The origin of grasslands in the temperate forest zone of east-central Europe: long-term legacy of climate and human impact

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Abstract

The post-glacial fate of central European grasslands has stimulated palaeoecological debates for a century. Some argued for the continuous survival of open land, while others claimed that closed forest had developed during the Middle Holocene. The reasons behind stability or changes in the proportion of open land are also unclear. We aim to reconstruct regional vegetation openness and test the effects of climate and human impact on vegetation change throughout the Holocene. We present a newly dated pollen record from north-western fringes of the Pannonian Plain, east-central Europe, and reconstruct Holocene regional vegetation development by the REVEALS model for 27 pollen-equivalent taxa. Estimated vegetation is correlated in the same area with a human activity model based on all available archaeological information and a macrophysical climate model. The palaeovegetation record indicates the continuous presence of open land throughout the Holocene. Grasslands and open woodlands were probably maintained by local arid climatic conditions during the early Holocene delaying the spread of deciduous (oak) forests. Significantly detectable human-made landscape transformation started only after 2000 BC. Our analyses suggest that Neolithic people spread into a landscape that was already open. Humans probably contributed to the spread of oak, and influenced the dynamics of hazel and hornbeam.

Keywords

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1 Introduction

Early Holocene climate changes triggered major ecosystem changes resulting in the spread of trees in northern latitudes. In Central Europe, temperate deciduous trees are believed to have eventually formed forests (although the structure of these forests has been long subject to a heated scientific debate e.g., Vera, 2000; Birks, 2005; Mitchell, 2005). Along with this natural process, people started to intensively shape the landscape as agricultural practises expanded in the Neolithic.

In the lowlands of east-central Europe open vegetation currently represents an abundant habitat type harbouring many grassland plant taxa (Chytrý, 2010). The fate of these taxa in the Late Quaternary has puzzled scientists for many decades. The crucial question is how grassland taxa survived in the developing forests of the early Holocene (Gradmann, 1933; Ložek, 1971, 2011; Vera, 2000; Magyari et al., 2010; Hejcman et al., 2013). There appears to be evidence that in some regions wooded steppe persisted until (and therefore predates) the adoption of sedentary lifestyle and agriculture in the Neolithic. For example in the heart of the Pannonian Plain such open spaces created an important baseline for the expansion of Neolithic farming communities (Járai-Komlódi, 1968; Havinga, 1972; Magyari et al., 2010), whose vegetation management was difficult to detect by classical palaeoecological methods (Willis & Bennett, 1994; Magyari et al., 2012). However, in other regions such continuity of open habitats is less known and more debatable. In the north-western outcrops of the Pannonian Plain, where steppe communities occur at present, the results of several pollen records allowed for the possibility of the existence of species-rich steppes from the last glacial interstadial 1 (GI-1; 14 ka) until the Neolithic (7.5 ka BP; Svobodová, 1989, 1997), but other authors argued for the continuous afforestation of the region in the same period (Rybníčková & Rybníček, 1972).

To gain solid knowledge on the origins of grasslands and to disentangle the factors driving long-term changes or stability, one needs information on past vegetation, climate and human activities. However, each information type presents its own methodological challenges and interpreting the results in an interdisciplinary framework adds further complexity to the analysis. Data on past vegetation is usually derived from pollen. However, it is rather problematic to realistically reconstruct the proportion of open land based solely on pollen percentages (Sugita, 2007a; Gaillard et al., 2010; Kuneš et al., 2011). Quantitative vegetation reconstruction based on the understanding of pollen production and dispersal can remedy this problem. Recent model calibrations allow researchers to obtain robust reconstructions of past land cover, especially as regards the ratio of forest and open land (Hellman et al., 2008; Mazier et al., 2012; Abraham et al., 2014).

Climatic conditions and various types of activities by human populations are considered to be important factors shaping vegetation and maintaining open land (Mercuri et al., 2011; Connor et al., 2013; Feurdean et al., 2015). Climate models were shown to be important for the evaluation of past vegetation patterns (Gaillard et al., 2010; Pielke et al., 2011), however, for local studies climate patterns based on Global or Regional Climate Models (Strandberg et al., 2014) do not provide the desired site-specific spatial resolution. As an alternative,

several studies used site-specific, locally calibrated climate models (Bryson, 2005), which provided 100-year time resolution (Higgins & MacFadden, 2009; Riehl et al., 2009). As far as human activities are concerned, different models of population densities for particular time periods emerged with the help of archaeological and historical data (Pongratz et al., 2008; Kaplan et al., 2009; Gaillard et al., 2010; Shennan et al., 2013). Nevertheless, such models concerned continental to global scales and are much too coarse to be meaningfully applied on a regional scale. There are ongoing efforts to reconstruct prehistoric regional population dynamics with the help of 14C dating (e.g., Whitehouse et al., 2014; Hinz et al., 2012; Shennan et al., 2013; Lechterbeck et al., 2014). Unfortunately, there are several problematic issues connected to these procedures indicating that the results can be biased by several factors, such as sampling strategies including site density (Mercuri, 2014), period preferences or changes in mobility and subsistence strategies (Contreras & Meadows, 2014; Crombé & Robinson, 2014). To derive more exact information on regional, archaeologically reflected human activities in a long-term perspective, a model based on a detailed and complete archaeological survey is essential.

In this study we combine three models to reconstruct Holocene vegetation dynamics in a spatially defined area. Firstly, we use the pollen record from the extinct Lake Vracov, situated in the north-western part of the Pannonian Plain, to create a REVEALS vegetation model of the area. Secondly, we review all existing excavation reports to gather information on the location, dating and identified activities of the archaeological sites and finds of the same area to produce reliable estimates of human occupancy through a Monte Carlo simulation-based model. Thirdly, we use a macrophysical climate model for the area as an independent data source of past climate. We address the following questions: i) What was the extent of open land since the beginning of the Holocene and did grassland vegetation persist until anthropogenic deforestation? ii) How did vegetation respond to climate changes in the area? iii) Can we track specific patterns in human-vegetation interactions?

2 Material and methods

2.1 Site description

The extinct Lake Vracov, nowadays transformed into a fishpond, is located on the Bzenecký brook in the floodplains of the Morava river in the north-western part of the Pannonian Plain (Fig. 1) in the Czech Republic. The area is formed by Upper Quaternary deposits of blown sands and loess with chernozem underlain by Neogene and Pliocene brackish and freshwater sediments. The high content of calcium and magnesium in these deposits created higher salinity in the water of the lake. To be able to compare vegetation, climate and human occupancy, an area of 25 km around the lake was selected (Fig. 1). This study area comprises the Outer Western Carpathians and vales along the Morava river. Lowlands along the Morava river lie between 150 and 275 m a.s.l. and are framed by 30 m high terraces covered by eolic loess. Vast areas of eolic sands with dunes of 13 m height occur on the right side of the Morava river between Vracov and Hodonín (Havlí ek & Zeman, 1986). The northern part of the area is bordered by the hills of Ždánice Forest and Ch iby, while the south-eastern edge is formed by the White Carpathians (Czudek, 1972).

2.2 Present-day vegetation

The lowlands of the Morava river host riverine forests, meadows, mires and sand steppes. The riverine forests are influenced by the Carpathian mesophyticum and consist of *Ulmenion* with *Fraxinus* species (Chytrý, 2013). In drier places at upper elevations *Carpinus betulus* and *Acer campestre* are frequent. Alder carrs with dominant *Alnus glutinosa* are not very common. Acidophilous oak or hornbeam-oak forests occur on sandy soils and were partly changed to semi-natural pine forests. On smaller patches, willow carrs with *Salix cinerea, S.aurita* and *Betula pubescens* developed. Sand steppes are represented by *Corynephorus canescens*, *Filago arvensis*, *F. minima*, *Plantago psyllium*, *Spergula pentandra*, *Veronica dillenii*, *Linaria genistifolia*, *Thymus serpyllum* and *Armeria elongata* (Chytrý, 2010). The vegetation of the hills (Ch iby and Ždánice forest) belongs to the supracolline or montane belts with beech or oak-hornbeam forests. In the south and south-west, forest vegetation mixes with the xerothermic flora of the Pannonian thermophyticum.

The largest part of the landscape consists of agricultural land (European Environmental Agency, 2013). According to potential natural vegetation maps (Bohn et al., 2000), the study area lies within the range of the occurrence of Pannonian lowland mixed pedunculate oak forests (Fig. 1). The vegetation of these forests co-occurs with dry grasslands (*Festuca rupicola*) and scrubs (*Prunus fruticosa, P. tenella*) as well as with sand steppes (Chytrý, 2010). Links of this unit with other semi-open and open vegetation further to the east are illustrated in Fig. 1.

2.3 Palaeovegetation data and model

The pollen record originated from sediments of the extinct Lake Vracov, which had been created by a dam formed by late-glacial fluvial and eolian processes (Havlí ek et al., 1995). The initial mineral sedimentation changed to organogenic accumulation of algal gyttja at the beginning of the Holocene. Open water lake surface existed until the Middle Holocene when partial terrestrialization started as documented by layers of mosses and sedge-moss communities (Rybní ková & Rybní ek, 1972; Rybní ek, 1983; Svobodová, 1997). The lake basin was drained one hundred years ago. Sediments were sampled from the bottom of the drained lake by Kamil Rybní ek in 1967. Altogether ca. 80 profiles were taken for the purpose of pollen or macroremains analyses. Three profiles were earlier analysed for pollen: DU-1-B (Rybní ková & Rybní ek, 1972), DU-7-K (Sládková-Hynková, 1974) and DU-7-D (Svobodová, 1997). Plant macroremains were analysed in only one profile (DU-1-B) (Rybní ková & Rybní ek, 1972; Rybní ek, 1983). In this study we used the DU-7-D pollen profile from the central part of the extinct lake, which is accessible in the Czech Pollen Database (Kuneš et al., 2009). We newly obtained material for dating from the stored profile.

The pollen diagram (see Supplementary Fig. 1) was newly zoned using optimal splitting by sum of squares in Psimpoll v. 4.26 (Bennett, 2009). All terrestrial pollen was included in the zonation. Significant zones were delimited by comparison with broken-stick model (Bennett, 1996).

Vracov was a medium sized lake (22 ha) and studies have shown that such a lake realistically portraits regional vegetation (Mazier et al., 2012; Abraham et al., 2014). To

estimate regional vegetation composition, which in turn enabled us to determine the ratio of forest and open land, the REVEALS model (Sugita, 2007b) was applied to the original pollen counts for 500-year intervals. Altogether 27 taxa were selected (Table 1) for which relative pollen productivities, one of the most important model input parameters, were available and tested for the region (Abraham & Kozáková, 2012; Abraham et al., 2014). Other parameters included the fall speed of pollen (Table 1) and wind speed, which was set according to average measured values to 4 m/s. The spatial extent of the region (Zmax) was set to 25 km, which is consistent with the size of the lake and previous simulations (Hellman et al., 2008; Abraham et al., 2014). The Sugita dispersal/depositional lake model (Sugita, 1993) was used to calculate regional vegetation composition (Sugita, 2007b). Calculations were made in R (Abraham et al., 2014; R Core Team, 2014). The REVEALS model does not consider any vegetation growing within the sedimentation basin. As the Vracov site represents a shallow lake, considerable amounts of vegetation could be producing pollen in the littoral part of the lake. We tried to avoid this problem and thus improve the estimates of regional open land by differentiating *Phragmites* during pollen analysis and excluding Cyperaceae from the model.

