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Ph.D. study program: Botany

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Anthropogenic impact on landscape transformation and vegetation changes reflected in pollen spectra from Central-Eastern Europe.

Antropogenní vliv na změny krajiny a vegetace odrážející se v pylových spektrech středovýchodní Evropy.

PhD Thesis

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Prague, 2016

Authorship statement

Chapter 1: Jamrichová E, Potůčková A, Hajnalová M, Barta P, Tóth P, Kuneš P (2014) Early occurence of oak-dominated forest in northern part of the Little Hungarian Plain, SW Slovakia. *The Holocene*, 24, 1810-1824.

- coring and sampling: EJ
- pollen analysing: EJ
- writing: EJ, PK, AP, MH, Contribution total of EJ: 75 %

Chapter 2: Hájková P, Jamrichová E, Horsák M, Hájek M (2013) Holocene history of *Cladium mariscum* dominanted calcareous fen: vegetation stability and landscape development. *Preslia*, 85, 317 – 332.

- coring and sampling: EJ, MHa
- pollen analysing: EJ
- writing: PH, EJ, MHo, MHa Contribution total of EJ: 50 %

Chapter 3: Jamrichová E, Szabó P, Hédl R, Kuneš P, Bobek P, Pelánková B (2013) Continuity and change in the vegetation of a Central European oakwood. *The Holocene*, 23, 46-56.

- coring and sampling: RH, EJ
- pollen analysing: EJ
- writing: EJ, PS, RH, PK Contribution total of EJ: 50 %

Chapter 4: Jamrichová E, Hájková P, Horsák M, Rybníčková E, Lacina A, Hájek M (2014) Landscape history, calcareous fen development and historical events in the Slovak Eastern Carpathians. *Vegetation History and Archaeobotany*, 23, 497-513.

- coring and sampling: PH, MHo, MHa
- pollen analysing: EJ, ER
- writing: EJ, PH, MHo, MHa Contribution total of EJ: 50 %

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Eva Jamrichová

Brno, 29th February, 2016

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Acknowledgements

In the first place, I hereby wish to thank my supervisor Petr Kuneš who encouraged and supported and helped me whenever I needed and gave me lots of useful advice. Another person I would like to thank is Helena Svitavská-Svobodová, who guided me in the field of palynology. I would also like to thank Michal Hájek and Petra Hajková, as well as Libor Petr and Lydie Dudová for many inspiring and fruitful discussions and exchanges of ideas during the numerous field trips and conferences.

I also greatly thank all of my friends and colleagues from the Department of Vegetation Ecology in Brno for a creative atmosphere and for sharing their remarks about present vegetation and human interactions, which helped me understand the interplay between our fields. I acknowledge Radim Hédl for his continuous support of palaeoecology at the Department of Vegetation Ecology, where I did most of my palynological work.

My thanks also go to Maruška Hajnalová, Radka Kozáková, Zuzana Plesková, Malvína Čierniková, Honza Roleček, Michal Horsák, Daniel Dítě and other friends and colleagues for being available whenever I needed help or to relax.

Many thanks also belong to all co-authors of my publications, for without them the papers would not have existed.

My biggest thanks, however, must go to my family and especially to Slavo for his support and patience.

The results of this PhD thesis were obtained as part of projects No. IAA600050812 and KJB601630803 of the Grant Agency of the Academy of Sciences of the Czech Republic (GAAV), and P504/11/0429 of the Czech Science Foundation (GAČR).

Abstract

The present thesis focuses on the impact of human communities on postglacial vegetation changes and landscape transformation in the region of Central-Eastern Europe. The main aim of the study was to evaluate how past human activities are reflected in pollen spectra from different types of mostly small-sized sites. Since the Middle Holocene onwards, human impact contributed to the formation and spread of various types of open habitats, altered the vegetation composition by introducing new species, influenced forest structure and supported the acceleration of geomorphic processes such as soil erosion or sediment accumulation. Human-induced alteration of the landscape cover and vegetation composition is reflected in pollen spectra, but it is often difficult to identify. Considered as direct evidence of human activities are the presence of pollen grains of cultivated plants in pollen spectra. Besides, there are several indirect traces of human impact on the landscape such as the spread of secondary anthropogenic indicators (apophytes), fluctuation in pollen curves of trees as a consequence of change in landscape cover or woodland composition, increases of micro-charcoal particles due to human-induced fire or erosion processes. **Chapter 1** presents confirmation of the assumption that Neolithic human impact is nearly undetectable in pollen spectra; however, several indirect traces suggest the presence of humans in the close vicinity of the study site. **Chapters 2** and **4** discuss how past human activities contributed to the formation and spread of various types of open habitats, which would probably not have existed without disturbances and management. Pollen analysis of two small forest hollows from the subcontinental oakwood Dúbrava (**Chapter 3)** shows that changes in medieval woodland management dramatically influenced the species composition of this temperate woodland and contributed to the persistence of its unique vegetation composition.

Precise identification of past human activities in pollen spectra contributes to answering questions about the history of human settlement in the study region, about the factors behind the landscape and vegetation changes and about the origin, history and survival of (semi-)open habitats.

Abstrakt

Prezentované práce je zaměřena na vliv lidských společenství na změny vegetace a transformace krajiny v regionu střední Evropy. Hlavním cílem studie bylo zhodnotit, jak se minulá lidské činnosti odráží v pylových spekter z různých typů a většinou malých lokalit. Člověk svou činností přispěl ke vzniku a šíření různých typů otevřených stanovišť, změnil složení vegetace introdukováním nových druhů, ovlivnil strukturu lesů a podpořil zrychlení geomorfologického procesů, jako je eroze půdy nebo hromadění sedimentů. Změny ve složení vegetace vyvolané činnosti člověka se odráží v pylových spektrech. Za přímý důkaz lidské činnosti v pylových spektrech je považována přítomnosti pylových zrn pěstovaných rostlin. Existuje také několik nepřímých stop indikujících lidský vliv na krajinu, jako je šíření sekundárních antropogenních indikátorů (apophyty), fluktuace v pylových křivkách dřevin v důsledku změn v pokryvu krajiny nebo složení lesa, zvýšení mikro-uhlíků v důsledku lidmi založených požáru nebo erozní procesy způsobenými lidskou aktivitou. V **kapitole 1** se potvrdil předpoklad, že dopad neolitické lidské činnosti v krajině je v pylových spektrech téměř neviditelná, nicméně, několik nepřímých stop indikují přítomnost lidských komunit v těsné blízkosti místa studie. V **kapitole 2** a **4** je diskutováno, jak minulé lidské aktivity přispěly ke vzniku a šíření různých typů bezlesých stanovišť, které by pravděpodobně neexistovaly bez jakýchkoli rušivých zásahů či hospodaření. Pylová analýza dvou malých sníženin v subkontinentálním dubovém lese Dúbrava (**kapitola 3**) ukazují, že změny v obhospodařování lesa ve středověku výrazně ovlivnili jeho druhovou skladbu a přispěl k přetrvávání unikátnímu složení vegetace studovaného lesa.

Přesnější identifikace minulé lidské činnosti v pylových spektrech může přispět k otázce historie lidského osídlení ve studovaném regionu, k objasnění faktorů, které způsobili změny v krajině a vegetace a k objasnění původu, historie a přežívání (polo)- otevřených stanovišť v průběhu holocénu.

Introduction

Humans have periodically influenced the landscape for thousands of years. Various activities of human communities triggered (whether accidentally or intentionally) the formation and spread of various types of open habitats (e.g., Behre, 1981; Hájková et al., 2011, Chapter 2, 4), changed the vegetation composition by introducing new species, influencing the forest structure (e.g., Gardner, 2002; Chapter 1, 3) and supporting the acceleration of geomorphic processes such as soil erosion or (flood induced) sediment accumulation (Willis et al., 1998; Chapter 1). There is a growing body of evidence from Central and Northern Europe that human activity played a crucial role in both the formation of grasslands and altered forest composition as far back as the Iron Age (Bruun et al., 2001; Pokorný et al., 2006; Pärtel et al., 2007) or even further (Rösch, 1996; Baumann and Poschlod, 2008; Dutoit et al., 2009; Magyari et al., 2010).

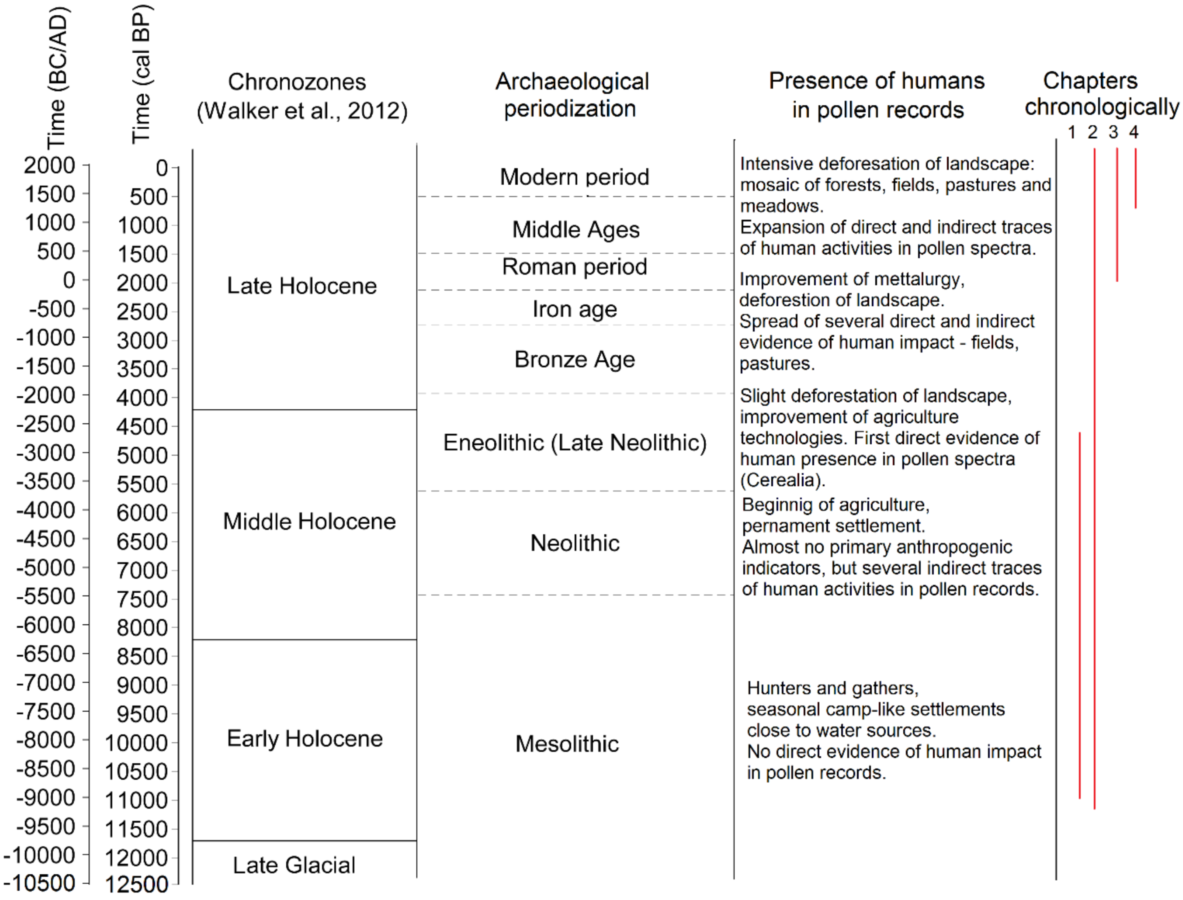
Significant signal of human presence in the landscape is in palynological record provided by the continual occurrence of cultivated plants (Cerealia). However, various indirect vegetation cues also suggest the influence of human communities (Figure 1).

It is argued that vegetation started to be intentionally influenced by people when the first agrarian communities settled in the landscape. In the last few decades, a still increasing number of studies focus on the detection of pre-agrarian (Mesolithic) human landscape impact (Innes and Blacford, 2003; Innes et al., 2013). Mesolithic seasonal camp-like settlements were located near water sources in wetlands and floodplain forests (Sümegi, 2013). Parts of forests were cleared, mainly for better accessibility and visibility (Mellars and Dark, 1998), besides wood (Chiverrell et al., 2004), but clearings were created also for social reasons (Davies et al., 2005). Moreover, the creation of temporarily open areas in floodplain forest possibly attracted game (Innes and Blackford, 2003). All of these activities can be reflected in pollen diagrams by increases in herbal pollen types (including apophytes), the spread of light-demanding shrubs and increases in charcoal particles (e.g. Chapter 1).

Later on, after the establishment of early farming communities in the landscape, human impact on the landscape environment progressively increased. It has been argued that the major drivers of landscape transformation were either agricultural activities (e.g., Behre, 1981) or different types of woodland management (Rackham, 2003), or both. Neolithic life remained strongly adapted to the forest ecosystem and utilized it extensively (Kalis et al., 2003). Woodlands were exploited for firewood and timber, felled to make room for arable fields and settlements, or as woodland pastures and sources of leaf fodder. Nonetheless, the population density during this period was rather small (Zimmermann et al., 2009), and Neolithic subsistence did not significantly alter the woodland vegetation in the vicinity of their settlements (Marinova and Thiebult, 2008). The prevalent form of woodland management in Neolithic Europe is thought to be ‘leaf-fodder husbandry’. This is characterized by small-scale clearings just large enough to harbour both settlements and small fields (Behre, 1988). Intensive forms of garden agriculture (Jones, 2005) practised in Central Europe during the Neolithic period (Bogaard, 2004) relied on manual hoe cultivation of very small plots of arable land. Moreover, the first Central European farmers settled in naturally treeless stands in loess areas (Bogaard, 2004; Hajnalová, 2007) or in open woodlands covering the Central European lowlands during that time (e.g., Kuneš et al., 2015). Therefore, deforestation and slash-and-burn management (Landnám model; Iversen, 1941), broadly applied in Northern Europe (Kalis and Meurers-Balke, 1998), was not required in the area of Central Europe (Willis, 2007). Additionally, small plots of arable land (Bogaard, 2004) and small population density (Zimmermann et al., 2009) led to human occupancy during the Neolithic that is almost imperceptible in pollen diagrams (Willis and Bennet, 1994). Nevertheless, there are several indications suggesting the presence of human communities in the landscape, for example, the spread of tall herbs vegetation, fluctuations in curves of trees, spread of light-demanding shrubs or development of secondary forest communities.

From the Eneolithic (Late Neolithic)/Bronze Age towards to the younger periods, mining and metallurgy, improvement of farming techniques (introduction of ard cultivation is assumed; Halstead, 1995) and enlargement of fields promoted increasing population density (Lang et al., 2000 – 2003). Lowland woodland areas started to be more intensively explored and cleared, and natural treeless vegetation got replaced by an anthropogenic steppe shaped by agricultural and pastoral activities (e.g., Chapter 2). Mountainous areas were less affected by humans during prehistory. An increasing number of studies, however, demonstrate that prehistoric peoples intensively or extensively affected the mountains by several types of activities. Higher elevated landscapes could be used for cattle grazing (in forested and deforested areas) or for selective tree felling (e.g., Moe and van der Knaap, 1990; Dreslerová, 2015; Kozáková et al., 2015; Schumacher et al., 2015). The utilization of higher elevated areas rapidly increased in the Middle Ages and during several colonization waves in the 13th and 19th centuries (Great colonization; Wallachian colonization, German colonization) when settlement had penetrated most intensively into previously unpopulated areas (Rybníček and Rybníčková, 2008; Wacnik, 1995, 2001; Margeliewski et al., 2010).

Figure 1.: Chronological framework and periodization used in the thesis.

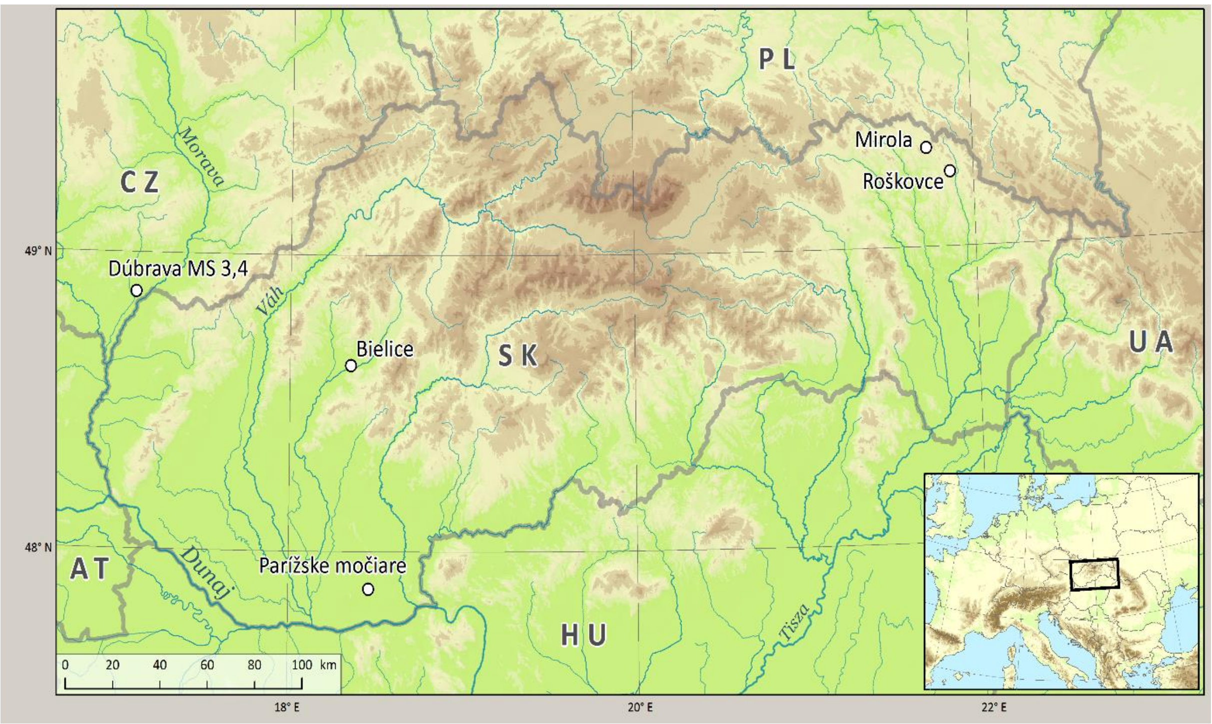


New villages were established in woody parts of mountain foothills, resulting in gradual deforestation followed by exploitation of the acquired open areas. Deforestation contributed to significant changes in local condition leading to hydrological changes, accumulation and erosion of sediments (Chapter 1), and landslides (Stankoviansky and Barka, 2007; Chapter 4). On the other hand, most modern calcareous spring fens developed after the deforestation of existing forest springs during the Wallachian colonization in the Western Carpathians (Hájek et al., 2011; Hájková et al., 2011; Chapter 4). Maintaining these ecosystems, which harbour many endangered and relict species, depends on management practices (mowing and grazing), and most of them cannot exist at all without management (Hájek et al., 2008).

Generally, since the Eneolithic/Bronze Age, and mainly during the Middle Ages, deforestation of the landscape, expansion of human-induced habitats (fields, pastures, meadows) and woodland management became clearly apparent in pollen diagrams as various types of direct (occurrence of primary anthropogenic indicators) or indirect evidence (occurrence of secondary anthropogenic indicators, changes in landscape cover and in woodland composition, increase in charcoal concentration, erosion) of human activities in the landscape.

The present thesis focuses on the detection of past human impact on the landscape and vegetation through the identification of various direct and indirect evidence of human activities in pollen records from the region of Central-Eastern Europe (Figure 2). More precise identification of past human activities in pollen spectra may help to (i) assess the history of human settlement in the study region; (ii) distinguish among the roles of different factors (be it natural or artificial) behind landscape and vegetation changes; and to (iii) determine the origin, extent of continuity and survival of various types of (semi-)open habitats such as open oakwoods, grasslands, spring fens, etc., which would not have existed without disturbances.

Figure 2.: Location of the study area in Central-Eastern Europe and its altitudinal variation (in metres). PL: Poland; CZ: Czech Republic; AU: Austria; SK: Slovakia; HU: Hungary; UK: Ukraine. List of localities: Parížske močiare (Chapter 1); Bielice (Chapter 2); Hodonîska Dúbrava Wood: MS3, MS4 (Chapter 3); Roškovce, and Miroľa (Chapter 4).



Direct evidence of human activities

Primary anthropogenic indicators – anthropophytes (species that do not belong to the native flora, such as cultivated species).

Cerealia

Pollen of cereals is the most important indicator connected with the presence of humans (Behre, 1981). Cereals have pollen with characteristic morphological features (Beug, 2004) and are divided into several types: Cerealia undif., *Triticum*-type, *Avena*-type, *Hordeum*-type, *Secale*. Their presence in pollen records needs to be considered with caution, however. Besides cultivated plants, pollen types of all of these taxa can also include pollen of wild-growing grasses originating from local wild-growing vegetation in the area under consideration (Marinova et al., 2012). In Central Europe, the *Hordeum*-type also includes several wild grasses naturally growing in Central Europe, for example, *Agropyron junceum, A. intermedium* or *Hordeum murinum* (Ellenberg, 1996; Jašková, 2008). The *Secale* pollen type also includes *Secale sylvestre*, which grows on sandy soils in steppe vegetation (Dostál and Červenka, 1991, Hoskovec, 2011). Pollen diagrams from Central Europe often contain finds of single pollen grains of Cerealia (Cerealia undif., *Hordeum*-type, *Secale*) during the Mesolithic period, which can be interpreted as pre-Neolithic grain cultivation (Gehlen and Schön, 2003). However, pre-Neolithic grain cultivation remains to be verified by archaeobotanical evidence, and the presence of single pollen grains of grasses larger than 45 µm are regarded as native, wild-growing grasses (Behre, 2007).

Nonetheless, the continual pollen curves of Cerealia pollen (not merely single pollen grains) recorded along with higher amounts of pollen of secondary anthropogenic indicators (e.g., *Plantago lanceolate*-type, *Polygonum aviculare*-type, *Rumex acetosa/acetossella*-type) clearly indicate the presence of humans in the landscape.

Archaeobotanical finds demonstrate that crop cultivation started since 5500 BC/7500 cal BP (Neolithic) in the lowlands of Central Europe. Among the first cultivated crops in Central Europe were *Triticum monnococum* and *T. dicoccum* (Bogaard, 2004; Hajnalová, 1993; Kočár and Dreslerová, 2010). The first noticeable change in crop cultivation occurred in the Eneolithic (Late Neolithic), when *Hordeum* became an important crop (Šálková et al., 2012), and since the Late Iron Age, when it prevailed (together with *T. dicoccum* and *T. spelta*) in grain finds (Kočár and Dreslerová, 2010). From that time, higher amounts of *Avena* and *Secale* have also been found. In the Roman period, the dominant cereal was still *Hordeum*, followed by *T. dicoccum* and *Panicum miliaceum, T. aestivum/turgidum, Secale* and *Avena*. *Hordeum* and *T. dicoccum* are the most important cereals in the rare finds from the Migration Period (Dreslerová and Kočár, 2013).

In contrast to archaeobotanical evidence, finds of Cerealia pollen (*Triticum*-type) were very scarce during the Neolithic period. Considering that Neolithic agriculture was based on small-scale horticulture in small, intensively managed fields (Bogaard, 2004), pollen of autogamous *Triticum* with low pollen productivity can be difficult to detect palynologically. Even if a peat profile contains Neolithic ceramic shards, its pollen spectrum may not hold evidence of direct human impact (Petr et al., 2014). The occurrence of fields in landscapes covered by open woodlands might also complicate the transport of pollen of cereals into sedimentation basins. Higher trees could serve as a pollen filter and therefore prevent the accumulation of pollen in basins (Kreutz, 2008). Pollen grains of the Cerealia (including the *Triticum*-type) started to continually occur since the Eneolihic (Late Neolithic) or from the Bronze Age onwards (Chapter 1, 2; Petr et al., 2013, 2014; Jankovská and Pokorný, 2013; Kuneš et al., 2015), probably as a results of more extensive agricultural practices, for example, improving ploughing technology and the use of livestock, connected with larger plots of arable land (Neustupný, 1978). At that time, population density increased (Zimmerman et al., 2009) with consequent higher demands on the environment (Kaplan et al., 2009). Deforestation increased, which presumably facilitated the transportation of pollen grains (included Cerealia) in the landscape. On the other hand, pollen grains of the *Secale* are very often recorded since the Neolithic period, possibly because of different pollination strategies among the three main cereals: anemogamous *Secale* and autogamous *Triticum* and *Hordeum* (Vuorela, 1973), which could have caused the overrepresentation of rye in pollen diagrams (Broström et al., 2008). Based on archaeobotanical finds, *Secale* is scarcely found since the Early Bronze Age and grain-rich finds are documented from the La Tène period (Dreslerová and Kočár, 2013). Nonetheless, the occurrence of *Secale* in pollen diagrams before the LaTéne/Roman period is interpreted rather as a non-cultivated species of rye growing in natural vegetation or as an arable weed (Behre, 1992). Small-scale cultivation of rye since the Bronze Age cannot be ruled out, however.

Besides pollen of cereals and their weeds, that of other cultivated plants, such as *Cannabis sativa, Linum usitatissimu* or *Fagopyrum esculentum*, can also be regarded as primary anthropogenic indicators in pollen diagrams from Central Europe.

Hemp (*Cannabis sativa* L.)

Archaeobotanical finds have confirmed the cultivation of hemp since the La Téne/Roman period, with an increasing tendency since the Early Middle Ages (Opravil, 1983; Hajnalová, 1999; Mercuri et al., 2002; Kočár and Dreslerová, 2010). The presence of *Cannabis* pollen could point to hemp cultivation for seeds and fibre (Behre, 1981). From the morphological point of view, pollen of *Cannabis* is difficult to distinguish from pollen of *Humulus* (Beug, 2004, but see Punt and Clark, 1984). In pollen sequences, the two pollen types are often merged into a broader group referred to as *Humulus/Cannabis*, Cannabaceae (Beug, 2004) or the *Humulus lupulus*-type (Punt and Clarke, 1984), which comprises both genera. However, based on the identification key proposed by Punt and Clark (1984), it is possible to distinguish between *Humulus*-type and *Cannabis*–type species. *Humulus lupulus* naturally grows in wet forests, and besides cultivated *Cannabis sativa*, the presence of *Cannabis ruderalis* in open nutrient enriched stands in Central–Eastern Europe also needs to be taken into consideration. Sporadic presence of *Cannabis* pollen can be generally interpreted as an indicator of open ruderal country (cf. Chapter 2). On the other hand, the unusual higher amount of *Cannabis* pollen may to be attributed to the retting process, especially when recorded in sediments of small water basins (Schofield et al., 2005). Based on ethnological sources from Central Europe, bundles of hemp were submerged predominantly in natural water bodies, mostly small in diameter, which warm up quicker in sunlight, which accelerated the process of fibre retting (Obršlík, 1981; Březinová, 1997). Thermal water sources with higher mineral content were also used for retting (Podolák, 1952; Suchora et al., 2015). Stems of hemp have higher technological qualities when they are harvested during flowering time (Široká, 2007), and retting of male plants for fibres could have left a strong signal in pollen records (Mercuri et al., 2002). Therefore, the unusual higher amount of *Cannabis* pollen could serve as an indicator of hemp cultivation, especially when recorded in small or thermal waterbodies.

Flax (*Linum usitatissimum* L.)

In Central Europe, *Linum usitatissimum* (flax) was cultivated for textile and oil production since the Neolithic period (Opravil, 1981; Zohary and Hopf, 1988; Hajnalová, 1993; Kočár and Dreslerová, 2010). *Linum usitatissimum* is an autogamous plant with low pollen productivity and is only sporadically traced in pollen diagrams (Behre, 1981). Pollen grains of flax can be identified to the *Linum usitatissimum*-type, which also includes its ancestor *L. bienne* (*angustifolium*) (Beug, 2004). However, this archaeophyte does not naturally occur in the area of Central Europe, therefore sporadic (sometimes single) finds of pollen grains of the *L. usitatissimum* type could indicate flax cultivation in the nearest vicinity of study sites (Jahns, 1999; Mehl et al., 2015). For textile production, flax was processed by retting similar to hemp. However, retting of flax is better detectable by plant macro-remains analyses compared to pollen analyses because of its low pollen productivity (e.g., Beug, 2011; Herbig and Sirocko, 2012; Rasmussen, 2005).

Buckwead (*Fagopyrum esculentum* L.)

In Central Europe, regular finds (of macro-remains and pollen) of *Fagopyrum esculentum* occur since the High Middle Ages (Opravil, 1974; Zemanek et al., 2009; Jankovská, 2011). The history of buckwheat in Central and Eastern Europe was studied by Opravil (1974). He assumed that *Fagopyrum esculentum* arrived in Central Europe with the Tartar invasion in the 13th century from the south via the Danube and also outside the Carpathian Arch via Poland (Opravil, 1974; Zemanek et al., 2009). Archaeobotanical finds confirmed its sporadic occurrence since the Early Middle Ages (9–10th century; Aslaben, 1995) with an increased proportion of finds since the 12th–13th century (Opravil, 1974, 1990; Zemanek et al., 2009). Pollen of *Fagopyrum* from the periods prior to the Middle Ages sporadically occurs in Northern and Central Europe (in the Czech Republic for example: Pokorný et al., 2008; Břízová et al., 1999; for more sites, see de Klerk et al., 2015). However, the presence of *Fagopyrum* prior to the Middle Ages is often interpreted as a result of long-distance transport, contamination during coring or misidentification (de Klerk et al., 2015). Long-distance transport and misidentification can be ruled out because *Fagopyrum esculentum* has rather large and heavy pollen grains with a characteristic morphological structure (Beug, 2004). Besides *F. esculentum*, the *Fagopyrum esculentum*-type also includes *F. tatricum,* which is a wild form of buckwheat naturally occurring in Tibet, Sichuan, Kashmir and Pakistan (Hanelt, 2001), so presence of *F. esculentum*-type in pollen slides from Central Europe can be interpreted as human impact. It is possible that buckwheat occurred earlier than the Middle Ages as a weed in crop fields (Nalepka, 2003; de Klerk et al., 2015).

Indirect evidence of human activities

Secondary anthropogenic indicators – apophytes (species that belong to the native flora but benefit from human activity)

The work by Behre (1981, 1986) defines secondary pollen indicators as follows: ‘Apophytes occur naturally in small habitats or niches and were favoured by the activities of man when he opened the landscape or created ruderal stands that were occupied by nitrophilous species.’ The classification of secondary anthropogenic indicators published by Behre (1981, 1986) has been widely used in many studies; however, selected groups of human-induced habitats (fields, fallow land, pastures, etc. see Behre 1981) have been improved and adapted to regional environmental condition of Europe – see, for example, Berglund and Ralska-Jasiewiczowa (1986) for Sweden, Vorren (1986) for Norway, Hicks (1988) for Finland, Brun (2011) for France; Mercuri et al. (2013) for Italy; Marinova and Atanassova (2006) for Bulgaria, Bottema and Woldring (1990) for the Meditterian region. In Central Europe, the improved classification of secondary human indicators was used in a study from Poland (Latalowa, 1992).

Behre (1981) often considers whole families or genera as secondary anthropogenic indicators, which may include plant species with opposite ecological requirements. Moreover, many of the species included in pollen types occurred not only in anthropogenic habitats, but also in natural vegetation. For example, the family Chenopodiaceae also includes many nitrophilous species. The same applies to the genus *Artemisia*, which is considered an indicator of ruderal habitats and pathways though in the region of Central-Eastern Europe, *Artemisia* continually occurred since the Late Glacial period (e.g., Petr et al., 2013; Chapter 1, 2). Similarly, the most important and widely used secondary human indicators in pollen spectra (*Plantago lanceolate*-type, *Plantago media/major, Juniperus*, *Urtica* or *Polygonum aviculare*-type) are usually interpreted as a consequence of pasturage, ruderalization and trampling (Hicks et al., 1988; Latalowa, 1992; Marinova et al., 2012; Kozáková et al., 2015; etc.). On the other hand, all of these species naturally grow in the study region, and their natural occurrence is possible. For example, the pre-Neolithic occurrence of ruderal taxa like *Urtica, Polygonum aviculare, Plantago lanceolata* or Chenopodiaceae may indicate the occurrence of Mesolithic settlement activities, especially if they co-occurred in the same period. On the other hand, the spread of trampled and ruderal habitats could also be associated with the presence of herds of large herbivores (Jankovská, 1994). Moreover, many ruderal taxa, such as *Polygonum aviculare* and Chenopodiaceae, inhabit bottoms of lakes exposed in summer, so natural factors such as dry climate might contribute to the spread of ruderal communities (Magyari et al., 2010; Chapter 1).

Another way of interpreting secondary anthropogenic indicators is to merge them into broader functional groups based on ecological requirements of plant species included in each pollen type. The merging of herbal pollen taxa into broader groups could lead to a more objective assessment of landscape changes as a consequence of human impact or natural agents (Chapter 2). Based on this classification, the impact of prehistoric human impact appears to have contributed to keeping forests open enough for the survival of light-demanding species. Nonetheless, the ecological classification of species assigned to pollen types may not be transferable across different landscapes and different times. Many species included in pollen types have quite different ecology, which makes the classification of some pollen types into broader ecological groups difficult. On the other hand, some pollen types may provide certain indicator value in a specific region and period (e.g., Kozáková and Boháčová, 1998; Chapter 2).

The presence of secondary anthropogenic indicators in pollen spectra needs to be considered very carefully in the context of whole pollen assemblages and with respect to evidence of primary anthropogenic impact (Marinova et al., 2012).

Change in woodland structure

Since the Middle Holocene, forests had been periodically influenced by human impact, and landscape utilization became the most large-scale disturbance affecting forest ecosystems of the temperate zone (Sala et al., 2000). Traditional management went on practically unchanged for thousands of years and was abandoned only recently (e.g. Rackham, 2003; Billamboz, 2003; Haneca et al., 2005; Szabó, 2010). The last 7500 years of woodland management included woodland pasture, collecting and storage of leaf fodder, ring-barking, pollarding, coppicing and shredding (Moe and Rackham, 1992; Göranson, 1986; Dreslerová, 2012). Woodland had been used for grazing of pigs, cattle, horses, sheep, geese and goats. Trees were coppiced or pollarded for firewood or cut for timber, and tree shredding produced leaf-hay for animals in late summer or autumn (Ellenberg, 1996; Bergmeier et al., 2010). Archaeological records confirm the use of different forest species for leaf fodder, depending on regional vegetation and the availability of woody species (see Hejcmanová et al., 2013). The nutrient value of leaves used for foddering also possibly affected the selective exploitation of woodlands. For example, *Quercus*, *Carpinus* and *Fagus* are low-quality forage and are avoided by cattle whereas trees with high nutrient quality, such as *Fraxinus, Tilia, Ulmus* and *Acer,* are preferred by cattle, so they were possibly preferentially harvested by man for winter foddering. Cattle and pigs feeding on tree seedlings and young trees hindered forest rejuvenation. Browsing on bark and twigs has serious consequences for tree species such as *Fagus* (beech). *Quercus* (oak), on the other hand, was avoided by livestock because its bark and leaves are unpalatable. In addition, rooting by pigs has a positive effect on the germination of oak (Stobbe, 1996). Woodland grazing creates open patches or grasslands where oak is more likely to establish (Rackham, 2003). On the other hand, woodland pasture had a negative effect on *Pinus* (pine), which does not regenerate when cut down or browsed by animals (Kreutz, 2008). Forest grazing also promotes the spread of light-demanding shrubs such as *Cornus mas*, *Cornus sanguinea* and *Sambucus* due to opening of the canopy (Moskal-de Hoyo, 2013).

