



A complex insight into the Late Quaternary history of Bohemian-Moravian Highlands summit

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Abstract Peat is an important archive allowing the reconstruction of past mire environments and surrounding vegetation. The Pihoviny site, one of the oldest peat deposits in the Bohemian-Moravian Highlands, was analysed for macrofossils and pollen and compared with other profiles in the region. The local mire development started in the Late Glacial as sedge-moss quaking fen with tundra elements characterised by high mineral richness and groundwater level. During the Early Holocene, it developed through the rich fen with hummocks, willow and reed stage to the waterlogged spruce forest, which persisted for thousands of years until the post-mediaeval deforestation. The recent mire vegetation developed 300 years ago due to human-induced deforestation. Further, we revealed high regional synchronicity among pollen profiles in the Early-Holocene (10,000–9000 cal BP), when open-canopy pine-birch forests transformed into closed-canopy deciduous forests

due to climate improvement. Contrary, the Late-Holocene transformation to beech-fir forests was not synchronous, suggesting another driver than climate, likely human activities. Although pollen of both late-successional trees occurred since the Early Holocene, their expansion began much later, 5500–3500 (beech) and 3500–2500 cal BP (fir). Numerous spruce macrofossils suggest its pollen's local origin in the waterlogged spruce forest. Our results support the need for active management to sustain open mire vegetation and prevent spontaneous forest regrowth, recently boosted by climate warming. Palaeoecological analyses reconstructed a mosaic of waterlogged spruce and terrestrial beech-fir forests in the landscape, which should be restored to increase forest resistance against bark-beetle breakdowns and other disturbances in future.

Keywords Macrofossils · Peat · Pollen diversity · Radiocarbon dating · Transfer function · Vegetation succession

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Introduction

Mires represent very important and interesting habitats from many points of view. They host highly specialised and diversified vegetation and related animal communities (Holmen et al. 1967; Rydin and Jeglum 2013; Horsáková et al. 2018). Further, they accumulate a considerable carbon amount in peat due to the stable

high groundwater level blocking decomposition processes (Joosten et al. 2017). Because of their sensitivity to any changes in the water regime, they belong among the most threatened habitats of Europe (Janssen et al. 2016; Chytrý et al. 2019; Spitale 2021). Mires are also very exceptional because they represent natural archives. They store direct information not only about their development and history thanks to keeping plant and animal macrofossils but also about the surrounding landscape thanks to the pollen archived in the peat (Barber 1993). Thus, it is possible to reconstruct the history of this unique habitat and relate it to the changes in climate and local environmental conditions, which can help us predict future development and threats.

The Bohemian-Moravian Highlands was and still is one of the most important regions for the mire biota within the Czech Republic (Rybníčková 1974; Peterka et al. 2014) even if many sites have been destroyed or disturbed in the last decades. Moreover, mires in this area still harbour many glacial relics of vascular plants (Čech et al. 2021) and especially bryophytes (Rybníček 1966; Štechová et al. 2014; Hájková et al. 2018). Despite the common presence of peat-forming substrates, relatively few modern palaeoecological studies exist from the area (e.g. Břízová 2009; Szabó et al. 2017; Roleček et al. 2020). The palaeoecological research of the Bohemian-Moravian Highlands started in the interwar period by Rudolph (1927), Salaschek (1936) and Puchmajerová (1944) in the Dářko peat bog situated close to the study site Pihoviny in the Žďárské vrchy Hills. Later, some studies focusing mainly on the pollen analysis followed and described profiles, either dated by radiocarbon method (e.g. Rybníček and Rybníčková 1968; Rybníčková and Rybníček 1988; Břízová 2009; Szabó et al. 2016), or with estimated age according to pollen spectra (e.g. Kneblová-Vodičková 1966; Jankovská 1971; Rybníčková 1974). Recently all known ages of the Bohemian-Moravian Highland mires were summarised by Peterka et al. (2022a). The detailed studies on local plus regional vegetation history, involving both the macrofossil records and pollen data of sufficient quality and with radiocarbon dating, were conducted only in the Dářko (Břízová 2009; Roleček et al. 2020) and the Kameničky site (Rybníčková and Rybníček 1988).

Based on the above-mentioned overview of published palaeoecological works, it is evident that

new modern multi-proxy radiocarbon-dated studies involving plant macrofossils and pollen data are needed in the region. This study brings a complex palaeoecological survey of the Pihoviny fen, originating around 14,000 cal BP (Peterka et al. 2022a, b). Thus, it is the oldest known mire in the region, together with the Dářko peat bog (Roleček et al. 2020). As the macrofossil data are only at the disposal of the current bog environment (Dářko) and tall-herb wetland vegetation (Kameničky), the macrofossil record from the Pihoviny site is the first one sampled in the low-productive minerotrophic fen habitat. The main aim of the research is to explore the history of this fen habitat type since the Glacial period and to assess if the recent minerotrophic fens and fen meadows in the region are a young vegetation type that originated after the anthropogenic deforestation, as was traditionally supposed (Rybníček and Rybníčková 2000) or they have more extended continuity. The complex palaeoecological research of the peat profile from the Pihoviny fen can substantially improve the knowledge on the vegetation development of the top parts of the Bohemian-Moravian Highlands (specifically Žďárské vrchy Hills) as well as on the development of local fen vegetation.

Methods

Study Site and Sediment Sampling

The Pihoviny site (49°39'32"N, 15°58'17"E; Figure 1) is situated in the heart of Žďárské vrchy Hills (northern part of the Bohemian-Moravian Highland), below the Žákova hora Mt with Nature reserve preserving primaeval beach-fir forests. The site is located on both sides of the road between the Cikháj and Herálec villages (1.2 km north of Cikháj) at an altitude of 680 m a.s.l. There is a mosaic of poor and moderately-rich fens, fen meadows and submontane *Nardus* grasslands surrounded by spruce forests (partly waterlogged) and alder carrs (for details, see Šíroková 2022). The recent fen vegetation is dominated, for example, by *Carex echinata*, *C. nigra*, *C. rostrata*, *Comarum palustre*, *Valeriana dioica* among vascular plants and *Aulacomnium palustre*, *Calliergonella cuspidata*, *Sphagnum palustre*, *S. recurvum* agg. and *S. teres* among bryophytes. Sub-recently rare bryophyte species *Hamatocaulis vernicosus* and

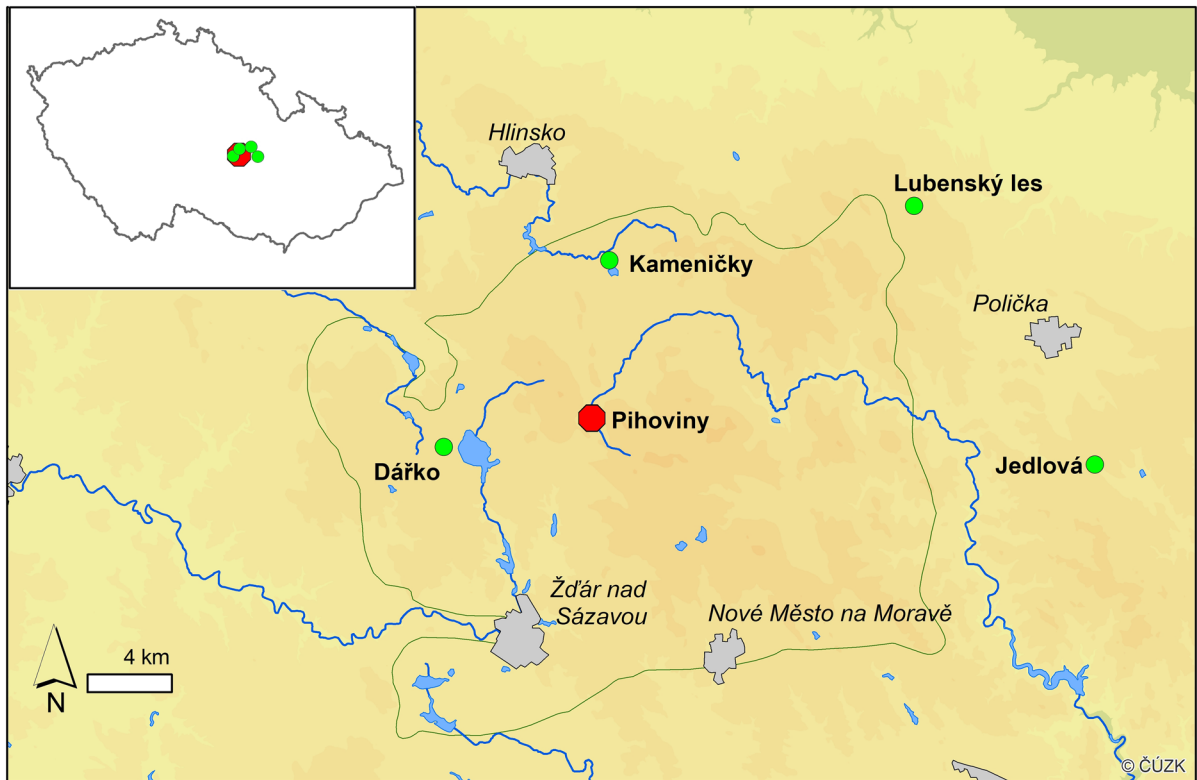


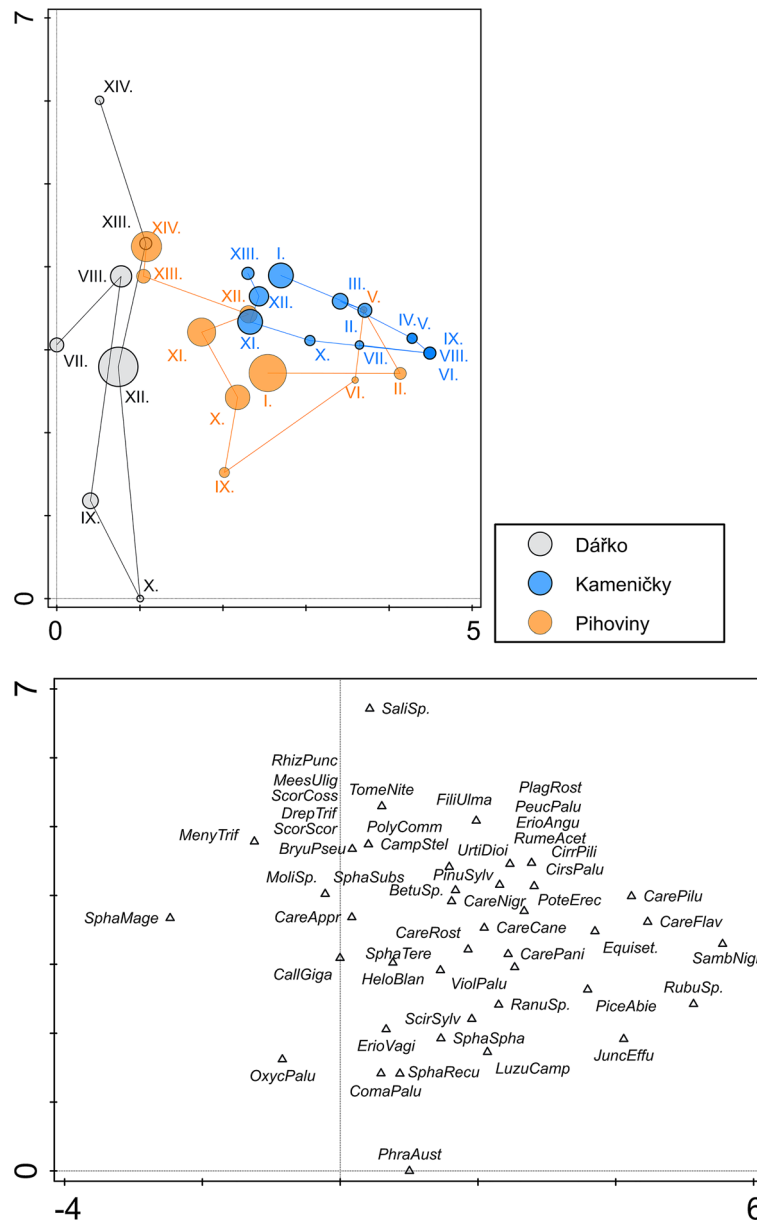
Fig. 1 Map of the study region with the position of Pihoviny sites and other profiles used for comparison. The dark green line shows the border of the phytogeographical district Žďárské vrchy Hills.

