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White Carpathian grasslands: can local ecological factors explain their extraordinary species richness?

Bělokarpatské louky: mohou lokální ekologické faktory vysvětlit jejich výjimečné druhové bohatství?

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Semi-dry grasslands in the White Carpathian (Bílé Karpaty) Mountains on the Czech-Slovak border are famous for their extremely high species richness. In places they contain more than 130 species of vascular plants per 100 m^2 and for some plot sizes they hold world records in the number of vascular plant species, but the reasons for this are poorly understood. Here we ask whether the high number of species in these grasslands can be explained by local ecological factors. We compared the White Carpathian grasslands with similar grasslands in adjacent areas in the west (southern Moravia) and the east (Inner Western Carpathians), which are on average notably poorer in species than those in the White Carpathians. In both of these areas, we sampled grasslands that were among the species-richest in the regional context and had a similar physiognomy, species composition and ecology as those in the White Carpathians. We found 75 sites with >70 and >25 species of vascular plants per 100 m^2 and 1 m^2, respectively, in which we recorded species composition and local environmental conditions, including precipitation, soil depth, soil pH and nutrient concentrations, above-ground biomass production and nutrients in plant biomass. Although the White Carpathian grasslands were considerably richer in species than the richest grasslands in the adjacent regions, there were no differences in the values of the factors studied that could provide an unequivocal explanation of their high species richness. However, the values of the factors studied were within the ranges reported in the literature as conducive to high species richness in temperate grasslands. We conclude that the high species richness recorded in the White Carpathian grasslands cannot be explained by a single factor. It results from a unique combination of regional factors (long history of these grasslands, large size of individual grassland areas and their existence in a landscape mosaic with forests, scrub and small wetlands), local abiotic factors (soil pH, soil nutrient status, moisture regime and resulting grassland productivity that are suitable for many species from the regional species pool) and management (low fertilizer input and mowing once a year in late spring or summer).

Keywords: Bílé Karpaty, Czech Republic, diversity, dry grassland, meadow, nutrients, productivity, Slovakia, soil pH, vascular plants, Western Carpathians

Introduction

The highest numbers of vascular plant species in areas smaller than 100 m^2 worldwide are found in temperate dry and semi-dry grasslands (van der Maarel & Titlyanova 1989, Kull & Zobel 1991, Zobel 1992, Cantero et al. 1999, Vasilevich 2009, Wilson et al. 2012). Even in the context of this generally species-rich vegetation, semi-dry grasslands of the White Carpathians (Bílé Karpaty), a mountain range on the border between the Czech Republic and Slovakia, have an exceptionally high local species richness. Klimeš et al. (2001) reported at least 67 and 88 vascular plant species in plots of 1 and 4 m^2, respectively, in the grasslands in the Čertoryje National Nature Reserve in the south-western part of the White

Carpathians. We recorded 105 vascular plant species per 16 m^2, 116 per 25 m^2, 131 per 49 m^2 and 133 per 100 m^2 at the same site (Z. Preislerová, formerly Otýpková, & M. Chytrý, unpublished data). A recent review of the global literature on species-rich plant communities (Wilson et al. 2012) indicates that the first three of these values are the highest numbers of species reported for areas of these sizes worldwide. However, the reasons for the extraordinary species richness in these grasslands have not been satisfactorily explained so far.

Local species richness can be affected by regional factors such as evolutionary and migration history (Zobel 1992, 1997, Ricklefs & Schluter 1993), or local factors such as abiotic environment and interspecific interactions (Grime 1979, Huston 1979). Typically, factors of both groups play some role, but their relative importance varies among sites and community types. Hájková et al. (2011) concluded, based on phytogeographical, archaeological and palaeoecological evidence, that the White Carpathian grasslands are of prehistoric origin. They also hypothesized that the long-term continuity of the White Carpathian grasslands, which may have existed throughout the Holocene in some places, is one of the key factors contributing to their high species richness. Although Hájková et al. (2011) emphasized the role of regional factors, there is little information on the local environmental factors prevailing in the White Carpathian grasslands (Klimeš 1997, Kubíková & Kučera 1999, Dvořáková 2009) and there is no synthesis of their role in shaping the species diversity in this ecosystem.

It is striking that in the White Carpathian semi-dry grasslands (*Brachypodio pinnati-Molinietum arundinaceae* association; Tlusták 1975, Chytrý 2007, Škodová et al. 2008, 2011) there are more than 90 species of vascular plants per 100 m^2 at most sites, whereas in floristically and physiognomically similar semi-dry grasslands in areas adjacent to the White Carpathians this value is rarely exceeded. If the high species richness in the White Carpathian grasslands is to be attributed to local factors, there should be a noticeable difference in the values of certain local factors, or combinations of factors, for the grasslands in the White Carpathians and those in adjacent areas. Therefore, we sampled and compared grasslands in the White Carpathians and similar grasslands in the areas adjacent in the west (southern Moravia) and the east (Inner Western Carpathians). In addition to species composition, we recorded several variables that are known to affect species richness in grasslands: precipitation as a broad-scale surrogate for water availability (Whittaker & Niering 1975, Adler & Levine 2007, Cheng et al. 2011), soil depth as a fine-scale surrogate for water availability, soil pH (Pärtel 2002, Schuster & Diekmann 2003, Chytrý et al. 2007), soil nutrients (Crawley et al. 2005, Hejcman et al. 2010), nutrient concentration in plant biomass (Braakhekke & Hooftman 1999) and above-ground biomass at the peak of the growing season as a measure of productivity (Grime 1979, Tilman & Pacala 1993).

