, Komárek J. 1982. Das Vorkommen einiger Chlorokokkalalgen in böhmischen Spätglazial und Postglazial. *Folia Geobotanica et Phytotaxonomica* 17: 165–195.

Jankovská V, Kuneš P, Van Der Knaap WO. 2007. 1. Fláje-Kiefern (Krušné Hory Mountains): Late Glacial and Holocene vegetation development. *Grana* 46: 214–216.

Jankovská Z. 2006b. *Lesní požáry v ČR (1992-2004) – příčiny, dopady a prevence.* Masaryk University in Brno,

Janská V, Jiménez-Alfaro B, Chytrý M, et al. 2017. Palaeodistribution modelling of European vegetation types at the Last Glacial Maximum using modern analogues from Siberia: Prospects and limitations. *Quaternary Science Reviews* 159: 103–115.

Jenč P, Peša V. 2003. Využívání severočeských převisů v pravěkém a historickém. In *Mezolit severních Čech. Komplexní výzkum skalních převisů na Českolipsku a Děčínsku, 1978-2003*. Svoboda J (eds). Brno; 97–104.

Jenč P, Peša V. 2013. Markvartická kotlina v Českém středohoří: příspěvek ke struktuře pravěkého osídlení podhorských oblastí na severu Čech. *Archeologie ve středních Čechách* 17: 555–573.

Johnson DL, Keller EA, Rockwell TK. 1990. Dynamic Pedogenesis: New Views on Some Key Soil Concepts, and a Model for Interpreting Quaternary Soils. *Quaternary Research* 33: 306–319.

Johnstone JF, Chapin FS. 2006. Fire interval effects on successional trajectory in boreal forests of northwest Canada. *Ecosystems* 9: 268–277.

Kalis AJ, Merkt J, Wunderlich J. 2003. Environmental changes during the Holocene climatic optimum in central Europe - Human impact and natural causes. *Quaternary Science Reviews* 22: 33–79.

Kane VR, Lutz J a., Alina Cansler C, et al. 2015. Water balance and topography predict fire and forest structure patterns. *Forest Ecology and Management* 338: 1–13.

Kaplan JO, Pfeiffer M, Kolen JCA, et al. 2016. Large scale anthropogenic reduction of forest cover in last glacial maximum Europe. *PLoS ONE* 11: 1–17.

Kappenberg A, Lehndorff E, Pickarski N, et al. 2019. Solar controls of fire events during the past 600,000 years. *Quaternary Science Reviews* 208: 97–104.

Keeley JE, Pausas JG, Rundel PW, et al. 2011. Fire as an evolutionary pressure shaping plant traits. *Trends in Plant Science* 16: 406–411.

Keeley JE, Rundel PW. 2005. Fire and the Miocene expansion of C4 grasslands. *Ecology Letters* 8: 683–690.

Kelly R, Chipman ML, Higuera PE, et al. 2013. Recent burning of boreal forests exceeds fire regime limits of the past 10,000 years. *Proceedings of the National Academy of Sciences* 110: 13055–13060.

Kelly RF, Higuera PE, Barrett CM, et al. 2011. A signal-to-noise index to quantify the potential for peak detection in sediment–charcoal records. *Quaternary Research* 75: 11–17.

Kirchgeorg T, Schüpbach S, Kehrwald N, et al. 2014. Method for the determination of specific molecular markers of biomass burning in lake sediments. *Organic Geochemistry* 71: 1–6.

Knicker H. 2011. Pyrogenic organic matter in soil: Its origin and occurrence, its chemistry and survival in soil environments. *Quaternary International* 243: 251–263.

Knipping M. 1989. *Zur spät- und postglazialen Vegetationsgeschichte des Oberpfälzer Waldes.* J. Cramer, Borntraeger: Berlin Stuttgart.

Komárek J, Jankovská V. 2001. Review of the Green Algal Genus Pediastrum; Implication for Pollenanalytical Research. *Bibliotheca Phycologica* 108: 1–127.

Körner C. 1998. A re-assessment of high elevation treeline positions and their explanation. *Oecologia* 115: 445–459.

Kozáková R, Pokorný P, Peša V, et al. 2015. Prehistoric human impact in the mountains of Bohemia. Do pollen and archaeological data support the traditional scenario of a prehistoric "wilderness"? *Review of Palaeobotany and Palynology* 220: 29–43.

Krawchuk MA, Moritz MA. 2011. Constraints on global fire activity vary across a resource gradient. *Ecology* 92: 121–132.

Kreuz A. 2008. Closed forest or open woodland as natural vegetation in the surroundings of Linearbandkeramik settlements? *Vegetation History and Archaeobotany* 17: 51–64.

Kula E, Jankovská Z. 2013. Forest fires and their causes in the Czech Republic (1992 – 2004). *Journal of Forest Science* 59: 41–53.

Kuna M, Danielisová A. 2014. *Archaeological atlas of Bohemia: selected sites from prehistory to the 20th century.* Institute of Archaeology, Praha - Academia: Praha.

Kuneš P, Abraham V, Kovarik O, et al. 2009. Czech Quaternary Palynological Database – PALYCZ. *Preslia (Prague)* 81: 209–238.

Kuneš P, Jankovská V. 2000. Outline of Late Glacial and Holocene Vegetation in a Landscape with Strong Geomorphological Gradients. *Geolines* 11: 112–114.

Kuneš P, Odgaard BV, Gaillard M-J. 2011. Soil phosphorus as a control of productivity and openness in temperate interglacial forest ecosystems. *Journal of Biogeography* 38: 2150–2164.

Kuneš P, Pelánková B, Chytrý M, et al. 2008a. Interpretation of the last-glacial vegetation of eastern-central Europe using modern analogues from southern Siberia. *Journal of Biogeography* 35: 2223–2236.

Kuneš P, Pokorný P, Šída P. 2008b. Detection of the impact of early Holocene hunter-gatherers on vegetation in the Czech Republic, using multivariate analysis of pollen data. *Vegetation History and Archaeobotany* 17: 269–287.

Kuneš P, Svobodov H, Macek M, et al. 2015. The origin of grasslands in the temperate forest zone of east-central Europe : long-term legacy of climate and human impact b. 116: 15–27.

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

Küster H. 1997. The role of farming in the postglacial expansion of beech and hornbeam in the oak woodlands of central Europe. *The Holocene* 7: 239–242.

Kuuluvainen T. 2002. Disturbance dynamics in boreal forests: defining the ecological basis of restoration and management of biodiversity. *Silva Fennica* 36: 5–11.

de Lafontaine G, Payette S. 2011a. Shifting zonal patterns of the southern boreal forest in eastern Canada associated with changing fire regime during the Holocene. *Quaternary Science Reviews* 30: 867–875.

de Lafontaine G, Payette S. 2011b. Long-term fire and forest history of subalpine balsam fir (Abies balsamea) and white spruce (Picea glauca) stands in eastern Canada inferred from soil charcoal analysis. *The Holocene* 22: 191–201.

Lang G. 1994. *Quartäre Vegetationsgeschichte Europas. Methoden und Ergebnisse.* Gustav Fischer Verlag: Jena, Stuttgart, New York.

Lee S, Wolberg G, Shin SY. 1997. Scattered data interpolation with multilevel B-splines. *IEEE Transactions on Visualization and Computer Graphics* 3: 228–244.

Legendre P, Legendre L. 2012. *Numerical Ecology.* Elsevier:

Leuschner C, Ellenberg H. 2017. *Ecology of Central European Forests.* Springer International Publishing: Cham.

Leys B, Carcaillet C. 2016a. Subalpine fires: the roles of vegetation, climate and, ultimately, land uses. *Climatic Change* 135: 683–697.

Leys B, Carcaillet C, Blarquez O, et al. 2014. Resistance of mixed subalpine forest to fire frequency changes: the ecological function of dwarf pine (Pinus mugo ssp. mugo). *Quaternary Science Reviews* 90: 60–68.

Leys B, Higuera PE, McLauchlan KK, et al. 2016b. Wildfires and geochemical change in a subalpine forest over the past six millennia. *Environmental Research Letters* 11: 125003.

Lisitsyna O V., Giesecke T, Hicks S. 2011. Exploring pollen percentage threshold values as an indication for the regional presence of major European trees. *Review of Palaeobotany and Palynology* 166: 311–324.

Litt T, Brauer A, Goslar T, et al. 2001. Correlation and synchronisation of Lateglacial continental sequences in northern central Europe based on annually laminated lacustrine sediments. *Quaternary Science Reviews* 20: 1233–1249.

Litt T, Schölzel C, Kühl N, et al. 2009. Vegetation and climate history in the Westeifel Volcanic Field (Germany) during the past 11 000 years based on annually laminated lacustrine maar sediments. *Boreas* 38: 679–690.

Lloret F, Estevan H, Vayreda J, et al. 2005. Fire regenerative syndromes of forest woody species across fire and climatic gradients. *Oecologia* 146: 461–468.

Long CJ, Whitlock C, Bartlein PJ, et al. 1998. A 9000-year fire history from the Oregon Coast Range, based on a high-resolution charcoal study. *Canadian Journal of Forest Research* 28: 774–787.

Lotter AF, Ammann B, Sturm M. 1992. Rates of change and chronological problems during the late-glacial period. *Climate Dynamics* 6: 233–239.

Ložek V. 1997. Nálezy z pískovcových převisů a otázka degradace krajiny v mladším pravěku v širších souvislostech. *Ochrana přírody* 52: 146–148.

Ložek V. 1998. Late Bronze Age environmental collapse in the sandstone areas of northern Bohemia. In *Mensch und Umwelt in der Bronzezeit Europas*. B H (eds). Oetker-Voges-Verlag: Kiel; 57–60.

Lundström US, van Breemen N, Bain D. 2000. The podzolization process. A review. *Geoderma* 94: 91–107.

Lynch JA, Clark JS, Stocks BJ. 2004. Charcoal production, dispersal, and deposition from the Fort Providence experimental fire: interpreting fire regimes from charcoal records in boreal forests. *Canadian Journal of Forest Research* 34: 1642–1656.

Macklin MG, Johnstone E, Lewin J. 2005. Pervasive and long-term forcing of Holocene river instability and flooding in Great Britain by centennial-scale climate change. *The Holocene* 15: 937–943.

Magny M. 2004. Holocene climate variability as reflected by mid-European lake-level fluctuations and its probable impact on prehistoric human settlements. *Quaternary International* 113: 65–79.

Magny M, Bégeot C, Guiot J, et al. 2003. Contrasting patterns of hydrological changes in europe in response to holocene climate cooling phases. *Quaternary Science Reviews* 22: 1589–1596.

Marcisz K, Gałka M, Pietrala P, et al. 2017. Fire activity and hydrological dynamics in the past 5700 years reconstructed from Sphagnum peatlands along the oceanic–continental climatic gradient in northern Poland. *Quaternary Science Reviews* 177: 145–157.

Marlon J, Bartlein PJ, Whitlock C. 2006. Fire-fuel-climate linkages in the northwestern USA during the Holocene. *The Holocene* 16: 1059–1071.

Marlon JR, Bartlein PJ, Daniau A-L, et al. 2013. Global biomass burning: a synthesis and review of Holocene paleofire records and their controls. *Quaternary Science Reviews* 65: 5–25.

Marlon JR, Bartlein PJ, Gavin DG, et al. 2012. Long-term perspective on wildfires in the western USA. *Proceedings of the National Academy of Sciences of the United States of America* 109: E535-43.

Mason SLR. 2000. Fire and Mesolithic subsistence — managing oaks for acorns in northwest Europe ? *Palaeogeography, Palaeoclimatology, Palaeoecology* 164: 139–150.

McWethy DB, Higuera PE, Whitlock C, et al. 2013. A conceptual framework for predicting temperate ecosystem sensitivity to human impacts on fire regimes. *Global Ecology and Biogeography* 22: 900–912.

Mellars P. 1976. Fire Ecology, Animal Populations and Man: a Study of some Ecological Relationships in Prehistory. *Proceedings of the Prehistoric Society* 42: 15–45.

Meyer GA, College M. 1995. Fire and alluvial chronology in Yellowstone National Park : Climatic and intrinsic controls on Holocene geomorphic processes. *Geological Society of America Bulletin* 107: 1211–1230.

Meysman FJR, Middelburg JJ, Heip CHR. 2006. Bioturbation: a fresh look at Darwin's last idea. *Trends in Ecology and Evolution* 21: 688–695.

Michéli E et al. 2007. *World Reference Base for Soil Resources 2006, First Update 2007 World Soil Resources Reports No 103.* FAO: Rome.

Migoń P, Duszyński F, Goudie A. 2017. Rock cities and ruiniform relief: Forms – processes – terminology. *Earth-Science Reviews* 171: 78–104.

Mikuláš R, Adamovič J, Hartel H, et al. 2007. Elbe Sandstones (Czech Republic/Germany). In *Sandstone Landscapes*. Hartel H, Cílek V, Herben T, Jackson A, Williams R (eds). Academia: Prague; 326–328.

Milad M, Schaich H, Bürgi M, et al. 2011. Climate change and nature conservation in Central European forests: A review of consequences, concepts and challenges. *Forest Ecology and Management* 261: 829–843.

Ministry of Agriculture of the Czech Republic. 2018. *Zpráva o stavu lesa a lesního hospodářství České republiky v roce 2017 [Report on the state of forests and forestry in the Czech Republic by 2017].* Ministry of Agriculture of the Czech Republic: Prague.

Miola A. 2012. Tools for non-pollen palynomorphs (NPPs) analysis: A list of Quaternary NPP types and reference literature in english language (1972-2011). *Review of Palaeobotany and Palynology* 186: 142–161.

Molinari C, Bradshaw RHW, Risbøl O, et al. 2005. Long-term vegetational history of a Picea abies stand in south-eastern Norway : Implications for the conservation of biological values. 126: 155–165.

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

Morales-Molino C, García-Antón M. 2014. Vegetation and fire history since the last glacial maximum in an inland area of the western Mediterranean Basin (Northern Iberian Plateau, NW Spain). *Quaternary Research* 81: 63–77.

Morgan P, Hardy CC, Swetnam TW, et al. 2001. Mapping fire regimes across time and space: Understanding coarse and fine-scale fire patterns. *International Journal of Wildland Fire* 10: 329.

Müller J, Bußler H, Goßner M, et al. 2008. The European spruce bark beetle Ips typographus in a national park: From pest to keystone species. *Biodiversity and Conservation* 17: 2979–3001.

Němec A. 1940. Studie o minerální výživě odumírajícího smrkového porostu v polesí Sv. Tomáš na Šumavě. *Lesnická práce* .

Niklasson M, Granstrom A. 2000. Numbers and Sizes of Fires: Long-Term Spatially Explicit Fire History in a Swedish Boreal Landscape. *Ecology* 81: 1484.

Niklasson M, Zin E, Zielonka T, et al. 2010. A 350-year tree-ring fire record from Białowieża Primeval Forest, Poland: implications for Central European lowland fire history. *Journal of Ecology* 98: 1319–1329.

Normand S, Ricklefs RE, Skov F, et al. 2011. Postglacial migration supplements climate in determining plant species ranges in Europe. *Proceedings of the Royal Society B: Biological Sciences* 278: 3644–3653.

Novák J, Abraham V, Houfková P, et al. 2017a. History of the Litovelské Pomoraví woodland (NE Czech Republic): A comparison of archaeo-anthracological, pedoanthracological, and pollen data. *Quaternary International* 1–11.

Novák J, Abraham V, Kočár P, et al. 2017b. Middle- and upper-Holocene woodland history in central Moravia (Czech Republic) reveals biases of pollen and anthracological analysis. *The Holocene* 27: 349–360.

Novák J, Sádlo J, Svobodová-Svitavská H, et al. 2012. Unusual vegetation stability in a lowland pine forest area (Doksy region, Czech Republic). *The Holocene* 22: 947–955.

Novák J, Svoboda J, Šída P, et al. 2015. A charcoal record of Holocene woodland succession from sandstone rock shelters of North Bohemia (Czech Republic). *Quaternary International* 366: 25–36.

Novák J, Trotsiuk V, Sykora O, et al. 2014. Ecology of Tilia sibirica in a continental hemiboreal forest, southern Siberia: An analogue of a glacial refugium of broad-leaved temperate trees? *The Holocene* 24: 908–918.

Ohlson M, Brown KJK, Birks HJB, et al. 2011. Invasion of Norway spruce diversifies the fire regime in boreal European forests. *Journal of Ecology* 99: 395–406.

Ohlson M, Ellingsen VM, del Olmo MV, et al. 2017. Late-Holocene fire history as revealed by size, age and composition of the soil charcoal pool in neighbouring beech and spruce forest landscapes in SE Norway. *The Holocene* 27: 397–403.

Ohlson M, Kasin I, Wist AN, et al. 2013. Size and spatial structure of the soil and lacustrine charcoal pool across a boreal forest watershed. *Quaternary Research* 80: 417–424.

Ohlson M, Korbøl A, Økland RH. 2006. The macroscopic charcoal record in forested boreal peatlands in southeast Norway. *The Holocene* 16: 731–741.

Ohlson M, Tryterud E. 2000. Interpretation of the charcoal record in forest soils: forest fires and their production and deposition of macroscopic charcoal. *The Holocene* 10: 519–525.

Oldfield F, Crowther J. 2007. Establishing fire incidence in temperate soils using magnetic measurements. *Palaeogeography, Palaeoclimatology, Palaeoecology* 249: 362–369.

