Understanding the extreme species richness of semi-dry grasslands in east-central Europe: a comparative approach

Srovnávací analýza mimořádně druhově bohatých širokolistých suchých trávníků východní části střední Evropy

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East-central European semi-dry grasslands hold several world records in small-scale vascular plant species richness. However, the reasons for the peculiarity of these grasslands are not well known, which hinders a better understanding of the mechanisms of species coexistence. We suggest that one of the reasons for this gap in our knowledge is the lack of basic information on the geographical distribution of these grasslands, their species richness, species composition and site conditions. Here we report new sites of extremely species-rich semi-dry grasslands in the foothills of the Eastern Carpathians in the south-western Ukraine. Using comparison with other sites with extremely species-rich semi-dry grasslands in the peri-Carpathian region and beyond, we show that these grasslands share many important features, including similar species composition, occurrence of species with disjunct distributions, site conditions, landscape context, long history of human influence and traditional management practice. Based on these findings, we suggest that continuity on a large (Pleistocene-Holocene) time scale and regularly practiced management that reduces the asymmetry in competition (typically mowing and absence of fertilizer application) may be the crucial factors responsible for the extremely high local species richness in east-central European semi-dry grasslands. We also suggest that this richness largely originates from an ancient pool of species of Eurasian forest-steppe and hemiboreal forests.

K e y w o r d s: Czech Republic, disjunct distribution, environmental history, forest-steppe, hemiboreal forests, meadows, mowing, Prut-Siret interfluve, relict species, site conditions, species coexistence, Romania, Slovakia, Transylvanian Plateau, Ukraine, White Carpathians

Introduction

European semi-dry grasslands are remarkable for their extremely high small-scale vascular plant species richness (Wilson et al. 2012). High numbers of species and occurrence of rare species stimulated not only substantial efforts for the conservation and restoration of these grasslands (Jongepierová et al. 2007, Sammul et al. 2008, Prach et al. 2013) but also keep provoking scientific interest. It is believed that the study of habitats with extraordinary species richness may help understand the mechanisms of species coexistence (Levine & HilleRisLambers 2012, Wilson et al. 2012). Some of the species-rich grasslands are now among the best studied habitats in Europe. Since Kull & Zobel (1991) presented their

record-holding count of the number of vascular plant species in Estonian wooded meadows there have been a further 20 studies on these meadows published in Web of Knowledge journals. Similarly grasslands in the White Carpathians (Bílé/Biele Karpaty Mts) in the Czech Republic and Slovakia have been thoroughly studied since Klimeš et al. (2001) published their species richness maxima, with more than 10 related studies appearing in Web of Knowledge journals over the last decade. In spite of this scientific effort, the authors of recent papers agree that reasons for the peculiarity of these grasslands are not well understood (Aaavik et al. 2008, Hájková et al. 2011, Merunková et al. 2012).

We suggest that the lack of understanding may be partly ascribed to the lack of basic information on the geographical distribution of these grasslands, their species richness, species composition and site conditions. Wilson et al. (2012) were the first to compile worldwide data on vascular plant species richness in contiguous areas of from 1 mm^2 up to 1 ha. Semi-dry grasslands dominated most of the records at the smaller scale up to 50 m^2; surprisingly, more than 50% of these records come from unpublished data. Only recently, Dengler et al. (2012) published details on a newly discovered record-holding site on the Transylvanian Plateau, Romania. The species richness of Romanian semi-dry grasslands of the *Festuco sulcatae-Brachypodietum pinnati* association reach record values for areas of 0.1 and 10 m^2 and have many similar features with the grasslands in the White Carpathians, including a similar species composition. In addition, the record-holding Estonian wooded meadows show many similarities (Kull & Zobel 1991). These findings indicate a promising way of improving our understanding of these grasslands and the causes of their extreme species richness: a search for other extremely species-rich grasslands on a geographical scale and comparison of their species richness, species composition and habitat conditions with the known sites. This suggestion may seem impractical due to the scarcity of extremely species-rich grasslands and their unpredictable distribution; however, here we provide an example of a successful application of this approach.

Looking for analogues of the extremely species-rich White Carpathian grasslands, the first author came across a report of grassland with *Pedicularis exaltata* in the foothills of the Eastern Carpathians in the Ukraine (Kahalo et al. 2009). *Pedicularis exaltata* is a remarkable species from a phytogeographical point of view, with distributional centre in the montane zone of the Eastern Carpathians and several disjunct occurrences in the foothills and lowlands of east-central Europe (Hendrych & Hendrychová 1989). The westernmost site of its distributional range is situated in the extremely species-rich semi-dry grasslands of the White Carpathians, more than 500 km from the nearest known site (Hájková et al. 2011). The first author assumed that the occurrence of *Pedicularis exaltata* in a similar landscape context (Carpathian foothills adjacent to a forest-steppe region) in the Ukraine might indicate occurrence of similar vegetation. This assumption proved justified.

The aims of this study are to provide basic information on recently identified extremely species-rich semi-dry grasslands in the Ukraine and compare their species richness, species composition and habitat conditions with that of semi-dry grasslands in the White Carpathians and Transylvania, as well as with other east-central European semi-dry grasslands. We expect that such a comparison may help us determine the reasons for the extraordinary species richness of these grasslands. We also want to stimulate further study of extremely species-rich grasslands at a geographical scale.

Material and methods

Study area

The recently identified extremely species-rich semi-dry grasslands are located in the Prut-Siret interfluve: a hilly region in the foothills of the Eastern Carpathians, south and west of the city of Černivci, in south-western Ukraine (Fig. 1). The most species-rich and extensive of the grasslands is located at Dzjurkač (also called Revnjanskoe) near the village of Spas'ka, where *Pedicularis exaltata* also occurs. It is a complex of about 20 ha of mown meadows, abandoned areas with tall herbaceous plants and small woodlands situated about 10 km west of Černivci. This site is known to local botanists and phytosociological data on its grasslands were recently published by Tokarjuk et al. (2009); however, their extreme species richness has received little attention. The site occupies a gentle north-facing slope of a ridge rising above the river Prut. The ridge forms a natural boundary between the rolling landscapes of the Prut-Siret interfluve (a part of the Pre-Carpathian Depression) to the south and the relatively flat landscape of the Volyn-Podolian Upland (a part of the East European Plain) to the north. The ridge culminates in Cecyna hill (537 m a.s.l.). Another site with similar vegetation, Pidokruh, is located on slopes and foothills of Okruh hill near the village of Zavoloka, on the south-western periphery of Černivci.

