# Prehistoric origin of the extremely species-rich semi-dry grasslands in the Bílé Karpaty Mts (Czech Republic and Slovakia)

**Prehistorický původ extrémně druhově bohatých subxerofilních luk v Bílých Karpatech**

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Bílé Karpaty Mts harbour some of the most species-rich managed grasslands in Europe, which contain a number of rare and disjunctly distributed species. Besides specific local environmental factors, the long Holocene history may explain the uniqueness of these grasslands. However, historical interpretations of the palaeoecological evidence from the region are far from unequivocal. While palaeomalacological data indicate persistence of open habitats throughout the entire Holocene, fragmentary pollen data support the hypothesis of a medieval origin of the grasslands. This paper reviews the available phytogeographical, archaeological and palaeoecological knowledge that provides indirect evidence for a prehistoric origin of the grasslands in the Bílé Karpaty Mts. High concentration of rare heliophilous species with a disjunct distribution in the south-western part of the Bílé Karpaty Mts suggest their long-term persistence. The archaeological findings provide evidence for the existence of prehistoric human settlement in this region since the Neolithic (Middle Holocene). Direct evidence for the existence of open human-influenced habitats before medieval times, based on the results of a multi-proxy analysis (macrofossils, molluscs and pollen) of an organic sediment dated back to Roman Age, is also provided. The results indicate the existence of an ancient cultural landscape with a mosaic of open grasslands, natural forests and fields. It is concluded that the evidence presented in this paper supports the hypothesis of prehistoric, rather than a medieval origin of the species-rich grasslands in the Bílé Karpaty Mts.

K e y w o r d s: Czech Republic, disjunct distribution, environmental history, Holocene, macrofossils, molluscs, palaeoecology, pollen, relict species, semi-dry grasslands, Slovakia, species richness

## Introduction

Development of grassland vegetation in Central Europe has been closely connected with human activities. Natural grasslands are largely confined to ecologically extreme habitats where the competition from trees is low, e.g. steep sunny slopes with shallow dry soils, rocky outcrops, oligotrophic waterlogged fens or the alpine zone (Ellenberg 1988, Ložek

2007, Poschlod et al. 2009). However, most of the Central European grasslands in favourable habitats are human-made and when unmanaged, they usually successionally change towards scrub and forest vegetation (Ellenberg 1988, Hansson & Fogelfors 2000, Moog et al. 2002). Grazing and mowing have created characteristic cultural landscapes with an important proportion of grassland communities all over Europe (Birks et al. 1988).

Calcareous semi-dry grasslands in the Bílé Karpaty Mts (south-eastern Czech Republic, south-western Slovakia), classified as *Brachypodio pinnnati-Molinietum arundinaceae* association (Chytrý et al. 2007), belong to the most remarkable European grassland communities (Jongepierová 2008, Jongepier & Jongepierová 2009). Their extraordinarily high local species richness ($\alpha$-diversity) surpasses that of most other European grassland communities and is comparable to that of the species-richest zonal steppes (Klimeš 2008). In addition, grasslands of the Bílé Karpaty Mts are unique due to numerous occurrences of plant species that are rare or absent in neighbouring regions and have areas of distribution that are characteristically disjunct (Podpěra 1951, Grulich 2008). This ecologically diverse group includes mainly species of continental steppe and heliophilous montane species growing at rather low altitudes (Table 1).

Causes of the high species richness and the unique species composition, however, are not fully understood. Both specific local environmental factors (Klimeš 1997, Kubíková & Kučera 1999, Klimeš 2008) and historical factors (Sillinger 1929, Grulich 2008, Ložek 2008) are hypothesized to determine this pattern. While ecological research has helped to partly clarify the role of environmental factors and management (Klimeš 1997, Klimeš & Klimešová 2001), scarcity of palaeoecological data has remained the major impediment to understanding the role of history in regional grassland development. Improving the knowledge of environmental history of the Bílé Karpaty Mts is all the more urgent, as several recent studies from different regions have identified significant relationships between grassland history and species richness (e.g. Cousins & Eriksson 2002, Chýlová & Münzbergová 2008, Karlík & Poschlod 2009). Land-use history and the age of grasslands may go back as far as the Iron Age (Bruun et al. 2001, Pärtel et al. 2007) or even earlier (Pärtel & Zobel 1999, Baumann & Poschlod 2008, Dutoit et al. 2009, Henry et al. 2010). Growing palaeoecological evidence for grassland occurrence in Central Europe during prehistoric times (e.g. Rösch 1996, Waller & Hamilton 2000, Pokorný et al. 2006, Baumann & Poschlod 2008, Magyari et al. 2010, Poschlod & Baumann 2010) supports the assumption that prehistoric agriculture was able to maintain a sufficiently open landscape to facilitate heliophilous species survival from the Neolithic onwards.

Due to the lack of organic sediments suitable for pollen and plant macrofossil preservation in the Bílé Karpaty Mts, palaeoecological pollen data available come only from spring fen sediments dated to Late Holocene and mostly located outside the centre of distribution of the species-rich grasslands (Rybníček & Rybníčková 2008). These pollen data indicate a late medieval deforestation of lower altitudes and foothills (11th–13th centuries) and even later deforestation of higher altitudes (since the 15th century on during the Walachian colonization; Rybníček & Rybníčková 2008). Presence of pollen grains of light-demanding species (such as *Achillea* type, *Centaurea scabiosa*, *Geranium* sp., *Melampyrum* sp., *Plantago lanceolata*, *P. media*, *Succisa pratensis* and *Thalictrum* sp.) in older sediments was not interpreted as evidence for the existence of grasslands.

Table 1. – List of light-demanding vascular plant species with disjunct distributions occurring in the Bílé Karpaty Mts. Data on distribution were taken from Čeřovský et al. (1999), Dostál (1986, 1989), Grulich (2008), Jongepier & Pechanec (2006), Meusel et al. (1965–1992), Řepka (1993) and other sources. Threat status of the species in the Czech Republic (A2 – missing, C1 – critically threatened, C2 – strongly threatened) follows Holub & Procházka (2000). Second column presents the number of sites in the Bílé Karpaty Mts (all/recently confirmed). Closely adjacent localities are considered as one. Distance to the nearest site was measured as the shortest distance between any site outside the Bílé Karpaty Mts and the nearest site in the Bílé Karpaty Mts. Numbers of sites are those recorded in the BKFLORA database (Jongepier & Jongepierová 2006, Jongepier & Pechanec 2006).