Browsing and selective harvesting of trees thus possibly affected their expansion or suppression in prehistory (Kalis et al., 2003; Hejcmanová et al., 2013). For example, selective harvesting of elm during the Neolithic period might have contributed to the decline of elm, which is broadly recorded by pollen assemblages in Europe (Troels-Smith, 1960; Iversen, 1973; Ralska – Jasiewiczowa et al., 2003; Magyari et al., 2012). Moreover, increasing abundance of *Corylus, Ulmus* or *Fraxinus* might indicate woodland pasture or coppicing because these species have a strong resprouting ability (e.g., Magyari et al., 2001, 2008; Gardner 2002).

The traditional forest management practices (e.g., coppicing, pasturing, haymaking, pannaging, bee-keeping; see Szabó, 2010) removed organic matter and nutrients from forest soil (Vild et al., 2013) and kept the woodlands open enough to allow the survival of light-demanding species including oak and hazel. It is highly plausible that forest management, which favoured light-demanding forest species, contributed to the maintenance of temperate oakwoods up until the recent period (see Chapter 3). The recent abandonment of traditional forest management practices has led to the decline of oakwoods throughout Europe over the last few decades (Kwiatkowska, 1994; Jakubowska-Gabara, 1996; Roleček, 2007; Hédl et al., 2010). Abandonment of cleared areas of forest (meadows, pastures and fields) has led to the 'secondary' woodland succession started by pioneer and light-demanding trees and shrubs such as *Betula, Fraxinus, Corylus* or *Pinus*. The reforestation of pastures or fields set off a secondary forest cycle beginning with the expansion of tall herbs, continued by the spread of pioneer trees such as *Betula, Fraxinus* or *Corylus* and ending with the original forest types (Kalis et al., 2003).

Woodland management is difficult to detect in pollen spectra. The fluctuation of curves of certain trees might be associated with woodland management, although natural causes can never be entirely rejected. On the other hand, the presence of coprophilous fungi, such as

Sporormiella, in pollen slides clearly indicates grazing by herbivores (domesticated or wild; Baker et al., 2013). Also, changes in the curves of herbal species, especially those associated with pastures and meadows, might help identify prehistoric woodland management. Still, the suppression of flowering of grasslands due to browsing and trampling, reflected in the decline of NAP (Non-Arboreal Pollen) values, needs to be taken into account (Kreutz, 2008). Nonetheless, knowledge of the archaeological or historical context of the study area can aid the interpretation of changes in pollen spectra with respect to past woodland management (e.g., Chapter 3).

Change in landscape cover

The most important anthropogenic impact on landscape cover was the clearing of forests to make room for fields and pastures, and the exploitation of forests for firewood and timber (Kaplan et al., 2009). This resulted in a gradual decline in the extent of forested areas whereas the extent of secondary non-forested areas increased. Land cover changes are inferred from pollen diagrams based on the AP (Arboreal) to NAP (Non-Arboreal Pollen) ratio. Some palynologists argue that if AP reaches more than 80% of the total pollen sum (TS), forest vegetation should be reconstructed, that less than 70% indicates the forest-steppe zone and that lower percentages (less or qual to 50%) indicate the steppe zone (Magyari et al., 2010; Svenning 2002). However, this relationship is not easy to interpret due to biases caused by different pollen productivity and dispersal of different species (e.g., Sugita, 1994; Sugita et al., 1999). For example, during the Middle Holocene, the AP:NAP ratio indicates densely forested areas in Central Europe, which is in contradiction with the presence of light-demanding species. Central European lowland woodlands were dominated by light-demanding oak, so oak-dominated forest communities presumably had an open canopy structure (Ralska-Jasiewiczowa et al., 2003; Chytrý, 2012). Also, the continual occurrence of heliophilous herbal pollen (e.g., *Artemisia*) throughout the Holocene corresponds to a (semi-)open landscape. The openness of the Middle Holocene landscape is also supported by assemblages of fossil molluscs (Pokorný et al., 2015; Chapter 1, 2).

Since the Eneolithic (Late Neolithic)/Bronze Age, people started to explore the landscape more deeply. Human-induced deforestation and consequent mowing or grazing played an important role in the creation, expansion and maintenance of open areas, where many light-demanding species could survive through the Middle Holocene until today (Hájková et al., 2011; Hájek et al., 2016; Chapter 2, 4). This is reflected in the higher amount of herbal pollen types, including primary and secondary anthropogenic indicators, caused by the expansion of fields, pastures and meadows. Forests were also more intensively explored due to the development of ore processing. All of these changes should be reflected in a decline of the AP:NAP ratio as a consequence of dramatic changes in landscape cover. In the same period, however, late-successional trees (*Fagus, Abies* and *Carpinu*s) immigrated into the area of Central Europe, forming dense forests. Moreover, the abandonment of the open landscape often resulted in onset of secondary woodland succession. This could be reflected as no change in the AP:NAP ratio or as its fluctuation (Petr et al., 2013; Chapter 2).

In conclusion, from the Neolithic onwards, human-induced deforestation and increasing of utilization of the landscape resulted in changes in landscape cover. This should be reflected in pollen spectra as changes in the AP:NAP ratio. In some cases, however, the AP:NAP ratio was rather stable during the entire prehistoric period (Chapter 1, 2). It is therefore necessary to interpret the whole pollen spectra and in most cases also employ other proxies (e.g. fossil molluscs and plant macro remains) could help resolve questions about changes in landscape cover (Hájková et al., 2011; Chapter 1, 2).

Erosion processes reflected in local vegetation changes

The more than 7000 years of human impact on the landscape influenced not only the vegetation, but also soil properties. Changes in soil properties due to human activities are a very complex topic, which cannot be resolved only by biological proxies. Enhanced soil erosion with consequent accumulation of colluvial sediments in the catchment areas of wetlands or mires could lead to changes of local wetland or mire vegetation reflected in pollen spectra. In Central Europe, agrarian utilization of deforested landscapes by ploughing, digging, hoeing and fertilization often resulted in soil erosion and gullying (Gerlach and Eckmeier, 2012; Dotterwiech, 2008). Soil erosion and associated down-slope sedimentation is an important and widespread phenomenon throughout Central Europe (Bell, 1992). During the Neolithic period, extensive utilization of the landscape did not lead to soil erosion (Willis and Bennet, 1994). This had changed prior to the younger periods, however. Intensive deforestation of slopes and the use of tillage in agricultural practice initiated soil erosion processes (Evans, 1990), predominantly in loessic hilly areas (Stankoviansky, 2008; Smetanová, 2011). Soil erosion is reflected in archaeological contexts as a consequence of more effective ploughing and deeper tillage (Neustupný, 1978, Beneš, 1995). As already mentioned, erosion processes are hard to detect in pollen profiles. One of the possible signals in pollen spectra associated with erosion are rapid increases in *Alnus* pollen. Accumulation of colluvial sediments possibly supported the development of *Alnus* stands in the vicinity of study sites (Pokorný, 2005; Chapter 2). Sediment erosion can also be detected based on the presence of certain types of non-pollen palynomorphs, which are commonly found in pollen preparations. One of the most important indicators of soil erosion in organic sediments are spores of arbuscular mycorrhizal fungi or HdV-207 (van Geel, 1986; van Geel et al., 1989), type HdV-1103, or *Glomus* sp. (van Geel et al., 1989), which sporulate below ground. However, the interpretations differ depending on the type of sediment (see Kolaczek et al., 2013).

Erosion or accumulation of allochtonous sediments in the alluvia of watercourses is mainly reflected in changes of sediment properties (Chapter 1). Changes in lithology due to erosion processes can be detected by sedimentological analyses such as loss on ignition (LOI) and magnetic susceptibility (MS) measurements. These two methods allow us to estimate the proportion of organic carbon, carbonate and mineral matter in sediments (Dearing et al., 1981; Boyle, 2004; Snowball et al., 1999). Organic and mineral matter can have an autochthonous origin, if it comes from the study site (bioproduction, biogenic silica and carbonate), or it can be allochtonous, if it comes from the catchment area of the study site (mineral in-wash due to catchment instability; Birks and Birks, 2006). Briefly, LOI analysis indicates the percentage of carbonates or organic material in accumulated sediments whereas results of measurement of MS analysis provide information about import of clastic sediment eroded in the catchment area of sediment input (e.g., Nazarok et al., 2014).

Charcoal particles in pollen slides

The history of fire events in the surroundings of coring sites used to be reconstructed by measuring microscopic and macroscopic charcoal concentrations in the sedimentary sequence. Fire activity is usually determined by estimating peaks in charcoal accumulation (stratigraphic levels with abundant charcoal) in the sedimentary record (Whitlock and Larsen, 2001). Microscopic charcoal is usually determined during pollen analysis, but this brings several limitations. One of them is that charcoal particles can get broken during the preparation of pollen samples, creating an artificially higher abundance of charcoal particles (Whitlock and Larsen, 2001). Another limitation of counting micro-charcoals during pollen analyses is that it can detect only the presence of fire activity, not its frequency. The frequency of fires can only be estimated if charcoal particles are counted in continuous samples, and sub-sampling of palaeoecological profiles for pollen analysis is usually not sufficiently continuous. In the identification of local fire activity, the use of other proxies, such as macroscopic charcoal or changes in lithology, are required as confirmation (Whitlock and Larsen, 2001). Elevated microcharcoal concentrations probably tend to reflect more regional fire activity (Whitlock and Larsen, 2001; Tinner et al., 1998) whereas macroscopic charcoals reflect local fires (e.g. Gardner and Whitlock, 2001). In Central Europe, higher micro-charcoal concentrations are often observed in Early Holocene stages. This is attributed to the climate conditions during the Early Holocene, characterized by higher temperatures and low precipitation, increasing natural fire frequency (cf. Feurdean et al., 2013). However, intentional setting of fires by Mesolithic populations must also be considered. Many studies show links between forest clearings and fires in the Mesolithic (e.g., Simmons, 1996; Moore, 2000; Wacnik, 2009; Regnell, 2012), which were possibly triggered by human-induced opening of the canopy (Tolksdorf et al., 2013; Innes et al., 2013).

During the Neolithic period, fire activity was reflected in higher concentrations of micro-charcoal particles only to a small extent (Petr et al., 2013, Chapter 2). This is attributed to the pointlessness of deforesting the lowland landscape, which was open enough (Kuneš et al., 2015). Although some studies of rather small sites (forest hollows) have shown an increase in charcoal particles during the Neolithic period with no dramatic changes in the curves of trees (Chapter 1). In such cases, higher charcoal concentrations can indicate the use of fire for domestic purposes (mainly if an increase in charcoal particles corresponds with the expansion of settlements documented by archaeological records). Anthracological analyses of samples from archaeological situations have shown that during the Neolithic/Eneolithic (Late Neolithic) period, firewood was collected randomly and almost non-selectively around settlements (Heiss and Oeggl, 2008). The charcoal taphonomy could thus be compared with that of pollen spectra (Théry-Parisot et al., 2010).

Towards the younger periods of prehistory, higher amounts of micro-charcoal particles tended to be recorded, accompanied by a decline in the curves of trees and spread of herbaceous pollen types. Furthermore the spread of pioneer trees (as part of secondary forest cycles) was connected with post-fire forest succession (Kalis et al., 2003). All of these changes, detected in pollen spectra, could be associated with fires lit with the intent of replacing forests with fields, pastures or for metallurgy (Chapter 1, 2). As regards metallurgy and smelting processes, intentional selection of trees as firewood needs to be considered. Anthracological analyses from prehistoric mining sites revealed selective collection of firewood, as people distinguished between hardwood and softwood (Heiss and Oeggl, 2008).

Nonetheless, micro-charcoal particles counted during pollen analyses could bring valuable information about past human activities. Compared to macro-charcoal evidence, however, they can provide more detailed and important information about forest composition and exploitation, especially if the charcoals were sampled in archaeological contexts (Théry-Parisot et al., 2010).

Summary and main questions of the work

This thesis discusses prehistoric human impacts during the Holocene based on case studies of pollen analyses carried out in Central-Eastern Europe (Figure 2). One of the main aims of the thesis was to find out whether it is possible to trace the history of human settlement in pollen spectra from different types of natural archives. The study sites are situated in a variety of landscapes (a lowland woodland, a lowland wetland, foothills of mountains) and sedimentary environments (an interdunal depression, a lowland wetland, a spring fen and a hot thermal spring), which allowed us to paint a more complete picture of different types of anthropogenic impact.

The other aim of this thesis was to ascertain whether it is possible to distinguish between changes in landscape and vegetation structure conditioned by natural factors (e.g., climate changes) and by human activities. To answer this question, the results of pollen analysis are complemented by results from other disciplines such as analyses of (micro- and macro-) charcoal, plant and mollusc macro-remains, and sedimentological analyses. The results obtained are also discussed in the context of archaeological and historical sources, which can be used for interpreting of pollen data. Comparison of pollen spectra with results from various other disciplines allowed us to determine how past human activities influenced forest composition since the Neolithic period onwards and how human impact contributed to the origin, continuity and survival of different types of (semi-)open habitats through the Holocene.

Chapter 1 *Early occurrence of temperate oak-dominant forest in the northern subunit of the Little Hungarian Plain, SW Slovakia* focuses on the detection of prehistoric human impact in the old settlement zone, which was densely settled since the Neolithic period. In this chapter, we ask whether it is possible to disentangle the drivers of environmental changes in the landscape and wetland habitats as a result of short-term climate variation or disturbances such as fire or human intervention. To resolve this problem and to understand the complex picture of the long-term dynamics of vegetation and landscape transformation and its response to climate fluctuations and human impact, various proxy data (pollen and macrofossil analyses, loss on ignition, magnetic susceptibility) were integrated in the study. The palaeoecological record was correlated with a macrophysical climate model and archaeological data. The results show that the transformation of the landscape and forest communities was triggered by climatic events up to the Middle Holocene, when disturbances caused by humans became the dominating influence on the landscape and vegetation. Prehistoric human impact resulting in deforestation contributed to soil erosion processes followed by rapid accumulation of clay sediment.

Chapter 2 *The whole Holocene history of a Cladium mariscus-dominated calcareous fen on warm springs: vegetation stability, relictualism and landscape development* addresses the topic of the whole-Holocene persistence of open steppes or dry grasslands and open wetlands in the Pannonian/Carpathian borderland. This chapter also focuses on the role of prehistoric human intervention on the continuity and survival of different types of open-country habitats. The continuity of temperate grasslands throughout the entire Holocene is still a topic of debate. In humid periods of the Middle Holocene, closed-canopy forests started to spread and open habitats retreated. The spread of agriculture that started in Central European lowlands ca 7500 cal BP had a counteracting effect: The landscape was gradually deforested, and cattle grazing, burning, crop cultivation and mowing supported the spread of species growing in open habitats. Our study confirms the whole-Holocene persistence of an open steppe and/or dry grasslands and open wetlands in this region. It also reveals coincidences between the history of human settlement, local development of the fen and regional changes in the representation of particular habitats, including managed mesic and semi-dry grasslands, since the Bronze Age.

Chapter 3 *Continuity and change in the vegetation of a Central European oakwood* examines evidence as to whether oakwoods can be characterized by long-term stability and what may be the driving forces of the observed stability or change. To answer these questions in a well-defined case study, we examined the history of a large subcontinental oakwood (Dúbrava) in the southeastern Czech Republic by applying interdisciplinary methods using palaeoecological and archival sources. The results show that the present oakwood was established in the mid-14th century by an abrupt change from shrubby, hazel-dominated vegetation to an oakwood. This change was most probably caused by a ban on oak felling in 1350 AD. From the 14th to the late 18th century, the Dúbrava woodland had multiple uses, of which woodland pasture and hay cutting kept the woodland considerably open. The unique vegetation of the Dúbrava woodland was largely shaped by medieval woodland management. It was further maintained by multiple use management in the early modern period and subsequently drastically reduced in extent by modern forest plantations, which are still being planted to date. We conclude that the Dúbrava woodland did not show long-term stability and that its species composition has dramatically changed over the last two millennia.

Chapter 4 *Landscape history, calcareous fen development and historical events in Slovak Eastern Carpathians.* In this article, we explore the interference among human activities, landscape development and changes in calcareous spring fens. The results show that humans were the main drivers of landscape transformation in the last millennium and that they directly created spring fen ecosystems through deforestation and also influenced fen species composition by husbandry activities. Moreover, the development of the both study sites illustrates how man-made spring fens, important present-day refugia of endangered wetland species, are influenced by different types of human management. We conclude that these ecosystems are sensitive to changes in management practice and that most of them cannot exist without management**.**

Early occurrence of temperate oak-dominated forest in the northern part of the Little Hungarian Plain, SW Slovakia

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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 at Parížske močiare marshes was investigated for pollen, plant macro-remains, molluscs, organic content, and magnetic susceptibility. The palaeoecological record extends from the Pleistocene–Holocene transition (≥ 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 the 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, most probably human activities became 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.

Key words: lowland wetland, palaeoecology, multi-proxy, *Quercus*, climate, disturbances

Introduction

The transition from Late Glacial to early Holocene is the key period for understanding of today's biota composition. The increase in temperature and precipitation recorded at around 13,000 years 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; Tóth et al., 2012, Feurdean et al., 2014) with a significant impact on vegetation (Birks and Ammann, 2000; Tinner and Lotter, 2001; Feurdean et al., 2008; Magyari et al., 2012a; Dudová et al., 2014). 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 (11,700–4200 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 Bennet, 2008; Stewart and Lister, 2001). The existence of glacial refugia of temperate trees has been recently shown in the Carpathian Basin (Willis et al., 1995; Magyari et al., 1999; Willis et al., 2000; Birks and Willis, 2008) but has not yet been confirmed in the Little Hungarian Plain. Between 11,500–9500 cal BP, temperate trees (*Corylus, Quercus, Ulmus, 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 the 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, and magnetic susceptibility) to investigate sediments in the Parížske Močiare Marshes 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 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 of mixed oak forest development during the periods of early and middle Holocene.

Material and Methods

The study site

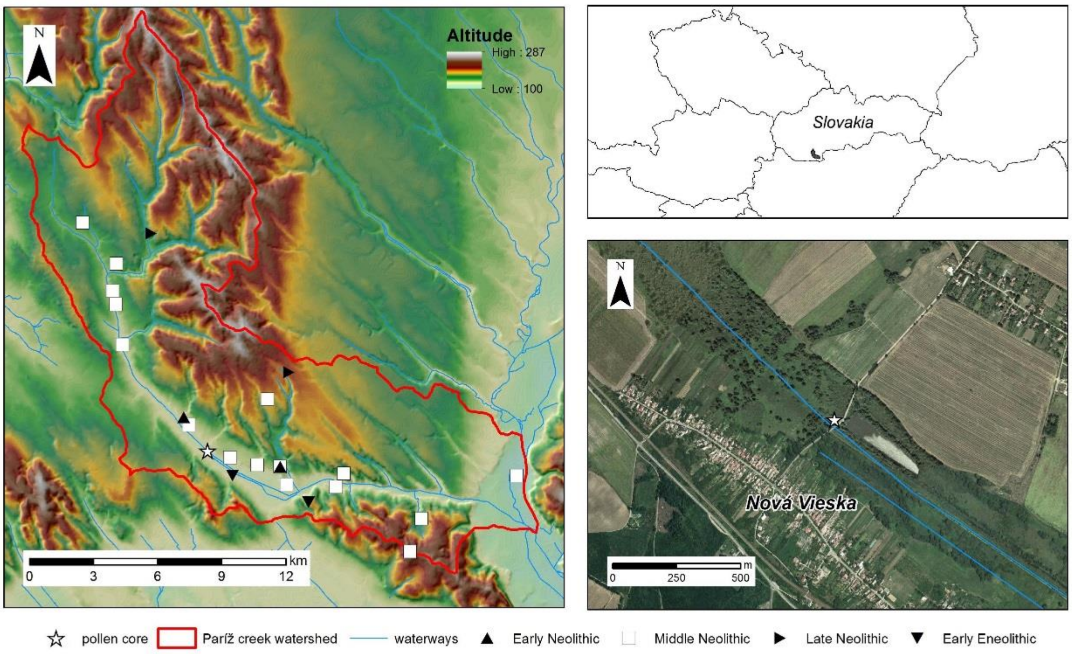
The Parížske močiare marshes (PM) are a National Nature Reserve and one of the most important wetlands in Slovakia. The site is located in a shallow valley on a floodplain of the Paríž Creek, in the Podunajská nížina lowland, the northern subunit of the Little Hungarian Plain (Figure 1). Today, the climate of the site's surroundings is warm and somewhat dry, with an approximate mean annual temperature of 8–9°C (mean January temperature from -1 to -4°C; mean July temperature from 20.5 to 19.5°C). Mean 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 lead 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 (*Phragmito-Magnocaricetea*). In the northern part, these change to mesophilous meadows (*Molinio-Arrhenatheretea*). Alluvial forests (class *Salicetea purpurae*) 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). Thirty-six 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).

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



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, organic content (OC), and magnetic susceptibility (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 cm^3. 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 cm^3.

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-gray clay and small stones; molluscs shells
340-360	As1Sh2Dl1Th+Gs+A	Dark-brown decomposed woody/sedge peat with admixture of clay
360-387	Sh2Dl2Gs+A	Dark-brown decomposed woody peat
387-420		Quercus sp. trunk
420-440	As3Dl1Th+Gg(min)+A	Light-brown clay with layers of woody peat and small stones; molluscs shells
440-450	As1Sh2Dl1Ga+A	Dark-brown woody peat with admixture of clay
450-460		Quercus sp. wood
460-470	Sh2Dl2	Dark-brown decomposed woody peat
470-480	As1Sh2Dl1	Dark-brown decomposed woody peat with narrow layers of light-brown clay; molluscs shells
480-498	Sh2Dl2	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; Dl – 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.

Magnetic susceptibility and organic content (weight loss on ignition [LOI]) measurements

Magnetic susceptibility (MS) was determined using a Kappabridge KLY-2 device. The results were normalised to obtain mass-specific magnetic susceptibility in $m^3.kg^{-1}.10^{-9}$. MS results provide information about the import of allogenic material eroded from the surrounding basin (e.g., Nazarok et al., 2014).

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

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 Clark, 1984) and pollen atlases (Reille, 1992, 1995, 1998). Non-pollen palynomorphs follow van Geel et al. (1980–1981). The nomenclature of pollen types follows Beug (2004) and Punt and Clark (1984) for the family Apiaceae.

Fire history surrounding the coring site 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 cm^{-3} (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 psimpoll 4.27 (Bennett, 1993–2009).

Macrofossil analyses

Sediment for macrofossil analyses was rinsed through a 200-μm sieve. Plant diaspores and other remains were examined under a stereomicroscope at a magnification of 12× and higher. For determination of plant macro-remains, several atlases and books were used (i.e. Bojnanský and Fargašová, 2007; Cappers et al., 2006; Berggren, 1969; 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. 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 psimpoll 4.27 (Bennett, 1996).

Macrophysical climate model

Due to 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 astrononomical 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. Riehl et al., 2008; Higgins and McFadden, 2009; Dreslerová, 2011; Hajnalová, 2012). 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

Eleven samples of terrestrial plant macrofossils were dated using ^{14}C accelerator mass spectrometry (AMS) facility 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 Rijkuniversitet, 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 1950 AD, with 95.4% probability.

Results and interpretations

Stratigraphy and sediment description

The deposit of organic woody material accumulated on 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 clayey, woody, and mollusc layers rich in calcium carbonate ($CaCO_3$) (Table 1). The material accumulated above the oak trunk at 385–360 cm (Table 1) was most probably re-bedded, as indicated by two reversed radiocarbon data. At a 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 interrupt 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 due to an 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 curve of MS increased. This indicates increased input of allogenic material as a result of soil erosion. From 320 cm to the top of the core, the minerogenic sediment formed from erosion of the slopes surrounding the basin.

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

Samples (lab. code)	**ID**	**Depth (cm)**	**Dating method**	**^{14}C age (uncal BP)**	**Calibrated ^{14}C age (cal BP) (95,4% c.i.)**	**Mean calibrated ^{14}C age (cal BP) (95,4% c.i.)**	**Material**
UG-10035	PM 1	500-498	AMS	96760 ± 30	11238-11167	11201	Seeds
UG-10036	PM 2	490-488	AMS	9230 ± 30	10500-10276	10390	Seeds
UG-10037	PM 3	460-458	AMS	9120± 30	10300-10221	10268	seeds, buds
UG-10038	PM 4	440-438	AMS	8390 ± 30	9487-9308	9421	seeds, buds
DSH-4415	PM 9	424-422	AMS	8380± 120	9546-9033	9343	seeds, buds
*UG-10039	PM 5	380-378	AMS	8830± 30	10147-9709	9914	Buds
*UG-10040	PM 6	360-358	AMS	9080±30	10261-10196	10232	Seeds
GRA-56625	PM 11	360-359	AMS	7975±60	9002-8643	8834	Seeds
UG-10041	PM 10	340-338	AMS	5210±25	5995-5916	5960	Seeds
DSH-4414	PM 7	330-329	AMS	4810±59	5653-5330	5525	Seeds
UG-10042	PM 8	322-320	AMS	4800±20	5594-5476	5521	Seeds

Abbreviations: cal: calibrated ages; BP: Before Present (1950); AMS: Accelerator Mass Spectrometry.

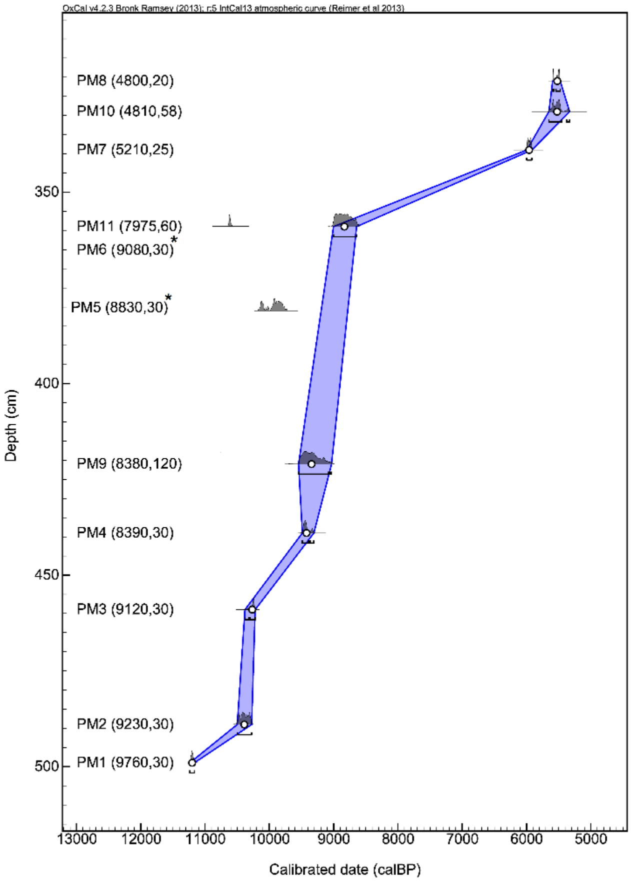


Figure 2.:

Age–depth relationship model of the Parížske močiare marshes profile based on nine radiocarbon dates produced in OxCal 4.1.
cal: calibrated ages; BP: Before Present (1950 AD).
Dates *PM5 (8830,30) and *PM6 (9080,30) were excluded from the age–depth model.

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).

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 arboreal pollen types and of Poaceae (50%) and *Artemisia* (5%) from herbaceous pollen types. Pollen grains of mesophilous trees (*Quercus* and *Ulmus)* were sporadically detected.

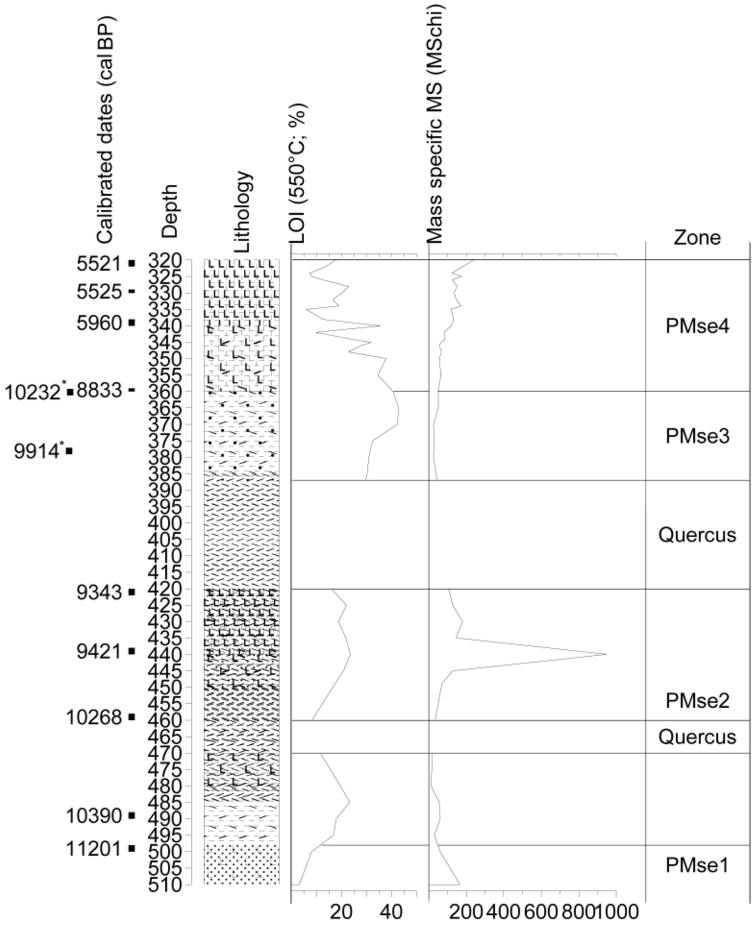


Figure 3.: Results of organic content (LOI) and magnetic susceptibility measurement from the Parížske močiare marshe profile.
()* – date excluded from the depth–age model.

<u>Phase 2: The Early-Holocene landscape transformation</u>

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 then 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.

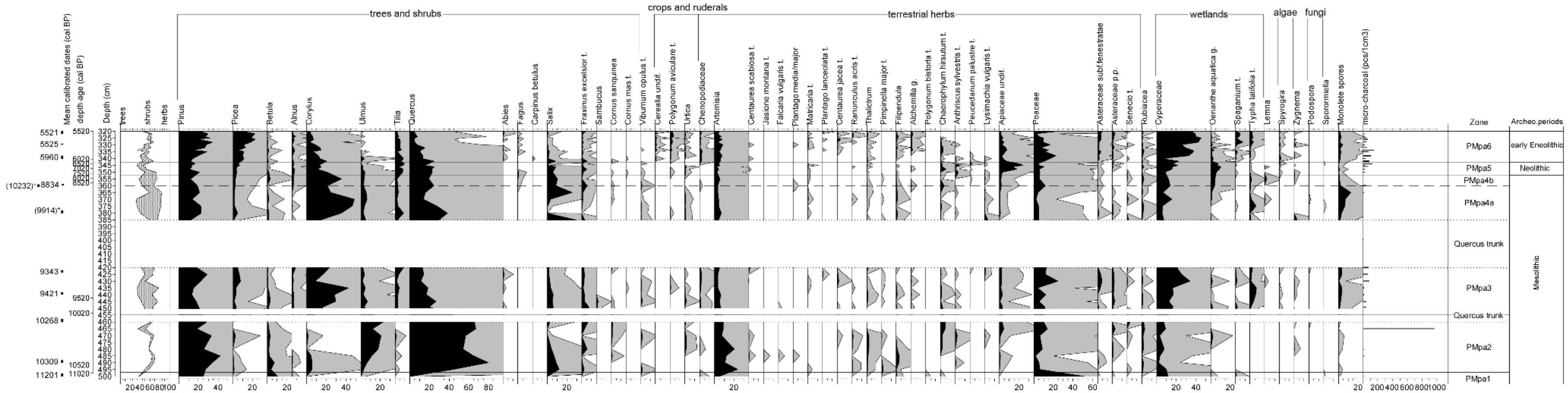
Pollen grains of *Plantago lanceolata* t. and *Polygonum aviculare* t. appeared for the first time. Scarce occurrence of coprophilous fungi (*Podospora*) indicated grazing animals. A small amount of micro-charcoal was recorded. Above this zone, at 420–385 cm, an oak trunk was present in the core.

Phase 3: The mid-Holocene landscape changes

Pollen analysis in the next phase (**Zone PMpa4**; 385–352 cm; ?–7685 cal BP) showed the same trends as the previous zone. Radiocarbon dating suggested occurence 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 (*Cornus 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 (c.f. 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 (Cerealia). Large amounts of micro-charcoal particles indicated the occurrence of fire.

Figure 4.: Percentage pollen diagram of selected pollen types from the Parížske močiare marshes profile.



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

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 evolution of the wetland in 34 plant macrofossil samples and 16 mollusc macrofossil samples relative 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, Potamogeton 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 Amman, 2000), Poland (Galka 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 (Petr et al., 2013; Gałka et al., 2014). The few records of mollusc species indicated open (probably damper) habitats and shallow marshes.

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*, *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*, etc. aquatics *Ceratophyllum demersum*, *Ceratophyllum submersum*, *Chara sp.*, *Lemna minor*/*gibba*, ephippia 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 *Oxyloma 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.