Opravil E. 2003. Rostlinné makrozbytky. In *Mezolit severních Čech. Komplexní výzkum skalních převisů na Českolipsku a Děčínsku, 1978-2003*. Svoboda J (eds). Archeologický ústav AV ČR Brno,: 38–42.

Oris F, Ali AA, Asselin H, et al. 2014. Charcoal dispersion and deposition in boreal lakes from 3 years of monitoring: Differences between local and regional fires. *Geophysical Research Letters* 41: 6743–6752.

Pals JP, Van Geel B, Delfos A. 1980. Paleoecological studies in the Klokkeweel bog near hoogkarspel (prov. of Noord-Holland). *Review of Palaeobotany and Palynology* 30: 371–418.

Paritsis J, Veblen TT, Holz A. 2014. Positive fire feedbacks contribute to shifts from Nothofagus pumilio forests to fire-prone shrublands in Patagonia. *Journal of Vegetation Science* 26: n/a-n/a.

Pausas JG. 2006. Simulating Mediterranean landscape pattern and vegetation dynamics under different fire regimes. *Plant Ecology* 187: 249–259.

Pausas JG, Keeley JE. 2009. A Burning Story: The Role of Fire in the History of Life. *BioScience* 59: 593–601.

Pausas JG, Paula S. 2012. Fuel shapes the fire-climate relationship: evidence from Mediterranean ecosystems. *Global Ecology and Biogeography* 21: 1074–1082.

Pausas JG, Ribeiro E. 2013. The global fire-productivity relationship. *Global Ecology and Biogeography* 22: 728–736.

Pausas JG, Ribeiro E. 2017. Fire and plant diversity at the global scale. *Global Ecology and Biogeography* 26: 889–897.

Pausas JG, Vallejo VR. 1999. The role of fire in European Mediterranean ecosystems. In *Remote Sensing of Large Wildfires*. Springer Berlin Heidelberg: Berlin, Heidelberg; 3–16.

Pavlů I, Zápotocká M. 2013. *Prehistory of Bohemia 2. The Neolithic.* Institute of Archaeology, Czech Academy of Sciences:

Payette S. 1992. Fire as a controlling process in the North American boreal forest. In *A Systems Analysis of the Global Boreal Forest*. Shugart HH, Leemans R, Bonan GB (eds). Cambridge University Press: Cambridge; 144–169.

Payette S, Delwaide A, Schaffhauser A, et al. 2012. Calculating long-term fire frequency at the stand scale from charcoal data. *Ecosphere* 3: 1–16.

Peichlová M. 1979. *Historie vegetace Broumovska [Vegetation history of the Broumovsko region].* Academy of Science CR, Průhonice,

Perşoiu A, Onac BP, Wynn JG, et al. 2017. Holocene winter climate variability in Central and Eastern Europe. *Scientific Reports* 7: 1196.

Pessenda LCR, Gouveia SEM, Aravena R. 2001. Radiocarbon Dating of Total Soil Organic Matter and Humin Fraction and Its Comparison with 14C Ages of Fossil Charcoal. *Radiocarbon* 43: 595–601.

Phillips JD. 2006. Deterministic chaos and historical geomorphology: A review and look forward. *Geomorphology* 76: 109–121.

Phillips S, Anderson R, Schapire R. 2006. Maximum entropy modeling of species geographic distributions. *Ecological Modelling* 190: 231–259.

Piha A, Kuuluvainen T, Lindberg H, et al. 2013. Can scar-based fire history reconstructions be biased? An experimental study in boreal Scots pine. *Canadian Journal of Forest Research* 43: 669–675.

Pini R, Ravazzi C, Raiteri L, et al. 2017. From pristine forests to high-altitude pastures: an ecological approach to prehistoric human impact on vegetation and landscapes in the western Italian Alps. *Journal of Ecology* 105: 1580–1597.

Pisaric MFJ. 2002. Long-distance transport of terrestrial plant material by convection resulting from forest fires. *Journal of Paleolimnology* 28: 349–354.

Pitkänen A, Huttunen P. 1999. A 1300-year forest-fire history at a site in eastern Finland based on charcoal and pollen records in laminated lake sediment. *The Holocene* 9: 311–320.

Plíva K. 1991. *Přírodní podmínky v lesním plánování.* ÚHUL: Brandýs nad Labem.

Pokorný P. 2002. A high-resolution record of Late-Glacial and Early-Holocene climatic and environmental change in Czech Republic. *Quaternary International* 91: 101–122.

Pokorný P. 2005. Role of man in the development of Holocene vegetation in Central Bohemia. *Preslia* 113–128.

Pokorný P, Chytrý M, Juřičková L, et al. 2015. Mid-Holocene bottleneck for central European dry grasslands: Did steppe survive the forest optimum in northern Bohemia, Czech Republic? *The Holocene* 25: 716–726.

Pokorný P, Kuneš P. 2005. Holocene acidification process recorded in three pollen profiles from Czech sandstone and river terrace environments. *Ferrantia* 44: 101–107.

Pokorný P, Novák J, Šída P, et al. 2017. Vývoj vegetace severočeských pískovcových území od pozdního glaciálu po střední holocén [Vegetation development of northern-Bohemian sandstone areas since the Late Glacial to the Middle Holocene]. In *Mezolit severních Čech 2 [Mesolithics of northern Bohemia 2]*. Svoboda J (eds). Archeologický ústav AV ČR, Brno: 11–37.

Pokorný P, Šída P, Chvojka O, et al. 2010. Palaeoenvironmental research of the Schwarzenberg Lake, southern Bohemia, and exploratory excavations of this key Mesolithic archaeological area. *Památky archeologické* 101: 5–38.

Power MJ, Codding BF, Taylor AH, et al. 2018. Human Fire Legacies on Ecological Landscapes. *Frontiers in Earth Science* 6: 1–6.

Power MJ, Marlon J, Ortiz N, et al. 2008. Changes in fire regimes since the Last Glacial Maximum: an assessment based on a global synthesis and analysis of charcoal data. *Climate Dynamics* 30: 887–907.

Preston CM, Schmidt MWI. 2006. Black (pyrogenic) carbon: a synthesis of current knowledge and uncertainties with special consideration of boreal regions. *Biogeosciences* 3: 397–420.

Punt W et al. 1976. *The Northwest European Pollen Flora, vol 1 (1976); vol 2 (1980); vol 3 (1981); vol 4 (1984); vol 5 (1988); vol 6 (1991); vol 7 (1996); vol 8 (2003).* Elsevier: Amsterdam.

R Development Core Team. 2013. *R: A Language and Environment for Statistical Computing.* R Foundation for Statistical Computing: Vienna.

Ramsey C. 2009. Bayesian analysis of radiocarbon dates. *Radiocarbon* 51: 337–360.

Ramsey, Ramsey CB. 2009. Dealing with outliers and offsets in radiocarbon dating. *Radiocarbon* 57: 217–235.

Randuška D. 1982. Forest typology in Czechoslovakia. In *Application of vegetation science to forestry. Handbook of vegetation science 12*. Jahn G (eds). The Hague: Dr. W. Junk Publishers: 147–178.

Ravazzi C. 2002. Late Quaternary history of spruce in southern Europe. *Review of Palaeobotany and Palynology* 120: 131–177.

Regnell M. 2012. Plant subsistence and environment at the Mesolithic site Tågerup, southern Sweden: New insights on the "Nut Age." *Vegetation History and Archaeobotany* 21: 1–16.

Reille M. 1992. *Pollen et spores d'Europe et d'Afrique du Nord.* Laboratoire de Botanique historique et Palynologie: Marseille.

Reille M. 1995. *Pollen et spores d'Europe et d'Afrique du Nord - supplement 1.* Laboratoire de Botanique Historique et Palynologie:

Reille M. 1998. *Pollen et spores d'Europe et d'Afrique du Nord - supplement 2.* Laboratoire de Botanique Historique et Palynologie:

Reimer P, Baillie M, Bard E. 2009. IntCal09 and Marine09 radiocarbon age calibration curves, 0-50,000 yeats cal BP. *Radiocarbon* 51: .

Reimer PJ, Bard E, Bayliss A, et al. 2013. IntCal13 and Marine13 Radiocarbon Age Calibration Curves 0–50,000 Years cal BP. *Radiocarbon* 55: 1869–1887.

Remy CC, Fouquemberg C, Asselin H, et al. 2018. Guidelines for the use and interpretation of palaeofire reconstructions based on various archives and proxies. *Quaternary Science Reviews* 193: 312–322.

Renssen H, Seppä H, Heiri O, et al. 2009. The spatial and temporal complexity of the Holocene thermal maximum. *Nature Geoscience* 2: 411–414.

Richter HG, Grosser D, Heinz I, et al. 2004. IAWA List of microscopic features for softwood identification. *IAWA Journal* 25: 1–70.

de Rigo D, Libertà G, Houston Durrant T, et al. 2017. *Forest fire danger extremes in Europe under climate change: variability and uncertainty.* Publications Office of the European Union: Luxembourg.

Rius D, Vannière B, Galop D. 2009. Fire frequency and landscape management in the northwestern Pyrenean piedmont, France, since the early Neolithic (8000 cal. BP). *Holocene* 19: 847–859.

Rius D, Vannière B, Galop D, et al. 2011. Holocene fire regime changes from multiple-site sedimentary charcoal analyses in the Lourdes basin (Pyrenees, France). *Quaternary Science Reviews* 30: 1696–1709.

Robin V, Bork H-R, Nadeau M-J, et al. 2013a. Fire and forest history of central European low mountain forest sites based on soil charcoal analysis: The case of the eastern Harz. *The Holocene* 24: 35–47.

Robin V, Knapp H, Bork HR, et al. 2013b. Complementary use of pedoanthracology and peat macro-charcoal analysis for fire history assessment: Illustration from Central Germany. *Quaternary International* 289: 78–87.

Robin V, Nadeau M-J, Grootes PM, et al. 2016. Too early and too northerly: evidence of temperate trees in northern Central Europe during the Younger Dryas. *New Phytologist* 212: 259–268.

Robin V, Nelle O. 2014. Contribution to the reconstruction of central European fire history, based on the soil charcoal analysis of study sites in northern and central Germany. *Vegetation History and Archaeobotany* 23: 51–65.

Robin V, Nelle O, Talon B, et al. 2018. A comparative review of soil charcoal data: Spatiotemporal patterns of origin and long-term dynamics of Western European nutrient-poor grasslands. *The Holocene* 28: 1313–1324.

Roebroeks W, Villa P. 2011. On the earliest evidence for habitual use of fire in Europe. *Proceedings of the National Academy of Sciences* 108: 5209–5214.

Roepke A, Krause R. 2013. High montane-subalpine soils in the Montafon Valley (Austria, northern Alps) and their link to land-use, fire and settlement history. *Quaternary International* 308–309: 178–189.

Rogers BM, Soja AJ, Goulden ML, et al. 2015. Influence of tree species on continental differences in boreal fires and climate feedbacks. *Nature Geoscience* 8: 228–234.

Rösch M. 1993. Prehistoric land use as recorded in a lake-shore core at Lake Constance. *Vegetation History and Archaeobotany* 2: 213–232.

Rösch M. 2013. Land use and food production in Central Europe from the Neolithic to the Medieval period: change of landscape, soils and agricultural systems according to archaeobotanical data. In *Economic archaeology: from structure to performance in European archaeology*. Kerig T, Zimmermann A (eds). Habelt: Bonn; 109–127.

Rösch M, Ehrmann O, Herrmann L, et al. 2002. An experimental approach to Neolithic shifting cultivation. *Vegetation History and Archaeobotany* 11: 143–154.

Ruddiman WF. 2003. The Anthropogenic Greenhouse Era Began Thousands of Years Ago. *Climatic Change* 61: 261–293.

Sádlo J, Herben T. 2007. Disturbance, denudation/accumulation dynamics and vegetation patterns in sandstone regions. In *Sandstone Landscapes*. Hartel H, Cílek V, Herben T, Jackson A, Williams R (eds). Academia: Prague; 205–211.

SAGA Development Team 2007. *SAGA Development Team 2007.* SAGA – System for Automated Geoscientific Analysis, http://www.saga-gis.org.:

Šamonil P, Daněk P, Schaetzl RJ, et al. 2015. Soil mixing and genesis as affected by tree uprooting in three temperate forests. *European Journal of Soil Science* 66: 589–603.

Šamonil P, Doleželová P, Vašíčková I, et al. 2013a. Individual-based approach to the detection of disturbance history through spatial scales in a natural beech-dominated forest. *Journal of Vegetation Science* 24: 1167–1184.

Šamonil P, Moravcová A, Pokorný P, et al. 2018. The disturbance regime of an Early Holocene swamp forest in the Czech Republic, as revealed by dendroecological, pollen and macrofossil data. *Palaeogeography, Palaeoclimatology, Palaeoecology* 507: 81–96.

Šamonil P, Schaetzl RJJ, Valtera M, et al. 2013b. Crossdating of disturbances by tree uprooting: Can treethrow microtopography persist for 6000 years? *Forest Ecology and Management* 307: 123–135.

Šamonil P, Valtera M, Bek S, et al. 2011. Soil variability through spatial scales in a permanently disturbed natural spruce-fir-beech forest. *European Journal of Forest Research* 130: 1075–1091.

Šamonil P, Vašíčková I, Daněk P, et al. 2014. Disturbances can control fine-scale pedodiversity in old-growth forests: is the soil evolution theory disturbed as well? *Biogeosciences* 11: 5889–5905.

Sass O, Heel M, Leistner I, et al. 2012. Disturbance, geomorphic processes and recovery of wildfire slopes in North Tyrol. *Earth Surface Processes and Landforms* 37: 883–894.

Sauer D, Sponagel H, Sommer M, et al. 2007. Podzol: Soil of the year 2007. A review on its genesis, occurrence, and functions. *Journal of Plant Nutrition and Soil Science* 170: 581–597.

Schaetzl RJ. 1994. Changes in O-Horizon Mass, Thickness and Carbon Content Following Fire in Northern Hardwood Forests. *Vegetatio* 115: 41–50.

Schaetzl RJ, Rothstein DE, Samonil P. 2018. Gradients in Lake Effect Snowfall and Fire across Northern Lower Michigan Drive Patterns of Soil Development and Carbon Dynamics. *Annals of the American Association of Geographers* 108: 638–657.

Schaetzl RJ, Thompson ML. 2015. *Soils: Genesis and Geomorphology.* Cambridge University Press: Cambridge; New York.

Scherjon F, Bakels C, MacDonald K, et al. 2015. Burning the Land. *Current Anthropology* 56: 299–326.

Schmidt MWI, Noack AG. 2000. Black carbon in soils and sediments: Analysis, distribution, implications, and current challenges. *Global Biogeochemical Cycles* 14: 777–793.

Schneider CA, Rasband WS, Eliceiri KW. 2012. NIH Image to ImageJ: 25 years of image analysis. *Nature Methods* 9: 671–675.

Schoeneberger PJ, Wysicki DA, Benham EC, et al. 1998. *Field Book for Describing and Sampling Soils.* Natural Resources Conservation Service, USDA, National Soil Survey Center: Lincoln.

Schweingruber FH. 1990. *Anatomie europäischer Hölzer – Anatomy of European woods.* Eidgenössische Forschungsanstalt für Wald, Schnee und Landschaft, Birmensdorf. Haupt: Bern und Stuttgart.

Schweingruber FH. 2011. *Anatomie europäischer Hölzer - Anatomy of European Woods.* Verlag Kessel: Remagen-Oberwinter.

Schwörer C, Colombaroli D, Kaltenrieder P, et al. 2015. Early human impact (5000-3000 BC) affects mountain forest dynamics in the Alps. *Journal of Ecology* 103: 281–295.

Schwörer C, Kaltenrieder P, Glur L, et al. 2014. Holocene climate, fire and vegetation dynamics at the treeline in the Northwestern Swiss Alps. *Vegetation History and Archaeobotany* 23: 479–496.

Scott AC. 2010. Charcoal recognition , taphonomy and uses in palaeoenvironmental analysis. *Palaeogeography, Palaeoclimatology, Palaeoecology* 291: 11–39.

Scott AC, Glasspool IJ. 2006. The diversification of Paleozoic fire systems and fluctuations in atmospheric oxygen concentration. *Proceedings of the National Academy of Sciences* 103: 10861–10865.

Selsing L. 2016. *Intentional fire management in the Holocene with emphasis on hunter-gatherers in the Mesolithic in South Norway.* Museum of Archaeology, University of Stavanger: Stavanger.

Shakesby RA. 2011. Post-wildfire soil erosion in the Mediterranean: Review and future research directions. *Earth-Science Reviews* 105: 71–100.

Shanahan TM, Hughen KA, McKay NP, et al. 2016. CO2 and fire influence tropical ecosystem stability in response to climate change. *Scientific Reports* 6: 29587.

Šída P, Prostředník J, Kuneš P. 2011. New Radiocarbon Data for the North Bohemian Mesolithic. *IANSA* II: 151–157.

Šída P, Prostředník J, Pokorný P. 2014. The Mesolithic of the Bohemian Paradise sandstone region. *The Dolní Věstonice Studies* 20: 109–116.

Simmons IG, Innes JB. 1987. Mid-holocene adaptations and later Mesolithic forest disturbance in Northern England. *Journal of Archaeological Science* 14: 385–403.

Singh N, Abiven S, Torn MS, et al. 2012. Fire-derived organic carbon in soil turns over on a centennial scale. *Biogeosciences* 9: 2847–2857.