In this paper, we ask whether there are some local environmental factors that are consistently different in the species-rich grasslands of the White Carpathians and the species-poorer but otherwise similar grasslands in adjacent areas, and if so, whether these factors can be considered as the main or partial causes of the high species richness recorded in the White Carpathian grasslands.

Study area

The White Carpathians (Bílé Karpaty) is a mountain range situated on the border between the Czech Republic and Slovakia (48°49'–49°08' N, 17°19'–18°08' E; highest altitude 970 m; Kuča et al. 1992, Otýpková et al. 2011). The adjacent area in southern Moravia is located to the west of the White Carpathians (48°47'–49°18' N, 16°31'–17°21' E) and that in the Inner Western Carpathians to the east (48°20'–49°07' N, 18°15'–21°18' E). The altitudinal range of the grassland plots studied in these three areas is 313–622 m (White Carpathians), 185–378 m (southern Moravia) and 334–972 m (Inner Western Carpathians).

The White Carpathians and the adjacent area of southern Moravia are in the flysch zone of the Outer Western Carpathians. Flysch landscapes are characterized by gentle slopes, rounded ridges and broad shallow valleys. Flysch bedrock, a sequence of alternating layers of Palaeogene sandstones and claystones, is easily eroded and subjected to frequent landslides. Its claystone layers are impervious to water, which often results in the formation of seepages on slopes. Soils on flysch are usually deep, with texture ranging from clayey-loamy at sites where claystones prevail to loamy-sandy on sandstones. They vary in calcium carbonate content but the pH (H_2O) is hardly ever less than 5 (Kuča et al. 1992, Mackovčin et al. 2002, 2007). At some of the sites sampled in southern Moravia flysch is overlain by loess. The study area in the Inner Western Carpathians consists of metamorphic and intrusive igneous rocks penetrated by volcanic rocks that are locally covered by various sedimentary rocks (Lexa et al. 2000). A common feature of the sites sampled is a significant content of calcium carbonate and deep to moderately deep soils.

Sites sampled in the White Carpathians range in mean annual temperatures from 6.6 to 8.7 °C, in southern Moravia from 8.1 to 9.3 °C and in the Inner Western Carpathians from 5.4 to 8.4 °C. Their mean annual precipitation ranges from 665 to 835 mm, 561 to 635 mm and 646 to 906 mm, respectively (interpolated values from climatic atlases; Lapin et al. 2002, Tolasz et al. 2007).

Material and methods

We sampled semi-dry and dry grasslands in the White Carpathians, southern Moravia and Inner Western Carpathians in May and June of 2008 and 2009. In all regions, the sites sampled were selected subjectively with the aim to record the most species-rich grasslands. Sites with species-rich grasslands were selected based on the species-rich plot records contained in Czech and Slovak vegetation-plot databases (Chytrý & Rafajová 2003, Janišová & Škodová 2007), literature records and suggestions from local experts. The grasslands were mostly dominated by *Brachypodium pinnatum*, *Bromus erectus*, *Carex humilis* or *C. montana* and belonged to the *Bromion erecti*, *Cirsio-Brachypodion pinnati* or *Festucion valesiacae* alliances (Chytrý 2007, Illyés et al. 2007, Janišová 2007, Dúbravková et al. 2010). Most grasslands in the White Carpathians were mown once a year in June or July as a part of nature conservation management (Jongepierová et al. 2008a). In the other areas some grasslands were mown and others abandoned. Few sites were extensively grazed. At 91 sites (37 in the White Carpathians, 34 in southern Moravia and 20 in the Inner Western Carpathians; Fig. 1), grasslands were sampled using plots of 1 and 100 m^2 in area with the former nested within the latter. Only species of vascular plants, including seedlings of woody plants, were recorded.

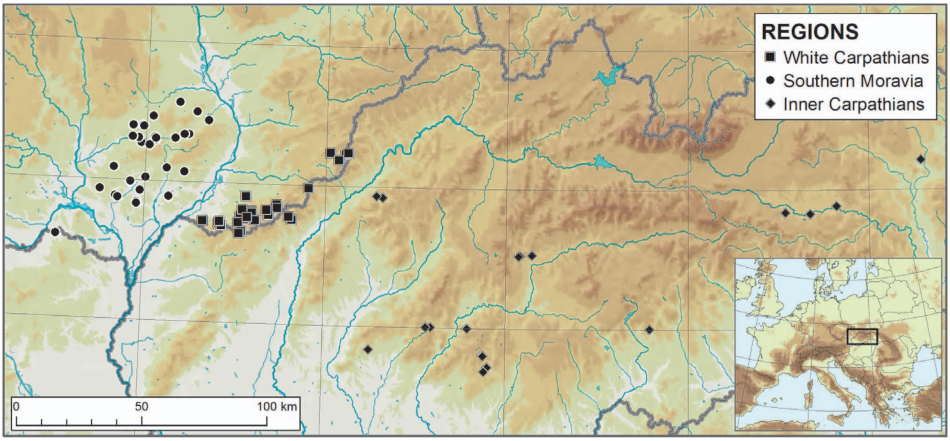

Fig. 1. – Map showing the locations of sites sampled in southern Moravia, White Carpathians and Inner Western Carpathians.