2.4 Archaeological data and human activity model

Prehistoric human activities included a diverse range of practices, such as dwelling, burying, building and using hillforts and enclosures, pasture, agriculture, mining, ritual practices, travelling, trade and exchange, tree felling, foraging and hunting. However, only some of these activities are detectable in the archaeological record. From existing excavation reports, published reports and other grey literature we excerpted information on the location, dating and identified human activities of the archaeological sites and finds from the same region as was used for calculating the REVEALS model. We included in the analysis every civil parish which at least partly belonged to the 25 km buffer zone around the lake (Fig. 1). In total 212 parishes were included in the study. Archaeological data were collected from three main sources: unpublished excavation reports stored at the archive of the Institute of Archaeology, Czech Academy of Sciences, Brno; published short reports of the Institute of Archaeological Heritage Management Brno (Čižmář et al., 2000; Čižmář & Geislerová, 2006), and finally published topographic summaries with archaeological survey results from the vicinity of the early medieval centre at Mikulčice (Poláček, 1997, 1998, 1999, 2005). The main analytical unit was the archaeological component, which is defined as a spatially continuous set of finds delineated by their function (e. g. residential) and chronological position (e. g. Early Bronze Age). Thus a typical archaeological component in our analysis could be for example the Neolithic layer in a multi-phase settlement, a few early Bronze Age burials at a multi-phase cemetery, an un-stratified single Iron Age brooch or an early medieval hillfort. To be able to include spatially less accurate data from pre-WWII period excavation reports, spatial accuracy was set at the level of individual parishes. Temporal uncertainties caused mainly by undiagnostic finds were quantified and simulated with the help of Monte Carlo simulations. We modelled the temporal dynamics and uncertainty of the four main component types (single finds, settlements, burial grounds, hoards), which provided us with an insight into the character of the available archaeological record. To mitigate the effects of archaeological research intensity, we also calculated parish occupancy likelihood as the proportion of simulation runs in which individual parishes were simulated

as occupied (for further details, see Kolá et al. in press.). We used parish occupancy likelihood as the basic human activity model and differentiated human activity models according to main component types for comparison with the results of the REVEALS model and in further calculations. For the calculation of the human activity model based on parish occupancy likelihood only settlements, burial sites and hoards were used in order to avoid large uncertainties generated by single finds.

2.5 Climate model

Today's climate at the site is warm and medium dry to slightly wet (mean annual temperature 9.0 °C, mean annual precipitation 569 mm). Due to the absence of any locally derived palaeoclimatic proxies, we used a macrophysical climate model (MCM) as an independent data source. MCM represents a heat-budget model derived from orbital forcing, variations in atmospheric transparency, and the principles of synoptic climatology (Bryson, 2005). This heat budget model is locally calibrated by a long series of meteorological data. MCM yields high resolution (100-year averages for each month), is site specific (it implicitly includes local influences, such as topography) and has already been successfully tested against proxy data (Higgins & MacFadden, 2009; Riehl et al., 2009; Dreslerová, 2012; Jamrichová et al., 2014). Based on MCM we calculated Holocene climatic parameters (temperature and precipitation in monthly averages) for Velké Pavlovice, a meteorological site 29 km west of the pollen sampling point, where observations for a 30-year period were available (Czech Hydrometeorological Institute). This site has a climate (9.2 °C; 563 mm) similar to that at the pollen site.

2.6 Chronology

Eleven radiocarbon dates were available for the Lake Vracov profile DU-7-D (Table 2). Two of them had been obtained earlier (Svobodová, 1997) using beta counting. Plant remains were dated by Accelerator Mass Spectrometry in the Pozna Radiocarbon Laboratory. Due to the overall absence of plant remains, three samples were treated with heavy liquid low carbon sodium polytungstate to separate the pollen-rich organic material. Samples were pre-treated with hot HF to remove inorganic particles, sieved, diluted by 10% HCl and sodium hexametaphosphate, and finally treated with hot HF to remove remaining inorganic particles. The remaining samples were then screened to remove rootlets and residues were dated by Beta Analytic, Miami.

An age-depth model was constructed using a Bayesian approach implemented in Bacon (Blaauw & Christen, 2011), based on the IntCal13 calibration curve and prior information assuming a mean accumulation rate of 20 yrs/cm and accumulation shape 1.5. Three dates were initially excluded from the age-depth model. One had too low organic content (Poz-51954) and yielded too young a date, the other two originated from the basal layer (Beta36494, Hv1868), which we expect to have been affected by post-depositional processes. These dates, however, originate from late-glacial deposits, which we do not discuss any further.

The chronological control for the Holocene part of the record consists of 5 radiocarbon dates, which are coupled in the age-depth model with the pre-Holocene dates. The model

exhibits a rather low accumulation rate for the major part of the Holocene (8000–1 BC), which, when combined with the 3 dates that control the model, creates uncertainties in dating. As a result, larger errors occur in the dating of biostratigraphic events (zones) (Fig. 3, Supplementary Fig. 1).

2.7 Numerical analyses

Results of the REVEALS, human activity and climate models were analysed numerically to elucidate palaeoclimatic and human induced palaeovegetational context. We used the direct ordination technique of Redundancy Analysis (RDA) implemented in the Vegan package (Oksanen et al., 2013) in R (R Core Team, 2014). As the first run, REVEALS-based vegetation percentages were analysed using climate variables and the proportion of human activity in the area as constraining environmental variables. In the second run, we used pollen percentages in order to evaluate correlations of rare pollen indicators, which were not included in the REVEALS calculations. Logarithmic transformation of pollen percentages was used in this case. In both runs time was used as a covariable to remove the effects of Holocene migrations.

3 Results

3.1 Age-depth model

The results of all 11 radiocarbon dates are shown in Table 2. The lowest 3 dates were excluded from the age-depth model, which is shown in Fig. 2. The accumulation rate during the early Holocene was quite low and the distance between dated points was rather large, which resulted in higher uncertainties for this period.

3.2 Palaeovegetation

Regional vegetation cover estimated by the REVEALS model for 27 pollen taxa is shown in Fig. 3. The diagram summarizes pollen versus vegetation proportions in 500-year intervals for the entire Holocene. Four vegetation zones were distinguished and are denoted as Early Holocene (10000–6500 BC), Middle Holocene (6500–3000 BC), Late Holocene I (3000–1 BC) and II (AD 1–1000). Their correspondence to pollen accumulation zones (PAZ) in the pollen diagram (Supplementary Fig. 1) is only approximate due to coarser time resolution (sampling strategy) of the REVEALS model. The last 1000 years were excluded from the numerical analyses because no appropriate archaeological data could be obtained.

3.2.1 Early Holocene (10000–6500 BC)—Vegetation was dominated by *Pinus* (40–60%) and *Betula* (10–20%) during the Early Holocene. The ratio of open land was the highest at this time (27%), apart of the youngest time interval. *Corylus* increased up to 20% at the end of this zone. Vegetation appears to have been open pine-birch forests.

3.2.2 Middle Holocene (6500–3000 BC)—At the beginning of this zone *Picea* expanded to 20%, *Corylus* expanded somewhat later. *Ulmus* and *Quercus* were present but not expanding. The ratio of open land was lower than in the previous phase and fluctuated depending on the amount of *Corylus* in the vegetation. *Pinus* remained a dominant

component of the vegetation. Forests were mostly coniferous with dominant pine and spruce.

3.2.3 Late Holocene I (3000–1 BC)—*Pinus* decreased to 20% at the beginning of the Late Holocene. This was accompanied by an increase in *Corylus* and later also in *Quercus* (both up to 20%). *Fagus* and *Carpinus* started to expand at the end of this zone. The landscape became more forested in the middle of this phase and cereal fields started to expand with a time-lag between 1500–1000 BC. Forests became predominantly deciduous.

3.2.4 Late Holocene II (AD 1–1000)—This phase was marked by massive human impact indicated by the enlargement of cereal fields and open land. *Pinus* and *Picea* dropped to 10%. *Quercus* became dominant in the forests together with *Carpinus* and later *Fagus*. *Corylus* declined. In the last time window half of the landscape is estimated to have been deforested.

3.3 Archaeology and human activity model

Altogether 3116 unique archaeological components were registered in the study area. Activity area classification resulted in 639 residential components, 550 burial components, 1801 single finds, 60 hoards and 66 other activity areas (hillforts, enclosures, specialized production places etc.).

The dataset served for the creation of a cumulative plot of 1000 Monte Carlo simulation runs for each dated component with the initial duration of time blocks set at 500 years. The results showed the temporal dynamics of the four basic behavioural categories: settlements, burial sites, single finds and hoards (Fig. 4). The generic trend of the curves for each component category at the regional scale showed a significant increase in the archaeological record at the beginning of the Neolithic in ca. 5500 BC. However, the archaeological evidence decreased after 4500 BC showing the lowest values between 4000 and 3000 BC. After 3000 BC increases in the archaeological evidence could be observed, especially in the burial record. The burial evidence then steadily decreased until the period AD 500–1000, when it increased again. For the settlement record in particular we registered rises and falls during the Neolithic and Eneolithic. The lowest evidence in the Eneolithic (particularly between 4000 and 3000 BC) was followed by a gradual increase from 3000 to 1000 BC. From that point onwards a more stable but slightly decreasing tendency in the settlement and burial ground curves was observed. After AD 500 another increase in the archaeological record was registered.

The human activity model showed that 20% of the landscape was affected by humans during the Neolithic (5500–4000 BC) (Fig. 4). A remarkable decrease could be observed between 4000–2500 BC followed by an abrupt increase to 40%. Major fluctuations of human activity happened since 2500 BC, especially during the Migration Period (AD 1–500).

3.4 Climate model

The MCM model provided monthly means of temperature, precipitation and evaporation in 100-year intervals (Fig. 4). For comparison with palaeovegetation and human activity data,

we selected January and July temperatures, summer precipitation (sum of April–July) and potential summer evaporation. Three main climatic phases could be observed in the climatic model. The first phase (10000–7500 BC) was characterized by rather high but fluctuating July temperature and very low January temperature. Precipitation was quite low (140 mm), but fluctuating evaporation created changing regimes from dry to more humid. The second phase (7500–3500 BC) exhibited relatively stable conditions, although January temperature was slowly rising to –3 °C. Precipitation remained low and high evaporation created very arid conditions during summer. The last phase (from 3500 BC) showed temperatures very close to recent conditions. Precipitation was higher, but fluctuating, creating short periods of summer droughts.

3.5 Numerical analyses

The ordination diagram of the first RDA analysis of REVEALS-based vegetation proportions and environmental variables is shown in Fig. 5. The first two RDA axes explained 39% of the total variability in the modelled vegetation data. A positive correlation can be seen between human occupancy and summer precipitation. *Quercus, Betula* and open land are correlated positively with these two variables. By contrast, *Pinus* is correlated with high July temperatures.

The second RDA analysis of pollen proportions and environmental variables is shown in Fig. 6. In this case only 14% of the total variability in the pollen data was explained by the first two RDA axes. The analysis revealed a strong correlation of human occupancy with many pollen taxa (*Plantago major*-type, *P. lanceolata, Artemisia, Ranunculus, Anemone, Viola palustris*-type, *Filipendula*).

4 Discussion

4.1 The dynamics of forest and open land during the Holocene

The dynamics of main vegetation patterns exhibited unusual stability with no recorded abrupt changes during the Holocene. Palaeovegetation records (Fig. 3, see also Supplementary Fig. 1) indicated a large proportion of herbs/open land with only one significant change around AD 1000.

In the following, we discuss stability and change in vegetation driven mainly by internal ecosystem dynamics and forces.

4.1.1 Early Holocene Phase ~10000–6500 BC (VR 1, VR 2 in pollen diagram)

—The pre-Holocene pollen record was dominated by *Pinus* with continuous curves of many herbs indicating open and cold conditions (Chenopodiaceae, *Artemisia, Thalictrum* etc.) with no or little evidence of more demanding species. The start of the Holocene was delimited in the pollen record (see Supplementary Fig. 1) by the sudden increases of green coccal algae (*Pediastrum, Tetraedron* and *Scenedesmus*) and aquatic plant taxa (*Nymphaea, Potamogeton*), which probably reflected increasing productivity triggered by increasing water temperature and nutrient availability. A further sign of the start of the Holocene was the increase in *Juniperus* pollen. A slow and gradual postglacial increase in the pollen of temperate deciduous trees (*Quercus, Corylus*) is a characteristic feature of this area

(Rybníčková & Rybníček, 1972; Svobodová, 1997; Břízová, 2009) in contrast to more eastern parts of the Pannonian Plain (Willis et al., 1997; Magyari et al., 2010; Hájková et al., 2013; Petr et al., 2013; Jamrichová et al., 2014).