Skre O, Wielgolaski FE, Moe B. 1998. Biomass and chemical composition of common forest plants in response to fire in western Norway. *Journal of Vegetation Science* 9: 501–510.

Skrzypek G, Baranowska-Kącka A, Keller-Sikora A, et al. 2009. Analogous trends in pollen percentages and carbon stable isotope composition of Holocene peat — Possible interpretation for palaeoclimate studies. *Review of Palaeobotany and Palynology* 156: 507–518.

Smith BD. 2011. General patterns of niche construction and the management of "wild" plant and animal resources by small-scale pre-industrial societies. *Philosophical Transactions of the Royal Society B: Biological Sciences* 366: 836–848.

Speranza A. 2000. *Solar and anthropogenic forcing of late-Holocene vegetation changes in the Czech Giant Mountains.* University of Amsterdam,

Speranza A, Hanke J, van Geel B, et al. 2000a. Late-Holocene human impact and peat development in the Černá Hora bog, Krkonoše Mountains, Czech Republic. *The Holocene* 10: 575–585.

Speranza A, Van Der Plicht J, Van Geel B. 2000b. Improving the time control of the Subboreal/Subatlantic transition in a Czech peat sequence by 14C wiggle-matching. *Quaternary Science Reviews* 19: 1589–1604.

Stahli M, Finsinger W, Tinner W, et al. 2006. Wildfire history and fire ecology of the Swiss National Park (Central Alps): new evidence from charcoal, pollen and plant macrofossils. *The Holocene* 16: 805–817.

Stalling H. 1987. *Untersunchungen zur spät-und postglazialen Vegetationsgeschichte im Bayerischen Wald.* Georg-August-Universität, Göttingen.

Stambaugh MC, Guyette RP. 2008. Predicting spatio-temporal variability in fire return intervals using a topographic roughness index. *Forest Ecology and Management* 254: 463–473.

Stebich M, Litt T. 1997. Das Georgenfelder Hochmoor ein Archiv fur Vegetations. *Siedlungs und Bergbaugechichte* 209–216.

Stein A, Gerstner K, Kreft H. 2014. Environmental heterogeneity as a universal driver of species richness across taxa, biomes and spatial scales. *Ecology Letters* 17: 866–880.

Stivrins N, Soininen J, Amon L, et al. 2016. Biotic turnover rates during the Pleistocene-Holocene transition. *Quaternary Science Reviews* 151: 100–110.

Stockmarr J. 1971. Tablets with Spores used in Absolute Pollen Analysis. *Pollen et Spores* 13: 615–621.

Švarcová M. 2012. *Postglaciální historie lokálních fenoménů horské vegetace západních Čech [Postglacial vegetation historz of local phenomena in western Bohemia].* MSc. thesis, Charles University in Prague,

Svenning J. 2002. A review of natural vegetation openness in north-western Europe. *Biological Conservation* 104: 133–148.

Svoboda J. 2003. Mezolitické osídlení severních Čech. In *Mezolit severních Čech. Komplexní výzkum skalních převisů na Českolipsku a Děčínsku, 1978-2003*. Svoboda J (eds). Archeologický ústav AV ČR: Brno; 77–96.

Svoboda J, Hajnalová M, Horáček I, et al. 2007. Mesolithic settlement and activities in rockshelters of the Kamenice river canyon, Czech Republic. *Eurasian Prehistory* 5: 95–127.

Svoboda J, Pokorný P, Horáček I, et al. 2018. Late Glacial and Holocene sequences in rockshelters and adjacent wetlands of Northern Bohemia, Czech Republic: Correlation of environmental and archaeological records. *Quaternary International* 465: 234–250.

Svobodová H. 2002. Preliminary results of the vegetation history in the Giant Mountains (Úpská rašelina mire and Černohorská rašelina bog). *Opera Corcontica* 39: 5–15.

Svobodová H. 2004. Vývoj vegetace na Úpském rašeliništi v holocénu [Development of the vegetation on Úpské rašeliniště Mire in the Holocene]. *Opera Corcontica* 41: 124–130.

Svobodová H, Reille M, Goeury C. 2001. Past vegetation dynamics of Vltavský luh, upper Vltava river valley in the Šumava mountains. Czech Republic. *Vegetation History and Archaeobotany* 10: 185–199.

Svobodová H, Soukupová L, Reille M. 2002. Diversified development of mountain mires, Bohemian Forest, Central Europe, in the last 13,000 years. *Quaternary International* 91: 123–135.

Sweeney CA. 2004. A key for the identification of stomata of the native conifers of Scandinavia. *Review of Palaeobotany and Palynology* 128: 281–290.

Szabó P, Kuneš P, Svobodová-Svitavská H, et al. 2016. Using historical ecology to reassess the conservation status of coniferous forests in Central Europe. *Conservation Biology* 1: 1–35.

Tinner W, Colombaroli D, Kołaczek P, et al. 2015. Long-term hydrological dynamics and fire history over the last 2000 years in CE Europe reconstructed from a high-resolution peat archive. *Quaternary Science Reviews* 112: 138–152.

Tinner W, Conedera M, Ammann B, et al. 1998. Pollen and charcoal in lake sediments compared with historically documented forest fires in southern Switzerland since AD 1920. *The Holocene* 8: 31–42.

Tinner W, Conedera M, Ammann B, et al. 2005. Fire ecology north and south of the Alps since the last ice age. *The Holocene* 15: 1214–1226.

Tinner W, Conedera M, Gobet E, et al. 2000. A palaeoecological attempt to classify fire sensitivity of trees in the southern Alps. *The Holocene* 10: 565–574.

Tinner W, Hofstetter S, Zeugin F, et al. 2006a. Long-distance transport of macroscopic charcoal by an intensive crown fire in the Swiss Alps - implications for fire history reconstruction. *Holocene* 16: 287–292.

Tinner W, Hubschmid P, Wehrli M, et al. 1999. Long-term forest fire ecology and dynamics in southern Switzerland. *Journal of Ecology* 87: 273–289.

Tinner W, Lotter AF. 2006b. Holocene expansions of Fagus silvatica and Abies alba in Central Europe: where are we after eight decades of debate? *Quaternary Science Reviews* 25: 526–549.

Tinner W, Nielsen EH, Lotter AF. 2007. Mesolithic agriculture in Switzerland? A critical review of the evidence. *Quaternary Science Reviews* 26: 1416–1431.

Titiz B, Sanford RL. 2007. Soil charcoal in old-growth rain forests from sea level to the continental divide. *Biotropica* 39: 673–682.

Tolasz R et al. 2007. *Climate atlas of Czechia.* Český hydrometeorologický ústav/Univerzita Palackého v Olomouci: Praha/Olomouc.

Tollefsrud MM, Kissling R, Gugerli F, et al. 2008. Genetic consequences of glacial survival and postglacial colonization in Norway spruce: combined analysis of mitochondrial DNA and fossil pollen. *Molecular Ecology* 17: 4134–4150.

Touflan P, Talon B. 2009. Spatial reliability of soil charcoal analysis: The case of subalpine forest soils. *Écoscience* 16: 23–27.

Treml V, Jankovská V, Petr L. 2008. Holocene dynamics of the alpine timberline in the High Sudetes. *Biologia* 63: 73–80.

Tsoar A, Allouche O, Steinitz O, et al. 2007. A comparative evaluation of presence-only methods for modelling species distribution. *Diversity and Distributions* 13: 397–405.

TU Dresden Institut für Photogrammetrie und Fernerkundung (IPF) PF. 2005. Geoinformationsnetzwerke für die grenzüberschreitende Nationalparkregion Sächsisch- Böhmische Schweiz (GeNeSiS). .

Turkington A V., Paradise TR. 2005. Sandstone weathering: A century of research and innovation. *Geomorphology* 67: 229–253.

Turner R, Roberts N, Eastwood WJ, et al. 2010. Fire, climate and the origins of agriculture: micro-charcoal records of biomass burning during the last glacial-interglacial transition in Southwest Asia. *Journal of Quaternary Science* 25: 371–386.

Tüxen R. 1956. *Die heutige potentielle natürliche Vegetation als Gegenstand der Vegetationskartierung, Angewandte Pflanzensoziologie.* Stolzenau/Weser.

Vachula RS, Richter N. 2017. Informing sedimentary charcoal-based fire reconstructions with a kinematic transport model. *The Holocene* 095968361771562.

Vachula RS, Russell JM, Huang Y, et al. 2018. Assessing the spatial fidelity of sedimentary charcoal size fractions as fire history proxies with a high-resolution sediment record and historical data. *Palaeogeography, Palaeoclimatology, Palaeoecology* 508: 166–175.

Vannière B, Blarquez O, Rius D, et al. 2016. 7000-year human legacy of elevation-dependent European fire regimes. *Quaternary Science Reviews* 132: 206–212.

Vanniere B, Power MJ, Roberts N, et al. 2011. Circum-Mediterranean fire activity and climate changes during the mid-Holocene environmental transition (8500-2500 cal. BP). *The Holocene* 21: 53–73.

Vannière B, Power MJ, Roberts N, et al. 2011. Circum-Mediterranean fire activity and climate changes during the mid-Holocene environmental transition (8500-2500 cal. BP). *The Holocene* 21: 53–73.

Vera FWM. 2002. *Grazing Ecology and Forest History.* CABI Publishing: Wallingford.

Verboom WH, Pate JS. 2006. Bioengineering of soil profiles in semiarid ecosystems: the ‘phytotarium’ concept. A review. *Plant and Soil* 289: 71–102.

Vočadlová K, Petr L, Žáčková P, et al. 2015. The Lateglacial and Holocene in Central Europe: a multi-proxy environmental record from the Bohemian Forest, Czech Republic. *Boreas* 44: 769–784.

Volařík D, Hédl R. 2013. Expansion to abandoned agricultural land forms an integral part of silver fir dynamics. *Forest Ecology and Management* 292: 39–48.

Walker M, Johnsen S, Rasmussen SO, et al. 2009. Formal definition and dating of the GSSP (Global Stratotype Section and Point) for the base of the Holocene using the Greenland NGRIP ice core, and selected auxiliary records. *Journal of Quaternary Science* 24: 3–17.

Walker MJC, Berkelhammer M, Björck S, et al. 2012. Formal subdivision of the Holocene Series/Epoch: a Discussion Paper by a Working Group of INTIMATE (Integration of ice-core, marine and terrestrial records) and the Subcommission on Quaternary Stratigraphy (International Commission on Stratigraphy). *Journal of Quaternary Science* 27: 649–659.

Wanner H, Solomina O, Grosjean M, et al. 2011. Structure and origin of Holocene cold events. *Quaternary Science Reviews* 30: 3109–3123.

Welzholz JC, Johann E. 2007. History of Protected Forest Areas in Europe. In *COST Action E27. Protected forest areas in Europe - analysis and harmonisation (PROFOR): results, conclusions and recommendations*. Federal Research and Training Centre for Forests, Natural Hazards and Landscape (BFW): Vienna; 17–40.

Wheeler EA, Baas P, Gasson PE. 1989. IAWA List of microscopc features for hardwood identification - With an appendix on non-anatomical information. *Iawa Bulletin* 10: 219–332.

Whitlock C, Higuera PE, McWethy DB, et al. 2010. Paleoecological Perspectives on Fire Ecology: Revisiting the Fire-Regime Concept. *The Open Ecology Journal* 3: 6–23.

Whitlock C, Larsen C. 2001. Charcoal as a fire proxy. In *Tracking Environmental Change Using Lake Sediments: Vol. 3 Terrestrial, Algal, and Siliceous Indicators*. Smol JP, Birks HJP, Last WM (eds). Dordrecht: Kluwer Academic Publishers: 75–97.

Whitlock C, Millspaugh SH. 1996. Testing the assumptions of fire-history studies: an examination of modern charcoal accumulation in Yellowstone National Park, USA. *The Holocene* 6: 7–15.

Wilby A. 2002. Ecosystem engineering: a trivialized concept? *Trends in Ecology & Evolution* 17: 307.

Wild J, Macek M, Kopecky M, et al. 2013. Temporal and spatial variability of microclimate in sandstone landscape: detailed field measurement.

Willis K, Van Andel TH. 2004. Trees or no trees? The environments of central and eastern Europe during the Last Glaciation. *Quaternary Science Reviews* 23: 2369–2387.

Winkler MG. 1985. Charcoal analysis for paleoenvironmental interpretation: A chemical assay. *Quaternary Research* 23: 313–326.

Wolf M, Lehndorff E, Mrowald M, et al. 2014. Black carbon: Fire fingerprints in Pleistocene loess–palaeosol archives in Germany. *Organic Geochemistry* 70: 44–52.

Wooster MJ, Zhang YH. 2004. Boreal forest fires burn less intensely in Russia than in North America. *Geophysical Research Letters* 31: 2–4.

Young RW, Wray RAL, Young ARM. 2009. *Sandstone landforms.* Cambridge University Press: Cambridge.

Zackrisson O. 1977. Influence of Forest Fires on the North Swedish Boreal Forest. *Oikos* 29: 22.

Zackrisson O, Nilsson M, Wardle D. 1996. Key ecological function of charcoal from wildfire in the Boreal forest. *Oikos* .

Zennaro P, Kehrwald N, Marlon J, et al. 2015. Europe on fire three thousand years ago: Arson or climate? *Geophysical Research Letters* 42: 5023–2033.

Zennaro P, Kehrwald N, Mcconnell JR, et al. 2014. Fire in ice : two millennia of Northern Hemisphere fire history from the Greenland NEEM ice core. *Climate of the Past* 809–857.

Zimmerman AR. 2010. Abiotic and Microbial Oxidation of Laboratory-Produced Black Carbon (Biochar). *Environmental Science & Technology* 44: 1295–1301.

Zvelebil M. 1994. Plant Use in the Mesolithic and its Role in the Transition to Farming. *Proceedings of the Prehistoric Society* 60: 35–74.

Zvelebil M. 2008. Innovating Hunter-Gatherers: The mesolithic in the Baltic. *Mesolithic Europe* 18–44.

Appendix 1. Supplemental information for Chapter 4

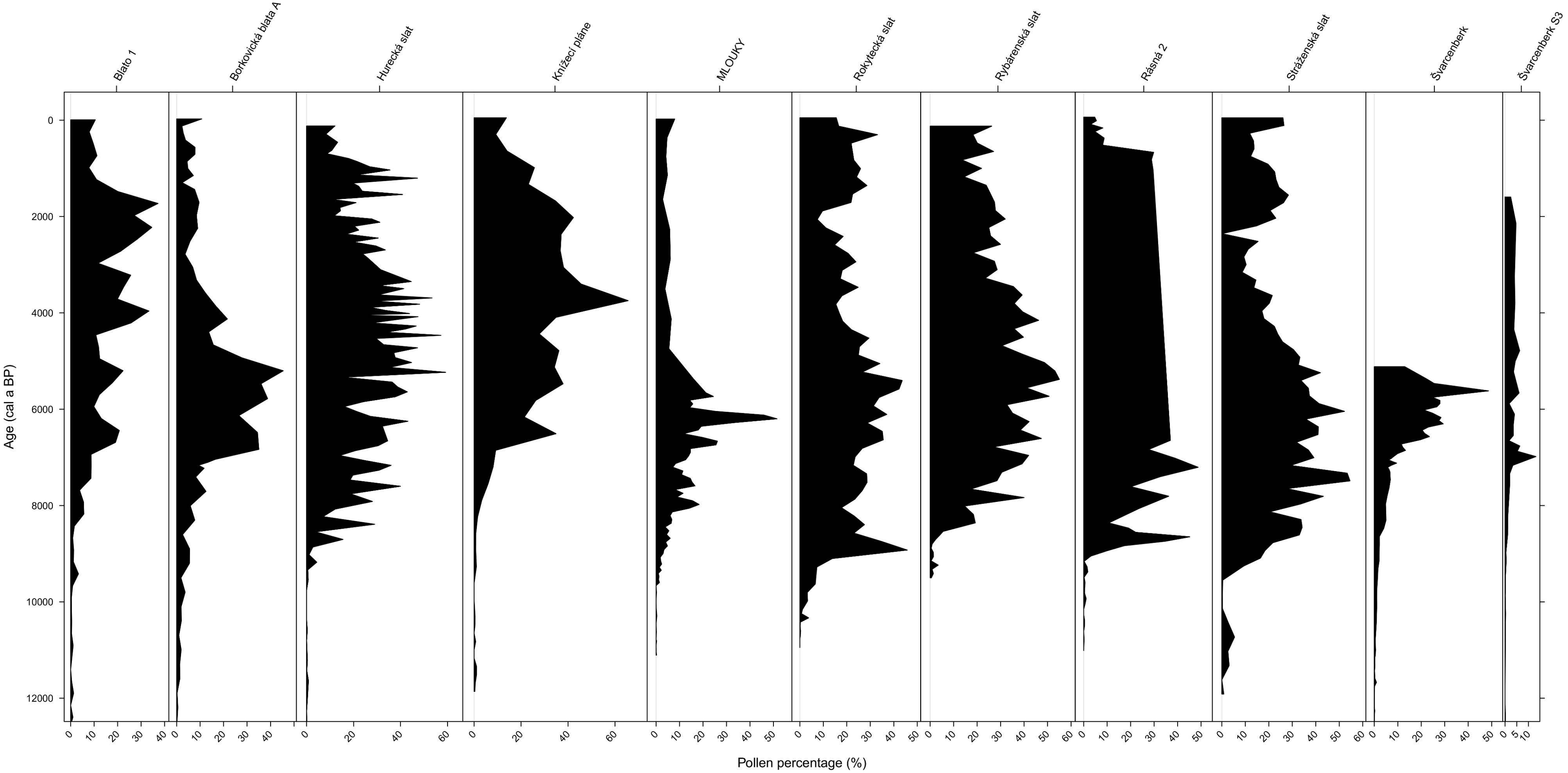


Figure S1. A compilation of ^{14}C-dated pollen records from southern Bohemia depicting *Picea abies* expansion. List of sites: Bláto 1 ; Borkovická blata A ; Hůrecká slať ; Knížecí pláně ; Mokré louky „MLOUKY“ ; Rokytecká slat ; Rybárenská slať ; Řásná 2 ; Stráženská slať ; Švarcenberk ; Švarcenberk S3 . Data extracted from Czech Quaternary Palynological Database (PALYCZ) https://botany.natur.cuni.cz/palycz/.

