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Patterns and drivers of phytodiversity in steppe grasslands of Central Podolia (Ukraine)

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Abstract We asked: (i) Which environmental factors determine the level of α-diversity at several scales and β-diversity in steppic grasslands? (ii) How do the effects of environmental factors on α- and β-diversity vary between the different taxonomic groups (vascular plants, bryophytes, lichens)? We sampled nested-plot series ranging from 0.0001 to 100 m^2 and additional 10-m^2 plots, covering different vegetation types and management regimes in steppes and semi-natural dry grasslands of Central Podolia (Ukraine). We recorded all terricolous taxa and used topographic, soil, land-use and climatic variables as predictors.

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Richness-environment relationships at different scales and across taxonomic groups were assessed with multimodel inference. We also fitted power-law species-area relationships, using the exponent (z value) as a measure of β-diversity. In general, the richness values in the study region were intermediate compared to those known from similar grasslands throughout the Palaearctic, but for 1 cm^2 we found seven species of vascular plants, a new world record. Heat index was the most important factor for vascular plants and bryophytes (negative relation), while lichen diversity depended mainly on stone and rock cover (positive). The explanatory power of climate-related variables increased with increasing grain size, while anthropogenic burning was the most important factor for richness patterns at the finest grain sizes (positive effect). The z values showed more variation at the finest grain sizes, but no significant differences in their mean between scales. The results highlight the importance of integrating scale into ecological analyses and nature conservation assessments in order to understand and manage biological diversity in steppe ecosystems.

Keywords Biodiversity · Bryophyte · Lichen · Scale dependence · Species-area relationship · Species richness

Introduction

Temperate grasslands are known for their high, and in some cases extraordinary, small-scale diversity of vascular plants (Wilson et al. 2012; Chytrý et al. 2015) as well as bryophytes and lichens (Dengler 2005; Löbel et al. 2006). Extremely high richness values ("world records") have mostly been recorded from semi-natural stands that have been subjected to low-intensity agricultural management for long periods (Dengler et al. 2014), but similar species densities are found in natural Palaearctic steppes. For example, Alekhin (1986) reports 77 species of vascular plants on 1 m^2 and 120 species on 100 m^2 for a northern forb steppe in the Kursk region of Russia. Along with high phytodiversity, steppe ecosystems provide refuges for a large number of rare and endangered animal and plant species, and they can be considered one of the global biodiversity hotspots (Habel et al. 2013). Although the steppes of Eurasia are one of the most threatened biomes worldwide (Werger and van Staalduinen 2012), we are only starting to understand the relevant environmental and biological processes that cause this unique biodiversity.

Various factors influence plot-scale ($\leq$1000 m^2) plant species richness in Palaearctic grasslands, with soil reaction and land use being the most prominent ones (Dengler et al. 2014). Typically, plant species richness (total or vascular plants) in European grasslands increases linearly with soil pH or peaks around or slightly below the neutral point (Schuster and Diekmann 2003; Löbel et al. 2006; Becker and Brändel 2007; Olsson et al. 2009; Merunková et al. 2014). This is largely in accordance with the theories of Pärtel (2002) and

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Ewald (2003), who stated that glacial refugia in Europe were dominated by base-rich substrata, leading to a higher regional pool of species in the current vegetation adapted to such conditions, which is also reflected at the plot scale. However, there are also a few cases in which pH was not a determining factor of plot-scale richness of European dry grasslands (Turtureanu et al. 2014: Transylvania) or even had a negative effect (Palpurina et al. 2015: in one of the studied Bulgarian regions). Phytodiversity in European grasslands is further strongly influenced by land use type and intensity. Extremely high richness values are typically found in semi-natural sites that have been mown regularly over long periods (Dengler et al. 2014). For example, mown steppe-like grasslands in Transylvania (Romania) were much richer than the grazed or unused/abandoned counterparts (Turtureanu et al. 2014). Concerning grazing, both Dupré and Diekmann (2001) in Sweden and Škornik et al. (2010) in Slovenia found highest plot-scale richness at light to moderate grazing intensity, which declines both towards heavy grazing and towards abandonment, in agreement with the Intermediate Disturbance Hypothesis (Grime 1973; Connell 1978). In some studies other factors also had a strong influence, such as heat index and therewith drought (Turtureanu et al. 2014: negative effect), microrelief (Löbel et al. 2006: positive effect) or mesoclimate (Palpurina et al. 2015: positive effect of mild winters).

While it has long been known that the relationships of species composition (e.g. Reed et al. 1993) and species diversity (e.g. de Bello et al. 2007; Giladi et al. 2011) to environmental drivers vary with the grain size of the observed system, this is only rarely taken into account when comparing results from studies using different plot sizes. For diversity-environment relationships, Shmida and Wilson (1985) hypothesized that with increasing area from 0.1 m^2 up to the terrestrial surface of the world, species richness patterns are determined successively by niche relations, habitat diversity, mass effect and ecological equivalency. Breaking this conceptual model down to concrete variables, several recent meta-analyses have provided valuable insights into vegetation diversity patterns. The relative importance of soil vs. climatic variables increases towards small grain sizes (Siefert et al. 2012), and the generally positive heterogeneity-diversity relationship becomes negative towards very small grain sizes (Tamme et al. 2010). However, Turtureanu et al. (2014) is probably the first study that directly analysed the relative importance of a broad set of different environmental variables for phytodiversity patterns across seven orders of magnitude of spatial grain. Largely in agreement with the above-mentioned theoretical and meta-analytical studies, they demonstrated for Transylvanian dry grasslands that soil variables were most important at grain sizes of 0.01 m^2 and under, litter cover and heat index were most important at intermediate grain sizes (0.01–10 m^2), while land use and mesoclimate were most important at 1–100 m^2. However, more datasets sampled with such a multi-scale approach from grasslands in other regions as well as other habitat types are needed to assess which of these patterns are generally valid, and which are specific to the Transylvanian study.

