Tuexenia 36: 337–358. Göttingen 2016.
doi: 10.14471/2016.36.015, available online at www.tuexenia.de

Diversity and functional composition of alpine grasslands along an elevational transect in the Gran Paradiso National Park (NW Italy)

Diversität und funktionelle Zusammensetzung alpiner Grasländer entlang eines Höhentransektes im Gran Paradiso-Nationalpark (Nordwest-Italien)

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Abstract

Elevational gradients in high mountain ranges are particularly suitable to study and understand patterns and drivers of plant community diversity and composition, yet there are only few studies that explicitly addressed this topic for the European Alps. Here we analysed an elevational gradient in grasslands of the Gran Paradiso National Park (NW Italy) from c. 1,700 to 3,100 m a.s.l. We recorded vascular plant species composition in 13 100-m² plots, each with two series of nested subplots from 0.0001 to 10 m², as well as a set of environmental parameters (topography, soil). Beta-diversity was assessed via the *z*-values of power-law species-area relationships, both across all plot sizes and from one plot size to the next bigger one. Diversity-environment relationships were assessed with multi-model inference based on Akaike information criterion (AIC), while scale dependence in *z*-values across plot sizes was analysed with an ANOVA. Life forms and three major functional traits (specific leaf area = SLA, canopy height, seed mass) were derived from trait databases to calculate fractions of life forms and community-weighted means for the metric traits. Species richness on 100 m² ranged from 17 to 65, with a mean of 43.5. The *z*-values were within a typical range known for European grasslands (mean: 0.227), with non-significant scale dependence. The importance of environmental factors for richness changed across grain sizes, with inclination (positive effect), mean soil depth and soil skeleton content (both: negative effect) being most influential at grain sizes of 0.0001–1 m². By contrast, soil pH was most important (with a unimodal relationship) for 10 and 100 m². After accounting for the other environmental factors, elevation showed a moderate unimodal relationship only for the two largest grain sizes. By contrast, functional composition showed strong and mostly significant relationships with elevation: hemicryptophytes and geophytes became rarer and chamaephytes more frequent, while community-weighted means of SLA, canopy height and seed mass decreased. Our findings highlight the scale dependence of biodiversity patterns, thus pointing to the need of multi-scale sam-

Manuscript received 21 March 2016, accepted 27 April 2016
Co-ordinating Editor: Anikó Csecserits

pling to reach comprehensive understanding. Further, we could provide one of the first documentations of biodiversity and functional composition along an elevational gradient in the Alps, some in agreement with expectations, others not. This suggests that more extensive studies with a similar design in this and other regions of the Alps could be a valuable contribution to the understanding of how environmental factors drive components of biodiversity as well a functional community assembly.

Keywords: alpha-diversity, altitudinal gradient, beta-diversity, biodiversity, community-weighted mean, life form, multi-model inference, nested plot, plant functional trait, species-area relationship (SAR)

Erweiterte deutsche Zusammenfassung am Ende des Artikels

1. Introduction

Elevational gradients have attracted the interest of ecologists and biogeographers for a long time as they show in an exemplary manner how biodiversity responds to a major environmental factor (MACARTHUR 1972, RAHBEK 1995, NOGUÉS-BRAVO et al. 2008, SEIPEL et al. 2012). Among others, an increase in elevation is connected with major changes in climatic conditions, such as temperature and amount of precipitation (RAHBEK 2005), resulting in steep environmental gradients across relatively short distances. This is why elevational gradients have long been taken as a mirror for latitudinal gradients across a much smaller spatial distance (RAHBEK 1995). This extreme environmental variation at short distances makes elevational gradients the perfect "laboratory" to investigate large-scale hypotheses (KÖRNER 2000).

Given that latitudinal diversity gradients are predominantly monotonously decreasing towards the poles (ROSENZWEIG 1995, GASTON & SPICER 2004), one could assume that the same pattern should hold for elevational gradients. Indeed, RAHBEK (1995) in his review on 90 studies found decreasing richness with elevation (either monotonously or first horizontal, then decreasing) in 33 cases. However, he found an even slightly larger number of studies with hump-shaped relationships (36). He further pointed to the fact that finding a monotonous decrease often was connected either to lacking standardisation of area across the altitudinal bands or to cutting off the lower part of the gradient. Therefore, he proposed, based on the existing data and analyses, a unimodal relationship between species richness and elevation with its peak at intermediate elevation as the general model. This hypothesis triggered new studies, further supporting the idea of a hump-shaped relation between species diversity and altitude (e.g. GRYTNES 2003, RAHBEK 2005, BRUUN et al. 2006, MAHDAVI et al. 2013). However, even when using standardised areas and sampling complete gradients, there is no unanimous support of a unimodal relationship, indicating that other environmental factors should be taken into account, too.

One explanation for inconsistent results among richness-elevation studies could be that this relationship is scale-dependent, meaning that it changes its shape when looking at different spatial grain sizes. There are few studies on this topic (e.g. AUSTRHEIM 2002, review in RAHBEK 2005), some of which found scale dependence, others not. The scale dependence of diversity-environment relationships is an old concept in ecology (SHMIDA & WILSON 1985), but only through some recent meta-analyses we know that there is indeed a strong and systematic reversal in prevalence of factors driving biodiversity at different spatial extents and grain sizes (FIELD et al. 2009, SIEFERT et al. 2012). Specifically for plant diversity, SIEFERT et al. (2012) concluded that soil factors are more important at the smallest grain sizes, while climatic variables become more relevant at larger scales. While these two meta-

analyses covered a very broad range of grain sizes (from square metres to thousands of square kilometres), they included only few studies on the smallest grain sizes, such as square centimetres to 100 m². The latter should be most interesting from an ecological point of view because at these scales individuals of different species interact with each other and with their abiotic environment, while the patterns at larger grain sizes could be seen as emergent properties of the patterns at small grain. Recent direct comparisons of different small grain sizes in various types of Palaearctic grasslands have demonstrated that the relative importance of factors strongly changes across grain sizes of that range (TURTUREANU et al. 2014, KUZEMKO et al. 2016, POLYAKOVA et al. 2016) – often, but not always in agreement with the predictions of SHMIDA & WILSON (1985). This calls for more data to reach a more comprehensive understanding.

Another approach to capture the scale dependence of diversity is to characterise species-area relationships (DRAKARE et al. 2006, DENGLER et al. 2009a). Since power laws generally fit species-area relationships well (DENGLER et al. 2009a, TRIANTIS et al. 2012), particularly at small spatial grain sizes (FRIDLEY et al. 2005, DENGLER & BOCH 2008), the exponent z of the power law has become a major descriptor of species-area relationships, which allows comparisons between different ecological situations (DRAKARE et al. 2006, CHIARUCCI et al. 2006). At the same time, z-values are a measure of β-diversity (JURASINSKI et al. 2009, POLYAKOVA et al. 2016). Moreover, "local" z-values allow easy testing whether there is scale dependence in species turnover as found in some studies (CRAWLEY & HARRAL 2001, TURTUREANU et al. 2014), but not in others (KUZEMKO et al. 2016).

One can also describe community composition and diversity in terms of functional aspects. The easiest way are spectra of life forms, which are commonly used in textbooks to represent differences between floras of different parts of the world (e.g. DIERSCHKE 1994), but have hardly been applied to describe systematic changes in community composition along continuous environmental gradients (but see PAVÓN et al. 2000). Closer to ecosystem functioning are plant functional traits (VIOLLE et al. 2007), whereby the three LHS traits – specific leaf area [SLA], canopy height and seed mass – are considered to reflect the main axes of plant strategies particularly well (WESTOBY 1998, MOOG et al. 2005). Stressful or resource-limited environments filter for a certain set of traits (BERNARD-VERDIER et al. 2012), which is specifically true for the changing climatic conditions along elevational gradients. Since special climatic conditions favour special adaption strategies, they thereby favour a certain plant trait (PELLISSIER et al. 2010, DUIVENVOORDEN & CUELLO A. 2012).

Given the high relevance of elevational gradients for understanding plant diversity patterns and community assembly rules, it is astonishing that from the European Alps as one of the otherwise best-studied high mountain ranges so little is known. We are not aware of any study on elevational gradients of plot-scale plant species richness, except for a report from a Swiss biodiversity monitoring scheme (BAFU 2009), which has gone largely unrecognised in the scientific discussion: There the authors could show that in 10-m² grassland plots, randomly distributed across the country, vascular plant species richness strongly increases from the colline (c. 28 species) via the montane (c. 33) to the subalpine belt (c. 44). Analyses of scale-dependent phytodiversity patterns and their drivers, as, for example, AUSTRHEIM (2002) in Norwegian and TURTUREANU et al. (2014) in Romanian semi-natural grasslands, are not known from the Alps, and the understanding of small-scale β-diversity patterns is generally limited. Also the functional aspect of plant community composition along elevation gradients has hardly been studied in the Alps (but see PELLISSIER et al. 2010). The aim of our study thus was to contribute to filling this knowledge gap by studying these aspects

along an elevational gradient in grasslands of the Italian Alps. Specifically, we asked three research questions: (1) Which are the main environmental factors driving species richness at plot scale (with special focus on elevation), and does their importance change across spatial scales? (2) How do species-area relationships of these grasslands behave in terms of potential changes of their slopes (*z*-values) across spatial scales and in relation to environmental parameters? (3) How does the functional composition of the communities change along the elevational gradient?

