Detecting ecological signatures of long-term human activity across an elevational gradient in the Šumava Mountains, Central Europe

Vachel Kraklow, Dagmar Dreslerová, Andrei-Cosmin Diaconu, Alice Moravcová, Martin Kadlec, Daniel Nývlt, Willy Tinner, Marco Heurich, Walter Finsinger, Angelica Feurdean, et al.

Kraklow VA, Dreslerová D, Diaconu A-C, Moravcová A, Kadlec M, Nývlt D, Tinner W, Heurich M, Finsinger W, Feurdean A, *et al.* 2024. Detecting ecological signatures of long-term human activity across an elevational gradient in the Šumava Mountains, Central Europe. *Quaternary Science Reviews* **344**: 108944.

Detecting ecological signatures of long-term human activity across an elevational gradient in the Šumava Mountains, Central Europe

Vachel A. Carter[*1,2,3], Dagmar Dreslerová[4], Andrei-Cosmin Diaconu[5], Alice Moravcová[1], Martin Kadlec[6], Daniel Nývlt[6], Willy Tinner[7], Marco Heurich[8,9,10], Walter Finsinger[11], Angelica Feurdean[12], Petr Kuneš[1], Gabriela Florescu[1,13]

[1] Department of Botany, Charles University, Prague, Czechia
[2] Department of Geography, University of Utah, Salt Lake City, Utah, USA
[3] Earth and Environmental Sciences Division, Los Alamos National Laboratory, Los Alamos, NM, USA
[4] Institute of Archaeology of the Czech Academy of Sciences, Praha, Czechia
[5] Department of Geology, Babeş-Bolyai University, Kogalniceanu, 1, 400084, Cluj-Napoca, Romania
[6] Department of Geography, Masaryk University, Brno, Czech Republic
[7] Institute of Plant Sciences and Oeschger Centre for Climate Change Research, University of Bern, Switzerland
[8] Department of National Park Monitoring and Animal Management, Bavarian Forest National Park, Freyunger Str. 2, 94481 Grafenau, Germany
[9] Chair of Wildlife Ecology and Management, Faculty of Environment and Natural Resources, University of Freiburg, Tennenbacher Straße 4, 79106 Freiburg, Germany
[10] Institute of Forestry and Wildlife Management, Inland Norway University of Applied Science, NO-2480 Koppang, Norway
[11] ISEM, University of Montpellier, CNRS, IRD, Montpellier, France
[12] Department of Physical Geography, Goethe University, Altenhöferallee 1, 60438 Frankfurt am Main, Germany
[13] Department of Geography, Stefan cel Mare University of Suceava, Romania

*Corresponding author: vachel.carter@gmail.com

Written for: Quaternary Science Reviews

Keyword: peat bog, testate amoebae, water table depth, hydroclimate, fire, pollen, plant macrofossils, climate change, human impact, Holocene, generalized additive models

Abstract

Central European mountains, including the Šumava Mountains located along the Czechia/Germany border, have a long and rich anthropogenic history. Yet, documenting prehistoric human impact in central European mountain environments remains a challenge because of the need to disentangle climate and human-caused responses in terrestrial systems. Here, we present the first reconstructed water table depths (WTDs) from two sites, Pěkná and Blatenská slať, located in the Šumava Mountains. We compare these local hydroclimate records with new and published pollen, non-pollen palynomorphs (NPPs), plant macrofossils, geochemistry and archeological records to investigate how hydroclimate and human activities impacted forest succession and fire activity throughout the Holocene across an elevational gradient. Using a generalized additive model, our results suggest that changes in forest succession and fire activity have been primarily caused by climate throughout the Holocene. However, humans have been utilizing mountain environments and their resources continuously since ~4600–4250 cal yr BP, thus playing a secondary role in modifying forest succession to increase resources beneficial to both humans and grazers. Over the last 1000 years, we provide evidence of directly observed human-caused modifications to the landscape. These results contribute to a growing body of literature illustrating human activities and landscape modifications in central European mountains.

1. Introduction

European mountain environments have a long and rich history with humans, particularly the Alps and Carpathians (Schmidl et al., 2005; Lutz and Pernicka, 2013; Geantă et al., 2014; Kothieringer et al., 2015; Feurdean et al., 2016; Schumacher et al., 2016; Finsinger et al., 2018; Gilck and Poschlod, 2019; Carter et al., 2020; Florescu et al., 2024). For example, alpine farming in the Alps has been a beneficial style of land use after 7000–6500 cal yr BP, with the most unambiguous evidence starting ~4200 cal yr BP, due to the vast open grasslands which were utilized by humans and livestock during the summer season (Hafner and Schwörer, 2018; Gilck and Poschlod, 2019; Tinner, 2023; Tinner et al., 2023). In the Carpathians, mountain farming has been documented since ~4400–3500 cal yr BP across a wide spectrum of elevations (Geantă et al., 2014; Feurdean et al., 2016; Feurdean et al., 2017; Lestienne et al., 2023). However, despite having a rich archeological history in the lowlands, it is believed that human impact in Central European mountains with lower elevations was less intense than in other European mountains (Rösch, 2000; Robin et al., 2013; Henkner et al., 2018) likely because of local contingencies, including the occurrence of denser forests and the lack of a treeless alpine zone (Dreslerová et al., 2020a). Documenting prehistoric human impact in Central European mountains remains a challenge, which inhibits our ability to assess potential legacies of past environmental changes, including past land uses, on contemporary forest structure and function (Willis and Birks, 2006), which ultimately also influence modern forest succession (Josefsson et al., 2009).

One of Central Europe's largest forested landscapes is located along the Czechia-Germany border (Šumava National Park, Czechia, and Bavarian Forest National Park, Germany). Together, both National Parks form the great Bohemian Forest Ecosystem and are part of the Natura 2000 network and UNESCO Biosphere Reserve, which was established to protect the most endangered flora and fauna in Central Europe (Krzystek et al., 2020). Upper Palaeolithic and Mesolithic archeological sites have been found at high elevations in the Šumava Mountains (Dreslerová et al., 2020b), with pollen taxa indicative of human activity documented since the Neolithic (Svobodová et al., 2001; Svobodová et al., 2002; Carter et al., 2018a) illustrating that the region has a long archeological history, making it an ideal place to investigate the extent of human impact on the landscape (Kozáková et al., 2020). However, there appears to be a boundary of ~600 m asl separating sub-montane settlements from non-settled land which is associated with suitable agropastoral farming (Dreslerová et al., 2020a).

Previous paleoecological studies from the region have investigated long-term anthropogenic impacts in the Šumava Mountains (Carter et al., 2018a; Kozáková et al., 2020). Using a macrophysical climate model to reconstruct local climate, Carter et al. (2018a) suggest increased fire activity in the early Holocene was likely driven by climate, despite archeological evidence illustrating high populations of Mesolithic communities in the region. Additionally, Carter et al., (2018a) suggest that increased fire activity ~2500 cal yr BP was not climatically-driven, but instead a result of increased anthropogenic activities which agrees with recent research by Kozáková et al. (2020) who found increasing anthropogenic impact, including fire activity, since the Late Bronze and Iron Ages. Both studies suggest that changes in forest succession since the last millennia were likely due to increasing human activities. However, validating anthropogenic impacts from paleoecological records from the Šumava Mountains has been challenging because of the lack of local proxy-based records of climate which are needed to disentangle climate vs anthropogenically-induced changes. The only local record of climate that exists from the Šumava Mountains spans the Late Glacial-Early Holocene transition (Mateo-Beneito et al. 2024). While the macrophysical climate model attempted to separate any anthropogenic signature from climatically-driven events (Carter et al., 2018a), until now, no local record of Holocene climate exists from the Šumava Mountains making it difficult to validate that changes in forest succession and fire activity are driven by human activity, and not from climate.

To fill in this gap, we present the first records of hydroclimate associated with long-term climate changes. Specifically, we present reconstructed water table depths (WTDs) from two new peat bog records, one from a mid-elevation locality located near the 600 m asl agropastoral boundary (Pěkná, 730 m asl), and one from a high elevation locality (Blatenská slať, 1275 m asl) to investigate whether the ecological impact of human activities varied spatially across an elevation gradient. Ombrotrophic peat bogs are excellent recorders of past hydrological changes due to their surface being directly coupled to rainfall, temperature, and humidity (Blackford, 2000). As

such, these depositional environments may be useful in disentangling climate versus anthropogenically-induced changes in vegetation assemblages and fire regimes. By comparing a local record of climate (via testate amoebae reconstructed WTDs) with new and published pollen, non-pollen palynomorphs (NPPs), plant macrofossils, geochemistry (see Schafstall et al., 2024) and archeological records, we aim to determine how 1) Holocene hydroclimate patterns varied across an elevational gradient and how changes in hydroclimate impacted forest succession and fire activity throughout the Holocene, and 2) whether changes in forest succession and fire activity were caused by climate and/or humans.

2. Study Sites

Pěkná (48°50'26.451", 13°56'14.9922") is a mid-elevation (730 m asl) peat bog located in an open valley near the village of Pěkná on the southern margin of the Šumava National Park (Figure 1). Pěkná is comprised of three bogs that span an area of 1.38 km^2, with the coring locality being located in the middle bog; the middle bog's area is 0.7 km^2. The peat bog is ~50 m from the Vltava River and ~5 km from Lipno reservoir. Pěkná is located <12 km from known Mesolithic and Bronze Age archeological sites and is roughly ~15 km from the nearest historic trading route (Dreslerová et al., 2020b). Local vegetation consists of mostly bog pine (*Pinus rotundata*), with *Betula pubescens*, *Pinus sylvestris*, and *Picea abies* towards the bog edge. Herb and shrub vegetation consists of *Sphagnum* sp., *Vaccinium* sp., *Eriophorum vaginatum*, *Andromeda polifolia*, *Oxycoccus palustris*, and *Melampyrum*.

By contrast, Blatenská slať (48°58′19.227″N, 13°27′18.699″E) is a high elevation (1275 m asl) raised peat bog located at the highest point in the Modravské slatě bog complex saddled between Blatný vrch peak and Studená hora peak near the village of Modrava (Schafstall et al., 2024) (Figure 1). The bog, with a size of 0.71 km^2, includes two large and several smaller peatland ponds. Blatenská slať is located <10 km from known Mesolithic archeological sites and is roughly ~10 km from the nearest historic trading route. Blatenská slať is approximately 33 km from the Pěkná peat bog. Local vegetation is covered by hummocks and hollows comprised of *Andromedo polifoliae- Sphagnetum magellanici* with marginal zones formed by *Pinus unicinata* subsp. *uliginosa* (Neuman) Businsky and shrub layers of *Vaccinium myrtillus*. Towards the bog edge and regionally, *Picea abies* dominates with a stand of *Abies alba* ~2 km away (Schafstall et al., 2024).

3. Methods

3.1 Core retrieval

In June 2019, sediment cores were extracted from Pěkná, and in October 2019, sediment cores were extracted from Blatenská slať. For Pěkná, a 419 cm composite sediment profile composed of two cores (PEK1 and PEK2) was extracted from the center of the Pěkná peat bog (48.8420614 N, 13.9382436 E). PEK 1 was extracted using a prototype percussion corer with a sediment chamber of 3 m in length and 10 cm in diameter, and PEK 2 with a modified Livingstone piston

corer with a sediment chamber of 1 m in length and a diameter of 6 cm (Merkt and Streif, 1970). The upper-most 254 cm of continuous, undisturbed peat was collected from the first core (PEK1), and the lower portion of the composite profile (165 cm) was collected from PEK2. Core correlation was done on the overlapping sequence based on visual peat stratigraphy and magnetic susceptibility data. Peat cores were transported to Charles University where they were subsampled at 1 cm intervals for paleoecological analysis.

For Blatenská slať, two parallel cores (BL1 and BL2) totaling 319 cm in depth were collected from the center of Blatenská slať using a modified Livingstone piston corer (see Schafstall et al., 2024 for further details).

3.2 Geochronology and Radiocarbon dating

For Pěkná, peat age-depth relations were established using thirteen ^{14}C dates of bulk peat and macrofossils and a ^{210}Pb series using a Bayesian method in rbacon package in R (Blaauw and Christen, 2011) (see Table 1). All ^{14}C dates were calibrated using the IntCal20 dataset (Reimer et al., 2020) (Figure 2). All measured ages were included using a Student-t distribution for ^{14}C ages and a normal distribution for ^{210}Pb ages. Based on lithology, two sedimentation zones were implemented in the age-depth model by adding a boundary at 350 cm and constraining their mean accumulation rate by 20 yr/cm for the upper part and 50 yr/cm for the lower part. The age-depth model partitioned the core into 85 sections, estimating the accumulation rate for each segment using a Markov Chain Monte Carlo (MCMC) approach.

For Blatenská slať, twelve ^{14}C dates of bulk peat and macrofossils, and a ^{210}Pb series were used to create peat age-depth relations (for details see Schafstall et al., 2024). All ^{14}C dates from both sites were analyzed at Isotoptech Zrt. located in Debrecen, Hungary, and the ^{210}Pb profile was analyzed at the Faculty of Science, Institute of Geochemistry, Mineralogy and Mineral Resources, Charles University.

3.3 Testate Amoebae analysis and water table reconstruction

Testate amoebae were used to reconstruct water table depth (i.e., groundwater levels) at both sites. Testate amoebae were analyzed at 3–5 cm intervals for both Pěkná and Blatenská slať using 1 cm^3 of sediment per sample. The samples were prepared following standard procedures (Hendon and Charman, 1997). At least 150 testate amoebae shells were counted and identified at each level under a stereomicroscope at 400× magnification using available taxonomic classifications (e.g. Mazei and Tsyganov, 2006). The quantitative reconstruction of water table depth was obtained using the pan-European transfer function of Amesbury et al. (2016).

3.4 Analysis of paleoclimate simulations

Following Schafstall et al. (2024), we retrieved simulated climatic variables (mean annual temperature (MAT °C), temperature of the wettest quarter of the year (T WetQ (°C)), and

precipitation of the wettest quarter of the year (WetQ PP (mm)) for the past 12,500 years from the CHELSA climate database (Karger et al., 2023). All data were first cropped to a 1 km window around Pěkná and Blatenská slat', and then the resulting values were extracted from .tif files using R statistical software (R Core Team, 2023).

3.5 Geochemical analysis and magnetic susceptibility

Geochemistry and magnetic susceptibility were used to investigate erosional and depositional activity at both sites. Elemental composition was determined using X-ray fluorescence spectroscopy (XRF). Individual dried (at 37 °C) samples in plastic bags were analyzed with a hand-held Innov-X DELTA analyzer in Geochem-Vanad mode. The total measurement time (6 minutes) was automatically divided into two phases: heavy elements (beam 40 kV) and light elements (beam 10 kV). Similarly, magnetic susceptibility was measured on the same samples. Using the Kappabridge MFK1-FA (AGICO, Inc.), which allows directly measuring mass-specific magnetic susceptibility (χ), the samples were analyzed at two frequencies (low 976 Hz and high 15,616 Hz) with an induced magnetic field of 200 $A \cdot m^{-1}$. Low-frequency magnetic susceptibility (χ_{LF}) and high-frequency magnetic susceptibility (χ_{HF}) were then obtained, but we only present χ_{LF}. We then verified through experimentation that plastic bags do not affect the mentioned analyses. In both cases, the values are many orders of magnitude lower, as they are made of diamagnetic material and thus do not significantly skew the results.

For both sites, heavy metal and carbonate-related elements (i.e., Fe, Ca, Pb) were normalized with Zr, which is the most stable lithogenic element within our record, to differentiate the source of Fe and Ca since these elements can have both authigenic and allogenic origin (Engstrom and Wright, 1984; Boyle, 2001). We also used the ratio, Rb/Sr, as an indicator of weathering intensity in each catchment (Chen et al., 1999).

3.6 Pollen, coprophilous fungi, plant macrofossils, and pollen richness and diversity

Pollen analysis was used to reconstruct regional changes in vegetation at Pěkná and Blatenská slať. Pollen analysis was conducted contiguously at 2 cm resolution from both sites (see Schafstall et al., 2024). Pollen processing utilized acid-base rinse procedures following Faegri et al. (1989) using 1 cm^3 of sediment per sample. For both Pěkná and Blatenská slať, two *Lycopodium* tablets (X=9,666 grains/tablet, Batch #3862) were added to each sample prior to pollen processing and used as an exotic tracer to calculate both pollen concentration (grains cm^3) and pollen accumulation rates (pollen influx; grains cm^{-2} yr^{-1}) (Stockmarr, 1972). A minimum of 500 terrestrial pollen grains were identified at a magnification of 400× with the aid of identification keys (Beug, 2004; Punt, 1976–1996). Pollen counts were converted into pollen percentages based on the abundance of each pollen type relative to the sum of all identified terrestrial pollen. To investigate anthropogenic influences at Pěkná and Blatenská slať, we used anthropogenic pollen indicators (Behre, 1981, 1988; Behre et al., 2023) which were grouped following Deza-Araujo et al., 2020: (i) primary anthropogenic indicators (cultivars), (ii)

adventive anthropogenic indicators (plants introduced with agriculture), and (iii) apophytes (native plant species favored by human activities) (Table 2). We also used the ratio of arboreal (AP) to non-arboreal pollen (NAP) to investigate canopy openness. A ratio of pioneer species (*Pinus* + *Betula*) to late-successional species (*Picea abies* + *Abies* + *Fagus*) was also used to investigate trends in forest succession over time. Additionally, coprophilous fungi spores (*Podospora*, *Sordaria*, *Tripterospora*, and *Sporormiella*) were used to identify grazing by domestic or wild herbivores (Baker et al., 2013).

Plant macrofossil analysis was used to explore changes in local vegetation assemblages. For both sites, plant macrofossils were analyzed using a stereomicroscope at a magnification of 15–50× and were identified with the aid of identification keys (Cappers et al., 2006; Bojňanský and Fargašová, 2007; Katz et al., 1977; Tomlinson, 1985) and the herbarium collection at Charles University. For Pěkná, macrofossils analysis was conducted every 2–3 cm and concentrations of plant macrofossils were adjusted to a constant volume of 15 cm^3 using procedures described by Birks (2007). For Blatenská slať, macrofossil analysis was conducted every 2 cm on average, with the top 14 cm pooled into one sample due to low sample size (see Schafstall et al., 2024). Plant macrofossils were not adjusted to a constant volume, and instead were presented as percentages, not concentrations.

To investigate biodiversity dynamics at each site, we calculated pollen-assemblage richness and diversity (Hill, 1973) following Finsinger et al. (2017). Specifically, we calculated N0, which is the total number of taxa in an assemblage, N1 which is the number of common taxa, and N2 which is the number of dominant taxa (Hill, 1973). Instead of using an analytical approach (Birks and Line, 1992), we resampled randomly and without replacement the pollen counts 1000 times to the smallest sample size (here n =177 for Pěkná, and 514 for Blatenská slať) prior to estimating N0, N1, and N2, to provide mean estimates and 95% confidence intervals of N0, N1, and N2 (Felde et al., 2016). Evenness was estimated as the ratio of dominant taxa relative to all taxa present in an assemblage using the N2/N0 ratio (Birks et al., 2016a). Pollen-assemblage richness and diversity were calculated following Finsinger et al., (2017) using the 'vegan' package (Oksanen et al., 2016) in R (R Core Team, 2023).

3.7 Charcoal analysis

Microscopic-charcoal was counted simultaneously with pollen analysis on the pollen slides (Finsinger and Tinner, 2005) at a magnification of 400× and was used to reconstruct regional fire activity (Tinner et al., 1998). Microscopic charcoal counts were transformed to concentrations (particles cm^{-3}) and charcoal accumulation rates (CHAR; the number of particles cm^{-2} yr^{-1}) using the software program, Tilia (Grimm, 2004). Macroscopic charcoal was used to reconstruct local-to-regional fire activity at Pěkná and Blatenská slať. Macroscopic charcoal was analyzed at 1 cm resolution at Pěkná and 0.5 cm resolution at Blatenská slať using sub-samples of 2 cm^3 from each site. Samples from both sites were left in 10 ml of sodium hexametaphosphate for 24

hr to disaggregate organic matter, and then 5 ml of sodium hypochlorite (10% NaOCl) to bleach non-charred material. Macroscopic charcoal was gently sieved through a 125 μm sieve and was analyzed using a stereomicroscope at a magnification of 15–50×.

Macrocharcoal morphologies were used to reconstruct the type of biomass burned from each site (i.e., a qualitative metric of fuel burnt/fire intensity) (Umbanhowar and Mcgrath, 1998; Enache and Cumming, 2006). Macrocharcoal morphologies were identified following Enache and Cumming (2006) and Mustaphi and Pisaric (2014), and were classified as wood, herb, grass and undifferentiated. Macroscopic charcoal counts, including macrocharcoal morphologies, were transformed to concentrations (particles cm^{-3}) and charcoal accumulation rates (CHAR; the number of particles cm^{-2} yr^{-1}). Macroscopic charcoal counts were then broken into a low-frequency component, known as charcoal background (BCHAR), and a peaks component (CHARpeak) using an interpolated temporal resolution of 30-years $sample^{-1}$ (for Pěkná) and 35-years $sample^{-1}$ (for Blatenská slať) using the program, CharAnalysis (Higuera et al., 2009). BCHAR was determined using a robust LOWESS regression with a moving-window width of 900 years (for Pěkná) and 1000 years (for Blatenská slať) which resulted in a robust signal-to-noise index (SNI) > 3.0 (Kelly et al., 2011). CHARpeak values were calculated as residuals from BCHAR and were separated from the background noise with a locally defined threshold using the 99th percentile of a Gaussian mixture model. The identified CHARpeaks were then screened with a minimum count peak-screening test (Higuera et al., 2010).

