



Human impact on open temperate woodlands during the middle Holocene in Central Europe



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ABSTRACT

Temperate oak-dominated woodlands are plant communities characterized by relatively open canopy structure and often rich assemblages of light-demanding understorey species. This vegetation prevailed in Central European lowlands during the early and middle Holocene. Where open woodlands persisted in later periods, several main factors might have prevented the expansion of shade-tolerant tree species: climate, soil, and disturbances. The last factor includes both natural and human induced agents (fire, grazing of wild or domestic herbivores, management). In our study we focused on the relative impact of the humans and climate on long-term forest vegetation changes in the northwestern part of the Pannonian Basin. Two peat cores covering the vegetation history of the past 12,000 years have been investigated by means of pollen and charcoal analyses. Palaeoecological data were interpreted in the context of a climatic model and archaeological evidence. Our results showed that the early Holocene vegetation in the study region was composed of open wooded steppe with the dominance of pine. Succession to temperate oak and hazel woodland started in about 7500 cal BP and coincides with the first traces of permanent human settlement in the vicinity of both study sites. Since the Neolithic, different types of woodland management have created a more open forest structure, which has benefited light-demanding trees, such as oak and hazel. However, during the middle Holocene several humid oscillations were recorded, which might have triggered the expansion of temperate woodlands. Although the natural or anthropogenic drivers behind the dynamics of temperate woodland could not be separated from each other, it seems probable that long-term human impact influenced the dynamics of temperate woodlands from the middle and late Holocene until the present.

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1. Introduction

Open temperate oakwoods are considered to be the natural vegetation in the lowland areas of Europe with warm, relatively moist summers and mild winters (Zólyomi, 1957; Ellenberg, 1996; Bohn and Neuhäusl, 2000; Bohn et al., 2003). Currently such oakwoods are confined to the warmer and drier parts of the gradients of mean annual temperature and moisture. Their distribution range includes lowlands

and hilly landscapes in the continental and partly oceanic climatic zones of Europe. Typical features are the dominance of oak species (*Quercus* spp.), a well-developed shrub layer with light-demanding species, such as *Corylus avellana*, *Cornus* spp. or *Ligustrum*, and a species-rich herb layer (Roleček, 2013; Chudomelová et al., 2017).

Based on palaeoecological results, temperate oakwoods started to spread to the Central European landscape during the early Holocene (Jamrichová et al., 2013, 2017). By the middle Holocene they were common in European lowlands, but in the late Holocene oaks gave way to expanding late-successional tree species such as *Fagus*, *Abies* and *Carpinus* (e.g. Rybníčková and Rybníček, 1972; Magyari et al., 2010; Petr et al., 2013). Open temperate oakwoods have been significantly affected by human communities since prehistory, being mostly

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transformed into fields and pastures. Many extant temperate oakwoods are remnants of the past distribution at sites unsuitable for agriculture or competitive mesophilous trees, i. e. beech and hornbeam (Chytrý, 1997). Open oakwoods are currently among the most threatened forest plant communities of Eurasia, rapidly succumbing to succession following the abandonment of traditional management (Hédl et al., 2010; Chudomelová et al., 2017).

Oak requires enough light during the regeneration phase (e.g. Collins and Battaglia, 2008; Gardiner and Hodges, 1998; Von Lüpke, 1998). Associated oak-dominated forest communities require relatively open canopy structure for their development (Roleček, 2013). However, temperate oakwoods in the middle Holocene also included noble hardwood species, such as *Tilia* and *Ulmus*. These species can create shady mature forest stands, which disadvantages light-demanding species in the forest understory. Therefore, it is difficult to explain the co-occurrence of oak, hazel and noble hardwoods in the fossil record unless other factors controlling for the persistence of mixed communities are taken into account (Ralska-Jasiewiczowa et al., 2003; Chytrý, 2012). Factors that might have prevented the establishment of closed forests due to the expansion of shade-tolerant tree species are climate, soil and disturbances. The last factor includes natural agents (fire, grazing of large herbivores) and human impact (various forms and intensity of woodland management including clearance, burning and woodland pasture).

During and after the middle Holocene, humans began to significantly influence European forests (Behre, 1981; Rackham, 2003). Since then, deforestation and management have become the most important large-scale disturbances affecting forest ecosystems (Kaplan et al., 2009). An effective way of forest suppression, for example for agricultural purposes, is by fire. The presence of fire in the palaeorecord has been significantly associated with human populations since the Mesolithic (Kuneš et al., 2008; Regnell, 2012; Tolksdorf et al., 2013). Fire affects forest productivity (Nave et al., 2011) and its occurrence maintains canopy openness, thus supporting light-demanding species in the forest understory. Human-induced forest fires could have contributed to the early Holocene expansion of hazel (Regnell, 2012). Since the Neolithic, the impact of humans on woodland communities has progressively increased as the remaining forests became increasingly utilized as resources of fuelwood and building material (Dufraisse, 2008). Traditional forest management practices (e.g., coppicing, pasturing, haymaking, pannage; Szabó, 2010) removed large amounts of organic matter and nutrients from forests. They also contributed to keeping the forest canopy relatively open, thereby facilitating the occurrence of light-demanding woody species including oak and hazel. Forest management practices controlled the distribution of forest species in terms of canopy opening (Coles, 1978) but also influenced their dynamics (expansion/decline) (Lang, 1994; Ralska-Jasiewiczowa et al., 2003; Hejmanová et al., 2013). For example, selective harvesting of elm during the Neolithic might have contributed to the elm decline broadly detected in the fossil pollen record throughout Europe (Iversen, 1973; Ralska-Jasiewiczowa et al., 2003; Magyari et al., 2012). It is likely that forest management favouring light demanding tree species contributed to the persistence of temperate oakwoods up to the present (Jamrichová et al., 2013). Nonetheless, the role of humans in the postglacial development of temperate forests is combined with the effects of natural factors, mainly climate and substrates. Previous studies considered natural factors as the decisive drivers of the persistence of open woodland communities (Huntley, 1990). A more recent view suggested that more than 7500 years of forest management have significantly contributed to this persistence (Ralska-Jasiewiczowa et al., 2003). Apparently, both types of factors likely played important roles in the dynamics of temperate tree populations and need to be equally considered in palaeoecological studies. Interdisciplinary approaches could help to better understand the interactions among vegetation, climate and humans in the past (e.g., Szabó and Hédl, 2011; Schwörer et al., 2015).

In this study we focused on the origins and development of temperate oakwoods in the northwestern part of the Pannonian Basin during the middle Holocene. One of the studied sites is located within an ancient oakwood, where previous palaeoecological analysis demonstrated the impact of medieval and modern management on current species composition (Jamrichová et al., 2013; Szabó et al., 2017). The second profile came from a region with exceptionally early Holocene presence of oak (Jamrichová et al., 2014). We examined two parallel explanations of the Holocene history of open temperate woodlands in Central Europe:

- i) Natural conditions were the main factor behind the establishment and maintenance of open temperate oakwoods throughout the early and middle Holocene.
- ii) Prehistoric human impact significantly contributed to the development of open temperate oakwoods.

2. Material and methods

2.1. Study sites

Dúbrava Wood (N 48°52.038', E 17°06.144', 190 m a.s.l.) and Parížske Mire (N 47°52.389', E 018°27.918', 123 m a.s.l.) are situated in the Lower Moravian Basin and in the northwestern part of the Pannonian Basin, respectively (Fig. 1). Climate in Dúbrava Wood is warm and slightly dry with ca. 8–9 °C average annual temperature and 500–550 mm of precipitation (Tolasz et al., 2007). Parížske Mire has a warm and dry climate with mild winters. Average precipitation is 550–650 mm and average temperature is 9 °C (Hreško, 2005). Dúbrava Wood lies within the wider alluvium of the Morava River on blown sand quaternary deposits of 150–200 cm depth (Novák and Pelíšek, 1943). Loess and calcareous sands represent the main soil substrate in the vicinity of Parížske Mire (Šály and Šurina, 2012). Current habitats include thermophilous Pannonian oakwoods on loess (alliance *Aceri tatarici-Quercion*), the Pannonian variant of oak-hornbeam forests (alliance *Carpinion*), alluvial forests (alliance *Alnion incanae*) and alder cars (alliance *Alnion glutinosae*) (Chytrý, 2013) in Dúbrava Wood (Fig. A.1). Parížske Mire is currently covered mainly by reed-beds (class *Phragmito-Magnocaricetea*) with transitions to mesophilous meadows (class *Molinio-Arrhenatheretea*) and fragmentary alluvial forests (class *Salicetea purpurae*) (Halada and David, 2005). The surroundings of the site are completely deforested and utilized for agricultural purposes (Fig. A.2).