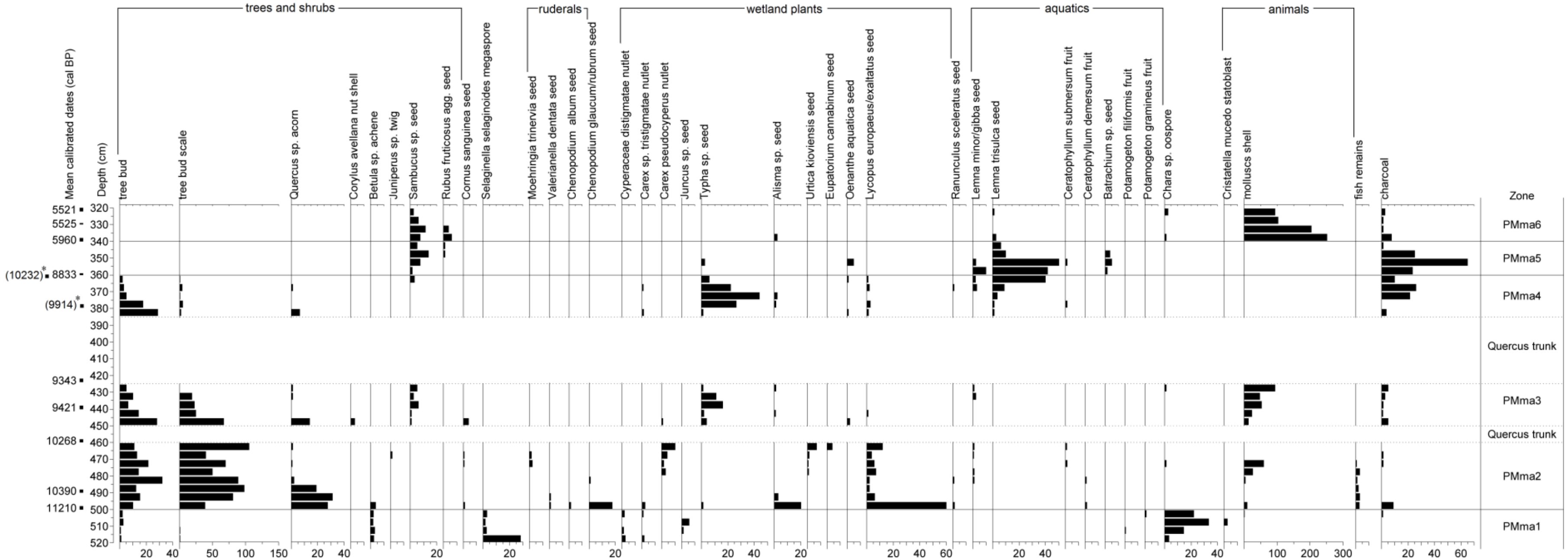
In the next step in wetland development (**Zones PMma3, PMmo3**; 450–420 cm; about 9844–9325 cal BP), the initial high peak of *Quercus* sp. with occurrence of shrubs (*Corylus avellana*, *C. sanguinea*) gradually declined. The predominance of *Sambucus nigra*/*racemosa* took place afterwards. Among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

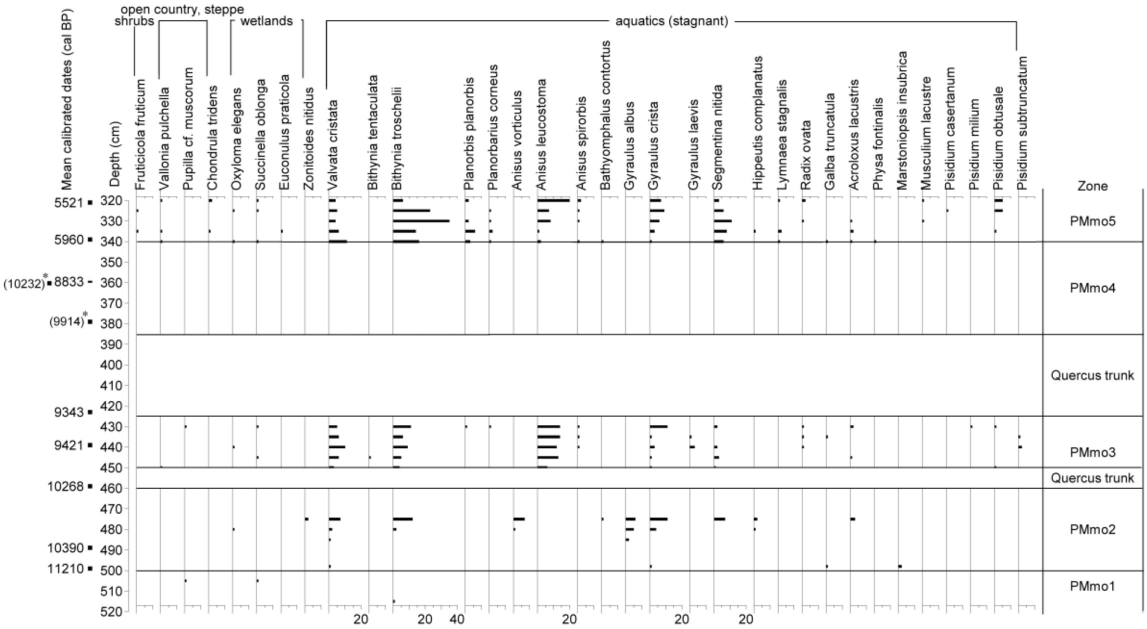
The sediment at 385–360 cm (**Zone PMma4**; ?–8945 cal BP) was most probably redeposited, though plant macro-remains displayed the similar trend as the previous zone (Zone PMma3; 450–420cm), namely, the decline of deciduous trees from their initial dominance. The amount of macro-charcoal is high.

Figure 5.: Plant macro-remains diagram from the Parížske močiare marshes profile in absolute numbers.



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

Figure 6.: Mollusc diagram from the Parížske močiare marshes profile in absolute numbers.



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

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 *Ceratophyllum submersum*, *O. aquatica*, and *Lemna trisulca*. Such conditions lasted until about 8834 cal BP (**Zone PMma5**; 360–340 cm, 8945–5960 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 *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. nigra*/*racemosa*, *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 of these zones (i.e., *Bithynia troschelii*, *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 the one hand, and shrubby places (*Fruticicola fruticum*) on the other.

The macrophysical climatic model (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 characterized 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 δ18O record of the Greenland ice core records – the Preboreal oscillation (Rassmussen 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 and 10.4°C, with slowly declining annual precipitation that reached a minimum (457 mm) at 5000 cal BP. The model reconstructed five additional humid phases, at 9200, 8000, 7800, 6500, and 5400 to 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 the unusual early occurrence of oak (forest) and examine the underlying environmental drivers, including climate change and disturbances by fire or human activities.

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

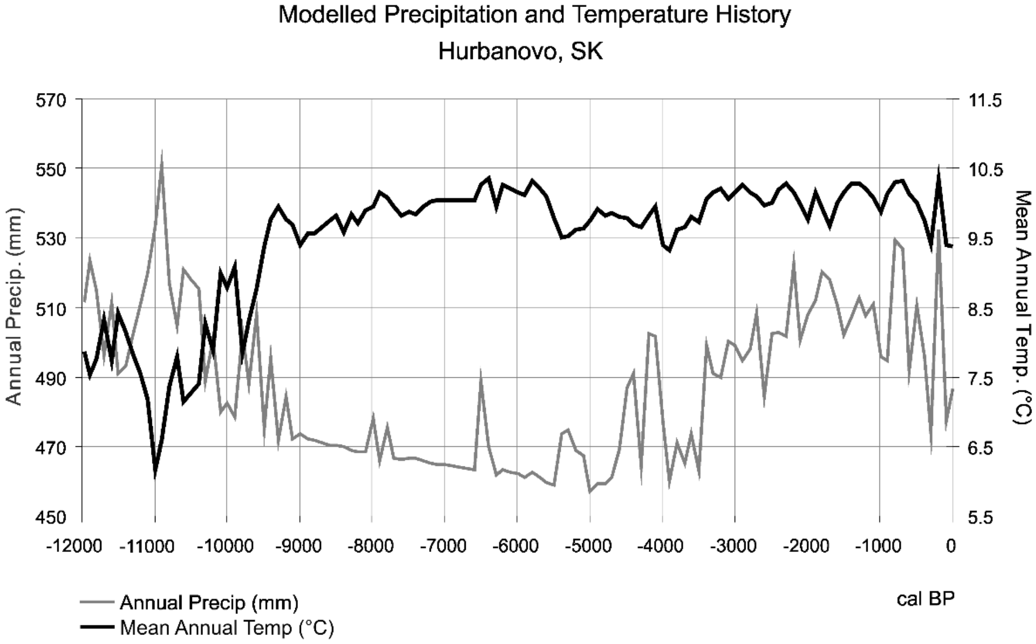
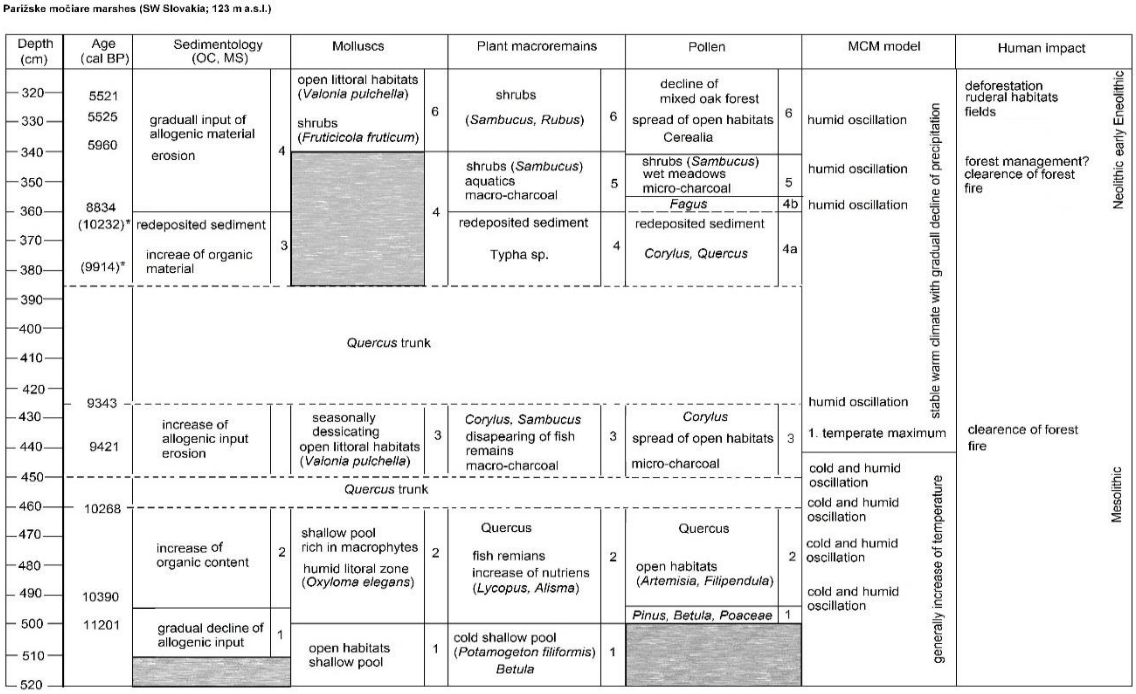


Figure 8.: Summarised development of upland vegetation and wetland environment of the Parížske močiare marshes profile based on all obtained proxies.



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

The 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 the open character and low productivity of 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., *Potamogeton filiformis*) declined, while thermophilous and deciduous forest species (*Quercus*) began to appear. However, finds of cold-adapted snail *Marstoniopsis insubrica* in the assemblages of 500–495 cm, the first find of this species in Slovakia (Horsák et al., 2013), 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 was indicated by the presence of steppe elements in the vegetation (Brewer et al., 2002) and lower value of arboreal pollen (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 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., Willis et al., 1995, 2000; Willis and Andel, 2004; Birks and Willis, 2008; Tzedakis et al., 2013). The 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 the 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.

The Early Holocene expansion of mixed oak forest

The expansion of temperate trees occurred between 11,201–10,780 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 (Willis et al., 1995, 1997; Magyari et al, 2010; Hájková et al., 2013; Petr et al., 2013). 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 survival (Ellenberg, 1996). During the Early Holocene, forest taxa dominated pollen assemblages (almost 90% of the TS; Figure 4) and plant macro-remains (Figure 5). However, the presence of steppe herbaceous taxa (e.g. *Artemisia* and *Centaurea scabiosa* t.) and wet meadow taxa (e.g. *Filipendula* and *Chaerophyllum hirsutum* t.) indicate persistence of open patches on loess slopes as well as within the floodplains (Magyari et al., 2010; Hájková et al., 2013). 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 13,000–11,000 years BP (Brewer et al., 2002), reaching the southern part of Central Europe at around 9000 years 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 (Huntley and Birks, 1983; Tallantire, 2002; Giesecke et al., 2011). 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 such an expansion (Huntley, 1993; Finsinger et al., 2006; 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, i.e. a shallow, permanent pool/lake. A similar cold, wet oscillation was clearly detected in various proxies in the South Carpathian Mountains as well (Buczkó et al., 2012; Tóth et al., 2012).

Corylus started to expand at about 9840 cal BP (Figures 4, 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. The cold, humid oscillations reconstructed by the MCM model may have contributed to the reduction of fires during these periods. However, the 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, 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; Wacnik, 2009; Regnell, 2012; Sümegi, 1999), 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 was based 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 11,000–10,200 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 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 (ca. 11,500 cal BP) in the central part of the Carpathian Basin – Great Hungarian Plain (c.f., Sümegi et al., 2002; Jakab et al., 2004). Similarly, the spread of *Quercus* before *Corylus* had been recorded in lowlands of SE Europe, e.g. Romania (Feurdean et al., 2007) or Bulgaria (Connor et al., 2013). It is very plausible, that 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 indictor (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 Paríž Creek valley most probably spanned from 7450–6250 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 Thiébault, 2008). Grazing thins the forest canopy and promotes the spread of light-demanding shrubs such as *Cornus mas*, *C. sanguinea*, and *Sambucus* (Moskal-de 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 (Rackman, 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 (Stankoviansky, 2008; Smetanová, 2011). 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.

Conclusions

Fossil assemblages from Parížske močiare marshes 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 due to 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, 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 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 *Quercu*s. 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 the further accumulation of organic material by 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).

Acknowledgements

The research was supported by the project grant GAČR P504/11/0429, institutional support of Masaryk University, and the long-term research development project no. RVO 67985939. It was also supported by the Slovak Grant Agency VEGA (project no. 1/0477/11) and by the Slovak Research and Development Agency (contract no. APVV-0598-10). We are grateful to Pavla Žáčková, Petra Hájková, and Peter Pišút for the help with separation and identification of macro-remains selected for the dating process, Leona Chadimová for MS measurement, Hilary Birks for the help with interpretation of analysis of plant macro-remains, and Zuzana Formánková for laboratory work. This manuscript was improved by suggestions of Pál Sümegi

and an anonymous reviewer. We also thank Simon Connor for linguistic corrections and helpful comments.

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Holocene history of a *Cladium mariscus*-dominated calcareous fen in Slovakia: vegetation stability and landscape development

Holocenní historie vápnité slatiny s dominantní mařicí pilovitou na Slovensku: vegetační stabilita a vývoj krajiny

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Dedicated to Kamil Rybníček and Eliška Rybníčková on the occasion of their 80th birthday

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Abstract

There are very few palaeoecological studies of thermal springs in Central Europe, despite the fact that they are extreme but stable habitats that enabled the long-term survival of certain species and are located in areas for which there is little data about landscape history. In western Slovakia, close to Malé Bielice village at the northern margin of the Pannonian-Carpathian boundary, a peat-forming warm spring is uniquely preserved, and it still harbours a rare plant, *Cladium mariscus*. This site is located in a region that is noteworthy for the occurrence of many rare, light-demanding species that have disjunct distributions or are at the limits of their distributions, which may indicate a long history of treeless habitats there. The geographical position of this study site thus provides a great opportunity to address the perennial debate about *in situ* relicts and the continuity of grasslands throughout the forest optimum. We analyzed a Holocene sediment core for macrofossils of vascular plants, bryophytes and molluscs, and for pollen, which were surprisingly preserved in rather high diversity, which enabled a detailed reconstruction of the landscape history. We further reviewed the archaeological evidence. Using this multi-proxy approach, we were able to confirm (i) the early expansion of mesophilous trees (*Ulmus*, *Fraxinus*, *Tilia* and *Quercus*) in northern parts of the Carpathian-Pannonian boundary, but the onset of this expansion could not be dated precisely, (ii) the continual persistence of the *Cladium mariscus* population in the fen and (iii) existence of open steppes and/or dry grasslands and open wetlands in this region throughout the Holocene. Since the Bronze Age, there are coincidences in the history of human settlement, local development of the fen and regional changes in the representation of particular habitats, including managed wet, mesic and semi-dry grasslands.

Keywords: archaeophytes, grassland persistence, macrofossils, molluscs, multi-proxy, pollen, radiocarbon dating, human influence

Introduction

Thermal springs in Central Europe are extreme habitats with stable conditions and potential refugia where light- and warm-demanding wetland species could survive during the whole Holocene or even during former periods (Diaconeasa and Popa, 1964). Most thermal springs are utilized for spa purposes and as a consequence the vegetation is destroyed. In western Slovakia, close to the town of Partizánske (the Malé Bielice village) at the Pannonian-Carpathian interface, one wetland patch around a warm spring still persists and harbours rare fen species such as *Cladium mariscus* and *Schoenus nigricans* (Ambros, 1996). These species are rare and strictly protected in several countries in central Europe (Feráková et al., 2001; Piękoś-Mirkowa and Mirek, 2006; Grulich 2012). *Cladium mariscus* is a light-demanding species with wide ecological amplitude, growing in both calcium-rich wetlands in areas with a subcontinental climate and on sandy soils in areas with an oceanic climate (Galka and Tobolski, 2012). It is assumed that low availability of nutrients (nitrogen, phosphorus) is also important for its occurrence (Balátová-Tuláčková, 1991; Pokorný et al., 2010). Because in peat deposits seeds and pollen of *Cladium mariscus* are usually well preserved and identifiable it is possible to study the population dynamics and continuity of its occurrence (cf. Hafsten, 1965; Pokorný et al., 2010, Galka and Tobolski, 2012). In Central Europe, *Cladium mariscus* is considered to be a relict from earlier periods of the Holocene (Brande, 2008; Pokorný et al., 2010). The fossil records from the Middle Holocene are the most frequent and this species is usually not present in the youngest phases of fen development. Further, there is the fossil record from the MIS 3 interstadial period from Belgium (Haest et al., 1986: 38–42 000 uncal BP). It therefore seems that *Cladium mariscus* could be considered as a warm-stage relict in Europe. In Slovakia, the fossil record is fragmentary with *Cladium* detected in sedimentary fill in a palaeomeander of the River Danube in the La Tène period (Pišút and Procházka, 2012) and in the Šúr palaeolake in the Danube lowland south of the Malé Karpaty Mts in the Middle Holocene (Žáčková, *in verb*). The aim of this study is to trace the history of *Cladium mariscus* populations in Slovakia, where warm springs could have been one of its potential long-lasting refugia.

The study site is located at the southern margin of the Inner Western Carpathians (middle-Nitra Basin), an area for which there is currently no radiocarbon-dated palynological data (compare Kuneš et al., 2009). Thus, it provides an opportunity to fill the gap in our palaoeocological knowledge of the Pannonian-Carpathian interface. Two important questions can be addressed: the spread of mesophilous trees (*Ulmus*, *Fraxinus*, *Tilia* and *Quercus*) in the Early Holocene and continuity of grasslands throughout the forest optimum. In the region where the warm spring studied is located, some range-margin disjunct populations of southern elements occur (e.g., *Aethionema saxatile* and *Cotinus coggygria*; Ambros, 1996; Čeřovský et al., 1999). Hence, timing of appearance of mesophilous tree pollen in the profile and knowledge of landscape development could bring certain indirect evidence to the question when did these disjuctions originate.

The continuity of temperate grasslands throughout the entire Holocene is the second still unresolved problem. Although older studies did not acknowledge continual survival of steppe elements in Central Europe (e.g. Rybníčková and Rybníček, 1972), there is a growing body of evidence that human activity played a crucial role in both the formation of grasslands and the alteration of forest composition from Neolithic times onwards (Pokorný et al., 2006; Baumann and Poschlod, 2008; Dutoit et al., 2009, Magyari et al., 2010). In the Middle Holocene, closed-canopy forests started to spread, whereas heliophilous and open grassland species retreated. The spread of agriculture that started in Central European lowlands ca 7500 cal BP had a counteracting effect: landscape was step-by-step deforested and cattle grazing, burning and crop cultivation facilitated the spread of heliophilous species. Thus, in the regions that were colonized during Neolithic and Late Neolithic, the pool of Early Holocene heliophilous species may have been preserved and the development of heliophilous vegetation may have been more or less continuous during the Holocene. Hájková et al. (2011) summarized the evidence supporting this hypothesis for the White Carpathians, another region at the western Carpathian-Pannonian boundary, where species considered to be Early Holocene elements disjunctly occur despite the absence of naturally treeless habitats. The study site is located in the early-colonized region with archaeological records since Early Neolithic periods (Točík, 1970) when human activities could have helped to maintain a treeless vegetation throughout the Holocene forest optimum (Late Neolithic period), which is considered to have been a bottleneck for the survival of light-demanding species (Ložek, 2008). Without human influence, treeless vegetation can survive only on sites, which are edaphically unfavourable for tree growth, such as rocky outcrops. Disjunct occurrences of some light-demanding steppe or semi-dry- and mesic-grassland species in the wider surroundings of the study site (e.g. *Crepis sibirica*, *Gypsophyla fastigiata*, *Peucedanum carvifolia* and *Tephroseris integrifolia* subsp. *moravica*; Hlaváček et al., 1984; Ambros, 1996; Janišová et al., 2012) resemble the above mentioned White-

Carpathian story and indicate that the study profile could be suitable for tracing the Holocene survival of light-demanding species.

Our study thus addresses not only the processes affecting large-scale landscape transformations but also local “ahistoric” processes that resist them and contribute to the formation of recent diversity patterns. We (i) explore the development of local fen habitats and *Cladium mariscus* persistence around warm springs using multi-proxy methods (pollen, macrofossils of plants and molluscs, radiocarbon dating); (ii) document the spread of mesophilous trees since the Early Holocene (iii) search for evidence of continuity of open grassland vegetation and (iv) trace the history of human settlement in pollen records, with an emphasis on the distribution of grassland habitats.

Methods

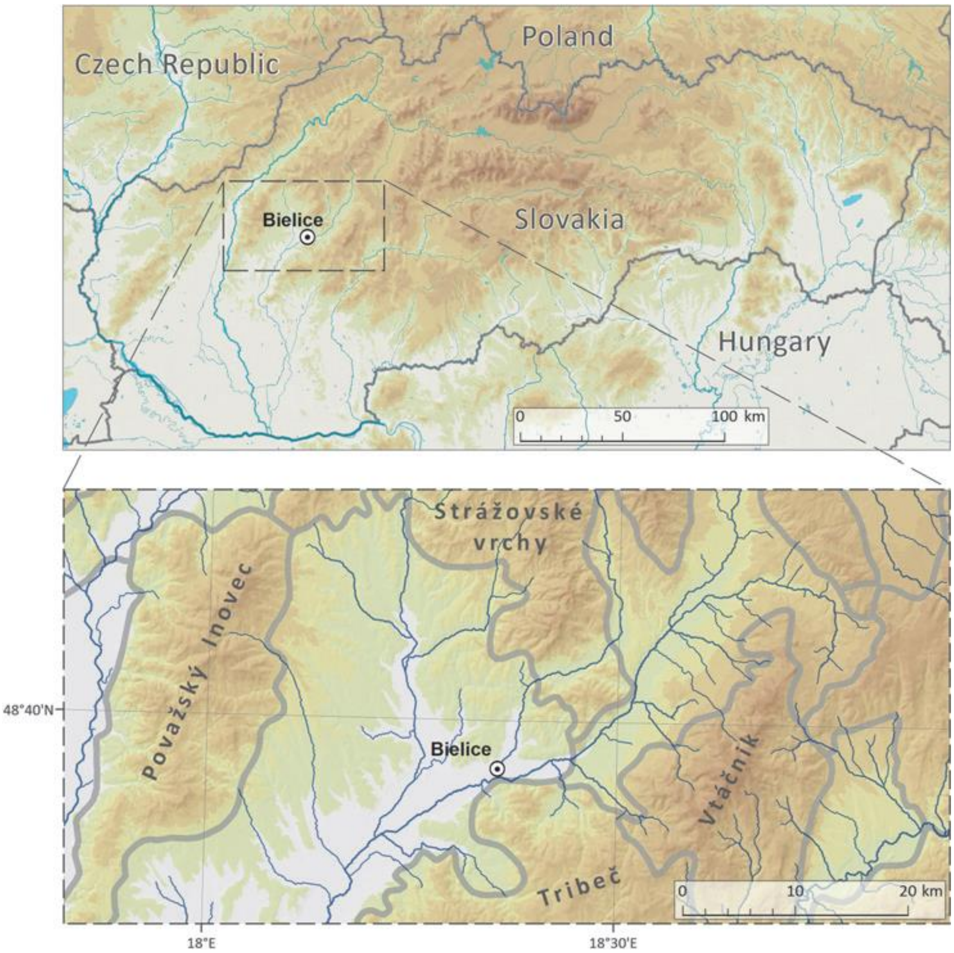
Study site

The study site is located near the Malé Bielice village in the middle-Nitra Basin (western Slovakia), which separates Považský Inovec, Strážovské vrchy and Tribeč Mountains (Figure 1) and links with Podunajská lowland in the south. Geomorphologically, it belongs to the Inner Western Carpathian Mountains. The study site is 185 m a. s. l. and supplied with warm spring groundwater (about 40 °C). It is one of four recent localities of the relict and critically endangered species, *Cladium mariscus* (Eliáš et al., 2003), even though the water level was reduced by drawing off spring water from this site in the past. Vegetation belongs to the *Magnocaricion elatae* alliance (Oťaheľová et al., 2001). Fen vegetation is overgrown by *Phragmites australis* and is extremelly poor in species, but the population of *Cladium* remains viable. The fen peat is 240 cm thick and accumulated on fluvial sands. Climate at the site is warm and slightly dry with a 8–9 °C mean annual temperature and 550–600 mm mean annual precipitation (http://geo.enviroportal.sk/atlassr/).

The study site is in the valley of the river Nitra and surrounded by loess slopes on the northern edge and flood terraces in the east (http://mapserver.geology.sk; Figure 1). This kind of landscape has attracted people since prehistoric times. In Central Europe, the first agricultural cultures were at naturally sheltered sites with favourable soil and climatic conditions located mainly on loess terraces and slopes (Hajnalová, 2007, Bogaard, 2004). This region is in an old-settlement zone; the oldest known archaeological records are for the middle Pleistocene (Bárta, 1965; Kaminská, 2008) and the fossil remains of *Mammoth primigenius* were discovered near the study site (Bárta, 1965).

The oldest known agricultural settlements in the vicinity of the site date back to the Early Neolithic (Linear Pottery culture; ca 5700–5000 BC; 7650–6950 cal BP) through Late Neolithic (Lengyel III; ca 4700–4400 BC; 6650–6350 cal BP) and Bronze Age onwards (Lusatian Culture; 1300–700 BC; 3250–2650 cal BP) (Točík, 1970; Veliačik, 1988). Rich settlement records are dated to the Iron Age (Hallstatt; ca 700–450 BC; 2650–2400 cal BP; La Tène; ca 450–0 BC; 2400–1950 cal BP) and they probably occur there because of the occurrence of iron ore and gold in the nearest mountains (Wiedermann, 1985; Veliačik, 1988; Vangľová, 2008). Human occupation of this landscape continues through Slavic Time (6th–12th the century AD; 1250–650 cal BP) up to the present. First written evidence about the nearest villages is for the second half of the 13th century AD; 550 cal BP (Kropilák et al., 1977–1978).

Figure 1.: Location of the study site in the middle-Nitra Basin (SW Slovakia).



Sediment sampling and analyses

Material for palaeoecological analyses was collected using a Russian-type peat-corer (Eijkelkamp, Giesbeek, The Netherlands) to obtain two cores that were collected close to each other. The physical properties of the sediments were described following Troels-Smith (1955; for detail see Table 1). Profiles of all proxies were divided into developmental zones based on results of constrained cluster analysis based on sum of squares (Coniss analysis, implemented in Tilia program; Grimm, 2011).

Material for pollen analyses from both profiles were sub-sampled (volume of 1 cm^3) at 10cm intervals along the profile and processed using standard techniques (Faegri and Iversen, 1989) with *Lycopodium* added as a marker (Stockmarr, 1971). In the bottom part of the profile, where the depth-age model indicated that 40 cm spaned almost five thousand years, we sampled certain sequences at 2 cm intervals (207–197 cm) and 3 cm intervals (198–187 cm) in order to identify or rule out a possible hiatus.

Samples containing clastic material were pre-treated with cold concentrated HF (hydrogen fluoride) for 24 hours and then KOH (potassium hydroxide) solution before acetolysis. At least 500 pollen grains of terrestrial plants per sample were identified using Beug (2004), Punt and Clark (1984) for the family Apiaceae, or pollen atlases (Reille, 1992, 1995, 1998). For the determination of non-pollen palynomorphs van Geel et al. (1980–1981) and van Geel et al. (2003) was used. The nomenclature of pollen types follows Punt and Clark (1984) and Beug (2004). The concentration of microscopic pieces of charcoal was determined using particle counts and compared with *Lycopodium* counts (Whitlock and Larsen, 2001; Tinner and Hu, 2003).

Pollen data are presented in two percentage pollen diagrams. In the first the development of forests, ruderal and dry habitats is presented. In the second is the pollen of species that grow mainly in wetland and wet meadow habitats. Spores and Non-Pollen Palynomorphs (NPP) are also included in the second pollen diagram. The percentages of the different pollen taxa was based on pollen sums of arboreal and non-arboreal pollen (AP+NAP = 100%). The percentages of wetland taxa, spores and non-pollen palynomorphs were related to the extended sum (i.e. AP+NAP+wetland+spores+NPP = 100%). In addition to classic pollen diagrams, we constructed a synoptic diagram, in which particular pollen taxa were classified into groups according to the habitat requirements of the plant species involved. We created these groups in order to trace the changes in the representation of open habitats, especially particular types of grasslands. We classified all pollen taxa. Collective pollen taxa, especially those at the family level, were merged into the group of unclassified herbaceous taxa named “indifferent ecology”. This group also includes Poaceae, because they may dominate dry grasslands, wetlands and open Carpathian forests; but some authors use Poaceae as indicators of grasslands. Nevertheless, the majority of this group is considered to grow in open habitats, including steppes. Chenopodiaceae, which are used as steppe indicators (Magyari et al., 2010), were placed in the group “open-country ruderals”, because macrofossils of *Chenopodium album* agg. were found at the study site. This group may also indicate steppe and halophytic habitats, especially in the first phase of the Holocene. We are aware that some taxa are difficult to classify, but we believe that using this approach led to a more objective assessment of landscape changes than relying on particular pollen taxa. For the list of taxa included in each of the groups and comments on species classification see Appendix 1. For photographic documentation of *Cladium* pollen and *Sporormiella* t. spores see Appendix 2 and 3. All pollen diagrams were constructed using Tilia software v. 1.7.16 (Grimm 2011).

Five centrimeters wide samples for macrofossil and mollusc analyses (50 cm^3) were taken discontinuously apart at 5 cm intervals and sieved into three fractions (200–630 μm, 0.630–1 mm, > 1 mm). Larger fractions were analyzed using a dissection stereomicroscope at magnifications of 10–40x and each slide (1 cm^3 of the finest fraction) was examined at 100–400x magnification to identify small seeds (e.g., *Juncus*) and oogonia of *Chara vulgaris*. Seeds and plant tissues were determined according to Mauquoy and van Geel (2007), Velichkewicz and Zastawniak (2008), Cappers et al., (2012) and other available identification literature. Macrofossils were also checked against the reference seed collection of the Institute of Botany, Academy of Sciences of the Czech Republic. Schweingruber (1978) was used for determining wood fragments and Hedenäs (2003) for bryophytes. Values are presented as absolute numbers (seeds, bryophytes, molluscs) or as volume percentages (plant tissues and woods). Mollusc shells were separated from other macrofossils and determined according to Ložek (1964) and M. Horsák's personal reference collection, using a dissection stereoscopic microscope. Remnants of slugs were not considered. Nomenclature of vascular plants follows Marhold and Hindák (1998), that of bryophytes Hedenäs (2003) and molluscs Horsák et al. (2010). Both, macrofossil and mollusc diagramms were created using C2 software (Juggins, 2003).

Table 1.: Stratigraphy and description of fen peat in the Male Bielice profile. Components: Tb (Hyp) – moss peat, Th – herbaceous peat, Tl – wood peat, Dh – herbaceous detritus, Dl – wood detritus, GCa – calcium carbonate precipitation, Ga – sand, [A] – charcoal.

Depth (cm)	**Troels-Smith system**	**Description**
0-40	Th3, GCa1, Dh+	Sedge peat with an admixture of $CaCO_3$, root zone
40-55	Th4, Tb+, Dh+	Sedge peat without $CaCO_3$
55-120	Th3, GCa1, Tb (Hyp)++, Dh+	Brown-moss/sedge peat with $CaCO_3$ deposits
120-240	Th2, Tl2, Tb(Hyp)+, Dh+, Dl+, [A]	Sedge/wood peat with small admixture of bryophytes and charcoals
below 240	As2, Gg(min)2	Solid clay with small stones

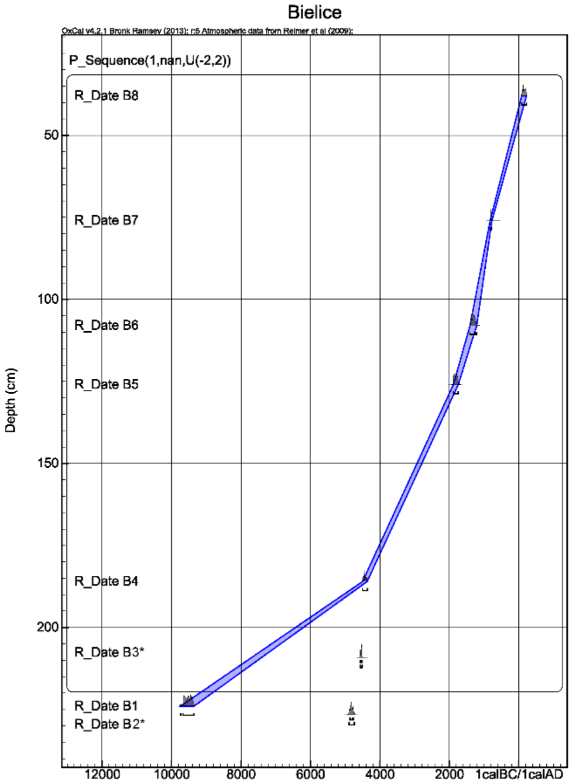
Chronology

Based on distinct changes in pollen diagrams we identified eight layers that were AMS radiocarbon dated. Dominant plant macrofossils were isolated from respective layers and sent for dating to the Centre for Applied Isotopes Studies, University of Georgia, Athens, GA, USA (UG-) (Table 2). A depth-age relationship model was constructed using OxCal 4.1 (Bronk Ramsey, 2009; Figure 3). An IntCal09 calibration curve (Reimer et al., 2009) was used to calibrate radiocarbon dates. In the main text, age of each sample refers to centre of interpolated calibrated age before year AD 1950 (i.e. BP=0), with a 95.4% probability. In the archaeological context, we additionally use also years BC/AD. Dating of samples (single seeds of *Schoenoplectus*) from the depths of 205–207 cm (6250 cal BP) and 225–227 cm (6623 cal BP) gave results that do not correspond with pollen spectra indicating an Early Holocene age. Because both these dates are based on a single seed, we considered these results to be a product of bioturbation processes in grazed spring fens and as a consequence rely more on bulk dating (see Discussion for further argumentation). That is why we did not include these two dates in the depth-age model and decided instead to date a bulk sample from the bottom layer.

Table 2.: Results of 14C dating of the Male Bielice peat profile. *UGAMS 12321 and 12322 according to the pollen record (for detail see Chronology section in the Methods) are not reliable and were not included into the depth-age model (see Discussion for details). Identity of seeds used for dating: [1]*Schoenoplectus*, *Cladium*; [2]*Schoenoplectus*; [3]*Schoenoplectus, Cladium*, *Lycopus*.