3.8 Statistical Analyses

To disentangle climate versus human-induced activities across an elevational gradient, we used a multivariate generalized additive model (GAM; Hastie and Tibshirani, 1986) implemented in the 'mgcv' package (Wood, 2006). To account for the high temporal variability within each of the time-series, all datasets were first binned into 100-year intervals by taking the average of each binned window. We then tested the relationships between hydroclimate (i.e., WTD) and humans (i.e., the sum of primary and adventive pollen indicators) set as the predictor variables, and different response variables that document changes in vegetation, fire and geochemistry. Additionally, because many of the primary and adventive pollen indicators are included in the NAP sum, we removed these taxa from the NAP sum to ensure these taxa were not biasing the GAM results. In each simulation, we used a Gaussian distribution with an identity link function.

A principal component analysis (PCA) was used to describe the main features of the palynological record and assess whether the primary, adventive and apophyte pollen taxa clustered together. Correlation matrices were used using PAST software (Hammer et al., 2001).

4 Results

4.1 Chronology and core lithology

The calibrated modeled mean basal age for Pěkná is 12,600 cal yr BP (Figure 2). Peat deposition rates were relatively steady with a mean of 30 years per centimeter throughout the entire record. The lower unit of the Pěkná peat core (12,640-11,430 cal yr BP) contains *Carex* peat with decomposed fragments of ligneous and herbaceous materials along with fine and coarse sand (SI Figure 1). Sand disappears from the Pěkná peat core ~11,279 cal yr BP and *Carex* continues to dominate until ~8850 cal yr BP. A transition to *Eriophorum* peat was recorded at 8850 cal yr BP until ~7900 cal yr BP. *Sphagnum* peat with *Eriophorum* then dominates until 6500 cal yr BP, and then switches to *Eriophorum* peat until 2500 cal yr BP. Brief episodes of *Sphagnum*-dominated peat occurred during that time frame, specifically between 5400–5200 cal yr BP and 4700–3900 cal yr BP. The profile then briefly switches to *Sphagnum* peat ~2500 cal yr BP until 1700 cal yr BP when it returns to *Eriophorum* peat mixed with Ericaceae roots until ~500 cal yr BP. The last 500 years have been *Sphagnum*-dominated peat (SI Figure 1).

The calibrated basal age for Blatenská slat' is 7300 cal yr BP (Schafstall et al., 2024). Peat deposition rates were relatively steady with a mean of 20 years per centimeter throughout the entire record. The lithology of the Blatenská slat' is mainly comprised of reddish brown or dark brown slightly fibrous decomposed material, except between 4800–4450 cal yr BP (depths ~182–210 cm) and the last ~100 years (i.e., the top 10cm), which is comprised of slightly reddish/dark brown undecomposed peat (see Schafstall et al. 2024). *Sphagnum medium/S. divinum* dominates throughout the entire profile, with *S. cf angustifolium* only being present from 7300–2000 cal yr BP (SI Figure 2). *Sphagnum fuscum* and *S.* sect. *acutifolia* are also only present between 5500–4500 cal yr BP.

4.2. Reconstructed water table depth

At Pěkná, reconstructed WTDs were low, ranging between 28–20 cm below the peat surface starting ~10,500 until 7500 cal yr BP, with a period of extremely low values ~28–27 cm between 9750–9200 cal yr BP (Figure 3). *Cryptodifflugia oviformis* and *Cryptodifflugia pusilla* are high between 12,500–8000 cal yr BP before decreasing; in the case of *C. pusilla* it disappears from the record entirely (SI Figure 3). Around 8000 cal yr BP, *Archerella flavum* and *Assulina muscorum* increase and dominate along with *D. pulex*. Other taxa that appear ~8000–7500 cal yr BP include *Arcella catinus*, *Assulina seminulum*, *Bullinularia indica*, *Heleopera petricola*, and *Hyalosphenia elegans*. WTDs increased starting ~7500 cal yr BP and remained relatively high, oscillating between 18-10 cm until ~1600 cal yr BP before decreasing again in conjunction with *Archerella flavum* and *Assulina muscorum* dominance. WTDs remained low between 1600–0 cal yr BP, ranging between 24–20 cm in conjunction with *Cryptodifflugia oviformis* dominance, before quickly increasing again over the modern period.

At Blatenská slať, reconstructed WTDs show similar patterns as Pěkná, with generally higher values (between 18–8 cm) between 7300–2200 cal yr BP in conjunction with *Archerella flavum* dominance (SI Figure 4). WTDs decrease ~2200 cal yr BP and remain low, ranging between 26-

24 cm until ~400 cal yr BP in conjunction with a rise in *Cryptodifflugia oviformis* and *Nebela militaris* dominance. WTDs slightly increased over the last few centuries to 16 cm.

4.3. Reconstructed minerogenic component changes

At Pěkná, minerogenic input (Rb/Sr) was very strong between 12,600–11,000 cal yr BP and again between 9500–8200 cal yr BP (Figure 3). Minerogenic input has also increased since the turn of the 20th century. Authigenic Ca and Fe (Ca/Zr and Fe/Zr) both increase ~10,500 cal yr BP (Figure 3). However, the increase in Ca is short-lived while Fe remains high until ~6200 cal yr BP. Authigenic Ca increases again between 8000–5500 cal yr BP and over the last 500 years. Pb/Zr has only been present at high values in the last 2000 years. χ_{LF} shows several sporadic erosional events ~7200, 6000 and 3000 cal yr BP, before increasing over the last 1000 years (Figure 3).

At Blatenská slať, minerogenic input is generally low until ~4500 cal yr BP, then sporadically fluctuates until ~2500 cal yr BP before remaining high until present (Figure 3). Authigenic Ca and Fe are both high at the onset of the record until ~4500 cal yr BP when both decline. Ca increases again between ~3300–2000 cal yr BP and then between 500–100 cal yr BP. Pb/Zr is only present, at high values, over the last 1000 years. χ_{LF} shows relatively high erosional activity between 7300–4200 cal yr BP and then a dramatic increase over the last 50 years (Figure 3).

4.4 Reconstructed vegetation history

Locally, the Pěkná peat bog was dominated by *Carex* (*C. rostrata*, *C. cf. canescens*, *C. cf. elata*, *C.* sp.) from 12,600–8000 cal yr BP before transitioning to *Eriophorium vaginatum* (SI Figure 5). *Eriophorium vaginatum* macrofossils were consistently present throughout the entire record. Regionally, pioneer species, *Pinus* and *Betula* pollen, dominated the forest canopy at Pěkná between 12,642–7500 cal yr BP, averaging 42% and 13%, respectively. The AP:NAP ratio was low during the same time frame, but increases and remains high between 8200–1000 cal yr BP (Figure 4). *Picea abies* pollen percentages begin to increase ~8500 cal yr BP, and rise to dominance between 8500–3500 cal yr BP, ranging between 20%–73%. Between 3500 and -42 cal yr BP, *Picea abies* pollen percentages increase averaging 19% of the total pollen rain, and then increase to an average of 30% over the last 70 years. *Corylus* pollen is present at Pěkná, but at relatively low percentages (average of 13%) between 12,642–6150 cal yr BP. The Pioneer:Successional ratio begins to decrease ~8500 cal yr BP, switching to a successional-dominated forest ~7300 cal yr BP. *Corylus* pollen decreases ~6050 cal yr BP, ranging from 1–9% from 6050 cal yr BP present. *Fagus* pollen begins to increase ~7950 cal yr BP, remaining <5% of the total pollen rain between 7950–6400 cal yr BP. *Fagus* pollen increases and fluctuates between 8%-23% between 6400–280 cal yr BP, and then decreases to <5% of the total pollen rain until the present. *Abies* pollen first appears ~6350 cal yr BP and averages <3% of the total pollen rain until ~5500 cal yr BP. *Abies* then increases to an average of 18% between 5500–650 cal yr BP before decreasing to <2% at present. *Pinus* undiff. pollen percentages begin to increase

~3500 cal yr BP, averaging 20% until ~1150 cal yr BP, and then increasing dramatically to an average of 34% in the last millennia (reaching a maximum of 51% at the turn of the 20th century). AP:NAP decreases over the previous 1000 years, overlapping with an increase in Pioneer:Successional values at Pěkná. Rarefied pollen richness (N0) shows generally low values throughout the entire record, except for over the last 1000 years (Figure 4). Pollen evenness (N2/N0) shows elevated diversity between 9000–7500 cal yr BP and again between 4000–1000 cal yr BP. Apophyte percentages have been present since the onset of the record, with high percentages (>2%) between 12500–11000 cal yr BP and again over the last 1500 years, peaking at 8% ~74 cal yr BP. Whereas adventive pollen percentages were first documented ~11,150 cal yr BP, which was one finding of *Polygonum aviculare*-type (SI Figure 5). Adventives, being comprised primarily of *Plantago lanceolata*, appear consistently starting ~4600 cal yr BP at low values (<1%) before peaking ~2% at 150 cal yr BP. Primary pollen indicators first appear 1450 cal yr BP with the arrival of *Secale*, and peak ~3% ~260 cal yr BP. Coprophilous fungi were found at Pěkná but in low percentages (<2%). *Sordaria* was the most common coprophilous fungi sporadically found; ~8500 and 8000 cal yr BP, between 3500–750 cal yr BP, and over the last 500 years. *Podospora* was also found but was less common than *Sordaria*; ~4800 cal yr BP, ~2500 cal yr BP, and in the last 300 years. *Tripterospora* was found at 3750 cal yr BP and again sporadically between 400–74 cal yr BP.

At Blatenská slať, the local peat bog was dominated by *Sphaghnum medium/divinum* and *Eriophorium vaginatum* the entire Holocene, with occasional findings of *S.* cf. *angustifolium*, *S.* sect. *Acutifolia*, *S. fuscum, S. majus* and *S.* sect. *Subsecunda* (SI Figure 2). Regionally, *Pinus* pollen percentages are high (maximum of 68%) at the onset of the Blatenská slať record, which overlaps with high Pioneer:Successional values (Figure 4). *Pinus* pollen then dramatically declines to 30% ~7200 cal yr BP as *Picea abies* pollen continues to rise to dominance, averaging 63% between 7200–4250 cal yr BP. *Fagus* pollen is present but low (<6%) at the onset of the record until ~6600 cal yr BP, and then increases to an average of 16% until the last 100 years. *Fagus* pollen then decreases to an average of 7%. *Abies* pollen average <2% between 7300–4600 cal yr BP and then dramatically increases to an average of 27% (maximum of 60%) between 4600–250 cal yr BP. *Abies* pollen percentages average 6% over the last 200 years. High AP:NAP values occur between 6500–4300 cal yr BP, with a brief increase ~5500 cal yr BP. Low AP:NAP values occur between 4300–2200 cal yr BP and again over the last 1000 years, while high AP:NAP values briefly occur between 2200–1000 cal yr BP (Figure 4). Low Pioneer:Successional values are documented between 6500–1500 cal yr BP, with a short-lived increase in values centered ~4200 cal yr BP. Pioneer:Successional values then increase and remain high until present. Rarefied pollen richness (N0) at Blatenská slať shows generally higher values ~7300–5000 cal yr BP, 4000–3000 cal yr BP and again over the last 1000 years (Figure 4). Pollen evenness (N2/N0) shows a general increasing trend in diversity over time until ~1000 cal yr BP when pollen evenness declines. Apophyte percentages have been present since the onset of the record, with peaks >2% between 4000–3000 cal yr BP and over the last 1000 years.

Additionally, adventives, which are comprised primarily of *Centaurea cyanus* and *Plantango lanceolatea,* have been present since the onset of the record, however, have been consistently present since ~4250 cal yr BP. Primary pollen indicators first appear ~5550 cal yr BP with one finding of *Cannabis*. However, primary pollen indicators have been consistently present starting ~950 cal yr BP. *Sordaria* was sporadically found ~6500 cal yr BP and over the last 1000 years. *Podospora* was only found ~6500 and ~4200 cal yr BP.

4.5 Reconstructed fire history

At Pěkná, local biomass burning (i.e., CHAR) was generally low throughout the record, except between 8500–7000 cal yr BP, ~6600 cal yr BP and ~5800 cal yr BP when biomass burning increased (Figure 7). Fire frequency was at its maximum ~10,500 cal yr BP. Fire frequency ranged from 2–3 fires/1000 years between 8000–3500 cal yr BP before declining to <1 fire/1000 years at present. Charred macrofossils and microCHAR generally follow the same pattern as CHAR (Figure 7). The analysis of morphology-based fuel types revealed that wood CHAR dominated with an average of 0.07 particles cm^{-2} yr^{-1} throughout the record (Figure 7), reaching a maximum of 2.7 particles cm^{-2} yr^{-1} at ~5550 cal yr BP. Grass CHAR averaged 0.07 particles cm^{-2} yr^{-1} the entire record, reaching a maximum ~8100 cal yr BP. Other noticeable grass CHAR events occurred ~6300 cal yr BP, ~6250 cal yr BP, and 5550 cal yr BP. Herb CHAR averaged 0.22 particles cm^{-2} yr^{-1} throughout the record with seven peaks greater than 2 particles cm^{-2} yr^{-1}; ~7600, ~ 8670 cal yr BP, ~8000 cal yr BP, ~7650 cal yr BP, ~7700 cal yr BP, ~7660, and ~8650.

At Blatenská slať, local biomass burning was low throughout most of the Holocene, except at the onset of the record ~7250–6500 cal yr BP (Figure 7). Fire frequency was high for this site at the onset of the record between 7250–5650 cal yr BP and again over the last 250 years. Between 3700–2400 cal yr BP, fire frequency declined to 0 fires/1000 years. Only six fire episodes were detected from the Blatenská slať record. Wood CHAR averaged 0.1 particles cm^{-2} yr^{-1} throughout the record with a maximum of 0.27 particles cm^{-2} yr^{-1} at 6500 cal yr BP (Figure 7). Grass CHAR averaged 0.01 particles cm^{-2} yr^{-1} throughout the record with a peak at ~6500 cal yr BP. Finally, Herb CHAR averaged 0.1 particles cm^{-2} yr^{-1} with a maximum ~7000 cal yr BP. No charred macrofossils were identified from Blatenská slať during macrofossil analysis. Regionally, biomass burning also follows a similar pattern as CHAR (Figure 7).

4.6 Generalized Additive Models

4.6.1. Climate response curves

When investigating the response between hydroclimate and forest succession variables, response curves illustrate a statistically significant decreasing relationship between WTD and the AP:NAP ratio ($p<0.0124$), and a significant increasing relationship with the Pioneer:Successional ratio ($p<0.00001$) (Figure 5). No significant relationships were found between WTD and pollen richness ($p=0.525$), pollen evenness ($p=0.338$), and coprophilous fungi ($p=0.496$). WTD was found to have a significant relationship with sedimentation rate ($p<0.0344$), the Fe/Zr ratio

($p<0.00001$), and the Rb/Sr ratio ($p<0.0001$) (Figure 6). Additionally, no significant relationship was found between WTD and the Ca/Zr ratio ($p=0.0622$), although this is trending towards significant. Finally, when investigating the response between hydroclimate and fire variables, response curves for Pěkná show a statistically significant increasing relationship with CHAR ($p<0.0145$), grass CHAR ($p<0.0262$), charred macrofossils ($p<0.00556$), and microcharcoal ($p<0.00001$) (Figure 8). In significant relationships were found between WTD and wood CHAR ($p=0.116$) and herb CHAR ($p=0.38$) (not shown in figures).

Response curves for Blatenská slať illustrate significant relationships between hydroclimate and the Pioneer:Successional ratio ($p<0.000271$), pollen richness ($p<0.0878$), and pollen evenness ($p<0.0222$) (Figure 5). No significant relationships were found between climate and the AP:NAP ratio ($p=0.988$). Significant relationships were found between hydroclimate and the Ca/Zr ratio ($p<0.000134$), the Fe/Zr ratio ($p<0.00001$) and the Rb/Sr ratio ($p<0.00001$) (Figure 6). No significant relationship was found between WTD and sedimentation rate ($p=0.283$) at Blatenská slať. Lastly, modeled response curves suggest no significant relationships between hydroclimate and fire variables; CHAR ($p=0.363$), grass CHAR ($p=0.329$), micro-charcoal ($p=0.714$) (Figure 8). No significant relationships were found between climate and wood CHAR ($p=0.759$) and herb CHAR ($p=0.374$) (not shown).

4.6.2. Anthropogenic response curves

For Pěkná, significant relationships were found between primary and adventive pollen indicators and coprophilous fungi ($p<0.00001$), and pollen richness ($p<0.00001$) (Figure 5). Insignificant relationships were found with the AP:NAP ratio ($p=0.196$), the Pioneer:Successional ratio ($p=0.194$), pollen evenness ($p=0.347$) (Figure 5), the Ca/Zr ratio ($p=0.224$), Fe/Zr ratio ($p=0.093$), Rb/Sr ratio (0.424), and sedimentation rate ($p=0.0826$) (Figure 6), and CHAR ($p=0.176$), grass CHAR ($p=0.228$), microcharcoal ($p=0.892$), charred macrofossils ($p=0.185$) (Figure 8). Additionally, no significant relationship was found between primary and adventive pollen indicators and wood CHAR ($p=0.318$) and herb CHAR ($p=0.386$) (not shown). The only significant relationships found between apophyte pollen indicators at Pěkná were with AP:NAP ($p<0.00001$), pioneer:successional ($p<0.0299$), pollen evenness ($p<0.00161$), pollen richness ($p<0.00001$), coprophilous fungi ($p<0.00001$) (SI Figure 6), and sedimentation rate (0.0122) (SI Figure 7). No significant relationships were found with apophytes and Ca/Zr ($p=0.0912$), Fe/Zr ($p=0.136$), and Rb/Sr ($p=0.381$) (SI Figure 7), or any fire variable; CHAR ($p=0.258$), Grass CHAR ($p=0.249$), charred macrofossils ($p=0.23$), microCHAR ($p=0.398$) (SI Figure 8), herb CHAR ($p=0.681$), or wood CHAR ($p=0.534$) (not shown).

Response curves for Blatenská slať illustrate significant relationships between primary and adventive pollen indicators and the AP:NAP ratio ($p<0.000202$), pollen richness ($p<0.00001$), pollen evenness ($p<0.0274$) and coprophilous fungi ($p<0.00278$) (Figure 5), sedimentation rates ($p<0.00104$) and the Ca/Zr ($p<0.00001$), Fe/Zr ($p<0.00001$) and Rb/Sr ratios ($p<0.00001$)

(Figure 6). No significant relationships were found with the pioneer:successional ratio (p=0.116) (Figure 5), CHAR (p=0.474), grass CHAR (p=0.209), microCHAR (p=0.423) (Figure 8), and herb CHAR (p=0.933) (not shown). While not significant, a relationship trending towards significant was found between primary and adventive pollen indicators and wood CHAR (p=0.0619) (not shown). The only significant relationships found between apophyte pollen indicators at Blatenská slať were with AP:NAP (p<0.00001), pioneer:successional (p<0.00431), coprophilous fungi (p<0.0428), pollen richness (p<0.00001) (SI Figure 6), all geochemistry variables, Ca/Zr (p=0.00283), Fe/Zr (p=0.00236), Rb/Sr (p=0.000175) and sedimentation rate (0.0404) (SI Figure 7). No significant relationships were found between apophytes and pollen evenness (p<0.85) (SI Figure 7), CHAR (p=0.615), grass CHAR (p=0.54), microCHAR (p=0.601) (SI Figure 8), or herb CHAR (p=0.872), and wood CHAR (p=0.488) (not shown).

4.7 Principal Component Analysis

For both sites, the PCA results based on selected pollen types and the total number of samples are shown in SI Figure 9 and 10. For Pěkná, the eigenvalues of the first two principal components were 9.52 and 6.8, respectively. The first and second principal components altogether accounted for 28.7% of the variance in fossil pollen assemblages. Taxa having large scores on PC1 are predominately primarily primary, adventive and apophyte pollen types.

For Blatenská slať, the eigenvalues of the first two principal components were 7.72 and 5.3, respectively. The first and second principal components altogether accounted for 24.3% of the variance in fossil pollen assemblages. Fossil pollen that corresponds with PC1 are mainly primary, adventive and apophyte pollen types.

5 Discussion

5.1 Local wetland vegetation dynamics and establishment of testate amoebae records

At Pěkná, at the onset of the record ~12,500 cal yr BP until ~9000 cal yr BP, macrofossils of several *Carex* taxa (*C. vesicaria*, *C. canescens*, *C. elata*, *C. rostrata*), and other wetland plants such as *Eriophorum vaginatum*, *Equisetum fluviatile*, *Filipendula ulmaria* and *Comarum palustre* (SI Figure 1) along with maximum Cyperaceae and Poaceae pollen percentages (SI Figure 5) indicate a tall-sedge marsh vegetation of Magno-Caricion elatae alliance. This alliance occupies the littoral zones of oligotrophic and mesotrophic water bodies where the water table is above the soil surface during most of the growing season (Šumberová et al. 2011). Magno-Caricion elatae alliance also represents the later stages in hydric succession of cut-off meanders within the floodplain of the Upper Vltava River (Bufková et al. 2005), suggesting that the Pěkná peat bog was originally an oxbow lake along the Upper Vltava River in the final stage of terrestrialization. High Rb/Sr, which is an indicator of erosion, suggests the oxbow lake was regularly influenced by local flooding until ~11,000 cal yr BP (Figure 3). High concentrations and percentages of pioneer species, such as *Pinus* sp. (likely *Pinus rotundata* and/or *P. sylvestris* based on modern vegetation assemblages) and *Betula pendula/pubescens* macrofossils and pollen

indicate both regional forestation and forestation of the peatland surface ~10,500 cal yr BP. Peat growth comprised primarily of *Eriophorum* peat coupled with wood fragments suggests a transition of a tall-sedge marsh into an oligotrophic groundwater-fed fen overgrown by trees starting ~10,500 cal yr BP and transitioning into peatbog shortly thereafter. As a result of peat formation, testate amoebae first appear ~10,500 cal yr BP (SI Figure 3), and thus provide a record of hydroclimate since ~10,500 cal yr BP at Pěkná (Figure 3). At Blatenská slať, the peat bog established ~7250 cal yr BP (Schafstall et al., 2024), which coincides with the first appearance of testate amoebae (SI Figure 4), thus providing a record of hydroclimate overlap between the two sites over the last ~7200 years.