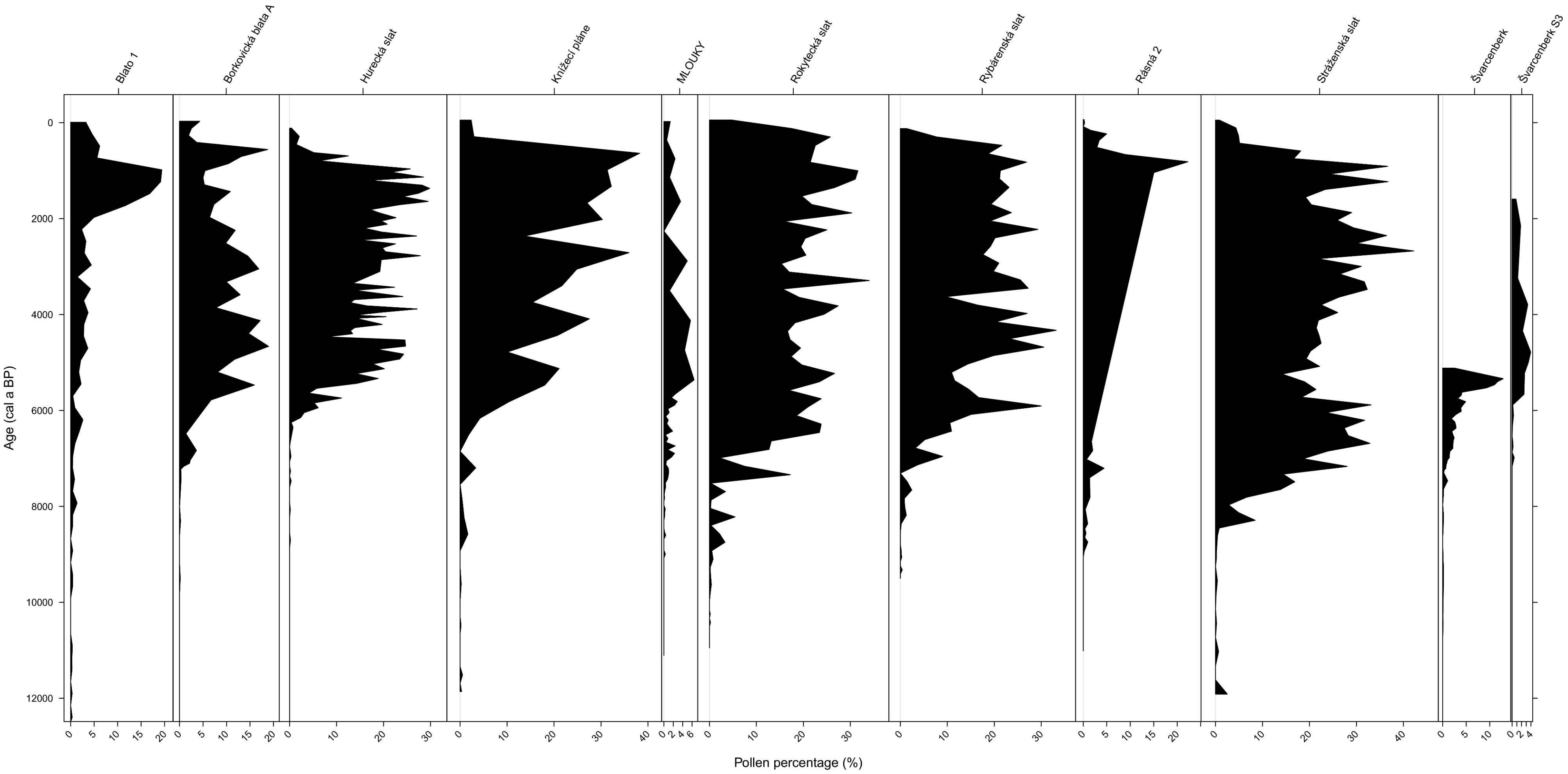


Figure S2. A compilation of ^{14}C-dated pollen records from southern Bohemia depicting *Fagus sylvatica* expansion. List of sites: Bláto 1; Borkovická blata A; Hůrecká slať; Knížecí pláně; Mokré louky „MLOUKY“; Rokytecká slať; Rybárenská slať; Řásná 2; Stráženská slať; Švarcenberk ; Švarcenberk S3 . Data extracted from Czech Quaternary Palynological Database (PALYCZ).

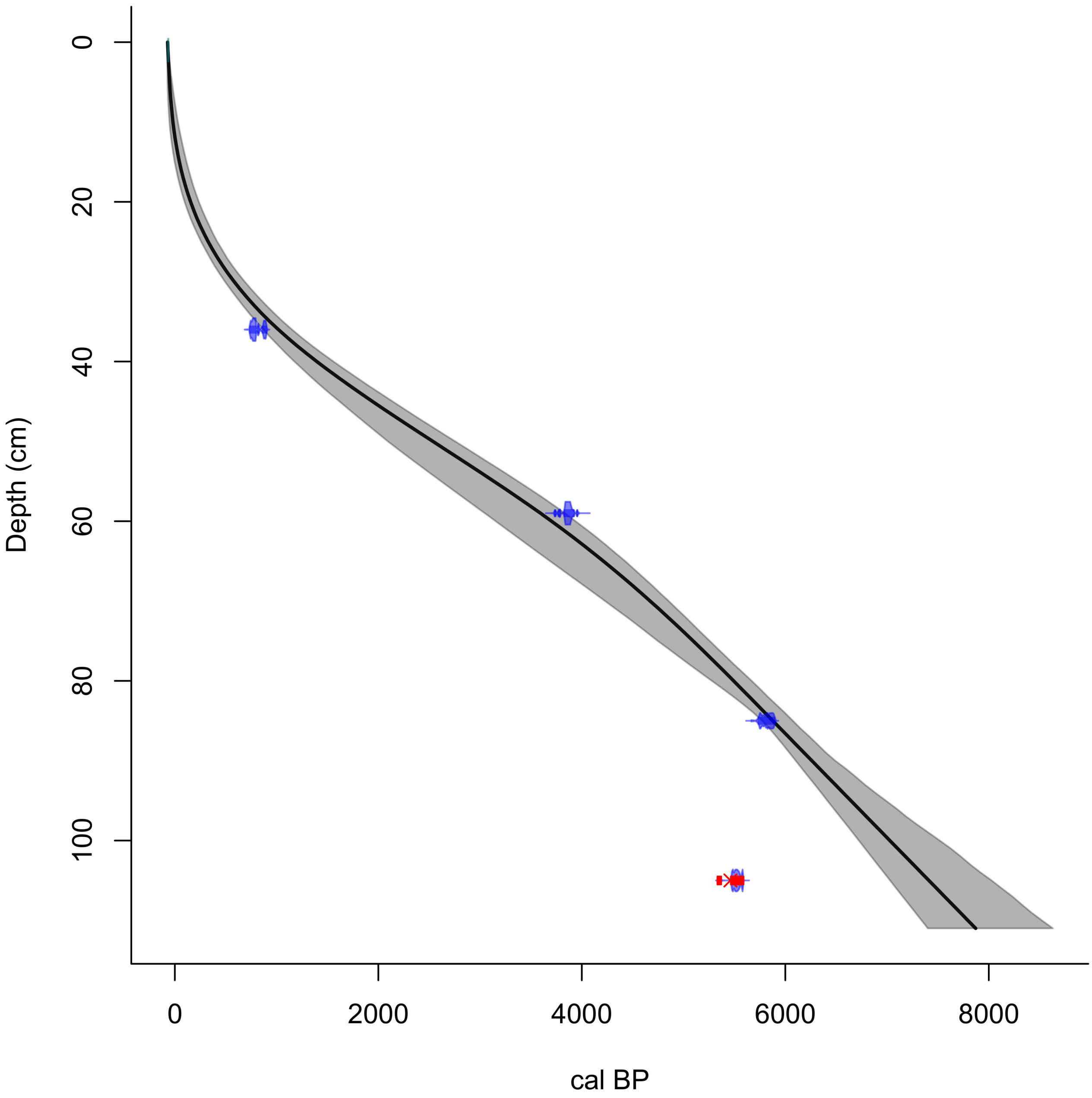


Figure S3. The age-depth model for Žofín peat bog profile.

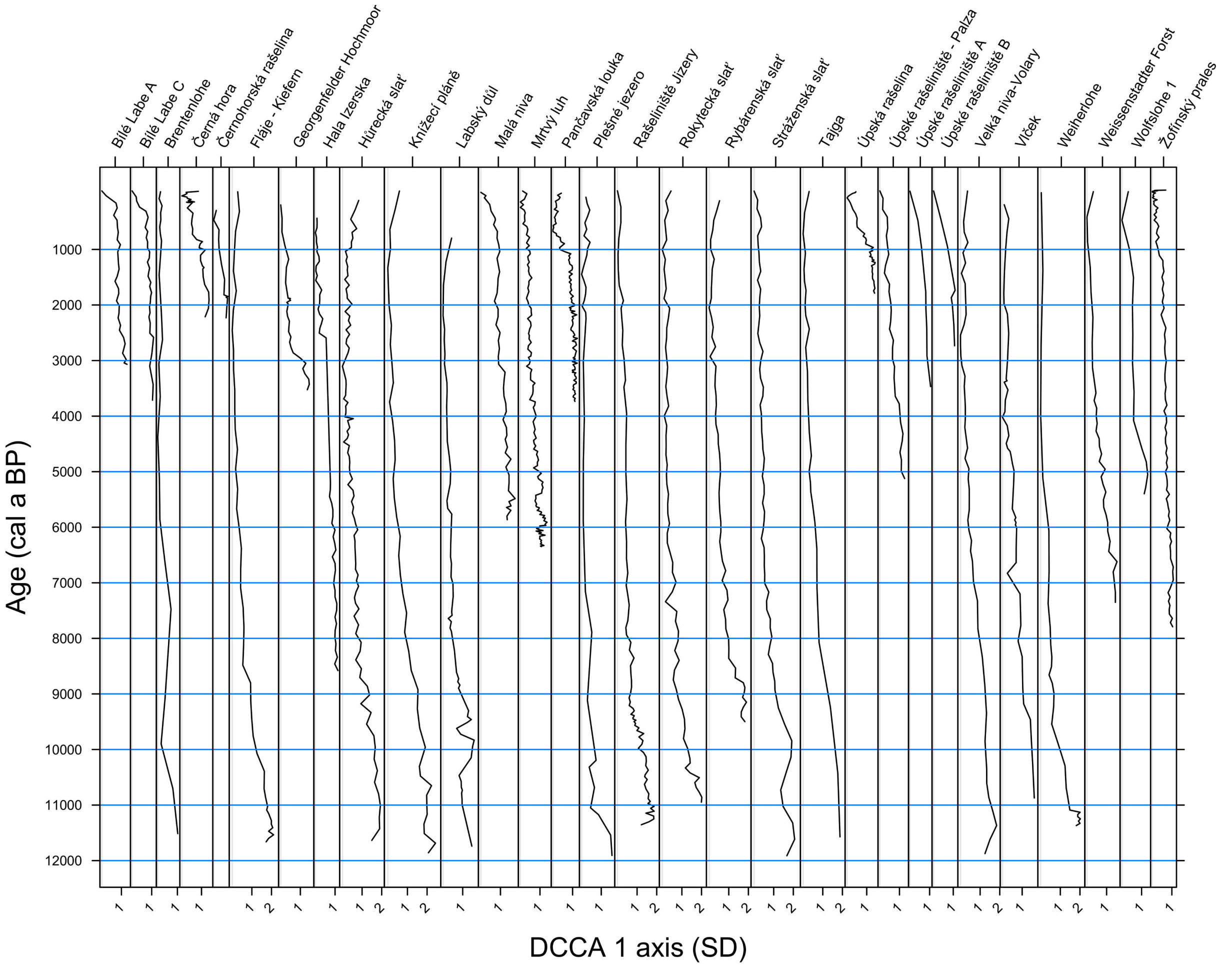
Table S1. Radiocarbon dating of soil charcoal particles and macroremains from the peat bog core.

Lab code	Site	Location	Context	Depth (cm)	Material dated	^{14}C a BP (±σ)	Calibrated age range (cal a BP; 2σ)	Median age (cal a BP)	Fire event
DeA-7648	Sonda 1	48.663201°N; 14.707003°E	topsoil	5-8	Pinus charcoal	9811±56	11338-11136	11227	1
LTL14777A	Sonda 1	48.663201°N; 14.707003°E	topsoil	10-14	Fagus charcoal	561±45	652-516	591	12
LTL14778A	Sonda 1	48.663201°N; 14.707003°E	subsoil	20-32	Picea charcoal	5997±45	6955-6726	6836	10
LTL14779A	Sonda 1	48.663201°N; 14.707003°E	subsoil	45-55	Pinus charcoal	9317±80	10708-10270	10515	3
LTL14780A	Sonda 1	48.663201°N; 14.707003°E	subsoil	65-75	Picea charcoal	6404±50	7425-7258	7341	9
LTL14781A	Sonda 1	48.663201°N; 14.707003°E	subsoil	90-100	Picea charcoal	5756±45	6660-6447	6556	11
DeA-7643	Sonda 2	48.663311°N; 14.706696°E	topsoil	1-5	Picea charcoal	582±20	642-539	606	12
LTL14783A	Sonda 2	48.663311°N; 14.706696°E	subsoil	20-30	Pinus charcoal	9239±70	10576-10246	10410	3
LTL14784A	Sonda 2	48.663311°N; 14.706696°E	subsoil	40-50	Pinus charcoal	9830±50	11335-11175	11237	1
LTL14785A	Sonda 2	48.663311°N; 14.706696°E	subsoil	60-70	Pinus charcoal	8978±75	10258-9795	10089	5
LTL14786A	Sonda 2	48.663311°N; 14.706696°E	subsoil	90-100	Picea charcoal	6860±70	7842-7581	7700	8
LTL14752A	Sonda 3	48.664665°N; 14.706416°E	topsoil	4-7	Abies charcoal	after 1950 AD	-	-	14
LTL14978A	Sonda 3	48.664665°N; 14.706416°E	subsoil	20-30	Picea charcoal	6508±45	7504-7319	7426	9
LTL14754A	Sonda 3	48.664665°N; 14.706416°E	subsoil	40-50	Picea charcoal	7771±50	8633-8430	8547	7
LTL14755A	Sonda 3	48.664665°N; 14.706416°E	subsoil	60-70	Picea charcoal	7681±50	8561-8391	8473	7
LTL15590A	Sonda 3	48.664665°N; 14.706416°E	subsoil	60-70	Pinus charcoal	8396±55	9522-9292	9425	6
LTL14756A	Sonda 4	48.664867°N; 14.706480°E	topsoil	4-8	Fagus charcoal	319±35	474-303	388	13
LTL14757A	Sonda 4	48.664867°N; 14.706480°E	subsoil	20-30	Pinus charcoal	8795±80	10156-9564	9841	5
LTL14758A	Sonda 4	48.664867°N; 14.706480°E	subsoil	40-50	Picea charcoal	268±40	465-0	328	13
LTL14759A	Sonda 4	48.664867°N; 14.706480°E	subsoil	60-70	Picea charcoal	7821±50	8767-8455	8602	7
LTL14760A	Sonda 5	48.665005°N; 14.708626°E	topsoil	6-10	Abies charcoal	208±40	314-0	182	14
DeA-7645	Sonda 5	48.665005°N; 14.708626°E	topsoil	6-10	Pinus charcoal	9468±43	11066-10578	10711	2
LTL15591A	Sonda 5	48.665005°N; 14.708626°E	subsoil	40-50	Picea charcoal	6935±45	7918-7675	7763	8
DeA-7751	Sonda 5	48.665005°N; 14.708626°E	subsoil	40-50	Pinus charcoal	9096±46	10388-10189	10245	4
LTL14764A	Sonda 6	48.665058°N; 14.709068°E	topsoil	5-10	Abies charcoal	343±40	489-309	395	13
LTL15592A	Sonda 6	48.665058°N; 14.709068°E	subsoil	20-30	Picea charcoal	5540±45	6413-6276	6341	11
LTL14766A	Sonda 6	48.665058°N; 14.709068°E	subsoil	40-50	Pinus charcoal	9489±70	11090-10574	10781	2

