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SPECIAL FEATURE: MACROECOLOGY OF VEGETATION

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Fine-grain beta diversity of Palaearctic grassland vegetation

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Abstract

Questions: Which environmental factors influence fine-grain beta diversity of vegetation and do they vary among taxonomic groups?

Location: Palaearctic biogeographic realm.

Methods: We extracted 4,654 nested-plot series with at least four different grain sizes between 0.0001 m² and 1,024 m² from the GrassPlot database, covering a wide

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range of different grassland and other open habitat types. We derived extensive environmental and structural information for these series. For each series and four taxonomic groups (vascular plants, bryophytes, lichens, all), we calculated the slope parameter (*z*-value) of the power law species–area relationship (SAR), as a beta diversity measure. We tested whether *z*-values differed among taxonomic groups and with respect to biogeographic gradients (latitude, elevation, macroclimate), ecological (site) characteristics (several stress–productivity, disturbance and heterogeneity measures, including land use) and alpha diversity (*c*-value of the power law SAR).

Results: Mean *z*-values were highest for lichens, intermediate for vascular plants and lowest for bryophytes. Bivariate regressions of *z*-values against environmental variables had rather low predictive power (mean $R^2 = 0.07$ for vascular plants, less for other taxa). For vascular plants, the strongest predictors of *z*-values were herb layer cover (negative), elevation (positive), rock and stone cover (positive) and the *c*-value (U-shaped). All tested metrics related to land use (fertilization, livestock grazing, mowing, burning, decrease in naturalness) led to a decrease in *z*-values. Other predictors had little or no impact on *z*-values. The patterns for bryophytes, lichens and all taxa combined were similar but weaker than those for vascular plants.

Conclusions: We conclude that productivity has negative and heterogeneity positive effects on *z*-values, while the effect of disturbance varies depending on type and intensity. These patterns and the differences among taxonomic groups can be explained via the effects of these drivers on the mean occupancy of species, which is mathematically linked to beta diversity.

KEYWORDS
disturbance, elevation, fine-grain beta diversity, heterogeneity, land use, macroecology, mean occupancy, Palaearctic grassland, productivity, scale dependence, species–area relationship (SAR), *z*-value

1 | INTRODUCTION

One of the central aims of ecology and evolutionary biology is to understand the drivers of biological diversity at different spatial and temporal scales (Allan et al., 2011; Isbell et al., 2011). A crucial dimension of biological diversity is β-diversity, the variability in species composition between local communities (Anderson et al., 2011). At large spatial grain sizes (≥ 100 km²) and along latitudinal and elevation gradients, important drivers of β-diversity are macroclimate and dispersal barriers (Qian, 2009; Qian et al., 2013; Pinto-Ledezma et al., 2018). At medium (0.01 km² to <100 km²) and small spatial grain sizes (< 0.01 km² or 1 ha; grain size classification modified from Field et al., 2009), the drivers are much less understood, although microclimate and soil variability are known to influence small-scale community composition (Opedal et al., 2015; Ulrich et al., 2017). A better understanding of drivers of fine-grain β-diversity would support a more informed application of this biodiversity dimension in vegetation ecology, conservation and management measures, and allow more reliable inter- and extrapolations of species richness to other fine grain sizes. Transferring results from coarse-grain β-diversity studies is not possible, as several studies have shown strong changes in patterns and drivers of β-diversity across grain sizes (Veech & Crist, 2007; Sreekar et al., 2018).

Species–area relationships (SARs) describing the increase of species richness with area are another major research focus of ecology and biogeography (Connor & McCoy, 1979; Drakare et al., 2006; Dengler, 2009). SARs can be constructed in various ways, among them, with nested and non-nested sampling units (Dengler et al., 2020a). There is growing evidence that among the numerous proposed SAR functions (Tjørve, 2003; Dengler, 2009), the power function ($S = c\,A^z \Leftrightarrow \log S = \log c + z \log A$; where S is species richness, A is area, and c and z are fitted parameters) provides the best fit in most cases (Connor & McCoy, 1979; Dengler, 2009; Triantis et al., 2012; Matthews et al., 2016; Dengler et al., 2020a). The parameters of SAR functions (and specifically the exponent z of the power law) are widely used for comparing the shape of SARs of taxonomic groups with different dispersal abilities (Patiño et al., 2014), assessing the impact of anthropogenic disturbance on species assemblages (Tittensor et al., 2007), and quantifying the expected species loss due to habitat area reduction (He & Hubbell, 2011).