5.2 Synchronous Holocene hydroclimate and forest succession, yet asynchronous fire regimes across the Šumava Mountains

Early Holocene hydroclimate reflects dry conditions above the modern agropastoral boundary Dreslerová et al., 2020a), likely in response to high summer insolation which induced warmer- and drier-than-present continental conditions (Berger and Loutre, 1991; Heiri et al., 2003; Fohlmeister et al., 2013) (Figure 3). This is further supported by the CHELSA model which shows the lowest precipitation values for the entire Holocene occurring between 12,000–8000 cal yr BP. Additionally, the CHELSA simulated climate shows the warmest temperatures during the wettest quarter (i.e., summer) occurred between 10,000–8000 cal yr BP. This time period overlaps with the forestation of the Pěkná peatbog by early successional species *Pinus* and *Betula* (Figure 4). Modeled response curves illustrate local climate as the dominant driver of forest succession, with early pioneer species dominating when the water table is low (<20 cm) (Figure 5). Additionally, response curves show a significant relationship with local hydroclimate and landscape openness at Pěkná, with NAP dominating when the WTD is low. Moreover, authigenic Ca and Fe (Ca:Zr and Fe:Zr) increase ~10,500 cal yr BP suggesting the peatbog surface was seasonally dry and exposed to oxygen at this time (Figure 3). Modeled response curves illustrate strong relationships between WTDs and the Fe/Zr and Rb/Sr ratios (Figure 6), demonstrating hydroclimates influence on local peatbog surface dynamics. Warm and dry summer conditions coupled with a landscape dominated by early successional fire-adapted species resulted in more frequent biomass burning. For example, the first appearance of charred macrofossils, specifically charred bryophytes and wood, occurred around ~10,500 cal yr BP, with high concentrations of other charred macrofossils such as pine needles, leaves, moss, *Carex* and *Eriophorum* until ~7300 cal yr BP (Figure 7). GAM response curves further support a significant relationship between hydroclimate (WTD) and local biomass burning (charred macrofossils) (Figure 8). Additionally, the highest CHAR and microCHAR values of the entire record also occur between 11,000–7300 cal yr BP (Figure 7), with response curves illustrating a strong influence of hydroclimate on local and regional fire activity. Specifically, when WTDs are low, ranging between 15–25 cm, all charcoal-related variables drastically increase suggesting that when peat surface conditions are dry, the environment at Pěkná is especially prone to fire activity (Figure 8). The significant relationship between WTD and macrocharcoal, particularly

grass charcoal, supports the fact that fine fuels burned better under drier conditions (Turetski et al., 2014; Feurdean et al., 2022). Furthermore, macrocharcoal morphology data further support the charred macrofossil data in that both understory (herbs) and canopy (shrubs and wood) were burning, potentially indicating both low and high severity fires on the peat surface (Figure 7). High-severity fires are also inferred from the dramatic decrease in forest canopy pollen ~8,500 cal yr BP (Figure 4), as well as by high concentrations of *Cenococcum geophilum*, a soil fungus that can be used as a proxy for soil erosion (Kroll, 1988), and an indicator of stress on vegetation as a result of chronic drought (Pigott, 1982; Coleman et al., 1989; Hasselquist et al., 2005) (Figure 7), as well as the presence of *Gelasinospora*, another soil fungus indicative of fire activity (van Geel, 1978). Interestingly, the highest peaks in CHAR occurred ~8000 cal yr BP, which is similar to other findings of high CHAR at this time (Carter et al., 2018a; Florescu et al., *in review*). This supports other regional paleofire reconstructions that indicate high fire activity in the Šumava Mountains in the early Holocene (Carter et al., 2018a; Mateo-Beneito et al., 2024; Florescu et al., *in review*), Czechia (Bobek et al., 2019), and across Europe (Vannière et al., 2016; Feurdean et al., 2020). Similarly, Cagliero et al. (2023) also illustrate a positive relationship between climate (i.e., July temperature) and biomass burning in the Dinaric Alps supporting the strong influence of summer temperatures on fire activity. While the Blatenská slať record does not extend beyond 7300 cal yr BP, the highest peaks in CHAR occurred at the onset of the record (Schafstall et al., 2024), further supporting regional burning across all elevations in the Šumava Mountains at this time (Figure 7).

Starting ~7250 cal yr BP until 2200 cal yr BP, local hydroclimate records illustrate generally higher WTDs at both sites during this time, suggesting relatively cooler and wetter conditions overall, an inference supported by the CHELSA climate model which simulates cooler temperatures of the wettest quarter (Figure 3). However, WTDs do fluctuate indicating drought episodes and drying of the peat bog surfaces, which is supported by generally higher Ca/Zr and/or Fe/Zr at both sites until ~5500–4500 cal yr BP. Relatively synchronous responses in forest succession were recorded near the agropastoral boundary and at the highest elevations in the Šumava Mountains as a result of cooler and wetter conditions. Specifically, *Picea abies* dominated at both sites (Figure 4), which mirror other paleoecological reconstructions illustrating *P. abies* as the dominant forest canopy cover during the mid-Holocene (Svobodová et al., 2001, 2002; Carter et al., 2018a; Florescu et al., *in review*). Carter et al. (2018b) suggested that approximately 50% of the total land-cover across the entire Šumava Mountains was comprised of *P. abies* during the mid-Holocene. Our records suggest that higher elevations (i.e., Blatenská slať, 1275 m asl) was comprised of ~75% *P. abies*, while mid-elevations (i.e., Pěkná, 730 m asl) was comprised of ~40%. Increased forest density, low species richness and low evenness and wetter conditions coincided with *P. abies* dominance at both sites, indicating fewer species in the environment (Figure 5). Understory microclimates in *P. abies*-dominated forests are typically cooler, with abundant surface litter and acidic soils (Augusto et al., 2003; Colombaroli et al., 2012), which would impact pollen richness, particularly understory taxa in

these forested ecosystems (Figure 4). Modeled relationships further support the notion that regional forest succession and composition was climatically-driven between 7000–4000 cal yr BP.

Because of cooler and wetter conditions, coupled with *P. abies* dominance, it would be expected that fire activity decreases as *P. abies* is a fire-avoidant species. However, *P. abies* establishment and rise to dominance in the Šumava Mountains occurred under elevated fire activity (Carter et al., 2018a). The rise to dominance of *P. abies* under elevated fire activity has also been witnessed in the Dinaric Alps (Cagliero et al., 2023) and Carpathians (Feurdean et al., 2012; Finsinger et al., 2018) suggesting a similar driver at the regional scale. At Pěkná, local fire activity is inferred from sporadic increases in charred macrofossils between 7700–4500 cal yr BP (Figure 3). Seasonally dry peatbog surfaces, which led to local fire activity at Pěkná, is supported by increased concentrations of *E. vaginatum* macrofossils and increased authigenic Ca. However, while increased authigenic Ca is also witnessed at Blatenská slať between 7000–4000 cal yr BP, local fire activity essentially disappears from the record ~6000 cal yr BP. The synchroneity in forest composition points to climate as the primary driver, yet asynchronous fire regimes points to another ignition source (i.e. not climate) for fires at mid-elevations.

Picea abies began to decrease at Pěkná starting ~5000 cal yr BP, likely because mean annual temperatures were too warm at this particular elevation (Figure 3). Mean annual temperatures may have reached a critical threshold ~4000 cal yr BP at higher elevations, which resulted in a drastic change in vegetation composition. Specifically, forests drastically changed from a *P. abies*-dominated forest to *Abies alba*-dominated forest at Blatenská slať, with higher pollen richness and slightly higher pollen evenness (Figure 4). The high proportion of *A. alba* at Blatenská slať (~60%) are the first-ever reported at any site in the Šumava Mountains, which Schafstall et al. (2024) suggest may be a result of climate conditions becoming drier coupled with essentially no disturbance events in the surrounding environment. While a brief period of increased *Eriophorum vaginatum* ~4000 cal yr BP may suggest drier conditions locally (Figure 3), the testate-derived hydroclimate does not illustrate any drastic decrease in WTDs ~4000 cal yr BP. In fact, WTDs continued to oscillate at higher values until ~2000 cal yr BP before decreasing to some of the lowest values recorded. We therefore propose that the increase in *Abies alba* was related to warming winter temperatures, likely spreading the species upslope from refuge from warmer temperatures at lower elevations. This assumption is based on the fact that temperate *Abies alba* is far more sensitive to winter frost and late frost than boreal *Picea abies* (Ellenberg, 2009; Lang et al., 2023).

Local WTDs illustrate a major drought occurring between 2200–500 cal yr BP across the Šumava Mountains. WTDs decrease earlier at Blatenská slať around ~2200 cal yr BP with consistently high percentages of *E. vaginatum* macrofossils indicating unstable hydrological conditions, whereas WTDs decrease ~1500 cal yr BP at Pěkná. The presence of *Calluna*

macrofossils further supports drier conditions at Pěkná over the last 1000 years (SI Figure 1). As a result of exceptionally dry conditions, similar to those witnessed in the early Holocene, forest density shifted to a more open landscape dominated by early pioneer species, which is supported by modeled response curves. *Picea abies* increases ~1000 cal yr BP at Blatenská slať (Figure 4), likely in response to warmer temperatures (i.e. upslope migration). However, the Little Ice Age (LIA, 1450–1500 CE; Matthews and Briffa, 2005) does overlap with part of this time. Thus, the cool and wet LIA conditions may have favored *P. abies* growth (Grabner, 2017). Because of warm and exceptionally dry conditions, coupled with a landscape abundant with pioneer species, it would be expected that fire activity increases over the last 2000 years. Interestingly, we see a slight increase in CHAR at Blatenská slať and decreasing CHAR at Pěkná (Figure 7). We speculate that the major drought witnessed between 2200–500 cal yr BP may have been primarily a winter-season drought, resulting in less snow at higher elevations. This may potentially explain why Blatenská slať experienced slightly more fire activity than Pěkná due to fuels being drier-than-normal. Alternatively, these results may indicate that humans were primarily using fire at higher elevations. However, because no significant relationships were found between hydroclimate and any fire variable at Blatenská slať, this alludes to other factors being the primary driver behind the increase in fire activity at higher elevations over the last 2000 years.

5.3 How did human activities influence forest succession and composition?

While hydroclimate has been the dominant driver of forest succession and composition, we cannot refute the possibility of humans as a secondary driver of landscape change. Archeological evidence documents human presence as early as the Mesolithic across the entire Šumava Mountain region (Fröhlich, 2003; Šída et al., 2011; Čuláková et al., 2012; Eigner et al., 2017; Kapustka et al., 2019; Kozáková et al., 2020), and near the vicinity of Pěkná (Vencl, 2006; Šída et al., 2008; 2012). Additionally, Blatenská slať is located <1 km of an old Medieval route (Kozáková et al., 2020), which was important for trading salt, metals and other goods (Svobodová et al., 2001). At the mid-elevation site, Pěkná, both coprophilous fungi and adventive pollen indicators have been continuously present since ~4600 cal yr BP, which reflects livestock roaming on the landscape (Ptáková et al., 2021). Modeled response curves demonstrate a significant relationship between primary and adventive pollen indicators and coprophilous fungi, pollen evenness and pollen richness at (Figure 5), as well as apophyte pollen indicators and all forest succession/landscape openness variables (SI Figure 6). Over the last 3000 years, pollen richness (N0) has been slowly increasing at Pěkná in conjunction with a slow transition from a successional-dominated canopy to an early pioneer-dominated canopy (Figure 4). While the AP:NAP ratio suggests the landscape was still very much dominated by trees, pioneer taxa such as *Betula pubescens*, *Pinus sylvestris* and *P. rotunda* were increasing at this time. These taxa are more light-demanding than late-successional species like *Picea abies* (Beck et al., 2016; Houston Durrant et al., 2016), suggesting the landscape was not as dense as the AP:NAP ratio suggests. Macrofossil evidence further supports the relatively consistent presence of *Pinus* on the

Pěkná peatbog since ~4000 cal yr BP (SI Figure 1). Regular grazing would have maintained an intermediate state between open pasture and closed woodland, typical of a woodland pasture environment (Vera, 2000; Hartel et al. 2015). This intermediate state would have favored understory herb and shrub growth beneficial for grazers. These results suggest that the Vltava River floodplain near Pěkná was likely frequently visited by grazers, which likely attracted hunters, should these have been wild game instead of domesticated livestock. However, if these were domesticated livestock, either scenario points to human presence. Additionally, the proximity to the Vltava River would have been beneficial for human occupation not only for mobility purposes, but also easy access to water and food. Increases in adventive pollen indicators overlap with the first appearance, and continued presence of primary pollen indicators including cultivars ~1450 cal yr BP (Figure 4). This suggests that humans were beginning to utilize agropastoral farming near Pěkná, which is ~100 m upslope from the modern-day agropastoral farming boundary (Dreslerová et al., 2020a). Increasing Pb/Zr over the last 2000 years is likely associated with the regional mining of ore (Veron et al., 2014) (Figure 3). Forests in the Šumava Mountains were used for charcoal and potash production for local iron smelters in the 16th century (Veselý et al., 1993), and glassworks in the 14th century (Fröhlich, 2003). Pb as well as Cu and Co are common colorant elements used in glassworks, especially blue glassworks (Bidegaray and Pollard, 2018; Zlámalová Cílová et al., 2021) which were popular glassworks for the region. Starting ~1200 cal yr BP, evidence of human activities directly modifying the local environment is evident in the Pěkná record, with a relatively large increase in primary and adventive pollen indicators (Figure 4). This overlaps with the pioneer:successional ratio illustrating more early pioneer taxa on the landscape. The largest ecosystem change has occurred over the last 500 years, with the decline of *Abies alba* at Pěkná likely associated with deforestation (Kolář et al., 2021). The large increase in NAP over the last 500 years illustrates a growing demand of agriculture and pasture area at lower elevations.

While we hypothesized human impact would be greater at Pěkná due to its proximity to the modern-day agropastoral farming boundary, surprisingly, we found comparable evidence of human impact at Blatenská slať. Similar to Pěkná, adventive pollen indicators have been consistently present since ~4250 cal yr BP suggesting human utilization of high elevation forests. Modeled response curves demonstrate that a more open landscape with higher NAP species and pollen richness is associated with higher primary and adventive human indicator pollen (Figure 5) and apophyte pollen indicators at Blatenská slať (SI Figure 6). Two time periods with higher NAP species and pollen richness occurred, first between 4000–2000 cal yr BP and then over the last 1000 years. During each of these periods, a similar environmental scenario that occurred at Pěkná also occurred at Blatenská slať. For example, pollen richness (N0) was exceptionally high during these two time periods, with rapid fluctuations in the pioneer:successional ratio suggesting a mixture of each forest type. While not significant, there appears to be a relationship trending towards significant with human activities and both the pioneer:successional ratio ($p=0.07280$), and coprophilous fungi ($p=0.074$). The modeled relationships between human

pollen indicator taxa, pollen richness and coprophilous potentially point to an environment with a higher mosaic of species richness that would have been favorable for gathering seasonally ethnobotanically important species found at higher elevations. Additionally, the potentially semi-open woodland may have been favorable for seasonal pastoralism. While we cannot say for certain that the time period between 4000–2000 cal yr BP with higher pollen richness and landscape openness was attributed directly to human influence, we can speculate that humans were utilizing resources at higher elevations during this period. However, there is more circumstantial evidence suggesting direct human impact at higher elevations over the last 1000–500 years. Notably, the drastic increase in Pb/Zr and primary indicator pollen taxa point to direct human influence in the region. Additionally, the drastic increase in *Picea abies* over the last 1000 years may have been a result of human management. Specifically, historical timber construction in the present-day Czech Republic included *P. abies* and *Abies alba* (Kolář et al., 2021). Starting in the mid-17th century onward, but perhaps as early as the end of the 14th century (e.g. in southern Germany), *Picea abies* was likely planted across the study region due to increasing construction demand (cf. Hölzl, 2010; Antoine et al., 2024). Additionally, *Picea abies* has also been shown to benefit from grazing and browsing (Ellenberg, 2009; Rey et al., 2013; Schwörer et al., 2015; Lang et al., 2023). Our results indeed illustrate the consistent presence of *Sporormiella* over the last 500 years which may have contributed to the recent expansion of *P. abies* (Figure 4). Deforestation at higher elevations likely increased local weathering of the Blatenská slať catchment over the last 1000 years, as indicated by increasing Rb/Sr (Figure 3). Modeled response curves demonstrate a significant relationship between primary and adventive pollen indicator taxa and the Rb/Sr ratio (Figure 6). Lastly, the decrease in forest cover and decline in pollen evenness over the last 1000 years supports previous quantitative REVEALS land-cover reconstructions which illustrate increasing landscape openness, especially over the last 500 years (Carter et al., 2018b). These data contribute to the growing body of literature illustrating how human deforestation has impacted vegetation composition and diversity over time (Antoine et al., 2024).

5.4 What drove the observed asynchronous changes in fire activity?

Approximately 96% of all modern wildfires in the European Union are caused by humans, which are being exacerbated by recent climate change (European Commission Joint Research Centre, 2023). Historic fires were likely also dominated by human ignition sources for pastoral purposes across Europe and in the Šumava Mountains. However, pastoral fires in the Šumava Mountains are unlikely to be detected by anthropogenic indicators, likely because there is a lack of pollen or spore evidence for pastoralism in this region (Kozáková et al., 2020). As such, modeled response curves do not show a relationship between primary and adventive pollen indicators, apophyte pollen indicators, and any fire variable. Instead GAM response curves illustrate a strong positive relationship between hydroclimate and every fire variable at Pěkná (Figure 8). However, this could be an artifact of the GAMs, as there are fewer observations using the sum of primary and adventive pollen indicator taxa as the predictor variable than the number of testate amoebae

observations as the predictor variables (see vertical dashed lines on GAMS x-axes; Figures 5, 6 and 8).

It was likely that humans were utilizing fire, but not enough to override climate as the dominant driver of fire. This is supported by local paleofire lacustrine-based reconstructions that document an increase in fire frequency in response to human occupation (Carter et al., 2018a; Florescu et al., *in review*). Lacustrine-based paleofire records are likely more reflective of regional activity, whereas peatbog-based paleofire records are more localized. Therefore, without direct archeological evidence documenting the physical presence of humans at Pěkná and Blatenská slať, the likelihood of finding any anthropogenically-related fire signal decreases, as does that ability to create a realistic estimate of population size of prehistoric communities from the area, which is a current challenge in the field of archeology (Kolář et al., 2022). Other studies from Europe have demonstrated the ability of humans to override climate as the primary driver of fire activity (e.g. Rey et al., 2013; 2019). However, these studies come from the Alps where the use of fire to create of maintain high-altitude pastures has been well documented (Pini et al., 2017; Gilck and Poschlod, 2019; Dietre et al., 2020). As Kozáková et al. (2020) suggest, the absence of a treeless zone in Šumava Mountains makes it more challenging to identify pastoral fires or other human-fire related activities. Such inferences showing a close link between land use and fire may depend on different climatic, vegetational and cultural settings as well as the sufficient preservation or investigation of the archeological remains. For example, Carter et al. (2021) showed that humans overrode climate as the dominant driver of fire in a high-elevation fire-prone mixed-conifer forest in south-central Utah, USA. Specifically, they showed that a 600-year period of elevated CHAR was associated with the farming-based Fremont culture, who likely used frequent, low-severity fire to increase plant resources beneficial for human usage. Because that specific study site had onsite archeological evidence (i.e., hearths), the odds of identifying a human-fire signature increased substantially. Additionally, the high prevalence of radiocarbon-dated archeological sites surrounding their study site allowed for creating a summed probability distribution (SPDs) which was used to distinguish human-caused fires from naturally caused ones. However, we acknowledge that the climate, vegetation, and fire regimes vary substantially between south-central Utah, USA (Carter et al., 2021) and Central Europe (this study or the Alps).

Conclusions

Documenting prehistoric human impact in Central European mountain environments has been a challenge. However, our study has demonstrated that long-term human impacts have left legacy effects on modern forest succession in central European mountain environments. By presenting the first records of reconstructed water table depths (WTDs) from the Šumava Mountains, our study demonstrated that major changes in forest succession primarily resulted from climate. Yet humans likely played a secondary role in modifying forest succession to increase resources beneficial to both humans and grazers over the last ~4600 years. However, the influence of

human activities in modifying forest succession increased substantially over the past 1000 years at both sites. We expected to see a larger anthropogenic footprint at Pěkná, as there is a higher prevalence of human settlements nearby. However, we found comparable evidence of human impact at Blatenská slať, especially over the last 1000 years. We were unable to document the use of fire as a tool to manipulate landscapes, and that the main driver of local and regional fire is climate. Our inability to provide direct evidence of people utilizing fire as a landscape management tool may be attributed to the lack of archeological evidence documenting human habitation at Pěkná and Blatenská slať or to local settings (e.g. lacking natural grasslands at higher elevations, humid conditions preventing large-scale burning, a lack of flammable vegetation, or the more localized nature of peatbog records versus regional-scale lacustrine records). Additional archeological evidence and sedimentary DNA data from the Šumava Mountains are desperately needed to better disentangle humans' role in altering vegetation assemblages and fire regimes prior-to the High Middle Ages.