| Species | Number of sites | Nearest site outside the Bílé Karpaty Mts | Location of compact distribution range |
|---|---|---|---|
| *Allium victorialis*, C2 | 1/1 | Javorníky Mts, Slovakia, ca 70 km | (sub)alpine zone in the Alps and the Carpathians |
| *Carex depressa* subsp. *transsilvanica* | 1/1 | Štiavnické vrchy Mts, Slovakia, ca 130 km | Eastern and Southern Carpathians, Balkans, Middle East (requires further taxonomical study) |
| *Crocus albiflorus*, C1 | 1/1 | Wienerwald, Austria, ca 160 km; Vizovické vrchy Mts, Czech Republic, ca 35 km, native? | the Alps and Dinarids |
| *Danthonia alpina*, C1 | 13/7 | Štiavnické vrchy Mts, Slovakia, ca 130 km | no compact range; rather abundant at middle altitudes in the Balkans, Apennines and Dinarids, on the margins of the Carpathians and the Alps |
| *Gentiana acaulis*, A1 | 1/0 | Moravskoslezské Beskydy Mts, Czech Republic, ca 90 km, native?; Joglland, Austria, ca 220 km | (sub)alpine zone of the Alps |
| *Lathyrus pannonicus* subsp. *pannonicus*, C1 | 4/3 | Malé Karpaty Mts, Slovakia, ca 55 km | perhaps an endemic taxon of the Pannonian lowland (requires further taxonomical study) |
| *Lilium bulbiferum*, C2 archaeophyte? | 11/4 | Nízký Jeseník Mts, Czech Republic, ca 90 km; Malá Fatra Mts, Slovakia, ca 90 km | no compact range (European montane species) |
| *Pedicularis exaltata*, C1 | 1/1 | Romania, ca 520 km | no compact range; spot distribution in Romania, Ukraine and Poland |
| *Peucedanum carvifolia*, C1 | 1/1 | Malé Karpaty Mts, Slovakia, ca 45 km | no compact range; spot distribution from Spain to the Ural Mts |
| *Potentilla micrantha*, C2 | 9/9 | Považský Inovec Mts, Slovakia, ca 40 km; Hanácká pahorkatina Hills, Czech Republic, 70 km | Apennines, Dinarids, Balkans, east coast of Black Sea, North Africa; spot distribution in Central Europe |
| *Pseudolysimachion spurium*, C1 | 11/1 | Malé Karpaty Mts, Slovakia, ca 65 km | from eastern Poland and Lithuania to Siberia; spot distribution in Central Europe |
| *Senecio erucifolius*, C1 | 10/0 | Valtická pahorkatina Hills, Czech Republic, ca 65 km, Záhorská nížina Lowland, Slovakia, ca 60 km | distributed from Atlantic ocean to Eastern Siberia, Mongolia and China; spot distribution in Central Europe. |
| *Senecio umbrosus*, C2 | 25/>10 | Strážovské vrchy Mts, Slovakia, ca 35 km | no compact range; spots in Poland, Western Carpathians, Dinarids and Balkan mountains |
| *Serratula lycopifolia*, C1 | 18/6 | Kyjovská pahorkatina Hills, Czech Republic, ca 35 km | Ukraine east of Dniestr and southern Russia; spot distribution in Western and Central Europe |
| *Tephroseris longifolia* subsp. *moravica*, C1 | 9/4 | Tribeč Mts, Slovakia, ca 60 km | no compact range; endemic taxon of western part of the western Carpathians isolated from other populations of *T. longifolia* s.l. |
| *Veratrum nigrum*, C1 | 3/3 | Middle Dyje valley, Czech Republic, ca 120 km | from eastern Poland to Siberia; spot distribution in western and Central Europe |

On the contrary, palaeomalacological analyses indicate the presence of treeless patches throughout the whole climatic optimum (Atlantic and Epiatlantic periods, ca 6500–1400 BC) and gradual deforestation from the Subboreal period on (ca 1400 BC; Ložek 2008). How dry-grassland snail species have survived in the Bílé Karpaty Mts during the spread of shade-tolerant competitive tree species (particularly *Fagus sylvatica* and *Carpinus betulus*) nevertheless remains unclear. Ložek (2008) hypothesizes the crucial role of large-herbivore grazing, as well as the influence of prehistoric human settlement since the Bronze Age, which probably resulted in the development of small patches of grassland vegetation.

The hypothesis of a long Holocene history of grasslands in the Bílé Karpaty Mts is further supported by the occurrence of rare heliophilous vascular plant species with disjunct distributions. Some of the species are supposed to have been more frequent in the cold periods of glacial cycles in Central Europe, when dry continental climate maintained open landscapes with abundant grassland vegetation (Ložek 2007). The unusual concentration of these species is hypothesized to be of relict origin: the species have presumably survived here since the times of naturally open landscape in the Early Holocene (ca 9500–6500 BC; Ložek 2007). Again, the mechanisms of survival of the heliophilous species through the period of Holocene forest spread, in regions lacking rocks and other extreme habitats, remain unclear.

Data on regional environmental history was gathered from different sources in order to evaluate the above hypotheses on the age of the grasslands. The data on the distribution of rare heliophilous species with disjunct distributions in the Bílé Karpaty Mts was obtained from the literature. All of the archaeological records of human settlement between the Neolithic and Iron Age in this region, which previously were largely scattered in local journals or even unpublished, were reviewed in order to check their spatial relationships to the area of distribution of species-rich semi-dry grasslands. It is assumed that archaeological evidence of human settlement since the Atlantic period in the area where the species-rich grasslands with rare heliophilous species occur would give support to the hypothesis that these grasslands are relicts of heliophilous communities of the Early Holocene. Further, an attempt was made to enrich the direct palaeoecological evidence for the environmental history in the Bílé Karpaty Mts. A field survey yielded fossil organic sediment in the alluvium of the Velička river near Velká nad Veličkou village, right in the centre of the south-western part of the Bílé Karpaty Mts, where the most species-rich grasslands occur. This sediment was analysed using the multi-proxy approach, including analyses of plant macrofossils (seeds, bryophyte leaves), pollen and molluscs in order to obtain more detailed evidence of the past landscape structure. It was assumed that unequivocal palaeoecological evidence for prehistoric origin of regional grassland communities might help to explain their extreme species richness. Based on this evidence an attempt was made to construct a possible scenario of Holocene development of the landscape in the Bílé Karpaty Mts.

## Materials and methods

*Study area and vegetation characteristics*

Bílé Karpaty Mts belong to the Flysch Belt of the Outer Western Carpathians, which originated in the Cretaceous and Tertiary together with the the Rhenodanubian Flysch of the Eastern Alps (Froitzheim et al. 2008). Carpathian Flysch consists of an alternating sequence of sedimentary rocks of different grain size, mostly sandstones and claystones of variable thickness. Flysch properties determine the topography and hydrogeology of the region. Landslides are common, denuding the bedrock and often changing the location of springs. In the south-western part of the Bílé Karpaty Mts, the Hluk development of the Bílé Karpaty Unit belonging to the Magura group of nappes prevails. It is characterized by the dominance of claystones rich in calcium carbonate and poor in silica. This easily eroded bedrock has resulted in the development of characteristic landscape with long gentle slopes, broad valleys and rounded ridges. Both surface and ground water is rich in calcium that abundantly precipitates around springs as calcareous tufa. On the other hand, the highest ridges (Velká Javořina, 970 m a.s.l.; Velký Lopeník, 911 m a.s.l.) are mostly formed of calcareous sandstones of the Vlára flysch development, which are also common in the north-eastern part of the mountain range. The territories of Bystrica and Rača Units are not considered in this paper as the species-rich grasslands of *Brachypodio-Molinietum* association do not occur there. Along the eastern boundary of the mountain range a narrow klippen belt passes, built of limestones and marlstones of Cretaceous and Paleogenic age (Buday 1967, Pechanec & Jongepierová 2008).

