



# Scale-dependent patterns and drivers of vascular plant, bryophyte and lichen diversity in dry grasslands of the Swiss inneralpine valleys

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## Abstract

The inner-alpine dry valleys of the Swiss Alps are characterized by subcontinental climate, leading to many peculiarities in dry grassland species composition. Despite their well-known uniqueness, comprehensive studies on biodiversity patterns of the dry grasslands in these valleys were still missing. To close this gap, we sampled 161 10-m<sup>2</sup> vegetation plots in the Rhône, Rhine and Inn valleys, recording vascular plants, terricolous bryophyte and lichen species, as well as environmental data. Additionally, we tested the scale-dependence of environmental drivers using 34 nested-plot series with seven grain sizes (0.0001–100 m<sup>2</sup>). We analysed the effects of environmental drivers related to productivity/stress, disturbance and within-plot heterogeneity on species richness. Mean species richness ranged from 2.3 species in 0.0001 m<sup>2</sup> to 58.8 species in 100 m<sup>2</sup>. For all taxa combined, the most relevant drivers at the grain size of 10 m<sup>2</sup> were southing (negative), litter (negative), mean annual precipitation (unimodal), gravel cover (negative), inclination (unimodal) and mean annual precipitation (unimodal). For vascular plants the pattern was similar, while bryophyte and lichen richness differed by the opposite relationship to mean annual precipitation as well as negative influences of mean herb layer height, grazing and mowing. The explained variance of the multiple regression model increased with grain size, with very low values for the smallest two grain sizes. While southing and litter had high importance for the five larger grain sizes, pH and gravel cover were particularly important at the intermediate grain sizes, and inclination and mean annual precipitation for the two largest grain sizes. The findings emphasize the importance of taxonomic group and grain size for patterns and drivers of species richness in vegetation, consistent with ecological theory. Differences in the diversity–environment relationships among the three taxonomic groups can partly be explained by asymmetric competition that leads to low bryophyte and lichen diversity where vascular plants do well and vice versa. The relatively low alpha diversity of vascular plants in dry grasslands in Swiss inner-alpine valleys compared to similar communities in other parts of the Palaearctic remains puzzling, especially because Swiss stands are often large and well-preserved.

**Keywords** Biodiversity · Bryophyte · Dry grassland · Lichen · Scale dependence · Vascular plant

## Introduction

The xerothermic vegetation of the central valleys of the Alps has long attracted the interest of botanists (Christ 1879; Braun-Blanquet and Richard 1950; Braun-Blanquet 1961; Schwabe and Kratochwil 2004; Dengler et al. 2019b). The macroclimate of these valleys strongly deviates from their

surroundings, as they are situated between the barriers of high mountain systems which largely block rain-carrying clouds. These valleys, therefore, constitute dry islands within the generally precipitation-rich European Alps. Together with the partly very low valley bottoms (sometimes only a few hundred metres above sea level), this leads to a relatively warm and dry climate, in strong contrast to the surrounding mountains (Braun-Blanquet 1961; Dengler et al. 2020c).

The climate, topography and isolated position lead to many peculiarities in flora and vegetation, partly resembling

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the Eastern European steppe vegetation. Apart from xerothermic forests and shrublands, different types of dry grasslands are a dominating feature of these landscapes (Braun-Blanquet 1961). These dry grasslands comprise diverse vegetation types, some growing on rocky outcrops with very shallow soils, others on slightly deeper soils. Below the alpine zone, most of these dry grasslands belong to semi-natural grasslands originating from centuries of low-intensity agriculture. Natural grasslands are rare and restricted to sites where forest growth is limited by particular soil or topographic conditions, e.g. rocky slopes with skeletal soils (Braun-Blanquet 1961; Boch et al. 2020; Dengler et al. 2020c). In the central valleys of the Alps, widespread Central European dry grassland species meet with steppic species whose main distribution is in the central part of Eurasia. In addition, dealpine, submediterranean and Southwest European xerothermic species occur together with a few narrow endemics of the Alps (Becherer 1972; Wohlgemuth 1996; Dengler et al. 2019a).

While dry grasslands in most other parts of Europe have been intensively studied during recent decades with respect to biodiversity, ecology and conservation (see reviews by Dengler et al. 2014; 2020c, Dengler and Tischew 2018; Boch et al. 2020), comprehensive studies on diversity patterns in dry grasslands along environmental gradients from the Swiss Rhône, Rhine and Inn valleys are missing (but see Boch et al. 2019a, 2021; Dengler et al. 2019b). Older literature mainly focussed on vegetation classification and the floristic and ecological characterization of dry grasslands (e.g. Christ 1879; Frey 1934; Braun-Blanquet 1961; Schwabe and Kratochwil 2004). However, knowledge on the distribution, ecology and biodiversity status of these dry grasslands is critical for developing management and conservation strategies. In Switzerland, this is of particular importance, as dry grasslands are among the most threatened vegetation types (Delarze et al. 2016). It has been estimated that about 95% of the dry grassland area in Switzerland has been lost since 1900, mainly due to land-use intensification or abandonment (Lachat et al. 2010), and habitat quality is still decreasing (Boch et al. 2019b). Consequently, 35% of about 350 dry grassland vascular plant species in Switzerland are currently considered threatened (Bornand et al. 2016).

Species richness in plant communities is controlled by a multitude of drivers (Grace 1999) which act simultaneously. Applying the concepts of Grime (1973), potential drivers can be grouped into those related to the stress–productivity axis and those related to the disturbance axis (Huston 2014), both of which are strongly modified by changing land-use systems and intensity (Allan et al. 2014). Generally, maximum fine-grain richness should be expected at intermediate levels of productivity and disturbance (Grime 1973; Huston 2014). However, what can be considered intermediate productivity depends on the level of disturbance and what

can be considered intermediate disturbance depends on the level of productivity; thus, looking at the variables individually might yield positive, unimodal or negative relationships (Huston 2014). More recently, the heterogeneity of either productivity- or disturbance-related factors became a focus of diversity theory as a variable that nearly universally increases species richness (Tamme et al. 2010; Stein et al. 2014). Previous studies in Palaeartic grasslands found that specific drivers might be particularly relevant in one region but not in others (reviewed by Dengler et al. 2014), thus demonstrating the need to study such relationships in multiple regions and consider a large set of different drivers to achieve a more systematic understanding.

Most of the studies dealing with drivers of species diversity in grasslands focused on vascular plants (see review in Dengler et al. 2014), while the knowledge for bryophytes and lichens is still fragmentary. However, these two taxonomic groups often constitute a large fraction of the overall species diversity in dry grassland vegetation. Particularly in rocky and sandy dry grasslands, the fraction of non-vascular taxa can be substantial, sometimes exceeding the number of vascular plant species (Löbel and Dengler 2008; Dengler et al. 2020b). Some studies found that bryophyte diversity is positively related to vascular plant diversity (Löbel et al. 2006; Müller et al. 2019) and to that of several invertebrate taxa, and even has the strongest relation with the diversity of a wide range of other taxa (“multidiversity”; Manning et al. 2015). However, studies investigating vascular plants, bryophytes and lichens simultaneously are rare (Löbel et al. 2006; Turtureanu et al. 2014; Zulka et al. 2014). This lack of multi-taxon studies in vegetation is problematic, as bryophytes and lichens are known to react sensitively to different environmental conditions, such as soil pH (Löbel et al. 2006), and nutrient supply (Boch et al. 2018b), vascular plant cover (Löbel et al. 2006; Boch et al. 2016, 2018a) and biomass (van Klink et al. 2017; Boch et al. 2018b). Therefore, it is important to understand how bryophyte and lichen richness in vegetation types is related to a wide array of potential drivers.

