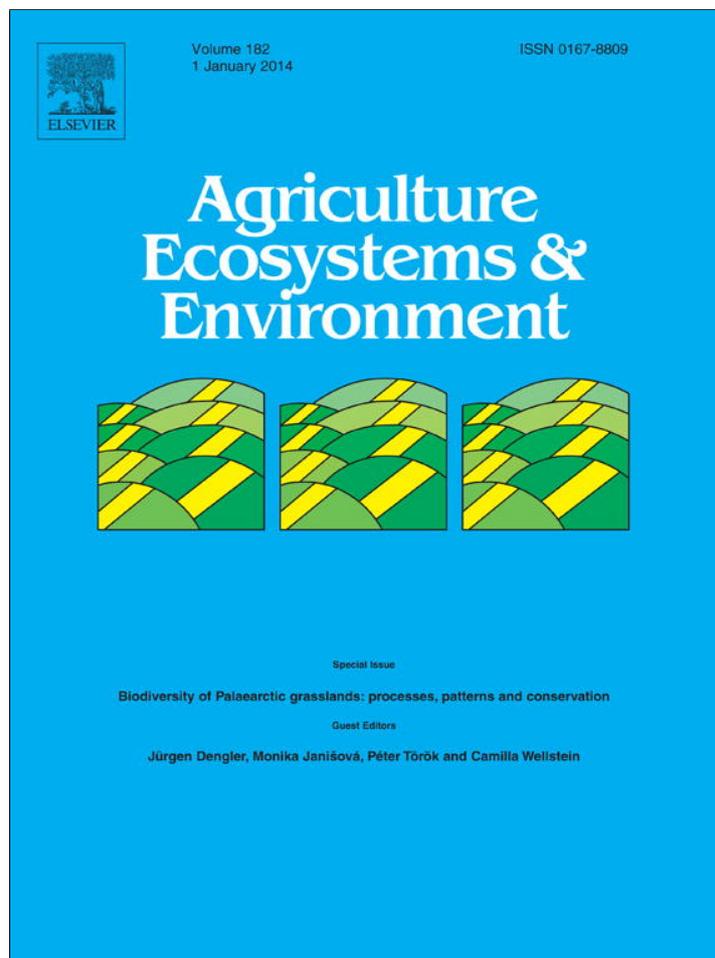


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## Scale- and taxon-dependent biodiversity patterns of dry grassland vegetation in Transylvania

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## ABSTRACT

Patterns of biodiversity may vary across spatial scales and between taxonomic groups; therefore, specific studies are needed to provide insights into factors driving community structure. Semi-natural grasslands are among the most biodiverse ecosystems, providing a suitable model for examining key ecological mechanisms. We analysed dry grasslands in Transylvania (Romania), which harbor extraordinarily species-rich plant communities, including the global maxima for two small grain sizes. We sampled data of vascular plants, bryophytes, and lichens in both nested and separate plots. We used soil, topographic, climatic, and land-use variables as predictors. Species richness at seven grain sizes (0.0001–100 m<sup>2</sup>) was modeled as a function of these predictors by generalized linear models, followed by multimodel inference over all possible variable combinations with AIC<sub>c</sub>. We also fitted power-law species–area relationships (SARs), both across the full range and for each transition of two subsequent plot sizes, as they provide a way of assessing  $\beta$ -diversity (through  $z$ -values) and its dependence on environmental variables. We found large differences in factors between scales and taxonomic groups, which generally supports the hypothesis that niche-related variables are important at very fine scales, while heterogeneity and disturbance-associated parameters become influential at larger scales. We explained the differences among the responses of taxonomic groups by their ecology. The exponents of the power-law SARs ( $z$ ) for total richness were higher than in most other European dry grasslands, demonstrating that  $\beta$ -diversity is also extraordinary here. Further, the  $z$ -values showed strong and unexpected scale dependence, peaking at 0.01–0.1 m<sup>2</sup>, and exponentially decreasing above these grain sizes. In conclusion, our study highlights the strong scale dependence of diversity–environment relationships, both in the case of  $\alpha$ - and  $\beta$ -diversity, while emphasizing the importance to study multiple taxonomic groups.

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## 1. Introduction

In Europe, some of the most biodiverse and threatened habitats are found in agricultural landscapes (Billeter et al., 2008; Oppermann et al., 2012). In contrast to the more homogenous natural vegetation cover, these cultural landscapes are characterized by a mosaic of many different natural, semi-natural and artificial habitat types. The so-called semi-natural open habitats have been shaped mainly through traditional low-intensity agricultural practices, which have supported the enrichment and diversification of the vegetation (Oppermann et al., 2012; van Elsen, 2000). In particular, semi-natural grassland ecosystems may support extraordinarily high numbers of plant species compared to other community types, both at small scale (Hájková et al., 2011;

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Kull and Zobel, 1991; Pärtel et al., 2005; Wilson et al., 2012) and when considering the species pool (Hobohm and Bruchmann, 2009; Korneck et al., 1998). However, intensification of agriculture from the 1950s onwards, and lately the large-scale abandonment of grasslands due to various social and economic factors, led to a substantial modification of existing plant assemblages and loss of species richness (e.g. Enyedi et al., 2008; Henle et al., 2008). The Transylvanian Plateau, located within the Carpathian arch and occupying almost a third of Romania's territory, still harbors large areas of extraordinarily species-rich dry grassland vegetation (Cremene et al., 2005; Dengler et al., 2012a). Grazing, and to a lesser extent mowing, have been the most common land use types in this region for several hundred years (Enyedi et al., 2008; Ruprecht, 2006). Many Natura 2000 sites have been designated in Romania, but as in other parts of Europe, they do not sufficiently cover the range of existing species-rich grasslands (Rozbrojová et al., 2010).

The majority of studies on biodiversity patterns and on the effects of management practices in semi-natural grasslands have been conducted in the largely fragmented and intensified farmlands of Central, Western and Northern Europe (e.g. Cousins et al., 2003; Billeter et al., 2008). The results may therefore not be directly transferable to Romania, where traditional land-use systems with low-intensity grasslands still cover vast, contiguous areas (Akeroyd and Page, 2011; Veen et al., 2009).

Species–area relationships (SARs: Connor and McCoy, 1979; Dengler, 2009a) are fundamental means of describing biodiversity patterns across scales, and they can usually be well fit by the power law ( $S = cA^z$ , where  $c$  and  $z$  are modeled parameters; e.g. Dengler, 2009a; Wilson et al., 2012). The exponent  $z$  can be seen as a measure of spatial turnover and allows for comparisons across systems, taxonomic groups, and scales (e.g. Crawley and Harral, 2001; Drakare et al., 2006). Beyond this, diversity–environment relationships may also change with spatial scale (de Bello et al., 2007; Giladi et al., 2011; Reed et al., 1993; Reitalu et al., 2012, 2014; Schmiedel et al., 2010). Therefore, analyzing only one spatial scale might lead to inappropriate conclusions.

The majority of studies on plant species diversity in Europe and its relationship with abiotic factors, as well as management types, have focused on a single taxonomic group, mostly vascular plants (e.g. Alard and Poudevigne, 2000; Auestad et al., 2007; Klimek et al., 2007). However, the influences of environmental parameters are often taxon-specific (Becker and Brändel, 2007; Löbel et al., 2006). Therefore, studying more than one major taxonomic group is beneficial both for providing advice for conservation planning and for understanding ecological principles. In European dry grasslands, vascular plants bryophytes and lichens exhibit contrasting diversity patterns in relation to environmental drivers (e.g. Becker and Brändel, 2007; Dolnik and Breuer, 2008; Löbel et al., 2006).

In this paper, we therefore used multi-scale and multi-taxon sampling in the Transylvanian dry grasslands, which include the world records of vascular plant species richness at 0.1 m<sup>2</sup> and 10 m<sup>2</sup> (Wilson et al., 2012), to shed light on the patterns and underlying drivers of biodiversity. We addressed two main questions: (i) How is  $\alpha$ -diversity at several scales (ranging from 0.0001 m<sup>2</sup> to 100 m<sup>2</sup>), and  $\beta$ -diversity (expressed as the  $z$ -value of the power-law SAR) related to environmental factors? (ii) How do  $\alpha$ - and  $\beta$ -diversity depend on the taxonomic group considered (all “plants” combined, vascular plants, bryophytes and lichens separately)?

## 2. Methods

### 2.1. Study area

The study was conducted in the Transylvanian Plateau and its peripheries, a hilly region in the centre of Romania (45°40′–47°50′

N, 23°00′–25°40′ E, 200–700 m a.s.l.; Fig. 1). The climate is subcontinental-temperate (see El. Appendix A), and oak-hornbeam forests are considered to be the potential natural vegetation (Bohn et al., 2004). Humans have been present in the region for several millennia, and nowadays the landscape is characterized by a mosaic of arable fields, old-fields, xeric grasslands on steep slopes, and relatively small forest patches. A more detailed description of the study area, including vegetation, can be found in Dengler et al. (2012a).

### 2.2. Field sampling

The sampling aimed to capture the geographic and ecological variation in the dry grasslands of the region. Sampling was mainly carried out in protected areas, as these are typically well preserved. We sampled 20 nested-plot series (Fig. 1) covering different management regimes and vegetation types of the phytosociological class *Festuco-Brometea*. The nested-plot series (“biodiversity plots”) follow the basic concept proposed by Dengler (2009b), with square-shaped subplots of 0.0001, 0.001, 0.01, 0.1, 1, and 10 m<sup>2</sup> arranged in two opposite corners of a 100-m<sup>2</sup> (10 m × 10 m) plot. In order to increase the data set for one spatial scale in a less time-consuming manner, we recorded 42 additional single plots of 10 m<sup>2</sup> (“normal plots”; for detailed information, see Dengler et al., 2012a). Two of the normal plots had to be excluded due to missing soil data, so that in total there were eighty plots of 10 m<sup>2</sup>. All plots were placed in visually homogeneous stands. All macroscopically visible terricolous photosynthesizing organisms (vascular plants, bryophytes, lichens and cyanobacteria—henceforth referred to as plants) were recorded (any-part or shoot-presence system; see Dengler, 2008). The plot data are available from the database EU-00-003 (Dengler et al., 2012b), registered in the Global Index of Vegetation-Plot Databases (GIVD; Dengler et al., 2011).

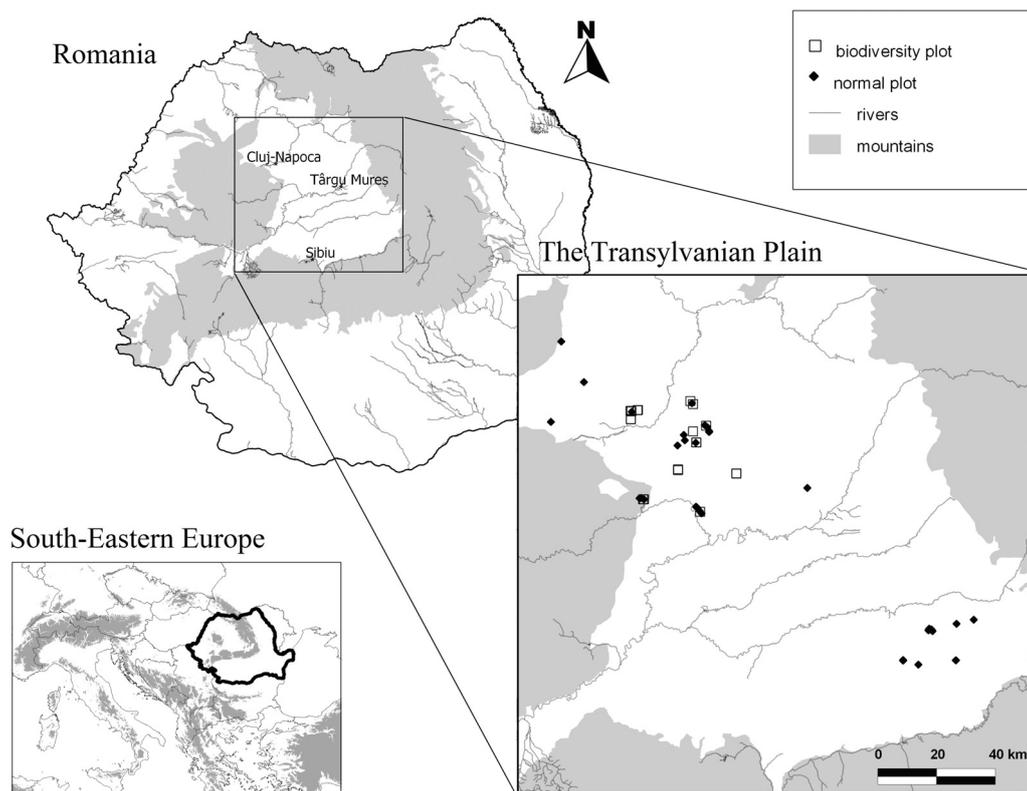
### 2.3. Environmental parameters

For each 10-m<sup>2</sup> plot, we determined geographic coordinates and altitude of a defined corner with a GPS device. Slope, aspect, and microrelief (as vertical deviation of the surface from an idealized plane over short distances) were determined in the field, while the cover of litter, open soil, as well as stones and rocks combined was estimated. Heat load index was calculated from slope and aspect (Olsson et al., 2009). Land use was roughly classified into “mown”, “grazed”, and “unused” (i.e. natural or abandoned grasslands) according to the dominant regime in the last few years based on appearance during sampling and site knowledge. We took a mixed soil sample to measure pH (in water) and humus content and to determine fractions of clay, silt, and sand semi-quantitatively (see Dengler et al., 2012a for details). We used climatic variables related to productivity and some potentially limiting bioclimatic factors (El. Appendix A), extracted from the WorldClim database (Hijmans et al., 2005; <http://www.worldclim.org/>).

