Conservation targets from the perspective of a palaeoecological reconstruction: the case study of Dářko peat bog in the Czech Republic

Paleoekologická rekonstrukce vývoje rašeliniště Dářko a její vztah k cílům ochrany přírody

Jan Roleček[1,2], Helena Svitavská Svobodová[3,4], Eva Jamrichová[3], Lydie Dudová[3], Petra Hájková[2,3], Günther Kletetschka[5,6,7], Petr Kuneš[4] & Vojtěch Abraham[4]

[1]*Czech Academy of Sciences, Institute of Botany, Department of Vegetation Ecology, Lidická 25/27, CZ-602 00 Brno, Czech Republic, e-mail: honza.rolecek@centrum.cz;* [2]*Department of Botany and Zoology, Faculty of Science, Masaryk University, Kotlářská 2, CZ-611 37 Brno, Czech Republic, e-mail: buriana@sci.muni.cz;* [3]*Czech Academy of Sciences, Institute of Botany, Laboratory of Palaeoecology, Lidická 25/27, CZ-602 00 Brno, Czech Republic, e-mail: helena.svitavskasvobodova@ibot.cas.cz, eva.jamrichova@ibot.cas.cz, cvilinek@gmail.com;* [4]*Department of Botany, Faculty of Science, Charles University, Benátská 2, CZ-128 01 Praha 2, Czech Republic, e-mail: vojtech.abraham@gmail.com, petr.kunes@natur.cuni.cz;* [5]*Czech Academy of Sciences, Geological Institute, Rozvojová 269, CZ-165 00 Prague 6, Czech Republic, e-mail: gk@natur.cuni.cz;* [6]*Department of Applied Geophysics, Charles University, Albertov 6, CZ-128 00 Prague 2, Czech Republic;* [7]*Geophysical Institute, University of Alaska Fairbanks, 903 N Koyukuk Drive, Fairbanks, AK 99775, USA*

Roleček J., Svitavská Svobodová H., Jamrichová E., Dudová L., Hájková P., Kletetschka G., Kuneš P. & Abraham V. (2020) Conservation targets from the perspective of a palaeoecological reconstruction: the case study of Dářko peat bog in the Czech Republic. – Preslia 92: 87–114

We analysed a continuous and well-dated record of pollen, non-pollen palynomorphs, geochemistry and plant macroremains from the best preserved peat bog in the Bohemian-Moravian Highlands (Czech Republic). Dářko peat bog is an isolated site of a pine bog woodland dominated by the central-European endemic *Pinus uncinata* subsp. *uliginosa*. It is protected as a National Nature Reserve and a Site of Community Importance. We describe major patterns and interesting details of the development of this site since the Late Glacial and provide a historical context for some natural phenomena of high conservation value. Until the High Middle Ages, macroclimate and autogenic succession appear to have been the main drivers of both the local and regional development of vegetation. The pine-dominated Late Glacial vegetation with cold-loving taxa survived until the first millennia of the Holocene. The first Late Glacial and Holocene record of *Isoëtes lacustris* outside its present range in this country indicates the presence of a cold oligotrophic waterbody in this period. *Corylus*, *Picea* and mixed oak forest taxa started to expand already around 10,500 cal. BP. Indicators of a warm oceanic climate appeared around 7700 cal. BP and the AP:NAP ratio increased gradually up to its Holocene maximum close to 99%. Around 6800 cal. BP, the minerotrophic wetland developed into an ombrotrophic bog. *Picea*, *Fagus* and *Abies* started to dominate the pollen assemblage around 5500 cal. BP. Between AD 1100 and 1350, an abrupt change in the vegetation started, which coincided with the High Medieval colonization of the region. The pronounced peak of Pb in the geochemical record between AD 1200 and 1650 reflects extensive metallurgical activities in a wider area. Valuable pine bog woodland appeared only around AD 1500, when pine expanded. This late expansion, also recorded elsewhere, may have been triggered by human activities, which challenges the present non-intervention management of this habitat. The present marginal occurrence of fen species in the bog lagg may be considered a relict of Late Glacial and Early Holocene minerotrophic fen vegetation, the

doi: 10.23855/preslia.2020.087

preservation of which requires active management. This study shows how palaeoecological knowledge helps explain present patterns in the composition of a valuable protected site. This knowledge may be used in prioritising conservation and in communicating the nature conservation goals to the public.

K e y w o r d s: Bohemian-Moravian Highlands, conservation priorities, Holocene, human impact, landscape history, Late Glacial, mire, palaeoecology, rare species, relict, vegetation

Introduction

An historical perspective is of great importance for biodiversity conservation (Davies & Bunting 2010, Wingard et al. 2017). It helps explain trends in the development of ecosystems, their stability, vulnerability and potential (Willis & Birks 2006, Jamrichová et al. 2013, Reitalu et al. 2014). It also provides narratives that contextualize present biological phenomena, which is relevant both for their scientific exploration (Nerlich et al. 2016) and communication with the public (Hockings et al. 1998). Peat bogs are an excellent system in this respect as they are valuable natural sites of high conservation concern (Lindsay 1995, Joosten et al. 2017) and simultaneously preserve an archive of information on the history of the local and regional environments (Barber 1993, Chapman et al. 2003).

The Bohemian-Moravian Highlands are an extensive upland region situated on the eastern periphery of the Central European Uplands. It connects the Sudetes Mts in the north with the Bohemian Forest region in the south. At the same time, it is a major obstacle to migration and transport between the lowland regions in the Bohemian Cretaceous Basin and the Outer Carpathian Depression. Due to its flat topography and sufficient rainfall, it is an important wetland area (Mackovčin & Sedláček 2002, Demek & Mackovčin 2006). One of the pivotal areas of this region is the Dářská brázda Furrow, situated on a watershed near the historical border between Bohemia and Moravia. It harbours a large wetland complex on its flat bottom, part of which is Dářko peat bog – the largest and best preserved peat bog in the Bohemian-Moravian Highlands.

Dářko peat bog is protected as a National Nature Reserve and Site of Community Importance. A rich mire biota occur here, including an isolated population of a rare bog pine (*Pinus uncinata* subsp. *uliginosa*) (Bastl et al. 2008, Businský 2009) and other habitat specialists of various taxonomic groups, including bryophytes (*Sphagnum rubellum*, *S. magellanicum* s.l., *Cephaloziella elachista*), vascular plants (*Andromeda polifolia*, *Vaccinium uliginosum*, *Carex chordorrhiza*) and insects (the ant *Formica picea*, the butterfly *Vacciniina optilete*) (Mackovčin & Sedláček 2002, www.prirodavysociny.cz). Dářko peat bog has become a classical site for studies in palaeoecology (Rudolph 1927, Salaschek 1935, Puchmajerová 1943, 1944) and mire ecology (Domin 1923, Klika & Šmarda 1944, Holubičková 1961, Rybníček 1964, Neuhäusl 1972, 1975, Peterka 2013). The latest papers related to its history appeared only recently (Břízová 2009, 2014).

Despite the considerable accumulation of knowledge, a palaeoecological reconstruction of the genesis of Dářko peat bog and the surrounding landscape suffers from uncertainties, which may hinder its effective conservation. For example, while the grasslands on the periphery of the peat bog are actively managed (Peterka 2015), non-intervention management is practised in the pine bog woodland. This distinction is based, among others, on assumptions about the natural development of pine bog woodland (www.cittadella.cz/europarc). The legitimacy of such assumptions should be subject to palaeoecological scrutiny.

Here, we deal with an evaluation and absolute dating of potential key events in the development of Dářko peat bog, such as the Late Glacial – Holocene transition, fen-bog transition and Medieval colonization of the surrounding landscape by humans. Our final goal was to assess the changes in the composition of the local plant assemblages, paying particular attention to the history of the present conservation targets, mainly the pine bog woodland and species of rich fen vegetation.

Material and methods

Study area

Dářko peat bog is situated in the central part of the Czech Republic, near the historical border between Bohemia and Moravia (Fig. 1). It is part of a large wetland complex. The part investigated is called Padrtiny and covers 145 ha, including a lagg. The peat is up to 8.6 m deep, with an estimated volume of 6.2 million m^3 (Neuhäusl 1975). The altitude is around 620 m a.s.l., the mean annual temperature is around 6.0 °C and the annual precipitation around 750 mm (Vesecký 1961). The core part of the peat bog is protected as the Dářko National Nature Reserve (64 ha) and it is also included at a Site of Community Importance Dářská rašeliniště (390 ha) and in the Žďárské vrchy Protected Landscape Area. It is the only site for the central-European endemic bog pine (*Pinus uncinata* subsp. *uliginosa*; syn. *P. rotundata*, *P. mugo* subsp. *rotundata*) in the central part of the Bohemian-Moravian Highlands (Businský 2009). The conservation is further focused on the biota of spruce bog woodlands, transitional mires and intermittently wet meadows.

Dářko peat bog developed in a tectonic depression, the Dářská brázda Furrow, which lies on an important physiographic crossroads in the Bohemian-Moravian Highlands (Demek & Mackovčin 2006). In this area, the Železné hory Mts, the Hornosázavská pahorkatina Upland and the Křižanovská vrchovina Upland meet the Žďárské vrchy Mts, one of the highest parts of the Bohemian-Moravian Highlands (maximum altitude 836 m a.s.l.). This area is also the watershed of the Sázava and Doubrava rivers. The geological settings are diverse and have influenced the historical development of this peat bog. While acidic Proterozoic and Palaeozoic plutonic and metamorphic rocks (gneiss, migmatite, granodiorite) prevail in most of the surroundings, the bedrock of the actual peat bog consists of Cretaceous sediments (marlstone, sandstone), which are often less acidic (calcareous). Situated adjacent to the peat bog is the largest fishpond in the Bohemian-Moravian Highlands, Velké Dářko (206 ha), which was constructed in the late 15th century (David 2001).

Field sampling

A profile of the sediment was obtained from the deepest part of the peat bog (49°38'16"N, 15°52'33"E, 622 m a.s.l) using a modified Livingstone piston corer (6 cm in diameter) on 9 August 2016. The length of the core was compressed from 8.53 to 7.31 m during the extraction process. A description of the deposits was done in the field. The material

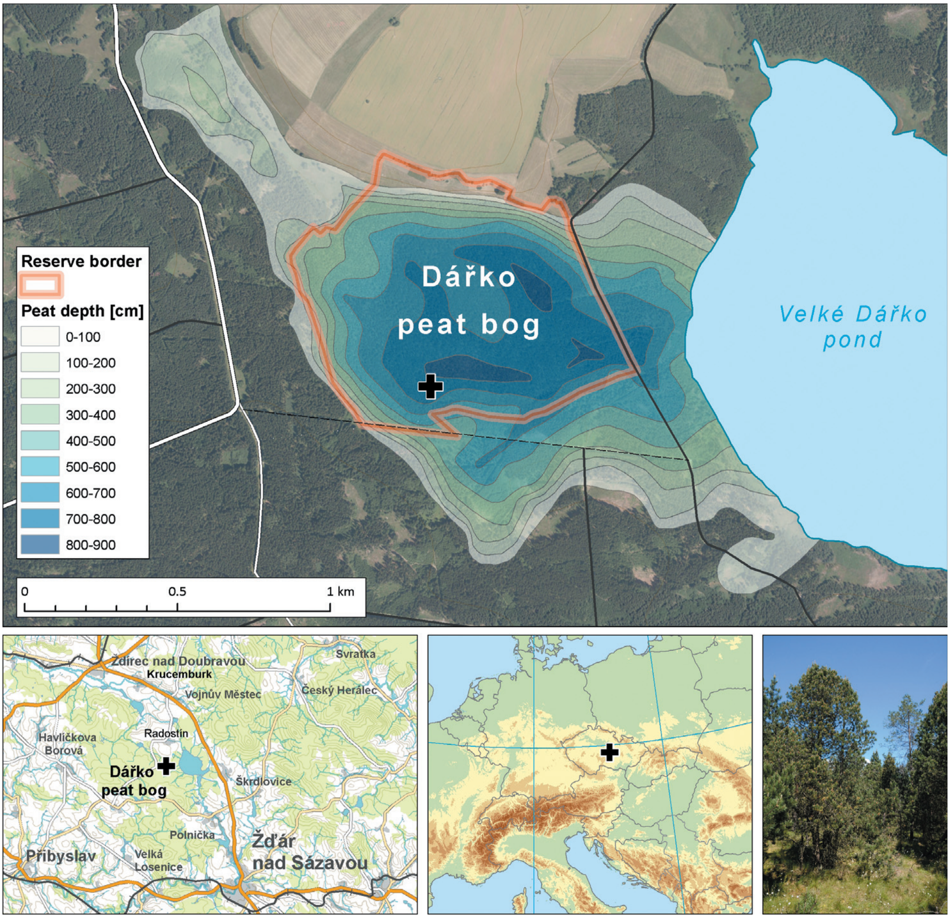


Fig. 1. – Map of the area studied. The cross indicates the position of the coring site. The border of the Dářko National Nature Reserve is used for Dářko peat bog delimitation. Peat depths are redrawn after Neuhäusl (1975). A photo of the present state of the pine bog woodland with *Pinus uncinata* subsp. *uliginosa* and *Eriophorum vaginatum* is included.

obtained was wrapped in plastic bags and transported to the Laboratory of Palaeoecology in Brno, where samples of the material (volume 1 cm^3) were taken at 10 cm intervals for pollen analysis. After analysis and radiocarbon dating (see below), layers corresponding to particularly interesting periods (Late Glacial and Pleistocene – Holocene transition; medieval and modern eras) were subsampled at 5 cm intervals and analysed.