The inconclusive results about the effects of different drivers on species richness might partly be due to different grain sizes that have been studied. It has been proposed theoretically (Shmida and Wilson 1985) and later shown in several meta-analyses that spatial scale can influence the relative importance (Field et al. 2009; Siefert et al. 2012) or even the direction of the impact of certain drivers (Tamme et al. 2010). Studies with nested-plot data of dry grasslands in different Palaeartic regions have confirmed strong scale effects (Turtureanu et al. 2014; Kuzemko et al. 2016; Polyakova et al. 2016; Dembicz et al. 2021a). In agreement with theory and the mentioned meta-analyses, these studies found the strongest effects of soil variables mostly at the smallest grain size and a prevalence of climate variables at

larger grain sizes, but there were also many regional differences. Multi-scale sampling does not only allow an analysis of the drivers of  $\alpha$ -diversity at different grain sizes, but also the application of species-area relationships (SARs) to study fine-grain  $\beta$ -diversity. SARs have been modelled with many different functions, with the power law ( $S = c A^z$  with  $S$  = species richness,  $A$  = area,  $c$  and  $z$  modelled parameters) prevailing (Arrhenius 1921; Martín and Goldenfeld 2006; Dengler 2009). Recently it has been shown with an extensive dataset of nested-plot data from open vegetation types across the Palearctic biogeographic realm that this function is generally the best SAR model also at fine grains in continuous habitats (Dengler et al. 2020a). The exponent  $z$  can then be used as a valid measure of  $\beta$ -diversity (Koleff et al. 2003; Jurasinski et al. 2009; Polyakova et al. 2016; Dembicz et al. 2021b). However, previous studies did not yield consistent results on the drivers of  $z$  values or the question whether  $z$  values are completely scale-invariant. Some studies found a slight peak of local  $z$  values for grain sizes around 0.01–0.1 m<sup>2</sup> (Turtureanu et al. 2014; Polyakova et al. 2016), while others did not find any scale dependence (Kuzemko et al. 2016; Dembicz et al. 2021a).

To shed light on these open points, the Eurasian Dry Grassland Group conducted an international research expedition to the dry grasslands of the three valley systems of the Swiss Alps with pronounced continental climate (Dengler et al. 2020b). Combined with some other datasets using the same methodology, these data were then used to address the following questions: (i) How does species richness across

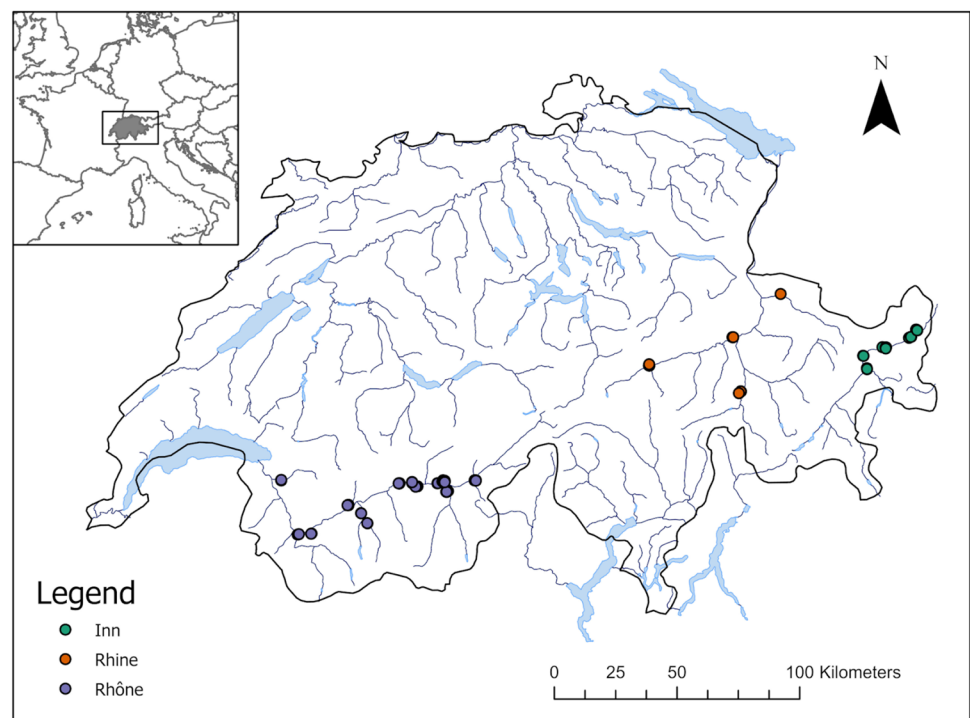
scales in these grasslands compare to that of other grassland habitats in the region and elsewhere? (ii) Which structural and environmental drivers are most important for the biodiversity patterns across taxonomic groups and spatial scales? (iii) Which factors drive fine-grain  $\beta$ -diversity ( $z$  values), and is there a scale-dependency of local  $z$  values?

## Methods

### Study system

We selected 27 study sites along the inneralpine valley systems of Switzerland within the river catchments of the Rhône (14), Rhine (5) and Inn (8), the numbers reflecting the different spatial extents of dry grasslands in these catchments (Online Resource 1). The sites extended from 6.98° N – 10.38° N and 46.12° E – 46.98° E and covered an elevational gradient from 511 to 1574 m a.s.l. (Fig. 1). Bedrock composition was diverse, including limestone, granite, metamorphic rocks (gneiss, amphibolite), flysch, moraine and alluvial deposits, with base-rich substrata prevailing overall. Regarding climate, the Rhône valley is the driest and most continental, followed by the Inn valley, while the Rhine valley is the least continental. Mean annual precipitation varies considerably, from 670 to 1,345 mm (DaymetCH database, see below). Most sites are legally protected grasslands of national importance (Eggenberg et al. 2001; see Online Resource 1). Within a site, plots were selected

**Fig. 1** Location of the sampling sites in three river catchments in Switzerland



to capture the existing diversity of ecologically and physiognomically varying dry grassland types (e.g. meso-xeric vs. xeric, skeleton-rich vs. fine-soil rich, north-facing vs. south-facing slopes). The studied communities belong to the vegetation classes *Festuco-Brometea* and *Sedo-Scleranthetea* (Dengler et al. 2020b).

### Field sampling and lab measurements

We primarily used so-called “EDGG Biodiversity Plots” ( $n = 34$ ; see Online Resource 1) to address the scale-dependence of plant diversity (Dengler et al. 2016). These are square plots of 100 m<sup>2</sup>, with two nested subplot series of 0.0001, 0.001, 0.01, 0.1, 1 and 10-m<sup>2</sup> plots in two opposite corners of the largest plot. In addition, we sampled 93 10-m<sup>2</sup> plots, resulting in a total of 161 10 m<sup>2</sup> plots. Of these, 107 were located in the Rhône catchment, 23 in the Rhine catchment and 31 in the Inn catchment (Online Resource 1). Most of the plots ( $n = 139$ ) were sampled during the 12th Field Workshop of the Eurasian Dry Grassland Group (EDGG; [www.edgg.org](http://www.edgg.org)) in 2019 (Dengler et al. 2020b), while a smaller proportion stems from sampling in the village Ausserberg in Valais in 2018 (published in Dengler et al. 2019b) and from a few other occasions in the years 2019–2020. Sampling was conducted in the months of May ( $n = 137$ ), June ( $n = 8$ ) and September ( $n = 16$ ), i.e. at phenological stages at which experienced botanists could recognize more or less the complete species composition. To test whether sampling time could have introduced a bias, we compared total species richness (all taxonomic groups) of the 10-m<sup>2</sup> plots sampled in May with those sampled later in the year, but the means were nearly identical (35.0 in May vs. 34.4 in later months).