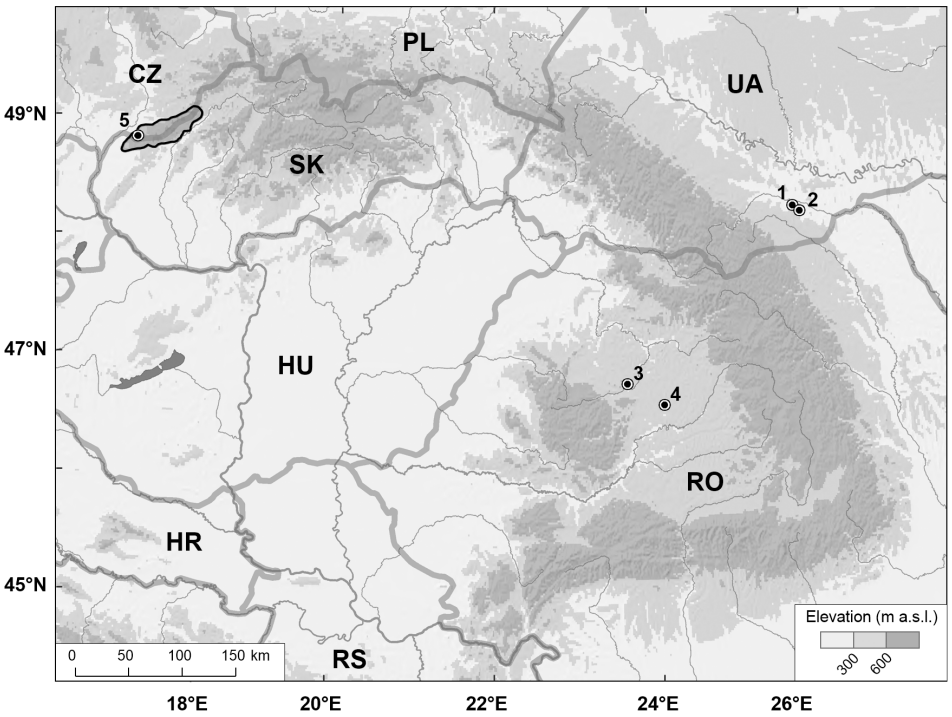


Fig. 1. – Map of the area studied. Site numbers: 1 – Dzjurkač, Prut-Siret interfluve; 2 – Pidokruh, Prut-Siret interfluve; 3 – Fânaţele Clujului, Transylvania; 4 – Rezervaţia de bujori de stepă, Transylvania; 5 – Čertoryje, White Carpathians. Boundaries of the White Carpathians are marked by a black line (Bílé/Biele Karpaty Protected Landscape Areas boundaries are used for simplicity).

Table 1. – Main geographical and ecological characteristics of the sites of extremely species-rich semi-dry grasslands in east-central Europe. Climatic data were taken from the WorldClim model (Hijmans et al. 2005) for the Ukrainian and Transylvanian sites and from local sources summarized in Vesecký (1961) for the White Carpathians. All bedrocks are mostly calcareous sediments.

Site	Prut-Siret interfluve, Dzjurkač	Prut-Siret interfluve, Pidokruh	White Carpathians	Transylvania, Rezervaţia Fânaţele Clujului	Transylvania, Rezervaţia de bujori de stepă
Country	Ukraine	Ukraine	Czech Republic, Slovakia	Romania	Romania
Latitude	48°18'	48°15'	48°49–48°57'	46°50'	46°39'
Longitude	25°48'	25°53'	17°20'–17°40'	23°39'	24°06'
Altitude (m a.s.l.)	350–500	250–300	250–690	480–600	400–450
Area	20 ha	30 ha	20 000 ha	100 ha	4 ha
Bedrock	Neogene	Neogene	Palaeogene	Neogene	Neogene
Mean annual temperature	7.5 °C	8.5 °C	7.0–8.5 °C	8.0 °C	8.5 °C
Mean annual precipitation	690 mm	640 mm	630–840 mm	620 mm	610 mm
Prevailing traditional management	mowing	mowing	mowing	mowing	mowing
Maximum species richness	90 (9 m^2)	71 (9 m^2)	105 (16 m^2)	99 (10 m^2)	78 (10 m^2)
Maximum species richness standardized to 10 m^2	92.8	73.2	91.4	99	78
Mean species richness	52.4 (9 m^2)	54.8 (9 m^2)	71.2 (16 m^2)	84.7 (10 m^2)	73.5 (10 m^2)
Mean species richness standardized to 10 m^2	54.0	56.5	62.0	84.7	73.5
No. of relevés analyzed	36	8	104	7	4

According to the historical records (Rudolph 1911) this type of grassland used to be more widespread in this region. Main geographical and ecological characteristics of the two sites are summarized in Table 1; characteristics of other sites of extremely species-rich grasslands in the peri-Carpathian region are included for comparison.

Data preparation and analyses

We assembled vegetation-plot data from the study area collected by the authors of this paper between 2004 and 2012. The data are phytosociological relevés recorded on plots of 9 m^2 (16 m^2 in one case; this relevé was not included in mean species richness calculations) for which all the species of vascular plants were recorded (based on the presence of shoots) and their covers estimated using the classical Braun-Blanquet scale (Dengler et al. 2008) with the first and second degrees (codes r and +) lumped together. Altogether we collected 44 relevés; 36 from Dzjurkač and eight from Pidokruh. For the analysis of compositional similarity, we randomly selected eight relevés from the Dzjurkač subset to obtain a more balanced structure of the Ukrainian dataset. All Ukrainian relevés are stored in a database registered in Global Index of Vegetation-Plot Databases (Dengler et al. 2011) under the identifier EU-UA-002.

To put the Ukrainian relevés into a broader context, we supplemented the dataset with 3721 relevés of Czech dry grasslands (assigned to *Festuco-Brometea* class by their authors) from the Czech National Phytosociological Database (CNPD; Chytrý & Rafajová

2003) and 82 relevés of Romanian dry grasslands published by Dengler et al. (2012). The Czech data included 104 relevés of extremely species-rich semi-dry grasslands assigned to the *Brachypodio pinnati-Molinietum arundinaceae* association by their authors. The Romanian data included 11 relevés of the extremely species-rich semi-dry grasslands of the *Festuco sulcatae-Brachypodietum pinnati* association. The Czech data came from a geographically stratified subset of CNPD prepared for the Vegetation of the Czech Republic project. For details of the stratification procedure and other aspects of the Czech dataset see Chytrý (2007) or Roleček (2007). Prior to the analyses, all records of identical species in different vegetation layers were merged. All tree species were deleted. Undetermined taxa and taxa determined to genus level were deleted except for some abundant but taxonomically complicated and/or often misidentified taxa: *Alchemilla* sp. (all records of the genus included), *Cuscuta* sp. (all records of the genus included), *Crataegus* sp. (all records of the genus included), *Rosa* sp. (all records of the genus included except for the morphologically and ecologically conspicuous *R. gallica* and *R. pimpinellifolia*) and *Taraxacum* sp. (all records of the genus included). The taxonomical concepts and nomenclature were unified according to Ehrendorfer (1973); exceptions and species not included in this reference but mentioned in this paper are listed in Electronic Appendix 1. To analyze the similarity between Ukrainian, Czech and Romanian relevés, we calculated a distance matrix based on Euclidean distance. To visualize the relationships in the matrix, we clustered the relevés using Ward's algorithm in PC-ORD 5.0 (McCune & Mefford 1999) and JUICE 7.0 (Tichý 2002) software. To evaluate the differences in species composition of the extremely species-rich semi-dry grasslands at different sites, we tabulated frequencies of the 30 most abundant species and 30 most diagnostic species (10 for each site). Diagnostic species were identified using the phi coefficient standardized for unequal group sizes (Tichý & Chytrý 2006) in JUICE 7.0. Species with a non-significant diagnostic value ($\alpha = 0.05$) were excluded from the list using Fisher's exact test. To indicate differences in environmental conditions of the vegetation at different sites, we calculated the unweighted mean Ellenberg indicator values (EIVs; Ellenberg et al. 1992) for all the species in each relevé and illustrated their distribution within the groups using box-and-whisker plots. Because we compared analogous types of vegetation with similar species composition and few eastern elements, we consider the use of EIVs (originally proposed for west-central Europe) as a convenient solution. Statistical significance of the differences in mean EIVs was tested using Kruskal-Wallis test and multiple comparisons in Statistica software (StatSoft 2011).