2. Study area

Our study was conducted in the northern part of the Gran Paradiso National Park, in the SW part of the European Alps, politically belonging to the autonomous Italian Region of Aosta Valley. The sampling in this study took place in the Valnontey Valley on the mainly eastern facing slope reaching from the village of Valnontey at 1,666 m a.s.l. up to the Col Lauson at 3,299 m a.s.l. (45.58° N, 7.31° E; Fig. 1).

While the bottom of the Aosta valley at 480–720 m a.s.l. is one of the driest regions in the entire Alps with only 490–550 mm of mean annual precipitation, the precipitation increases slightly with elevation, reaching about 700 mm in Cogne (1,550 m a.s.l.), just below our study transect (BRAUN-BLANQUET 1961). At the elevation of our study sites, one can assume similar values as for the Gran Cot meteorological station, located about 4 km to the east at 2,279 m a.s.l., with 670 mm mean annual precipitation and 1.1 °C mean annual temperature (LO RUSSO et al. 2013). The geology of the bedrock is diverse and varies locally: although the escarpment is mainly dominated by calcitic rocks, gneiss as well as diabase and amphibolite can also be encountered (DI PASQUALE 1961).

While the lower altitudes are dominated by forests with interspersed semi-natural, mostly dry grasslands, above 2,200 m a.s.l., the landscape is mainly characterised by alpine grasslands, rocks and ravines. Above roughly 2,700 m a.s.l., the vegetation is sparse, and loose gravel and rocks become the dominant elements of the landscape.

The vegetation in the park is partly influenced by past and present human activity: Even within the borders of the national park, low-intensity grazing by sheep is maintained in some areas, and some forests are managed. Numerous hiking paths and tourists that can be encountered up to the Refugio Vittorio Sella at 2,585 m a.s.l. provide evidence of human influence. Beyond the Refugio, the area is populated by herds of ibex (*Capra ibex*) as well as other alpine mammals. The ibex was also the main reason for the establishment of the National Park in 1922 as the first in Italy and the second in the entire Alps (BIBELRIETHER & SCHREIBER 1989).

3. Methods

3.1 Field sampling

In order to stratify the field sampling according to the main gradient, we divided the sampled slope into seven elevational belts of 200 m, between c. 1,700 and c. 3,100 m a.s.l. In each of these belts, we localised two sampling sites that met specific criteria: we avoided wetlands, rock outcrops, forest, screes and areas with high human influence and positioned the sampling sites in a minimum distance of 10 m to such regions. As only one suitable site could be identified for the belt of 1,700–1,900 m a.s.l., 13 instead of 14 sites were sampled in total, from the valley bottom of Valnontey up to

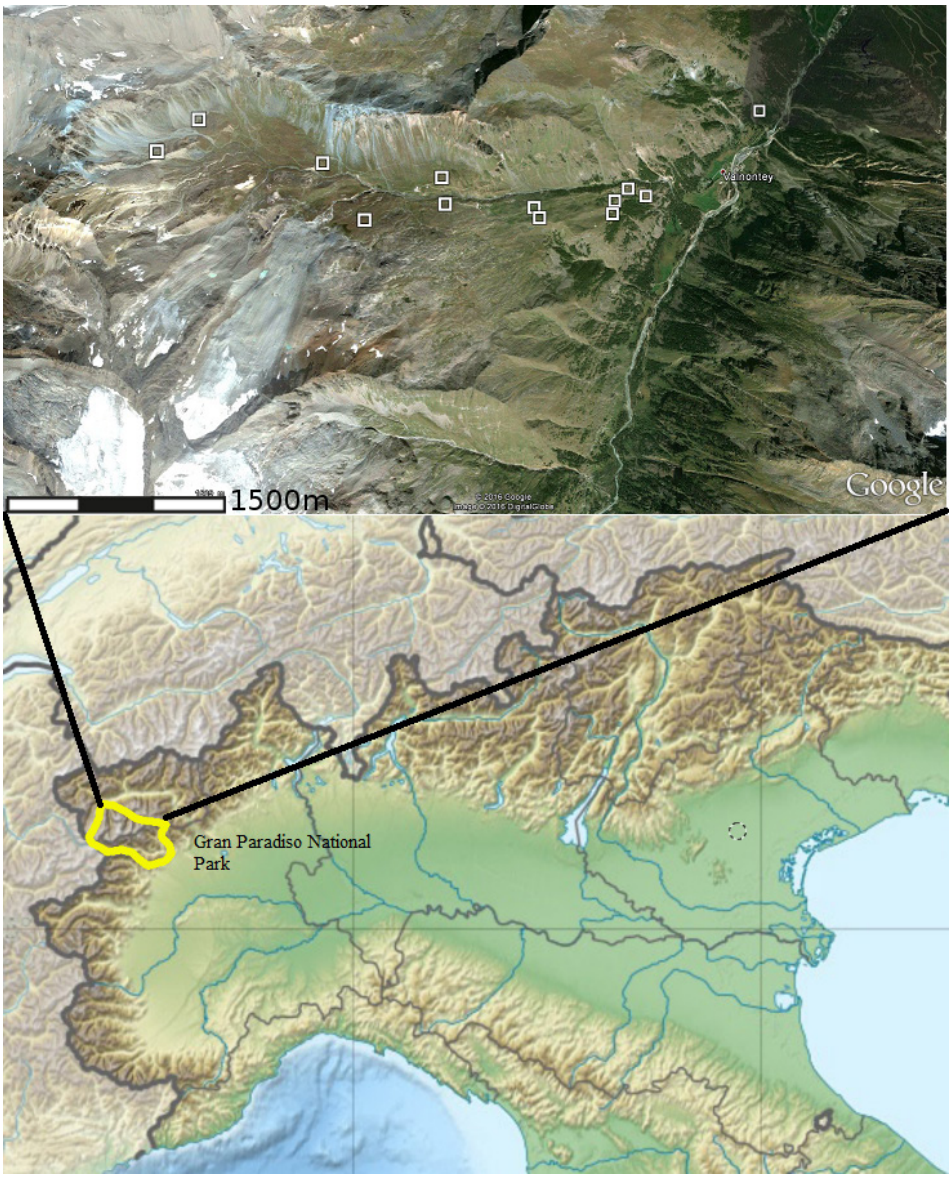


Fig. 1. Map of the study area, located in the Gran Paradiso National Park in NW Italy. The white squares indicate the location of the100-m² plots, each containing two nested-plot series of smaller plots (Satellite image: Google Earth).

Abb. 1. Karte des Untersuchungsgebiets, dem Gran Paradiso Nationalpark in NW-Italien. Die weißen Quadrate zeigen die Lage der 100-m² Plots, welche jeweils zwei ineinander geschachtelte Plotserien enthalten (Satellitenbild: Google Earth).

the Col Lauson. Syntaxonomically, the subalpine stands mainly belonged to the class *Festuco-Brometea*, while the alpine stands were distributed between three grassland classes (*Elyno-Seslerietea albicantis*, *Caricetea curvulae*, *Molinio-Arrhenathertea*: *Poion alpinae*), with transitions towards *Thlaspietea rotundifolii* and *Salicetea herbaceae* (syntaxonomy according to THEURILLAT et al. 1995).

At each site we delimited a square-shaped 100-m² plot, which was then sampled with the nested-plot design of DENGLER (2009b) in the variant of TURTUREANU et al. (2014). This means that in two opposite corners of the 100-m² plot, nested series of square-shaped subplots of the sizes 0.0001 m², 0.001 m², 0.01 m², 0.1 m², 1 m² and 10 m² were placed and sampled (Fig. 2). Coordinates and elevation of each 100-m² plot were determined with a handheld GPS (global positioning system) device, and the four corners were marked for potential future revisiting studies by inserting magnets into the soil.

In the 100-m² plot as well as in each subplot, we recorded all vascular plant species present, following the any-part-system (= shoot presence; see DENGLER 2008). For each 10-m² plot, we also recorded the following structural and environmental variables: cover of the herb layer, average height of the herb layer, maximum height of the herb layer, litter cover, slope inclination, slope aspect (transformed for further analyses into the southing component = -cos (angle)), microrelief (maximum deviation of the soil surface from an idealised plane cutting through the plot), soil depth (determined with a pointed iron pole). Furthermore, we took a mixed soil sample from the top 10 cm in several random locations within the 10-m² subplots, which was then air-dried for further analyses. In the laboratory, pH (in aqua dest.), C and N content (with a C/N analyser) and skeleton content (mass fraction of particles > 2 mm) were determined. Table 1 provides descriptive statistics of all structural and environmental parameters.

3.2 Statistical analyses

The statistical analyses were performed within the R software environment (R CORE TEAM 2015). Residuals were visually inspected for approximate normal distribution and homoscedasticity (QUINN & KEOUGH 2002), and since no serious deviations were detected, we applied parametric tests on non-transformed data.