rare sedge *Carex dioica* were reported from the locality (Štechová et al. 2014; Kaplan et al. 2015). Since 2003, the vegetation has been regularly managed by mowing once a year with exporting mown biomass out of the locality. Coring took place on September 29, 2020. The studied profile was taken in the deepest part of the fen using a gouge auger (6 cm diameter, 100 cm length). The depth of the profile was 174 cm, and two overlapping cores were taken. The peat sediment was visually described in the field, stored in plastic tubes, and transported into the laboratory for further processing.

Palaeoecological Analyses

The peat core was divided in the laboratory into 3 cm long sub-samples. 23 samples were analysed for macrofossil, 53 for pollen and 57 for LOI (Loss on ignition) analysis. Plant macrofossils were extracted from a 50 ml volume of sediment using wet sieving on sieves with mesh diameters of 1 mm, 0.63 mm

and 0.20 mm and handpicked from the sediment. Plant macrofossils were identified under a dissecting microscope according to Smith (1996), Cappiers et al. (2006), Velichkevich and Zastawniak (2006, 2008), Lüth (2019), other available identification literature and the reference seed collection of the Institute of Botany of the Czech Academy of Sciences. Macrofossil abundance is presented as absolute numbers per sample for countable fossils or as volume percentages for bryophytes, tissues and wood fragments. The proportions of particular sediment components (plant tissues, bryophytes, wood etc.) were estimated after wet sieving. Wood remains were identified with the help of an online key (www.woodanatomy.ch). The samples for pollen analysis were processed by standard palynological procedures (Faegri and Iversen 1989). Hydrofluoric acid was used to remove mineral particles. At least 300 terrestrial pollen grains were counted per sample, and the pollen grains were identified using standard keys and pollen atlases (Beug 2004; Reille 1995). Nomenclature of pollen types follows Beug



(2004). Results of pollen analysis are presented in percentages, where the percentage of pollen taxa is based on a sum of terrestrial pollen with the exclusion of pollen of (semi-)aquatic plants, spores and non-pollen palynomorphs. Their percentage values were calculated based on the sum of all pollen grains counted in the sample. The samples for LOI analysis were dried at 105 °C for 48 h and combusted at 550 °C for 3 hours. LOI at 550 °C reflects a weight percentage of organic matter. LOI measurements followed Heiri et al. (2001) and Holliday (2004).

Radiocarbon Dating and Depth-Age Modelling

Selected plant macrofossils (seeds, bryophytes, wood, charcoal and needles) were used for radiocarbon AMS dating in the laboratory (Isotoptech Zrt., Debrecen, Hungary, ten dates). All dates were calibrated using the IntCal 20 calibration curve for the Northern Hemisphere (Reimer et al. 2020). The depth-age model was calculated using the P_Sequence function with the k_0 parameter equal to 0.5 cm^{-1} and $\log_{10}(k/k_0)$ equal to 0.3 in Oxcal 4.4. software (Bronk Ramsey 2008) based

◀**Fig. 2** DCA ordination diagram of macrofossils from the Pihoviny, Dářko and Kameničky sites. The size of the sample symbols of samples is proportional to species richness. Eigenvalues: 1st axis: 0.6504 (13.72% of explained variation), 2nd axis: 0.3308 (6.98%). The layers were merged to millennia BP as indicated with Roman numerals. Fifty species with the highest fit are shown. Species abbreviations: BetuSp.: *Betula* sp., BryuPseu: *Bryum pseudotriquetrum*, CallGiga: *Calliergon giganteum*, CampStel: *Campylium stellatum*, CareAppr: *Carex appropinquata*, CareCane: *Carex canescens*, CareFlav: *Carex flava*, CareNigr: *Carex nigra*, CarePani: *Carex panicea*, CarePilu: *Carex pilulifera*, CareRost: *Carex rostrata*, CirrPill: *Cirriphyllum pilliferum*, CirsPalu: *Cirsium palustre*, ComaPalu: *Comarum palustre*, DrepTrif: *Drepanocladus trifarius*, Equiset: *Equisetaceae*, ErioAngu: *Eriophorum angustifolium*, ErioVagi: *Eriophorum vaginatum*, FiliUlma: *Filipendula ulmaria*, HeloBlan: *Helodium blandowii*, JuncEffu: *Juncus effusus*, LuzuCamp: *Luzula campestris* agg., MeesUlig: *Meesia uliginosa*, MenyTrif: *Menyanthes trifoliata*, MoliSp.: *Molinia* sp., OxycPalu: *Oxycoccus palustris* (*Vaccinium oxycoccos*), PeucPalu: *Peucedanum palustre*, PhraAust: *Phragmites australis*, PiceAbie: *Picea abies*, PinuSylv: *Pinus sylvestris*, PlagRost: *Plagiomnium rostratum*, PolyComm: *Polytrichum commune*, PoteErec: *Potentilla erecta*, RanuSp.: *Ranunculus* sp., RhizPunc: *Rhizomnium punctatum*, RubuSp.: *Rubus* sp., RumeAcet: *Rumex acetosa*, SaliSp.: *Salix* sp., SambNigr: *Sambucus nigra*, ScirSylv: *Scirpus sylvaticus*, ScorCoss: *Scorpidium cossonii*, ScorScor: *Scorpidium scorpioides*, SphaMag: *Sphagnum magellanicum* s. lat. (*medium/divinum*), SphaRecu: *Sphagnum recurvum* agg., SphaSpha: *Sphagnum* sect. *Sphagnum* (excl. *S. magellanicum* s.lat.), SphaSubs: *Sphagnum subsecundum*, SphaTere: *Sphagnum teres*, TomeNite: *Tomentypnum nitens*, UrtiDioi: *Urtica dioica*, ViolPalu: *Viola palustris*.

on a Bayesian approach. Moreover, we implemented the most distinct boundaries in the lithological composition to introduce the changes in the accumulation rates. We used the following boundaries: 25 cm (more organic/ more inorganic sediment), 98 cm (brown/ dark brown colour of sediment), 138 cm (slightly/strongly decomposed sediment), 142 cm (strongly/slightly decomposed sediment), 163 (organic/sandy sediment) and 165 cm (sandy/organic sediment). All ages mentioned in the Results and Discussion are based on the depth-age model (median values) and given in calibrated years before the present (before 1950; cal BP) rounded to the nearest 50. Division of the Holocene follows Walker et al. (2012) throughout the text.

Data Analysis

The macrofossil diagram was created using C2 software (Juggins 2003), and the pollen diagram using Tilia v. 1.7.16 (Grimm 2011). The Tilia software

was also used to perform cluster analysis (CONISS) with square root transformation of percentage pollen data. The same cluster analysis was also applied to the macrofossil data, which were transformed to the 0-1-2 abundance scale. This transformation was done because of the incomparable counts among the analysed biotic proxies (i.e., vascular plant seeds in absolute numbers, vascular plant tissues, moss tissues, and wood in percentages). When the macrofossil abundance of species in the sample was below or equal to the median, the species obtained 1; when its abundance was higher than the median, the species received 2. If more macrofossil types represented the species (e.g. seeds, needles, bud scales etc.), they were summed up before the transformation. Because the samples were not contiguously analysed, the boundaries among particular zones of pollen and macrofossil diagrams were placed between two adjacent samples. The pollen diversity curve was calculated as pollen numbers rarefacted for the sum of 300 pollen grains in the PolPal for Excel (Nalepka and Walanus 2003; https://adamwalanus.pl/polpal_excel.html).

Multivariate analyses of macrofossil data were also conducted on the data transformed to the 0-1-2 abundance scale. Species-by-sample matrix of plant macrofossil data was subjected to detrended correspondence analysis (DCA) in Canoco 5 (Šmilauer and Lepš 2014). Multivariate time series analysis was also performed in Canoco 5 software on presence-absence macrofossil data averaged by millennia BP (in Fig. 2 indicated with roman numerals) and with down-weighting of rare species. Species-by-sample matrix of macrofossil data from Pihoviny, Kameničky and Dářko was subjected to unconstrained detrended correspondence analysis (DCA). Based on plant macrofossil records, past groundwater pH and Ellenberg indicator values for moisture and nutrients were reconstructed using a transfer function published in the work of Šímová et al. (2019). The calibration dataset contained 751 modern assemblages of bryophytes and vascular plants from mires in Czechia, Slovakia and Poland, supplemented by direct water pH measurements and Ellenberg indicator values (Ellenberg and Leuschner 2010). Species nomenclature was unified among the profiles to avoid potential bias caused by unequal identification. For that reason, *Cenococcum geophilum* was deleted from the Pihoviny profile, *Betula* and *Salix* were used only on the level of

Table 1 Results of radiocarbon ^{14}C dating (AMS method) for profile under study. The symbol * refers to the outlier excluded from the depth-age model

Laboratory code	Depth [cm]	^{14}C AMS	Calibrated ranges (95.4 %) [cal. BP]	Median [cal. BP]	Material
DeA-27978	21–24	232 ± 23	313–270 (53.4 %), 210–197 (2.8 %), 188–150 (37.9 %), 11–... (1.3 %)	283	Charcoals
DeA-33335	27–30	2049 ± 33	2111–1923 (93.8 %), 1904–1893 (1.6 %)	1995	<i>Rubus</i> seed, charred <i>Picea</i> needles
DeA-27975	36–39	3711 ± 27	4149–4110 (14.7 %), 4102–3976 (80.4 %), 3938–3935 (0.4 %)	4041	Wood
DeA-33336	57–60	7759 ± 48	8633–8620 /1.8 %), 8604–8420 (93.7 %)	8528	Wood
DeA-33337*	75–78	7622 ± 51	8538–8350 (95.4 %)	8415	<i>Viola palustris</i> seeds, <i>Picea</i> needles
DeA-27974	99–102	9338 ± 49	10,697–10,383 (95.4 %)	10,546	<i>Carex</i> + <i>Urtica</i> seeds, <i>Picea</i> needles
DeA-27973	138–141	9607 ± 47	11,173–10,989 (39.1 %), 10,980–10,764 (56.4 %)	10,942	<i>Potentilla erecta</i> + <i>Viola palustris</i> seeds, <i>Picea</i> needles
DeA-33338	159–162	11,126 ± 147	13,297–13,268 (2.1 %), 13,250–12,760 (93.3 %)	13,023	<i>Carex</i> seeds, <i>Poaceae</i> nodus, <i>Scorpidium cossonii</i> stems+leaves
DeA-33864*	163,5–165	10,913 ± 47	12,918–12,744 (95.4 %)	12,814	<i>Carex</i> seeds, <i>Drepanocladus trifarius</i> stems+leaves
DeA-27972	168–171	12,104 ± 57	14,091–13,805 (95.4 %)	13,961	<i>Scorpidium cossonii</i> and <i>Campylium stellatum</i> stems+leaves, <i>Carex</i> seeds

genus and *Sphagnum angustifolium*, *S. fallax* and *S. flexuosum* were merged to the *S. recurvum* agg. in all profiles. The nomenclature used in the text follows Danihelka et al. (2012) for vascular plants and Kučera et al. (2012) for bryophytes.