Acknowledgements

We would like to thank Vojtěch Abraham and Jan Šašek for their help in the field at Pěkná, and Daniel Vondrák and Nick Schafstall for their help in the field at Blatenská slať. Additionally, we would like to thank Viktor Goliáš for his contribution on ^{210}Pb dating. This project was funded by the Czech Science Foundation, BOBAFIRES project #19-14271Y and BESTFORCE project #20-13368S, by Masaryk University project MUNI/A/1323/2022, by RES-HUM - CZ.02.01.01/00/22_008/0004593 (MEYS + EU), and by the Laboratory Directed Research and Development program at Los Alamos National Laboratory under project number 20230864PRD3.

References:

1. Amesbury, M.J., Swindles, G.T., Bobrov, A., Charman, D.J., Holden, J., Lamentowicz, M., Mallon, G., Mazei, Y., Mitchell, E.A.D., Payne, R.J., Roland, T.P., Turner, T.E., Warner, B.G., 2016. Development of a new pan-European testate amoeba transfer function for reconstructing peatland palaeohydrology. Quaternary Science Reviews 152, 132–151, https://doi.org/10.1016/j.quascirev.2016.09.024.
2. Antoine, E., Marquer, L., Muigg, B., Tegel, W., Bisson, U., Bolliger, M., Herzig, FF., Heussner, K.-U., Hofmann, J., Kontic, R., Kyncl, T., Land, A., Lechterbeck, J., Leuschner, H.H., Linderholm, H.W., Neyses-Eiden, M., Rösch, M., Rzepecki, A., Walder, F., Weidemüller, J., Seim, A. 2024. Legacy of last millennium timber use on plant cover in Central Europe: Insights from tree rings and pollen. Science of the Total Environment 922, 171157, https://doi.org/10.1016/j.scitotenv.2024.171157.
3. Augusto, L., Dupouey, J.-L., Ranger, J. 2003. Effects of tree species on understory vegetation and environmental conditions in temperate forests. Annuals of Forest Science 60, 823–831, https://doi.org/10.1051/forest:2003077.

4. Baker, A.G., Bhagwat, S.A., Willis, K.J., 2013. Do dung fungal spores make a good proxy for past distribution of large herbivores? Quaternary Science Reviews 62, 21–31, https://doi.org/10.1016/j.quascirev.2012.11.018
5. Behre, K.-E. 1981. The interpretation of anthropogenic indicators in Pollen Diagrams. Pollen Spores, 23, 225–245.
6. Behre, K.-E. 1988. The role of man in European vegetation history. In: Huntley, B., Webb, T. (Eds.) Vegetation History. Handbook of Vegetation Science, Springer, Dordrecht, 633672, https://doi.org/10.1007/978-94-009-3081-0_17.
7. Behre, K.-E., van der Knapp, W.O., Lang, G., Morales-Molino, C., Tinner, W. In: Anthropogenic changes to vegetation, Lang, G., Ammann, B., Behre, K.-E., Tinner, W. (Eds). 2023, pp. 363–408.
8. Beck, P., Caudullo, G., de Rigo, D., Tinner, W. 2016. Betula pendula, Betula pubescens and other birches in Europe: distribution, habitat, usage and threats. In: San-Migeul Ayanz, J., de Rigo, D., Caudullo, G., Houston Durrant, T., Mauri, A. (Eds.) European Atlas of Forest Tree Species. Publi. Off. EU, Luxembourg, pp. e010226+.
9. Berger, A., and Loutre, M.F., 1991. Insolation value for the climate of the last 10 million 775 years. Quaternary Science Reviews 10, 297–317, https://doi.org/10.1016/0277-3791(91)90033-Q.
10. Beug, H.-J. 2004. Leitfaden der Pollenbestimmung für Mitte leuropa und angrenzende Gebiete. Verlag Dr Friedrich Pfeil, Munich.
11. Bidegaray, A-I., and Pollard, A.M. 2018. Tesserae Recycling in the Production of Medieval Blue Window Glass. Archaeometry 60, 784–796, https://doi.org/10.1111/arcm.12350
12. Birks, H.J.B., Line, J.M. 1992. The use of rarefaction analysis for estimating palynological richness from Quaternary pollen-analytical data. The Holocene, 2, 1–10, https://doi.org/10.1177/095968369200200101.
13. Birks, H.H., 2007. Plant macrofossil introduction. In: Elias, S.A. (Ed.), Encyclopedia of Quaternary Science, vol. 3. Elsevier, Amsterdam, pp. 2266–2288.
14. Birks, H.J.B., Felde, V.A., Bjune, A.E., Grytnes, J.-A., Seppä, H., Giesecke, T. 2016. Does pollen-assemblage richness reflect floristic richness? A review of recent developments and future challenges. Review of Palaeobotany and Palynology, 228, 1–25, https://doi.org/10.1016/j.revpalbo.2015.12.011.
15. Blaauw, M., and Christeny, J.A., 2011. Flexible paleoclimate age-depth models using an autoregressive gamma process. Bayesian Analysis 6, 457–474. https://doi.org/10.1214/11-BA618.
16. Blackford, J.J., 2000. Palaeoclimatic records from peat bogs. Trends in Ecology and Evolution. 15, 193–198, https://doi.org/10.1016/S0169-5347(00)01826-7.
17. Bobek, P., Svobodová-Svitavská, H., Pokorný, P., Šamonil, P., Kuneš, P., Kozáková, R., Abraham, V., Klinerová, T., Gabriela Švarcová, M., Jamrichová, E., Krauseová, E., Wild, J. (2019). Divergent fire history trajectories in Central European temperate forests revealed a

pronounced influence of broadleaved trees on fire dynamics. Quaternary Science Reviews 225, 105865, https://doi.org/10.1016/j.quascirev.2019.105865.
18. Bojňanský, V and Fargašová, A. 2007. Atlas of Seeds and Fruits of Central and East-European Flora Springer, Dordrecht, The Netherlands.
19. Boyle, J.F. 2001. Inorganic geochemical methods in paleolimnology. In: Last W, Smol JP (Eds.) Tracking environmental change using lake sediments, physical and geochemical methods. Kluwer, Dordrecht, pp 83–142.
20. Bufková, I., Prach, K., Bastl, M. 2005. Relationship between vegetation and environment within the montane flood plain of the Upper Vltava River (Šumava National Park, Czech Republic). Silva Gabreta, 2, 5–76.
21. Cagliero, E., Paradis, L., Marchi, N., Lisztes-Szabó, Z., Braun, M., Hubay, K., Sabatier, P., Čurovič, M., Spalevic, V., Motta, R., Lingua, E, Finsinger, W. 2023. The role of fire disturbances, human activities and climate change for long-term forest dynamics in upper-montane forests of the central Dinaric Alps. The Holocene 33(7), 827–841, https://doi.org/10.1177/09596836231163515.
22. Carter, V.A., Moravcová, A., Chiverrell, R.C., Clear, J.L., Finsinger, W., Dreslerová, D., Halsall, K., Kuneš, P. 2018a. Holocene-scale fire dynamics of central European temperate spruce-beech forests. Quaternary Science Reviews 191, 15–30, https://doi.org/10.1016/j.quascirev.2018.05.001.
23. Cappers, R.T.J., Bekker, R.M., Jans, J.E.A. 2006. Digitale Zadenatlas Van Nederland Barkhuis Publishers, Groningen.
24. Carter, V.A., Chiverrell, R.C., Clear, J.L., Kuosmanen, N., Moravcová, A., Svoboda, M., Svobodová-Svitavská, H., van Leeuwen, J.F.N., van der Knapp, W.O., Kuneš, P. 2018b. Quantitative Palynology Informing Conservation Ecology in the Bohemian/Bavarian Forests of Central Europe. Frontiers in Plant Science 8, 2268, https://doi.org/10.3389/fpls.2017.02268.
25. Carter, V.A., Bobek, P., Moravcová, A., Šolcová, A., Chiverrell, R.C., Clear, J.L., Finsinger, W., Feurdean, A., Tanţău, I., Magyari, E., Brussel, T., Kuneš, P. 2020. The role of climate-fuel feedbacks on Holocene biomass burning in upper-montane Carpathian forests. Global and Plantetary Change 193, 103264, https://doi.org/10.1016/j.gloplacha.2020.103264.
26. Carter, V.A., Brunelle, A., Power, M.J., DeRose, R.J., Bekker, M.., Hart, I., Brewer, S., Spangler, J., Robinson, E., Abbott, M., Maezumi, S.Y., Codding, B.F. 2021. Legacies of Indigenous land use shaped past wildfire regimes in the Basin-Plateau Region, USA. Communications Earth and Environment 2, 72, https://doi.org/10.1038/s43247-021-00137-3.
27. Chen, J., An, Z., Head, J., 1999. Variation of Rb/Sr ratios in the Loess-paleosol sequences of central China during the last 130,000 years and their implications for monsoon paleoclimatology. Quaternary Research 51, 215–219. https://doi.org/10.1006/qres.1999.2038.
28. Coleman, M.D., Bledsoe, C.S., Lopushinsky, W. 1989. Pure culture response of ectomycorrhizal fungi to imposed water stress. Canadian Journal of Botany, 67, 29–39, https://doi.org/10.1139/b89-005.

29. Colombaroli, D., Beckmann, M., van der Knapp, W.O., Curdy, P., Tinner, W. 2012. Changes in biodiversity and vegetation composition in the central Swiss Alps during the transition from pristine forest to first farming. Biodiversity Research 19, 157–170, https://doi.org/10.1111/j.1472-4642.2012.00930.x.
30. Čuláková, K., Eigner, J., Metlička, M., Přichystal, A. and Řezáč, M. 2012. Horské mezolitické osídlení u Javoří pily, obec Modrava, okres Klatovy. Archeologie ve středních Čechách 16, 19–28.
31. Deza-Araujo, M., Morales-Molino, C., Tinner, W., Henne, P.D., Heitz, C., Pezzatti, G.B., Hafner, A., Conedera, M. 2020. A critical assessment of human-impact indices based on anthropogenic pollen indicators. Quaternary Science Reviews 236, 106291, https://doi.org/10.1016/j.quascirev.2020.106291.
32. Dietre, B., Reitmaier, T., Walser, C., Warnk, T., Unkel, I., Hajdas, I., Lambers, K., Reidl, D., Nicolas Hass, J. 2020. Steady transformation of primeval forest into subalpine pasture during the Late Neolithic to Early Bronze Age (2300−1700 BC) in the Silvretta Alps, Switzerland. The Holocene 30(3), 355–368, https://doi.org/10.1177/0959683619887419.
33. Dreslerová, D., Romportl, D., Čišecký, Č., Fröhlich, J., Michálek, J., Metlička, M., Parkman, M., Pták, M., 2020a. At the end of the world? Settlement in the Šumava mountains and foothills in later prehistory. Praehistorische Zeitschrift 95, 1–23, https://doi.org/10.1515/pz-2021-0019.
34. Dreslerová, D., Kozáková, R., Metlička, M., Brychová, V., Bobek, P., Čišecký, Č., Demján, P., Lisá, L., Pokorná, A., Michálek, J., Strouhalová, B., Trubač, J., 2020b. Seeking the meaning of a unique mountain site through a multidiscplinary approach. The Late La Tène site at Sklářské Valley, Šumava Mountains, Czech Republic. Quaternary International 542, 88–108, https://doi.org/10.1016/j.quaint.2020.03.013.
35. Dreslerová, D., Venclová, N., Demján, P., Kyselý, R., Matoušek, V., 2022. Did they leave or not? A critical perspective on the beginnings of the La Tène period in Bohemia. Archaeologické rozhledy 74, 505–537, https://doi.org/10.35686/AR.2022.24.
36. Eigner, J., Kapustka, K., Parkman, M., Řezáč, M. 2017. Mezoliticke osidleni Šumavy pohledem studia surovin kamennych artefaktů z lokalit Javoři Pila 1 a Nova Pec [Mesolithic occupation of the Bohemian Forest according to the study of raw materials for lithic production from the sites of Javoři Pila 1 and Nova. Silva Gabreta 23, 33–44.
37. Ellenberg, H., 2009. Vegetation Ecology of Central Europe, 4th ed. Cambridge University Press, Cambridge.
38. Enache, M.D., Cumming, B.F., 2006. Tracking recorded fires using charcoal morphology from the sedimentary sequence of Prosser Lake, British Columbia (Canada). Quaternary Research 65, 282–292, https://doi.org/10.1016/j.yqres.2005.09.003.
39. Engstrom, D.R., Wright, H.E., Jr 1984. Chemical stratigraphy of lake sediments as a record of environmental change. In: Haworth EY, Lund JWG (Eds.) Lake sediments and environmental history. Leicester University Press, Leicester, pp 11–68.

40. European Commission, Joint Research Centre, San-Miguel-Ayanz, J., Durrant, T., Boca, R. 2023. Forest fires in Europe, Middle East and North Africa 2022, Publications Office of the European Union. https://data.europa.eu/doi/10.2760/348120.
41. Faegri, K., Kaland, P.E., and Krzywinski, 1989. Textbook of Pollen Analysis. Wiley, New York.
42. Feurden, A., Spessa, A., Magyari, E.K., Willis, K.J., Veres, D., Hickler, T. 2012. Trends in biomass burning in the Carpathians region over the last 15,000 years. Quaternary Science Reviews 45, 111–125, https://doi.org/10.1016/j.quascirev.2012.04.001.
43. Feurdean, A., Gałka, M., Tanţău, I., Geantă, A., Hutchinson, S.M., Hickler, T. 2016. Tree and timberline shifts in the northern Romanian Carpathians during the Holocene and the response to environmental changes. Quaternary Science Reviews 134(15), 100–113, https://doi.org/10.1016/j.quascirev.2015.12.020.
44. Feurdean, A., Florescu, G., Vannière, B., Tanţău, I., O'Hara, R.B., Pfeiffer, M., Hutchinson, S.M., Gałka, M., Moskal-del Hoyo, M., Hickler, T., 2017. Fire has been an important driver of forest dynamics in the Carpathian Mountains during the Holocene. Forest Ecology and Management 389, 15–26, https://doi.org/10.1016/j.foreco.2016.11.046.
45. Feurdean, A. Vasiliev, I. 2019. The contribution of fire to the late Miocene spread of grasslands in eastern Eurasia (Black Sea region). Scientific Reports 9, 6750, https://doi.org/10.1038/s41598-019-43094-w.
46. Feurdean, A., Vannière, B., Finsinger, W., Warren, D., Connor, S.C., Forrest, M., Liakka, J., Panait, A., Werner, C., Andrič, M., Bobek, P., Carter, V.A., Davis, B., Diaconu, A.-C., Dietze, E., Feeser, I., Florescu, G., Gałka, M., Giesecke, T., Jahns, S., Jamrichová, E., Kajukało, K., Kaplan, J., Karpińska-Kołaczek, M., Kołaczek, P., Kuneš, P., Kupriyanov, D., Lamentowicz, M., Lemmen, C, Magyari, E.K., Marcisz, K., Marinova, E., Niamir, A., Novenko, E., Obremska, M., Pędziszewska, A., Pfeiffer, M., Poska, A., Rösch, M., Słowiński, M., Stančikaitė, M., Szal, M., Święta-Musznicka, J., Tanţău, I., Theuerkauf, M., Tonkov, S., Valkó, O., Vassiljev, J., Veski, S., Vincze, I., Wacnik, A., Wiethold, J., Hickler T. 2020. Fire hazard modulation by long-term dynamics in land cover and dominant forest type in eastern and central Europe. 17(5), 1213–1230, https://doi.org/10.5194/bg-17-1213-2020.
47. Feurdean, A., Diaconu, A.-C., Pfeiffer, M., Gałka, M., Hutchinson, S.M., Butiseaca, G., Gorina, N., Tonkov, S., Niamir, A., Tanţău, I., Zhang, H., Kirpotin, S. 2022. Holocene wildifre regimes in western Siberia: interaction between peatland moisture conditions and the composition of plant functional types. Climate of the Past 18(6), 1255–1274, https://doi.org/10.5194/cp-18-1255-2022.
48. Finsinger, W., and Tinner, W. 2005. Minimum count sums for charcoal-concentration estimates in pollen slides: accuracy and potential errors. The Holocene 15(2), 293–297, https://doi.org/10.1191/0959683605hl808rr.
49. Finsinger, W., Morales-Molino, C., Gałka, M., Valsecchi, V., Bojovic, S., Tinner, W. 2017.

Holocene vegetation and fire dynamics at Crveni Potok, a small mire in the Dinaric Alps (Tara National Park, Serbia). Quaternary Science Reviews 167, 63–77, http://dx.doi.org/10.1016/j.quascirev.2017.04.032.
50. Finsinger, W., Fevre, J., Orbán, I., Pál, I., Vincze, I., Hubay, K., Birks, H.H., Braun, M., Tóth, M., Magyari, E.K. 2018. Holocene fire-regime changes near the treeline in the Retezat Mountains. (Southern Carpathians, Romania). Quaternary International 477(30), 94–105, https://doi.org/10.1016/j.quaint.2016.04.029.
51. Fröhlich, J. 2003. Sklářství Šumavy (*Glass-making in Šumava*). In: Šumava. Příroda, historie, život. Baset, pp 1–799.
52. Florescu, G., Tinner, W., Feurdean, A., Finsinger, W., Kuneš. P., Vondrák, D., Heurich, M., van der Knaap, P. Kletetscka, G., Kraklow, V. (in review). Forest composition and density shaped long-term fire regimes and lake-catchment interactions in the Bavarian mountain temperate mixed forests, Central Europe.
53. Florescu, G., Hutchinson, S.M., Gałka, M., Mîndrescu, M., Tantău, I., Petras, A., Feurdean, A. 2024. The legacy of millennial-scale land-use practices on landscape composition, diversity and slope erosion in the subalpine areas of Eastern Carpathians, Romania. The Holocene 34(4), 467–486, https://doi.org/10.1177/09596836231219473.
54. Fohlmeister, J., Vollweiler, N., Spötl, C., Mangini, A., 2013. COMNISPA II: Update of a 931 mid-European isotope climate record, 11 ka to present. The Holocene 23(5), 749–754. doi: 932 10.1177/0959683612465446.
55. Geantă, A., Gałka, M., Tanţău, I., Hutchinson, S.M., Mîndrescu, M., Feurdean, A. 2014. High mountain region of the Northern Romanian Carpathians responded sensitively to Holocene climate and land use changes: A multi-proxy analysis. The Holocene 24(8), 944–956, https://doi.org/10.1177/0959683614534747.
56. Grabner, M. 2017. Werkholz: Eigenschaften und historische Nutzung 60 mitteleuropäischer Baum- und Straucharten. Verlag Dr, Kessel, Remagen-Oberwinter.
57. Grimm, E.C. 2004. TILIA and TGView. Springfield: Illinois State Museum, Research and Collection Center.
58. Gilck, F., and Poschlod, P., 2019. The origin of alpine farming: A review of archaeological, linguistic and archaeobotanical studies in the Alps. The Holocene 29, 1503–1511, https://doi.org/10.1177/0959683619854511.
59. Hafner, A., Schworer, C., 2018. Vertical mobility around the high-alpine Schnidejoch Pass. Indications of Neolithic and Bronze Age pastoralism in the Swiss Alps from paleoecological and archaeological sources. Quaternary International 484, 3–18, https://doi.org/10.1016/j.quaint.2016.12.049.
60. Hammer, O., Harper, D.A.T., Ryan. D. 2001. PAST: Paleontological Statistics Software Package for Education and Data Analysis. Palaeontologia Electronica 4(1), 1–9.
61. Hartel, T., Plieninger, T., Varga, A. 2015 Wood-pastures in Europe. In: Kirby KJ, Watkins C (Eds.) Europe's changing woods and forests: from wildwood to managed landscapes. CABI Publishing, Wallingford, pp 61–76.

