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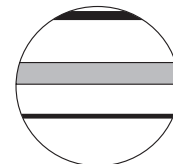
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Abstract

Using a multi-proxy analysis of a postglacial sedimentary sequence from a lowland wetland, we address the possible drivers of change in the wetland habitats and surrounding landscapes of southwestern Slovakia. A 5 m-deep core in the Pářížske močiare marshes was investigated for pollen, plant macro-remains, molluscs, organic content and magnetic susceptibility. The palaeoecological record extends from the Pleistocene–Holocene transition ($\geq 11,200$ cal. BP) to the 5th millennium cal. BP and was correlated with a macrophysical climate model (MCM) and archaeological data. Our results show the transformation of an open parkland landscape with patches of coniferous forest to a temperate deciduous forest at the onset of the Holocene. The record is remarkable for an early occurrence of *Quercus* pollen and macro-remains around 11,200 cal. BP and its early expansion (10,390 cal. BP) in the vegetation. Such an early spread of *Quercus* has not previously been recorded in the region, where *Corylus* is usually the first to expand among temperate trees. This unusual development of forest communities was most probably triggered by a short-lived increase in precipitation and decrease in temperature, as reconstructed by the MCM model. Higher moisture availability and low temperature inhibited *Corylus* and favoured the spread of *Quercus*. Later, the climate became drier and warmer, which, together with fires, supported the expansion of *Corylus*. Since 7300 cal. BP, human activities became most likely the dominant influence on the landscape. Deforestation contributed to soil erosion, which halted the accumulation of organic material after 5520 cal. BP, followed by the accumulation of clay sediments.

Keywords

climate, disturbances, lowland wetland, multi-proxy, palaeoecology, *Quercus*

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Introduction

The transition from the Late Glacial to the early Holocene is the key period for understanding of today's biota composition. The increase in temperature and precipitation recorded at around 13,000 yr BP initialised spreading of temperate forest species from their glacial refugia to northern areas, whereas short-lived restriction (cold and dry) of the climatic excursions caused reduction of these populations (Brewer et al., 2002). The climate of the early Holocene was unstable and several short-lived (cold and humid) oscillations occurred (Blockley et al. 2012). All of these events were recorded in northern Europe (e.g. Björck et al., 1997), but their appearance has been documented also in Central Europe (e.g. Haas et al. 1998; Magny et al., 2003) and Central-eastern Europe (e.g. Feurdean et al., 2008, 2014; Tóth et al., 2012), with a significant impact on vegetation (Birks and Ammann, 2000; Dudová et al., 2014; Feurdean et al., 2008; Magyari et al., 2012a; Tinner and Lotter, 2001). Except climate, several other factors such as distance of refugia (Birks and Line, 1993), seed dispersal, migration rate (Iversen, 1960), interactions between species (Birks, 1986) and disturbances such as fire and human intervention (Keller et al., 2002) contributed to the spread of temperate forest elements during the early and middle Holocene (11,700–6200 cal. BP; Walker et al., 2012) and

caused differences in the timing of their expansion (Finsinger et al., 2006).

The geographical position of the northern part of the Carpathian Basin (Little Hungarian Plain) on the edge of the Western Carpathians plays an important role in today's florogenesis of Central Europe in terms of the existence of cryptic glacial refugia as well as migration route of thermophilous species (Provan and Bennett, 2008; Stewart and Lister, 2001). The existence of glacial refugia of temperate trees has been recently shown in the Carpathian Basin (Birks and Willis, 2008; Magyari et al. 1999; Willis et al.

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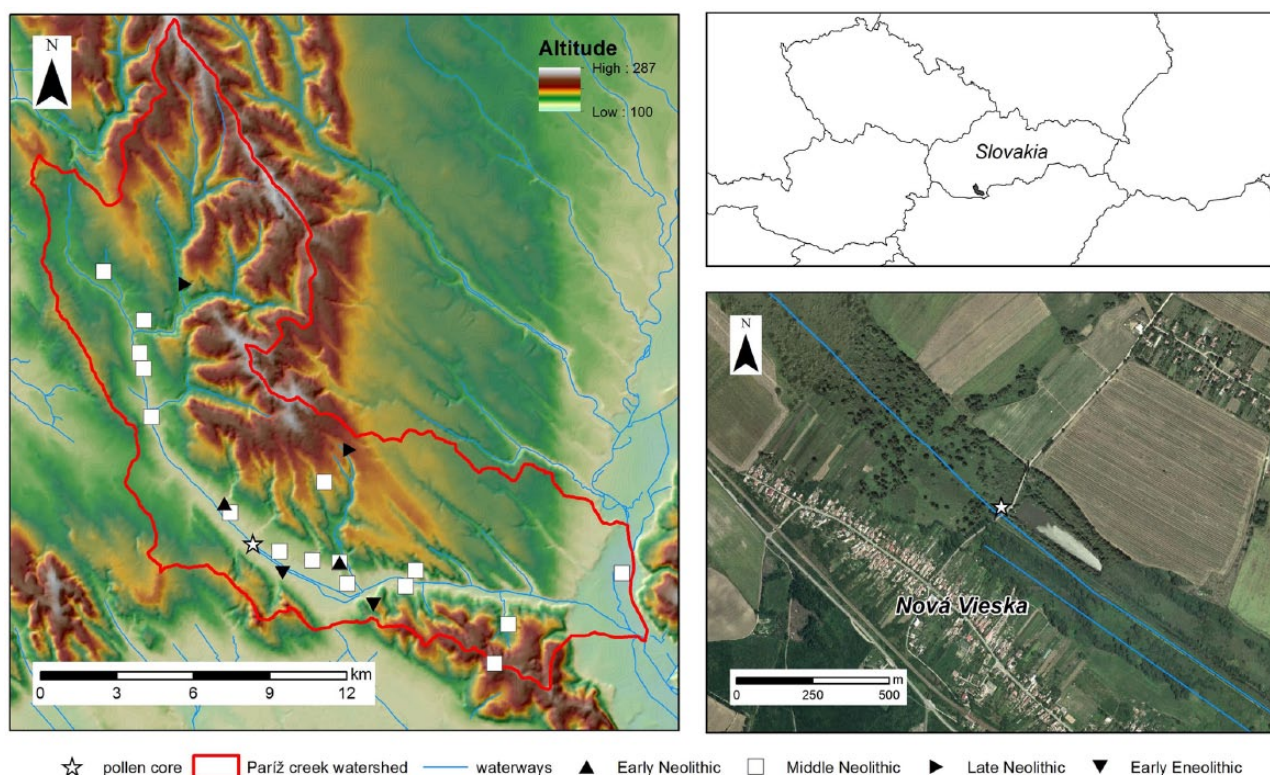


Figure 1. Localisation of the coring site in the Parížske močiare marshes and archaeological sites in the Paríž creek watershed.

1995, 2000) but has not yet been confirmed in the Little Hungarian Plain. Between 11,500–9500 cal. BP, temperate trees (*Corylus*, *Quercus*, *Ulmus* and *Tilia*) spread to the landscape of Carpathian Basin forming species-rich communities of mixed oak forest (e.g. Sümegi et al., 2012); however, spatial differences were recorded in the early Holocene forest composition (e.g. Sümegi et al., 2002). Despite this information, we lack studies that would confirm survival and spread of thermophilous species during the Late Glacial and early Holocene period in the Little Hungarian Plain. Two records partially deal with this problem (Hájková et al., 2013; Petr et al., 2013). Both suggest the early Holocene spread of temperate trees (*Quercus*, *Ulmus*, *Tilia* and *Corylus*) into the transition zone between the Carpathian Basin and the Western Carpathians, but do not have appropriate dating.

We used multiple proxies (pollen, plant macrofossils, molluscs, organic content (OC) and magnetic susceptibility (MS)) to investigate sediments in the Parížske Močiare Marshes (PM) Reserve, an area continuously occupied by humans since the Early Neolithic Period (7500 cal. BP). Our goal was to reconstruct the character of the landscape and marsh environments during the unstable condition of the Pleistocene/Holocene transition and early Holocene period and to detect possible human intervention on the landscape since the early Holocene period.

