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

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
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.

**Key words:** 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 m³ (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
obtained was wrapped in plastic bags and transported to the Laboratory of Palaeoecology in Brno, where samples of the material (volume 1 cm³) 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 cm³) 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...
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 | 14C 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-969599      | 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, Ti, 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. Vaccinio-Pinetum, 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 (LPAGZ) in the development of Dářko peat bog (their dating is based on the depth-age model):

LPAGZ 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, *Hippophae rhamnoides, Ephedra* and *Juniperus*) and a rich spectrum of pollen of herbaceous plants (e.g. *Achillea, Artemisia, Aster tripolium* type, *Brassicaceae, Asteraceae* subfam. *Cichorioideae, Cerasium, 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,* and ferns. The occurrence of algae (*Botryococcus, Scenedesmus, Tetraedron*), and spores and pollen of aquatic macrophytes (*Isoëtes lacustris*, *Myriophyllum alterniflorum, Myriophyllum spicatum*) indicate a stagnant water environment. *Pinus* stomata were also present. The AP:NAP ratio is close to 80%.

LPAGZ 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.

LPAGZ 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
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.
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:
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, Carex appropinquata, Carex 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 canescens) 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 oxyccocos 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 (Grušlich 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 warnstorffii-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
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 recurvicaulis-Caricetum lasiocarpaceae (Hálek & 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 oxyccocos* 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 (Businsky 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 uncom-
mon 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). Usu-
ally 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. For-
est canopies were dominated by Pinus sylvestris, P. cembra and Betula. Using the mod-
er analogy 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 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 occurred, 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, Milítký 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 relics 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*/*Betula 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).

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**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 výskytům ve větrného bruchového 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 zasažujeme do historických souvislostí některé přírodní jevy cenné z hlediska ochrany přírody. Až do vrcholného středověku se jako hlavní hybná síla vývoje mimo kulturního vlivu a autogenní sukcese. Vývoj vegetace počíná již v období neolitu a v podstatě zůstává nezměněný až do přibližně 7400 let před naším letopočtem. Ještě před 6400 lety začíná začínají se objevovat první viditelné změny v mikrovektoru, představující první fázi přechodu od vytrvalého k lesnímu až do purpurového feny. Zastoupení pylu dřevin se postupně zvyšuje, až k holocennímu maximu blížící se 99 %. Minerotrofní slatinný mokřad se zmenšuje v ombrotrofní vrchoviště asi před 6800 lety. Smrk, buk a jinde začínají se objevovat první známé výskytu v pylovém záznamu převažovat asi před 5500 lety. Řádná změna vegetačního pokryvu začíná již v období před 8000 lety a pokračuje až do současné doby. Výskyt slatiništních specialit (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 ochranného managementu. Naše studie ukazuje, jak mohou paleokeologické poznatky přispět k pochopení současného družstva spojeného s lidským vlivem na lokalitu a okolí. Tyto poznatky mohou být využity ke stanovení priorit ochrany území a k vysvětlování cílů ochrany přírody široké veřejnosti.

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