The analysed organic material from Dúbrava Wood was obtained from a treeless wetland of ca. 20–30 m in diameter and the pollen record reflected mostly local vegetation (Calcote, 1995; Sugita, 1994). The site is therefore suitable for a stand-scale palynological study (Bradshaw, 2013). The cored site at Parížske Mire was situated on the edge of a water body that was created after the extraction of a ca. 200 ha peatbog. The pollen profile probably reflected vegetation on a more regional scale (Sugita, 1994).

2.2. Preparation and processing of palaeoecological data

2.2.1. Sampling

Material for palaeoecological analyses was collected in September 2012 by digging from the wall of a pit using metal boxes of 10 × 10 × 50 cm³ (82 cm long; Dúbrava) and by coring using an open tube core with 8 cm diameter (300 cm long; Parížske Mire). The organic material was later described following Troels-Smith (1955) and subsampled in the laboratory. The Dúbrava Wood profile was subsampled into 2 cm units for pollen (volume 1 cm³) and macro-charcoal analyses (volume 2 cm³). The Parížske Mire profile was subsampled for pollen analyses by 3 cm (300–221 cm) and 6 cm (221–0 cm), each of volume 1 cm³. Macro-charcoals larger than 125 µm were counted during

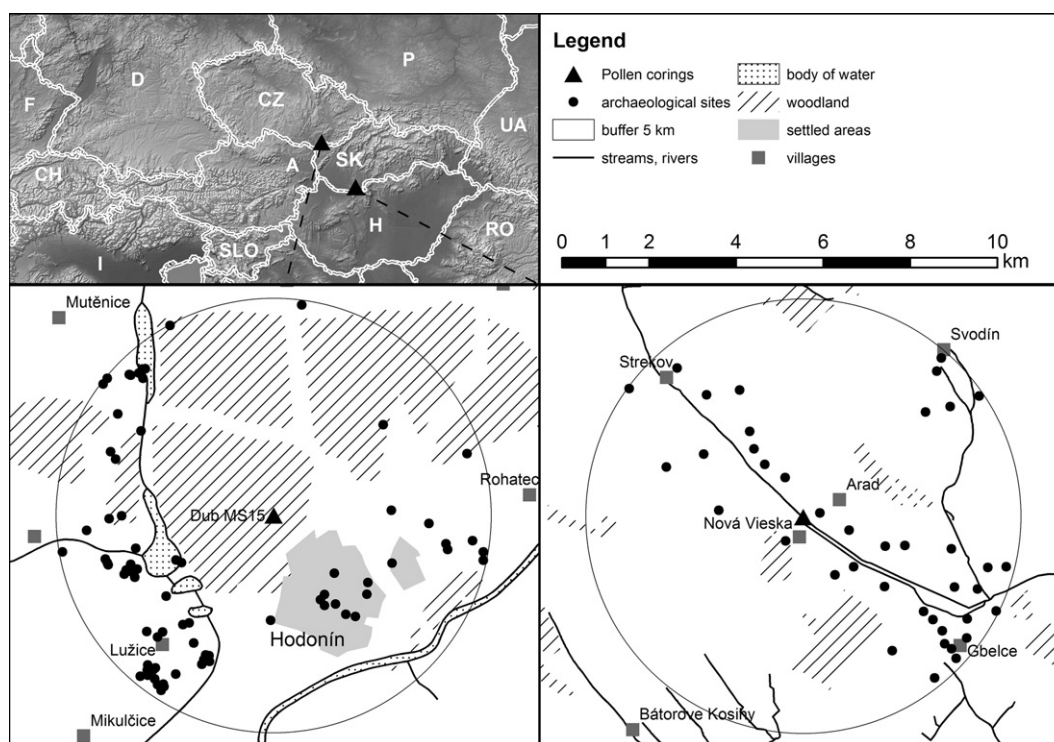


Fig. 1. Map of Central Europe depicting the study area with detailed overviews of the study sites and localization of known archaeological sites.

macrofossil analysis, for which the sediment was subsampled at 6 cm intervals (volume of 50 cm³).

2.2.2. Pollen analysis

The preparation of samples for pollen analysis followed standard techniques (Faegri and Iversen, 1989). Samples containing mineral material were pre-treated with cold concentrated HF for 24 h and then processed by KOH and acetolysis. At least 500 terrestrial pollen grains were identified using standard key and photo collections (Beug, 2004; Reille, 1992; Punt and Clarke, 1984 for family Apiaceae). For the determination of non-pollen palynomorphs we used Van Geel et al. (1980–1981). The nomenclature of pollen types follows Beug (2004) and Punt and Clarke (1984).

Pollen data are presented in percentage pollen diagrams constructed in the Tilia software v. 1.7.16, which was also used for cluster analysis through Coniss (Grimm, 2011). Total pollen sum (TS) was calculated based on the terrestrial pollen sum, excluding (semi)aquatic plants, pteridophyta, algae, fungi, and other non-pollen palynomorphs (NPP). The percentages of pollen taxa were based on pollen sums of arboreal and non-arboreal pollen (TS = AP + NAP = 100%). The percentages of (semi)aquatic taxa, spores, and NPP were related to the extended sum [AP + NAP + (semi)aquatic + spores + NPP = 100%].

Pollen diversity in the samples was expressed in terms of the Shannon-Wiener diversity index. It followed the standard formula (Eq. (A.1)).

2.2.3. Charcoal analysis

Fire history at the sites was reconstructed through the quantification of macroscopic and microscopic charcoal concentration. Pollen-slide microscopic charcoals are thought to reflect more regional fire activity (Clark, 1988; Tinner et al., 1998), whereas macroscopic charcoals local fires (Whitlock, 2001).

Microscopic charcoal analysis was performed during pollen analysis. Charcoal was quantified using particle counts in relation to *Lycopodium* counts to give charcoal concentration in particles per cm⁻³

(Whitlock and Larsen, 2001; Tinner and Hu, 2003). Charcoal concentration was then converted to charcoal accumulation rate (pieces per cm⁻²·year⁻¹) by multiplying it by the sediment accumulation rate.

The quantity of macroscopic charcoals was obtained by wet sieving the continuous series of samples from Dúbrava Wood. The extracted material was deflocculated with 10% KOH and non-charred organic particles were bleached by 3% hydroxide peroxide (Schlachter and Horn, 2010). Charcoal particles were identified according to their characteristic angular shape, sharp edges and black color (Enache and Cumming, 2006) and size fractions larger than 125 μm were counted. Their quantification was performed by optical analysis of microphotographs processed by ImageJ software (Schneider et al., 2012). For Pařížské Mire, macro-charcoal particles were counted during the analysis of plant macro-remains. We focused on the same size class >125 μm. All macro-charcoal concentration series were transformed to accumulation rates.

2.2.4. Magnetic susceptibility

Magnetic susceptibility (MS) of the deposits was determined using the Agico Ltd. KLY4 Kappabridge device. Results were normalized by sample weight to get mass specific magnetic susceptibility in 10⁻⁸ m³ kg⁻¹. The results of MS analysis provide information about the input of inorganic material eroded in the catchment area including surrounding slopes (e.g., Nazarov et al., 2014).

2.3. Chronology

Based on the visual examination of pollen diagrams (see below), we determined layers in profiles to be dated by Accelerator Mass Spectrometry (AMS) (Table 1). Charcoals and seeds of terrestrial herbs were isolated from the selected layers and sent for dating to the Centre for Applied Isotopes Studies, University of Georgia, Athens, GA, USA (UG-), Center voor Isotopenzoek, Rijksuniversiteit, Groningen, Netherland (GRA-) and Centre for Isotopic Research on Cultural and Environmental

Table 1
Results of ^{14}C dating (AMS method) from the two profiles. Calibrated ages are median values and intervals of the calibrated 2σ range BP. Abbreviations: cal – calibrated age. BP – Before Present (1950). Dates marked by asterisk (*) were excluded from age-depth modelling.