### 2.4. Analyses of richness–environment relationships

Generalized linear models with Poisson distribution of errors were used to fit species richness from 0.0001 to 100 m<sup>2</sup> ( $n = 40$  for first six scales;  $n = 20$  for 100 m<sup>2</sup>). Additionally, total, vascular plant, bryophyte, and lichen richness were modeled separately at 10-m<sup>2</sup> ( $n = 80$ , including the nested and the additional individual plots).

Multi-collinearity between the continuous variables was checked using pairwise Pearson correlations for the nested set of plots used in cross-scale modeling of total richness and, separately, for taxon-wise species richness at 10 m<sup>2</sup>. Two predictors were considered as collinear when  $|r| > 0.7$ , and in such cases we kept the one we considered more meaningful (El. Appendix B). In addition, the quadratic terms of the variables were included when they were



**Fig. 1.** Map of the study area and spatial distribution of the nested-plot series and normal plots. Note that in cases where the plots were very close to each other, not all symbols are visible.

significant in single-parameter models (El. Appendix B). Land-use type was coded using dummy variables.

Overdispersion in the full parameter models was tested by estimating the dispersion parameter (i.e. by dividing Pearson's  $\chi^2$  by the degrees of freedom;  $n-p$ , where  $n$  is the number of observations in  $p$  parameters; Logan, 2010). Since its value indicated violations of the assumption, we assumed a negative binomial distribution of errors to account for overdispersion. The candidate models were constructed using the `glm.nb` function in the MASS package (Ripley et al., 2012) for R (R Development Core Team, 2010).

Corrected Akaike's Information Criteria ( $AIC_c$ ) were used to select the best models. From the set of candidate models constructed from all possible combinations of predictors, we calculated the differences in  $AIC_c$  values as  $\Delta AIC_{c,i} = AIC_{c,i} - \text{minimum } AIC_c$ , across all models in the set. We report on all models with  $\Delta AIC_{c,i} < 2$ , as they have substantial support (Burnham and Anderson, 2002). We transformed  $AIC_{c,i}$  values into Akaike weights ( $w_i$ , i.e. the probability that a given model is the best within the set; Burnham and Anderson, 2002; Johnson and Omland, 2004). As a complementary measure of statistical support, we used evidence ratio ( $ER = \text{likelihood}_{\text{best model}} / \text{likelihood}_{i\text{-th model}}$ , where  $\text{likelihood} = \exp(-1/2 \times \Delta_i)$ ; Johnson and Omland, 2004). To summarize the information across the numerous possible predictor combinations, we provide the relative importance of predictors (i.e. range 0–1, where 1 indicates that the variable is part of all models with statistical support; Burnham and Anderson, 2002). Calculations were carried out using the `dredge` function of the MuMIn R package (version 1.7.11; Bartoń, 2012).

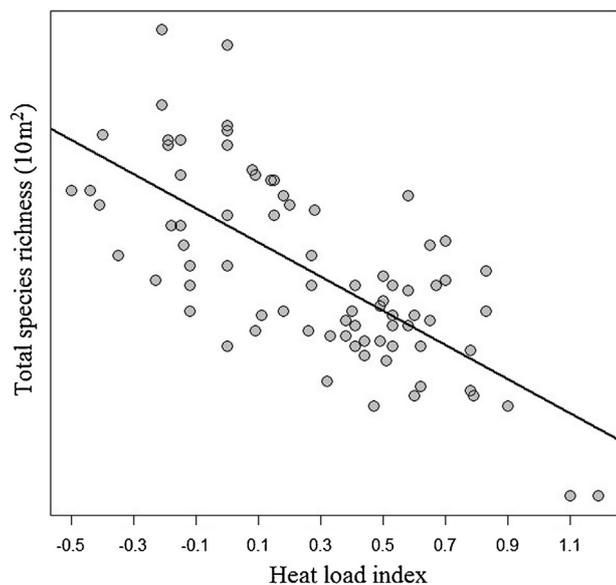
We checked for spatial autocorrelation for the 10-m<sup>2</sup> subplots within biodiversity plots by a Moran's  $I$  test based on a list of neighboring plots (distance interval of 0–20 m), using the `spdep` R package (version 0.5-46; Bivand, 2012). This test did not detect any significant spatial autocorrelation in the final models.

## 2.5. Analyses of species–area relationships

SARs were fitted using the power-law function because it performed particularly well in previous multimodel comparisons at small grain sizes (Dengler, 2009a; Dengler and Boch, 2008b), and its parameters are well understood. The exponents of the power-law function, the so-called  $z$ -values, are a universal means of comparing species–area relationships (e.g. Drakare et al., 2006; Dengler, 2009a) and they can be considered as a measure of  $\beta$ -diversity (Crist and Veech, 2006). We therefore used the  $z$ -values modeled in  $S$ -space (i.e. the untransformed scale of  $S$  values) and tested their dependence on environmental factors with the approach used for  $\alpha$ -diversity (see Section 2.4).

First, the power law function was fitted in  $S$ -space with non-linear regression in Statistica 10 (StatSoft Inc., 2011; 0.1 as starting values and 0.5 as step-width) because, unlike fitting in log  $S$ -space (i.e. the log-transformed scale of  $S$  values), zero values for richness can be handled in a statistically sound manner (Dengler, 2009a). Fitting was performed for all plants, vascular plants, bryophytes and lichens, and for each of the 20 nested-plot series separately, using for the plot sizes below 100 m<sup>2</sup> the average richness values of the two subplots in opposite corners.

Second, instead of assuming that a single power law describes the increase of richness correctly across spatial scales, we divided the empirical relationship into segments and tested whether their  $z$ -values differ (Dengler, 2009a). We therefore calculated these local  $z$ -values for the all transitions between subsequent richness values for all 20 nested-plot series. The resulting values were then subjected to a main-effects ANOVA in Statistica 10, with scale and series ID as the two factors. Finally, we calculated mean local  $z$ -values for transitions of subsequent plot sizes, when looking separately at vascular plants, bryophytes and lichens, and when grouping the data



**Fig. 2.** Visualization of the relationship of total plant species richness at 10 m<sup>2</sup> ( $n = 80$ ) to the most influential predictor according to Table 3 and Electronic Appendix F, heat load index.

of total richness according to the three land-use types and the three main grassland types (see Dengler et al., 2012a).

### 3. Results

#### 3.1. Overall plant diversity

Across all 10-m<sup>2</sup> plots, 422 taxa were determined: 366 vascular plants (86.7%), 41 bryophytes, 14 lichens, and one genus of macroscopic cyanobacteria (*Nostoc* sp.). At plot scale, the dominance of vascular plants was even stronger, accounting for 94.4% of the mean species richness (Table 1). Non-vascular plants were unevenly distributed between plots, with the standard deviation often exceeding the means (Table 1).

#### 3.2. Diversity–environment relationships

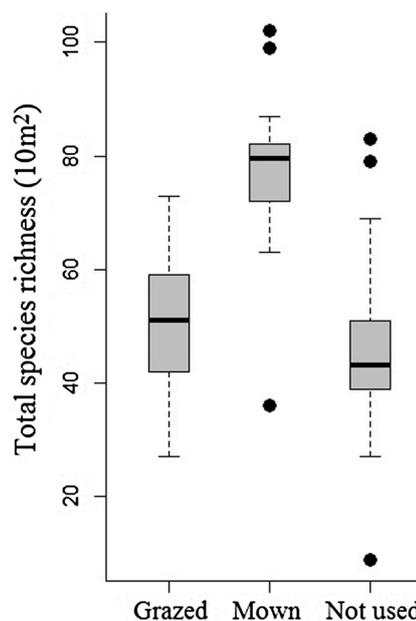
##### 3.2.1. Total plant species richness across scales

The relative importance of predictors changed across scales (Table 2, El. Appendices A and D). A highly relevant variable at very fine scales was the humus content. By contrast, microrelief and land-use type (i.e. mowing) became important predictors only at larger scales (Table 2, El. Appendix D). In addition to these parameters, also heat load index, litter cover, and altitude played an appreciable role, but not for the whole range. Although minimum temperature of the coldest month was highly important from 0.1 to 100 m<sup>2</sup> (El. Appendix D), it showed only marginal effects in the best models (Table 2).

##### 3.2.2. Species richness of taxonomic groups at 10 m<sup>2</sup>

The models are presented in Table 3 as well as in Electronic Appendices E and F. For total richness, the two most influential parameters were heat load index (Fig. 2) and land use (Fig. 3).

For vascular species richness, the most important predictors were heat load index, microrelief, clay content, temperature annual range, and management type (i.e. no usage) (El. Appendix F). All these predictors had a negative effect on species richness (Table 3). Although clay content was included in the best model, it had a weak and non-significant effect.



**Fig. 3.** Visualization of the relationship of total plant species richness at 10 m<sup>2</sup> ( $n = 80$ ) to the second most influential predictor according to Table 3 and Electronic Appendix F, land-use type. Note that this figure does not account for the other potentially influential covariates, which explains that in Electronic Appendix F the effect of Unused vs. Grazed is larger than Mown vs. Grazed while in the visualization it appears the other way round.

In the case of bryophyte species richness, heat load index, stone cover, and humus content were relatively important (El. Appendix F). While both heat load index and humus content had a negative influence, stone cover had a statistically significant weakly positive influence (Table 3).

For lichen species richness, microrelief, humus content, and minimum temperature of the coldest month were the most important predictors (El. Appendix F). The relationship with microrelief was unimodal, and both humus content and minimum temperature of the coldest month had a strong positive effect (Table 3).

#### 3.3. Species–area relationships

The overall slope ( $z$ ) of the power-law SARs (modeled in  $S$ -space) for all taxonomic groups combined ranged from 0.159 to 0.264, with a mean of 0.207.

##### 3.3.1. Scale-dependence of $z$ for total plant richness

For the “local”  $z$ -values, series ID had no effect, while scale was highly influential. The mean  $z$ -value increased steeply from 0.0001–0.001 m<sup>2</sup> to 0.01–0.1 m<sup>2</sup>. Above these grain sizes, a more or less exponential decrease in  $z$ -values occurred (Fig. 4).

When comparing the three land-use types, the mean species-area curves of grazed and unused grasslands were nearly indistinguishable and that of mown sites was higher (El. Appendix G.A). When considering the local  $z$ -values (El. Appendix G.B), the three curves coincide with the overall pattern shown in Fig. 4. The local  $z$ -values did not differ significantly between land-use types for any of the spatial transitions (ANOVAs not shown).