62. Hasselquist, N., Germino, M.J., McGonigle, T., Smith, W.K. 2005. Variability of Cenococcum colonization and its ecophysiological significance for young conifers at alpine–treeline. New Phytologist 165, 867–873, doi: 10.1111/j.1469-8137.2005.01275.x.
63. Hastie, T.J., and Tibshirani, R.J., 1986. Generalized Additive Models. Statistical Science 1(3), 297–318, https://www.jstor.org/stable/2245459.
64. Heiri, O., Lotter, A.F., Hausmann, S., Kienast, F. 2003. A chironomid-based Holocene summer air temperature reconstruction from the Swiss Alps. The Holocene 13, 477–484, https://doi.org/10.1191/0959683603hl640ft.
65. Hendon, D., and Charman, D.J., 1997. The preparation of testate amoebae (Protozoa: rhizopoda) samples from peat. The Holocene 7, 199–205, https://doi.org/10.1177/095968369700700207.
66. Henkner, J., Ahlrichs, J., Fischer, E., Fuchs, M., Knopf, T., Rösch, M., Scholten, T., Kühn, P. 2018. Land use dynamics derived from colluvial deposits and bogs in the Black Forest, Germany. Journal of Plant Nutrition Soil Science 181(2), 240–260, https://doi.org/10.1002/jpln.201700249.
67. Higuera, P.E., Brubaker, L.B., Anderson, P.M., Hu, F.S., Brown, T.A., 2009. Vegetation mediated the impacts of postglacial climate change on fire regimes in the south-central Brooks Range, Alaska. Ecological Monographs 79, 201–219, https://doi.org/10.1890/07-2019.1.
68. Higuera, P.E., Gavin, D.G., Bartlein, P.J., Hallett, D.J., 2010. Peak detection in sediment-charcoal records: Impacts of alternative data analysis methods on fire-history interpretations. International Journal of Wildland Fire 19, 996–1014, https://doi.org/10.1071/WF09134.
69. Hill, M.O., 1973. Diversity and Evenness: A Unifying Notation and Its Consequences. Ecology 54, 427–432, https://doi.org/10.2307/1934352.
70. Hölzl, R. 2010. Historicizing sustainability: German scientific forestry in the eighteenth and nineteenth centuries. Science as Culture 19(4), 431–460, https://doi.org/10.1080/09505431.2010.519866
71. Houston Durrant, T., de Rigo, D., Caudullo, G., 2016. Pinus sylvestris in Europe: distribution, habitat, usage and threats. In: San-Miguel-Ayanz, J., de Rigo, D., Caudullo, G., Houston Durrant, T., Mauri, A. (Eds.), European Atlas of Forest Tree Species. Publ. Off. EU, Luxembourg, pp. e016b94+
72. Josefsson, T., Hörnberg, G., Östlund, L., 2009. Long-term human impact and vegetation changes in a Boreal Forest Reserve: Implications for the Use of Protected Areas as Ecological References. Ecosystems 12, 1017–1036, https://doi.org/10.1007/s10021-009-9276-y.
73. Kapustka. K., Walls, M., Eigner, J. 2019. Beginnings of mountain settlement in Czech Republic - a case study from the Bohemian Forest. In: Pelisiak A, Nowak M and Astaloş C (Eds.) People in the Mountains – Current Approaches to the Archaeology of Mountainous Landscapes. Oxford: Archaeopress Archaeology, pp. 185–195.

74. Karger, D.N., Nobis, M.P., Normand, S., Graham, C.H., Zimmermann, N., 2023. CHELSA-TraCE21k – High resolution (1 km) downscaled transient temperature and precipitation data since the Last Glacial Maximum. Climates of the Past 19, 439–456, https://doi.org/10.5194/cp-19-439-2023
75. Katz, N.J., Katz, S.V., Skobeyeva, E.I. 2007. Atlas of plant remains in peat (in Russian). Nedra-press, Moscow.
76. Kelly, R.F., Higuera, P.E., Barrett, C.M., Hu, F.S., 2011. A signal-to-noise index to quantify the potential for peak detection in sediment-charcoal records. Quaternary Research 75, 11–17, https://doi.org/10.1016/j.yqres.2010.07.011.
77. Kolář, J., Dobrovolný, P. Szabó, P., Mikita, T., Kyncl, T., Kyncl, J., Sochová, I., Rybníček, M. 2021. Wood species utilization for timber constructions in the Czech lands over the period 1400–1900. Dendrochronologia, 70, 125900, https://doi.org/10.1016/j.dendro.2021.125900.
78. Kolář, J., Macek, M., Tkáč, P., Novák, Abraham, V., 2022. Long-term demographic trends and spatio-temporal distribution of past human activity in Central Europe: Comparison or archaeological and palaeocological proxies. Quaternary Science Reviews 297, 107834, https://doi.org/10.1016/j.quascirev.2022.107834.
79. Kothieringer, K., Walser, C., Dietre, B., Reitmaier, T., Haas, J.N., Lambers, K. 2015. High impact: early pastoralism and environmental change during the Neolithic and Bronze Age in the Silvretta Alps (Switzerland/Austria) as evidenced by archaeological, palaeoecological and pedological proxies. Zeitschrift für Geomorphologie 59, 177–198, 10.1127/zfg_suppl/2015/S-59210.
80. Kozáková, R., Bobek, P., Dreslerová, D., Abraham, V., Svobodová-Svitavská, H., 2020. The prehistory and early history of the Šumava Mountains (Czech Republic) as seen through anthropogenic pollen indicators and charcoal data. The Holocene 31(1), 145–159, https://doi.org/10.1177/0959683620961484.
81. Kroll, H. 1988. Das Allerletzte. Cenococcum geophilum. – Archäologische Informationen. Mitteilungen zur Ur- und Frühgeschichte 11(1), 111.
82. Krzystek, P., Serebryanyk, A., Schnörr, C., Červenka, J., Heurich, M., 2020. Large-scale mapping of tree species and dead trees in Šumava National Park and Bavarian Forest National Park using lidar and multispectral imagery. Remote Sensing 12(4), 661, https://doi.org/10.3390/rs12040661.
83. Lang, G., Ammann, B., Behre, K.-E., Tinner, W., 2023. Quaternary Vegetation Dynamics of Europe. Haupt, Bern.
84. Lestienne, M., Jamrichová, E., Kuosmanen, N, Diaconu, A.-C., Schafstall, N., Goliáš, V., Kletetschka, G., Šulc, V., Kuneš, P. 2023. Development of high diversity beech forest in the eastern Carpathians. Journal of Biogeography 50, 699–714, https://doi.org/10.1111/jbi.14562.
85. Lutz, E., and Pernicka, E., 2013. Prehistoric copper from the Eastern Alps. Open Archaeometry, 1(1), 1–25, https://doi.org/10.4081/arc.2013.e25.

86. Mateo-Beneito, A., Florescu, G., Tátosová, J., Carter, V.A, Chiverrell, R., Heiri, H., Vasiliev, I., Kuosmanen, N., Kuneš, P. 2024. Multi-proxy temperature and environmental reconstruction during the Late Glacial and Early Holocene in the Bohemian Forest, Central Europe. Quaternary Science Reviews 331, 108647, https://doi.org/10.1016/j.quascirev.2024.108647.
87. Matthews, A and Briffa, K.R. 2005. The 'little ice age': re-evaluation of an evolving concept. Geografiska Annaler: Series A, Physical Geography 87(1), 17–36, https://doi.org/10.1111/j.0435-3676.2005.00242.x.
88. Mazei, Y., Tsyganov, A., 2006. Freshwater Testate Amoebae. KMK, Moscow.
89. Merkt, J., Streif, H.J., 1970. Stechrohrbohrger¨ate für limnische und marine Lockersedimente. Geologisches Jahrbuch 88, 137–148.
90. Mustaphi, C.J.C., Pisaric, M.F.J., 2014. A classification for macroscopic charcoal morphologies found in Holocene lacustrine sediments. Progress in Physical Geography 38, 734–754, https://doi.org/10.1177/0309133314548886.
91. Oksanen, J., Blanchet, G.B., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Szoecs, E., Wagner, H., 2017. vegan: Community Ecology Package. R package version 2.4-1. https://CRAN.R-project.org/package=vegan.
92. Pigott, C.D. 1982. Survival of mycorrhiza formed by Cenococcum geophilum Fr. in dry soils. New Phytologist 92, 513–517, http://www.jstor.org/stable/2434235.
93. Pini, R., Ravazzi, C., Raiteri, L., Guerreschi, A., Castellano, L., Comolli, R. 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(6), 1580–1597, https://doi.org/10.1111/1365-2745.12767.
94. Ptáková, M., Pokorný, P., Šída, P., Novák, J., Horáček, I., Juřičková, L., Meduna, P., Bezděk, A., Myšková, E., Walls, M., Poschlod, P. 2021. From Mesolithic hunters to Iron Age herders: a unique record of woodland use from eastern central Europe (Czech Republic). Vegetation History and Archaeobotany 30, 269–286, https://doi.org/10.1007/s00334-020-00784-0.
95. Punt, W. 1976-1996. The northwest European pollen flora 1-7. Elsevier, Amsterdam.
96. R Core Team, 2023. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/
97. Reimer, P.J., Austin, W.E.N., Bard, E., Bayliss, A., Blackwell, P.G., Bronk Ramsey, C., Butzin, M., Cheng, H., Edwards, R.L., Friedrich, M., Grootes, P.M., Guilderson, T.P., Hajdas, I., Heaton, T.J., Hogg, A.G., Hughen, K.A., Kromer, B., Manning, S.W., Muscheler, R., Palmer, J.G., Pearson, C., Van Der Plicht, J., Reimer, R.W., Richards, D.A., Scott, E.M., Southon, J.R., Turney, C.S.M., Wacker, L., Adolphi, F., Büntgen, U., Capano, M., Fahrni, S.M., Fogtmann-Schulz, A., Friedrich, R., Köhler, P., Kudsk, S., Miyake, F., Olsen, J., Reinig, F., Sakamoto, M., Sookdeo, A., Talamo, S., 2020. The IntCal20 Northern Hemisphere Radiocarbon Age Calibration Curve (0-55 cal kBP). Radiocarbon 62, 725–757. https://doi.org/10.1017/RDC.2020.41

98. Rey, F., Schwörer, C., Gobet, E., Colombaroli, D., van Leeuwen, J.F.N., Schleiss, S., Tinner, W., 2013. Climatic and human impacts on mountain vegetation at Lauenensee (Bernese Alps, Switzerland) during the last 14,000 years. The Holocene 23, 1415–1427, https://doi.org/10.1177/0959683613489585.
99. Rey, F., Gobet, E., Schwörer, C., Wey, O., Hafner, A., Tinner, W. 2019. Causes and mechanisms of synchronous succession trajectories in primeval Central European mixed *Fagus sylvatica* forests. Journal of Ecology 107, 1392–1408, https://doi.org/10.1111/1365-2745.13121.
100. Robin, V., Bork, H-R., Nadeau, M-J., Nelle, O. 2013. 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(1), 35–47, https://doi.org/10.1177/0959683613515727.
101. Rösch, M., 2000. Long-term human impact as registered in an upland pollen profile from the southern Black Forest, south-western Germany. Vegetation History and Archaeobotany 9, 205–218, https://doi.org/10.1007/BF01294635.
102. Schafstall N, Helena Svitavská-Svobodová H, Kadlec M, Gałka M, Kuneš P, Bobek P, Goliáš V, Pech P, Nývlt D, Hubený P, Kuosmanen N, Carter VA, Florescu G. 2024. The absence of disturbances promoted the expansion of silver fir (Abies alba) in the Bohemian Forest under drier conditions. Palaeogeography, Palaeoclimatology, Palaeoecology 653(1), 111950, https://doi.org/10.1016/j.palaeo.2023.111950.
103. Schmidl, A., Kofler, W., Oeggl-Wahlmüller, N., Oeggl, K.D., 2005. Land use in the eastern Alps during the Bronze Age - an archaeobotanical case study of a hilltop settlement in the Montafon (western Austria). Archaeometry 47(2), 455–470, https://doi.org/10.1111/j.1475-4754.2005.00213.x.
104. Schwörer, C., Colombaroli, D., Kaltenrieder, P., Rey, F., Tinner, W., 2015. Early human impact (5000-3000 BC) affects mountain forest dynamics in the Alps. Journal of Ecology 103, 281–295, https://doi.org/10.1111/1365-2745.12354.
105. Schumacher, M., Schier, W., Schütt, B., 2016. Mid-Holocene vegetation development and herding-related interferences in the Carpathian region. Quaternary International 415, 253–267, https://doi.org/10.1016/j.quaint.2015.09.074.
106. Šída, P., Fröhlich, J., Chvojka, O. 2008. Pozdně paleolitická a mezolitická stanoviště na horní Vltavě u Perneku. Nové poznatky o předneolitickém osídlení Lipenska, Archeologické výzkumy v jižních Čechách 21, 3–29.
107. Šída, P., Eigner, J., Fröhlich, J., Moravcová, M. and Franzeová, D. 2011. Doba kamenná v povodí horní Otavy. Plzeň, Západočeská univerzita v Plzni.
108. Šída, P., Franzeová, D., Moravcová, M. 2012. Raw material sources and the possibility of studying hunter-gatherer mobility as seen on selected Late Upper Palaeolithic and Mesolithic Sites in Bohemia. Natural Sciences in Archaeology 3(1), 117–129.
109. Stockmarr, J. 1972. Tablets with spores used in absolute pollen analysis. Pollen Spores 13, 614–621.

110. Šumberová, K., Hájková, P., Chytrý, M., Hroudová, Z., Sádlo, J., Hájek, M., Hrivnák, R., Navrátilová, J., Hanáková, P., Ekrt, L., Ekrtová, E. 2011. Vegetace rákosin a vysokých ostřic (Phragmito-Magno-Caricetea). Marsh vegetation. – In: Chytrý M. (ed.), Vegetace České republiky. 3. Vodní a mokřadní vegetace [Vegetation of the Czech Republic 3. Aquatic and wetland vegetation], p. 386–579, Academia, Praha.
111. Svobodová, H., Soukupová, L., and Reille, M., 2002. Diversified development of mountain mires, Bohemian Forest, Central Europe, in the last 13,000 years. Quaternary International 91(1), 123–135, https://doi.org/10.1016/S1040-6182(01)00106-9.
112. Svobodová, H., Reille, M., and Goeury, C., 2001. Past vegetation dynamics of Vltavský luh, upper Vltava River valley in the Šumava mountains, Czech Republic. Vegetation History and Archaeobotany 10(4), 185–199, https://doi.org/10.1007/PL00006930.
113. Tinner, W., Conedera, M., Ammann, B., Gaggeler, H.W., Gedye, S., Jones, R., Sagesser, B. 1998. Pollen and charcoal in lake sediments compared with historically documented forest fires in southern Switzerland since AD 1920. The Holocene 8, 31–42, https://doi.org/10.1191/095968398667205430.
114. Tinner, W., Lang, G., Schwörer, C. 2023. Treeline and timberline dynamics. In: Lang, G., Ammann, B., Behre, K.-E., Tinner, W., 2023. Quaternary Vegetation Dynamics of Europe. Haupt, Bern, pp. 455–466.
115. Tinner, W. 2023. Long-term disturbance ecology. In: Lang, G., Ammann, B., Behre, K.-E., Tinner, W., 2023. Quaternary Vegetation Dynamics of Europe. Haupt, Bern, pp. 467–485.
116. Tomlinson, P. 1985. An aid to the identification of fossil buds, bud-scales and catkin-bracts of British trees and shrubs. Circaea 3, 45–130.
117. Turetsky, M.R., Benscoter, B., Page, S., Rein, G., van der Werf, G.R., Watts, A. 2014. Global vulnerability of peatlands to fire and carbon loss. Nature Geoscience 8, 11–14, https://doi.org/10.1038/ngeo2325.
118. Umbanhowar, C.E., Mcgrath, M.J., 1998. Experimental production and analysis of microscopic charcoal from wood, leaves and grasses. The Holocene, 8(3), 341–346, https://doi.org/10.1191/095968398666496051.
119. van Geel, G., 1978. A paleoecological 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), 1–120, 10.1016/0034-6667(78)90040-4.
120. Vannière, B., Blarquez, O., Rius, D., Doyen, E., Brücher, T., Colombaroli, D., Connor, S., Feurdean, A., Hickler, T., Kaltenrieder, P., Lemmen, C., Leys, B., Massa, C., Olofsson, J. 2016. 7000-year human legacy of elevation-dependent European fire regimes. Quaternary Science Reviews, 132, 206–212, https://doi.org/10.1016/j.quascirev.2015.11.012.
121. Vencl, S. 2006. Nejstarší osídlení jižních Čech. Praha, Archeologický ústav Akademie věd ČR.

122. Vera, F.W.M., 2000. Grazing ecology and forest history. CABI Publishing, Wallingford. pp 1–506.
123. Veron, A., Novak, M., Brizova, E., Stepanova, M. 2014. Environmental imprints of climate changes and anthropogenic activities in the Ore Mountains of Bohemia (Central Europe) since 13 cal. ka BP. The Holocene 24(8), 919–931, https://doi.org/10.1177/0959683614534746.
124. Veselý, J., Almquist-Jacobson, H., Miller, L.M., Norton, S.A., Appleby, P., Dixit, A.S., Smol, J.P. 1993. The history and impact of air pollution at Čertovo Lake, southwestern Czech Republic. Journal of Paleolimnology 8, 211–231, https://doi.org/10.1007/BF00177857.
125. Willis, K.J., and Birks, H.J.B. 2006. What is natural? The need for a long-term perspective in biodiversity conservation. Science 314, 1261–1265, DOI: 10.1126/science.1122667
126. Wood, S.N., 2006. Generalized Additive Models: an introduction with R. Boca Raton: CRC/Chapman & Hall
127. Zlámalová Cílová, Z., Gelnar, M., Randáková, S. 2021. Trends in Colouring Blue Glass in Central Europe in Relation to Changes in Chemical Composition of Glass from the Middle Ages to Modern Ages. Mineral 11(9), 1001, https://doi.org/10.3390/min11091001.

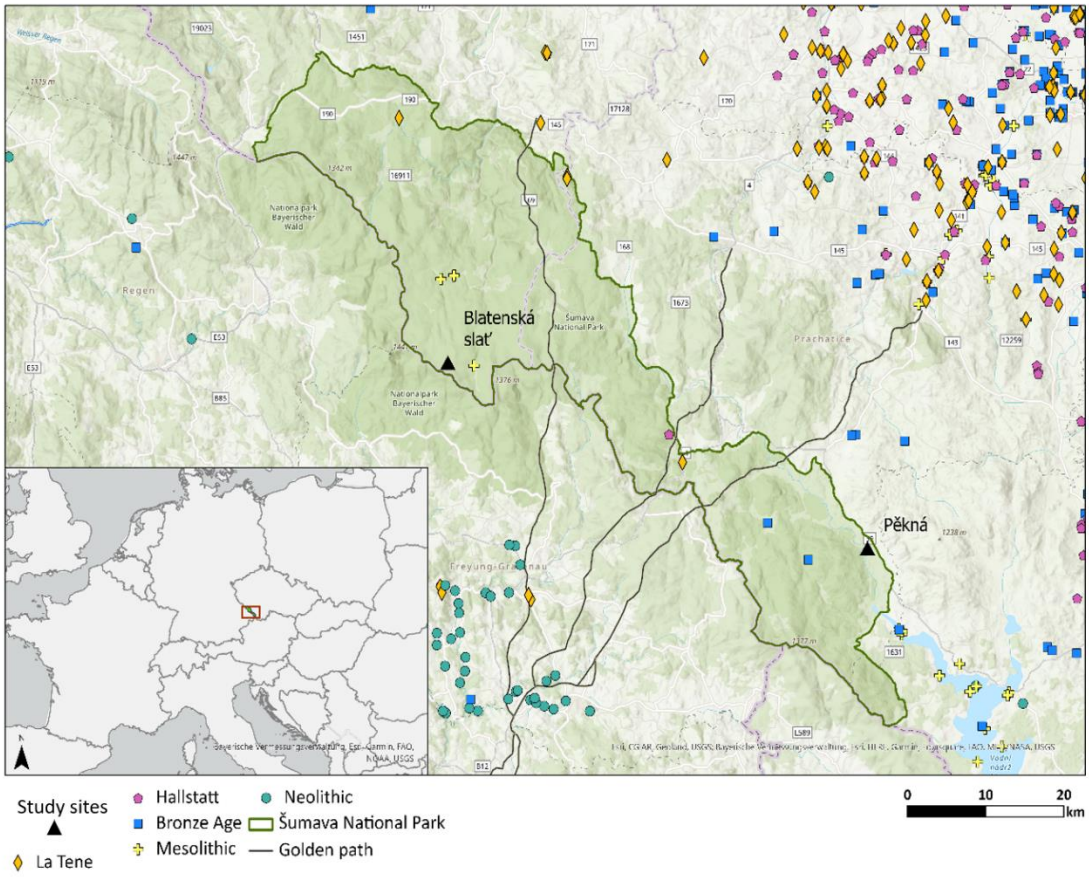


Figure 1. Map showing the location of Pěkná (730 m asl) and Blatenská slať (1275 m asl) peat bogs located in Šumava National Park on the border of Czechia, Germany and Austria (small inset figure), in relation to known archeological sites (main figure); Mesolithic sites (yellow '+'), Neolithic sites (green dots), Bronze Age sites (blue squares), Early Iron Age – Hallstatt sites (pink hexagon), Late Iron Age – La Tène sites (orange triangles); black triangles are our study sites. The three black lines that transect the Bohemian Forest Ecosystem are known historic trading routes. Image by Č. Čišecký.