A soil probe was used to measure soil depth at three places within each 100 m^2 plot and the results averaged. Soil samples were collected at a depth of 3–10 cm at three places within each 100 m^2 plot and subsequently mixed for each plot. They were used to determine the following chemical properties: (1) Soil pH was measured after 12-hour extraction in distilled water (soil/water ratio 2/5). (2) Plant available phosphorus, potassium and calcium in Mehlich III extracts were determined by means of spectrophotometry (phosphorus) and atomic absorption spectrophotometry (potassium and calcium). (3) C/N ratio was determined as the ratio of organic carbon, estimated based on the loss on ignition, and total nitrogen, determined using the Kjehldahl method (Zbíral 2005).

Above-ground biomass (including standing dead biomass but excluding litter) was clipped at 0.5–1 cm above ground in four subplots of 0.0625 m^2 within each 1 m^2 plot. Samples from the subplots were pooled, oven-dried and weighed. Biomass dry weight was recalculated as g/m^2. Biomass was analysed for nitrogen, phosphorus, potassium and calcium. For the nitrogen determination, dry material was mineralised using sulphuric acid and hydrogen peroxide, and the nitrogen concentration determined by distillation. For determination of the other elements (P, N and Ca), material was mineralised by heating it in a microwave oven and then determined using the methods mentioned above (Zbíral 2005).

As we were interested in the species-richest grasslands, we included in the analysis only those sites that contained at least 70 vascular plant species per 100 m^2 and, at the same time, at least 25 species per 1 m^2. The resulting data set contained 75 plots, including 35 from the White Carpathians, 22 from southern Moravia, and 18 from the Inner Western Carpathians.

The differences between the three regions were tested using ANOVA and Tukey post-hoc tests. Univariate relationships between species richness, biomass and environmental variables were quantified using Pearson correlations. The computations were performed using STATISTICA 9 (www.statsoft.com).

In addition to the analyses of environmental factors, we performed a redundancy analysis (RDA) of a matrix of species × sites in CANOCO 4.5 (ter Braak & Šmilauer 2002), in which the number of species in 100 m^2 plots was used as a single constraining variable. Species cover values recorded on the Braun-Blanquet scale were replaced by mid-percentage values for each degree and square-root transformed. This analysis was done in order to control for the possible effect of any unmeasured environmental factors: if the species-rich plots were consistently characterized by a group of species with certain ecological requirements, it might indicate factors responsible for high species richness.

Results

Species richness of grasslands in the White Carpathians was significantly higher than in similar grasslands in southern Moravia and the Inner Western Carpathians (Figs 2a, 2b). The maximum number of species of vascular plants recorded in grasslands in the White Carpathians was 133 and 59 in plots of 100 and 1 m^2, respectively. In southern Moravia the corresponding numbers were 108 and 50, and in the Inner Western Carpathians, 100 and 49 species.

The precipitation recorded at the sites sampled in southern Moravia was significantly less than at the sites in the other two regions (Fig. 2c). There was no difference in soil depth between regions (Fig. 2d). The soil pH recorded at the White Carpathian sites was significantly lower than at the sites in the other two regions (Fig. 2e), but there was a broad overlap in the pH values recorded in the three regions. When only those sites with pH values that were within the range recorded in the White Carpathians (5.4–7.2) were compared, the White Carpathian grasslands were consistently richer in species (Fig. 3). Soil phosphorus and calcium concentrations recorded at the southern Moravian sites were higher (Figs 2f, 2h), but there was no difference in soil potassium concentration and C/N ratio (Figs 2g, 2i). Above-ground biomass was lowest in the Inner Western Carpathians and highest in the White Carpathians, but again values for the different regions overlapped considerably (Fig. 2j). When only sites with more than 200 g/m^2 (dry weight) of biomass were compared, the grasslands in the White Carpathians were richer in species than those in the other regions (Fig. 4). The concentrations of nitrogen and phosphorus in the plant biomass collected at the southern Moravian sites were higher (Figs 2k, 2l) than in the plant biomass collected in the other regions. Potassium in biomass was lowest in the Inner Western Carpathians and highest in southern Moravia (Fig. 2m), while the regions did not differ in the concentration of calcium in the biomass (Fig. 2n). The N/P ratio was higher in the White Carpathians than in southern Moravia (Fig. 2o).

In the White Carpathians, species richness and biomass were positively correlated based on the data collected from both plot sizes (1 m^2: $r = 0.34$, $P = 0.047$; 100 m^2: $r = 0.34$, $P = 0.047$). Species richness in 1 m^2 plots was negatively correlated with the potassium content of the soil in the White Carpathians ($r = –0.37$, $P = 0.027$). All other correlations of species richness with the measured variables were not significant within the White Carpathian data set. The dry weight of the above-ground biomass collected in the White Carpathians was negatively correlated with the nitrogen concentration in the biomass ($r = –0.55$, $P = 0.001$), while the other variables were not correlated with the dry weight of biomass.