##### 3.3.2. Effects of taxonomic groups

The species–area relationships of vascular plants were indistinguishable from the patterns for total richness (see El. Appendix H in comparison with Fig. 4). The overall  $z$ -values of bryophytes were significantly lower than those of vascular plants. The scale-dependence of the  $z$ -values was even more pronounced for

**Table 1**

Overview of the species richness (mean ± SD) encountered in the 20 nested-plot series ( $n = 20$  for 100 m<sup>2</sup>;  $n = 40$  for smaller plot sizes).

Area [m <sup>2</sup> ]	All taxa			Vascular plants	Bryophytes	Lichens
	Min	Max	Mean ± SD	Mean ± SD	Mean ± SD	Mean ± SD
0.0001	0	5	2.6 ± 1.5	2.3 ± 1.4	0.2 ± 0.4	0.0 ± 0.0
0.001	0	9	4.6 ± 2.4	4.2 ± 2.1	0.4 ± 0.6	0.0 ± 0.0
0.01	3	20	10.2 ± 5.1	9.6 ± 4.7	0.6 ± 0.7	0.0 ± 0.0
0.1	7	45	22.8 ± 10.3	21.1 ± 9.9	1.5 ± 1.1	0.2 ± 0.5
1	18	82	40.0 ± 15.5	37.5 ± 15.3	2.2 ± 1.3	0.4 ± 0.7
10	37	101	60.5 ± 17.4	57.2 ± 17.4	2.8 ± 1.7	0.6 ± 1.0
100	58	134	88.2 ± 24.0	83.3 ± 24.2	3.8 ± 2.2	1.2 ± 2.3

bryophytes than for vascular plants. At all spatial scales, the  $z$ -values of bryophytes were lower than those of vascular plants, and these differences were significant at nearly all spatial scales (El. Appendix H). Due to their rarity, we could only include  $z$ -values for lichens in the analysis at larger scales, where an ANOVA with a HSD post hoc test revealed that they were significantly lower than those of vascular plants for the transitions 0.1–1 m<sup>2</sup> and 1–10 m<sup>2</sup>, and significantly higher than those of bryophytes at 10–100 m<sup>2</sup>.

#### 4. Discussion

##### 4.1. Diversity–environment relationships

###### 4.1.1. Total plant species richness across scales

This study reinforces the theory that species richness–environment relationships are strongly scale-dependent (Field et al., 2009; Siefert et al., 2012). Generally, our results are in accordance with the conceptual model of Shmida and Wilson (1985), which states that niche relations are the prevailing drivers

of richness at the finest scales, while environmental heterogeneity is more important at intermediate scales. These outcomes show that multi-scale sampling approaches allow a wide-ranging interpretability of diversity patterns with limited additional sampling effort.

At the finest scales considered here (i.e. 0.0001–0.1 m<sup>2</sup>), humus content was always an important parameter. This finding is consistent with the prediction that niche relations, which are mainly determined by resource factors, have a greater influence at very small scales (Shmida and Wilson, 1985; Siefert et al., 2012). The hump-shaped relationship of richness with humus (Table 2) can broadly be related to the intermediate disturbance hypothesis (IDH: Connell, 1978; Grime, 1973) since humus content increases when soils remain undisturbed. The low negative effect of soil pH on plant diversity (Table 2) is unexpected, as numerous studies found strong effects of pH in European grasslands (e.g. Chytrý et al., 2003; Reitalu et al., 2014; Schuster and Diekmann, 2003). This striking pattern is usually explained by the dominance of calciphilous species in the regional species pools (Ewald, 2003; Pärtel, 2002),

**Table 2**

Parameterization of the best models according to the AIC<sub>c</sub>-based selection for explaining species richness at 0.0001, 0.001, 1, 10 and 100 m<sup>2</sup> as well as  $z$ -values across scales (calculated in  $S$ -space). The predictors included in the full models are given in Electronic Appendices B and D; see Electronic Appendix A for predictor abbreviations. Std. coef., standardized coefficients; SE, standard errors.

Diversity parameter	Average (± SD)	Predictor	Std. coef.	SE	$p$
0.0001 m <sup>2</sup> ( $n = 40$ )	2.6 (1.5)	Hum	0.550	0.156	<b>&lt;0.001</b>
		Hum <sup>2</sup>	−0.200	0.067	<b>0.003</b>
0.001 m <sup>2</sup> ( $n = 40$ )	4.6 (2.4)	Hum	0.561	0.117	<b>&lt;0.001</b>
		Hum <sup>2</sup>	−0.245	0.056	<b>&lt;0.001</b>
0.01 m <sup>2</sup> ( $n = 40$ )	10.2 (5.1)	Hum	0.364	0.093	<b>&lt;0.001</b>
		Hum <sup>2</sup>	−0.182	0.039	<b>&lt;0.001</b>
		pH	−0.153	0.088	0.080
		Litt	−0.101	0.058	0.084
0.1 m <sup>2</sup> ( $n = 40$ )	22.8 (10.3)	Mown vs. grazed	0.366	0.105	<b>&lt;0.001</b>
		Hum	0.347	0.068	<b>&lt;0.001</b>
		Litt	−0.172	0.040	<b>&lt;0.001</b>
		Hum <sup>2</sup>	−0.161	0.029	<b>&lt;0.001</b>
		MinTemp	0.069	0.041	0.100
		Temp	0.058	0.043	0.175
1 m <sup>2</sup> ( $n = 40$ )	40.0 (15.5)	Rel	0.026	0.051	0.610
		Mown vs. grazed	0.257	0.073	<b>&lt;0.001</b>
		Rel	−0.176	0.052	<b>&lt;0.001</b>
		Litt	−0.142	0.030	<b>&lt;0.001</b>
		Heat	−0.136	0.038	<b>&lt;0.001</b>
		MinTemp	0.060	0.026	<b>0.020</b>
10 m <sup>2</sup> ( $n = 40$ )	53.4 (18.3)	Rel <sup>2</sup>	0.040	0.021	0.050
		Mown vs. grazed	0.264	0.058	<b>&lt;0.001</b>
		Heat	−0.100	0.029	<b>&lt;0.001</b>
		Litt	−0.096	0.023	<b>&lt;0.001</b>
		Rel	−0.088	0.040	<b>0.027</b>
		MinTemp	0.080	0.020	<b>&lt;0.001</b>
100 m <sup>2</sup> ( $n = 20$ )	88.2 (24.0)	Rel <sup>2</sup>	0.037	0.015	<b>0.014</b>
		Mown vs. grazed	0.457	0.108	<b>&lt;0.001</b>
		MinTemp	0.098	0.038	<b>0.010</b>
		Rel	0.046	0.056	0.417
$z$ values ( $n = 20$ )	0.21 (0.03)	Rel <sup>2</sup>	0.044	0.049	0.369
		Heat	0.014	0.004	<b>0.003</b>
		Litter	0.011	0.004	<b>0.022</b>
		MinTemp	0.008	0.004	0.062

Significant  $p$ -values are in bold.

**Table 3**  
Parameterization of the best models according to the AIC<sub>c</sub>-based selection for taxon-wise species richness at 10 m<sup>2</sup> (n=80). The predictors included in the full models are given in Electronic Appendices B and F; see Electronic Appendix A for predictor abbreviations. Std. coef., standardized coefficients; SE, standard errors.

Species group	Average (± SD)	Predictor	Std. coef.	SE	p
All	53.5 (18.3)	Heat	-0.246	0.028	<b>&lt;0.001</b>
		Unused vs. Grazed	-0.200	0.065	<b>0.004</b>
		TempRange	-0.134	0.034	<b>&lt;0.001</b>
		Rel	-0.106	0.050	<b>0.033</b>
		Clay	-0.047	0.029	0.112
		Rel <sup>2</sup>	0.039	0.013	<b>0.004</b>
Vascular plants	50.3 (17.6)	Heat	-0.234	0.028	<b>&lt;0.001</b>
		Unused vs. Grazed	-0.222	0.065	<b>&lt;0.001</b>
		Rel	-0.139	0.050	<b>0.005</b>
		TempRange	-0.132	0.034	<b>&lt;0.001</b>
		Rel <sup>2</sup>	0.047	0.013	<b>&lt;0.001</b>
		Clay	-0.047	0.029	0.107
Bryophytes	2.8 (2.3)	Heat	-0.618	0.081	<b>&lt;0.001</b>
		Hum	-0.293	0.102	<b>0.004</b>
		Hum <sup>2</sup>	0.152	0.041	<b>&lt;0.001</b>
		Stones	0.027	0.010	<b>&lt;0.001</b>
Lichens	0.3 (0.9)	Rel	1.383	0.478	<b>0.004</b>
		Hum	0.748	0.136	<b>&lt;0.001</b>
		Rel <sup>2</sup>	-0.292	0.109	<b>0.007</b>
		MinTemp	0.164	0.070	<b>0.019</b>

Significant p-values are in bold.

but our plots probably spanned too small a range of pH (6.1–8.4 in H<sub>2</sub>O) to reveal a similar relationship.

For grain sizes of 0.01–10 m<sup>2</sup>, litter cover had an important negative effect. Although litter may generally have a positive effect on plant recruitment in dry grasslands, large amounts inhibit seedlings (Loydi et al., 2013), leading to stands dominated by a few dominant, perennial species, which do not need to regenerate in

order to persist. In Transylvania, litter has previously been shown to negatively affect dry grassland vegetation (Ruprecht et al., 2010).

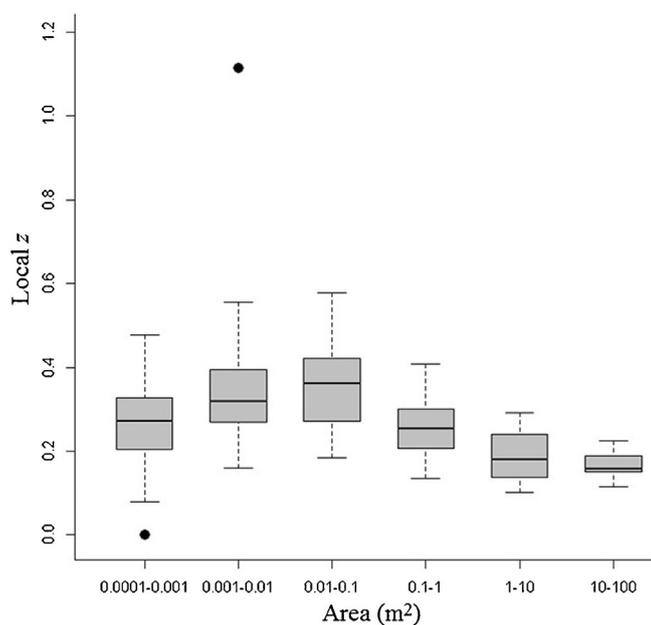
Heat load index was a strong and negative predictor, but only at 1 and 10 m<sup>2</sup>. Heat load reduces water availability (Pausas and Austin, 2001) in such relatively hot and dry sites. In addition, highest heat load is connected with very steep slopes, which are affected by continuous erosion. By contrast, in northern central and northern Europe, where extreme summer drought is not an issue, solar radiation has repeatedly been shown to have a positive effect on grassland diversity (Klimek et al., 2007; Olsson et al., 2009; Pykälä et al., 2005).

Microrelief played an important role in the richness models from 0.1 to 100 m<sup>2</sup>, though the effect varied from positive to u-shaped. The heterogeneity-diversity hypothesis (HDR) assumes that heterogeneous environments can host more species because of more available niches (see Lundholm, 2009; Tamme et al., 2010). Tamme et al. (2010) found that the positive effect of spatial heterogeneity increases with grain size and turns negative below 0.01 or 0.001 m<sup>2</sup>, which is consistent with our findings.

Finally, consistent with Field et al. (2009) and Siefert et al. (2012) we found that climatic variables gain importance with increasing grain size, despite the fact that we used very small grain sizes compared to the coarse resolution of Worldclim data. Minimum winter temperature (range: -8.9 to -5.9 °C) exerted significant effects from 0.01 m<sup>2</sup> upwards. The positive effect of cold winters could be due to shorter vegetation periods, when interspecific competition among the grassland-dominating hemicryptophytes (which renew their above-ground biomass each summer) is reduced (Dengler and Boch, 2008a).