The area lies on a steep climatic gradient with warm foothills, moderately warm hilly landscapes with the species-rich grasslands and cool mountain ridges; average annual temperatures range approximately from 4.5 to 9.5 °C. The precipitation sums are rather high due to orographic precipitation; average annual sums range approximately from 600 to 1000 mm (Quitt 1971, Pechanec & Jongepierová 2008).

The species rich semi-dry grasslands occur mainly in the south-western part of the Bílé Karpaty Mts. The prevailing grassland vegetation type is usually classified within the *Bromion erecti* or *Cirsio-Brachypodion pinnati* alliances and *Brachypodio pinnati-Molinietum arundinaceae* association (Tlusták 1975, Chytrý et al. 2007, Škodová et al. 2008). The grasslands are characterized by relatively high productivity and extremely high species richness. Klimeš et al. (2001) identified up to 99 vascular plant species per 4 $m^2$. Usually 60 to 70 species are found in a vegetation plot of 16 $m^2$ (Tlusták 1975, Klimeš 2008, Škodová et al. 2008). The vegetation is composed of grasses (*Avenula pubescens*, *Brachypodium pinnatum*, *Bromus erectus*, *Festuca rupicola* and *Molinia arundinacea*), sedges (*Carex caryophyllea*, *C. michelii* and *C. montana*) and a high number of broad-leaved herbaceous plants, including many orchids. Another feature characteristic of these grasslands is the presence of intermittently-wet meadow species (*Betonica officinalis*, *Galium boreale*, *Inula salicina*, *Molinia arundinacea*, *Potentilla alba*, *Sanguisorba officinalis* and *Serratula tinctoria*), which may indicate temporary moistening in the upper soil layers, perhaps caused by a high clay content. Vegetation also includes many (sub)continental species and species with disjunct distributions, sometimes considered as ancient relicts (see the list of species with disjunct distributions in the Table 1).

Nomenclature follows Kubát et al. (2002) for vascular plants except for *Carex depressa* subsp. *transsilvanica* (Schur) Richter, Hill et al. (2006) for bryophytes and Juřičková et al. (2001) for molluscs.

*Distribution of prehistoric human settlement, Brachypodio-Molinietum grasslands and species with disjunct distributions*

Information on human settlement of the study area between the Neolithic and Iron Age was compiled both from published and unpublished sources and critically reviewed. Archaeological records were divided into six categories according to their age: Neolithic, Linear Ware culture; Neolithic, Moravian Painted Ware culture; Early Eneolithic, Moravian Painted Ware culture, Lengyel development; Late Eneolithic, Corded Ware culture; Bronze Age; Iron Age. According to the intensity of settlement, records were divided into four categories: hilltop settlement, settlement, burial ground and fragmentary record. The archaeological records in the distribution range of *Brachypodio-Molinietum* grasslands were mapped. Lowlands around the Morava, Váh, Olšava and Myjava rivers, with dense continuous human settlement since the Early Neolithic, were not reviewed in detail. In the north-eastern part of the Bílé Karpaty Mts, the study was restricted to the territory of flysch sediments of the Bílé Karpaty Unit and the klippen belt; the territories of Rača and Bystrica Units were not considered, as *Brachypodio-Molinietum* grasslands do not occur there.

The distribution of *Brachypodio-Molinietum* grasslands is that of Sillinger (1929) who mapped this type of vegetation before the agriculture intensification in the second half of the 20th century. A database of vegetation records that includes data from both the Czech and Slovak parts of the study area (Škodová et al. 2008) were also used to complete Sillinger's map. To select the records of *Brachypodio-Molinietum* association, the formal definition published in Chytrý et al. (2007) was used and made more restrictive by using the condition of presence of the *Serratula tinctoria* sociological species group (at least two species out of *Betonica officinalis*, *Galium boreale* subsp. *boreale*, *Potentilla alba* and *Serratula tinctoria* had to be present in the record). This analysis recognized only a few additional sites not included on Sillinger's map, particularly in the klippen belt region. In the resulting map, the sites that harbour rare heliophilous species with disjunct distributions, i.e. the hypothesized relicts of the era before the Atlantic and Subboreal spread of shade-tolerant competitive trees, were highlighted. These hypothesized relict species (Table 1) were selected using the following criteria: (i) a light-demanding or moderately shade-tolerant species; (ii) a species with a disjunct distribution range and discontinuous distribution in Central Europe (the nearest occurrences are usually more than 50 km distant from the study area, with several exceptions of spot distribution ca 35–45 km distant; see Table 1); (iii) a species growing in semi-natural habitats (avoiding field margins and field fallows) and preferring deep soils (to diminish the possibility of survival on open calcareous rocks – klippen belt in the study area – instead of grassland patches).

*Sediment description and palaeoecological analyses*

The analysed organic sediment originates from the valley bottom of the river Veličká near Velká nad Veličkou village (Fig. 1). It was buried by alluvial sediments ca 230 cm below the surface and found during excavation at a local sewerage plant in 1995. The sediment was sampled by a local amateur naturalist Josef Vaněk and stored in two sealed plastic bags in a cold cellar. We learned about the existence of this sediment during a field survey in 2009.