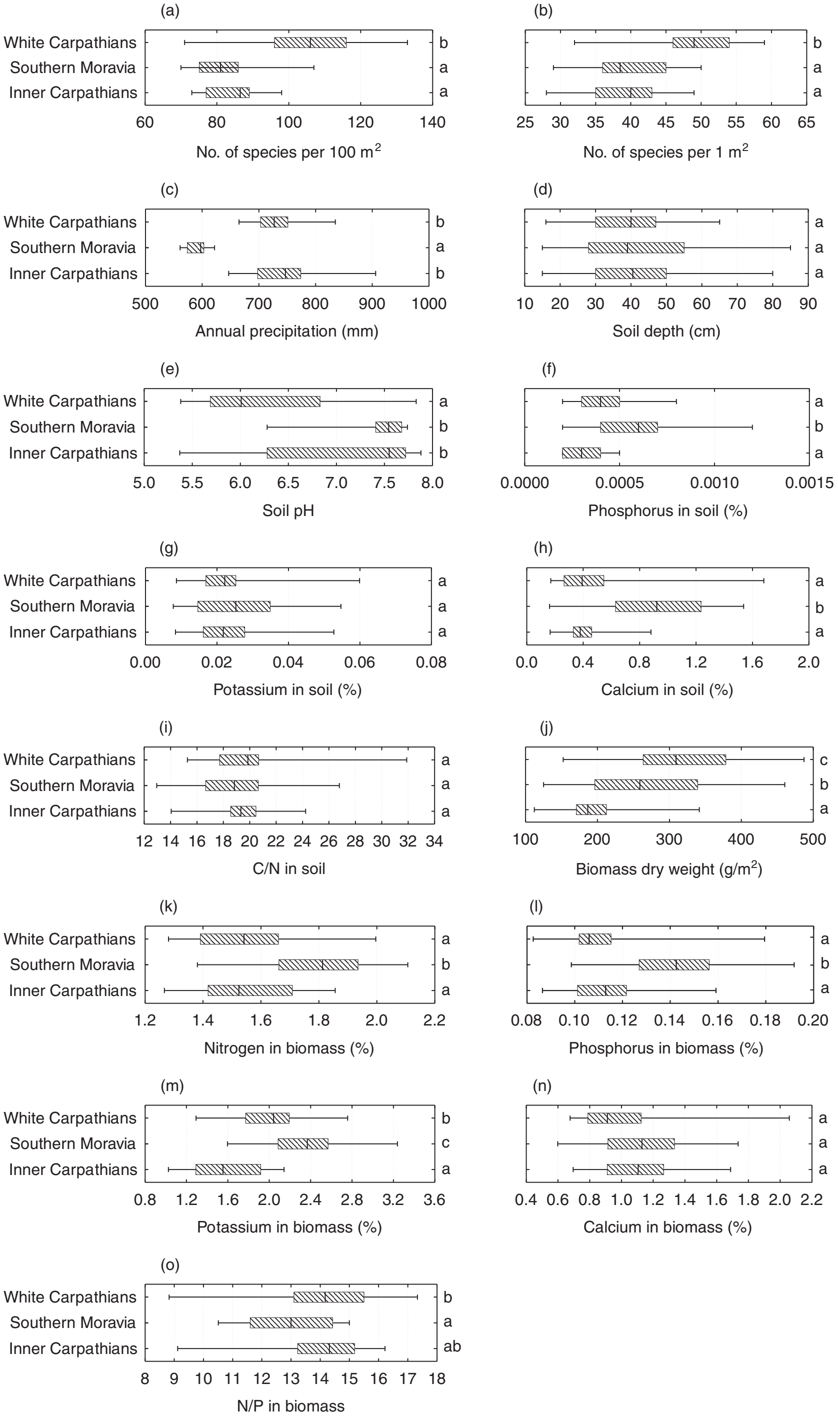

Fig. 2. – Comparison of species richness and local site factors recorded in the White Carpathians, southern Moravia and the Inner Western Carpathians. Medians, quartiles, minimum and maximum values are shown. Groups with the same letters are not statistically different (ANOVA with post-hoc Tukey test at $P < 0.05$).

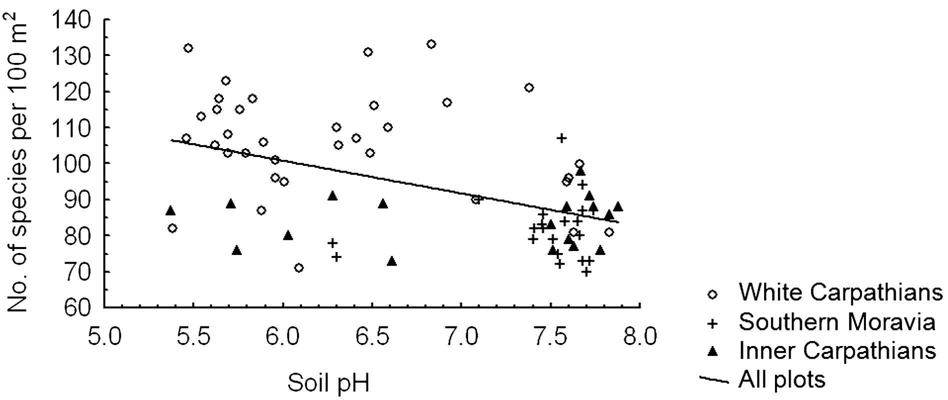

Fig. 3. – Number of vascular plant species recorded in grassland plots of 100 m^2 plotted against soil pH. The relationships for each of the three regions studied were not significant and the line is fitted for the significant regression of values for all the plots sampled in the three regions ($R^2 = 0.23$, $P < 0.001$).