While β-diversity and SARs are widely studied, there is little awareness that these two concepts are closely related. MacArthur (1965) implicitly suggested that the slope parameter *z* of nested SARs can be used as a measure of β-diversity and the intercept as a measure of α-diversity, but this was later dismissed by Connor and McCoy (1979). Koleff et al. (2003) demonstrated mathematically that the exponent *z* of the power function is indeed a direct measure of β-diversity. Similarly, Ricotta et al. (2002) proposed the use of the slope parameter b_1 of species accumulation curves (SACs; for differences from SARs, see Dengler et al., 2020a) modelled with a logarithmic function ($S = b_0 + b_1 \log A$) as a measure of multiplicative β-diversity. Jurasinski et al. (2009) listed slope parameters of nested SARs as the third concept of proportional diversity, next to additive and multiplicative β-diversity, but indicated that they are only rarely applied.

More recently, Polyakova et al. (2016; see also Sreekar et al., 2018) re-introduced *z*-values as a valid measure of multiplicative β-diversity in continuous habitats. If the SAR is modelled with a power function, the slope parameter *z* is calculated by:

$$z = \frac{\log\left(\frac{S_2}{S_1}\right)}{\log\left(\frac{A_2}{A_1}\right)} \quad (1)$$

where S_2 and S_1 are the species richness values of the grain sizes A_2 and A_1, respectively, with $A_2 > A_1$. Therefore, if the sampling takes place in nested plots, S_2 can be interpreted as γ-diversity and S_1 as (averaged) α-diversity:

$$z = \frac{\log\left(\frac{\gamma}{\bar{\alpha}}\right)}{\log\left(\frac{A_\gamma}{A_{\bar{\alpha}}}\right)} \quad (2)$$

Defining multiplicative β-diversity as

$$\beta_{mult} = \frac{\gamma}{\bar{\alpha}} \quad (3)$$

it follows that

$$z = \frac{\log(\beta_{\text{mult}})}{\log\left(\frac{A_\gamma}{A_\alpha}\right)} \quad (4)$$

Accordingly, *z*-values are the logarithms of "conventional" multiplicative β-diversity, divided by the logarithm of the ratio of the considered areas. The advantage of this approach is that the resulting value allows direct comparison of β-diversity values irrespective of the relative increase in area between the α- and γ-level.

The slope *z* of nested power function SARs within a continuous habitat (in contrast to island SARs where each area represents a different, spatially separate unit) is also linked to the average sparsity of species (Storch, 2016) in terms of the proportion of occupied subplots: the sparser the species are on average in the sampling plots (i.e. the lower their mean occupancy is), the steeper the SAR slope. Intuitively, if all species occur in each subplot of a larger plot, the SAR slope approaches zero, while if all species exclusively occupy just one subplot, the slope approaches one. There is a mathematical relationship between mean species' occupancy and the SAR slope (Šizling & Storch, 2004), but the prediction of SAR slopes would require complete information on all species occupancies within a given plot (i.e. the total number of occupied subplots for each species), which is not available in most nested-plot data (usually only a very small subset of all potential subplots of smaller grain size within a larger plot is sampled, thus precluding a realistic estimate of occupancy). Still, one can predict that any factor affecting mean species occupancy in a sampling design will also influence the SAR slope (Šizling & Storch, 2004). This finding enables the investigation of the effects of taxonomic group and ecological factors on species occupancy and thus SAR slopes. Results of the few, mostly regional, empirical studies on drivers of fine-grain *z*-values in vegetation are largely idiosyncratic and inconclusive (Appendix S1). For instance, certain types of disturbances, like grazing, may selectively decrease the occupancy of grassland plant species, creating opportunities for others (Loucougaray et al., 2004), thus possibly increasing the SAR slope. In contrast, other disturbances may selectively eliminate the sparsest species, increasing overall mean species occupancy, and thus decreasing the SAR slope. In this context of multiple possible responses, a comparative empirical study of SAR slopes is needed to shed light on the causal pathways through which individual environmental factors affect species occupancies and SAR slopes.