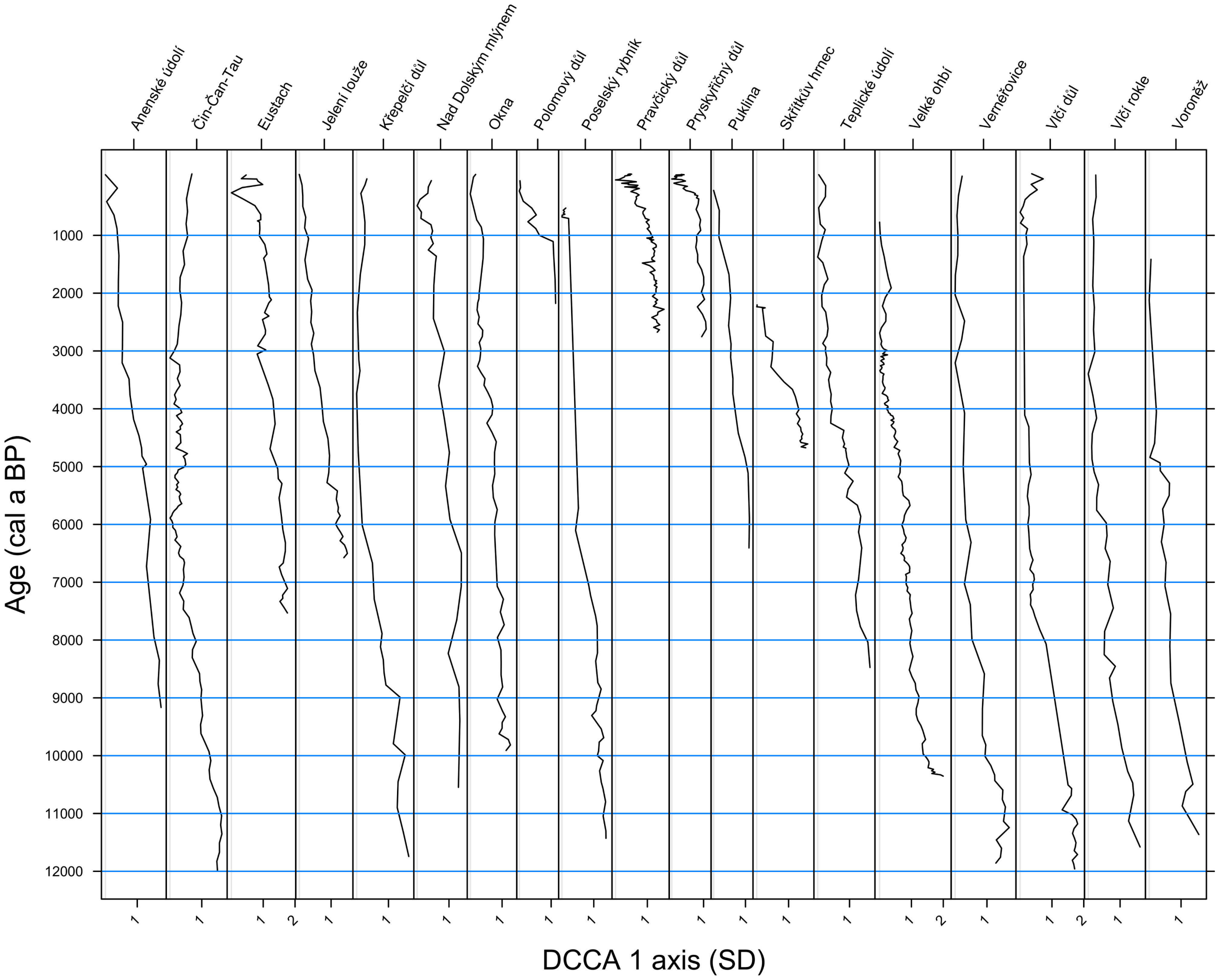
Lab code	Site	Location	Context	Depth (cm)	Material dated	^{14}C a BP (±σ)	Calibrated age range (cal a BP; 2σ)	Median age (cal a BP)	Fire event
LTL14767A	Sonda 6	48.665058°N; 14.709068°E	subsoil	60-70	Picea charcoal	5823±45	6735-6503	6631	11
DeA-7753	Sonda 6	48.665058°N; 14.709068°E	subsoil	60-70	Pinus charcoal	8941±47	10214-9914	10053	5
LTL14768A	Sonda 7	48.669005°N; 14.708762°E	topsoil	10-15	Fagus charcoal	393±40	515-316	451	13
LTL14769A	Sonda 7	48.669005°N; 14.708762°E	subsoil	20-30	Pinus charcoal	9541±70	11142-10608	10894	2
LTL15593A	Sonda 7	48.669005°N; 14.708762°E	subsoil	20-30	Picea charcoal	8395±60	9527-9281	9420	6
LTL14770A	Sonda 7	48.669005°N; 14.708762°E	subsoil	40-50	Pinus charcoal	9241±70	10578-10246	10412	3
LTL14771A	Sonda 7	48.669005°N; 14.708762°E	subsoil	60-70	Picea charcoal	8874±80	10201-9695	9978	5
LTL14772A	Sonda 8	48.669025°N; 14.708349°E	topsoil	10-16	Abies charcoal	181±45	303-0	174	14
LTL14773A	Sonda 8	48.669025°N; 14.708349°E	subsoil	20-30	Abies charcoal	512±45	640-496	535	12
LTL14774A	Sonda 8	48.669025°N; 14.708349°E	subsoil	40-50	Pinus charcoal	9217±85	10588-10227	10394	3
LTL15594A	Sonda 8	48.669025°N; 14.708349°E	subsoil	40-50	Picea charcoal	6292±45	7320-7029	7219	9
LTL14775A	Sonda 8	48.669025°N; 14.708349°E	subsoil	60-70	Pinus charcoal	6000±50	6975-6720	6840	10
LTL14776A	Sonda 8	48.669025°N; 14.708349°E	subsoil	80-90	Picea charcoal	5712±45	6633-6408	6502	11
CRL16-363	Peat profile	48.664441°N; 14.705347°E	peat bog	36	bulk peat	885±25	906-732	791	-
CRL16-357	Peat profile	48.664441°N; 14.705347°E	peat bog	59	Abies needles	3563±29	3966-3726	3863	-
CRL16-356	Peat profile	48.664441°N; 14.705347°E	peat bog	85	Picea needles+seeds	5052±31	5903-5727	5821	-
CRL16-358	Peat profile	48.664441°N; 14.705347°E	peat bog	105-106	plant tissue	4770±31	5590-5333	5519	-

Table S1 (Continued). Radiocarbon dating of soil charcoal particles and macroremains from the peat bog core.

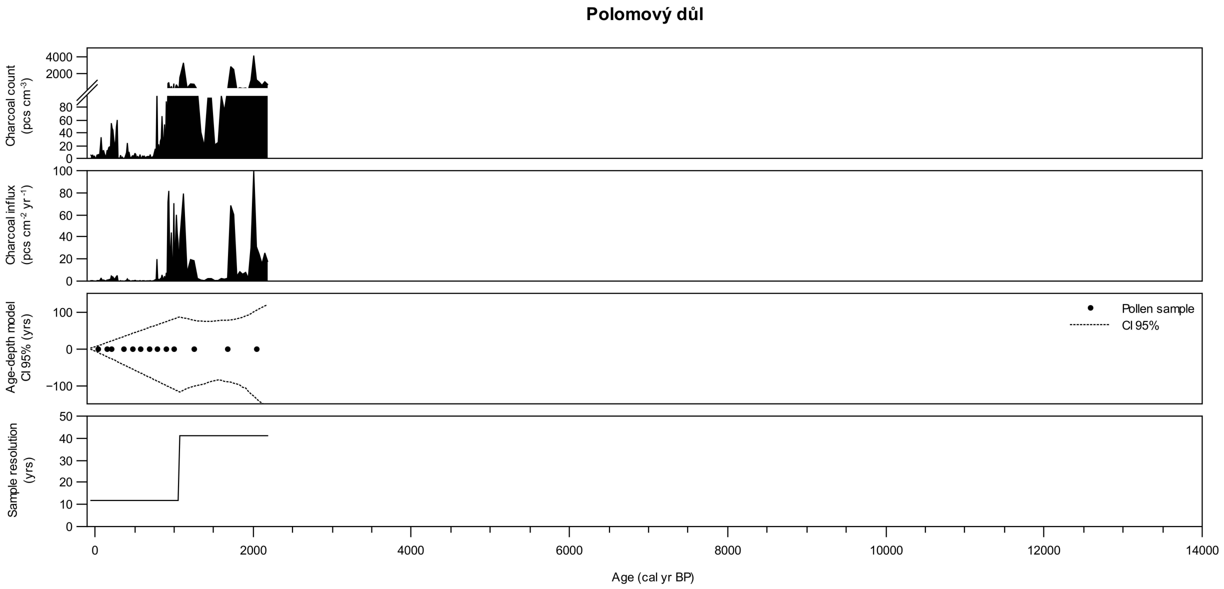
Appendix 2. Supplemental information for Chapter 5



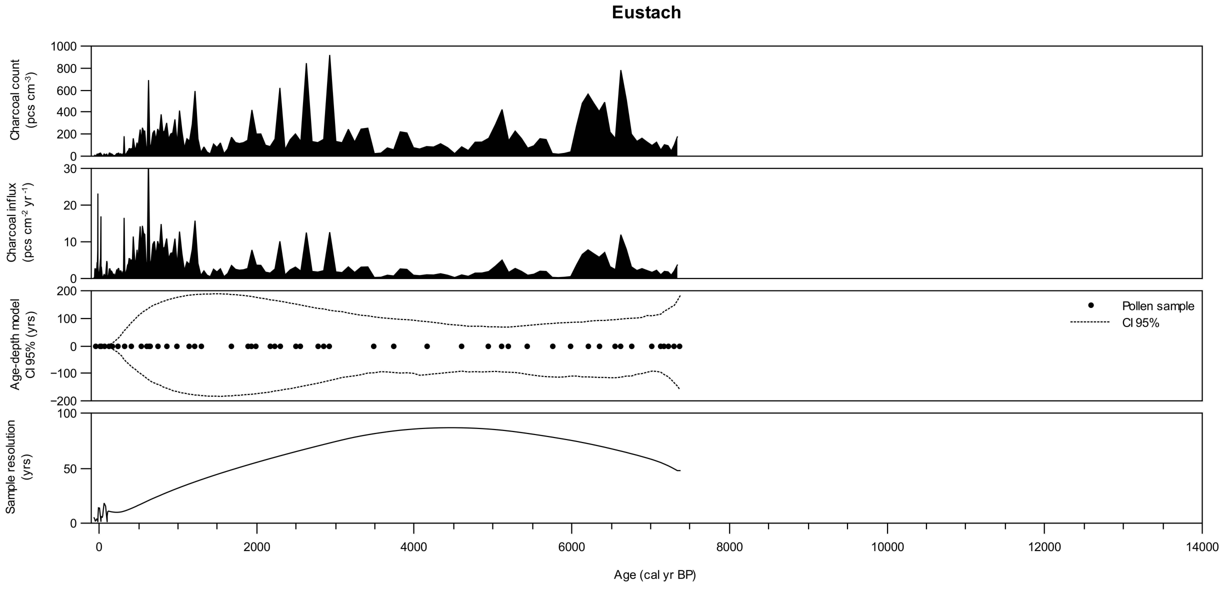
Supplementary Figure 1. Sample scores on the first DCCA axis (time-constrained) deduced from pollen sequences located in the mountain sub-region.



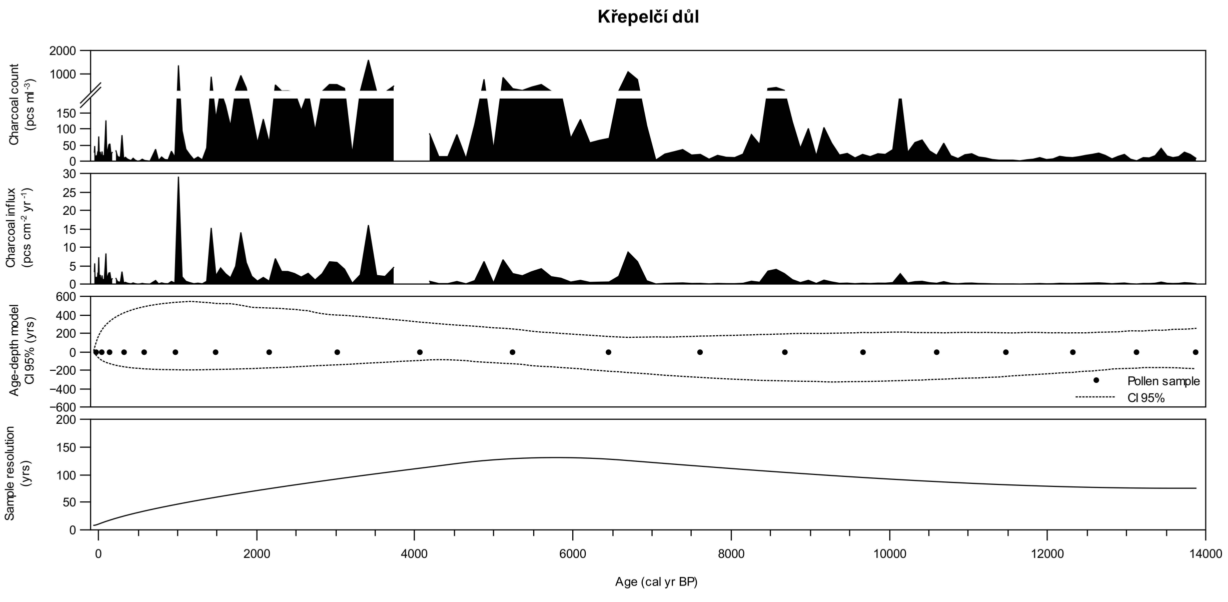
Supplementary Figure 2. Sample scores on the first DCCA axis (time-constrained) deduced from pollen sequences located in the sandstone sub-region.


Polomový důl

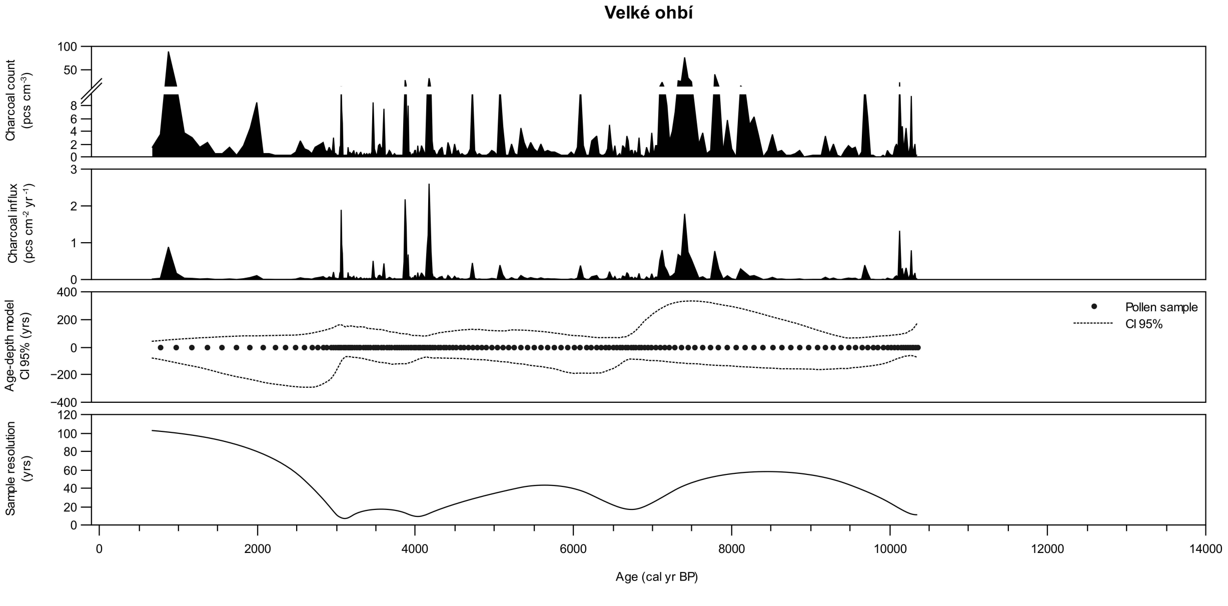
Supplementary Figure 3. Polomový důl - macro-charcoal influx series (CHAR) used for the calculation of regional charcoal composites. Charcoal concentration, charcoal influx (CHAR), sample age uncertainty given by an age-depth model (95 % confidence interval), pollen sample position and sample resolution.