Pollen analysis

The preparation of pollen samples followed standard procedures (Faegri & Iversen 1989). We added five tablets of *Lycopodium* spores to each sample of known volume (1 cm^3) prior to chemical treatment to determine the pollen concentration and subsequently pollen influx of arboreal taxa and charcoal concentration according to Stockmarr (1971). Each tablet with batch number 3862 contained 9666 spores. Arboreal taxa included all woody species (trees, shrubs and dwarf shrubs). Samples containing mineral material were pretreated with cold concentrated HF and then processed with KOH and subjected to acetolysis. Not less than 1000 terrestrial arboreal and non-arboreal pollen grains were identified using standard pollen keys (Punt 1976–2003, Beug 2004, Punt & Hoen 2009), microphotographic atlases (Reille 1992–1998) and the reference collection of the Institute of Botany, Czech Academy of Sciences (IB CAS). During the pollen analysis, we also analysed fossils of pteridophytes, bryophytes, fungi, algae, charcoal dust and other non-pollen palynomorphs (NPPs), which were counted and identified using the keys of van Geel (1978), van Geel et al. (1989, 2003), Pals et al. (1980), Speranza et al. (2000), Cugny et al. (2010) and an online database of non-pollen objects (http://nonpollenpalynomorphs.tsu.ru). Pollen percentages were calculated based on the total pollen sum (TS) of arboreal and non-arboreal pollen (TS = AP + NAP = 100%) and plotted against depth and time using Tilia v. 1.7.16 software (Grimm 2011). The percentages of (semi)aquatic taxa (or local taxa), spores and other NPPs were calculated in relation to the TS (cf. Berglund & Ralska-Jasiewiczowa 1986). Diagrams were divided into zones using sums-of-squares partitioning and the statistical significance of the zones was evaluated using the broken-stick model in the Psimpoll 4.27 program (Bennett 1993).

Macroremain analysis

Plant macrofossils were extracted from sediment samples of 10–20 ml volume by wet-sieving using sieves with mesh diameters of 1 mm, 0.63 mm and 0.2 mm. Plant macrofossils were then hand-picked from Petri dishes. The percentages of particular components in the sediment (e.g. wood, bryophytes, plant tissues) were estimated after wet sieving. Plant remains were identified under a dissecting microscope according to Cappers et al. (2006), Hedenäs (2003) and other available identification literature and the reference seed collection of IB CAS. Wood fragments were identified with the help of an on-line key (http://www.woodanatomy.ch). The values of all macrofossils are presented as absolute numbers per sample for countable fossils and as volume percentages for bryophytes, tissues and wood fragments. Only samples from the period between 13,400 and 6000 cal. BP were analysed to assist in the interpretation of peat bog vegetation in the critical periods of the Late Glacial – Holocene transition and fen-bog transition. Particular developmental zones in the macrofossil diagram were delimited using Coniss cluster analysis in the Tilia software. The Probabilistic Vegetation Key (Tichý & Chytrý 2019) was used to interpret the zones in terms of extant vegetation types: the identities of all the species of vascular plants recorded in a particular zone were entered into a key and the most probable vegetation type identified by the algorithm was chosen. The vegetation types considered correspond to the concept in the Vegetation of the Czech Republic monograph (Chytrý 2007–2013).

Radiocarbon dating

The profile was dated using the radiocarbon AMS (accelerator mass spectrometry) method in the Poznań Radiocarbon Laboratory. Bulk peat 1 cm thick was used for the dating of 14 samples and seeds of terrestrial plants for one sample. A depth-age model was created using the Bayesian age-depth modelling in the Bacon program (Blaauw & Christen

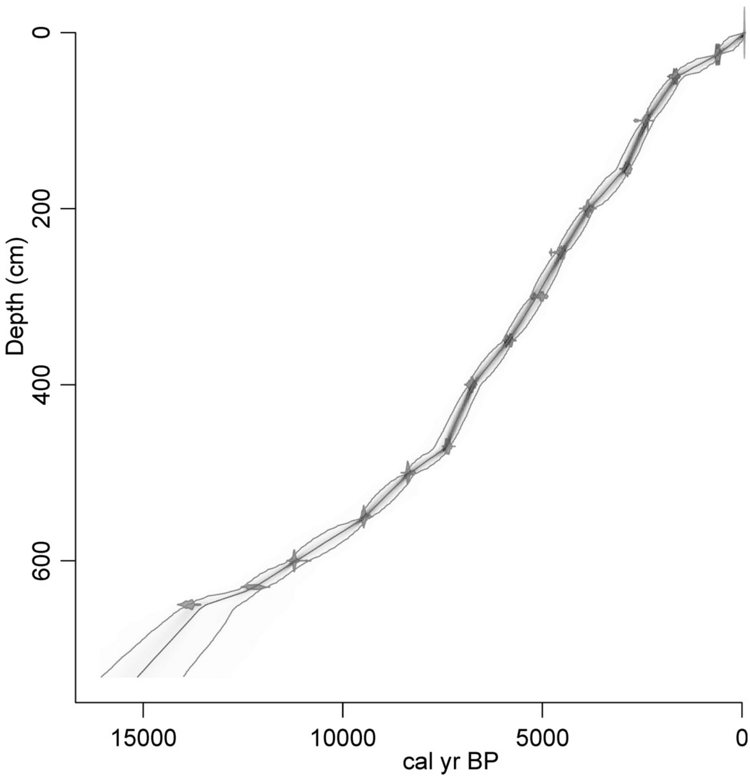


Fig. 2. – Depth-age model of Dářko core: mean value (central dotted line), distributions of calibrated ^{14}C dates (dark grey polygons) and distributions of modelled ages for all depths (light grey grid). The age between the bottom ^{14}C date and the base of the core was extrapolated due to the lack of datable material.

2011). All ages mentioned in the Results and Discussion are based on the depth-age model, if not specified otherwise. Throughout the text, we use calibrated ages before AD 1950 (cal. BP; Reimer et al. 2013) rounded to the nearest 50, with the exception of the chapters related to late human impact, where the age of the Gregorian calendar is used for comparability with archaeological and historical sources.

Geochemical analysis

We used X-ray fluorescence (XRF) scans to determine the elemental composition of the sediment (Rollinson 2014). For this we built a programmable horizontally moving platform connected to a personal computer. Each sediment core was placed in a sediment holder and covered with a polyethylene membrane. The XRF analyses were carried out along the cores at 2 mm intervals, using a 2.2 mm collimated beam, with 6 minutes of exposure at each core location. We used the Geochem mode with two beams (up to 11 keV for 3 minutes for lighter elements, and up to 50 keV for 3 minutes for heavier elements). Variations in Rb were used to create a single depth scale (Kletetschka et al. 2018).

Taxonomic concepts and nomenclature

Taxonomic concepts and plant names follow Danihelka et al. (2012) for vascular plants (with the exception of *Potentilla palustris* (L.) Scop.), Smith (1996) for bryophytes except *Sphagnum* mosses, and Laine et al. (2018) for *Sphagnum* mosses. We use the name *Sphagnum magellanicum* s.l. for *S. medium*/*divinum*, which were not distinguished until recently (Laine et al. 2018).

Results

Chronology

The results of the AMS dating of 15 samples from the Dářko core are provided in Table 1. The calibrated age (2 sigma) of the peat bog base is 14,050–13,700 cal. BP. The corresponding depth-age model, depicted in Fig. 2, estimates the onset of peat accumulation close to 13,400 cal. BP. The age of the gravel base of the core at 732 cm was extrapolated to ~15,100 cal. BP. The model shows a rather regular accumulation during the entire Holocene period, with relatively lower accumulation rates between 12,000 and 6450 cal. BP (~0.045 cm/year), higher rates between 6450 and 1750 cal. BP (ca 0.07 cm/year) and again lower rates between 1750 cal. BP and the present (~0.03 cm/year).

Table 1. – Radiocarbon AMS dates recorded for different depths of the Dářko core.

Depth (cm)	Laboratory code	^{14}C age (years BP)	Material dated
25	Poz-102334	615 ± 30	terrestrial seeds
50	Poz-96597	1765 ± 30	Bulk
100	Poz-92954	2370 ± 30	Bulk
155	Poz-96599	2775 ± 35	Bulk
200	Poz-92953	3560 ± 30	Bulk
250	Poz-96600	4050 ± 35	Bulk
300	Poz-92952	4435 ± 35	Bulk
350	Poz-96601	5100 ± 40	Bulk
400	Poz-92951	5945 ± 35	Bulk
470	Poz-96602	6450 ± 40	Bulk
500	Poz-92950	7540 ± 40	Bulk
550	Poz-96603	8440 ± 40	Bulk
600	Poz-92949	9790 ± 50	Bulk
630	Poz-102690	10360 ± 60	Bulk
650	Poz-96756	11990 ± 60	Bulk

Stratigraphy

The basal layers of the profile (750–650 cm) are composed of clayey and sandy material that accumulated in a shallow still waterbody. The rest of the profile consists of decomposed peat, with an admixture of wood remains in the lower part (650–553 cm). A detailed description is provided in Table 2.

Table 2. – Stratigraphy and description of the analysed sediment. Abbreviations according to Troels-Smith (1955): Gmin – Grana minora, Gmaj – Grana majora, Sh – Substantia humosa, Th – Turfa herbacea, Tl – Turfa lignosa.

Depth (cm)	Troels-Smith classification	Sediment description
0–11	Th4	Undecomposed peat with plant roots and tissues
11–22	Sh2; Th2	Slightly decomposed peat with visible plant macro-remains; pale-brown colour.
22–560	Sh4	Highly decomposed peat; dark-brown colour.
560–650	Sh3; Tl1	Highly decomposed peat with admixture of woody remains; dark-brown colour.
650–730	Sh1; Gmin3	Clay and sand with admixture of decomposed organic matter; grey colour.
730	Gmaj4	Coarse sand with gravel; grey colour.

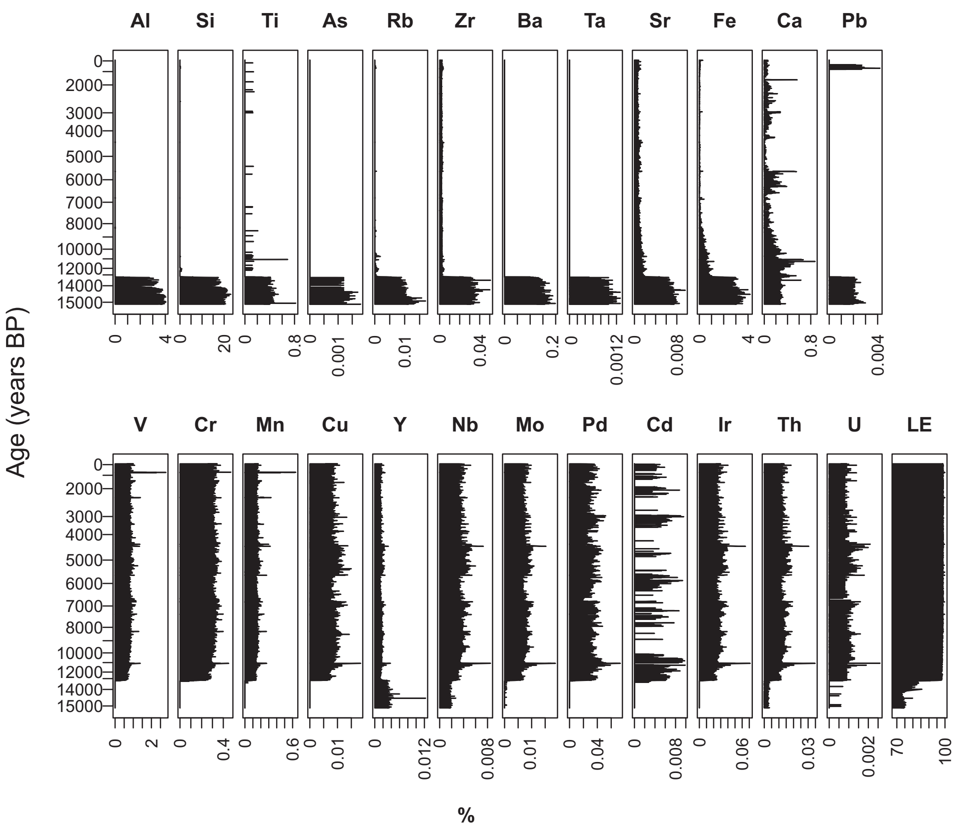


Fig. 3. – Elemental composition of Dářko peat bog sediment, determined using X-ray fluorescence. LE – light elements (from hydrogen to sodium).

Geochemistry

Temporal changes in the elemental composition of the sediment are shown in Fig. 3. In the lower part of the profile (730–650 cm; Late Glacial), high amounts of Al, K, Si, Tl, Fe, As, Zr and Sr indicate intense erosion in the vicinity of the site with a high input of clastic allochthonous material into the sedimentation basin. The high amount of Si may also be related to the aquatic environment and the occurrence of diatoms. Around 13,400 cal. BP, there was a rapid decline in all the mentioned elements, whereas Mn, Cu, Th and Cd increased. This indicates a decline in erosion, stabilization of the vegetation in the vicinity of the site and accumulation of organic material. The gradual decline in Ca may be related to the decline in calcium carbonate in the environment. Its first minimum occurred around 8300 cal. BP and may indicate a transition to acidic conditions due to the accumulation of peat isolating the surface from the calcareous bedrock. A similar gradual decline was recorded for Fe. Later periods when Ca increased may be connected with Ca uptake by deep-rooting plants (e.g. *Vacciniaceae*, trees). The pronounced peak of Pb between ~750 and 300 cal. BP reflects extensive metallurgical activities in a wider area.