While bryophytes and lichens can make up a large proportion of the overall phytodiversity of Palaearctic dry grasslands (Dengler 2005), their diversity-environment relationships are far less well studied than those of vascular plants and, if so, often in separate studies (e.g. Müller et al. 2012) that make it hard to draw comparisons with vascular plants. Nevertheless, comparative studies in dry grasslands on the Swedish island of Öland (Löbel et al. 2006) and in Transylvania (Turtureanu et al. 2014) indicate some general trends regarding contrasting responses of vascular plant, bryophyte and lichen diversity to environmental drivers: On Öland, soil pH had a unimodal effect on the richness of vascular plants but a positive effect on that of non-vascular plants, while microtopography was positive for vascular plants and bryophytes, but not for lichens (Löbel et al. 2006). In

Transylvania, vascular plant diversity was strongly driven by type of land use and mesoclimate, while for non-vascular plants in general humus content of the soil and, particularly for terricolous bryophytes, the rockiness of the soil surface played a bigger role (Turtureanu et al. 2014). These few examples already indicate that for a general understanding of commonalities and differences in diversity-environment relationships of different taxa, more data from other study systems are needed.

One of the countries characterized by a high diversity of grasslands of both natural and anthropogenic origin is Ukraine (Bilyk 1973a, b; Solomakha 2008). The steppe and forest-steppe zones cover about 73 % of the total area of Ukraine (Moysienko et al. 2014) and are assumed to have grasslands as natural vegetation (Bohn et al. 2004). However, the precise border of the area of natural steppes varies according to the reference (Didukh and Shelyag-Sosonko 2003; Bohn et al. 2004), and thus also the assessment what is a natural steppe and what a semi-natural grassland. Today, most Ukrainian grassland, be it natural or semi-natural, has been transformed into arable fields. High nature value grasslands are typically preserved only in small patches in protected areas, steep slopes of valleys and ravines, burial mounds and ancient settlements (Korotchenko and Peregrym 2012; Moysienko et al. 2014). According to rough estimates, natural steppe vegetation today occupies no more than one percent of the territory of Ukraine, but at the same time, these steppe fragments conserve about 30 % of the plant and animal species listed in the Red Book of Ukraine (Burkovsky et al. 2013). This situation highlights the importance of conserving the remaining steppe areas. A better understanding of the factors causing this high diversity would help to implement conservation management more effectively.

Podolia is a region of particular importance for the study of biodiversity patterns in Ukrainian steppe communities, because it is located at the border of the forest zone (where steppe-like grasslands are all semi-natural) to forest-steppe and steppe zones (which represent the western margin of the continuous Eurasian distribution of meadow steppes and grass steppes; Didukh and Shelyag-Sosonko 2003). In a previous paper, Kuzemko et al. (2014) showed that the mean plant species richness at a grain size of 10 m^2 is relatively low in the Central Podolian steppes compared to steppe-like semi-natural grasslands in the Ukrainian Pre-Carpathians (Roleček et al. 2014) and Transylvania, Romania (Dengler et al. 2012; Turtureanu et al. 2014) as well as to steppes of central Siberia (Polyakova et al. unpublished). This ecologically and biogeographically unexpected finding could have multiple causes and calls for a deeper understanding of the drivers of phytodiversity in Central Podolian steppes, both from the regional perspective and as a contribution to a synthetic model of phytodiversity for all Palaearctic grasslands (Dengler et al. 2014). Moreover, it is not clear whether this relatively lower richness is related to the structure of the studied communities and whether it holds across spatial scales.

Considering all of the above, we address the following questions in this article: (i) Which environmental factors determine the level of α-diversity at several scales (ranging from 0.0001 to 100 m^2) and β-diversity (expressed as the z value of the power-law SAR) in the region of Central Podolia? (ii) How do α- and β-diversity within the different taxonomic groups (vascular plants, bryophytes and lichens) differ in their dependence on environmental factors (soil, topographic, climatic and land-use variables)? This work complements a previous study using the same data set for vegetation classification (Kuzemko et al. 2014) by adding an in-depth analysis of the richness-environment relationships in the nested plot systems in the Central Podolian steppes and placing these in the broad context of dry grasslands across the Palaearctic.

Methods

Study area

The study area covers Central Podolia (48.95°–48.10°N and 27.55°–29.35°E), the central, lower lying part of the Podolian Upland (73–251 m a.s.l.), which is located in the south-western part of Ukraine (Fig. 1), at the north-western border of the steppic biogeographic region of Europe (Liamine 2002a; b). The climate is temperate-subcontinental with a mean annual temperature of about 7–9 °C and 600–650 mm annual precipitation (Lipinsky et al. 2003). The geobotanical zone of this region is a matter of debate, with Didukh and Shelyag-Sosonko (2003) assigning the territory of Central Podolia completely to the Forest-Steppe zone, while Bilyk (1977) and Bohn et al. (2004) consider it largely as part of the broadleaved forest region. This means that there is no consensus as to which degree the steppic grasslands of the region are natural. More specifically, the potential natural vegetation according to Bohn et al. (2004) is mainly East Polish-Ukrainian lime-pedunculate oak-hornbeam forests with smaller patches of Podolian-Moldavian thermophilous hornbeam-pedunculate oak forests and East pre-Carpathian-Moldavian sessile oak-hornbeam forests. A more detailed description of the study area, including vegetation, can be found in Kuzemko et al. (2014).