#### 4.1.2. Effect of land use

For grain sizes of 0.1–100 m<sup>2</sup>, land use was included in all models (El. Appendix C), and it had by far the strongest effect in the best models (Table 2), consisting of a pronounced increase in richness in mown compared to grazed or unused grasslands. The relative richness difference between the land-use types was nearly scale-invariant (see El. Appendix G.A). The pattern was essentially the same when analyzing all 10-m<sup>2</sup> plots without accounting for other predictors, but the unused plots were species-poorer than the grazed (Fig. 3). When accounting for the other environmental factors, in this case the additional positive effect of mowing vs. grazing was reduced while the negative effect of not using vs. grazing



**Fig. 4.** Box-whisker plots of the scale-dependence of the power-law z-values of total plant richness on area. Medians (horizontal lines within boxes), inter-quartile ranges (boxes), outliers (whiskers) and extreme values (black points) of the “local” z-values for transitions from one to the next plot size are given. Series ID had no effect in the ANOVA ( $p = 0.917$ ), and the effect of scale was highly significant ( $p < 0.001$ ). At the smallest scale (0.0001–0.001 m<sup>2</sup>) the mean z-value was 0.254, which increased to the maxima of 0.363 for 0.001–0.01 m<sup>2</sup> and 0.355 for 0.01–0.1 m<sup>2</sup>, with the mean at the first transition being raised by an extreme outlier, without which it would be only 0.324. Above these scales, the decrease in z-values led to a mean value of only 0.165 for the transition 10–100 m<sup>2</sup>. Note that z-values above 1 are theoretically impossible for true spatial means of species densities, but can occur when one or both of the respective means are biased due to the low replication ( $n = 2$ ).

became stronger. This change from single to multiple regression can be explained by confounding effects of other parameters, e.g. steep, southwards facing slopes are either grazed or unused, but they cannot be mown.

The increase of species richness under either grazing or mowing is consistent with the intermediate disturbance hypothesis (Grime, 1973) as these grasslands are managed in a low-intensity manner. Studies in Europe have shown that abandonment decreases richness both compared to grazing and mowing (Dupré and Diekmann, 2001; Jacquemyn et al., 2011; Losvik, 1999; Vassilev et al., 2011; Wanner et al., 2014) Compared to the extreme diversity losses in consequence of abandonment reported by these studies, our mean difference between unused and grazed grasslands appears moderate (Fig. 3).

Most remarkable was that meadows were much richer than pastures (Fig. 3). Interestingly, not only the Transylvanian but nearly all extraordinarily species rich grasslands of Europe have a long history of mowing (e.g. Merunková et al., 2012; Kull and Zobel, 1991). The vertical structure of grassland communities is dependent on management history, and the regional species pool might be modified through the intensity of competition (Zobel, 1992). This mechanism might have encouraged the increase in the number of mowing-tolerant species in grasslands that have been mown for several centuries. So far, the findings of the few studies in European grassland types are heterogeneous regarding vascular plant richness in meadows vs. pastures (e.g. Fischer and Wipf, 2002; Hansson and Fogelfors, 2000; Stammel et al., 2003; Wellstein et al., 2007). For grazing, contrasting effects at different levels of productivity have been already proposed (Milchunas et al., 1988; Bakker et al., 2006). By contrast, a similar dependence of mowing effects on biodiversity is not known. In a situation with low to no fertilization and low disturbance as in the Transylvanian dry grasslands, the positive difference between mowing and grazing might be particularly high.

#### 4.2. Species–area relationships

We found that in Transylvania, the  $z$ -values of total richness average 0.207 in  $S$ -space, corresponding to 0.275 in log  $S$ -space (Dengler et al., 2012a), and this is distinctly higher than in other dry grasslands across Europe (Chiarucci et al., 2006; Dengler, 2005; Dengler and Boch, 2008b; Dolnik and Breuer, 2008). This highlights that these grasslands are not only globally outstanding with regard to small-scale  $\alpha$ -diversity (Wilson et al., 2012), but in comparison with other European dry grasslands, also with regard to small-scale  $\beta$ -diversity. Only de Bello et al. (2007), who studied  $z$ -values (0.01–100 m<sup>2</sup>, log  $S$ -space) in Spanish grasslands found higher species turnover in some cases.

Unexpectedly,  $z$ -values in our study were neither affected by vegetation type (Dengler et al., 2012a) nor by land-use type (see Table 2 and El. Appendix D). Dupré and Diekmann (2001) found that SARs in abandoned plots were clearly steeper than in grazed plots in Sweden, and it is unclear why this pattern did not emerge in Transylvania (see El. Appendix G.A). In our study, the predictors generally explained little in the variability of  $z$ -values, with litter cover and heat load index having a negative effect. This could be explained in that both extreme south facing slopes and high litter cover negatively affect most species, leading to lower richness at smaller scales, while due to the inherent heterogeneity of topography and litter distribution at larger spatial scales the more sensitive species normally still find some suitable patches. Chiarucci et al. (2006) found a clear negative effect of productivity on  $z$ -values. While we did not measure productivity directly, it can be safely assumed that meso-xeric stands are more productive, but their  $z$ -values in our case did not differ significantly (Dengler et al., 2012a; Table 7).

While  $z$ -values in the SARs of the Estonian dry grasslands were largely scale-invariant (Dengler and Boch, 2008b), we found a pronounced scale-dependence in our case (Fig. 4, El. Appendices G.B and H), probably because in Estonia cryptogams play a much bigger role in the overall communities (see Boch and Dengler, 2006).

#### 4.3. Particularities of bryophytes and lichens

##### 4.3.1. Cryptogam richness

One interesting aspect of the Transylvanian dry grasslands is their low diversity of cryptogams (Table 1), as they were much rarer compared to *Festuco-Brometea* grasslands in other parts of Europe (Boch and Dengler, 2006; Dengler, 2005; Löbel and Dengler, 2008). At plot scale, cryptogams in these studies contributed much more to overall plant species richness (Saaremaa: 28%; Öland: 8–32%; NE Germany: 12–14%) than in Transylvania (5.6%, see Table 1). While bryophytes, despite being species-poor, reached considerable cover in some of our plots (Dengler et al., 2012a), lichens were absent from most of the 10-m<sup>2</sup> plots. One possible explanation could be the increased drought and higher temperatures in southern and eastern Europe. However, higher proportions of cryptogams were found at 10 m<sup>2</sup> also in Bulgaria (Pedashenko et al., 2013) and Ukraine (A. Kuzemko et al., unpubl.).

##### 4.3.2. Environment–diversity relationships of cryptogams

Overall, 10-m<sup>2</sup> richness of taxonomic groups showed contrasting patterns in relation to the predictors, which is in accordance with most diversity studies in grasslands (e.g. Austrheim, 2002; Jeschke et al., 2008; Löbel et al., 2006; Virtanen and Crawley, 2010). These differences probably arise from distinct life history traits of cryptogams (Pharo and Beattie, 1997).

Like vascular plants, bryophytes were negatively affected by heat load (Table 3). This indicates that the steep southwards facing slopes are eroded, hostile habitats, inducing drought stress for rootless bryophytes (e.g. Grytness et al., 2006; Herben, 1987). While lichens are on average better drought-adapted than bryophytes (Pharo and Beattie, 1997), this could not explain the lack of a relationship with heat load. The only community type in the study with notable lichen presence were the rocky grasslands, with a mean of 3.0 lichen species on 10 m<sup>2</sup>. These communities occur particularly on south-facing, but less steep slopes, with a considerable cover of stones, which support cryptogam colonization also on the surrounding soil.

Humus content was most influential for the richness of cryptogams. However, the direction of the relationship was u-shaped for bryophytes and positive for lichens. The response of the bryophytes might be caused by opposite preferences of the two most relevant groups: the short-lived acrocarpous mosses prefer raw soil with low humus content, while the perennial pleurocarpous mosses grow on well-developed soils with high humus content. Unexpectedly, soil pH did not play a role for the cryptogam groups, in contrast to the findings of other studies (e.g. Löbel et al., 2006), but the reason could simply be the short pH gradient studied.

While vascular plant richness showed a u-shaped response to microrelief, lichens showed a unimodal response. For bryophytes, this factor did not play any role. This strongly deviates from the situation in more flat dry grasslands (Löbel et al., 2006), where the richness of all three taxonomic groups increased with microrelief.

While land use type was highly influential for vascular plant richness, it did not affect the cryptogam groups appreciably. By contrast, Eskelinen and Oksanen (2006) and Virtanen and Crawley (2010) found strong negative effects of grazing intensity on plot-scale richness of cryptogams. One probable explanation is that we did not distinguish different land-use intensities but only land-use types.

#### 4.3.3. SARs of cryptogams

The  $z$ -values of bryophytes were lower than those of vascular plants at all spatial scales. Since  $z$ -values are a measure of species turnover, we can conclude that  $\beta$ -diversity of bryophytes is generally lower than for vascular plants, meaning that they occur more evenly in space. Bryophytes, with their extremely light spores, are less dispersal-limited, and have relatively wider niches. For lichens, the  $z$ -values for the largest transition (10–100 m<sup>2</sup>) were higher than those of bryophytes and vascular plants, albeit insignificantly so for the latter (see El. Appendix F). One reason could be that the similarity of habitat requirements of most lichen species restricts their occurrence to micro-habitats that occur only locally but then typically host several species at once. Such extremely clumped distributions are mathematically reflected by high  $z$ -values.

## 5. Conclusions

This study shows that diversity–environment relationships are strongly scale-dependent, and that neglecting the scale can lead to incorrect generalizations. Therefore, we recommend using multi-scale sampling approaches with limited additional sampling effort in order to allow for a much more general interpretability of diversity patterns. Similarly, studying multiple taxonomic groups was highly informative in this case as it yielded different patterns and drivers for the three taxonomic groups, which could be related to their biology. At least in this case, none of the groups could reasonably be used as a surrogate for the diversity of the others.

While some of the grasslands included in this study were previously known to contain globally extraordinary  $\alpha$ -diversity values at plot scale (Dengler et al., 2012a; Wilson et al., 2012), we could demonstrate that also  $\beta$ -diversity (expressed as  $z$ -value of the power-law SAR) is unusually high. Finally, the extraordinary small-scale richness of Transylvanian dry grasslands highlights their need for protection, both for reasons of biodiversity conservation and as an excellent study system for ecological theories. As the particularly high richness values were always connected to traditional low-intensity management, it is fundamental to maintain these practices as a core element of High Nature Value farming.

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## Appendices A–H. Supplementary data

Supplementary material related to this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.agee.2013.10.028>.