Samples (lab. code)	Depth (cm)	Abbreviation	^{14}C age (uncal BP)	Calibrated ^{14}C age (cal BP) (95,4% c.i.)	Mean	Material (seeds and charcoals)
Dúbrava Wood						
UG-12662	80–82	MS15_1	10,280 ± 60	12,384–11,815	12,066	charcoals
UG-13655	66–68	MS15_2	5960 ± 25	6883–6729	6790	charcoals
UG-12667	46–48	MS15_3	3680 ± 25	4090–3925	4021	<i>Carex</i> sp.
UG-13654	38–40	MS15_4	280 ± 30	452–155	358	<i>Carex</i> sp.
UG-12666	28–30	MS15_5	240 ± 25	422–150	244	<i>Carex</i> sp.
Parížske Mire						
DSH-4419	287	PM2_1	10,064 ± 94	11,983–11,270	11,623	<i>Schoenoplectus tabernemontani</i>
GRA-56487	271–277	PM2_2	7705 ± 45	8581–8412	8489	<i>Schoenoplectus</i> tab., <i>Carex</i> sp.
DSH-4416*	252–258*	PM2_3*	6350 ± 162*	7567–6895*	7254*	<i>Schoenoplectus</i> tab.
GRA-56425	252–258	PM2_4	5585 ± 40	6439–6298	6364	<i>Schoenoplectus</i> tab.
UG-19702	240–246	PM2_5	4400 ± 25	5041–4874	4962	<i>Schoenoplectus</i> tab., <i>Carex</i> sp.
GRA-56486	210–216	PM2_6	2200 ± 35	2320–2128	2226	<i>Schoenoplectus</i> tab., <i>Carex</i> sp.
GRA-56621	176–182	PM2_7	1855 ± 50	1898–1629	1787	<i>Sambucus ebulus</i>
GRA-56618	134–140	PM2_8	1310 ± 50	1311–1087	1233	<i>Schoenoplectus</i> tab., <i>Carex</i> sp.
DSH-4418	72–78	PM2_9	941 ± 53	938–763	850	<i>Sambucus ebulus</i>
GRA-56613*	36–42*	PM2_10*	470 ± 120*	673–287*	477*	<i>Carex</i> sp.

Heritage (CIRCE), Italy (DSH-) (Table 1). Radiocarbon ages were calibrated using the IntCal13 calibration curve (Reimer et al., 2013). Depth-age models were created with P_Sequence (a Bayesian model of deposition) implemented in Oxcal 4.2.1 (Bronk Ramsey, 2011). At Parížske Mire, two dates were detected as outliers (DSH-4418 and DSH-4416) in Outlier analysis (Bronk Ramsey, 2009) and excluded

from the depth-age model. Due to potential changes in the sedimentation rate, the command Boundary was used (Fig. 2). In Dúbrava Wood, boundaries were placed at 71 cm (sand/clay sediment) and at 40 cm (clay/organic sediment). In Parížske Mire, the command boundary was applied at 277 cm (sand/peat) and at 126 cm (brown peat/clay).

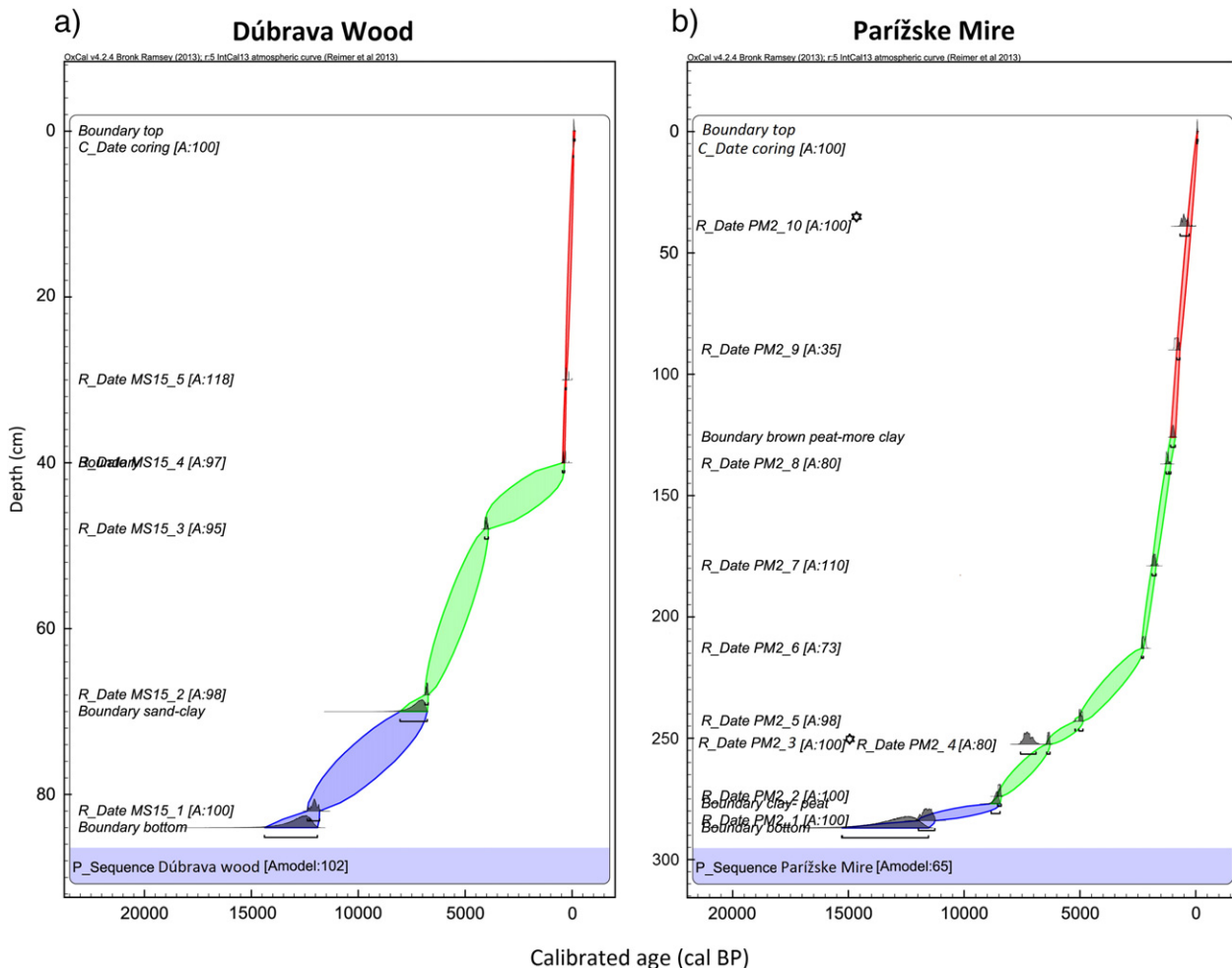


Fig. 2. Age-depth models for a) Dúbrava Wood and b) Parížske Mire. Dates marked by asterisk (*) were excluded from age-depth modelling.

2.4. Climate reconstruction

The climate history of the study region was reconstructed using the Macrophysical Climate Model (MCM; Bryson and McEnaney DeWall, 2007). This model is site-specific (that is, it includes local influences, such as topography) and has been successfully used in several palaeoecological studies (e.g., Hajnalová, 2012; Kuneš et al., 2015; Jamrichová et al., 2014). Two MCM models were built based on temperature and precipitation measurements for the period 1961–1990 from the two meteorological stations closest to the sites: Velké Pavlovice (data by the Czech Hydrometeorological Institute) for Dúbrava Wood and Hurbanovo (data by the Slovak Hydrometeorological Institute) for Parížske Mire.

2.5. Archaeological evidence of human activity

Archaeological evidence of past human activities was collected from a buffer zone of 5 km around the profiles. For Dúbrava Wood, the data were extracted from the LONGWOOD archaeological database (Kolář et al., 2016a, 2016b), which includes information from unpublished excavation reports from the Archive of the Institute of Archaeology of the Czech Academy of Sciences, Brno. Additionally, published summaries or short reports were used (Čížmář et al., 2000; Čížmář and Geislerová, 2006; Poláček, 1997, 1998, 1999, 2005). For Parížske Mire, the data source was the Slovakian national archaeological database (CEANS), which comprised unpublished excavation reports and short reports as well as summarized information from published scientific literature (Bujna et al., 1993). This database is maintained at the Institute of Archaeology of the Slovak Academy of Sciences, Nitra. These data were combined with a catalogue of archaeological sites from the Neolithic to the Early Bronze Age (Tóth, 2014). Inspired by the Archaeological Database of Bohemia (Kuna and Křivánková, 2006), we approached the archaeological dataset as archaeological sites, composed of components. Archaeological components are defined as spatially continuous sets of finds characterized by their function (e.g. residential, burial) and chronological position (e.g. Neolithic, Únětice culture, Iron Age) (Kuna, 2004).