Field sampling

The field sampling was carried out in the second half of July 2010. Sample plots were selected to represent the variability of dry grassland communities in the study region as fully as possible (Fig. 1). We sampled 21 nested-plot series covering different regimes of land-use and vegetation types. The nested-plot series ("biodiversity plots") follow the concept proposed by Dengler (2009b), with square-shaped subplots of 0.0001, 0.001, 0.01, 0.1, 1, and 10 m^2 arranged in two opposite corners of a 100-m^2 (10 m × 10 m) plot. In addition, we sampled 184 additional normal plots of 10 m^2. We recorded all terricolous vascular plants, bryophytes and lichens that were superficially present (i.e. shoot presence). Twenty-three normal plots and five subplot series (i.e. corners) from biodiversity plots were excluded in some analyses due to missing soil data.
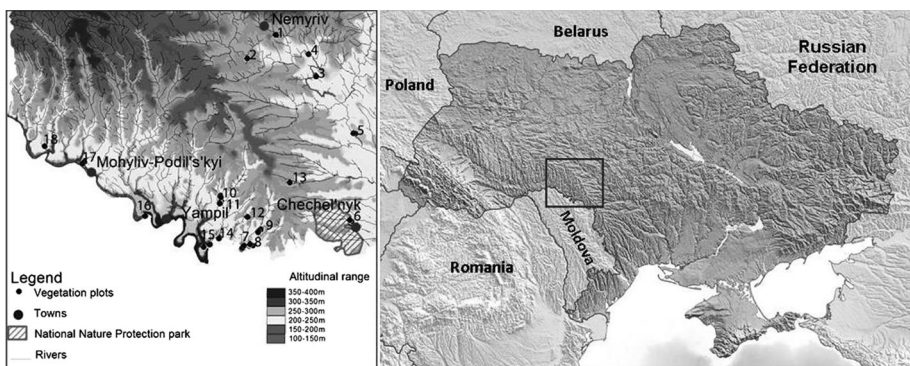
Fig. 1 Location of the studied 19 grassland sites in Central Podolia, within Ukraine

Structural and environmental parameters

For each 10-m^2 plot we estimated the cover of the shrub, herb and moss layers and that of litter, gravel as well as stones and rocks. We determined geographic coordinates and altitude with GPS (several different devices, all with an approximate accuracy of 5 m), aspect with a compass and slope with an inclinometer. The latter two parameters were used to calculate the heat index according to Olsson et al. (2009). Microrelief was measured as maximum vertical deviation from an imaginary plane through the plot. We classified the present land use into rough, quasi-metric categories regarding "grazing intensity" (mostly by cattle; 0 = not grazed, 1 = low, 2 = medium, 3 = high) and "burning" (0 = no; 1 = yes) based on our knowledge of the sites and/or visible signs in the plots.

Mixed soil samples were taken for determination of soil texture type (estimation of fractions of sand, silt and clay), skeleton content, pH, electric conductivity, organic C and total N content as well as C_{org}/N_{tot} ratio (see Kuzemko et al. 2014 for details). We used climatic variables related to productivity and some potentially limiting bioclimatic factors (Online Resource 1), extracted from the WorldClim database at an approximate 1-km resolution (Hijmans et al. 2005; http://www.worldclim.org).

Analyses of richness-environment relationships

Richness-environment relationships were assessed for total species richness separately at each of the different scales ranging from 0.0001 to 100 m^2 ($n = 42$ for smaller grain sizes; $n = 21$ for 100 m^2). The patterns of total, vascular plant, non-vascular plant, bryophyte and lichen richness were compared at 10-m^2 grain size in a larger number of plots ($n = 198$; including the nested and the additional individual plots).

Collinearity between the continuous variables was checked using pairwise Pearson correlations for the 198 10-m^2 plots. Two predictors were considered as collinear when $|r| > 0.7$, and in such cases we kept the one we considered ecologically more meaningful. The *Percentage of silt* was dropped due to high correlation with *Percentage of sand* (r = −0.90). *Total N* was removed in favour to *Organic C* (r = 0.95) and *Mean annual temperature* replaced *Elevation* (r = −0.83) and *Temperature of the coldest quarter* (r = 0.99). *Annual precipitation* replaced *Temperature seasonality* (r = −0.74) and *Precipitation of the driest quarter* replaced *Precipitation seasonality* (r = −0.86) and *Percentage winter precipitation* (r = 0.88).

Generalized linear models with Poisson error distribution were applied within an information-theoretical approach that allows estimating variable importance based on automated model selection within subsets of a supplied "global" model (Burnham and Anderson 2002 implemented in R-package *MuMIn* version 1.14; Bartoń 2015). *MuMIn* estimates variable importance by building models of all possible variable combinations. The importance of single variables is quantified as the sum of Akaike weights over all models including the explanatory variable. The approach may become computationally intensive as the number of independent variables increases. Therefore, prior to each analysis, all variables unrelated to species richness in individual models were identified (AIC$_c$ of model including the variable +2 > AIC$_c$ of the null model glm ($y = 1$)). For the analysis of richness of different species groups at the 10-m^2 scale, all variables unrelated to richness of the group under focus were dropped. In contrast, for the analysis on different scales only those variables that were unrelated to species richness at all scales were dropped from the global model in order to compare the importance of the variables

between the grain sizes. Explanatory variables were transformed, if necessary, to improve model residuals (see Online Resource 1). A quadratic term of a variable was additionally included into the full model if the quadratic term improved model performance in unimodal models (ΔAIC_c to null model >2). Quadratic terms were only included in models if the non-quadratic term was also present; thus they can never reach higher importance in the results. Variable coefficients were integrated over all models using function *model.avg* in *MuMIn*.

