Holocene history and environmental reconstruction of a Hercynian mire and surrounding mountain landscape based on multiple proxies

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A B S T R A C T

We discovered the first peat section covering the entire Holocene in the Hrubý Jeseník Mountains, representing an island of unique alpine vegetation whose history may display transitional features between the Hercynian and Carpathian regions. We analysed pollen, plant macrofossils (more abundant in bottom layers), testate amoebae (more abundant in upper layers), peat stratigraphy and chemistry. We found that the landscape development indeed differed from other Hercynian mountains located westward. This is represented by *Pinus cembra* and *Larix* during the Pleistocene/Holocene transition, the early expansion of spruce around 10,450 cal yr BP, and survival of *Larix* during the climatic optimum. The early Holocene climatic fluctuations are traced in our profile by species compositions of both the mire and surrounding forests. The mire started to develop as a calcium-rich percolation fen with some species recently considered to be postglacial relicts (*Meesia triquetra*, *Betula nana*), shifted into ombrotrophy around 7450 cal yr BP by autogenic succession and changed into a pauperised, nutrient-enriched spruce woodland due to modern forestry activities. We therefore concluded that its recent vegetation is not a product of natural processes. From a methodological viewpoint we demonstrated how using multiple biotic proxies and extensive training sets in transfer functions may overcome taphonomic problems.

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Introduction

The Hrubý Jeseník Mountains (northern Sudetes, Hercynian Mountains, Czech Republic), represent an isolated island of high-mountain vegetation with a high biodiversity and relictualism (Jeník et al., 1980), located at the interface between two important European mountain systems, the Hercynian and the Carpathian mountain ranges. Despite this uniqueness, its full Holocene history is unknown. Most research was focussed on the second half of the Holocene (Rybníček and Rybníčková, 2004; Treml et al., 2008; Dudová et al., 2010, 2013; Novák et al., 2010), except one fragmentary record from the Boreal period (Dudová et al., 2010). Thus, information about changes during the late glacial/early Holocene transition and after the 8.2 ka cold event (Rohling and Pälike, 2005; Rasmussen et al., 2007) is lacking in the Jeseníky Mountains, unlike for other Sudeten Mountains located westwards (e.g., Rybníček and Rybníčková, 1968; Svobodová et al., 2001, 2002; Jankovská, 2007; Engel et al., 2010). The opportunity to investigate the whole Holocene landscape and environmental development in the Hrubý Jeseník Mountains arose recently, when an old peat

deposit at the Skřítek mire was discovered. It appeared that this deposit complements perfectly the profile we have already published from the summit Vozka raised bog located nearby (19 km), which covers the younger period of the last 6000 years (Dudová et al., 2013). In addition, a different hydrological context (minerotrophy) as well as a better preservation of macrofossils enabled us to reconstruct the succession of the mire vegetation, which was expected to differ from that found in the Vozka bog. The existence of recent data on environmental characteristics and species composition of testate amoebae and vegetation from the same area (Hájková et al., 2011; Hájek et al., 2013; Jiroušek et al., 2013) enables us to conduct detailed multi-proxy paleoreconstructions using transfer functions based on both testate amoebae and macrofossils.

Multi-proxy analysis is a useful modern tool of palaeoecology that provides evidence concerning ecosystem development, landscape processes, and hydrological and climate changes (Chambers et al., 2012). Plant macrofossils and testate amoebae are the most common biotic proxies used for reconstructing the local development of mire ecosystems and often complement each other (Mitchell et al., 2013). Whereas testate amoebae are commonly used for direct reconstruction of surface wetness and pH with the help of modern species–environment matrices (Charman et al., 2007; Payne et al., 2011), plant macrofossils are mostly used for a qualitative interpretation of vegetation types (Birks and

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Seppä, 2010) while the use of quantitative reconstruction of environmental variables (transfer functions) is rare (Mitchell et al., 2013). In contrast, pollen assemblages represent a proxy that usually reflects vegetation changes rather on a regional scale and they are sensitive to changes in temperature, humidity, soil development, and human impact (Seppä, 2007). Local mire development can be partly independent from the wider landscape and subsequently driven by autogenic processes, such as peat accumulation (Walker, 1970; Dudová et al., 2013), but partly it can be influenced also by regional drivers such as changes in climate (water regime, Swindles et al., 2007), forest cover in catchment (water regime, trophic level; Speranza et al., 2000; Lamentowicz et al., 2007), or human impact (Sjögren et al., 2007). In this study, we reconstructed landscape and environmental changes using macrofossils of bryophytes and vascular plants, testate amoebae, pollen and non-pollen palynomorphs, dry bulk density, ash content, charcoal, and peat chemistry. To reconstruct the most important ecological factors, we used a comprehensive training dataset of vascular plants and bryophytes, accompanied by direct water pH measurements and ecological indicator values for moisture. The use of a macrofossil transfer function is a relatively innovative method in palaeoecological research, because it requires collaboration between palaeoecologists and vegetation scientists to use sufficiently large datasets of vegetation plots and ecological measurements. As the applicability of macrofossil-based transfer functions recently began to be tested (Väliranta et al., 2012; Mitchell et al., 2013), we aim to contribute by using an extensive training data set from a database of vegetation-plot records.

The main aims of the study are (i) to analyse landscape development from the late glacial/early Holocene transition up to the present time at the Hercynian–Carpathian interface; (ii) to trace the local wetland succession using plant and testate amoebae communities and to reconstruct local environmental development using both the peat physical–chemical properties and the species composition of two different biotic proxies; and (iii) to reveal whether local development reflects changes in climate and landscape vegetation cover.

Material and methods

Site

Skřítek mire is located in the southern foothills of the main ridge of the Hrubý Jeseník Mountains, which constitute the highest area of the Jeseníky (Gesenke) mountain range. It is the eastern-most Hercynian mountain region that reaches the alpine belt (Fig. 1). The study site is an extensive, formerly raised bog at an elevation of 860–820 m, close to the Skřítek saddle in the municipality of Sobotín. The locality is a National Nature Reserve (166 ha) since 1955. It is situated in a shallow valley with many small streams. Its bedrock comprises gneiss, phyllite, and metagranite. The recent vegetation consists of *Picea* forests (partly waterlogged) with rare, isolated patches of open mire belonging to the *Caricion canescenti-nigrae* and *Sphagno recurvi–Caricion canescentis* alliances (for details, see Chytrý, 2011). The site is surrounded and partly covered by *Picea* plantations. Pollen from another profile (173 cm deep), cored in the centre of the bog, was analysed recently as a master's thesis (Mušálková, 2010), however due to contamination of the upper 160 cm of the sediment (indicated by high amount of pollen of temperate trees in the late glacial and early Holocene periods) the profile is not used for comparison in this paper, except for one radiocarbon date of bottom sample (see Table 1).

Sediment sampling and analyses

The peat profile was collected from an area with the deepest sediment (49°59′28.7″N, 17°9′31.7″E). The peat from 250 to 413 cm was cored using a percussion drilling corer; whereas the peat from 0 to 250 cm was cut off in the form of five monoliths from open excavation and stored in metal boxes (50 × 10 × 10 cm). For pollen analysis, the core was subsampled every 10 cm, except for the bottom and the upper part of section, where samples were taken every 5 cm and 2.5 cm, respectively. Macrofossil analysis was carried out on
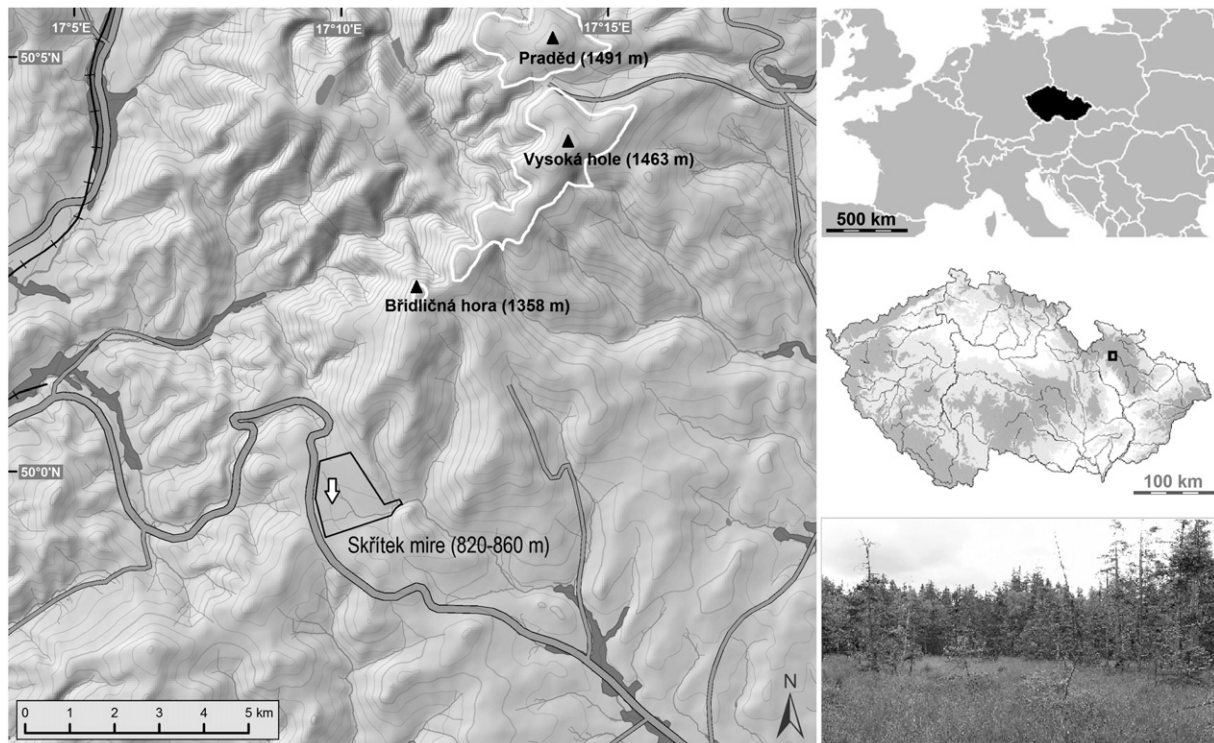

Figure 1. Site map of Skřítek mire, situated in the southern foothills of the Hrubý Jeseník Mountains, Czech Republic. The approximate position of the natural treeline is depicted by a white line. The arrow points at the place where the profile was taken.