To provide an even more general picture of the Ukrainian extremely species-rich semi-dry grasslands, we compared frequencies of the species present in Ukrainian relevés with those in synoptic tables of semi-dry grasslands published by Illyés et al. (2007), Chytrý (2007) and Dengler et al. (2012). Illyés et al. (2007) published a synthesis of *Brachypodium pinnatum* and *Bromus erectus* dominated grasslands, mostly belonging to *Bromion erecti* and *Cirsio-Brachypodion pinnati* alliances (broad-leaved semi-dry grasslands), for most countries of central Europe (from Germany to north-western Romania). Chytrý (2007) published a synthesis of all types of dry grassland in the Czech Republic. We excerpted the frequency columns corresponding to associations of *Bromion* and *Cirsio-Brachypodion* alliances, including the *Brachypodio-Molinietum* association. From the study of Dengler et al. (2012) we took all the frequency columns corresponding to associations from several different alliances of dry grasslands occurring in Transylvania. As some

of the published synoptic tables do not include information on rare species (with a frequency < 20% in all columns), we modified accordingly all the frequency columns compared. As a result, the comparison is based on the frequencies of the 367 most abundant species, which may be viewed both as a disadvantage (data incompleteness) and an advantage (noise reduction). According to our pilot analyses, the inclusion of 50 rare species had virtually no effect on the results. In cases when different taxonomical concepts were used in different sources, the broader taxonomical concept was used for a particular taxon and more narrowly defined taxa were merged. For the analysis of similarity of frequency columns, we calculated a distance matrix based on Euclidean distance. To visualize the similarity, we clustered the columns using Ward's algorithm and ordinated them in two-dimensional space using non-metric multidimensional scaling in Statistica software (StatSoft 2011).

Calculations of species richness were performed on full species lists (including juvenile trees and shrubs). To compare species richness per relevé (alpha-diversity) among regions where relevés were recorded in different sized plots, we standardized the richness values using a power function (Dengler 2009), assuming a z-value equal to 0.294, as reported for semi-dry *Brachypodietalia pinnati* grasslands in Transylvania (Dengler et al. 2012).

Results

Species richness

Comparison with other extremely species-rich semi-dry grasslands (Table 1) shows that both newly identified sites in the Ukraine have a slightly lower standardized mean species richness than sites in the White Carpathians and markedly lower than Transylvanian sites (for the latter, however, there were very few relevés available). The standardized maximum species richness for Dzjurkač, however, is slightly higher than that for the record-holding site in the White Carpathians (Čertoryje nature reserve) and slightly lower than that for the record-holding site in Transylvania (Fânaţele Clujului nature reserve). The other Ukrainian site, Pidokruh, has a moderate standardized maximum species richness, which is slightly lower than that of the species poorer site in Transylvania (Rezervaţia de bujori de stepă nature reserve). The maximum number of vascular plants per 9 m^2 at Dzjurkač (90) is the highest reported in scientific literature (Wilson et al. 2012, J. Dengler pers. comm.). A comparison with the maxima recorded for different sized plots published by Wilson et al. (2012) is provided in Fig. 2. Full record-holding relevé is included in Electronic Appendix 2.

Species composition

Comparison with other types of dry grasslands in central Europe based on species frequencies (Fig. 3) revealed that Ukrainian extremely species-rich semi-dry grasslands are most similar to the *Brachypodio-Molinietum* association in Chytrý (2007) and Illyés et al. (2007). Cluster analysis of individual relevés gave a similar result and revealed that the similarity between the Ukrainian and Czech extremely species-rich semi-dry grasslands may be at the level of a phytosociological association (see dendrogram in Electronic Appendix 3). Therefore, we suggest classifying the Ukrainian grasslands within the

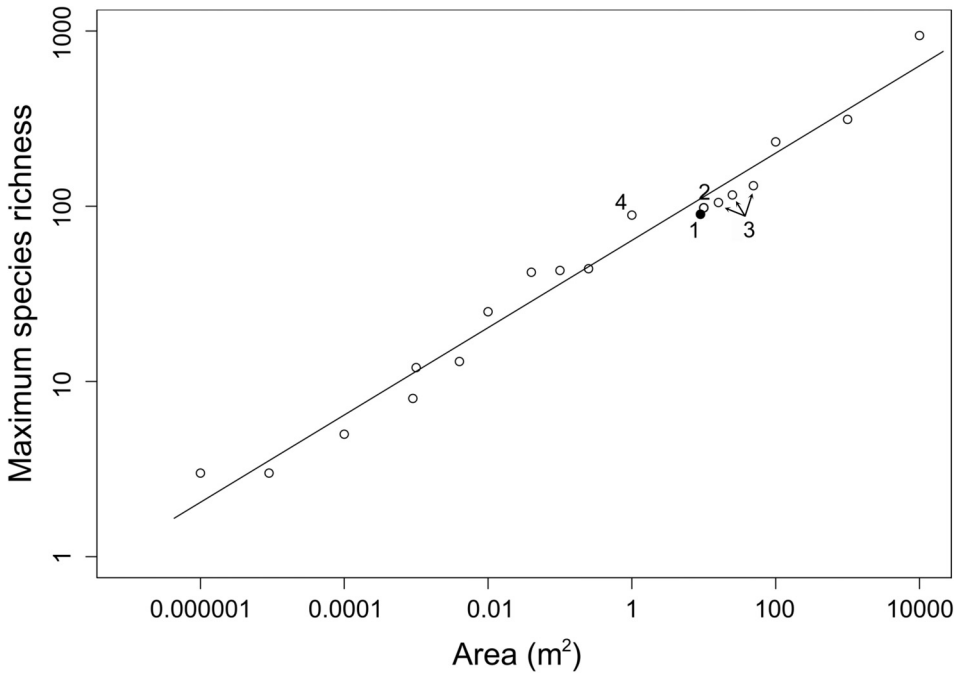


Fig. 2. – Maximum species richness of vascular plants per 9 m^2 plot in semi-dry grasslands at Dzjurkač in the Ukraine compared in the log-log space with world records published by Wilson et al. (2012) for a range of plot sizes. Site numbers: 1 – Dzjurkač, Ukraine; 2 – Fânaţele Clujului, Romania; 3 – Čertoryje, Czech Republic; 4 – Sierras de Comechingones, Argentina. Only sites with values recorded at spatial scale close to that used at Dzjurkač are marked with numbers.

Brachypodio-Molinietum association, first described from the White Carpathians (Klika 1939, Chytrý 2007) or, alternatively, describing a new, closely related and geographically vicarious association.