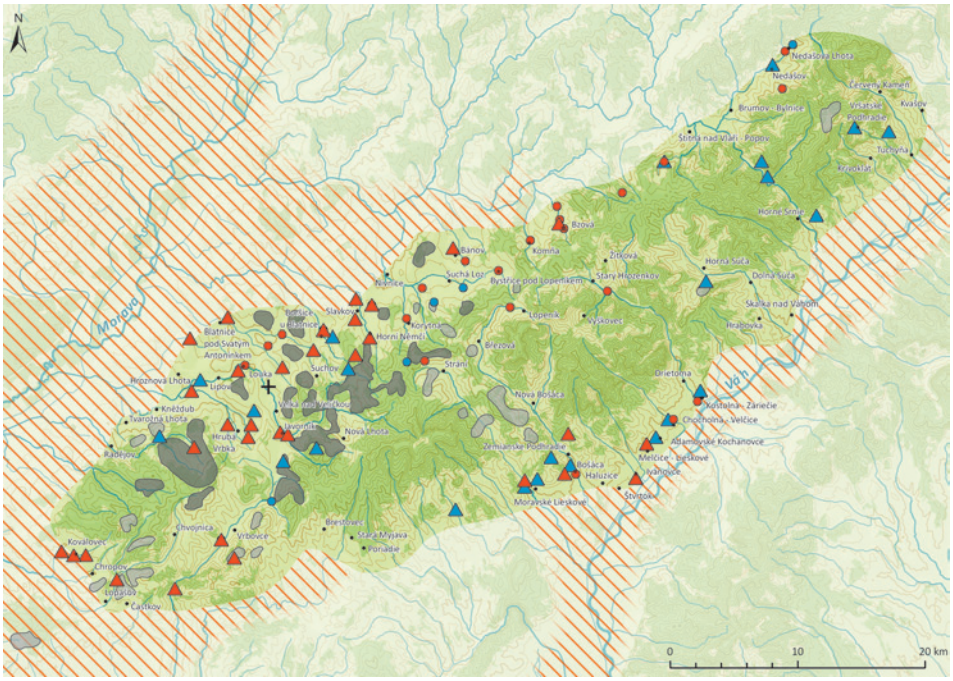



Fig. 1. – The distribution of *Brachypodio pinnati-Molinietum arundinaceae* grasslands (grey segments) and prehistoric archaeological records from the Neolithic to Bronze Age (triangles and circles). It is apparent that the distribution of species-rich grasslands largely overlaps early (Neolithic, Eneolithic) human settlement. Distribution of *Brachypodio-Molinietum* grasslands is based on both historical data (Sillinger 1929) and the analysis of databased vegetation plots (see Materials and methods for details). Darker grey colour of grassland segments indicates the occurrence of at least two plant species with disjunct distributions listed in Table 1. Archaeological records of significant human settlement (hilltop settlements, villages, burial sites) are indicated by triangles; fragmentary records are indicated by small circles. Settlement age categories are indicated by different coloured symbols: red – Neolithic and Eneolithic; blue – Bronze Age (including the transitional period between Late Eneolithic and Early Bronze Age). When archaeological sites provide evidence for various periods, only the oldest record was mapped. Only the territories of the Bílé Karpaty geological unit and the klippen belt were mapped. Hatching indicates neighbouring lowlands along the Morava, Olšava, Myjava and Váh rivers with well-documented intense prehistoric settlement. See Electronic Appendix 1, 2 for complete list of archaeological records in all prehistoric periods in a wider territory. Cross indicates location of the analysed sediment.

Standard plant macrofossil analysis according to Berglund (1986) was carried out. In total, 3.5 l volume of the sediment was analysed. Macrofossils were identified using Beijerinck (1976) and Bojňanský & Fargašová (2007) for seeds and Smith (1980) for bryophytes. Most seeds were also compared with the reference collection of the Institute of Botany, Academy of Sciences of the Czech Republic, Průhonice (http://www.ibot.cas.cz). Wood pieces were not identified because of their poor preservation. Pollen analysis was carried out using standard methods according to Faegri & Iversen (1989). Sediment sample was prepared by the acetolysis method (Erdtman 1960) after pre-treatment with cold concentrated hydrofluoric acid for 24 hours. Pollen frequency was low and pollen grains were not well preserved. Altogether 313 pollen grains of terrestrial plants were determined. Pollen was identified using the reference collection, Moore et al. (1991), Beug

(2004) and Reille (1992, 1995, 1998), pollen type nomenclature follows Beug (2004). Molluscs were extracted from the sediment (sample volume 6 l) using the standard wet-sieving of the sediment (Ložek 1964). After drying, shells were separated from the remaining material by hand-sorting under a stereo microscope, identified and counted.

*Radiocarbon dating*

One piece of wood and a sample of twelve *Sambucus nigra/racemosa* seeds were radiocarbon-dated at the Center for Applied Isotope Studies, University of Georgia, Athens, USA, using Accelerator Mass Spectrometry (AMS). The $^{14}C$ dates were calibrated using IntCal09 calibration curve in the OxCal4 software (Bronk Ramsey 2009). The abbreviation BP (Before Present) refers to uncalibrated age, while abbreviations BC (Before Christ) and AD (Anno Domini) refer to calibrated ages throughout the text.

## Results

*Prehistoric settlement density in relation to semi-dry grasslands and species with disjunct distributions*

Distribution of species-rich semi-dry grasslands largely overlaps the distribution of prehistoric settlement (Fig. 1, Electronic Appendix 1). The earliest prehistoric settlement in the region is dated to the Early Neolithic. The Linear Ware culture settlement reached the periphery of the area of distribution of the species-rich grasslands (maximum 3.5 km from the Čertoryje nature reserve, Přední louky meadows and Búrová nature reserve). During the Early Eneolithic (Moravian Painted Ware culture), settlement penetrated deeper into the mountains and during the Bronze Age, it spanned virtually the whole present-day range of the *Brachypodio-Molinietum* grasslands (Fig. 1). Moreover, the early-colonized sites often harbour several later cultures, through the Bronze and Iron Ages up to the Middle Ages. For example, the Vojšice archaeological site located on the border of the best known grassland nature reserve in the Bílé Karpaty Mts, Čertoryje, provided evidence for human settlement since the Early Eneolithic (the Moravian Painted Ware culture, Lengyel development, ca 4000 BC), through Late Eneolithic (the Corded Ware culture), Late Bronze Age (the Urnfield culture), Late Iron Age (La-Tène and Roman periods), Early Middle Ages (the Great Moravian period) until High Middle Ages. Čertoryje nature reserve is also the richest site of the species with disjunct distributions in the Bílé Karpaty Mts. Generally, the fit between the distribution of species-rich semi-dry grasslands and early human settlement is even better, when only the grasslands harbouring at least two disjunctly distributed species are considered (see darker grey coloured grassland segments in Fig. 1). Such grasslands are concentrated in the south-westernmost part of the Bílé Karpaty Mts, between the villages of Bánov and Radějov, where the evidence for Neolithic or Eneolithic settlement is abundant. On the other hand, there is a much lower density of prehistoric human settlement in the northern part of the Bílé Karpaty Mts (though lack of archaeological data from this region may be perhaps partly ascribed to less intensive research), which coincides with the fragmentary distribution of *Brachypodio-Molinietum* grasslands and sporadic occurrence of the species with disjunct distributions. Moreover, the northernmost sites of *Brachypodio-Molinietum* (Vršatské Podhradie, Horná Súča) are located close to the sites of Bronze Age

settlement. Both latter sites are also specific due to their occurrence in the proximity of extreme habitats of the klippen belt limestone rocks (Vršatec and Krasín, respectively).

*Characteristics of the analysed sediment*

*Sambucus nigra/racemosa* seeds from the sediment were dated to 1770±25 14Cyr BP, which corresponds to 140–325 years AD (2σ calibrated age), i.e. the Roman Age. The analysed wood piece was dated to 2200±30 14Cyr BP (380–203 years BC; 2σ calibrated age), i.e. the Younger Iron Age (La-Tène period). The difference between the two dates cannot be interpreted equivocally, as the sedimentary sequence could not be studied in detail due to the sampling scheme. The organic layer was ca 10 cm thick, not structured and consisted of pieces of wood, seeds, leaves, pieces of wood charcoal (up to 5 cm), snail shells and a large admixture of clay. The sediment was originally buried by clay material, perhaps from the collapse of an eroded river bank. The lack of structure and the occurrence of species of fluvial habitats suggest that the sediment was deposited during a short period. If this assumption is correct, the older age of the piece of wood could be explained by its origin from an old tree or by redeposition from older floodplain sediments. Then, the whole sediment may originate from the Roman Age. However, it cannot be excluded that this deposit is older and of La-Tène origin.