Grasslands are inherently fine-grain communities with the maximum compositional variability appearing at very fine scales, usually below 1 m² (Bartha et al., 2004, 2011). The vegetation of Palaearctic grasslands is particularly suitable for studying fine-grain β-diversity as it regularly contains three taxonomic groups with contrasting ecological properties (vascular plants, bryophytes, lichens). Moreover, such grasslands occur under very diverse site conditions (e.g. from sea level to more than 5,000 m a.s.l., from very wet to very dry sites) and management regimes (e.g. natural, semi-natural, intensified; Dengler et al., 2020b). Since Palaearctic grasslands are known to exhibit extreme variation in small-scale species richness, from monospecific systems to the world records in vascular plant species richness below 100 m² (Wilson et al., 2012; Dengler et al., 2016a), we expect that fine-grain β-diversity values will also cover a broad range.

Here, we use the extensive GrassPlot database (Dengler et al., 2018), which provides multi-scale species richness data of grasslands and other non-forested habitats across the whole Palaearctic biogeographic realm, to test how fine-grain β-diversity (measured as *z*-values of nested-plots SARs) is related to multiple potential drivers. We expected that higher fine-grain heterogeneity will increase fine-grain β-diversity, but theoretical predictions for the role of other environmental factors were unclear due to their possible contradictory effects (see Appendix S1). Thus, we addressed the following research questions:

1. How do *z*-values differ among three *taxonomic groups* (vascular plants, bryophytes, and lichens)?

2. How do *z*-values vary in relation to large-scale *biogeographic characteristics*, such as latitude, elevation and macroclimate?
3. How are *z*-values related to small-scale *ecological characteristics*, related to stress–productivity, disturbance and heterogeneity?
4. How are *z*-values related to α-*diversity*?

2 | METHODS

2.1 | Vegetation-plot data

We used plot data from the collaborative vegetation-plot database GrassPlot (Biurrun et al., 2019; Dengler et al., 2018; https://edgg.org/databases/GrassPlot) registered as EU-00-003 in the Global Index of Vegetation-Plot Databases (GIVD; Dengler et al., 2011). GrassPlot assembles vegetation-plot data, together with methodological, environmental and structural information from grasslands and other non-forest vegetation types (rocks and screes, deserts, ruderal communities etc.) from the Palaearctic biogeographic realm. GrassPlot specifically collects multi-scale data sets from nested-plot sampling schemes (e.g. Dengler et al., 2016b) with areas from 0.0001 to 1,024 m².

We retrieved all nested-plot series from GrassPlot (v.2.04 on 20 March 2020) that contained at least four different grain sizes (4,654 series, consisting of 164,578 individual plots). All series had information on *vascular plants*, 890 on terricolous (soil-dwelling) *bryophytes*, 894 on terricolous *lichens*, and 862 on all three taxonomic groups, i.e. the total species richness of the vegetation (hereafter termed *complete vegetation*). We refer to the four categories (complete vegetation, vascular plants, bryophytes, lichens) together as the *four taxonomic groups*.

For those nested-plot series with more than one plot for certain grain sizes, we averaged richness values per grain size. Thus, we obtained one single richness value for each grain size within each nested-plot series and for each taxonomic group. The plots were distributed across 34 different countries from 28.5° N to 70.0° N and 16.2° W to 161.8° E, and covered an elevation gradient from 0 m to 4,387 m a.s.l. (Figure 1 and Appendix S2). They included a wide range of different vegetation types (natural grasslands, secondary grasslands, azonal communities, dwarf shrublands, tall forb and ruderal communities and semi-deserts); in fact, the selection criteria of GrassPlot (Dengler et al., 2018) include 63% of all distinguished habitat types in the European part of the realm (Janssen et al., 2016).FIGURE 1 Density and spatial distribution of the 4,654 nested-plot series in the Palaearctic biogeographic realm containing information on vascular plant species that were analysed in this study. The colour scale indicates the number of available series per 10,000-km² grid cell. The map uses the Lambert Azimuthal Equal-Area projection.