Table 1

Radiocarbon dates of samples from the Skřítek mire. Abbreviations: GrN: Centre for Isotope Research, Rijksuniversiteit Groningen, the Netherlands; UGAMS: Centre of Applied Isotope Studies, The University of Georgia, USA; AMS: Acceleration Mass Spectrometry; BP: before present (before AD 1950). The date GrN-41368 was published in Mušálková (2010).

Laboratory number	Method	Depth (cm)	Material	14C age BP	Calibrated age BP (range 95.4%)
UGAMS-10459	AMS	12–13	*Picea* needle fragment	350 ± 50	310–490
UGAMS-12338	AMS	22–23	*Picea* needle	1150 ± 20	890–1 170
UGAMS-12339	AMS	39.5–40.5	*Picea* needle fragment	3980 ± 30	4360–4530
UGAMS-10460	AMS	48–48.5	Cone scales	4280 ± 35	4740–4960
UGAMS-10461	AMS	74–75	Spindles	4540 ± 25	5060–5320
UGAMS-10462	AMS	234–235	*Carex* cf. *limosa* seeds	7320 ± 50	8010–8300
UGAMS-8174	AMS	269–271	*Carex* cf. *limosa* seeds	8550 ± 40	9480–9710
UGAMS-8173	AMS	349–351	Seeds	9330 ± 40	10,420–10,670
UGAMS-8172	AMS	399–401	*Carex* seeds	9980 ± 40	11,460–11,680
UGAMS-8171	AMS	409–411	*Carex* seeds	9970 ± 40	11,460–11,610
GrN-41368	AMS	165–168	Bulk	11,520 ± 50	13,490–13,250

discontinuous samples taken at intervals of 5 cm, except for the upper part where samples were taken at intervals of 2.5 cm. Testate amoebae were analysed every 10 cm (410–180 cm), 5 cm (175–50 cm), or 2.5 cm (47.5–0 cm). Dry bulk density and ash content were analysed every 10 cm (410–50 cm) or 2.5 cm (47.5–0 cm).

For pollen analysis, samples of 1–2 cm^3 of peat were acetolysed according to the standard methods of Faegri and Iversen (1989). Tablets with *Lycopodium* markers were added to the samples to calculate the pollen concentration (Stockmarr, 1971). Pollen was identified using the reference literature (Punt, 1976; Punt and Clarke, 1980, 1981, 1984; Punt et al., 1988, 1995, 2003; Moore et al., 1991; Punt and Blackmore, 1991; Reille, 1992; Beug, 2004) and the reference collection at the Institute of Botany ASCR. The determination of spores and non-pollen objects followed Moore et al. (1991) and van Geel et al. (1980, 1981, 2003).

Peat samples for testate amoebae analysis (1 cm^3 volume) were macerated for 24 h in distilled water. Tests were determined in 1 ml of solution (= one slide) with the help of Bartoš (1954), Ogden and Hedley (1980), Laminger et al. (1981) and Charman et al. (2000). Where test concentrations were low, a maximum of five slides (= 5 ml of solution) was scanned.

For macrofossil analysis, peat monoliths 5 cm long (ca. 100 cm^3 volume) were rinsed with running water on 1 mm, 630 μm, and 200 μm mesh-size sieves. We used a higher resolution (2.5 cm long monolith of 50 cm^3 volume) for the upper 50 cm due to a low accumulation rate. Seeds were identified according to Berggren (1969) and Cappers et al. (2012), wood fragments according to Schweingruber (1978), bryophytes according to Hedenäs (2003) and species missing in this source according to Smith (1996). Leaf and tissue identification followed Mauquoy and van Geel (2007). The material was also compared with the macrofossil reference collection at the Institute of Botany ASCR.

For dry bulk density and ash content, samples of 6 cm^3 were cut from the peat section. Peat samples were dried for seven days at room temperature, dried at 105°C for 1 h to remove the air moisture, then weighed, burnt for 3 h at 550°C in a kiln, and reweighed.

For pH and conductivity measurements, a solution was prepared from a dried peat sample: distilled water mixture (1:5). The total concentration of cations (metals) in the peat samples was determined after extraction by aqua regia (HCl:HNO$_3$:H$_2$O = 3:1:4) and measured using an atomic absorbance spectrometer. Because we found a discrepancy between the results of the total concentration of calcium (solubilised by aqua regia) and the conductivity of the peat solution, we further analysed the calcium concentration in the water solution using an atomic absorbance spectrometer.

Data processing

The age–depth model is based on terrestrial plant macrofossils from ten levels radiocarbon-dated by Accelerator Mass Spectrometry. The

dates were calibrated with the IntCal09 calibration curve (Reimer et al., 2009). The age–depth model was created by OxCal 4.1 (Ramsey, 2009). In the main text, the age of each sample refers to the centre of an interpolated calibrated age BP (before present, i.e., before AD 1950), with a 95.4% probability.

The results of pollen, macrofossil, and testate amoebae analyses are presented in diagrams made by Polpal 11.11 (Nalepka and Walanus, 2003). In the pollen diagram, zones were delimited according to the most important changes in taxa assemblages; in the macrofossil and testate amoebae diagrams, zones were delimited with the help of agglomerative cluster analysis (ConsLink).

To carry out the palaeoenvironmental reconstruction using transfer functions, two calibration (training) data sets from Central Europe were applied. These were selected in such a way to cover the two most important and most causal ecological factors that structure species composition of mire vegetation, i.e., the water pH and water regime (Hájek et al., 2006, 2013; Jabłońska et al., 2011, Rydin & Jeglum 2013). The first data set contains 97 modern assemblages of testate amoebae, which are excellent indicators of moisture conditions (Lamentowicz and Mitchell, 2005; Mitchell et al., 2008, 2013), accompanied by directly measured mean water table depths. The second set contains 923 modern assemblages of bryophytes and vascular plants, accompanied by direct water pH measurements and ecological indicator values for moisture. For data sources and methodological details, see Supplementary material S1. Detrended correspondence analysis (DCA) of the second training data set (bryophytes + vascular plants) confirmed that water pH (major gradient) and moisture (secondary gradient) are indeed the major factors that predominantly structure species composition pattern in this data set (for DCA diagram and eigenvalues of axes see Supplementary material S2) and that they are only slightly intercorrelated. In order to avoid any confounding effect of pH in moisture reconstruction (see Juggins, 2013), we modelled the relationship between pH and moisture using Generalised Additive Model (GAM), which exhibited higher adjusted R-square statistics than did either linear or quadratic model, and used residuals from this relationships ("residual Ellenberg moisture") in the transfer function. Nevertheless, the GAM model confirmed low relationship between the two variables (Rsq = 0.11; e.d.f. = 4.019). For the structure of testate amoebae data, see Jiroušek et al. (2013).

For the macrofossil transfer function, we used log-transformation of species abundance data in the training data set and presence–absence data in the testing data set. This different approach was applied because the abundance of vascular plants and bryophytes in the training set was in percentages, whereas the abundance of macrofossils had to be expressed in variety of scales and ways: tissues were in percentages, seeds in absolute numbers and some of species were even represented by different types of macrofossils (e.g., seeds, spindles and tissues of *Eriophorum vaginatum*). In the case of testate amoebae, we used log-transformation of species abundance data in both the training and the

testing set. The root mean-square error of prediction (RMSEP) with bootstrap cross-validation was calculated (Crowley, 1992). The model with the lowest RMSEP (weighted averaging) was used. Analyses were carried out using C2 software (Juggins, 2003).

Results

Radiocarbon dating

The peat started to accumulate before 11,500 cal yr BP, according to the two deepest samples (Table 1). Samples UGAMS-8171 and UGAMS-8172 are inverted, but their ranges of 95.4% probability overlapped considerably. Due to this inversion, one age (11,500 cal yr BP) is used for all samples from 413 to 400 cm in the main text. According to the age–depth model (Fig. 2), the accumulation of peat was relatively rapid until approximately the upper 40 cm. The large difference between

the age of samples UGAMS-12338 and UGAMS-12339 (Table 1) indicates a hiatus or peat compression because of mineralisation between 40.0 and 22.5 cm.