## References

- Akeroyd, J.R., Page, N., 2011. Conservation of High Nature Value (HNV) grassland in a farmed landscape in Transylvania, Romania. *Contrib. Bot.* 46, 57–71.
- Alard, D., Poudevigne, I., 2000. Diversity patterns in grasslands along a landscape gradient in northwestern France. *J. Veg. Sci.* 11, 287–294.
- Auestad, I., Knut, R., Økland, R.H., 2007. Scale-dependence of vegetation–environment relationships in semi-natural grasslands. *J. Veg. Sci.* 19, 139–148.
- Austrheim, G., 2002. Plant diversity patterns in semi-natural grasslands along an elevational gradient in southern Norway. *Plant Ecol.* 161, 193–205.
- Bakker, E.S., Ritchie, M.E., Olff, H., Milchunas, D.G., Knops, J.M.H., 2006. Herbivore impact on grassland plant diversity depends on habitat productivity and herbivore size. *Ecol. Lett.* 9, 780–788.
- Bartoň, K., 2012. Multi-Model Inference, Package MuMIn, (<http://cran.r-project.org/web/packages/MuMIn/index.html>).
- Becker, T., Brändel, M., 2007. Vegetation–environment relationships in a heavy metal-dry grassland-complex. *Folia Geobot.* 42, 11–28.
- Billetter, R., Liira, J., Bailey, D., Bugter, R., Arens, P., Augenstein, I., Aviron, S., Baudry, J., Bukacek, R., Burel, F., Cerny, M., De Blust, G., De Cock, R., Diekotter, T., Dietz, H., Dirksen, J., Dormann, C., Durka, W., Frenzel, M., Hamersky, R., Hendrickx, F., Herzog, F., Klotz, S., Koolstra, B., Lausch, A., Le Coeur, D., Maelfait, J.P., Opdam, P., Roubalova, M., Schermann, A., Schermann, N., Schmidt, T., Schweiger, O., Smulders, M.J.M., Speelmans, M., Simova, P., Verboom, J., van Wingerden, W., Zobel, M., Edwards, P.J., 2008. Indicators for biodiversity in agricultural landscapes: a pan-European study. *J. Appl. Ecol.* 45, 141–150.
- Bivand, R., 2012. Spatial Dependence: Weighting Schemes, Statistics And Models Package spdep, (<http://cran.r-project.org/web/packages/spdep/index.html>).
- Boch, S., Dengler, J., 2006. Floristische und ökologische Charakterisierung sowie Phytodiversität der Trockenrasen auf der Insel Saaremaa (Estland). *Arb. Inst. Landschaftsökol. Münster* 15, 55–71.
- Bohn, U., Gollub, G., Hettwer, C., Neuhauslová, Z., Raus, T., Schlüter, H., Weber, H., Hennekens, S. (Eds.), 2004. Map of the Natural Vegetation of Europe. Scale 1: 2 500 000. Interactive CD-ROM: Explanatory Text, Legend, Maps. Bundesamt für Naturschutz, Bonn.
- Burnham, K.P., Anderson, D.R., 2002. Model Selection and Multimodel Inference—A Practical Information-Theoretic Approach, 2nd edn. Springer, New York.
- Chiarucci, A., Viciani, D., Winter, C., Diekmann, M., 2006. Effects of productivity on species–area curves in herbaceous vegetation: evidence from experimental and observational data. *Oikos* 115, 475–483.
- Chytrý, M., Tichý, L., Roleček, J., 2003. Local and regional patterns of species richness in central European vegetation types along the pH/calcium gradient. *Folia Geobot.* 38, 429–442.
- Connell, J.H., 1978. Diversity in tropical rain forests and coral reefs. *Science* 199, 1302–1310.
- Connor, E.F., McCoy, E.D., 1979. The statistics and biology of the species–area relationship. *Am. Nat.* 113, 791–833.
- Cousins, S.A.O., Lavorel, S., Davies, I., 2003. Modelling the effects of landscape pattern and grazing regimes on the persistence of plant species with high conservation value in grasslands in south-eastern Sweden. *Landscape Ecol.* 18, 315–332.
- Crawley, M.J., Harral, J.E., 2001. Scale dependence in plant biodiversity. *Science* 291, 864–868.
- Cremene, C., Groza, G., Rakosy, L., Schileyko, A.A., Baur, A., Erhardt, A., Baur, B., 2005. Alterations of steppe-like grasslands in Eastern Europe: a threat to regional biodiversity hotspots. *Conserv. Biol.* 19, 1606–1618.
- Crist, T.O., Veech, J.A., 2006. Additive partitioning of rarefaction curves and species–area relationships: unifying  $\alpha$ -,  $\beta$ -, and  $\gamma$ -diversity with sample size and habitat area. *Ecol. Lett.* 9, 923–932.
- de Bello, F., Lepš, J., Sebastià, M.-T., 2007. Grazing effects on the species–area relationship: variation along a climatic gradient in NE Spain. *J. Veg. Sci.* 18, 25–34.
- Dengler, J., 2005. Zwischen Estland und Portugal—Gemeinsamkeiten und Unterschiede der Phytodiversitätsmuster Europäischer Trockenrasen. *Tuexenia* 25, 387–405.
- Dengler, J., 2008. Pitfalls in small-scale species–area sampling and analysis. *Folia Geobot.* 43, 269–287.
- Dengler, J., 2009a. Which function describes the species–area relationship best?—a review and empirical evaluation. *J. Biogeogr.* 36, 728–744.
- Dengler, J., 2009b. A flexible multi-scale approach for standardised recording of plant species richness patterns. *Ecol. Indic.* 9, 1169–1178.
- Dengler, J., Boch, S., 2008a. Forest–edge communities (*Trifolium–Geranietaea sanguinea*) on the island of Saaremaa (Estonia): phytosociology and biodiversity patterns. *Mitt. Arbeitsgem. Geobot. Schleswig-Holstein* 65, 257–286.
- Dengler, J., Boch, S., 2008b. Sampling–design effects on properties of species–area curves—a case study from Estonian dry grassland communities. *Folia Geobot.* 43, 289–304.
- Dengler, J., Jansen, F., Glöckler, F., Peet, R.K., De Cáceres, M., Chytrý, M., Ewald, J., Oldeland, J., Finckh, M., Lopez-Gonzalez, G., Mucina, L., Rodwell, J.S., Schaminée,

- J.H.J., Spencer, N., 2011. The Global Index of Vegetation-Plot Databases (GIVD): a new resource for vegetation science. *J. Veg. Sci.* 22, 582–597.
- Dengler, J., Becker, T., Ruprecht, E., Szabó, A., Becker, U., Beldean, M., Bitá-Nicolae, C., Dolnik, C., Goia, I., Peyrat, J., Sutcliffe, L.M.E., Turtureanu, P.D., Uğurlu, E., 2012a. *Festuco-Brometea* communities of the Transylvanian Plateau (Romania)—a preliminary overview on syntaxonomy, ecology, and biodiversity. *Tuexenia* 32, 319–359.
- Dengler, J., Todorova, S., Becker, T., Boch, S., Chytrý, M., Diekmann, M., Dolnik, C., Dupré, C., Giusso del Galdo, G.P., Guarino, R., Jeschke, M., Kiehl, K., Kuzemko, A., Löbel, S., Otýpková, Z., Pedashenko, H., Peet, R.K., Ruprecht, E., Szabó, A., Tsiripidis, I., Vassilev, K., 2012b. Database Species–Area Relationships in Palaearctic Grasslands. *Biodivers. Ecol.* 4, 321–322.
- Dolnik, C., Breuer, M., 2008. Scale dependency in the species–area relationship of plant communities. *Folia Geobot.* 43, 305–318.
- Drakare, S., Lennon, J.J., Hillebrand, H., 2006. The imprint of the geographical, evolutionary and ecological context on species–area relationships. *Ecol. Lett.* 9, 215–227.
- Dupré, C., Diekmann, M., 2001. Differences in species richness and life-history traits between grazed and abandoned grasslands in southern Sweden. *Ecography* 24, 275–286.
- Enyedi, Z.M., Ruprecht, E., Deak, M., 2008. Long-term effects of the abandonment of grazing on steppe-like grasslands. *Appl. Veg. Sci.* 11, 55–62.
- Eskelinen, A., Oksanen, J., 2006. Changes in the abundance, composition and species richness of mountain vegetation in relation to summer grazing by reindeer. *J. Veg. Sci.* 17, 245–254.
- Ewald, J., 2003. The calcareous riddle: why are there so many calciphilous species in the central European flora? *Folia Geobot.* 38, 357–366.
- Field, R., Hawkins, B.A., Cornell, H.V., Currie, D.J., Diniz-Filho, J.A.F., Guégan, J.-F., Kaufman, D.M., Kerr, J.T., Mittelbach, G.G., Oberdorff, T., O'Brien, E.M., Turner, J.R.G., 2009. Spatial species–richness gradients across scales: a meta-analysis. *J. Biogeogr.* 36, 132–147.
- Fischer, M., Wipf, S., 2002. Effect of low-intensity grazing on the species-rich vegetation of traditionally mown subalpine meadows. *Biol. Conserv.* 104, 1–11.
- Giladi, I., Ziv, Y., May, F., Jeltsch, F., 2011. Scale-dependent determinants of plant species richness in a semi-arid fragmented agro-ecosystem. *J. Veg. Sci.* 22, 983–996.
- Grime, J.P., 1973. Competitive exclusion in herbaceous vegetation. *Nature* 242, 344–347.
- Grytness, J.A., Heegaard, E., Ihlen, P.G., 2006. Species richness of vascular plants, bryophytes, and lichens along an altitudinal gradient in western Norway. *Acta Oecol.* 29, 241–246.
- Hájková, P., Roleček, J., Hájek, M., Horsák, M., Fajmon, K., Polák, M., Jamrichová, E., 2011. Prehistoric origin of the extremely species-rich semi-dry grasslands in the Bile Karpaty Mts (Czech Republic and Slovakia). *Preslia* 83, 185–204.
- Hansson, M., Fogelfors, H., 2000. Management of a semi-natural grassland: results from a 15-year-old experiment in southern Sweden. *J. Veg. Sci.* 11, 31–38.
- Henle, K., Alard, D., Clitherow, J., Cobb, P., Firbank, L., Kull, T., McCracken, D., Moritz, R.F.A., Niemela, J., Rebane, M., Wascher, D., Watt, A., Young, J., 2008. Identifying and managing the conflicts between agriculture and biodiversity conservation in Europe—a review. *Agric. Ecosyst. Environ.* 124, 60–71.
- Herben, T., 1987. Bryophytes in grassland vegetation sample plots: what is their correlation with vascular plants? *Folia Geobot. Phytotaxon.* 22, 34–41.
- Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G., Jarvis, A., 2005. Very high resolution interpolated climate surfaces for global land areas. *Int. J. Climatol.* 25, 1965–1978.
- Hobohm, C., Bruchmann, I., 2009. Endemische Gefäßpflanzen und ihre Habitat in Europa—Plädoyer für den Schutz der Grasland-Ökosysteme. *Ber. Reinhold-Tüxen-Ges.* 21, 142–161.
- Jacquemyn, H., Van Mechelen, C., Brys, R., Honnay, O., 2011. Management effects on the vegetation and soil seed bank of calcareous grasslands: an 11-year experiment. *Biol. Conserv.* 144, 416–422.
- Jeschke, M., Kiehl, K., Pfadenhauer, J., Gigon, A., 2008. Langfristige Auswirkungen ehemaliger Bewirtschaftungsvarianten auf die Diversität von Blütenpflanzen, Moosen und Flechten eines Kalkmagerrasens. *Bot. Helv.* 118, 95–109.
- Johnson, J.B., Omland, K.S., 2004. Model selection in ecology and evolution. *Trends Ecol. Evol.* 19, 101–108.
- Klimek, S., Kemmermann, A.R., Hofmann, M., Isselstein, J., 2007. Plant species richness and composition in managed grasslands: the relative importance of field management and environmental factors. *Biol. Conserv.* 134, 559–570.
- Korneck, D., Schnittler, M., Klingenstein, F., Ludwig, G., Takla, M., Bohn, U., May, R., 1998. Warum verarmt unsere Flora?—Auswertung der Roten Liste der Farn- und Blütenpflanzen Deutschlands. *Schriftenr. Vegetationskd.* 29, 299–444.
- Kull, K., Zobel, M., 1991. High species richness in an Estonian wooded meadow. *J. Veg. Sci.* 2, 715–718.
- Löbel, S., Dengler, J., 2008. [“2007”]. Dry grassland communities on southern Öland: phytosociology, ecology, and diversity. *Acta Phytogeogr. Suec.* 88, 13–31.
- Löbel, S., Dengler, J., Hobohm, C., 2006. Species richness of vascular plants, bryophytes and lichens in dry grasslands: the effects of environment, landscape structure and competition. *Folia Geobot.* 41, 377–393.
- Logan, M., 2010. *Biostatistical Design and Analysis Using R: A Practical Guide*. Wiley-Blackwell, Oxford.
- Losvik, M.H., 1999. Plant species diversity in an old, traditionally managed hay meadow compared to abandoned hay meadows in southwest Norway. *Nord. J. Bot.* 19, 473–487.
- Loydi, A., Eckstein, R.L., Otte, A., Donath, T.W., 2013. Effects of litter on seedling establishment in natural and semi-natural grasslands: a meta-analysis. *J. Ecol.* 101, 454–464.
- Lundholm, J.T., 2009. Plant species diversity and environmental heterogeneity: spatial scale and competing hypotheses. *J. Veg. Sci.* 20, 377–391.
- Merunková, K., Preislerová, Z., Chytrý, M., 2012. White Carpathian grasslands: can local ecological factors explain their extraordinary species richness? *Preslia* 84, 311–325.
- Milchunas, D.G., Sala, O.E., Lauenroth, W.K., 1988. A generalized model for the effects of grazing by large herbivores on grassland community structure. *Am. Nat.* 132, 87–106.
- Olsson, P.A., Mårtensson, L.-M., Bruun, H.H., 2009. Acidification of sandy grasslands—consequences for plant diversity. *Appl. Veg. Sci.* 12, 350–361.
- Oppermann, R., Beaufoy, G., Jones, G. (Eds.), 2012. *High Nature Value Farming in Europe: 35 European Countries—Experiences and Perspectives*. Verlag region-alkultur, Ubstadt-Weiher.
- Pärtel, M., 2002. Local plant diversity patterns and evolutionary history at the regional scale. *Ecology* 83, 2361–2366.
- Pärtel, M., Bruun, H.H., Sammuli, M., 2005. Biodiversity in temperate European grasslands: origin and conservation. *Grassl. Sci. Eur.* 10, 1–14.
- Pausas, J.G., Austin, M.P., 2001. Patterns of plant species richness in relation to different environments: an appraisal. *J. Veg. Sci.* 12, 153–166.
- Pedashenko, H., Apostolova, I., Boch, S., Ganeva, A., Janišová, M., Sopotlieva, D., Todorova, S., Ūnal, A., Vassilev, K., Velev, N., Dengler, J., 2013. Dry grasslands of NW Bulgarian mountains: first insights into diversity, ecology and syntaxonomy. *Tuexenia* 33, 309–346.
- Pharo, E., Beattie, A.J., 1997. Bryophyte and lichen diversity: a comparative study. *Aust. J. Ecol.* 22, 151–162.
- Pykälä, J., Luoto, M., Heikkinen, R.K., Kontula, T., 2005. Plant species richness and persistence of rare plants in abandoned semi-natural grasslands in northern Europe. *Basic Appl. Ecol.* 6, 25–33.
- R Development Core Team, 2010. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna.
- Reed, R.A., Peet, R.K., Palmer, M.W., White, P.S., 1993. Scale dependence of vegetation–environment correlations: a case study of a North Carolina piedmont woodland. *J. Veg. Sci.* 4, 329–340.
- Reitalu, T., Purschke, O., Johansson, L.J., Hall, K., Sykes, M.T., Prentice, H.C., 2012. Responses of grassland species richness to local and landscape factors depend on spatial scale and habitat specialisation. *J. Veg. Sci.* 23, 41–51.
- Reitalu, T., Helm, A., Pärtel, M., Bengtsson, K., Gerhold, P., Rosén, E., Takkis, K., Znamenskiy, S., Prentice, H.C., 2014. Determinants of fine-scale plant diversity in dry calcareous grasslands within the Baltic Sea region. *Agric. Ecosyst. Environ.* 182, 59–68.
- Ripley, B., Venables, B., Hornik, K., Gebjardt, A., Firth, D., 2012. *Support Functions and Datasets for Venables and Ripley's MASS*. Package MASS. (<http://cran.r-project.org/web/packages/MASS/index.html>).
- Rozbrojová, Z., Hájek, M., Hájek, O., 2010. Vegetation diversity of mesic meadows and pastures in the West Carpathians. *Preslia* 82, 307–332.
- Ruprecht, E., 2006. Successfully recovered grassland: a promising example from Romanian old-fields. *Restor. Ecol.* 14, 473–480.
- Ruprecht, E., Enyedi, M.Z., Eckstein, R.L., Donath, T.W., 2010. Restorative removal of plant litter and vegetation 40 years after abandonment enhances re-emergence of steppe grassland vegetation. *Biol. Conserv.* 143, 449–456.
- Schmiedel, U., Dengler, J., Luther-Mosebach, J., Gröngroft, A., Mucche, G., Petersen, A., Strohbach, B.J., Jürgens, N., 2010. Patterns and dynamics of vascular plant diversity along the BIOTA transects in southern Africa. In: Schmiedel, U., Jürgens, N. (Eds.), *Biodiversity in Southern Africa. Volume 2: Patterns and Processes at Regional Scale*. Klaus Hess, Göttingen, pp. 118–135.
- Schuster, B., Diekmann, M., 2003. Changes in species density along the soil pH gradient—evidence from German plant communities. *Folia Geobot.* 38, 367–379.
- Shmida, A., Wilson, M.V., 1985. Biological determinants of species diversity. *J. Biogeogr.* 12, 1–20.
- Siefert, A., Ravenscroft, C., Althoff, D., Alvarez-Yépez, J.C., Carter, E.C., Glennon, K.L., Heberling, J.M., Jo, I.S., Pontes, A., Sauer, A., Willis, A., Fridley, J.D., 2012. Scale dependence of vegetation–environment relationships: a meta-analysis of multivariate data. *J. Veg. Sci.* 23, 942–951.
- Stammel, B., Kiehl, K., Pfadenhauer, J., 2003. Alternative managements on fens: response of vegetation to grazing and mowing. *Appl. Veg. Sci.* 6, 245–254.
- StatSoft Inc., 2011. *STATISTICA. Data Analysis Software System, Version 10* ([www.statsoft.com](http://www.statsoft.com)).
- Tamme, R., Hiiesalu, I., Laanisto, L., Szava-Kovats, R., Pärtel, M., 2010. Environmental heterogeneity, species diversity and co-existence at different spatial scales. *J. Veg. Sci.* 21, 796–801.
- van Elsen, T., 2000. Species diversity as a task for organic agriculture in Europe. *Agric. Ecosyst. Environ.* 77, 101–109.
- Vassilev, K., Pedashenko, H., Nikolov, S.C., Apostolova, I., Dengler, J., 2011. Effect of land abandonment on the vegetation of upland semi-natural grasslands in the Western Balkan Mts, Bulgaria. *Plant Biosyst.* 145, 654–665.
- Veen, P., Jefferison, R., de Smidt, J., van der Straaten, J. (Eds.), 2009. *Grasslands in Europe of High Nature Value*. KNNV Publishing, Zeist.
- Virtanen, R., Crawley, M.J., 2010. Contrasting patterns in bryophyte and vascular plant species richness in relation to elevation, biomass and Soay sheep on St Kilda, Scotland. *Plant Ecol. Divers.* 3, 77–85.
- Wanner, A., Suchrow, S., Kiehl, K., Meyer, W., Pohlmann, N., Stock, M., Jensen, K., 2014. Scale matters: Impact of management on plant species richness and