Eustach

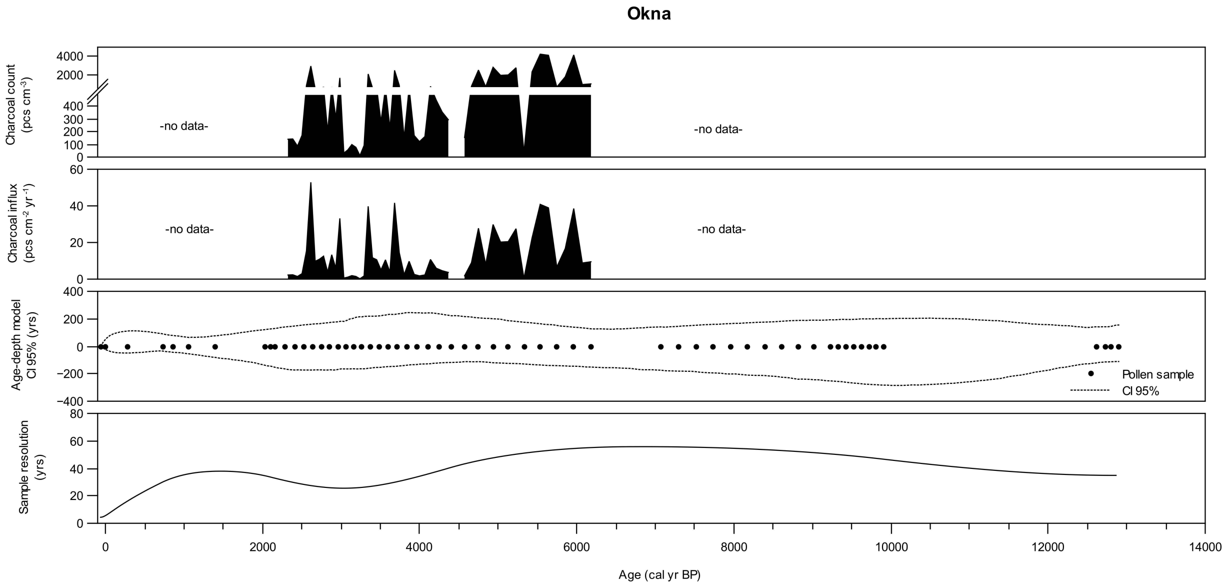
Supplementary Figure 4. Eustach - macro-charcoal influx series (CHAR) used for the calculation of regional charcoal composites. Charcoal concentration, charcoal influx (CHAR), sample age uncertainty given by an age-depth model (95 % confidence interval), pollen sample position and sample resolution.



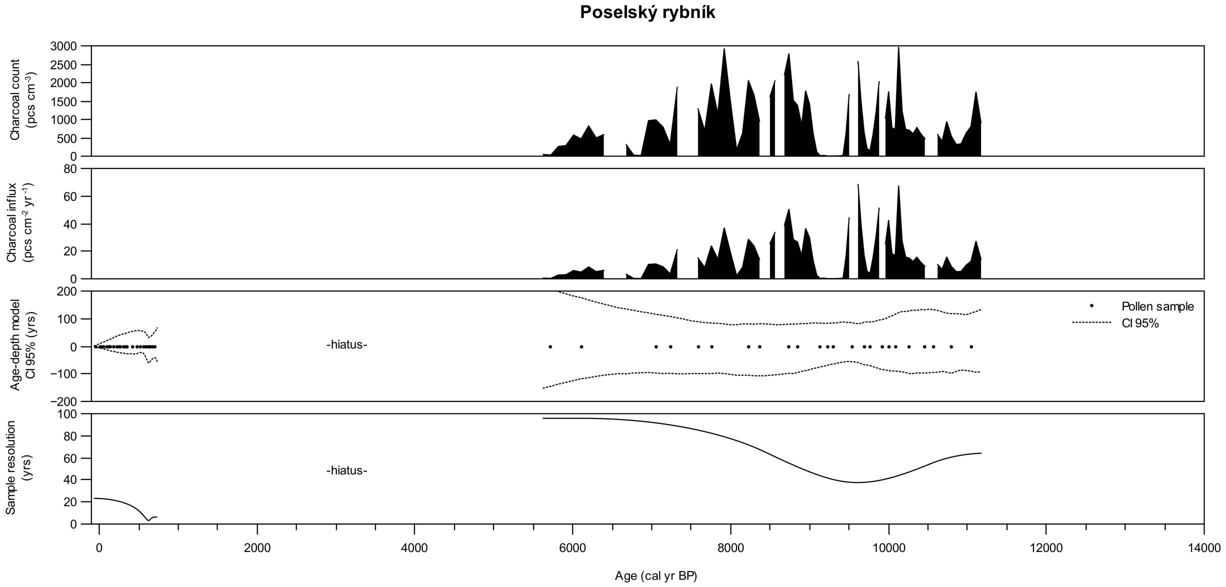
Supplementary Figure 5. Křepelčí důl - macro-charcoal influx series (CHAR) used for the calculation of regional charcoal composites. Charcoal concentration, charcoal influx (CHAR), sample age uncertainty given by an age-depth model (95 % confidence interval), pollen sample position and sample resolution.



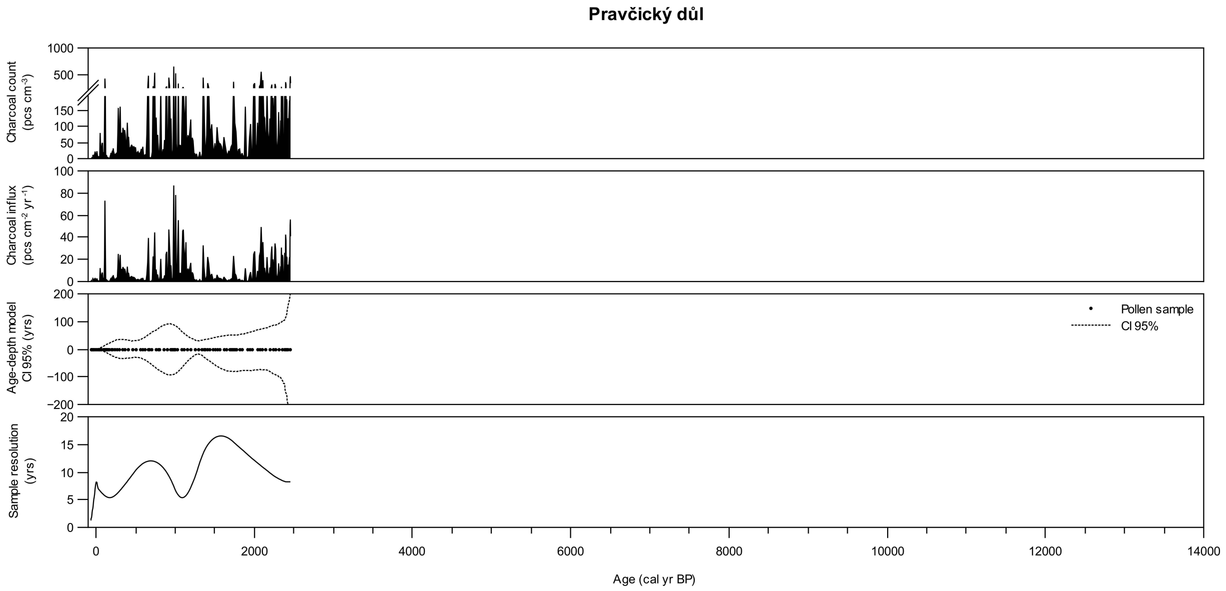
Supplementary Figure 6. Velké ohbí - macro-charcoal influx series (CHAR) used for the calculation of regional charcoal composites. Charcoal concentration, charcoal influx (CHAR), sample age uncertainty given by an age-depth model (95 % confidence interval), pollen sample position and sample resolution.



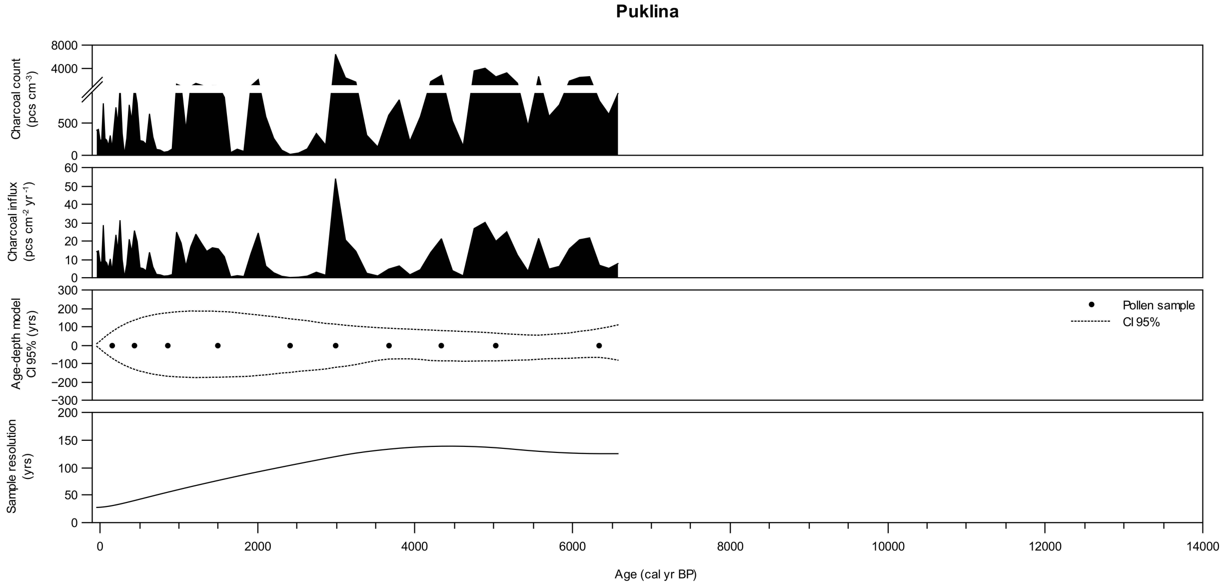
Supplementary Figure 7. Okna - macro-charcoal influx series (CHAR) used for the calculation of regional charcoal composites. Charcoal concentration, charcoal influx (CHAR), sample age uncertainty given by an age-depth model (95 % confidence interval), pollen sample position and sample resolution.



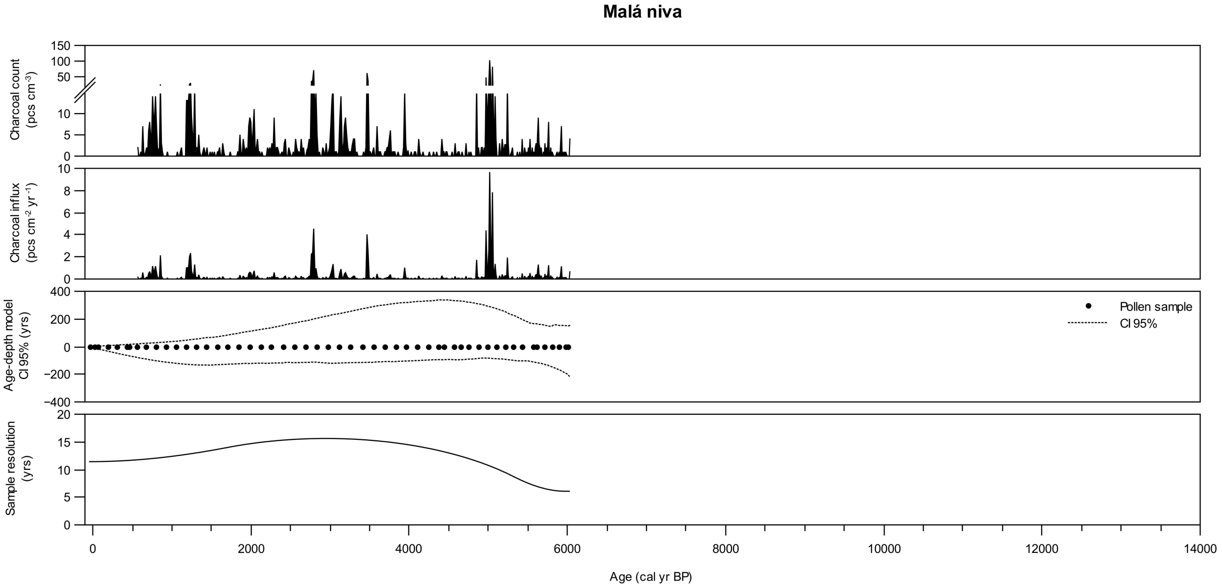
Supplementary Figure 8. Poselský rybník - macro-charcoal influx series (CHAR) used for the calculation of regional charcoal composites. Charcoal concentration, charcoal influx (CHAR), sample age uncertainty given by an age-depth model (95 % confidence interval), pollen sample position and sample resolution.



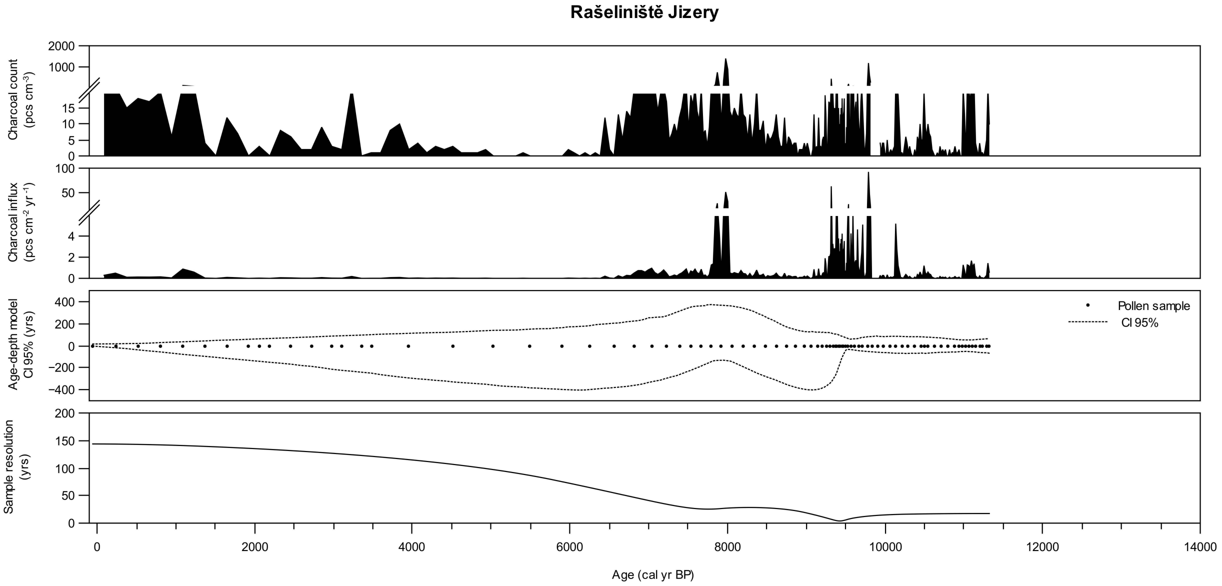
Supplementary Figure 9. Pravčický důl - macro-charcoal influx series (CHAR) used for the calculation of regional charcoal composites. Charcoal concentration, charcoal influx (CHAR), sample age uncertainty given by an age-depth model (95 % confidence interval), pollen sample position and sample resolution.



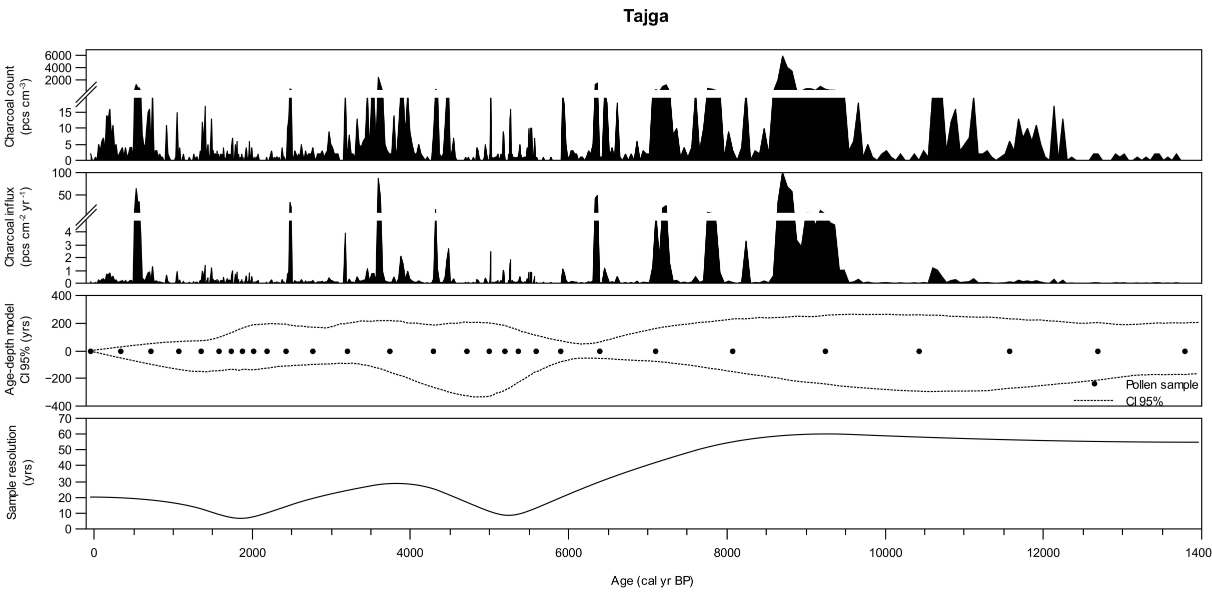
Supplementary Figure 10. Puklina - macro-charcoal influx series (CHAR) used for the calculation of regional charcoal composites. Charcoal concentration, charcoal influx (CHAR), sample age uncertainty given by an age-depth model (95 % confidence interval), pollen sample position and sample resolution.