Pollen analysis

The pollen diagram was divided into seven main zones and several subzones, according to pollen assemblages (Fig. 3):

Zone SKRp-1 (413–345 cm, around 11,500–10,490 cal yr BP) corresponds to open pine–birch forest vegetation with dominance of *Pinus sylvestris* t. and *Betula alba* t. and presence of *Pinus cembra* t. and *Betula nana* t. Subzone SKRp-1A (413.0–407.5 cm, around 11,500 cal yr BP) is characterised by a peak of *Larix* pollen and by indicators of open steppe and/or tundra elements (peak of Poaceae and presence of *Botrychium*, *Helianthemum* t., *Allium* t., and *Pulsatilla* t.). In the following subzones, SKRp-1B (407.5–387.5 cm, around 11,500–11,250 cal yr BP), 1C
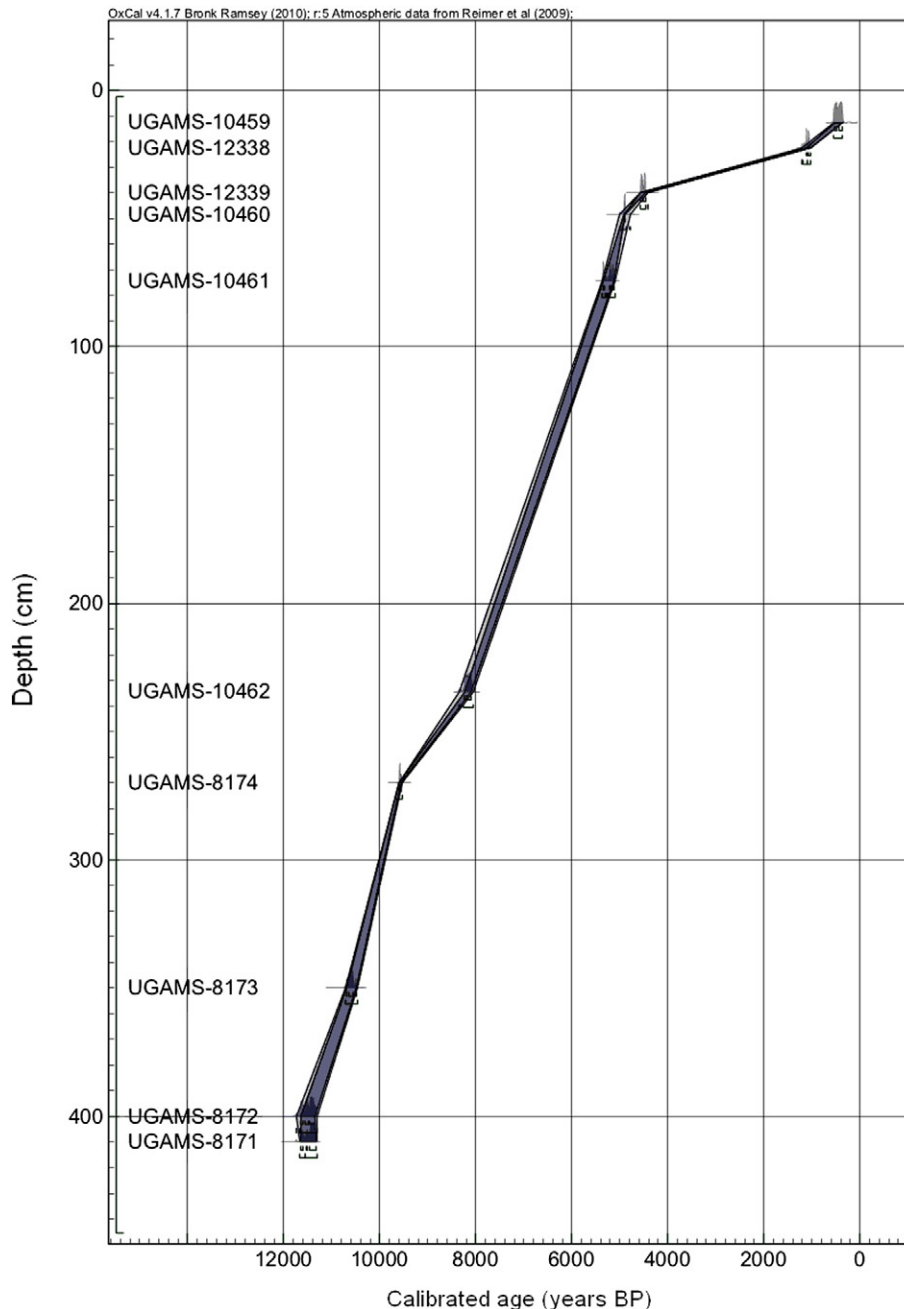

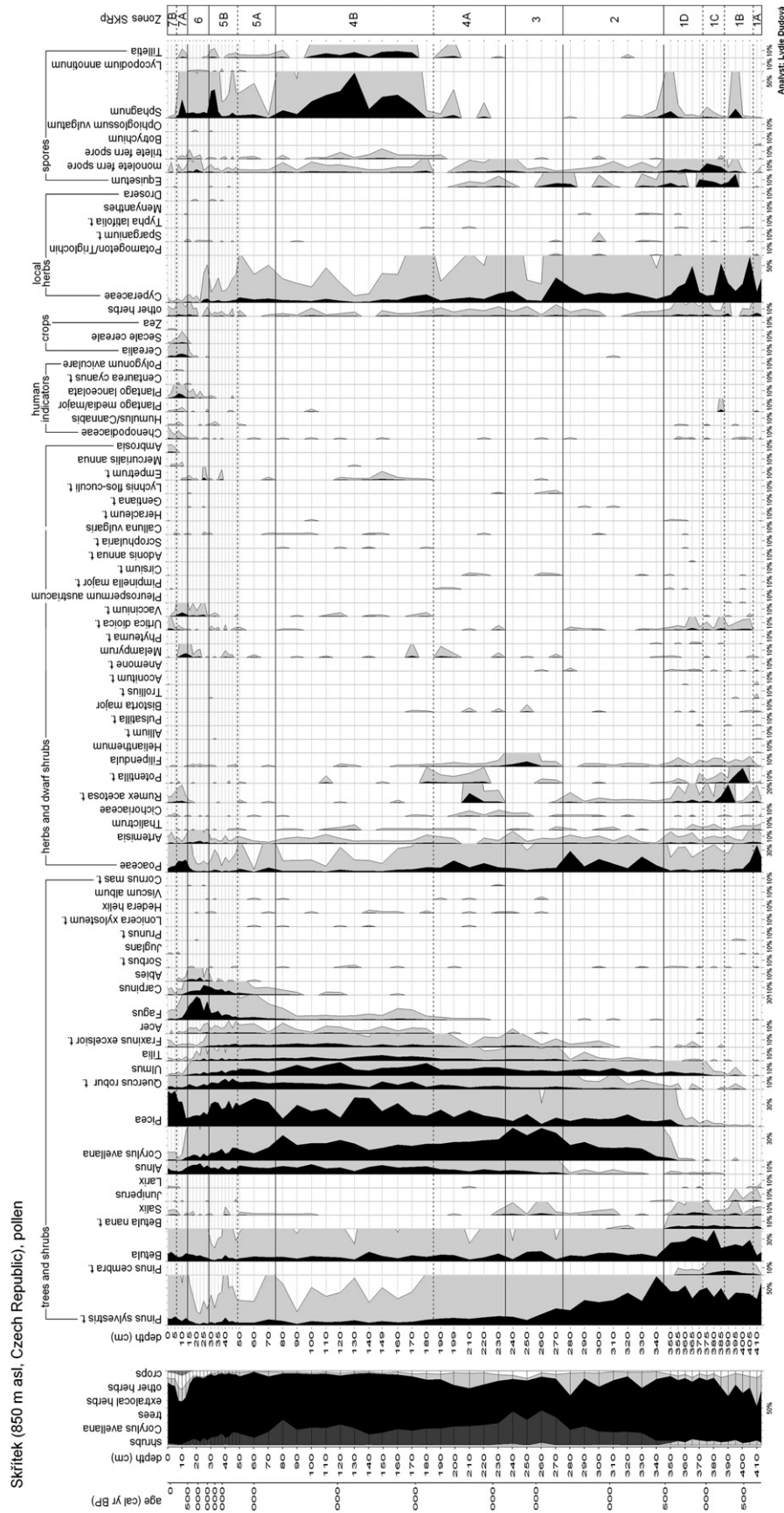**Figure 2.** Age–depth relationship of Skřítek mire, based on 10 radiocarbon dates.

Figure 3. Pollen diagram of Skřítek mire based on the total pollen sum (except local herbs). The time scale is given in calibrated years BP (before AD 1950); the cumulative tree/herb pollen diagram is based on a pollen sum without local and extralocal herbs (*Poaceae*, *Rumex acetosa* t., and *Potentilla* t.).