- vegetation type diversity in Wadden Sea salt marshes. *Agric. Ecosyst. Environ.* 182, 69–79.
- Wellstein, C., Otte, A., Waldhardt, R., 2007. Impact of site and management on the diversity of central European mesic grassland. *Agric. Ecosyst. Environ.* 122, 203–210.
- Wilson, J.B., Peet, R.K., Dengler, J., Pärtel, M., 2012. Plant species richness: the world records. *J. Veg. Sci.* 23, 796–802.
- Zobel, M., 1992. Plant species coexistence—the role of historical, evolutionary and ecological factors. *Oikos* 65, 314–320.

**Electronic Appendix A**

Summary data of environmental variables used to model total, vascular, non-vascular, bryophyte, and lichen species richness at 10 m<sup>2</sup> ( $n = 80$ ). For land-use type, the number of plots in each of the category is given in brackets. SD, standard deviation. When interpreting our results, it is crucial to keep in mind that the environmental predictors were not necessarily obtained at the same spatial scale as the richness values, but usually represent average values for the 10-m<sup>2</sup> plots or, in the case of climatic variables, modelled values for a grid cell of approx. 1 km<sup>2</sup> size.

	Abbreviation	Mean	SD	Minimum	Maximum
Altitude (m a.s.l.)	Alt	484	80	296	692
Inclination (°)	Incl	25	12	0	50
Heat load index	Heat	0.28	0.38	-0.50	1.19
Microrelief (cm)	Rel	8	9	1	50
Humus content (%)	Hum	10.6	5.4	1.1	30.1
pH (H <sub>2</sub> O)	pH	7.6	0.6	6.1	8.4
Clay content (%)	Clay	24.6	11.6	2.5	50.0
Silt content (%)	Silt	59.3	18.2	5.0	77.0
Sand content (%)	Sand	16.0	17.9	4.8	92.5
Litter cover (%)	Litt	24	23	1	90
Stone and rock cover (%)	Stone	3	11	0	70
Annual mean temperature (°C)	Temp	8.5	0.4	7.5	9.6
Maximum temperature of warmest month (°C)	MaxTemp	24.3	0.6	22.6	25.7
Minimum temperature of coldest month (°C)	MinTemp	-7.5	0.7	-8.9	-5.9
Temperature annual range (°C)	TempRange	31.8	0.8	30.0	33.0
Annual precipitation (mm)	Precip	611.3	15.4	582.0	671.0
Land use type	Mown (14), grazed (41), unused (25)				

## **Electronic Appendix B**

Detection of multi-collinearity among predictor variables and overview of those predictors entered into the full models.

First, when multi-collinearity was analyzed for cross-scale models, humus was highly correlated with sand (0.78) and stones (0.73), while the last two were also correlated (0.96). Annual mean temperature had a strong relationship with maximum temperature of the warmest month (0.99), annual temperature range (0.86), and annual precipitation (−0.75). Maximum temperature of the warmest month was highly correlated with annual temperature range (0.89), while minimum temperature of coldest month was negatively related to annual temperature range (−0.77). Therefore, altitude, heat load index, microrelief, humus, pH, clay, silt, annual mean temperature, minimum temperature of coldest month, and land-use type were kept in the full models of total richness across scales.

Secondly, for the taxon-specific richness at 10 m<sup>2</sup>, the *r* correlation coefficient between silt and sand content was −0.80. Annual mean temperature was highly correlated with altitude (−0.78), annual precipitation (−0.82), and maximum temperature of warmest month (0.96), while the latter had a high negative relationship with annual precipitation (−0.79). As a result, heat load index, microrelief, humus, pH, clay, sand, litter, stone, annual mean temperature, minimum temperature of coldest month, temperature annual range, and land-use type were kept in the full models for richness of all groups at 10 m<sup>2</sup>.

We also included the second-order terms for humus content and microrelief since they were significant for nearly all single-parameter models in both analyses presented above.

### Electronic Appendix C

AIC<sub>c</sub>-based model selection for total species richness at 0.0001, 0.001, 0.01, 0.1, 1, 10, and 100 m<sup>2</sup> as well as for *z*-values across all scales (calculated in *S*-space). AIC<sub>c</sub> = Akaike information criterion corrected for small sample sizes; Δ<sub>*i*</sub> = AIC<sub>*c,i*</sub> difference; ER = evidence ratio. All models with Δ<sub>*i*</sub> < 2 are provided. The predictors used in the full model are presented in Electronic Appendices B and D; see Electronic Appendix A for predictor abbreviations.