Only models for total- and vascular plant species richness showed significant overdispersion according to *dispersion test* in R-package *AER* version 1.2–4 (Kleiber and Zeileis 2008). Repeating those model runs using a quasi-Poisson error distribution did not change results qualitatively. Residuals for none of the models showed significant spatial autocorrelation as tested using function *moran.test* in R-package *spdep* version 0.5–88 (Bivand and Piras 2015).

In order to compare explained variation of models on different scales, McFadden's pseudo-R^2 (1—(log likelihood of the full model/log likelihood of the null model)) was calculated. Note that McFadden's pseudo-R^2 is not directly comparable to common R^2 measures as it tends to be much smaller than 1.

Analyses of species-area relationships

Species turnover (β-diversity) was assessed via species-area relationships (SARs). SARs can usually be well approximated via power laws at any spatial scale (Connor and McCoy 1979; Dengler 2009a) and particularly at small grain sizes in continuous vegetation (Dengler and Boch 2008). The exponent z of the power law can be used as an informative tool to compare β-diversity between habitats, taxa and scales (Drakare et al. 2006). For each or the 21 nested-plot series we fitted a power function in double-log space, i.e. $\log_{10} S = \log_{10} c + z \log_{10} A$, with S = species richness, A = area in m^2 and c = richness on one unit area (here: 1 m^2) with linear regression, resulting in an overall z-value. Second, we calculated "local" z-values, i.e. those for the transition between two subsequent grain sizes, to test whether β-diversity depends on spatial grain size, i.e. the actual relationship deviates from a perfect power law (Turtureanu et al. 2014).

Results

Richness values of taxonomic groups

A total of 712 taxa were identified in the dataset of 10-m^2 plots ($n = 226$): 581 vascular plants (81.6 %), 75 bryophytes, 54 lichens, one macroscopic taxon of algae and one of cyanobacteria (18.4 % non-vascular plants). At the analysed grain sizes, the proportion of vascular plants gradually increased from 84.7 % at 0.0001 m^2 to 90.9 % at 100 m^2. The richness of bryophytes considerably exceeded that of lichens at all scales (Online Resource 2). Vascular plants in general were fairly evenly distributed among the plots, while the distribution was more uneven in the case of bryophytes and particularly of lichens (consider the ratios of standard deviations to means in Online Resource 2). Noteworthy is the complete absence of lichens on our smallest plots of 0.0001 and 0.001 m^2.

Taxon-dependence of richness-environment relationships

Multimodel inference yielded heat index (negative) and annual mean temperature (unimodal) as the most important factors for total species richness of the vegetation at the 10-m^2 grain size, followed by burning (positive), cover of litter (negative), cover of stones (unimodal) and grazing intensity (positive) (Table 1). Since vascular plants accounted for

Table 1 Predictors of 10-m^2 richness for all taxa and the individual taxonomic groups based on multimodel inference ($n = 198$)

	All species	Vascular plants	Non-vascular plants	Bryophytes	Lichens
Topography					
Inclination			0.77+	0.91+	0.32+
Heat index	**1.00−**	**1.00−**	**1.00−**	**1.00−**	0.49−
Microrelief	0.47+		0.62+	0.46+	**0.68+**
Soil surface and texture					
Cover stones and rocks	**0.85+**	**0.96+**	**1.00+**	**0.99+**	**0.99+**
+Cover stones and rocks^2	**0.80−**	**0.93−**	0.34−	0.26−	0.44−
Cover gravel			**1.00−**	**0.98−**	
Cover litter	**0.86−**	**0.95−**			
Skeleton	0.34+		**0.83+**		**0.89+**
Clay	**0.66+**	**0.68+**			**0.64+**
+Clay^2	**0.53−**	0.46−			0.31−
Soil chemistry					
pH		0.26+	**0.89−**	0.43−	**0.74−**
Conductivity		0.29+	0.47−	**0.73−**	**0.59−**
CaCO3		0.28+	0.48+	0.42+	0.29−
C.org	0.33+	0.34+			
+C.org^2	0.10−	0.09−			
C/N	**0.65−**	**0.87−**	**0.51−**	0.29−	**0.53−**
Mesoclimate					
Annual mean temperature	**1.00+**	**1.00+**	0.40−	0.35−	0.36−
+Annual mean temperature^2	**1.00−**	**1.00−**	0.10−	0.09+	0.10+
Precipitation of driest quarter	0.34−	**0.53+**	**0.53+**	**0.72+**	**0.65+**
+Precipitation of driest quarter^2	0.10−	0.22−	0.16−	0.19+	0.26−
Land use					
Grazing intensity	**0.84+**	**0.90+**	**0.95−**	**0.93−**	**0.54−**
Burning	**0.96+**		0.27−	0.26+	

The table indicates the importance value of each variable and the direction of the relationship. The relationship is derived from the mean model coefficients across all possible models, weighted by their Akaike weights (see Methods). Importance values ≥0.5 (i.e. those occurring in 50 % or more of the plausible models) are set in bold. Gaps indicate those variables that were excluded prior to analyses as they did not show a relation with the dependent variable in a univariate model (ΔAIC_c to null model <2); this was true across all five taxa for Sand, Temperature annual range and Annual precipitation

the biggest fraction of total richness, the resulting model for this group did not deviate much from the overall model. The main differences were that burning had no influence, soil pH, limestone content and conductivity had a weak positive effect (vs. none for total richness), while precipitation of the driest quarter had a unimodal relation (vs. negative for total richness) (Table 1).