Pollen and NPP assemblages

Based on the total composition of pollen assemblages (Figs 4 and 5), we delimited seven local pollen analytical zones (LPAZ) in the development of Dářko peat bog (their dating is based on the depth-age model):

LPAZ DAR 1 (650–575 cm; 13 400–10 250 cal. BP) is characterized by high abundance of *Pinus sylvestris*, *Salix*, *Betula pubescens* type pollen, regular occurrence of cold-tolerant trees and shrubs (*Pinus cembra*, *Betula nana* type, *Hippophaë rhamnoides*, *Ephedra* and *Juniperus*) and a rich spectrum of pollen of herbaceous plants (e.g. *Achillea*, *Artemisia*, *Aster tripolium* type, *Brassicaceae*, *Asteraceae* subfam. *Cichorioideae*, *Cerastium*, *Cerinthe*, *Sagina apetala* group, *Scleranthus perennis*, *Chenopodiaceae*, *Galium*, *Thalictrum, Potentilla, Helianthemum, Trollius, Plantago lanceolata* type and *Dryas octopetala*). The pollen spectrum of the local vegetation includes a high amount of graminoids and herbs, mainly *Cyperaceae*, *Poaceae*, *Filipendula* and ferns. The occurrence of algae (*Botryococcus*, *Scenedesmus*, *Tetraedron*), and spores and pollen of aquatic macrophytes (*Isoëtes lacustris*, *Myriophyllum alterniflorum*, *M. spicatum*) indicate a stagnant water environment. *Pinus* stomata were also present. The AP:NAP ratio is close to 80%.

LPAZ DAR 2 (575–525 cm; 10,250–8890 cal. BP) is characterized by a change in dominance from *Pinus sylvestris* type to *Corylus* and *Betula pubescens* type. Pollen of temperate broadleaved trees (*Ulmus*, *Quercus* and *Tilia*) increased, whereas *Pinus cembra* and *Betula nana* type pollen decreased. In the local vegetation, *Cichorioideae* and *Poaceae* pollen reached Early Holocene maxima, whereas that of other local herbaceous plants decreased. Water algae nearly disappeared, whereas pollen of minerotrophic wetland species (e.g. *Menyanthes trifoliata*, *Typha angustifolia*, *T. latifolia*) appeared.

LPAZ DAR 3 (525–445 cm; 8890–7330 cal. BP) is characterized by an increase in pollen of temperate broadleaved trees (*Quercus*, *Fraxinus, Tilia*, *Ulmus*). Pollen of *Picea* gradually increased, whereas *Corylus* pollen abruptly decreased and *Betula pubescens* type pollen reached its Holocene maximum. *Fagus* pollen was recorded regularly in low amounts. In the local vegetation, *Sphagnum* spores increased and became dominant. Higher amounts of *Cyperaceae* and frequent *Peucedanum* and *Thalictrum* pollen was

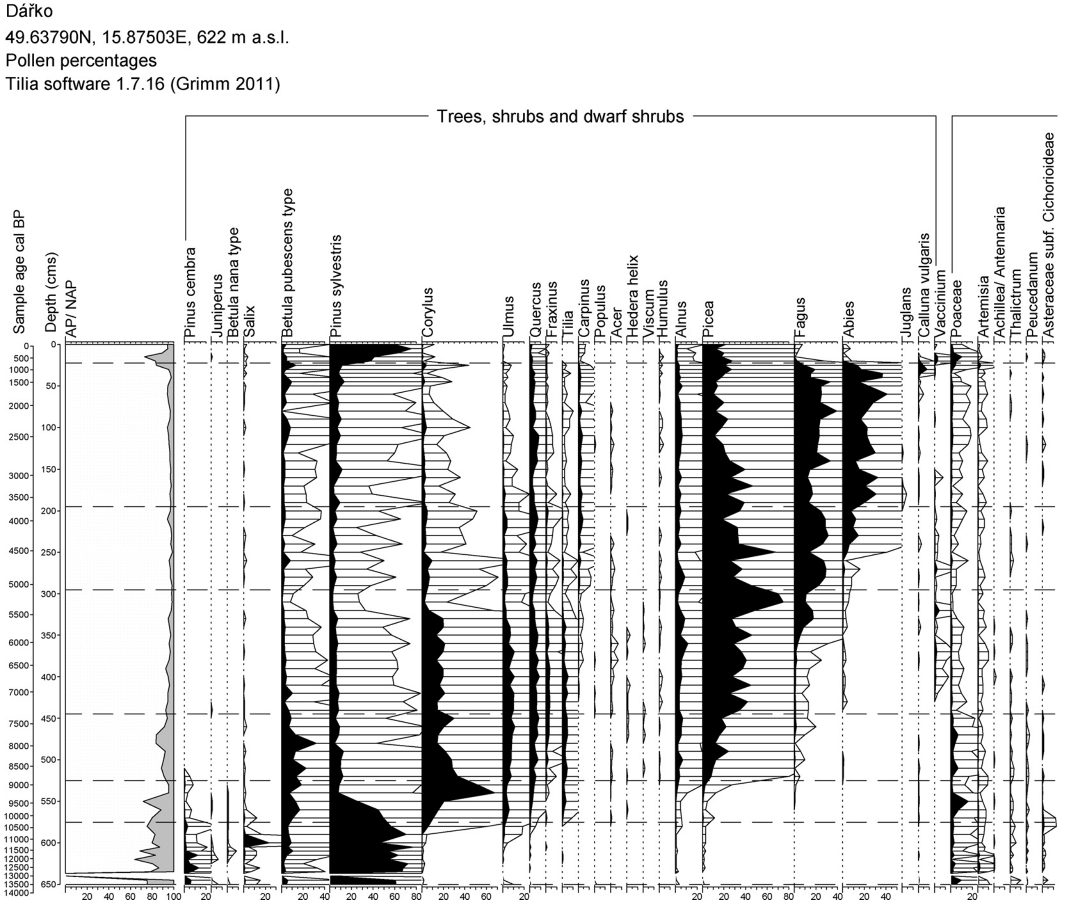
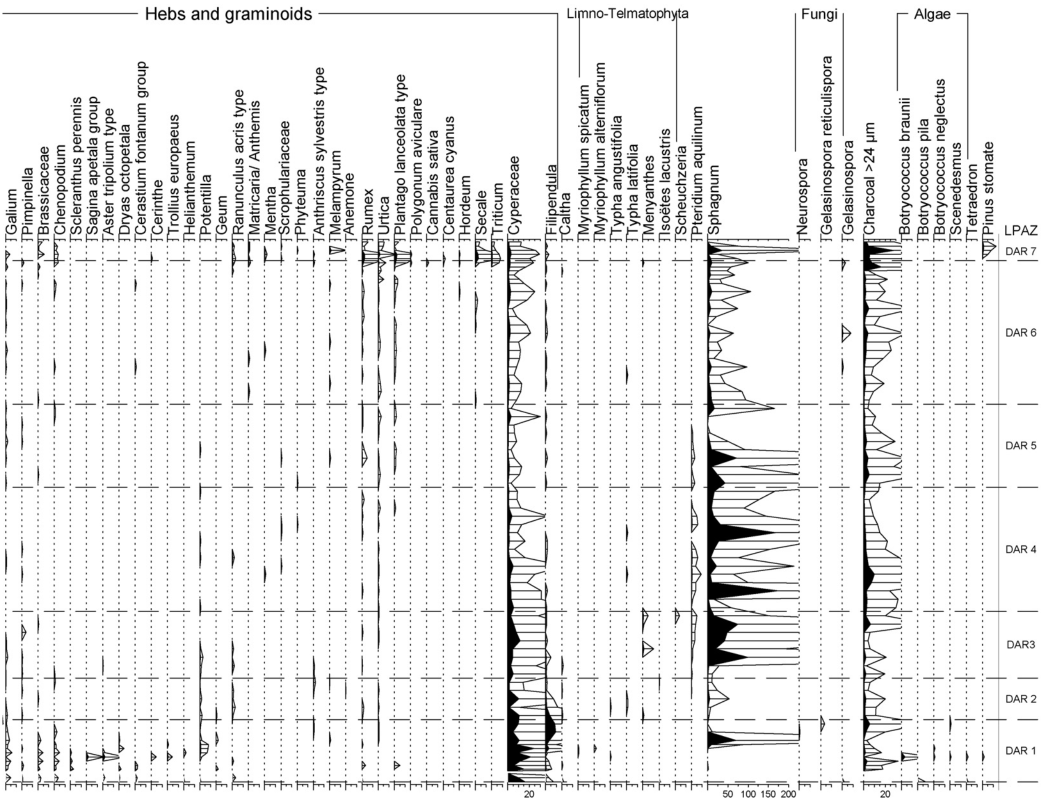


Fig. 4. – Percentage pollen diagram of selected pollen types belonging to different ecological groups. AP/NAP = ratio of arboreal pollen (AP) to non-arboreal pollen (NAP).

also recorded. *Menyanthes* pollen was still present and *Scheuchzeria* pollen was also found. Spores of coprophilous fungi (*Cercophora*, *Sporormiella*, *Sordariaceae*), which occurred continuously from the profile base, disappeared around 7750 cal. BP. Charcoal and spores of the fire-tolerating *Pteridium aquilinum* increased. The AP:NAP ratio was close to 90%. Among fungal remains, *Bysothecium circinans* (HdV-16), growing on graminoids, and HdV-18 ascospores, confined to *Eriophorum vaginatum*, prevailed. HdV-54 mycelia are related to *Sphagnum* peat.

LPAZ DAR 4 (445–295 cm; 7330–5080 cal. BP) is characterized by the dominance of pollen of *Picea*, *Corylus* and broadleaved trees (*Quercus*, *Acer*, *Tilia*, *Ulmus*, *Populus*, *Fraxinus*). *Betula pubescens* type decreased, *Fagus* pollen gradually increased, *Abies* and *Carpinus* pollen appeared. Of the local species, *Sphagnum* spores still dominated with fluctuating abundance, and *Vaccinium* pollen appeared and maintained a continuous presence. Pollen of other herbaceous plants was recorded in low amounts and the AP:NAP ratio increased to over 95%. NPPs (e.g. the fungi *Helicoön pluriseptatum*,



Entophlyctis lobata, *Microthyrium*, *Actinopeltis,* testate amoebe *Assulina muscorum*, *Arcella* and *Amphitrema*, and rotifer *Habrotrocha*) indicate a switch to ombrotrophic conditions around 6800 cal. BP. The peak of charcoal and *Pteridium aquilinum* spores suggest an increased occurrence of fires.

LPAZ DAR 5 (295–195 cm; 5080–3730 cal. BP) is characterized by a steep increase in *Fagus* pollen to its first Holocene maximum at the expense of *Corylus* and other broad-leaved trees, except *Quercus*. *Picea* remained the main dominant in the pollen assemblage, with fluctuating abundance. *Abies* and *Carpinus* pollen increased. Pollen of some indirect human indicators (e.g. *Urtica*, *Rumex acetosa* type, *Plantago lanceolata* type) appeared, and pollen of *Calluna*, *Poaceae* and various herbaceous plants (*Artemisia*, *Brassicaceae*, *Cichorioideae*, *Melampyrum*, *Pimpinella*, *Thalictrum*) was frequently recorded. However, the abundance of herbaceous plant pollen remained low and the AP:NAP ratio rarely dropped below 95%. Charcoal and *Pteridium aquilinum* spores declined towards the end of this zone.