In each plot and subplot, all vascular plants, terricolous bryophytes and lichens with shoot-presence in the plots were recorded. Most bryophyte and lichen species were collected and identified in the laboratory. At the grain size of 10 m<sup>2</sup>, the percent cover of each species was estimated, and we recorded the following structural and environmental parameters (Online Resource 2): mean annual temperature, mean annual precipitation, inclination, aspect, microrelief, herb layer height, soil pH, conductivity, soil depth, stone cover, litter cover, gravel cover, grazing and mowing. The *coordinates* and the *elevation* were determined using a handheld GPS. *Aspect* and *inclination* were measured in degrees using a compass, and inclinometer or a smartphone, respectively. For the analyses, we took the *southing* component of aspect, i.e.  $-\cos(\text{aspect})$ , ranging from  $-1$  on northern to  $+1$  on southern slopes. The percent cover of the tree, shrub, herb and cryptogam layer was estimated, as well as the percent cover of all layers together (hereafter: ‘total vegetation’). In addition, the percent cover of abiotic layers like litter, dead wood, stone, gravel and fine soil was estimated. The

*vegetation height* and *soil depth* were measured at five random points within each plot using a plastic disc and an iron pole, respectively. We then used mean vegetation height as a proxy for standing biomass and mean soil depth for the analysis. Further, we measured *maximum microrelief* perpendicular to a pole of 80 cm length placed on the soil surface where it showed the greatest difference in relief (Dengler et al. 2016). For soil property measures, soil samples of the uppermost 15 cm were taken at five random locations and then mixed. The soil samples were air-dried to measure *soil pH* and *electrical conductivity* with a multi-parameter probe (HANNA instruments HI 12,883, Woonsocket, Rhode Island, USA) in a suspension of 10 g soil and 25 ml distilled water. We assessed land use as the presence of *grazing* and *mowing*, respectively, both as binary variables by evaluating traces like faeces, signs of grazing or presence/absence of pasture weeds. *Mean annual temperature* and *mean annual precipitation* were derived from the DaymetCH dataset (D. Schmatz, WSL, Birmensdorf, unpublished, see <https://www.wsl.ch/de/projekte/climate-data-portal.html#tabellement1-tab1>, version of September 2021). This dataset of 100-m resolution for the period 1981–2010 was created with the interpolation software Daymet (Thornton et al. 1997), based on the daily measured values of all weather stations of MeteoSwiss and the digital elevation model DHM25 of Swiss-Topo. We decided against the widely used CHELSA climate dataset (Karger et al. 2017) because it underestimates the annual precipitation in our studied sites by on average nearly 200 mm as the comparison of DaymetCH and CHELSA data showed, while DaymetCH data were consistent with the climatic normal for the climate stations nearby. For the comprehensive list of variables, see Online Resource 1. The data are available from the GrassPlot database (dataset CH\_D; Dengler and Tischew 2018, Dengler et al. 2018b; <https://edgg.org/databases/GrassPlot>).

### Statistical analyses of species richness–environment relationships

In order to avoid multicollinearity, we first prepared a correlation matrix of all available metric predictor variables (environmental variables or proxies thereof) (Online Resource 3). Following the recommendation by Dormann et al. (2013), if two variables were highly correlated (Pearson’s  $|r| \geq 0.6$ ), we always retained the ecologically more meaningful variable (Online Resource 3). The selection ended up with the following 14 predictors: southing, inclination, maximum microrelief, mean soil depth, mean herb layer height, litter cover, stone cover, gravel cover, grazing, mowing, soil pH, electrical conductivity, mean annual temperature and mean annual precipitation.

First, we modelled species richness at the 10-m<sup>2</sup> grain size for vascular plants, bryophytes, lichens and all three



groups combined. We checked if the models were improved by the addition of a quadratic term. The quadratic terms of inclination and stone cover were added to the full models as these strongly improved model performance ( $\Delta\text{AICc} > 5$  in the model with quadratic term compared to the one without). This led to a final selection of 17 predictor variables. We started by calculating generalised linear models (GLMs) with negative binomial distribution for each of the four richness variables using the MASS package (Venables and Ripley 2002). Spatial autocorrelation in the model residuals was tested using the Moran's *I* test (Paradis and Schliep 2018). Only in the case of bryophyte richness did significant spatial autocorrelation occur. Thus, for this taxonomic group, we applied a generalised linear mixed-effect model (GLMM) with scaled values and plot ID nested in site ID as random factors. This random factor combination successfully removed spatial autocorrelation from the residuals. We then compared the GLMM to the corresponding negative binomial GLM using AICc values. We calculated the effect of the predictor variables on species richness by conducting a multimodel inference using the MuMIn package (Bartoń 2019). Using the *dredge* function, we generated a set of models with combinations of fixed effect terms. The relative importance value of the variables was derived as the sum of Akaike weights over all possible models containing the variable.

Additionally, we modelled total species richness for each of the seven grain sizes. Due to the smaller dataset size of the nested-plot series, in these models we dropped the four predictors with the lowest variable importance in the previous model (electrical conductivity, stone cover squared, grazing and mowing) and calculated a model for each grain size. No significant overdispersion or spatial autocorrelation occurred in these models, except for total species richness in three smallest grain sizes where we found overdispersion (thus the results of these models should be treated with caution). The effects of important predictors on species richness of taxonomic groups were visualised as predicted values based on the averaged models.

### Analyses of species–area relationships and $\beta$ -diversity

For each nested-plot series, we fitted a power-law species–area relationship (SAR) to the data of total species richness after averaging the richness values of the two sub-series, using linear regression in double-log space. The slope parameter of the SAR ( $z$  value) can be used as a measure of fine-grain  $\beta$ -diversity (Juraskinski et al. 2009; Polyakova et al. 2016). When species richness equalled zero in smaller grain sizes, these grain sizes were not used in the regression of that nested-plot series. The dependence of  $z$  values on

environmental predictors was then modelled similarly to the grain size models, but with a Gaussian error distribution.

To test for potential scale-dependence of  $z$  (Crawley and Harral 2001; Turtureanu et al 2014), we calculated “local  $z$  values” (Williamson 2003), i.e. the slopes of the SAR in double-log representation between two subsequent grain sizes (provided each had a richness  $> 0$ ) for each of the 34 nested-plot series. These local  $z$  values of the six grain-size transitions were then compared with an ANOVA, taking series ID as error term, followed by Tukey's post-hoc test.

## Results

### Species richness across scales

In total, we recorded 818 taxa, of which 629 were vascular plants (77%), 109 bryophytes (13%) and 80 lichens (10%). Mean total species richness ranged from 2.3 species in 0.0001 m<sup>2</sup> to 58.8 species in 100 m<sup>2</sup> (Table 1). Across all grain sizes, vascular plants had the highest mean species richness, followed by bryophytes and lichens. The maximum total species richness at 100-m<sup>2</sup> scale was 113 species in a meso-xeric grassland in the Rhône catchment above the village of Ausserberg, from which 110 species were vascular plants and three bryophytes. The maximum richness at 100 m<sup>2</sup> for bryophytes and lichens was 19 and 24 species, respectively (Table 1).