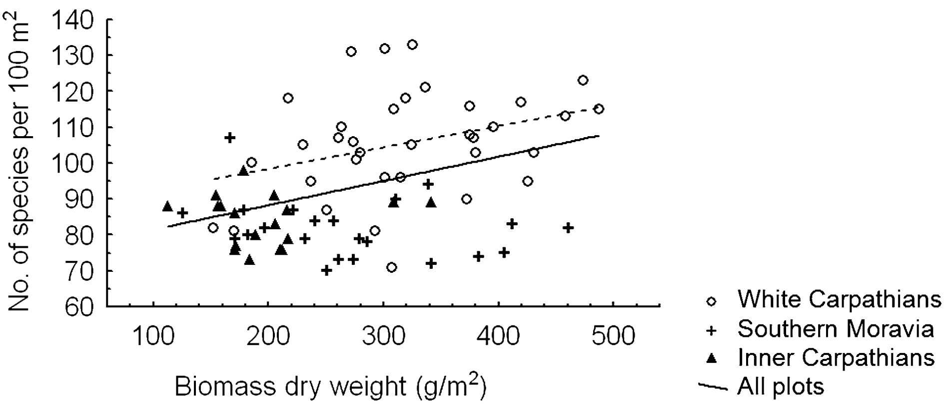

Fig. 4. – Number of vascular plant species recorded in grassland plots of 100 m^2 plotted against above-ground biomass production. Lines are fitted for significant regressions (White Carpathian plots: $R^2 = 0.11$, $P = 0.047$; all plots: $R^2 = 0.15$, $P < 0.001$). For the grasslands in southern Moravia and Inner Western Carpathians the relationships were not significant.

Across all three regions, species-richest plots were characterized by several species that were missing or rare in species-poorer plots (Table 1). Most of these species are common in the White Carpathian grasslands but rare in grasslands in adjacent regions, as indicated by a parallel analysis of the fidelity of species to the three regions (results not shown). These species differ in their ecological requirements, but many are typical of wet, intermittently wet or mesic soils, acidic substrates, forests and forest fringes.

Table 1. – Species with the highest affinity to species-rich plots. The first 40 species with the highest scores (in descending order) on constrained axis of RDA ordination where number of species in 100 m^2 plots was used as the only canonical variable.

Valeriana stolonifera subsp. *angustifolia*
Trifolium rubens
Sanguisorba officinalis
Lathyrus niger
Clematis recta
Lathyrus latifolius
Symphytum tuberosum
Asperula tinctoria
Campanula patula
Campanula persicifolia
Myosotis arvensis
Molinia arundinacea
Anacamptis pyramidalis
Carex panicea
Pulmonaria angustifolia
Carex montana
Ajuga reptans
Holcus lanatus
Serratula tinctoria
Inula salicina
Potentilla erecta
Anthoxanthum odoratum
Gymnadenia conopsea
Prunella grandiflora
Betonica officinalis
Cruciata glabra
Potentilla alba
Allium carinatum
Centaurea jacea
Leucanthemum vulgare agg.
Calamagrostis arundinacea
Carex pallescens
Cirsium pannonicum
Galium boreale
Danthonia decumbens
Taraxacum sect. *Ruderalia*
Trifolium campestre
Campanula glomerata
Trisetum flavescens
Ranunculus auricomus agg.

Discussion

Local species richness of vascular plants in the White Carpathian grasslands is considerably higher than in similar species-rich grasslands in adjacent regions of southern Moravia and the Inner Western Carpathians. However, the striking difference in species richness is not paralleled by differences in any of the local factors measured. Only soil pH was lower and biomass dry weight higher in the White Carpathian grasslands than in the species-rich grasslands in both adjacent regions. The other factors measured were not significantly higher or lower in the White Carpathians than in both adjacent regions. However, even the differences in soil pH and biomass seem to be insufficient to account for the high species richness of the White Carpathian grasslands.

The soil pH of the White Carpathian grasslands is lower than in species-poorer grasslands in the adjacent regions. In addition, species richness within the White Carpathian grasslands decreases with soil pH and calcium content (Dvořáková 2009), although in our data set this relationship was not significant. This seemingly conflicts with the results of studies that demonstrate that species richness of temperate grasslands increases with soil pH (e.g. Schuster & Diekmann 2003, Crawley et al. 2005). Local species richness-pH relationship is usually explained by the species pool effect, which reflects the predominance of base-rich or base-poor soils during evolutionary history, and resulting over-representation of calcicole or calcifuge species in regional species pools (Pärtel 2002, Ewald 2003). In temperate Europe, this theory would predict higher species richness on calcareous substrates because of the predominance of base-rich soils during the cold and dry periods of the Pleistocene (Chytrý et al. 2003, Ewald 2003). However, it is important to consider the range of the pH values recorded. Our sample of pH values from all three regions ranged from 5.4 to 7.9, while the positive richness-pH relationship is commonly observed only up to a pH of around 5 or 6 (Janssens et al. 1998, Schuster & Diekmann 2003, Crawley et al. 2005). At higher pH values species richness typically levels off and finally declines towards the extreme end of the pH gradient. If species richness declines within the range of pH values of 5.5–7.5, it is probably caused by some other factors co-varying with pH, e.g. drought (Chytrý et al. 2007). We believe that pH higher than 5 is a necessary condition for high species richness in all the regions studied, but differences in pH within the sampled range of 5.4–7.9 have negligible effects on variation in species numbers. This conclusion is supported by the facts that (1) for the same pH values within the range of pH 5.4–7.2, White Carpathian grasslands are consistently richer in species than those in adjacent regions, and (2) within our White Carpathian data set soil pH does not co-vary with species richness.