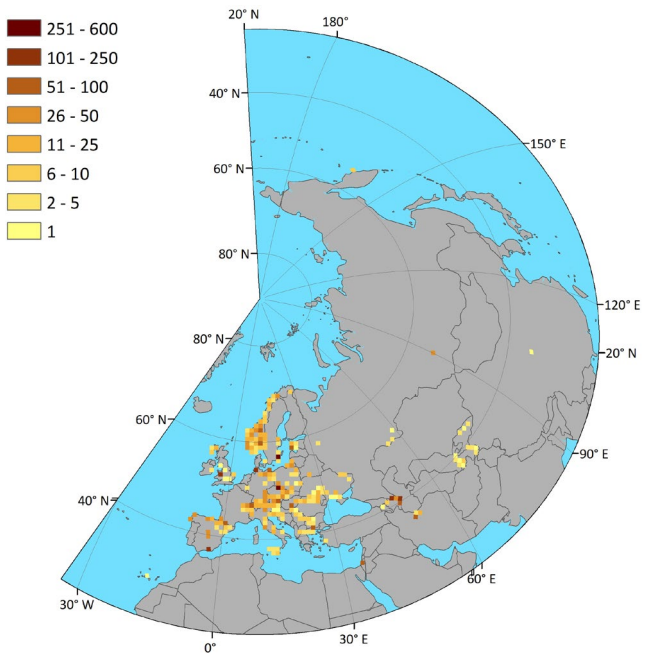


FIGURE 1 Density and spatial distribution of the 4,654 nested-plot series in the Palaearctic biogeographic realm containing information on vascular plant species that were analysed in this study. The colour scale indicates the number of available series per 10,000-km² grid cell. The map uses the Lambert Azimuthal Equal-Area projection

2.2 | SAR modelling

We fitted a power function to each data set representing a taxonomic group within a nested-plot series, using the non-transformed "*S*-space" ($S = c\,A^z$, where S is species richness, A is area in m², and c and z are fitted parameters) and the "logarithmic *S*-space" ($\log_{10} S = \log_{10} c + z \log_{10} A$). Both approaches are valid, have been widely used in the literature, and have different strengths and limitations (see Dengler, 2009; Dengler et al., 2020a). Due to the different treatment of the error structure, the parameter estimates in the two mathematical spaces usually deviate. Generally, fitting in *S*-space gives more weight to good fit at larger grain sizes, whereas fitting in log *S*-space gives more weight to good fit at smaller grain sizes and typically reduces heteroscedasticity in the residuals.

To fit the power model in log *S*-space, we used linear regression and the standard 'lm' function in R (R Core Team, 2018). The fitting in *S*-space followed the approach of Dengler et al. (2020a; see also Matthews et al., 2019a). We applied non-linear regression using the 'mle2' function in the *bbmle* R package (Bolker & R Core Team, 2017). Starting parameter values were derived from fitting the linear model in log *S*-space. In a small number of cases where the resultant *S*-space model did not converge, we iterated across a range of different starting parameter values to achieve convergence (see Dengler et al., 2020a). To avoid problems with fitting in log *S*-space, we assigned small non-zero values to any subplot with observed values of $S = 0$ (see Dengler et al., 2020a). For both the *S*-space and log *S*-space fitted models, we stored the *z*- and *c*-values.

2.3 | Predictor variables

In addition to the taxonomic group, we used a wide range of plot characteristics available from GrassPlot and related to our research questions (for further details and references, see Appendix S3, for the number of plots used in each analysis see Appendix S6). We grouped them into three categories: *biogeographic characteristics*, *ecological characteristics* and *α-diversity*. The ecological characteristics were further subdivided into those related to the *stress–productivity* and *disturbance* axes (Grime, 1977; Huston, 2014) as well as to *heterogeneity* (Lundholm, 2009; Stein et al., 2014), in order to connect with well-established theories of α-diversity. However, we acknowledge that some variables are only weakly connected to the respective group or might contain elements of more than one group.

As *biogeographic characteristics*, we used two variables related to major biogeographic theories (*latitude* and *elevation*) and four major climatic variables (*mean annual temperature*, *temperature seasonality*, *mean annual precipitation*, *precipitation seasonality*). While latitude and most of the elevation data were provided by the original data set collectors, missing elevation data and the other four variables were derived from external sources using the plot coordinates (for details, see Appendix S3).

The *stress–productivity* variables refer to the stress–productivity axis of Grime (1977; productivity in Huston, 2014): We used *soil pH* and *soil depth mean* as soil-related stress measures, assuming a U-shaped relationship of stress with soil pH (nutrient uptake is limited at both high and low pH, with additional toxicity effects at low pH; see Lambers et al., 2008) and a negative relationship with soil depth (see Appendix S1). Further, we classified plots into those that receive (anthropogenic) *fertilization* vs those that do not. Finally, we used *herb layer cover* as a proxy of productivity. While at cover values below 90% there should be a reasonably good correlation of standing biomass with herb layer cover (Ónodi et al., 2017), we acknowledge that for very high cover values the relationship likely will disappear as the biomass then mainly is determined by vegetation height.