### The three river catchments in comparison

The topographic, soil and land use conditions were rather similar in the three river catchments (Online Resource 4). Major differences only occurred for elevation and the elevation-related climatic variable mean annual temperature and mean annual precipitation (Online Resource 4). Mean annual temperature was highest for the plots in the Rhône catchment (8.3 °C), intermediate in the Rhine catchment (6.8 °C) and lowest in the Inn catchment (5.1 °C). With around 800 mm, mean annual precipitation was similar in the Rhône and Inn catchments, but less variable in the latter, while it was much higher in the Rhine catchment (1055 mm). At the 10-m<sup>2</sup> scale, mean species richness values were very similar across the three catchments, e.g. for total species richness 34.0 species in the Rhône, 38.8 species in the Rhine and 36.0 species in the Inn catchment (Online Resource 4). There was no problematic autocorrelation for any taxonomic group that could be removed by adding catchment as a random factor to a GLMM (see Methods section), indicating that the small differences in richness patterns among the catchments were fully explained by the environmental predictors used in the regressions.

**Table 1** Summary of species richness values (number of species recorded in a plot) for different plot sizes and different taxonomic groups

Area [m <sup>2</sup> ]	<i>n</i>	All taxa			Vascular plants			Bryophytes			Lichens		
		Min	Max	Mean ± SD	Min	Max	Mean ± SD	Min	Max	Mean ± SD	Min	Max	Mean ± SD
0.0001	68	0	5	2.3 ± 1.1	0	5	2.0 ± 1.2	0	3	0.3 ± 0.6	0	1	0.04 ± 0.2
0.001	68	1	8	3.6 ± 1.8	0	8	3.0 ± 1.6	0	4	0.5 ± 0.9	0	3	0.1 ± 0.4
0.01	68	2	14	6.3 ± 2.8	0	11	5.1 ± 2.5	0	4	0.9 ± 1.2	0	6	0.3 ± 1.0
0.1	68	4	24	11.9 ± 4.2	3	20	10.0 ± 3.9	0	6	1.5 ± 1.6	0	7	0.5 ± 1.2
1	68	10	38	20.8 ± 5.7	5	38	17.6 ± 5.8	0	8	2.2 ± 2.1	0	7	1.0 ± 1.6
10*	68	17	59	34.7 ± 9.1	7	54	28.9 ± 8.9	0	13	3.6 ± 3.2	0	23	2.2 ± 3.5
10**	161	9	59	35.1 ± 9.3	7	55	29.3 ± 8.9	0	15	3.9 ± 3.4	0	23	1.9 ± 3.2
100	34	29	113	65.2 ± 2.5	17	110	48.5 ± 6.9	0	19	6.4 ± 4.6	0	24	4.0 ± 5.2
<i>z</i> value	34 <sup>+</sup>	0.16	0.31	0.24 ± 0.03	0.16	0.35	0.24 ± 0.04	0.09	0.60	0.23 ± 0.13	0.05	0.34	0.23 ± 0.09

The *z* values were derived from power-law species-area relationships fitted across the seven grain sizes of the nested plots. Note that the plots of areas ≤ 10 m<sup>2</sup> in each biodiversity plot were considered as independent observations. *n* – number of plots, SD – standard deviation

\*Only 10-m<sup>2</sup> plots from biodiversity plots

\*\*All 10-m<sup>2</sup> plots

<sup>+</sup> *n* = 32 for bryophytes and lichens

### Diversity–environment relationships of different taxonomic groups

The variance of species richness explained by our multiple regression models varied from only 15% for lichens via 34% for vascular plants and 36% for all taxa to 46% (66% including the random factors) for bryophytes (Table 2). The most important predictors for richness of all taxa were southing (negative), litter cover (negative), mean annual precipitation (unimodal with peak around 1100 mm), gravel cover (negative), inclination (unimodal with peak around 40°), maximum microrelief (positive) and stone cover (unimodal with peak around 55%) (Table 2, Fig. 2). When comparing the three taxonomic groups, only a few of the tested predictors had a consistent direction of the effect across all three, namely litter (negative), gravel cover (negative) and electrical conductivity (negative, but of low importance in all groups) (Table 2, Fig. 2). As the most species-rich taxonomic group, vascular plants showed patterns largely consistent with those reported for all taxa, except that soil pH (negative), mean soil depth (positive), mowing (positive), and grazing (positive) were more important. The species richness model for bryophytes differed from that for vascular plants mainly in the two climatic variables (mean annual precipitation being unimportant, while mean annual temperature being important) and mean herb layer height, grazing and mowing all having a clear negative relationship, while that of stone cover was pronouncedly unimodal with a peak around 45% (Fig. 2). Lichens differed from the two other taxonomic groups by showing positive relationship with soil pH. Although inclination had a negative quadratic term for all taxa combined and separately (Table 2), an actual unimodal relationship occurred only for all taxa together and

vascular plants, while the curve was monotonously increasing for bryophytes and monotonously decreasing for lichens (Fig. 2).

### Diversity–environment relationships across spatial scales

The importance of the analysed variables differed strongly and systematically across the seven spatial grain sizes (Fig. 3; Online Resource 5). Southing and litter cover had a strong negative impact on species richness at most grain sizes, whereas inclination was a strong positive predictor for 10- and 100-m<sup>2</sup> plots. Mean annual precipitation had strong unimodal impact on richness in larger grains (1–100 m<sup>2</sup>). The smallest grain sizes (0.0001 m<sup>2</sup> and 0.001 m<sup>2</sup>) had no predictor with a relative importance greater than 0.5. The explained variance of species richness was highest for 100-m<sup>2</sup> plots ( $R^2_{\text{adj.}} = 0.60$ ) and almost negligible for the two smallest grain sizes (Fig. 4, Online Resource 5).

### Species–area relationships

The overall *z* values of all taxa ranged from 0.16 to 0.31 with a mean of 0.24 (Table 1). The strongest predictors for *z* values were mean annual precipitation (unimodal), mean annual temperature (positive), and inclination (u-shaped relationship; Online Resource 5). The explained variance of *z* values was relatively high compared to that of species richness at the different spatial scales ( $R^2_{\text{adj.}} = 0.60$ ). The local *z* values for all taxa ranged from 0 to 0.602 with a mean of 0.235. Across the considered spatial grain sizes, they were highest for the transition from 0.01 to 0.1 m<sup>2</sup> with

**Table 2** Relative importance of predictors based on multimodel inference fitted to total, vascular plant, bryophyte and lichen species richness in 10-m<sup>2</sup> plots ( $n = 161$ )

Category	Predictor	All taxa	Vascular plants	Bryophytes	Lichens
Productivity/ stress	Mean annual precipitation	0.97 (+)	1.00 (+)	0.32 (–)	0.55 (+)
	Mean annual precipitation (quadratic)	0.90 (–)	0.98 (–)	0.33 (+)	0.63 (–)
	Mean annual temperature	0.25 (+)	0.27 (–)	0.58 (+)	0.69 (+)
	Southing	1.00 (–)	0.97 (–)	0.96 (–)	0.35 (+)
	Soil pH (H <sub>2</sub> O)	0.40 (–)	0.71 (–)	0.43 (–)	0.86 (+)
	Electrical conductivity	0.24 (–)	0.24 (–)	0.25 (–)	0.27 (–)
	Mean soil depth	0.38 (+)	0.75 (+)	0.78 (–)	0.32 (–)
	Mean herb layer height	0.24 (–)	0.52 (+)	0.88 (–)	1.00 (–)
	Litter	1.00 (–)	0.98 (–)	0.72 (–)	0.25 (–)
Disturbance	Inclination	0.99 (+)	0.99 (+)	0.82 (+)	0.40 (–)
	Inclination (quadratic)	0.89 (–)	0.85 (–)	0.41 (–)	0.56 (–)
	Grazing	0.33 (+)	0.73 (+)	0.69 (–)	0.37 (–)
	Mowing	0.30 (+)	0.85 (+)	0.66 (–)	0.86 (–)
Heterogeneity	Maximum microrelief	0.59 (+)	0.25 (–)	0.27 (+)	0.75 (+)
	Stone cover	0.50 (+)	0.39 (–)	0.71 (+)	0.99 (+)
	Stone cover (quadratic)	0.36 (–)	0.41 (–)	0.60 (–)	0.76 (–)
	Gravel cover	0.99 (–)	1.00 (–)	0.34 (–)	0.40 (–)
	<i>Adjusted R</i> <sup>2</sup>	0.36	0.34		0.15
	<i>R</i> <sup>2</sup> <sub>GLMMm</sub>			0.46	
	<i>R</i> <sup>2</sup> <sub>GLMMr</sub>			0.20	
<i>R</i> <sup>2</sup> <sub>GLMMC</sub>			0.66		