(387.5–372.5 cm, 11,250–10,970 cal yr BP), and 1D (372.5–345.0 cm, 10,970–10,490 cal yr BP), the representation of *Poaceae* pollen decreases, while pollen indicators of moister and/or species-richer grasslands are common (tall moisture-demanding herbs *Filipendula*, *Aconitum*, *Bistorta major*, and nutrient-demanding *Urtica dioica*). The subzones are delimited by coinciding distinct changes in pollen and spore taxa: subzones SKRp-1B and 1C are delimited by the disappearance of *Juniperus* pollen, the appearance of *Alnus* pollen, and a higher presence of fern spores. A line between subzones SKRp-1C and 1D is drawn by a decline of *P. cembra* t. and an increase in *Ulmus* and *Salix* pollen. An important switch in dominants takes place at 355 cm and 350 cm, where *P. cembra* t. disappears during the expansion of *Corylus* and *Picea*.

At the base of zone SKRp-2 (345–275 cm, 10,490–9590 cal yr BP), *B. nana* t. and *Salix* decline, while *Corylus* continues to rise. *P. sylvestris* t., *Corylus*, *Picea*, *Ulmus*, and *Poaceae* pollen are dominant. After the expansion of *Picea*, *Corylus*, and *Ulmus*, the character of the vegetation changes to less open stands as supported by a coinciding decline in light-demanding shrubs and herbs (except *Poaceae*). In this zone, *Alnus*, *Quercus*, and *Tilia* pollen are constantly present.

Zone SKRp-3 (275–235 cm, 9590–8220 cal yr BP) is delimited by a dominance of *Corylus* pollen and less *Poaceae*. *P. sylvestris* t. decreases in this zone, while *Quercus*, *Tilia*, *Fraxinus*, *Alnus*, and *Salix* increase. At around 8220 cal yr BP (zones SKRp-3/4), the peak of *Corylus* ends while the abundance of moisture-demanding *Picea* starts to increase.

Zone SKRp-4 (235–75 cm, 8220–5210 cal yr BP) is characterised by the dominance of *Corylus* and *Picea* and maximum values of broadleaved trees. In subzone 4A (235–185 cm, 8220–7240 cal yr BP), there is more *P. sylvestris* t. and *Poaceae* pollen. Subzone 4B (185–75 cm, 7240–5210 cal yr BP) is characterised by maximum abundance of *Ulmus*, *Tilia*, and *Fraxinus*, a high amount of *Alnus* and *Quercus*, and stable presence of *Acer*. *Fagus* pollen is constantly present in the pollen spectra from this subzone.

In zone SKRp-5 (75–28.75 cm, 5210–2280 cal yr BP), a gradual switch in dominance of pollen spectra takes place: *Fagus* and *Carpinus* pollen increase, while *Corylus*, *Ulmus*, *Fraxinus*, and later also *Picea*, decrease.

Zone SKRp-6 (28.75–13.75 cm, 2280–490 cal yr BP) is characterised by the highest values of *Fagus*, *Carpinus*, and *Abies* and low values of other trees. Alteration of the vegetation in the wide area by human activities is implied by *Artemisia* and *Plantago lanceolata* pollen as well as by the first appearance of microcharcoals (22.5 cm, 1080 cal yr BP). Deforestation, indicated by a decrease in all trees except *Betula* and *Pinus* and an increase in herbs and microcharcoal, is detected at 570 cal yr BP (15 cm).

Zone SKRp-7 (13.75–0 cm, 490–(−60) cal yr BP) is delimited by a decrease in *Fagus*, *Carpinus*, *Corylus*, *Ulmus*, and *Abies* pollen and a coinciding increase in *Poaceae*. Later, *Picea* pollen abruptly increases. In addition, a high amount of *Cerealia*, *Rumex*, and *P. lanceolata*, *Chenopodiaceae*, *Urtica*, *Secale*, *Mercurialis annua*, and *Ambrosia* is present in this zone.

Macrofossil analysis

The profile was divided into eight zones (Fig. 4):

Zone SKRm-1 (407–382 cm, around 11,500–11,140 cal yr BP) is characterised by dominance of *Carex rostrata*, *C. canescens*, and *Comarum palustre* seeds. The bryophyte layer is represented by *Sphagnum teres* and *Calliergon stramineum* stems and leaves.

Zone SKRm-2 (377–272 cm, 11,050–9540 cal yr BP) is characterised by the dominance of *Carex appropinquata* seeds. At the beginning, species from the former zone still occur, while later tissues of *Phragmites australis* and the bryophytes *Hamatocaulis vernicosus*, *M. triquetra*, and *Warnstorfia exannulata* appear. Other species, such as *Sparganium minimum* and *Epilobium palustre* are represented by lower seed abundance. *Betula pubescens* seeds occur almost throughout the whole zone (377–292 cm), while *B. nana* seeds are present in only one sample (347–342 cm).

In Zone SKRm-3 (267–202 cm, 9400–7550 cal yr BP), the peat is dominated by plant tissues of *P. australis* and wood fragments of *Betula* and *Picea abies*. Wood appears for the first time in this zone. *Equisetum* tissues occur in lower amounts. *Carex limosa* seeds occur constantly throughout the zone, whereas *Menyanthes trifoliata* and *C. appropinquata* appear in the upper portion.

Zone SKRm-4 (197–142 cm, 7460–6440 cal yr BP) is characterised by the appearance of *E. vaginatum*. The peat comprises almost exclusively *Eriophorum* tissues and "spindles". The amount of wood decreases considerably. Seeds of *C. limosa*, *C. rostrata*, *C. elongata*, and *Potentilla erecta* are in low abundance.

In Zone SKRm-5 (137–82 cm, 6350–5320 cal yr BP), *Sphagnum magellanicum* appears, which together with *E. vaginatum* tissues forms the main component of the peat. The 82–87 cm layer is characterised by more *Picea* wood (50%) and needles. All fen species (e.g., *C. limosa*) are absent in this zone.

Zone SKRm-6 (77–29.5 cm, 5230–2420 cal yr BP) is similar to the former zone, but *S. magellanicum* is less represented. *Sphagnum* sect. *Cuspidata* and leaves of *Vaccinium oxycoccos* agg. occur in some samples.

Zone SKRm-7 (27–14.5 cm, 1940–530 cal yr BP) is dominated by *P. abies* wood. *E. vaginatum* tissues almost disappear and seeds of *Rubus* cf. *idaeus* and fungal sclerotia occur in low abundances.

Zone SKRm-8 (12–0 cm, 380–0 cal yr BP) is dominated by *P. abies* wood and *Sphagnum capillifolium* stems and leaves. In the uppermost sample, *E. vaginatum* tissues and spindles re-appear.

Testate amoebae analysis

The upper part of the profile (from 165 cm upwards) was divided into five zones (Fig. 5). The minerotrophic part of the profile (410–165 cm) is characterised by a very poor representation of testate amoebae species and low abundances; nine samples were completely without testate amoebae. This was probably caused by unfavourable conditions for test preservation (fen peat) and humification of peat. Only *Amphitrema flavum*, *Arcella catinus*, *Centropyxis minuta*, *Heleopera sphagni*, *Hyalosphenia papilio*, and *Trigonopyxis arcula* occurred in low abundance. Such a poor record does not allow any ecological interpretation or reconstruction.

Zone SKRt-1 (165–85 cm, 6770–5380 cal yr BP) is characterised by higher species richness and higher abundances compared to the lower parts of the profile. *Assulina seminulum* and *A. flavum* start to dominate, whereas other species such as *A. catinus*, *Cyclopyxis arcelloides*, *H. papillio*, *Nebela militaris*, and *T. arcula* are less abundant. Synchronously with *S. magellanicum*, *H. sphagni* appears and increases in abundance at the end of this period.

Zone SKRt-2 (80–70 cm, 5290–5130 cal yr BP) is characterised by the dominance of *H. sphagni*, whereas *A. flavum* decreases and *A. seminulum* disappears. *Arcella hemisphaerica* occurs exclusively in this layer.

Zone SKRt-3 (65–32.5 cm, 5060–3000 cal yr BP) is dominated by *A. flavum*. *A. seminulum* appears again, and *H. sphagni* decreases in abundance.

In the zone SKRt-4 (30–20 cm, 2520–910 cal yr BP), *Cryptodifflugia oviformis* starts to dominate, whereas *A. flavum* disappears, with the exception of the 20 cm layer.

Zone SKRt-5 (17.5–0 cm, 740–0 cal yr BP) is characterised by a change of dominants; *C. oviformis* is substituted by *T. arcula*. *Hyalosphenia subflava*, *N. militaris*, and *Cryptodifflugia sacculus* occur as subdominant species. In the uppermost layers, *Difflugia fallax*, *Euglypha compressa*, *E. rotunda*, *Heleopera petricola*, *Cryptodifflugia compressa*, and *Trinema lineare* occur in low abundance.