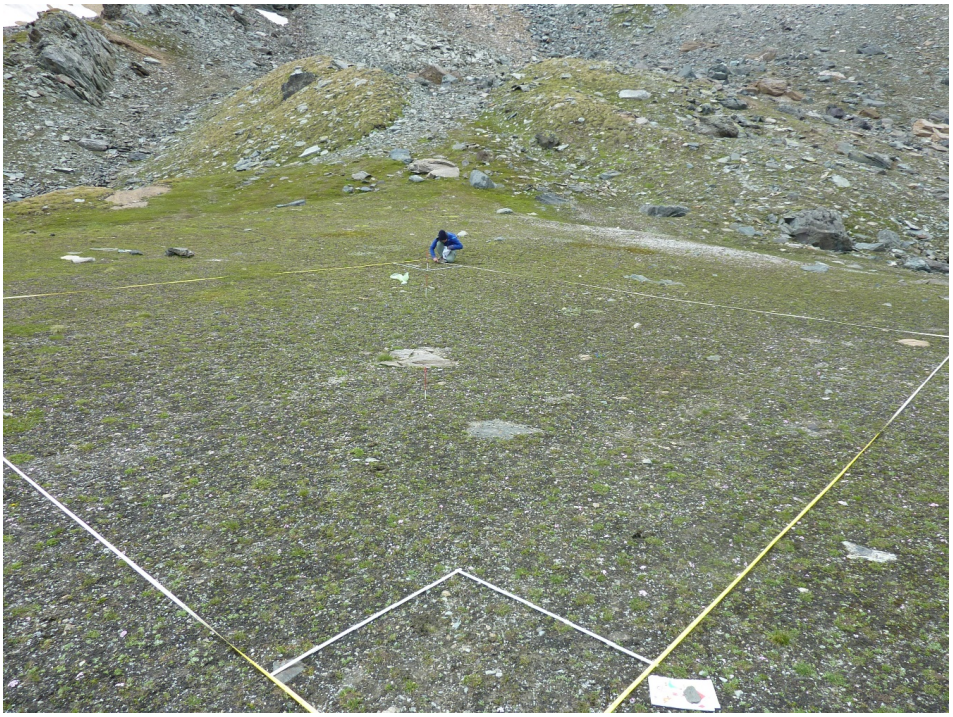


Fig. 2. The field sampling of a plot at 3,022 m a.s.l. (Photo: F. Weiser, 16 August 2014).

Abb. 2. Datenaufnahme für einen Plot auf 3.022 m ü. NN (Foto: F. Weiser, 16.08.2014).

3.2.1 Species-area relationships

Species-area relationships (SARs) were fitted using the power-law function $S = c\,A^z$, where S is the number of species, A the plot area, and c and z are two fitted parameters. This model has been proven to give good model fits, especially for small plot sizes (e.g. DENGLER 2009a). We calculated overall z-values for each 100 m² plot by fitting linear regressions to the data in double-log space (i.e. $\log S = \log c + z \log A$). We used the exponent z as a measure of β-diversity (JURASINSKI et al. 2009), which is particularly useful as it standardises multiplicative β-diversity by the ratio of the grain sizes used for α- and γ-diversity (POLYAKOVA et al. 2016). For the smaller grain sizes, we used the arithmetic mean of the richness of the two corners, and in the one case where the smallest subplots in both corners were void of vascular plant species, we assumed a value of 0.125 to allow the calculation of the logarithm. The use of 0.125 is based on the view that the calculated mean richness values are estimates for the true mean richness values, which must always be > 0. With two replicates, the estimated (calculated) mean richness values can be 0, 0.5, 1 etc., which represent the ranges]0, 0.25[, [0.25, 0.75[, [0.75, 1.25[etc. and thus the range mid-points 0.125, 0.5, 1 etc. This rationale (SCHMIEDEL et al. 2012) avoids an arbitrary transformation of all values, such as log (x + 1) or log (x + 0.00001), which is frequently used, but also strongly criticised (WILSON 2007).

Additionally, we assessed the scale dependence of z-values by calculating within each 100 m² plot for each transition between two subsequent plot sizes the local slope, which in our case simply was $z_{A\text{-}10A} = \log_{10} S_{10A} - \log_{10} S_A$ (see TURTUREANU et al. 2014). We then subjected these data to a repeated-measures analysis of variance (ANOVA) to test whether the local z-value changed across these grain-size transitions.

3.2.2 Diversity-environment relationships

Diversity-environment relationships were assessed for a total of eight biodiversity measures: We used species richness at the seven grain sizes of 0.0001 to 100 m² as measure of α-diversity and the overall z-values as measure of β-diversity. We had 26 replicates for α at the smaller grain sizes and 13 for α at 100 m² and for β.

For the environmental predictors of Table 1 (except for the four last, which were considered as structural parameters of the vegetation), we tested for multi-collinearity by using pairwise Pearson correlations. Two parameters were considered to be collinear if $|r| > 0.8$. In such cases we kept the predictor we thought to be ecologically more meaningful or more widely used in comparable studies. Therefore, we kept pH, which was highly negatively correlated with C/N, and carbon content, which was highly positively correlated with nitrogen content (Table 2). Additionally, we included squared terms of elevation and pH because richness has often been shown to be unimodally related to these parameters.

For each of the eight diversity measures, we calculated generalised linear models with Poisson error distribution. To test the model assumptions, we examined the data for overdispersion by estimating a dispersion parameter using the *AER* package in R (KLEIBER & ZEILEIS 2008). Additionally, we tested for autocorrelation between the 10-m² subplots as our units with the least spatial distance to each other. The applied Moran's I test within the *spdep* package (BIVAND et al. 2013, BIVAND & PIRAS 2015) revealed no spatial autocorrelation in the final models.

We assessed the diversity-environment relationship in the multimodel inference framework (BURNHAM & ANDERSSON 2002), as implemented in the *MuMIn* package for R (version 1.15.1; BARTOŃ 2015). Using the *dredge* function, all possible predictor combinations were tested, and each of the resulting many models assessed using the Akaike information criterion for small n (AICc; BURNHAM & ANDERSSON 2002). Each model was then weighted with its Akaike weight, which describes its probability of being the best model within the set of compared models (JOHNSON & OMLAND 2004). Summing the Akaike weights of all models containing a particular predictor gives the importance value of this predictor, ranging from 0 to 1.

With *MuMIn* we also derived an averaged model (JOHNSON & OMLAND 2004). From this we extracted the signs of the parameters. Furthermore, we calculated McFadden's pseudo R^2 with the *pscl* package for R (JACKMAN 2015). Finally, we graphically visualised the direction of the impact of the pairs of the most influential parameters for some of the biodiversity measures with the package *visreg* as 3D plots (BREHENY & BURCHETT 2016).

Table 1. Mean, standard deviation (SD), minimum and maximum of environmental and structural parameters for the 26 10-m² plots.

Tabelle 1. Mittelwert, Standardabweichung (SD), Minima und Maxima der Umwelt- und Strukturparameter der 26 10-m²-Aufnahmeflächen.

	Mean	SD	Minimum	Maximum
Elevation [m a.s.l.]	2435	363	1737	3022
Inclination [°]	19.3	10.2	0.0	38.0
Southing	-0.24	0.81	-1.00	0.92
Mean microrelief [cm]	5.0	2.8	1.4	13.2
Mean soil depth [cm]	22.1	11.5	10.0	50.6
Skeleton content [%]	14.0	8.4	2.0	37.0
Soil reaction (pH)	4.92	0.68	3.73	6.41
N [%]	0.40	0.17	0.07	0.70
C [%]	4.67	2.14	0.69	8.44
C/N	11.5	1.1	9.0	13.2
Cover herb layer [%]	80.6	22.0	30.0	100.0
Average height herb layer [cm]	14.8	10.2	2.0	40.0
Maximum height herb layer [cm]	46.5	29.0	4.0	101.0
Litter cover [%]	17.2	25.1	0.0	90.0

Table 2. Correlation matrix of the predictor variables. Correlations with $|r| > 0.8$ are indicated in bold. The parameters in italics were not considered in the multiple regressions because of high collinearity with another variable.

Tabelle 2. Korrelationsmatrix der Umweltvariablen. Korrelationen mit $|r| > 0.8$ sind in Fettdruck hervorgehoben. Die kursiv gesetzten Variablen wurden in den multiplen Regressionen wegen hoher Kollinearität mit einer anderen Variable nicht berücksichtigt.