Nevertheless, the vegetation at the Dzjurkač and Pidokruh sites in the Ukraine differs appreciably (see Electronic Appendix 2 for full frequency tables). There are more species of mesic meadows (e.g. *Arrhenatherum elatius*, *Anthoxanthum odoratum*, *Gladiolus imbricatus*, *Holcus lanatus* and *Trisetum flavescens*), tall herbaceous plants (e.g. *Equisetum telmateia*, *Laserpitium latifolium*, *Pteridium aquilinum* and *Veratrum nigrum*) and (sub)montane species (e.g. *Hypericum maculatum*, *Pedicularis exaltata* and *Veratrum album* subsp. *lobelianum*) in the Dzjurkač grasslands, which from a syntaxonomical point of view are transitional between *Cirsio-Brachypodion*, *Arrhenatherion elatioris* and *Polygono-Trisetion flavescentis* alliances (see the analysis in Electronic Appendix 4). This is reflected in the significantly higher EIVs for moisture and nutrients (Fig. 4) and corresponds well with the relatively high altitude of this site (Table 1) and position on a northern slope with the occurrence of moist depressions. On the other hand, the vegetation at Pidokruh includes more species of basiphilous dry grasslands and thermophilous herbaceous fringes (e.g. *Bupleurum falcatum*, *Carex montana*, *Cirsium pannonicum*, *Genista tinctoria*, *Inula hirta*, *I. salicina*, *Melampyrum cristatum*, *Peucedanum cervaria*, *Scabiosa ochroleuca* and *Thesium linophyllon*). This is reflected in a significantly higher Ellenberg

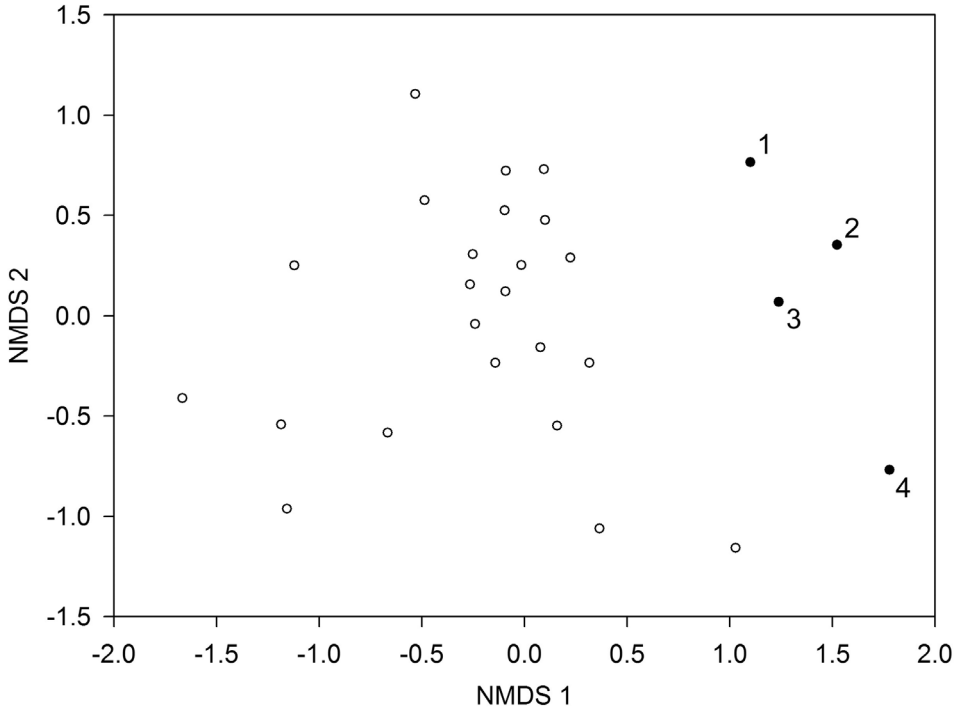


Fig. 3. – Non-metric multidimensional scaling plot showing the similarity of the different types of dry and semi-dry grasslands in central Europe. The calculation is based on the matrix of Euclidean distances between the frequency columns. Legend: 1 – cluster D in Illyés et al. (2007), mostly *Brachypodio-Molinietum* grasslands in the Czech Republic and Slovakia; 2 – *Brachypodio-Molinietum* grasslands in the Czech Republic according to Chytrý (2007); 3 – Ukrainian grasslands at Dzjurkač and Pidokruh (species frequencies based on 16 relevés, eight from each site); 4 – Transylvanian *Festuco-Brachypodietum* grasslands according to Dengler et al. (2012; species frequencies based on 11 relevés, seven from Fânaţele Clujului and four from Rezervaţia de bujori de stepă); empty circles – other types of dry grasslands occurring from Germany to Transylvania published in Chytrý (2007; only *Cirsio-Brachypodion* and *Bromion* grasslands are included), Illyés et al. (2007) and Dengler et al. (2012).

indicator values for temperature, light, soil reaction and continentality (Fig. 4) and corresponds well with the position of this site at a lower altitude (Table 1) and at the foot of a south-western slope.

The extremely species-rich semi-dry grasslands in Romania share many features with those in the Ukraine and Czech Republic (Table 2). However, in terms of their total species composition they are more similar to the *Polygalo majoris-Brachypodietum pinnati* association. Included in this association are broad-leaved semi-dry grasslands of the Pannonian region that have higher numbers of drought-tolerant species than *Brachypodio-Molinietum* grasslands. This is also the case for the Romanian sites with high frequencies of drought-tolerant species, such as *Agropyron intermedium*, *Carex michelii*, *Centaurea triumfettii*, *Echium russicum*, *Iris aphylla*, *Koeleria macrantha*, *Linum nervosum*, *Seseli annuum*, *Teucrium chamaedrys* and *Veronica prostrata* (see also Table 3). Their EIVs for moisture are the lowest and for temperature the highest of the communities compared (Fig. 4). As these grasslands exhibit some unique features, we support their current classification as a separate association *Festuco sulcatae-Brachypodietum pinnati* (*Cirsio-Brachypodion*