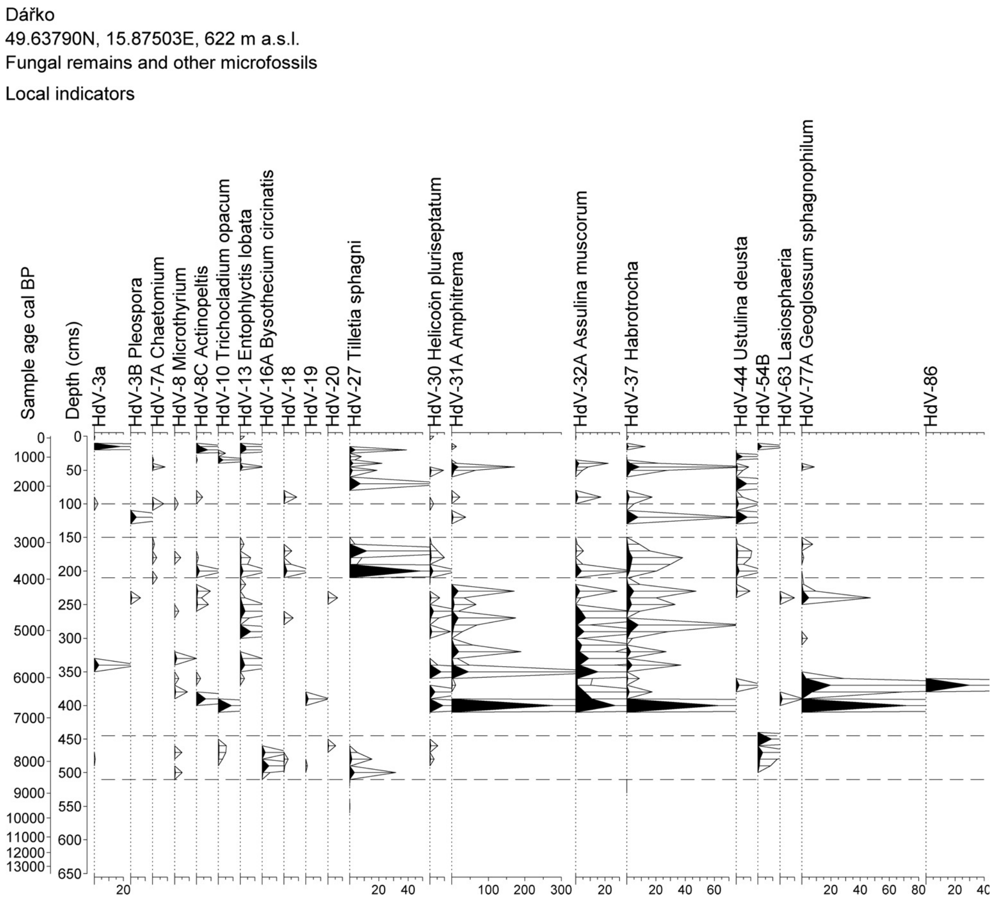
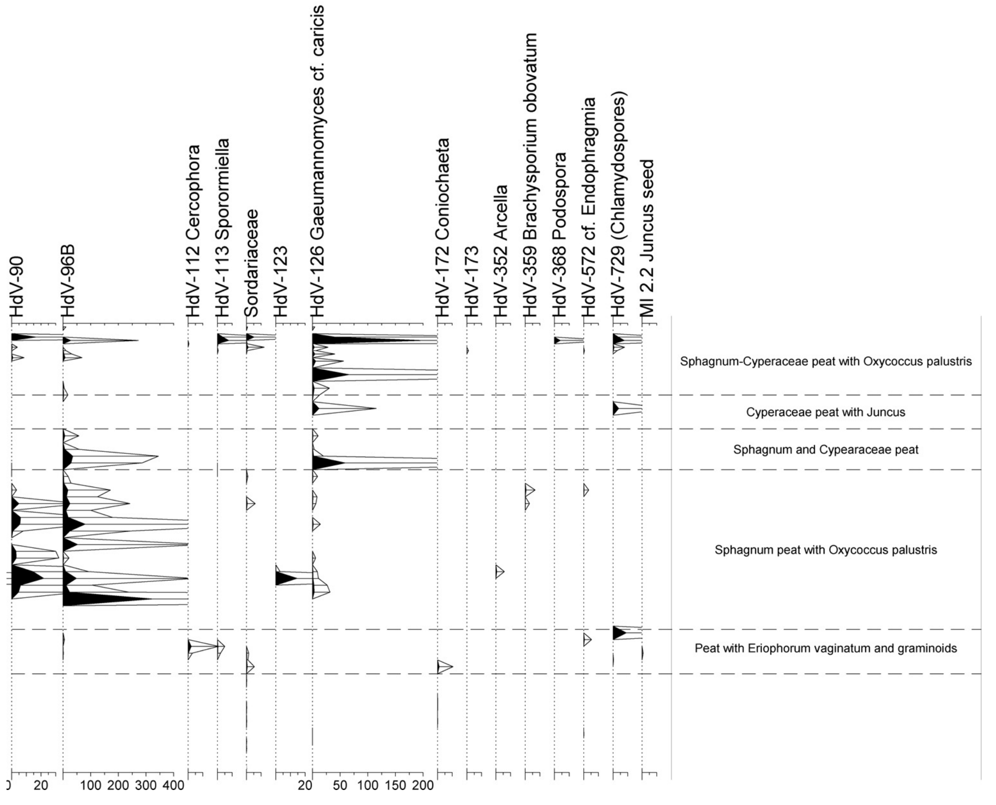


Fig. 5. – Diagram of fungal remains and other selected non-pollen microfossils.

LPAZ DAR 6 (195–22.5 cm, 3730–540 cal. BP) is characterized by a co-dominance of *Picea*, *Fagus* and *Abies* pollen and maximum abundance of *Carpinus* pollen. Since 3700 cal. BP, single pollen grains of cereals (*Secale*) and weeds (*Anthemis arvensis* type) indicate human activity in a wider area. Around 1000 cal. BP, *Calluna* pollen and charcoal markedly increased. Up to 540 cal. BP, many human indicators characteristic of the following period (see below) appeared in the pollen spectra. The AP:NAP ratio fell below 95% only in the second half of the period. Of the NPPs, ascospores of *Ustulina deusta*, which is common on the roots of deciduous trees, were regularly present. The frequent occurrence of hypopodia of *Gaeumannomyces* cf. *caricis* is linked to the presence of local *Carex* species and *Tilletia sphagni* indicates *Sphagnum* peat. At the end of this zone, a rapid increase of spores of coprophilous fungi was recorded, together with spores indicating drier local conditions.

LPAZ DAR 7 (22.5–0 cm, 540–0 cal. BP) is characterized by an abrupt increase and dominance of *Pinus sylvestris* type pollen and the appearance of *Pinus* stomata. *Fagus*, *Abies* and *Carpinus* pollen declined or almost disappeared, while *Picea* pollen remained



high. Pollen of *Vaccinium* type, *Poaceae*, many herbaceous plants (*Anthriscus sylvestris* type, *Brassicaceae*, *Cichorioideae*, *Chenopodiaceae*, *Melampyrum*, *Mentha*, *Plantago lanceolata* type, *Ranunculus acris* type, *Rumex*, *Urtica*), weeds (*Anthemis arvensis* type, *Centaurea cyanus*), crops (*Triticum* type, *Secale*, *Hordeum* type), spores of coprophilous fungi and charcoal remained high or decreased, partly due to the shading by abundant *Pinus* pollen. The AP:NAP ratio dropped to 75% before local spread of *Pinus*.

The pollen influx of arboreal taxa varied greatly and differed significantly between the bottom (up to ~500 cm; ~8350 cal. BP) and upper layers. Median of the bottom layers (around 12,000 grains cm^{-2} year^{-1}) is approximately four times greater than that in the upper layers (around 3000 grains cm^{-2} years^{-1}) (Fig. 7).

Macroremains

Based on the CONISS cluster analysis we delimited four main developmental zones in the period between 13,400 and 6000 cal. BP (Fig. 6). In the Late Glacial (Phase 1:

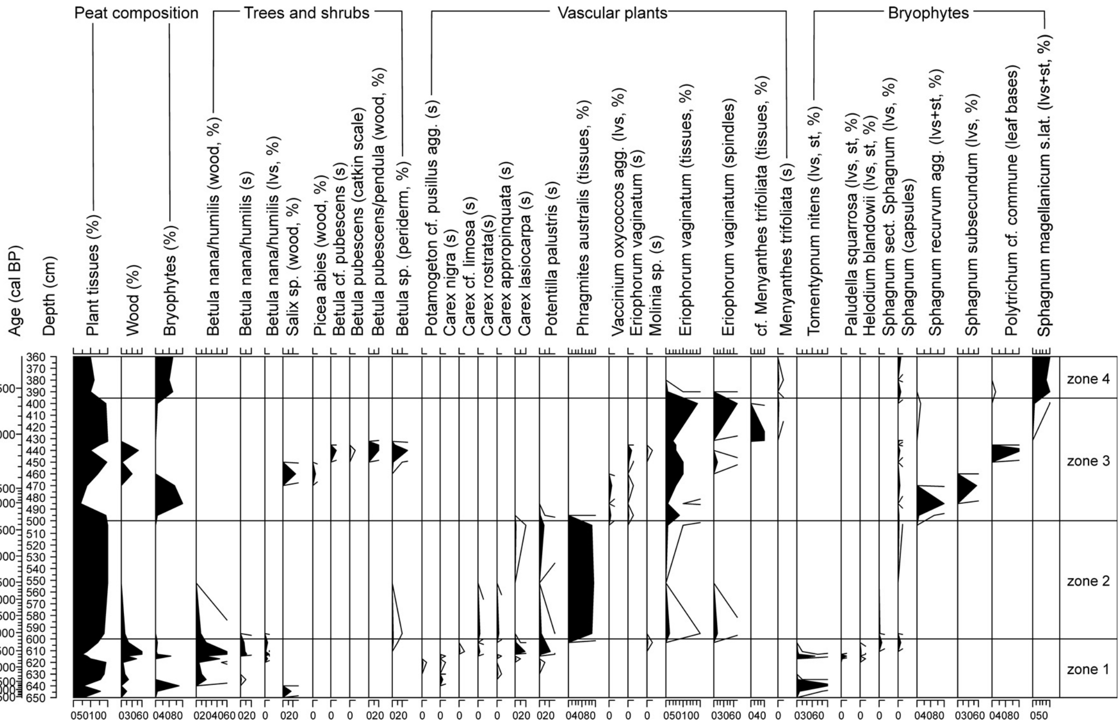


Fig. 6. – Macrofossil diagram of Dářko peat bog sediment. Values are absolute numbers per sample for countable fossils and volume percentages for bryophytes, tissues and wood fragments (then indicated as a %). Abbreviations: s (seeds of plants), lvs+st (leaves and stems of bryophytes). Exaggeration multiplier 10 was applied (line above the black curve).

650–600 cm; 13 500–11,100 cal. BP), the peat was predominately formed by undecomposed plant tissues with a high admixture of *Betula nana/humilis* wood and bryophyte stems and leaves in some layers. Of vascular plants, *Carex nigra*, *C. appropinquata, C. lasiocarpa* and *Potentilla palustris* seeds were mainly present. As for bryophytes, stems and leaves of the low hummock-forming species *Tomentypnum nitens*, *Paludella squarrosa* and *Helodium blandowii* were present. Of the vegetation types considered, the association *Menyantho-Sphagnetum teretis* (alliance *Sphagno warnstorfii-Tomentypnion nitentis*) has the highest probability of identity with this zone (72.1%). Around 11,100 cal. BP (beginning of Phase 2; 600 cm), tissues of *Phragmites australis* started to dominate in the peat (about 70 %). Seeds of some sedges and *Potentilla palustris* were still present and tissues and spindles of *Eriophorum vaginatum* newly appeared in the peat. Of the considered vegetation types, the association *Sphagno recurvi-Caricetum lasiocarpae* (alliance *Sphagno-Caricion canescentis*) has the highest probability of identity with this zone (65.0%). Around 8300 cal. BP (beginning of Phase 3; 500 cm) tissue of *Phragmites* completely disappeared from the peat, whereas that of *Eriophorum vaginatum* increased, leaves of *Vaccinium oxycoccos* agg. appeared and *Sphagnum recurvum* agg. and *S. subsecundum* started to dominate. Between 7400 and 7300 cal. BP, tissue of *Sphagnum* locally disappeared and around 7150 cal. BP, leaf bases of *Polytrichum* cf. *commune* appeared in the peat. Wood of *Salix* (25%) and *Picea* (5%) was present in a layer dated to 7350 cal. BP and wood of *Betula pubescens/pendula* in the layers dated between 7150 and 7100 cal. BP. *Eriophorum vaginatum* was present continuously between 8300 and 6700 cal. BP (Phase 3: 500–400 cm). Of the considered vegetation types, the association *Sphagno recurvi-Caricetum rostratae* (alliance *Sphagno-Caricion canescentis*) has the highest probability of identity with this zone (91.7%). After 6700 cal. BP, stems and leaves of *Sphagnum magellanicum* s.l. started to dominate in the peat, whereas the tissues of *Eriophorum vaginatum* disappeared. Due to the low number of macroremains of vascular plants analysed, this zone was not interpreted in terms of extant vegetation types using a numerical algorithm.

Discussion

Initiation of the peat bog

Continuous and rather intense accumulation of peat throughout the profile, exceptional in the region of the Bohemian-Moravian Highlands (cf. e.g. Szabó et al. 2017), allowed us to construct a precise depth-age model. Dářko peat bog originated during the Late Glacial: radiocarbon dating of the peat bog base close to 14,000 cal. BP (13,400 cal. BP according to the depth-age model) roughly corresponds to the age reported by Břízová (2009). The limnic sediment at the base of the peat bog was not analysed in detail, as it contained few fossils. However, pollen and spores of *Isoëtes lacustris*, *Myriophyllum alterniflorum*, *Potamogeton* spp. and aquatic algae (*Botryococcus*, *Scenedesmus*, *Tetraedron*, *Zygnemataceae*) in the contiguous peat layers (Fig. 7) indicate the presence of a cold oligotrophic waterbody during the onset of peat accumulation. Whether there was a lake or just a system of small pools remains uncertain. Pollen and macroremains of aquatic species were present in low numbers, so we suppose that they were transported to the sediment from adjacent waterbodies. Some finds are of biogeographical importance, as *Isoëtes* and *Myriophyllum* are now rare and endangered species in the Czech Republic (Grulich 2017). For *Isoëtes* this is the first Late Glacial and Holocene record outside its present range in this country and adjacent mountain ranges (Kuneš et al. 2009, Břízová 2011, Hájková et al. 2018).