Samples	**Depth (cm)**	**Dating method**	**Age in uncal BP**	**Cal a AD/BC (95.4%-Interval)**	**Cal a BP (95.4% c.i.)**	**Material**
UGAMS 12327 (B8)	37-39	AMS	1860 ± 20	85-222 AD	1865-1728	Seeds[1]
UGAMS 12326 (B7)	75-77	AMS	2620 ± 25	826-776 BC	2776-2726	Seeds[2]
UGAMS 12325 (B6)	107-109	AMS	3040 ± 30	1406-1213 BC	3356-3163	seeds[1]
UGAMS 12324 (B5)	125-127	AMS	3480 ± 25	1885-1740 BC	3835-3690	seeds[1]
UGAMS 12323 (B4)	185-187	AMS	5620 ± 20	4499-4368 BC	6449-6318	Seeds[3]
UGAMS 12322* (B3)	205-207	AMS	5440± 20	4342-4259 BC	6292-6209	Seeds[2]
UGAMS 12321* (B2)	225-227	AMS	5830± 240	4790-4556 BC	6740-6506	Seeds[2]
UGAMS 12763 (B1)	223-224	AMS	10000 ± 30	9743-9356 BC	11693-11306	bulk

Figure 2.: Depth-age relationship for the Malé Bielice profile based on six radiocarbon dates.



Results

Stratigraphy

The peat is mainly composed of sedge peat (*Cladium*, *Schoenoplectus*) and in the upper part there is a slight admixture of calcium carbonate (0–120 cm) and mollusc shells (0–150 cm). Large quantities of wood fragments are present in the lower peat layers (125–240 cm). Generally, the peat is characterized by a rather high decomposition rate, probably promoted by hot water (cf. Taylor and Dykstra, 2005). Bryophytes occur in low quantities in the middle part of the profile and are not very-well preserved. The core used for macrofossil and mollusc analyses was about 15 cm longer than that used for pollen analysis, because the oldest (bottom) layer was slightly thicker. For detailed information about the stratigraphy and peat composition see Table 1 and Figure 2 (macrofossils).

Pollen

Based on cluster analysis, the pollen diagram was divided into the four main phases and two sub-phases (Figure 4, 5).

1. The first zone Bpa1 (227–212 cm; 11 475–9568 cal BP) is characterized by the dominance of *Pinus* with an admixture of *Larix*, *Juniperus*, *Betula* and *Salix*. Among the different pollen types of herbaceous plants, Poaceae and *Artemisia* dominated. Pollen of *Picea* and mesophilous trees (*Quercus*, *Ulmus* and *Corylus*) is also present. Pollen of trees makes up almost 75% of the total pollen sum (TS), but the presence of species such as Poaceae, Rubiaceae, Chenopodiaceae, *Artemisia*, *Matricaria* t.. and *Cladium mariscus* clearly indicate the presence of open habitats.

2. The second zone Bpa2 (212–182 cm; 9568–6174 cal BP) is characterized by a great increase in the pollen of mesophilous trees (*Alnus*, *Ulmus*, *Tilia*, *Quercus* and *Fraxinus*), decline in that of *Pinus* and complete disappearance of that of *Larix* from the pollen record. Pollen of light-demanding *Corylus* shrubs also significantly increases. Pollen grains of *Fagus* occur sporadically. Among the pollen of herbaceous plants, species of wet habitats (e.g. *Senecio* t., *Petasites*, *Peucedanum palustre* t. and *Primula farinosa* t.) occur in higher quantities. Cyperaceae markedly increase and taxa indicating open water appear (*Lemna* and *Alisma* t.).

3. In the third zone Bpa3 (182–112 cm; 6174–3640 cal BP) pollen of *Fagus*, *Carpinus* and *Abies* is present. Pollen of herbaceous plants indicates the presence of dry and mesic

meadows (*Cephalaria/Dipsacus*, *Jasione montana* t., *Falcaria vulgaris* t. and *Plantago lanceolata* t.), wetlands (*Cladium mariscus*) and nutrient-rich habitats (S*olanum dulcamara*, *Chelidonium majus, Urtica* and *Bidens*). Cerealia pollen (*Triticum* t.; found at the end of this zone) indicates human settlement. In the wetland, green algae *Botryoccoccus* rapidly increases and Cyperaceae decline.

In the sub-zone Bpa3b (112–62 cm; 3640–2392 cal BP) pollen of *Fagus*, *Carpinus* and *Tilia* clearly declines, whereas that of *Alnus* rapidly increases. Higher quantities of *Betula* are also recorded. Among the pollen of herbaceous plants the increase in that of cereals (*Triticum* t. and *Secale*), ruderals (*Polygonum aviculare* t.) and pasture plants (e.g. *Eryngium campestre* t., *Orlaya grandiflora* t. and *Plantago lanceolata* t.) indicates presence of dry-grasslands and pastures. Concerning local taxa, *Botryococcus* suddenly declines and Cyperaceae increases, which indicates a lowering of the water table.

4. At the beginning of the sub-zone Bpa4a (62–32 cm; 2392–1563 cal BP), the amount of pollen of Cerealia, ruderal-, meadow- and pasture indicating taxa increases and *Juniperus* re-appears, implying the spread of pastures. In the second part of the zone, there is a marked decrease in the amount of Cerealia and *Juniperus* pollen and increase in that of wet-meadow species (*Filipendula*, *Trifolium badium* t. and *Gentiana pneunomonanthe* t.). *Botryococcus* re-appears and Cyperaceae decline and the quantity of micro charcoals increases.

The last pollen sub-zone Bpa4b (32–7 cm; 1563–405 cal BP) is characterized by a decline in tree pollen (AP decreases to 50%) and an increase in that of vegetation associated with the presence of humans; pollen of *Fagopyrum* is recorded for the first time and that of *Secale* increases continuously from the beginning of this zone. Of the ruderal species, a large quantity of *Cannabis* pollen is recorded. The increase in pollen of taxa indicating nutrient-rich habitats is also recorded (*Urtica*, *Bidens* and *Chenopodiaceae*).

Figure 3.: Macrofossil diagram. Main components of the peat are placed at the beginning of the diagram and presented in relative percentages. Countable plant remains are given in absolute numbers (seeds of vascular plants, oogonia, bryophyte stems), uncountable material (wood, plant tissues) in percentages in terms of volume. Oogonia of *Chara vulgaris* and seeds of *Juncus articulatus* were counted in 1 mL of the finest fraction of the sediment.

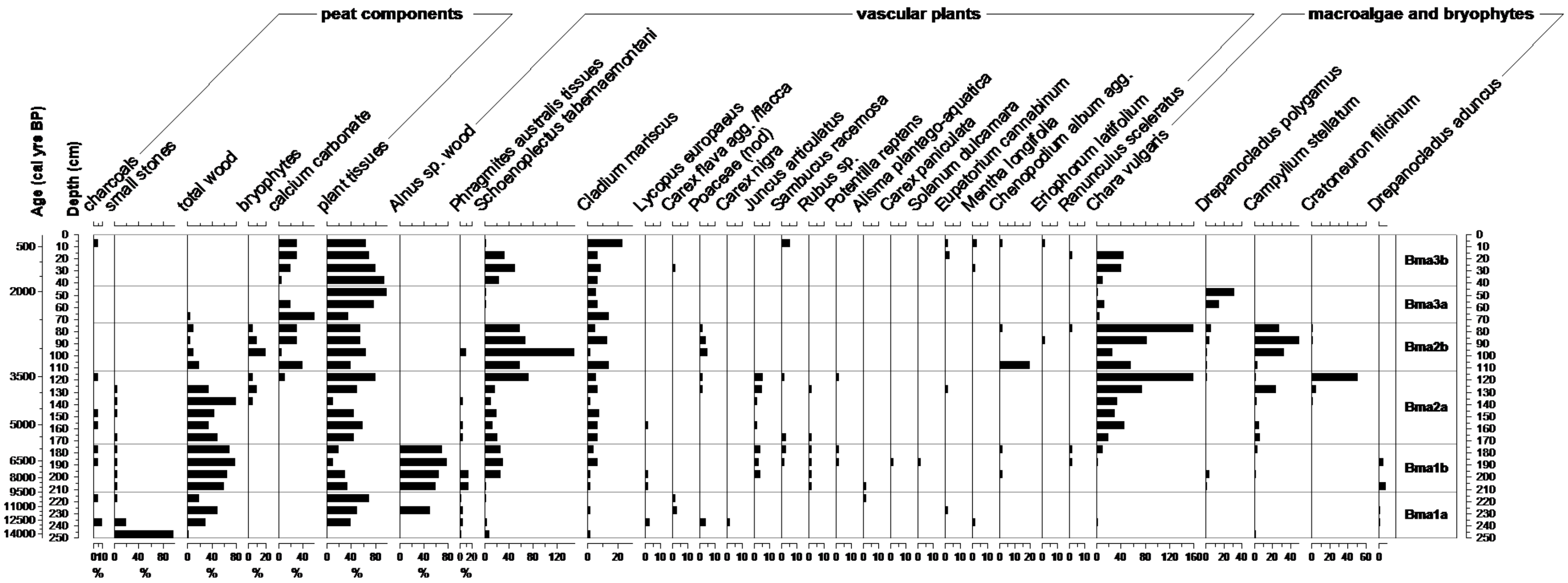


Figure 4.: Percentage pollen diagram of trees, ruderals and dry-grassland species. The percentages of of individual pollen taxa are based on pollen sums of arboreal and non-arborea pollen (AP+NAP = 100%).

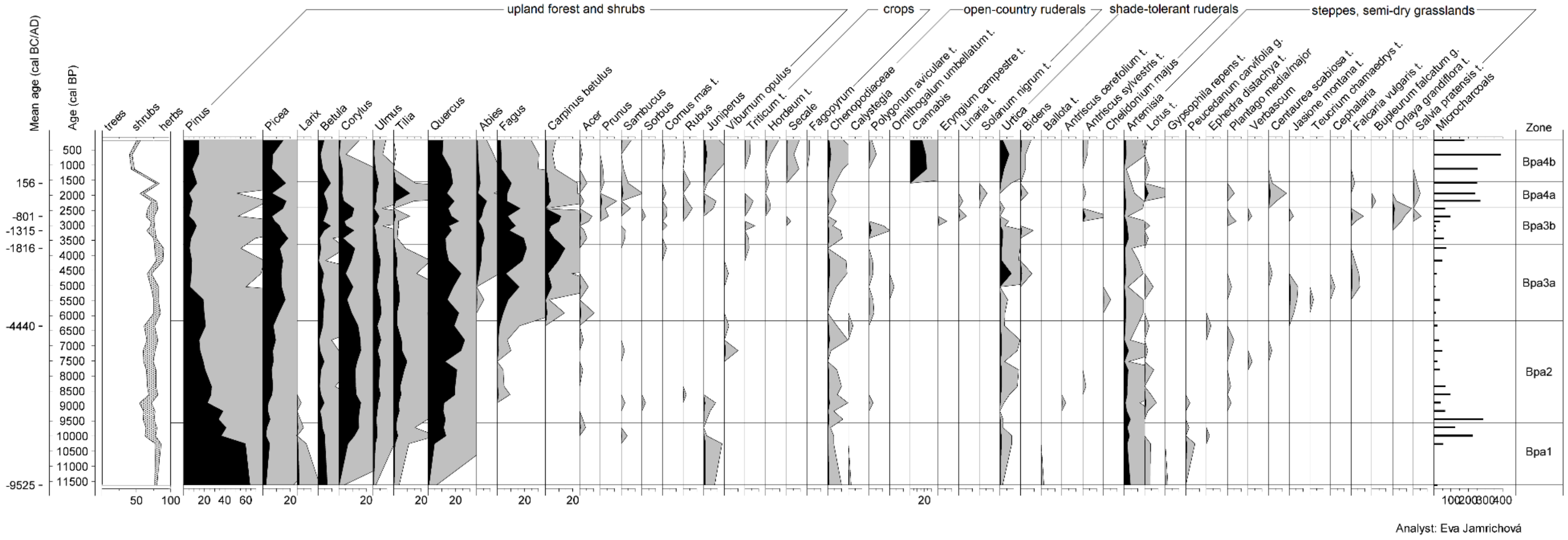
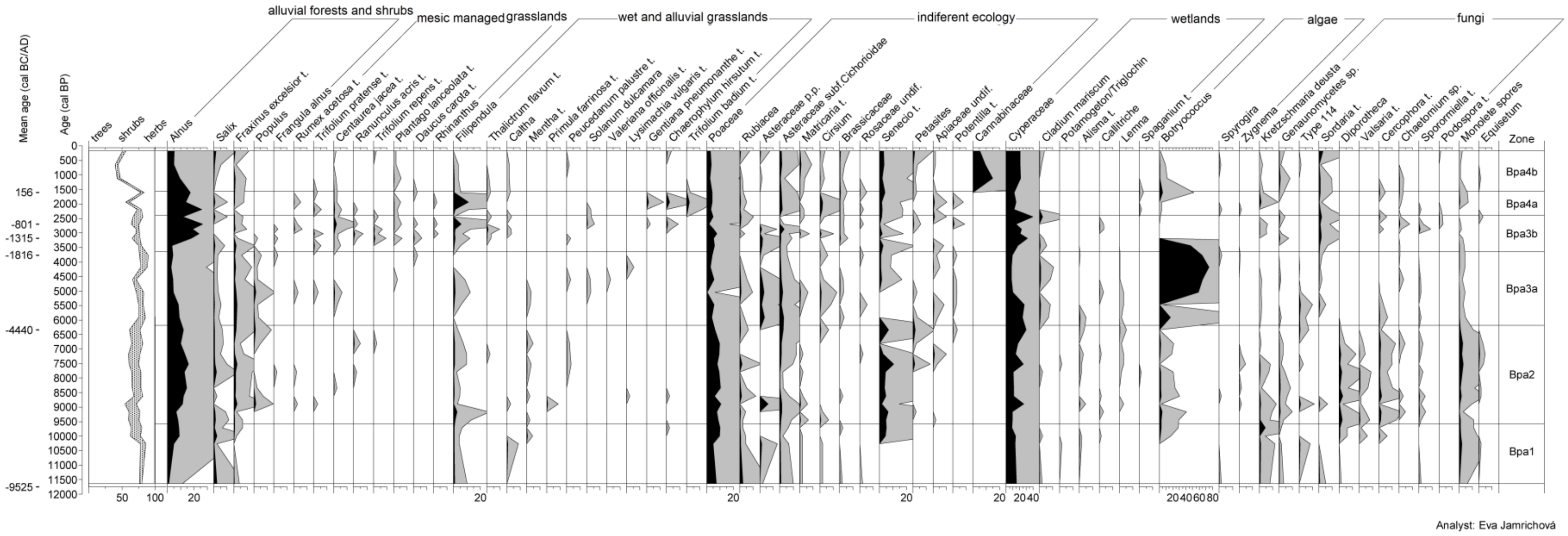


Figure 5.: Percentage pollen diagram of species preferring wetland and wet meadow habitats. Spores and non-pollen palynomorphs (NPP) are also included. The percentages of individual pollen taxa are based on pollen sums of arboreal and non-arboreal pollen (AP+NAP = 100%). The percentages of wetland taxa, spores and non-pollen palynomorphs are based on the extended sum (i.e., AP+NAP+wetland+spores+NPP = 100%).



Macrofossils

On the basis of cluster analysis, we divided the macrofossil diagram into three main phases and three sub-phases (see Figure 3). The local vegetation remained stable throughout the time span of this profile; seeds of *Schoenoplectus tabernemontani* and *Cladium mariscus* are present continuously.

1. Zone Bma1a (250–215 cm; 14 396–9886 cal BP according to the depth-age model used: see Chronology section for details) represents the oldest phase of fen development. Seeds of *Cladium mariscus*, *Schoenoplectus tabernaemontani*, *Eupatorium cannabinum*, *Mentha longifolia* and *Lycopus europeus*, sedges *Carex flava* agg. and *C. nigra* are present, but in low quantities. Small amounts of *Alnus* wood indicates presence of alder-carr in the vicinity of the fen or scattered trees growing directly in the fen, but we cannot exclude underground origin of the pieces of wood, which implies that *Alnus* may not have been present at this stage in the development of the fen.

In sub-zone Bma1b (210–175 cm; 9409–5898 cal BP) the abundance of seed of *Cladium* and *Schoenoplectus* increases. Seeds of *Rubus* and *Sambucus* indicate shrubby vegetation in the vicinity. Seeds of other fen (*Juncus articulatus* and *Carex paniculata*) or nitrophilous wetland species growing on disturbed fen peat (*Ranunculus sceleratus*, *Chenopodium album* agg. and *Potentilla reptans*) are also present. These species together with the moss *Drepanocladus aduncus* indicate fluctuating and seasonally strong decreases in the water level. There is an increase in the quantity of *Alnus* wood, indicating a more closed canopy. A small quantity of oogonia of *Chara vulgaris* is recorded at the end of this zone.

2. Zone Bma2a (170–115 cm; 5652–3452 cal BP) is similar to the previous one, but there is a greater abundance of oogonia of *Chara vulgaris*, which indicates wetter conditions, probably small fen pools. Bryophytes are less abundant (*Campylium stellatum, Cratoneuron filicinum*).

At the beginning of the sub-zone Bma2b (110–75 cm; 3358–2691 cal BP) there is a greater quantity of *Chenopodium album* agg. seeds, which together with the decrease in the quantity of *Alnus* wood recorded could indicate the presence of humans. At that time trees were probably being felled and the fen disturbed or grazed. There is also an increase in precipitation of calcium carbonate and in the abundance of heliophilous species such as *Schoenoplectus tabernaemontani* (seeds) and *Campylium stellatum* (stems with leaves).

3. Zone Bma3a (70–45 cm; 2601–1927 cal BP) is characterized by the absence of seeds of *Schoenoplectus tabernemontani*. There is a markedly lower abundance of oogonia of *Chara vulgaris*, which indicate a decrease in water level. Further, there is a strong decrease in the total

amount of bryophytes and *Campylium stellatum* is replaced by *Drepanocladus polygamus*. There is a decrease in precipitation of calcium carbonate at the end of this period.

At the beginning of sub-zone Bma3b (40–5 cm; 1854–171 cal BP), *Schoenoplectus* seeds re-appear and *Chara vulgaris* oogonia increase in abundance. Later, in the most recent part of this zone, oogonia disappear and *Schoenoplectus* seeds disappear almost completely, indicating a decrease in water level. In contrast, the seeds of *Cladium mariscus* become more abundant.

Molluscs

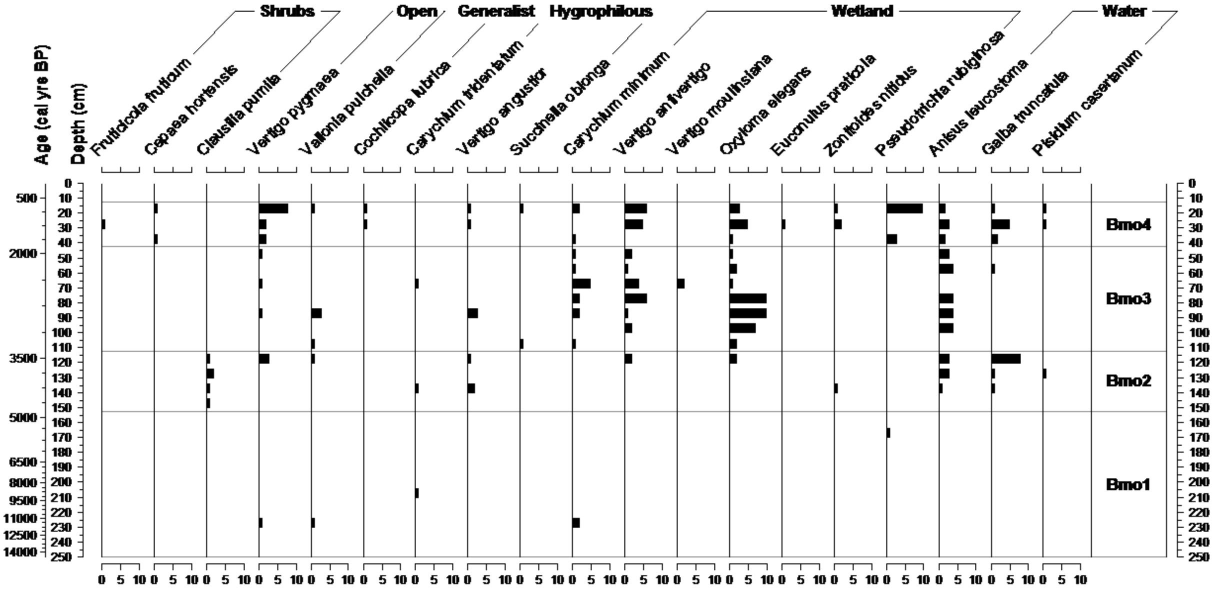
Based on the cluster analysis, four mollusc assemblage zones were distinguished (Figure 6). Most of the interpretations are based more on changes in species abundances than on species turnover, as the latter is likely to be linked with sub-optimal conditions for shell preservation in most layers. Unfortunately, shells in layers from a depth of 140 cm down to the bottom (entire zone Bmo1 and the oldest part of the zone Bmo2) were extremely poorly preserved due to the low concentration of calcium carbonate and a high quantity of wood, which provided only very limited material for reconstruction.

1. In the first zone Bmo1 (250–155 cm, 14 396 – 4955 cal BP) there is only extremely poor material, consisting of only a few shells in only some layers. The species recorded, *Vallonia pulchella* and *Vertigo pygmaea*, are characteristic of fully open habitats, which indicates the existence of an open-fen at this site.

2. In the second zone Bmo2 (150–115 cm; 4709–3452 cal BP), *Clausilia pumila*, a species of wet and alluvial habitats, is present. This might indicate, along with the absence of typical open habitat species in the deeper layers of this zone, an increase in the abundance of shrubs. At the end of this zone, two open-habitat species appear and in the subsequent layer *C. pumila* disappears completely.

3–4. In the zones Bmo3 (110–45 cm, 3358–1927 cal BP) and Bmo4 (40–5 cm, 1854–171 cal BP), several wetland species (e.g. *Oxyloma elegans* and *Vertigo antivertigo*) are very abundant, particularly in the third zone, which indicates a high and stable water table and succession into stable open calcareous fen. Another fen species, *Vertigo moulinsiana*, which is sensitive to intensive grazing, is also present in one layer of the zone Bmo3. Zones 3 and 4 differ in the dominance of the open-country snail *Vertigo pygmaea*, which is more abundant in the youngest layers.

Figure 6.: Mollusc diagram. Data are in absolute numbers of shells. Species are classified into main ecological groups according to Ložek (1964).



Discussion

Chronology

Our presumption that the basal layers are of the Early Holocene age, as indicated by the bulk dating (11 500 cal BP), is supported by two pieces of evidence. First, the Early Holocene is indicated in the record by a steep and rapid decline in the dominance of *Pinus*. In Central Europe *Pinus* was also locally dominant in the Middle Holocene (e.g. Pokorný and Kuneš, 2005) but only in areas where the edaphic conditions were unsuitable for other trees, which is not our case. In addition, we do not know of a steep decline in the abundance of *Pinus* occurring around 6500 cal BP anywhere else and the results from other profiles at the Carpathian-Pannonian border clearly indicate that up to the Middle Holocene *Pinus* pollen is also not abundant (Magyari et al., 1999; 2001; Petr et al., 2013; unpublished data of E.J.). Second, the Early Holocene age is indicated by an uninterrupted pollen curve for *Larix* up to 211 cm. Current information indicates that *Larix* dissapeared in the region of the Carpathian-Pannonian border prior to the Middle Holocene (Magyari et al., 1999; 2001; unpublished data of E.J.) and its occurrence during the Middle and Late Holocene is documented only in northern Slovakia, in the Tatra Mts (Rybníčková and Rybníček, 2006), Orava, Spiš, Liptov and Horehronie regions

(Jankovská, 1988; Hájek et al., 2011; Rybníček and Rybníčková, 2002; unpublished data of E. J.), in the Slovenský raj Mts and the Turčianska Basin. Also data from the Mitická slatina site (located ca 25 km from the study site), based on AMS dating of more seeds, suggest that *Larix* occurred together with an abundance of *Pinus* and some mesophilous trees in the Lateglacial (12 900 cal BP) but disappered during the Early Holocene.

The difference between single-seed and bulk dating may be due to a bioturbation that transported seeds from upper to lower layers. This might include root growth of reed (*Phragmites australis*), activity of invertebrates generally living in rather deep layers in spring fens or frequent grazing, which is well-documented in our fossil record. Contamination during coring also cannot be excluded. The hard-water effect (Grimm et al., 2009) is probably of little importance in this case, because (i) we dated fen and not aquatic bulk deposits (note that fen vegetation usually photosynthesizes above the water-table), (ii) the bulk sample did not contain grains of calcium carbonate or snail shells, (iii) our results for other spring fens in the Western Carpathians are very similar in terms of the dates for bulk and seed samples (unpublished data). Note that seed re-deposition could happen very easily, because the bottom layer is very compressed with 40 cm equivalent to almost five thousand years. We do not know the reason for the different rates of accumulation in bottom layers and the rest of profile, but high mineralization due to lower water supply is a possible reason.

As a result of dating constraints, the age of the Early Holocene sequence (up to ca 7000 cal BP) is only inferred from the depth-age model and not based on individual AMS dates obtained for material within this zone. The pollen spectrum (absence of *Carpinus, Abies* and crops and high representation of *Pinus*, *Corylus* and *Tilia*) conforms to the prediction of the depth-age model and indicates an Early-Holocene age, but the fossil record in this sequence may not be complete. Scarce occurrence of *Fagus* could point to a hiatus in the record, but the amount of pollen is rather low. Moreover, pollen of *Fagus* occurs in early Holocene sequencies in the profile collected at Šúr (western Slovakia; Petr et al., 2013) and Santovka (south-western Slovakia; Petr et al. 2012), which indicates the occurrence of beech during the Early Holocene period in the foothills of the Western Carpathians.

Local vegetation

Our results indicate the continual presence of *Cladium mariscus* at the study site. Similarly, *Cladium mariscus* seeds are recorded in different Holocene periods in fens in northeastern Poland (Galka and Tobolski, 2012), northern Germany (Michaelis, 2002), central Bohemia

(Hrabanovská černava; Petr, 2005), northwestern Bohemia (Pokorný et al., 2010) and southern Slovakia (Žáčková *in verb.*), which indicate its continuous presence in calcareous fens in Europe during the Holocene. As the distribution of this species is limited by low winter temperatures of below 2°C, which damage its meristems (Conway, 1938), and a low number of frost-free days (Salmina 2004), it was probably not widespread during the Glacial periods, but direct palaeoecological evidence is scarce. Thermal springs may have been refugia during the Glacial period, but our fossil record cannot indicate whether it was present before the start of the Holocene. This species probably spread after the climate improved in the Early Holocene and its decline probably did not start before the formation of the High Medieval landscape, when sedimentation of nutrient-rich flood loams caused by errosion after human-deforestation started (Pokorný et al., 2010). Further, eutrophication and drainage during the last decades resulted in a strong reduction in the number of localities for *Cladium* in Central Europe (Eliáš et al., 2003; Pokorný et al., 2010).

The community with *Cladium mariscus* studied was rather stable with only small changes connected with fluctuating water level. The presence of *Alnus* wood, *Eupatorium cannabinum*, *Mentha longifolia*, *Potentilla reptans* and *Ranunculus sceleratus* seed in the period between ca 13 700 and 6000 cal BP is characteristic of a fluctuating water level and higher nutrient supply. *Alnus* wood in the bottom part of the profile (up to 175 cm; ca 6000 cal BP), along with pollen and seeds of light-demanding plants, indicate alder carr with an open canopy or a mosaic of open fen habitat and scattered *Alnus* trees. Later, the level of the water increased and then remained stable (ca. 5100 cal BP), which is indicated by the presence of a high abundance of *Chara vulgaris* oogonia and *Botryococcus* characteristic of calcareous-fen pools. This change may be due to a change in the position of the spring or to climate moistening, the latter is documented as occurring in this period (ca. 5500–5000 cal BP) in the Eastern Carpathians (Magyari et al., 2009; 2013) and Great Hungarian Plain (Magyari et al., 2010; increase in *Fagus* associated with an increase in humidity). During this period the vegetation consisted of reed swamp dominated by tall graminoids (*Cladium*, *Schoenoplectus* and *Phragmites*) and tall herbaceous plants (*Eupatorium* and *Lycopus*), but lacked a well-developed bryophyte layer. It probably corresponds to the present-day vegetation of the *Magnocaricion elatae* Koch 1926 alliance, which is the most common current vegetation type with *Cladium mariscus* (Eliáš et al., 2003). The important finding is that of *Primula farinosa* (see comment on this pollen type in Electronic Appendix 1) in the Early Holocene period. This species prefers ancient *Caricion davallianae* calcareous fens which initiated in the Lateglacial or Early Holocene (Hájek et al., 2011), but till present there was no direct evidence of its occurrence in those periods in the Western Carpathians. Its occurrence in the profile studied suggests that low-sedge brown-moss vegetation co-existed in a mosaic of *Cladium* stands. Such a mosaic may also have developed in younger phases of fen development, even if it is not documented by pollen, because pollen record of entomogamous herbaceous plants might mirror a very local pattern.

The site was probably repeatedly influenced by human activities (probably grazing) occurring at the latest from the Bronze Age, which is indicated by the high presence of *Chenopodium album* seeds. Another explanation could be that the origin of the *Chenopodium* seeds is natural and due to disturbance by wild herbivores or drying out of fen peat; *Chenopodiaceae* can grow on exposed mudflats or dessicated surfaces of fens (e.g. Magyari et al., 2010, 2012). These natural events might explain the occurrence of *Chenopodium album* seeds in older parts of the profile. Grazing by domesticated or wild herbivores is further indicated by the presence of spores of coprophilous fungi (*Sporormiella* t.) and absence of the calcareous-fen snail *Vertigo moulinsiana* (cf. Ausden et al., 2005) from all but one layer of the profile. Grazing could increase the input of nutrients into the ecosystem, which probably limited the occurrence of low-productive *Caricion davallianae* vegetation. High-productive vegetation consisting of tall graminoids and tall herbaceous plants might be further supported by the high water temperature of the warm springs, which probably increases the mineralization rate (Taylor and Dykstra, 2005) and the associated nutrient release. A high rate of decomposition might also account for the steep depth-age curve in the basal part of the profile.

The most recent change in vegetation caused by an anthropogenic water-level decrease is reflected in the disappearance of *Schoenoplectus tabernaemontani*, whose seeds are present in the sub-recent sample collected from 5–10cm below the surface, and recent spread of *Phragmites australis.* As a disturbed water regime is considered to be the reason for the recent extinction of *Cladium mariscus* at many sites (Eliáš et al., 2003), the future of this species at the study site is uncertain.

Early spread of mesophilous trees

As expected, we documented the occurrence of some mesophilous trees (*Ulmus, Fraxinus*, *Tilia* and *Quercus*) from the beginning of sediment accumulation, dated roughly to the Early Holocene, even though the abundances of these trees was less than those reported for more southern locations: northern Hungary (Magyari et al., 2010) and southern Slovakia (Petr et al., 2013; unpublished data of E.J.). Occurrence of local Glacial refugia for these trees more to the north is suggested by Magri (2008) and Willner et al. (2009) but not verified, thus it is likely that mesophilous trees spread from Pannonian Glacial refugia (e.g. Birks and Willis 2008; Sümegi et al., 2013) northwards to a small basins surrounded by mountain ranges (Tríbeč Mountains, 829 m a.s.l. and Považský Inovec Mountains, 1042 m a.s.l. in our case). Later, these mesophilous trees increased in abundance, probably after an improvement in climate when, simultaneously, open-country species (*Artemisia* and Chenopodiaceae) decreased and Poaceae increased. However, in deciduous forests at the Pannonian-Carpathian boundary there is characteristically also a great abundance of Poaceae (e.g., *Brachypodium pinnatum*). Because the dating of the basal layer of the profile is somewhat uncertain and of poor resolution (see chapter Chronology in Discussion), further research is needed to reconstruction more precisely the spread of mesophilous trees in the region studied.

Continuity of treeless vegetation

Landscape openness is usually measured in terms of the AP (Arboreal Pollen) and NAP (Non-Arboreal Pollen) ratio in pollen records. Generally, if AP makes up more than 80% of total pollen, it indicates forest vegetation, less than 70% forest-steppe and lower percentages (less or equally to 50%) steppe (Svening et al., 2002; Magyari et al., 2010). Using other palaeoecological proxies, such as macrofossils of plants and snails, may also be used to determine the level of landscape openness (Svenning et al., 2002), though they may reflect rather local conditions. Our pollen diagram indicates that arboreal pollen prevailed from the beginning of the accumulation of organic matter (about 80%). A similar AP:NAP ratio is recorded during the Pleistocene/Holocene transition at the Vracov site (South Moravia, northwestern margin of the Pannonian lowland; Rybníčková and Rybníček, 1972). The AP percentages are greater than 75% in most of the profile, which might indicate a densely forested landscape. Nevertheless, this contradicts not only the clearly open character of local wetland vegetation (indicated by the plants *Cladium mariscus*, *Schoenoplectus tabernaemontani* and snails *Vallonia pulchella* and *Vertigo pygmaea*) but also clear evidence of the presence of open-grassland and steppe patches (Figure 4). Indeed, recent studies indicate that the relationship between the AP percentage and representation of forests is more complicated than previously thought (e.g. Sugita et al., 1999; Pelánková et al., 2008; Magyari et al., 2010). Recent surface samples from floodplains in wooded steppe, where improved moisture conditions result in the development a local forest, often contain > 75% of AP and as a consequence it is difficult to distinguish continuous forest from wooded steppe (Magyari et al., 2010). This may also apply to the site studied, which is situated in a waterlogged basin where *Picea*- and *Alnus*-forests were probably abundant (cf. Figure 4). The results from southern Siberia indicate that pollen spectra consisting of between 50–80% AP are recorded not only in open *Larix* and *Pinus sylvestris* forests, but also in meadow steppes in a forest-steppe landscape (Pelánková et al., 2008). We conclude that in the Pleistocene/Holocene transition and Early Holocene in the area studied there were open coniferous forests with *Pinus sylvestris* and *Larix,* similar to those reconstructed in other regions of the Western Carpathian mountains (Jankovská, 1988; Jankovská and Pokorný, 2008) and Pannonian Basin (Sümegi et al., 2001), where they occured in a mosaic with treeless habitats such as fens and steppes. These forests may have been similar to the southern-Siberian *Pinus-Larix* hemiboreal forests, which are rather open, with many light-demanding species and high species richness (Chytrý et al., 2012). They dominated the landscape, but the exact ratio of forested and treeless habitats cannot be assessed accurately.