The specific aims are to (1) investigate the establishment of temperate trees at the onset of the Holocene, (2) assess the postglacial development of temperate trees around the study site and to find site-specific patterns (if any) in the postglacial development of forest communities, and (3) determine whether climatic oscillation or disturbances by fire and/or human impact represented critical factors for the development of mixed oak forests during the periods of early and middle Holocene.

Material and methods

The study site

The PM National Nature Reserve is one of the most important wetlands in Slovakia. The site is located in a shallow valley on a

floodplain of the Paríž Creek, in the Podunajská nížina lowland, the northern subunit of the Little Hungarian Plain (Figure 1). Today, the climate of the site surroundings is warm and somewhat dry, with an approximate mean annual temperature of 8–9°C (mean January temperature from –1°C to –4°C; mean July temperature from 20.5°C to 19.5°C). Annual precipitation is about 530–650 mm (<http://geo.enviroportal.sk/atlassr/>).

The study area is tectonically young and intersected by faults that have helped form the valley (Mazúr and Lukniš, 1978). These faults have caused blockage of the valley and formation of a flow-through lake. Impeded local hydrological drainage led to accumulation of organic material. Today, the marshes fill the lowermost part of the valley, which is 9 km long and 1 km wide at the widest part. The eastern slopes of the valley are steep, up to 59°, while the western slopes are flatter, with a maximum inclination of 5° (Hreško et al., 2005). Chernozems are the dominant soil type of the Paríž catchment (70%), but luvisols and/or cambisols cover 30% (Šály and Šurina, 2012). Today, the site is vegetated mainly with reed beds (*Phragmites-Magnocaricetea*). In the northern part, these change to mesophilous meadows (*Molinio-Arrhenatheretea*). Alluvial forests (class *Salicetea purpureae*) also occur in fragments (Halada and David, 2005). The coring site (N 47°52'29.77"; E 18°27'41.17"; 123 m a.s.l.) was situated near the village of Nová Vieska, in a shallow part of the mire, just outside the protected area.

Settlement history

The watershed of Paríž Creek is a part of the southwest Slovakian traditional habitation zone, with prominent settlement records from the Upper Palaeolithic onwards (Bárta, 1965). A total of 36 archaeological sites from the early Holocene to mid-6th millennium cal. BP were mapped in the watershed. In our study, only 23 well-described sites were used (Figure 1), representing the early, middle and late Neolithic (7700–6100 cal. BP) and early Eneolithic (early Copper Age; 6100–5521 cal. BP) periods (Tóth et al., 2011).

Table 1. Stratigraphy and description of peat deposits at Parížske močiare marshes according to Troels-Smith (1955).

Depth (cm)	Troels-Smith system	Description
315–340	As3Sh1Th+Gg(min)+	Dark-grey clay and small stones; mollusc shells
340–360	As1Sh2D11Th+Gs+A	Dark-brown decomposed woody/sedge peat with admixture of clay
360–387	Sh2D12Gs+A	Dark-brown decomposed woody peat
387–420		<i>Quercus</i> sp. trunk
420–440	As3D11Th+Gg(min)+A	Light-brown clay with layers of woody peat and small stones; mollusc shells
440–450	As1Sh2D11Ga+A	Dark-brown woody peat with admixture of clay
450–460		<i>Quercus</i> sp. wood
460–470	Sh2D12	Dark-brown decomposed woody peat
470–480	As1Sh2D11	Dark-brown decomposed woody peat with narrow layers of light-brown clay; mollusc shells
480–498	Sh2D12	Dark-brown decomposed woody peat
498–510	Ga3Ag1	Grey calcareous fluvial sands
510–515	Ag3Gs1Gg(maj)+	Grey silty sand with pebbles

Components: Ag – silt; As – clay; D1 – woody peat; Ga – fine sand; Gs – coarse sand; Gg(min) – little stones (2–6 mm); Gg(maj) – gravels (6–20 mm); Sh – entirely decomposed organic material; Th – herbaceous peat; A – charcoal.

Palaeoecological analyses

Material for palaeoecological analyses was obtained in 2010 using a percussion drilling set. The 520-cm-long sediment core (5-cm diameter) was stored in plastic (PVC) tubes. Sediment stratigraphy and lithological properties were described following Troels-Smith (1955; Table 1). Material for pollen, OC and MS analyses was sub-sampled at 5-cm intervals (510–350 cm) or 2-cm intervals (350–320 cm), each sample with a volume of 1 cm³. Sediment for macrofossil analyses (analysis of plant macro-remains and molluscs) was sub-sampled at 5-cm intervals (520–320 cm), each sample having a volume of 50 cm³.

MS and OC (weight loss on ignition) measurements. MS was determined using a Kappabridge KLY-2 device. The results were normalised to obtain mass-specific MS in m³/kg/10⁹. MS results provide information about the import of alloegenic material eroded from the surrounding basin (e.g. Nazarok et al., 2014).

Samples for determination of OC were dried for 7 days at room temperature, then dried at 105°C for 1 h to remove air moisture before ignition for 3 h at 550°C (Heiri et al., 2001) in order to determine OC (loss on ignition (LOI)).

Pollen analysis. Samples for pollen analyses were prepared by a standard procedure (Erdtman, 1960; Faegri and Iversen, 1989). A known amount of *Lycopodium* spores was added to each sample prior to chemical treatment. Samples containing clastic material were pre-treated with concentrated HF and then processed using KOH and acetolysis (Faegri and Iversen, 1989). At least 500 terrestrial pollen grains were identified in each sample using pollen keys (Beug, 2004; Punt and Clarke, 1984) and pollen atlases (Reille, 1992, 1995, 1998). Non-pollen palynomorphs follow van Geel et al. (1980). The nomenclature of pollen types follows Beug (2004) and Punt and Clarke (1984) for the family Apiaceae.

Fire history of the coring site surroundings was reconstructed through measurement of microscopic and macroscopic charcoal concentration in the sedimentary sequence. Microscopic charcoal was determined during pollen analysis and quantified using particle counts in relation to *Lycopodium* counts to give the charcoal concentration in particles/cm³ (Tinner and Hu, 2003). Macroscopic charcoal was determined during plant macrofossil analysis.

Pollen percentages were calculated based on the total sum (TS) of terrestrial arboreal pollen (AP) and non-arboreal pollen (NAP) (AP + NAP = 100%), with exclusion of aquatic and local mire plants, Pteridophyta, algae, fungi and other non-pollen palynomorphs. The percentage of spores and non-pollen palynomorphs is related to the extended sum (AP + NAP + spores and non-pollen palynomorphs = 100%). The pollen diagram was drawn in Tilia v.

1.7.16 (Grimm, 2011). The pollen profile was divided into local pollen analytical zones based on optimal splitting by information content using the broken-stick model to determine a statistically valid number of zones, as implemented in the program pspoll 4.27 (Bennett, 1996).

Macrofossil analyses. Sediment for macrofossil analyses was rinsed through a 200-µm sieve. Plant diaspores and other remains were examined under a dissecting microscope at a magnification of 12× and higher. For determination of plant macro-remains, several atlases and books were used (i.e. Berggren, 1969; Bojnanský and Fargašová, 2007; Cappers et al., 2006; Katz et al., 1977; Velichkevich and Zastawniak, 2006, 2008), together with reference material of recent fruits and seeds. Mollusc shells were separated from other macrofossils and determined under a dissecting microscope according to Ložek (1964) and M. Horsák's personal reference collection. Remnants of slugs were not considered. The nomenclature of molluscs follows Horsák et al. (2013a). Macrofossil diagrams were created in Tilia v. 1.7.16 (Grimm, 2011). To determine the number of significant zones in the diagram, a cluster analysis with optimal splitting by sums-of-squares was used based on the broken-stick model in the program pspoll 4.27 (Bennett, 1996).

Macrophysical climate model. Because of the absence of any local palaeoclimatic data for the region, we used the macrophysical climate model (MCM) as an independent data source. MCM is a 'heat-budget model predicted on orbital forcing, variations in atmospheric transparency, and the principles of synoptic climatology' (Bryson 2005; Bryson and McEnaney DeWall, 2007). The MCM does not use any biological proxies and is derived from astronomical data (Milankovitch cycles) and a radiocarbon-dated series of over 2400 volcanic eruptions (for the method, see Bryson and McEnaney DeWall, 2007), locally calibrated by a long series of meteorological data. The model has a high resolution (single centuries, 100-year averages by month), is site-specific (implicitly includes local influences like topography), provides research with testable hypotheses (Hajnalová, 2012) and has already been successfully verified against proxy data elsewhere (in archaeology cf. Dreslerová, 2011; Hajnalová, 2012; Higgins and McFadden, 2009; Riehl et al., 2008). We built the MCM for Hurbanovo, which is 20 km west from the sampling point and represents the closest meteorological station. The observed climate of Hurbanovo for 1961–1990 (provided by the Slovak Hydrometeorological Institute in Bratislava) was used in the MCM.