3. Results

3.1. Chronology and sedimentation rates

We obtained reliable depth-age models for both profiles (Fig. 2), with the agreement value of 65% (Parížske Mire) and 102% (Dúbrava Wood) between calibrated and modelled values. The sedimentation rate in Parížske Mire was very low (ca. 0.002 cm/year) in the bottom part (286–273 cm), higher between 273 and 256 cm (ca. 0.01 cm/year). The sedimentation rate declined between 256 and 126 cm to ca.

0.005 cm/year and increased towards to the upper part of the sediment (ca. 0.08 cm/year). The sedimentation rate in Dúbrava Wood was low (0.002 cm/year) in the bottom part of the profile (82–68 cm). Between 68 and 40 cm the sedimentation rate was 0.007 cm/year and from 40 cm towards the top of the profile it increased to 0.06 cm/year.

3.2. Magnetic susceptibility variations

Organic material started to accumulate on pure sand deposits in Dúbrava Wood (total length of the profile: 82 cm). Most of the sediment consists of clay with a low proportion of organic material (Table 2). From 71 cm (ca. 7900 cal BP), the admixture of fine sand decreased towards the top of the profile with a synchronous increase in the amount of decomposed plant remains. Magnetic susceptibility values rose from the section bottom upwards to ca. 71 cm (7900 cal BP) (Figs. A.3 and 5). After that, MS showed slight variations up to ca. 62 cm (6000 cal BP) followed by a gradual decline towards the top of the section.

At Parížske Mire (total length of the section: 286 cm), most of the organic sediment consists of decomposed peat intercalated with sandy and clayey layers (Table 2). Organic sediment started to accumulate on fluvial sands with a gradual increase in organic material towards to the top of the section. Between 271 and 256 cm (8200–7300 cal BP), the sedimentation of organic material ended with a sand layer with roots of plants indicating a possible hiatus in the sedimentation record. After that, the sedimentation continued by organic material abundant in plant macro-remains and with a gradual increase in the proportion of clay (from 126 cm; ca. 970 cal BP) towards the top of the sediment. Variations in magnetic susceptibility (Figs. A.3 and 6) clearly reflected changes in the lithology of the sediment. Higher magnetic susceptibility values corresponded with inorganic sandy or clayey deposits containing higher concentrations of ferromagnetic particles, whereas lower values reflected higher contents of diamagnetic organic matter.

3.3. Vegetation development

Based on the results of cluster analysis, the pollen record was divided into three main phases (Figs. 3 and 4). The first phase was common for both sites and covered almost 4000 years of the postglacial development from the early to the middle Holocene. The length of the second phase differed between the sites. At Parížske Mire, it covered ca. 5300 years, whereas in Dúbrava Wood it lasted almost 7200 years from the middle Holocene until the Middle Ages, revealing a unique stability in species composition at this site. The third phase differed between the sites. Nonetheless, during the first and second phases the two sites showed similar trends in postglacial vegetation development. Pollen diversity generally increased with time at both sites (Figs. 5 and 6) showing fluctuations whose frequency depended on the density of pollen samples.

Table 2

Stratigraphy and description of organic deposits from the two sites according to Troels-Smith (1955). Components: As - clay, Ga - fine sand, Gs - coarse sand, Sh - entirely decomposed organic material, Th - herbaceous peat.

	Troels-Smith	Description of composition of sediment
Dúbrava Wood		
0–40 cm	Sh3, Th1	Organic sediment with gradual increase in plant remains towards to the top of sediment; dark brown color
40–71 cm	Sh3, Ga1	Organic sediment with admixture of fine sand, sporadic occurrence of charcoal; dark brown color
71–82 cm	Sh2, As2, Ga2	Clayey-organic and sediment with sand; dark-brown color
82–95 cm	Gs4	Grey coarse sand
Parížske Mire		
0–40 cm	Sh3, As1	Highly decomposed clayey-organic sediment with plant roots; black-grey color
40–126 cm	Sh2, As2	Clayey-organic sediment with admixture of un-decomposed plant remains and roots; black-brown color
126–246 cm	Sh3	Organic sediment with admixture of molluscs shells and roots of plants; black-grey color
246–256 cm	Sh3, Ga1	Decomposed organic sediment with admixture fine sand
256–271 cm	Ga4	Fine grey sand
271–277 cm	Sh2, Ga2	Sandy-organic sediment, roots of plants; grey-brown color
277–286 cm	Sh2, As3, Ga2	Clayey-organic sediment with admixture of sand, in 286 cm calcium carbonate; light brown color
286–300 cm	Gs4	Coarse fluvial sands; grey color

Dúbrava Wood

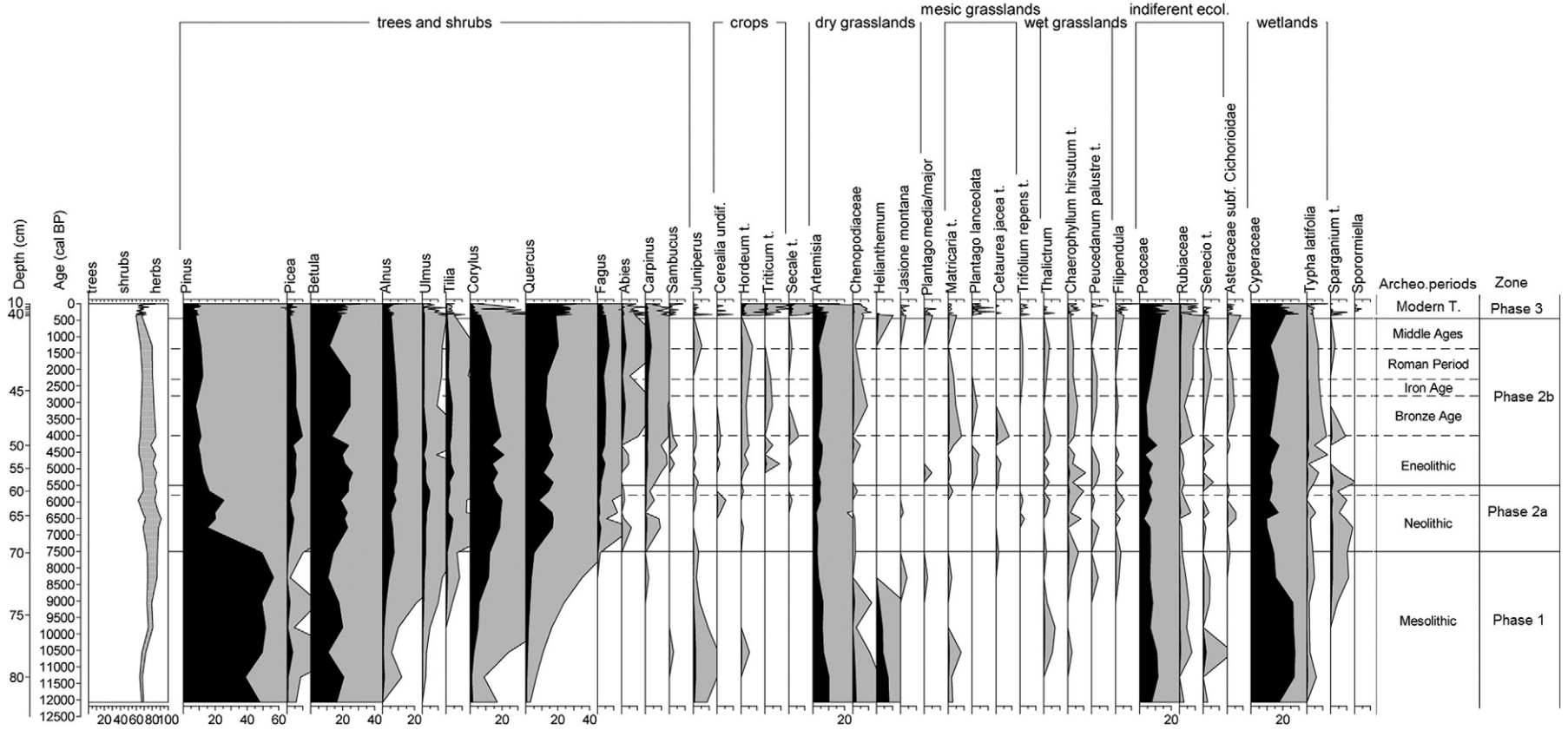


Fig. 3. Percentage pollen diagrams of selected pollen types and spores from Dúbrava Wood.