The AP percentages remained stable during the entire prehistoric period, even if the composition of forest species changed; this is caused by differences in production of pollen among different species of trees (e.g. Prentice, 1985; Sugita, 1994; Sugita et al., 1999), the large proportion of light-demanding shrubs in the AP sum in most periods, and changing ratio of local (floodplain) and regional (upland) pollen influx. Because even some types of Carpathian-Pannonian deciduous forests usually have an open structure and many light-demanding species are present (Roleček, 2005) it is difficult to distinguish between a mosaic of large areas of steppe with forested patches and open forests. Our data suggests that Early- and Middle-Holocene forests (~9500–6500 cal yr BP; see chapter Chronology for discussion on dating) were composed mainly of light-demanding *Quercus* with an admixture of *Corylus*. They should be open, because both hazel and oak seedlings need high light intensities to survive. These *Quercus-Corylus* forests were kept open by various natural factors. First, climate in the Pannonian lowland was rather dry and relatively warm (Magyari et al., 2010; unpublished data of E.J.). Second, edaphic factors (soil properties, nutrient availability, geomorphology) might co-determine the existence of species-rich open forests (Svenning, 2002; Bradshaw et al., 2005, Sümegi et al., 2012). Third, disturbances caused by large native herbivores (Vera, 2000), natural fires (Chytrý et al., 2010) or human activity in the Mesolithic (Tallantire, 2002; Kuneš et al., 2008) could also have contributed to keeping forests open enough for survival of light-demanding species. The high number of particles of micro-charcoal found in this period indicates that fires were important regardless of whether they were started by man during the Mesolithic (Mason, 2000) or by natural events. Grazing by large herbivores is well indicated by the presence of spores of coprophilous fungi (*Sporormiella* genus) in organic deposits

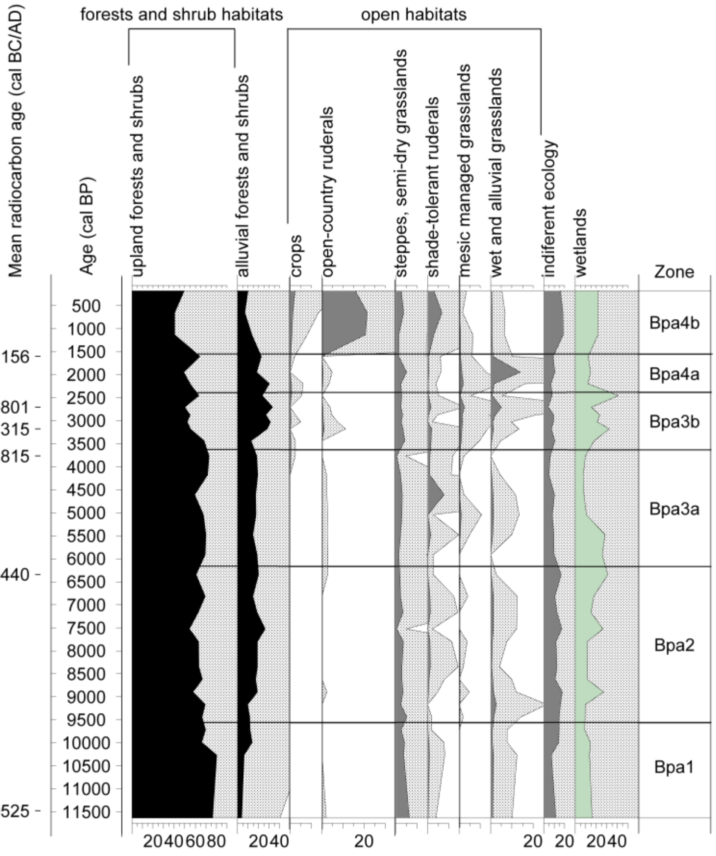
(Ahmed and Cain, 1972), even though present in low amounts of below 1% (Davis and Shafer, 2006). We recorded *Sporormiella* t. spores from the Pleistocene/Holocene transition, which indicates possible influence of large herbivores in a pre-agriculture period. Concerning steppe vegetation, it surely existed in Central-European lowlands before man established settlements there (WallisDeVries et al., 2002) at least on south facing slopes and dry plateaus (Dúbravková and Hajnalová, 2012). In the study area, continental steppe vegetation probably persisted on loess loams situated on slopes close to the study site (http://mapserver.geology.sk), whereas wet and mesophilous meadows occurred in the floodplain. Steppe occurrence is well indicated by *Artemisia* and Chenopodiacaeae. Although these taxa may indicate human settlements, their occurrence before the Neolithic is likely to be connected with either steppes or halophytic habitats in the steppe zone (Eliáš et al., 2013).

After 4000 cal BP (the Bronze Age), the AP frequencies started to fluctuate, probably as a consequence of an increasing representation of species of managed grasslands, crops and some dry-grassland species, and spread of *Fagus* and *Carpinus*. The synoptic pollen diagram (Figure 7) reveals that around 3700 cal BP the most important bottleneck for light-demanding species ocurred. It is indicated by a decline of all grassland, open-country ruderal and open-wetland species, and unlike the previous bottleneck at the Boreal/Atlantic boundary around 7500 cal BP it was further associated with a decline in pollen of unclassified non-arboreal taxa (including Poaceae) and an increase of upland forests. This period corresponds to the expansion of *Fagus* and *Carpinus*, which is generally attributed to soil deterioration due to nutrient leaching (Berglund, 1986; Pokorný and Kuneš, 2005), fluctuating human activity (Pokorný, 2005) and/or increase in the availability of moisture during the growing-season in the Pannonian lowland (Magyari et al., 2010). This phase of the Holocene was apparently also crucial for the survival of light-demanding species in another region at the Pannonian-Carpathian boundary, the White Carpathians (Hájková et al., 2011). In the study region and the White Carpathians, *Fagus* and *Carpinus* expansion is closely associated with agriculture intensification at the onset of the Bronze Age. In the profile studied, enhanced human activity between 3700 and 3500 cal BP is indicated by the occurrence of coprophilous fungi (*Sporormiella* t., *Sordaria* t., *Chaetomium* sp.), the plant *Plantago lanceolata* (indicating managed grasslands), and a general increase in species of all grassland types (wet, mesic and dry) and open-country ruderals (Figure 7).

Coincidence between pollen and archaeological records

The human settlement of the study area is documented by archaeological records since the Early Neolithic (~5700–5000 BC; Točík, 1970) but there is no clear pollen evidence such as presence of Cerealia pollen or increase in microcharcoals. There are records of a Neolithic settlement ca 3 km from the site analyzed, but the small-scale garden agriculture typical of that period (Bogaard, 2004) probably accounts for the absence of Ceralia in pollen records. As the population density of Neolithic farmers was sparse, they did not have a marked effect on the landscape. Moreover, the first farmers tended to settle in naturally treeless areas in those parts of Central Europe covered with loess (Bogaard, 2004; Hajnalová, 2007), therefore deforestation was not required (Willis, 2007).

Figure 7.: Synoptic pollen diagram. All pollen taxa are classified into groups according to habitat requirements of the plant species involved. Group “wetlands” is not included in the total sum. For the list of taxa belonging to particular groups and comments on species classification see Appendix 1.



During Late Neolithic (Eneolithic), agricultural practices were developed (Hajnalová, 2007), but there is still no evidence of the presence of Cerealia during that time in the study area, possibly the distance from the human settlements at that time limited the input of crop pollen. Dreslerová and Pokorný (2004) document that even large water bodies in a less geomorphologically structured landscape can have catchment areas of only 800–1000 m in radius and that small water bodies catch only local pollen. Even though we did not record cereals for this period, changes in the composition of grassland species indicate human activity, mainly grazing, in the surrounding landscape, during the Late Neolithic.

The first occurrence of *Triticum* t. pollen is dated to ca 4000 cal BP (127 cm, 3765 cal BP; 1816 BC Bronze Age). The Bronze Age (~4250–2650 cal BP; 2300–700 BC; Barta, 2009) is characterized by an improvement in farming techniques (use of ard and yoke; Hajnalová, 2012), ore mining and metal processing, which markedly affected the landscape. The decline in mesophilous trees (*Fagus* and *Carpinus*) and increase in *Alnus* after 3500 cal BP might be due to an increase in human pressure. Deforestation and tillage resulted in soil erosion in the area of loessic hilly lands (Stankoviansky, 2008; Smetanová, 2011) and development of *Alnus* carrs (cf. Pokorný, 2005). On the other hand, deforestation of south-exposed slopes allowed the development of dry grasslands (Dúbravková and Hajnalová, 2012). This process may account for the gradual spread of dry-grassland species, especially those recorded in the pollen diagram that indicate disturbance (*Orlaya grandiflora* t. and *Eryngium campestre* t.). Dry grasslands were grazed, mowed or burned to keep them open in order to obtain hay for livestock (Bylebyl, 2007). Woodlands were probably grazed as well, which led to a decrease in canopy cover and spread of the light-demanding shrubs *Cornus mas*, *Frangula* and *Sambucus* (cf. Moskal-del Hoyo, 2013). According to Marinova and Thiébault (2008), presence of *Cornus mas* together with *Sambucus* is associated with human activity, such as canopy opening and, in the case of *Sambucus*, nutrient-enrichment and disturbance. Alternatively, light-demanding shrubs might have survived in forests not affected by human activity but growing on shallow soils in limestone rocky places in the Strážovské vrchy Mts. Forest grazing probably also resulted in open oak forests (oak pollen increased) and suppressed shady beech forests in that period (Figure 4: zone Bpa3b).

Further intensification of agriculture occurred in the Iron Age (67 cm; 2500 cal BP, 560 BC), i.e. the period when numerous settlements are recorded in the study region. At that time settlement intensity increased due to iron and gold ore mining in the closest mountains (Vangľová, 2008). There is evidence of prehistoric mining on the north-eastern slopes of the Považský Inovec Mountains, only ca 25 km from the study site (Lukačka, 2006). The increase in the concentration of micro-charcoal in the pollen diagram probably reflects strong exploitation of the surrounding landscape (deforestation and metallurgy). During the La Tène period (around 80 BC), human activity around fortified settlements increased (Vangľová, 2008), which might account for the *in situ* decline in Cerealia associated with a clear peak in species indicating wet and alluvial grasslands. Dry-grassland species also increased, but less so. These changes may suggest a general change from crop cultivation to grassland management. Because the stability of wet grasslands is more dependent on mowing than dry grasslands (Galvánek and Lepš, 2009), the changes recorded for the La Tène period might suggest the presence of hay meadows in the study area, which corresponds to the results of the meta-analysis of Western and Central European archaeobotanical data (Hodgson et al., 1999).

After temporary decline in agriculture, the representation of grassland and open-country ruderal species steeply increased, coinciding with Slavic settlement of the region.

Conclusions

The warm-spring fen-peat profile collected close to the Malé Bielice village contained not only macrofossils of plants and molluscs, but also an extraordinary high number of pollen taxa, which is an uncommon feature of calcium-rich lowland fens. Our multi-proxy palaeoecological study of this profile confirmed (i) the early spread of mesophilous trees (*Ulmus*, *Fraxinus*, *Tilia* and *Quercus*) into the northern part of the Carpathian-Pannonian boundary, but unfortunatelly it was not possible to date it accurately, (ii) the survival of *Cladium mariscus* population throughout the Holocene, (iii) the Holocene persistence of open-country habitats (calcareous fens, dry grasslands) in the region, which may explain the occurrence of rare light-demanding species and (iv) the coincidences between the history of human settlement and the spread of particular types of grassland at the Pannonian-Carpathian boundary.

Acknowledgements

We dedicate this study to Eliška Rybníčková and Kamil Rybníček, who conducted one of the first multi-proxy palaeoecological studies on the Pannonian-Carpathian boundary, on their 80th birthday. We are grateful to Libor Petr and Stanislav Němejc for help with the profile sampling, Zuzana Formánková for laboratory work and three reviewers for valuable comments. The research was funded by grant GAČR P504/11/0429, institutional support of Masaryk University and long-term research development project no. RVO 67985939.

Souhrn

Historie slatin na teplých pramenech je ve střední Evropě téměř neprobádaná (s výjimkou teplých pramenů v Rumunsku), přestože jsou to extrémní stanoviště se stabilními podmínkami, které mohou umožňovat dlouhodobé přežívání druhů. Studovali jsme vápnitý sediment, který se začal ukládat na začátku holocénu u Malých Bielic (u města Partizánske na západním Slovensku) na vývěru teplého pramene s teplotou okolo 40 °C. Tato lokalita se zachovala do současnosti a vyskytuje se na ní vzácný druh *Cladium mariscus*. Důležité je, že se nachází v oblasti, odkud paleoekologická data dosud zcela chyběla a kde se v současnosti vyskytují vzácné světlomilné druhy, které zde mají izolované výskyty nebo jsou zde na okraji svého areálu rozšíření. Jejich přežívání během klimatického optima, kdy expandoval v krajině les, není doposud plně vysvětleno a právě paleoekologické metody mohou přispět k vysvětlení současného prostorového vzoru (*pattern*) ve výskytu těchto druhů. Studované území v kotlině řeky Nitry představuje také severní výběžek panonské nížiny do Západních Karpat, což bylo důležité pro šíření mezofilních dřevin v raném holocénu. Detailní mezioborové studium tohoto slatinného sedimentu zahrnující analýzu pylových zrn, rostlinných makrozbytků, schránek měkkýšů a stratigrafii doplněnou radiokarbonovým datováním nám umožnila potvrdit 1) časnou expanzi mezofilních dřevin (*Ulmus, Fraxinus, Tilia, Quercus*) v severních částech karpatsko-panonské hranice; 2) reliktní charakter a dlouhodobé přežívání izolované populace *Cladium mariscus* na slatiništi, syceném teplým pramenem; 3) kontinuální výskyt otevřených stanovišť (slatiny, stepi/suché trávníky) v krajině během celého holocénu, což mohlo významně ovlivnit přežívání vzácných světlomilných druhů v krajině a 4) vliv lidské činnosti na šíření jednotlivých typů nelesní vegetace na karpatsko-panonské hranici, který se významně projevoval od doby bronzové. Člověk začal v krajině intenzivněji působit právě v okamžiku rozmachu bukových a habrových lesů a pravděpodobně tak zabránil vyhynutí řady světlomilných druhů.

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Continuity and change in the vegetation of a Central European oakwood

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Abstract

The issue of continuity in deciduous oakwood vegetation has been in the forefront of woodland ecological studies for many decades. The two basic questions that emerge from existing research are whether or not oakwoods can be characterized by long-term stability and what may be the driving forces of the observed stability or change. To answer these questions in a well-defined case study, we examined the history of a large subcontinental oakwood (Dúbrava) in the southeastern Czech Republic with interdisciplinary methods using palaeoecological and archival sources. Palaeoecology allowed us to reconstruct the vegetation composition and fire disturbances in Dúbrava in the past 2000 years, while written sources provided information about tree composition and management from the 14th century onwards. The pollen profiles show that the present oakwood was established in the mid-14th century with an abrupt change from shrubby, hazel-dominated vegetation to oak forest. This change was most probably caused by a ban on oak felling in 1350 AD. From the 14th to the late 18th century Dúbrava had multiple uses, of which wood-pasture and hay-cutting kept the forest considerably open. The second remarkable change was dated to the late 18th century, when multiple-use management was abandoned and Dúbrava was divided into pasture-only and coppice-only parts. The last major shift occurred in the mid-19th century, when modern forestry and Scotch pine plantation became dominant. We conclude that Dúbrava Wood did not show stability on the long run and that its species composition has dramatically changed during the last two millennia. The most important driving force in the shaping and maintenance of the unique vegetation of Dúbrava was human management.

Key words: temperate oakwood, palynology, written sources, *Quercus*, management history, ecosystem stability, historical ecology

Introduction

Deciduous oakwoods have been on the decline for a century all over Europe, because oaks fail to regenerate. This phenomenon is often referred to as ‘Oak Change’ or ‘Oak Decline’ (Watt, 1919; Rackham, 2008). Available studies attribute it to various plant diseases (e.g. *Microsphaera alphitoides, Phytophthora* species), decline in human management or a combination of various factors (Luisi et al., 1993; Jung et al., 2000). Nonetheless, the term ‘oakwood’ denotes more than the dominance of oak species in the tree layer – deciduous oakwoods are specific biotic assemblages with many species more or less confined to this type of biotope (Ellenberg, 1996; Konvička et al., 2004).

The issue of continuity in deciduous oakwood vegetation has been in the forefront of woodland ecological studies for many decades. The two basic questions that emerge from existing research are whether or not oakwoods can be characterized by long-term stability and what may be the driving forces of the observed stability or change. Some scientists argued that deciduous oakwoods are the natural vegetation of the relatively warm and dry areas of Europe (Zólyomi, 1957; Ellenberg, 1996; Bohn and Neuhäusl, 2000), and are therefore stable communities occupying a restricted range of ecological conditions for several millennia. Others claimed that human management (burning, pasturing, litter raking and coppicing) rather than natural conditions played a decisive role in the maintenance of European deciduous oakwoods. This view is supported by the recent notable decline of oakwood species assemblages and the ‘invasion’ of hornbeam, maples, ash and lime following the abandonment of traditional management (Kwiatkowska et al., 1997; Roleček, 2007; Hédl et al., 2010). This opinion connects the stability of oakwoods to continuity of management on a millennial case, which implies fluctuations in vegetation with changes in human population densities around particular oak forests.

While the question of stability vs. change can be approached using a single disciplinary perspective (such as palynology, Huntley and Webb, 1988; Ritchie, 1995; Segerström, 1997), the study of driving forces requires a multi-proxy approach (Bürgi et al., 2004; Pechony and Shindell, 2010; Ireland et al., 2011). The comparison of natural scientific data with historical written sources is particularly useful in this respect, since historical sources can provide a framework of interpretation for palaeoecological data (Veski et al., 2005; Lindbladh et al., 2007). Archival data have been successfully used to detect driving forces of vegetation stability and change (Bürgi, 1999; Szabó, 2010b).

In this paper we present the results of interdisciplinary research on the long-term dynamics of a large lowland oakwood. This wood is among the best preserved subcontinental deciduous oakwoods in Central Europe (Roleček, 2007). Our study covers the past two millennia, and we integrate i) pollen and macro-charcoal data from two small forest hollows, and ii) archival written documents on species composition and management at the site. We aim to answer the following two questions:

1) Is the oakwood at the study site characterized by long-term stability in species composition or were there significant changes during the past two millennia?

2) What were the driving forces of stability or change? Was the role of natural factors or human management apparently more important?

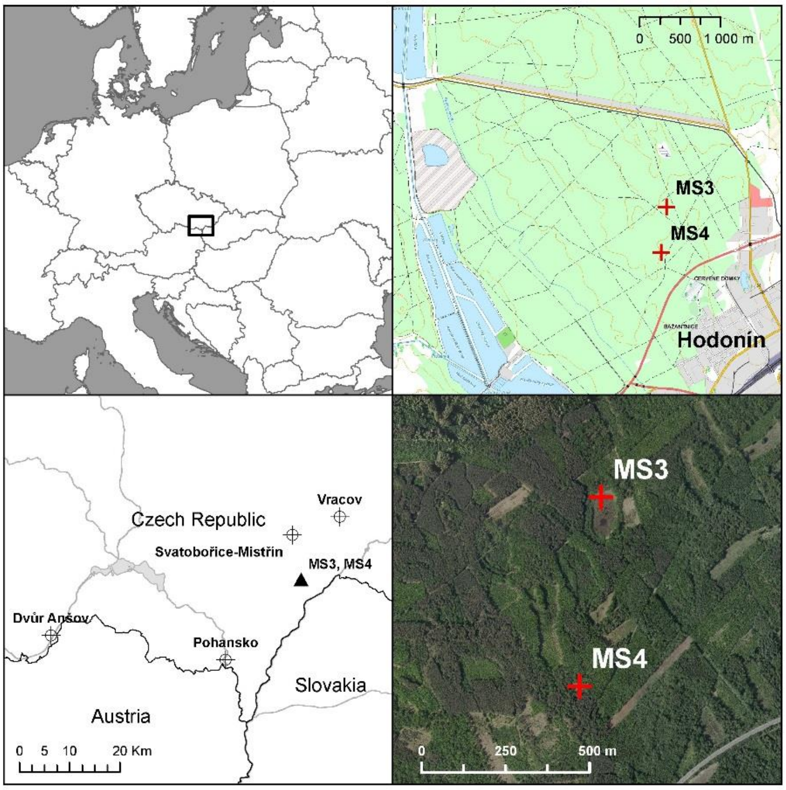
Materials and Methods

Study site

Hodonínská Dúbrava is a large (ca. 3300 ha) and relatively well-preserved ancient woodland (Figure 1). It is the core site of a specific type of subcontinental oakwoods, *Carici fritschii-Quercetum roboris* (Chytrý, 1997; Roleček, 2007) – a community endemic to this and a few adjacent sites. Due to low ground water levels, other vegetation types, such as alluvial forests (*Alnion incanae*) and alder carrs (*Alnion glutinosae*) also occur. At higher and drier elevations mesic oak-hornbeam woods (*Carpinion*) prevail. Approximately half of the forest has been turned into Scotch pine plantations in the 19th and 20th centuries.

Dúbrava is located at the NW edge of the Pannonian Basin (17°05´00´´E, 48°52´40´´N; Figure 1). Climate is 'humid continental' (cf. Peel et al., 2007). It is relatively warm and dry with ca. 9ºC of average annual temperature and 500–550 mm of precipitation (Tolasz et al. 2007). The site is gently sloping towards the SW, with elevations from 164 to 242 m. Dúbrava lies on the fringe of the wide alluvium of the Morava river, on 150–200 cm deep quaternary blown sand deposits (Novák and Pelíšek, 1943). Soils are extremely nutrient poor arenic dystric cambisols (AOPK CR 2002–2010), slightly acidic and prone to desiccation (Novák and Pelíšek, 1943). The water table fluctuates during the year. The settlement history of the area is typical of Central European lowlands. People have been living in the region since the Palaeolithic with population peaks in the Early Copper (4000–3400 BC), Late Bronze (1200–750 BC) and Late Iron Ages (400–1 BC) (Měřínský and Šmerda, 2008a). Dúbrava Wood historically belonged to the estate of Hodonín.

Figure 1.: Localization of Dúbrava Wood in Czech Republic with position of previously published pollen profiles in study area.



Palaeoecological analyses

The SW part of Dúbrava with numerous spring-submerged depressions was surveyed in 2008. Guidance by R. Řepka helped us locate 15 sites. We chose the six best preserved sites for coring using a Russian corer in 2008. All profiles were re-sampled for pollen analysis in July 2009, mostly taken from a trench using 10x10x50 cm metal boxes. All profiles were analysed for pollen at 5 cm resolution. Following the results of this preliminary analysis and radiocarbon dating (Table 1), we chose two pollen profiles denoted MS3 and MS4. The two sites represent treeless wetlands of ca. 50–100 m in diameter. Vegetation is dominated by reed (*Phragmites communis*) at MS3 and by sedges (*Carex* spp.) at MS4. The nearest vicinity of both wetlands is forest of *Quercus petraea*, *Quercus robur* and *Pinus sylvestris*.

Organic sediments from MS3 and MS4 stored in metal boxes were sub-sampled by 1 cm. 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 hours and then processed by KOH and acetolysis. At least 500 pollen grains were identified using standard key and photo collections (Beug, 2004; Reille, 1992, 1995, 1998); for the determination of non-pollen palynomorphs we used van Geel et al. (1980–1981). The nomenclature of pollen types follows Beug (2004).

Macrocharcoal analysis was carried out on the same sections as the pollen analysis. Sediments were sampled continuously at 1 cm increments using calibrated sampler of 2 ml volume. The macrocharcoal analysis of MS3 took a place after the removal of parts of sediment for radiocarbon dating, therefore charcoal data from some parts are missing. Extracted material was deflocculated with 10% KOH and subsequently non-charred organic particles were bleached by 3% hydrogenoxid (Schlachter, 2010). Particles larger than 125 μm were separated from the samples by wet sieving. Quantification of charred particles was performed using optical analysis of microphotographs processed by ImageJ software (Rasband, 1997). Charcoal fragments were identified according their black and characteristic shape /Enache and Cumming, 2006).

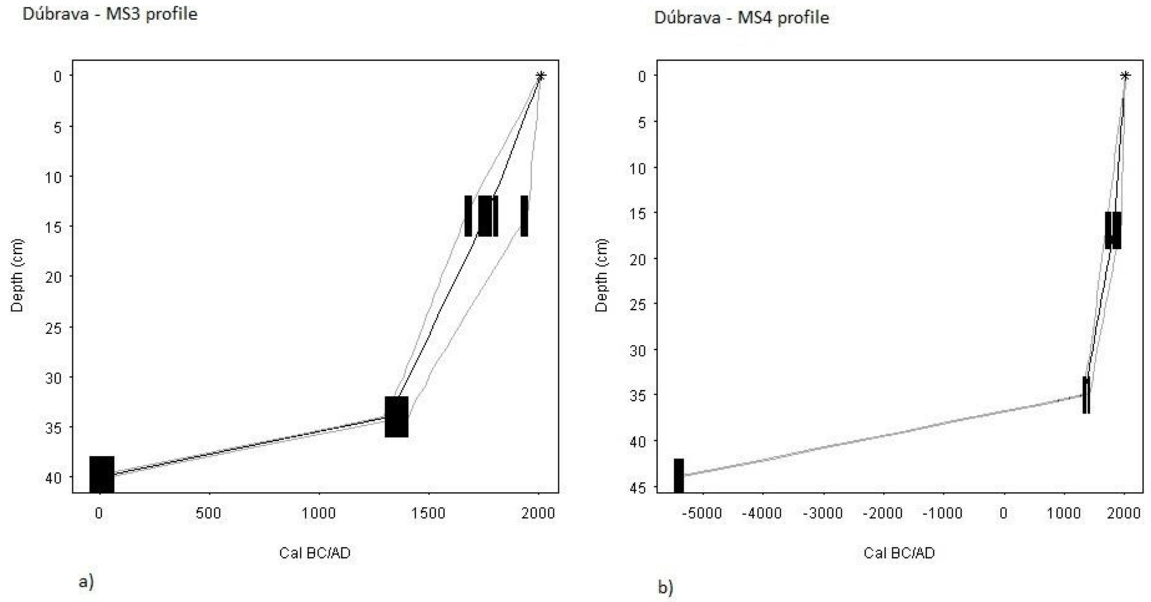
Pollen data are presented as percentages calculated based on terrestrial pollen sum, from which aquatics and local mire plants, pteridophyta, algae, fungi and other non-pollen palynomorphs were excluded. Charcoal concentration is expressed as the number of pieces per 2 ml. Percentage pollen diagrams with macrocharcoal histograms were created in Tilia v. 1.7.16 (Grimm, 2011). The pollen profiles were divided into three (MS3) or four (MS4) pollen zones based on the results of ConsLink and visual analyses. For a comparison of archival and pollen data, it is necessary to understand the relevant source area of pollen (RSAP) (Sugita, 1994). In the case of small basins situated within forests Sugita (1994) estimated the RSAP to be 50–100 m and about 40–50% of pollen coming from trees growing within this radius, while the rest (background pollen) originating from outside the RSAP. Calcote (1995) confirmed this estimation by empirical research of fossil pollen in forest hollows.

Selected plant macrofossils or charcoal taken from three depths in each profile were used for AMS radiocarbon dating in the Center for Applied Isotopes Studies, University of Georgia, Athens, GA, USA. An age-depth relationship model was constructed for both profiles using Clam v.1.0 R code (Blaauw, 2010, R development Core Team 2008). IntCal04 calibration curve (Reimer et al., 2004) was used to calibrate radiocarbon dates. To estimate the age of every pollen sample, linear interpolation between the midpoints of calibrated dated levels was applied (Table 1). The age-depth model was forced to go through 0 cm = 2009 BC/AD (BC ages are negative) (Figure 2). In this paper we use calibrated years. The radiocarbon date of the organic sediment from the base of the MS4 profile (5413 BC obtained from charcoal) gave a result apparently too old when compared with the MS3 profile, and was not used. This date may have resulted from the sandy base allowing the vertical migration of plant macroremains and charcoal. However, the date could possibly be correct, which would refer to slow accumulation of organic material. Nonetheless, the continuous presence of *Juglans*, which is known to be a Roman import in the region (Hajnalová, 2001), in both profiles appears to indicate that the base of MS4 is unlikely to be older than the Roman Period.

Table 1: Calibration of radiocarbon dates of the MS3 and MS4 profiles. Abbreviation: AD = Anno Domini (after Christ), BC = before Christ, BP = before present (1950).

Depth (cm)	**Lab code**	**Sample ID**	**Dated material**	**^{14}C - age (BP)**	**Calibrated ^{14}C-age**	
					Mean	**Range**
40 – 38	UG-7745	MS3,1	Charcoal	2000 ± 25	6 AD	47 BC – 60 AD
34 – 32	UG-7744	MS3,2	Carex seeds	610 ± 25	1349 AD	1297 AD – 1401 AD
14 – 12	UG-7743	MS3,3	Carex seeds	170 ± 20	1808 AD	1665 AD – 1950 AD
44 – 42	UG-8518	MS4	Charcoal	6420± 25	5413 BC	5472 BC – 5341 BC
35 – 33	UG-747	MS4,2	seeds, charcoal	560 ± 25	1368 AD	1313 AD – 1424 AD
17 – 15	UG-7746	MS4,3	Carex seeds	120 ± 25	1809 AD	1681 AD – 1937 AD

Figure 2. Age – depth relationship of a) MS 3 and b) MS4 profiles based on three radiocarbon dates for each profile.



Abbreviations: cal = calibrated ages, AD = Anno Domini (after Christ), BC = before Christ.

Archival research

To find out about the history of management and vegetation in Dúbrava, we studied the written records produced by the Hodonín estate administration from the 14th to the 20th centuries. All sources are presently kept at the Moravian Archives (MZA) in Brno. Written sources are precisely dated, which allowed us to establish a firm chronology of management changes. When compared to data on management, for most of the study period information on vegetation was patchy and rather vague. However, for the last two centuries precise data are available on tree species composition. The following kinds of sources were used:

1) *Charters* are records of legal transactions. The first charters dealing directly with Dúbrava are from the mid-14th century, while the last ones are from the 18th century.

2) *Urbaria* are conscriptions of all incomes from an estate. Four *urbaria* survive that provide relevant information about the Hodonín estate. They date from 1600 (MZA F5 kniha 1a, analyzed in Chocholáč, 1994), ca. 1654 (incomplete: MZA F5 kniha 1), 1691 (MZA F5 kniha 3) and 1805 (MZA F5 kniha 4).

3) *Estate conscriptions* describe the value of landed property in a given historical moment. A detailed conscription survives from 1692 (MZA F5 kniha 5).

4) *Account books* were kept by woodland owners to register incomes generated by the cutting and selling of underwood and timber. For Dúbrava only a few remain, covering the years 1765–1772 (MZA F5 karton 538).

5) *Forestry management plans* (FMP) are detailed surveys containing information on the name, size and position of each woodlot, as well as on tree composition and forest structure, supplemented by current and planned management. FMPs of Dúbrava are from 1851 (MZA F5 kniha 232), 1864 (MZA F5 kniha 233-236, 238, 240) 1906 (MZA F5 kniha 242, 244, 245), 1925 (MZA F263 kniha 1), 1936 (MZA F263 kniha 4, 5) and 1952 (MZA F302 kniha 4).

6) *Forestry documents* were produced by the local forestry administration. Such documents include e.g. various surveys of woodland areas, discussion on types of management and detailed diaries of yearly activities.

7) *Large-scale maps* (ca. 1: 30 000 and larger) are generally available in the Czech Lands from the 18th century onwards. We used three nationwide surveys prepared by the Austrian Army in 1764–1783, 1836–1852 (both 1: 28 800) and 1876–1880 (1: 25 000), available online at http://oldmaps.geolab.cz. A much more detailed (1: 2880) set of maps were drawn in 1824–1843 as part of the so-called Stable Cadastre (Bičík et al., 2001). Finally, maps

produced as parts of forestry management plans were used. Three sets of maps survive from Hodonín: 1851 (MZA F5 mapa 54–59), 1884 (MZA F5 mapa 60–64, note that the FMP itself is lost) and 1906 (MZA F5 mapa 65–70).

Results

Pollen stratigraphy and vegetation history

Based on changes in dominant taxa (Table 2), the pollen diagrams were divided into three (MS3) or four (MS4) phases. The first three phases are highly similar in both profiles, while the fourth one, covering the second half of the 20th century, is visible only in MS4 (Figures 3 and 4). Historical documents show corresponding results; major management changes happened approximately in the transition periods between the pollen zones. Because of the high similarity between the pollen spectra and historical sources, the results are presented jointly.

Roman Period to the High Middle Ages (1st century AD – mid-14th century AD) – Phase 1

At the beginning of the sedimentation process dated to the 1st century AD, Dúbrava consisted mainly of light-demanding woody species, such as *Corylus* (19%) and *Betula* (17%). The relatively low proportion of tree pollen and of *Juniperus* (3%) also suggests open forest vegetation. A high amount of pollen of coniferous trees, such as *Picea* (18%) and *Abies* (6%) was also recorded. *Corylus* produces little pollen as an understorey species (Rackham, 1988). The observed high amount of *Corylus* in the profile suggests that it had a dominant position in the vegetation (Gardner, 2002), and that its pollen spread was hardly hindered by overstorey vegetation. This and the presence of *Juniperus* allow us to interpret the vegetation in the nearest vicinity of the study site as shrubby woodland. Such vegetation is implied in the original, High Medieval name of Dúbrava, which was Klečka. This name was first recorded in a charter interpolation from 1350 AD (Boček, 1839: 204–205). In Old Czech, ‘klečka’ refers to a place with shrubs (Gebauer, 1970). The basal layers of both profiles contained low amounts of charcoal particles. These provided no evidence fort local fire events, which could have been connected to the shrubby vegetation dominated by *Corylus* (cf. Tinner et al., 2005). The composition of herbaceous pollen in Phase 1 indicates the presence of an intensively managed landscape.

Table II: Characteristics of main phases based on changes in pollen taxa and historical events.

	Cal. AD	MS3		MS4		Written sources
		max. %	min. %	max. %	min. %	
Phase 4		n/a	n/a	*Betula*, *Populus*		Dominance of high forests, afforestation of open areas, abandonment of drainage canals
	1941	---	***Corylus***, *Picea*	Cerealia *Zea mays* *Typha latifolia* *Fraxinus*	*Artemisia* Chenopodiaceae Cyperaceae ***Corylus***	
Phase 3		*Loranthus europaeus*, Poaceae, *Equisetum*	*Artemisia*, Asteraceae subf.cichorioidae, Scrophulariaceae, Rubiaceae, Cyperaceae, *Typha latipholia t.*	---	Rubiaceae	Strict coppicing regime in woodland later to be replaced by high-forests, grubbing out of one third of the Wood and turning it into pasture. Digging of of drainage canals. Beginning of *Pinus* plantations.
	1808/1809	***Quercus***, *Betula*, *Pinus*	*Tilia*, *Alnus*	***Quercus***, *Pinus*	*Picea*, *Ulmus*, *Alnus*	End of multiple management, separation of pasture and woodland
Phase 2		Chenopodiaceae, Asteraceae, Rubiaceae, *Rumex acetosa t.*, *Rhinanthus*, *Polygonum persicaria* , Cerealia, *Secale*, *Podospora*, *Sporormiella*	---	Chenopodiaceae, Asteracaeae, Brassicaceae, *Lotus t.*, Rubiaceae, *Filipenula*, *Chaeorphyllum, hirs. t.*, *Plantago lanceolata.*, *Polygonum aviculare*, *Secale*	---	Multiple-use management: wood-pasture, hay meadows, coppicing, pannage, wild-fruit and oak gall collection, beehives and arable fields in the Wood. Gradual change in name from Klečka ('place with shrubs') to Dúbrava ('oakwood')
	1349 /1348	***Corylus*** , *Picea*, *Abies*, *Ulmus*, *Tilia*, *Juniperus* *Alnus glutinosa*	***Quercus***, *Pinus*,	***Corylus***, *Picea*, *Tilia*, *Ulmus*, *Juniperus* *Alnus glutinosa*	***Quercus***, *Pinus*	Ban on cutting oaks
Phase 1		*Artemisia*, Silenaceae, *Senecio t.*, Scrophulariaceae, *Valeriana off. t.*, *Polygonum aviculare*, *Polygonum persicaria*, Cyperaceae, *Typha latifolia t.*, *Sparganium*	Cerealia, *Secale*	Silenaceae, Ranunculaceae, *Senecio t.*, Daucaceae, *Geranium*, *Polygonum persicaria*	Cerealia, *Secale*	Original name Klečka refers to shrubby vegetation
	6					

Abbreviations: cal = calibrated ages, AD = Anno Domini (after Christ), max% = maximum (or increasing) of pollen percentage, min% = minimum (or decreasing) of pollen percentage.