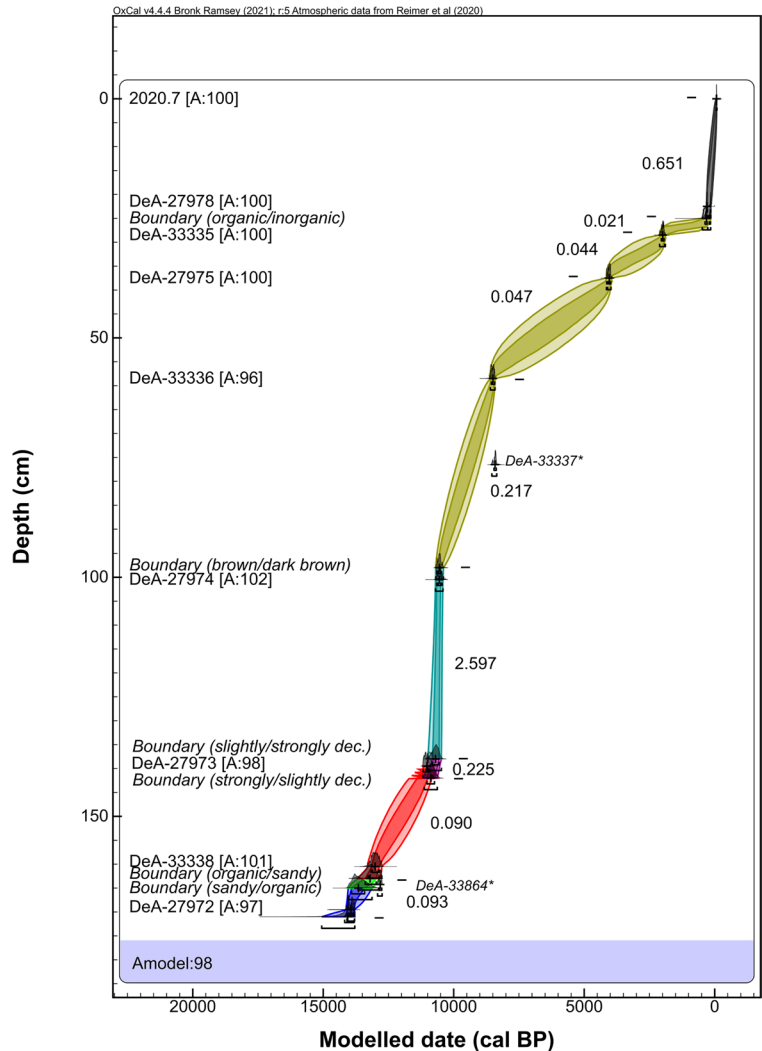
To assess possible similarities or differences in the regional forest development since the Late Glacial, we have compared the percentage pollen data of selected trees (*Pinus sylvestris* t., *Picea*, *Corylus*, *Ulmus*, *Tilia*, *Quercus*, *Abies*, *Fagus*) and Arboreal Pollen (AP) among available pollen sites with sufficient radiocarbon dating in the study region (Žďárské vrchy Hills): Pihoviny (this study), Kameničky (Rybníčková and Rybníček 1988), Dářko (Roleček et al. 2020), Jedlová and Lubenský Les (Szabó et al. 2016). The pollen data were obtained from the PALYCZ database (Kuneš et al. 2009; <https://botany.natur.cuni.cz/palycz>) and transformed into percentage values. The synoptic pollen diagrams for each tree taxa were created in the C2 program.

Results

Dating, Depth-Age Modelling and Peat Accumulation

Using radiocarbon dating of plant macrofossils, we obtained ten radiocarbon AMS dates. We discovered that the peat started accumulating ca 14,000 years ago in the Late Glacial period (see Table 1). Two of the radiocarbon dates were reversed with the adjacent dates and exhibited a very low agreement index, deeply below the threshold value of 60% (for more information, see Bronk Ramsey 2008); thus, we excluded them from the model as outliers. Then, we obtained a reliable depth-age model, which reached the agreement value of 98% between calibrated and modelled values (Fig. 3). The error values of modelled dates varied distinctly. The most precise dating is available for the last 300 years (error range 20–95 years) and between 10,650 and 10,500 cal BP (75–90 years). On the contrary, the highest inaccuracy of modelled dates is between 8450 and 450 cal BP (200–650 years). The error

Fig. 3 Depth-age model calculated for the profile Pihoviny based on the P_Sequence function. The accumulation rates are given in mm/year for particular accumulation zones. The symbol * refers to the outlier excluded from the depth-age model. Abbreviations: A - percentage agreement between calibrated and modelled values, dec. – decomposed.



values in other profile parts mostly varied between 100 and 300 years. The accumulation rate differed throughout the peat profile as well and varied from the very low values 0.021–0.047 mm.year⁻¹ in the middle part (8500–300 cal BP; 58.5–22.5 cm) to the high values 2.597 mm.year⁻¹ in the Early Holocene (10,700–10,550 cal BP; 138–98 cm) and the upper part of the profile (300–(sub)recent; 22.5–6 cm, 0.651 mm.year⁻¹).

Sediment Description and LOI

The organic matter started accumulating on the bottom's clayish bedrock (cf. Table 2). A still high admixture of clay characterised the first organic layer (171–165 cm). The narrow sandy layer between 163

and 165 cm suggests some activity of neighbouring streams (13,200–13,650 cal BP). Later the undecomposed brown moss-sedge peat started to accumulate (156–163 cm), being more decomposed more up (142–156 cm). From 138 cm up, the sediment was strongly decomposed, and the wood amount continually increased. In the depth of 33 to 35 cm, the thin layer with a higher proportion of clay was present, suggesting mineral flushes from the surrounding. The layer between 20 and 6 cm was also characterised by inorganic admixture. Results of LOI analysis correspond well with the higher mineral content and low organic matter (Fig. 4a) in the bottom (162–171 cm) and in the upper part of the profile (9–18 cm). A high decrease in organic matter in the middle of the profile (76.5 cm, 9450 cal BP) was also recorded. Organic

Table 2 Lithological zones of the profile under study

Depth (cm)	Description	Colour
0–6	Root zone, not analysed	-
6–20	Organic sediment with a small inorganic admixture and roots	Grey
20–25	Transition zone	
25–33	Organic sediment, a high proportion of roots	Dark brown
33–35	Clayish sediment	Grey
35–98	Organic sediment with an admixture of undecomposed wood and charcoals	Dark brown
98–138	Strongly decomposed organic sediment with undecomposed wood and plant tissues	Brown
138–142	Slightly decomposed organic sediment	Rusty brown
142–156	Strongly decomposed organic sediment	Brown
156–163	Organic sediment with undecomposed bryophytes	Red brown
163–165	Sandy layer	Light grey
165–171	Organic sediment with a high admixture of clay	Grey brown
171–174	Clay	

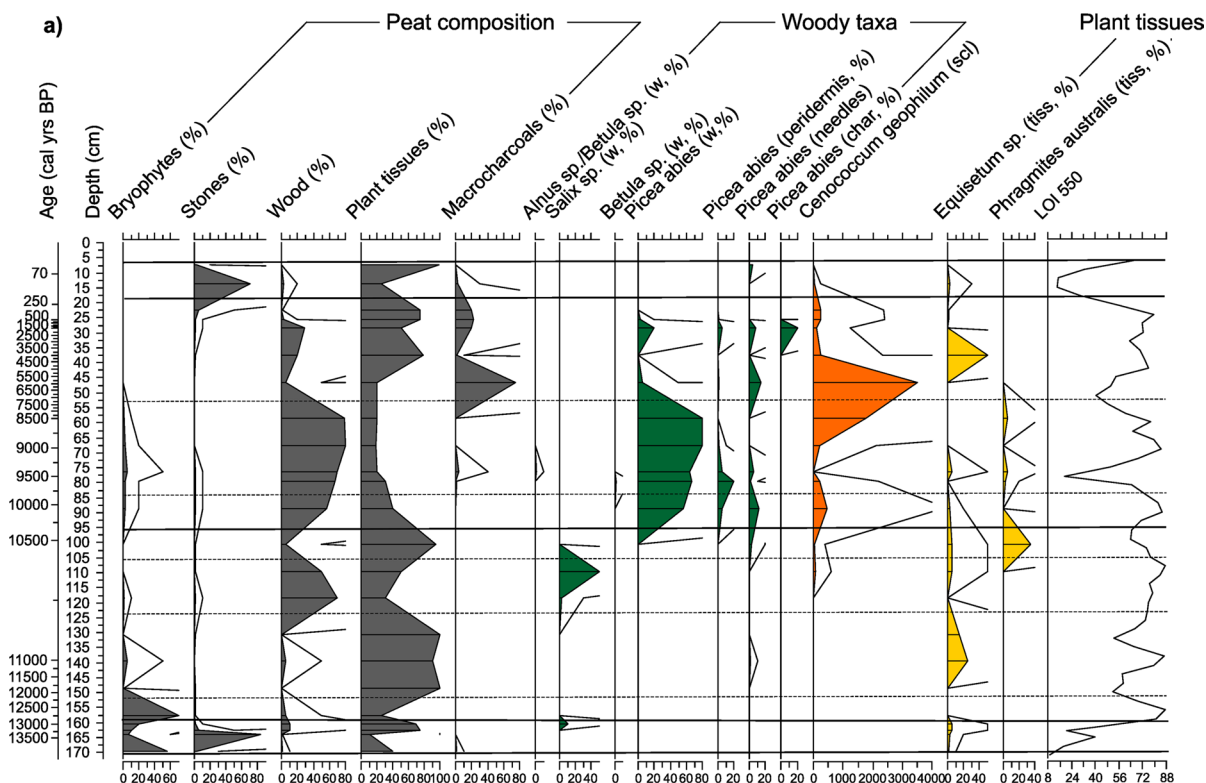


Fig. 4 Macrofossil diagram of Pihoviny peat profile (3a: Peat composition, Woody taxa, Plant tissues and LOI; 3b: Bryophytes and Vascular plants). Values are in percentages when indicated by %; otherwise, they are in absolute numbers.