Importance values  $\geq 0.5$  (i.e. variable occurs in more than 50% of plausible models) are in bold. Positive (+) and negative (–) relationships are indicated. In the case of quadratic terms, a negative sign means a unimodal relationship, a positive sign a u-shaped relationship. Predictors are grouped into three categories related to different ecological theories. The variances explained by adjusted  $R^2$ , the fixed effects ( $R^2_{GLMMm}$ ), the random factors site and plot ID ( $R^2_{GLMMr}$ ) and the whole model ( $R^2_{GLMMC}$ ) are also given

significant differences across grain sizes (Tukey's post-hoc test,  $p < 0.05$ ; Fig. 5).

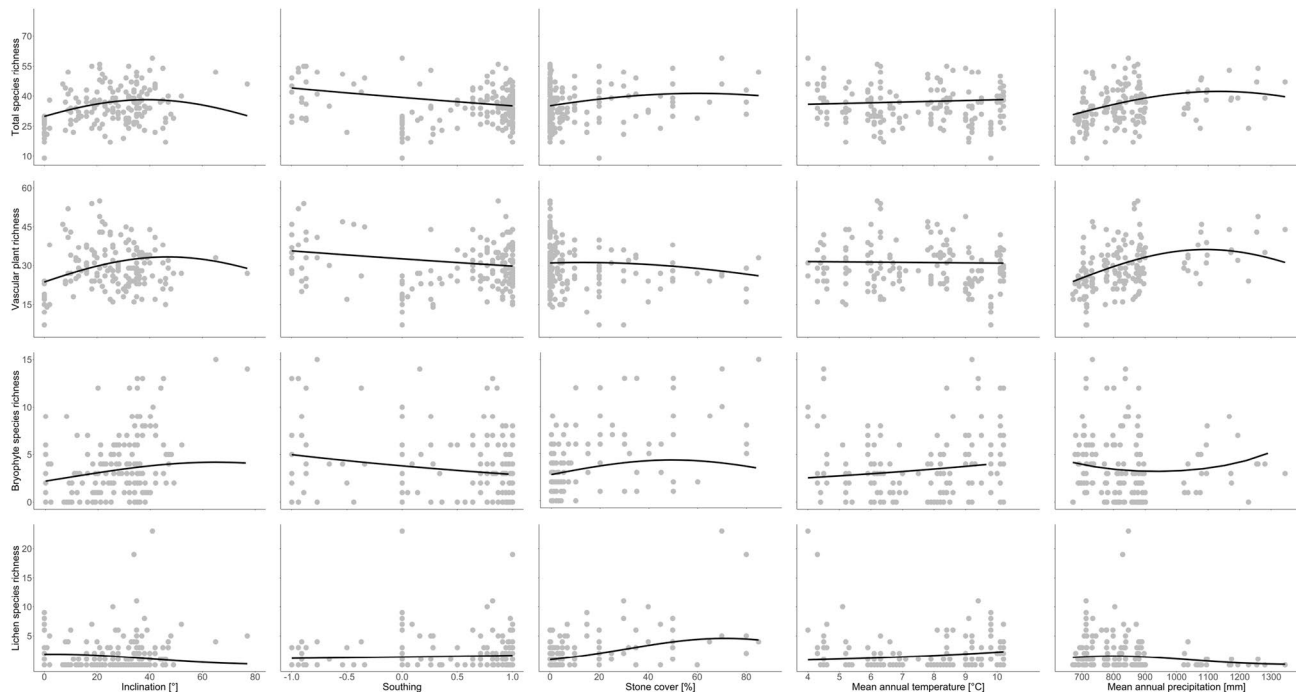
## Discussion

### Species richness at different scales

Comparing the vascular plant data from our nested-plot series to the average of *Festuco-Brometea* nested plots from across the Palaearctic with identical or very similar sampling approaches (shoot presence, seven standard grain sizes; values available from the GrassPlot Diversity Explorer, v.2.10 at <https://edgg.org/databases/GrasslandDiversityExplorer>, accessed on 5 April 2022; see Biurrun et al. 2021), the stands in the central valleys of Switzerland were poorer. This is true across all seven studied grain sizes, with differences ranging from 8% at 0.0001 m<sup>2</sup> to 27% at 0.1 m<sup>2</sup>. At 10 m<sup>2</sup>, our average was 28.9 species vs. the Palaearctic average of 36.9 ( $n = 358$ ). Below-average vascular plant species richness (in relation to other stands of the class) was previously also observed for the Aosta valley (35 species at 10 m<sup>2</sup>; Wiesner et al. 2015) and the inneralpine dry valleys

of Austria (34.2 species at 10 m<sup>2</sup>; Magnes et al. 2021). This pattern was unexpected, as dry grasslands, at least in the Rhone valley, the Inn valley and the Aosta valley still cover extensive areas and appear well-conserved compared to other regions in Europe. Moreover, the isolated character of continental central valleys in mountain massifs cannot be causal, as two other EDGG Field Workshops in the Apennines (49.5 species in 10 m<sup>2</sup>; Filibeck et al. 2018) and the Caucasus (48.7 species in 10 m<sup>2</sup>; Aleksanyan et al. 2020) in rather comparable situations found above-average richness. Also, base-rich alpine grasslands in the Swiss Alps are systematically richer (median of approx. 50 species in 10 m<sup>2</sup>; Dengler et al. 2020d). Similarly, bryophytes were systematically poorer in species in our plots than the Palaearctic average, except in 10 m<sup>2</sup> and 100 m<sup>2</sup> (<https://edgg.org/databases/GrasslandDiversityExplorer>). By contrast, lichen species richness was clearly higher in the Swiss inneralpine stands of *Festuco-Brometea* than those elsewhere, albeit at a very low level (e.g. on average 2.2 species vs. 1.1 species in 10 m<sup>2</sup>; <https://edgg.org/databases/GrasslandDiversityExplorer>).

One explanation for this puzzling finding might be the biogeographical history of the species pool (Zobel 2016).



**Fig. 2** Effects of inclination, southing, stone cover, mean annual temperature and mean annual precipitation on total, vascular plant, bryophyte and lichen species richness from the full multiple regression models. Displayed are the original richness data and the predic-

tions from general linear models and linear mixed-effect model. Each dot represents one or several 10-m<sup>2</sup> plots ( $n = 161$ ). Inclination, stone cover and mean annual precipitation had quadratic relationships (see Table 2)

The Alps were covered by a huge ice shield during the last glacial period, preventing any in-situ survival of plants with the exception of nunataks on mountain tops (Pan et al. 2020). While the species pool of alpine grasslands probably found sufficiently large refugia along the ice-free margins of the Alps (Tribisch and Schönswetter 2003), the majority of more thermophilous steppe species probably went extinct. Recolonisation from steppe areas further to the east seems to have played a rather minor role for the inner valleys of the Alps (Kirschner et al. 2020), resulting in a significantly smaller pool of steppe species in the Alps compared to other regions.