The REVEALS model suggested that there was open vegetation in the study area, consisting mainly of pine and birch. Grasslands constituted up to 30% of the vegetation in this period (Fig. 3), as shown by continuous curves of light-demanding terrestrial plants, e.g. *Thalictrum,* Apiaceae*, Rumex* and *Plantago.* The structure of such vegetation could be explained either as a mosaic of open vegetation and dense forest (forest steppe) or as a savannah-like vegetation with a combination of scattered trees, shrubs and a productive herb layer. Revealing such details in structure is unfortunately beyond the abilities of the model. Nevertheless the model confirms that large open patches existed at this time. According to a semi-quantitative reconstruction, forest steppes in the Great Hungarian Plain reached their greatest extent in the same period (Magyari et al., 2010), but temperate trees, such as *Quercus, Ulmus* and *Corylus* also attained high proportions. *Quercus* and *Corylus* were also confirmed to have expanded earlier further to the north (Petr et al., 2013; Jamrichová et al., 2014). In our case such expansion occurred only at the end of this phase (~7000 BC). Contrary to our findings, previous pollen studies at our site assumed continuous afforestation of the area around Vracov from Allerød (GI 1; 12000 BC) until the Subboreal (~2500 BC). Rybníčková & Rybníček (1972) argued that the disappearance of light demanding taxa and the occurrence of e.g. *Hedera helix* would imply only a limited occurrence of relic stands of woodland steppe (*Quercion pubescentis*) and that chernozem soils, which are often linked with the distribution of steppe vegetation (Ložek, 2011; Antoine et al., 2013), developed only during the late glacial and subsequently degraded under forest cover. Although chernozem occurs today in southern Moravia, its origin and evolution in a Central European context is still unclear and fuels discussion (Eckmeier et al., 2007). Chernozem seems to be resistant against colonization by trees (Vysloužilová et al., 2014).

Fossil land snails remain the only direct evidence for stand scale vegetation openness in our region (Ložek, 2001; Sümegi et al., 2012; Juřičková et al., 2013; Pokorný et al., 2015). A significant habitat of steppe vegetation including calcareous grasslands occurs immediately south-west of the study region in the Pálava mountains. The persistence of snails of open habitats during the Holocene was reported near this area in the floodplains of the river Dyje (Vašátko & Ložek, 1973). Furthermore, vegetation linked to deep soils represents another widespread habitat in southern Moravia which could harbour steppe plant species in the Holocene (Ložek, 2011).

Forests in northern Europe were also rather open in the same period (Nielsen et al., 2012; Theuerkauf et al., 2014). A combination of factors was suggested to have driven this openness, including soil conditions and seasonal dryness (degree of continentality). The role of large herbivores in maintaining open landscapes has been subject to a heated debate (Vera, 2000; Svenning, 2002; Birks, 2005; Mitchell, 2005). Although the Holocene fauna was impoverished in comparison with previous temperate stages, there were still large grazers present, such as aurochs (Bradshaw et al., 2003) and wild horses, which were able to live in open pine forests (Sommer et al., 2011). The presence of dung spores found during pollen analysis is an important indicator of the presence of grazers. Several types may be

included, such as *Sporormiella*, *Sordaria* and *Podospora* (van Geel, 2001; Baker et al., 2013). In our profile, only Sordariaceae spores were found and only in the Late Holocene period (see Supplementary Fig. 1). We therefore assume that large herbivores did not play an important role in maintaining vegetation openness.

The highest ratio of forested land occurred at the end of this phase, when temperate deciduous taxa (*Corylus*, *Ulmus* and *Quercus*) started to expand. The REVEALS model showed a decrease in grasslands to 15%, which probably resulted from the gradual closing of forest vegetation through the expansion of shade tolerant trees.

Further occurrence of pollen taxa including *Ephedra fragilis*-type, *Juniperus*, *Senecio*, *Campanula*, *Jasione*, Rubiaceae and *Cirsium*, but also of pollen types that are regarded as anthropogenic indicators, such as *Plantago lanceolata, P. major/media*-type, *Rumex* and *Urtica,* can be seen in this phase (see Supplementary Fig. 1). Although in low frequencies and quantities, these taxa could indicate the persistence of open habitats (wet and dry grasslands) in the region. Recording poor pollen producers in a largely forested landscape can be problematic as tested on lake sediments in Estonia (Meltsov et al., 2011, 2013), therefore even single pollen occurrences of such taxa may be of high value.

4.1.2 Middle Holocene Phase ~6500–3000 BC (VR 3 in pollen diagram)—

According to the REVEALS model, this phase commenced with the maximum recorded proportion of forested land leaving only 12.5% to open land. However, the dominant pine with an admixture of birch suggests the existence of open hemiboreal forests harbouring light demanding taxa similar to those currently found in southern Siberia (Chytrý et al., 2012). At the start of this phase pine decreased from 60 to 50 % of the total vegetation, but, rather surprisingly, remained dominant. As our study area covers a partly hilly landscape, we expected spruce to expand in this phase. From among deciduous taxa *Corylus* became abundant, while oak and elm remained insignificant admixture trees. Contrary to our findings, in other areas of Central Europe *Quercus* and *Corylus* outcompeted pine in the lowlands (Magyari et al., 2010; Petr et al., 2013; Jamrichová et al., 2014; Marquer et al., 2014; Trondman et al., 2015), and spruce prevailed at higher elevations (Trondman et al., 2015; Abraham V. et al. in prep). The persistence of pine vegetation during the Middle Holocene in our region could be linked the widespread sandy soils (Culek, 1996) and climate (see discussion below).

The ratio of open land remained high at ca. 20% through the entire period. This could be the result of the continuity of pine-dominated vegetation, a legacy of the previous phase. However, increasing human activities, which started with the Neolithic after 5500 BC (Fig. 4), could also play a significant role. The continuous occurrence of pollen indicators of open grassland as discussed in the previous subchapter could be observed here as well.

Generally speaking, the landscape remained open during the Middle Holocene. When compared to the Early Holocene, the most notable change occurred in tree species composition through the expansion of *Corylus* and *Picea*.

4.1.3 Late Holocene Phases I and II from ~3000 BC (VR 4 + VR 5 in pollen diagram)—A remarkable change denoting the start of this phase was a sharp decline in *Pinus* accompanied by an increase in temperate deciduous trees, mainly oak. Moreover, *Fagus* increased at around 1500 BC together with the first occurrences of cereal pollen (Fig. 4; Supplementary Fig. 1). Beech probably expanded in the hilly part of the study region creating mixed stands with spruce. Lowland vegetation changed into oak forests on more fertile soils leaving pine dominant on poorer sandy soils. In Phase II, hornbeam became a major player in forest vegetation accompanied by the ongoing expansion of cereal fields. A comparison with other records in the area suggests that hornbeam was much more frequent in the hills towards the north-east (Rybní ek & Rybní ková, 2008). The entire phase is characterized by significant human impact, which may have played a major role in shaping the vegetation (see discussion below). The dynamics of open land (grasslands and cereal fields) did not indicate any expansion until AD 250. The pollen diagram shows an increase in anthropogenic pollen indicators, such as Chenopodiaceae, *Plantago lanceolata, P. major/ media-type, Rumex* and *Urtica* together with the more frequent occurrence of grassland indicators (see Supplementary Fig. 1). This suggests the intensification of grazing in the open areas. A similar pattern in the occurrence of cereals with anthropogenic indicators was found at other southern Moravian sites from approx. 3400 BC (Svobodová, 1989, 1997).

Overall trends in the dynamics of open land during the Holocene demonstrated exceptional stability: approximately 20% of the landscape was covered by non-forest vegetation from the earliest stages of the Holocene until the High Middle Ages. Moreover, forests during the key early phase of the Holocene were predominantly pinewoods, which probably had a more open character and could harbour many light demanding and steppe taxa.

4.2 Vegetation-climate feedbacks

Holocene vegetation dynamics was traditionally interpreted in the framework of climatic events. Mostly the rise in temperature would have created conditions for the spread of forests at the start of the Holocene. In classic studies, vegetation development in pollen diagrams was described as a succession of biostratigraphic zones characterized mainly by the degree of humidity and temperature (Firbas, 1949).

In the case of the Lake Vracov pollen diagram, we could distinguish only four zones relevant for Holocene vegetation development. The boundaries of the first three zones were placed at or near major climatic events – the start of the Holocene and the 8.2 and 4.2 events (Walker et al., 2012) – implying that vegetation change might have been triggered by climate in these cases. The beginning of the Holocene was detected in other, nearby pollen records as the expansion of tree pollen, mainly *Pinus* and *Betula* accompanied by a reduction in herb pollen (Rybní ek & Rybní ková, 1996). At these sites, which are characterized by milder conditions than our study site, such changes were interpreted as immediate reactions to climate change. By contrast, in the lowlands of the Pannonian Plain a decrease in tree pollen at the beginning of the Holocene was observed (Hájková et al., 2013; Sümegi et al., 2013; Jamrichová et al., 2014). This seems to have resulted from specific conditions in which rising temperatures increased aridity.

The most discussed climatic event at 8.2 ka shows an indisputable imprint in proxy data in the North Atlantic region of Europe (Wiersma & Renssen, 2006) as well as in the Mediterranean (Pross et al., 2009). In northern Europe, this event seems to have suppressed temperate trees probably as a result of winter and early spring cooling (Seppä et al., 2007). In central-western Europe the cooling suppressed *Corylus* allowing for the subsequent expansion of *Fagus* and *Abies* causing climatically driven changes of terrestrial ecosystems (Tinner & Lotter, 2001). Such reorganization can be also seen in numerous other records in central Europe (Giesecke et al., 2011). However, in the more continental environment of eastern Europe the visibility of this phenomenon in pollen data is much more disputable (Feurdean et al., 2014). The effects of the event proved untraceable even in a high-resolution record (Pokorný et al., 2010). By contrast, the Lake Vracov record reflected significant vegetation change at or very near 6200 BC. We recorded an increase in pine and a decrease in non-arboreal pollen and coccal green algae. A sudden increase in open land could be observed between 6000–5500 BC in the REVEALS model together with an increase in Cyperaceae pollen (not included in REVEALS). These features may point at climatically induced changes in the lake basin, such as water level changes, causing hiatuses in sedimentation recorded in the littoral part of the lake (Rybníčková & Rybníček, 1972; Rybníček, 1983). Nevertheless, during this time sedimentation rates were the lowest in Lake Vracov. The resulting high uncertainties in the age-depth model (Fig. 2) make it almost impossible to distinguish and separate the 9.3 and 8.2 events from each other.

The middle-late Holocene boundary derived from a global aridification event at 4.2 ka (Walker et al., 2012) is more problematic to detect in Europe. Statistically, our boundary between Middle and Late Holocene (Fig. 3) corresponds to the 4.2 event. However, it may also be correlated to the 3500 BC event, which was characterized by a robust change from somewhat dry and warm climate to colder and wetter conditions and a more shifting climatic regime (Dreslerová, 2012) and was documented in numerous proxy data around the world (Shuman, 2012). Unlike the 8.2 event, this change was also recorded in the MCM model (Fig. 4) leading to increasing summer precipitation, decreasing evaporation, warmer winters and colder summers. The change, denoted in our profile as the start of the Late Holocene, was characterized by a substantial decrease in pine pollen and an expansion of deciduous taxa (mainly oak). *Fagus* and *Carpinus* appeared at this time as well. However, with the expansion of Eneolithic people (Dreslerová, 2012) it remains difficult to fully disentangle anthropogenic and climate driven changes in ecosystems (see further discussion).