Two of the main factors in the overall and vascular model, cover of stones and rocks as well as heat index, had similar effects also on the diversity of non-vascular plants, although the unimodal component of rocky surface was less pronounced for these taxa and the heat index was only included in about one half of the models for lichens. By contrast, some variables not relevant for vascular plants (and often also not for the total richness), were influential for the two non-vascular groups (Table 1). Most prominent were inclination and microrelief, which had always a positive effect. Interestingly, several variables showed opposite effects for vascular plants and non-vascular plants, namely grazing intensity (positive for vascular, negative for non-vascular), pH and conductivity (positive for vascular, negative for non-vascular) and annual mean temperature (unimodal for vascular, negative for non-vascular). The diversity-environment relationships for bryophytes and lichens were similar, except for surface cover of gravel that only played a role for bryophytes (negative), while skeleton (positive) and clay content (unimodal) were only included in the lichen model.

The explanatory power of the environmental variables as indicated by McFadden's pseudo-R^2 was highest for the richness of lichens ($R^2 = 0.35$) followed by non-vascular plants ($R^2 = 0.19$), bryophytes ($R^2 = 0.15$) and vascular plants ($R^2 = 0.10$). The model explaining overall richness reached an R^2 of 0.10.

Scale-dependence of richness-environment relationships

The explanatory power of the derived diversity-environment relationships in the 21 biodiversity plots was good for 100 m^2, but continuously decreased towards 0.01 m^2, with very low pseudo-R^2 values for the smallest three grain sizes (Fig. 2). In general,
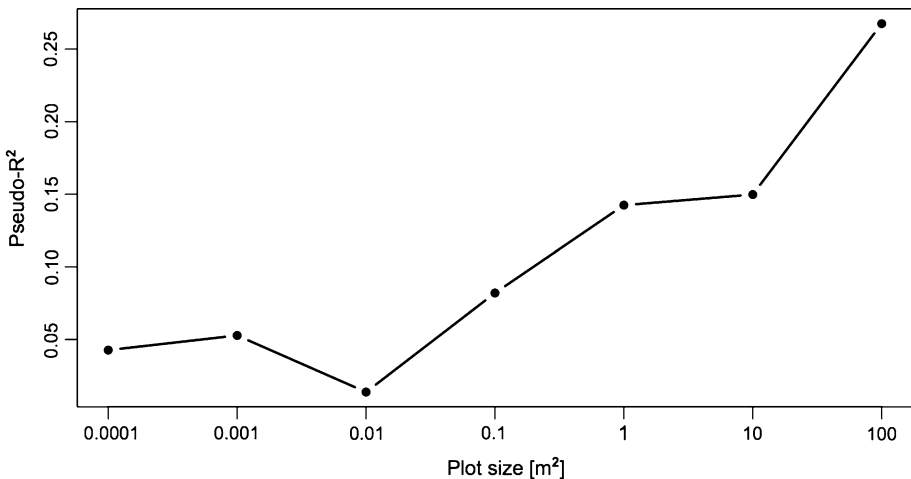
Fig. 2 Change of the explanatory power of the richness-environment relationships for all taxa across the studied spatial scales, ranging from 0.0001 to 100 m^2. Note that McFadden's pseudo-R^2 is not comparable to common R^2 measures as it tends to be small

heat index was the most influential factor for total species richness (negative relationship) from 0.01 m^2 upwards and was included in nearly all models from 0.1 m^2 upwards (Fig. 3; Table 2). The presence of burning was influential only at the two smallest grain sizes below 0.01 m^2 (positive). Conversely, the cover of litter had a strong positive influence only at our coarsest grain size (100 m^2). The various soil-related variables (texture and chemistry) generally had only moderate influence and typically reached their greatest influence for intermediate grain sizes (1 or 10 m^2) (Fig. 3). The two mesoclimatic variables of the full model, annual mean temperature and precipitation of the driest quarter, generally increased in their influence with increasing grain size (Fig. 3). The influence of microrelief on total diversity was low across all scales, with changing direction (Fig. 3; Table 2). Some variables exhibited systematic shifts in the direction of their influence on richness across the scales (Table 2). For example, while having a big negative effect on richness at the larger grain sizes, heat index became a (weak) positive factor at 0.001 and 0.0001 m^2. Cover of stones and rocks, on the other hand, affected diversity negatively at small scales, but positively at larger scales.
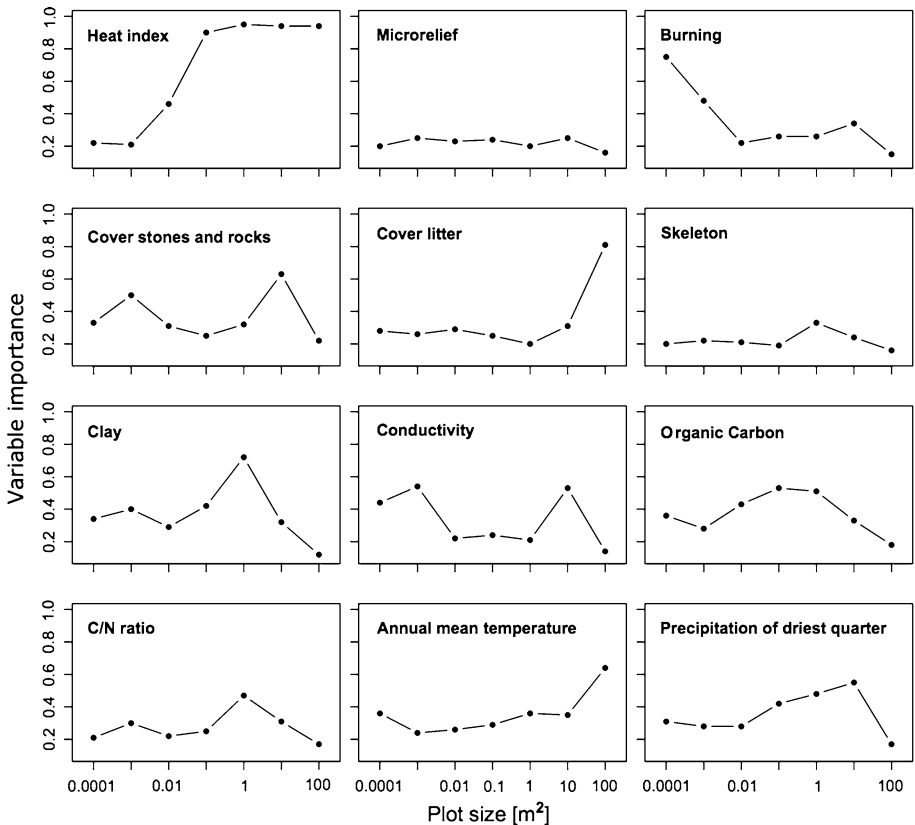
Fig. 3 Change of relative importance of the 12 variables included in the full models for total species richness across the studied spatial scales from 0.0001 to 100 m^2