Palaeoenvironmental reconstruction

We reconstructed changes in water pH and peat moisture based on plant ecological indicator values for the entire profile. In addition, water level (WL, in cm below the apical parts of mosses) inferred from testate
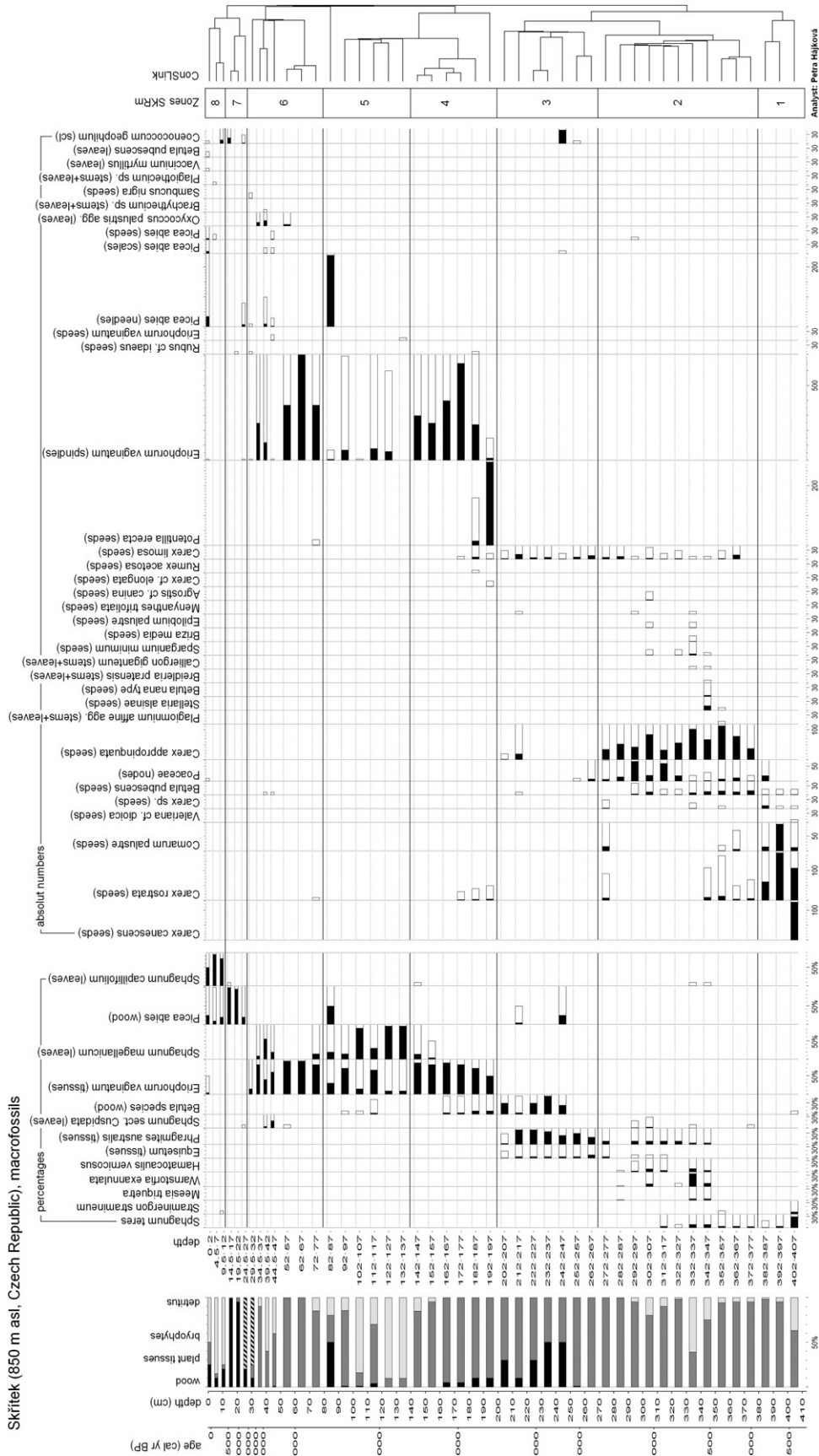
Figure 4. Macrofossil diagram of Skřítek mire; the approximate time scale is given in calibrated years BP (before AD 1950). Uncountable macrofossils (plant tissues, wood, bryophytes) are given as percentages; countable macrofossils (seeds and fruits, scl: sclerotia, spindles, needles) are presented in absolute numbers.
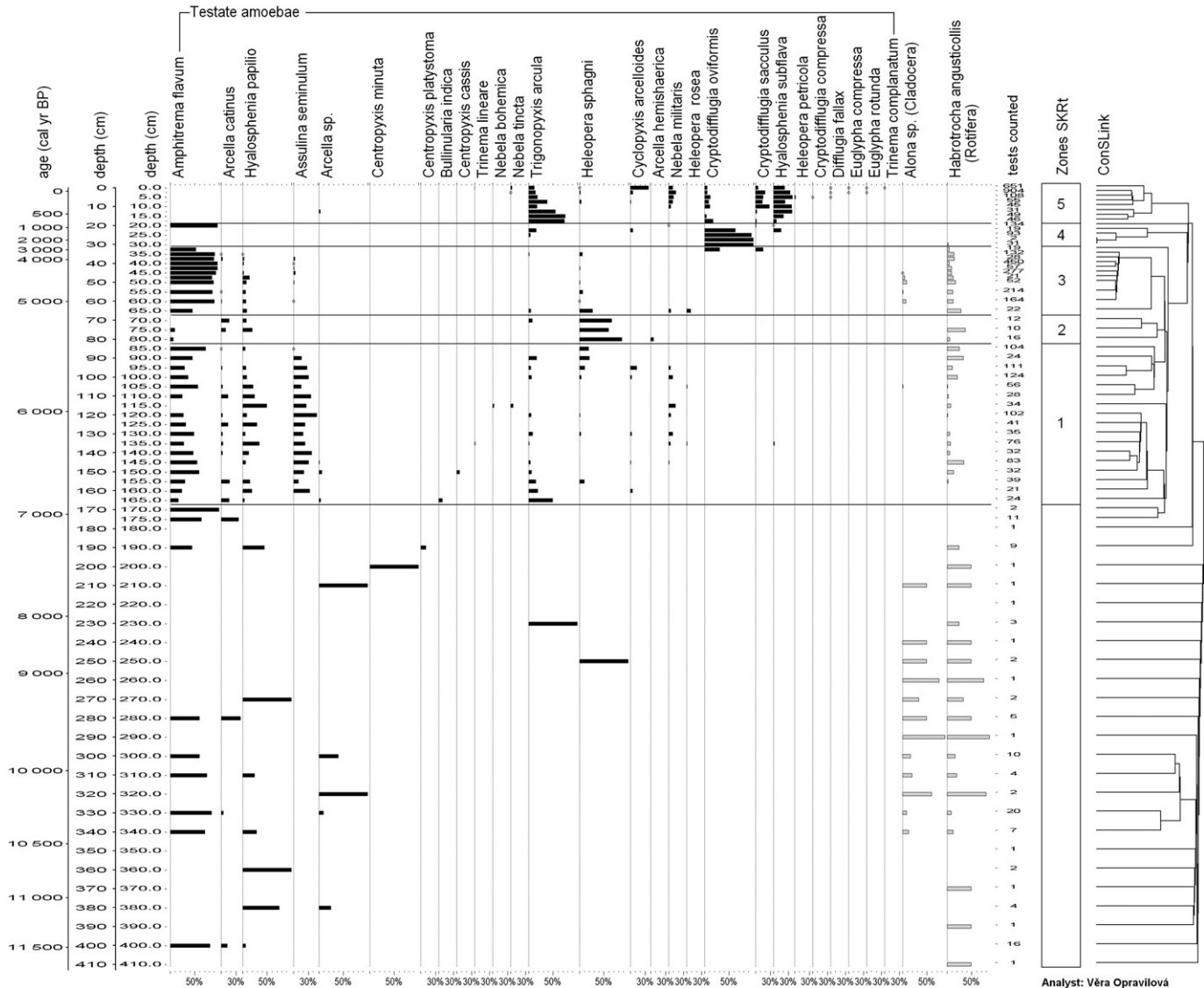
Skřítek (850 m asl, Czech Republic), testate amoebae

Figure 5. Testatae amoebae diagram of Skřítek mire in percentages; the approximate time scale is in calibrated years BP (before AD 1950).

amoebae was reconstructed for the upper part of the profile (Fig. 6). The relationships between the observed and predicted values of WL (testate amoebae), pH and moisture and the values of RMSEP and maximum bias indicate a high quality of the transfer function models and their usefulness for the reconstructions (see Fig. 7). The species composition of vascular plants and bryophytes based on macrofossils reveals two different developmental stages: minerotrophic fen, with a water pH of 6.0 and ombrotrophic bog, with a pH of 3.5. The fen–bog transition lasted over 700 years (between 7510 and 6770 cal yr BP; 200–160 cm) and is recognised by a steep decline in the reconstructed water pH and by a striking decrease in iron and potassium in the peat. Reconstructed moisture also decreased in this transitional zone. The initial phase of development in the early Holocene (407–382 cm; 11,450–11,100 cal yr BP) is characterised by a lower reconstructed pH and a higher reconstructed moisture compared with the rest of the minerotrophic stage (382–202 cm; 11,100–7510 cal yr BP). Another change in water chemistry was reconstructed for the youngest part of the mire development (from 27 cm upwards; 2040 cal yr BP). The reconstructed water pH increased, which relates to modern human-induced changes in the locality (artificial drainage and afforestation).