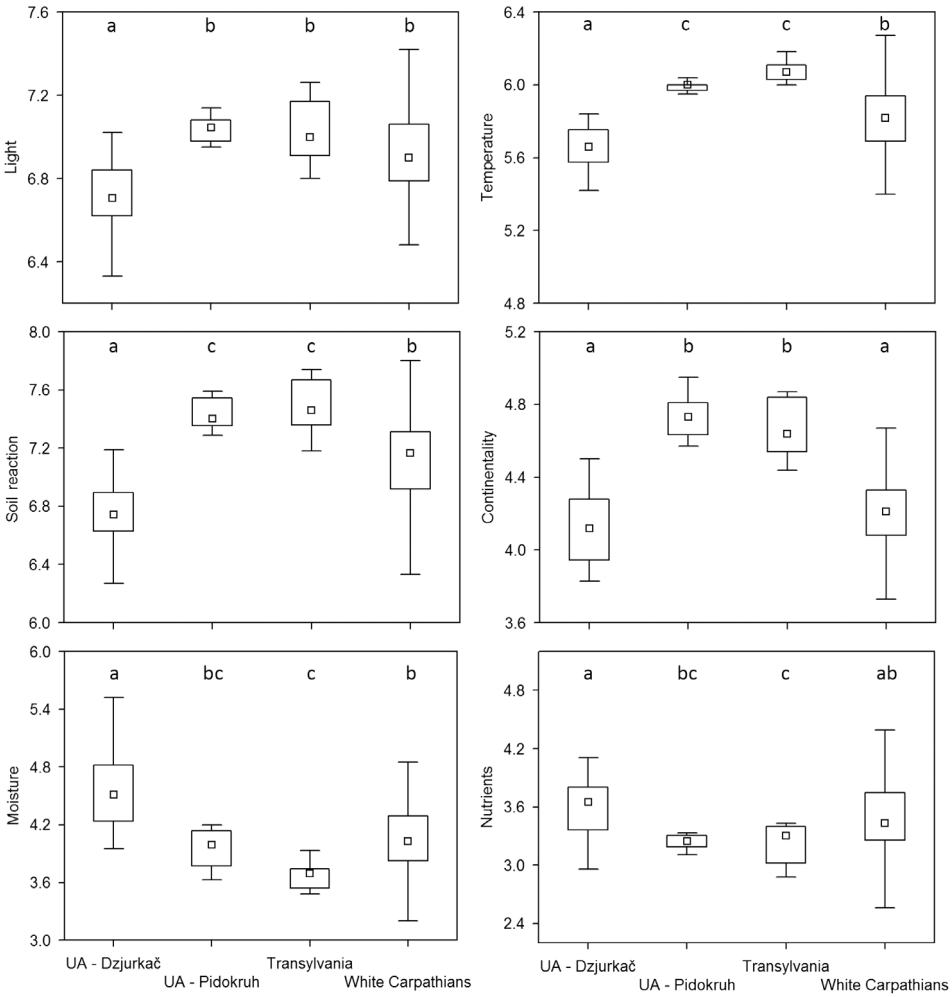


Fig. 4. – Differences in mean Ellenberg indicator values for light, temperature, soil reaction, continentality, moisture and nutrients between the extremely species-rich semi-dry grasslands at the two newly identified sites in the Ukraine (UA) and those in Transylvania and the White Carpathians.

alliance). Their differentiation from other types of east-central European semi-dry grassland is also well illustrated by their remote position on the ordination plot based on species frequencies (Fig. 3).

Discussion

Our findings rank the semi-dry grasslands in the Prut-Siret interfluve in the Ukraine among the places with the world's highest species richness at the scale of about 10 m^2 (Wilson et al. 2012). Even more interestingly, these grasslands are very similar in several respects to other extremely species-rich grasslands in east-central Europe.

Table 2. – Thirty most frequent species in the extremely species-rich semi-dry grasslands in the three regions compared. Species are sorted according to mean frequencies. Legend: f_{UA} – percentage frequency in 16 Ukrainian relevés (eight from Dzjurkač and eight from Pidokruh); f_{WC} – percentage frequency in 104 White Carpathian relevés; f_{TR} – percentage frequency in 11 Transylvanian relevés (seven from Fânaţele Clujului and four from Rezervaţia de bujori de stepă).

Species	f_{UA}	f_{WC}	f_{TR}
Filipendula vulgaris	100	81	100
Dactylis glomerata	83	85	100
Brachypodium pinnatum	72	86	100
Achillea millefolium agg.	67	85	100
Trifolium montanum	78	68	100
Campanula glomerata	83	59	100
Lotus corniculatus	83	59	100
Knautia arvensis agg.	72	63	91
Betonica officinalis	72	71	82
Cruciata glabra	83	49	91
Plantago lanceolata	50	71	100
Ranunculus polyanthemos	56	63	100
Briza media	72	65	82
Plantago media	56	62	100
Galium verum agg.	61	84	73
Leucanthemum vulgare agg.	83	56	64
Viola hirta	50	47	100
Cirsium pannonicum	50	73	73
Festuca ser. *Valesiacae*	28	65	100
Leontodon hispidus	50	59	82
Salvia pratensis	44	64	82
Carex montana	72	62	55
Primula veris	50	71	64
Centaurea jacea agg.	78	50	55
Centaurea scabiosa s. l.	56	34	91
Thesium linophyllon	50	44	82
Coronilla varia	50	24	100
Medicago sativa agg.	78	32	64
Tanacetum corymbosum	78	47	45
Dianthus carthusianorum agg.	33	33	100

Table 3. – Thirty species most differentiating the extremely species-rich semi-dry grasslands in the three regions compared. Percentage frequencies of 10 species with highest diagnostic values are given for each region (in grey). Species are sorted according to decreasing diagnostic value measured by the phi coefficient. For legend see Table 2.

Species	f_{UA}	f_{WC}	f_{TR}
Peucedanum oreoselinum	50	0	0
Trifolium pannonicum	44	0	0
Equisetum telmateia	39	0	0
Cichorium intybus	39	1	0
Potentilla erecta	67	29	0
Ferulago sylvatica	28	0	0
Laserpitium latifolium	44	13	0
Gymnadenia conopsea	50	20	0
Erigeron annuus	22	0	0
Pteridium aquilinum	22	0	0
Bromus erectus agg.	0	71	0
Lathyrus latifolius	0	51	0
Trifolium rubens	0	45	0
Koeleria pyramidata	0	43	0
Lathyrus pratensis	0	41	0

Species	f_{UA}	f_{WC}	f_{TR}
Helianthemum nummularium agg.	6	49	0
Colchicum autumnale	11	54	0
Potentilla heptaphylla	0	51	9
Pulmonaria angustifolia	0	35	0
Trisetum flavescens	17	56	0
Iris aphylla	0	0	73
Agropyron intermedium	17	16	100
Echium russicum	0	5	73
Centaurea triumfettii	0	6	73
Crepis nicaeensis	0	0	64
Teucrium chamaedrys	11	11	82
Seseli annuum	0	5	64
Veronica austriaca agg.	11	25	91
Carex michelii	0	24	82
Koeleria macrantha	6	9	73

Table 4. – Thirty species most differentiating *Brachypodio-Molinietum* grasslands in the Ukraine and the White Carpatians from other east-central European types of dry grasslands (3631 Czech and Transylvanian relevés were used for comparison). Species are sorted according to decreasing maximum diagnostic value in any of the two columns measured by the phi coefficient. For legend see Table 2. Frequency code"present" indicates the species is present in the relevés from Dzjurkač but was excluded from the analysis during the random subset selection described in the Material and methods.

Species	f_{UA}	f_{WC}
Cruciata glabra	83	49
Sanguisorba officinalis	72	60
Potentilla alba	72	70
Potentilla erecta	67	29
Serratula tinctoria	61	63
Carex montana	72	62
Lathyrus latifolius	present	51
Filipendula vulgaris	100	81
Colchicum autumnale	11	54
Campanula glomerata	83	59
Molinia caerulea agg.	56	51
Trifolium pannonicum	44	0
Cirsium pannonicum	50	73
Trifolium rubens	0	45
Gymnadenia conopsea	50	20
Ononis arvensis	44	12
Trisetum flavescens	17	56
Rumex acetosa	6	60
Primula veris	50	71
Betonica officinalis	72	71
Tanacetum corymbosum	78	47
Equisetum telmateia	39	0
Leucanthemum vulgare agg.	83	56
Laserpitium latifolium	44	13
Pulmonaria angustifolia	0	35
Equisetum arvense	39	1
Peucedanum oreoselinum	50	0
Agrostis tenuis	72	36
Lilium martagon	39	18
Trifolium montanum	78	68

Total species composition

Results of our numerical analyses reveal that the floristic composition of the extremely species-rich semi-dry grasslands at the three sites is very similar. Vegetation at these sites may be classified in single phytosociological alliance (*Cirsio-Brachypodion*, i.e. broad-leaved semi-dry grasslands with a subcontinental distribution) and vegetation at the sites in the White Carpathians and the Ukraine perhaps even in single phytosociological association (*Brachypodio-Molinietum*). The similarity suggests a possible link between extremely-high species richness and particular species composition. This idea is supported by the similarity with another record-holding extremely species-rich grassland community, occurring more than 1000 km to the north – Estonian wooded meadows. Of the 73 species of herbaceous plants and graminoids cited by Kull & Zobel (1991) as occurring in the species-richest places in the Laelatu wooded meadow, 40 occurred also in our relevés of *Brachypodio-Molinietum* grasslands in the White Carpathians and the Ukraine. Moreover, of the 30 species with highest fidelity to *Brachypodio-Molinietum* grasslands (Table 4), seven occur also at Laelatu: *Campanula glomerata*, *Filipendula vulgaris*, *Leucanthemum vulgare* agg., *Molinia caerulea* agg., *Potentilla erecta*, *Primula veris* and *Serratula tinctoria*. A similar species-rich grassland was reported also from Styria, Austria (Steinbuch 1995); it was formally described as *Cirsio pannonici-Brometum* association. We suggest that this similarity in species composition of extremely species-rich semi-dry grasslands supports species pool-based explanations of species richness, which will be discussed further below.