Variables	Δ <sub><i>i</i></sub>	<i>w<sub>i</sub></i>	ER
<b>0.0001 m<sup>2</sup> (n = 40)</b>			
Hum, Hum <sup>2</sup>	–	0.0157	1.00
Hum, Hum <sup>2</sup> , Litt	0.91	0.0099	1.57
Hum, Hum <sup>2</sup> , Unused vs. Grazed	1.17	0.0087	1.79
Rel <sup>2</sup> , Hum, Hum <sup>2</sup>	1.65	0.0069	2.28
Rel, Hum, Hum <sup>2</sup>	1.77	0.0065	2.42
Hum, Hum <sup>2</sup> , Temp	1.81	0.0063	2.47
<b>0.001 m<sup>2</sup> (n = 40)</b>			
Hum, Hum <sup>2</sup>	–	0.0225	1.00
Rel, Hum, Hum <sup>2</sup>	0.55	0.0171	1.32
Hum, Hum <sup>2</sup> , pH	1.33	0.0116	1.95
Rel <sup>2</sup> , Hum, Hum <sup>2</sup>	1.45	0.0109	2.06
Hum, Hum <sup>2</sup> , Unused vs. Grazed	1.81	0.0091	2.47
Hum, Hum <sup>2</sup> , Mown vs. Grazed	1.86	0.0089	2.53
Hum, Hum <sup>2</sup> , Temp	1.92	0.0086	2.61
Rel, Hum, Hum <sup>2</sup> , pH	1.96	0.0085	2.66
Hum, Hum <sup>2</sup> , Litt	1.98	0.0084	2.70
Alt, Hum, Hum <sup>2</sup>	2.00	0.0083	2.71
Hum, Hum <sup>2</sup> , Clay	2.01	0.0082	2.74
Hum, Hum <sup>2</sup> , Silt	2.31	0.0071	3.18
Heat, Hum, Hum <sup>2</sup>	2.33	0.0070	3.21
Rel, Hum, Hum <sup>2</sup> , Unused vs. Grazed	2.47	0.0065	3.45
Hum, Hum <sup>2</sup> , MinTemp	2.48	0.0065	3.45
<b>0.01 m<sup>2</sup> (n = 40)</b>			
Litt, Hum, Hum <sup>2</sup> , pH	–	0.0165	1.00
Litt, Hum, Hum <sup>2</sup> , Mown vs. Grazed	0.31	0.0141	1.17
Litt, Hum, Hum <sup>2</sup>	0.46	0.0131	1.26
Hum, Hum <sup>2</sup> , pH	0.48	0.0130	1.27
Litt, Hum, Hum <sup>2</sup> , Unused vs. Grazed	0.88	0.0106	1.55
Litt, Hum, Hum <sup>2</sup> , Mown vs. Grazed, Temp	1.54	0.0077	2.16
Litt, Hum, Hum <sup>2</sup> , Temp	1.84	0.0066	2.51
Litt, Hum, Hum <sup>2</sup> , pH	2.00	0.0061	2.72
<b>0.1 m<sup>2</sup> (n = 40)</b>			
Litt, Hum, Hum <sup>2</sup> , Rel, Temp, MinTemp, Mown vs. Grazed	–	0.0539	1.00
Litt, Hum, Hum <sup>2</sup> , Rel <sup>2</sup> , Temp, MinTemp, Mown vs. Grazed	1.14	0.0304	1.77
<b>1 m<sup>2</sup> (n = 40)</b>			
Heat, Rel, Rel <sup>2</sup> , Litt, MinTemp, Mown vs. Grazed	–	0.0204	1.00
Alt, Rel, Hum, Litt, MinTemp, Mown vs. Grazed, Unused vs. Grazed	0.18	0.0186	1.09
Alt, Rel, Hum, Hum <sup>2</sup> , Litt, MinTemp, Mown vs. Grazed	0.53	0.0157	1.30
Alt, MinTemp, Litt, Hum, Rel, Mown vs. Grazed	0.58	0.0153	1.34
Heat, Rel, Rel <sup>2</sup> , Clay, Litt, MinTemp, Mown vs. Grazed	0.75	0.0140	1.46
Alt, Heat, Rel, Litt, MinTemp, Mown vs. Grazed	0.84	0.0134	1.52
Alt, Heat, Rel, Hum, Litt, MinTemp, Mown vs. Grazed	0.87	0.0132	1.54
Alt, Heat, Rel, Litt, MinTemp, Mown vs. Grazed, Unused vs. Grazed	1.06	0.0120	1.70
Heat, Rel, Litt, MinTemp, Mown vs. Grazed	1.16	0.0114	1.79
Alt, Rel, Rel <sup>2</sup> , Hum, Litt, MinTemp, Mown vs. Grazed, Unused vs. Grazed	1.62	0.0091	2.25

<b>Variables</b>	$\Delta_i$	$w_i$	<b>ER</b>
<b>10 m<sup>2</sup> (n = 80)</b>			
Heat, Rel, Rel <sup>2</sup> , Litt, Clay, MinTemp, Mown vs. Grazed	0.00	0.0309	1.00
Alt, Heat, Rel, Rel <sup>2</sup> , Litt, Clay, MinTemp, Mown vs. Grazed	1.09	0.0180	1.72
Heat, Rel, Rel <sup>2</sup> , Litt, MinTemp, Mown vs. Grazed	1.25	0.0165	1.87
Alt, Heat, Litt, MinTemp, Mown vs. Grazed	1.63	0.0137	2.26
Heat, Litt, MinTemp, Mown vs. Grazed	1.68	0.0134	2.31
<b>100 m<sup>2</sup> (n = 20)</b>			
Rel, Rel <sup>2</sup> , MinTemp, Mown vs. Grazed	–	0.1143	1.00
Rel, Rel <sup>2</sup> , MinTempMown vs. Grazed, Unused vs. Grazed	0.40	0.0935	1.22
Rel, Rel <sup>2</sup> , Litt, MinTemp, Mown vs. Grazed	1.28	0.0602	1.90
<b>Total z values</b>			
Heat, Litter, MinTemp	–	0.4561	1.00
Heat, Litter	0.86	0.2965	1.54
Heat, Litter, Altitude, MinTemp	1.22	0.2474	1.84

### Electronic Appendix D

Estimates of the relative importance of predictor variables used for modeling total richness at 0.0001, 0.001, 0.01, 0.1, 1, 10 and 100 m<sup>2</sup> as well as for  $z$ -values across all scales (calculated in  $S$ -space). The presented values are the sums of the Akaike weights across all candidate models where a certain variable occurs. Values higher than 0.5 are in bold.

Diversity parameter	Heat	Rel	Rel <sup>2</sup>	Litt	Hum	Hum <sup>2</sup>	pH	Clay	Silt	Temp	MinTemp	Altitude	Unused vs. Grazed	Mown vs. Grazed
0.0001 m <sup>2</sup> ( $n = 40$ )	0.376	0.237	0.231	0.328	<b>0.704</b>	<b>0.653</b>	0.259	0.258	0.272	0.223	0.203	0.230	0.294	0.277
0.001 m <sup>2</sup> ( $n = 40$ )	0.260	0.357	0.255	0.227	<b>0.969</b>	<b>0.966</b>	0.288	0.264	0.244	0.214	0.203	0.216	0.235	0.239
0.01 m <sup>2</sup> ( $n = 40$ )	0.368	0.240	0.209	<b>0.634</b>	<b>0.828</b>	<b>0.828</b>	0.434	0.192	0.207	0.256	0.200	0.213	0.286	0.375
0.1 m <sup>2</sup> ( $n = 40$ )	0.292	<b>0.504</b>	0.339	<b>1.000</b>	<b>0.885</b>	<b>0.885</b>	0.254	0.186	0.211	0.488	<b>0.517</b>	0.241	0.269	<b>0.960</b>
1 m <sup>2</sup> ( $n = 40$ )	<b>0.608</b>	<b>0.956</b>	0.456	<b>1.000</b>	0.446	0.340	0.209	0.254	0.217	0.293	<b>0.912</b>	<b>0.604</b>	0.390	<b>0.996</b>
10 m <sup>2</sup> ( $n = 40$ )	<b>0.690</b>	<b>0.679</b>	<b>0.503</b>	<b>0.997</b>	0.312	0.264	0.212	0.428	0.189	0.202	<b>0.995</b>	<b>0.661</b>	0.327	<b>1.000</b>
100 m <sup>2</sup> ( $n = 20$ )	0.117	<b>0.906</b>	<b>0.806</b>	0.374	0.138	0.126	0.109	0.119	0.089	0.097	<b>0.979</b>	0.313	0.375	<b>0.999</b>
$z$ -value	<b>0.618</b>	0.200	0.259	<b>0.638</b>	0.229	0.199	0.361	0.148	0.187	0.165	0.416	0.197	0.114	0.125

## Electronic Appendix E

AIC<sub>c</sub>-based model selection for the four species groups ( $n = 80$ ). AIC<sub>c</sub> = Akaike information criterion corrected for small sample sizes;  $\Delta_i = AIC_{c,i}$  difference; ER = evidence ratio. All models with  $\Delta_i < 2$  are presented. The predictors used in the full model are listed in Electronic Appendices B and F; see Electronic Appendix A for predictor abbreviations.

Variables	$\Delta_i$	$w_i$	ER
<b>Total richness</b>			
Heat, Rel, Rel <sup>2</sup> , Clay, TempRange, Unused vs. Grazed	–	0.0052	1.00
Heat, Rel, Rel <sup>2</sup> , TempRange, Unused vs. Grazed	0.04	0.0051	1.02
Heat, Rel, Rel <sup>2</sup> , Litt, Clay, TempRange, Unused vs. Grazed	0.72	0.0036	1.44
Heat, Rel, Rel <sup>2</sup> , Clay, Hum <sup>2</sup> , Sand, TempRange, Unused vs. Grazed	0.81	0.0035	1.50
Heat, Rel, Rel <sup>2</sup> , Hum <sup>2</sup> , TempRange, Unused vs. Grazed	0.84	0.0034	1.52
Heat, Rel, Rel <sup>2</sup> , Hum <sup>2</sup> , Sand, TempRange, Unused vs. Grazed	0.99	0.0032	1.64
Heat, Rel, Rel <sup>2</sup> , Clay, Hum <sup>2</sup> , TempRange, Unused vs. Grazed	1.31	0.0027	1.93
Heat, Rel, Rel <sup>2</sup> , TempRange, Unused vs. Grazed, Mowed vs. Grazed	1.35	0.0027	1.96
Heat, Rel, Rel <sup>2</sup> , Litt, TempRange, Unused vs. Grazed	1.39	0.0026	2.01
Heat, Rel, Rel <sup>2</sup> , Clay, Sand, TempRange, Unused vs. Grazed	1.40	0.0026	2.02
Heat, Rel, Rel <sup>2</sup> , Clay, Temp, TempRange, Unused vs. Grazed	1.44	0.0025	2.05
Heat, Rel, Rel <sup>2</sup> , Clay, TempRange, Unused vs. Grazed, Mowed vs. Grazed	1.46	0.0025	2.08
Heat, Rel, Rel <sup>2</sup> , Clay, MinTemp, TempRange, Unused vs. Grazed	1.46	0.0025	2.08
Heat, Hum <sup>2</sup> , TempRange, Unused vs. Grazed	1.54	0.0024	2.16
Heat, Rel, Rel <sup>2</sup> , Hum, TempRange, Unused vs. Grazed	1.56	0.0024	2.18
Heat, Rel, Rel <sup>2</sup> , Clay, Temp, MinTemp, Unused vs. Grazed	1.64	0.0023	2.27
Heat, Rel, Rel <sup>2</sup> , Clay, Hum, Hum <sup>2</sup> , TempRange, Unused vs. Grazed	1.66	0.0023	2.29
Heat, Rel <sup>2</sup> , TempRange, Unused vs. Grazed	1.90	0.0020	2.59
Heat, Rel, Rel <sup>2</sup> , Sand, TempRange, Unused vs. Grazed	1.92	0.0020	2.62
Heat, Rel <sup>2</sup> , Hum <sup>2</sup> , TempRange, Unused vs. Grazed	1.94	0.0020	2.64
Heat, Rel, Rel <sup>2</sup> , MinTemp, TempRange, Unused vs. Grazed	1.98	0.0019	2.69
Heat, Rel, Rel <sup>2</sup> , Hum, Sand, TempRange, Unused vs. Grazed	1.99	0.0019	2.70
Heat, Rel, Rel <sup>2</sup> , Temp, TempRange, Unused vs. Grazed	1.99	0.0019	2.70
<b>Vascular plant richness</b>			
Heat, Rel, Rel <sup>2</sup> , Clay, TempRange, Unused vs. Grazed	–	0.0100	1.00
Heat, Rel, Rel <sup>2</sup> , TempRange, Unused vs. Grazed	0.10	0.0095	1.05
Heat, Rel, Rel <sup>2</sup> , Clay, Sand, TempRange, Unused vs. Grazed	0.17	0.0092	1.09
Heat, Rel, Rel <sup>2</sup> , Litt, Clay, TempRange, Unused vs. Grazed	0.80	0.0067	1.49
Heat, Rel, Rel <sup>2</sup> , TempRange, Unused vs. Grazed, Mowed vs. Grazed	0.86	0.0065	1.54
Heat, Rel, Rel <sup>2</sup> , Clay, TempRange, Unused vs. Grazed, Mowed vs. Grazed	0.93	0.0063	1.59
Heat, Rel, Rel <sup>2</sup> , Sand, TempRange, Unused vs. Grazed	1.06	0.0059	1.70
Heat, Rel, Rel <sup>2</sup> , Clay, Temp, TempRange, Unused vs. Grazed	1.07	0.0058	1.71
Heat, Rel, Rel <sup>2</sup> , Clay, MinTemp, TempRange, Unused vs. Grazed	1.10	0.0058	1.73
Heat, Rel, Rel <sup>2</sup> , Clay, Temp, MinTemp, Unused vs. Grazed	1.25	0.0054	1.87
Heat, Rel, Rel <sup>2</sup> , Litt, Clay, Sand, TempRange, Unused vs. Grazed	1.27	0.0053	1.89
Heat, Rel, Rel <sup>2</sup> , Stones, Clay, TempRange, Unused vs. Grazed	1.45	0.0048	2.06
Heat, Rel, Rel <sup>2</sup> , Litt, TempRange, Unused vs. Grazed	1.55	0.0046	2.17
Heat, Rel, Rel <sup>2</sup> , Clay, Sand, TempRange, Unused vs. Grazed, Mowed vs. Grazed	1.64	0.0044	2.27
Heat, Rel, Rel <sup>2</sup> , Clay, Hum <sup>2</sup> , Sand, TempRange, Unused vs. Grazed	1.71	0.0042	2.35
Heat, Rel, Rel <sup>2</sup> , MinTemp, TempRange, Unused vs. Grazed	1.80	0.0041	2.46
Heat, Rel, Rel <sup>2</sup> , Stones, TempRange, Unused vs. Grazed	1.81	0.0040	2.47
Heat, Rel, Rel <sup>2</sup> , Litt, Clay, Temp, TempRange, Unused vs. Grazed	1.82	0.0040	2.49
Heat, Rel, Rel <sup>2</sup> , Temp, TempRange, Unused vs. Grazed	1.82	0.0040	2.49
Heat, Rel, Rel <sup>2</sup> , Litt, Clay, MinTemp, TempRange, Unused vs. Grazed	1.83	0.0040	2.49
Heat, Rel, Rel <sup>2</sup> , Temp, MinTemp, Unused vs. Grazed	1.87	0.0039	2.55