Chronology. A total of 11 samples of terrestrial plant macrofossils were dated using ¹⁴C accelerator mass spectrometry (AMS) facility

Table 2. Results of ^{14}C dating from Parižske močiare marshes peat profile. *UGAMS10039 and *UGAMS 10040 were excluded from the depth-age model (for details, see Chronology).

Samples (lab. code)	ID	Depth (cm)	Dating method	^{14}C age (uncal. BP)	Calibrated ^{14}C age (cal. BP) (95, 4% CI)	Mean calibrated ^{14}C age (cal. BP) (95, 4% CI)	Material
UG-10035	PM 1	500–498	AMS	9676 \pm 30	11238–11167	11201	Seeds
UG-10036	PM 2	490–488	AMS	9230 \pm 30	10500–10276	10390	Seeds
UG-10037	PM 3	460–458	AMS	9120 \pm 30	10300–10221	10268	Seeds, buds
UG-10038	PM 4	440–438	AMS	8390 \pm 30	9487–9308	9421	Seeds, buds
DSH-4415	PM 9	424–422	AMS	8380 \pm 120	9546–9033	9343	Seeds, buds
*UG-10039	PM 5	380–378	AMS	8830 \pm 30	10147–9709	9914	Buds
*UG-10040	PM 6	360–358	AMS	9080 \pm 30	10261–10196	10232	Seeds
GRA-56625	PM 11	360–359	AMS	7975 \pm 60	9002–8643	8834	Seeds
UG-10041	PM 10	340–338	AMS	5210 \pm 25	5995–5916	5960	Seeds
DSH-4414	PM 7	330–329	AMS	4810 \pm 58	5653–5330	5525	Seeds
UG-10042	PM 8	322–320	AMS	4800 \pm 20	5594–5476	5521	Seeds

cal.: calibrated ages; BP: Before Present (1950); AMS: accelerator mass spectrometry.

of the Centre for Applied Isotope Studies, University of Georgia, USA (sample code: UG-); the Centre for Isotopic Research on Cultural and Environmental Heritage (CIRCE) (DSH-); and the Rijksuniversiteit, Groningen, the Netherlands (GRA-) (Table 2). Two results of radiocarbon dating (UG-10039 and UG-10040) resulted in reversed ages and indicated that the sedimentation rate was not uniform.

To model ages of samples and for calibration of ^{14}C ages, we used P_Sequence of OxCal 4.1 with event spacing of 0.1 cm (Bronk Ramsey, 2008, 2009, 2011) and IntCal13 (Reimer et al., 2013). The age–depth model was sustainable only if the two aberrant dates (UG-10039, UG-10040) were designated as outliers (Figure 2). In the subsequent sections, the age of each sample refers to the centre of interpolated calibrated age before year BP, with 95.4% probability.

Results and interpretations

Stratigraphy and sediment description

The deposit of organic woody material accumulated on the top of fluvial sands (520–500 cm) and has a maximum depth of 180 cm (500–320 cm). Most of the organic sediment consists of decomposed peat with interlaid clay, wood and mollusc layers rich in calcium carbonate (CaCO_3) (Table 1). The material accumulated above an oak trunk at 385–360 cm (Table 1) was most probably re-bedded, as indicated by two reversed radiocarbon data. At the depth of 320 cm, sedimentation of organic material ceased and was overlaid by minerogenic sediment.

According to sediment composition and analysis of OC and MS, five main zones were distinguished in the profile (Figure 3). In the lower part of the sediment record (**Zone PMse1**; 510–498 cm), gradually declining MS but increasing OC imply reduction of allogenic input. The next phase (**Zone PMse2**; 498–420 cm) was characterised by a fluctuation in values of OC and MS, indicating the accumulation of organic sediment and gradual infilling of the depression by mineral material. The peak of MS at 440 cm was remarkable, suggesting inflow of mineral material. Another oak trunk at depth 420 and 387 cm interrupts the accumulation of other organic material in the profile. At 387 cm (**Zone PMse3**; 387–360 cm), directly above the oak trunk, accumulation of woody organic sediment recommenced, indicated by an increasing trend of OC values and declining MS values. The woody organic material was finally replaced by gradual incorporation of clay at 360 cm. This part of the sediment was redeposited, probably because of the event also connected with the deposition of the oak trunk. The proportion of clay particles increased towards the top of the sediment (**Zone PMse4**; 360–320 cm), reflected in the trend of both sediment analyses – the curve of OC declined, whereas the

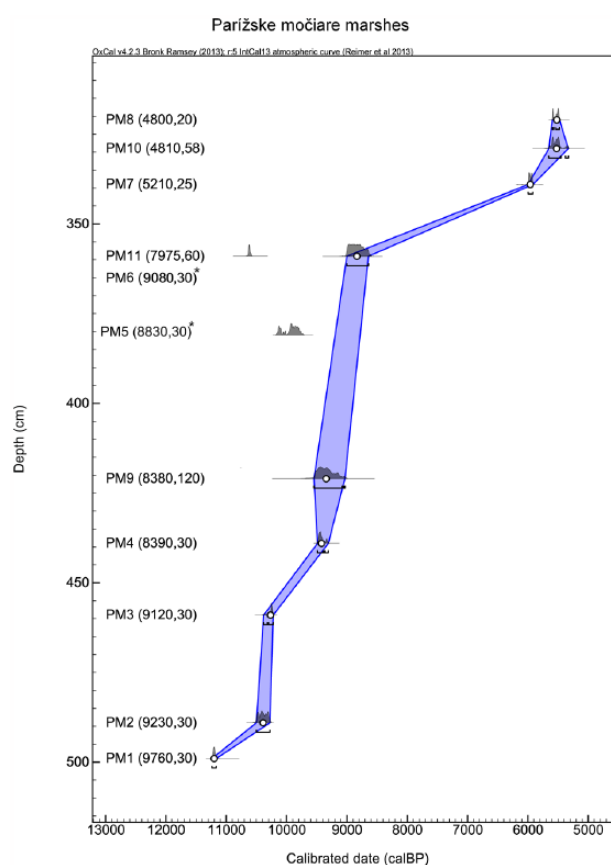


Figure 2. Age–depth relationship model of the Parižske močiare marshes profile based on nine radiocarbon dates produced in OxCal 4.1.

cal.: calibrated ages; BP: Before Present (1950).

Dates *PM5 (8830,30) and *PM6 (9080,30) were excluded from the age–depth model.

curve of MS increased. This indicates increased input of allogenic material as the result of soil erosion. From 320 cm to the top of the core, a minerogenic sediment formed from erosion of the slopes surrounding the basin appeared.

Regional vegetation development

Based on pollen analysis and dating, regional vegetation development was divided into three main phases. The pollen record consists of 43 samples divided into six zones (Figure 4).

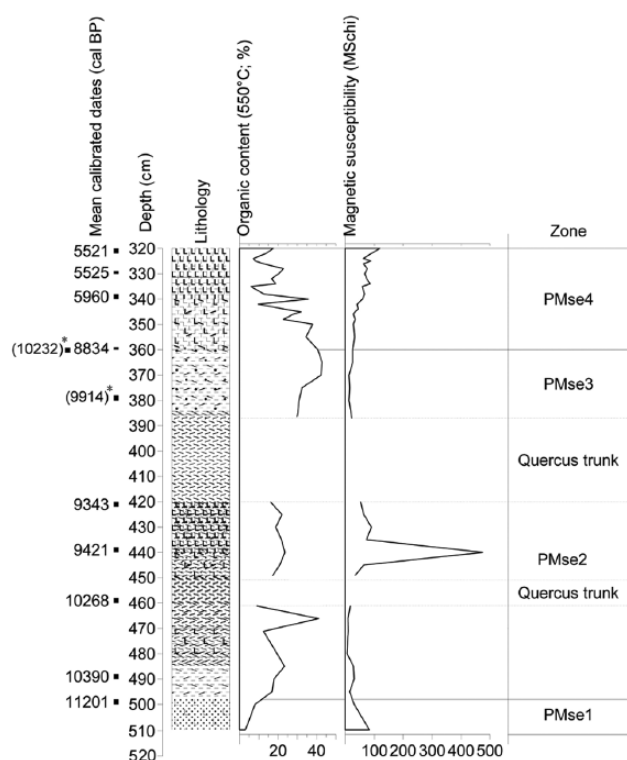


Figure 3. Results of organic content (LOI) and magnetic susceptibility measurement from the Parížske močiare marshes profile.