The dry weight of the above-ground biomass harvested at the peak of the growing season, as measured in this study, is a good surrogate of the net annual primary productivity, because in the grasslands studied herbaceous species are dominant while there are very few and a low biomass of woody species. Thus the relationship between species richness and biomass reported here can be interpreted as the diversity-productivity relationship. At the local scale, the diversity-productivity relationship is usually unimodal (Grime 1979, Tilman 1982, Tilman & Pacala 1993). In temperate grasslands, local species richness usually increases with biomass up to about 200–300 g/m^2 (Zobel & Liira 1997, Ma et al. 2010) and decreases when the biomass dry weight exceeds approximately 400–500 g/m^2 (Moore & Keddy 1989, Zobel & Liira 1997, Crawley et al. 2005, Hejcman et al. 2010, but see Adler et al. 2011 and the subsequent debate). The biomass recorded in the White Carpathian grasslands in this study ranged from 152 to 487 g/m^2 and was 217–487 g/m^2 in the richest plots with more than 110 species per 100 m^2. Thus productivity in the White Carpathian grasslands clearly falls within the productivity range that supports the highest species richness in temperate grasslands. However, even within this range the White Carpathian grasslands are considerably richer in species than the richest grasslands in the adjacent regions. Thus productivity, like soil pH, can also be considered as necessary but not sufficient condition for maintenance of the extremely high species richness in the White Carpathian grasslands.

Other local factors measured or their combinations also do not provide unequivocal explanation of the extremely high species richness in the White Carpathian grasslands, although they are most probably within the ranges that support a high species richness. For example, soil extractable phosphorus and potassium in the White Carpathian grasslands are within the range that is consistent with high species richness in European grasslands (Janssens et al. 1998, Hejcman et al. 2010). However, soil potassium values in the White Carpathian grasslands do not differ from values found in the species-poorer southern Moravian and Inner Western Carpathian grasslands, and soil phosphorus values, which are on average slightly higher in southern Moravia, still broadly overlap the values recorded in the White Carpathians. Similarly, the N/P ratio of the plant biomass is about 14–15 in the richest grasslands of the White Carpathians, indicating nearly optimal balance of limiting resources. Under such conditions, it is supposed that different plant species are limited by different resources, competition is thus limited and high species richness is maintained (Braakhekke & Hooftman 1999, Güsewell et al. 2005). However, also in this case, the same N/P ratios were found in species-poorer grasslands in the Inner Western Carpathians.

Thus a clear explanation for the unique high species richness in the White Carpathian grasslands remains elusive. Most probably it results from a particular combination of several factors that are conducive to high species richness:

The first group of factors includes regional ones, especially the hypothetical prehistoric origin of the White Carpathian grasslands. Hájková et al. (2011) indicated that the most species-rich grasslands in the White Carpathians occur in areas with dense human settlement since the Neolithic, and palaeoecological evidence of open landscape in the same areas goes back to the Eneolithic (Copper Age). There is growing evidence that species richness of European grasslands is positively related to their age (Pärtel & Zobel 1999, Bruun et al. 2001, Pärtel et al. 2007, Waesch & Becker 2009), and this also may be the case for the White Carpathians. Phytogeographical data on isolated occurrences of several rare species in the White Carpathian grasslands (reviewed by Jongepierová et al. 2008b and Hájková et al. 2011) indicate that some of these grasslands may have developed directly from the early Holocene open birch-pine woodlands and thus inherited a significant part of the putative high diversity of their herb layer (Chytrý et al. 2010). However, grasslands in the adjacent region of southern Moravia are also situated in an area settled since the Neolithic and many of them harbour isolated occurrences of rare species, indicating their old age; in spite of this, they have much lower species richness than their counterparts in the White Carpathians.

Another regional effect on the high species richness in the White Carpathian grasslands may be the size of the grassland areas. For example, the sites with the highest species richness occur in the Čertoryje National Nature Reserve, which has an area of nearly 7 km^2 (including the buffer zone), of which most is covered by grassland (Bravencová 2003). The Theory of Island Biogeography (MacArthur & Wilson 1967) predicts that larger patches of a single habitat should have higher species richness not only if the total patch is considered, but also within small plots sampled in this patch. Studies of other European grasslands tend to confirm this prediction (e.g. Öster et al. 2007). Early studies on the White Carpathian grasslands (Sillinger 1929) show that in the 1920s there were more large tracts of meadows than today, but many of them were ploughed in the period of socialist agriculture, mainly in the 1970s (Futák et al. 2008).