The *disturbance* variables refer to disturbance sensu Grime (1977) and Huston (2014), meaning destruction or removal of accumulated bio- and necromass. Therefore, *litter cover* was used as an adverse proxy of disturbance (Appendix S1). We also consider *slope inclination* as related to disturbance because erosion increases with inclination. Furthermore, we extracted the following measures of anthropogenic disturbance from GrassPlot: *naturalness* (at two levels) and presence of the management types *livestock grazing*, *mowing* and *burning*. Naturalness at coarse level indicates whether grassland is natural or secondary, while naturalness at fine level refers to the intensity of human impact on vegetation within each of the two coarse categories (for details, see Appendix S3).

The *heterogeneity* variables are those that describe the small-scale variability of stress–productivity and/or disturbance, usually determined within the largest or second-largest grain plot of each nested series: *Soil depth CV* indicates the variability of soil depth within a plot; *microtopography* refers to deviations from a smooth plane, which could lead to small-scale differences in soil moisture; *rock and stone cover* is related to variation in soil depth, microclimate and erosion; *shrub layer cover* is related mainly to variation in light and moisture conditions.

As a measure of *α-diversity*, we used the *c-value* from the SAR modelling (see above). The *c-value* is the predicted average species richness at the unit area, i.e. in our case in 1 m².

2.4 | Analyses of the *z*-values

We tested how the modelled *z*-values of the power function depended on our four groups of predictors: taxonomic group, biogeographic characteristics, ecological (site) characteristics and α-diversity. We excluded nested-plot series with no reported species for the investigated taxonomic group as well as the very few nested-plot series where the model fitting did not converge or resulted in theoretically impossible values of $z > 1$ (Williamson, 2003). In consequence, for *S*-space we had estimated *z*-values for 4,554 series for vascular plants, 716 for bryophytes, 400 for lichens and 862 for complete vegetation (numbers differ slightly for log *S*-space).

As only a small fraction of our data set contained all variables of interest, we decided to test the effect of each of them independently, similar to the study of Drakare et al. (2006) for *z*-values and Dengler et al. (2020a) for shapes of SARs. From a statistical point of view multiple regressions, which analyse a multitude of predictors simultaneously, including potential interactions, might be considered advantageous. However, in our case such an approach would have drastically reduced the spatial coverage or forced us to restrict ourselves to those variables that can be retrieved from global databases at coarser grains instead of using our in-situ determined fine grain data. For the continuous variables (see Appendix S3), we used bivariate linear regressions to test for their potential influence on the *z*-values of the three taxonomic groups and complete vegetation. To account for potential hump-shaped or U-shaped relationships, we implemented a second-order polynomial function but removed the quadratic term if non-significant. To allow for the assessment of more complex non-linear relationships, we additionally visualized a polynomial surface using local fitting as implemented in the R package *stats* by the 'loess' function (with smoothing parameter α set to 0.8). For categorical predictors (see Appendix S3), we applied analysis of variance (ANOVA), followed by Tukey's post hoc test (R package *stats*) and *multcompView* (Graves et al., 2019) to identify homogeneous groups. The comparison of taxonomic groups was additionally carried out for only those nested-plot series where all three taxonomic groups had been recorded simultaneously. In this case, we used a mixed-effects model with plot series ID as a random factor (intercept). The mixed-effects model was implemented using the R package *lme4* (version 1.1-19; Bates et al., 2015) followed by a Tukey's post hoc test as implemented in the function 'glht' of the R package *multcomp* (version 1.4-8; Hothorn et al., 2008).

3 | RESULTS

The results obtained for *S*-space and log *S*-space were qualitatively similar; in log *S*-space on average the modelled *z*-values were slightly higher and R^2_{adj} about 25% higher than in *S*-space (for *n*, R^2_{adj}, parameter estimates and *p*-values in both *S*-spaces, see Appendix S6). Thus (and to be consistent with Dengler et al., 2020a), we report here the results in *S*-space in detail (results in log *S*-space are shown in Appendix S5). We focused primarily on the results for vascular plants, for which we have the most comprehensive data set. Generally, the results for bryophytes, lichens and complete vegetation were similar; thus, we mention them only when there were important deviations. As we tested numerous bivariate relationships with large amounts of observations, the results of significance tests should be viewed with caution. While we report all significant relationships in the *Results*, we focus the *Discussion* on those relationships with a relevant amount of explanatory power (mostly $R^2_{adj} > 0.02$).