Table 2 Parameter estimates for the seven spatial grain sizes of α-diversity and of the overall z-value as measure of β-diversity based on multimodel inference ($n = 21$ for 100 m^2 and 37 for all smaller grain sizes)

	0.0001 m^2	0.001 m^2	0.01 m^2	0.1 m^2	1 m^2	10 m^2	100 m^2	z
Topography								
Heat index	0.22+	0.21+	0.46−	**0.90−**	**0.95−**	**0.94−**	**0.94−**	0.20−
Microrelief	0.20+	0.25−	0.23−	0.24−	0.20−	0.25+	0.16+	0.20−
Soil surface and texture								
Cover stones and rocks	0.33−	0.50−	0.31+	0.25−	0.32+	**0.63+**	0.22+	0.26−
+Cover stones and rocks^2	0.10−	0.14−	0.11−	0.06+	0.06−	0.17−	0.06−	0.03+
Cover litter	0.28+	0.26+	0.29+	0.25−	0.20−	0.31−	**0.81+**	**0.83+**
Skeleton	0.20+	0.22−	0.21−	0.19+	0.33+	0.24+	0.16+	0.15−
Clay	0.34+	0.40+	0.29+	0.42−	**0.72−**	0.32−	0.12−	0.17+
+Clay^2	0.07−	0.08−	0.09−	0.09−	0.29−	0.05−	0.02+	0.03−
Soil chemistry								
Conductivity	0.44+	**0.54+**	0.22+	0.24+	0.21+	**0.53+**	0.14−	0.15−
C_{org}	0.36−	0.28+	0.43+	**0.53+**	**0.51+**	0.33+	0.18+	0.16+
+C_{org}^2	0.14−	0.06−	0.28−	0.41−	0.36−	0.16−	0.06−	0.02+
C/N	0.21+	0.30+	0.22−	0.25+	0.47−	0.31−	0.17−	0.17−
Mesoclimate								
Annual mean temperature	0.36+	0.24−	0.26+	0.29+	0.36+	0.35+	0.64−	0.24−
+Annual mean temperature^2	0.09−	0.05+	0.06−	0.07−	0.19−	0.17−	0.54+	0.03+
Precipitation of driest quarter	0.31−	0.28+	0.28+	0.42+	0.48+	**0.55+**	0.17−	0.19+
+Precipitation of driest quarter^2	0.08−	0.08−	0.08−	0.10−	0.14−	0.35−	0.03−	0.02+
Land use								
Burning	**0.75+**	0.48+	0.22+	0.26+	0.26+	0.34+	0.15+	0.15−

The table indicates the importance value of each variable and the direction of the relationship. The relationship is derived from the mean model coefficients across all possible models, weighted by their Akaike weights (see Methods). Importance values ≥0.5 (i.e. those occurring in 50 % or more of the plausible models) are set in bold. The following variables were excluded prior to analyses as they did not show a relationship with the dependent variable in univariate models at any scale (ΔAIC_c to null model <2): Inclination, Cover gravel, Sand, pH, CaCO$_3$, Temperature annual range, Annual precipitation, Grazing intensity

Species-area relationships

The overall z-values (all taxa, across all grain sizes) as measure of β-diversity ranged from 0.185 to 0.340, with a mean of 0.243. They were not particularly well explained by the measured environmental factors, with cover of litter being the most consistent positive predictor across the plausible models (Table 2). The local z values showed more variation at the smallest grain sizes, but no significant differences in their mean between scales (repeated measures ANOVA: $p = 0.145$).