Variables	$\Delta_i$	$w_i$	ER
Heat, Rel, Rel <sup>2</sup> , Stones, Litt, Clay, TempRange, Unused vs. Grazed	1.89	0.0039	2.57
Heat, Rel, Rel <sup>2</sup> , Litt, Clay, Temp, MinTemp, Unused vs. Grazed	1.93	0.0038	2.62
<b>Bryophyte richness</b>			
Heat, Stones, Hum, Hum <sup>2</sup>	–	0.0252	1.00
Heat, Rel <sup>2</sup> , Stones, Hum, Hum <sup>2</sup>	0.74	0.0174	1.45
Heat, Rel, Stones, Hum, Hum <sup>2</sup>	1.09	0.0146	1.72
Heat, Stones, Hum, Hum <sup>2</sup> , MinTemp	1.23	0.0136	1.85
Heat, Stones, Hum, Hum <sup>2</sup> , TempRange	1.84	0.0100	2.51
Heat, Litt, Stones, Hum, Hum <sup>2</sup>	1.95	0.0095	2.65
Heat, Rel <sup>2</sup> , Stones, Hum, Hum <sup>2</sup> , MinTemp	1.96	0.0094	2.67
Heat, Stones, Hum, Hum <sup>2</sup> , Unused vs. Grazed	1.97	0.0094	2.67
<b>Lichen richness</b>			
Rel, Rel <sup>2</sup> , Hum, MinTemp	–	0.0048	1.00
Rel, Rel <sup>2</sup> , Clay, Hum, MinTemp	0.60	0.0035	1.35
Rel, Rel <sup>2</sup> , Hum, pH, MinTemp	0.86	0.0031	1.53
Clay, Hum <sup>2</sup> , MinTemp	0.97	0.0029	1.62
Heat, Rel, Rel <sup>2</sup> , Hum, MinTemp	1.10	0.0027	1.73
Rel, Rel <sup>2</sup> , Hum, Hum <sup>2</sup> , MinTemp	1.38	0.0024	2.00
Rel, Rel <sup>2</sup> , Clay, Hum <sup>2</sup> , MinTemp	1.49	0.0023	2.10
Rel, Rel <sup>2</sup> , Clay, Hum, pH, MinTemp	1.68	0.0021	2.32
Heat, Rel, Rel <sup>2</sup> , Clay, Hum, MinTemp	1.69	0.0020	2.33
Rel, Rel <sup>2</sup> , Hum, Temp, TempRange	1.81	0.0019	2.47
Rel, Rel <sup>2</sup> , Litt, Hum, MinTemp	1.83	0.0019	2.49
Rel, Rel <sup>2</sup> , Hum, Sand, MinTemp	1.84	0.0019	2.51
Clay, Hum, MinTemp	1.87	0.0019	2.55
Stones, Hum <sup>2</sup> , MinTemp	1.95	0.0018	2.65

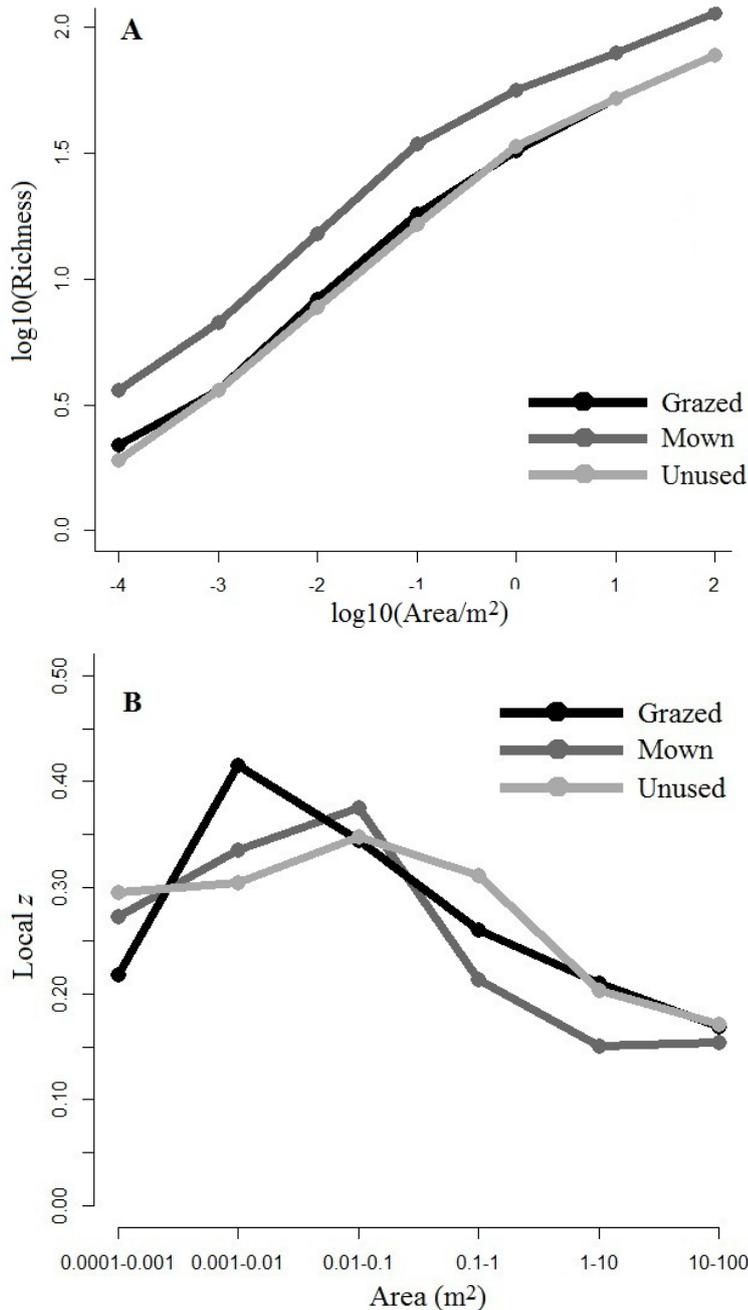
### Electronic Appendix F

Estimates of the relative importance of predictor variables used for modeling total, vascular, bryophyte and lichen species richness at 10 m<sup>2</sup>. Values higher than 0.5 are in bold.

Species group	Heat	Rel	Rel <sup>2</sup>	Litt	Stones	Hum	Hum <sup>2</sup>	pH	Clay	Sand	Temp	MinTemp	TempRange	Unused vs. Grazed	Mown vs. Grazed
All	<b>1.000</b>	<b>0.583</b>	<b>0.695</b>	0.433	0.251	0.369	<b>0.500</b>	0.235	<b>0.502</b>	0.344	0.364	0.430	<b>0.770</b>	<b>0.884</b>	0.389
Vascular plants	<b>1.000</b>	<b>0.780</b>	<b>0.850</b>	0.376	0.366	0.271	0.291	0.225	<b>0.526</b>	0.328	0.354	0.432	<b>0.757</b>	<b>0.904</b>	0.393
Bryophytes	<b>1.000</b>	0.315	0.338	0.260	<b>1.000</b>	<b>0.954</b>	<b>0.959</b>	0.230	0.233	0.236	0.246	0.308	0.266	0.256	0.248
Lichens	0.319	<b>0.546</b>	<b>0.536</b>	0.247	0.400	<b>0.554</b>	<b>0.526</b>	0.332	0.429	0.262	0.326	<b>0.649</b>	0.371	0.312	0.239

### Electronic Appendix G

Visualization of the effect of land use on species-area curves. Displayed are mean values for total richness (A) and local  $z$ -values (B) of nine grazed, six mown and five unused nested-plot series. Note that the high value for mowing at 0.001–0.01 is caused by one mathematically correct but theoretically impossible extreme value (1.114; see Fig. 4 for explanation). If this value were removed from the calculation, the mean value here would be 0.327 instead of 0.415, i.e. actually lower than the value at 0.01–0.1 (0.345).



### Electronic Appendix H

Visualization of the scale-dependence of the power-law  $z$ -values of taxon richness on area in the biodiversity plots ( $n = 20$ ). Displayed are mean values for the “local”  $z$ -values for transitions from one to the next grain size. Since  $z$ -values can only be calculated for transitions where mean richness is  $> 0$  already for both plot sizes of the pair, calculations for bryophytes and lichens were based on a smaller number of replicates or, in the case of lichens, impossible at some smaller scales (i.e. in all nested plot series they had a recorded average richness of 0 species at the smaller scales). For the 0.1–1, 1–10, and 10–100 m<sup>2</sup> transitions, the calculations were based only on  $n = 4–9$  for lichens. The overall  $z$ -values of bryophytes in  $S$ -space with a mean of 0.171 (SD = 0.083) were significantly lower than those of vascular plants with a mean of 0.208 (SD = 0.026), i.e. paired  $t$ -test;  $n = 20$ ;  $p = 0.027$ . The differences between the  $z$ -values of bryophytes and vascular plants were significant at all spatial scales, except the smallest and the largest (0.0001–0.001 m<sup>2</sup>:  $p = 0.076$ ; 0.001–0.01 m<sup>2</sup>:  $p = 0.001$ ; 0.01–0.1 m<sup>2</sup>:  $p = 0.010$ ; 0.1–1 m<sup>2</sup>:  $p = 0.004$ ; 1–10 m<sup>2</sup>:  $p < 0.001$ ; 10–100 m<sup>2</sup>:  $p = 0.135$ ;  $t$ -test).