Rich fen and Phragmites-dominated fen

Plant macroremains and pollen provide convincing evidence for the development of rich fen vegetation during the Late Glacial and Early Holocene (13,400–11,100 cal. BP). The species composition of the fossils resembles moderately calcium-rich sedge-moss fens of the phytosociological association *Menyantho trifoliatae-Sphagnetum teretis* from the alliance *Sphagno warnstorfii-Tomentypnion nitentis* (Hájek & Hájková 2011, Mucina et al. 2016, Peterka et al. 2017). This is indicated by the presence of ecological specialists such as *Carex appropinquata*, *C. lasiocarpa*, *Potentilla palustris*, *Triglochin* sp. (the latter only as pollen) and the mosses *Tomentypnum nitens*, *Helodium blandowii* and *Paludella squarrosa*. For *Helodium* this is the fourth fossil record from the Czech Republic (Hájková et al. 2018). We assume that the present rare occurrence of the fen specialists *Carex chordorrhiza* and *C. lasiocarpa* in the lagg of the peat bog may be a relict of this

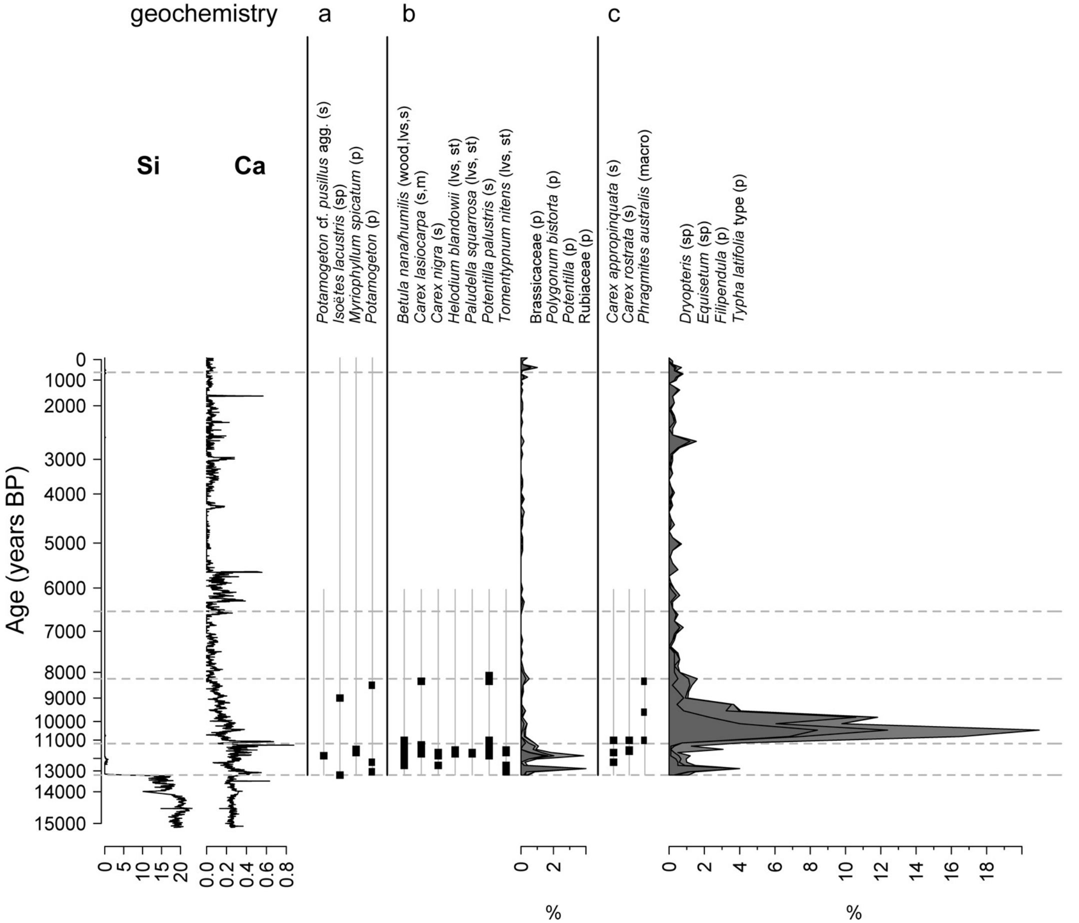
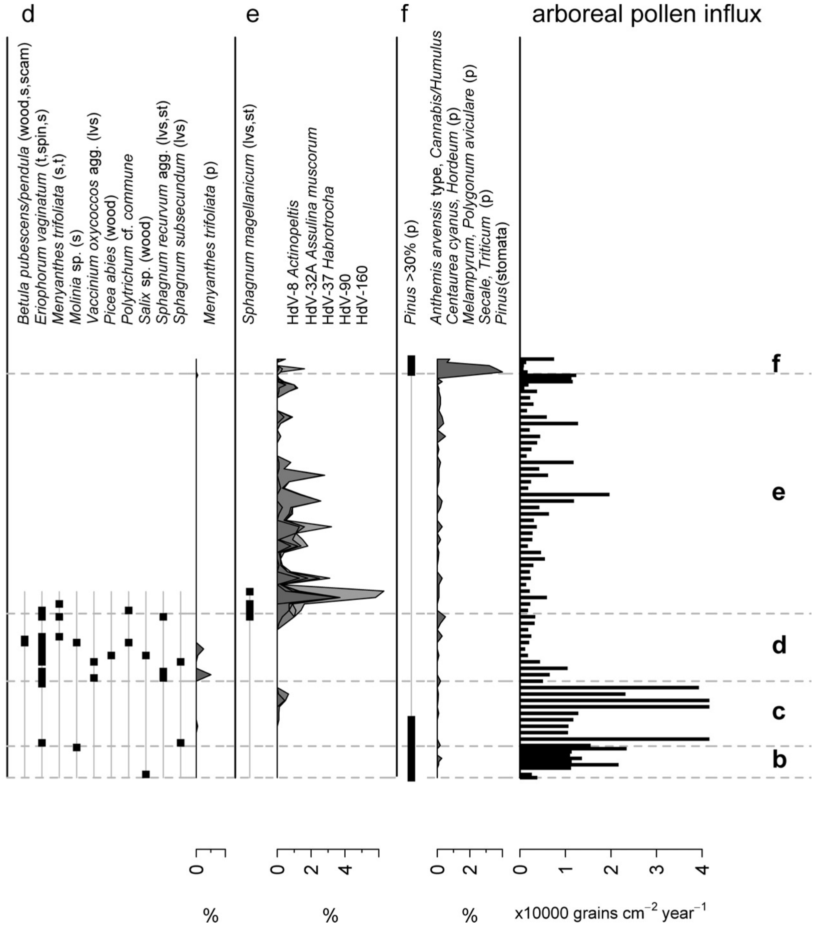


Fig. 7. – Summarizing stratigraphic plot of selected proxies, indicating major phases in the development of the Dářko peat bog: a – aquatic taxa, b – rich fen phase/taxa, c – *Phragmites*-dominated poor fen phase/taxa, d – *Eriophorum vaginatum*-dominated poor fen phase/taxa, e – open bog phase/taxa, and f – pine bog woodland phase/taxa and indicators of human activity. The type of fossil is abbreviated in parentheses: fr – fruits, lvs – leaves, npp – non-pollen palynomorphs, p – pollen, s – seeds, sp – plant spores, spin – spindles, st – bryophyte stems, t – other tissues. Presences (black squares) or pollen percentages (grey polygons) are shown.

developmental phase. The local vegetation is even classified in the above-mentioned association *Menyantho-Sphagnetum* (Peterka 2013, Lysák 2018). Another characteristic taxon, *Betula nana/humilis*, was rather abundant in the profile around the Late Glacial – Holocene transition. Salaschek (1935) identified similar remnants of leaves and fruit as *Betula nana*. This species, nowadays rare and considered to be a relict in central Europe (Lang 1994, Dítě et al. 2018), is currently absent from the entire Bohemian-Moravian Highlands (Kaplan et al. 2019).

The rich fen developed into poor fen dominated by *Phragmites australis* around 11,100 cal. BP. This phase lasted up to around 8300 cal. BP. Some rich fen species (e.g. *Carex lasiocarpa*) were still present, but *Sphagnum* and the acidophyte *Eriophorum*



vaginatum appeared and the species composition started to resemble poor fens of the *Sphagno-Caricion canescentis* alliance, particularly the association *Sphagno recurvi-Caricetum lasiocarpae* (Hájek & Hájková 2011). This association was recently also reported from the Dářko peat bog lagg (Lysák 2018).

Besides the characteristic species composition, the relatively high base content of the fen environment is indicated by maximum levels of Ca in the geochemical record of the initial rich-fen zone. The source of Ca in the predominantly acidic landscape was most likely the local bedrock formed by Cretaceous sediments, which contain calcium carbonate. Throughout the *Phragmites*-dominated phase, the amount of Ca gradually decreased. This was probably connected with the isolation of the fen surface from the mineral-rich groundwater by an increasingly thick layer of peat (Hughes & Barber 2004).

Fen-bog transition

Transition from a base-rich fen supplied with groundwater to a base-poor bog dependent on precipitation is a major event in the development of a peat bog and has profound consequences for biodiversity (Rybníček 1984, Zobel 1988, Granath et al. 2010). It seems that in the case of Dářko peat bog it was a gradual process, which varied in its timing and duration in different parts of the basin (cf. Rudolph 1927, Salaschek 1935, Puchmajerová 1944). It appears that at the bottom of the basin from which we obtained the profile (Fig. 1), the supply of groundwater was restricted and the transition to ombrotrophy began relatively early. A *Phragmites*-dominated poor fen disappeared here around 8300 cal. BP, near the Early-Middle Holocene boundary (Walker et al. 2019). It was replaced by a poor fen dominated by *Eriophorum vaginatum*, *Sphagnum recurvum* agg. and *S. subsecundum*. *Eriophorum vaginatum* increased in abundance, *Vaccinium oxycoccos* agg. newly appeared and *Menyanthes trifoliata* was recorded repeatedly. The vegetation might have been similar to the association *Sphagno recurvi-Caricetum rostratae* from the alliance *Sphagno-Caricion canescentis* (Hájek & Hájková 2011). Also this association was recently reported occurring at Dářko peat bog (Peterka 2015). Change in the sedimentary environment was accompanied by a marked decline in the influx of arboreal pollen, concurrent with the retreat of the high pollen producers *Pinus*, *Betula* and *Corylus*. Around 6800 cal. BP, poor fen species disappeared and an ombrotrophic bog developed. This is clearly indicated by the dominance of *Sphagnum* (mainly *S. magellanicum* s.l.), the appearance of pollen of *Vacciniaceae* and abundant presence of NPPs belonging to different taxonomic groups, including testate amoebae (*Amphitrema* sp., *Assulina muscorum*), rotifers (*Habrotrocha* sp.) and fungi (*Geoglossum* sp.). Such a species assemblage comes close to the alliance *Sphagnion magellanici*, which is still present in the open parts of the pine bog forest (Peterka 2013).

Ca and Fe levels in the peat decreased close to minimum during the fen-bog transition, which is in accordance with the switch to ombrotrophy. While Fe values have remained low up to the present, Ca levels have periodically increased. One such marked increase occurred concurrently with the establishment of the bog (around 6900 cal. BP). We assume that this may be connected with the recorded spread of *Vacciniaceae*, as these low growing shrubs are adapted to a low Ca availability and might have enriched the environment through their efficient uptake of Ca (Ingestad 1973) from deeper layers of peat.

Interestingly, a similar pattern of fen-bog transition, including a *Phragmites*-dominated phase, is reported from the Eastern Sudetes Mts by Dudová et al. (2014). They also report similar changes in geochemistry, with Ca and Fe showing similar patterns. However, the timing of the phases differs somewhat, which supports our assumption that the process was driven (or at least substantially modified) by local conditions, particularly the supply of groundwater.

Origin of pine bog woodland

Bog pine (*Pinus uncinata* subsp. *uliginosa*) is the most characteristic tree of central-European peat bogs (Businský 2009, Heuertz et al. 2010). Its disjunct distribution indicates an ancient, relict origin of its present occurrence. Indeed, we recorded a high amount of *Pinus* pollen and few stomata in the Late-Glacial deposits of Dářko peat bog. Unfortunately, these may also belong to Scots pine (*Pinus sylvestris*), the more common species of pine in the area studied. During the early Holocene, pines retreated and were uncommon until the youngest phase of the Late Holocene. A comeback of pines took place around AD 1500, when the *Pinus* pollen curve rose steeply. *Pinus* stomata appeared soon after, suggesting that pine bog woodland vegetation was formed at that time. Expansion of pine was preceded by a period of increase in the pollen of *Calluna* (from around AD 900 AD) and microcharcoal (from around AD 1000), indicating drier conditions and/or increased human impact.

Late expansion of bog pine was also reported from other peat bogs in central Europe (e.g. Hahne 1992, Mitchell et al. 2001, Svobodová et al. 2002, Dudová et al. 2010). Usually it is attributed to desiccation of the surface of the peat bog. Mitchell et al. (2001) even report a dry initial phase with high abundance of *Calluna* in the Swiss Jura Mts, which resembles that recorded at Dářko peat bog. In addition to broad-scale natural drivers, such as the Medieval climate optimum (around AD 950–1100; Mann et al. 2009), local drivers might have contributed to this environmental change. Velké Dářko fishpond, adjacent to Dářko peat bog, was constructed shortly before pine expansion (between AD 1480 and 1493; David 2001) and so the drainage of the peat bog might partially have been connected with this activity. Already Salaschek (1935) notes the late expansion of bog pine at Dářko peat bog and discusses its possible link to artificial drainage. Nevertheless, he favours natural succession of the peat bog as the reason. In addition, we suggest that mesoclimatic change resulting from deforestation of the surrounding landscape during the Late Medieval colonization might have been a part of this process. Besides drier soil conditions, increased nutrient availability, resulting either from peat mineralization or burning, might have supported the recorded changes in vegetation (Kučerová et al. 2008, Navrátilová 2013).

Because the nearest sites for *Pinus uncinata* subsp. *uliginosa* are more than 80 km from Dářko peat bog, we assume that this species survived in low abundance at this site (most probably in the lagg) during the entire Holocene and that its late expansion is just a result of its quantitative spread. This assumption agrees with the conclusion of Rudolph (1927), who considers this species to be native and even reports finding seeds of bog pine in the basal peat layers. However, the seeds do not differ much from those of the common *Pinus sylvestris* (Bojňanský & Fargašová 2007), so this identification may require revision.