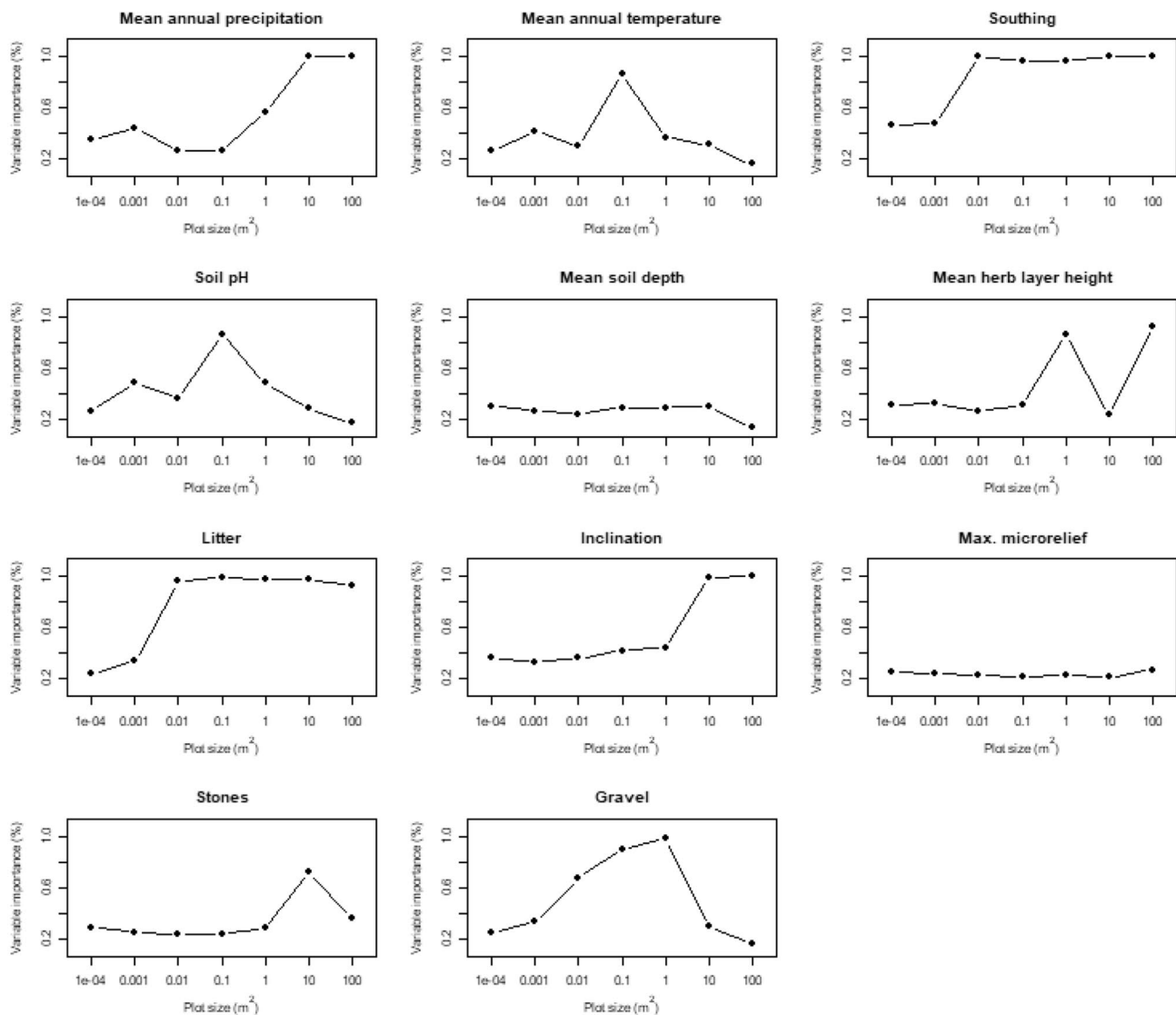
Differentiated by catchment, our mean vascular plant species richness data at 10 m<sup>2</sup> were 28.8 (Rhône), 33.6 (Rhine) and 27.7 (Inn) for. This corresponds quite well to the data from the national monitoring program of the sites of national importance in Switzerland (WBS), with higher number of replicates that were sampled at optimum phenological stage, with 26.7 for the Western Central Alps (Rhône) and 34.6 for the Eastern Central Alps (Rhine and Inn) (Bergamini et al. 2019). This confirms that our sampling was mostly comprehensive. Compared to the Jura Mts. in Switzerland with 40.4 vascular plants in 10 m<sup>2</sup>, the plots in the inneralpine dry valleys are generally poorer in species, which might be attributed to the more pronounced summer drought that excludes various less drought-tolerant species from the grasslands.

### Factors influencing diversity of taxonomic groups at 10 m<sup>2</sup>

We found pronounced differences in the diversity–environment relationship between all three taxonomic groups considered. This is consistent with results of previous comparative studies on the plot-scale richness of these groups (Löbel et al. 2006; Turtureanu et al. 2014; Kuzemko et al. 2016; Polyakova et al. 2016; Dembicz et al. 2021a) and can be explained by their different ecological requirements and life histories.

Our proxies for the *productivity–stress axis* of Grime (1973) mostly showed inconsistent patterns across the three taxonomic groups. Only litter cover, which reflects both productivity and absence of disturbance, was negative for all of them. The strongest predictor of this variable group was mean annual precipitation, showing unimodal relationships for vascular plants and total richness, with maxima around 1000–1100 mm—as expected along a stress–productivity gradient (Grime 1973): below that amount of precipitation apparently edaphically dry sites become so stressful that only few species can exist, while above the maximum conditions become so benign that competition increasingly excludes species from the system. By contrast, lichen species richness peaked at lower precipitation and bryophyte richness even showed an inverse pattern compared to the



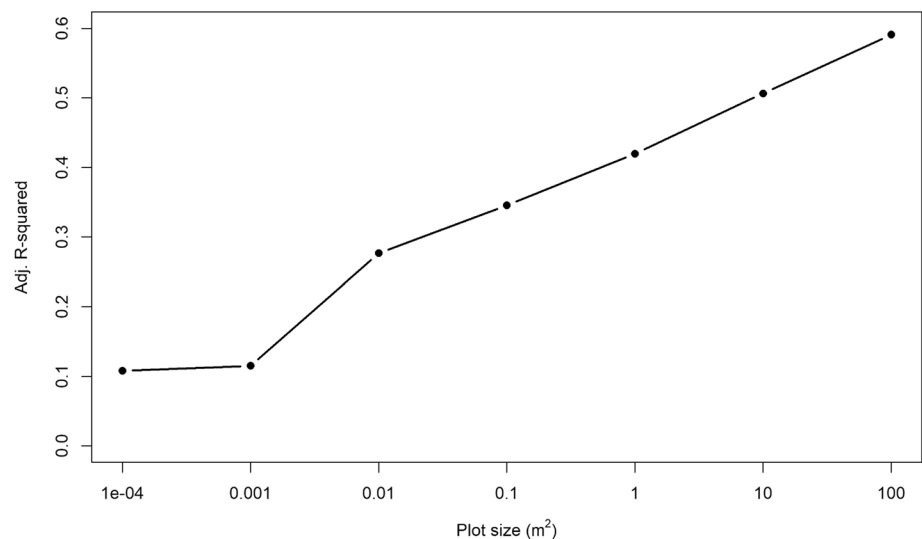


**Fig. 3** Variable importance of predictors for total species richness at seven spatial scales (plot sizes) ( $n=68$  for 0.0001–10 m<sup>2</sup>;  $n=34$  for 100 m<sup>2</sup>) derived from multimodel inference