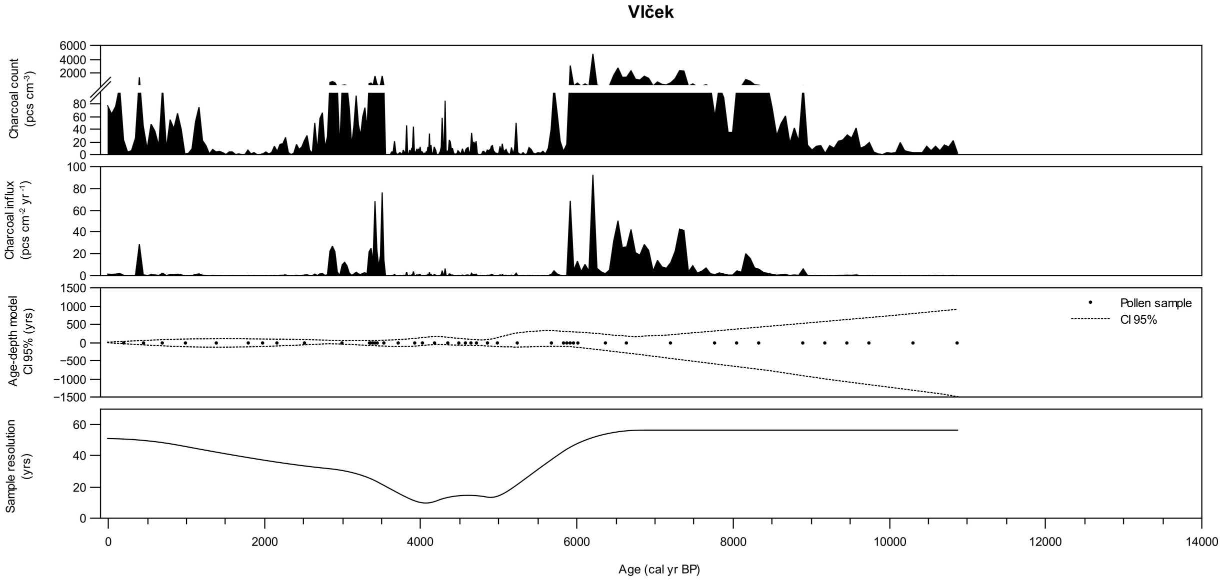
Supplementary Figure 11. Malá niva - macro-charcoal influx series (CHAR) used for the calculation of regional charcoal composites. Charcoal concentration, charcoal influx (CHAR), sample age uncertainty given by an age-depth model (95 % confidence interval), pollen sample position and sample resolution.



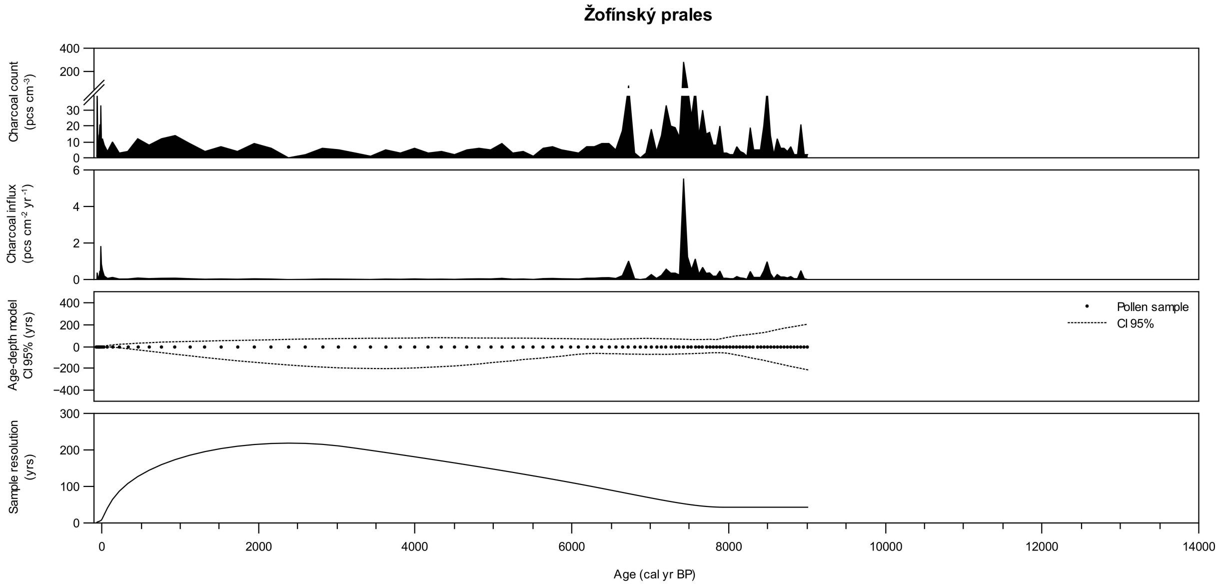
Supplementary Figure 12. Rašeliniště Jizery- macro-charcoal influx series (CHAR) used for the calculation of regional charcoal composites. Charcoal concentration, charcoal influx (CHAR), sample age uncertainty given by an age-depth model (95 % confidence interval), pollen sample position and sample resolution.



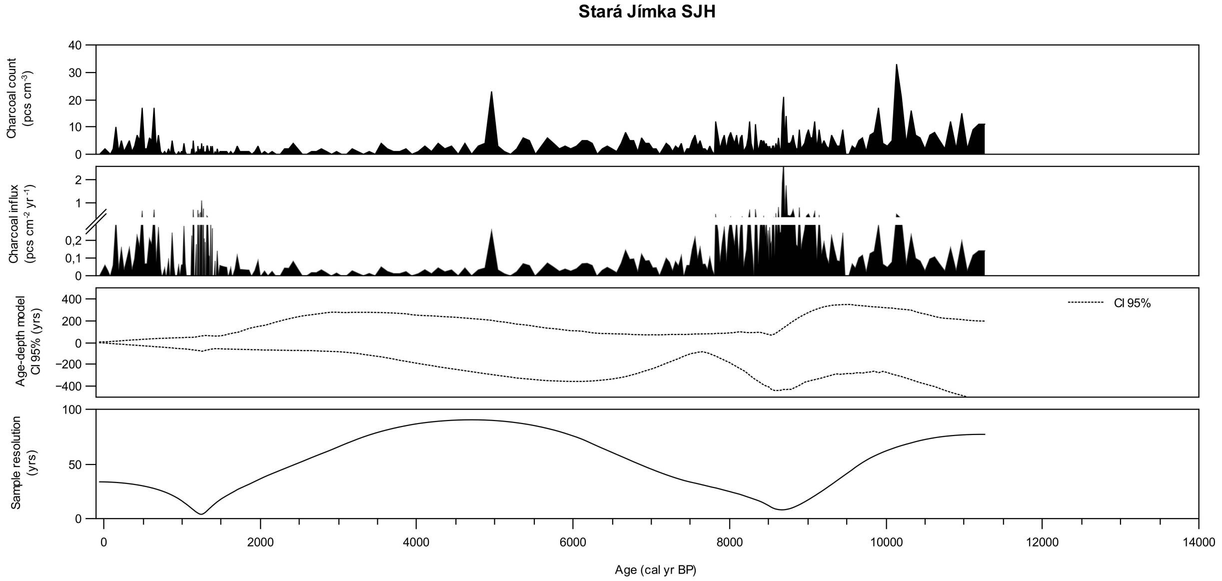
Supplementary Figure 13. Tajga - macro-charcoal influx series (CHAR) used for the calculation of regional charcoal composites. Charcoal concentration, charcoal influx (CHAR), sample age uncertainty given by an age-depth model (95 % confidence interval), pollen sample position and sample resolution.



Supplementary Figure 14. Vlček - macro-charcoal influx series (CHAR) used for the calculation of regional charcoal composites. Charcoal concentration, charcoal influx (CHAR), sample age uncertainty given by an age-depth model (95 % confidence interval), pollen sample position and sample resolution.



Supplementary Figure 15. Žofínský prales - macro-charcoal influx series (CHAR) used for the calculation of regional charcoal composites. Charcoal concentration, charcoal influx (CHAR), sample age uncertainty given by an age-depth model (95 % confidence interval), pollen sample position and sample resolution.



Supplementary Figure 16. Stará Jímka SJH - macro-charcoal influx series (CHAR) used for the calculation of regional charcoal composites. Charcoal concentration, charcoal influx (CHAR), sample age uncertainty given by an age-depth model (95 % confidence interval), pollen sample position and sample resolution.

Supplementary Table S1. List of radiocarbon dates

Locality	Region	Location (WGS 84)	Lab code	^{14}C Age ±2σ	Median cal BP	Interval cal BP ±2σ	Taxon	Material	Depth (cm)	Context	Reference
NP České Švýcarsko	Sandstones	50,87271°N; 14,36286°E	LTL8202A	1449 ±45	1344	1285-1476	Quercus sp.	wood charcoal	15-20	soil	(1)
NP České Švýcarsko	Sandstones	50,892°N; 14,42573°E	LTL8203A	3174 ±50	3399	3249-3555	Pinus sp.	wood charcoal	12-16	soil	(1)
NP České Švýcarsko	Sandstones	50,892°N; 14,42573°E	LTL8204A	6625 ±45	7513	7437-7575	Pinus sp.	wood charcoal	19-30	soil	(1)
NP České Švýcarsko	Sandstones	50,8799°N; 14,28503°E	LTL8205A	4546 ±45	5167	5046-5435	Picea abies	wood charcoal	21-30	soil	(1)
NP České Švýcarsko	Sandstones	50,88521°N; 14,28766°E	LTL8206A	236 ±45	275	0-437	Larix decidua	wood charcoal	3-10	soil	(1)
NP České Švýcarsko	Sandstones	50,88521°N; 14,28766°E	LTL8207A	350 ±45	400	311-496	Pinus sp.	wood charcoal	14-26	soil	(1)
NP České Švýcarsko	Sandstones	50,89364°N; 14,40741°E	LTL8208A	368 ±30	433	316-503	Pinus sp.	wood charcoal	4-8	soil	(1)
NP České Švýcarsko	Sandstones	50,89364°N; 14,40741°E	LTL8209A	2626 ±40	2755	2716-2845	Pinus sp.	wood charcoal	10-16	soil	(1)
NP České Švýcarsko	Sandstones	50,89364°N; 14,40741°E	LTL8210A	7132 ±50	7959	7848-8029	Picea abies	wood charcoal	19-26	soil	(1)
NP České Švýcarsko	Sandstones	50,88248°N; 14,41543°E	LTL8211A	340 ±45	395	307-494	Pinus sp.	wood charcoal	9-12	soil	(1)
NP České Švýcarsko	Sandstones	50,88248°N; 14,41543°E	LTL8212A	1074 ±40	983	927-1061	Pinus sp.	wood charcoal	15-20	soil	(1)
NP České Švýcarsko	Sandstones	50,88248°N; 14,41543°E	LTL8213A	6356 ±50	7293	7175-7418	Quercus sp.	wood charcoal	23-30	soil	(1)
NP České Švýcarsko	Sandstones	50,8854°N; 14,32689°E	LTL8214A	after 1950 AD	50	46-54	Fagus sylvatica	wood charcoal	0-6	soil	(1)
NP České Švýcarsko	Sandstones	50,8854°N; 14,32689°E	LTL8215A	1650 ±45	1552	1413-1693	Fagus sylvatica	wood charcoal	6-10	soil	(1)
NP České Švýcarsko	Sandstones	50,8854°N; 14,32689°E	LTL8216A	1667 ±45	1574	1417-1701	Fagus sylvatica	wood charcoal	37-50	soil	(1)
NP České Švýcarsko	Sandstones	50,88622°N; 14,35134°E	LTL12347A	1351 ±45	1280	1182-1342	Pinus sp.	wood charcoal	11-15	soil	(1)
NP České Švýcarsko	Sandstones	50,88622°N; 14,35134°E	LTL12349A	9727 ±65	11151	10793-11254	Pinus sp.	wood charcoal	34-51	soil	(1)
NP České Švýcarsko	Sandstones	50,86856°N; 14,42339°E	LTL12350A	961 ±45	859	782-960	Pinus sp.	wood charcoal	40-50	soil	(1)
NP České Švýcarsko	Sandstones	50,90842°N; 14,42139°E	LTL12351A	5844 ±45	6660	6509-6776	Pinus sp.	wood charcoal	60-75	soil	(1)
NP České Švýcarsko	Sandstones	50,90842°N; 14,42139°E	LTL12352A	9528 ±55	10868	10664-11099	Pinus sp.	wood charcoal	32-49	soil	(1)
NP České Švýcarsko	Sandstones	50,90842°N; 14,42139°E	LTL12353A	818 ±35	727	680-789	Pinus sp.	wood charcoal	10-15	soil	(1)
NP České Švýcarsko	Sandstones	50,89622°N; 14,35406°E	LTL12354A	617 ±45	601	541-665	Quercus sp.	wood charcoal	39-50	soil	(1)
NP České Švýcarsko	Sandstones	50,89622°N; 14,35406°E	LTL12355A	4225 ±45	4745	4616-4864	Fagus sylvatica	wood charcoal	25-36	soil	(1)
NP České Švýcarsko	Sandstones	50,89622°N; 14,35406°E	LTL12356A	370 ±35	431	315-505	Quercus sp.	wood charcoal	8-10	soil	(1)
NP České Švýcarsko	Sandstones	50,8799°N; 14,28503°E	LTL12357A	938 ±45	851	746-932	Pinus sp.	wood charcoal	7-13	soil	(1)
NP České Švýcarsko	Sandstones	50,87271°N; 14,36286°E	LTL12358A	1399 ±40	1313	1270-1379	Quercus sp.	wood charcoal	2-10	soil	(1)
NP České Švýcarsko	Sandstones	50,88622°N; 14,35134°E	LTL12348A	178 ±45	173	0-302	Quercus sp.	wood charcoal	28-34	soil	(Bobek et al., 2018b)
NP České Švýcarsko	Sandstones	50,882868°N; 14,317496°E	LTL16049A	1256 ±45	1203	1070-1284	Picea abies	wood charcoal (5 pcs)	106	peat bog	(Bobek et al., 2018b)
NP České Švýcarsko	Sandstones	50,931874°N; 14,438233°E	DeA-10128	6154 ±32	7066	6960-7161	Picea abies	wood charcoal	122	peat bog	(Bobek et al., 2018b)
NP České Švýcarsko	Sandstones	50,932394°N; 14,439768°E	DeA-10130	3017 ±27	3209	3081-3337	Picea abies	wood charcoal	56-57	peat bog	(1)
NP České Švýcarsko	Sandstones	50,932394°N; 14,439768°E	DeA-10132	4644 ±30	5407	5310-5466	Pinus sp.	wood charcoal	72-73	peat bog	(Bobek et al., 2018b)
NP České Švýcarsko	Sandstones	50,932394°N; 14,439768°E	DeA-10133	5727 ±32	6520	6440-6634	Picea abies	wood charcoal (10 pcs)	81-82	peat bog	(Bobek et al., 2018b)
Okna	Sandstones	50,532066°N; 14,675933°E	Poz-33653	1390 ±80	1308	1097-1522	indet.	charcoal	87	peat bog	(3)
Okna	Sandstones	50,532066°N; 14,675933°E	UGAMS-3538	2150 ±25	2143	2046-2304	indet.	charcoal	105,5	peat bog	(3)
Okna	Sandstones	50,532066°N; 14,675933°E	Poz-33654	3900 ±60	4327	4152-4515	indet.	charcoal, plant + insect remains	178	peat bog	(3)
Okna	Sandstones	50,532066°N; 14,675933°E	Poz-33655	8860 ±90	9950	9633-10205	indet.	charcoal and plant remains	284	peat bog	(3)
Velké ohbí	Sandstones	50,604056°N; 16,127124°E	Poz-90315	1245 ±30	1205	1076-1271	cf Picea abies	wood charcoal, charred needles, seeds	11-14	peat bog	this study
Velké ohbí	Sandstones	50,604056°N; 16,127124°E	Poz-90283	4480 ±35	5166	4978-5291	indet.	charcoal, needles, wood	188-189	peat bog	this study
Velké ohbí	Sandstones	50,604056°N; 16,127124°E	Poz-90325	6180 ±40	7079	6951-7235	cf Picea abies	wood charcoal, charred needles, seeds	256-257	peat bog	this study
Slavkovský les	Mountains	50,02283°N; 12,69938°E	LTL14964A	262 ±35	309	0-455	Picea abies	wood charcoal	30-14	soil	this study
Slavkovský les	Mountains	50,03472°N; 12,7375°E	LTL14965A	5925 ±40	6747	6661-6857	Picea abies	wood charcoal	30-44	soil	this study
Boubínský prales	Mountains	48,973596°N; 13,814596°E	CRL16_092	5758 ±40	6558	6454-6658	Picea abies	wood charcoal	10-20	soil	this study
Boubínský prales	Mountains	48,973596°N; 13,814596°E	CRL16_093	7422 ±42	8258	8174-8345	Picea abies	wood charcoal	20-30	soil	this study
Boubínský prales	Mountains	48,973596°N; 13,814596°E	CRL16_094	8797 ±45	9825	9631-10146	Picea abies	wood charcoal	40-50	soil	this study
Boubínský prales	Mountains	48,973596°N; 13,814596°E	CRL16_095	8186 ±43	9132	9021-9272	Picea abies	wood charcoal	84-105	soil	this study
Boubínský prales	Mountains	48,973596°N; 13,814596°E	CRL16_096	8846 ±43	9949	9740-10158	Picea abies	wood charcoal	12-22	soil	this study
Boubínský prales	Mountains	48,973596°N; 13,814596°E	CRL16_097	6097 ±41	6969	6858-7157	Picea abies	wood charcoal	22-32	soil	this study