Landscape cover

During the Late Glacial and beginning of the Early Holocene, the landscape surrounding Dářko peat bog was probably covered by semi-open vegetation. Open-canopy forests with a species-rich herbaceous layer or a mosaic of forests and grasslands prevailed. Forest canopies were dominated by *Pinus sylvestris*, *P. cembra* and *Betula*. Using the modern analogue approach, they might be compared with current hemiboreal (subtaiga) or taiga forests, or perhaps a mixture of both, depending on site conditions and altitude (Chytrý et al. 2008, Kuneš et al. 2008, Janská et al. 2017). Heliophilous shrubs, including *Salix*, *Juniperus*, *Betula nana*/*humilis* and *Hippophaë rhamnoides*, were also present. Grasslands and understories of open-canopy forests were rich in steppe, tundra and mesic- and wet-grassland graminoids, herbaceous plants and low shrubs, e.g. *Adenostyles*, *Artemisia*, *Bistorta officinalis*, *Botrychium*, *Chenopodiaceae*, *Dryas octopetala*, *Ephedra*, *Filipendula*, *Helianthemum*, *Sagina*, *Thalictrum* and *Trollius*.

The detailed radiocarbon dating enabled us to confirm the persistence of some glacial elements (e.g. *Pinus cembra*) well into the Holocene. The subsequent changes in the composition of the dominant forest trees resulted in an important switch from competitively poor, cold-tolerant, heliophilous conifers and small-leaved deciduous species to relatively competitive, thermophilous and shade-tolerant broadleaved trees (*Corylus* and species of mixed oak forests). Their initial spread started around 11,100 cal. BP, when *Ulmus* and *Corylus* increased, followed by *Quercus* and *Tilia*. Around 9200 cal. BP, the pollen of *Corylus* became the most abundant in the pollen assemblage, replacing *Pinus*, which finished its rapid decline soon afterwards and only came back in recent times as *Pinus uncinata*). In wet places, *Alnus* and *Picea* spread during the second half of the Early Holocene. Abundance of *Picea* at mesic sites remains uncertain due to taphonomic complexities (Hájková et al. 2019), particularly the ability of the species to grow on peat bogs, as confirmed for our site by the find of stomata and wood of *Picea* in the peat. Similar interpretive difficulties pertain to *Betula*.

The humid climate of the Middle Holocene supported further spread of *Picea* and species of mixed oak forests. Regular presence of *Hedera* and *Viscum* confirms the relatively mild character of the climate (Iversen 1944). The landscape was probably densely forested, as indicated by the AP:NAP ratio, which increased to 99% around 5100 cal. BP. The more or less constant abundance of *Quercus*, however, indicates that habitat heterogeneity or disturbance have favoured the survival of some heliophilous and semi-shade species. In some periods, indicators of grazing and fires were recorded.

Picea remained dominant in the pollen spectrum even after the progressive spread of *Fagus*, *Carpinus* and *Abies* during the second half of the Middle Holocene. The simultaneous decline of *Corylus* and other broadleaved trees (except *Quercus*) indicates that these species might previously have occupied corresponding niches on mesic soils. Over much of the Late Holocene, the species composition of the dominant trees remained unchanged and corresponds quite well with the potential natural vegetation of the region (Neuhäuslová & Moravec 1997) – *Fagus*, *Abies-Fagus* and *Picea-Fagus*-dominated forests at high altitudes, *Picea*-dominated forests in waterlogged places, and *Quercus*, *Abies-Quercus* and *Quercus-Carpinus*-dominated forests at low altitudes. It is unclear to what extent this pattern was influenced by natural or human-driven disturbances. Some options are discussed below.

Early spread of broadleaved trees

As described above, the spread of temperate broadleaved trees in the area studied (after 11,100 cal. BP) was only slightly delayed after the Early Holocene climatic amelioration. We suggest this indicates there was no climatic limitations for these species (such as drought in the warm and dry lowlands; Kuneš et al. 2015) and that their Late Glacial distribution ranges were not far away. The early spread of broadleaved trees is noted by Puchmajerová (1944), but we cannot support her suggestion that these species survived from the previous interglacial.

It is worth mentioning that other important temperate broadleaved trees, *Fagus* and *Carpinus*, also spread rather early (cf. Wiezik et al. 2020). A low abundance of *Fagus* pollen was continuously present already at the end of the Early Holocene. The substantial increase in the abundance of its pollen that occurred much later (around 5800 cal. BP), appears to support the hypothesis of Giesecke & Brewer (2018), who claim that the postglacial spread and quantitative expansion of these species were two distinct processes (see Birks 2019 for a review of this topic). Quantitative expansion of the late disperser *Carpinus* (Kuneš & Abraham 2017) occurred soon after 5000 cal. BP at the site studied, i.e. even slightly earlier than that of *Abies*.

Human impact

Up to the end of the first millennium AD, macroclimate and autogenic succession appear to have been the main drivers of the development of both local and regional vegetation. Medieval colonization of the central part of the Bohemian-Moravian Highlands changed this picture. Between AD 900–1000, peaks of *Calluna* pollen and microcharcoal indicate burning, which might have been connected to the clearing of forest by man. Coprophilous fungi also appeared, suggesting grazing by domestic animals. Hypothetically, these phenomena might have been connected to the existence of an Early Medieval trail connecting Bohemia and Moravia, which was later called the Libická stezka trail (Květ 2003). Its routing and even existence before the High Middle Ages are, however, uncertain (Slavík 2010, Jílková 2012). Moreover, as mentioned above, the increase in *Calluna* and charcoal may also have been caused by drier conditions, perhaps resulting from the onset of the Medieval climate optimum around AD 950 (Mann et al. 2009).

A conspicuous drop in the abundance of arboreal pollen occurred between AD 1150 and 1350, accompanied by an increase in diverse indicators of human activities, including cereals, weeds, ruderals and grassland species. The timing corresponds well with the historical data on the foundation of important nearby settlements: Žďár nad Sázavou (AD 1252; Geisler & Malý 2006) and Krucemburk (around AD 1250; Doležel 2004). In the same period there is an increase in Pb in the geochemical records, apparently originating from the atmospheric deposition of emissions from Ag metallurgy (Holub & Malý 2012, Holub 2015). Unfortunately, without further study we cannot determine whether the emissions originated from sources in the Havlíčkův Brod ore district or from sources in the Kutná Hora ore district, which were more distant, but by an order of magnitude richer (Holub 2015). The deposition seems to have peaked around AD 1350 and ceased close to AD 1650; however, dating uncertainty is relatively high due to the rather coarse resolution of the analysis and fluctuations in the calibration curve (Reimer et al. 2013).

Recent findings concerning pre-Medieval human activities at higher altitudes in the Bohemian-Moravian Highlands (Hejhal 2009) indicate that searching for their possible traces in our record makes sense. Although there is no convincing signal of human indicators before the Early Middle Ages, we would like to point out several phenomena. First, there is conspicuous covariation of microscopic charcoal and spores of the pyrophytic fern *Pteridium aquilinum* during most of the Middle Holocene, indicating a considerable incidence of fires in the area studied. It peaked around 6750 cal. BP. Although the fires might have had natural causes, we cannot exclude human interventions. Around 4650 cal. BP, a short fluctuation occurred, during which *Betula* and *Poaceae* markedly increased, together with slight increases in some other heliophilous taxa such as *Rumex acetosa* type, *Salix* and *Thalictrum*. Also a few spores of coprophilous fungi appeared after a long absence. Interestingly, in the same period, a major change in the forests of the surrounding landscape occured, with *Carpinus* and *Abies* increasing and *Tilia* and *Corylus* decreasing. It is possible that humans played a role in this change, as suggested earlier for other places in central Europe (Küster 1997, Kozáková et al. 2011). The first single pollen grains of cereals (*Secale*) and presumed weeds (*Anthemis arvensis* type) were detected around 3500 cal. BP. We cannot rule out their origin in low-intensity Bronze Age agriculture or in the wider surroundings. Archaeological evidence of human presence during this period mainly originates from the Havlíčkův Brod region (Hejhal 2009).

Between AD 200 and 600 (Roman and Migration periods), a slight increase in heliophilous trees and shrubs (*Betula*, *Corylus*) and several human indicators, including *Calluna*, *Chenopodiaceae*, *Plantago lanceolata* and *Urtica*, was recorded. These ruderal and open-landscape taxa indicate rather low-intensity human use of the area, i.e. lacking large-scale deforestation or permanent agriculture. It might also be related to the existence of an ancient long-distance communication, as repeatedly suggested based on some archaeological finds (particularly Byzantine coins; Drápelová 2007, Militký 2010). However, the available evidence is still sparse.

Implications for conservation

Our study complements and in several respects clarifies the picture of Dářko peat bog development provided by previous studies. We see several points relevant for nature conservation. First, the present main conservation target, i.e. pine bog woodland dominated by *Pinus uncinata* subsp. *uliginosa*, is of recent origin. In spite of its high conservation value, it may be even viewed as the result of peat bog degradation (although other explanations are also possible). We show that the peat bog was more open during most of the Holocene, thus providing more habitats for heliophilous species. Development towards a more wooded state in the last 100 years is also reported by vegetation scientists (see summary in Peterka 2013) and is visible on aerial photographs dating from 1949 or later (http://www.geoservice.army.cz/historicke-lms). In this respect, loss of bog specialists such as the sedge *Carex pauciflora* and the butterflies *Coenonympha tullia* and *Colias palaeno* over the last decades (Beneš et al. 2002, Peterka 2013, http://www.lepidoptera.cz) challenges the present non-intervention management of the pine bog woodland. Partial drainage of the peatbog and surrounding forests in the 19th and 20th centuries (www.cittadella.cz/europarc) most likely contributed to this development (Lysák 2018). We see the need for a thorough restoration of the water regime and active support of open habitats in the woodland. The currently practiced mowing of fragments of fens and intermittently wet meadows in the peat bog lagg (Peterka 2015) is therefore commendable and should be extended. In historical terms, the most valuable species of plants occurring here (e.g. *Carex chordorrhiza* and *C. lasiocarpa*) may be viewed as remarkable relicts of the Late Glacial and Early Holocene developmental phases of the peat bog. We admit, however, that conservation planning has to involve also other criteria, such as species and habitat rarity, level of threat and role in the ecosystem (Regan et al. 2007, Moilanen et al. 2011), which may either support or contradict the historical perspective.

We would also like to highlight the fossil finds of rare habitat specialist species, such as the fen moss *Helodium blandowii*, aquatic species of boreal lakes *Isoëtes lacustris* and *Myriophyllum alterniflorum* and characteristic glacial elements such as *Pinus cembra*, *Betula nana*/*humilis*, *Hippophaë rhamnoides*, *Adenostyles*, *Dryas octopetala* and *Ephedra*. These finds are not only relevant to the knowledge of the species, but also enrich the story of the past of the site studied and the surrounding landscape. The social significance of such stories may be used to communicate the nature conservation goals to the public (Hockings et al. 1998).

Acknowledgements

The Nature Conservation Agency of the Czech Republic is acknowledged for granting permission to core the sediment, Luděk Čech for support and literature, Ondřej Hájek for drawing the map, J. W. Jongepier and Tony Dixon for linguistic check, Dušan Lekeš for field assistance, Filip Lysák and Tomáš Peterka for consultations, and Jolana Hrubá and Marian Takáč for help with the XRF measurements. This study was financed by the Czech Science Foundation (grant no. 16-10100S). JR, HSS, EJ, LD and PH were further supported by the long-term developmental project of the Czech Academy of Sciences (RVO 67985939). Support for GK came from the CSF 20-08294S and RVO 67985831.

Souhrn

Studovali jsme dobře datovaný nepřetržitý záznam pylu, nepylových palynomorf, rostlinných makrozbytků a chemických prvků v nejlépe dochovaném rašeliništi na Českomoravské vrchovině. Rašeliniště Dářko je významná botanická lokalita, známá například izolovaným výskytem vrchovištního blatkového boru. Je chráněna jako národní přírodní rezervace a je součástí evropsky významné lokality Dářská rašeliniště. V předkládané studii popisujeme hlavní rysy a zajímavé zvláštnosti vývoje lokality od pozdní doby ledové po současnost a zasazujeme do historických souvislostí některé přírodní jevy cenné z hlediska ochrany přírody. Až do vrcholného středověku se jako hlavní hybná síla vývoje místní i regionální vegetace jeví makroklima a autogenní sukcese. Vegetace pozdní doby ledové s dominancí borovice a zastoupením chladnomilných druhů se zde zachovala až do prvních tisíciletí holocénu. První fosilní nález šídlatky jezerní z období pozdního glaciálu a holocénu mimo její současný areál v pohraničních pohořích ukazuje na existenci chladné oligotrofní vodní plochy na lokalitě. Líska, smrk a druhy smíšených doubrav se začaly šířit brzy, přibližně před 10500 lety. Indikátory teplého oceanického klimatu (břečťan, jmelí) se objevily asi před 7700 let. Zastoupení pylu dřevin se postupně zvyšovalo až k holocennímu maximu blížícímu se 99 %. Minerotrofní slatinný mokřad se změnil v ombrotrofní vrchoviště asi před 6800 lety. Smrk, buk a jedle začaly v pylovém záznamu převažovat asi před 5500 lety. Náhlá změna vegetačního pokryvu začala mezi lety 1100 a 1350 n.l., současně s vrcholně středověkou kolonizací oblasti. Výrazný nárůst obsahu olova v geochemickém záznamu mezi lety 1200 a 1650 n.l. je spojen s hutněním stříbra v širším okolí. Blatkový bor se začal šířit až kolem roku 1500 n.l. Tento pozdní původ, pozorovaný i na dalších lokalitách ve střední Evropě, může souviset s lidským vlivem na lokalitu a okolní krajinu, což zpochybňuje dnes praktikovaný bezzásahový režim ochrany tohoto biotopu. Výskyt slatiništních specialistů (např. *Carex lasiocarpa*, *C. chordorrhiza*) v laggu vrchoviště lze v souladu s našimi výsledky chápat jako cenný relikt pozdně glaciální a raně holocenní mokřadní vegetace, jehož zachování vyžaduje pokračování aktivního ochranářského managementu. Naše studie ukazuje, jak mohou paleoekologické poznatky přispět k pochopení současného druhového složení vegetace cenného chráněného území. Tyto poznatky mohou být využity ke stanovení priorit ochrany území a k vysvětlování cílů ochrany přírody široké veřejnosti.