	Altitude [m]	Inclination [°]	Maximum microrelief [cm]	Mean soild epth [cm]	Skeleton content [%]	pH	N [%]	C [%]	C/N
Inclination [°]	-0.75	–	–	–	–	–	–	–	–
Maximum microrelief [cm]	-0.09	0.27	–	–	–	–	–	–	–
Mean soil depth [cm]	0.37	-0.51	-0.35	–	–	–	–	–	–
Skeleton content [%]	-0.30	0.06	-0.12	0.40	–	–	–	–	–
pH	0.17	-0.44	-0.40	0.65	0.26	–	–	–	–
N [%]	*-0.47*	*0.51*	*0.15*	*-0.63*	*-0.15*	*-0.65*	–	–	–
C [%]	-0.39	0.50	0.19	-0.67	-0.22	-0.72	***0.98***	–	–
C/N	*-0.09*	*0.49*	*0.39*	*-0.69*	*-0.38*	***-0.81***	*0.53*	*0.65*	–
Southing	-0.40	0.36	-0.20	-0.26	-0.04	0.11	*0.28*	0.17	*-0.20*

3.2.3 Functional composition

We characterised the plants in the plots functionally according to their Raunkiaer life form and the three LHS traits (specific leaf area [SLA], canopy height and seed mass), which are considered to be particularly important to characterise different functional dimensions (WESTOBY 1998). We could derive the data for most of the species from the LEDA (KLEYER et al. 2008) and BiolFlor (KLOTZ et al. 2002) databases. When LEDA provided different values for one species, we used their arithmetic mean for the further analyses. Seed mass and life form were completely taken from BiolFlor. Due to extremely skewed distributions, we used log-transformed values for canopy height and seed mass as usually done (WESTOBY 1998).

Life forms were analysed by calculating the fraction of the five main life forms (phanerophytes, chamaephytes, hemicryptophytes, geophytes and therophytes) presence/absence-based for the 13 100-m² plots. In the case of the LHS traits, we calculated community-weighted means (CWMs) for the 26 10-m² plots for which we had cover data. Data of LHS traits were available for species accounting for approx. 75% of all cover and life forms for species accounting for 92% of all occurrences. The fraction data of the five life forms as well as the CWMs of the LHS traits were then subjected to linear regressions against elevation.

4. Results

4.1 Diversity and species-area relationships

Mean species richness (shoot presence) of vascular plants ranged from 2.1 species on 1 cm² (0.0001 m²) via 18.7 species on 1 m² to 43.5 species on 100 m² (Table 3). At all spatial scales, there was considerable variation between plots, e.g. 0–5 species on 1 cm² and 17–65 species on 100 m². While the standard deviation of richness increased considerably with grain size, the coefficient of variation decreased slightly, from c. 57% at 1 cm² to 36% at 100 m².

The overall *z*-values of the power-law species-area relationships ranged from 0.183 to 0.315 in the 13 100-m² plots, with a mean of 0.227 (Table 3). The local *z*-values showed more variation and a slight, but insignificant peaked at the transition from 0.01 to 0.1 m² (Fig. 3).

Table 3. Descriptive statistics of vascular plant diversity found in the plots. Given are the species richness of plot sizes from 0.0001 to 100 m² (as measures of α-diversity) and the total *z*-values (as measure of β-diversity).

Tabelle 3. Deskriptive Statistik der Gefäßpflanzendiversität in den Aufnahmeflächen. Angegeben sind der Artenreichtum für Flächengrößen von 0,0001 bis 100 m² (als Maß für α-Diversität) und die Gesamt-*z*-Werte (als Maß für β-Diversität).

Biodiversity measure	Minimum	Maximum	Mean	SD
0.0001-m² richness	0	5	2.1	1.2
0.001-m² richness	0	6	3.7	1.5
0.01-m² richness	1	12	6.2	2.8
0.1-m² richness	1	23	12.2	5.7
1-m² richness	4	29	18.7	6.8
10-m² richness	9	42	28.0	9.7
100-m² richness	17	65	43.5	15.7
Total *z*-value	0.183	0.315	0.227	0.036

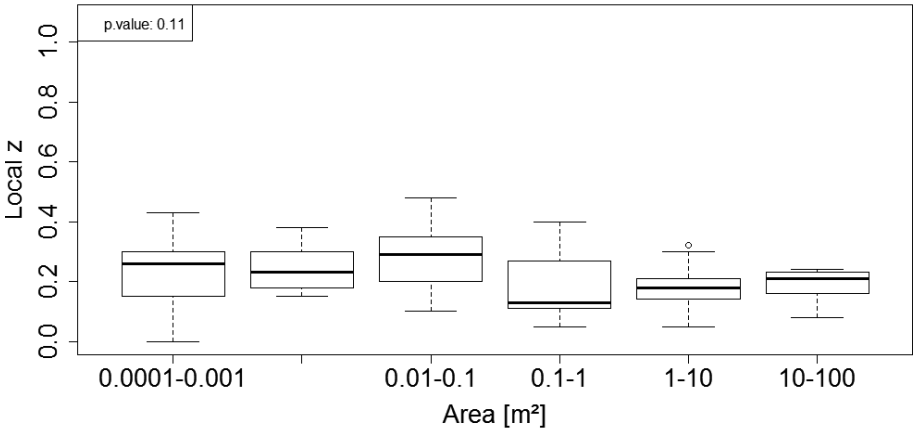


Fig. 3. Scale dependence of the *z*-values (slope of the power-law species-area relationship in the log-log representation). Local *z*-values refer to the transition from one plot size to the next larger plot size.

Abb. 3. Skalenabhängigkeit der *z*-Werte (Steigung der Potenzfunktion der Artenzahl-Areal-Beziehung in der doppellogarithmischen Darstellung). Die lokalen *z*-Werte beziehen sich auf den Übergang von der kleineren zur nächstgrößeren Plotgröße.

4.2 Diversity-environment relationships

The α-diversity was influenced by different environmental parameters at different spatial scales. The most relevant parameters across the scales were inclination, mean soil depth, pH and skeleton content (Table 4): Inclination had a positive relationship at all scales, but was most influential at 1 and 10 m². Mean soil depth influenced species richness always negatively, with strongest effects between 0.001 and 1 m². Species richness showed a unimodal relationship to soil reaction at the grain sizes from 0.1 to 100 m², but particularly at the two largest plot sizes. Skeleton content had a negative effect, which was most pronounced at 0.01 to 0.1 m². All other variables never exceeded 50% variable importance. Of these, elevation tended to have a unimodal relationship at the coarser grain sizes and southing a positive relationship at the smaller grain sizes, whereas carbon (humus) content and microrelief did not have a clear directional effect at any grain size. For some of the plot sizes, we visualise the trend surfaces of the relationships regarding the main environmental drivers in Figure 4. The explanatory power of the models was low for the four smallest grain sizes with a McFadden's pseudo-R^2 of only about 10%, but then continuously increased with grain size to reach about 45% at the 100-m² scale (Fig. 5).

While the α-diversities were well explained by the measured environmental parameters, this was not the case for the *z*-values (β-diversity), where no predictor had more than 22% of importance and McFadden's pseudo-R^2 was close to zero (Fig. 5).

4.3 Functional composition

Among the life forms, hemicryptophytes prevailed in all plots with about 40–80% of all species, followed by chamaephytes, while none of the other three life forms ever contributed more than 10% to the vascular plant species richness. Three life forms showed a significant dependence on elevation (Fig. 6): hemicryptophytes and geophytes decreased, while chamaephytes increased their relative importance.

Table 4. Variable importance based on multi-model inference for the species richness of plot sizes from 0.0001 to 100 m² (as measures of α-diversity) and the total z-values (as measure of β-diversity). Importance values range from 0 to 1, the latter meaning that the respective variable is included in all statistically relevant models; values above 0.5 are hightlighted in bold. The symbol ↑ (grey) indicates a positive relationship, the symbol ↓ (white) a negative relationship; a "↓" for the squared terms of elevation or pH indicates unimodal relationships.

Tabelle 4. Variablenbedeutung (*variable importance*) für die Artenzahlen der Plotgrößen zwischen 0,0001 m² und 100 m² (als Maßen der α-Diversität) und der z-Werte (als Maß der β-Diversität) basierend auf *multi-model inference*. Die Variablenbedeutung kann Werte zwischen 0 und 1 annehmen, wobei 1 bedeutet, dass der jeweilige Parameter in allen statistisch relevanten Modellen enthalten ist. Werte über 0,5 sind durch Fettdruck hervorgehoben. Das Symbol ↑ (grau) weist auf einen positiven, das Symbol ↓ (weiß) auf einen negativen Einfluss hin; ein „↓" bei den quadratischen Termen weist auf eine unimodale Beziehung hin.