LOI: loss on ignition.

(*) – date excluded from the depth–age model.

Phase 1: The initial stage. The initial stage of upland vegetation development (**Zone PMpa1**; 500–497.5 cm, 11,201–10,998 cal. BP) was characterised by the dominance of *Pinus* (25%), *Betula* (10%) and, to a lesser extent, *Salix* (8%) from AP types and of Poaceae (50%) and *Artemisia* (5%) from herbaceous pollen types. Pollen grains of mesophilous trees (*Quercus* and *Ulmus*) were sporadically detected.

Phase 2: Early Holocene landscape transformation. The first pronounced change in the landscape took place at around 11,000 cal. BP (**Zone PMpa2**; 497.5–455 cm, 10,998–10,056 cal. BP), accompanied by a decline of numerous cold-tolerant taxa. The proportion of *Pinus* pollen decreased to less than 10%, allowing the spread of pollen from temperate trees and shrubs (*Quercus*, *Ulmus*, *Tilia*, *Fraxinus* and *Cornus sanguinea*). The amount of *Quercus* increased rapidly, and oak reached almost 80% of the total sum of terrestrial pollen. Among herbaceous pollen types, pollen grains of *Artemisia* (10%), *Jasione montana* t., *Plantago media/major* and *Centaurea scabiosa* t. indicate the presence of steppe vegetation, while *Pimpinella major* t. and *Filipendula* record the occurrence of more mesic open habitats. The next change in forest dominance occurred at a depth of around 455 cm (**Zones PMpa3**; 455–420 cm; 10,056–9325 cal. BP), when a rapid increase of *Corylus* (30%) was recorded, with synchronous decline of *Quercus* (30%) and *Ulmus* (5%). Qualitative and quantitative increases of herbaceous pollen suggested the spread of various open habitats. Pollen grains of *Plantago lanceolata* t. and *Polygonum aviculare* t. appeared for the first time. Scarce occurrence of coprophilous fungi (*Podospora*) indicated grazing animals. A small amount of micro-charcoal was recorded. Above this zone, at 420–385 cm, an oak trunk was present in the core.

Phase 3: Mid-Holocene landscape changes. Pollen analysis in the next phase (**Zone PMpa4**; 385–352 cm; ?–7685 cal. BP) showed the same trends as in the previous zone. Radiocarbon dating suggested occurrence of redeposited material in the lower part of this zone (**Zone PMpa4a**; 385–360 cm). Among arboreal taxa, *Corylus* dominated (38%), admixed with *Quercus*, *Betula*, *Pinus* and *Salix*. The presence of spores of coprophilous fungi (*Podospora* and *Sporormiella*) indicated grazing. From 360 cm (**Zone PMpa4b**; 360–352 cm), pollen of *Fagus* started to continually occur. In the next zone (**Zone PMpa5**; 352–341 cm; about 7685–6104 cal. BP), a slight change in abundance of deciduous tree pollen was detected. *Quercus* pollen did not change significantly, while *Corylus* and *Ulmus* declined slightly and *Fraxinus*, *Tilia* and *Picea* increased slightly. More pollen from light-demanding shrubs (*C. sanguinea* and *Sambucus*) implied the spread of open vegetation patches. Pollen of wetland and alluvial plants occurred in higher quantities (e.g. *Lysimachia vulgaris* t. and *Peucedanum palustre* t.) and *P. aviculare* t. reappeared. The recorded decline in Chenopodiaceae, with consequent increase of Apiaceae, probably reflected a more seasonally stable water level and replacement of ruderal communities by wet meadows (cf. Magyari et al., 2010). Spores of *Sporormiella* suggested grazing. Towards the end of this zone, micro-charcoal particles appeared in higher quantities.

The last significant change in the character of the landscape (**Zone PMpa6**; 341–320 cm; 6104–5521 cal. BP) is linked to the decline of deciduous trees (*Quercus*, *Corylus*, *Ulmus*, *Salix* and *Fraxinus*) and the appearance of pollen grains of cereals. Pollen of deciduous trees (*Quercus*, *Ulmus*, *Fraxinus* and *Corylus*) decreased synchronously with the increase of conifers (*Pinus* and *Picea*). This probably reflected the decline in closed canopy around the study site, which allowed pollen input from regional vegetation (coniferous trees). Among herbaceous types, there was an increase in pollen types indicating the creation and spread of new open habitats such as mesic meadows (*Centaurea jacea* t., *P. lanceolata* t.), ruderal habitats (*P. aviculare* t., *Urtica*) and fields (Cerealialia). Large amounts of micro-charcoal particles indicated the occurrence of fire.

Development of the local environment within the marshes

To obtain a complex picture about development of a wetland environment, results of plant and mollusc macrofossil analyses are presented together. The diagrams show the succession of the wetland in 34 plant macrofossil samples and 16 mollusc macrofossil samples related to the six main zones (Figure 5) and four zones, respectively (Figure 6). Development of the marsh environment was divided into three main phases.

Phase 1: The initial stage. The sediment from the oldest period (**Zones PMma1**; **PMmo1**; 520–500 cm; older than 11,201 cal. BP) contained molluscs and plant macrofossils, but only the latter had sufficient information for palaeoecological interpretation. Plant macrofossil assemblages were characterised by the presence of *Selaginella selaginoides*, *Betula* sp., Cyperaceae, *Carex canescens* and *Juncus* sp. The presence of a water body was indicated by macrofossils of *Chara* sp., *Potamogeton gramineus*, *P. filiformis* and bryozoan *Cristatella*. The cold-preferring, light-demanding species *S. selaginoides* was also determined as a typical plant of Younger Dryas in the Swiss Alps (Tobolski and Ammann, 2000), Poland (Gałka and Sznel, 2013) and Denmark (Mortensen et al., 2011); *P. filiformis* is an arctic-alpine species today, but during the Late Glacial, it was widespread in Central Europe (Gałka et al., 2014; Petr et al., 2013). The few records of mollusc species indicated open (probably damper) habitats and shallow marshes.