Discussion

Richness values of taxonomic groups

Comparing our results of the species richness of Central Podolian steppes with those of other dry and steppic grasslands across the Palaearctic (Table 3) revealed that we have recorded a new "world record" at 0.0001 m^2 grain size. While the previously known maximum was five species of vascular plants (Wilson et al. 2012; Chytrý et al. 2015), we found seven species on 1 cm^2 (shoot presence) twice in Ukraine: between the villages Chetvertynivka and Mytkivka (Trostyanets district, Vinnytsia region) and near Faihorog village (Kryzhopil district, Vinnytsia region). In the first case it was a mesoxeric grassland on granite assigned to the *Fissidens viridulus-Festuca rupicola* community (order *Brachypodietalia pinnati*); in the second case a xeric grassland on limestone of the *Salvia nutans-Carex humilis* community (order *Festucetalia valesiacae*; for details on syntaxonomic placement, see Kuzemko et al. 2014). For 0.001 m^2, our maximum value was also quite high: with 11 species of vascular plants we found a higher diversity than any other study of Table 3 and just one species less than the world record in a limestone grassland in Sweden (Wilson et al. 2012). For the grain sizes from 0.01 m^2 upwards, the Central Podolian mean and maximum vascular plant richness values were clearly below those for the semi-natural steppic grasslands of Transylvania and slightly below those of the true steppes in South Siberia (Khakassia), but they were similar to those in Bulgarian dry grasslands and above those of Mediterranean grasslands of Sicily (Table 3).

In contrast to the other taxonomic groups, we found no lichen species at plot sizes below 0.01 m^2. Fruticose as well as foliose lichens occurred only sparsely in the denser grassland vegetation, building clumped stands in suitable microhabitats, e.g. gaps and surrounding small rocky outcrops. Due to the small number of replicates, the chances of encountering lichens in the small subplots were therefore quite small. By contrast, at least some bryophytes reached high cover values (see Kuzemko et al. 2014), leading to a higher chance of their being present at the smallest scales. Thus, lichens contribute proportionally more to species richness at medium to larger scales.

Taxon-dependence of richness-environment relationships

The strong inverse relationship of the species richness to the heat index of total, vascular, bryophyte and to a lesser extent also lichen richness is consistent with the findings of Turtureanu et al. (2014) for Transylvania. Steep south-west facing slopes under summer-warm conditions provide a quite hostile environment that seemingly excludes many species from the stands, mainly because of drought stress. The same factor is considered responsible for the sharp decline in species richness of the steppe communities at the transition from the northern forb steppe to the southern grass steppes (Alekhin 1986). Unlike the situation in central and northern Europe (Schuster and Diekmann 2003; Löbel et al. 2006), soil pH (and related soil factors) played only a minor positive role for vascular plant species richness. This could be related to a rather short pH gradient and a high mean (Online Resource 1) for the Ukrainian study sites, which is typical for continental regions. Similarly, Turtureanu et al. (2014) in Romania did not find a pH effect on vascular plant species richness and Palpurina et al. (2015) in one region of Bulgaria even a negative relationship. Richness of non-vascular plants showed a clear negative relationship to soil pH in strong contrast to the situation in Öland, where Löbel et al. (2006) found a strong

Table 3 Comparison of mean and maximum richness values of vascular plants (shoot presence) found in Central Podolia with those found in other natural and semi-natural dry grasslands of the Palaearctic

Country	Region	Reference	Number of replicates	Statistics	$0.0001\ m^2$	$0.001\ m^2$	$0.01\ m^2$	$0.1\ m^2$	$1\ m^2$	$10\ m^2$	$100\ m^2$
Ukraine	Central Podolia	This paper	42-226-21	Max	7	**11**	13	21	42	64	86
				Mean	2.5	4.0	7.3	13.8	24.4	37.2	66.8
Germany	Upper Franconia	(Hopp and Dengler 2015)	2-2-1	Max	4	9	**19**	31	43	55	65
				Mean	**4.0**	**6.5**	**14.0**	25.0	37.0	47.5	65.0
Romania	Transylvania	Dengler et al. (2012)	40-82-20	Max	5	8	18	43	79	98	**127**
				Mean	2.3	4.2	9.6	21.1	37.5	49.7	83.3
Bulgaria	NW Bulgarian mountains	Pedashenko et al. (2013)	30-98-15	Max	6	9	14	25	36	60	87
				Mean	2.3	3.9	7.6	13.3	22.8	34.1	56.7
Italy	Sicily	Dembicz et al. (unpublished)	42-67-21	Max	4	9	14	27	39	68	98
				Mean	1.7	3.2	6.4	12.8	21.0	35.4	55.4
Russia	Khakassia	(Polyakova et al. unpublished)	78-132-39	Max	5	9	17	28	52	72	94
				Mean	2.1	4.0	8.2	17.3	29.7	43.9	65.3

Maxima within this comparison are shown in bold, minima in italics and current world records are underlined. The number of replicates is given in the sequence $<10\ m^2$–$10\ m^2$–$100\ m^2$

positive relationship. It might be that the relationship in Podolia was not caused by soil reaction itself but rather the fact that the few sites with low pH in Podolia were those close to granite outcrops, where the herb layer was rather sparse and thus allowed a relatively dense cryptogam layer to develop. Grazing intensity had a strong effect on the diversity of all taxonomic groups. However, this was not as suggested by the Intermediate Disturbance Hypothesis (Grime 1973; Connell 1978) and found, for example, in grasslands by Škornik et al. (2010). Instead, we found a positive relationship for vascular plants and negative ones for bryophytes and lichens. An explanation might be that even the most intensively grazed plots in our study were still only moderately grazed when viewed in a wider context. By contrast, cryptogams in pastures might be more affected by trampling of herbivores than by their grazing, and this could exclude sensitive and slow-growing bryophytes and lichens at much lower land use intensities. These results are similar to the finding of Müller et al. (2012) that land use negatively affects bryophyte diversity in (mostly mesic) grasslands.