Focussing on the water regime, the greatest wetness was reconstructed for the initial phase (11,500–11,150 cal yr BP; 410–380 cm) and for the upper part of the minerotrophic stage from 9670 to 7550 cal yr BP (282–202 cm, Fig. 6). A steep moisture decline was reconstructed at the beginning of the fen–bog transition. From this point, reconstructed moisture (by macrofossils) continually but slightly increased up to 2040 cal yr BP (in 27.5 cm) and subsequently decreased. The WL indicated by testate amoebae fluctuated more distinctly. The highest WL (5 cm below the surface) was reconstructed for 5290 cal yr BP (80 cm; SKRt-2), whereas the lowest WL (ca 17 cm below the surface) occurred three-times: after the fen–bog transition (165 cm, 6860 cal yr BP), in the middle of the bog phase (115 cm, 5940 cal yr BP) and sub-recently (15–12.5 cm, 570–400 cal yr BP). The testate amoebae species that predominantly indicated hydrological fluctuation are the moisture-demanding *A. flavum* (optimum in transfer function −9.6 cm) and *H. sphagni* (optimum −7.4 cm) and the drought-tolerant *T. arcula* (optimum −14.8 cm) and *A. seminulum* (optimum −13 cm). These preferences agree with indications from the literature (Lamentowicz and Mitchell, 2005; Payne et al., 2006).
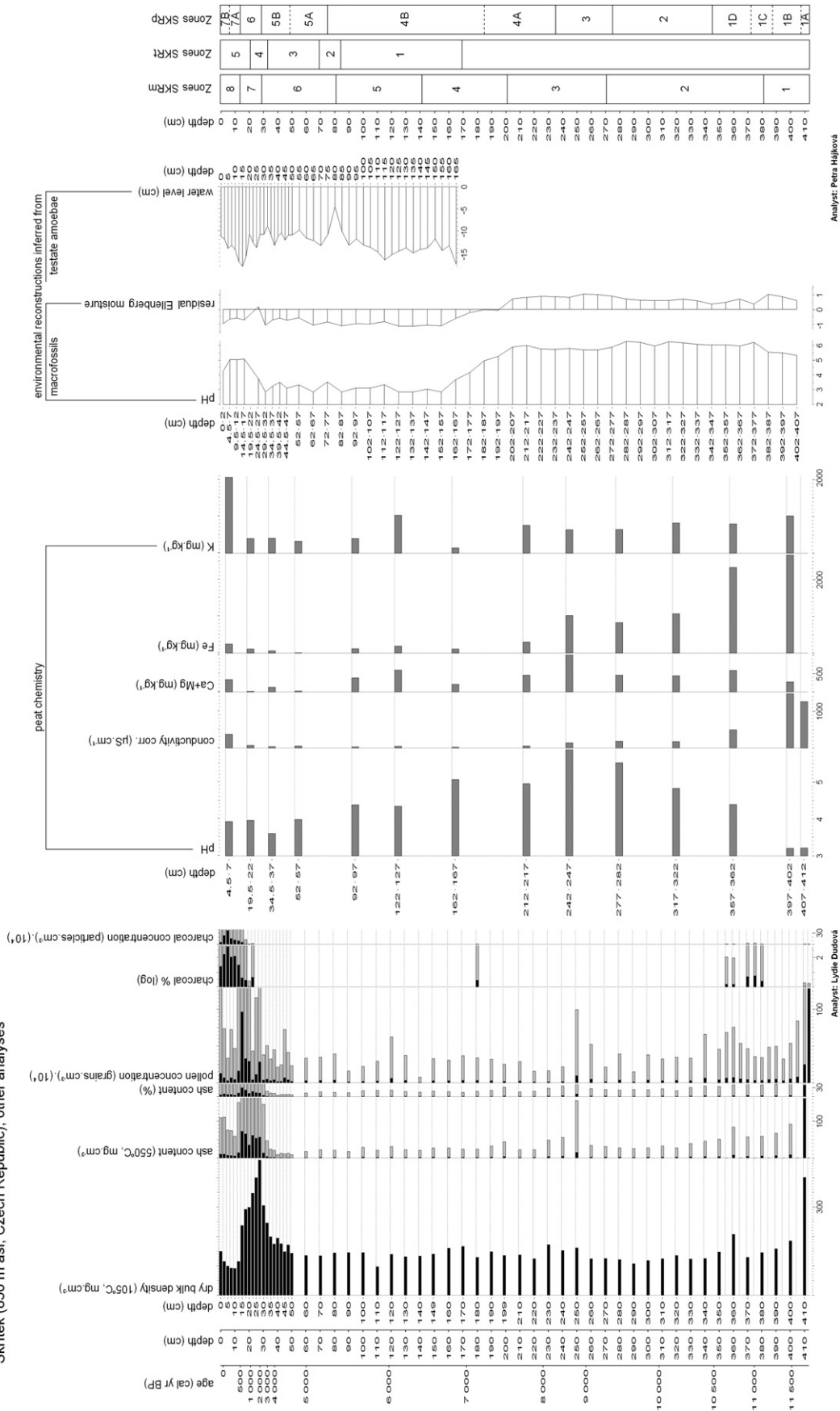
Figure 6. Results of peat analyses (dry bulk density, ash content, pollen concentration, microcharcoals, pH, conductivity, calcium + magnesium, iron, and potassium), reconstructions inferred from macrofossils (water pH and and residual Ellenberg indicator values for moisture) and from testate amoebae (water level). Note the different scales of curves.
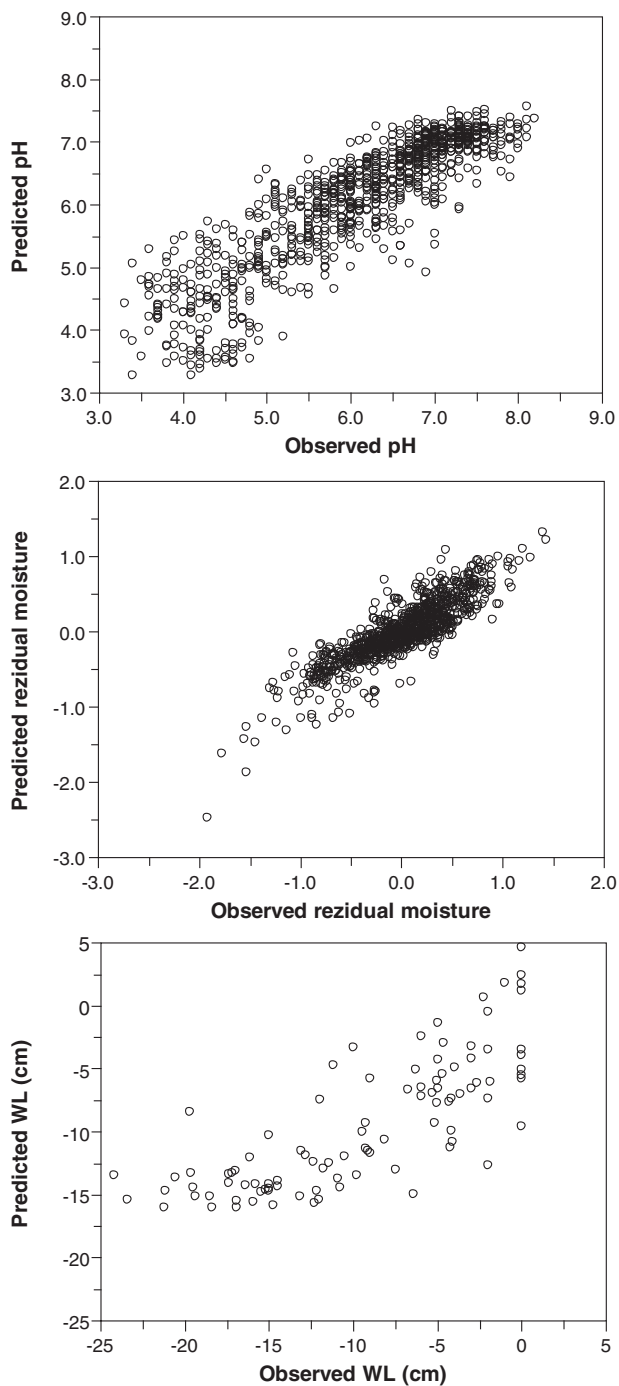
Figure 7. Comparison of observed and predicted values of water level depth (WLD, in cm below the surface) inferred from testate amoebae and pH and residual Ellenberg moisture inferred from macrofossils. The model with the lowest RMSEP (weighted averaging) was used. Both, plant and testate amoebae training data used were in percentages logarithmically transformed. Model parameters: water pH: WA_INV model, RMSEP 0.55805, r^2_{Boot} 0.76293, max bias$_{Boot}$ 0.88436; residual Ellenberg moisture: WA_INV, RMSEP 0.26169, r^2_{Boot} 0.71856, max bias$_{Boot}$ 0.43394; and WLD: WA_INV, RMSEP 4.5189, r^2_{Boot} 0.56405, max bias$_{Boot}$ 10.236.