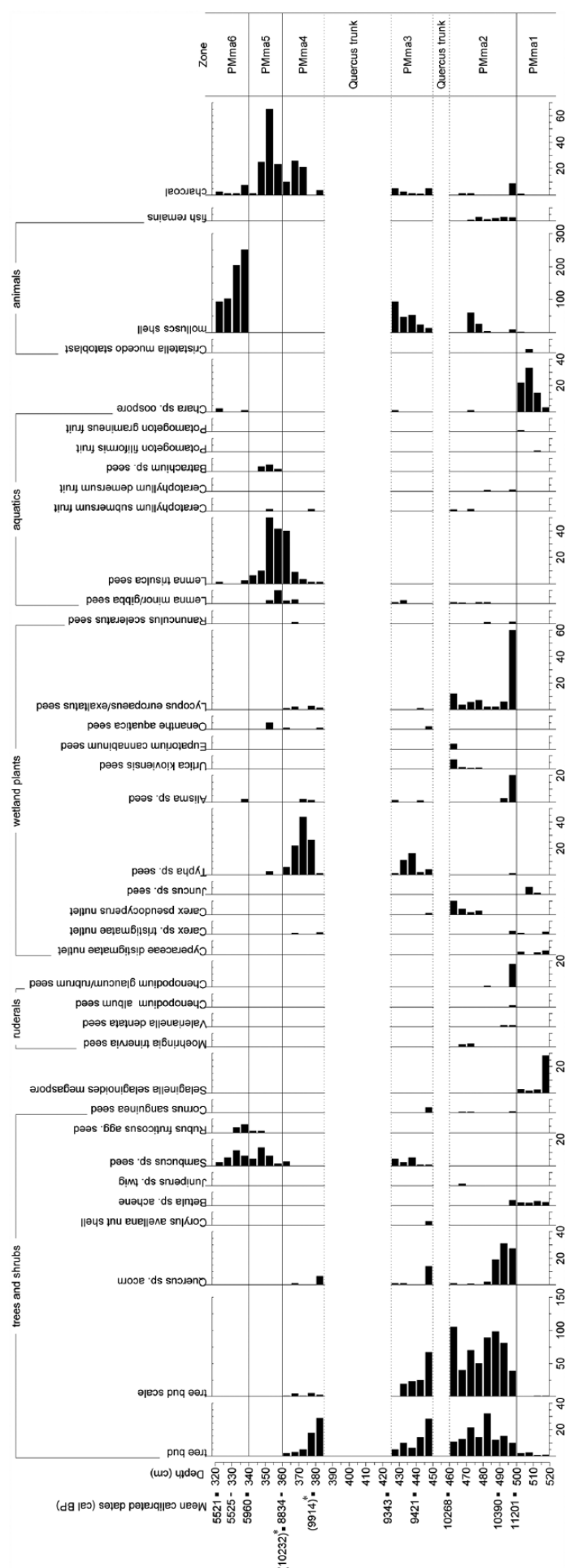


Figure 5. Plant macro-remains diagram from the Parízske močiare marshes profile in absolute numbers. (*) – date excluded from the depth–age model.

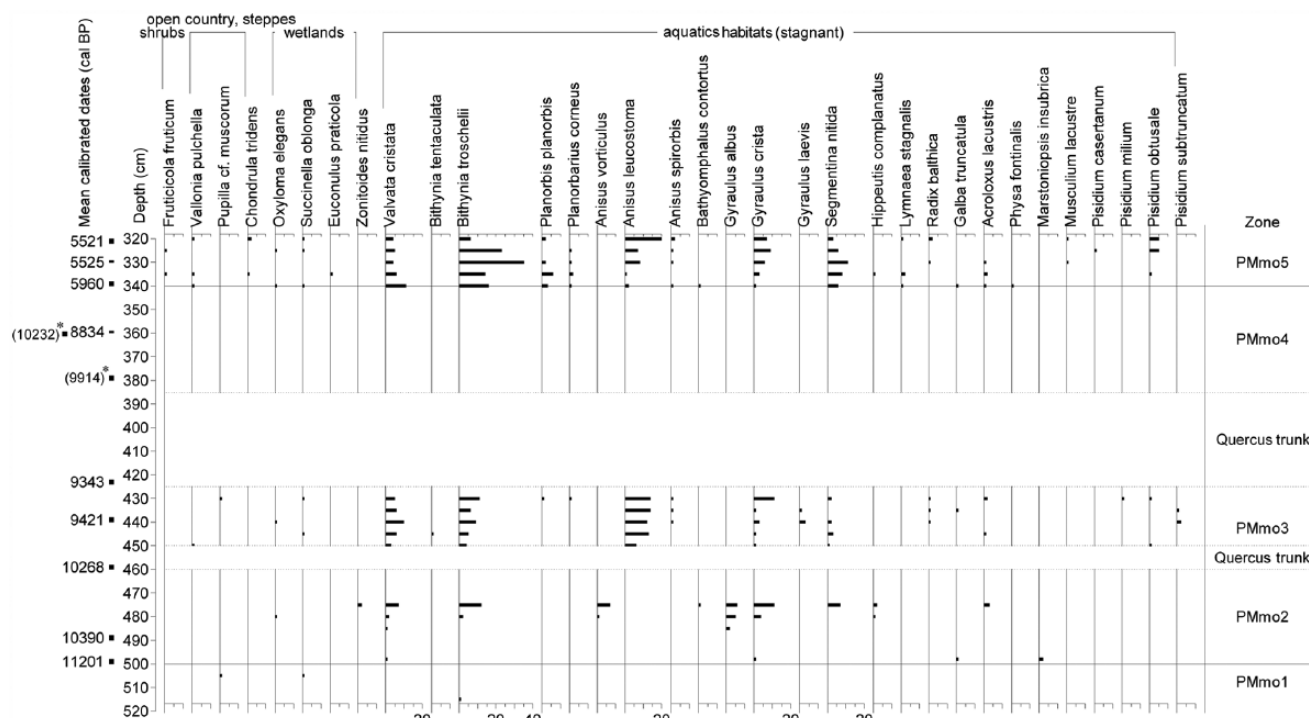


Figure 6. Mollusc diagram from the Parižské močiare marshes profile in absolute numbers.
(*) – date excluded from the depth–age model.

Phase 2: The early Holocene transformation of marshes. At the beginning of this phase (**Zones PMma2, PMmo2**; 500–460 cm; about 11,201–10,268 cal. BP), there was a rapid increase in the abundance of macrofossils of annual ruderal herbs, such as *Chenopodium glaucum/rubrum*, *Chenopodium album* agg. and *Valerianella dentata*, as well as wetland species (*Alisma* sp., *Lycopus europaeus/exaltatus*, *Ranunculus sceleratus* and *Typha latifolia/angustifolia*, etc.). Trees and shrubs expanded immediately, represented in the macrofossil record by *Quercus* sp. and *C. sanguinea*. The presence of heliophilous shrubs, *Juniperus* sp. and *C. sanguinea* suggested open vegetation. In the second half of the zone, herbaceous species increased, especially wetland plants *Carex pseudocyperus*, *L. europaeus*, *Urtica kioviensis*, *Solanum dulcamara* and so on. Aquatics *Ceratophyllum demersum*, *C. submersum*, *Chara* sp., *Lemna minor/gibba*, ehippia of the aquatic crustacean order Cladocera and fish scales pointed to the existence of a shallow pool/lake. The recorded mollusc species represented a mixture of species inhabiting stagnant water habitats (many aquatic species) and a humid littoral zone in its vicinity (*Zonitoides nitidus* and *Oxytoma elegans*). Aquatic species indicated a shallow pool/lake with a rich cover of macrophytes, but the pool was rather permanent and of the lower tropical level, as suggested by *Anisus vorticulus*. The record of freshwater snail *Marstoniopsis insubrica* at the very bottom of this layer was remarkable, namely, with respect to its postglacial spread northward.

In the next step in wetland development (**Zones PMma3, PMmo3**; 450–420 cm; about 9844–9325 cal. BP), the initial high peak of *Quercus* sp. with the occurrence of shrubs (*Corylus avellana* and *C. sanguinea*) gradually declined. The predominance of *Sambucus nigra/racemosa* took place afterwards. Among the wetland plants present were *Alisma* sp., *Oenanthe aquatica*, *Carex vesicaria*, *C. pseudocyperus* and so on. The trophic level of the environment increased, as indicated by the appearance of *T.*

angustifolia/latifolia, *Sparganium* sp. and *Daphnia ehippia*. The aquatic vegetation was dominated by *Chara* sp. and *Lemna* sp. Fish macrofossils disappeared, but molluscs rapidly increased in this zone. The data suggest sedimentation at the bottom of shallow pool, probably seasonally desiccating during drier months or years. Freshwater snails and bivalves were recorded in great abundance (172 shells in total) and diversity (16 species). Besides many aquatic mollusc species, only five specimens of three land-snail species were found. These species indicated the presence of littoral marshy habitats (*O. elegans*), which were without trees or shrubs, as suggested by two open country species (e.g. *Vallonia pulchella*). The small amount of macro-charcoal indicated fires. At a depth of 420–385 cm, a trunk of *Quercus* sp. was found.

Phase 3: The mid-Holocene formation of wetland. At the beginning of this phase, a considerable gap in the succession of mollusc communities was found (**Zone PMmo4**; 385–340 cm). This was probably caused by a lower amount of calcium carbonate and/or at the same time a higher content of organic matter; thus, all shells were probably dissolved by organic acids in the sediment.