Increasing summer precipitation at 3500 BC probably triggered the further expansion of *Picea* in hilly stands, a tree most competitive in moist conditions (Ellenberg & Leuschner, 1996; Henne et al., 2011). Further on hazel started to outcompete pine at lower elevations, whereas the ratio of open land remained stable.

According to the RDA analysis (Fig. 5), *Quercus* and open land vegetation were strongly correlated with increasing summer precipitation (see also van der Knaap et al., 2010), confirming that increasingly wet conditions at 3500 BC could trigger the expansion of oak and the opening of the landscape. On the other hand pine was strongly correlated with high July temperatures suggesting that its dominance was mainly driven by the strongly continental climate of the first half of the Holocene. Temperate deciduous trees (*Corylus,*

Tilia, Ulmus) were more strongly correlated with increasing winter temperature suggesting that they favoured milder winters and were relatively resistant to dryness.

4.3 The role of human activity in vegetation dynamics

According to our human activity model, the first major impact on the landscape around Lake Vracov took place after ca. 5500 BC with the start of the Neolithic. The impact of Mesolithic people remains problematic to detect, because records consist of roughly dated single finds and the capabilities Mesolithic communities to influence vegetation at the landscape scale are a matter of ongoing discussion (Behre, 2007; Tinner et al., 2007; Kuneš et al., 2008). Hunter-gatherer communities could be responsible for an increase in *Corylus* during the Mesolithic period (Kuneš et al., 2008; Regnell 2012), whereas a gradual decrease in *Corylus* at the end of the Mesolithic and start of the Neolithic, which was probably triggered by climate, could facilitate the transition to agriculture and grazing (Regnell 2012). The lowest ratio of human occupancy in the post-Neolithic period in our study region was observed during the Eneolithic (between 4000–2500 BC).

The pollen record did not show any changes in anthropogenic indicators after 5500 BC, because such taxa had already been present in the landscape. Approximately 20% of the landscape was affected by people at that time, which roughly corresponds to the ratio of landscape openness. A similar ratio of vegetation openness was estimated during the Early Iron Age for central Europe (Dreslerová, 1995; Kaplan et al., 2009). A slight expansion of forests could be observed again at 4000–3500 BC, correlated with the decrease of registered human activity during the Eneolithic, which might have created space for the forest to regenerate. However, such remarkable decrease in human activity could also be explained by the decreased visibility of archaeological finds in the landscape as a result of specific types of dwellings, erosion/accumulation processes or specific subsistence strategies. In this period *Quercus* expanded significantly for the first time (Figs 3 and 4). As discussed earlier, these vegetation changes could also be triggered by a major climatic change at 3500 BC. Vegetation changes were arguably brought on by the combined effects of human activities and climate.

Another enormous increase in human activity started with the final phase of the Eneolithic at 2500 BC. At this time another increase in *Quercus* occurred in the vegetation model suggesting that oak was supported by human activities. Ordination analysis also showed a strong correlation of oak abundance and human activity in the study area. Such findings were recently tested on historical data in the same area showing the spread of oak after a ban on oak cutting and the promotion of forest grazing in the Late Middle Ages (Jamrichová et al., 2013). In lack of direct evidence, it is more challenging to explain the connections between oak and human activities in prehistory. An important aspect may have been grazing. *Quercus* thrives under grazing pressure by herbivores (cattle, horse and deer; Olff et al., 1999), which could partly explain why it was a favourite tree in managed forests. It has also been the choice of timber for building purposes since prehistory and was valued as a producer of acorns for domestic pigs (Rackham, 2003). Moreover, its occurrence was linked with pollen indicators of grazing, such as *Rumex acetosa*-type and *Plantago lanceolata*. Surprisingly, the ratio of forest increases together with the first occurrence of cereal fields

(Figs 3 and 4). Along with increasing crop cultivation, *Quercus* became dominant in forests to be joined by expanding *Carpinus* after 500 BC. Hornbeam could prevail later, following changes in forest utilization, the reduction of grazing and the start of coppicing. Oak was often related to an increase in the occurrence of fires (Abrams, 1992; Chytrý et al., 2010), as large individuals are able to survive fires and regeneration benefits from them (Ellenberg & Leuschner, 1996; Mason, 2000). Unfortunately our data did not include charcoal, but the analysis of a forest hollow in the study area (Jamrichová et al. 2013) demonstrated that fire did not play a major role in forest dynamics in the past two millennia.

Open land and the emergence of secondary forests (*Betula*) were also correlated with human occupancy, which reflected the effects of deforestation. Surprisingly, we did not observe any correlation between cereal fields and human occupancy. This is due to the fact that cereal pollen was not recorded during the Neolithic period, when extensive human activity was modelled in the area. Cereals used and cultivated at that time were several species of *Triticum* (*T. monococcum, T. dicoccum, T. aestivum*) and *Hordeum vulgare* (Dreslerová & Ko ár, 2013). A possible explanation of the disproportions between expected and observed estimates of cereal fields during these prehistoric times may lie in the differential pollen production of those ancient cereal species from the present ones. A lack of cereals during the Neolithic was observed at other nearby sites as well (Jamrichová E. in prep.). In southern Europe, Neolithic agricultural practices were also found to have had much lower impact than Bronze Age forest management on pollen rain (Mecuri, 2014). Different agricultural practices have to be taken into account when interpreting such disproportions. This certainly raises the need for further multidisciplinary studies (Hjelle et al. 2012).

Because the REVEALS model provides insights into only a few dominant taxa, for which measures of pollen productivity are available, we attempted a detailed analysis of pollen finds with information on human activity and climate. As expected, we found a strong correlation of humans to *Artemisia*, *Plantago major/media*, *P. lanceolata* and *Ranunculus*, which are usually interpreted to indicate pastures, meadows or ruderal communities (Behre, 1981; Svobodová, 1990; Gaillard, 2013). Other pasture pollen taxa such as *Rumex acetosa*-type, *Potentilla*, Cruciferae and *Filipendula* were only weakly correlated to humans. Other taxa that are commonly interpreted as indicators of anthropogenic habitats (Gaillard, 2013; Mercuri et al., 2013), e.g. *Centaurea nigra*-type, *C. cyanus*, Asteraceae Cichorioidae, *Polygonum aviculare*-type, *P. persicaria*, *Urtica*, Chenopodiaceae, Rubiaceae, *Campanula*-type, did not exhibit any positive correlation with human occupancy. These taxa can also be linked to different natural open habitats and our analysis suggests that they existed naturally in the landscape before the start of the Neolithic.

5 Conclusions

Combined regional palaeoenvironmental data (palaeovegetation, human occupancy and climate) brought new evidence on the dynamics of open land in the Holocene. Modelled regional palaeovegetation from the north-western edge of the Pannonian Plain suggested that there was continuous and stable openness in the landscape during the entire Holocene. Grasslands and open woodlands were maintained in the lowlands by climatic conditions during the early Holocene. Lower winter and higher summer temperatures accompanied by

much higher aridity than today delayed the spread of deciduous forests. Neolithic people spread into the landscape and probably started using and maintaining existing open habitats. We detected clearly anthropogenic landscape transformation only after 2000 BC. Humans probably facilitated the spread of oak, which had been triggered by increasing precipitation, and contributed to the dynamics of hazel and hornbeam.

Appendix A. Supplementary data

Refer to Web version on PubMed Central for supplementary material.

Acknowledgements

References

Abraham V, Kozáková R. Relative pollen productivity estimates in the modern agricultural landscape of Central Bohemia (Czech Republic). Review of Palaeobotany and Palynology. 2012; 179:1–12.

Abraham V, Oušková V, Kuneš P. Present-day vegetation helps quantifying past land cover in selected regions of the Czech Republic. PLoS ONE. 2014; 9:e100117. [PubMed: 24936973]

Abrams MD. Fire and the development of oak forests. BioScience. 1992; 42:346–353.

Antoine P, Rousseau D-D, Degeai J-P, Moine O, Lagroix F, Kreutzer S, Fuchs M, Hatté C, Gauthier C, Svoboda J, Lisá L. High-resolution record of the environmental response to climatic variations during the Last Interglacial–Glacial cycle in Central Europe: the loess-palaeosol sequence of Dolní Věstonice (Czech Republic). Quaternary Science Reviews. 2013; 67:17–38.

Baker AG, Bhagwat SA, Willis KJ. Do dung fungal spores make a good proxy for past distribution of large herbivores? Quaternary Science Reviews. 2013; 62:21–31.

Behre K-E. The interpretation of anthropogenic indicators in pollen diagrams. Pollen et Spores. 1981; 23:225–245.

Behre KE. Evidence for Mesolithic agriculture in and around Central Europe? Vegetation History and Archaeobotany. 2007; 16:203–219.

Bennett KD. Determination of the number of zones in a biostratigraphical sequence. New Phytologist. 1996; 132:155–170.

Bennett, KD. Psimpoll and pscomb programs for plotting and analysis. Uppsala University; Uppsala: 2009.

Birks HJB. Mind the gap: how open were European primeval forests? Trends in Ecology & Evolution. 2005; 20:154–156. [PubMed: 16701360]

Blaauw M, Christen JA. Flexible paleoclimate age-depth models using an autoregressive gamma process. Bayesian Analysis. 2011; 6:457–474.

Bohn, U., Gollub, G., Hettwer, C. Karte der natürlichen Vegetation Europas / Map of the Natural vegetation of Europe. Bundesamt für Naturschutz, Bonn; Bad Godesberg: 2000.

Bradshaw RHW, Hannon GE, Lister AM. A long-term perspective on ungulate-vegetation interactions. Forest Ecology and Management. 2003; 181:267–280.

Břízová E. Quaternary environmental history of the Čejčské Lake (S. Moravia, Czech Republic). Bulletin of Geosciences. 2009; 84:637–652.

Bronk Ramsey CB. Bayesian analysis of radiocarbon dates. Radiocarbon. 2009; 51:337–360.

Bryson, R. Archeoclimatology. Encyclopedia of World Climatology. Oliver, JE., editor. Springer; Netherlands: 2005. p. 58-63.

Chytrý, M. Vegetace eské republiky 1. Travinná a ke í ková vegetace – Vegetation of the Czech Republic 1. Grassland and Heathland Vegetation. Academia; Praha: 2010.

Chytrý, M. Vegetace eské republiky 4. Lesní a k ovinná vegetace – Vegetation of the Czech Republic 4. Forest and scrub vegetation. Academia; Praha: 2013.

Chytrý M, Danihelka J, Horsák M, Ko í M, Kubešová S, Lososová Z, Otýpková Z, Tichý L, Martynenko VB, Baisheva EZ. Modern analogues from the Southern Urals provide insights into biodiversity change in the early Holocene forests of Central Europe. Journal of Biogeography. 2010; 37:767–780.

Chytrý M, Ermakov N, Danihelka J, Hájek M, Hájková P, Horsák M, Ko í M, Kubešová S, Lustyk P, Otýpková Z, Pelánková B, et al. High species richness in hemiboreal forests of the northern Russian Altai, southern Siberia. Journal of Vegetation Science. 2012; 23:605–616.

ižmá , M., Geislerová, K. Výzkumy–Ausgrabungen 1999–2004. Ústav archeologické památkové pé e Brno; Brno: 2006.

ižmá , M., Geislerová, K., Unger, J. Výzkumy–Ausgrabungen 1993–1998. Ústav archeologické památkové pé e Brno; Brno: 2000.

Connor SE, Ross SA, Sobotkova A, Herries AIR, Mooney SD, Longford C, Iliev I. Environmental conditions in the SE Balkans since the Last Glacial Maximum and their influence on the spread of agriculture into Europe. Quaternary Science Reviews. 2013; 68:200–215.

Contreras DA, Meadows J. Summed radiocarbon calibrations as a population proxy: a critical evaluation using a realistic simulation approach. Journal of Archaeological Science. 2014; 52:591–608.