References

Barber K. E. (1993) Peatlands as scientific archives of past biodiversity. – Biodiversity and Conservation 2: 474–489.

Bastl M., Burian M., Kučera J., Prach K., Rektoris L. & Štech M. (2008) Central European pine bogs change along an altitudinal gradient. – Preslia 80: 349–363.

Beneš J., Konvička M., Dvořák J., Fric Z., Havelda Z., Pavlíčko A., Vrabec V. & Weidenhoffer Z. (eds) (2002) Motýli České republiky: rozšíření a ochrana I, II [Butterflies of the Czech Republic: distribution and conservation I, II]. – Společnost pro ochranu motýlů, Praha.

Bennett K. D. (1993) PSIMPOLL 2.27: program for plotting pollen diagrams and analysing data. – Department of Plant Sciences, Cambridge University, Cambridge.

Berglund B. & Ralska-Jasiewiczowa M. (1986) Pollen analysis and pollen diagrams. – In: Berglund B. E. (ed.), Handbook of Holocene palaeoecology and palaeohydrology, p. 455–485, John Wiley & Sons, Chichester.

Beug H.-J. (2004) Leitfaden der Pollenbestimmung für Mitteleuropa und angrenzende Gebiete. – Verlag Dr. Friedrich Pfeil, München.

Birks H. J. B. (2019) Contributions of Quaternary botany to modern ecology and biogeography. – Plant Ecology and Diversity 12: 189–385.

Blaauw M. & Christen J. A. (2011) Flexible paleoclimate age-depth models using an autoregressive gamma process. – Bayesian Analysis 6: 457–474.

Bojňanský V. & Fargašová A. (2007) Atlas of seeds and fruits of Central and East-European Flora. The Carpathian Mountains region. – Springer, Dordrecht.

Břízová E. (2009) Dynamika vývoje lesní vegetace na Českomoravské vrchovině z pohledu palynologie [Dynamics of forest vegetation in the Bohemian-Moravian Uplands from a palynological point of view]. – Zprávy České botanické společnosti 44, Materiály 24: 45–58.

Břízová E. (2011) Quillwort (*Isoëtes*), a mysterious plant from the Czech Republic. – Acta Musei Nationalis Pragae, series B – Historia Naturalis, 67: 25–34.

Břízová E. (2014) Nové poznatky o výskytu organických sedimentů stáří pozdního glaciálu a holocénu v České republice [New data on the organic sediments of the Late Glacial-Holocene age in the Czech Republic]. – Zprávy o geologických výzkumech 2014: 47–54.

Businský R. (2009) Borovice blatka v novém pojetí [A new concept in bog pine]. – Zprávy České botanické společnosti 44: 35–43.

Cappers R. T. J., Bekker R. M. & Jans J. E. A. (2006) Digitale Zadenatlas van Nederland / Digital seed atlas of the Netherlands. – Barkhuis Publishing, Groningen.

Chapman S., Buttler A., Francez A. J., Laggoun-Défarge F., Vasander H., Schloter M., Combe J., Grosvernier P., Harms H., Epron D., Gilbert D. & Mitchell E. (2003) Exploitation of northern peatlands and biodiversity maintenance: a conflict between economy and ecology. – Frontiers in Ecology and the Environment 1: 525–532.

Chytrý M. (ed.) (2007–2013) Vegetace České republiky 1–4 [Vegetation of the Czech Republic 1–4]. – Academia, Praha.

Chytrý M., Danihelka J., Kubešová S., Lustyk P., Ermakov N., Hájek M., Hájková P., Kočí M., Otýpková Z., Roleček J., Řezníčková M., Šmarda P., Valachovič M., Popov D. & Pišút P. (2008) Diversity of forest vegetation across a strong gradient of climatic continentality: Western Sayan Mountains, southern Siberia. – Plant Ecology 196: 61–83.

Cugny C., Mazier F. & Galop D. (2010) Modern and fossil non-pollen palynomorphs from the Basque mountains (western Pyrenees, France): the use of coprophilous fungi to reconstruct pastoral activity. – Vegetation History and Archaeobotany 19: 391–408.

Danihelka J., Chrtek J. & Kaplan Z. (2012) Checklist of vascular plants of the Czech Republic. – Preslia 84: 647–811.

David J. (2001) „miesto pusté a diel lesem zarostlé" (k zaniklým osadám Darov a Osralov někdejšího Čáslavského kraje) [“a deserted and partly overgrown place” (on abandoned settlements of Darov and Osralov of the former Čáslav region)]. – Sborník Havlíčkobrodské společnosti pro povznesení regionálně historického povědomí 1: 21–23.

Davies A. L. & Bunting M. J. (2010) Applications of palaeoecology in conservation. – The Open Ecology Journal 3: 54–67.

Demek J. & Mackovčin P. (eds) (2006) Hory a nížiny. Zeměpisný lexikon ČR [Mountains and lowlands. Geographical lexicon of the Czech Republic]. – AOPK ČR, Brno.

Dítě D., Hájek M., Svitková I., Košuthová A., Šoltés R. & Kliment J. (2018) Glacial-relict symptoms in the Western Carpathian flora. – Folia Geobotanica 53: 277–300.

Doležel J. (2004) Cruciburgensis monetae magister: několik poznámek k problému jeho identifikace [Cruciburgensis monetae magister: several comments on the problem of his identification]. – Archeologické rozhledy 56: 401–416.

Domin K. (1923) Problémy a metody rostlinné sociologie a jejich použití pro výzkum lučních a pastvinných porostů republiky Československé [Problems and methods of plant sociology and their application in the research on meadows and pastures of the Czechoslovak Republic]. – Ministerstvo zemědělství republiky Československé, Praha.

Drápelová P. (2007) Mincovnictví v Justiniánově době [The coinage in the age of Justinian]. – Bc. thesis, Charles University, Prague.

Dudová L., Hájek M. & Hájková P. (2010) The origin and vegetation development of the Rejvíz pine bog and the history of the surrounding landscape during the Holocene. – Preslia 82: 223–246.

Dudová L., Hájková P., Opravilová V. & Hájek M. (2014) Holocene history and environmental reconstruction of a Hercynian mire and surrounding mountain landscape based on multiple proxies. – Quaternary Research 82: 107–120.
Faegri K. & Iversen J. (1989) Textbook of pollen analysis. – John Wiley & Sons, Chichester.
Geisler M. & Malý K. (2006) Výsledek výzkumné sezóny 2004 a doklady železářské produkce ze středověkého městečka ve Žďáru nad Sázavou [Results of research season 2004 and evidence of medieval iron production in the town of Žďár nad Sázavou]. – Archeologia Technica 17: 107–110.
Giesecke T. & Brewer S. (2018) Notes on the postglacial spread of abundant European tree taxa. – Vegetation History and Archaeobotany 27: 337–349.
Granath G., Strengbom J. & Rydin H. (2010) Rapid ecosystem shifts in peatlands: linking plant physiology and succession. – Ecology 91: 3047–3056.
Grimm E. C. (2011) Tilia version 1.5.12. – Illinois State Museum, Springfield.
Grulich V. (2017) Červený seznam cévnatých rostlin ČR [The Red List of vascular plants of the Czech Republic]. – Příroda, Praha, 35: 75–132.
Hahne J. (1992) Untersuchungen zur spät-und postglazialen Vegetationsgeschichte im nordöstlichen Bayern (Bayerisches Vogtland, Fichtelgebirge, Steinwald). – Flora 187: 169– 200.
Hájek M. & Hájková P. (2011) Vegetation of fens, transitional mires and bog hollows. – In: Chytrý M. (ed.), Vegetation of the Czech Republic 4. Forest and scrub vegetation, p. 614–704, Academia, Praha.
Hájková P., Jamrichová E., Wiezik M., Peterka T., Petr L., Singh P., Máliš F., Fajmonová Z. & Hájek M. (2019) Spruce representation in zonal woodlands may be overestimated when using pollen spectra from peatlands. – Review of Palaeobotany and Palynology 271: 104104.
Hájková P., Štechová T., Šoltés R., Šmerdová E., Plesková Z., Dítě D., Bradáčová J., Mútňanová M., Singh P. & Hájek M. (2018) Using a new database of plant macrofossils of the Czech and Slovak Republics to compare past and present distribution of hypothetically relict fen mosses. – Preslia 90: 367–386.
Hedenäs L. (2003) The European species of the *Calliergon-Scorpidium-Drepanocladus* complex, including some related or similar species. – Meylania 28: 1–117.
Hejhal P. (2009) Pravěké a raně středověké osídlení české části Českomoravské vrchoviny [Prehistoric and early medieval settlement in the Bohemian part of the Bohemian-Moravian Highlands]. – PhD. thesis, Masaryk University, Brno.
Heuertz M., Teufel J., González-Martínez S. C., Soto A., Fady B., Alía R. & Vendramin G. G. (2010) Geography determines genetic relationships between species of mountain pine (*Pinus mugo* complex) in western Europe. – Journal of Biogeography 37: 541–556.
Hockings M., Carter B. & Leverington F. (1998) An integrated model of public contact planning for conservation management. – Environmental Management 22: 643–654.
Holub M. (2015) Modelování historické primární produkce stříbra v hlavních rudních revírech Čech a přilehlé části Moravy [Results of the mathematic models of the historical silver production from main ore districts of the Bohemia and adjacent part of the Moravia]. – Acta Rerum Naturalium 18: 9–20.
Holub M. & Malý K. (2012) Separátní hutnění galenitových, stříbrem bohatých rud těžených na Českomoravské vrchovině [Separate smelting of galena ore rich in silver from Bohemian-Moravian Highlands]. – Acta Rerum Naturalium 12: 1–14.
Holubičková B. (1961) Studie o vegetaci blat II. (Rašeliniště u Velkého Dářka) [A study of peatland vegetation II. (Velké Dářko peatbog)]. – Sborník VSŽ, Praha, 1960: 151–180.
Hughes P. D. M. & Barber K. E. (2004) Contrasting pathways to ombrotrophy in three raised bogs from Ireland and Cumbria, England. – Holocene 14: 65–77.
Ingestad T. (1973) Mineral nutrient requirements of *Vaccinium vitis idaea* and *V. myrtillus*. – Physiologia Plantarum 29: 239–246.
Iversen J. (1944) *Viscum*, *Hedera* and *Ilex* as climate indicators. – Geologiska Föreningen i Stockholm Förhandlingar 66: 463–483.
Jamrichová E., Szabó P., Hédl R., Kuneš P., Bobek P. & Pelánková B. (2013) Continuity and change in the vegetation of a Central European oakwood. – Holocene 23: 46–56.
Janská V., Jiménez-Alfaro B., Chytrý M., Divíšek J., Anenkhonov O., Korolyuk A., Lashchinskyi N. & Culek M. (2017) Palaeodistribution modelling of European vegetation types at the Last Glacial Maximum using modern analogues from Siberia: prospects and limitations. – Quaternary Science Reviews 159: 103–115.
Jílková H. (2012) Komunikační systémy v regionu Poličky a jejich sídelní kontext [The communications systems of Polička region and their settlement context]. – Bc. thesis, Charles University, Prague.
Joosten H., Tanneberger F. & Moen A. (eds) (2017) Mires and peatlands of Europe. Status, distribution and conservation. – Schweizerbart, Stuttgart.