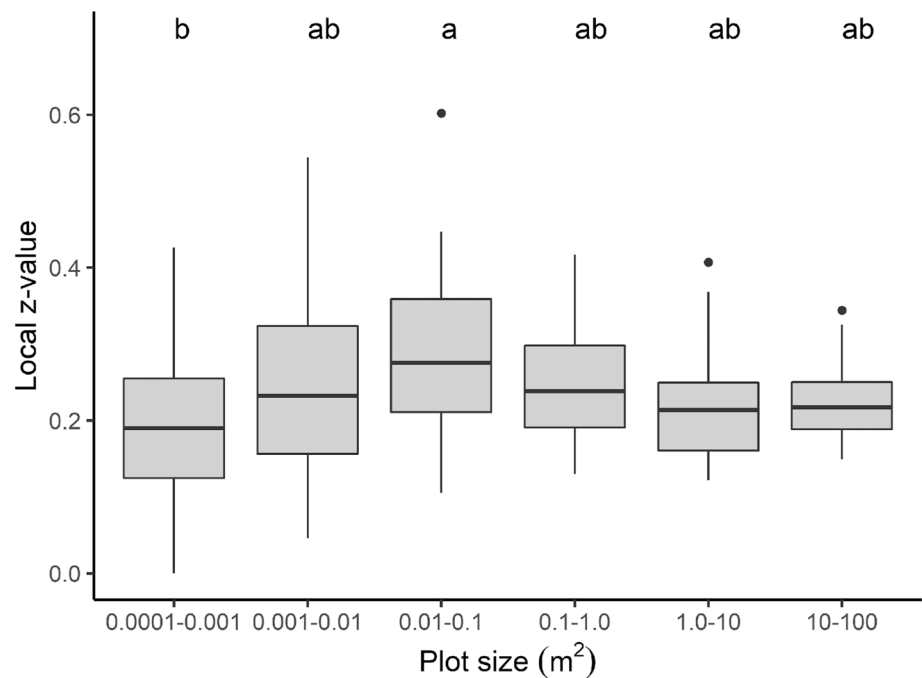
vascular plants (u-shaped), which both probably could be explained by asymmetric competition, suppressing a diverse cryptogam layer where vascular plants thrive. Mean annual temperature showed opposite patterns for vascular plants (slightly richer at higher elevation with cooler climate) and non-vascular plants (particularly rich in the warmer lowlands). Our findings of richness–climate relationships for vascular plants, via the strong negative correlation with elevation ( $r=-0.99$ ) indicate increasing richness with elevation, which differs from the predominantly reported mid-elevational peak (McCain and Grytnes 2010). A possible explanation is that we sampled not the full elevation gradient, but only the increasing part of the hump, and thus missed the decreasing part at higher elevations. This fits to the fact that plot-based studies in Swiss grasslands found

richness peaks between 1100 and 1600 m a.s.l. (Descombes et al. 2017; Boch et al. 2019b), while our highest plot was at 1574 m a.s.l. A particularly strong negative predictor of total, vascular and bryophyte richness was southing, which can be explained by the more stressful conditions in south-facing slopes vs. flat or north-facing areas. This is consistent with the strong negative effect of heat load index (a composite variable mainly based on aspect) found in Transylvanian dry grasslands (Turtureanu et al. 2014). Mean soil pH, which is often a particularly relevant parameter for plot-scale species richness (e.g. Schuster and Diekmann 2003; Löbel et al. 2006; Boch et al. 2016, 2018a), typically with a unimodal response, in our case showed opposing effects for the three taxonomic groups: negative for vascular plants, weak for bryophytes and positive for lichens. This might be related to

**Fig. 4** The explained variance expressed by adjusted  $R^2$  for the models of total species richness for the individual plot sizes ( $n = 68$  for 0.0001–10 m<sup>2</sup>;  $n = 34$  for 100 m<sup>2</sup>)



**Fig. 5** Boxplots of local  $z$  values as measures of  $\beta$ -diversity across spatial scales (transitions between two subsequent plot sizes). Different letters denote significant differences in mean  $z$  values between transitions (Tukey's posthoc test at  $\alpha = 0.05$ )



the fact that vascular plants prefer slightly more developed soils which coincides with decalcification, whereas lichens profit among the base-rich dry grasslands from the most extreme sites (highest pH) due to lower vascular plant competition. Last, mean herb layer height, which, in the way it was measured, reflects standing biomass and vegetation density, was strongly negative for the two non-vascular groups, but slightly positive for the vascular plants themselves. The strong negative effect of standing biomass of vascular plants on richness of the two other groups again could be explained by asymmetric competition for light (Löbel et al. 2006; Boch et al. 2016, 2018a, b).

According to the Intermediate Disturbance Hypothesis (IDH; Connell 1978; see also Grime 1973; Huston 2014), one should expect maximum richness at intermediate levels of *disturbance*. We considered here three proxies of disturbance as follows: slope inclination related to erosion, and the two land-use variables grazing and mowing. While the quadratic term of inclination was negative in all models, we found a peak inside the possible values only for total richness and vascular plants, where highest diversity occurred at around 40°, thus in agreement with the IDH. By contrast, lichens showed a monotonously decreasing and bryophytes a monotonously increasing relationship with slope angle. This does not conflict with the IDH per se, but highlights the taxon

and context dependency of what can be considered “intermediate” (see Huston 2014). Grazing and mowing, which we had only as rough binary variables, showed contrasting effects on vascular plant richness (weakly positive) and on the richness of the two non-vascular groups (negative). Since farmers who are managing these legally protected grasslands of national importance must follow restrictions regarding mowing, stocking density and fertilization, land-use intensity in these low-productivity systems can be described as low to moderate. Thus, our plots rather reflect the increasing part of the IDH, which is supported in the case of vascular plants. However, for bryophyte and lichen richness, even this low land-use intensity obviously was already too much. This is in agreement with Allan et al. (2014), who found bryophyte and lichen diversity to be highest at very low land-use intensities and rapidly declining values already at moderate land-use intensity in German grasslands. In addition, Boch et al. (2018b) found strong negative direct effects of land-use intensity and indirect negative effects of land-use intensity via increased vascular plant biomass on bryophyte richness in German and Swiss grasslands. Increased vascular plant biomass can lead to competitive exclusion of bryophyte and lichens species and consequently lower species richness of these groups (Löbel et al. 2006; Boch et al. 2016, 2018b).