Crombé P, Robinson E. 14C dates as demographic proxies in Neolithisation models of northwestern Europe: a critical assessment using Belgium and northeast France as a case-study. Journal of Archaeological Science. 2014; 52:558–566.

Culek, M. Biogeografické len ní R. Enigma; Praha; 1996.

Czudek, T. Geomorfologické len ní SR. Academia; Praha: 1972.

Dreslerová, D. A settlement-economic model for a prehistoric microregion: settlement activities in the Vino stream basin during the Hallstatt period. Whither archaeology? Papers in honour of Evžen Neustupný. Kuna, M., Venclová, N., editors. Institute of Archaeology; Praha: 1995. p. 145-160.

Dreslerová D. Human response to potential robust climate change arend 5500 cal BP in the territory of Bohemia (Czech Republic). Interdisciplinaria Archaeologica. 2012; 3:43–56.

Dreslerová D, Ko ár P. Trends in cereal cultivation in the Czech Republic from the Neolithic to the Migration period (5500 b.c.-a.d. 580). Vegetation History and Archaeobotany. 2013; 22:257–268.

Eckmeier E, Gerlach R, Gehrt E, Schmidt MWI. Pedogenesis of chernozems in Central Europe — A review. Geoderma. 2007; 139:288–299.

Ellenberg, H., Leuschner, C. Vegetation Mitteleuropas mit den Alpen: in ökologischer, dynamischer und historischer Sicht. Ulmer; Stuttgart: 1996.

European Environmental Agency. Corine Land Cover 2006 seamless vector data. Copenhagen: 2013.

Feurdean A, Per oiu A, Tan u I, Stevens T, Magyari EK, Onac BP, Markovi S, Andri M, Connor S, F rca S, Gałka M, et al. Climate variability and associated vegetation response throughout Central and Eastern Europe (CEE) between 60 and 8 ka. Quaternary Science Reviews. 2014; 106:206–224.

Feurdean A, Marinova E, Nielsen AB, Liakka J, Veres D, Hutchinson SM, Braun M, Timar-Gabor A, Astalos C, Mosburgger V, Hickler T. Origin of the forest steppe and exceptional grassland diversity in Transylvania (central-eastern Europe). Journal of Biogeography. 2015; doi: 10.1111/jbi.12468

Firbas, F. Spät- und nacheiszeitliche Waldgeschichte Mitteleuropas nördlich der Alpen. Gustav Fischer Verlag; Jena: 1949.

Gaillard, M-J. POLLEN METHODS AND STUDIES | Archaeological Applications. Encyclopedia of Quaternary Science (Second Edition). Elias, SA., Mock, CJ., editors. Elsevier; Amsterdam: 2013. p. 880-904.

Gaillard M-J, Sugita S, Mazier F, Trondman A-K, Broström A, Hickler T, Kaplan JO, Kjellström E, Kokfelt U, Kuneš P, Lemmen C, et al. Holocene land-cover reconstructions for studies on land cover-climate feedbacks. Climate of the Past. 2010; 6:483–499.

Giesecke T, Bennett KD, Birks HJB, Bjune AE, Bozilova E, Feurdean A, Finsinger W, Froyd C, Pokorný P, Rösch M, Seppä H, et al. The pace of Holocene vegetation change – testing for synchronous developments. Quaternary Science Reviews. 2011; 30:2805–2814.

Gradmann R. Die Steppenheidetheorie. Geographische Zeitschrift. 1933; 39:265–278.

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

Havinga AJ. A palynological investigation in the Pannonian climate region of lower Austria. Review of Palaeobotany and Palynology. 1972; 14:319–352.

Havlíek, P., Krejí, O., Novák, Z., Stráník, Z., Uhlíová, I. Geological map of the Czech Republic - Sheet 32 - 22 Hodonín. Czech Geological Survey; Praha: 1995.

Havlíek P, Zeman A. Kvartérní sedimenty moravské ásti vídeské pánve. Anthropozoikum. 1986; 17:9–41.

Hejcman M, Hejcmanová P, Pavlu V, Beneš J. Origin and history of grasslands in Central Europe – a review. Grass and Forage Science. 2013; 68:345–363.

Hellman SEV, Gaillard M-J, Broström A, Sugita S. The REVEALS model, a new tool to estimate past regional plant abundance from pollen data in large lakes: validation in southern Sweden. Journal of Quaternary Science. 2008; 23:21–42.

Henne PD, Elkin CM, Reineking B, Bugmann H, Tinner W. Did soil development limit spruce (*Picea abies*) expansion in the Central Alps during the Holocene? Testing a palaeobotanical hypothesis with a dynamic landscape model. Journal of Biogeography. 2011; 38:933–949.

Higgins P, MacFadden BJ. Seasonal and geographic climate variabilities during the Last Glacial Maximum in North America: Applying isotopic analysis and macrophysical climate models. Palaeogeography Palaeoclimatology Palaeoecology. 2009; 283:15–27.

Hinz M, Feeser I, Sjögren K-G, Müller J. Demography and the intensity of cultural activities: an evaluation of Funnel Beaker Societies (4200–2800 cal BC). Journal of Archaeological Science. 2012; 39:3331–3340.

Hjelle KL, Kaland S, Kvamme M, Lødøen TK, Natlandsmyr B. Ecology and long-term land-use, palaeoecology and archaeology – the usefulness of interdisciplinary studies for knowledge-based conservation and management of cultural landscapes. International Journal of Biodiversity Science, Ecosystem Services & Management. 2012; 8:321–337.

Jamrichová E, Potuková A, Horsák M, Hajnalová M, Barta P, Tóth P, Kuneš P. Early occurrence of temperate oak-dominated forest in the northern part of the Little Hungarian Plain, SW Slovakia. Holocene. 2014; 24:1810–1824.

Jamrichová E, Szabó P, Hédl R, Kuneš P, Bobek P, Pelánková B. Continuity and change in the vegetation of a Central European oakwood. The Holocene. 2013; 23:46–56.

Járai-Komlódi M. The late glacial and Holocene flora of the Great Hungarian Plain. Annales Universitatis Scientiarum Budapestinensis de Rolando Eötvös Nominatae Sectio Biologica. 1968; 9–10:199–225.

Juiková L, Horáková J, Jansová A, Ložek V. Mollusc succession of a prehistoric settlement area during the Holocene: A case study of the eské stedohoí Mountains (Czech Republic). Holocene. 2013; 23:1811–1823.

Kaplan JO, Krumhardt KM, Zimmermann N. The prehistoric and preindustrial deforestation of Europe. Quaternary Science Reviews. 2009; 28:3016–3034.

Koláj, Macek M, Tká P, Szabó P. Spatio-temporal modelling as a way to reconstruct patterns of past human activities. Archaeometry. (in press).

Kuneš P, Abraham V, Kováík O, Kopecký M. PALYCZ contributors. Czech Quaternary Palynological Database – PALYCZ: review and basic statistics of the data. Preslia. 2009; 81:209–238.

Kuneš P, Pokorný P, Šída P. Detection of impact of Early Holocene hunter-gatherers on vegetation in the Czech Republic, using multivariate analysis of pollen data. Vegetation History and Archaeobotany. 2008; 17:269–287.

Kuneš P, Odgaard BV, Gaillard M. Soil phosphorus as a control of productivity and openness in temperate interglacial forest ecosystems. Journal of Biogeography. 2011; 38:2150–2164.

Lechterbeck J, Edinborough K, Kerig T, Fyfe R, Roberts N, Shennan S. Is Neolithic land use correlated with demography? An evaluation of pollen-derived land cover and radiocarbon-inferred demographic change from Central Europe. The Holocene. 2014; 24:1297–1307.

Ložek V. K otázce stepí ve st ední Evrop . Zprávy eskoslovenské botanické spole nosti. 1971; 6:226–232.

Ložek V. Molluscan fauna from the loess series of Bohemia and Moravia. Quaternary International. 2001; 76–7:141–156.

Ložek, V. Po stopách prav kých d j . O silách,které vytvážely naši krajinu. Doko án; Praha: 2011.

Magyari EK, Chapman JC, Passmore DG, Allen JRM, Huntley JP, Huntley B. Holocene persistence of wooded steppe in the Great Hungarian Plain. Journal of Biogeography. 2010; 37:915–935.

Magyari EK, Chapman J, Fairbairn AS, Francis M, Guzman M. Neolithic human impact on the landscapes of North-East Hungary inferred from pollen and settlement records. Vegetation History and Archaeobotany. 2012

Marquer L, Gaillard M-J, Sugita S, Trondman A-K, Mazier F, Nielsen AB, Fyfe RM, Odgaard BV, Alenius T, Birks HJB, Bjune AE, et al. Holocene changes in vegetation composition in northern Europe: why quantitative pollen-based vegetation reconstructions matter. Quaternary Science Reviews. 2014; 90:199–216.

Mason SLR. Fire and Mesolithic subsistence - managing oaks for acorns in northwest Europe? Palaeogeography Palaeoclimatology Palaeoecology. 2000; 164:139–150.

Mazier F, Gaillard M-J, Kuneš P, Sugita S, Trondman A-K, Broström A. Testing the effect of site selection and parameter setting on REVEALS-model estimates of plant abundance using the Czech Quaternary Palynological Database. Review of Palaeobotany and Palynology. 2012; 187:38–49.

Meltsov V, Poska A, Odgaard BV, Sammul M, Kull T. Palynological richness and pollen sample evenness in relation to local floristic diversity in southern Estonia. Review of Palaeobotany and Palynology. 2011; 166:344–351.

Meltsov V, Poska A, Reitalu T, Sammul M, Kull T. The role of landscape structure in determining palynological and floristic richness. Vegetation History and Archaeobotany. 2013; 22:39–49.

Mercuri AM, Sadori L, Uzquiano Ollero P. Mediterranean and north-African cultural adaptations to mid-Holocene environmental and climatic changes. The Holocene. 2011; 21:189–206.

Mercuri AM, Mazzanti MB, Florenzano A, Montecchi MC, Rattighieri E, Torri P. Anthropogenic pollen indicators (API) from archaeological sites as local evidence of human-induced environments in the Italian peninsula. Annali di Botanica. 2013; 3:143–153.

Mercuri AM. Genesis and evolution of the cultural landscape in central Mediterranean: the "where, when and how" through the palynological approach. Landscape Ecology. 2014; 29:1799–1810.

Mitchell FJG. How open were European primeval forests? Hypothesis testing using palaeoecological data. Journal of Ecology. 2005; 93:168–177.

Nielsen AB, Giesecke T, Theuerkauf M, Feeser I, Behre K-E, Beug H-J, Chen S-H, Christiansen J, Dörfler W, Endtmann E, Jahns S, et al. Quantitative reconstructions of changes in regional openness in north-central Europe reveal new insights into old questions. Quaternary Science Reviews. 2012; 47:131–149.

Oksanen J, Blanchet FG, Kindt R, Legendre P, O'Hara RB, Simpson GL, Solymos P, Stevens MHH, Wagner H. vegan: Community Ecology Package, v. 2.0-10. 2013

Olff H, Vera FWM, Bokdam J, Bakker ES, Gleichman JM, de Maeyer K, Smit R. Shifting mosaics in grazed woodlands driven by the alternation of plant facilitation and competition. Plant Biology. 1999; 1:127–137.

Petr L, Žá ková P, Grygar TM, Píšková A, K ížek M, Treml V. Šúr, a former late glacial and Holocene lake at the westernmost margin of the Carpathians. Preslia. 2013; 85:239–263.

Pielke RA, Pitman A, Niyogi D, Mahmood R, McAlpine C, Hossain F, Goldewijk KK, Nair U, Betts R, Fall S, Reichstein M, et al. Land use/land cover changes and climate: modeling analysis and observational evidence. Wiley Interdisciplinary Reviews: Climate Change. 2011; 2:828–850.