Kaplan Z., Danihelka J., Chrtek J., Kirschner J., Kubát K., Štech M. & Štěpánek J. (eds) (2019) Klíč ke květeně České republiky [Key to the flora of the Czech Republic]. Ed. 2. – Academia, Praha.
Kletetschka G., Vondrák D., Hrubá J., Procházka V., Nábělek L., Svitavská-Svobodová H., Bobek P., Hořická Z., Kadlec J., Takáč M. & Stuchlík E. (2018) Cosmic-impact event in lake sediments from central Europe postdates the Laacher See eruption and marks onset of the Younger Dryas. – The Journal of Geology 126: 561–575.
Klika J. & Šmarda J. (1944) Rostlinně sociologický příspěvek k poznání rašelinišť a luk na Žďársku a Novoměstsku [Phytosociological contribution to the knowledge of peatlands and meadows in Žďár and Nové Město regions]. – Věstník Královské České Společnosti Nauk, ser. math.-nat. 1944/7: 1–60.
Kozáková R., Šamonil P., Kuneš P., Novák J., Kočár P. & Kočárová R. (2011) Contrasting local and regional Holocene histories of *Abies alba* in the Czech Republic in relation to human impact: evidence from forestry, pollen and anthracological data. – Holocene 21: 431– 444.
Kučerová A., Rektoris L., Štechová T. & Bastl M. (2008) Disturbances on a wooded raised bog: how windthrow, bark beetle and fire affect vegetation and soil water quality? – Folia Geobotanica 43: 49– 67.
Kuneš P. & Abraham V. (2017) History of Czech vegetation since the Late Pleistocene. – In: Chytrý M., Danihelka J., Kaplan Z. & Pyšek P. (eds), Flora and vegetation of the Czech Republic, p. 193–227, Springer, Cham.
Kuneš P., Abraham V., Kovářík O., Kopecký M. & PALYCZ contributors (2009) Czech Quaternary Palynological Database – PALYCZ: review and basic statistics of the data. – Preslia 81: 209–238.
Kuneš P., Pelánková B., Chytrý M., Jankovská V., Pokorný P. & Petr L. (2008) Interpretation of the last-glacial vegetation of eastern-central Europe using modern analogues from southern Siberia. – Journal of Biogeography 35: 2223– 2236.
Kuneš P., Svobodová-Svitavská H., Kolář J., Hajnalová M., Abraham V., Macek M., Tkáč P. & Szabó P. (2015) The origin of grasslands in the temperate forest zone of east-central Europe: long-term legacy of climate and human impact. – Quaternary Science Review 116: 15– 27.
Küster H. (1997) The role of farming in the postglacial expansion of beech and hornbeam in the oak woodlands of central Europe. – Holocene 7: 239–242.
Květ R. (2003) Duše krajiny. Staré stezky v proměnách věků [Soul of the landscape. Old trails transforming over the ages]. – Academia, Praha.
Laine J., Flatberg K. I., Harju P., Timonen T., Minkkinen K. J., Laine A., Tuittila E.-S. & Vasander H. T. (2018) *Sphagnum* mosses: the stars of European mires. – Sphagna Ky, Helsinki.
Lang G. (1994) Quartäre Vegetationsgeschichte Europas. – Fischer, Jena.
Lindsay R. (1995) Bogs: the ecology, classification and conservation of ombrotrophic mires. – Scottish Natural Heritage, Edinburgh.
Lysák F. (2018) Návrh revitalizačních opatření na území EVL Dářská rašeliniště [Proposal of revitalization measures for the territory of the SCI Dářská rašeliniště]. – Ms., AOPK ČR, Praha.
Mackovčin P. & Sedláček M. (eds) (2002) Chráněná území ČR. VII. Jihlavsko [Protected areas of the Czech Republic. VII. Jihlava region]. – AOPK ČR & EkoCentrum Brno, Praha.
Mann M. E., Zhang Z., Rutherford S., Bradley R. S., Hughes M. K., Shindell D., Caspar A., Faluvegi G. & Ni F. (2009) Global signatures and dynamical origins of the Little Ice Age and Medieval Climate Anomaly. – Science 326: 1256–1260.
Militký J. (2010) Nálezy antických mincí v Čechách a jejich historický význam [Finds of ancient coins in Bohemia and their historical importance]. – PhD. thesis, Charles University, Prague.
Mitchell E. A., van der Knaap W. O., van Leeuwen J. F., Buttler A., Warner B. G. & Gobat J. M. (2001) The palaeoecological history of the Praz-Rodet bog (Swiss Jura) based on pollen, plant macrofossils and testate amoebae (*Protozoa*). – Holocene 11: 65–80.
Moilanen A., Anderson B. J., Eigenbrod F., Heinemeyer A., Roy D. B., Gillings S., Armsworth P. R., Gaston K. J. & Thomas C. D. (2011) Balancing alternative land uses in conservation prioritization. – Ecological Applications 21: 1419–1426.
Mucina L., Bültmann H., Dierßen K., Theurillat J.-P., Raus T., Čarni A., Šumberová K., Willner W., Dengler J., Gavilán R., Chytrý M., Hájek M., Di Pietro R., Pallas J., Daniëls F., Bergmeier E., Guerra A., Ermakov N., Valachovič M., Schaminée J., Lysenko T., Didukh Y., Pignatti S., Rodwell J., Capelo J., Weber H., Dimopoulos P., Aguiar C., Hennekens S. & Tichý L. (2016) Vegetation of Europe: hierarchical floristic classification system of vascular plant, bryophyte, lichen, and algal communities. – Applied Vegetation Science 19 (Suppl. 1): 3–264.
Navrátilová J. (2013) *Vaccinio-Pinetum montanae* Oberdorfer 1934. – In: Chytrý M. (ed.), Vegetation of the Czech Republic 4. Forest and scrub vegetation, p. 426–429, Academia, Praha.

Nerlich B., Elliott R. & Larson B. (eds) (2016) Communicating biological sciences: ethical and metaphorical dimensions. – Routledge, London.
Neuhäusl R. (1972) Vegetationsverhältnisse des hydrographischen Gebietes der Moore am Teich Velké Dářko. – Folia Geobotanica et Phytotaxonomica 7: 105–165.
Neuhäusl R. (1975) Hochmoore am Teich Velké Dářko. Vegetace ČSSR, A9. – Academia, Praha.
Neuhäuslová Z. & Moravec J. (eds) (1997) Mapa potenciální přirozené vegetace České republiky [Map of potential natural vegetation of the Czech Republic]. – Kartografie, Praha.
Pals J. P., van Geel B. & Delfos A. (1980) Palaeocological studies in the Klokkeweel bog near Hoogkarspel (Prov. of Noord-Holland). – Review of Palaeobotany and Palynology 30: 371–418.
Peterka T. (2013) Vegetace rašelinišť severovýchodní části Českomoravské vrchoviny a její vztah k vlastnostem prostředí [Mire vegetation of the northeastern part of the Českomoravská vrchovina highland and its relationships to environmental characteristics]. – Ms. thesis, Masaryk University, Brno.
Peterka T. (2015) Žďár Hills. – In: Chytrý M., Danihelka J. & Michalcová D. (eds), Botanical excursions in Moravia. Field guide for the 58th IAVS Symposium, p. 19–36, Masaryk University, Brno.
Peterka T., Hájek M., Jiroušek M., Jiménez-Alfaro B., Aunina L., Bergamini A., Dítě D., Felbaba-Klushyna L., Graf U., Hájková P., Hettenbergerová E., Ivchenko T. G., Jansen F., Koroleva N. E., Lapshina E. D., Lazarević P. M., Moen A., Napreenko M. G., Pawlikowski P., Plesková Z., Sekulová L., Smagin V. A., Tahvanainen T., Thiele A., Biţa-Nicolae C., Biurrun I., Brisse H., Ćušterevska R., De Bie E., Ewald J., FitzPatrick Ú., Font X., Jandt U., Kącki Z., Kuzemko A., Landucci F., Moeslund J. E., Pérez-Haase A., Rašomavičius V., Rodwell J. S., Schaminée J. H. J., Šilc U., Stančić Z. & Chytrý M. (2017) Formalized classification of European fen vegetation at the alliance level. – Applied Vegetation Science 20: 124–142.
Puchmajerová M. (1943) Rašeliniště v oblasti Žďárských vrchů na Českomoravské vysočině [Peatbogs in the region of Žďárské vrchy Mts in the Bohemian-Moravian Highlands]. – Zemědělský archiv, Praha, 34/6: 3–20.
Puchmajerová M. (1944) Rašeliniště u Velkého Dářska podle rozborů rašeliny [Velké Dářko peatbog according to peat analysis]. – Sborník České akademie technické 18: 451–483.
Punt W. (ed.) (1976–2003) The Northwest European pollen flora I–VIII. – Elsevier, Amsterdam.
Punt W. & Hoen P. P. (2009) The Northwest European pollen flora, 70: *Asteraceae–Asteroideae*. – Review of Palaeobotany and Palynology 157: 22–183.
Regan H. M., Davis F. W., Andelman S. J., Widyanata A. & Freese M. (2007) Comprehensive criteria for biodiversity evaluation in conservation planning. – Biodiversity and Conservation 16: 2715–2728.
Reille M. (1992–1998) Pollen et spores d'Europe et d'Afrique du Nord. – Laboratoire de botanique historique et palynologie, Marseille.
Reimer P. J., Bard E., Bayliss A., Beck J. W., Blackwell P. G., Bronk Ramsey C., Buck C. E. E., Cheng H., Edwards R. L., Friedrich M., Grootes P. M., Guilderson T. P., Haflidason H., Hajdas I., Hatté C., Heaton T. J., Hoffmann D. L., Hogg A. G., Hughen K. A., Kaiser K. F., Kromer B., Manning S. W., Niu M., Reimer R. W., Richards D. A., Scott E. M., Southon J. R., Staff R. A., Turney C. S. M. & van der Plicht J. (2013) IntCal13 and Marine13 radiocarbon age calibration curves 0–50,000 years cal BP. – Radiocarbon 55: 1869–1887.
Reitalu T., Kuneš P. & Giesecke T. (2014) Closing the gap between plant ecology and Quaternary palaeoecology. – Journal of Vegetation Science 25: 1188–1194.
Rollinson H. R. (2014) Using geochemical data: evaluation, presentation, interpretation. – Routledge, London.
Rudolph K. (1927) Profil radostínského rašelinného ložiska u rybníka Velké Dářsko [A section of Radostín peat sediment near Velké Dářsko pond]. – Časopis Národního musea 101: 45–50.
Rybníček K. (1964) Die Braunmoorgesellschaften der Böhmisch-mährischen Höhe (Tschechoslowakei) und die Problematik ihrer Klassifikation. – Preslia 36: 403–415.
Rybníček K. (1984) The vegetation development of Central European mires. – In: Moore P. D. (ed.), European mires, p. 177–201, Academic Press, London.
Salaschek H. (1935) Paläofloristische Untersuchungen mährisch-schlesischer Moore. – Beihefte zum Botanischen Centralblatt, B 54: 1–58.
Slavík J. (2010) Krucemburk a život koželužské rodiny Skřivanových – Binkových 1623–1948 [Krucemburk and the life of Skřivan – Binko's tanner family 1623–1948]. – PhD. thesis, Charles University, Prague.
Smith A. J. E. (1996) The moss flora of Britain and Ireland. – Cambridge University Press, Cambridge.
Speranza A., Hanke J., van Geel B. & Fanta J. (2000) Late-Holocene human impact and peat development in the Černá Hora bog, Krkonoše Mountains, Czech Republic. – Holocene 10: 575–585.
Stockmarr J. (1971) Tablets with spores used in absolute pollen analysis. – Pollen et Spores 13: 615–621.
Svobodová H., Soukupová L. & Reille M. (2002) Diversified development of mountain mires, Bohemian Forest, Central Europe, in the last 13,000 years. – Quaternary International 91: 123–125.

Szabó P., Kuneš P., Svobodová-Svitavská H., Švarcová M. G., Křížová L., Suchánková S., Müllerová J. & Hédl R. (2017) Using historical ecology to reassess the conservation status of coniferous forests in Central Europe. – Conservation Biology 31: 150–160.
Tichý L. & Chytrý M. (2019) Probabilistic key for identifying vegetation types in the field: a new method and Android application. – Journal of Vegetation Science 30: 1035–1038.
Troels-Smith J. (1955) Karakterisering af løse jordarter [Characterization of unconsolidated sediments]. – Reitzels Forlag, København.
van Geel B. (1978) A palaeoecological study of Holocene peat bog sections in Germany and The Netherlands, based on the analysis of pollen, spores and macro- and microscopic remains of fungi, algae, cormophytes and animals. – Review of Palaeobotany and Palynology 25: 1–120.
van Geel B., Buurman J., Brinkkemper O., Schelvis J., Aptroot A., van Reenen G. & Hakbijl T. (2003) Environmental reconstruction of a Roman Period settlement site in Uitgeest (The Netherlands) with special reference to coprophilous fungi. – Journal of Archaeological Science 30: 873–883.
van Geel B., Coope G. R. & van der Hammen T. (1989) Palaeoecology and stratigraphy of the Lateglacial type section at Usselo (The Netherlands). – Review of Palaeobotany and Palynology 60: 25–129.
Vesecký A. (ed.) (1961) Podnebí Československé socialistické republiky. Tabulky [Climate of the Czechoslovak Socialistic Republic. Tables]. – Hydrometeorologický ústav, Praha.
Walker M., Gibbard P., Head M. J., Berkelhammer M., Björck S., Cheng H., Cwynar L. C., Fisher D., Gkinis V., Long A., Lowe J., Newnham R., Rasmussen S. O. & Weiss H. (2019) Formal Subdivision of the Holocene Series/Epoch: a Summary. – Journal of the Geological Society of India 93: 135–141.
Wiezik M., Jamrichová E., Hájková P., Hrivnák R., Máliš F., Petr L., Jankovská V., Čierniková M. & Hájek M. (2020) The Last Glacial and Holocene history of mountain woodlands in the southern part of the Western Carpathians, with emphasis on the spread of *Fagus sylvatica*. – Palynology (in press, doi: 10.1080/01916122.2019.1690066).
Willis K. J. & Birks H. J. B. (2006) What is natural? The need for a long-term perspective in biodiversity conservation. – Science 314: 1261–1265.
Wingard G. L., Bernhardt C. E. & Wachnicka A. H. (2017) The role of paleoecology in restoration and resource management: the past as a guide to future decision-making: review and example from the Greater Everglades ecosystem, USA. – Frontiers in Ecology and Evolution 5: 11.
Zobel M. (1988) Autogenic succession in boreal mires: a review. – Folia Geobotanica & Phytotaxonomica 23: 417–445.

Received 18 February 2020
Revision received 3 May 2020
Accepted 6 May 2020