Biodiversity measure	0.0001	0.001	0.01	0.1	1	10	100	Total z
Elevation [m a.s.l.]	0.32 ↓	0.21 ↓	0.31 ↓	0.22 ↑	0.21 ↓	0.35 ↑	0.42 ↑	0.15 ↑
Elevation [m a.s.l.]^2	0.33 ↓	0.21 ↓	0.32 ↓	0.23 ↑	0.21 ↓	0.36 ↓	0.44 ↓	0.15 ↑
Carbon content [%]	0.23 ↑	0.21 ↓	0.21 ↑	0.20 ↓	0.22 ↓	0.18 ↑	0.09 ↑	0.15 ↓
Inclination [°]	**0.50** ↑	0.24 ↑	0.28 ↑	**0.52** ↑	**0.93** ↑	**0.98** ↑	0.17 ↑	0.15 ↓
Max. microrelief [cm]	0.25 ↓	0.19 ↓	0.20 ↓	0.18 ↓	0.23 ↓	0.31 ↓	0.17 ↑	0.16 ↓
Mean soil depth [cm]	0.29 ↓	**0.85** ↓	**0.58** ↓	**0.70** ↓	**0.68** ↓	0.33 ↓	0.20 ↓	0.17 ↑
pH	0.21 ↓	0.20 ↑	0.23 ↑	0.26 ↑	0.33 ↑	**0.70** ↑	**0.77** ↑	0.22 ↑
pH^2	0.22 ↓	0.21 ↑	0.23 ↑	0.26 ↓	0.33 ↓	**0.68** ↓	**0.74** ↓	0.22 ↑
Skeleton content [%]	0.40 ↓	0.27 ↓	**0.64** ↓	**0.57** ↓	0.20 ↓	0.17 ↓	0.08 ↑	0.19 ↑
Southing	0.24 ↑	0.24 ↑	0.41 ↑	0.28 ↑	0.32 ↑	0.19 ↓	0.10 ↓	0.16 ↓

The CWMs of specific leaf area (SLA) ranged from about 12 to 24 mm²/mg and exhibited a slight non-significant decreasing trend with elevation (Fig. 7a). By contrast, for both canopy height and seed mass, elevation exerted a strong and highly significant negative effect on the CWMs (Fig. 7b–c).

5. Discussion

5.1 Diversity of the studied grasslands in comparison with other studies

When comparing our mean vascular plant species richness values to those of (dry) grasslands across the Palaearctic sampled with the same methodology (Table 3 in KUZEMKO et al. 2016), they are similar for the two smallest grain sizes, but show more and more negative deviations for the larger grain sizes. With a mean of 18.7 species on 1 m², the grasslands of the Gran Paradiso National Park are poorer than any of the six regions compiled by KUZEMKO et al. (2016) and have only about 50% of the mean richness found in the most diverse grasslands of Transylvania (DENGLER et al. 2012). At the 10-m² and 100-m² scale, the ratio is slightly higher with 56% and 52%, respectively. The relationship between the maximum values from our study and the maximum values found anywhere else in Palaearctic grasslands (WILSON et al. 2012, CHYTRÝ et al. 2015, KUZEMKO et al. 2016) shows a similar pattern: While at 1 cm² our five species are close to the known world record of seven species in

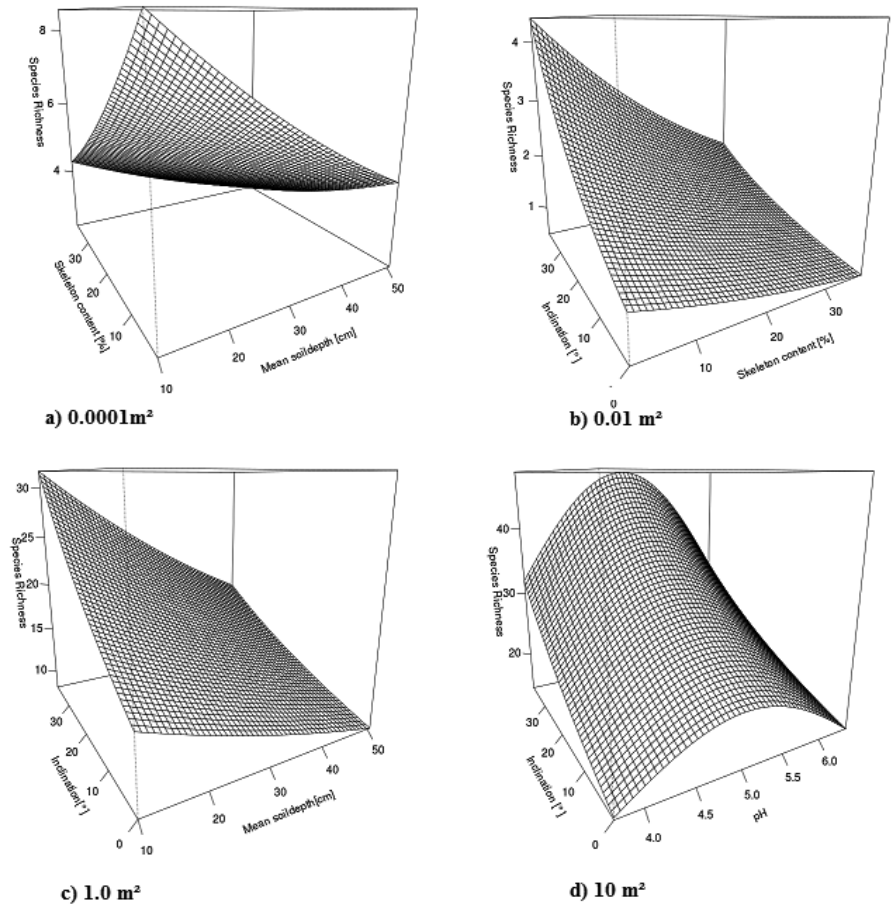


Fig. 4. Visualisation of the effect of main environmental factors on vascular plant species richness via response surfaces at four different grain sizes.

Abb. 4. Darstellung der Effekte einiger besonders einflussreicher Faktoren auf die Artenzahl der Gefäßpflanzen anhand von 3D-Grafiken für vier verschiedenen Plotgrößen.

Ukrainian steppic grasslands (KUZEMKO et al. 2016), our maxima fall off more and more compared to the Palaearctic records with increasing grain size. For example, at 100 m² our maximum of 65 species is only 49% of the maximum known from the White Carpathians in the Czech Republic (CHYTRÝ et al. 2015).

The *z*-values as measures of multiplicative *β*-diversity were within the typical range reported for a wide variety of dry grasslands in Europe (DENGLER 2005). Similar to TURTUREANU et al. (2014) and POLYAKOVA et al. (2016), we found the species-area relationship to be steepest around 0.01–0.1 m², though insignificantly so in our case. However, it is currently not well understood why in some cases species-area relationships have a clear scale dependence at these small scales (CRAWLEY & HARRAL 2001), but not in others (DENGLER & BOCH 2008, KUZEMKO et al. 2016).

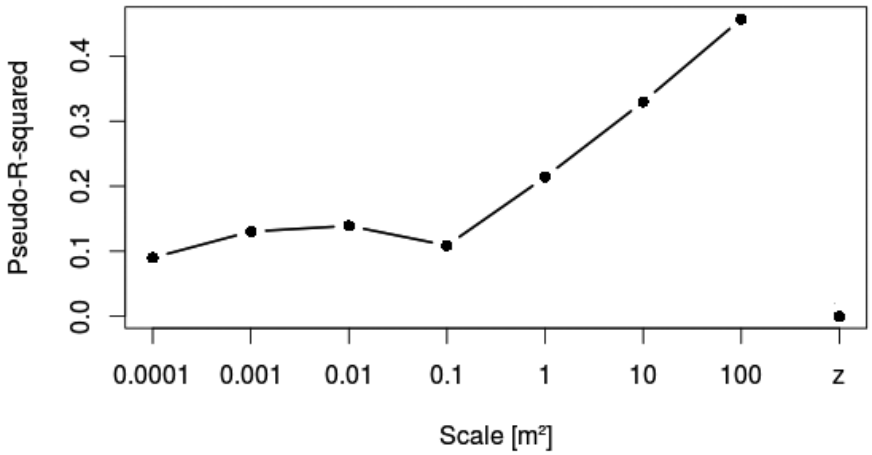


Fig. 5. Explanatory power of the multiple regression models for the α-diversity (species richness) at seven grain sizes and the β-diversity (z-value) expressed as McFadden's pseudo-R^2. Note that McFadden's pseudo-R^2 cannot directly be compared with conventional R^2-values as they tend to be lower.

Abb. 5. Erklärungskraft der multiplen Regressionsmodelle für die α-Diversität (Artenreichtum) auf sieben Skalengrößen und für die β-Diversität (z-Wert) ausgedrückt durch McFaddens Pseudo-R^2. Pseudo-R^2-Werte können nicht direkt mit dem herkömmlichen R^2-Werten verglichen werden, da erstere tendenziell niedriger sind.