Pokorný P, Šída P, Chvojka O, Žá ková P, Kuneš P, Sv tlík I, Veselý J. Palaeoenvironmental research of the Schwarzenberg Lake, southern Bohemia, and exploratory excavations of this key Mesolithic archaeological area. Památky archeologické. 2010; 101:5–38.

Pokorný P, Chytrý M, Juřičková L, Sádlo J, Novák J, Ložek V. Mid-Holocene bottleneck for central European dry grasslands: Did steppe survive the forest optimum in northern Bohemia, Czech Republic? The Holocene. 2015; 25:716–726.

Poláček, L. Studien zum Burgwall von Mikulčice. Band 2. Institute of Archaeology, Academy of Sciences of the Czech Republic Brno; Brno: 1997.

Poláček, L. Studien zum Burgwall von Mikulčice. Band 3. Institute of Archaeology, Academy of Sciences of the Czech Republic Brno; Brno: 1998.

Poláček, L. Studien zum Burgwall von Mikulčice. Band 4. Institute of Archaeology, Academy of Sciences of the Czech Republic Brno; Brno: 1999.

Poláček, L. Studien zum Burgwall von Mikulčice. Band 6. Institute of Archaeology, Academy of Sciences of the Czech Republic Brno; Brno: 2005.

Pongratz J, Reick C, Raddatz T, Claussen M. A reconstruction of global agricultural areas and land cover for the last millennium. Global Biogeochemical Cycles. 2008; 22:16.

Pross J, Kotthoff U, Müller UC, Peyron O, Dormoy I, Schmiedl G, Kalaitzidis S, Smith AM. Massive perturbation in terrestrial ecosystems of the Eastern Mediterranean region associated with the 8.2 kyr BP climatic event. Geology. 2009; 37:887–890.

R Core Team. R: A language and environment for statistical computing. R Foundation for Statistical Computing; Vienna: 2014.

Rackham, O. Ancient woodland. Its history, vegetation and uses in England. 2d edition. Castlepoint Press; Dalbeattie: 2003.

Regnell M. Plant subsistence and environment at the Mesolithic site Tågerup, southern Sweden: new insights on the "Nut Age.". Vegetation History and Archaeobotany. 2012; 21:1–16.

Reimer P. IntCal13 and Marine13 radiocarbon age calibration curves 0–50,000 years cal BP. Radiocarbon. 2013; 55:1869–1887.

Riehl S, Pustovoytov KE, Hotchkiss S, Bryson RA. Local Holocene environmental indicators in Upper Mesopotamia: Pedogenic carbonate record vs. archaeobotanical data and archaeoclimatological models. Quaternary International. 2009; 209:154–162.

Rybníček K. The environmental evolution and infilling process of a former lake near Vracov (Czechoslovakia). Hydrobiologia. 1983; 103:247–250.

Rybníček, K., Rybníčková, E. Czech and Slovak Republics. Paleoecological events during the last 15000 years. Berglund, BE.Birks, HJB.Ralska-Jasiewiczowa, M., Wright, HE., editors. John Wiley & Sons; Chichester, New York, Brisbane, Toronto, Singapore: 1996. p. 488-490.

Rybníček K, Rybníčková E. Upper Holocene dry land vegetation in the Moravian–Slovakian borderland (Czech and Slovak Republics). Vegetation History and Archaeobotany. 2008; 17:701–711.

Rybníčková E, Rybníček K. Erste Ergebnisse paläogeobotanischer Untersuchungen des Moores bei Vracov, Südmähren. Folia Geobotanica & Phytotaxonomica. 1972; 7:285–308.

Seppä H, Birks HJB, Giesecke T, Hammarlund D, Alenius T, Antonsson K, Bjune AE, Heikkila M, MacDonald GM, Ojala AEK, Telford RJ, Veski S. Spatial structure of the 8200 cal yr BP event in northern Europe. Climate of the Past. 2007; 3:225–236.

Shennan S, Downey SS, Timpson A, Edinborough K, Colledge S, Kerig T, Manning K, Thomas MG. Regional population collapse followed initial agriculture booms in mid-Holocene Europe. Nature Communications. 2013; 4

Shuman B. Patterns, processes, and impacts of abrupt climate change in a warm world: the past 11,700 years. Wiley Interdisciplinary Reviews: Climate Change. 2012; 3:19–43.

Sládková-Hynková, H. Paleogeobotanická studie rašelinišťu Vracova. MSc. Thesis, Department of Plant Biology, Faculty of Science, University of Brno; Brno: 1974.

Sommer RS, Benecke N, Lõugas L, Nelle O, Schmölcke U. Holocene survival of the wild horse in Europe: a matter of open landscape? Journal of Quaternary Science. 2011; 26:805–812.

Strandberg G, Kjellström E, Poska A, Wagner S, Gaillard M-J, Trondman A-K, Mauri A, Davis BAS, Kaplan JO, Birks HJB, Bjune AE, et al. Regional climate model simulations for Europe at 6 and 0.2 k BP: sensitivity to changes in anthropogenic deforestation. Climate of the Past. 2014; 10:661–680.

Sugita S. A model of pollen source area for an entire lake surface. Quaternary Research. 1993; 39:239–244.

Sugita, S. POLLSCAPE Model. Encyclopedia of Quaternary Science. Scott, AE., editor. Elsevier; Oxford: 2007a. p. 2561-2570.

Sugita S. Theory of quantitative reconstruction of vegetation I: pollen from large sites REVEALS regional vegetation composition. Holocene. 2007b; 17:229–241.

Sümegi, P., Persaits, G., Gulyás, S. Woodland-Grassland Ecotonal Shifts in Environmental Mosaics: Lessons Learnt from the Environmental History of the Carpathian Basin (Central Europe) During the Holocene and the Last Ice Age Based on Investigation of Paleobotanical and Mollusk Remains. Ecotones Between Forest and Grassland. Myster, RW., editor. Springer; New York: 2012. p. 17-57.

Sümegi, P., Szilágyi, G., Gulyás, S., Jakab, G., Molnár, A. The late Quaternary paleoecology and environmental history of Hortobágy, a unique mosaic alkaline steppe from the heart of the Carpathian Basin. Steppe Ecosystems: Biological diversity, management and restoration (Environmental Research Advances). Morales Prieto, MB., Traba Diaz, J., editors. Nova Science Publishers; 2013. p. 165-193.

Svenning J-C. A review of natural vegetation openness in north-western Europe. Biological Conservation. 2002; 104:133–148.

Svobodová H. Rekonstrukce p írodního prost edí a osídlení v okolí Mist ína. Palynologická studie [Reconstruction of natural environment and human settlement round about Mist ín. A palynological study]. Památky archeologické. 1989; 80:188–206.

Svobodová H. Vegetace jižní Moravy v druhé polovin prvého tisíciletí. Archeologické rozhledy. 1990; 42:170–205.

Svobodová, H. Vývoj vegetace jižní Moravy b hem pozdním glaciálu a holocénu [Vegetation development of southern Moravia during the Late Glacial and Holocene]. Diss. Thesis, Institute of Botany; AS R Pr honice: 1992.

Svobodová H. Die Entwicklung der Vegetation in Südmähren (Tschechien) während des Spätglazials und Holozäns - eine palynologische Studie. Verhandlungen der Zoologisch-Botanischen Gesellschaft in Österreich. 1997; 134:317–356.

Theuerkauf M, Bos JAA, Jahns S, Janke W, Kuparinen A, Stebich M, Joosten H. *Corylus* expansion and persistent openness in the early Holocene vegetation of northern central Europe. Quaternary Science Reviews. 2014; 90:183–198.

Tinner W, Lotter AF. Central European vegetation response to abrupt climate change at 8.2 ka. Geology. 2001; 29:551–554.

Tinner W, Nielsen EH, Lotter AF. Mesolithic agriculture in Switzerland? A critical review of the evidence. Quaternary Science Reviews. 2007; 26:1416–1431.

Trondman A-K, Gaillard M-J, Mazier F, Sugita S, Fyfe R, Nielsen AB, Twiddle C, Barratt P, Birks HjB, Bjune AE, Björkman L, et al. Pollen-based quantitative reconstructions of Holocene regional vegetation cover (plant functional types and land-cover types) in Europe suitable for climate modelling. Global Change Biology. 2015; 21:676–697. [PubMed: 25204435]

van der Knaap WO, van Leeuwen JFN, Svitavská-Svobodová H, Pidek IA, Kvavadze E, Chichinadze M, Giesecke T, Kaszewski BM, Oberli F, Kalni a L, Pardoe HS, et al. Annual pollen traps reveal the complexity of climatic control on pollen productivity in Europe and the Caucasus. Vegetation History and Archaeobotany. 2010; 19:285–307.

van Geel, B. Non-Pollen Palynomorphs. Tracking Environmental Change Using Lake Sediments. Smol, JP.Birks, HJB.Last, WM.Bradley, RS., Alverson, K., editors. Springer; Netherlands: 2001. p. 99-119.

Vašátko J, Ložek V. Der holozäne Bodenkomplex von Pavlov und seine Bedeutung für die Landschaftsgeschichte des südmährischen Tschernosemgebietes. Zprávy Geografického ústavu SAV. 1973; 10:1–10.

Vera, FWM. Grazing ecology and forest history. CABI publishing; New York: 2000.

Vysloužilová B, Danková L, Ertlen D, Novák J, Schwartz D, Šefrna L, Delhon C, Berger J-F. Vegetation history of chernozems in the Czech Republic. Vegetation History and Archaeobotany. 2014; 23:97–108.

Walker MJC, Berkelhammer M, Björck S, Cwynar LC, Fisher DA, Long AJ, Lowe JJ, Newnham RM, Rasmussen SO, Weiss H. Formal subdivision of the Holocene Series/Epoch: a discussion paper by a working group of INTIMATE (Integration of ice-core, marine and terrestrial records) and the Subcommission on Quaternary Stratigraphy (International Commission on Stratigraphy). Journal of Quaternary Science. 2012; 27:649–659.

Whitehouse NJ, Schulting RJ, McClatchie M, Barratt P, McLaughlin TR, Bogaard A, Colledge S, Marchant R, Gaffrey J, Bunting MJ. Neolithic agriculture on the European western frontier: the boom and bust of early farming in Ireland. Journal of Archaeological Science. 2014; 51:181–205.

Wiersma AP, Renssen H. Model–data comparison for the 8.2 ka BP event: confirmation of a forcing mechanism by catastrophic drainage of Laurentide Lakes. Quaternary Science Reviews. 2006; 25:63–88.

Willis KJ, Bennett KD. The Neolithic transition - fact or fiction? Palaeoecological evidence from the Balkans. The Holocene. 1994; 4:326–330.

