



Contrasting Holocene environmental histories may explain patterns of species richness and rarity in a Central European landscape



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ABSTRACT

The south-western part of the White Carpathians (Czech Republic, Slovakia) is known for its exceptional grassland diversity and occurrence of many species with disjunct distribution patterns, including isolated populations of continental forest-steppe species. The north-eastern part of the mountain range lacks many of these species and has clearly lower maxima of grassland species richness. While climatic and edaphic conditions of both regions largely overlap, their specific environmental history has been hypothesized to explain the exceptional richness in the south-western part. We explored an entire-Holocene record (9650 BC onwards), the first one from the north-eastern part, to find out whether differences in history may explain regional patterns of species rarity and richness. We analysed pollen, macrofossils and molluscs and dated the sequence with 13 radiocarbon dates. We further reconstructed past human activities using available archaeological evidence. Based on this analysis, the Early-Holocene landscape was reconstructed as semi-open with broad-leaved trees (elm and lime) appearing already around 9500 BC. Lime reached a relative abundance of as much as 60% around 8700 BC. All analysed proxies support the existence of dense lime-dominated woodland during the forest optimum starting after climate moistening around 6800 BC, some 2200 years before the first signs of slight forest opening in the Late Neolithic. During the Bronze and Iron Ages, human pressure increased, which led to a decrease in lime and an increase in oak, hornbeam, grasses and grassland snails; nevertheless, forests still dominated the landscape and beech spread when human impact temporarily decreased. Colonisation after AD 1350 created the modern grassland-rich landscape. All available evidence confirmed an early post-Glacial expansion of broad-leaved trees, supporting the hypothesis on their glacial refugia in the Carpathians, as well as presence of closed-canopy forest well before the Neolithic. This environmental history was unfavourable for the survival of Early-Holocene forest-steppe species in the north-eastern White Carpathians and may explain the impoverished grassland flora compared to the south-western part. We conclude that contrasting Holocene histories may explain those patterns in species richness and distributions, which cannot be explained by recent environmental conditions alone.

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1. Introduction

Distribution of biodiversity over the Earth's surface is highly uneven on different spatial scales (Gaston and Spicer, 2013; Pimm et al., 2014; Michalčová et al., 2014; Chytrý et al., 2015). Some regions display exceptional species diversity (richness hotspots;

Lennon et al., 2001) or exceptional concentrations of rare species (rarity hotspots; Williams et al., 1996; Ohlemüller et al., 2008; Crain and Tremblay, 2014). Knowledge of these hotspots is important for both regional and global conservation efforts, but we often lack information on their origin and mechanisms of maintenance of their diversity. Some studies emphasize the effects of specific local environmental conditions and their fluctuations, management, landscape complexity and connectivity (e.g., Fischer et al., 2014; Kormann et al., 2015; Mathar et al., 2015). However, not all rarity

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and richness hotspots are well explained by environmental factors (Lennon et al., 2011; Merunková et al., 2012). It was shown that historical factors shaping regional species pools and local survivals at large time scales may play a role as well (Svenning and Skov, 2007; Willner et al., 2009; Zobel et al., 2011; Horskák et al., 2012, 2015).

On the Holocene time scale, unique interactions between pre-historic agriculture, climate and local environment might have facilitated the development of rarity and richness hotspots in temperate landscapes (Pärtel et al., 2007; Hájková et al., 2011; Roleček et al., 2014; Pokorný et al., 2015). Testing such hypotheses is never straightforward, because historical factors acting in the Holocene are difficult to grasp numerically. Available palaeoecological data may limit relevance for addressing these hypotheses: they often detect patterns of vegetation development at too coarse scales and only rarely cover an entire-Holocene development directly within the richness and rarity hotspots. If they do so (e.g. Feurdean et al., 2015), comparative data for analogous sites outside the hotspot are usually missing. Discovering entire-Holocene palaeorecords relevant for the sites of interest is often a matter of chance and for many hotspots no suitable data are available. We feel that under such circumstances even palaeoecological studies based on the analysis of a single or a few profiles may bring important insights into regional environmental histories and the formation of specific biogeographical patterns (Colombaroli et al., 2013; Hájková et al., 2015; Feurdean et al., 2015; Kuneš et al., 2015).