Locality	Region	Location (WGS 84)	Lab code	^{14}C Age ±2σ	Median cal BP	Interval cal BP ±2σ	Taxon	Material	Depth (cm)	Context	Reference
Boubínský prales	Mountains	48,973596°N; 13,814596°E	CRL16_098	6075 ±41	6935	6793-7155	Picea abies	wood charcoal	42-51	soil	this study
Boubínský prales	Mountains	48,973596°N; 13,814596°E	CRL16_099	8773 ±44	9781	9564-10116	Picea abies	wood charcoal	51-71	soil	this study
Boubínský prales	Mountains	48,973596°N; 13,814596°E	CRL16_100	5857 ±42	6677	6555-6780	Picea abies	wood charcoal	1-14	soil	this study
Žofínský prales	Mountains	48,66471°N; 14,706462°E	LTL14777A	561 ±45	591	516-652	Fagus sylvatica	wood charcoal	10-14	soil	(2)
Žofínský prales	Mountains	48,66471°N; 14,706462°E	LTL14778A	5997 ±45	6836	6726-6955	Picea abies	wood charcoal	20-32	soil	(2)
Žofínský prales	Mountains	48,66471°N; 14,706462°E	LTL14779A	9317 ±80	10515	10270-10708	Pinus sp.	wood charcoal	45-55	soil	(2)
Žofínský prales	Mountains	48,66471°N; 14,706462°E	LTL14780A	6404 ±50	7341	7258-7425	Picea abies	wood charcoal	65-75	soil	(2)
Žofínský prales	Mountains	48,66471°N; 14,706462°E	LTL14781A	5756 ±45	6556	6447-6660	Picea abies	wood charcoal	90-100	soil	(2)
Žofínský prales	Mountains	48,66471°N; 14,706462°E	LTL14783A	9239 ±70	10410	10246-10576	Pinus sp.	wood charcoal	20-30	soil	(2)
Žofínský prales	Mountains	48,66471°N; 14,706462°E	LTL14784A	9830 ±50	11237	11175-11335	Pinus sp.	wood charcoal	40-50	soil	(2)
Žofínský prales	Mountains	48,66471°N; 14,706462°E	LTL14785A	8978 ±75	10089	9795-10258	Pinus sp.	wood charcoal	60-70	soil	(2)
Žofínský prales	Mountains	48,66471°N; 14,706462°E	LTL14786A	6860 ±70	7700	7581-7842	Picea abies	wood charcoal	90-100	soil	(2)
Žofínský prales	Mountains	48,66471°N; 14,706462°E	LTL14752A	after 1950 AD	50	46-54	Abies alba	wood charcoal	4-7	soil	(2)
Žofínský prales	Mountains	48,66471°N; 14,706462°E	LTL14978A	6508 ±45	7426	7319-7504	Picea abies	wood charcoal	20-30	soil	(2)
Žofínský prales	Mountains	48,66471°N; 14,706462°E	LTL14754A	7771 ±50	8547	8430-8633	Picea abies	wood charcoal	40-50	soil	(2)
Žofínský prales	Mountains	48,66471°N; 14,706462°E	LTL14755A	7681 ±50	8473	8391-8561	Picea abies	wood charcoal	60-70	soil	(2)
Žofínský prales	Mountains	48,66471°N; 14,706462°E	LTL15590A	8396 ±55	9425	9292-9522	Pinus sp.	wood charcoal	60-70	soil	(2)
Žofínský prales	Mountains	48,66471°N; 14,706462°E	LTL14756A	319 ±35	388	303-474	Fagus sylvatica	wood charcoal	4-8	soil	(2)
Žofínský prales	Mountains	48,66471°N; 14,706462°E	LTL14757A	8795 ±80	9841	9564-10156	Pinus sp.	wood charcoal	20-30	soil	(2)
Žofínský prales	Mountains	48,66471°N; 14,706462°E	LTL14758A	268 ±40	328	0-465	Picea abies	wood charcoal	40-50	soil	(2)
Žofínský prales	Mountains	48,66471°N; 14,706462°E	LTL14759A	7821 ±50	8602	8455-8767	Picea abies	wood charcoal	60-70	soil	(2)
Žofínský prales	Mountains	48,66471°N; 14,706462°E	LTL14760A	208 ±40	182	0-314	Abies alba	wood charcoal	6-10	soil	(2)
Žofínský prales	Mountains	48,66471°N; 14,706462°E	LTL15591A	6935 ±45	7763	7675-7918	Picea abies	wood charcoal	40-50	soil	(2)
Žofínský prales	Mountains	48,66471°N; 14,706462°E	LTL14764A	343 ±40	395	309-489	Abies alba	wood charcoal	5-10	soil	(2)
Žofínský prales	Mountains	48,66471°N; 14,706462°E	LTL15592A	5540 ±45	6341	6276-6413	Picea abies	wood charcoal	20-30	soil	(2)
Žofínský prales	Mountains	48,66471°N; 14,706462°E	LTL14766A	9489 ±70	10781	10574-11090	Pinus sp.	wood charcoal	40-50	soil	(2)
Žofínský prales	Mountains	48,66471°N; 14,706462°E	LTL14767A	5823 ±45	6631	6503-6735	Picea abies	wood charcoal	60-70	soil	(2)
Žofínský prales	Mountains	48,66471°N; 14,706462°E	LTL14768A	393 ±40	451	316-515	Fagus sylvatica	wood charcoal	10-15	soil	(2)
Žofínský prales	Mountains	48,66471°N; 14,706462°E	LTL14769A	9541 ±70	10894	10608-11142	Pinus sp.	wood charcoal	20-30	soil	(2)
Žofínský prales	Mountains	48,66471°N; 14,706462°E	LTL15593A	8395 ±60	9420	9281-9527	Picea abies	wood charcoal	20-30	soil	(2)
Žofínský prales	Mountains	48,66471°N; 14,706462°E	LTL14770A	9241 ±70	10412	10246-10578	Pinus sp.	wood charcoal	40-50	soil	(2)
Žofínský prales	Mountains	48,66471°N; 14,706462°E	LTL14771A	8874 ±80	9978	9695-10201	Picea abies	wood charcoal	60-70	soil	(2)
Žofínský prales	Mountains	48,66471°N; 14,706462°E	LTL14772A	181 ±45	174	0-303	Abies alba	wood charcoal	10-16	soil	(2)
Žofínský prales	Mountains	48,66471°N; 14,706462°E	LTL14773A	512 ±45	535	496-640	Abies alba	wood charcoal	20-30	soil	(2)
Žofínský prales	Mountains	48,66471°N; 14,706462°E	LTL14774A	9217 ±85	10394	10227-10588	Pinus sp.	wood charcoal	40-50	soil	(2)
Žofínský prales	Mountains	48,66471°N; 14,706462°E	LTL15594A	6292 ±45	7219	7029-7320	Picea abies	wood charcoal	40-50	soil	(2)
Žofínský prales	Mountains	48,66471°N; 14,706462°E	LTL14775A	6000 ±50	6840	6720-6975	Pinus sp.	wood charcoal	60-70	soil	(2)
Žofínský prales	Mountains	48,66471°N; 14,706462°E	LTL14776A	5712 ±45	6502	6408-6633	Picea abies	wood charcoal	80-90	soil	(2)
Žofínský prales	Mountains	48,66471°N; 14,706462°E	DeA-7648	9811 ±56	11227	11136-11338	Pinus sp.	wood charcoal	5-8	soil	(2)
Žofínský prales	Mountains	48,66471°N; 14,706462°E	DeA-7643	582 ±20	606	539-642	Picea abies	wood charcoal	1-5	soil	(2)
Žofínský prales	Mountains	48,66471°N; 14,706462°E	DeA-7645	9468 ±43	10711	10578-11066	Pinus sp.	wood charcoal	6-10	soil	(2)
Žofínský prales	Mountains	48,66471°N; 14,706462°E	DeA-7751	9096 ±46	10245	10189-10388	Pinus sp.	wood charcoal	40-50	soil	(2)
Žofínský prales	Mountains	48,66471°N; 14,706462°E	DeA-7753	8941 ±47	10053	9914-10214	Pinus sp.	wood charcoal	60-70	soil	(2)

Supplementary Table S1 (Continued). List of radiocarbon dates

Curriculum vitæ

Mgr. Přemysl Bobek
Birth: 26.3.1982 in Liberec, Czech Republic
Contact: premysl.bobek@ibot.cas.cz

Education:

- since 2008: Postgraduate studies at the Charles University in Prague, Department of Botany
  Dissertation: Holocene fire dynamics within the Northern Bohemia sandstone landscape Supervisor: doc. RNDr. Petr Kuneš Ph.D.

- 2002-2008: Master's degree at Charles University in Prague, Department of Botany .
  Thesis: Vývoj lesní vegetace Brd v novověku na základě antrakologické analýzy uhlíků z reliktů milířů.
  Supervisor: Mgr. Petr Kočár

Professional experience:

- Institute of Botany, The Czech Academy of Sciences, Laboratory of Paleoecology, since 2017
- The Silva Tarouca Research Institute for Landscape and Ornamental Gardening, since 2016 (half-time)
- Institute of Botany, The Czech Academy of Sciences, Department of GIS and Remote Sensing, since 2009-2016
- Charles University in Prague, Faculty of Sciences, Department of Botany, 2012-2015 (half-time)
- NATURA 2000 field mapping for AOPK
- Botanical field survey for Krkonoše National Park - KRNAP

Research projects

- Dynamika požárů lesní vegetace v pískovcových oblastech Čech a její vliv na současná společenstva, Grantová agentura UK, 2009-2011
- Prostorově vázané historické informace jako podklad pro plánování péče a rozvoj přírodě blízkých lesů v Česko-saském Švýcarsku / Raumbezogene historische Informationen als Grundlage für die Pflege- und Entwicklungsplanung naturnaher Wälder in der Sächsisch-Böhmischen Schweiz, Cíl 3/ Ziel 3, 4/2009 - 03/2012
- Pollen-based land-cover reconstruction - model testing and its implications for Holocene environmental change studies, The Czech Science Foundation, GAP504/12/0649, 2012-2015
- Coppice forests as the production and biological alternative for the future, The Ministry of Education, Youth and Sports, EE2.3.20.0267, 2012-2015
- Indikátory pro hodnocení přírodě blízkého prostředí / Indikatoren zur Bewertung der Naturnähe, *Cíl 3/ Ziel 3*, 2014
- A comparison of related pollen depositions of tundra in central-European mountains and in sub-artic around Abisko, INTERACT - International Network for Terrestrial Research and Monitoring in the Arctic, 2014
- Fire in postglacial Central Europe: neglected historical and present effect in forest dynamics, The Czech Science Foundation, GA14-22658S, 2014-2016
- Stopy katastrofy, která způsobila úhyn velkých savců a klimatické změny před 12 900 lety. The Ministry of Education, Youth and Sports, LK21303, 2013-2015
- Ecosystem engineering and soil complexity in old-growth temperate forests, The Czech Science Foundation, GA16-15319S, 2016-2018
- Late Holocene retrogression of forest ecosystems: Causes, processes and consequences for biodiversity, The Czech Science Foundation, 17-07851S, 2017-2019

- Hidden human prehistoric activities in the mountains. Archaeological and pollen evidence from the Šumava Mountains. The Czech Science Foundation, 17-17909S, 2017-2019

IF Publications:

view at ResearcherID: https://publons.com/researcher/2657975/premysl-bobek/

- Kletetschka G., Vondrák D., Hruba J., Prochazka V., Nabelek L., Svitavská-Svobodová H., **Bobek P.**, Horicka Z., Kadlec J., Takac M., & Stuchlik E. (2018): Cosmic-Impact Event in Lake Sediments from Central Europe Postdates the Laacher See Eruption and Marks Onset of the Younger Dryas. *The Journal of Geology*, 126, 561–575.
- **Bobek P.**, Svitavská H., Werchan B., Švarcová M. G., Kuneš P. (2018): Human-induced changes in fire regime and subsequent alteration of the sandstone landscape of Northern Bohemia (Czech Republic). The Holocene, 28, 427-443.
- **Bobek P.**, Šamonil P., Jamrichová E. (2018): Biotic controls on Holocene fire frequency in a temperate mountain forest, Czech Republic. *Journal of Quaternary Science* 33(8): 892-904.
- Jamrichová E., Hédl R., Kolář J., Tóth P., **Bobek P.**, Hajnalová M., Procházka J., Kadlec J., Szabó P., (2017): Human impact on open temperate woodlands during the middle Holocene in Central Europe. Rev. Palaeobot. Palynol. 245, 55–68.
- Adámek, M., **Bobek, P.,** Hadincová, V., et al. (2015) Forest fires within a temperate landscape: A decadal and millennial perspective from a sandstone region in Central Europe. For Ecol Manage 336:81–90.
- Jamrichová E, Szabó P, Hédl R, Kuneš P**, Bobek P**, Pelánková B. (2013) Continuity and change in the vegetation of a Central European oakwood. The Holocene, 23, 44–54.

Other publications:

view at ResearchGate: www.researchgate.net/profile/Premysl_Bobek

- Hošek J., Lisá L., **Bobek P.,** & Radoměřský T. (2019) "Usselo soils" - the Late Glacial marker horizon identified in the Labe River region (Central Bohemia, Czech Republic). *Geoscience Research Reports*, 52.
- Radomerský T., Kuneš P**., Bobek P.** (2017): Testing the distribution model of Ledum palustre L. using paleoecological data. *Geoscience Research Reports*, 50, 65–71.
- Matoušek V., **Bobek P**. (2017): Mokřinka a Čenkov-Komorsko. Srovnání výsledků systematického mezioborového studia pozůstatků pálení dřevěného uhlí na Křivoklátsku a v Brdech. Archeologie ve středních Čechách, 21, 425-435.
- **Bobek P**., Matoušek V. (2015): Mokřinka. Příspěvek ke studiu pálení dřevěného uhlí v Čechách v novověku. In: Matoušek V., Blažková K. (eds), Les a industrializace, Togga.
- **Bobek., P.** (2013): Dlouhodobý vliv požárů na složení vegetace. In: Seiler, U., Wild, J., (eds) Hist. Waldentwicklung der Sächsisch-Böhmischen Schweiz / Hist. vývoj lesa v Českosaském Švýcarsku. Rhombos-Verlag, Berlin, p 440.
- **Bobek, P.** (2008): Vývoj lesní vegetace Brd v novověku na základě antrakologické analýzy uhlíků z reliktů milířů. Thessis, dep. Katedra botaniky PřF UK.
- Abraham, V., **Bobek, P.**, Pokorný, P. (2007): Forest management and charcoal-burning activities in the modern history of Bohemian Switzerland. - In: Eurasian Perspectives on Environmental archaeology. The 2007 AEA Annual Conference, September 12-15, 2007, Poznan, Poland.
- **Bobek, P.** (2007): Vývoj lesní vegetace Brd v novověku – rekonstrukce na základě antrakologické analýzy uhlíků z reliktů milířů. Bioarcheologie v České Republice – Bioarchaeology in the Czech Republic (ed. by J. Beneš and P. Pokorný), Praha.

Selected conference contributions and Fellowship:

- Expedition: Svalbard 2015. Centrum polární ekologie, Jihočeská univerzita.
- Talk: Inter-regional comparison of the Holocene fire regimes in Bohemia (Czech Republic): spatio-temporal patterns and possible driving forces, 6th International Anthracology Meeting, University of Freiburg, 30.8.-6.9.2015.
- Talk: Fire disturbance regime within temperate forest: multiple-site charcoal and pollen record from the sandstone landscape, 9th European Palaeobotanical Palynological Conference (EPPC), Padova, 26-31 August 2014.
- Talk: Fire disturbance-driven vegetation dynamics under the sandstone landscape conditions in Northern Bohemia, 2nd International Workshop of Pedoanthracology, Kiel, 2013.

- Poster: Paleoekologický záznam v půdním prostředí: lesní vegetace holocénu Českého Švýcarska z pohledu pedoantrakologie X. sjezd České botanické společnosti, 3. – 7. září 2012, Praha

- Talk: Holocene fire dynamics and forest composition in the Elbe Sandstone area, Sandstone Landscape III conference, 25-27.4.2012, Kudowa Zdrój, Poland
- Talk: Holocénní dynamika požárů v pískovcové oblasti Českého Švýcarska, Konference České botanické společnosti Praha 26.-27.11. 2011
- Poster: Soil charcoal in sandstone landscapes - XVIII. INQUA Congress - the International Union for Quaternary Research, Bern, 21.-27.6.2011
- Poster: Holocénní dynamika požárů v oblasti NP Českosaské Švýcarsko, 3. konference České společnosti pro ekologii, Kostelec nad Černými lesy 21.–23. 10 2011.
- Poster: Wildfire in Bohemian Switzerland NP (Czech Republic): long-term dynamics and the impact on forest vegetation - BES Annual Symposium 2011: Forests and Global Change, University of Cambridge, 28 – 30.3.2011
- Poster: Wildfire in Bohemian Switzerland NP (Czech Republic): long-term dynamics and the impact on forest vegetation - 10th meeting on vegetation databases: Vegetation databases and spatial analysis, Freising, 19-21.9.2011
- Poster: Holocene fire dynamics and forest composition of Northern Bohemia sandstone areas - 5th International Meeting of Charcoal Analysis, Valencia, 5.-9.9.2011
- Poster: Reconstruction of modern woodland history revealed from anthracological studies of charcoal kiln sites in Brdy Mountains, Central Bohemia – Frontiers in Historical Ecology, Birmensdorf, 30.8.-2.9.2011
- Talk: 6. konference environmentální archeologie: Název příspěvku: Holocenní dynamika požárů lesní vegetace v NP České Švýcarsko
- Trees and Forests as Archives of Last Millenium Climate, 24-26 April 2008 in Gliwice-Niepolomice, Poland