*Species composition of the analysed sediment*

The analysed mollusc assemblage comprises a mixture of forest specialists (Table 2, group 1, e.g. *Helicodonta obvoluta*), generalists that avoid forests (Table 2, group 5, e.g. *Vallonia pulchella*) and dry grassland specialists (Table 2, group 4, e.g. *Granaria frumentum*). Distinctly different ecological requirements of the species would prevent them from co-occurring in one habitat. At the same time, the presence of alluvial and aquatic species confined to streams (mainly *Ancylus fluviatilis*) indicates that the analysed sediment was created by the activity of running water. As dead shells are not commonly transported over long distances by running water, the co-occurrence of species with different ecological requirements in one sedimentary layer suggests the existence of a mosaic of dry grassland and natural forest patches on a local rather than landscape scales. Several forest specialists, such as *Cochlodina orthostoma* and *Helicodonta obvoluta*, indicate nearby presence of well-developed forest habitats, since these species do not prefer shrubs or young forests. Some of the forest species (e.g. *Cochlodina orthostoma*, *Sphyradium doliolum* and *Discus perspectivus*) are currently quite rare in Bílé Karpaty Mts and are not recorded in the wide surroundings of the study site.

Macrofossil assemblage of vascular plants was also ecologically diverse as in the case of the molluscs (see Table 3). The species-richest ecological group is composed of indicators of human activities, mostly field weeds (e.g. *Euphorbia helioscopia*, *Thlaspi arvense*, *Viola arvensis* and *Veronica opaca* – the latter is currently a rare and critically threatened species in the Czech Republic) and species growing both in arable fields and other human-influenced habitats (*Atriplex* sp., *Chenopodium* spp. and *Cirsium arvense*). These species suggest the presence of agriculture and perhaps also some so far undiscovered settlement in the close vicinity of the study site. The moss species *Eucladium verticillatum* indicates occurrence of calcareous tufa incrustation in springs or small brooks near the river Veličká. Tall-sedge or fen vegetation near the river is indicated by a high representation of *Cyperaceae*

Table 2. – List of mollusc species with numbers of specimens identified in the sample. Ecological classification of the species follows Ložek (1964) and Lisický (1991), with few modifications. 1 – strict forest species; 2 – forest species frequently occurring also in other mesic habitats such as gardens, parks and shrubberies; 3 – species of damp forests; 4 – species inhabiting steppe habitats (dry grasslands), also tolerating forest-steppe conditions; 5 – open landscape species avoiding forest habitats; 6 – thermophilous and xerotolerant species living both in forest and grassland; 7 – mesophilous and mostly euryoecious species; 8 – hygrophilous species; 9 – extremely hygrophilous terrestrial species living in various types of wetland; 10 – aquatic species inhabiting various freshwater habitats.

| Ecological group | Species | No. of shells |
|---|---|---|
| 1 | *Platyla polita* (Hartmann, 1840) | 1 |
| | *Acathinula aculeata* (O. F. Müller, 1774) | 3 |
| | *Sphyradium doliolum* (Bruguičre, 1792) | 2 |
| | *Cochlodina laminata* (Montagu, 1803) | 2 |
| | *Cochlodina orthostoma* (Menke, 1830) | 1 |
| | *Discus perspectivus* (M. von Mühlfeld, 1816) | 5 |
| | *Aegopinella pura* (Alder, 1830) | 2 |
| | *Daudebardia rufa* (Draparnaud, 1805) | 3 |
| | *Helicodonta obvoluta* (O. F. Müller, 1774) | 4 |
| 2 | *Discus rotundatus* (O. F. Müller, 1774) | 2 |
| | *Alinda biplicata* (Montagu, 1803) | 3 |
| | *Monachoides incarnatus* (O. F. Müller, 1774) | 1 |
| | *Arianta arbustorum* (Linné, 1758) | 6 |
| | *Aegopinella minor* (Stabile, 1864) | 13 |
| | *Helix pomatia* Linné, 1758 | 5 |
| | *Vitrea crystallina* (O. F. Müller, 1774) | 4 |
| 3 | *Macrogastra ventricosa* (Draparnaud, 1801) | 3 |
| | *Clausilia pumila* C. Pfeiffer, 1828 | 1 |
| 4 | *Granaria frumentum* (Draparnaud, 1801) | 11 |
| | *Cepaea vindobonensis* (A. Férussac, 1821) | 1 |
| 5 | *Vallonia pulchella* (O. F. Müller, 1774) | 17 |
| | *Vallonia costata* (O. F. Müller, 1774) | 41 |
| 6 | *Cochlicopa lubricella* (Rossmässler, 1835) | 2 |
| 7 | *Cochlicopa lubrica* (O. F. Müller, 1774) | 3 |
| | *Vitrea contracta* (Westerlund, 1871) | 4 |
| | *Perpolita hammonis* (Ström, 1765) | 5 |
| 8 | *Carychium tridentatum* (Risso, 1826) | 9 |
| | *Succinella oblonga* (Draparnaud, 1801) | 8 |
| | *Trochulus villosulus* (Rossmässler, 1838) | 2 |
| 9 | *Carychium minimum* (O. F. Müller, 1774) | 1 |
| | *Zonitoides nitidus* (O. F. Müller, 1774) | 1 |
| 10 | *Bythinella austriaca* (von Frauenfeld, 1857) | 6 |
| | *Galba truncatula* (O. F. Müller, 1774) | 3 |
| | *Radix peregra* (O. F. Müller, 1774) | 7 |
| | *Ancylus fluviatilis* O. F. Müller, 1774 | 1 |
| | *Pisidium casertanum* (Poli, 1791) | 1 |
| | *Pisidium personatum* Malm, 1855 | 1 |

Table 3. – List of plant species identified during the macrofossil and pollen analysis. Vascular plants were identified from seeds and fruits (S+F, 33 taxa) or pollen grains (P, 38 taxa), bryophytes from stems with leaves (St+L, 3 species). In total, 3,500 ml of sediment was analyzed for macrofossils.