The south-western part of the White Carpathians (Western Carpathians Mts, Czech Republic and Slovakia) is a well-known example of a rarity and richness hotspot which is difficult to explain in terms of available environmental data. Neither the geological bedrock (calcareous flysch) nor the climate of this region are exceptional within Central Europe. Extreme habitats are lacking and there is no endemism. In spite of this, local semi-dry grasslands reach a uniquely high alpha diversity of vascular plants (Wilson et al., 2012; Chytrý et al., 2015), with a high representation of habitat specialists (Fajmonová et al., 2013) and disjunct occurrences of many species (Hájková et al., 2011), which has challenged scientists for decades (Sillinger, 1929; Podpěra, 1930; Nevole, 1947; Škodová et al., 2011; Michalcová et al., 2014). It has been hypothesized that the exceptional species richness is partially caused by the presence of light-demanding relicts of Early-Holocene forest-steppe communities (Podpěra, 1930; Ložek, 2008; Hájková et al., 2011; Roleček et al., 2015). This hypothesis is supported by complex, although incomplete, evidence. The early prehistoric agriculture in the region might have prevented complete forest encroachment and extinction of light-demanding species (Hájková et al., 2011). Shells of snails found in the Kazivec profile (Ložek, 2008; site 5 in Fig. 1) also suggest a continuous occurrence of open landscape during the forest optimum. However, precise dating of selected shells (M. Horskák, unpublished data) showed that individual layers of this sequence include different periods, thus the profile requires re-assessment. Continuous existence of steppe grasslands throughout the Middle-Holocene forest optimum was recently reported for the Morava river valley (Kuneš et al., 2015), a lowland region adjacent to the south-western White Carpathians (site 2 in Fig. 1). The lowland, however, does not support such a high alpha diversity, probably because of different site conditions and different history of human activities in the past centuries (Hájková et al., 2011).

Plant species composition in the north-eastern part of the White Carpathians is clearly separated from that of the south-west, while environmental conditions are less differentiated (Otýpková et al., 2011). The north-east is generally more humid and colder, but values of the main climatic characteristics of the two regions largely

overlap. The north-east is generally poorer in species (Otýpková et al., 2011), lacks world-record extremes of alpha-diversity (Chytrý et al., 2015) and harbours only few occurrences of rare species with disjunctive distribution ranges. Besides that, these species belong more often to Submediterranean or perialpine biogeographical elements (e.g. *Aposeris foetida*, *Aremonia agrimonoides*, *Carex ornithopoda*, *Hippocrepis comosa*, *Potentilla micrantha*, *Tephrosieris longifolia*) than to continental ones, which is typical of the south-west (Hájková et al., 2011; Otýpková et al., 2011). We explored whether these differences can be ascribed solely to (minor) differences in climate and geographical position, or whether they are the result of different Holocene environmental histories. For this purpose we utilised a newly discovered entire-Holocene palaeorecord in calcareous spring deposits located well inside the north-eastern part of the study area. We focused on interpretation of pollen and plant macrofossil data, but also involved fossil mollusc data and archaeological evidence.

2. Material and methods

2.1. Regional setting and field sampling

The study site is located close to the Mituchovci settlement (village of Horná Súča, Trenčín District, Slovakia), in the north-eastern part of the White Carpathians (Fig. 1) at an altitude of 438 m a.s.l. Geographical coordinates (WGS-84) are: 48°56'45" N; 17°58'24" E. In 2010 a 274-cm deep vertical cross-section through fen deposits was exposed, from which a profile was taken into metal boxes (50 × 10 × 10 cm). Moreover, 10–20 cm thick layers (according to lithological boundaries) were collected into plastic bags with the aim of obtaining more material for palaeomalacological research. In order to increase the resolution of the palaeomalacological data, the site was revisited in 2012, when an additional core was sampled close to the previous cross-section using a gouge auger of 100 cm long and 6 cm in diameter. Selected results from this core (Moutelíková, 2015) are also included.

2.2. Pollen, microcharcoal and macrofossil analyses

Our profile was sampled at intervals of 5 cm for pollen and microcharcoal analysis. Samples of 1–2 cm³ were acetolysed according to standard methods (Faegri and Iversen, 1989); some samples were additionally treated in HCl due to the large amount of carbonates. Tablets with *Lycopodium* markers were added to the samples in order to calculate pollen and charcoal concentrations (Stockmarr, 1971). Generally the samples were poor in pollen which was moreover badly preserved because of tufa (calcium carbonate) precipitation, therefore at least 100 grains, in some cases only 50 grains, were counted per sample. Bad preservation may affect percentages of some species, with coniferous trees, *Tilia* and *Corylus* being rather resistant to corrosion and/or oxidation, while *Quercus*, *Fagus*, *Acer*, *Fraxinus* and *Ulmus* being rather sensitive (Havinga, 1964). This might have affected especially *Tilia*, which was found in unusually high percentages in our study (see Section 3). We therefore compared its representation with a wider data set of pollen spectra from tufa fens (Hájek et al., 2011). We further confronted our pollen record with the curve of overall pollen concentration and sum of indeterminable pollen (unidentified mostly because of degradation and crumpling). To avoid possible preservation biases in microcharcoal, we calculated charcoal concentrations related to both the marker and the sum of other preserved microfossils. Only robust peaks appearing after application of both adjustments were interpreted.

Pollen was identified using standard literature (The Northwest

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