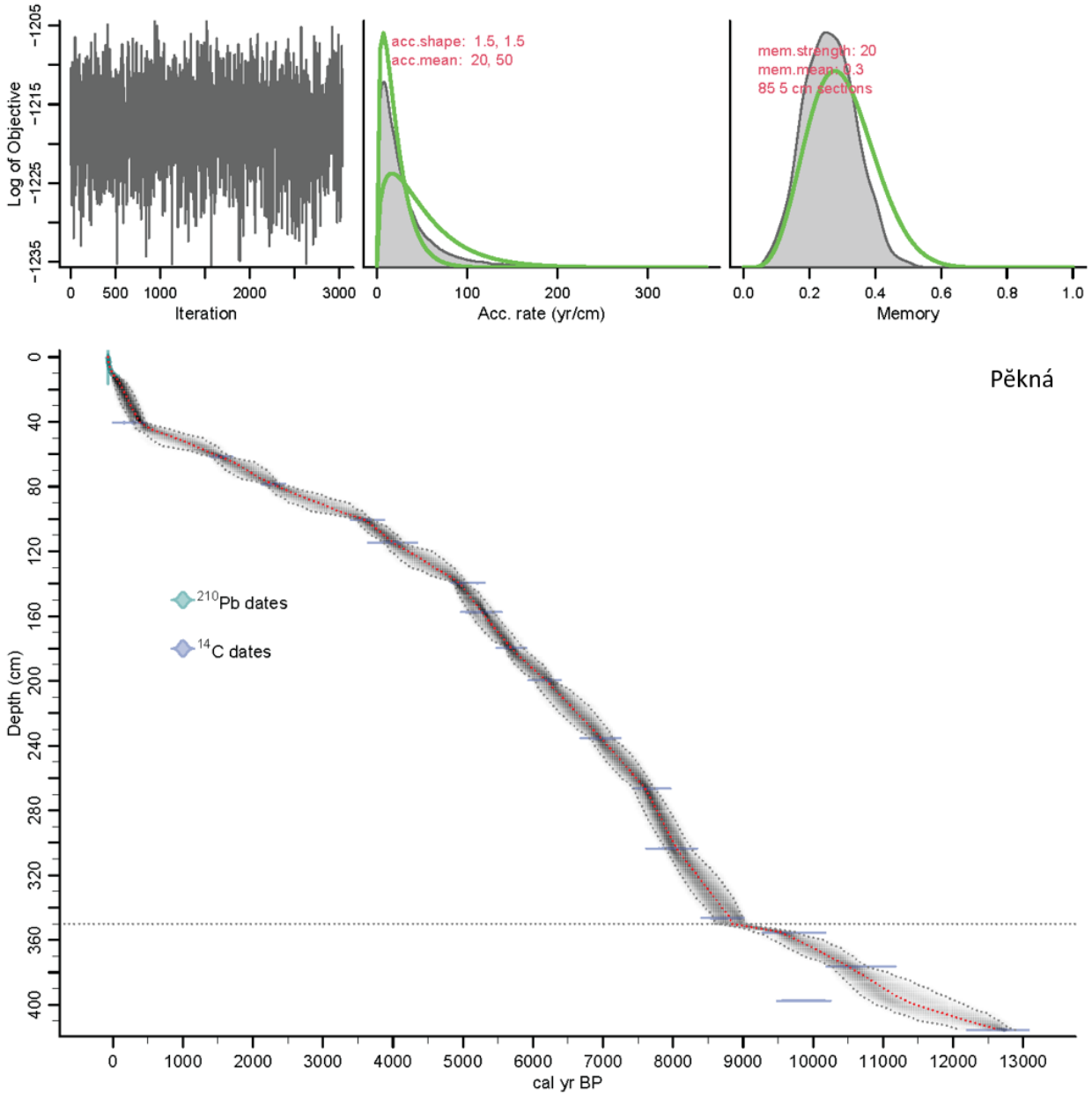


Figure 2. Age-depth model and lithology for Pěkná, Czechia. Age-depth relationships were established using thirteen ^{14}C dates of bulk peat and macrofossil origin, and a ^{210}Pb series (Appleby, 1978), and were modeled in 'rbacon' (Blaauw and Christen, 2011) using the IntCal20 dataset for ^{14}C ages (Reimer et al., 2020). The horizontal dotted line represents the sedimentation boundary between decomposed herbaceous peat and *Eriophorum* peat (see lithology in SI Figure 2). Different prior accumulation rate means were used for these two sections.

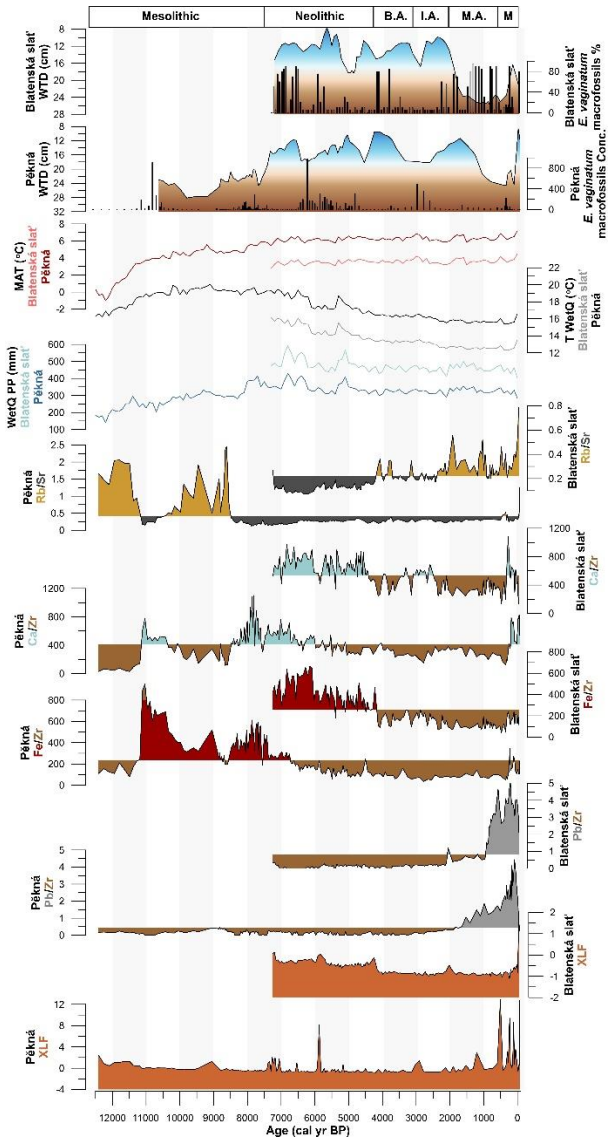


Figure 3. Reconstructed hydroclimate and geochemistry for Pěkná and Blatenská slať. From top to bottom (with Blatenská slať presented first since it is higher in elevation (1275 m asl) and Pěkná presented second (mid-elevation site, 730 m asl); Different archaeological time periods; testate amoebae reconstructed water table depths (WTDs; brown = drier, blue = wetter) with *Eriophorum vaginatum* macrofossils, an indicator of dry conditions, overlaid (black vertical bars); CHELSA modeled climate variables including mean annual temperatures (MAT; salmon = Blatenská slat, red = Pěkná), temperature of the wettest quarter (T WetQ; black = Blatenská slat, gray = Pěkná), precipitation for the wettest quarter (WetQ pp; light blue = Blatenská slat, dark blue = Pěkná) (Karger et al., 2023); Rb/Sr, an indicator of mineralogic input (gold = increased mineralogic input, black = decreased mineralogic input); Ca/Zr, an indicator of authigenic Ca (brown = decreased Ca, blue = increased Ca); Fe/Zr, an indicator of authigenic Fe (brown = decreased Fe, red = increased Fe); Pb/Zr, an anthropogenic indicator for mining activity (brown = decreased Pb, gray = increased Pb); low frequency magnetic susceptibility (χ_{LF}), an indicator of erosion (brow curves).

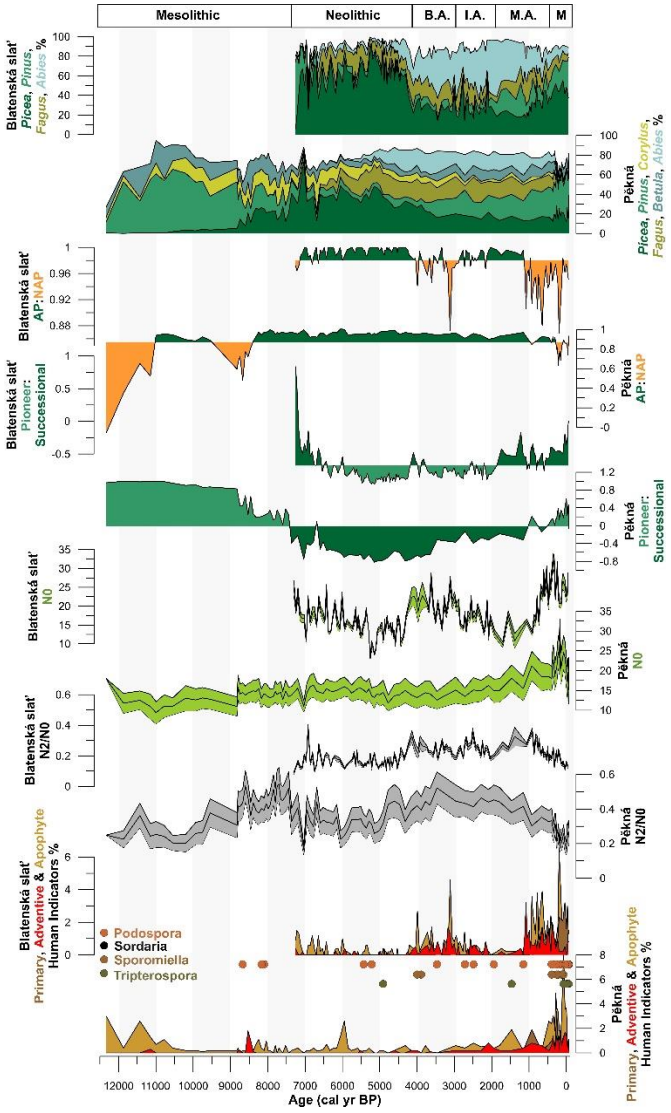


Figure 4. Reconstructed vegetation history for Pěkná and Blatenská slať. From top to bottom (with Blatenská slať presented first since it is higher in elevation (1275 m asl) and Pěkná presented second (mid-elevation site, 730 m asl); Different archaeological time periods; Dominant forest canopy pollen percentages (dark green curve= *Picea abies*, light green curve = *Pinus*, yellow curve = *Corylus*, olive curve = *Fagus*, dark blue curve = *Betula*, light blue curve = *Abies*); index of forest openness (arboreal pollen = dark green curve, non-arboreal pollen = orange curve), index of forest succession (light green curve = pioneer tree taxa, dark green curve = successional tree taxa); rarefied pollen richness (N0; green curve with gray confidence intervals) indicating periods of increased pollen diversity; pollen evenness (N2/N0; gray lines) indicating the potential dominance of pollen taxa within an ecosystem; primary (brow curve), adventive (red curve) and apophyte (gold curve) pollen indicator taxa indicating human activities overlaid with coprophilous fungi, an indicator of grazers (*Podospora* = orange dots, *Sordaria* = black dots, *Sporomiella* = brown dots, *Tripterospora* = green dots).

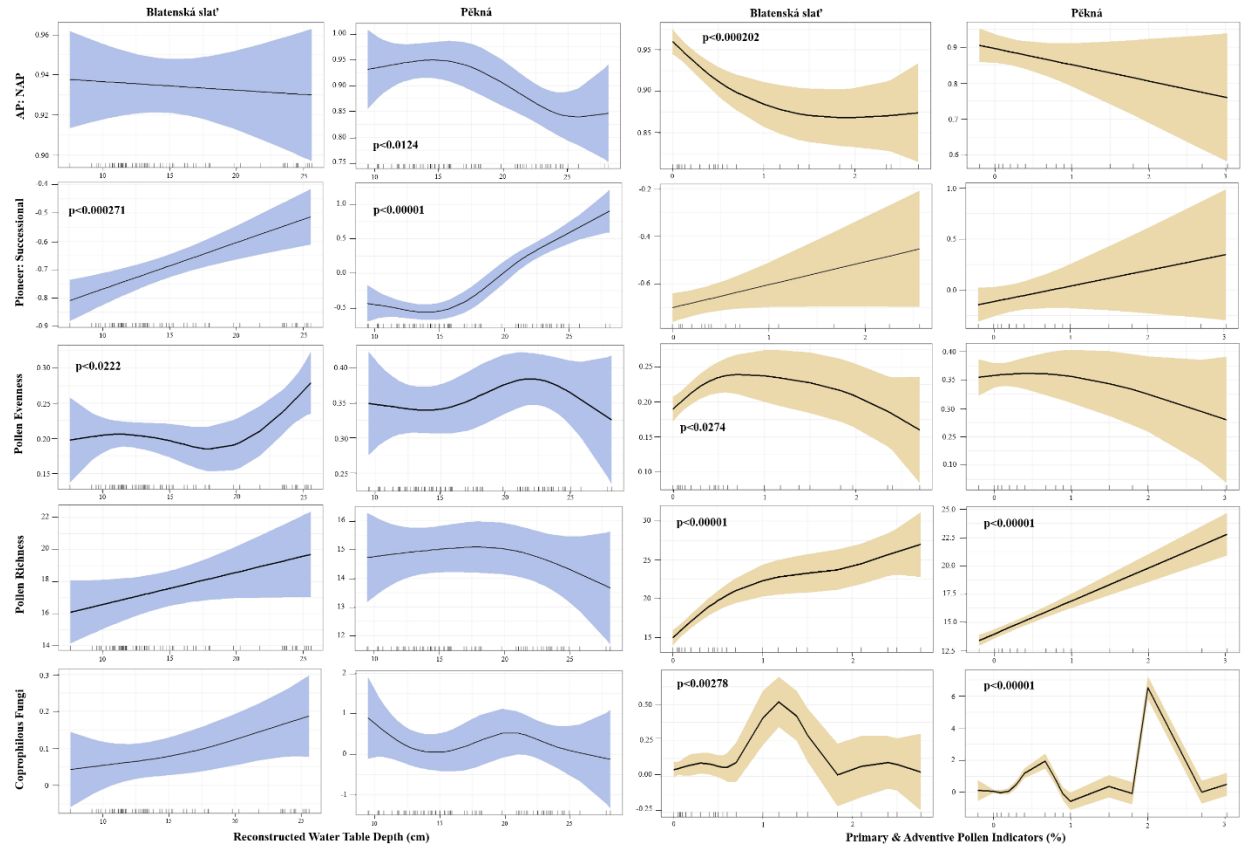


Figure 5. Model response curves showing the relationship between hydroclimate and anthropogenic indicators as independent variables and various forest succession, forest composition and pollen diversity variables at Blatenská slať' and Pěkná, Czechia. Blue curves are results for testate amoebae reconstructed water table depths (WTDs). Yellow curves are results for the sum of primary and adventive pollen indicators following Deza-Aruajo et al. 2020. Bold p-values indicate the relationship is statistically significant.

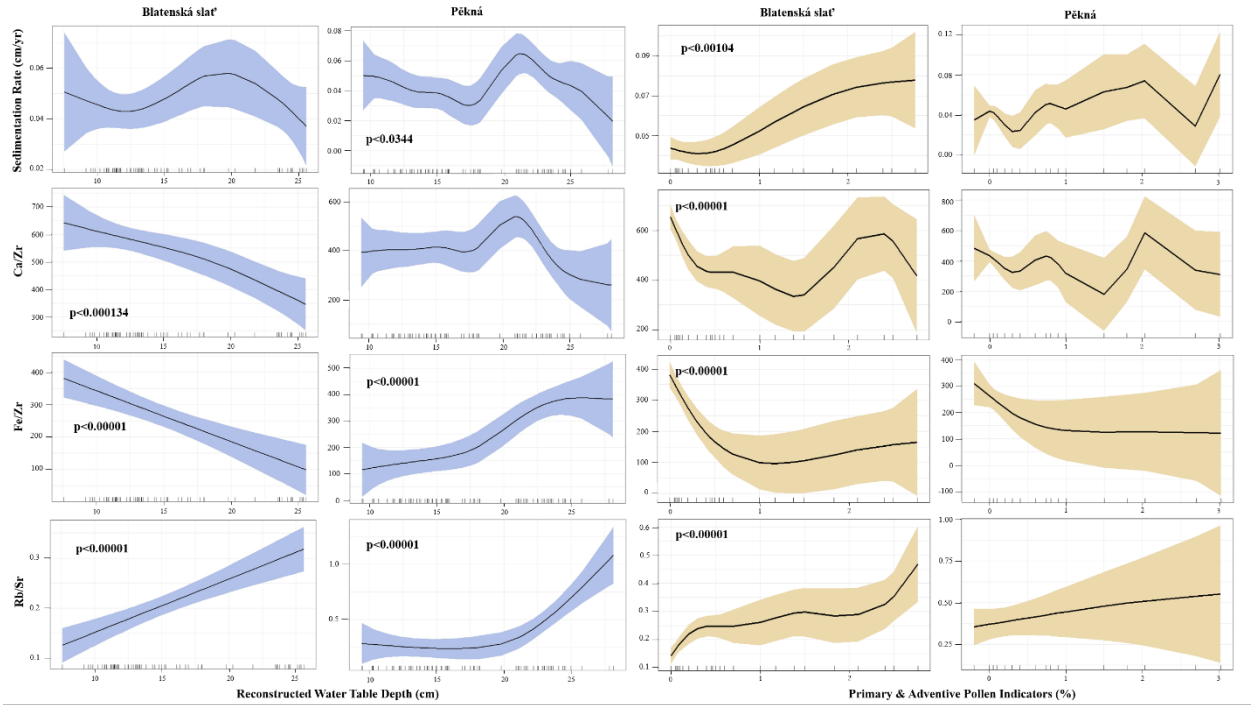


Figure 6. Model response curves showing the relationship between hydroclimate and primary and adventive pollen indicators, (i.e., anthropogenic indicators) as independent variables and various geochemistry variables used as indicators of erosional and depositional activity at Blatenská slať and Pěkná, Czechia. Blue curves are results for testate amoebae reconstructed water table depths (WTDs). Yellow curves are results for the sum of all primary and secondary pollen indicators. Bold p-values indicate the relationship is statistically significant.

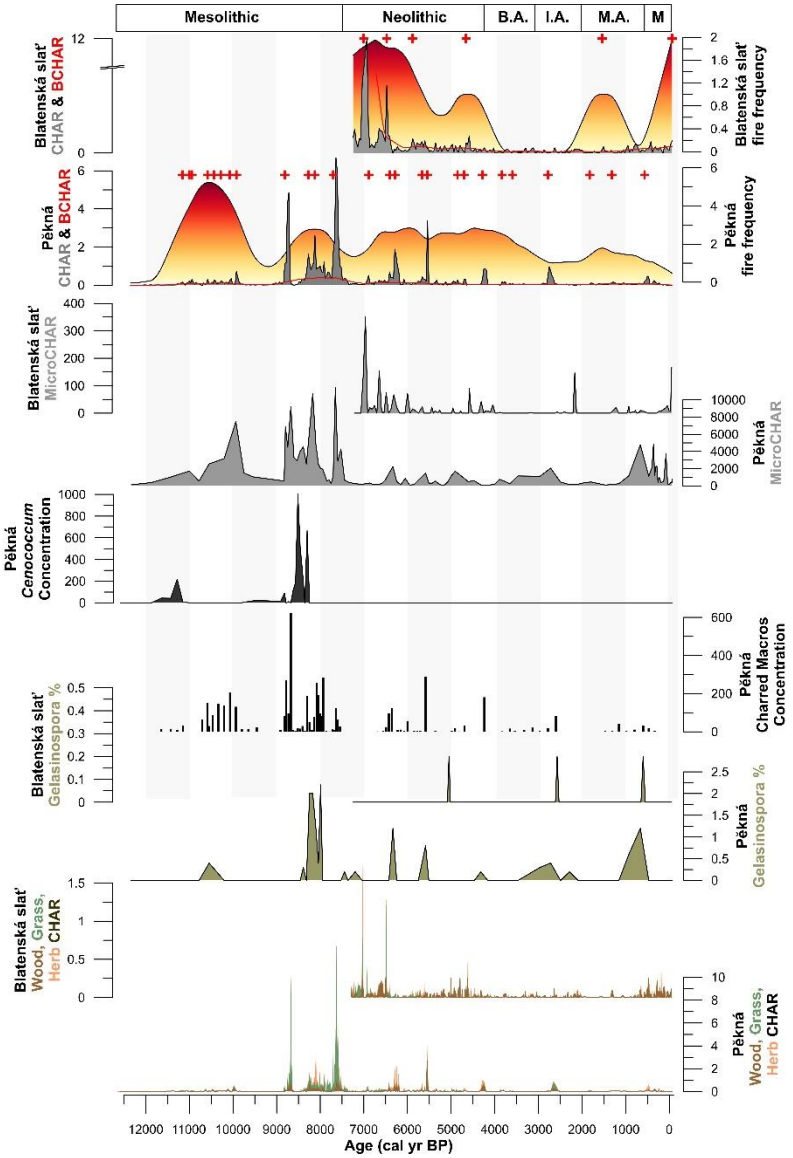


Figure 7. Reconstructed fire history for Pěkná and Blatenská slať. From top to bottom (with Blatenská slať presented first since it is higher in elevation (1275 m asl) than Pěkná (730 m asl); Different archaeological time periods; CHAR (particles per cm^{-2} yr^{-1}) (dark gray curve), with BCHAR (red line) indicates regional fire activity; fire frequency indicates fires/1000 years (filled colour curve); fire episodes are represented with a red '+' symbol; Microcharcoal (particles per cm^{-2} yr^{-1}) (dark gray curve), indicates regional biomass burning; *Cenococcum geophilum* concentrations (black curve), an indicator of soil erosion after fire (only observed at Pěkná); Charred macrofossil concentrations (black histogram) is the sum of all charred macrofossil data (only observed at Pěkná); *Gelasinospora* percentages (olive curve) indicates fire activity; Wood CHAR (brown curve), Grass CHAR (green curve), and Herb CHAR (salmon curve) indicate fuel source type; presented on a log scale to visually demonstrate the large abundance of woody charcoal.