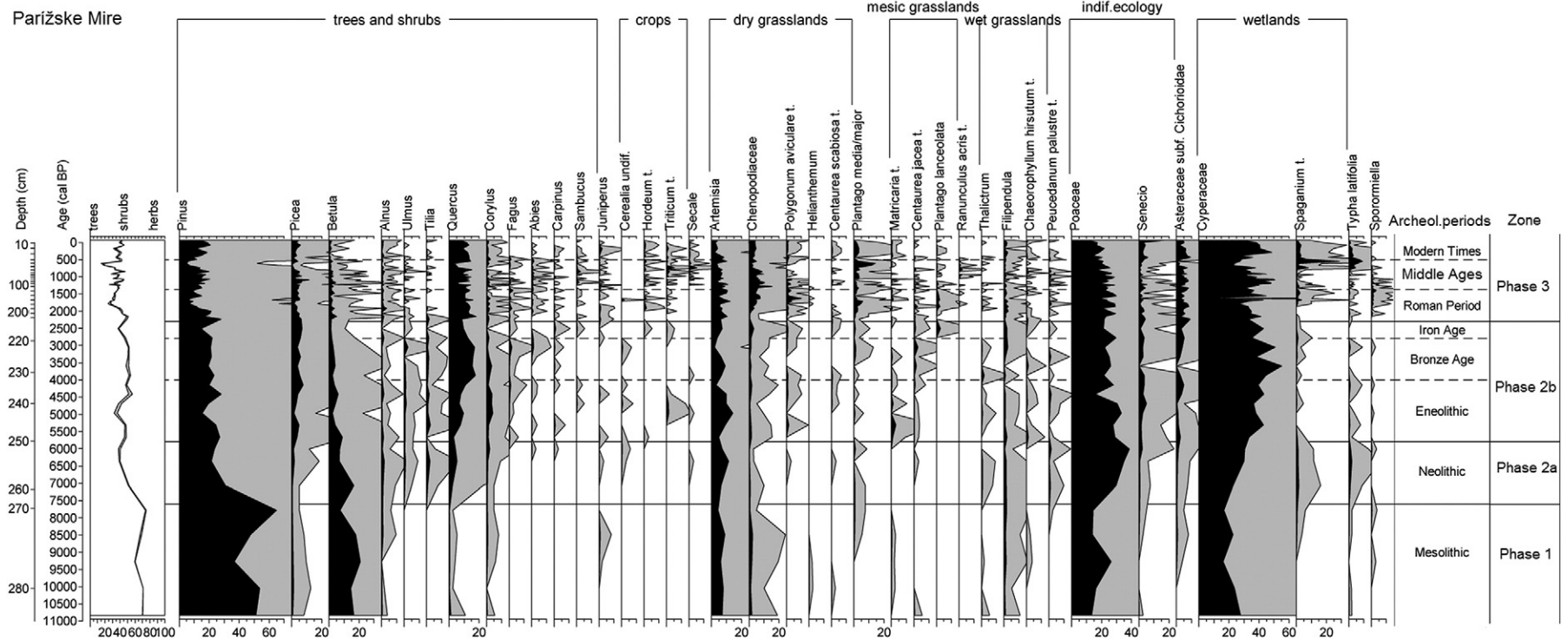


Fig. 4. Percentage pollen diagrams of selected pollen types and spores from Parižske Mire.

Dúbrava Wood

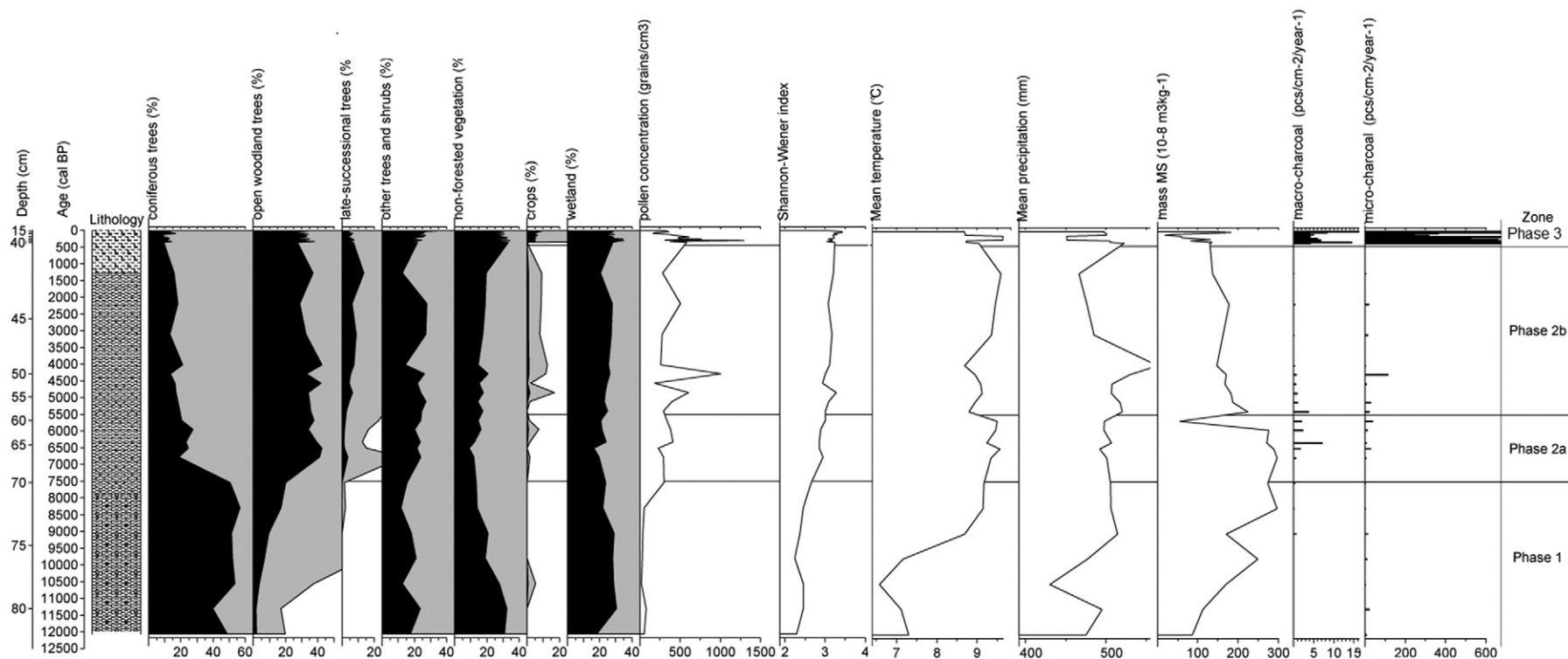


Fig. 5. Synoptic diagram from Dúbrava Wood summarizing the results of all performed analyses: pollen (in %), ecological index revealing pollen diversity, magnetic susceptibility ($10^{-8} \text{ m}^3 \text{ kg}^{-1}$), reconstructed annual temperature ($^{\circ}\text{C}$) and precipitation (mm) and micro- and macro-charcoal accumulation rates ($\text{pcs per cm}^{-2} \cdot \text{year}^{-1}$). Identified pollen types were merged into several functional groups: coniferous trees (*Pinus, Picea*), open temperate trees (*Quercus, Ulmus, Tilia, Corylus*), late-successional trees (*Fagus, Abies, Carpinus*), other trees and shrubs, non-forested vegetation (all identified pollen of terrestrial herbs), crops (*Cerealia undif., Hordeum, Triticum, Secale*) and wetland (pollen of (semi)-aquatic herbs and *Alnus*).