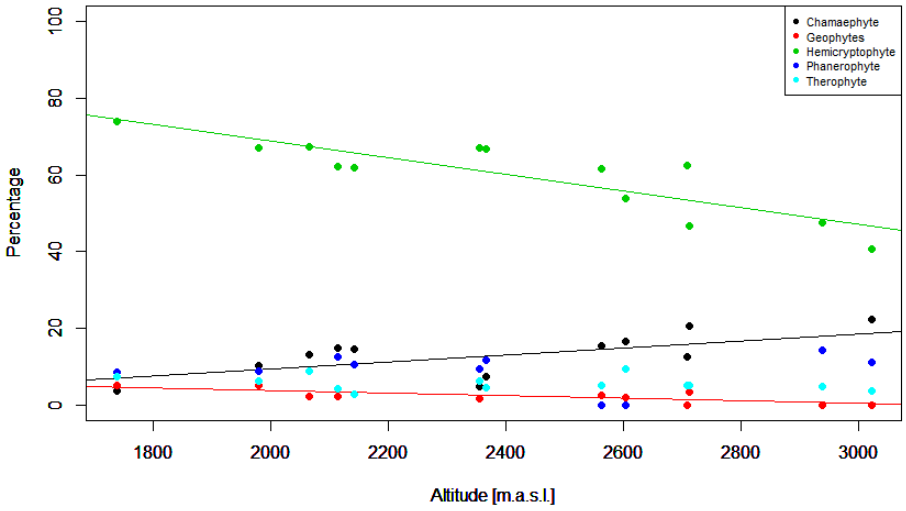


Fig. 6. Fractions of different life forms in the 100-m^2 plots (based on presence/absence) and their dependence on elevation. Linear regression lines are plotted when this relationship was significant (chamaephytes: $p = 0.016$, $R^2 = 0.37$; geophytes: $p = 0.004$, $R^2 = 0.50$; hemicryptophytes: $p < 0.001$; $R^2 = 0.72$).

Abb. 6. Anteile der verschiedenen Lebensformen der 100 m²-Plots (auf Präsenz/Absenz basierend) und deren Abhängigkeit von der Meereshöhe. Eine lineare Regressionslinie wurde gezogen, wenn eine signifikante Beziehung vorlag (Chamaephyten: $p = 0{,}016$; $R^2 = 0{,}37$; Geophyten: $p = 0{,}004$; $R^2 = 0{,}50$; Hemikryptophyten: $p < 0{,}001$; $R^2 = 0{,}72$).

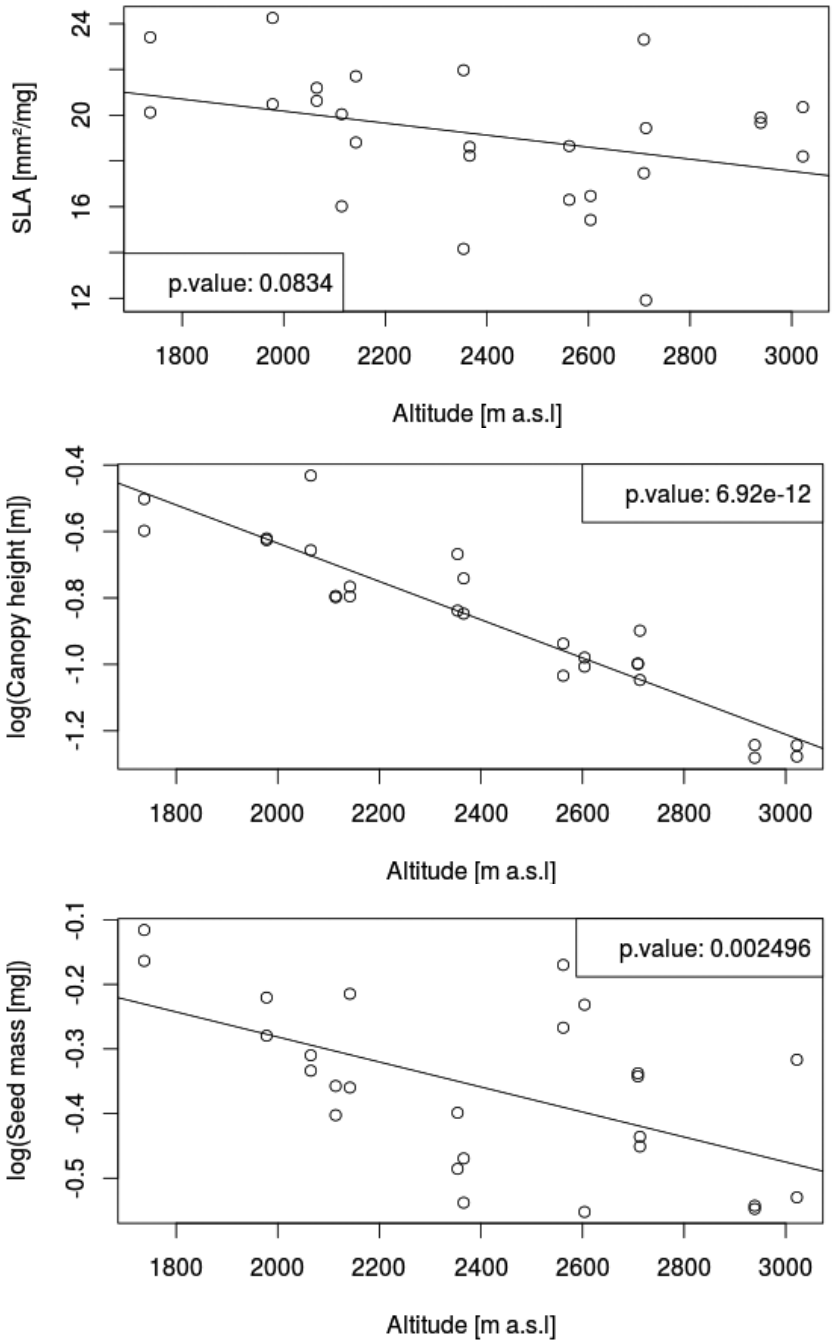


Fig. 7. Community-weighted means of the "Westoby traits" L (specific leaf area, SLA; R^2 = 0.08), H (canopy height; R^2 = 0.86) and S (seed mass; R^2 = 0.29) and their relation to elevation assessed with linear regression.

Abb. 7. Lineare Beziehung der gewichtete Mittelwerte der sogenannten "Westoby-Traits" L (spezifische Blattfläche, SLA; R^2 = 0,08), H (Wuchshöhe; R^2 = 0,45) und S (Samengewicht; R^2 = 0,59) zur Meereshöhe.

5.2 Diversity-environment relationships

Regarding the relevance of environmental parameters for vascular plant diversity, our results do not coincide well with the expectations. Based on the study of BAFU (2009) for grasslands in Switzerland, we would have expected an increase in species richness with elevation at least up to the upper end of the subalpine zone, with a slight decrease in the highest elevations. However, such a unimodal relationship (in accordance with the theory of RAHBEK 2005) was only found for the two largest grain sizes (10 and 100 m²) and had only about 40% importance after accounting for the other factors. Based on many previous studies, one would further expect a strong (typically increasing or unimodal) effect of soil pH on plot-scale plant species richness (e.g. SCHUSTER & DIEKMANN 2003), but in our case such a clear unimodal relationship was evident only for the two largest grain sizes (with 70–80% importance). Interestingly, we found three other variables to play the major role for diversity patterns at grain sizes of 0.0001–1 (–10) m², which we had not expected: inclination (positive for the whole range), mean soil depth and skeleton content (both negative for the middle part of this grain size range). These findings are not easily explained: Inclination might increase heterogeneity and thus the number of available niches, while habitats with deep soils provide a more homogenous environment with fewer niches. It might also be relevant that due to our relatively small plot number, inclination was not fully independent of elevation, but with r = -0.75 just below our threshold for $|r|$. This means that by chance at higher elevation we generally had flatter slopes. Thus, the seemingly positive effect of inclination on plant diversity might actually at least partly be a negative effect of elevation.

Our results generally agree with the notion that the relative importance of environmental factors on biodiversity patterns change with grain size as has been theoretically postulated (SHMIDA & WILSON 1985) and found in a few meta-analyses (e.g. FIELD et al. 2009, SIEFERT et al. 2012) as well as some multi-grain studies like ours (TURTUREANU et al. 2014, KUZEMKO et al. 2016, POLYAKOVA et al. 2016). As expected (SIEFERT et al. 2012), soil parameters, such as inclination, soil depth and skeleton content, were more influential at smaller grain sizes, while climate (in our case represented only by elevation) played at least some role only at the two largest grain sizes. By contrast, it was rather unexpected that another soil parameter, namely soil reaction, also was influential only at these relatively large grain sizes. The recorded increase of explanatory power of our diversity-environment relationships with spatial grain size matches the findings of KUZEMKO et al. (2016) and POLYAKOVA et al. (2016). Reasons might be that at the smallest scales, biotic rather than abiotic factors drive biodiversity. Moreover, the spatial mismatch of our environmental parameters (recorded at 10 m²) with the richness counts might have contributed to the low explanatory power; however, from 10 to 100 m², explanatory power increased, casting doubt on this explanation. In conclusion, our findings indicate that more studies with a rigorous sampling design are needed to fully understand the scale dependence of diversity-environment relationships.