In addition to their large area, these grasslands are in contact with natural forests and contain numerous solitary trees (Doležal et al. 2010), patches of scrub and small wetlands at seepage sites (Hettenbergerová & Hájek 2011, Schamp et al. 2011), which provide a constant source of propagules that could potentially enrich nearby grasslands. As a result, species-richest grasslands typically contain, in addition to grassland species, also species of forest fringes and forests (e.g. *Campanula persicifolia*, *Clematis recta*, *Lathyrus niger*, *Pulmonaria angustifolia*, *Symphytum tuberosum* and *Valeriana stolonifera* subsp. *angustifolia*).

The second group includes local abiotic factors, several of which were recorded in this study. As discussed above, most of these factors are within the range that is consistent with high species richness, but there is no single one that can account for the high species richness *per se*. There can also be other factors that we did not study in detail, especially soil moisture, which was approximated only by rough surrogates of precipitation and soil depth. Although precipitation is relatively high (around 700–750 mm/yr) and it is generally combined with deep soils in the White Carpathian grasslands, there are periods of summer drought, as indicated by the tree-ring analyses of solitary oak trees growing in these grasslands (Doležal et al. 2010). One of the reasons for summer water deficit can be the surface water runoff after episodic summer rain events, caused by the heavy texture of the clayey soils. Summer droughts may reduce the biomass of dominant species, thus allowing long-term persistence of poor competitors (Klimeš 2008). In contrast, the clayey soils may absorb water during periods of wet weather or after spring snow thaw, and retain it for a long time. In addition, the flysch bedrock is composed of alternating layers of claystone and sandstone, which respectively form poorly and well drained soils or soil horizons. The notion that changing moisture conditions are favourable, if not essential, to high species richness in semi-dry grasslands, is supported by the presence of numerous species typical of intermittently wet habitats (e.g. *Betonica officinalis*, *Galium boreale*, *Inula salicina*, *Molinia arundinacea*, *Potentilla alba* and *Serratula tinctoria*) among the species that, in our analysis, differentiate species-rich plots from species-poorer plots (Table 1). Besides many species typical of dry grasslands these meadows contain mesophilous species (e.g. *Anthoxanthum odoratum*, *Campanula patula*, *Centaurea jacea*, *Leucanthemum vulgare* and *Trisetum flavescens*) and moisture-demanding species (e.g. *Ajuga reptans*, *Carex pallescens*, *C. panicea* and *Sanguisorba officinalis*). Without temporal and spatial variability in moisture, the coexistence of drought-adapted, moisture demanding and transitional species in the White Carpathian grasslands (Chytrý 2007, Škodová et al. 2008, 2011) would not be possible, even if there were enough sources of diaspores from various habitats in the surroundings. Many of the southern Moravian grasslands we studied are also on flysch bedrock, but they occur in an area with lower precipitation, which may prevent long-term persistence of moisture demanding and forest species and limit species richness of these grasslands.

The third group of factors includes management. Until recent decades, the most species-rich meadows in the White Carpathians were traditionally mown for hay once a year and nature conservation management has been continuing with annual mowing since the 1990s (Futák et al. 2008). Studies clearly show that after abandonment, the species richness of these grasslands declines, most often due to spread of the competitive tall grass *Molinia arundinacea*, but re-introduction of mowing leads to relatively rapid restoration of a species-rich grassland (Klimeš et al. 2000, Klimeš 2008). However, though mowing is one of the necessary conditions, it is not sufficient to explain the high species richness alone, because some of the grasslands in the adjacent areas are also mown but have much fewer species than their counterparts in the White Carpathians.

We hypothesize that none of the above-mentioned factors on their own can account for the high species richness recorded in the White Carpathian grasslands; however, in the absence or under shifted values of one of the factors, the resulting species richness would be less, which may be the case for similar grasslands in the adjacent areas.