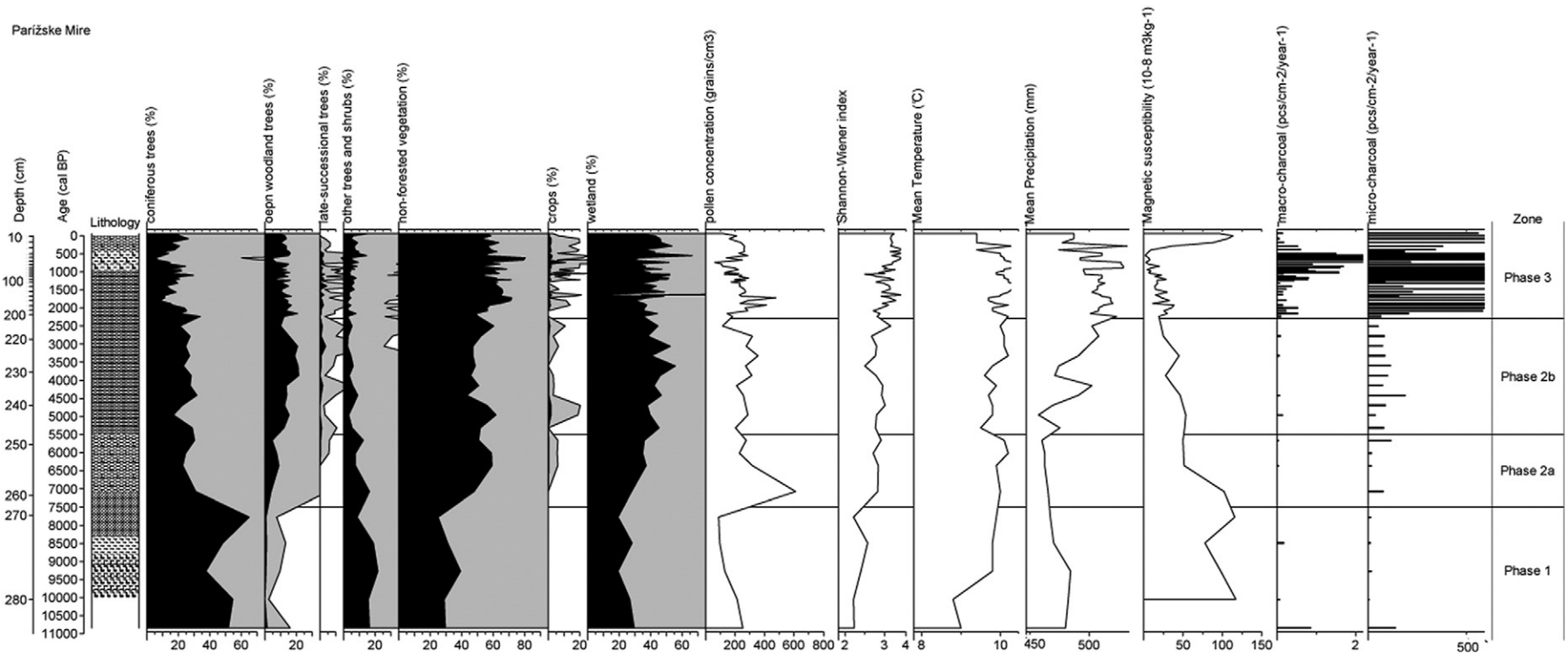


Fig. 6. Synoptic diagram from Parížske Mire summarizing results of all performed analyses. For description see Fig. 5.

The pollen assemblage from the oldest period (Phase 1: 11,000–7500 cal BP in Dúbrava Wood; 11,620–7600 cal BP in Parížske Mire) indicated a mosaic of steppe (*Artemisia*, *Helianthemum*, Poaceae) and forest elements (*Pinus*, *Betula*, *Juniperus*). In the pollen spectra *Pinus* dominated with an admixture of *Betula*, indicating open woodland. A slight spread of *Corylus* into the landscape occurred after ca. 9900 (Dúbrava Wood) and 9200 cal BP (Parížske Mire).

The first pronounced change at both sites occurred around 7600/7500 cal BP (Phase 2: 7500–500 cal BP at Dúbrava Wood and 7600–2300 cal BP at Parížske Mire) when the cool-mixed wooded steppe was replaced by temperate woodland. The proportion of *Pinus* declined to ca. 20%, whereas the abundance of temperate trees gradually increased. At both sites, *Quercus*, *Tilia* and *Ulmus* expanded first (Phase 2a: 7500–5400 cal BP at Dúbrava Wood and 7600–5800 cal BP at Parížske Mire) followed by *Fagus*, *Carpinus* and *Abies* (Phase 2b: 5800/5400–2300/500 cal BP). Among herbaceous pollen types, the occurrence of cereal (Cerealia undif.) implies human impact in the vicinity of the study sites after ca. 7000 cal BP at Parížske Mire and 6300 cal BP at Dúbrava Wood. From ca. 5500 cal BP, human induced habitats – fields (*Triticum* t.) and pastures (*Plantago lanceolata* t., *Centaurea jacea* t.) – expanded at Dúbrava Wood. At Parížske Mire, the spread of open habitats, such as mesic meadows (*Centaurea jacea* t., *Matricaria* t.), ruderal habitats (*Polygonum aviculare* t.) and fields (Cerealia undif.) occurred from ca. 5500–5000 cal BP.

The last change had a similar character at both sites, but occurred at different times: during the Iron Age (Phase 3: 2300 cal BP–recent) and the early Modern Times (Phase 3: 500 cal BP–recent) at Parížske Mire and at Dúbrava Wood, respectively. At Parížske Mire, this last transformation of the landscape is characterized by a gradual decline in temperate trees (except *Quercus*) probably as a reaction to the intensive deforestation of the landscape indicated by an increase in herbaceous pollen types. At the Dúbrava site, the last change is connected with a rapid decline of *Corylus* with a simultaneous increase in *Quercus*. High values of anthropogenic indicators at both sites suggested continuous and intensive land use.

3.4. Fire history

The accumulation rate of micro and macro charcoal particles showed low fire activity during the first phase of vegetation development (Phase 1: 11,000–7500 cal BP at Dúbrava Wood; 11,620–7600 cal BP at Parížske Mire). This changed during the middle Holocene when the amount of macro-charcoal particles rapidly increased indicating fire events in the vicinity of Dúbrava Wood. However, the influx of micro-charcoals remained low. At the Parížske Mire site, the accumulation rate of micro- and macro-charcoal was low during Phase 2a (7600–5500 cal BP) whereas at Dúbrava Wood (Phase 2a: 7500–5500 cal BP) there was a gradual increase. In Phase 2b (5500–500 cal BP at Dúbrava Wood and 5500–2300 cal BP at Parížske Mire) the accumulation rate of micro-charcoal rapidly increased probably as a reaction to increasing regional fire activity in the vicinity of both study sites. The influx of charcoal (both micro- and macro-) distinctly peaked during the younger periods (Phase 3: 500 cal BP–recent at Dúbrava Wood and 2300 cal BP–recent at Parížske Mire) (Figs. 5 and 6).

3.5. Climate history

Both climate models showed similar trends in climate history, therefore they are described together. Mean annual temperature and precipitation were considered. Three main phases of climate development could be distinguished (Fig. A.4): during Phase 1 (12000–9500 cal BP) several discrepancies in climate reconstructions between the two sites occurred. Nonetheless, the first phase could be characterized at both sites by a rise in temperature up to ca. 7.0 °C (Dúbrava Wood) and 7.5 °C (Parížske Mire), although with several cold oscillations. From this point onwards, the temperature was generally on the rise up to

the 8 °C at Dúbrava Wood and 9.5 °C at Parížske Mire at ca. 9400 cal BP. Summer temperatures higher than today were reconstructed for the early Holocene in East-Central Europe based on chironomids (Tóth et al., 2012) and declining lake levels (Feurdean, 2005; Magyari et al., 2009). Precipitation varied around 480 mm at both sites.

Phase 2 (9500–5500 cal BP) was a period of relatively stable and warm conditions with ca. 9.3 °C at Dúbrava Wood and 9.8 °C at Parížske Mire. At the beginning of this phase, temperature suddenly increased up to the ca. 9.2 °C at Dúbrava Wood and ca. 10 °C at Parížske Mire and stayed high, whereas precipitation remained low (ca. 500 mm at Dúbrava Wood and 450 mm at Parížske Mire). Similarly warm climate during the early to middle Holocene (Holocene Thermal Maximum) was described in the entire Northern Hemisphere (Wanner et al., 2008). For example, in the Eastern Carpathians such a warm period occurred between 9400 and 8900 cal BP (Tóth et al., 2015). Temperatures peaked between 6500 and 5800 cal BP at both sites (ca. 9.4 °C at Dúbrava Wood and ca. 10.2 °C at Parížske Mire). During this time, higher temperatures were also reconstructed based on chironomid head capsules in Eastern Slovakia (7700–5800 cal BP; Hájková et al., 2016) as well as in the eastern Alps (7900–4500 cal BP; Ilyashuk et al., 2011). After ca. 5800 cal BP, the temperature declined with minima slightly below 8.8 °C at Dúbrava Wood and 9.4 °C at Parížske Mire. Annual precipitation slowly declined with a minimum between ca. 5800 and 5600 cal BP (ca. 490 mm at Dúbrava Wood and 460 mm at Parížske Mire). The period between 6500 and 5900 was generally cold and dry on a global scale (Wanner et al., 2011).