Abbreviations: w (wood), char (charcoals), op (opercula of capsules), tiss (tissues), s (seeds), spindl (spindles), scl (sclerotia). LOI 550: Loss on ignition at 550 °C. Macrofossils were analysed by A. Šíroková and P. Hájková.

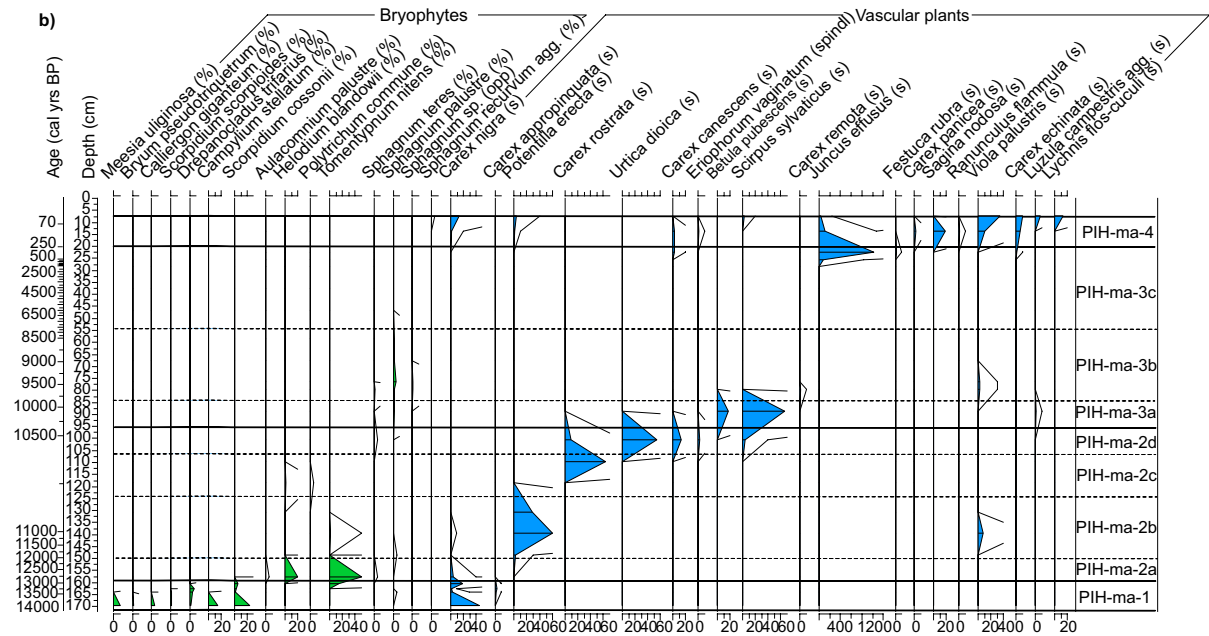


Fig. 4 (continued)

content in other parts of the profile was relatively high, and values varied between 41 and 87%.

Development of Local Fen Vegetation Since the Glacial Period

Development of the local fen vegetation started at ca 14,000 cal BP in the Late Glacial (see Fig. 4a, b). The four main developmental zones (three levels of divisions) and seven additional subzones (six levels of divisions) were delimited using cluster analysis. Initially, minerotrophic sedge-moss vegetation developed (**PIH-ma-1 zone**; 171–159 cm; 14,100–12,900 cal BP). The bryophyte layer was species-rich and dominated by *Scorpidium cossonii* and *Campylium stellatum*; other species co-occurred in lower abundances (e.g. *Bryum pseudotriquetrum*, *Calliergon giganteum*, *Drepanocladus trifarius*, *Meesia uliginosa*, *Scorpidium scorpioides*). Among vascular plants, *Carex appropinquata* and *C. nigra* seeds were recorded. Later the succession continued to the more successional advanced fen with low-hummocks built by *Tomentypnum nitens* (dom.), *Aulacomnium palustre*, *Helodium blandowii* and calcitolerant peat moss *Sphagnum teres*. In the herb layer, *C. nigra* and *Potentilla erecta* occurred (**PIH-ma-2a**; 159–153 cm; ca 12,900–12,300 cal BP). In the next zone (**PIH-ma-2b**;

153–124.5 cm; 12,300–10,650 cal BP), the bryophyte abundance strongly declined (only *T. nites* still occurred), and plant tissues (including *Equisetum* sp.) started to dominate in the peat. Among vascular plant macrofossils, seeds of *P. erecta* dominated, and seeds of *C. nigra* and *Viola palustris* occurred. Later, higher amount of wood (*Salix* sp.) first appeared in the sediment (**PIH-ma-2c**; 124.5–105 cm; 10,650–10,550 cal BP). Sclerotia of the ectomycorrhizal fungi *Cenococcum geophilum* also appeared, *Carex rostrata* dominated the herb layer, and *H. blandowii* and *Polytrichum commune* occurred in the bryophyte layer but in very low abundances. The last subzone of the second zone (**PIH-ma-2d**; 105–94.5 cm; 10,550–10,400 cal BP) was characterised by *Phragmites australis* tissues (ca 35%), *Carex canescens*, *Scirpus sylvaticus* and *Urtica dioica* seeds. The amount of wood decreased, and the first needles of *Picea abies* appeared. The third macrofossil zone is characterised by the high amount of wood and the presence of woody species (mostly *Picea*, but also *Betula*). The first subzone (**PIH-ma-3a**; 94.5–84 cm; 10,400–9850 cal BP) was characterised by a still semi-open canopy indicated by a high number of *Scirpus sylvaticus* seeds and the presence of *Luzula campestris* seeds. *Picea abies* dominated the tree layer (ca 60% of wood), but *Betula pubescens* was also present (17 seeds). In the moss layer, *Sphagnum palustre*

occurred. In the subzone **PIH-ma-3b** (84–52.5 cm; 9850–7300 cal BP), the wood of *Picea* strongly dominated (64–80%). There were also high abundances of *Cenococcum geophilum* sclerotia, low values of *Phragmites* tissues (ca 5%), leaves of *S. palustre* (1–2%) and opercula of *Sphagnum* capsules. At the beginning of this subzone, seeds of *Carex remota* and *Viola palustris* and leaves of *S. teres* were present. At the beginning of the next subzone (**PIH-ma-3c**; 52.5–18 cm; 7300–200 cal BP), a high amount of woody macro charcoal indicates repeated local fires (around 5950 cal BP, 75% of the sediment; 2000–300 cal BP, ca 20%) and abundance of *Cenococcum geophilum* sclerotia substantially increased. In this zone, mainly *Picea* macrofossils occurred (charcoals, needles, wood), and *Equisetum* tissues were present as well. The last sample of this zone is already transitional to the next zone, which is indicated by the high

abundance of *Juncus effusus* seeds. The last zone (**PIH-ma-4**; 18–6 cm; 200–10 cal BP) is characterised by the decrease of the wood amount and other macrofossils of *Picea*, whereas some fen-meadow species (re)appeared (*Carex canescens*, *C. echinata*, *C. nigra*, *C. panicea*, *Lychnis flos-cuculi*, *P. erecta*, *Ranunculus flammula* and others). The remarkable finding of *Sagina nodosa* seeds (13.5 cm; 100 cal BP; 1850 AD) occurred in the layer with low LOI and high inorganic admixture, indicating disturbances.

The Main Gradient in the Local Vegetation Composition

The gradient length in DCA analysis of macrofossil data is 5.07 units on the first axis and 2.53 on the second axis (Fig. 5). The first axis explains 17% and

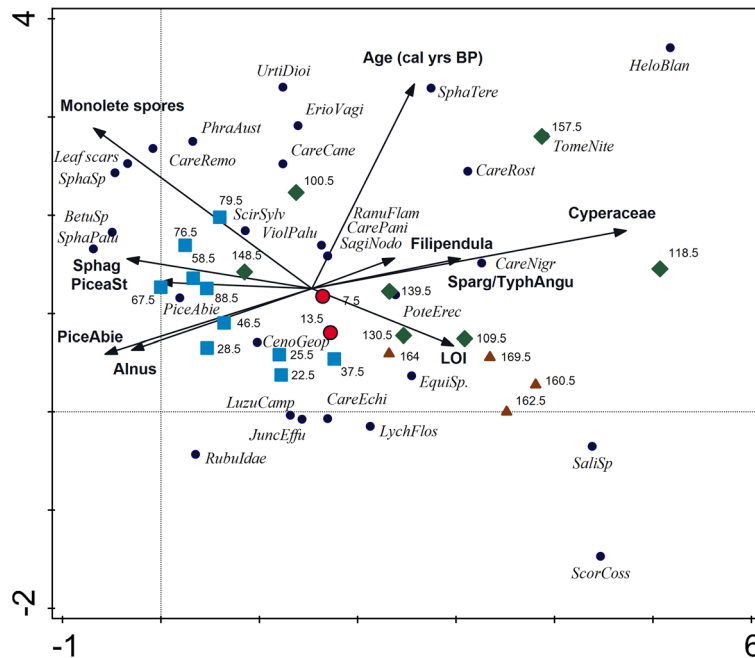


Fig. 5 DCA ordination diagram of macrofossils from the Pihoviny site. Eigenvalues: 1st axis: 0.7105 (17% of explained variation), 2nd axis: 0.3516 (8.4%). Black dots assign species. Thirty species with the highest fit are shown. Samples are classified according to affiliation to four developmental zones: PIH-ma-1 (brown triangles), PIH-ma-2 (green rhombs), PIH-ma-3 (blue squares) and PIH-ma-4 (red circles). The LOI and local pollen (black arrows) are passively projected onto the scatter plot (Sparg/TyphAngu = *Sparganium/Typha angustifolia*, LOI = Loss on ignition, Sphag = *Sphagnum*, Picea-St = *Picea stomata*, PiceAbie = *Picea abies*). Species abbreviations: BetuSp: *Betula* sp., CareCane: *Carex canescens*, CareEchi: *Carex echinata*, CareNigr: *Carex nigra*, CarePani:

Carex panicea, CareRemo: *Carex remota*, CareRost: *Carex rostrata*, CenoGeop: *Cenococcum geophilum*, EquiSp.: *Equisetum* sp., ErioVagi: *Eriophorum vaginatum*, HeloBlan: *Helodium blandowii*, JuncEffu: *Juncus effusus*, LychFlos: *Lychnis flos-cuculi*, LuzuCamp: *Luzula campestris* agg., PhraAust: *Phragmites australis*, PiceAbie: *Picea abies*, PoteErec: *Potentilla erecta*, RanuFlam: *Ranunculus flammula*, RubuIdae: *Rubus idaeus*, SagiNodo: *Sagina nodosa*, SaliSp: *Salix* sp., ScirSylv: *Scirpus sylvaticus*, ScorCoss: *Scorpidium cossonii*, SphaPalu: *Sphagnum palustre*, SphaSp: *Sphagnum* sp., SphaTere: *Sphagnum teres*, TomeNite: *Tomentypnum nitens*, UrtiDioi: *Urtica dioica*, ViolPalu: *Viola palustris*.

the second axis 8.4% of the compositional variation. The principal gradient in the species composition is driven by the canopy openness. In the left part of the diagram, the Middle-Holocene samples with macrofossils of woody species (*Picea abies*, *Betula* sp.) and species related to the forest (*Carex remota*, *Cenococcum geophilum*) and *Sphagnum palustre* are placed. The Late-Glacial and Early-Holocene samples with brown mosses are situated at the opposite end of the diagram. The youngest two samples (red circles) are placed in the middle and are composed of fen-meadow species like *Carex echinata*, *Juncus effusus*, *Lychnis flos-cuculi* and others. Pollen of local taxa passively plotted to the DCA diagram fit well with the principal gradient. Tree pollen (*Alnus*, *Picea abies*), monoete spores of ferns and stomata of *Picea* characterise the forest stage in the left, while pollen of Cyperaceae, *Filipendula* and *Sparganium/Typha angustifolia* is associated with the old samples in the right part of the diagram.

Quantitative Reconstruction of the Local Environmental Factors

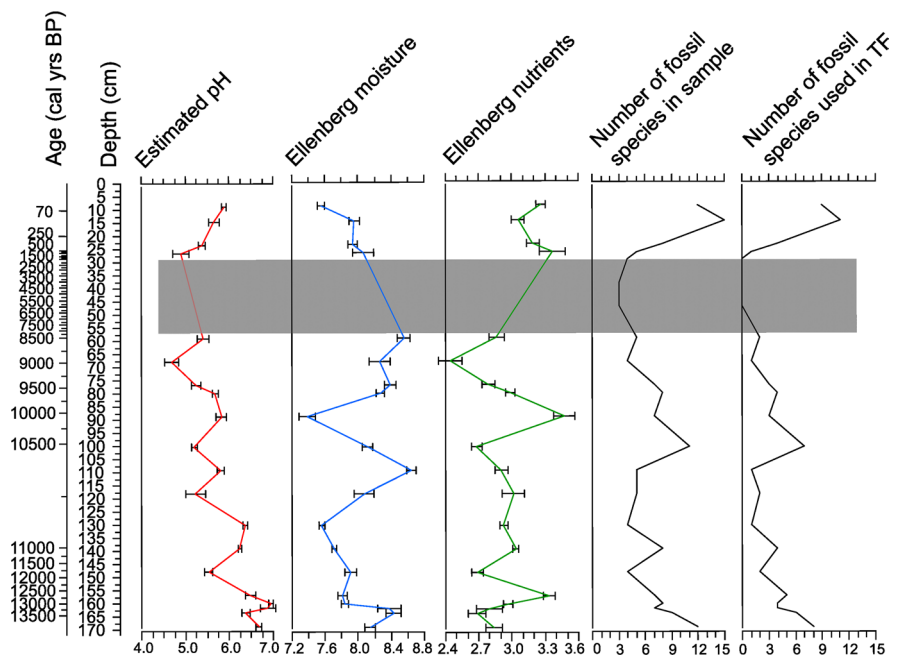
Estimated groundwater pH based on the modern training data set of samples-species matrix and measured pH reached the highest values at the beginning of the development (Fig. 6) when the pH between 6.5 and 7 was reconstructed for the initial

vegetation stage. Later during the hummock development, the influence of mineral-rich groundwater weakened, and the pH decreased to 5 in 9000 cal BP when the spruce, with its acidic litter, dominated the site. A few centuries ago, when the site was deforested, the pH values started to increase again, but only to the lower level of ca 6. Estimated Ellenberg moisture values have shown high wetness fluctuations within the entire profile. The wettest periods were at the beginning of the development (PIH-ma-1), during the stage PIH-ma-2c (*Carex rostrata* occurrence) and between 9500 and 8500 cal BP (PIH-ma-3b), when *Sphagna* occurred in the waterlogged spruce forest. Contrary, the lowest moisture was estimated for the stage PIH-ma-2b, with *Potentilla erecta* being the most abundant, PIH-ma-3a (ca 9900 cal BP) when *Scirpus sylvaticus* dominated the vegetation and sub-recent period (the last sample of PIH-ma-4). The nutrients mainly were reconstructed higher in the periods with lower moisture, with the highest values in the PIH-ma-2a zone (ca 12,800 cal BP), PIH-ma-3a (9900 cal BP) and in the last centuries (PIH-ma-4 zone).

Comparison with Kameničky and Dářko Profiles

The ordination diagram (Fig. 2) captures the main compositional changes in samples of plant

Fig. 6 Changes in the estimated values of groundwater pH, Ellenberg moisture and nutrients. The estimation is based on the calibration of the recent dataset and plant macrofossils. The shadow box indicates samples with any species used in the transfer function.



macrofossils from three nearby profiles in the Žďárské vrchy Hills. The gradient along the first ordination axis stretches from mires via mire and wet grasslands to forests. Mires (in the left part of the diagram) are indicated by a group of rich fen brown mosses (e.g. *Bryum pseudotriquetrum*, *Calliergon giganteum*, *Scorpidium cossonii*, *S. scorpioides*, *Tomentypnum nitens*; upper part of the diagram), and bog elements (*Eriophorum vaginatum*, *Sphagnum magellanicum* s.lat., *Vaccinium oxycoccus* agg.; bottom of the diagram). The middle part of the scatter comprises fen sedges (*Carex canescens*, *C. nigra*, *C. panicea*), other mire species (*Viola palustris*) and broad-leaved herbs (*Ranunculus* sp., *Rumex acetosa*). Of peat mosses, *Sphagnum teres* is present. Nutrient-demanding tall herbs (*Cirsium palustre*, *Filipendula ulmaria*, *Urtica dioica*) are concentrated in the upper part of the diagram. Forest species (*Picea abies*, *Rubus* sp., *Sambucus nigra*) are situated in the right part of the diagram.

The diagram shows that Pihoviny and Dářko sites harboured rich fens with brown mosses in the Late Glacial. Afterwards, bog species started to dominate in the Dářko site, while vegetation at Pihoviny site shifted towards communities with a higher proportion of broad-leaved species, albeit

still with fen elements, which occurred here ca 12,900–10,400 cal BP. Analogous vegetation was documented in the Kameničky profile. However, rich fen communities did not precede more productive grassland vegetation with tall forbs at this site. Both localities were later (between the 7th and 1st millennium BP) overgrown by forests, as suggested by macrofossils of *Picea abies* and other forest elements (*Rubus* sp., *Sambucus nigra*). The samples from the forest phase are species-poorer than others within the analysed dataset. During the last millennium, the vegetation changed to fen meadow (Pihoviny) or grassland with a mixture of tall-herb and mire species (Kameničky).

Development of Regional Vegetation Based on Pollen Data

The six pollen developmental zones were delimited using CONISS cluster analysis (Fig. 7). The oldest pollen developmental zone (**PIH-po-1**; 166–155.5 cm; 13,750–12,550 cal BP) dated to the Allerød (warmer period within Late Glacial) was characterised by high pollen abundance of *Pinus sylvestris* t., Poaceae and Cyperaceae and by the exclusive presence of *Alnus viridis*, which did not occur later on. *Salix* reached its highest pollen abundance in this

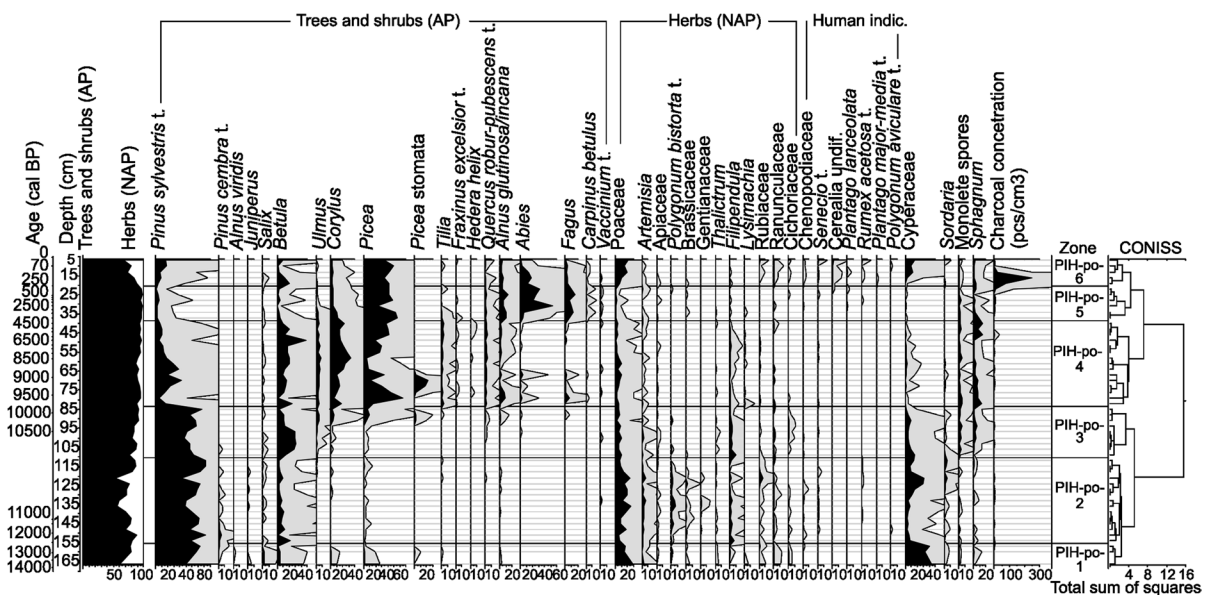


Fig. 7 Percentage pollen diagram of the selected taxa of the Pihoviny site. Grey silhouettes show exaggeration 10x. For full pollen diagrams see Supplementary Materials Figure S1. Pollen was analysed by L. Petr