Dry bulk density, ash content, and peat chemistry

Dry bulk density (Fig. 6) is relatively constant throughout the profile (between 100 and 200 mg·cm^{-3}), except for the basal sample (400 mg·cm^{-3}) and the layers between 32.5 and 15 cm (250–450 mg·cm^{-3}). Ash content shows similar trends and mostly varied up to 10 mg·cm^{-3} except for the basal sample (160 mg·cm^{-3}) and

the samples at a depth of 27.5–15 cm (around 60 mg·cm^{-3}). The percentage of ash content corresponds with the ash content in mg·cm^{-3}. The concentration of pollen per cm^3 correlated with the ash content percentage, as expected. Microcharcoal occurs particularly in the upper 15 cm (Fig. 6). The increase in microcharcoal in the peat clearly coincides with the decrease in dry bulk density and ash content between 15 cm and 12.5 cm.

pH is lowest in the deepest peat layer and increases to a maximum value of 5.89 at 242–247 cm. From 162 to 167 cm, pH decreases again, reaching values below 4.0 in the upper 50 cm. Contrary to pH, the highest values of conductivity (1487 μS cm^{-1}) is in the deepest layer and correlates with a calcium concentration in peat solution prepared in distilled water (760 mg·kg^{-1}, result not shown in Fig. 6). The concentration of calcium + magnesium (solution in *aqua regia*) increased throughout the minerotrophic phase of development, with a maximum in the 242–247 cm layer. The concentration of most elements distinctly decreased in or before the fen–bog transition (192–197 cm); the concentration of iron and calcium + magnesium decreased between 242 and 212 cm, whereas the concentration of potassium decreased later, between 212 and 162 cm. The lowest values of calcium + magnesium were measured between 57.0 and 19.5 cm. Values of conductivity and some elements (calcium + magnesium, iron, potassium) increased again in the sub-recent layer (4.5–7.0 cm).

We found a discrepancy between extremely high conductivity in the basal peat, which is much higher than in other layers, and the total calcium concentration, which does not differ as much in the basal sample. However, the analysis of calcium extracted by water shows that the basal sample is indeed rich in mobile calcium.

Discussion

Mire development and environmental changes

The macrofossil assemblages record one of the classical autogenic successional hydroseres (Walker, 1970). The development started from mineral-rich fen and continued through reed (*Phragmites*) swamp and birch (*Betula*) carr to ombrotrophic bog. A similar development was also documented from other parts of the Hercynian massif (Rybníček and Rybníčková, 1968; Jankovská, 1980) and throughout the world (e.g., Nicholson and Vitt, 1994; Hughes and Barber, 2003). We observed no reversals in this development or allogenically conditioned anomalies in the succession, such as those documented in the valley fens by Kulczynski (1949) or Hájková et al. (2012). The development ended with wet spruce forest, which was probably induced by human activity in the last few centuries.

Around 11,500 cal yr BP, shortly after the onset of the Holocene (cf. Rassmussen et al. 2006), organic matter started to accumulate in a strong spring discharge, which may have been triggered by an increased climate humidity. However, according to an unpublished master's thesis by Mušálková (2010), small patches with peat accumulation already existed at the site 2000 years previously (Table 1). At about 11,050 cal yr BP, macrofossils indicate a local water table decrease, which is in agreement with continued climate improvement indicated by pollen (*Ulmus* increased, *P. cembra* declined). The water regime stabilised, and low-sedge fen vegetation with *C. limosa* and the bryophytes *M. triquetra* and *H. vernicosus* developed. These bryophytes were generally more common during the late glacial and early Holocene (Rybníček and Rybníčková, 1968; Jankovská, 1980), but have recently become rare and endangered (Kučera et al., 2012). The development of a subsequent birch–reed stage was reflected by both macrofossils and local pollen. Environmental reconstruction based on macrofossils suggests that high wetness still persisted in the birch–reed stage.

The most pronounced change in the local development is the fen–bog transition (FBT), which took place about 7510 cal yr BP. Macrofossil evidence agrees well with peat chemistry, indicating higher pH in the

fen stage compared to the bog stage. Generally, all that is required for ombrogenous conditions is the separation of the growing peat surface from the groundwater. Autogenic peat accumulation is the most common and effective process to achieve this, as it can isolate the mire surface from mineral-rich groundwater (Hughes and Barber, 2004). This is exactly the case of the FBT recorded in this study, when at least 2 m of peat had accumulated at the moment of the switch between minerotrophy and ombrotrophy. The FBT is also well reflected in the striking decrease in iron and potassium in the peat (Fig. 6). The unchanged tree pollen curves during the FBT suggest that climate was rather stable, so it is likely that the FBT was not triggered by climate change. The water table was rather high before the FBT and declined after bog vegetation establishment. Such a development fits the "wet-mode of raised bog formation" described by Damman (1986) and Hughes and Barber (2003). The same process was further observed in one other mire in the study area, which is situated in a basin at a lower altitude (the Rejvíz mire; Dudová et al., 2010). In contrast, in the summit-raised bog of Vozka, located in the same mountain range, experienced the FBT, which was triggered by some allogenic and probably climatically-driven factor, as indicated by a water table decrease before the FBT (Dudová et al., 2013). The macrofossil species composition before the FBT strongly resembles that of the dry hummocky communities that preceded the FBTs in Great Britain (Hughes and Barber, 2003) and Sweden (Svensson, 1988). Analogous to the results of Hughes and Barber (2003, 2004), we thus confirmed contrasting pathways to ombrotrophy and different timings of the FBT within the study region of the Hrubý Jeseník Mountains: 7450 cal yr BP in Skřítek, 6010 cal yr BP in Rejvíz, and 2050 cal yr BP in the Vozka mire.

The last distinct change in fossil assemblages was once more connected with the hydrological regime. The 32.5–15.0 cm layer (3000–570 cal yr BP) is highly mineralised (high values of ash content and bulk density), which indicates a WL decrease. The age of the change in water regime is hardly determinable, because this thin peat layer represents a long period. The change might have occurred around AD 1450, when later less mineralised peat started to accumulate as is indicated by lower ash content and dry bulk density. It is notable that all proxies and measurements show an abrupt transition at about 15 cm. It might therefore be possible that there is a hiatus at this level. A hiatus at the top of a compacted peat layer is a common phenomenon that can be caused by human activity (Sjögren et al., 2007) or dry periods (Dudová et al., 2013). Hence, the WL might have decreased even later than around AD 1450. Post-sedimentation processes are also suggested by relatively high values of reconstructed WL for the mineralised layer and the subsequent water table decrease, clearly indicated by the peak of *T. arcula* between 17.5 and 12.5 cm depth (Fig. 5). This hydrological change might be due to human activity in the surrounding landscape, as is indicated by the abrupt increase in charcoal at 15 cm. The pollen curves of crops (*Cerealia*, *Secale*) and human indicators (*P. lanceolata*) increased or remained stable. However, we cannot exclude continual desiccation due to autogenic succession to the spruce forest because the mineralised layer has a unique assemblage of testate amoebae with dominant *C. oviformis* (an indicator of small hummocks; Mitchell et al., 1999) and a high amount of *Picea* wood in the peat. The presence of trees is also indicated by *Hyalosphenia subflava* (Mitchell et al., 1999).

Landscape transformations during the early Holocene

The early Holocene occurrence of open pine–birch forests with tall herb and steppe/tundra elements corresponds well with reconstructions in other Hercynian high-mountain ranges at the Czech–Polish and Czech–German border: Orlické Mountains (Madeyska, 2005), Krkonoše Mountains (Engel et al., 2010), Krušné Mountains (Jankovská et al., 2007; Břízová, 2010), and Šumava Mountains (Svobodová et al., 2001, 2002; Jankovská, 2006). However, the occurrence of *P. cembra* and *Larix* is rarely recorded elsewhere (Kuneš

and Jankovská, 2000; Jankovská, 2006, 2007;Engel et al., 2010). This pattern reflects differences in the early Holocene mountain vegetation between the Hercynian (western) and Carpathian (eastern) Czech Republic, with *P. cembra*–*Larix* forests being much more abundant in the Carpathians (Rybníček and Rybníčková, 2002; Jankovská and Pokorný, 2008; Kuneš et al., 2008). Even though the Jeseníky Mountains belong to the Hercynian unit, their eastward position close to the Carpathians probably determined the frequent occurrence of *Larix* and *P. cembra* in the early Holocene.

After the onset of the Holocene, increasing temperatures are reflected by the immigration of warmth-demanding trees. The Preboreal Oscillation (a cooling event around 11,400–11,300 cal yr BP; Rasmussen et al., 2007; Kobashi et al., 2008) is possibly reflected at Skřítek at 390 cm (11,290 cal yr BP) in the decrease of *Ulmus* and *Quercus* pollen. At around 11,250 cal yr BP, the establishment of *Ulmus* probably led to the decline in *Juniperus*. Later, around 10,950 cal yr BP, *P. cembra* declined as a consequence of the expansion of *Ulmus*, *Betula* and *Picea*. A similar event was recorded in the Krkonoše Mountains around 9150 cal yr BP (Engel et al., 2010). The later date of this event in the Krkonoše Mountains might be due to the high altitude. By analogy, a juniper decline is associated with *Betula* and *Pinus* expansion in the Bohemian Forest (Svobodová et al., 2002).

The expansion of *Picea* at 10,640 cal yr BP, recorded shortly before that of *Corylus*, occurred earlier than in other Hercynian mountains in the Czech Republic, where *Picea* expanded between 8500 and 9000 cal yr BP (Madeyska, 2005; Jankovská et al., 2007; Břízová, 2010). Conversely in the Western Carpathians, *Picea* has been abundant since 10,820 cal yr BP (Rybníček and Rybníčková, 2002) or even during the late glacial period (Jankovská and Pokorný, 2008).