Phase 3 (5500 cal BP–recent) began with a decline in temperature at both sites (to ca. 8.5 °C at Parížske Mire and 9.5 °C at Dúbrava Wood) with a coeval gradual rise in precipitation. This climate trend recorded by the MCM model could be linked with 5.5 event, when colder and wetter climate was recorded all over Europe (Magny and Haas, 2004). After ca. 4500 cal BP, precipitation increased with several dry fluctuations. This is in concordance with reconstructions of higher lake levels throughout Europe after 4500 cal BP (e.g., Magny et al., 2009).

3.6. Human history

Both study sites are situated in regions with a long history of agriculture (Fig. 1; Table A.1). The archaeological evidence of past human activities registered on these small areas had a relatively fragmentary character. Considering the phases of vegetation history, during the first phase (11600–7600/7500 cal BP) no traces of permanent human settlement were detected. During the second phase (7600–5500 cal BP), we registered the first human activities. Landscapes surrounding both sites were occupied by Neolithic and Early Eneolithic farming communities. From the beginning of the next vegetation phase (Phase 3, 5500–2300/500 cal BP) the two landscapes underwent different developments. Whereas Eneolithic human activities around the Dúbrava Wood profile were nearly non-existent, from around Parížske Mire we have the strongest evidence of prehistoric settlement activities. After the transition from the Eneolithic to the Bronze Age (4400–4200 cal BP), the landscape around Dúbrava Wood showed a relatively stable archaeological record of settlement areas, increasing especially with the beginning of the Medieval Period (1370–750 cal BP), indicating constant and regular land-use. In contrast, Parížske Mire showed only very scarce archaeological record until 750 cal BP.

4. Discussion

4.1. Holocene climate changes and the establishment of temperate woodlands

Pollen assemblages from the oldest period (since 11,600 cal BP) indicated a mosaic of steppe and forest elements (Figs. 3 and 4). The landscape probably had the character of cool-mixed wooded steppe (cf. Magyari et al., 2010) similar to early Holocene vegetation described

from the northern parts of the Pannonian Basin (Rybníčková and Rybníček, 1972; Svobodová, 1997; Magyari et al., 2010; Willis et al., 1995; Petr et al., 2013; Hájková et al., 2013).

The first major change in vegetation composition occurred between 9900 and 7500 cal BP (Figs. 5 and 6). It can be characterized as the gradual transition from cool-mixed wooded steppe to temperate woodland. This early Holocene change in dominant trees followed the development observed at other sites in the same region (Magyari et al., 2010, 2012; Hájková et al., 2013; Petr et al., 2013; Jamrichová et al., 2014), although this process was relatively slow and less pronounced at our two sites. Among the trees of temperate forests, *Corylus* started to expand first (ca. 10,000/9300–8750 cal BP), followed by *Quercus*, *Tilia*, *Ulmus* (7600–6800 cal BP) and finally by *Fagus*, *Carpinus* and *Abies* (5800–5200 cal BP). The direct presence of oak and hazel forests since at least 11,200 cal BP was documented by pollen and woody remains at Parížske Mire during a previous palaeoecological study (Jamrichová et al., 2014). Nonetheless, our new data suggest that temperate woodlands expanded into the broader region later, at ca. 7500 cal BP. These changes in tree dominants were probably associated with the increase in temperature since 9500 cal BP and in precipitation since 5500 cal BP (Figs. 5, 6 and A.4). That precipitation lagged behind temperature may have favoured hazel, which started to expand as the first among temperate trees. Its expansion during the early Holocene was often connected with an increase in temperature at low moisture (Huntley and Prentice, 1993; Finsinger et al., 2006).

Except for the relatively dry climate in the early Holocene, the delayed expansion of temperate tree species could be linked to soil conditions at the study sites. Dúbrava Wood is situated on extremely sandy soils with low fertility and low water retention. In combination with low precipitation, poor soil conditions could sustain pine forests and suppress the expansion of deciduous tree species except for *Corylus*. A similar situation was observed at other sites of the region (Kuneš et al., 2015; Svobodová, 1997). However, at Parížske Mire, fertile chernozem soils prevail, therefore soil fertility could not have been a limiting factor. We argue that the early Holocene spread of temperate trees in Central Europe was triggered by increased moisture conditions, either on a large scale by precipitation or locally due to substrate conditions. This is in congruence with the conclusions of Hájek et al. (2016) and Jamrichová et al. (2017) for the Western Carpathians, a region neighbouring the Pannonian Basin. Moisture availability rather than temperature alone was the main factor behind the expansion of temperate trees during the Late Glacial and early Holocene in Central European lowlands (Birks and Birks, 2014).

During the middle Holocene, temperature was high, whereas precipitation remained low with several humid oscillations in ca. 8500–8000 cal BP; 7700–7500 cal BP and 6500–6300 cal BP (Fig. A.4). The moistening of the climate in Central Europe was recorded after ca. 8600–8000 cal BP (Feurdean et al., 2014; Hájková et al., 2016). Pollen-based reconstructions from lakes in the Alps showed an increase in summer precipitation during 7700–7250 cal BP (Magny, 2004; Joannin et al., 2013). This may be a general pattern for Central Europe. The increase in precipitation was not conspicuous, but it could affect forest cover in the study region. In both pollen diagrams, the transition of the *Pinus* dominated vegetation into temperate woodland with dominant *Quercus* occurred at around 7600–7200 cal BP (Figs. 3 and 4). This could be driven by the gradual moistening of the climate recorded by regional climate reconstructions (e.g., Feurdean et al., 2013) or by a slight drop in temperature while precipitation increased (Dúbrava Wood) as indicated by our MCM model (Fig. A.4). Short-term declines in temperature were observed in ca. 7600–7300 and 7100–6900 cal BP by chironomid-based summer temperature in the Eastern Carpathians (Tóth et al., 2015). Cooler and wetter climate conditions were reconstructed from speleotherms in the Romanian Western Carpathians in ca. 7600–7300 cal BP (Tămaş et al., 2005) and in ca. 7100–7000 cal BP (Onac et al., 2002). The amount of *Quercus* in the pollen spectra increased since ca. 7500 cal BP, *Abies* and *Fagus* occurred regularly and *Picea* increased its abundance. Increases in *Picea* and *Fagus*

could indicate increased humidity, as spruce requires higher soil and air moisture availability and *Fagus* needs moist summers to survive but is limited by drought and cold winters (Feurdean et al., 2011). Nonetheless, we do not assume that beech and spruce spread into the landscape of the study region with its continental climate. In lowlands, they probably got established in more moist habitats in wet depressions (Chytrý, 2012).

The distinct decline in *Pinus* with a subsequent increase in temperate trees occurred already at the end of the Late Glacial or beginning of the Early Holocene in the Western Carpathians, which were probably sufficiently moist and warm during this period (Jamrichová et al., 2017). On the western margins of the Pannonian plain, the *Pinus-Quercus* transition occurred relatively late (between 8000 and 7500 cal BP (Abraham et al., 2016) or even later (after 4200 cal BP) in regions with sandy soils (Kuneš et al., 2015). Similarly, the *Pinus-Quercus* transition in ca. 8400–8000 cal BP was revealed in pollen data from Western Hungary (Szántó and Medzihradsky, 2004; Medzihradsky, 2001; Medzihradsky, 2005). A positive reaction of oak to increased precipitation was recorded during the early and late Holocene in our study region (Jamrichová et al., 2014; Kuneš et al., 2015). The local increase in moisture availability was reflected at both study sites through the analysis of plant macro-remains. Changes in substrate moisture and trophic were documented as an increase in seeds of aquatic macrophytes, such as *Potamogeton* sp., *Typha* sp. and *Alisma* sp. (see Figs. A.5 and A.6). Changes in lithological properties as well as an increase in MS at both sites after 8000 cal BP indicated increasing humidity at least on a local scale. At Parížske Mire after 8000–7300 cal BP, coarse sand accumulated probably due to fluvial activity of the nearest stream Paríž. At Dúbrava Wood, the results of MS revealed an increase in sedimentation of mineral material after 8000 cal BP (Figs. 5, 6 and A.3).