Species with disjunct distributions

The extremely species-rich semi-dry grasslands studied include a considerable number of rare heliophilous species with disjunct distributions in east-central Europe. For the White Carpathians, the information on these species is summarized by Hájková et al. (2011). Among the species mentioned by these authors, *Pedicularis exaltata* and *Veratrum nigrum* occur also at Dzjurkač in the Ukraine, together with *Adenophora liliifolia* and *Crepis sibirica*, whose distributions in central Europe are also characteristically disjunct. The concentrated occurrence of such species in the grasslands studied is noteworthy, as it may be of relict origin, i.e. the species may indicate a specific history of these grasslands (Ložek 2007, Hájková et al. 2011). As *Veratrum nigrum*, *Adenophora liliifolia* and *Crepis sibirica* are important elements of Eurasian forest-steppe, hemiboreal forests and continental forest meadows (Kleopov 1990, Ermakov & Maltseva 1999, Ermakov 2006) their co-occurrence suggests historical or migrational links between these grasslands and forest-steppe or hemiboreal forest vegetation. According to recent views, such vegetation could have been widespread in east-central Europe during early Holocene and, in some regions, also in the Pleistocene (Ložek 2007, Kuneš et al. 2008, Magyari et al. 2010). The long history of these ancient types of vegetation is reflected in the large size of their species pool (Ermakov & Maltseva 1999). Large species pool may then support their high small-scale species richness (Ermakov & Maltseva 1999, Chytrý et al. 2012) and possibly also a high species richness of their hypothetical successors in east-central Europe.

Remarkably, both of the extremely species-rich semi-dry grasslands in Transylvania also host heliophilous species with disjunct distributions. Fânaţele Clujului harbours a spectrum of regionally rare heliophilous elements, including the steppe species (*Psephellus*

trinervius), mesophilous species typical of hemiboreal forests and continental forest meadows (*Serratula coronata*), as well as species ranging from steppe to subalpine meadows (*Bulbocodium vernum*) (Dengler at al. 2012, Badarau 2013). The other Transylvanian site, Rezervaţia de bujori de stepă, was declared a nature reserve to protect the only population of the Pontic steppe species *Paeonia tenuifolia* in Transylvania (Cristea 1999). Again, the occurrence of such species may indicate that these grasslands are linked to ancient types of vegetation with large species pools.

Orchids

Brachypodio-Molinietum grasslands in the White Carpathians are also famous for their richness in orchids, with about 20 species of orchid occurring in this habitat (Jongepier & Jongepierová 1995). Accordingly, Dzjurkač in the Ukraine is a regionally important orchid site with 14 species (e.g. *Dactylorhiza sambucina* and *Gymnadenia conopsea* subsp. *densiflora*) occurring in area of about 20 ha. Comparable sites in the White Carpathians, e.g. Búrová (19 ha) and Dolnoněmčanské louky (29 ha) nature reserves, have 10 and 17 species of orchid, respectively (K. Fajmon, in litt.).

Grassland orchids are considered to be competitively weak species (Jersáková & Kindlmann 2004) sensitive to intensification of management, particularly the application of mineral fertilizers containing phosphorus (Hejcman et al. 2010), as well as to absence of management (Jersáková & Kindlmann 2004). Their abundant occurrence in relatively high-productive *Brachypodio-Molinietum* grasslands (Merunková et al. 2012) is attributed to regular biomass removal (Jersáková & Kindlmann 2004), typically by mowing (Futák et al. 2008). Cessation of mowing results in a fast retreat of some species of orchid, while their return after restoration of mowing may be slow (Jersáková et al. 2002); therefore an abundance of orchids may indicate these grasslands have regularly been mown for long periods of time.

Drier types of grasslands are considerably poorer in orchids (Jersáková & Kindlmann 2004). The availability of moisture may be the ultimate control of orchid occurrence, as shown e.g. by Scott & Carrey (2002) for *Gymnadenia conopsea*, the most common species of orchid in *Brachypodio-Molinietum* grasslands. This idea is supported also by the sub-Atlantic and sub-Mediterranean ranges of many orchids (Klotz et al. 2002). This may also account for the low numbers of orchids in some of the Transylvanian grasslands (Mititelu 1990), which are regularly mown, but experience somewhat drier, continental climate and contain more drought-tolerant species.

Site conditions

Comparison of site conditions recorded in the extremely species-rich semi-dry grasslands in the peri-Carpathian region (Table 1) revealed that they have several important ecological features in common. Compared to other *Festuco-Brometea* grasslands, they occur in places with a relatively cold (mean annual temperature 7.0–8.5 °C) and humid (mean annual precipitation 610–840 mm) mesoclimate. As this is coupled with the occurrence on deep, clayey soils, which retain water, they support more moisture-demanding species. Merunková et al. (2012) suggest that it is the temporal and spatial variability in moisture of clayey soils that facilitates coexistence of drought-adapted and moisture demanding

species in the White Carpathian grasslands. This suggestion, however, has not yet been adequately tested.

The bedrock is also similar at all the sites compared, consisting mainly of calcareous sediments of Tertiary age (mostly clays/claystones with sand/sandstone interbeds). Soils on such bedrock are mostly base-rich to moderately rich (Dengler et al. 2012, Merunková et al. 2012, V. A. Nikoryč, pers. comm.) and because of the evolutionary history of the central-European flora, they have larger species pools than base-poor soils (Pärtel 2002, Chytrý et al. 2003, Ewald 2003). Such bedrock is also unstable and slope movements (sliding, slumping) occur at all the sites compared or close by (Cristea 1999, Rudko 2005, Pechanec & Jongepierová 2008, Moldovan 2012). At some sites, these slope movements create a characteristically complex topography supporting a mosaic of wet, mesic and dry sites. Existence of such a mosaic may hypothetically increase local species richness through mass effect (Shmida & Ellner 1984, Merunková et al. 2012), which has been shown also for east-central European semi-dry grasslands (Janišová et al. 2014). In extreme cases, slope movements could also promote long-term survival of competitively weak heliophilous species either through repeated disturbance or by creating extreme sites with steep slopes and shallow soils; slumping hills at Fânaţele Clujului are the most striking example (Dengler et al. 2012, Moldovan 2012).