zone. Few pollen grains of *Pinus cembra* t. also occurred. The pollen of *Picea* (also stomata), *Corylus* and *Tilia* also appeared in this zone, even in very low quantities. The AP (arboreal pollen) varied between 60 and 80%. The next zone (**PIH-po-2**; 155.5–110.5 cm; 12,550–10,600 cal BP) was characterised by the presence of *Juniperus* and *Pinus cembra* t. pollen, still high but fluctuating *Pinus sylvestris* t. and Poaceae pollen. Values of AP decreased below 60%, but at the end of the zone, they increased again. Pollen of *Artemisia*, *Polygonum bistorta* t. and *Filipendula* increased, whereas pollen of Cyperaceae decreased in the zone beginning but temporarily increased again around 10,650 cal BP. Pollen of other herbs like Cichoriaceae, *Senecio* t., *Thalictrum* and Ranunculaceae also occurred. Gentianaceae appeared in the middle of the zone. The presence of *Sordaria* spores characterised the whole zone and mainly its end. At the beginning of the third zone (**PIH-po-3**; 110.5–83.5 cm; 10,600–9800 cal BP), pollen abundances of *Pinus sylvestris* t. slightly decreased, whereas the pollen of *Betula* steeply increased. Pollen of *Pinus cembra* t. disappeared at the beginning of this zone. Pollen of temperate trees and shrubs *Ulmus*, *Corylus* and *Quercus* started to occur, as well as monolete and *Sphagnum* spores. The fourth zone (**PIH-po-4**; 83.5–38.5 cm; 9800–4150 cal BP) represents the end of the Early Holocene and the entire Middle Holocene, and it was characterised by a very distinct decrease of pollen abundances of *Pinus sylvestris* t. and concurrently increase of pollen abundances of *Alnus glutinosa/incana*, *Corylus*, *Fraxinus*, *Picea*, *Quercus*, *Tilia* and *Ulmus*. Sporadic pollen of *Hedera helix* also occurred. *Abies*, *Carpinus* and *Fagus* pollen started to occur in low abundances and the pollen of Cyperaceae strongly decreased at the beginning of this zone. *Sordaria* spores almost disappeared. In the second part of the zone, microcharcoals started to occur continuously but in very low abundances. The next zone (**PIH-po-5**; 38.5–20.5 cm; 4150–250 cal BP) is characterised by the decrease of pollen abundances of some temperate trees (*Corylus*, *Fraxinus*, *Tilia*, *Ulmus*) and increase of *Abies* (between 3300 and 2500 cal BP from 5.9 to 53.6%), *Alnus* (ca 4000 cal BP), *Carpinus* (ca 3300 cal BP) and *Fagus* (ca 4000 cal BP) at the beginning of the zone. In the last zone (**PIH-po-6**; 20.5–7 cm; 250–50 cal BP), the previous species also declined as well as monolete spores, whereas Poaceae, Cyperaceae,

herbs and human indicator (including *Cerealia*) pollen increased their abundances or started to occur. Microcharcoals reached their highest concentration in ca 220 cal BP indicating landscape deforestation by fire. Arboreal pollen (AP) also declined in this period.

The pollen-based plant diversity (rarefacted to the pollen sum of 300 grains) varied between 13 and 26 pollen taxa during the Holocene. The highest values (higher than 20 pollen taxa) were reached in the very beginning in Late Glacial (23; ca 13,750 cal BP), in the Early Holocene (24; 10,700 cal BP) and distinctly increased in the last 200 years (22 to 26) because of the appearance of pollen taxa related to the anthropogenic impact (secondary and primary anthropogenic indicators, herbs related to meadows and pastures, cf. Fig. 8).

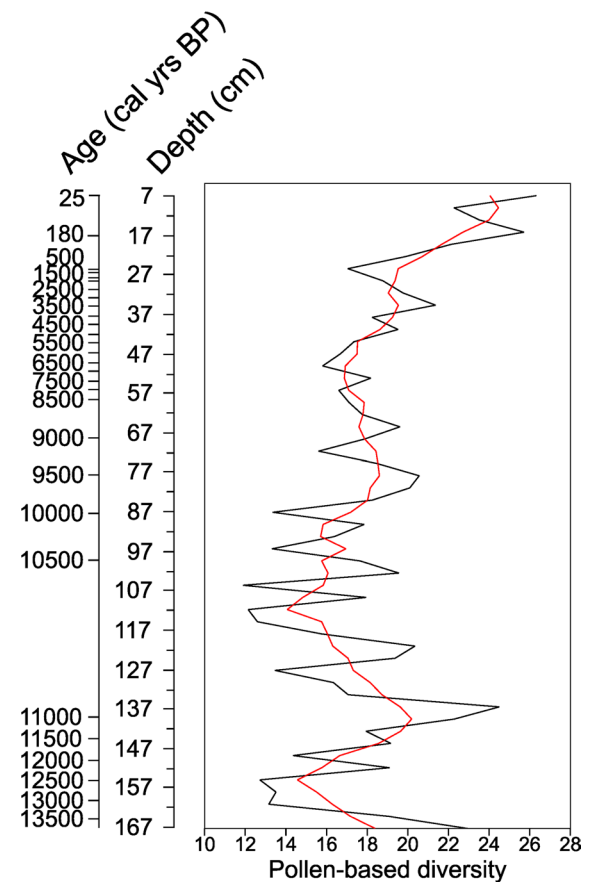


Fig. 8 Pollen-based diversity curve rarefacted to 300 pollen grains with smoothing line based on moving average (calculated from 5 last samples)

Changes in the Regional Forest Composition Based on the Synthesis of Pollen Data

The comparison of the selected pollen taxa among all

available pollen profiles in the study region reveals quite synchronous development of the landscape cover since the Late Glacial period (Fig. 9). During the Late Glacial period (since 14,000 cal BP), the

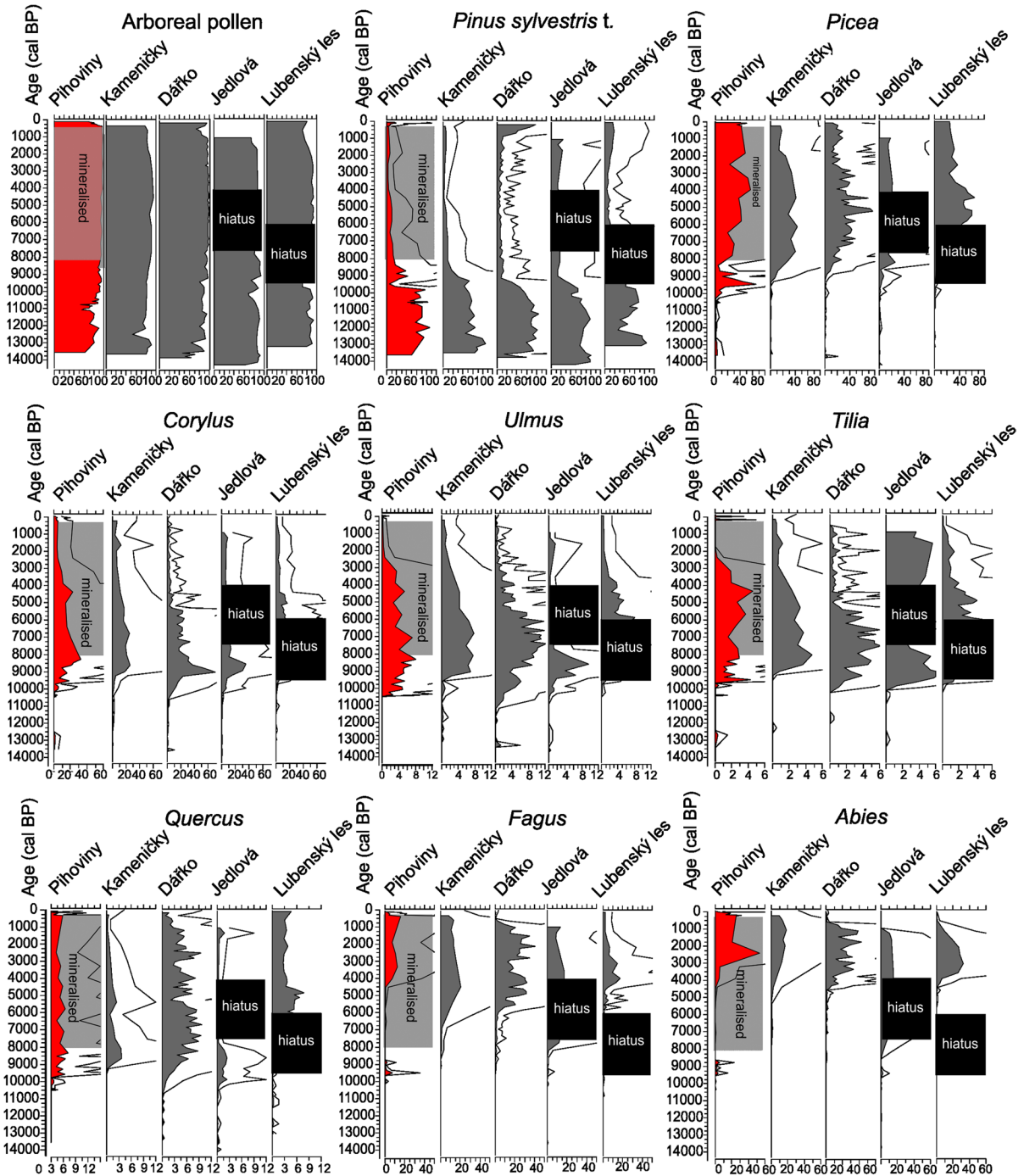


Fig. 9 Comparison of the pollen abundance (in percentages) changes of selected tree taxa among the profiles from the study region. Black boxes mark the profile parts with hiatuses presence. In such parts, species' onset or decrease is impossible to estimate

landscape was covered by a *Pinus*-dominated forest; however, the AP ratio indicates the semi-open character of the landscape. The situation changed in ca. 10,500 cal BP (Early Holocene) when the first temperate broad-leaved trees started to occur. Later they started to expand, *Ulmus* was the first (10,550 cal BP), followed by *Corylus* (10,200 ca BP), *Quercus* and *Tilia* (9700 cal BP). At the Dářko site, the expansion of broad-leaved trees began a little bit earlier (11,100 cal BP). The next change in the landscape cover of the study region occurred between 10,000 (Pihoviny, Jedlová) and 8500 cal BP (other sites) when *Picea* pollen substantially increased its abundance with a synchronous decline in *Pinus* pollen. The *Picea* expansion was the earliest in the Pihoviny (the most distinct; between 10,350 and 10,000 cal BP from 1.3% to 10%) and Jedlová (not so distinct, between 10,150 and 9350 cal BP; from 1.2 to 4.5%) sites among all comparing sites. At the same time, the spread of *Corylus* and other broad-leaved trees was also recorded. Possibly *Picea* spread on more mesic and waterlogged areas, whereas hazel and other temperate trees occupied drier stands. The last change in regional landscape development is connected with *Fagus* and *Abies* expansion and the decline of other temperate broad-leaved trees. The change in the abundance of broad-leaved tree dominants was not synchronous among sites; the time range was ca. 2000–3000 years. Although pollen of both late-successional trees *Abies* and *Fagus* occurred relatively early in the study region (since the Early Holocene), their expansion began much later. *Fagus* distinctly increased its pollen abundances (i.e. expanded) in ca. 5500 cal BP at Dářko and Kameničky sites, in ca. 4000 cal BP at Lubenský les and 3500 cal BP at Pihoviny. *Abies* expanded later than *Fagus*, in 3500 cal BP in Dářko and Lubenský les and in 2500 cal BP at Kameničky and Pihoviny.