The 8.2 ka event

A distinct decrease in *Corylus*, detected around 8220 cal yr BP at the Skřítek mire, might coincide with the rapid decline in temperature called the 8.2 ka event (Mayewski et al., 2004; Rasmussen et al., 2007; Fohlmeister et al., 2012). While in southern and northern Europe this cooling event led to drier conditions, the regions between 50° and 43° northern latitude experienced moister conditions because of decreasing evapotranspiration (Magny et al., 2003). A *Corylus* decline during the 8.2 ka event was recorded throughout temperate Europe between 45° and 57° northern latitude: in Ireland (Ghilardi and O'Connell, 2012), southern Sweden (Seppä et al., 2005; Wennerberg, 2005), Denmark (Rasmussen et al., 2008), western France (Naughton et al., 2007), Switzerland (Tinner and Lotter, 2001), and Poland (Ralska-Jasiewiczowa et al., 1998). The *Corylus* decline is generally explained as a consequence of increasing moisture that supports the expansion of taller, competitively stronger trees. At Skřítek mire, the increase in *Picea* coinciding with the decline in *Corylus* was slow and gradual and the increase in *Ulmus* and *Quercus* was rather minor. This implies that the cooling event could have a direct impact on the flowering of *Corylus*, whereas the consequent switch in dominance between *Corylus* and *Picea* was a longer and more gradual process.

The decrease in *Corylus* and increase in *Picea* pollen were recorded in the Jeseníky Mountains approximately at the same time as in all other Hercynian mountains of the Czech Republic (Svobodová et al., 2001, 2002; Madeyska, 2005; Jankovská et al., 2007; Břízová, 2010; Engel et al., 2010). The expansion of *Picea* was more intense there, as it was not yet established in those regions.

The middle and late Holocene

During the Holocene climatic optimum, mountain woodlands consisted mainly of *Picea* and *Corylus*, with admixture of *Ulmus* and *Quercus* in the study region (Dudová et al., 2010, 2013 and this study). Other tree species occurred at rather low altitudes (*Tilia*, *Fraxinus*, *Acer*) or in azonal habitats (*Alnus*, *Betula*, *Pinus*). A single *Larix* pollen

grain was found in the sample dated 7700 cal yr BP. Together with other late Holocene finds of *Larix* pollen in the same region (Mušálková, 2010; Dudová et al., 2013), this is important evidence of the presence of *Larix* trees during the Holocene, which is unique in the Hercynian part of the Czech Republic (Dudová et al., 2013).

In the northern foreland of the Alps, the *Fagus* expansion was likely triggered by the 8.2 ka event (Tinner and Lotter, 2001, 2006). In our study area, *Fagus* establishment, indicated by a continuous pollen curve since 7510 cal yr BP, was slightly delayed after the 8.2 ka event. After its establishment, *Fagus* occurred at low frequency until approximately 5290 cal yr BP, when it started to expand. This implies that the *Fagus* distribution was in equilibrium with the climate for more than 2000 years before its expansion.

The short-term decrease in *Corylus* and increase in *Picea* (and possibly also a slight short-term increase in *Fagus*) between 5200 and 5000 cal yr BP might reflect the shift to cooler and wetter climate recorded in the Alps during that time (5550–4950 cal yr BP, Magny and Haas, 2004). Moistening of the climate is also indicated by a conspicuous increase in WL prior to the *Picea* expansion reconstructed by testate amoebae (80 cm, 5290 cal yr BP).

After 4600 cal yr BP, the first expansion of *Fagus* and *Carpinus* led to a decrease in *Corylus* and *Ulmus*. During the second phase of *Fagus* and *Carpinus* expansion after 2280 cal yr BP, besides other trees, mainly *Picea* was affected. A similar two-phased pattern of *Fagus–Carpinus–Abies* expansion, with an initial impact on *Corylus* and subsequently on *Picea*, was observed at other sites of the Jeseníky Mountains (Rybníček and Rybníčková, 2004; Dudová et al., 2010, 2013). The first phase of *Fagus* and *Carpinus* expansion was probably enabled by soil deterioration due to nutrient leaching, caused by high precipitation in the Middle Holocene period (Berglund, 1986; Pokorný and Kuneš, 2005). Climate shifts to more humid conditions, supporting the ability of *Fagus* (and *Abies*) to outcompete other trees (Tinner and Lotter, 2006), are suggested as an alternative explanation for the gradual change in montane woodland composition during the late Holocene.

Modern human impact

Our results suggest that the landscape has been affected by human activity as late as 1080 cal yr BP (AD 870, 22.5 cm) matching the archaeological evidence about absence of human settlement before the Middle Ages (Podborský, 1993). At 570 cal yr BP (AD 1380, 15 cm), forest clearance took place close to the Skřítek site, according to a final decrease in *Fagus*, *Carpinus*, *Abies* and other trees and an abrupt increase in *Poaceae* and herbs. In addition, we recorded an increase in microcharcoal concentration, which might have been caused by charcoal production in the neighbourhood as indicated by a historical map from AD 1674 (Nožička, 1957).

Picea pollen has increased in abundance since 350 cal yr BP (AD 1600, 12.5/10.0 cm), during continuing deforestation, which is indicated by a decline in all other trees and an increase in human indicators. We consider the increase in *Picea* pollen rather as a percentage effect, because it is not accompanied by a decrease in non-arboreal pollen. A real expansion of *Picea* on previously deforested patches is possibly reflected by a further increase in *Picea* pollen and decrease in herb pollen around 150 cal yr BP (AD 1800, 7.5–5.0 cm, zone SKRp-7B). At that time, meadows that had been established during the eighteenth century at the Skřítek mire and in its vicinity (www.oldmaps.geolab.cz, accessed 25 January 2013) were probably partly abandoned.

Effectiveness of the transfer function approach for macrofossils

We verified the usefulness of macrofossils for quantitative reconstruction of environmental conditions such as base saturation, which is the most important factor that influences species composition of mire biota (Hájek et al., 2006, Rydin & Jeglum 2013). The macrofossil-based reconstruction correlates well with the results of peat analyses

and indicates two crucial events, i.e., the fen–bog transition and the sub-recent transformation to depauperate spruce forest caused by human impact.

As for other proxies, the reliability of reconstruction based on macro-fossils depends on the quality of both the training and the testing data sets as well as on appropriate selection of the causal environmental variables (Juggins, 2013). In our research, the macrofossil transfer function for moisture showed differences between the wet minerotrophic fen phase and the drier ombrotrophic bog phase, but it was not able to trace changes in water regime within a bog phase (see Fig. 6). The reason for the latter might be either the low number of fossilised species or the fact that contrary to testate amoebae, the bog vegetation does not reflect relatively small changes in water levels of about 5–10 cm. In addition, some bog species have quite wide tolerances to the water table (e.g. *S. capillifolium*, *E. vaginatum*, *Oxycoccus palustris* agg.) We therefore recommend combining the results from transfer functions based on multiple taxonomic groups that differ in taphonomy and in their response to environmental change (Jiroušek et al., 2013). Our experience fits well with the results of Väliranta et al. (2012) and Mitchell et al. (2013), who also compared reconstructions inferred from testate amoebae and macrofossils. However, discrepancies between proxies (e.g., occasional inconsistent episodes found in our study as well as in Väliranta et al., 2012), might indicate not only short-term fluctuations reflected just by one proxy due to its specific traits, but also an uncertainty in reconstruction caused by insufficient training or testing data. We therefore encourage palaeoecologists to collaborate more intensively with vegetation scientists who possess comprehensive vegetation-plot databases accompanied by ecological data based either on direct field measurements or on calibration through ecological indicator values. Such data could be successfully utilised in macrofossil transfer functions.

Conclusions

1. The discovery of the Skřítek peat profile in the Hrubý Jeseník Mountains had enabled the reconstruction of the Holocene history of the mire ecosystem as well as of the high-mountain region at the interface between the Hercynian and Carpathian mountain ranges.

2. In contrast to the general pattern in the western Hercynian Mountains, but similar to the Carpathians to the east, *P. cembra* and *Larix* were present during the early Holocene, *Picea* expanded at 10,640 cal yr BP, and *Larix* probably survived throughout the Holocene. These geographic relationships might be important in understanding recent distribution patterns of some plant species such as those of hemiboreal forests reaching their western range limit in the Hrubý Jeseník Mountains, e.g., *Crepis sibirica* and *Conioselinum tataricum* (Kaplan, 2012). The study area is also the only Hercynian mountain range where *Larix* is probably native.

3. Before the intensification of human impact around 1080 cal yr BP, large-scale vegetation changes were driven primarily by climate events (the Preboreal Oscillation, the 8.2 ka event, the cool–wet shift between 5550 and 5000 cal yr BP). During the 8.2 ka event, *Corylus* abundance decreased while *Picea* abundance increased. The literature review indicates that this vegetation change can be generalised for the Hercynian Mountains of the Czech Republic.

4. Reconstructions based on the individual proxies complemented each other because of different taphonomy and different rates of response to an environmental change. Mire succession was autogenic, with a rather rapid fen–bog transition. The mire succession was probably not affected by climate changes, except for one event around 11,050 cal yr BP. The present-day pauperised *Picea* phase is a result of modern development, probably connected to human activity.

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Acknowledgments

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