Landscape context

As mentioned in the Introduction, the landscapes around the Czech and Ukrainian sites with extremely species-rich semi-dry grasslands are similar. Both the south-western White Carpathians and the Prut-Siret interfluve are mostly hilly regions with a substantial cover of mesophilous broad-leaved forests and with a climate that is generally suitable for forest vegetation. In other words, the natural vegetation in most places of both regions is forest (Bohn & Neuhäusl 2000–2003). However, both regions are also situated on the periphery of large plains with forest-steppe climate and a significant representation of steppe species and vegetation. In the case of the White Carpathians, the surrounding lowlands along the Morava and Váh rivers are parts of the Pannonian Basin, an important forest-steppe region lying between the Alps, Carpathians and Balkan mountain ranges (Embleton 1984, Magyari et al. 2010, Chytrý 2012). In the case of Prut-Siret interfluve, the southern part of the Volyn-Podolian Upland to the north and the Dniestr-Prut-Siret interfluve to the south (mostly situated in Romania and Moldova) are again regions of relatively warm and dry continental climate supporting a forest-steppe vegetation (Marynyč 1989, Nedelea et al. 2009). Also the Transylvanian Plateau is a region of transitional character between forest and forest-steppe, both from the point of view of bioclimatology (Kun et al. 2004) and natural vegetation, in which thermophilous and mesophilous mixed oak woods prevail (Bohn & Neuhäusl 2000–2003). Transylvanian dry grasslands are mostly confined to isolated extreme sites on southern slopes and their surroundings; however, they include species with disjunct distributions and even endemics (Dengler et al. 2012), which suggests their refugial character and ancient origin.

In summary, the extremely species-rich semi-dry grasslands in the three regions compared occur in similar landscapes, with a prevalence of sites suitable for mesophilous species but with links to sources of forest-steppe species.

History of human influence

Hájková et al. (2011) suggest that the extreme species richness of semi-dry grasslands in the White Carpathians and local survival of rare heliophilous species with disjunct distributions may be partly ascribed to the long history and continuity of these grasslands maintained by human activities. The authors summarize archaeological evidence for prehistoric human settlement in this region since the Neolithic/Eneolithic and provide multiproxy evidence for the existence of a cultural landscape with a mosaic of open grasslands, natural forests and fields in the Roman Age at the latest. From this point of view it is remarkable that the sites of extremely species-rich semi-dry grasslands in the Ukraine and Romania are also situated in regions colonized early by prehistoric farmers. In the Ukraine, the surroundings of the city of Černivci harbour many remnants of Late Neolithic/Eneolithic Cucuteni-Trypillian culture (~4800–3000 BC; Passek 1961, Videjko & Burdo 2004). Archaeological evidence for settlements of this culture was found even at Spas'ka and Zavoloka, which are adjacent to the grasslands studied (Videjko & Burdo 2004). In Romania, Fânaţele Clujului is situated at the periphery of the city of Cluj-Napoca, just 7 km north of the city centre, where remnants of an Early Neolithic Starčevo-Criş culture (~6000 BC) settlement were found, and 9 km north-east of Baciu, an important archaeological site with evidence for human settlement in all major prehistoric periods, including Palaeolithic, Mesolithic and Early Neolithic (Spataro 2010, National Heritage Institute 2012). The other Romanian site, Rezervaţia de bujori de stepă, is situated 5 km north-west of Zau de Câmpie and 7 km east of Iacobeni, where remnants of Late Neolithic/Eneolithic Turdaş-Vinča culture (~4500–3700 BC) settlements were found (National Heritage Institute 2012). It is also of interest that in the close vicinity of the species-richest sites in the White Carpathians (Čertoryje nature reserve) and the Ukraine (Dzjurkač), remnants of early Slavic (8th–10th century AD) settlements were found (Tymoščuk 1981, Hájková et al. 2011).

Several authors provide evidence that species richness may be positively associated with the age of the grasslands on a millennial time scale (Bruun et al. 2001, Pärtel et al. 2005). Even if suitable management (mowing, grazing, burning) has not been continued for millenia, human activities kept the landscape open and thus might have facilitated the survival of a large pool of heliophilous species of early Holocene communities (forest-steppe, hemiboreal forests) during the spread of closed-canopy forest in the middle Holocene (Ložek 2007, Hájková et al. 2011). Long-term existence of human-managed open habitats might also have facilitated the immigration of species and even evolutionary changes in their fundamental niches promoting coexistence (Eriksson 2013).

Regarding more recent human influences, all the sites of extremely species-rich semi-dry grasslands compared were mown over the last few decades (Cristea 1999, Jongepierová et al. 2008, Dengler et al. 2012, I. I. Čornej, pers. obs.) and often have been traditionally used by local people for hay-making. Intensive management, such as application of mineral fertilizers, intensive grazing or ploughing was rare or absent (Artemčuk 1960, Korsós et al. 1997, Futák et al. 2008, Badarau 2013). The unusually low intensity of management was at several sites (e.g. the most species-rich sites in the White Carpathians and Dzjurkač in the Ukraine) probably the consequence of their locations in remote corners of their parishes. Continuity of mowing is an important determinant of species composition and richness also in Estonian wooded meadows (Aavik et al. 2008).

Mowing in the absence of fertilizer application increases local species richness in semi-dry grasslands through litter and biomass removal, suppression of dominants and support of low-growing competitively weak species (Klimeš et al. 2000, 2008, Klimeš & Klimešová 2001). As stated by Lepš (1999), mowing reduces the asymmetry in competition for light and decreases the probability of local extinction of weak competitors. According to Eriksson (2013), the management of grasslands promotes spatial stability of habitat conditions and thus reduces local extinction rates, which increases species occupancy and results in high local species richness. The cessation of mowing of semi-dry grasslands leads to an immediate decline in the abundance of many species and results in a marked decrease in local species richness (Klimeš et al. 2008).

The cessation of mowing is a serious threat to the extraordinary natural values of several of the sites studied. Over the last couple of years, the area regularly mown was greatly reduced at Dzjurkač and almost nil at Pidokruh in the Ukraine. These places are now extensively grazed and burnt in early spring. The traditionally mown grasslands at Fânaţele Clujului in Romania were recently also partly transformed into intensive cattle and sheep pastures (Badarau 2013).

Conceptual model of the species richness of peri-Carpathian extremely species-rich semi-dry grasslands

Zobel (1992) provided a conceptual model of plant species richness for Estonian extremely species-rich grasslands. His influential framework links evolutionary, historical and ecological factors and emphasizes their interplay. Among the individual factors, he emphasizes the existence of a large pool of basiphilous steppe plants (though filtered during migration to boreo-nemoral zone) and regular mowing, which controls the occurence of shading trees and shrubs and reduces the asymmetry in the competition for light.

Merunková et al. (2012) provided an analogous, but more inclusive model for extremely species-rich grasslands in the White Carpathians. These authors propose that the following factors support small-scale species richness: early human settlement (possibly enabling survival of a large early-Holocene species pool), a large area of grasslands (possibly increasing both total and local species richness according to the theory of island biogeography), existence of a mosaic of different habitats (possibly increasing local species richness through mass effect), high soil pH (supporting large pool of base-demanding species), convenient soil chemistry and productivity (falling within the range supporting high species richness in temperate grasslands), changing soil moisture (possibly supporting coexistence of drought-adapted, moisture demanding and 'transitional' species and suppressing their competitors) and mowing (preventing the spread of competitive species). The authors conclude that the high species richness recorded in the grasslands of White Carpathians cannot be explained by a single factor but is a result of a unique combination of many different factors.