The second major change in species composition occurred at around 5800–5500 cal BP (Figs. 5 and 6). It could be connected with a further increase in precipitation. During this period, shade-tolerant, late-succession species (*Fagus*, *Abies* and *Carpinus*) expanded in both pollen profiles. Based on the MCM model, temperature slightly declined and precipitation increased at 5800–5500 cal BP (Figs. 5, 6 and A.4). Proxy data from the Eastern Carpathians revealed a cooling of the climate and an increase in lake levels between 5500 and 4200 cal BP (Onac et al., 2002; Constantin et al., 2007; Magyari et al., 2009). A comparison of our data with other studies from the study region (Kuneš et al., 2015; Jamrichová et al., 2014) and more generally from the Carpathian-Pannonian borderland showed that late-successional trees expanded into the landscape in 5800–4500 cal BP (Gálová et al., 2016; Magyari et al., 2010; Feurdean, 2005). This concurs with our observations. However, the curves of other temperate trees did not significantly change (except for *Quercus* and *Corylus* at Parížske Mire). After ca. 7500–5500 cal BP, the amount of non-forest pollen types increased and pollen of cultivated plants regularly occurred (Figs. 5 and 6). It is possible that the enlargement of open areas also enlarged the pollen source area, and increased the abundance of regional pollen. The relatively low pollen abundances of all three late-successional trees may be due to long-distance transport from the nearest hills in the study region or from the adjacent Carpathians mountains where the expansion of *Fagus*-dominated forests was documented (e.g., Hájek et al., 2016; Hájková et al., 2013; Petr et al., 2013).

4.2. Local disturbances, human impact and temperate woodlands

Except for climate, the expansion and persistence temperate woodlands with dominant oak could have been caused by local disturbances (e.g., Feurdean et al., 2011). Shade intolerant oak requires periodic canopy disturbances to maintain its dominant position in forest ecosystems.

The expansion of light-demanding woody species, oak and hazel, coincides with the onset of the Neolithic period in 7500 cal BP (Figs. 3 and 4). It could be therefore plausibly associated with prehistoric woodland

management. The occurrence of Cerealia (Cerealia undif., *Hordeum* t. and *Secale* t.) indicated agricultural practices in the vicinity of the study sites. Human activities may have therefore positively affected the spread of open temperate woodlands. Since the Neolithic, woodlands have been used for fuelwood and building material, for the gathering of seeds, fruits and leaf fodder, and as woodland pasture (Kalis et al., 2003). Different types of woodland management could significantly affect woodland vegetation. Several anthracological studies of Neolithic settlements from Central Europe recorded the common occurrence of oak implying its significant presence in the surrounding landscape (e.g., Hajnalová and Hajnalová, 2005; Moskal-del Hoyo, 2013, 2016). Such forests were penetrated by people and utilized by different types of woodland management leading to the development of a mosaic-like forest. Historical management practices (e.g. coppicing or pollarding, Rackham, 1990) provided favourable conditions for the regeneration of light-demanding trees, such as *Quercus* or *Corylus*. A pollen diagram from northern Hungary showed several forest cycles dated to Neolithic (7200–6900 cal BP) or Eneolithic (6900–5200 cal BP) attributed to woodland management, possibly coppicing and pollarding (Gardner, 2002; Magyari et al., 2008). The coppicing of *Quercus* was identified in Great Britain and Flanders since the Neolithic (Rackham, 2003) or Roman Period (Haneca et al., 2005), respectively. Hazel twigs, catkins and branches might be used as winter livestock fodder (Favre and Jacomet, 1998). A specific role may have been played by wood-pasture. Grazing by large herbivores including cattle might have promoted oak reproduction in the early Holocene (Vera, 2000). Moreover, wood pasture is by definition grasslands with trees, therefore oak could get established easier in such open habitats (Rackham, 2003). Grazing by large herbivores is well indicated by the presence of spores of coprophilous fungi (*Sporormiella* genus). We recorded *Sporormiella* spores from the Early Holocene towards the top of the profile at Parížske Mire, indicating the possible influence of large herbivores on local vegetation (Fig. 4). Plant macro-remains analysis also revealed the spread of ruderal vegetation since the Neolithic, which might be attributed to the grazing directly at the site (Fig. A.6). At Dúbrava Wood, coprophilous fungi were absent in the prehistoric palaeoecological record (Fig. 3). However, the recorded increase in MS during the Neolithic implies the input of allochthonous material due to erosion, which could be caused by disturbances to local vegetation by grazing (Figs. 5 and A.4).

Oak expansion in ca. 7500 cal BP, can also be linked to an increased abundance of micro-charcoal in Dúbrava Wood, although the macro-charcoal accumulation rate remained low (Fig. 5). At Parížske Mire, the amount of (micro- and macro-) charcoal remained low (Fig. 6). It is also a period with increasing precipitation, which could lower the possibility of natural fire ignition. It seems that at least during the Neolithic period fire events did not affect the spread of oak-dominated forests. In ca. 6800–5300 cal BP (Dúbrava Wood) and after 5800 cal BP (Parížske Mire) a rapid increase in micro-charcoal was recorded. Fires might slow down the expansion of forests into the landscape, especially at lower altitudes (cf. Feurdean et al., 2013). In our study, however, the increase in fire activity coincides with the spread of forest elements. Fire could have positively affected oak and hazel at both sites. Periodic fires can create an open stand structure, which advances oak reproduction by suppressing competitors and allows oak to dominate even at sites that offer favourable conditions for shade tolerant species (Dey, 2002). There was also a visible spread in herbaceous pollen including primary and secondary anthropogenic indicators (gradual decline in AP:NAP ratio). Culturally this corresponded to the end of the Neolithic and the beginning of the Eneolithic. During the Eneolithic, a more extensive land-use of the landscape, such as swidden cultivation (slash-and-burn agriculture) could be assumed (Kolář et al., 2016a). In this light, it is possible that the (probably human induced) fire activities coincided with the openness of the landscape due to the spreading of anthropogenic habitats in the vicinity of both sites. From our data it is also visible that an increase in landscape openness benefits light-demanding trees, such as oak and hazel.

The increased human impact visible through a quantitative and qualitative increase in primary and secondary anthropogenic indicators in both pollen records after ca. 5500 cal BP implies an increase of landscape utilization (Figs. 3 and 4). The amount of archaeological data differed, but the impact on the landscape and vegetation was similar. The Eneolithic period in our study region was characterized by several changes in agriculture practices, including the use of the ard and cattle as a power source (Mischka, 2011; Bakker et al., 1999). Possible changes in subsistence strategies connected with the increasing importance of livestock husbandry resulted in an increase in grazing pressure. This was visible in the palaeoecological record as the continuous occurrence of grazing indicators (secondary anthropogenic indicators; e.g. Schumacher et al., 2016) or indicators of mesic managed grasslands (e.g., Hájková et al., 2013). In both pollen profiles it was obvious that the intensity of human impact positively correlated with the spread of light-demanding woody species, i.e. oak and hazel.

5. Conclusions

The development of temperate lowland woodland showed similar trends at both sites. Vegetation changed from cold wooded steppe with conifers to temperate forest during the middle Holocene (at 7600–7500 cal BP). Both sites showed an almost synchronous dynamics of oak-dominated woodland from the Neolithic to the Middle Ages. The expansion of temperate woodland coincides with the appearance of the first permanent settlements in the vicinity of both sites, documented in the pollen record by the spread of anthropogenic indicators as well as by charcoal particles. Therefore, the spread of open oak-dominated woodland could be associated with human presence since the Neolithic through various types of woodland management, such as woodland pasture or coppicing. Human induced disturbances contributed to the creation of open forest structure, where light-demanding trees, such as oak and hazel, expanded.

While temperate forests were expanding, several humid oscillations were recorded. It is possible that the increase in moisture availability during the middle Holocene allowed for the expansion of temperate trees into the lowlands of Central Europe forming open temperate woodlands. However, the rapid increase in precipitation after 5500 cal BP did not significantly affect the composition of open temperate woodlands, which stayed more or less unchanged up to 2300 cal BP.

We conclude that human activities played an important role in the dynamics of open woodland during the Holocene. Humans probably influenced the persistence of light-demanding woody species, although this impact could not be clearly separated from climatic factors, especially precipitation.

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Appendix A. Supplementary Data

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.revpalbo.2017.06.002>.

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