Scale-dependence of richness-environment relationships

For several of the analysed factors, we found that their relevance for diversity patterns differed considerably across spatial scales. This is generally in agreement with the expectation that diversity-environment relationships are not constant across grain sizes (Shmida and Wilson 1985; Siefert et al. 2012). Specifically, we could corroborate Siefert et al.'s (2012) prediction and result from their meta-analysis that mesoclimatic variables increase in relative importance with grain size. Our results also agree in many respects with findings for the dry grasslands of Transylvania (Turtureanu et al. 2014), in particular with regard to the dominant role of the heat index and litter cover at the larger grain sizes. While in Transylvania, land use type (i.e. mown vs. either grazed or non-used) was the most important factor at all the grain sizes from 0.1 m^2 upwards, this factor was not relevant in Central Podolia. The reason could simply be that in Central Podolia we had no mown grasslands, but only unused and grazed types of different intensity, which also in Transylvania hardly differed in their richness. While in Transylvania, humus content was the most important factor at the three smallest grain sizes with a unimodal relationship, such an influential unimodal relationship towards humus content (organic C) was found in Central Podolia at intermediate grain sizes only (0.1–1 m^2).

One important finding is the different explanatory power of our models for the different scales, which increased towards larger grain sizes (Fig. 2). One could argue that this could be caused by a mismatch between the spatial scales used for sampling of richness and for environmental variables, because we used the same set of environmental factors for modelling of richness across scales, most determined at the 10-m^2 scale and the mesoclimatic variables at the 1-km^2 scale. While this mismatch could explain the decrease of explanatory power towards grain sizes smaller than 10 m^2, this is not consistent with the strong further increase of explanatory power from 10 to 100 m^2. It would also not explain that the influence of burning increases towards the smallest grain sizes. While it would have been advantageous to measure all environmental variables at the same grain sizes as biodiversity, this would have come with much higher workload (for soil and topographic parameters) or have been impossible (for climate variables). We therefore believe that our approach to use environmental variables from the 10-m^2 scale as an approximation of the conditions at the smaller grain sizes might have introduced some additional noise (and thus likely lower explanatory power), but it should not have masked or changed actual patterns. The very low explanatory power at the smallest grain sizes might also be due to the fact that here co-occurrence of species is more "stochastic", i.e. less determined by

environmental factors but by biological processes like dispersal, lateral spread or species–species interactions.

Species-area relationships

The average total z value (in log S space) in Podolian dry grasslands (0.243) is at the upper margin of what was found in a review of European dry grasslands (Dengler 2005), but not as high as in Transylvania (0.275; Turtureanu et al. 2014). The z-values are a conventional and easily comparable measure of β-diversity (Drakare et al. 2006), but it is still not well understood what drives the variation in small-scale β-diversity among different grassland types in different regions.

Like Dengler and Boch (2008) in their study of Estonian dry grasslands, we did not find any scale dependency of the z values across the seven orders of magnitude studied, which contrasts to the pronounced scale-dependency (with a peak around 0.01–0.1 m^2) reported from Transylvania (Turtureanu et al. 2014). Our findings support the view of Dengler (2009a) that power laws are in most cases very good approximations for species-area relationships at small scales in continuous vegetation, with z-values being more or less constant over many orders of magnitude.

The reason why pronounced deviations from this general pattern are found in some exceptional cases, such as the Transylvanian dry grasslands, needs to be further explored with SAR data from other biogeographic and ecological contexts. The same is true for understanding the variation in z-values between different study regions. One possible research direction may be spatial scaling of environmental heterogeneity. The richness-environment relationship at one spatial grain size may be related to spatial heterogeneity of the focal environmental variable at the next smaller grain. Changes in local z values are thus particularly expected if spatial heterogeneity at a particular grain size is missing or removed (e.g. by land use). For future studies addressing scale dependent richness-environment relationships, the accumulating pool of highly standardised data from the EDGG Research Expeditions (Vrahnakis et al. 2013) could be a major source.

Conclusions

We have shown that the last remnants of Ukrainian steppe vegetation are particularly species rich at small scales, with a new world record of species richness at 0.0001 m^2 grain size. The number of vascular plants is above average in meso-xeric grassland types with less intensive heat development, while the occurrence of stones and more pronounced microrelief provide habitat for a relatively higher number of bryophyte and lichen species. Analysis of scale-dependence of richness-environment relationships revealed that the climate factors increase in importance with grain size while land use/soil-related variables decrease. Almost all identified drivers varied in importance or even direction with scale, and there were also pronounced differences in how the three studied taxonomic groups reacted to these drivers. This calls for caution when conclusions for ecological theory or conservation applications are drawn from studies involving only a single spatial scale or a single taxon. Instead, we recommend multi-scale and multi-taxon studies as an approach to gain more comprehensive and reliable insights, not only when designing conservation approaches for grassland vegetation. One important insight in our case was that land-use intensity (grazing, burning), albeit on an overall low level, had contrasting effects on the

taxonomic groups studied: While vascular plant species richness seemed to benefit from burning and more intense grazing, both were negative for bryophytes and lichens. This indicates that the current species richness of the vegetation cannot be maintained with a single "best" management practice, but rather needs a mosaic of different land uses. Comparing the identified drivers of phytodiversity in the steppe grasslands of Central Podolia with those in other regions allowed us to determine recurring patterns and mechanisms and to differentiate these from regional idiosyncrasies.

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