The high amount of *Artemisia*, Asteraceae, Silenaceae, Rubiaceae and *Valeriana officinalis* t. implies meadows. The constant occurrence of Cerealia indicates the presence of arable fields in the nearest vicinity of the site. Ruderal plants such as *Polygonum aviculare* t. and *Polygonum persicaria* indicate trampled habitats and cultivated land (Behre, 1981; Gaillard, 2007). At the end of Phase 1, the pollen of *Plantago lanceolate* t., *Rumex acetosa* t. and *Melampyrum* appeared. These could be connected with grazed grasslands.

Late Middle Ages to the Early Modern Period (mid-14th century AD – end of 18th century AD) – Phase 2

The first great change in forest composition occurred in the mid-14th century. It was recorded in both profiles and is dated 1348 AD (MS3) and 1369 AD (MS4). This event is characterized by a rapid increase in *Quercus* (30%, i.e. by 20%), and in *Pinus* (to 10%). It was accompanied by a strong decline in *Corylus* (6%), *Abies* (1%) and *Picea* (4%). *Betula* did not change. The dominance of oak, birch and pine has been characteristic for Dúbrava ever since the beginning of Phase 2.

Two charters refer to the active protection of oaks in Dúbrava precisely in this period. The first one is the above-mentioned interpolated charter from 1350, which gave the citizens of Hodonín the right to take dry wood and grass in the Wood but forbade them to fell living oaks (Boček, 1839: 204–205, for a discussion on the dating of the charter, see Měřínský and Šmerda, 2008b). The other one is the foundation charter of the Augustinian monastery in Brno from 1370 AD. It was included in this document that the tenants of the monastery had the right to cut timber and firewood in Dúbrava "with the exception of oak trees, which they must not cut down at all" (translation from Latin original, MZA F5 karton 11 inv. č. 744, fol. 25–32). The ban on cutting oaks was included in a number of privileges in later centuries as well (e.g. 1531 – MZA F5 karton 3 inv. č. 29; 1600 *urbarium* – MZA F5 kniha 1a).

In Phase 2 the maxima of *Quercus* in both profiles (34% MS3; 28% MS4) and the highest percentage of AP (78%) were recorded. The subsequent decrease in *Quercus* pollen is synchronous with an increase in the pollen of the other main tree species: *Carpinus*, *Fagus*, *Abies* and *Picea*. From the middle of the 14th century onwards, the general increase in Cerealia, the start of a continuous pollen curve of *Secale* and the occurrence of weeds (*Centaurea cyanus* – a typical high-medieval weed, *Papaver rhoeas*) may be connected with the expansion of arable land as a consequence of population growth in the surrounding area. The unchanged curves of *Plantago lanceolate* t., Rubiaceae, *Senecio* t., *Rumex acetosa* t., Chenopodiaceae and *Lotus* t. suggest the continuous presence of grasslands and pastures. This argument is also supported by findings of spores of coprophilous fungi (*Podospora, Sporormiella*) in the sediment. The pollen of *Juniperus* and the spores of *Sporormiella* are indicators of livestock farming (Davis, 1987).

We observed a gradual increase in charcoal particles throughout Phase 2. This could be connected with higher fire susceptibility of the vegetation caused by the expansion of *Pinus* or with the intensification of human activities in the vicinity of the study site. Higher concentrations of charcoal particles at the end of this phase in both profiles and a slight decrease in *Quercus* and increase in *Betula* and Cyperaceae may indicate a distinct fire event, however, the percentage of *Quercus, Betula* and Cyperaceae swiftly returned to their previous values.

In this period the name of the Wood changed. The original Klečka [‘a place with shrubs’] was gradually replaced by Dúbrava [‘oakwood’]. ‘Dúbrava’ was first used as a common noun that added information on the Wood (e.g. 1370: “the oakwood [dúbrava] that is called Klečka” – MZA F5 karton 11 inv. č. 744, fol. 25–32), and only later became a geographical name. The last occurrence of the name Klečka is from 1531 (MZA F5 karton 3 inv. č. 29), after that only Dúbrava was used. Two *urbaria* (1600 – MZA F5 kniha 1a; 1691 – MZA F5 kniha 3) provide detailed information on the management of Dúbrava. The most characteristic feature was multiple use, which included wood-pasture, pannage (the fattening of domestic pigs on acorns), hay cutting in woodland meadows, firewood cutting and the collecting of strawberries and oak galls. There were managed ponds, beehives and even arable fields within the Wood. The system was complex but not random: every use was carefully regulated temporally and spatially. The *urbaria* also include a description of the boundaries of Dúbrava, from which it is clear that the boundaries of the Wood were similar to those of today and that a few hundred metres from the pollen sites we investigated there were arable fields. Relatively little direct information is available on tree species in this period: apart from frequent references to acorns and oak galls, the 1692 estate conscription (MZA F5 kniha 5) mentioned that Dúbrava comprised mostly of oaks and partly of aspen and birch. The lack of *Pinus* in this list is noteworthy.

Figure 3: Percentage pollen diagram of selected pollen types with macro-charcoal concentrations from MS3 core. Parts of sediment without macrocharcoal analysis are marked as No Data.

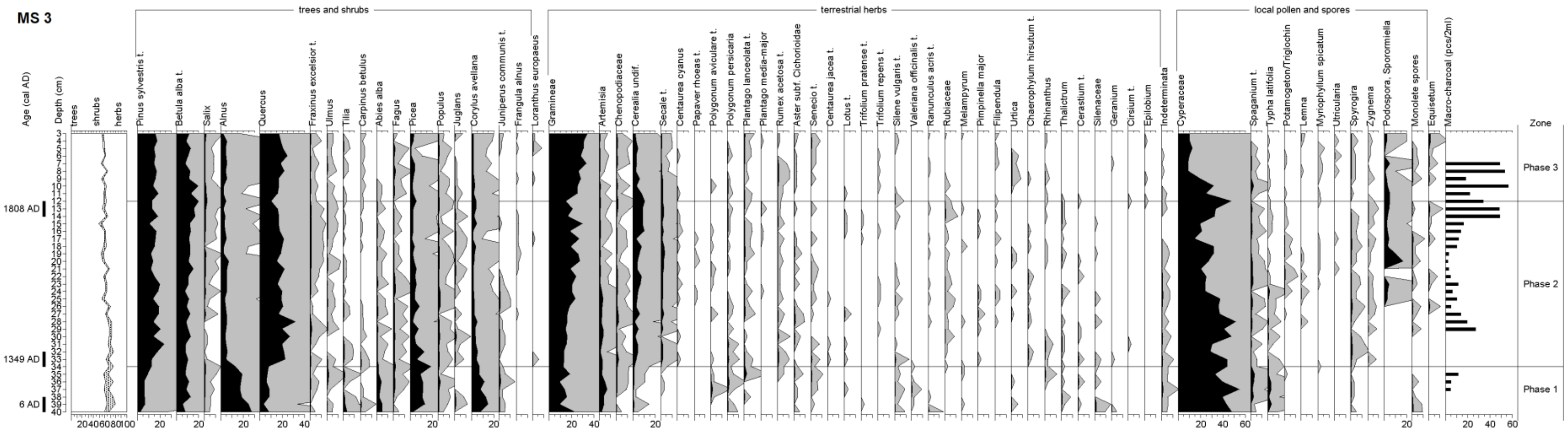
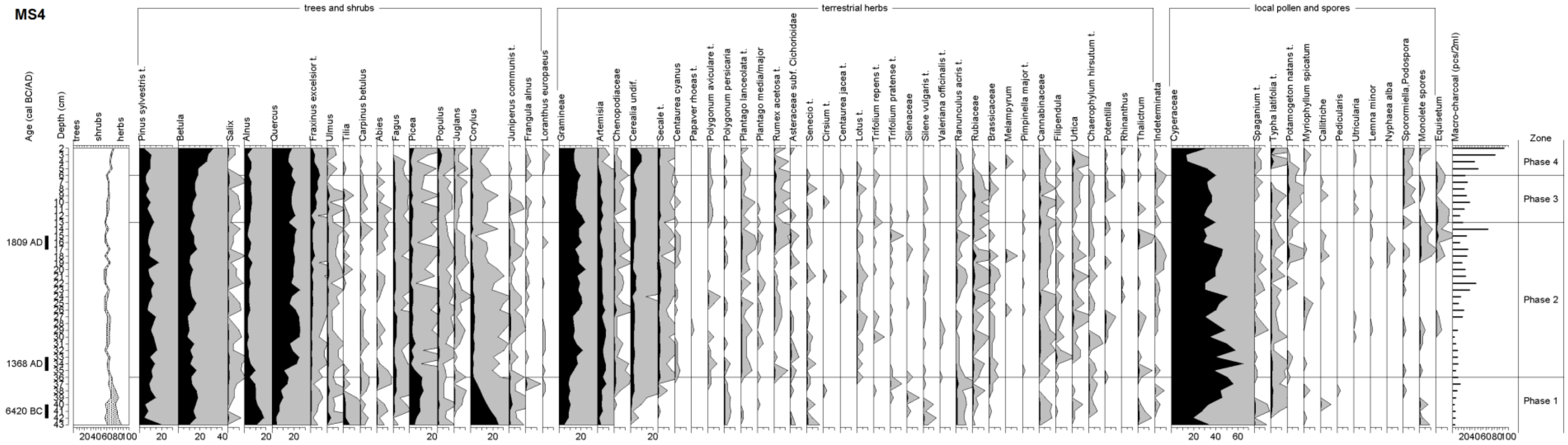


Figure 4. Percentage pollen diagram of selected pollen types with macro-charcoal concentrations from MS4 core.



Modern Period (19th century AD – present) – Phases 3 and 4

At the beginning of the 19th century the second major change in the composition of Dúbrava can be observed. In the pollen diagrams this was reflected by a change in tree composition. A moderate decline in *Quercus* and increase in *Betula*, *Pinus*, *Salix*, *Populus* and *Fraxinus* can be associated with several, possibly interacting factors. A significant decline in Cerealia and *Secale*, dated to the beginning of the 19th century, is visible in MS3 but not in MS4; the latter is characterized by an increase in *Polygonum aviculare* t., *Trifolium repens* t. and large quantities of coprophilous fungal spores (*Podospora*). The apparent contradiction (increase in human activities in MS4, decrease in MS3) can be explained by the different location of the profiles within the Wood.

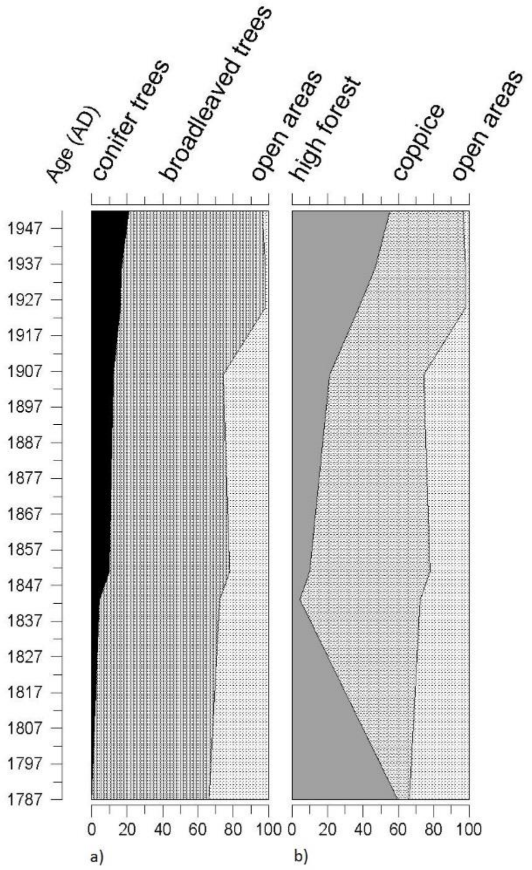
The last change was recognized only in MS4 and refers to Phase 4. It is dated to the mid-20th century and is characterized by a rapid increase in *Populus* and *Betula* and the disappearance of pasturing indicators, such as *Plantago lanceolate* t., *Trifolium repens* t. and Rubiaceae. It refers to the abandonment of pastures and fields inside or immediately outside the Wood and secondary succession with *Populus* and *Betula* as pioneer trees. The curve of *Quercus* rose again but it never reached the medieval maximum of the beginning of Phase 2. At the end of this phase we also recorded a decrease in the curves of other herbs, for example *Filipendula*, *Potentilla*, *Chaerophyllum hirsutum* t., Silenaceae. Macroscopic charcoal concentrations steeply increase towards the top of MS4. This indicates the presence of fire events in the fire-prone *Pinus* stands which were established by modern forestry. ´The increase in charcoal particles could be also associated with the construction of a railway line along Důbrava Wood. The first steam engine on the Emperor Ferdinand Northern Railway passed through the town Hodonín in 1841 AD (Vykoupil, 2008).

Written sources show a major management change at the beginning of Phase 3. In the late 1780s Dúbrava was divided into two parts. The larger part (ca. two thirds of the whole) was enclosed by a woodbank (Szabó, 2010a) and turned into a coppice, while on the remaining one third all trees were quickly removed and the area was turned into pasture. The former multiple management was abolished; pasturing, hay-cutting and pannage were banned. By the mid-nineteenth century, however, the forestry administration changed its mind about management and started transforming the coppices into high-forests, partly with the help of *Pinus* plantations. Timber producing high-forests (including plantations) have formed the majority management type since the 1950s (as witnessed by consecutive forestry management plans: 1851 – MZA F5 kniha 232; 1864 – MZA F5 kniha 233-236, 238, 240; 1906 – MZA F5 kniha

242, 244, 245; 1925 – MZA F263 kniha 1; 1936: MZA F263 kniha 4, 5; 1952 – MZA F302 kniha 4). There were continuous efforts to afforest the open areas in the Dúbrava, however, these were unsuccessful until the 1920s. The pastures created in the late 18th century did not last long, and by 1906 (MZA F5 kniha 242, 244, 245) they reverted back to woodland (Figure 5).

The hydrological regime of the Wood was also changed. Some time in the 19th-20th centuries much of the territory of Dúbrava was drained by a network of channels. These channels connected wetter areas and drained their water into larger canals that had been created in and around the Wood since the 15th century. These drainage channels are still visible in the field but are not maintained any more. Their dating is uncertain. The 1925 FMP (MZA F263 kniha 1) mentioned maintenance work on canals that were created before 1907, therefore we assume that the channels were dug already in the 19th century.

Figure 5: Changes in the amount of a) broadleaved forest, conifer forest and open areas b) high forest, coppice and open areas and in Dúbrava since the end of the 18th century. Data prior to 1851 are approximate.



Discussion

The combination of pollen analysis, macrocharcoal analysis and the study of historical documents provides synergetic results about vegetation stability and historical human impact in Dúbrava Wood. Palaeoecological analyses enabled us to reconstruct vegetation composition and fire disturbances during the past 2000 years while written archival material revealed information on tree composition and management practices for the past seven centuries.

Stability/change in species composition in a regional context

Our results show that in the study period the species composition of Dúbrava went through significant changes. In the 14th century the vegetation of Dúbrava Wood changed from shrubby growth composed mainly of *Corylus* and *Betula* to subcontinental oakwood. In the past two centuries mesophilous species started to spread and *Pinus* plantations appeared – this process continues up until the present.

To gain a more general picture of forest vegetation development in the study region, we used previously published palaeoecological data from four nearby sites: Vracov (Svobodová, 1997; Rybníčková and Rybníček, 1972), Svatobořice-Mistřín (Svobodová, 1989, 1997), Anšův Dvůr (Svobodová, 1990) and Pohansko (Svobodová, 1990; Doláková et al., 2010). They showed that *Quercus* started to spread in the study region in ca. 6900 BC. After this date, grassy subxerophilous oakwoods or mixed oak-lime-hornbeam forests developed in mesic conditions, and floodplain forests prevailed in wet conditions. All four pollen profiles recorded the dominant presence of *Quercus* from ca. 6900 BC to the Early Middle Ages, ca. 6th–9th centuries AD. Unlike at the other three sites, there were relatively high amounts of *Fagus* and *Abies* at Vracov from ca. 3900 BC onwards. This may have resulted from long-distance transport as the site represents a larger lake basin. In contrast to the vegetation recorded in the four profiles, from the 1st to the 14th centuries AD Dúbrava consisted mainly of *Corylus* and *Betula*. *Quercus*, *Tilia, Ulmus* and *Carpinus* occurred only as admixture species. However, we cannot tell whether the vegetation observed at the beginning of the study period had been stable in previous centuries or whether it was the result of recent changes.

The most significant spread of oak in Dúbrava was recorded at the beginning of 14th century. This process was accompanied by a decrease in other trees and shrubs, mainly *Corylus*. A comparison with other pollen diagrams from the region shows a similar decrease in *Corylus* and increase in *Quercus*, however, at a completely different date, in ca. 1200 BC (Svobodová, 1997). The massive spread of oak recorded in Dúbrava has no analogues in southern Moravian pollen profiles in this period, all four of which show a decline in *Quercus* starting from the Early Middle Ages.

The pollen profiles from Dúbrava ended with a visible decline in oak and an increase in ash, birch and pine in the 19th century. This increase in *Fraxinus* and *Pinus* was recorded in other pollen diagrams from study region as well. The spreading of *Fraxinus* in predominantly oak forests is probably a natural reaction to the absence of organic matter removal and is part of a gradual change to a shady mesic forest (Hofmeister et al., 2004; Hédl et al., 2010). *Pinus* spread mainly as a result of plantation forestry.

Driving forces of stability/change in species composition

A possible explanation of the rapid spread of *Quercus* in Dúbrava in the 14th century AD could be provided by the onset of the Little Ice Age (LIA), which began in ca. 1300 AD (Matthews and Briffa, 2005). Climate change (cooler and moisture conditions) could have influenced vegetation composition and cause the spreading of *Quercus*, which is less sensitive to late frosts than *Fagus*. In Białowieża forest (Poland), Mitchell and Cole (1998) attribute the dominance of *Quercus* to a competitive edge in edaphic conditions. However, Faliński (1986) described the dominance of *Quercus* in this forest as a result of grazing (herbivores and cattle). After a reduction in grazing, *Quercus* was replaced by *Carpinus*. In our study region, no other pollen profile records an increase in *Quercus* in the LIA; climate change is therefore unlikely to have caused the dramatic change in the vegetation of Dúbrava. Another possible explanation of the massive spread of oak is fire. Recent studies form North America show that the widespread occurrence and dominance of oak is the result of frequent fires (Abrahams, 1992). Today, oak is in decline because of fire suppression by humans, which leads to a gradual replacement of oak by shade-tolerant species (Dey, 2002; Little, 1974; Van Lear, 1991; Lorimer, 1993). However, the results of macrocharcoal analyses from Dúbrava showed no major fire event parallel with the sudden change in species composition at the beginning of Phase 2. There is some indication of a possible fire at the end of Phase 2, nevertheless even in this case higher concentrations of charcoal particles were not connected to any lasting influence on species composition. Fire is therefore unlikely to have been a driving force of species composition changes.

In a regional context, the changes in the species composition of Dúbrava Wood appear to be rather exceptional. In such cases, site history is often the best explanatory factor (Veski et al., 2005; Lindbladh et al., 2007; Ejarque et al., 2009). Two written documents mentioned the protection of oaks in the mid-14th century, which precisely coincides with the pollen data. However, the interpretation of these charters needs careful attention. Such bans were a commonplace in medieval charters and did not necessarily have to have any concrete consequences. In Sweden in the 18th and 19th centuries a similar ban is known to have caused a decline in oak numbers, although the socioeconomic conditions here very different from late medieval Moravia (Eliasson and Nilsson, 2002). Nonetheless, in our case the existence of two charters and a simultaneous increase in oak pollen can hardly be a coincidence. These charters indicate that from the middle of the 14th century oaks were in fact actively protected in Dúbrava, which led to changes in the vegetation. According the Vera Hypothesis (Vera, 2000), an increase in wood-pasture (also recorded in the two charters) could also have promoted oaks. Similar conclusions were arrived at for an earlier period at Pohansko, where the spread of *Quercus* accompanied by a slight decrease in *Tilia*, *Fraxinus* and *Ulmus* in ca. 600–700 AD was attributed mainly to grazing by pigs (Svobodová, 1990; Kratochvíl, 1981).

From the 14th to the late 18th century, Dúbrava had multiple uses, some of which (pasturing and hay cutting) kept the Wood relatively open. In this phase the maxima of *Quercus* in both profiles (34% MS3; 28% MS4) and the highest percentage of AP (78%) were recorded. This is confirmed by the 1692 estate conscription, which claimed that the Wood comprised mostly of oaks. The change in species composition (slight decline in *Quercus* and spreading of *Fraxinus*, *Betula*, *Populus* and *Pinus*) at the end of this period could have multiple reasons. One is a change in hydrological conditions (the construction of drainage channels), another could be windbreak as suggested by an increase in pioneer trees (*Populus* and *Betula*). Written documents show that multiple-use management ended exactly at this time, and the part where the forest hollows are situated was turned into pure coppice and some 50 years later into high-forest. Therefore the change in species composition can also be associated with a reduction of grazed areas (disappearance of pasturing indicators) and the gradual conversion to high-forest. A similar situation was observed in Białowieża forest (Faliński, 1986; Mitchell and Cole, 1998), where species of open habitats gradually declined and mesophytic tree species (*Carpinus*) replaced oak. This has lead to the loss of species assemblages typical for subcontinental oakwoods (Kwiatkowska et al., 1997).

Protecting the unique vegetation of subcontinental oakwoods

Open canopy oakwoods currently host many endangered species (Spitzer et al., 2008). To sustain their populations, these species had to find suitable habitats throughout the Holocene. It is often argued that open oakwoods with wood-pasture continuity must have been present since prehistoric times (e.g. Vera, 2000; Vodka et al., 2009). While this is certainly possible, other management types and tree species compositions could have provided equally suitable conditions. For example Milovice Wood, a large subcontinental oakwood not far from Dúbrava, was managed as a coppice-with-standards for at least six hundred years (Szabó, 2010b). Only when coppicing ceased did the subcontinental character of the vegetation begin to rapidly fade (Hédl et al., 2010). Our results indicate that the open woodland could have consisted of various community types. In Dúbrava, open forest communities were apparently present from the first millennium AD, while the oakwood fully developed only in the 14th century. This suggests that even from the point of view of species sensitive to canopy openness, open oakwoods might not have been the only option for survival in the Holocene.

Conclusions

We conclude that Dúbrava Wood did not show stability on the long run and that its species composition has dramatically changed during the last two millennia. From 0 to 1350 AD Dúbrava was almost certainly not an oakwood. The origins of its present species composition date back to the 14th century, when intentional management caused a shift from shrubby, hazel-dominated vegetation towards an oakwood. The most important driving force in the shaping and maintenance of the unique vegetation of Dúbrava was human management. Medieval management promoted oaks, and the open oakwoods were further maintained by multiple-use management in the Early Modern Period. They were subsequently drastically reduced in extent by modern forestry plantations continuing to date. The species in the herb layer could have been present in the millennia preceding the past two thousand years; however, until the 14th century they had to survive in other types of vegetation than subcontinental oakwoods.

Acknowledgements

This study was supported by grant no. IAA600050812 “Lowland woodland in the perspective of historical development” from the Grant Agency of the Academy of Sciences of the Czech

Republic and as a long-term research development project no. RVO 67985939. We would like to thank Radek Řepka for introducing us to the sites which were sampled for pollen. We are grateful to Dušan Lekeš for his help during fieldwork and to Zuzana Formánková for laboratory work.

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Landscape history, calcareous fen development and historical events in the Slovak Eastern Carpathians

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Abstract

We explored interactions among human activities, landscape development, and changes in biotic proxies in two small calcareous spring fens in the Slovak Eastern Carpathians, reaching back to ca. 930 AD. Results of pollen, plant macrofossil, and mollusc analyses were compared with the settlement history. The regional pollen record reflected historical events and changes in the settlement density very well at both study sites. The natural mixed fir–beech–spruce forests with fern undergrowth were suppressed and replaced with light-demanding trees in the periods of high human impact (e.g., Wallachian colonization). The study area was affected several times by wars and raids followed by a consequent decline in the settlement density. Some of these events are well reflected in the pollen records that document tree recovery and decline of cereals, weeds, and pasture indicators. In comparison, only some landscape changes were reflected in the local fen development. Both spring fens originated after deforestation, Roškovce around 1347 AD and Miroľa around 929 AD. The most pronounced change involving the water regime stabilization and undisturbed development of plant and mollusc communities took place after the decline in human impact. We conclude that humans were the main drivers of landscape transformation in the last millennium; they directly created spring-fen ecosystems through deforestation and influenced fen species composition through husbandry activities.

Keywords: forest development, multi-proxy, macrofossil, pollen, snail, spring fen

Introduction

In Central Europe, various human activities (e.g., deforestation, forest grazing, and agriculture) have significantly altered landscape structure and forest composition in the past. Such impacts often caused an extension of pastureland and supported the development of several new habitats such as meadows and spring fens (Behre, 1988; Willis, 1994; Gardner, 2002; Pokorný, 2005; Feurdean and Willis, 2008; Hájková et al., 2011). Although human-mediated, these habitats contain many endangered species. But the modern decline in traditional management practices (coppicing, forest pasture, and regular mowing) has resulted in a gradual impoverishment of their biodiversity (Mitchell and Cole, 1998; Feurdean and Willis, 2008; Jamrichová et al., 2013). Understanding the processes and conditions responsible for the origin and variability of these habitats can improve their protection and development of appropriate management practices (Willis and Birks, 2006; Feurdean, 2010; Vegas-Vilarúbia et al., 2011). Results of palaeoecological studies help to reveal the origin, disturbance regime, and natural variability of target habitats (Willis and Birks, 2006) and are a useful tool for nature conservancy (Chambers and Daniell, 2011).

Calcareous fens belong among the habitats of high biodiversity, with the occurrence of many habitat specialists and highly endangered species (Bedford and Godwin, 2003; Hájek et al., 2011). They belong to the most threatened habitats due to water regime changes (i.e., human-made drainage), eutrophication, and changes in agricultural practices, mainly during the last 50 years (Grootjans et al., 2005; Hájková and Hájek, 2011). The history of some recent calcareous fens was traced to the Late Glacial times (Yu et al., 2003; Hájek et al., 2011), but the number of such old calcareous fens is low. In the cultural landscape of Western and Central Europe, young calcareous fens prevail (Grootjans et al., 2006; Hájková et al., 2012). In the Western Carpathians, most modern calcareous spring fens (especially those in the Outer Western Carpathians) developed after the deforestation of existing forest springs (Hájek et al., 2011; Hájková et al., 2012). Therefore, deforestation and consequent mowing or grazing played an important role in the creation of favourable conditions for calcareous fen biota. Although relatively young, these fens represent important neorefugia of endangered and relict species once humans destroyed the oldest lowland fens. The old fens of Late Glacial age still have the most relict fen species and fen specialists (Hájek et al., 2011) and are the source of these species, which can migrate (or could have migrated during the last centuries) to newly originating fens. However, not all species have good dispersal ability, and the probability of colonization decreases with decreasing connectivity of fen sites, which has become evident in the last few decades.

In this study, we attempted to explore the palaeorecords from two calcareous spring fen deposits using a multi-proxy approach (analysis of pollen, plant macrofossils, and molluscs) to obtain a complex reconstruction of the fen and landscape development in the previously unexplored Slovak Eastern Carpathians. Analyses of plant macrofossils and molluscs provide information about the main successional trends in the habitat development, thus enabling a precise reconstruction of local history (Birks and Birks, 2006; Hájková et al., 2012). By contrast, pollen analyses capture regional landscape changes (Birks and Birks, 1980; Lamentowicz et al., 2008). Historical sources can provide valuable information on historical land-use, settlement structure, and socio-economic conditions (Foster et al., 1998, 2002; Goslar et al., 1999) as a useful framework for interpretation of the pollen data (Veski et al., 2005; Lindbladh et al., 2007). A combination of particular proxies that reflect both local and regional development of vegetation and habitat conditions can explore relationships between the surrounding landscape and the local fen ecosystem. We specifically explored the main driving forces behind landscape structure transformation and links between landscape changes and local fen development. In addition, we highlight the implications of this palaeoecological knowledge for fen conservation management.

Material and methods

Site description

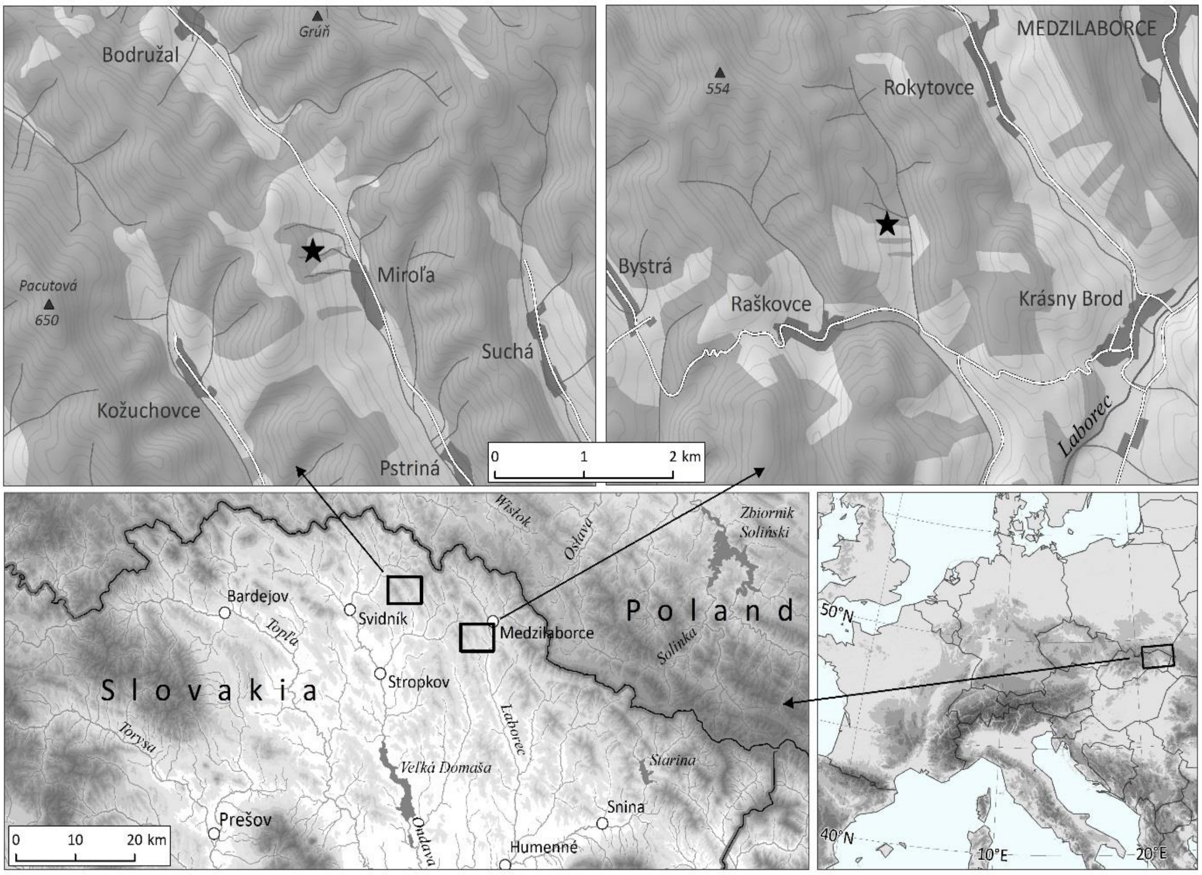
The studied fen sites, Roškovce (49.251389° N; 21.861944° E, open fen 700 m²) and Miroľa (49.332500° N; 21.726667° E, open fen 2100 m²), are situated in the flysch zone of the Outer Western Carpathian Mountains in the north-eastern part of Slovakia (Figure 1) geomorphologically belonging to the Laborecká Vrchovina Mountains. Both sites were developed on moderate slopes; they are situated at middle altitudes (Roškovce, 351 m a.s.l.; Mirol’a, 415 m a.s.l.) and are supplied by calcareous groundwater (electric water conductivity at 540 and 600 μS.cm^{-1}, respectively). Calcium carbonate (called tufa; $CaCO_3$) precipitation is characteristic of both sites. The vegetation can be classified as *Carici flavae–Cratoneuretum* (Roškovce) and *Valeriano–Caricetum flavae* (Miroľa) associations within the *Caricion davallianae* alliance (see Dítě et al., 2007), which is dominated by low sedges and so-called brown (non-sphagnaceous) mosses. The flysch bedrock is characterised by the alternation of sandstone and claystone, which supports frequent development of landslides, especially after landscape deforestation and the application of an intensive grazing. The climate of the sites' surroundings is slightly warm and humid with a 4–7 °C mean annual temperature and 800–900 mm of mean annual precipitation (http://geo.enviroportal.sk/atlassr/).

Cultural development in the study area

Archaeological finds document the settlement in the study area since the Late Neolithic (2000–1800 BC), which continued during the Bronze Age (1800–700 BC) and Roman Period (0–400 AD) (Vizdal, 2003). The oldest known finds of the Slavic settlement dated to the 6th century are situated in the foothills of the Eastern Carpathian Mountains. It is possible that other Slavic settlement artefacts could be discovered at higher altitudes, such as the Laborecká Vrchovina Mountains (Uličný, 2001). In the first half of the 11th century, the Hungarians conquered the study area, making it part of the Hungarian Kingdom (Pop, 2010). After the 11th century, the number of inhabitants in the region gradually increased. This is reflected in the settlement expansion and establishment of new villages (Uličný, 2001). In the mid-13th century, the Tatar invasion influenced settlement in the region. During the Tatar raids, many villages were destroyed or plundered, and most of inhabitants were killed. As a result, the majority of arable land was abandoned and depredated. These raids affected most strongly the north-eastern part of Hungarian Kingdom. Since the 13th century, colonisation by Germans (mostly the lowlands) and Ruthenians (Wallachian colonisation of the foothills) completed the population in the region (Pop, 2010; Rábik, 2012). In the study area, villages are established mainly on the margins of older settlements in the wooded part of the Eastern Carpathian foothills. Ruthenian shepherds settled new villages and farmed on the Wallachian custom (Uličný, 1990, 2001). From the 15th–16th centuries, many villages were temporarily or permanently abandoned because nobles frequently fought one another, which was followed by plunder. For example, after the invasion by Polish troops (1471–1473 AD) the number of settlements declined from 1565 in 1427 AD to 154 in 1492 AD (Rábik, 2012). There was a decrease in the population in the study region due to the Kuruc wars (1678–1711 AD), which had devastating economic consequences. The population of many Ruthenian villages also decreased because of emigration of their inhabitants or pervasive disease (plague) (Uličný, 2001; Pop, 2010). In the 18th century, the population of the Ruthenian villages increased, resulting in the emigration of inhabitants to the southern part of the Hungarian Kingdom, which provided better conditions for farming (Pop, 2010). In the 19th century, the cholera epidemic afflicted the region (1830–

1831 AD), followed by the famine of 1852 AD (Anonymous, 2011). During the second half of the 19th century, many people left the region and moved to the southern part of the Hungarian Kingdom or to the United States or Canada. During World War I and II, many villages were destroyed and burned, and the population decreased again (Pop, 2010).