The sediment at 385–360 cm (**Zone PMma4**; ?–8834 cal. BP) was most probably redeposited, although plant macro-remains displayed the similar trend as the previous zone (**Zone PMma3**; 450–420 cm), namely, the decline of deciduous trees from their initial dominance. The amount of macro-charcoal is high. Open waterlogged spaces were colonised by *T. angustifolia/latifolia*, *Alisma* sp. and *L. europaeus/exaltatus*. The existence of a shallow depression with water was confirmed by the presence of *C. submersum*, *O. aquatica* and *Lemna trisulca*.

Such conditions lasted until about 8834 cal. BP (**Zone PMma5**; 360–340 cm, 8834–5960 cal. BP), when species indicating stable water conditions reappeared (*Batrachium* and *O. aquatica*). At that time, macro-remains of deciduous trees (*Quercus* and *Corylus*) disappeared, whereas nitrophilous shrubs (*S. nigra/racemosa* and

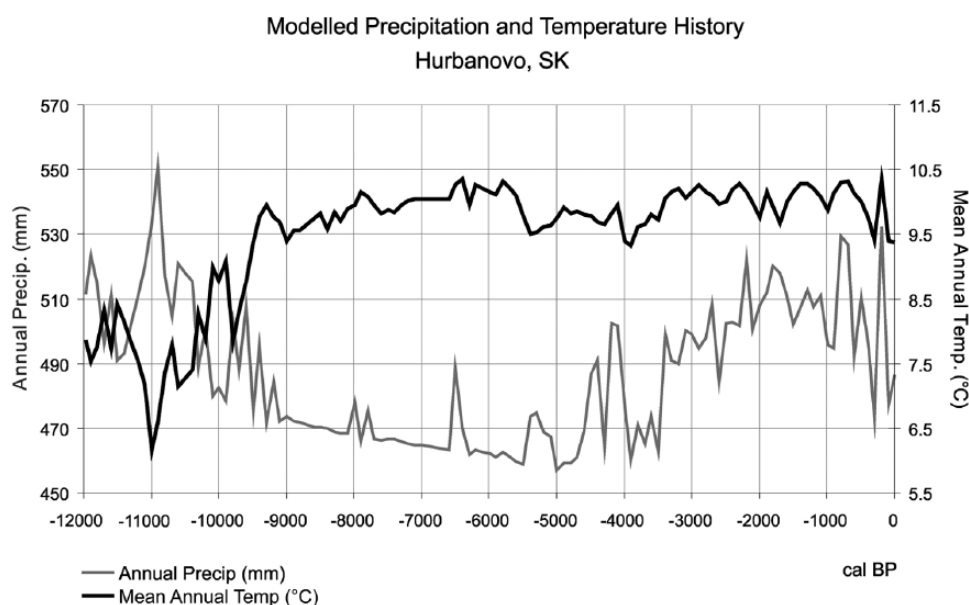


Figure 7. Modelled precipitation and temperature history for Hurbanovo, Slovakia.

Depth (cm)	Age (cal BP)	Sedimentology (OC, MS)	Molluscs	Plant macroremains	Pollen	MCM model	Human impact
320	5521	gradual input of allogenic material erosion	open littoral habitats (<i>Valonia pulchella</i>)	shrubs (<i>Sambucus, Rubus</i>)	decline of mixed oak forest	humid oscillation	deforestation ruderal habitats fields
330	5525		shrubs (<i>Fruticicola fruticum</i>)		spread of open habitats Cerealia		
340	5960						
350		redeposited sediment		shrubs (<i>Sambucus</i>) aquatics macro-charcoal	shrubs (<i>Sambucus</i>) wet meadows micro-charcoal	humid oscillation	forest management? clearance of forest fire
360	8834 (10232)*			redeposited sediment	<i>Fagus</i>	humid oscillation	
370							
380	(9914)*	increase of organic material		<i>Typha</i> sp.	redeposited sediment		
390							
400			<i>Quercus</i> trunk				
410							
420							
430	9343	increase of allogenic input erosion	seasonally desiccating open littoral habitats (<i>Valonia pulchella</i>)	<i>Corylus, Sambucus</i> disappearing of fish remains macro-charcoal	<i>Corylus</i> spread of open habitats micro-charcoal	humid oscillation	clearance of forest fire
440	9421					1. temperate maximum	
450			<i>Quercus</i> trunk				
460	10268	increase of organic content	shallow pool/lake rich in macrophytes humid littoral zone (<i>Oxyloma elegans</i>)	<i>Quercus</i> fish remains increase of nutrients (<i>Lycopodium, Alisma</i>)	<i>Quercus</i> open habitats (<i>Artemisia, Filipendula</i>)	cold and humid oscillation	generally increase of temperature
470						cold and humid oscillation	
480		gradual decline of allogenic input	open habitats shallow pool	cold shallow pool (<i>Potamogeton filiformis</i>) <i>Betula</i>	<i>Pinus, Betula, Poaceae</i>	cold and humid oscillation	
490	10390					cold and humid oscillation	
500	11201						
510							
520							

Figure 8. Summarised development of upland vegetation and wetland environment of the Parízske močiare marshes profile based on all obtained proxies.

(*) – date excluded from the depth–age model.

Rubus fruticosus) appeared. The large amount of charcoal suggested fire activity in this area. Later on (Zone PMma6; 340–320 cm, 5960–5521 cal. BP), tree macrofossils are absent from the sediment. Terrestrial vegetation was dominated by *S. nigralracemosa*, *R. fruticosus* agg. and wetland vegetation by *Carex riparia* and *Alisma* sp. Among aquatic flora, *Chara* sp. and *L. trisulca* occurred in this zone. The shell preservation was restored in the uppermost layers (Zone PMmo5; 340–320 cm, 5960–5521 cal. BP) of the profile. In

total, we obtained 272 shells of aquatic and 14 shells of terrestrial molluscs. The recorded species and their abundances indicated exactly the same conditions as reconstructed from the zone PMmo3 (450–425 cm). The most abundant freshwater snail species were the same in both these zones (i.e. *Bithynia trosschellii*, *Anisus leucostoma* and *Valvata cristata*). The recorded terrestrial snail species confirmed the existence of humid but open littoral habitats (e.g. *Euconulus praticola* and *V. pulchella*). The other two species, found only

in this zone, also showed the presence of dry steppe areas (*Chondrula tridens*) on one hand, and shrubby places (*Fruticicola fruticum*), on the other hand.

The MCM. According to the MCM, the climate history during the period covered by the PM record was divided into two major phases (Figure 7).

PMmcm1 (500–440 cm; 11,201–9422 cal. BP). According to the MCM, the first period is characterised by gradual increase in temperature but with several cold, wet oscillations.

At the beginning of organic sedimentation in the PM basin, the mean annual temperature was around 8.0°C and annual precipitation around 500 mm. Shortly afterwards, there was a strong cold and humid climatic oscillation, lasting from 11,100 to 10,900 cal. BP. This period correlates with the decline in solar activity as observed in the $\delta^{18}\text{O}$ record of the Greenland ice core records – the Preboreal oscillation (Rasmussen et al., 2007).

From this point, the temperature began increasing generally. This development was interrupted by four cold and wet oscillations of varying magnitude. During the most prominent one at 11,100–10,900 cal. BP, the mean annual temperature dropped to 6°C. The following oscillations at around 10,600–10,400 cal. BP, 10,200 cal. BP and 9800 cal. BP were milder. At 9300 cal. BP, the temperature reached its first Holocene maximum (9.95°C, 470 mm). According to the MCM, this was a period of relatively stable, warm conditions, oscillating between 9.4°C and 10.4°C, with slowly declining annual precipitation that reached the minimum (457 mm) at 5000 cal. BP. The model reconstructed five additional humid phases, at 9200, 8000, 7800, 6500 and 5400–5100 cal. BP.

Discussion

The combination of multiple analyses, including pollen, macrofossils and molluscs together with sediment analyses, provided complex data on the dynamics of local wetland environment and regional vegetation (Figure 8). Based on these data, we discuss below an unusual early occurrence of oak (forest) and examine the underlying environmental drivers, including climate change and disturbances by fire or human activities.