There is comprehensive evidence that any type of environmental *heterogeneity* across grain sizes increases species richness (Stein et al. 2014), and this relationship only might be reversed at very fine grain sizes far below 1 m<sup>2</sup> (Tamme et al. 2010). However, for maximum microrelief as our most direct measure of within-plot heterogeneity, we found mixed effects: While it positively influenced the species richness of all taxa and of lichens, there were only weak positive effects for bryophytes and even negative ones for vascular plants. This contrasts with the strong positive effect of microrelief on plot-scale richness of vascular plants found in dry grasslands of Sweden and Siberia (Löbel et al. 2006; Polyakova et al. 2016). We do not have a good explanation why the Swiss *intra-alpine* dry grasslands deviate here from similar plant communities elsewhere and from theoretical expectations. We also considered stone cover as a measure of heterogeneity, assuming highest heterogeneity and thus highest richness at intermediate levels of stone cover. However, while the relationships had a negative quadratic term for all three taxonomic groups, only in bryophytes showed a peak at intermediate stone covers, while vascular plants showed a monotonously decreasing and lichens a monotonously increasing curve (Fig. 2). Apparently, the areas with very shallow soils directly surrounding rocks and stones created spaces with low competition from vascular plants, beneficial for terricolous bryophytes and even more so for terricolous lichens, which overcompensated the loss of area by the stones themselves (as we did not record saxicolous species). On the other hand, for vascular plants, additional

rocks and stones inside the plot just meant a loss of inhabitable area. Finally, we tentatively also listed gravel cover under heterogeneity-related factors. However, here we found a negative effect on all taxonomic groups, but particularly so for vascular plants. The difference of gravel vs. stones and rocks could be that the former through its smaller weight can be more easily moved by various agents (wind, water, trampling) and thus damage surrounding plants, particularly small ones. Moreover, gravel, if not embedded in a matrix of fine soil, has an extremely low water-holding capacity and thus could even exclude most species due to desiccation.

### Diversity–environment relationships across spatial scales

We found that the explanatory power of our models for total richness was negligible for the two smallest grain sizes and then continuously increased towards 100 m<sup>2</sup>. Similarly, previous studies using the same method in dry grasslands of other regions (Kuzemko et al. 2016; Polyakova et al. 2016; Talebi et al. 2021; but see Dembicz et al. 2021a) found an increasing amount of explained variance with grain size. This makes sense for the following two reasons: (a) ecologically, one should expect species interactions (not covered by the measured environmental variables) to become more important towards finer grain sizes and thus lead to more variation and lower predictability, (b) methodologically, the scale mismatch increases also towards the smaller grain sizes as most predictors were measured for 10 m<sup>2</sup> and the climate variables for even larger grains<sup>2</sup>.

While some predictors had a strong and consistent effect across the studied grain sizes (southing and litter cover), mean annual precipitation was important only for the three largest grain sizes, whereas gravel cover had high importance for the intermediate grain sizes only (0.01–1 m<sup>2</sup>) and soil pH even changed the sign of the impact from positive at smaller grain sizes to slightly negative at larger ones. These findings are in agreement with the general notion that diversity–environment relationships are strongly scale-dependent (Shmida and Wilson 1985; Field et al. 2009; Siefert et al. 2012). Specifically, the shift in the relative importance of soil factors (like pH and gravel cover) at smaller grain sizes to climatic variables (e.g. mean annual precipitation) at larger ones agrees with theoretical expectations (Shmida and Wilson 1985; Siefert et al. 2012). It is also largely consistent with the results from similar studies on dry grassland vegetation in other parts of the Palaearctic (Turtureanu et al. 2014; Kuzemko et al. 2016; Dembicz et al. 2021a; Talebi et al. 2021).

## Species–area relationships

With a mean of 0.24, the  $z$  values found in the Swiss inner-alpine dry grasslands are intermediate. It exactly matches the mean value reported for more than 2000 nested-plot series of various grasslands and other open habitat types across the Palaearctic modelled in the same way (Dengler et al. 2020a: Supporting Information 9). Specifically for the two studied vegetation classes, *Festuco-Brometea* (large majority of plots) and *Sedo-Scleranthetea*, Dembicz et al. (2021c) report  $z$  values calculated in log- $S$  space of 0.239 and 0.325, respectively. Thus, in contrast to  $\alpha$ -diversity (see above),  $\beta$ -diversity (of which  $z$  values are a measure) is not outstanding in the region. Compared to other studies using the same method,  $z$  values were well explained by environmental variables, with an  $R^2$  of 0.60. The three most relevant predictors were mean annual precipitation (unimodal), mean annual temperature (positive) and inclination (negative). Maximum microrelief as our most direct measure of within-plot heterogeneity had a positive, but minor effect. These findings for  $z$  values of total species richness deviate quite strongly from the comprehensive study of Palaearctic open habitats (Dembicz et al. 2021b: Appendix S5) where the explained variance was low in general, and particularly low for the climate variables mean annual precipitation and mean annual temperature. Why these macroclimatic variables have such a strong influence on fine-grain beta diversity in our study system remains unclear for the time being.

Finally, when analysing the scale dependence of  $z$  values, we found a slight peak for the transition from 0.01 to 0.1 m<sup>2</sup> with decreases towards both the smaller and the larger grain sizes. These findings correspond to those in regional studies of Turtureanu et al. (2014), Polyakova et al. (2016) and Talebi et al. (2021), while other studies did not find a scale dependence of  $z$  values (Kuzemko et al. 2016; Dembicz et al. 2021b). This demonstrates that the scale dependence of  $z$  values in dry grasslands of the Palaearctic is generally weak, but if there is one, it always exhibits a peak at grain sizes clearly below 1 m<sup>2</sup>, pointing to a very fine-grained community organisation. In a recent Palaearctic synthesis, Zhang et al. (2021) found the same when basing the calculation of  $z$  values on shoot presence as we did. From a methodological point of view this means that, except for very detailed studies, one can safely analyse dry grasslands using the “normal” power function with a constant  $z$  value, as Dengler et al. (2020a) already concluded for all open habitat types in the Palaearctic.

## Conclusions and outlook

We found that patterns and drivers of species richness vary strongly between the three taxonomic groups (vascular plants, bryophytes and lichens) as well as across the seven studied grain sizes. This variation was mostly consistent with theoretical expectations and previous findings in other grassland types. Thus, our study contributes to an increasing knowledge of the often-neglected phenomena of taxon- and scale-dependence. It follows that one must be cautious, both in ecological research and biodiversity conservation, when transferring findings from other studies sampled with a different grain size or when considering one taxonomic group as surrogate for another. While the findings of this study largely confirmed our prior hypotheses, there were some unexpected deviations, e.g. the low importance of microrelief in the models and the high explained variance in the model for within-plot  $\beta$ -diversity ( $z$  values). Also, the low alpha diversity of vascular plants in Swiss inner-alpine valleys compared to dry grasslands in mountain valleys elsewhere in the Palaearctic remains puzzling. To understand the reasons for these unexpected patterns will require analysing alpha diversity of standard grain sizes with high-quality data across many regions in the Palaearctic simultaneously and including many potential drivers, an enterprise for which the steadily growing GrassPlot database (Dengler and Tischew 2018a, Dengler et al. 2018b; Biurrun et al. 2021) provides good opportunities.

**Supplementary Information** The online version contains supplementary material available at <https://doi.org/10.1007/s00035-022-00285-y>.

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**Author contributions** JD planned the research. All authors except MBe and SB were involved in the field sampling, ID identified the collected vascular plants, BC-M the bryophytes and SB the lichens, while MBe analysed the soils. MBe conducted the statistical analyses under the supervision of ID and JD. He also led the writing of the Methods and Results sections, while JD and SB drafted the Introduction and Discussion sections, and ID and WW gave major inputs. All authors checked, revised and approved the manuscript.

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**Data availability** The vegetation-plot data underlying this study are stored in the GrassPlot database (<https://edgg.org/databases/GrassPlot>), from which they can be requested according to the GrassPlot Bylaws.

**Code availability** The R code used for the analysis is available upon request from the first author.

## Declarations

**Conflict of interest** We declare no conflict of interest.

**Ethical approval** The field work in protected areas was permitted by the conservation authorities of the cantons of Vaud, Valais and Grisons.

**Consent to participate** Not applicable.

**Consent for publication** All authors have approved the submitted manuscript.

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