Discussion

Development of the Local Fen Vegetation

At the end of the last Glacial, boreal brown-moss quaking rich fen vegetation with glacial relics of bryophytes (*Drepanocladus trifarius*, *Scorpidium scorpioides*) occurred at the site. According to the European phytosociological synthesis, this vegetation

might belong to the *Stygio-Caricion limosae* alliance, which recently has a distribution centre in northern Europe (Joosten et al. 2017; Peterka et al. 2017), but was also verified for the Carpathians and adjacent regions (Peterka et al. 2018; Dřevojan et al. 2020). The presence of moss *Meesia uliginosa* in the macrofossil record from Pihoviny has shown that this vegetation could also contain some tundra elements recently occurring either more to the north or in the mountain areas (Hedenäs 2020; Hájková and Šíroková 2022). *Betula nana* or *B. humilis* represent other such elements which used to be found in the glacial peat and which were also recorded in the bottom sample of nearby Kocanda site dated again to the Late Glacial (Peterka et al. 2022a) and in the bottom of the Dářko site (Roleček et al. 2020). Vegetation of boreal quaking rich fens was probably relatively common in temperate Europe at the end of the Glacial and in the Early Holocene, as is documented by numerous macrofossil records of indicator species of bryophytes (van Geel et al. 1984; Magyari et al. 1999; Miola et al. 2006; Hájková et al. 2015; Hájková et al. 2018). In the study region of Bohemian-Moravian Highlands quaking, rich fen vegetation, even if already without tundra elements, was still present before 50–70 years (Rybníček 1966, Rybníček 1974). Still, recently it almost disappeared because of past disturbances, the absence of management and climate change (Peterka et al. 2014; Štechová et al. 2014).

Further brown-moss quaking rich fen vegetation was replaced by rich fens vegetation with calcium tolerant Sphagna (*Sphagno-Tomentypnion* alliance) characterised by hummock-building bryophytes, here *Tomentypnum nitens*, *Helodium blandowii*, *Aulacomnium palustre* and calcium tolerant *S. teres* in small quantities. Such development was accompanied by the decline of estimated water pH, which is related to the peat accumulation and acidification by bryophytes, especially by Sphagna (Andrus 1986; Soudzilovskaia et al. 2010). Hummocks elevated above the groundwater level were also reflected by lower estimated Ellenberg moisture values. Later on, since the beginning of the Holocene, the wetland communities with the dominance of vascular plants and only a small proportion of bryophytes developed. After the short stage with *Salix* dominance in 10,650–10,550 cal BP, *Phragmites australis* appeared and started to dominate (in ca 10,500 cal BP), like at the Dářko site (ca 11,000 cal BP; Roleček

et al. 2020). Contrary, *Phragmites* was missing in the fossil record of the Kameničky site (Rybníčková and Rybníček 1988). Whereas fen vegetation in Dářko mire developed to the bog, Kameničky and Pihoviny developed similarly to the waterlogged spruce forest. Thus it seems that *Picea abies* (together with *Abies*) was the tree often encroaching and dominating the mires in the Bohemian-Moravian Highlands, as was also documented during the archaeobotanical survey in the region (Hrubý et al. 2014). The occurrence of the waterlogged spruce forest is further in line with the study of Hájková et al. (2019) who demonstrated that spruce is the tree species most frequently colonises peatlands in central Europe and with Málek (1958), who considered spruce forest in Bohemian-Moravian Highlands native only on azonal waterlogged sites. Pollen record of the study profile has shown that some waterlogged forests in the broader surrounding were also composed of *Alnus glutinosa/incana*, even if macrofossils did not prove it either in Pihoviny or in Kameničky. The long occurrence of forested phase in mires, mainly in the Middle Holocene, was also documented in other European regions such as Western Carpathians (Margielewski et al. 2011; Hájková et al. 2012, 2020a, b; Schafstall et al. 2022). Interestingly, the forested stages (either with spruce or alder or both) could not only result in intensive peat decomposition and even the formation of stratigraphic hiatuses (Rybníček and Rybníčková 1987; Wójcicki and Nita 2017), but on the contrary, they could also be connected with higher accumulation rate (Michczyński et al. 2013). Probably, two contradictory processes can play a role here: the waterlogged forests produce more material (wood) to be accumulated, and at the same time, higher mineralisation mostly occurs under the trees. In the case of the studied profile Pihoviny, two stages with a high content of wood occurred, between 120 and 105 cm (10,650–10,550 cal BP) and between 90 and 55 cm (10,150–7850 cal BP). The first one was built by *Salix* wood and exhibited a very high accumulation rate (2.597 mm/year), whereas the second one was built by *Picea* wood and exhibited an intermediate accumulation rate (0.217 mm/year). Later on (7850–500 cal BP), the trees were still present as indicated by *Picea* needles, but the peat accumulation rate, as well as wood amount, strongly decreased, likely because of repeated fires indicated by macro charcoals.

Finally, the spruce forest was cut in the modern period (ca 450cal BP), and the recent moderately-rich fen and fen meadow developed. This finding is not surprising as it corresponds with the opinion of Rybníček and Rybníčková (2000), who expected that the majority of fen meadows in the region had originated secondarily after human-induced deforestation. Although this event might be understood as a return of low-productive minerotrophic mire, current vegetation in Pihoviny varies considerably from Late-Glacial or Early-Holocene communities. It comprises common fen species, such as *Carex canescens*, *C. nigra*, *Sphagnum palustre*, *S. teres* and *Viola palustris*. The different composition of current communities might be due to a restricted species pool that mainly contains species able to survive in the forest phase. The macrofossil record shows that some species (e.g. *Sphagnum palustre*, *S. teres* and *Viola palustris*) were present in some parts of the spruce forest stage; thus, they can survive the semi-open canopy of the waterlogged forest. On the other hand, the recent occurrence of *Carex dioica* (Kaplan et al. 2015), *Hamatocaulis vernicosus*, *Sphagnum warnstorffii* and *Tomentypnum nitens* (Štechová et al. 2014), i.e., species characteristic for the *Sphagno-Tomentypnion* alliance, may suggest that even light-demanding elements of rich fens might have survived forest phases *in situ* in small open patches. However, this question remains open because of the lack of direct evidence of the continual *in situ* survival of fen specialists. However, the correlation between the site age and the number of fen specialists suggests their long-term survival (Peterka et al. 2022b). Other filters of the former species pool are shifts in local environmental conditions, especially lower water pH and groundwater level (both proved by estimated Ellenberg values) when almost two metres of peat is accumulated and blocks the approach of the more mineral-rich groundwater from the underground. The species composition of sub-recent samples is similar to that of Kameničky site, which, however, tended to more productive wet grassland during the last centuries. This difference might be connected to a more intensive human impact. While Pihoviny site is situated more than 1 km from the nearest settlement, Kameničky site is close to the edge of the village. A relatively higher nutrient availability here might have been caused, for instance, by the higher intensity of

cattle grazing (compare Rybníčková and Rybníček 1988).

Vegetation of the Surrounding Landscape

The pollen analysis from the Pihoviny site revealed the landscape history from the Late Glacial period up to the recent period, even if the record of the Middle and Late Holocene is only with the low resolution because of peat mineralisation. Based on a comparison with other published profiles, it is evident that the landscape development was relatively synchronous in the whole study region. During the Late Glacial, the landscape was covered with cold-tolerant species with the domination of *Pinus* (both, *P. sylvestris* with high pollen abundance and *P. cembra* with low pollen abundance) and *Betula*. Although AP reached a higher value (~75%), implying a forested landscape, the landscape was rather semi-open, as is indicated by the occurrence of heliophilous pollen taxa (e.g. *Juniperus*, *Artemisia*, Poaceae). A similar landscape character with many light-demanding species was revealed at Dářko (AP~76%; Roleček et al. 2020) and Kameničky (AP ~78%; Rybníčková and Rybníček 1988). It seems that the whole region was semi-open, having a character of light taiga forest (with *Pinus* and *Betula*), as assumed by Roleček et al. (2020) in mosaic with steppe or tundra vegetation during the Late Glacial period. It is in concordance with higher elevated Hercynian mountains as Jeseníky Mts. (Dudová et al. 2014) or Šumava Mts. (Svobodová et al. 2002). The occurrence of some temperate trees already in the Glacial period is remarkable. The probable explanation is long-term dispersal from the adjacent glacial refugia in southern Moravia (Hošek, unpubl. data).

As the climate became more favourable at the beginning of the Holocene, the temperate biota around the Pihoviny site started to spread. Firstly, *Ulmus* expanded on dry areas (since 10,550 cal BP), followed by *Corylus* (10,200 cal BP) and *Quercus* and *Tilia* (9700 cal BP). These changes were very synchronous among sites in the study region, except for the Dářko site, where the spreading of temperate trees occurred a little bit earlier (11,000 BP). The reason for that could be the more extensive sedimentation basin which reflects more regional landscape changes (Roleček et al. 2020) or the position on the southwestern margin of the Žďárské vrchy

Hills (cf. Fig. 1) in a bit lower altitude (620 m a.s.l.) with different geomorphological settings (Demek and Mackovčín 2006) and on another bedrock (cretaceous sedimentary rocks). Nonetheless, the almost synchronous change in main tree dominants in all the profiles indicates that the transformation of the landscape cover from cold taiga forest to temperate broadleaved forest was mainly triggered by the short climate amelioration increasing available moisture for trees dated to the 10,300 cal BP (so-called Boreal oscillation; Bond et al. 2001). Although the deciduous trees started to penetrate the region and their pollen abundances gradually increased, the *Pinus*-dominated forests persisted until ca 9300–9000 cal BP when *Pinus* declined, which might be connected with climate humification in those times (Rasmussen et al. 2007). The persistence of *Pinus* forest until the Boreal period was also documented in the neighbouring regions such as the basins of southeastern Bohemia (Rybníčková 1974; Pokorný 2002). On the other hand, in the Šumava Mts as well as Jeseníky Mts, the *Pinus* retreat occurred earlier in ca 10,400 cal BP (Dudová et al. 2014; Svitavská Svobodová and Janský 2021). *Picea* was present in the low abundances from the beginning but substantially expanded around 10,000 cal BP around the Pihoviny site. In other places in the study region, the *Picea* spreading was a bit delayed (ca 8500 cal BP; Kameničky, Dářko). The reason for earlier expansion in the Pihoviny site might be the proximity of Svatka river, which was probably surrounded by waterlogged alluvial forest also containing *Picea*. However, even the effect of a slightly different meso-climate (relatively colder and shaded valley below the summit of the highlands) allowing scattered occurrences of *Picea* in the surrounding forests cannot be entirely excluded. During the middle Holocene, the AP reached the highest amount (ca 90%) in all study sites indicating a forested landscape. The pollen diversity was low, and the dominant trees during that time were *Picea*, *Corylus* and *Betula*, less *Tilia*, *Ulmus* and *Quercus*. When considering that spruce occurred mainly on mesic or waterlogged sites and that *Corylus* and *Betula* required light, the forest should be partly opened. Also, the presence of *Artemisia* pollen implies open spaces around study sites.