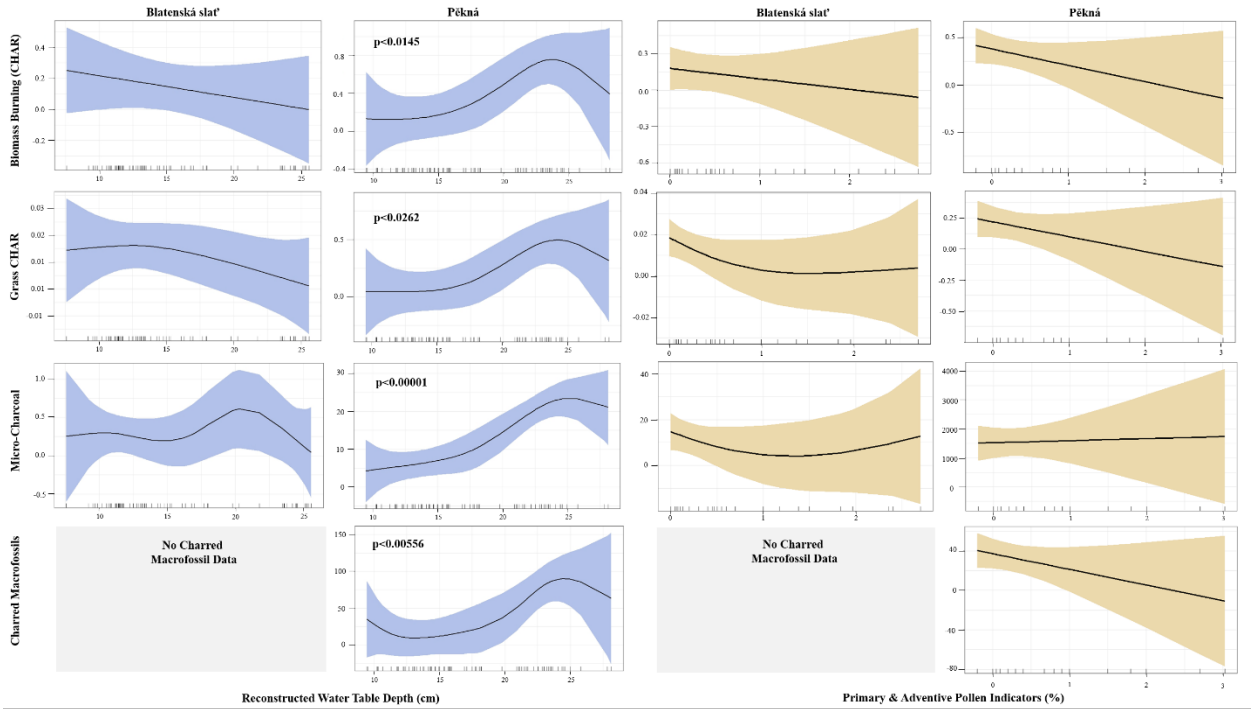


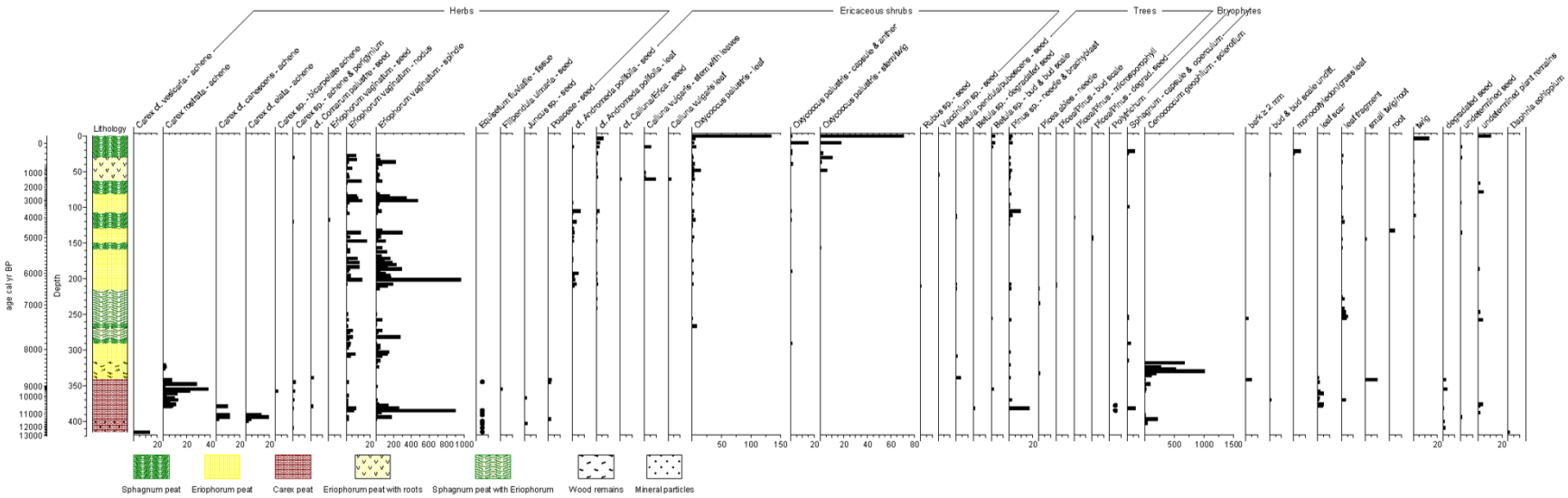
Figure 8. Model response curves showing the relationship between hydroclimate and anthropogenic indicators as independent variables and various fire variables indicator of fire activity at Blatenská slať and Pěkná, Czechia. Blue curves are results for testate amoebae reconstructed water table depths (WTDs). Yellow curves are results for the sum of primary and adventive pollen indicators following Dezu-Aruajo et al., 2020. Bold p-values indicate the relationship is statistically significant.

Table 1. Age-depth relations for Pěkná, Czechia.

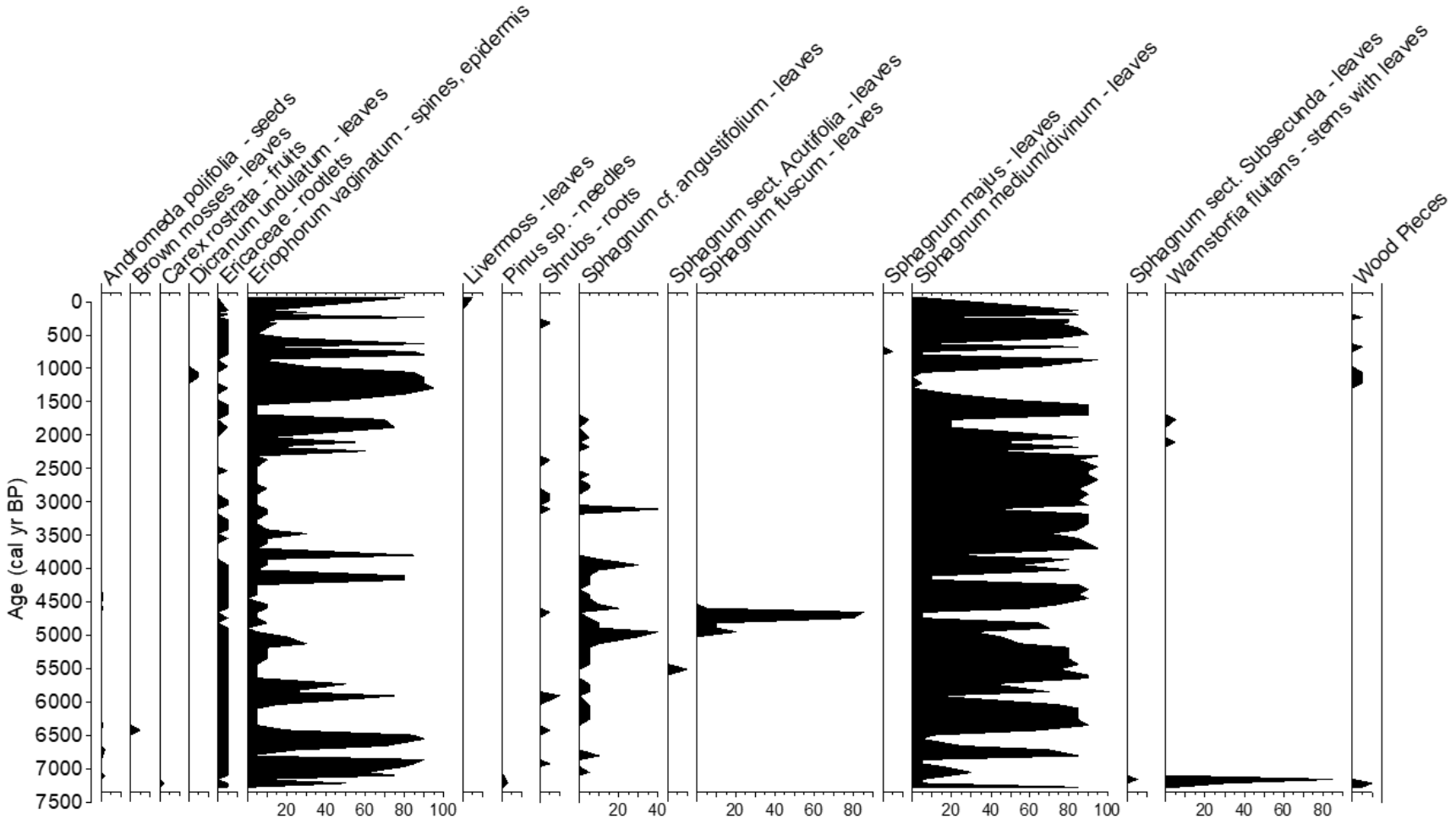
Isotope	Lab Code	Depth (cm)	Age (^{210}Pb / ^{14}C yr BP)	Sample Material
^{210}Pb		1	2017 ± 8.4	Bulk peat
^{210}Pb		2	2015 ± 8.3	Bulk peat
^{210}Pb		3	2012 ± 8.3	Bulk peat
^{210}Pb		4	2009 ±8.4	Bulk peat
^{210}Pb		6	2001 ± 8.5	Bulk peat
^{210}Pb		8	1990 ± 8.8	Bulk peat
^{210}Pb		10	1965 ± 11.4	Bulk peat
^{210}Pb		12	1918 ± 17.3	Bulk peat
^{14}C	DeA-22180	41	250 ± 25	Conifer needle, Ericaceae bud
^{14}C	DeA-26077	62	1653 ± 27	*Sphagnum* stems
^{14}C	DeA-22181	79	2289 ± 26	*Betula* twig
^{14}C	DeA-26078	101	3383 ± 38	*Sphagnum* stems
^{14}C	DeA-23068	115	3649 ± 46	*Oxycoccus* leaves, pine needle, *Carex* seeds
^{14}C	DeA-26079	140	4409 ± 36	*Sphagnum* stems
^{14}C	DeA-22181	158	4576 ± 35	*Sphagnum* stems
^{14}C	DeA-26080	180	4941 ± 37	*Sphagnum* stems
^{14}C	DeA-26081	200	5402 ± 41	*Sphagnum* stems
^{14}C	DeA-22183	236	6101 ± 41	*Sphagnum* stems
^{14}C	DeA-22184	267	6825 ± 68	Charred *Oxycoccus* leaves
^{14}C	DeA-22185	304	7143 ± 72	*Sphagnum* stems
^{14}C	DeA-26082	347	7852 ± 48	*Carex* seeds
^{14}C	DeA-22186	356	8608 ± 68	*Carex* seeds
^{14}C	DeA-22187	377	9348 ± 73	*Carex* seeds
^{14}C	DeA-26083	398	8800 ± 69	*Carex* seeds and leaf fragments
^{14}C	DeA-22188	416	10746 ± 73	*Carex* seeds and leaves

Table 2. Pollen taxa used to calculate primary and secondary pollen indicators, indicative of human influence on at the landscape at Pěkná and Blatenská slať, Czechia. Taxa were selected following Dezu-Aruajo et al., 2020.

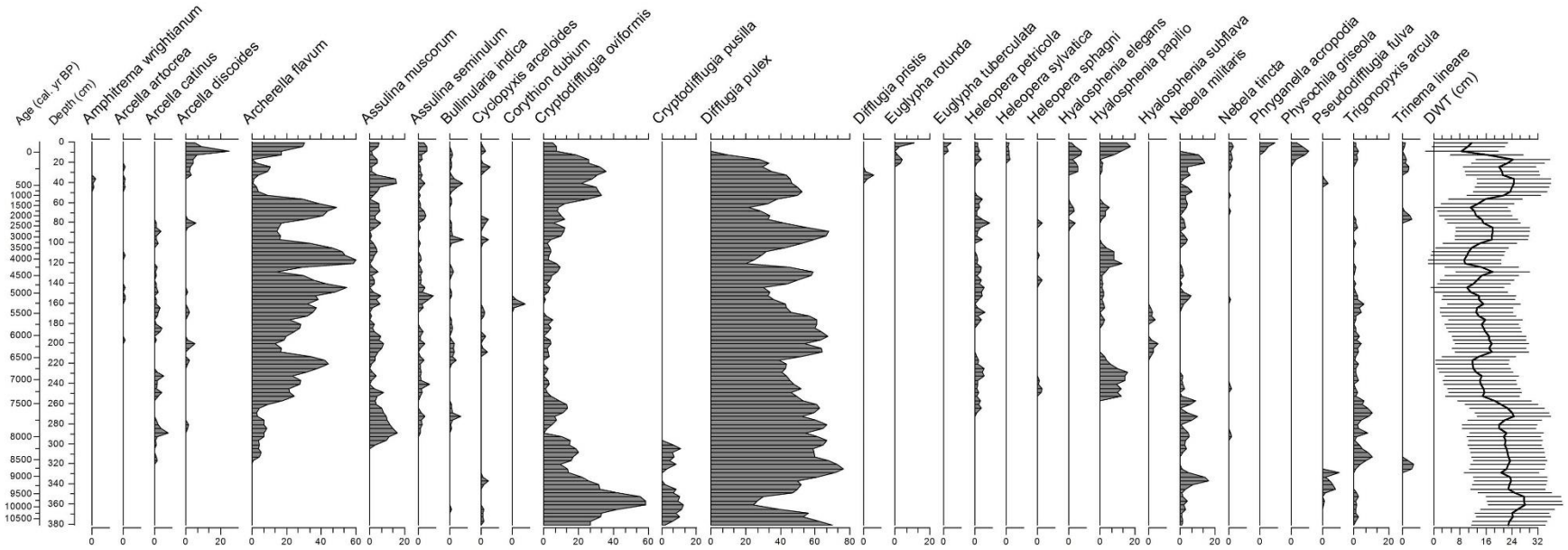
	Pěkná	**Blatenská slať**
Primary Indicators	*Secale*, *Juglans*	*Cannabis*-type, *Fagopyrum*, *Juglans*, *Secale*, *Triticum*-type, *Vicia*
Secondary Indicators (Adventives)	*Plantago lanceolata*, *Plantago major*, *Plantago sp.*, *Polygonum aviculare*-type	*Plantago lanceolata*, *Plantago major*, *Plantago sp.*, *Polygonum aviculare*-type,
Secondary Indicators (Apophytes)	*Juniperus*, *Calluna vulgaris*, *Artemisia*, *Melampyrum*, *Rumex*, *Trifolim*, *Urtica*	*Artemisia*, *Calluna vulgaris*, *Campanula*, *Juniperus*, *Melampyrum*, *Pteridium aquilinum*, *Rumex*, *Urtica*


Herbs
Ericaceous shrubs
Trees
Bryophytes
Lithology
age cal yr BP
Depth
Carex cf. vesicaria - achene
Carex rostrata - achene
Carex cf. canescens - achene
Carex cf. elata - achene
Carex sp. - bicarpellate achene
cf. Comarum palustre - seed
Eriophorum vaginatum - seed
Eriophorum vaginatum - nodus
Eriophorum vaginatum - spindle
Equisetum fluviatile - tissue
Filipendula ulmaria - seed
Juncus sp. - seed
Poaceae - seed
cf. Andromeda polifolia - seed
cf. Andromeda polifolia - leaf
cf. Calluna/Erica - seed
Calluna vulgaris - stem with leaves
Calluna vulgaris leaf
Oxycoccus palustris - leaf
Oxycoccus palustris - capsule & anther
Oxycoccus palustris - stem/twig
Rubus sp. - seed
Vaccinium sp. - seed
Betula pendula/pubescens - seed
Betula sp. - degraded seed
Betula sp. - bud & bud scale
Pinus sp. - needle & brachyblast
Picea abies - needle
Picea/Pinus - bud scale
Picea/Pinus - microsporophyll
Picea/Pinus - degrad. seed
Polytrichum
Sphagnum - capsule & operculum
Cenococcum geophilum - sclerotium
bark ≥ 2 mm
bud & bud scale undiff.
monocotyledon/grass leaf
leaf scar
leaf fragment
small twig/root
root
twig
decomposed seed
undetermined seed
undetermined plant remains
Daphnia ephippium
Sphagnum peat
Eriophorum peat
Carex peat
Eriophorum peat with roots
Sphagnum peat with Eriophorum
Wood remains
Mineral particles
charcoal ≥ 1 mm
charred Betula sp. seed
charred Betula sp. bud scale
charred Pinus sp. needle
charred Pinus sp. brachyblast
partly charred Pinus sp. needle with brachyblast
charred Pinus sp. - needle
charred Picea abies - needle
charred needle undetermined
charred Andromeda polifolia seed
charred Oxycoccus cf. palustris seed
partly charred Oxycoccus cf. palustris leaf
charred Oxycoccus cf. palustris stem
charred Vaccinium sp. seed
charred Carex cf. canescens - achene
charred Carex cf. elata/acuta - achene
charred Eriophorum vaginatum - spindle
charred Eriophorum vaginatum - nodus
charred Sphagnum leaves in assemblage
charred moss
partly charred moss
charred seed undiff.
charred leaf
partly charred leaf
charred bud
charred rootlet
charred bark
charred plant tissue
partly charred plant tissue
charred leaf in rosette

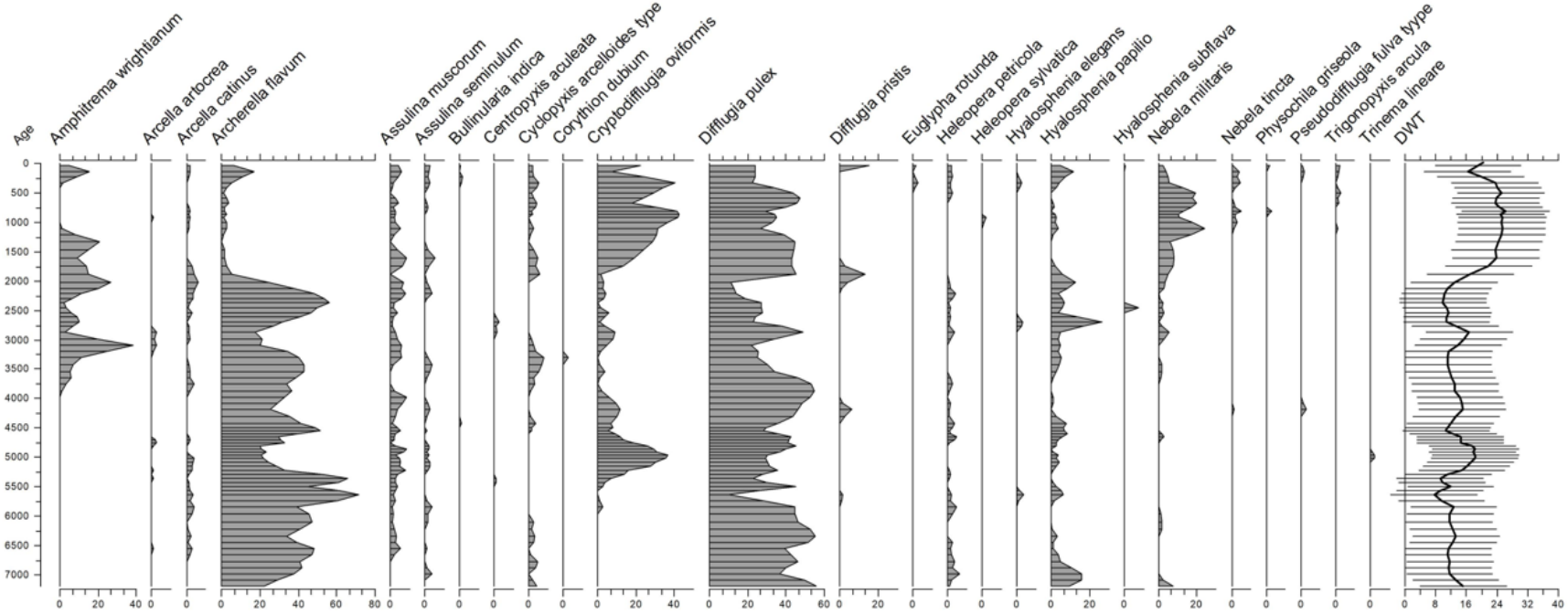
SI Figure 1. Full plant macrofossil diagram with core lithology for Pěkná, Czechia. Top panel are tree, shrub and herb macrofossils. Bottom panel are charred macrofossils only.