| Ecological group | Taxon | S+F | P | St+L |
|---|---|---|---|---|
| Trees and shrubs | *Acer campestre* | 11 | | |
| | *Alnus* sp. | | 9 | |
| | *Betula* sp. | | 7 | |
| | *Carpinus betulus* | 6 | | |
| | *Cornus mas* | 2 | | |
| | *Corylus avellana* | 10 | | |
| | *Fagus sylvatica* | 22 | 6 | |
| | *Juglans* sp. | | 3 | |
| | *Juniperus* sp. | | 4 | |
| | *Picea abies* | | 10 | |
| | *Pinus* sp. | | 41 | |
| | *Quercus* sp. | 2 | 12 | |
| | *Salix* sp. | | 3 | |
| | *Sambucus nigra/racemosa* | 78 | | |
| | *Staphyllea pinnata* | 24 | | |
| | *Tilia cordata/Tilia* sp. | 5 | 4 | |
| | *Ulmus* sp. | | 3 | |
| Cereals | *Cerealia* | | 1 | |
| | *Avena sativa* | 1 | | |
| Ruderals and weeds | *Artemisia* sp. | | 6 | |
| | *Atriplex* sp. | 37 | | |
| | *Ballota nigra* | 5 | | |
| | *Cirsium arvense* | 2 | | |
| | *Chenopodiaceae* | | 4 | |
| | *Chenopodium album* agg. | 34 | | |
| | *Ch. hybridum* | 19 | | |
| | *Euphorbia helioscopia* | 1 | | |
| | cf. *Galeopsis angustifolia* | 5 | | |
| | *Persicaria lapathifolia* | 11 | | |
| | *Persicaria mitis* | 1 | | |
| | *Plantago media/major* | | 1 | |
| | *Thlaspi arvense* | 1 | | |
| | *Veronica opaca* | 1 | | |
| | *Viola arvensis* | 1 | | |
| Nitrophytes | *Aegopodium podagraria* | 1 | | |
| | *Atropa bella-donna* | 1 | | |
| | *Rubus* sp. | 1 | | |
| | *Solanum* sp. | 2 | | |
| | *Stachys sylvatica* | 2 | | |
| | *Urtica dioica* | 5 | 2 | |
| Grassland and open forest species | *Ajuga reptans* | 2 | | |
| | *Laserpitium* cf. *latifolium* | | 1 | |
| | *Laserpitium pruthenicum* | 1 | | |
| | *Lychnis flos-cuculi* | 6 | | |
| | *Medicago lupulina* | 1 | | |
| | *Rhinanthus* sp. | 1 | | |
| | *Eurhynchium hians* | | | 1 |
| | *Rhytidiadelphus triquetrus* | | | 45 |
| Calcareous spring species | *Eucladium verticillatum* | | | 25 |
| Wetland species | *Cyperaceae* | | 145 | |
| | *Lemna minor* | | 1 | |
| | *Triglochin/Potamogeton* sp. | | 7 | |
| | *Valeriana dioica* type | | 2 | |
| Other species | *Aethusa cynapioides* | 3 | | |
| | *Allium* type | | 2 | |
| | *Asplenium* sp. | | 2 | |
| | *Asteraceae-Cichorioidae* | | 5 | |
| | *Brassicaceae* | | 1 | |
| | *Campanulaceae* | | 1 | |
| | *Cirsium* type | | 1 | |
| | *Dryopteris* sp. | | 4 | |
| | *Equisetum* sp. | | 3 | |
| | *Galium* sp. | | 1 | |
| | *Humulus/Cannabis* | | 2 | |
| | *Poaceae* | | 10 | |
| | *Potentilla* sp. | | 1 | |
| | *Ranunculus* type | | 3 | |
| | *Selaginella* sp. | | 2 | |
| | *Senecio* type | | 1 | |
| | *Taraxacum* sp. | | 1 | |
| | *Vicia* type | | 1 | |

pollen and the presence of *Valeriana dioica*-type pollen. Co-occurrence of trees and forest vascular plants with species of grassland and semi-open forests suggests the existence of a habitat mosaic in the surrounding landscape. Forest habitats were probably represented by alluvial alder forests (*Alnus* pollen) in the close vicinity of streams and mesic forests (e.g. *Acer campestre*, *Quercus* sp., *Tilia cordata* and *Ulmus* sp.) with thermophilous and semi-heliophilous species of shrub (*Cornus mas* and *Staphyllea pinnata*). *Eurhynchium hians*, *Rhytidiadelphus triquetrus*, *Lychnis flos-cuculi*, *Medicago lupulina*, *Rhinanthus* sp. and *Valeriana dioica* suggest presence of wet and mesic grasslands. *Laserpitium pruthenicum* and *L.* cf. *latifolium* are species of dry-mesic to intermittently wet grasslands and semi-open forests and are characteristic of the present landscape of the Bílé Karpaty Mts. *Juniperus communis* is an indicator of pastures.

## Discussion

These results provide evidence for the hypothesis of the prehistoric origin of the extremely species rich semi-dry grasslands in the Bílé Karpaty Mts. Although the sediment analysed does not cover prehistoric periods, both macrofossil and pollen data indicate the existence of cultivated landscape with a mosaic of forests and open habitats in the Roman Age at the latest, i.e. about one millennium earlier than suggested by previous palynological studies. Moreover, the review of archaeological records provided evidence for early (Neolithic, Eneolithic) human settlement in the south-western part of the Bílé Karpaty Mts and for frequent presence of different prehistoric human cultures in the region before the Slavic colonization in the Early Middle Ages. Therefore, it is suggested that the extreme species richness of the semi-dry grasslands of the *Brachypodio-Molinietum* association may be partly ascribed to the long history and continuity of these grasslands maintained by human activities (grazing, mowing and burning). It is also suggested that the early human activities might have prevented the spread of closed-canopy forests during the Atlantic period and thus facilitated local survival of the rare heliophilous species with disjunct distributions; some of these species may be relicts of the heliophilous communities of the Early Holocene.

### *Relationships between species richness and age of grasslands*

Species richness of grasslands is known to be influenced by a broad spectrum of ecological factors. During previous studies in the Bílé Karpaty Mts (e.g. Klimeš 1997, Dvořáková 2009), correlations were found between the fine-scale species richness and above ground biomass (negative), soil C/N ratio (negative) or Ca and Mg concentrations (positive on very fine scale, negative on coarser scale when species-poor stands on calcium extremely-rich skeletal soils were included). Except for local environmental factors, the number of species in a particular community is limited by the size of the regional species pool, which is determined by coarse-scale spatial and temporal processes such as evolution, migration and refugial history (Taylor et al. 1990, Eriksson 1993). However, within the same species pool, species richness of a particular community may be modified by local dispersal-related factors such as proximity of seed sources (Cantero et al. 1999, Bruun 2000), presence of dispersal vectors (Bruun et al. 2008) or permeability of the landscape for the species (Rédei et al. 2003).

The age and continuity of the habitat are another two factors related to colonization/extinction dynamics and therefore to species richness. While age indicates past opportunities for colonization (it is exhibited e.g. by higher proportion of slow-colonizing species in older habitats; Matlack 1994, Waesch & Beaker 2009), the (dis)continuity indicates the occurrence of species' extinctions due to habitat disturbance or a major change of environmental conditions. While exact habitat age is often unknown, its continuity in the last decades or centuries may often be determined based on the study of historical sources such as old maps or aerial photographs (e.g. Chýlová & Münzbergová 2008, Karlík & Poschlod 2009).

Several studies conducted in grasslands show that species richness is positively related to the age and continuity of the grassland. A study of Estonian calcareous grassland indicates that small-scale species richness depends on the continuity of the traditional management regime (Kull & Zobel 1991). In a study of a Swedish rural landscape, 17 species were positively associated with a long continuity of grassland management and only two with lack of management (Cousins & Eriksson 2001). Analysis of calcareous dry grasslands in southeastern Germany has revealed higher species richness in ancient than in recent grasslands (Poschlod et al. 2008), though another study from this region has shown no significant relationship between continuity and species richness (Karlík & Poschlod 2009).

Few studies have attempted to analyse the effects of prehistoric human activities on species richness of plant communities, obviously due to the lack of detailed historical data. A study of Estonian calcareous grassland has shown that both the size of the species pool and the local species richness are significantly related to human population density in the Late Iron Age (Pärtel et al. 2007). As the dry grasslands in the region are human-made, the density of prehistoric human population may indicate continuity of the grasslands. Positive relationship between species richness and the intensity of land use from the Iron Age onwards was also found in a coarse-scale study from eastern Denmark (Bruun et al. 2001).