Early Holocene establishment of mixed oak forest

Plant macrofossils from the oldest period (more than 11,201 cal. BP, 520–500 cm) indicated a cold climate and open character and low productivity of the local vegetation. The local condition of the marshes changed at around 11,200 cal. BP when the number of cold-tolerant plant taxa (e.g. *P. filiformis*) declined, while thermophilous and deciduous forest species (*Quercus*) began to appear. However, finds of cold-adapted snail *M. insubrica* in the assemblages of 500–495 cm, the first find of this species in Slovakia (Horsák et al., 2013b), suggest that the climate remained cold. The cold stage of the early Holocene, at around 11,200 cal. BP, was detected in a single pollen sample only (500 cm). The low temperature and precipitation here were indicated by the presence of steppe elements in the vegetation (Brewer et al., 2002) and lower value of AP (less than 40%). These suggested that the landscape had a character of open cool steppe with patches of trees formed under cold, dry climatic conditions (cf. Magyari et al., 2010).

Scattered occurrence of *Quercus* and *Ulmus* was documented by the analysis of pollen and macro-remains (*Quercus*), suggesting the establishment of a mixed oak forest in the study region during the cold stage of the early Holocene (about 11,200 cal. BP; Figure 7). Such an early record of temperate trees in a landscape of cool-mixed wooded steppe vegetation implied their early (probably Late Glacial) immigration to this site from their cryptic glacial refugia situated elsewhere in the Carpathian Basin (e.g. Birks and

Willis, 2008; Tzedakis et al., 2013; Willis et al., 1995, 2000; Willis and Andel, 2004). Continuous occurrence of pollen of *Quercus*, *Tilia*, *Ulmus* and *Corylus* around 11,300 cal. BP was also recorded in other pollen profiles from the Slovakian part of the Little Hungarian Plain, in localities Šúr (Petr et al., 2013) and Bielice (Hájková et al., 2013). It seems that the northern part of the Carpathian Basin might have been a refugium of these temperate trees or represent an area where they arrived soon after climate amelioration.

Early Holocene expansion of mixed oak forest

The expansion of temperate trees occurred between 11,201 and 10,780 cal. BP (500–495 cm). The change in landscape character and wetland environment is documented by significant changes in species composition recorded by macro-remains and pollen. The MCM model showed rising temperatures but decreasing precipitation (Figure 7). The marshes transformed from a cold pool/lake with low nutrient supply to a more eutrophic shallow pool/lake, and the pollen record showed replacement of cool-mixed wooded steppe by deciduous forest, similar to that of other marginal parts of the Carpathian Basin (Hájková et al., 2013; Magyari et al., 2010; Petr et al., 2013; Willis et al., 1995, 1997). The establishment of deciduous forest and reduction of open steppe patches probably contributed to soil stabilisation in the basin. This was reflected in declining MS values, as a result of declining mineral input into the basin (e.g. Willis et al., 1995).

The early Holocene forest was mainly composed of light-demanding *Quercus* with some *Ulmus*, and must have been relatively open because oak seedlings need sufficient light for their survival (Ellenberg, 1996). During the early Holocene, forest taxa dominated in pollen assemblages (almost 90% of the TS; Figure 4) and in plant macro-remains (Figure 5). However, the presence of steppe herbaceous taxa (e.g. *Artemisia* and *C. scabiosa* t.) and wet meadow taxa (e.g. *Filipendula* and *Chaerophyllum hirsutum* t.) indicates persistence of open patches on loess slopes as well as within the floodplains (Hájková et al., 2013; Magyari et al., 2010). Moreover, macrofossils of light-demanding shrubs, such as *Juniperus* and *C. sanguinea*, together with mollusc assemblages of species preferring open terrestrial habitats (e.g. *V. pulchella*; Figure 6), support the conclusion that the landscape had an open park-like character, which might allow the spread of light-demanding mixed oak forest.

The postglacial migration of temperate trees showed a quite specific phenomenon – the remarkable early occurrence of *Quercus* in both pollen and macro-remains (wood) since 11,200 cal. BP, which was followed by exceptionally early expansion (10,390 cal. BP). Such an early spread of *Quercus* was unknown in the study region until now. Oak was expected to spread from its southern refugia between 13,000 and 11,000 yr BP (Brewer et al., 2002), reaching the southern part of Central Europe at around 9000 yr BP. This is in accordance with the sites situated at the edge of the Western Carpathians and Carpathian Basin (Hájková et al., 2013; Petr et al., 2013), where expansion of oak started at around 9500 cal. BP. However, it does not correspond to our results, in which *Quercus* expanded into the vegetation considerably earlier. The early Holocene *Quercus* peak is also inconsistent with other palaeoecological results from Northwestern and Central Europe, showing expansion of mostly *Corylus* among temperate trees (Giesecke et al., 2011; Huntley and Birks, 1983; Tallantire, 2002). Warm summers, cold winters and less moisture availability of the early Holocene period recorded in Northern Hemisphere (Kutzbach and Webb, 1993) contributed to higher seasonality, which, together with frequent fires (Clark et al., 1989), could explain this expansion (Finsinger et al., 2006; Huntley, 1993; Magyari et al., 2010). However, the climate of the early Holocene was unstable, with several cold and humid oscillations,

which may have influenced the spread of temperate trees. Moreover, a humid climate would be expected to suppress natural fires. In the following section, we discuss the possible impact of the local climate conditions and disturbances on the expansion of temperate trees in the study region.

The role of climate oscillations. The expansion of *Quercus* before *Corylus* was recorded during the Allerød period (14,000–13,000 cal. BP) in the Southern Alps. Higher moisture availability and low temperatures inhibited hazel and favoured the spread of taller trees such as *Pinus* and mixed oak forest (Finsinger et al., 2006). It is plausible that in our study region, a short-lived climatic oscillation at the onset of the Holocene, when the climate became more humid and cold, suppressed the spread of *Corylus* and favoured *Quercus*. The local MCM model indicates a rapid increase in precipitation and cooling during the period of oak expansion, suggesting conditions favouring *Quercus* over *Corylus* (Figure 7). Fish remains and water molluscs found at the beginning of the Holocene also indicate wet conditions, that is, a shallow, permanent pool/lake. A similar cold, wet oscillation was clearly detected in various proxies in the South Carpathian Mountains as well (Buczko et al., 2012; Tóth et al., 2012).

Corylus started to expand at about 9840 cal. BP (Figures 4 and 5). For that period, the MCM model showed that the climate became drier and warmer in comparison with the previous phase, which probably supported a change in forest dominance as *Quercus* was suppressed by *Corylus*. Fish remains did not occur in this level of the profile and mollusc communities reflected seasonally fluctuating water levels, probably as a consequence of warmer, drier conditions (Figure 8). The significant increase in temperature (early Holocene thermal maximum) has also been reconstructed using chironomids in the Central-Eastern Alps around 10,200–7,800 cal. BP (Ilyashuk et al., 2011) and around 9970 cal. BP in the South Carpathian Mountains (Tóth et al., 2012).

The role of disturbances: Fire and human interference. Disturbances by fire or human intervention are considered to be one of the main factors influencing postglacial migration of trees (Huntley and Birks, 1983), although their role has often been neglected (Keller et al., 2002). Based on several long-term studies, fire favours *Corylus* over *Quercus* (Tinner et al., 1999). However, several studies support the role of fire as a disturbance factor causing the spread of oaks in eastern North America (Abrams, 1992; Dey, 2002). Our concern here is whether early Holocene fire dynamics contributed to the different timing of postglacial tree migration at our study site as well.

During the period of *Quercus* expansion, only a small amount of charcoal was found, indicating a low fire frequency. Cold, humid oscillations reconstructed by the MCM model may have contributed to the reduction of fires during these periods. However, a park-like character of the landscape was open enough to support establishment of a mixed oak forest, and therefore, disturbances creating open patches (such as fire) were not required to maintain oak populations. The amount of charcoal particles increased alongside *Corylus* expansion (Figures 4 and 5). This correlation between the increase in forest fire and expansion of *Corylus* has been documented in the Southern Alps as well. Forest fire supported the spread of hazel, helping to maintain its high population density (Finsinger et al., 2006). Hazel can sprout well after a fire (Delarze et al., 1992), and its pollen production increases after opening up of forests (Aaby, 1986). The climate reconstructed by the MCM model may have been dry enough to trigger natural lightning, increasing fire frequency (cf. Feurdean et al., 2013).