Willis KJ, Braun M, Sümegi P, Tóth A. Does soil change cause vegetation change or vice versa? A temporal perspective from Hungary. Ecology. 1997; 78:740–750.
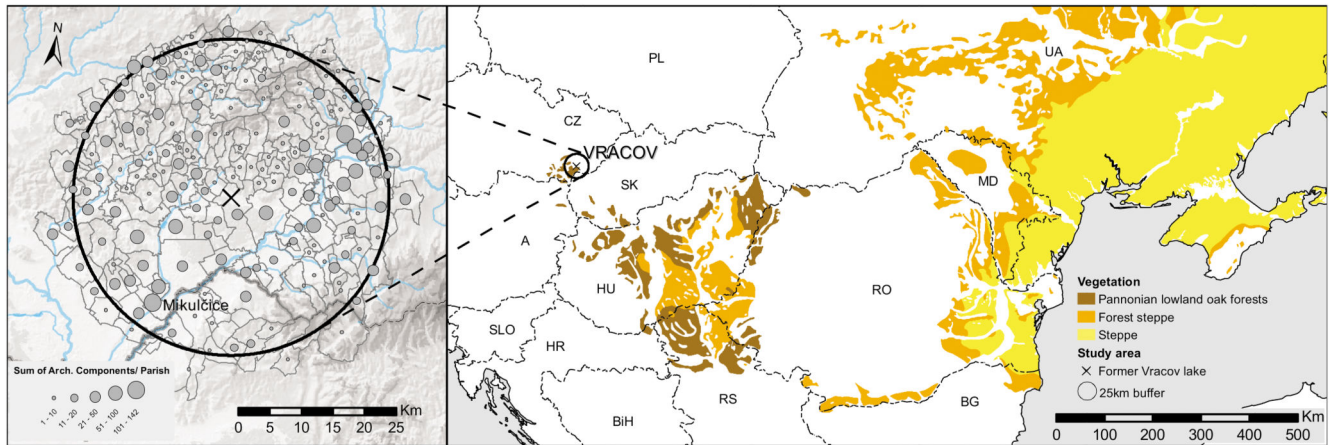
Fig. 1.
Right: Map of central and eastern Europe showing the location of Lake Vracov and the distribution of main vegetation types (steppe, forest steppe and Pannonian lowland oak forests) based on the potential natural vegetation map of Europe (Bohn et al. 2000). Left: Detailed map of the study area around Lake Vracov indicating the number of archaeological components (spatially continuous sets of finds delineated by their function and chronological position; for details see Materials and Methods section) in individual parishes.
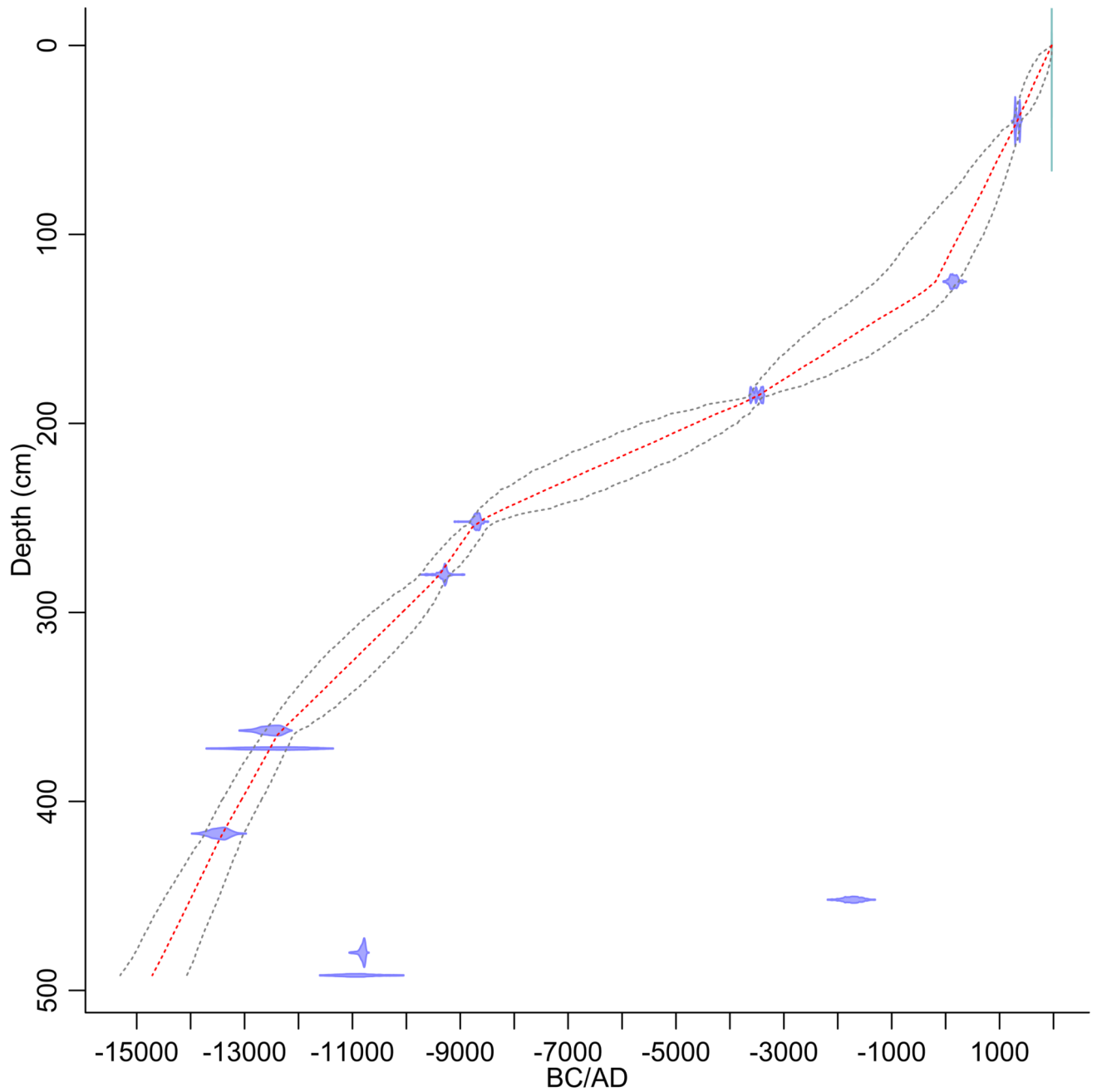
Fig. 2.
Age-depth model for the Lake Vracov pollen record constructed in Bacon v 2.2. Mean accumulation 20 yr/cm was used as a priori information. The three deepest dates were excluded from the model.
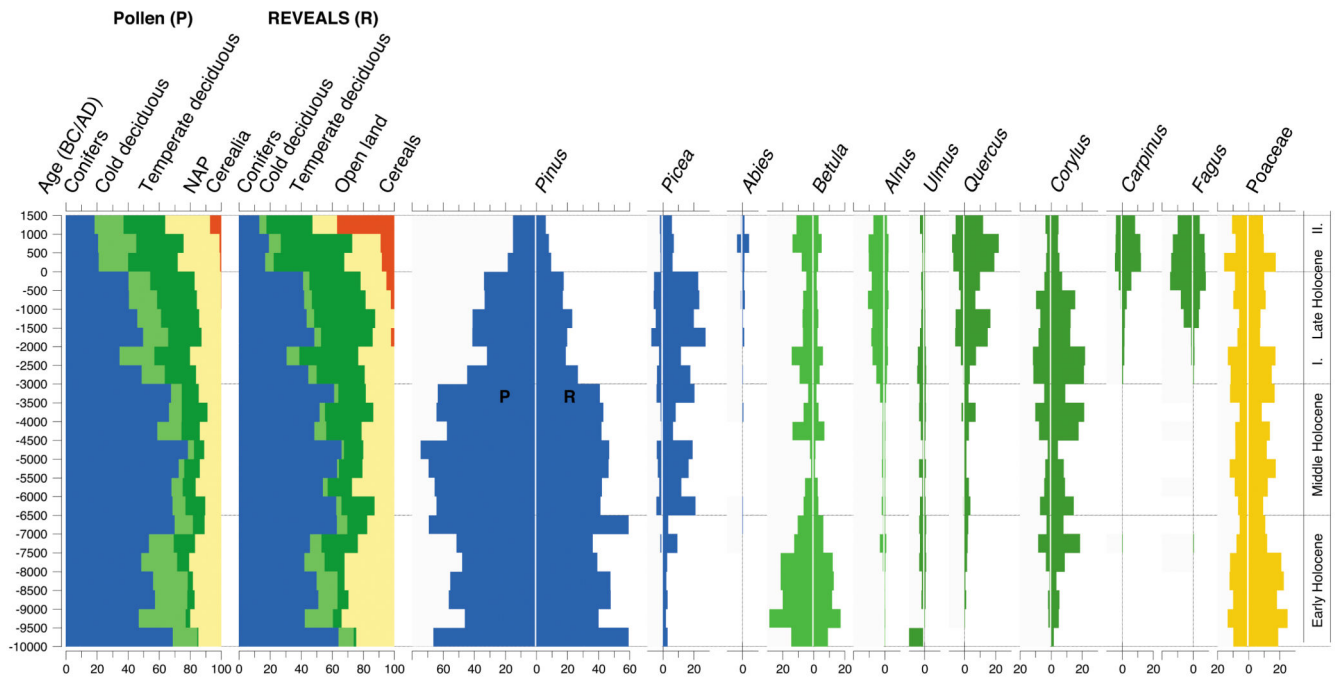
Fig. 3.

Percentage diagram showing Holocene REVEALS estimated vegetation (right columns, R) in the study area together with original pollen data (left columns, P) for comparison. Horizontal lines separate major vegetation zones analogous to pollen accumulation zones (see Appendix 1). Taxa are grouped into conifers (*Abies, Juniperus, Pinus, Picea*), cold deciduous trees (*Alnus, Betula, Salix*), temperate deciduous trees (*Carpinus, Corylus, Fagus, Quercus, Tilia, Ulmus*), open land - NAP (*Artemisia, Calluna vulgaris, Filipendula,* Chenopodiaceae, *Plantago lanceolata, P. media,* Poaceae, *Potentilla*-type, *Ranunculus acris*-type, Rubiaceae, *Rumex acetosa*-type, *Urtica*) and cereals (Cerealia-type, *Secale cereale*-type).
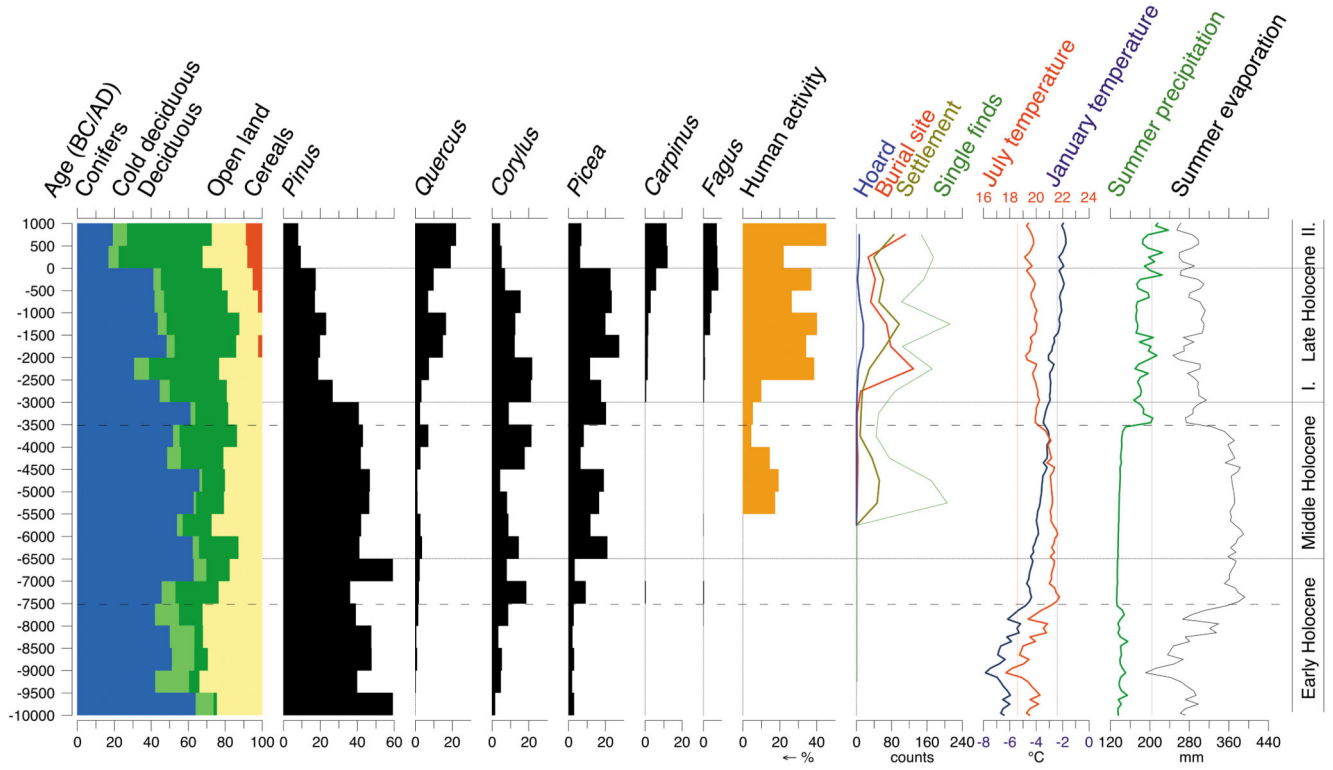
Fig. 4.