Altogether, although the effects of local environmental variables on species richness of the semi-dry grasslands in the Bílé Karpaty Mts are more straightforward and better studied, it is apparent that the legacies of ancient human activities may significantly shape their recent diversity patterns.

### *Possible relationship between the occurrence of species with disjunct distributions and local environmental history*

The concentration of species with disjunct distributions in the Bílé Karpaty Mts is conspicuous and was recognized during the early floristic and geobotanical research in the first half of the 20th century (e.g. Čoka 1906, 1907, Staněk 1926, 1927, Sillinger 1929, Podpěra 1951). Generally speaking, species with disjunct distributions are those whose distribution ranges are fragmented into geographically isolated parts. The causes may vary and the disjunctions may result either from spread or retreat of the species. A geographically restricted species' occurrence that is considered to result from its retreat from the surrounding area is often referred to as "relict" (Holmquist 1962). Although the relict character of species occurrence at a particular site is difficult to prove, a recent study from the Western Carpathians (Hájek et al. 2011) showed that in peatlands (history of which may be reconstructed using palaeoecological evidence), some species traditionally considered as relicts are significantly linked to sites with a long Holocene history. Also a high concentra-

tion of species with disjuct distributions at one site may suggest a refugium that has persisted for a long time (Hájek et al. 2009).

Fragmentation of species distribution ranges is frequently associated with a major change in the environment. Current flora and vegetation of Central European landscapes were predominantly formed during the Holocene (Ložek 1964, 2007, Berglund et al. 1996), during which there were, from the point of view of terrestrial organisms, three major environmental changes: (i) the warming at the transition between Pleistocene and Holocene (ca 9500 BC) accompanied by the retreat of glacial species and the spread of thermophilous species; (ii) the spread of closed-canopy forests during the warm and humid Atlantic period (ca 6500–1400 BC) accompanied by the retreat of heliophilous species and the spread of shade-tolerant species; (iii) the spread of agriculture that started in Central European lowlands ca 5500 BC and continued till the modern period, being accompanied by the retreat of closed-canopy forests and shade-tolerant species through human-induced deforestation and the spread of heliophilous species supported by cattle grazing, burning, crop cultivation and mowing. Significantly, the two latter environmental changes with largely counteracting effects occurred synchronously in the regions with early human settlement. This resulted in what some palaeoecologists (e.g. Ložek 2004) call "double-track development" of the Central European landscape: in the regions that were colonized early (Neolithic, Eneolithic; mostly warm and dry lowlands and adjacent hilly landscapes with base-rich soils), the pools of Early Holocene heliophilous species were mostly preserved and the development of heliophilous vegetation was more or less continuous during the Holocene; in contrast, the late colonized regions (mostly cold and humid uplands and mountains with base-poor soils) experienced a period of extensive closed-canopy forest spread and the Holocene development of heliophilous vegetation was discontinuous there. In other words, persistence of Early Holocene heliophilous species is supposed to play a bigger role in the lowlands, while colonization from distant refugia or from extreme treeless habitats like rocks, screes or fens is supposed to be more important in the uplands.

Taking into consideration the results of this analysis of prehistoric human settlement, it seems that the Bílé Karpaty Mts posses a rare combination of the features characteristic for the two contrasting "tracks" (i.e. development paths): a relatively humid climate with a steep temperature gradient from warm foothills to cool mountain tops, deep base-rich soils and early and rather intensive human settlement. Thus, it is likely that this rare combination might have facilitated local survival of isolated populations of steppe to montane heliophilous species during critical periods in the Holocene and the formation of their disjunct distribution ranges.

*Possible scenario of Holocene landscape development in the Bílé Karpaty Mts*

Based on the results of palaeoecological analyses conducted in the study area and its wide surroundings (Rybníčková & Rybníček 1972, Jankovská & Pokorný 2008, Ložek 2008), a possible scenario of the survival of light-demanding species in the study area was constructed (see also Fig. 2). In Early Holocene, landscape was initially covered by open *Betula* and *Pinus* stands with increasing admixture of *Quercus* and *Corylus*, with light-demanding species growing in the understorey. Many characteristic species of *Brachypodio-Molinietum* grasslands tolerate moderate shading from trees, as indicated by

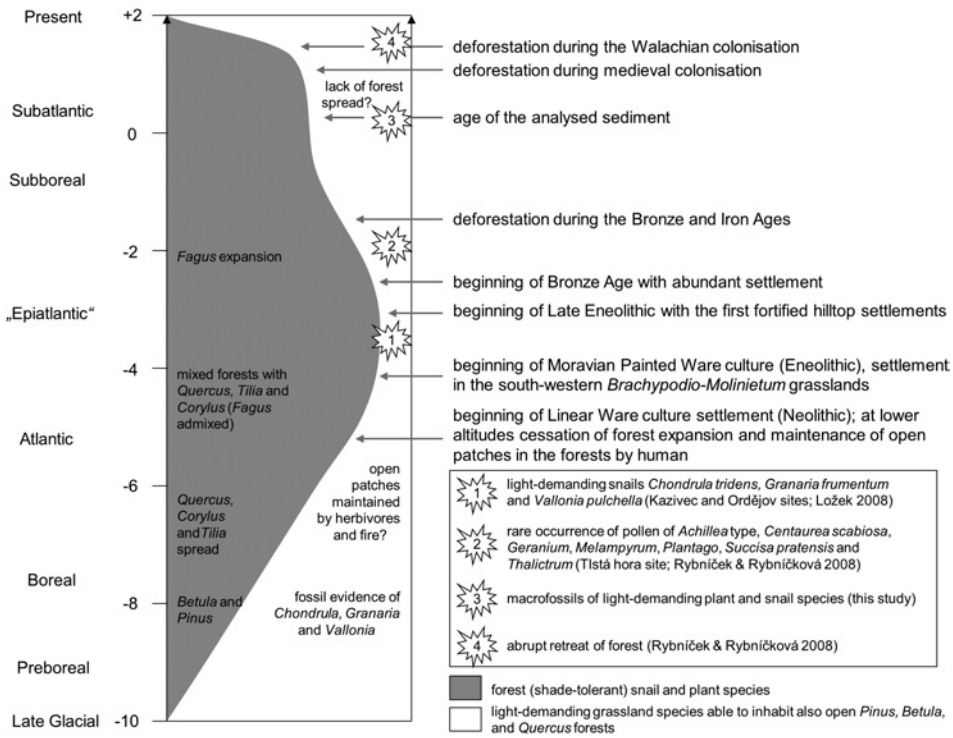



Fig. 2. – Hypothetical scheme of Holocene landscape development in the Bílé Karpaty Mts. The shape of the curve of forest/heliophilous species ratio is based on existing scarce palaeoecological evidence and further study may lead to its refinement.