Figure 1. Localization of the study sites in the Laborecká vrchovina Mountains (NE Slovakia) showing the position of the two analysed calcareous-fen sites.



Palaeoecological analyses

Material for palaeoecological analyses was collected on each site in August 2007 from the wall of a pit using two overlapping boxes and stored in metal boxes of 10×10×50 cm^3. Mollusc samples were collected alongside the boxes from six layers at each site. The depth of these layers varied between 10 and 22 cm and was 12.5 cm on average. The physical properties of the sediments were described in the field following Troels-Smith (1955; for details see Table 1). The stratigraphies of all proxies were divided into developmental zones based on constrained cluster analysis by sum-of-squares (Coniss analysis, implemented in Tilia program; Grimm 2011).

Table 1.: Stratigraphy and description of fen deposits in the Roškovce and Miroľa profiles.

Depth (cm)	Troels-Smith system	Description
Roškovce		
0-10	Th3, Dg1, Tb(Hyp)+, Dh+	Brown-moss/sedge peat with an admixture of $CaCO_3$, root zone
10-22.5	Dg3, Th1, Tb+, Dh+	Coarse-grained $CaCO_3$ deposits with small amount of organic
22.5-35	Th2, Dg2, Tb (Hyp)++, Dh+	Brown-moss/sedge peat with coarse-grained $CaCO_3$ deposits
35-46	Dg4, Th++, Tb(Hyp)+, Dh+	Fine-grained $CaCO_3$ deposits with small amount of organic
46-57	Tb(Hyp)3, Th1, Dg1, Dh+	Brown-moss/sedge peat with an admixture of $CaCO_3$
57-73	Th2, Tb(Hyp)2, Tl+, Dh+, [A]	Brown-moss/sedge peat with wood and charcoals
below 73	As4	Solid clay without stones
Miroľa		
0-25	Th2, Tb (Hyp)2, Dg+, Dh+, As+	Brown-moss/sedge peat with an admixture of $CaCO_3$
25-57	Th1, Tb (Hyp)1, Tl 1, As1, Gg(min)++, Dg+, Dh+, [A]	Brown-moss/sedge peat with clay, wood, small stones and charcoals
57-68	Th2, Tb (Hyp)2, Tl+, Dg++, Dh+, As+, [A]	Brown-moss/sedge peat with $CaCO_3$, wood and charcoals
68-80	Th2, T12, Tb (Hyp)++, Dg+, Dh+, As+, [A]	Wood/herbaceous peat with $CaCO_3$ and charcoals

Components: Tb (Hyp) – moss peat, Th – herbaceous peat, Tl – wood peat, Dh – herbaceous detritus, Dg – granular detritus (calcium carbonate), Dl – wood detritus, As – fine clay, Gg(min) – little stones, [A] – charcoal.

Pollen analysis

Material for pollen analyses from both profiles were sub-sampled at 5 cm intervals (volume of $1cm^3$) and processed using standard techniques (Faegri and Iversen 1989). Samples containing clastic materials were pre-treated with cold concentrated HF (hydrogen fluorid) for 24 hours and then processed by a KOH (potassium hydroxide) solution. At least 500 terrestrial pollen grains were identified according to Beug (2004), Punt and Clarke (1984) for the Apiaceae family, and pollen atlases (Reille, 1992, 1995, 1998). For the determination of non-pollen palynomorphs (NPP), van Geel et al. (1980–1981) was used. The nomenclature of pollen types follows Punt and Clarke (1984) and Beug (2004).

The pollen data are presented in percentage pollen diagrams. The total pollen sum (TS) was calculated based on the terrestrial pollen sum; (semi)aquatic plants, pteridophyta, algae, fungi, and the other non-pollen palynomorphs were excluded. 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 =F 100%). The pollen diagrams were constructed using Tilia software v. 1.7.16 (Grimm 2011).

Macrofossil analysis

Samples for macrofossil analysis (100 cm^3) were taken without gaps in 5–10 cm intervals taking visible stratigraphic changes into account, and sieved into three fractions (200–630 μm, 0.630–1 mm, > 1 mm). The two larger fractions were analysed using a stereomicroscope with a magnification of 10–40x; one slide of the finest fraction was examined at 100–400x magnification to identify small seeds (*Juncus*) and oogonia of *Chara vulgaris*. Seeds and plant tissues were determined according to Berggren (1969), Mauquoy and van Geel (2007), Cappers et al. (2012), and the other available identification literature. Macrofossils were also checked against the reference seed collection of the Institute of Botany, Academy of Sciences of the Czech Republic. Wood fragments were determined according to Schweingruber (1982); bryophytes were determined according to Smith (1996). Values are presented as absolute numbers per sample for countable fossils (seeds) or as volume percentages (bryophytes, plant tissues, and woods).

Malacological analysis

Molluscs were extracted from samples of 750–1000 ml volume by carefully washing each sample in a bowl-shaped sieve (mesh size 0.5 mm) to remove fine soil particles (see Horsák 2003). After drying, all shells and fragments were separated from the remaining material by hand-sorting under a dissecting microscope and then identified and counted. Molluscs were determined according to Ložek (1964) and M. Horsák’s personal reference collection. Remnants of slugs were not considered.

Results

Stratigraphy

The deposit at both sites was accumulated on clay bedrock with a maximum depth of 73 cm at the Roškovce site and 80 cm at the Miroľa site. Based on different compositions and representations of mineral particles and organic matter in the analysed sediments, the profiles were divided into six (Roškovce) and four layers (Miroľa). The 57–35 cm layer at the Miroľa site contained stones (15 cm in diameter), wood pieces (15×3 cm), and a high clay content, which indicates a landslide event (Table 1).

Table 2.: Results of radiocarbon dating from Miroľa and Roškovce peat profiles.

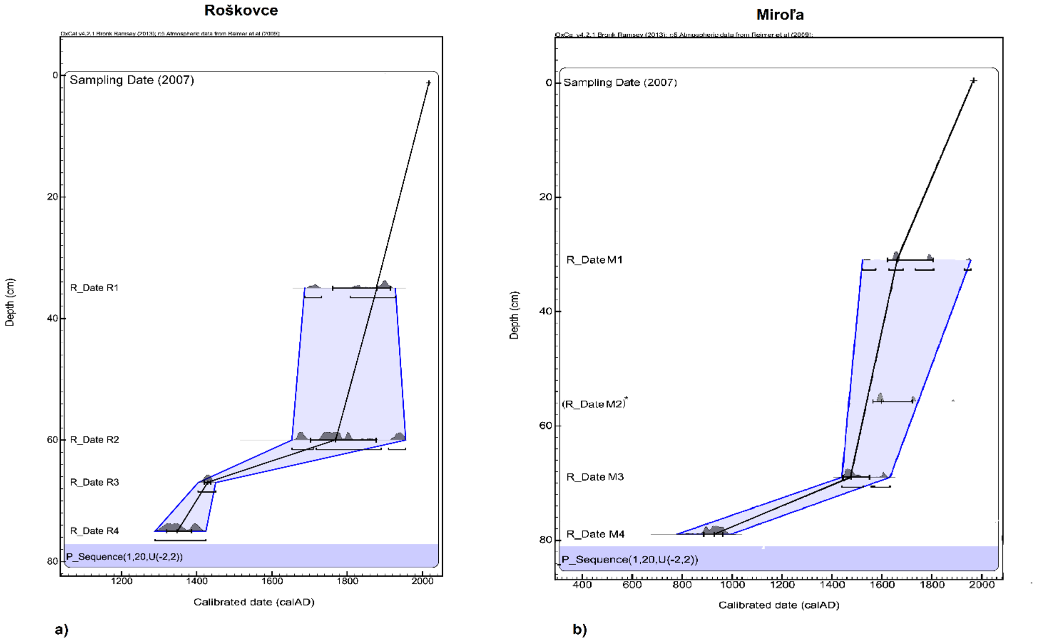
Samples (lab. code)	**Depth (cm)**	**Dating method**	**^{14}C age (uncal. BP)**	**Material**	**Calibrated ^{14}C age (cal.AD)**	
					Median (AD)	**Range (AD)** **95,4%**
Roškovce						
R1 (UG-10015)	35 - 37	AMS	60 ± 25	seeds	1878/	1694-1919
R2 (UG-10016)	58 - 60	AMS	170 ± 25	seeds	1769	1665-1954
R3 (UG-13297)	65 - 67	AMS	490 ± 20	seeds	1429	1412-1444
R4 (UG-10017)	73 - 75	AMS	590 ± 30	seeds	1347	1298-1413
Miroľa						
M1 (UG-11628)	30 - 32	AMS	240±25	seeds	1662	1529-1955
M2 (UG-11629)*	55 – 57	AMS	240±20*	seeds	1661*	1642-1952*
M3 (UG-13296)	68 - 70	AMS	390±20	seeds	1476	1445-1619
M4 (UG-11630)	78 - 80	AMS	1130±25	seeds	929	827-986

The radiocarbon date denoted by * was excluded from the depth–age model.

Chronology

Based on distinct changes in pollen diagrams, we determined the layers to be dated by AMS radiocarbon. Dominant plant macrofossils were isolated from the selected layers and sent for dating to the Centre for Applied Isotopes Studies, University of Georgia, Athens, GA, USA (UG-) (Table 2). Radiocarbon ages were calibrated using the IntCal09 calibration curve (Reimer et al., 2009). A depth–age model was created with P_Sequence (a Bayasian model of deposition) implemented in Oxcal 4.2.1 (Bronk Ramsey, 2008, 2009, 2013). At the Miroľa site, the radiocarbon age (M2) obtained for 54–52 cm depth was the same as for 32–30 cm (240±25(20) BP). We assume that the material (seeds) used for the dating was re-deposited from the upper layers due to a landslide event and excluded the date at 54–52 cm from the depth–age model (Figure 2). To estimate the age of each pollen sample, linear interpolation of the median of the calibrated level (with a 99, 7% probability) was implied.

Figure 2.: Depth–age relationship of the a Roškovce and b Miroľa profiles based on four (Roškovce) and three (Miroľa) radiocarbon dates. The date M2 from 54 to 52 cm depth in the Mirol'a profile was excluded from the depth–age model. The black line goes through the median value of calibrated levels and was set to intersect 0 cm = 2007 (sampling date).



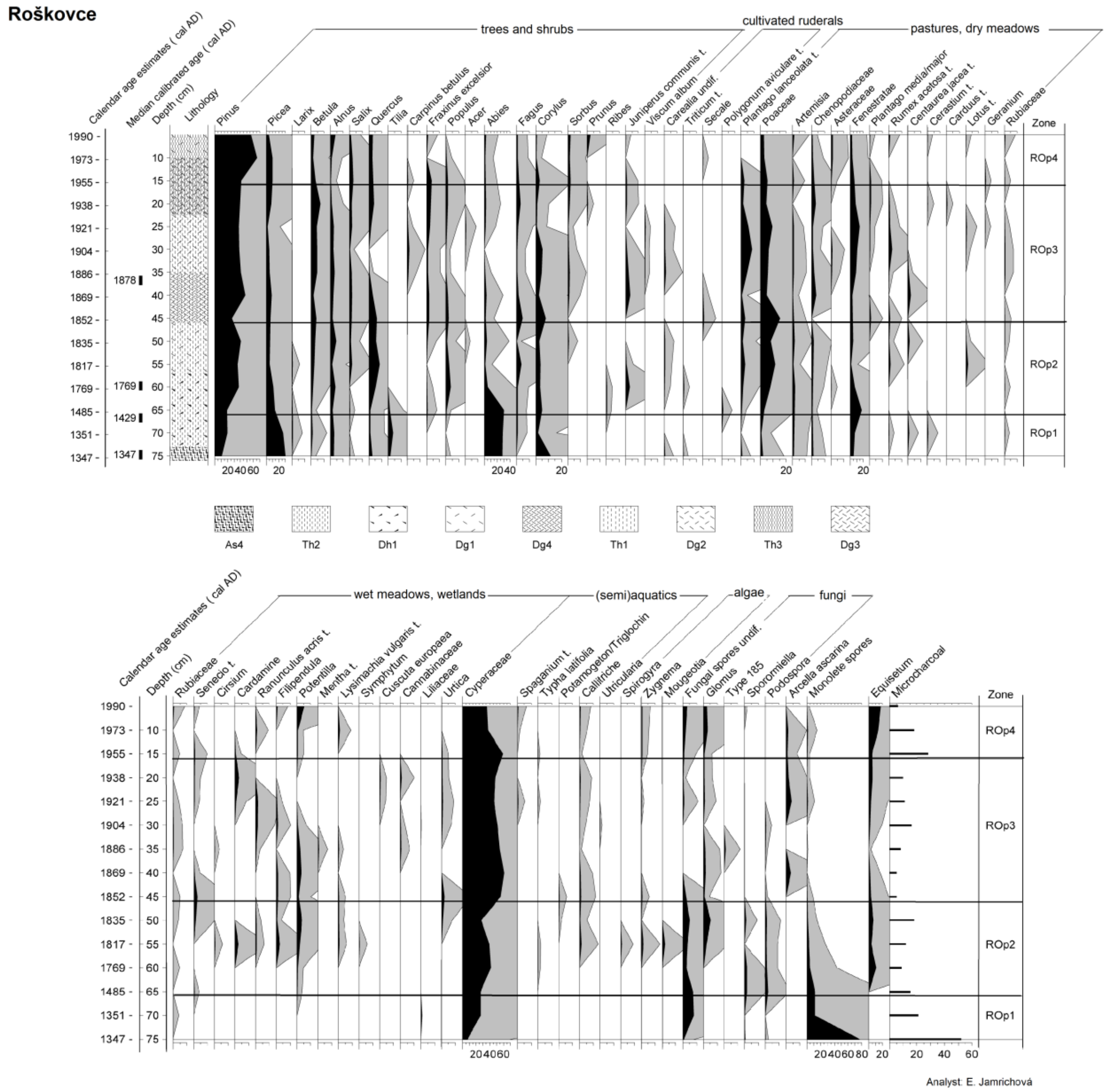
Pollen

Roškovce

We divided pollen diagrams into four main phases (Figure 3).

1. Zone ROp1 (75–67.5 cm; mid-14th century – first half of the 15th century AD) is characterised by the dominance of coniferous trees (*Abies* and *Picea* ca. 30%) with admixture of deciduous trees and shrubs. There was little herbaceous pollen, but the presence of Cerealia, *Plantago lanceolata* t., and meadow species (*Centaurea jacea* t., *Rumex acetosa* t., *Cerastium* t.) suggests the existence of arable land, open stands, and meadows in the vicinity of the study site. There was a high proportion of monolete fern spores.

Figure 3.: Percentage diagram of selected pollen and spores from the Roškovce site. The abbreviation of lithological components follows Troels-Smith (1955) (see Table 1).



2. Zone ROp2 (67.5–47.5 cm; first half of the 15th – first half of the 19th century AD) was characterised by a decline of coniferous trees (*Abies* 7%; *Picea* 15%) and an increase (qualitative and quantitative) of herbaceous pollen (e.g., Poaceae, *Lotus* t., *Ranunculus acris* t., *Rumex acetosa* t.) and indicators of human-induced habitats (e.g., Cerealia and *Polygonum aviculare* t.). These indicate an enlargement of open stands and intensification of agriculture. The presence of hygrophilous species (*Sparganium* t. and *Typha latifolia* t.) and green algae

(*Zygnema, Spirogyra, Mougeotia*) imply wetter habitat conditions. There were fewer monolete fern spores here than in the first zone.

3. Zone ROp3 (47.5–17.5 cm; first half of the19th – first half of the 20th century AD) is characterised by changes in local taxa. Cyperaceae increased, and the curves of green algae were interrupted (*Zygnema*) or absent (*Mougeotia, Spirogyra*) probably due to vegetation succession.

4. Zone ROp4 (17.5–5 cm; first half of the 20th – end of the 20th century AD). In the last zone, *Pinus* increased to 60% and other deciduous trees declined (*Betula, Populus, Fraxinus, Corylus*) or disappeared (*Carpinus*). Curves of meadow species increased, but the absence of cereals (except *Secale*) and pasture indicators suggests an overgrowth of abandoned fields and pastures. Among the local taxa, the proportion of Cyperaceae decreased.

Miroľa

The pollen profile from the Miroľa spring fen was divided into four zones (Figure 4).

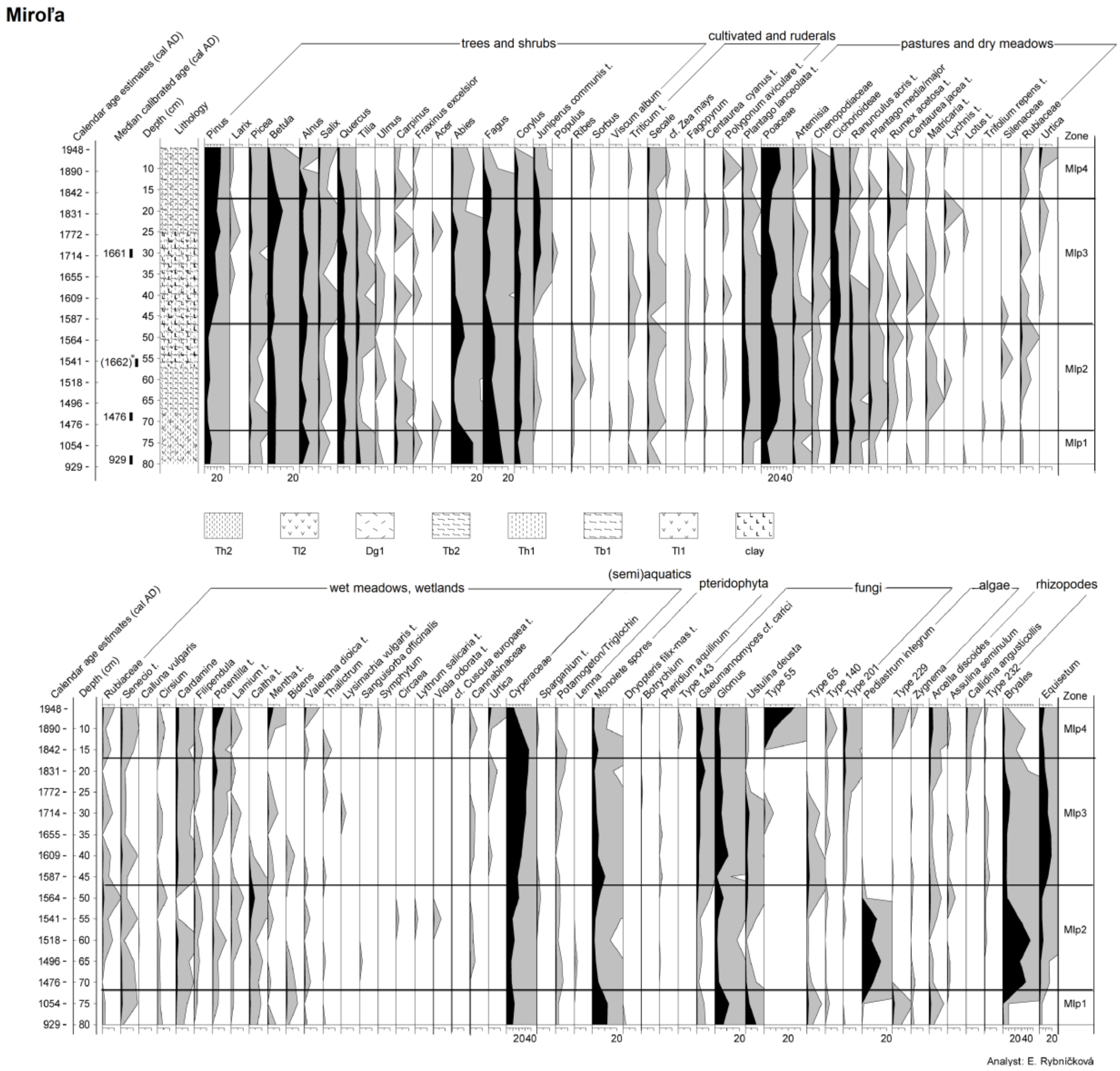
1. Zone MIp1 (80–72.5 cm; first half of the 10th – beginning of the 13th century AD) is characterised by the co-dominance of *Abies* (17%) and *Fagus* (16%). The composition of herbaceous species is linked with the existence of local open stands and meadows (e.g., *Centaurea jacea* t., *Mentha* t., *Bidens*) in the surroundings of the spring fen. Cerealia suggests the presence of fields. From local types, more monolete fern spores, fungal spores (Type 140, Type 201), and algae (*Zygnema*) were identified.

2. Zone MIp2 (72.5–47.5 cm; early 13th – second half of the16th century AD) is characterised by a decline in fir–beech forests at the beginning of zone, but fir was restored later to the amounts of the previous phase. Small fluctuations recorded in cereals reflect changes in agricultural practices. An increase in *Plantago lanceolata* t. and meadows species (e.g., Poaceae, *Ranunculus acris* t., and *Matricaria* t.) indicates an expansion of pasture and meadows. The appearance of *Pediastrum integrum* indicates the presence of open water; there was also a decline in monolete fern spores.

3. Zone MIp3 (47.5–17.5 cm; second half of the 16th – first half of the 19th century AD) is characterised by a spread of light-demanding trees and shrubs such as *Betula, Juniperus communis* t., and *Larix* due to a decline in the fir–beech forest. Fluctuations in the number of human indicators are recorded. The curve of Cyperaceae gradually increased, which implies vegetation succession. Eutrophication is indicated by fungus Type 140.

4. Zone MIp4 (17,5–5 cm; first half of the 19th – mid-20th century AD). Towards the end of the profile, almost all tree species' pollen declined, except *Pinus.* Among herb pollen, higher amounts of wet meadow species (*Potentilla* t., *Mentha* t., *Valeriana dioica* t.) were recorded. The curves of cereals and plants of trampled habitats (*Polygonum aviculare* t.) were restored, but declined again towards the upper part of profile. Within the local types, Cyperaceae declined, and higher amounts of Sordariaceous ascospores were identified, indicating an increase in nutrients.

Figure 4.: Percentage diagram of selected pollen and spores from the Miroľa site. The abbreviations of lithological components follow Troels-Smith (1955) (see Table 1).



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

Macrofossils

Roškovce

We divided the diagram into four zones (Figure 5).

1. Zone ROma1 (73–57 cm, mid-14th – end of the 18th century AD) represents an initial stage of development characterised by *Carex otrubae*, *Carex distans*, and wet meadow species (e.g., *Lychnis flos-cuculi*, *Caltha palustris*, and *Scirpus sylvaticus*), which all later disappeared from the profile. This layer is rich in bryophyte species. A high amount of *Potentilla erecta* and an increase in *Campylium stellatum* indicates fewer disturbances in the upper part of this zone.

2. Zone ROma2 (57–40 cm, end of 18th – second half of the 19th century AD) is characterised by *Blysmus compressus*, *Carex rostrata*, and *Chara vulgaris*, indicating a higher water level and a certain level of disturbance.

3. Zone ROma3 (40–16 cm, second half of the 19th – mid-20th century AD) is characterised by a sharp decline in *Blysmus compressus* and *Carex rostrata* and the disappearance of *Chara vulgaris.* The increase in *Carex panicea*, Poaceae, and *Potentilla erecta* and the appearance of *Scorpidium cossonii* (in the upper part) indicate a decline in water level and an undisturbed fen development; the site was mowed rather than grazed. The upper part of this zone is characterised by *Equisetum* tissues.

4. Zone ROma4 (16–0 cm, mid-20th century AD – present). The beginning of this zone has low values of *Carex panicea* and *Potentilla erecta*, which is followed by an increase in the sub-recent layers (0–10 cm). There were few vascular plant and bryophyte species.

Miroľa

The diagram was divided into five zones (Figure 6).

1. Zone MIma1 (80–74 cm, first half of the 10th – first half of the 12th century AD) is characterised by *Fagus sylvatica*, *Abies alba* (almost 40% of the deposit was wood), and the sciophilous grass *Glyceria nemoralis*. This indicates that the fen originated in fir–beech forest.

2. Zone MIma2 (74–46 cm, first half of the 12th – second half of the 16th century AD) is dominated by *Eleocharis uniglumis/palustris* and *Bidens cernua*. These species suggest a high water level (as do *Chara vulgaris* and *Carex otrubae*). A high nutrient supply is indicated by *Caltha palustris*, *Lycopus europaeus*, and *Scirpus sylvaticus*. Bryophytes *Calliergonella cuspidata*, *Cratoneuron filicinum*, and *Brachythecium rivulare* were also present. This zone is

relatively species-rich mainly due to a combination of ecologically different species groups (19 species in total).

Figure 5.: Macroremains diagram from the Roškovce site. Countable plant remains are in absolute numbers, others (wood, plant tissues) in volume percentages.

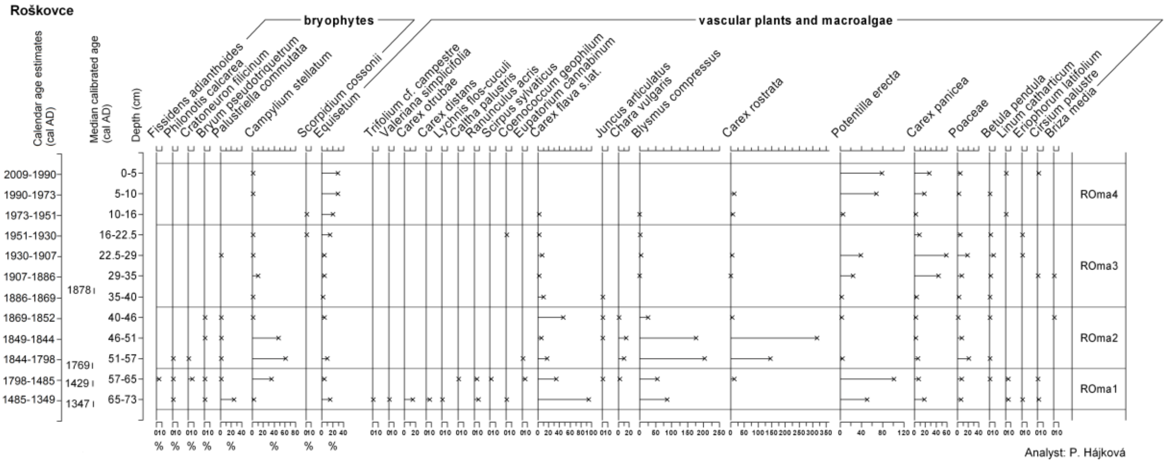
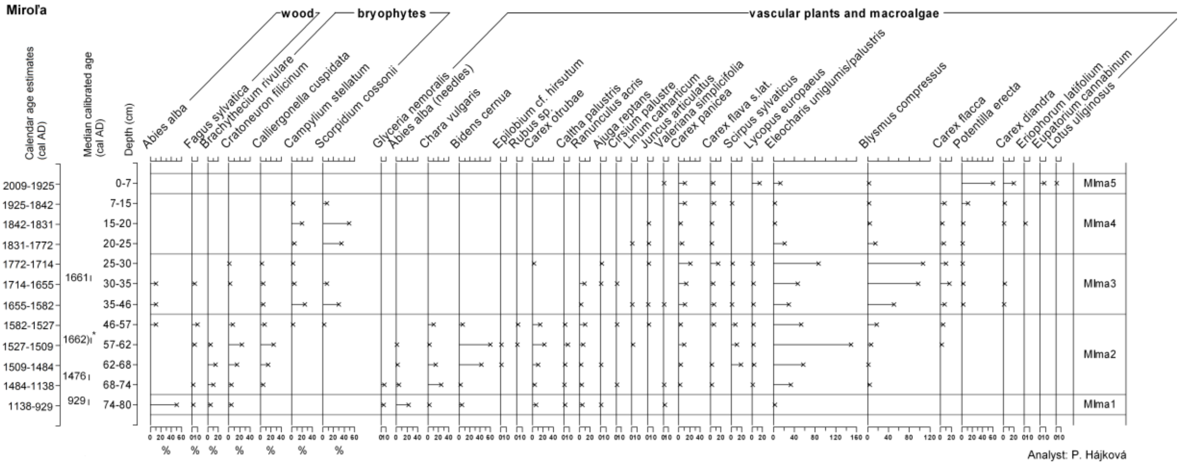


Figure 6.: Macroremains diagram from the Miroľa site. Countable plant remains are in absolute numbers, others (wood, plant tissues) in volume percentages.



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

3. Zone MIma3 (46–25 cm, second half of the 16th – second half of the 18th century AD) represents a transition between the earlier, nutrient-rich and disturbed zone and the subsequent zone with few nutrients. Forest species and some species with higher nutrient-demands had disappeared (*Bidens* and *Caltha*), but some remained (e.g., *Lycopus europaeus*, *Ranunculus*

acris, and *Calliergonella cuspidata*). *Blysmus compressus* became dominant in this zone, and the competitively weak low-sedge *Carex diandra* appeared. *Eleocharis uniglumis*/*palustris* indicates a rather high water level.

4. Zone MIma4 (25–7 cm, second half of the 18th – first half of the 20th century AD) is species poor (only 11 species in total) and is characterised by low sedges such as *Carex flava*, *C. flacca*, and *C. panicea* in the herb layer and *Campylium stellatum* and *Scorpidium cossonii* in the bryophyte layer. *Blysmus compressus* and *Eleocharis uniglumis*/*palustris* seeds still occur, but in low amounts.

5. Zone MIma5 (7–0 cm, first half of the 20th century AD – present) represents the most recent changes during the last century. *Carex diandra*, *Lycopus europaeus*, and *Potentilla erecta* increased and bryophytes (*Campylium stellatum* and *Scorpidium cossonii*) disappeared.

Molluscs

Roškovce

Four zones were distinguished (Figure 7). We documented a continuous succession of characteristic treeless-fen mollusc assemblage throughout the site.

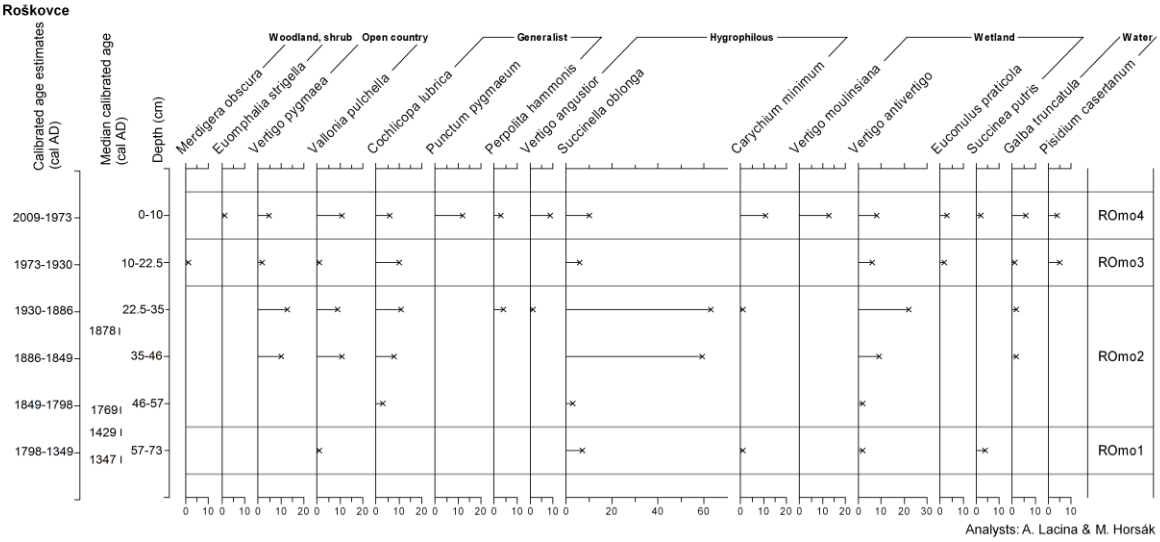
1. Zone ROmo1 (73–57 cm, mid-14th – end of the 18th century AD) had a few hygrophilous species and an open-country species, *Vallonia pulchella*.

2. Zone ROmo2 (57–22.5 cm; end of the 18th – first half of the 20th century AD) had at its beginning a distinct decrease in species richness; it dropped from five to three generalist species. This indicates disturbances caused by intensive cattle grazing. The number of species increased towards the younger periods: *Vertigo pygmaea*, *Vallonia pulchella*, and *Vertigo angustior* appeared; *Cochlicopa lubrica* increased, and *Succinella oblonga* became dominant.

3. Zone ROmo3 (22.5–10 cm, first half of the 20th – second half of the 20th century AD) had a notable decrease in the open-country species *Vallonia pulchella* and *Vertigo pygmaea* and a decrease in *Succinella oblonga* and *Vertigo antivertigo*. The decrease of the former two species indicate an invasion of shrubs and more shady conditions (suggested also by the record of *Merdigera obscura*), but the decrease of the latter two suggested less vegetation productivity and less representation of broad-leaved herbs. As these two processes are in opposition, these changes together indicate an increase in the water table and in spring water flow. This is supported by the appearance of *Pisidium casertanum*.

4. Zone ROmo4 (10–0 cm, second half of the 20th century AD – present) represents a well-developed, stable, species-rich fen community. Some fen specialists became more abundant (*Vertigo angustior*) or reached the site (hygrophilous and the relict species *Vertigo moulinsiana*). The increase in *Vallonia pulchella* and *Vertigo pygmaea* suggests more open conditions.

Figure 7.: Mollusc diagram from the Roškovce site in absolute numbers.



Miroľa

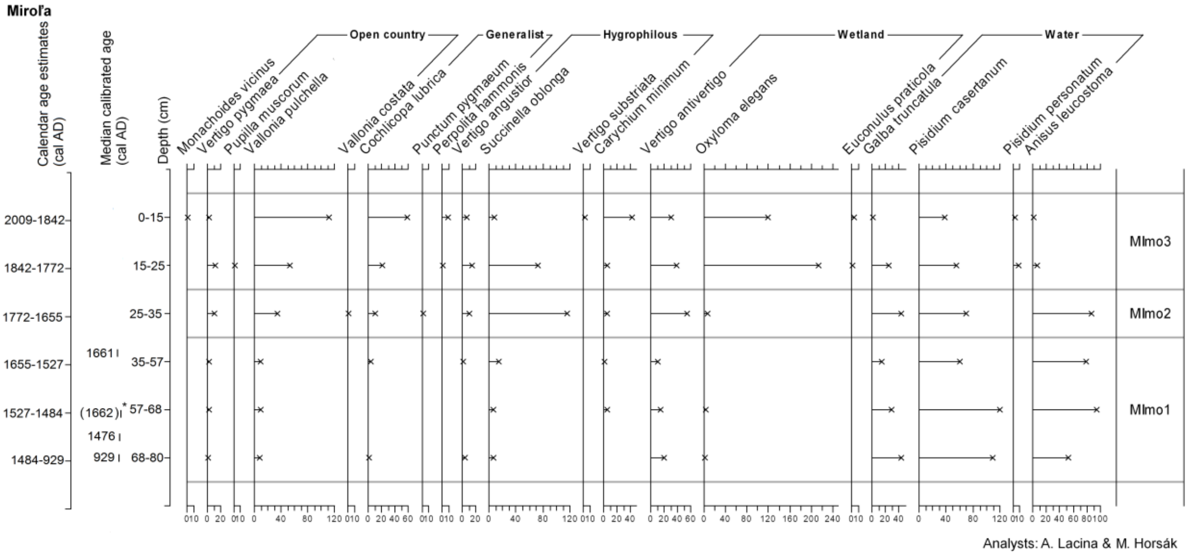
Three developmental zones were distinguished (Figure 8). The species composition was rather stable throughout the succession. Most interpretations reflect changes in species abundance. Based on species composition, it is clear that the site was fully open from the initial layer. Characteristic species of fully open habitats, *Vallonia pulchella* and *Vertigo pygmaea*, were found in all layers. There were no forest- or shrub-preferring species except one shell of *Monachoides vicinus* recorded in the uppermost layer.