The onset of the late-successional trees (*Abies*, *Fagus*) in the Pihoviny site occurred in two steps: the first short one (ca 9500–8800 cal BP) and the second more distinct one (since ca 3500 cal BP). Only

sporadic pollen was detected in the period between. The first Early-Holocene appearance of *Fagus* and *Abies* pollen was documented in the Pihoviny site as well as in the nearby Dářko peat bog (Roleček et al. 2020) and the Jedlová site (Szabó et al. 2016). It indicates quite early penetration of both trees into the study region, consistent with the European-scale synthesis provided by Brewer et al. (2017). Early occurrence of low pollen abundances of *Fagus* was also recorded in southern Czech regions, such as Šumava Mts. (ca 9500 cal BP; Svobodová et al. 2001) and Třeboň Basin (ca 9000 cal BP; Jankovská 1980; Pokorný and Jankovská 2000). It seems that the *Fagus* started to spread from the southern part of the Czech Republic (cf. also Abraham et al. 2016), similar to the Western Carpathian region (Wiezik et al. 2020), but single pollen grains have to be carefully interpreted when macrofossil record is missing. The contamination from the upper layers cannot be fully excluded, but no other pollen types indicate it. Nevertheless, the real expansion of *Fagus* and *Abies* occurred much later during the Late Holocene and was accompanied by a decline of temperate or noble hardwood trees. Interestingly, the transition from noble hardwood forest to the fir-beech forest was not synchronous among sites in the Žďárské vrchy Hills. *Fagus* expanded from 5500 to 3500 cal BP, while *Abies* from 3500 to 2500 cal BP. Such discrepancies pointed to non-climatic factors behind the *Fagus* expansion and fit well with the results of Pokorný (2005; Central Bohemia) and Dudová (2016; Jeseníky Mts), who suggested a crucial role of human activities in the *Fagus* spreading. Nevertheless, climate shifts to more humid and cold conditions could also support the ability of *Fagus* and *Abies* to outcompete other trees (Tinner and Lotter 2006). Nevertheless, we cannot completely rule out the influence of unprecise dating on the onset of the particular tree curves, as most of the profiles are minerotrophic fens with rather low peat accumulation, and low time resolution (Szabó et al. 2016; Rybníčková and Rybníček 1988).

The last significant change was the (post)mediaeval deforestation ca 450–200 years ago, reflected by a substantial decrease of *Abies*, *Fagus* and *Carpinus* pollen, an increase of pollen of pioneer trees (*Betula*, *Pinus*), non-arboreal pollen (NAP), and pollen abundances of Poaceae, Cyperaceae and microcharcoals. The course of the rarefaction pollen-diversity curve concords with general trends of the diversity

development documented by Roleček et al. (2021), who found lower diversity, increasing only in the Late Holocene for the mesic and montane Hercynia compared to warm Hercynia, Carpathians and Pannonia. Contrary to the general trend, we revealed some short-time higher values of pollen diversity also in the Late Glacial and Early Holocene. Also, the values of pollen richness in the study site varied within the same range (16–24 taxa) as average values for mesic and montane Hercynia (Roleček et al. 2020). The microcharcoal concentration in the Pihoviny site started to increase at ca 280 cal BP. This timing corresponds well with the foundation of glassworks in the nearby villages of Cikháj and Herálec in the 17th century (Bukáček 1958), which led to further logging of forests, including the surrounding of Žákova hora Mt. (Vrška et al. 1999). The clear-cuts probably caused increased local erosion. At the Pihoviny site, it is evidenced by a thin mineral layer inserted among the organic layers (ca 1850 AD). Such local erosion was documented elsewhere in the Hercynian uplands and mountains, where it often buried surfaces, including local waterlogged forests with *Abies* and *Picea* (Kaiser et al. 2020).

Important Findings of Plant Macrofossils

Bryophytes *Drepanocladus trifarius*, *Helodium blandowii*, *Meesia uliginosa* and *Scorpidium scorpioides* occurred in the profile's base. *H. blandowii* was further found in the second developmental zone. In the Czech Republic, the first two species are currently considered critically endangered, while the latter two belong among endangered (Kučera et al. 2012). However, the threat status of *M. uliginosa* should be reconsidered "regionally extinct" since the only current population belongs to related *M. minor* (Ellis et al. 2021). These mosses are assumed to be glacial relicts (Rybníček 1966; Dítě et al. 2018; Hájková et al. 2018) and indicators of well-preserved fens and other peatland habitats (e.g. Šoltés et al. 2004; Váňa 2006; Peterka et al. 2020). According to our knowledge, macrofossils of *M. uliginosa* have never been found in any peat profile in the Czech and Slovak Republic. The record from Pihoviny has already been published and discussed by Hájková and Široká (2022). The profile further contained *H. blandowii*. This species has been found only in four peat deposits in former Czechoslovakia (Hájková et al. 2018, 2020a, b). One

of the previous records comes from the nearby Dářko profile (Roleček et al. 2020). On the contrary, *D. trifarius* and *S. scorpioides* belong to relatively common components of old peat sediments, as their habitats (quaking brown-moss-rich fens) were probably widespread in central Europe in the late Glacial and Early Holocene (Hájková et al. 2018).

Seeds of *Sagina nodosa* occurred in the uppermost zone of the profile, in the zone dated to the second half of the 19th century. According to the macrofossil database of the Czech and Slovak Republic, the fossil seeds of this species were never found in the Czech and Slovak sediments (<https://www.sci.muni.cz/botany/mirecol/paleo>). However, recent work on the subfossil deposits of the Bohemian-Moravian Highlands (Šírká, in prep.) has proved the occurrence of fossil seeds in another locality (Louky u Černého lesa). The sub-recent records are in concordance with the work of Sutorý (1978) and the Pladias database (Chytrý et al. 2021) that summarise numerous historical localities (the second half of the 19th and first half of the 20th century) not only from the study region but from other regions in the Czech Republic. The species was probably common elsewhere in Central Europe (cf. Pawłowski et al. 1960; Sutorý 1992) but disappeared during the second half of the 20th century because of changes in landscape management. The layer with *S. nodosa* was characterised by a low value of LOI and high inorganic admixture indicating disturbances. This corroborates the knowledge that several fen species deserve oligotrophic sites with the untouched hydrological regime in combination with mild disturbances that suppress competitively superior vascular plants and bryophytes, reduce litter accumulation, remove the sod and thus maintain open patches supporting germination and seedling recruitment (Weltzin et al. 2005; Stammel et al. 2006; Singh et al. 2019, 2021).

Implications for Conservation

In the Bohemian-Moravian Highlands, fens and fen meadows are current biodiversity hotspots harbouring many endangered species (Štechová et al. 2014; Čech et al. 2021). These valuable habitats were, however, formed by natural processes as well as by human influence, i.e. landscape deforestation in the (post) mediaeval times and consequent agricultural management (hay-cutting or extensive pasture; Rybníček and

Rybníčková 2000). Regular mowing is hence essential to sustain open mire vegetation and prevent spontaneous forest regrowth (Moen et al. 1999; Hájková et al. 2022). Active mowing is even more needed concerning recent climate events (dry and hot summers; Koenig et al. 2018), which lower water-table depth, decrease environmental stress and make fens more susceptible to wood encroachment and other successional changes (Lamers et al. 2015; Hájek et al. 2020).

Common macrofossils of *Picea abies* in the profile give an argument for considering natural spruce forest in the region primarily as azonal vegetation of the waterlogged sites. Furthermore, palaeoecological analyses suggest a mosaic of spruce forests on wet sites and beech-fir forests on mesic sites in the Late Holocene. However, spruce monoculture plantations currently prevail over forests with natural or semi-natural species composition in the Žďárské vrchy Hills. Similarly to spruce plantations in other parts of the Czech Republic (Fanta and Petřík 2018), these forests are negatively affected by ongoing climate changes and consequently more endangered by calamities caused by bark beetle outbreaks or windstorms. The former composition of the tree layer, including a higher proportion of *Abies* and *Fagus*, should be restored to increase the stability of forests and prevent their breakdowns in future.

Conclusions

The fossil record of the studied Pihoviny site involves the last 14,000 years, which is one of the oldest records in the study region. The local fen vegetation developed from the sedge-moss quaking fen with tundra elements, through the hummock-building rich fen, *Salix* stage to the waterlogged spruce forest, which persisted over thousands of years. Finally, humans deforested the site, and open-fen vegetation was restored, but species composition was different than in the Late Glacial and Early Holocene. The reason could be different climate, different local conditions (lower reconstructed water pH, lower moisture and higher nutrients) or restricted species pool filtered by long forested stage. Two exceptional findings have been made: stems of the (sub) alpine species *Meesia uliginosa* in the Late Glacial layer and seeds of in Czechia recently extinct species *Sagina nodosa* in the (sub)recent layer. The regional vegetation developed from the semi-open landscape dominated by cold- and dry-tolerating trees (*Pinus*

sylvestris t., *Betula*) and Poaceae. *Pinus cembra* was also present until ca 10,600 cal BP. The *Pinus sylvestris* t. decline and the temperate tree onset occurred in the Early Holocene (between 10,200 and 9500 cal BP), which fits well with other fossil records from the region. The expansion of late-successional trees *Fagus* and *Abies* was less synchronised among profiles and varied between 5500 and 3500 in the case of *Fagus* and between 3500 and 2500 in the case of *Abies*. It could be influenced by human disturbances in forests, as is also reported from other regions, but non-precise dating cannot be ruled out. The pollen-based diversity was the highest in the last centuries when the pollen related to human activities increased its richness, which concurs with the general trend reconstructed for the mesic and montane Hercynia (Roleček et al. 2020).

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Author Contribution PH and TP conceived the ideas, coordinated the work and led the writing. PH, TP, LP and AŠ sampled profiles in the field. AŠ with the help of PH analysed plant macrofossils, LP made pollen and microcharcoal analyses, AŠ and LP analysed LOI. EJ prepared the pollen data from the study region for comparative figure. All authors contributed critically to the drafts and gave final approval for publication.

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Data Availability Pollen data are available in the PALYCZ database (Kuneš et al. 2009) and plant macrofossil data are at disposal in the Plant macrofossil database of the Czech and Slovak Republic (Hájková et al. 2018). The worksheet with pollen data used for comparative Fig. 9 is available as Table S1 in the electronic supplementary material.

Declarations

Conflicts of Interest The authors declare no conflict of interest.

Ethical Approval The research complies with the current laws of the Czech Republic. This article does not use animals and does not contain any studies with human participants performed by any of the authors. The authors have no ethical conflicts to disclose.

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