Intentional ignition by Mesolithic populations must also be considered. Many studies show links between forest clearings and fires in the Mesolithic (e.g. Moore, 2000; Regnell, 2012; Sümegi,

1999; Wacnik, 2009), possibly triggered by human impact (Tolksdorf et al., 2013). Moreover, the spread of light-demanding taxa such as *Corylus* has been linked to the occurrence of Mesolithic settlements (Kuneš et al., 2008; Regnell, 2012). Hazelnuts were a very valuable crop during the Mesolithic (Regnell, 2012), and their production increases after opening of the canopy (cf. Innes et al., 2013). During the period of *Corylus* expansion, *Fraxinus* and *Betula* increased as well. Both of these pioneer trees spread after deforestation of the floodplain forest, which might suggest intentional clearance of the landscape (Magyari et al., 2001, 2012b). The subsistence of Mesolithic groups in this region depended on hunting and gathering, with hunting considered dominant (Sümegi et al., 2013). Creation of temporarily open areas in floodplain forest may have attracted game (Innes and Blackford, 2003). Burning and clearance of the landscape might trigger erosion (Willis et al., 1998) as reflected in the curve of MS values (Figure 3). All of these changes may be attributed to the human presence in the landscape, particularly through the creation of seasonal camp-like settlements and intensive foraging favouring the expansion of forest clearings (Sümegi, 2013).

We conclude that in our area, disturbances by fire were most likely an important factor affecting postglacial dynamics of hazel populations, but had little or no influence on the establishment and expansion of oak populations. Therefore, a lack of forest fires may have delayed the spread of hazel during the early Holocene.

The early Holocene expansion of Quercus: Local or regional phenomenon?

The dominance of *Quercus* in forest vegetation in our profile was rather short and directly coincided with the cold, wet climatic events reconstructed by the MCM model between about 11,000 and 10,200 cal. BP. On the other hand, the short duration of oak dominance may have been caused by local wetland oak stands, indicated by fragments of oak wood in the sediment, whereas *Corylus* occupied well-drained parts in upper parts of the basin. This might cause that pollen production of taller *Quercus* over-shaded the pollen rain of *Corylus*, which could be therefore under-estimated in the pollen diagram. On the other hand, *Corylus* is not a good competitor against taller trees of mixed oak forests (Tallantire, 2002), and it is likely that spread of *Corylus* was inhibited in such forests with dominant *Quercus* and *Ulmus* (Feurdean et al., 2007). However, open forests with dominant *Ulmus/Quercus* also spread after the climate improvement (c. 11,500 cal. BP) in the central part of the Carpathian Basin – Great Hungarian Plain (cf. Jakab et al., 2004; Sümegi et al., 2002). Similarly, the spread of *Quercus* before *Corylus* had been recorded in lowlands of SE Europe, for example, Romania (Feurdean et al., 2007) and Bulgaria (Connor et al., 2013). It is very plausible that the recorded early Holocene expansion of *Quercus* could be associated with environmental conditions of large lowland areas, which differ in climate, soil and geomorphology from those in the marginal parts of the Carpathian Basin and foothills of the Carpathians (Sümegi et al., 2012).

Nevertheless, oak most likely occurred early in the study region and its spread might be caused by a combination of factors, such as the location of the study site near its cryptic glacial refugium in the Carpathian Basin and specific local climatic conditions favouring the expansion of oak during the early Holocene.

The middle Holocene development of mixed oak forest

The mixed oak forest that developed during the early Holocene experienced no compositional changes until about 7398 cal. BP, when minor changes in the pollen curves of deciduous trees were recorded. At that time, macro-remains of deciduous trees

disappeared, whereas nitrophilous shrubs (*S. nigra/racemosa*, *R. fruticosus*) reappeared. Later, around 5960 cal. BP, a decline in almost all deciduous trees was recorded. All of these changes in the vegetation and forest communities may be attributed to human impacts.

Although the primary anthropogenic indicator (Cerealia) was not found in the pollen record in the period of Neolithic (7500 cal. BP), there are indirect traces of human impact on the vegetation and forest communities. Archaeological mapping has documented 21 sites, including 15 rather extended villages, dated to the middle and late Neolithic in the study area (Figure 1). Based on radiocarbon dates of the archaeological sites in SW Slovakia and adjacent regions, middle and late Neolithic habitation of the Pariž Creek valley most probably spanned from 7450 to 6250 cal. BP (Barta et al., 2012). A large charcoal peak occurred around 350 cm (7398 cal. BP; Figures 4, 5), corresponding to the settlement expansion documented in archaeological records. The increase of shrubs recorded by both macrofossils and pollen assemblages could also imply increased human pressure, especially in terms of landscape openness, grazing and ruderalisation (Marinova and Thiébaut, 2008). Grazing thins the forest canopy and promotes the spread of light-demanding shrubs such as *Cornus mas*, *C. sanguinea* and *Sambucus* (Moskal-del Hoyo, 2013). Spores of *Sporormiella* suggest direct grazing on the site (Gill et al., 2013), and development of wet meadows, indicated by the increase of wet meadows species, could record pasturage on the floodplain (c.f. Magyari et al., 2010). Constant occurrence of *P. aviculare* pollen suggests the spread of trampled habitats. During this period, the increase in *Fraxinus* and *Tilia* pollen alongside declining *Corylus* and *Ulmus* is quite unusual, because *Corylus* and *Fraxinus* have similar autecology and would be expected to react similarly to climate changes (Rackham, 1980). It is possible that *Fraxinus* and *Tilia* benefitted from the decline of *Corylus* and *Ulmus*, hinting at tree felling or forest management (cf. Gardner, 2002; Magyari et al., 2001, 2008, 2012b).

Towards the end of sedimentation (at around 5960 cal. BP), temperate deciduous tree pollen (*Quercus*, *Corylus*, *Ulmus*, *Salix* and *Fraxinus*) started to decline. This, together with the higher amount of charcoal particles, suggests intentional deforestation (Figure 8). Moreover, the first Cerealia grains were recorded in this phase. The early Eneolithic Period (early Copper Age, 6000–5500 cal. BP) was documented at only two sites in the area, one of which is located approximately 1 km SE of the core site. The presence of Cerealia pollen and the scarcity of archaeological sites may be explained by the enlargement of field size during the Eneolithic (6100–4400 cal. BP) and the use of more developed technology. Improvement of ploughing technology potentially affected the geomorphology of the surrounding landscape. Deforestation and use of tillage in agricultural practices greatly contributed to soil erosion processes, predominantly in hilly areas covered by loess (Smetanová, 2011; Stankoviansky, 2008). Increasing MS values and declining OC in the sediment support the explanation that such erosion processes resulted in interruption of organic accumulation around 5520 cal. BP. Subsequently, organic sediment was buried under 320 cm of colluvial–fluvial sediments (fine sand and runoff from loess) eroded from the surrounded slopes.

Conclusion

Fossil assemblages from PM provide an important record of environmental changes in the northern part of the Carpathian Basin from the Pleistocene–Holocene transition (≥ 11200 cal. BP) through the early and middle Holocene (up to 5520 cal. BP). The sedimentation of organic material stopped because of strong human-induced deforestation of the temperate oak forest, contributing to soil erosion that buried the organic sediment under 320 cm of minerogenic sediment.

Based on the results of multi-proxy analyses, we conclude that during the cold stage of the Pleistocene/Holocene transition, the marshes had a character of a cold shallow pool surrounded by a cold steppe, with patches of coniferous forest. After amelioration of the climate, the study site transformed into a shallow eutrophic pool/lake surrounded by an open mixed oak forest. The detection of temperate trees (*Quercus* and *Ulmus*) during the cold phase of the early Holocene suggests their early immigration into the region or their presence in local refugia. The expansion of *Quercus* before *Corylus*, a specific phenomenon in postglacial tree migration, was most probably triggered by a short-lived climatic oscillation at the onset of the Holocene, when the climate became more humid and cold, which suppressed the spread of *Corylus* and favoured *Quercus*. Mixed oak forest has been affected by anthropogenic disturbance since the Neolithic (7500 cal. BP), and possibly earlier. Around 6000 cal. BP, deforestation began, leading to soil erosion, eventually halting further accumulation of organic material until 5520 cal. BP. The development of the mixed oak forest was predominantly influenced by climate and disturbances, such as fire, since the early Holocene and by human intervention since the mid-Holocene (Neolithic) and probably earlier (Mesolithic).

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