Diagram showing the general human activity model (parish occupancy likelihood) and differentiated human activity models in the study area, the results of the Macrophysical Climate Model (mean January temperature, mean July temperature, mean summer precipitation and mean summer evaporation) and major REVEALS-based vegetation components. Taxa are grouped as indicated in Fig. 3. Dotted horizontal lines separate major vegetation zones as in Fig. 3, dashed horizontal lines demarcate main climatic zones.
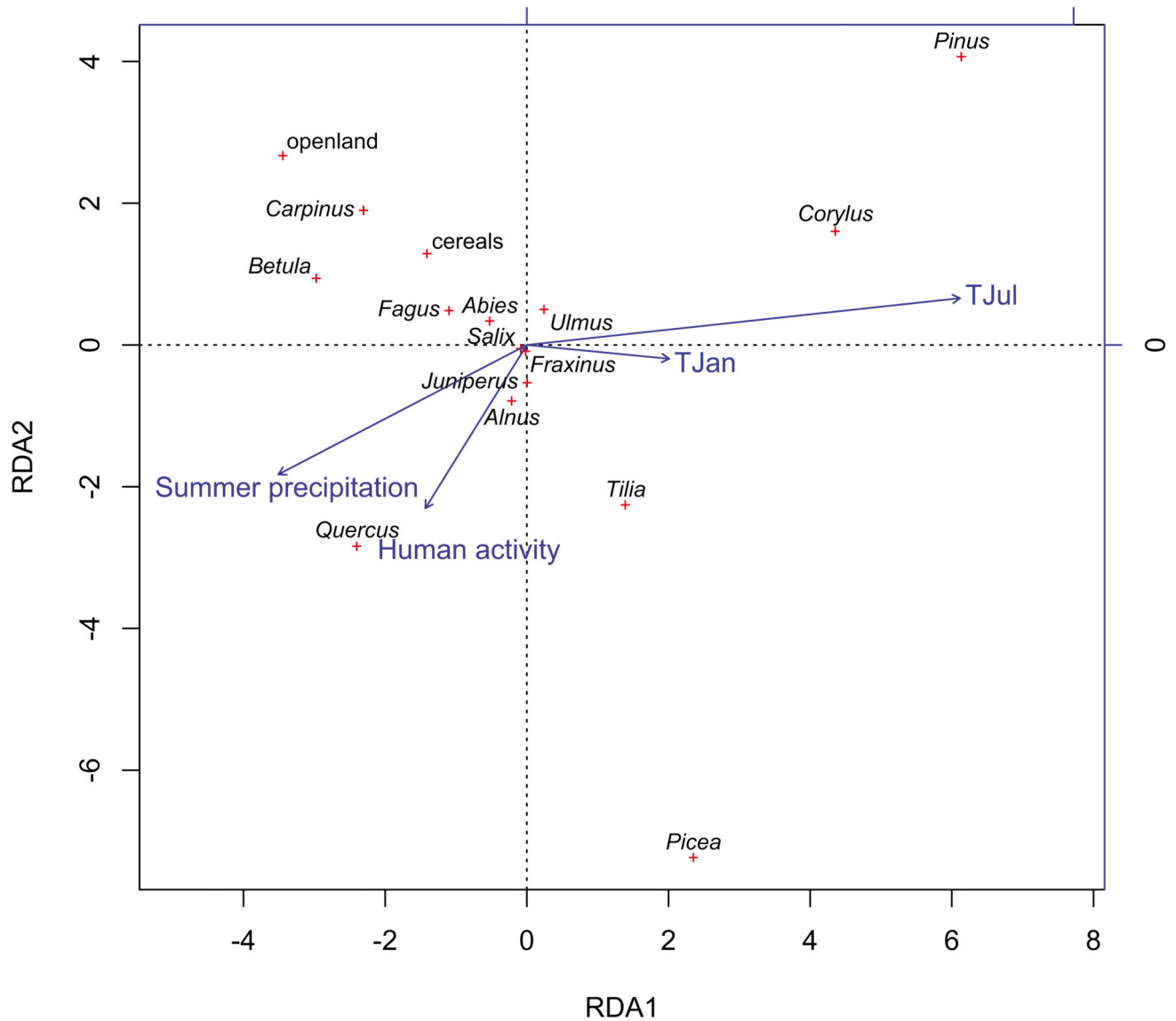
Fig. 5.
Redundancy analysis (RDA) biplot of REVEALS vegetation components correlated with environmental variables (human activity, summer precipitation, January (TJan) and July (TJul) temperatures).
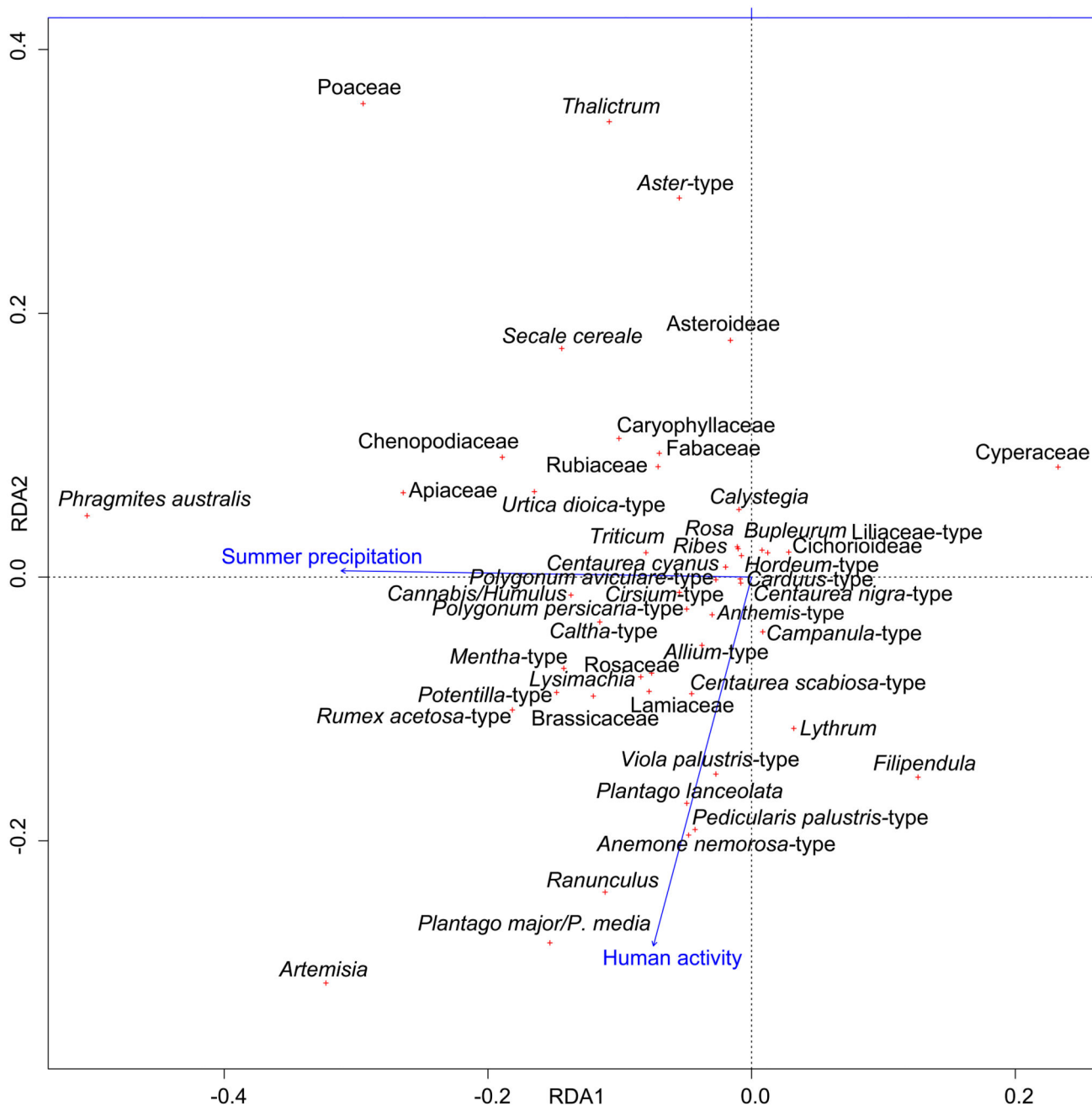
Fig. 6.
Redundancy analysis (RDA) biplot of selected pollen percentages correlated with environmental variables (human activity and summer precipitation).

Table 1

Pollen productivity estimates relative to Poaceae and their respective fall speeds used in the REVEALS model. Original PPEs were taken from the following publications: 1 – Abraham et al. (2014), 2 – Abraham & Kozáková (2012), 3 – Mazier et al. (2012).

	Relative pollen productivity	Fall speed of pollen – vg [m.s-1]	citation
Abies	12.77	0.12	1
Alnus	4.2	0.021	1
Artemisia	3.48	0.025	3
Betula	2.62	0.024	1
Calluna vulgaris	0.82	0.038	3
Carpinus	0.5	0.042	1
Cerealia-t	0.046	0.06	1
Corylus	1.4	0.025	1
Fagus	1.2	0.057	1
Filipendula	2.81	0.006	3
Fraxinus	0.18	0.022	1
Chenopodiaceae	4.28	0.019	2
Juniperus	2.07	0.016	3
Picea	0.47	0.056	1
Pinus	2	0.031	1
Plantago lanceolata	0.9	0.029	1
Plantago media	1.27	0.024	3
Poaceae	1	0.035	1
Potentilla-t	1.19	0.018	3
Quercus	0.42	0.035	1
Ranunculus acris-type	1.96	0.014	3
Rubiaceae	2.61	0.019	3
Rumex acetosa-type	2.14	0.018	3
Salix	2.31	0.022	1
Secale-t	3.02	0.06	3
Tilia	0.5	0.032	1
Ulmus	6	0.032	1
Urtica	10.52	0.007	2

Table 2

Radiocarbon ages for the Lake Vracov profile DU-7-D. Dates marked (*) originate from a previous study (Svobodová, 1992), dates marked (**) were rejected in the age-depth model. Dates were calibrated using the IntCal13 calibration curve (Reimer, 2013) in Oxcal (Bronk Ramsey, 2009).

Sample depth (cm)	Laboratory number	Material dated	Method	Radiocarbon age (^{14}C years BP)	Calibrated age (cal. years AD/BC)
39.5–40.5	Poz-51951	Seeds of *Carex*	AMS	670±30	AD 1274–1320 AD 1351–1391
124.5–125.5	Poz-51947	Plant remains	AMS	1870±50	AD 25–252 AD 305–311
184.5–185.5	Poz-51948	Plant remains	AMS	4715±35	3632–3560 3537–3494 3466–3375
252	Beta377320	Pollen extract	AMS	9410±40	8793–8604 8581–8575
280	Poz-51949	Seed of *Najas marina*	AMS	9830±60	9446–9211
362.5	Beta377321	Pollen extract	AMS	12390±50	12839–12197
372	HV-1868 *	Bulk organic fraction	BC	12260±372	13634–11487
417	Poz-51952	Plant remains	AMS	12890±90	13767–13187
452	Poz-51954	Plant remains	AMS	3410±120**	
480	Beta364949	Pollen extract	AMS	10880±50**	
487–497	HV-18599 *	Bulk organic fraction containing sand	BC	10985±355**	