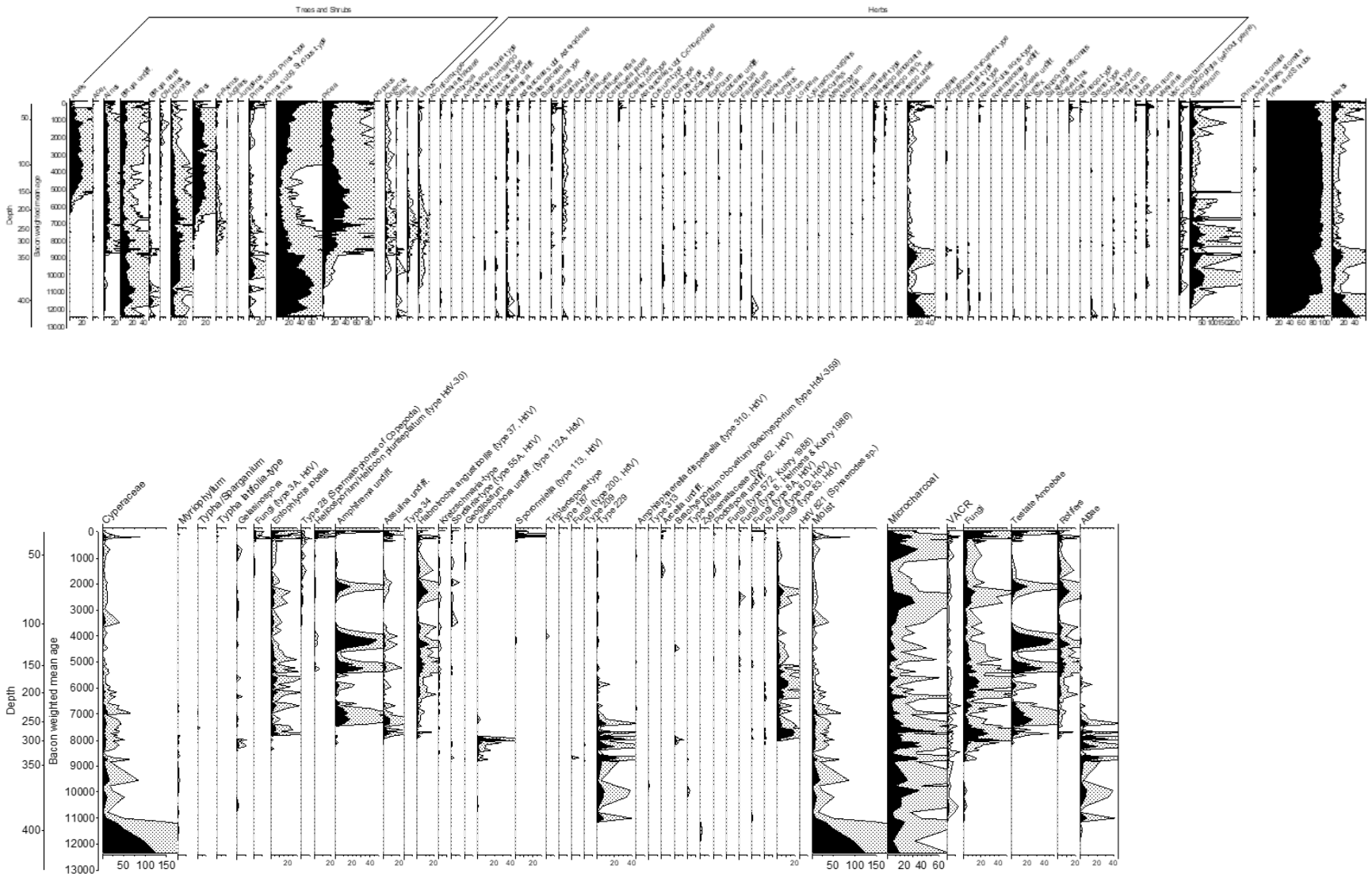
SI Figure 2. Full plant macrofossil diagram for Blatenská slať, Czechia.



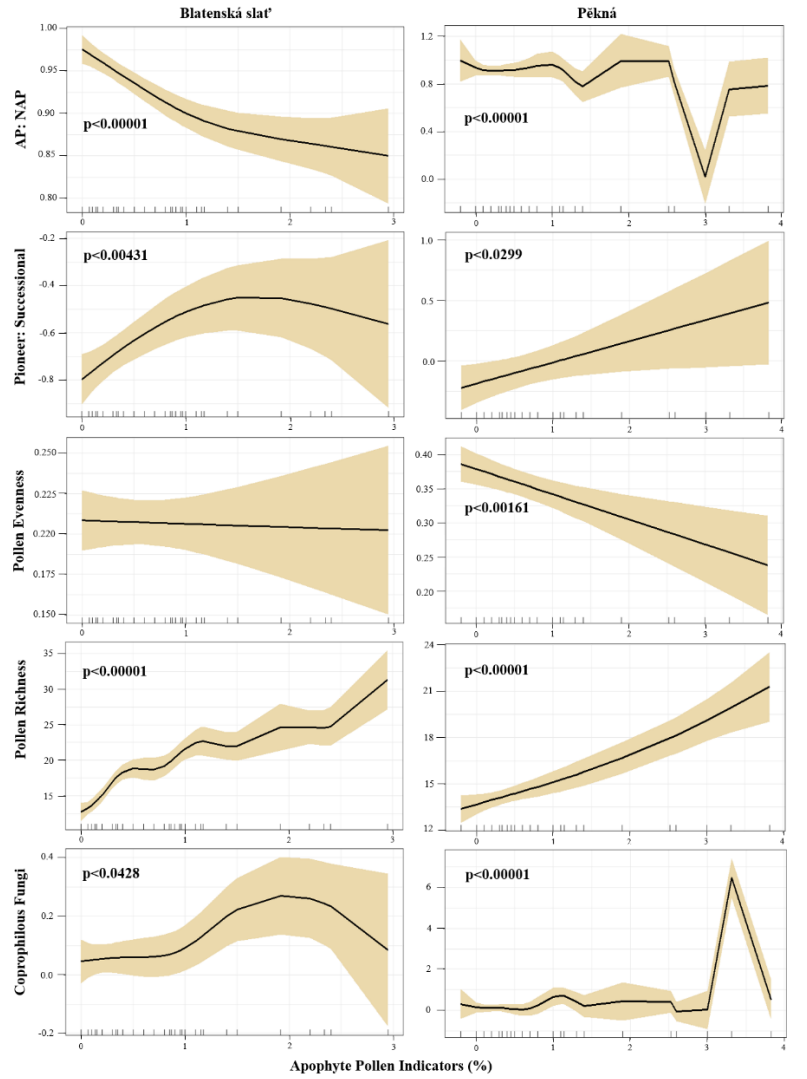
SI Figure 3. Full testate amoebae and reconstructed water table depth diagram for Pěkná, Czechia.



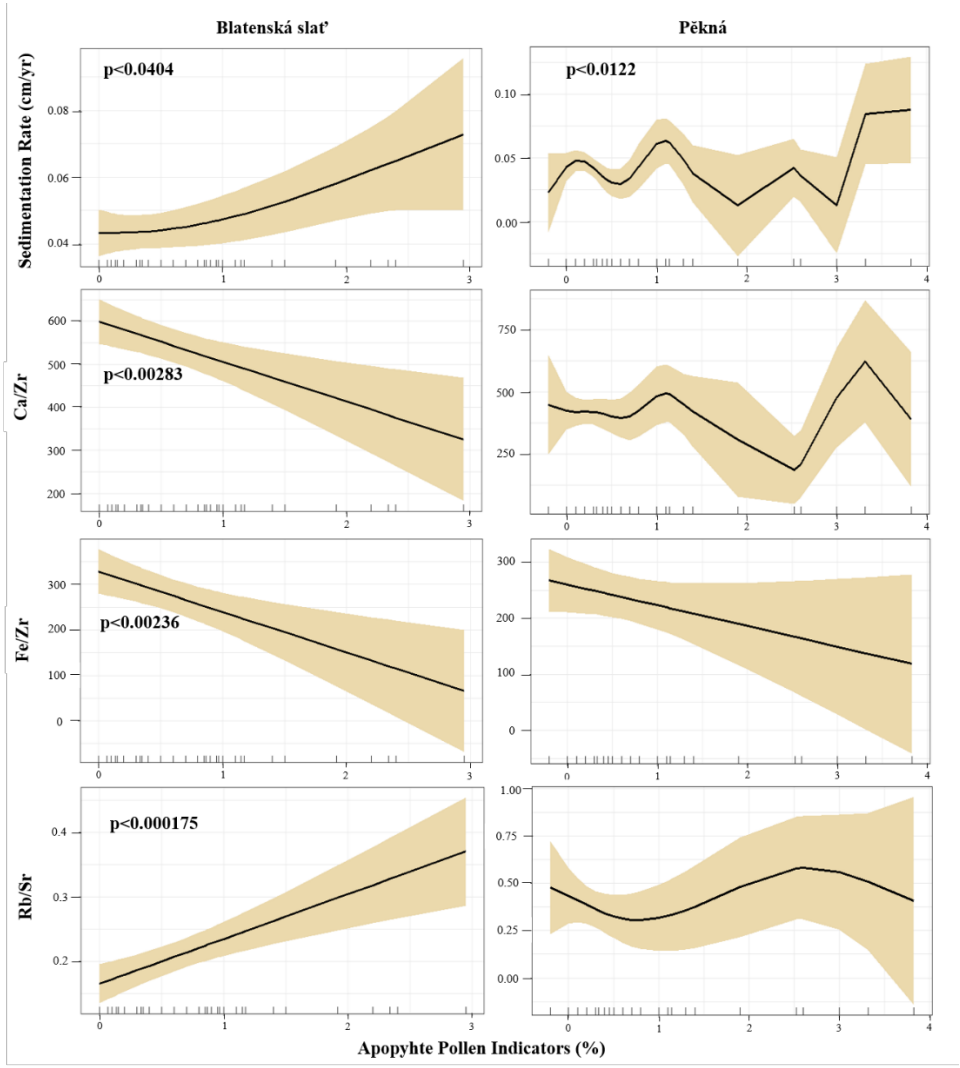
SI Figure 4. Full testate amoebae and reconstructed water table depth diagram for Blatenská slať, Czechia.



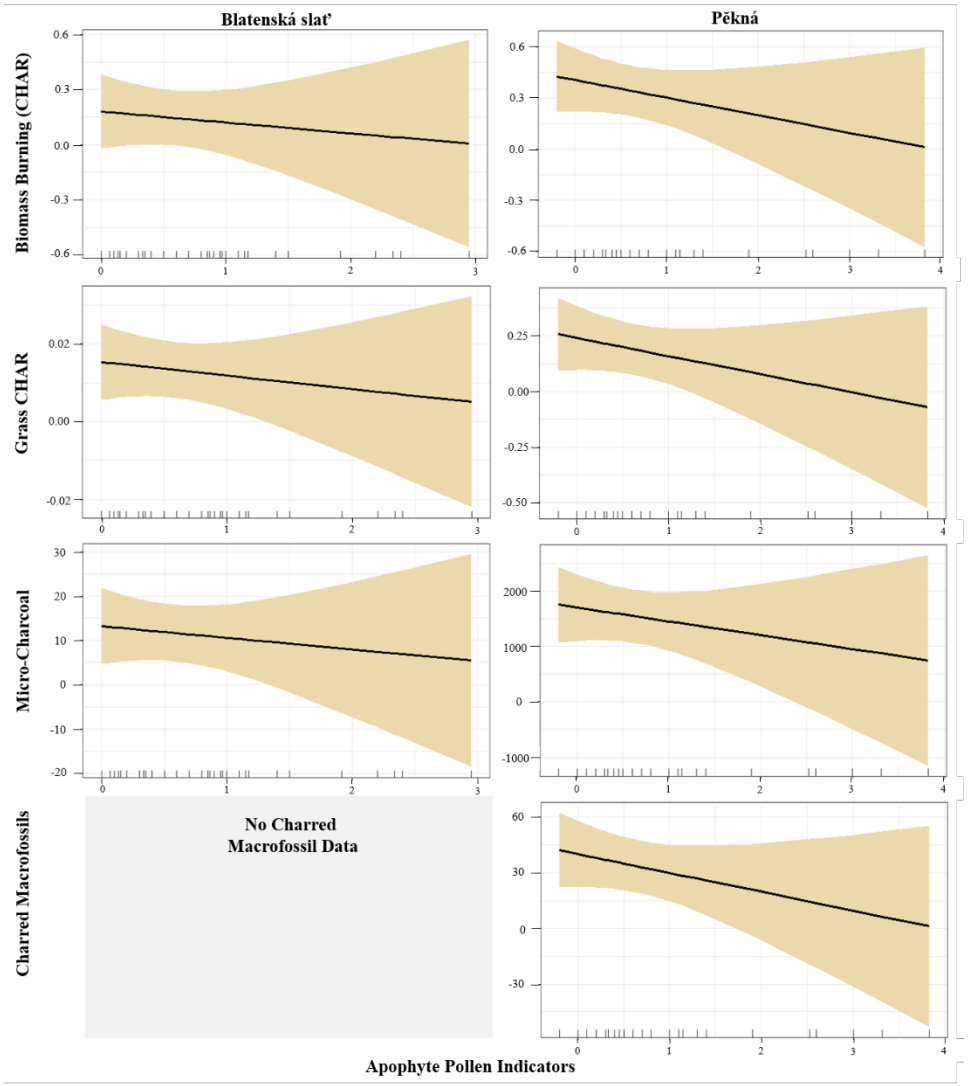
SI Figure 5. Full pollen diagram for Pěkná, Czechia. Top panel are tree, shrub and herb taxa. Bottom panel are aquatic and non-pollen palynomorph taxa.



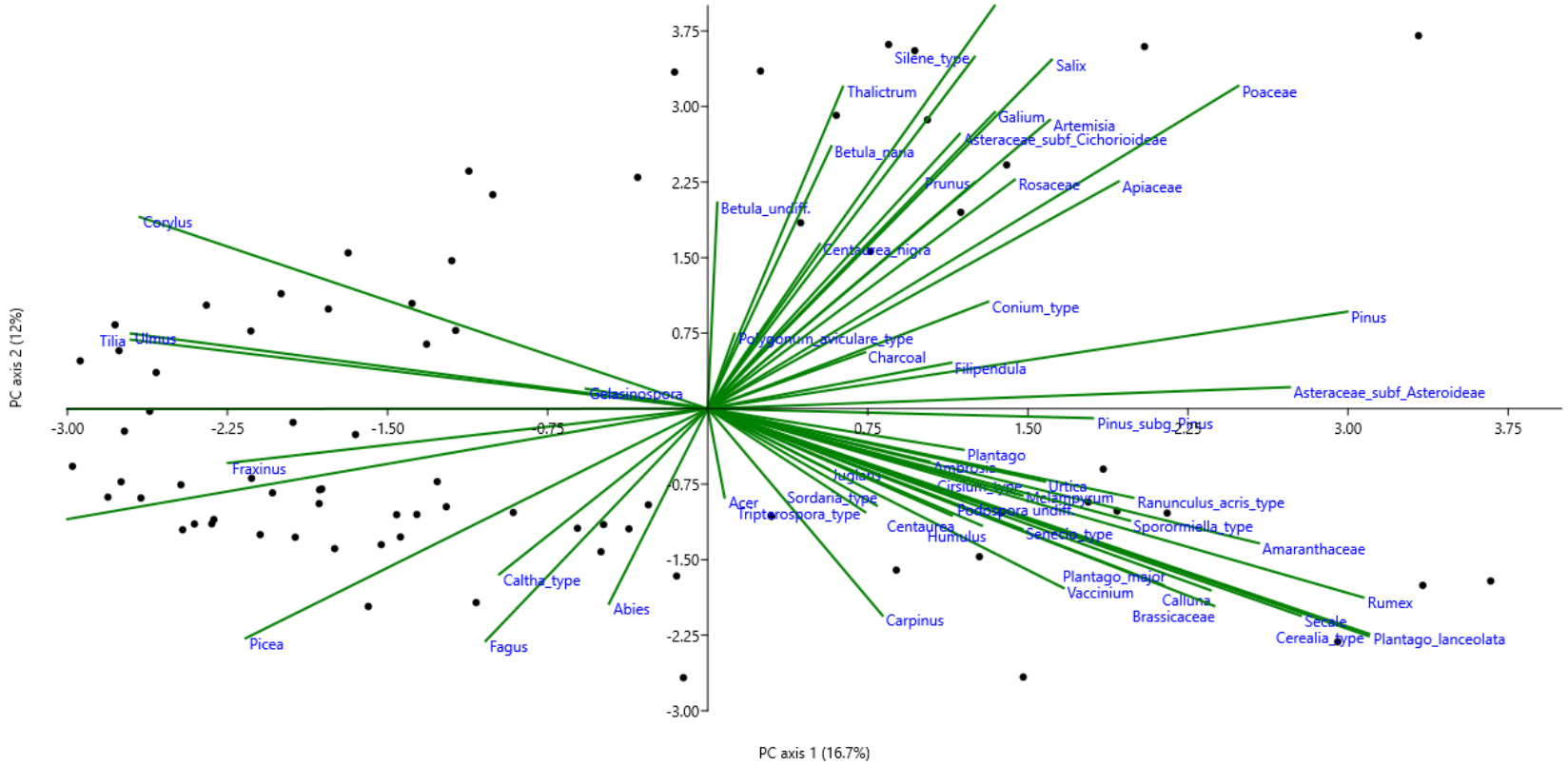
SI Figure 6. Model response curves showing the relationship between apophyte pollen indicators as independent variables and various forest succession, forest composition and pollen diversity variables at Blatenská slať and Pěkná, Czechia. Bold p-values indicate the relationship is statistically significant.



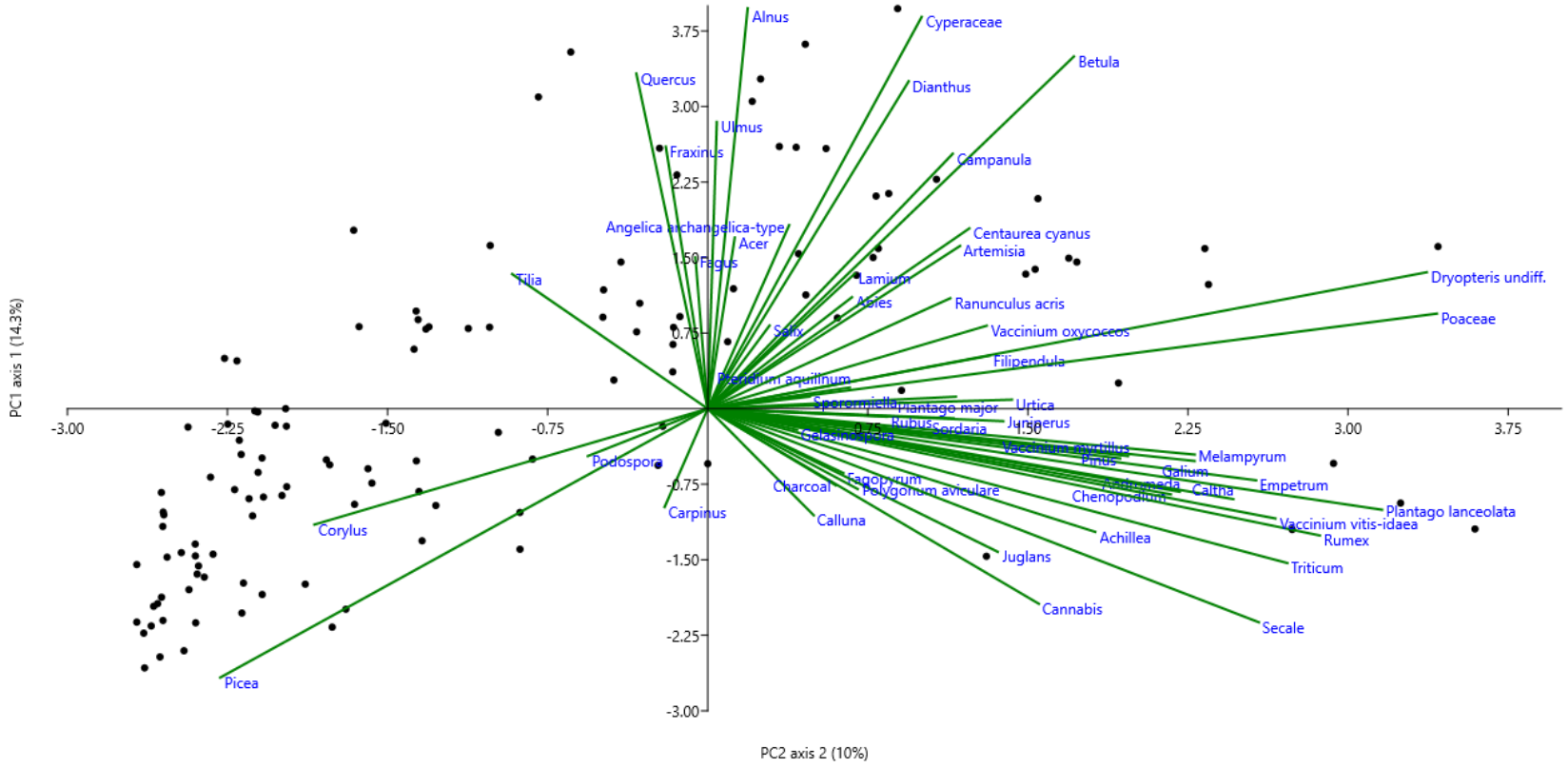
SI Figure 7. Model response curves showing the relationship between apophyte pollen indicators as independent variables and various geochemistry variables used as indicators of erosional and depositional activity at Blatenská slať and Pěkná, Czechia. Bold p-values indicate the relationship is statistically significant.



SI Figure 8. Model response curves showing the relationship between apophyte pollen as independent variables and various fire variables indicator of fire activity at Blatenská slať and Pěkná, Czechia. Bold p-values indicate the relationship is statistically significant.



SI Figure 9. PCA results for fossil pollen data from Pěkná, Czechia.



SI Figure 10. PCA results for fossil pollen data from Blatenská slat, Czechia.