5.3 Functional aspects of community assembly

While life form spectra are often used in text books to illustrate differences between main biomes of the Earth or among vegetation types in one region (DIERSCHKE 1994, RICHTER 2001), they have rarely been used along continuous environmental gradients such as elevation. One example is the study of MAHDAVI et al. (2013) along an elevational gradient in steppic grasslands of Iran. They found that from 1,000 to 4,000 m a.s.l., both hemicryptophyte and chamaephyte fraction increased monotonously, while therophytes decreased in

importance and geophytes showed a unimodal relationship with a peak between 2,500 and 3,300 m a.s.l. We also found a significant increase of chamaephyte fraction with elevation, which indicates that this life form might be advantageous at high elevation, independent of the climate characteristics. By contrast, hemicryptophytes show contrasting patterns in the Iranian mountains (increasing with elevation) and the Alps (decreasing). The reason could be that due to the much more pronounced summer drought in the lower elevations of the Iranian mountains (even in comparison to a relatively dry region in the Alps), hemicryptophytes are replaced by therophytes, reaching nearly 70% at 1,000 m a.s.l. In consequence, in Iran the successive replacement of therophytes by hemicrytophytes dominates the overall pattern rather than the replacement of hemicryptophytes by chamaephytes as in the Alps. With regard to the Alps, we are only aware of the coarse description of the situation in a valley of Ticino, Switzerland (DIERSCHKE 1994: Fig. 32), where the elevational gradient is shown in four zones and where, in agreement with our study, an increase of chamaephytes with elevation occurred, while a parallel decrease in hemicryptophytes was not visible.

Community-weighted means (CWMs) of traits are a valuable tool to characterise the response of plant community composition to environmental gradients, which has only just started to be explored (e.g. SHIPLEY 2010, BERNARD-VERDIER et al. 2012, PURSCHKE et al. 2015). Among eight tested traits, BERNARD-VERDIER et al. (2012) found that SLA, seed mass and plant height (in their case reproductive height vs. canopy height in ours) were among those that corresponded strongest with decreasing values to decreasing soil depth in Mediterranean grasslands. We found a similar and strong decline with elevation, indicating that very different types of environmental harshness (shallow soil = shortage of water and nutrients vs. high elevation = low temperature and short vegetation period) can have similar effects on community assembly. A decrease in plant height with elevation can be interpreted as a direct consequence of shorter vegetation periods, i.e. less time to build up plant organs, but also an adaptation because the higher the elevation the more dangerous it is to have organs that stick out of the snow in winter and then are exposed to extremely low temperatures without isolating snow. Lower SLA at higher elevation means that the leaves have more structural elements per unit area, making them more robust. This is particularly relevant for evergreen leaves of chamaephytes, whose fraction increases with elevation. Last but not least, the decrease in mean seed mass with increasing elevation is not so easily explained. One could assume that larger seeds (which store more resources for the seedling) would be a better strategy to ensure establishment under harsh conditions. However, both increasing harshness of the environment in Alpine grasslands and decreasing soil depth in Mediterranean rangelands are likely associated with an increased patchiness of the environment, with many patches not suitable at all. Under such circumstances, having only few large seeds might be more risky than having more but smaller seeds – because the higher the number of seeds, the higher the chance that at least some reach suitable microsites.

Erweiterte deutsche Zusammenfassung

Einleitung - Höhengradienten stehen schon seit langem im Fokus von Biogeographen und Ökologen da sie beispielhaft dafür stehen, wie Biodiversität auf einen einflussreichen Umweltfaktor reagiert (MACARTHUR 1972, RAHBEK 1995, NOGUÉS-BRAVO et al. 2008, SEIPEL et al. 2012). Neben monoton abnehmenden werden oft auch unimodale Beziehungen zwischen Meereshöhe und Artenzahl gefunden (RAHBEK 1995). Ein Grund hierfür ist die Skalenabhängigkeit der Artenzahl-Höhen Beziehung. Dass Biodiversitäts-Umweltbeziehungen von der betrachteten Skalengröße abhängen, ist ein bekanntes Prinzip in der Ökologie (SHMIDA & WILSON 1985, SIEFERT et al. 2012). Für Aufnahmeflächengrößen

zwischen 1 cm² und 100 m² wurde jüngst für verschiedene paläarktische Grasländern eine systematische Änderung der Bedeutung verschiedenen Faktorengruppen für die Ausprägung von Diversitätsmustern bestätigt (TURTUREANU et al. 2014, KUZEMKO et al. 2016, POLYAKOVA et al. 2016). Die Ergebnisse standen aber nicht immer im Einklang mit den Vorhersagen von SHMIDA & WILSON (1985), so dass weitere Daten benötigt werden, um die Zusammenhänge besser zu verstehen. Eine andere Möglichkeit die Skalenabhängigkeit der Diversität zu charakterisieren sind Artenzahl-Areal- Beziehungen (DRAKARE et al. 2006, DENGLER et al. 2009a). Diese werden meist gut über eine Potenzfunktion ($S = c\ A^z$, S = Artenzahl, A = Fläche, c und z = gefittete Parameter) beschrieben. Deren Exponent z ist ein Maß für multiplikative β-Diversität (JURASINSKI et al. 2009) und erlaubt es, zwischen unterschiedlichen ökologischen Situationen zu vergleichen (CHIARUCCI et al. 2006, DRAKARE et al. 2006). Diversität und Zusammensetzung von Pflanzengesellschaften können auch mit funktionellem Fokus beschrieben werden. Dies geschieht meist über die Lebensformen oder aber funktionellen Eigenschaften der Pflanzen (*plant functional traits*), wobei spezifische Blattfläche, Wuchshöhe und Samengewicht die drei Merkmale darstellen, welche die Lebensstrategie der Pflanze am besten widerspiegeln (WESTOBY 1998, MOOG et al. 2005). Je nach den anzutreffenden Umweltbedingungen verfolgen Pflanzen unterschiedliche Strategien und weisen zudem eine bestimmtes Kombination an Merkmalen auf (PELLISSIER et al. 2010, DUIVENVOORDEN & CUELLO A. 2012). Obwohl Höhengradienten besonders geeignet sind, den Zusammenhang von verschiedenen Aspekten der Diversität und Zusammensetzung von Pflanzengesellschaften und Umweltbedingungen zu analysieren, gibt es dazu kaum systematische Publikationen aus den europäischen Alpen. In unserer Arbeit untersuchen wir daher funktionelle Merkmale, Artenzahl-Areal- und Artenzahl-Umwelt-Beziehungen in Grasländern der italienischen Alpen, wobei drei Fragen im Vordergrund stehen: (1) Welche Umweltbedingungen sind entscheidend für die Artenzahl und wie ändert sich ihr Einfluss mit der Aufnahmeflächengröße? (2) Ist die Artenzahl-Areal-Beziehung selbst skalenabhängig? (3) Wie ändert sich die funktionelle Zusammensetzung der Gesellschaften entlang des Höhengradienten?

Methoden − Die Daten unserer Studie wurden im italienischen Gran Paradiso Nationalpark(Südwest-Alpen) erhoben. Das beprobte Transekt verlief an einem Osthang des Tales von Valnontey, einem Seitental des Aostatals mit einem mittleren Jahresniederschlag von etwa 700 mm und einer Jahresmitteltemperatur von 1,1 °C. Die Aufnahmeflächen lagen entlang eines Höhengradienten von 1.666 m ü. NN bis hinauf zum Col Lauson auf 3.299 m ü. NN (45,58° N, 7,31° E; Abb. 1). Die lokale Geologie wird von Kalkstein bestimmt, aber auch Diabas und Amphibolit kommen vor. Bis zu einer Höhe von 2.200 m ü. NN besteht die Vegetation hauptsächlich aus Wäldern, unterbrochen von halbnatürlichen Grasländern. Oberhalb schließen sich alpine Grasländer und Schuttfluren an, während sich oberhalb von 2.700 m ü. NN die geschlossene Vegetationsdecke auflöst.

Das Transekt wurde in sieben Höhenabschnitte von je 200 m unterteilt mit dem Ziel, für jeden derselben zwei Aufnahmeflächen von je 100 m² („Biodiversitäts-Plot“) anzulegen. Durch eine Vielzahl an Ausschlusskriterien (z. B. anthropogen beeinflusste Gebiete, Wälder, Feuchtgebiete) konnte auf 1.700−1.900 m ü. NN nur eine Fläche beprobt werden, was zu einer Gesamtzahl von 13 Biodiversitäts-Plots führte. Deren Design folgte DENGLERs (2009b) Vorschlag in der Variante von TURTUREANU at al. (2014): an zwei gegenüberliegenden Ecken jedes 100 m²-Plots wurde eine Reihe von ineinander geschachtelten Teilplots der Größen 0,0001 m², 0,001 m², 0.01 m², 0.1 m², 1 m² und 10 m² angelegt. Für Plots aller Größen wurden die vorkommenden Gefäßpflanzen mit der *shoot presence*-Methode aufgenommen. Auf den 26 10 m²-Plots wurde zusätzlich der Deckungsgrad der Arten in % geschätzt und verschiedene Umwelt- und Standortfaktoren aufgenommen, sowie eine Mischprobe der ersten 10 cm des Bodens an verschiedenen Stellen im Plot genommen, welche im Labor untersucht wurde (Tab. 1).