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Souhrn

Bělokarpatské louky jsou výjimečné svou velkou koncentrací druhů cévnatých rostlin, která místy přesahuje 60 druhů na ploše 1 m^2, 80 druhů na 4 m^2, 100 druhů na 16 m^2 či 130 druhů na 49 m^2. Tak velké druhové bohatství nemá ve střední Evropě obdoby a na některých velikostech ploch je dokonce rekordní i v celosvětovém měřítku. Jeho příčiny však nebyly dosud plně objasněny. Částečně je lze vysvětlit působením příznivých regionálních faktorů, zejména pravděpodobné dlouhodobé existence těchto luk od pravěku až do dneška, která umožnila přežívání mnoha světlomilných druhů typických pro vegetaci raného holocénu. Podobné typy travinné vegetace na jižní Moravě ale i přes obdobný historický vývoj zdaleka nedosahují takových koncentrací druhů na malých plochách, takže příčiny je třeba hledat i jinde. Tato práce zkoumá možný vliv některých lokálních faktorů na základě srovnání bělokarpatských luk s druhově chudšími trávníky jižní Moravy a Vnitřních Západních Karpat. V těchto územích jsme vybrali druhově nejbohatší porosty s podobným druhovým složením, fyziognomií a ekologií, jako mají bělokarpatské louky. Na 91 lokalitách jsme zaznamenali všechny druhy cévnatých rostlin na plochách 1 m^2 a 100 m^2, srážky, hloubku půdy, půdní pH, koncentrace hlavních živin v půdě, hmotnost nadzemní biomasy (jako míry produktivity) a koncentrace hlavních živin v biomase. Z nich jsme pro srovnávací analýzu vybrali 75 lokalit s více než 70 druhy cévnatých rostlin na plochu 100 m^2 a zároveň s více než 25 druhy na 1 m^2. Přestože byly bělokarpatské louky výrazně druhově bohatší než nejbohatší trávníky obou srovnávaných oblastí, mezi studovanými lokálními faktory jsme nenašli takové rozdíly, které by mohly větší koncentraci druhů na malých plochách v Bílých Karpatech samy o sobě vysvětlit. Hodnoty těchto faktorů ale spadaly do rozmezí, která podle studií z jiných oblastí umožňují velké druhové bohatství v travinných společenstvech. Naše výsledky a jejich srovnání s literaturou nasvědčují, že v případě bělokarpatských luk nelze určit jeden nebo několik málo faktorů, které by byly schopné vysvětlit jejich extrémně velké druhové bohatství. Místo toho zde zřejmě vznikla výjimečná souhra mnoha okolností, počínaje dávným původem luk, velkou rozlohou jednotlivých lučních komplexů a jejich výskytem v pestré mozaice lesů, křovin a mokřadů, přes vlhkostní režim, pH půdy, zásobení živinami a z toho vyplývající produktivitu, které vyhovují velké části druhů z regionální flóry, a konče pravidelným jednosečným obhospodařováním. Domníváme se, že při absenci nebo změně kteréhokoliv z těchto faktorů by unikátní druhové bohatství bělokarpatských luk bylo menší, než dnes pozorujeme.

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Vegetace Česke republiky 3. Vodní a mokřadní vegetace
[Vegetation of the Czech Republic 3. Aquatic and wetland vegetation]

Academia, Praha, 2011, 827 pp., ISBN 978-80-200-918-9

The third volume of the Czech national vegetation classification, dealing with aquatic and wetland vegetation, sets a new landmark in European vegetation research. On the one hand, it stands in the long tradition of European classification studies, starting about a century ago with the work of Josias Braun-Blanquet and followers (see Rodwell et al. 2002), on the other hand it reflects new developments – and raises the benchmark – in applying modern computer techniques to understand and document the variation in plant communities. Records taken from the field still form the basis, the so-called vegetation relevé: a description of a vegetation stand at a certain time, recording all species and their cover-abundance values. Based on a total set of 95,660 vegetation records in the Czech National Phytosociological Database, a vegetation classification at the level of association was performed using the supervised classification method Cocktail (Bruelheide 1995; Koči et al. 2003). After stratification, all together 10,279 relevés were assigned to associations of aquatic and wetland vegetation. This dataset was used for creating synoptic tables and determining diagnostic, constant and dominant species. The consequent way in which the data have been analysed reflects the critical attitude of the authors in nowadays vegetation research, in the same way as they proceeded in the previous two volumes of the overview, on grasslands and heathlands (Chytrý 2007) and on ruderal, weed, rock and scree vegetation (Chytrý 2009), respectively.

The overview of the Czech aquatic and wetland vegetation comprises three formation groups: aquatics, wetlands sensu stricto, and springs and mires. These groups comprise 10 formations, varying from free-floating aquatic plant communities, communities characterized by aquatic plants rooted in the bottom and stonewort communities, to plant communities of marshes, springs and bogs. They are classified in 10 classes, 37 alliances, and 176 associations. Given the fact that natural lakes are almost absent in Czech Republic, this diversity is surprisingly high. Natural habitats are concentrated in river floodplains (aquatic and wetland vegetation) and in precipitation-rich mountainous areas (spring and mire vegetation), whereas at other places artificial biotopes occur, including currently about 25,000 fishponds, ranging in size from a few hundred square metres to nearly 500 hectares.

The descriptions of the associations form the core of the book, following a standard format. Each description starts with the scientific name of the association, with code and author citation (according to the latest International Code of Phytosociological Nomenclature; Weber et al. 2000), followed by the vernacular name. In a small text box, synonyms are presented, as well as a list of diagnostic species and its formal definition. In separate paragraphs, attention is paid to items like vegetation structure, ecology, succession, management, distribution, variation and classification. At the end of the association descriptions, a summary in English is given. The distribution of each association is mapped in a geographical grid with cells of 5 minutes of geographical longitude by 3 minutes of latitude (approximately 5 × 5.5 km). Synoptic tables are given for groups of closely related associations, and the same applies for environmental factors, like Ellenberg indicator values (Ellenberg et al. 1992), altitudinal range and the cover of the herb layer. The book is illustrated with high-quality colour photographs. The book closes with more than 60 pages of references and an index of species and syntaxon names.

From the 1990s onwards, vegetation research in the Czech Republic has clearly gained ground in Europe once again after a rather long period of relative silence. This is illustrated by an impressive amount of scientific papers (e.g. on software development and on multivariate computer techniques), a number of successful international meetings organized in the country, and the prominent position of Czech vegetation scientists in international journals, organizations and working groups, like the European Vegetation Survey. The publication of the third volume of the Vegetation of the Czech Republic furthers this development. My only concern is that the book is written in the Czech language. As a consequence, the international public has to derive its information from the tables, maps, graphs, photographs and short summaries, or... has to learn how to read Czech.

Joop Schaminée

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