Here we propose a common model for peri-Carpathian extremely species-rich grasslands, based on their most striking similarities, which were discussed above. Similarity in species composition between different sites supports the species pool-based explanations of species richness. The occurrence of remnants of Neolithic/Eneolithic human settlements near to all the sites studied suggest an ancient age for these grasslands and their possible link with large species pools of early-Holocene heliophilous communities. This hypothesis is further supported by the occurrence of rare species with disjunct distributions at all

the sites compared. Ancient ages of these grasslands may also have a beneficial effect on immigration and evolutionary changes in species niches, which may promote their coexistence. The calcium-rich bedrock at all these sites favours most members of this predominantly basiphilous ancient species pool. Coexistence of species from different species pools could also play a role, as all the sites lie in or near borderlands between regions with prevailing mesic site conditions and regions of warmer and drier forest-steppe climate. Slope movements present at all the sites compared create a complex topography, which favours the development of a mosaic of wet, mesic and dry sites that may increase species richness through a mass effect. Extensive and repeated slope movements also possibly block succession at some sites and thus favour the long-term survival of heliophilous species. Semi-dry soils seem to enable drought-tolerant and mesophilous species to coexist. It is an intriguing question whether this coexistence is primarily determined by changing moisture (i.e. changing moisture serves as an equalizing or stabilizing mechanism of species coexistence; Chesson 2000), or whether changing moisture simply provides conditions that are tolerable for both drought-tolerant and mesophilous species, whose coexistence is controlled by some other factor. Such a controlling factor could be regular mowing in the absence of fertilizer application, the most common form of management at the sites compared. Mowing has been repeatedly identified as an important factor reducing the asymmetry in competition and promoting species coexistence in grasslands.

Interestingly, Chytrý et al. (2012) suggest an analogous model for the extremely species-rich forests in the Altai Mountains in southern Siberia. Altaian hemiboreal forests share many species with the east-central European semi-dry grasslands, as they have open, species-poor canopies and species-rich herbaceous understoreys. The model of these authors emphasizes similar aspects as Merunková et al. (2012) does for the grasslands in the White Carpathians, particularly the rare combination of several factors needed to achieve extremely high small-scale species richness. These factors include a rich regional flora, stability of the environment since the Pleistocene, heterogeneity of the montane forest-steppe landscape, an open canopy that ameliorates microclimate but does not exclude light-demanding species, a macroclimate that is not too harsh, mesic soils with a near-neutral pH and limited competition between the plants in the herb layer. The major difference from the above models proposed for grasslands is the hypothetical factor controlling competition in the herb layer: here it is not mowing, but the influence of trees on the herb layer. Chytrý et al. (2012) mention canopy shading, competition for water and nutrients from the trees and disturbance. We suggest that analogically to species-rich grasslands, competition for light may be the most important factor and that shading by trees may reduce the asymmetry in competition between plants in the herb layer and facilitate species coexistence in these forests. In any case, this is another example of a plant community whose extraordinary local species richness largely originates from an ancient pool of Eurasian forest-steppe and hemiboreal forest species.

Other record-holding sites

In addition to the sites already discussed, Wilson et al. (2012) report world records of vascular plant species richness for three other grassland sites: dry sandy grasslands in Germany, montane grasslands in Argentina and limestone grasslands in Sweden. Do these grasslands fit our model of species richness?

Comparison with German dry sandy grasslands is not straightforward, as they hold records at very small spatial scales (up to 1 cm^2) and are, therefore, difficult to compare with our sites. We also assume that the determinants of species richness at different scales may differ. At the same time, there is little data available on species richness at very small spatial scales and thus it is difficult to judge whether the reported values are exceptional or not.

Argentinean montane grasslands reach their species richness maxima at environmental conditions different from those of east-central European semi-dry grasslands. The richest plots are in extensively grazed and sporadically burnt short-grass communities growing on shallow soils that developed over crystalline bedrock (Cantero et al. 1999). When considering the consequences of these differences for our model of species richness, it should be noted that the species pool of Argentinean grasslands is quite different from that of our grasslands, as is their history: they evolved under light grazing pressure from a large native herbivore, *Lama guanicoe* (Cantero et al. 1999). In spite of these differences, Argentinean montane grasslands fulfil the basic conditions required by our model for extreme species richness to occur: continuity over a long period of time and management that reduces the asymmetry in competition (here it may be the long-lasting grazing).

Swedish record-holding grasslands belong to the well-studied *Veronica spicata-Avenula pratensis* community occurring at the Great Alvar on Öland island (Krahulec et al. 1986, van der Maarel & Sykes 1993). This community of extensively grazed semi-dry grasslands occurs on a limestone substrate covered with moraine sediments or weathering residuals of varying thickness, which produce soils of different depths, moisture regimes and pH values (Löbel & Dengler 2008). Various hypotheses have been proposed to account for their extremely high species richness, including the low productivity in the harsh climate of northern Europe, high spatio-temporal variability in environmental conditions (Löbel & Dengler 2008) and the peculiar carousel model (van der Maarel & Sykes 1993). Considering our conceptual model, we stress the large species pool of these grasslands and presence of endemic species (e.g. *Galium oelandicum*), which indicate their ancient origin; this is also supported by the results of palaeoecological studies (Königsson 1968).

Conclusions

Our results support Zobel's idea (Zobel 1992) that extremely high local species richness in grasslands appears where a large ancient species pool is enabled to coexist in a small area thanks to an external factor (typically regular mowing), which reduces the asymmetry in interspecific competition. Thus, although other factors certainly also play a role, continuity on a large (Pleistocene-Holocene) time scale and limited competition in the more recent history seem to be crucial factors responsible for the extremely high local species richness in east-central European semi-dry grasslands. We also suggest that the species pool of these grasslands is, for a substantial part, inherited from ancient communities of Eurasian forest-steppe and hemiboreal forests.

See www.preslia.cz for Electronic Appendices 1–4

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Souhrn

Širokolisté suché trávníky východní části střední Evropy patří k mimořádně druhově bohatým rostlinným společenstvům, držícím několik světových rekordů v počtu druhů cévnatých rostlin na malé prostorové škále. Příčiny této výjimečnosti nejsou dostatečně známy, což mimo jiné brání lepšímu porozumění mechanismům koexistence rostlinných druhů. Podle našeho názoru lze k poznání v této oblasti účinně přispět sběrem a publikováním základních informací o geografickém rozšíření těchto trávníků, jejich druhové bohatosti, druhovém složení a stanovištních podmínkách. V tomto příspěvku popisujeme nové lokality extrémně druhově bohatých širokolistých suchých trávníků z předhůří Východních Karpat na jihozápadní Ukrajině. Srovnáním s dalšími extrémně druhově bohatými trávníky známými z periferie Karpat v České republice a v Rumunsku a s dalšími typy středoevropských suchých trávníků se nám podařilo ukázat, že extrémně druhově bohaté trávníky jsou si v řadě ohledů podobné, a to jak celkovým druhovým složením a výskytem vzácných druhů s disjunktivním areálem, tak stanovištními podmínkami, krajinným kontextem, dlouhou historií lidského vlivu a způsobem obhospodařování. Tím je ve většině případů sečení bez častější aplikace minerálních hnojiv, intenzivní pastvy, rozorávání nebo jiných forem intenzivního hospodaření. Na základě těchto poznatků se domníváme, že k faktorům odpovědným za mimořádně velkou druhovou bohatost širokolistých suchých trávníků ve východní části střední Evropy patří zejména kontinuita jejich výskytu na velké časové škále (pleistocén až holocén) a také dlouhodobé obhospodařování (typicky sečení a nehnojení) vedoucí ke zmenšení asymetrie mezidruhové konkurence. Také se domníváme, že tato bohatost je do značné míry podmíněna časovou nebo prostorovou návazností na druhově bohatá archaická společenstva eurasijské lesostepi a hemiboreálních lesů.

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