their occurrence in continental hemi-boreal pine-birch forests of *Brachypodio pinnati-Betuletea pendulae* class (Ermakov et al. 2000), and the current occurrence of some of these species in semi-open forests in the study area. Later, mixed *Quercus* forests were formed that probably included many open patches with light-demanding species, because oak needs much light for regeneration (Le Duc & Havill 1998, Vera 2000). These patches might have been maintained by large herbivores or natural fires (Chytrý et al. 2010). The bottleneck for the survival of light-demanding species in the region came probably as late as in the Epiatlantic period due to the spread of shade-tolerant trees (Ložek 2008). However, Neolithic and Eneolithic human colonization of the region prevented the extinction of light-demanding species. In the late Subboreal and early Sub-Atlantic periods, beech (*Fagus sylvatica*), the tree which is able to restrict the light-demanding understorey species substantially (Ellenberg 1988), started to dominate the Central European forests (Rybníčková & Rybníček 1972, Rybníček & Rybníčková 2008). Nevertheless, human settlement during the Bronze Age and later kept the landscape open. Because beech spread can be accelerated in forests disturbed and then abandoned by man (Pokorný 2005), the continuity of settlement in a wider area might have been particularly important. The evidence for the existence of a cultivated landscape during the Roman Age and human settlement in Early Middle Ages (the Great Moravian period) also suggest a smaller role of for-

est spread during the Migration period which is reported for some other regions in Central Europe (Sádlo et al. 2005). In the central and northern parts of the Bílé Karpaty Mts, prehistoric settlement was not so dense and frequent and there are few *Brachypodio-Molinietum* grasslands and species with disjunct distributions there.

Indeed, local environmental conditions probably co-determined the unique species composition of the grasslands in the region. Heavy clayey calcium-rich soils are not easily leached and therefore the acidification during the Middle and Late Holocene, frequently observed in other parts of Central Europe (Ewald 2003, Sádlo et al. 2005, Pokorný & Kuneš 2005), may not have occurred and acted as a bottleneck for calcicole species. Further, early deforestation of the dry slopes located close to the densely populated Pannonian lowlands might have enabled immigration of thermophilous species from the south-east as early as the Atlantic period. Some of the disjunct species occurrences in the study area may have originated during this and later periods, because long-term existence of open habitats increased the probability of long-distance colonization even by poor colonizers. Also, it was hypothesized that the last Ice Age was warmer in the Bílé Karpaty Mts than in other mountains in the Czech Republic due to the contact with the Pannonian lowlands, which might have facilitated survival of some species specific for the region (Sillinger 1929, Ložek 2007).

Human settlement in the area of the present-day distribution of extremely species-rich grasslands (Vojšice) occurred also in Early and High Middle Ages, but was abandoned later. Abandoned grasslands were at those times perhaps extensively managed by people living in adjacent villages. In modern times, particularly in the last decades of intensive grassland management, relatively large distances from settlements might have been beneficial for the preservation of the high species richness and the archaic floristic and faunistic elements. This hypothesized concert of the Holocene environmental history, the early human settlement and its intensity, the geographical position on the boundary between different biogeographical regions and peculiar local environmental conditions might have yielded the unique grassland community.

See http://www.preslia.cz for Electronic Appendix 1, 2.

## Acknowledgements

We dedicate this paper to excellent geobotanists Pavel Sillinger (1905–1938) and Josef Podpěra (1878–1954) who first recognized the uniqueness of grasslands in the Bílé Karpaty Mts and explained it in terms of specific history.

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## Souhrn

Louky na vápnitém flyši Bílých Karpat patří k druhově nejbohatším travinobylinným společenstvům v Evropě. Jsou unikátní i svým druhovým složením, v němž se významně uplatňují druhy jinak ve střední Evropě vzácné,

mnohdy s disjunktivním areálem, jejichž výskyt v Bílých Karpatech je často výrazně geograficky izolovaný. Z ekologického hlediska jde o pestrou skupinu druhů, zahrnující prvky kontinentálních lesostepí, druhy rozšířené ve středních polohách pohoří jihovýchodní Evropy nebo subalpínské druhy, které se v Bílých Karpatech vyskytují v neobvykle nízkých nadmořských výškách. Příčiny extrémně vysoké druhové bohatosti a unikátního druhového složení bělokarpatských luk nejsou dosud jasné. Předpokládá se jak vliv lokálních faktorů prostředí (střídavě vlhké, hluboké jílovité půdy s dostatkem vápníku, vlhké a teplé klima, mozaikovitost krajiny), tak vliv historie území a jeho geografické polohy. Zatímco vliv lokálních faktorů prostředí byl již studován a zčásti prokázán, přímé paleoekologické doklady historie luční vegetace Bílých Karpat téměř chybějí kvůli nedostatku vhodných sedimentů. Současné studie z různých částí Evropy přitom přinášejí poznatky o průkazném vztahu mezi historií lučních biotopů a jejich druhovou bohatostí a o pravěké existenci suchých trávníků v oblastech s pravěkým osídlením. V Bílých Karpatech však pylová analýza sedimentů z několika pěnovcových pramenišť neprokázala existenci luk před středověkou a valašskou kolonizací, zatímco analýzy měkkýšů z jiných lokalit zde naznačují možnost přežívání nelesních biotopů v průběhu celého holocénu.

Tato práce shrnuje dosavadní znalosti o výskytu druhů s disjunktivním areálem, jejichž velká koncentrace může být zapříčiněna jejich dlouhodobým přežíváním v území. Přináší rovněž detailní rešerši archeologických nálezů z Bílých Karpat, která ukázala poměrně husté pravěké osídlení v území s výskytem druhově bohatých trávníků asociace *Brachypodio pinnati-Molinietum arundinaceae*, přičemž geografický vztah mezi pravěkým osídlením a rozšířením rostlinných druhů s disjunktivním výskytem je ještě těsnější. Pravěké osídlení bylo na mnoha lokalitách dlouhodobé nebo opakované, jak dokládají nálezy z neolitu, eneolitu, doby bronzové a doby železné. Některá sídliště ležela přímo na území dnešních nejcennějších luk (např. polykulturní lokalita Vojšice v NPR Čertoryje). Přímý důkaz o existenci člověkem ovlivněných biotopů před středověkou a valašskou kolonizací pak přináší námi provedená analýza makrozbytků, pylů a měkkýšů ze sedimentu pohřbeného v aluviu říčky Veličky u Velké nad Veličkou. Tato analýza prokázala výskyt druhů nelesních biotopů (např. rostliny *Laserpitium pruthenicum*, *Lychnis flos-cuculi*, *Medicago lupulina* a měkkýši *Granaria frumentum*, *Cepaea vindobonensis*, *Vallonia pulchella*) v tomto území v době římské (asi 250 n. l.).

Lidská činnost spojená s osídlením mohla ve zdejší krajině udržovat nelesní biotopy a umožnit přežívání světlomilných druhů během středního a pozdního holocénu, tedy v době expanze společenstev stinných bukových a habrových lesů. Osídlení jihozápadní části Bílých Karpat od neolitu dále považujeme za nepřímý doklad lokálního přežívání světlomilných druhů v průběhu celého holocénu, které mohlo mít v kombinaci se specifickými přírodními podmínkami a geografickou polohou zásadní vliv na současné druhové složení a druhovou bohatost bělokarpatských luk.

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