1. Zone MImo1 (80–35 cm, first half of the 10th – mid-17th century AD) had a high abundance of freshwater species (*Anisus leucostoma* and *Galba truncatula*), indicating a high water table. High amounts of *Pisidium casertanum* suggest the presence of spring streamlets.

2. Zone MImo2 (35–25 cm; mid-17th – second half of the 18th century AD) had *Succinella oblonga* and *Vertigo antivertigo* as dominant species, indicating a well-developed herb layer, possibly as a result of decreasing water table, followed by the release of nutrients.

3. Zone MImo3 (25–0 cm, second half of the 18th century AD – present) became drier as indicated by the decrease in all freshwater species and the increase of many terrestrial snail species. Notably higher amounts of *Cochlicopa lubrica*, *Perpolita hammonis* (at the upper part of the zone), and *Oxyloma elegans* confirmed an increase of nutrients and food sources, probably caused by a decrease in the water table. A rich population of *Vallonia pulchella* indicates a continued fully open character of the site.

Figure 8.: Mollusc diagram from the Miroľa site in absolute numbers.



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

Discussion

Landscape structure transformation – consequences of human impact or climatic change?

Reduction of ancient forests

The reduction of ancient forests and the spread of meadow species and anthropogenic indicators are the main features of the analysed pollen records. The development of both study fens started when natural fir–beech forests with an admixture of *Quercus*, *Betula*, *Tilia*, and *Carpinus* (Miroľa site) and fir–spruce forests with a low admixture of *Fagus* (Roškovce site) dominated the landscape. The understorey of these forests was probably rich in ferns (see also Jankovská, 1995; Rybníček and Rybníčková, 2008). A reduction in dominant trees caused an increase in light-demanding trees (*Quercus* and *Betula* at Roškovce site; *Pinus, Larix* and *Betula* at Miroľa site) as well as *Salix, Fraxinus,* and *Populus,* which tolerate periodic inundation (Wacnik, 1995). Our study, however, captures only the last phase of the development of natural fir–beech and fir–spruce forests. Other studies documented that these forests started to spread to the Lower Beskids region during the Subatlantic period (ca. 2500 cal BP; Krippel, 1971; Ralska-Jasiewiczowa, 1980; Tasenkević and Bezusko, 1982; Rybníček and Rybníčková, 1995; Wacnik, 1995, 2001; Szczepanek, 2001; Margielewski et al., 2010). Their reduction began in the Middle Ages as a consequence of the Wallachian colonisation (since the 13th century AD) when the settlement penetrated the Carpathians (Wacnik, 1995, 2001; Szczepanek, 2001; Margielewski et al., 2010), as we demonstrated in this study. The first decline of *Abies* and *Fagus* at the Miroľa site dates to the 15th century; the second occurred around the landslide at the end of 17th century. Such a decline (*Abies* and *Picea*) happened in the Roškovce site during the 18th century.

According to both pollen diagrams the woodland was transformed into arable land and grasslands (pastures and meadows), so we assume that human impact was the driving factor behind this significant landscape transformation.

Changing human impact

The relative representation of anthropogenic indicators (both for grazing and for crop cultivation) and forest trees has fluctuated since the beginning of organic accumulation (10th–14th century AD). Such changes were generally caused by fluctuating population density (Yeloff and van Geel, 2007; van Hoof et al., 2006), which were induced either by climatic or socioeconomic and political changes. These two factors may interact, as deterioration of climate often coincides with political conflicts and plague outbreaks (Yeloff and van Gell, 2007; Büntgen et al., 2013; Pfister and Brázdil, 2006). A long wet period during the harvest and a dry or cold spring might have a devastating impact on crop cultivation and lead to an agriculture economy crisis (Pfister and Brázdil, 2006; Možný et al., 2012). In order to explain the fluctuations in the agriculture intensity in our study area, we interconnected available data on political history, population density, and climate with our pollen records.

At the Miroľa site, the first deforestation took place in the 15th century. Extension of crop cultivation and grazing were recorded at both study sites even though this period was characterised by climate deterioration (Little Ice Age (LIA); Büntgen et al., 2013), which generally restricted crop cultivation. Intensive agriculture at both sites was probably connected with the colonization of mountain areas (Žadanský, 2002; Pop, 2010; Rábik, 2012). The second deforestation at the Miroľa site was indicated in the zone affected by the landslide. It was again synchronous with intensification of agricultural activities. At the same time, around 1661 AD, frequent floods were recorded in the study region (Stankoviansky and Pišút, 2011). That period falls within the coldest phase of the LIA (Maunder Minimum 1645–1715 AD; Luterbacher et al.¨, 2001), which was characterised by climate extremes (Büntgen et al., 2013).

Crop cultivation at the Miroľa site was later interrupted, likely due to the Kuruc uprising from 1678–1711 AD and the subsequent abandonment of villages from 1713–1714 AD (Kropilák et al., 1977). After the cold spells, rather positive temperature trends were reported during the 18th and 19th centuries (Büntgen et al., 2013), but crop cultivation at the Miroľa site has not recovered. But at the Roškovce site, the warm period coincided with land-use intensification and rapid deforestation in the second half of the 18th century. Coprophilous fungi (*Podospora* and *Sporormiella*) were recorded at that time, implying intensive cattle grazing directly on the study site. In the first half of the 19th century, a cholera epidemic (1830 AD) and drought followed by famine (1852 AD) afflicted the region (Anonymous, 2011; Büntgen et al., 2010), which led to a deterioration in the social situation and to the emigration of inhabitants in the region (Kropilák et al., 1977; Majo, 2012; Pop, 2010). These events are reflected in the profile by the interrupted curve of Cerealia pollen and by the peak of *Secale*, which is rather drought-tolerant (Murphy, 2007).

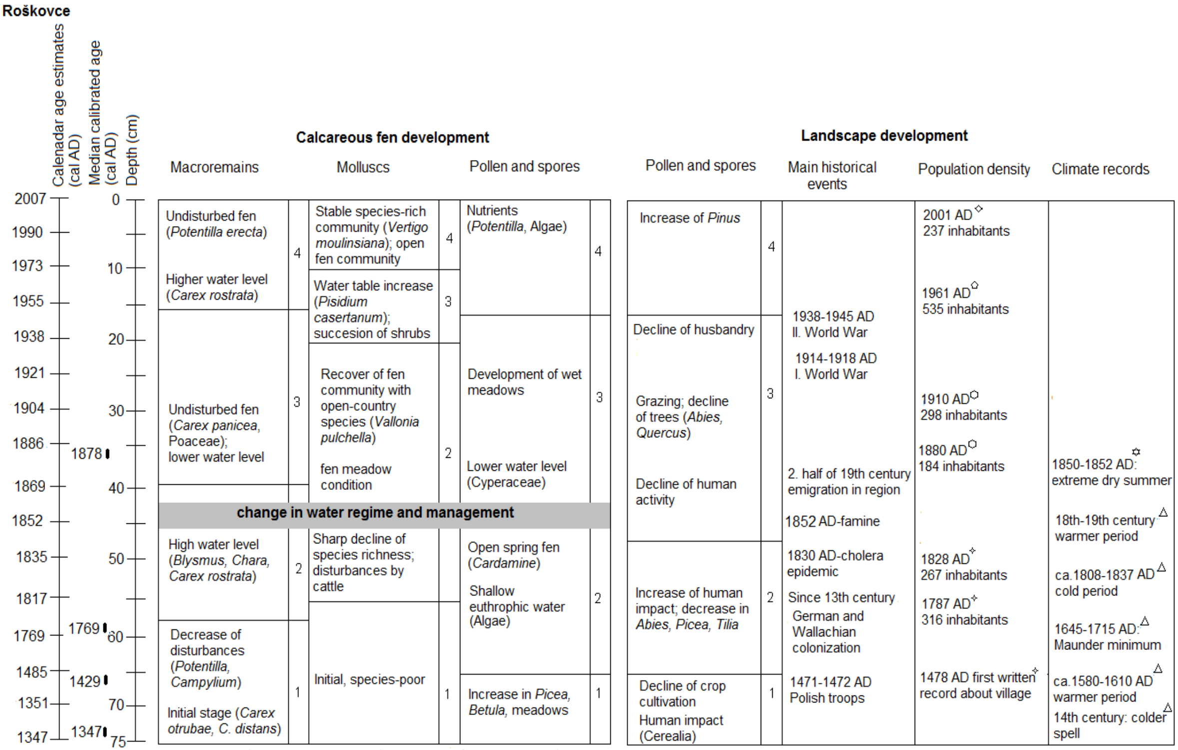
The last period of intensified agricultural activity started at the end of the 19th century at both sites and coincides clearly with an increase in population density (Kropilák et al., 1977; Majo, 2012). The amount of cereals (and later pasture indicators) decreased towards the uppermost layers while meadow indicators (Rubiaceae, *Potentilla* t., *Filipendula*) increased slightly as a result of the grazing reduction in the last few decades.

Our study demonstrates that fluctuation of agriculture intensity is not conditioned only by climatic changes, but also reflects political events such as the Kuruc uprising and colonisation or emigration waves.

Local development of spring fen

Both fens originated as open habitats after deforestation during the late Middle Ages. Deforestation generally increased the area of open habitats and led to increased rates of rainwater infiltration, decreased evapotranspiration, and ultimately resulted in a greater groundwater discharge (Jaworski, 1994; Lamentowicz et al., 2007). Because the accumulation of fen deposits started in particular profiles in different climatic periods (Miroľa in the Medieval Warm Period: MWP, 950–1250 AD; Roškovce in the Little Ice Age: LIA, 1300–1850 AD; Lamb, 1965; Matthews and Briffa, 2005), we conclude that climate did not trigger the fen initiation. Flysch bedrock with alternating sandstone and claystone is characterised by frequent landslides, which are important in the emergence of springs.

Figure 9.: Summarised development of regional and local vegetation of the Roškovce site based on all obtained proxies.



Sources: ✧Kropilák et al. (1977) ○ Majo (2012) ⌂ Kačur (2008) ◇ http://app.statistics.sk/mosmis/sk/run.html
✡Büntgen et al. (2010) △Büntgen et al. (2013)

A frequent spring-fen emergence after landscape deforestation was documented in the Western Carpathian flysch zone (Hájková et al., 2012), where many springs already existed in forests; these became spring fens after deforestation (Rybníčková et al., 2005; Hájek et al., 2011; Hájková et al., 2012).

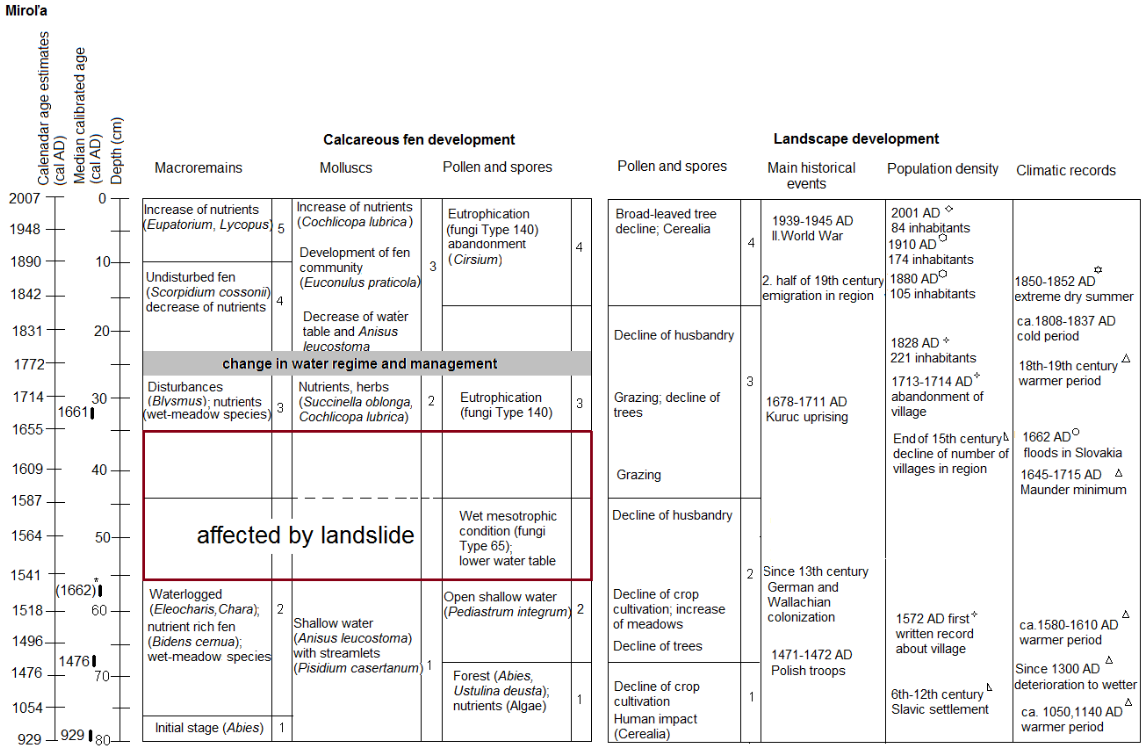
After the initial phase, the first important change indicated by local proxies was probably connected with the change in hydrological conditions. The increase of groundwater discharge, indicated by macrofossils (e.g., *Chara vulgaris*), desmids, diatoms, and green algae (*Zygnema*, *Spirogyra*, *Mougeotia*), was recorded at the Roškovce site (65–40 cm, ca. 1485–

1869 AD). Such a hydrological change could be caused by continuing deforestation as a consequence of increasing human population density in the region since the 15th century AD (Uličný, 1990, 2001; Rábik, 2012) and is well traced in pollen records as well. By contrast, the groundwater level was high already from the beginning of the Miroľa fen development, as indicated by the presence of hygrophilous molluscs. The small clam *Pisidium casertanum* and the plant *Glyceria nemoralis* indicate streamlets with running water. Later, small shallow pools with *Pediastrum integrum* appeared. Their nutrient-rich conditions are indicated by *Bidens cernua*, today a species of nutrient-rich fishponds and their summer-dried bottoms (Šumberová and Lososová, 2011). The 57–30 cm layer was most probably affected by a landslide, making the interpretation of this part of the profile difficult. The deposits in this layer were probably partially mixed, as suggested by the same radiocarbon age obtained from seeds at 32–30 cm (1662 AD) and at 57–55 cm (1661 AD). On the other hand, macrofossil change seems to be gradual. Local proxies indicate high nutrient supply by the presence of fungal ascospores Type 140, the land snail *Succinella oblonga,* and wet meadow plant species. *Blysmus compressus* indicates disturbed wet patches.

At both sites, the fen development terminated with undisturbed calcareous fen communities of both plants and molluscs that require a stable high water level near the fen surface and rather low nutrient content. This shift to undisturbed fen dates to the second half of 19th century at the Roškovce site and to the second half of 17th century at the Miroľa site. It was most likely triggered by the decline in grazing. It correlated with the population decline after the famine and cholera epidemic in Roškovce (Anonymous, 2011) and after the landslide and Kuruc uprising in Miroľa. A decrease in grazing activity is a complex factor involving both a lower nutrient supply and a lower level of disturbance. It can be followed by disappearance of open-water patches and by accelerated vegetation succession. In Miroľa, grazing cessation is reflected in changes in the bryophyte layer (the fen specialist *Scorpidium cossonii* started to dominate), the dominance of *Cyperaceae,* and the decline of nutrient-demanding wet-meadow species (e.g., *Calliergonella cuspidata* and *Scirpus sylvaticus*). In Roškovce, *Potentilla erecta*, Poaceae, and *Carex panicea* increased, and *Chara vulgaris* disappeared.

The sub-recent changes at the Roškovce site involved an increase in water level (indicated by *Zygnema, Equisetum, Sparganium* t., and *Pisidium casertanum*) and shrub encroachment indicated by the snail *Merdigera obscura*. Increasing productivity and nutrient availability, indicated by the snail *Cochlicopa lubrica* and the herbs *Eupatorium* and *Lycopus,* can be traced in the Miroľa fen. These sub-recent changes can be explained, in both sites, by the abandonment of fens and surrounding grasslands. Nevertheless, both sites are recently mown by nature conservancy authorities and host bryophyte, vascular plant, and mollusc communities rich in fen specialists.

Figure 10.: Summarised development of regional and local vegetation of the Miroľa site based on all obtained proxies.



Sources: ᐞRábik (2012) ✧Kropilák et al. (1977) ○ Majo (2012) ◇ http://app.statistics.sk/mosmis/sk/run.html
○Stankoviansky and Pišút (2011) △Büntgen et al.(2013)

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

Implication for conservation policy

Palaeoecological research can enlarge the knowledge obtained from short-term management experiments and thus may help to assess the most appropriate conservation management. Our research has shown that even though the vegetation disturbed by grazing was rather species-rich, it did not contain rich mollusc communities and recently endangered vascular plant species, including *Carex diandra*, the most endangered species present in a recent community. This accords with studies reporting sensitivity of snail communities to intensive grazing (Ausden et al., 2005). The endangered snail *Vertigo moulinsiana*, whose density has been substantially reduced by grazing according to Ausden et al. (2005), has appeared in the

Roškovce fen only after grazing cessation. On the other hand, we found that disturbed fens provide suitable conditions for *Blysmus compressus,* a species becoming rare because of abandonment of the use of fens. Nevertheless, we cannot exactly assess the intensity and dynamics of past disturbances. It seems that at the Miroľa site, intensive grazing led to the occurrence of the generalist plants *Bidens* and *Eleocharis,* indicating nutrient-rich, strongly disturbed wetlands rather than fens. Less grazing intensity led to the dominance of the fen specialists *Blysmus compressus, Scorpidium cossonii*, and *Campylium stellatum* and to enhanced bryophyte diversity. At the Roškovce site, moderate grazing indicated by coprophilous fungi led to the occurrence of some fen specialists tolerating disturbances (*Blysmus compressus*, *Campylium stellatum*). On the contrary, absence of management can strongly suppress light-demanding bryophyte species (cf. Hájková et al., 2009). This process probably happened at the Roškovce site, where upper fen layers are conspicuously poorer in bryophyte species as compared to deeper ones. The sub-recent changes were probably triggered by management cessation in the second half of 20th century, which led to shrub encroachment and increasing productivity because of a lack of disturbance and nutrient export (Güssewell et al., 1998; Diemer et al., 2001; Hájková et al., 2009). The described development illustrates how man-made spring fens, which are important present-day refugia of endangered wetland species, are maintained by a moderate management rather than abandonment or intensive grazing. Generally, these ecosystems are sensitive to changes in management practice and most cannot exist at all without some form of management, especially the small ones that developed at low-productive aquifers of the flysh bedrock (Hájek et al., 2008).

Acknowledgements

We are grateful to Barbora Pelánková for help with the profile samplings and to Zuzana Formánková for laboratory work. We would like to thank Pim van der Knaap and anonymous reviewer for useful critical comments and suggestion on the manuscript. The research was supported by the grant project GAČR P504/11/0429, institutional support of Masaryk University, and the long-term research development project no. RVO 67985939.

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Conclusions

Detailed conclusions are presented in the individual chapters. In summary, the aims of this thesis were threefold: (i) to trace the history of human habitation in pollen spectra from different types of natural archives; (ii) to distinguish between changes in landscape cover and vegetation structure driven by natural factors (climate change, fire) and those driven by anthropogenic impact; (iii) to find out whether and how past human activities contributed to the origin, persistence and survival of different types of (semi-)open habitats.

The thesis presents new original data mainly from the transitional zone of the Western Carpathians and the northern part of the Pannonian plain, which is an important area between two contrasting phytogeographical zones, but almost without any palaeoecological studies performed in recent years.

Pollen records from different types of mostly small-sized sites very well reflect settlement dynamics, historical events and changes in settlement density. Detailed analysis of human impact traced by pollen indicators yields valuable information about (pre-)historic landscape occupation, mainly in regions that have otherwise been poorly addressed by archaeological and historical research.

A comparison of various palaeoecological data (pollen analysis, plant and mollusc macro-remains, anthracology, and lithology) with archaeological and historical sources shows that natural agents (climate, fire, grazing of large herbivore) had a decisive role in vegetation changes until the Middle Holocene (ca. 7500 cal BP), when human activities started to more influence the vegetation and landscape cover.

Our study of prehistoric human impact on vegetation cover confirms the assumption that traces of Neolithic human influence are nearly undetectable in pollen profiles. Some of the results might nevertheless be seen as indirect evidence pointing to the impact of humans on the local landscape and vegetation: higher amounts of charcoal particles, spread of light-demanding shrubs or development of different types of grasslands (pastures and meadows).

It turns out that the presence of humans in the landscape sustained and supported the spread of various types of (semi-)open habitats: open oak woodlands, dry grasslands, steppes, calcareous fens and wetlands, which would probably not have survived the Middle Holocene expansion of shade-tolerant trees without disturbances. During the Middle Holocene, there was a critical bottleneck period (ca. 3700 cal BP) for the survival of light-demanding species in the region at the Pannonian-Carpathian boundary. It was most probably connected with increasing human pressure on the landscape.

Changes in medieval woodland management dramatically influenced the species composition of the subcontinental oakwood Dúbrava and contributed to the persistence of its unique vegetation composition.

Man-made deforestation of mountain landscapes over the last millennia contributed to the formation of numerous spring fens, which today harbour various endangered light-demanding species.

Our detailed assessment of evidence of past human activities in the pollen records has improved our knowledge about the origin, continuity, survival and persistence of heliophilous species and (semi-)open habitats. This knowledge could be later used for conservation efforts.

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Curriculum vitae

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Education

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- 2005–2009: PhD. degree, Department of Natural Sciences, The Constantine Philosopher University in Nitra, Slovakia, in: Environmentalistic, Conservation and Land-use (Thesis: *Selected landscape properties as settlement factors in Nitra region during the Neolithic, Eneoltihc (Late Neolithic) and the Bronze Age*).
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Abroad stays

- 3–4/2010: Institute of Plant Science, University of Bern, Switzerland
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Grant projects

Researcher:

- 2008-2012: Lowland woodland in the perspective of historical development (GAAV ČR IAA600050812). Project leader: Radim Hédl

- 2008-2011: Origin and development of the Western Carpathian calcareous-fens and their biota: the question of glacial relicts and refuges (GAAV ČR KJB601630803). Project leader: Michal Horsák
- 2011-2015: Environmental gradients, vegetation dynamics and landscape changes in the West Carpathians from the Late Glacial up to the present time (GAČR P504/11/0429). Project leader: Petra Hájková
- 2012-2016: Long-term woodland dynamics in Central Europe: from estimations to a realistic model (European Research Council (XE) FP7/2007-2013 ERC Grant agreement no. 278065). Project leader: Péter Szabó
- 2012-2015: Pollen-based land-cover reconstruction - model testing and its implications for Holocene environmental change studies **(**GA ČR P504/12/0649) Project leader: Petr Kuneš.

Publication activity

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Articles in peer reviewed journals

1. Hájek M, Horsák M, Tichý L, Hájková P, Dítě D, **Jamrichová E** (2010) Testing a relict distributional pattern of fen plants and terrestrial snail species at Holocene scale: a null model approach. *Journal of Biogeography,* 38: 742 – 755.
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(presenting author is underlined, P-poster, T-talk)

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Courses and workshop participation

- Workshop: Soil Micromorphology in General and Archaeological Context, January 2014, Brno, Czech Republic
- Workshop: The Theory of Pollen Analysis and Landscape Reconstruction Algorithm, February 2015, Czech Republic.
- Wood and Wood charcoal Analysis, February 2015, České Budějovice, Czech Republic.
- Summer school: COST-INTIMATE 2nd Training and Research School in Paleoclimatology, June 2013, Baile Tusnad, Romania.

Others

- 2011: Poster award: Eva Jamrichová, Szabo P, Hédl R, Kuneš P, Pelanková B: The role of management in the establishment of European oakwoods Frontiers in Historical Ecology, Birmensdorf, Switzerland.

Appendices

Hájková P., Jamrichová E., Horsák M. & Hájek M. (2013): Holocene history of a Cladium mariscus-dominated calcareous fen in Slovakia: vegetation stability and landscape development. Preslia 85: 289–315.

Appendix 1: Classification of pollen taxa into groups used in synoptic diagram. Pollen taxa follow Beug (2004). Footnotes are listed below the table.

Forests and shrub habitats	
Wet	Alnus, Salix, Fraxinus, Populus, Frangula
Dry	other trees and herb pollen types of forest understory (Corydalis cava t., Anemone nemorosa, Allium ursinum t.)
Open habitats	
Indiferent ecology (i.e., collective taxa)	Rubiaceae, Senecio t., Cirsium, Asteraceae-Cichoriodae, Potentilla t., Cyperaceae, Poaceae[1], Geranium, Matricaria t., Anagallis t., Brassicaceae, Vicia t., Rosaceae undif., Apiaceaea undif., Cannabinaceae, Empetraceae, Petasites
Wet and alluvial grasslands[2]	Caltha t., Filipendula[3], Chaerophyllum hirsutum t., Mentha t., Valeriana officinalis t., Lysimachia vulgaris t., Polygonum bistorta t., Gentiana pneumonanthe t. [4]., Trifolium badium t., Thalictrum flavum t., Sanguisorba officinalis, Ophioglossum, Primula farinosa t. [5], Peucedanum palustre t.
Steppes, semi-dry grasslands[6]	Artemisia, Ephedra distachya t., Jasione montana t., Orlaya grandiflora t., Cephalaria, Falcaria vulgaris t., Gypsophilla repens t. [7], Bupleurum falcatum g., Peucedanum carvifolia g., Plantago media/major[8], Salvia pratensis t., Centaurea scabiosa t., Verbascum, Teucrium chamaedrys t., Scabiosa, Lotus t. [9]
Mesic managed grasslands	Plantago lanceolata t., Rumex acetosa t., Trifolium pratense t., Centaurea jacea t., Trifolium repens t., Ranunculus acris t., Daucus carota t., Pimpinella major t., Rhinanthus t., Cerastium t., Heracleum sphondylium t.
Open-country ruderals	Chenopodiaceae[10], Eryngium campestre t., Linaria t., Ornithogalum umbellatum t., Solanum nigrum t., Polygonum aviculare t., Calystegia
Shade-tolerant ruderals[11]	Ballota t., Anthriscus cerefolium t., A. caucalis t., Chelidonium majus, Urtica, Anthriscus sylvestris t., Bidens, Persicaria maculosa t., Solanum dulcamara
Crops	Triticum t., Hordeum t., Secale, Fagopyrum
Wetlands[12]	Cyperaceae, Cladium mariscus[13], Oenanthe aquatica g., Sparganium t., Potamogeton/Triglochin, Callitriche, Alisma t., Lemna

Comments

[1] used as grassland indicator in some studies; may, however, include species of open oak forests at the Pannonian-Carpathian boundary and Early Holocene hemi-boreal forests (e.g., *Brachypodium pinnatum, Calamagrostis arundinacea* and *Melica* sp. div.)

[2] This group includes species which are diagnostic of mown wet grasslands of the *Calthion, Molinion* and *Deschampsion* alliances (Janišová et al. 2007), most of them have optimum in the *Calthion* alliance. This group includes also tall-herb species which grow in wet-meadow fallows dominated by *Filipendula ulmaria*. Analogous tall-herb habitats occurred in Early Holocene, what may explain the occurrence of this group in that period.

[3] This type comprises not only *F. ulmaria*, but also *F. vulgaris*. The latter species occur in semi-dry grasslands, but may grow also in wet *Molinion* grasslands. Because of a correlation between *Filipendula* peak and peaks of clear wet-meadow species, we classified this pollen type into this group.

[4] This type includes, from the relevant species, not only *Gentiana pneumonanthe*, but also *G. cruciata* and all Slovak *Centaurium* species. The latter species might occur also in semi-dry grasslands in the study region. We classified this type into wet grassland indicators because of correlation with other wet-grassland species. Anyway, no interpretations would change when this type will be classified within dry grasslands.

[5] This pollen type may include also *Cortusa mathiolii* and *Primula stricta*. Occurrence of *Cortusa mathiolii* at the study site is not probable because of specific ecological demands of this species (limestone rocks in high mountains or gorges). Similar, *Primula stricta* recently grows only in North Europe and its ecology is different (sand dunes, shore cliffs).

[6] This group includes true and salty steppes (*Artemisia* and *Ephedra*), whose prevalence is expected at the onset of the Holocene, as well as semi-dry grasslands (so called *meadow steppe*) which is recently largely managed by mowing or mild grazing. This group thus includes the classified which are considered as diagnostic of the *Bromion erecti* and *Cirsio-Brachypodion pinnati* alliances (Janišová et al. 2007).

[7] Includes *Gypsophila fastigiata*, recently rare species of dry grasslands and open pine forests.

[8] We are aware that this type includes not only *P. media*, but also *P. major*, however, both indicate non-forest habitats. Because of a correlation with a peak of dry-grassland species, we classified into this group.

[9] Lotus type is problematic to classify, because the most common species in the study area, *Lotus corniculatus*, is common in both, semi-dry and mesic managed grasslands. The group may futher include *L. angustissimus*, which occur in dry and halophytic grasslands in Hungary. Because of the occurrence in the Early Holocene, we included it into the group of semi-dry grasslands in order to avoid confusion associated with the existence of managed grasslands in that period. Anyway, its peak in Late Holocene was probably partially caused by extension of mesic maganed grasslands.

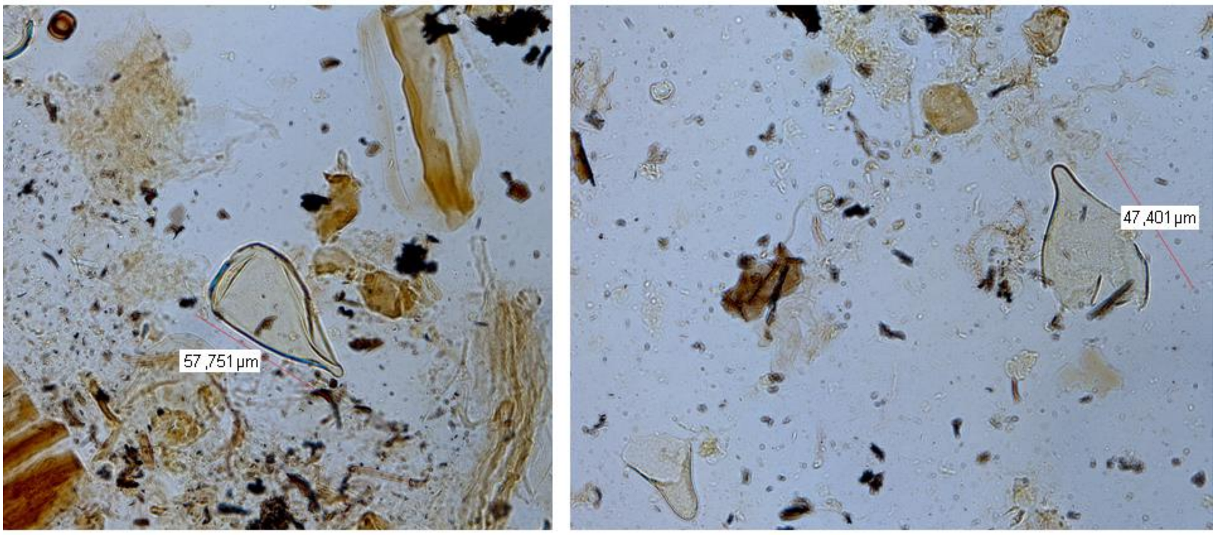
[10] Magyari et al. (2010) consider this type as steppe indicator; in our case caution is needed because of fossil seeds of *Chenopodium album* found in the profile.

[11] This group includes, for the sake of simplification, both drought- and warm-demanding and moist-demanding species. Both these groups inhabit abandoned grasslands and fields, margins of field tracks and intensively grazed places. The former group (*Ballota, Anthriscus cereifolius* and *A. caucalis*) further inhabits shrubs and disturbed forests with *Robinia* (an invasive species), *Quercus* or *Carpinus* at dry slopes of low altitudes, while other species may inhabit alluvial *Alnus* forests and surroundings of manure deposits.

[12] This group is excluded from Total Pollen Sum

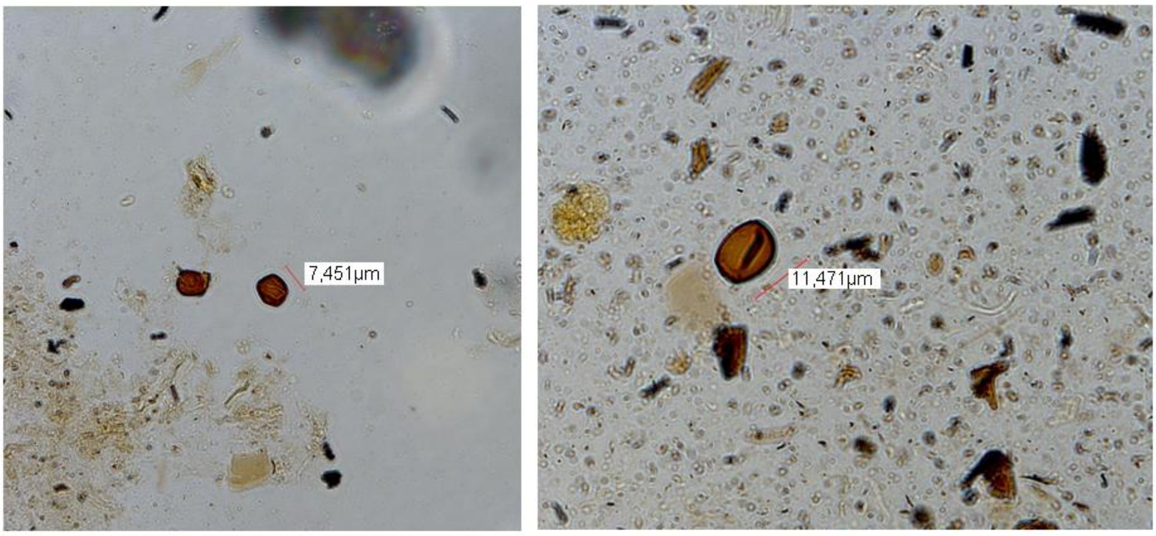
[13] *Cladium mariscus* pollen was distinguished from other Cyperaceae pollen by the presence of a finger-like projection on the apical side of a pollen grain. However, similar characters (transitional to those observed for *Cladium*) can be found on other Cyperaceae pollen, only pollen grains with clear and significant projection were identified as *Cladium mariscus*. For photographic documentation see Electronic Appendix 3.

Appendix 2: Photo documentation of *Cladium mariscus* pollen



Pollen grains of *Cladium mariscus* (magnification 400x)

Appendix 3: Photo documentation of *Sporormiella* t. spores



Spores of *Sporormiella* (magnification 400x)