Die Art-Areal Beziehungen wurden mittels der z-Werte des Potenzgesetzes über den ganzen Aufnahmeflächenbereich analysiert. Ferner wurden innerhalb jedes 100 m²-Plots zwischen den aufeinanderfolgenden Plotgrößen die lokale Steigung im doppellogarithmischen Raum, also ein „lokaler“ z-Wert berechnet (vgl. TURTUREANU et al. 2014). Um die Skalenabhängigkeit dieser lokalen z-Werte zu analysieren, wurden sie einer Varianzanalyse (ANOVA; „mit Messwiederholung“) unterworfen.

Bei die Analyse der Diversität-Umwelt-Beziehungen betrachteten wir die Artenzahlen der sieben Plotgrößen (0.0001 m² – 100 m²) als Maßen von α- Diversität und die z-Werte als Maß der multiplikativen β-Diversität. Die Umweltparameter wurden auf Kollinearität untersucht und bei hochkorrelierten Paaren ($|r| > 0.8$) wurde der Parameter behalten, welcher ökologisch relevanter erschien. Dann wurden für jedes der acht Biodiversitätsmaße generalisierte lineare Modelle sämtlicher Kombinationen der nicht hoch-korrelierten Umweltparameter berechnet. Die Technik der *multi-model inference* erlaubte dann jeweils die „Bedeutung" der Parameter (*variable importance*) zu ermitteln sowie ein „Durchschnitts-Model" und den McFaddens Pseudo-R^2-Wert zu bestimmen. Die einflussreichsten Parameter wurden schlussendlich als 3D-Plots visualisiert.

Schließlich charakterisierten wir die Pflanzen anhand ihrer Raunkiaer-Lebensformen und der drei LHS-Merkmale (spezifische Blattfläche [*specific leaf area*; SLA]; Wuchshöhe der photosynthetisierenden Organe [*canopy height*]; Samengewicht [*seed mass*]). Die Lebensformen analysierten wir, indem wir die Anteile der fünf Hauptlebensformen (Phanerophyten, Chamaephyten, Hemikryptophyten, Geophyten and Therophyten) für die 13 100 m²-Plots berechneten und in eine lineare Beziehung zur Meereshöhe stellten. Für die LHS-Merkmale wurden gewichtete Mittelwerte (*community-weighted means*, CWMs) berechnet, allerdings auf der Flächengröße von 10 m², da hierfür auch artspezifische Deckungsdaten erhoben worden waren. Diese CMWs wurden dann ebenfalls über eine lineare Regression mit der Meereshöhe analysiert.

Ergebnisse − Bei der Untersuchung der Artenvielfalt-Areal-Beziehung variierte die Artenzahl und die *z*-Werte über alle Plotgrößen hinweg stark. Die Details sind in Tabelle 3 und Abbildung 3 ersichtlich. Die Umweltfaktoren, welche die α- Diversität am meisten beeinflussten, waren Hangneigung (positiv), mittlere Bodentiefe (negativ), pH-Wert (unimodal) und Skelettanteil im Boden (negativ). Die auf den Umweltfaktoren basierenden Modelle erklärten auf den vier kleinen Skalengrößen nur einen geringen Anteil der Varianz (Pseudo-R^2-Werte von nur rund 10 %), doch stieg die Erklärungskraft bis auf 45 % (100 m²) an. Für die *z*-Werte zeigte kein Umweltparameter einen nennenswerten Einfluss. Die Analyse zur funktionellen Zusammensetzung zeigte für drei der fünf Lebensformen einen signifikanten Zusammenhang mit der Meereshöhe, wobei Hemikryptophyten in allen Plots mit einem Anteil von 40−80% die dominierende Lebensform waren. Hemikryptophyten und Geophyten zeigten mit der Meereshöhe eine signifikante Abnahme, während die Chamaephyten zunahmen. Die gewichteten Mittelwerte für zwei der drei LHS-Merkmal (Samengewicht und Wuchshöhe) wiesen eine stark negative Beziehung zur Meereshöhe auf, während SLA eine marginal signifikante, leichte Abnahme zeigte (Abb. 7).

Diskussion − Im Vergleich zu besonders artenreichen Kalkhalbtrockenrasen der Paläarktis sind die Plots im Gran Paradiso Nationalpark insgesamt artenärmer. Das Ergebnis zur Skalenabhängigkeit der *z*-Werte hingegen entspricht dem ähnlicher Studien, wenn es auch nicht signifikant ist (u. a. POLYAKOVA et al. 2016). Unsere Ergebnisse zur den Diversität-Umweltbeziehungen sind unerwartet im Vergleich mit anderen Studien. So war eine unimodale Beziehung zwischen der Artenzahl und der Höhe nur auf den beiden größten Flächengrößen zu beobachten. Überhaupt zeigte der Höhengradient nur relativ wenig Einfluss auf die Artenzahl (maximal 40 % Variablenbedeutung). Auch der pH-Wert, welcher in anderen Untersuchungen einen starken Einfluss auf die Artenzahl zeigte, hat in unseren Analysen nur einen signifikanten, unimodalen Einfluss auf den beiden größten Plotgrößen. Unerwarteterweise stellten stattdessen die mittlere Bodentiefe, Hangneigung und Skelettanteil drei besonders einflussreiche Variablen dar. Es kann allerdings nicht ausgeschlossen werden, dass der ermittelte positive Effekt der Hangneigung auf die Artenzahl teilweise einen negativen Effekt der Meereshöhe repräsentieren könnte, da durch Zufall die Plots in höheren Lagen weniger steil waren. Trotzdem ist ein positiver Einfluss der Hangneigung ökologisch erklärbar, da durch erhöhtes Gefälle die Habitatheterogenität erhöht wird und somit die Anzahl der verfügbaren Nischen steigt. Standorte mit tiefgründigem Boden hingegen bieten homogenere Bedingungen und somit weniger verfügbare Nischen. Unsere Ergebnisse bestätigen, dass auf kleineren Plotgrößen der Einfluss von Bodenparametern bedeutend ist (vgl. SIEFERT et al. 2012), während auf großen Skalen klimatische Faktoren (hier repräsentiert durch die Meereshöhe) eine größere Rolle spielen. Übereinstimmend mit anderen Studien (KUZEMKO et al. 2016,

POLYAKOVA et al. 2016) stieg das Erklärungspotential der Umweltparameter mit zunehmender Korngröße. Grund hierfür könnte sein, dass auf kleinen Plotgrößen biotische Faktoren einen größeren Einfluss haben, während auf größeren Plotgrößen die abiotischen Faktoren bedeutsamer werden.

Die Ergebnisse der Lebensformanalysen stehen grundsätzlich im Einklang mit dem viel gröberen Lehrbuchwissen zu Lebensformspektren verschiedener Floren (DIERSCHKE 1994). Eine kontinuierliche Zunahme der Chamaephyten mit der Höhe wurde auch im Elbrus-Gebirge im Nord-Iran gefunden (MAHDAVI et al. 2013). Unsere Ergebnisse bezüglich der LHS-Merkmale stehen im Einklang mit den Ergebnissen anderer Untersuchungen entlang anderer Umweltgradienten. Die allgemeine Abnahme der Wuchshöhe kann als Reaktion auf die kürzere Vegetationsperiode und die harscheren Umweltbedingungen mit zunehmender Höhe interpretiert werden. Die mit steigender Höhe robustere Pflanzenstruktur zeigt sich in der abnehmenden spezifischen Blattfläche. Die Abnahme des Samengewichts entlang des Höhengradienten ist kontraintuitiv. Zu erwarten wäre ein zunehmendes Samengewicht um die Keimungschance in der alpinen Zone zu steigern. Die vorgefundenen Werte legen nahe, dass eine andere Strategie, etwa die größtmögliche Streuung um einen geeigneten Standort zu erreichen, zu Tragen kommt.

Acknowledgements

The study was jointly planned by all authors, while field sampling was conducted by E.B. and F.W. as part of their Bachelor theses in Geoecology at the University of Bayreuth, in the framework of the ECOPOTENTIAL project (http://www.ecopotential-project.eu). The data were then re-analysed by the two for this paper under the supervision of J.D., while the manuscript was drafted by E.B., F.W. and J.D. and critically revised by all authors.

We are grateful to Carl Beierkuhnlein for contributing to the initial discussion of the study design and providing various support during the field campaign. We thank the Parco Nazionale Gran Paradiso for allowing us to conduct our research there and especially Roberto Cristofori for the permission to sleep in the mountain huts of the park rangers. Achaz von Hardenberg and Ramona Viterbi kindly provided us with permits and local support. Christine Pilsl, Eva Strätz and Reinhold Stahlmann equipped us with tools, instruments and maps, while Marga Wartinger conducted the soil analyses in the lab. Finally we thank Anikó Csecserits and two anonymous reviewers for a fast and thorough peer review and Aiko Huckauf for linguistic editing.

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Zeitschrift/Journal: Tuexenia - Mitteilungen der Floristisch-soziologischen Arbeitsgemeinschaft

Jahr/Year: 2016

Band/Volume: NS_36

Autor(en)/Author(s): Baumann Esther, Weiser Frank, Chiarucci Alessandro, Jentsch Anke, Dengler Jürgen

Artikel/Article: Diversity and functional composition of alpine grasslands along an elevational transect in the Gran Paradiso National Park (NW Italy) 337-358