3.1 | Taxonomic groups

The *z*-values of the taxonomic groups differed significantly, whether tested across all available data sets (ANOVA) or only for those data sets in which vascular plants, bryophytes and lichens were sampled simultaneously (mixed-effects model with plot ID as a random factor; Figure 2). The highest *z*-values across all data sets in *S*-space were found in lichens (mean ± standard deviation: 0.28 ± 0.14, median: 0.25), followed by vascular plants (0.23 ± 0.10, median: 0.21) and bryophytes (0.19 ± 0.11, median: 0.17). The order was the same when considering only nested-plot series where all three taxonomic groups had data, with lichens (0.29 ± 0.15, median: 0.26) followed by vascular plants (0.22 ± 0.05, median: 0.21) and bryophytes (0.20 ± 0.11, median: 0.18).

3.2 | Biogeographic characteristics

For vascular plants and bryophytes, *z*-values had a U-shaped, slightly negative relationship with *latitude* and a positive relationship with *elevation* (Figure 3 and Appendix S4). For lichens, the relationship between *z*-values and elevation was slightly hump-shaped, and the relationship with latitude was not significant (Appendix S4). For complete vegetation, only latitude showed a significant relationship, which was decreasing to slightly U-shaped (Appendix S4).

We found U-shaped relationships for *mean annual temperature*, *temperature seasonality* and *precipitation seasonality* in the case of vascular plants and bryophytes (Figure 3 and Appendix S4). Lichen *z*-values showed a U-shaped relationship only with temperature seasonality (Appendix S4). By contrast, the *z*-values of complete vegetation were negatively related to temperature seasonality and showed a U-shaped relationship with precipitation seasonality (Appendix S4). Only vascular plant *z*-values showed a significant, hump-shaped relationship with *mean annual precipitation* (Figure 3, Appendix S4).

3.3 | Ecological characteristics

For vascular plants and complete vegetation, *z*-values had hump-shaped relationships with *soil pH* (Figure 3, Appendix S4), while bryophytes and lichens did not show a significant pattern with this variable (Appendix S4). For vascular plants and complete vegetation, *z*-values had a negative and in the latter case slightly U-shaped

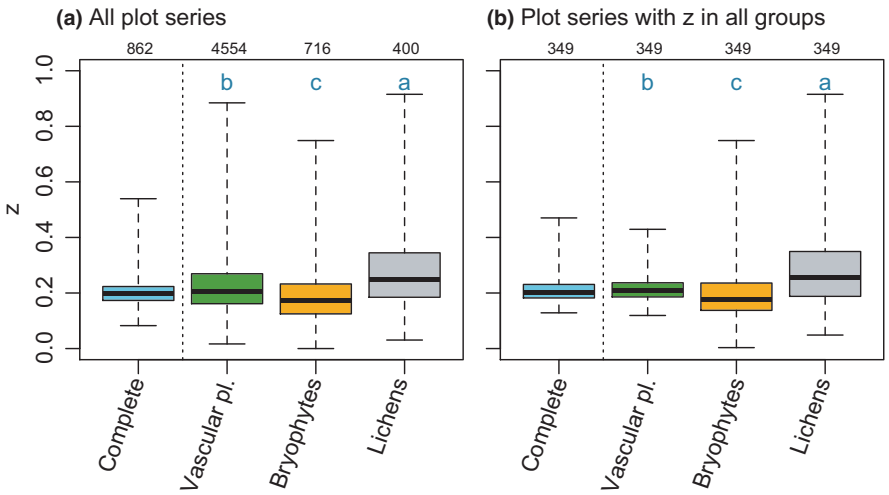


FIGURE 2 Differences in *z*-values (modelled in *S*-space) among the three taxonomic groups: vascular plants, bryophytes and lichens, and all these groups pooled together (a) across all available nested-plot series and (b) for the series with simultaneous data of all groups (note that the number of replicates in [b] is lower than for complete vegetation in [a] as in many plots bryophytes and lichens were considered, but absent). The values on top indicate the numbers of nested-plot series used, while the blue lowercase letters indicate significant differences among groups ($p < 0.05$) as tested with a Tukey post hoc test with ANOVA for (a) and a linear mixed effect model with plot series ID as random effect (on intercept) for (b)

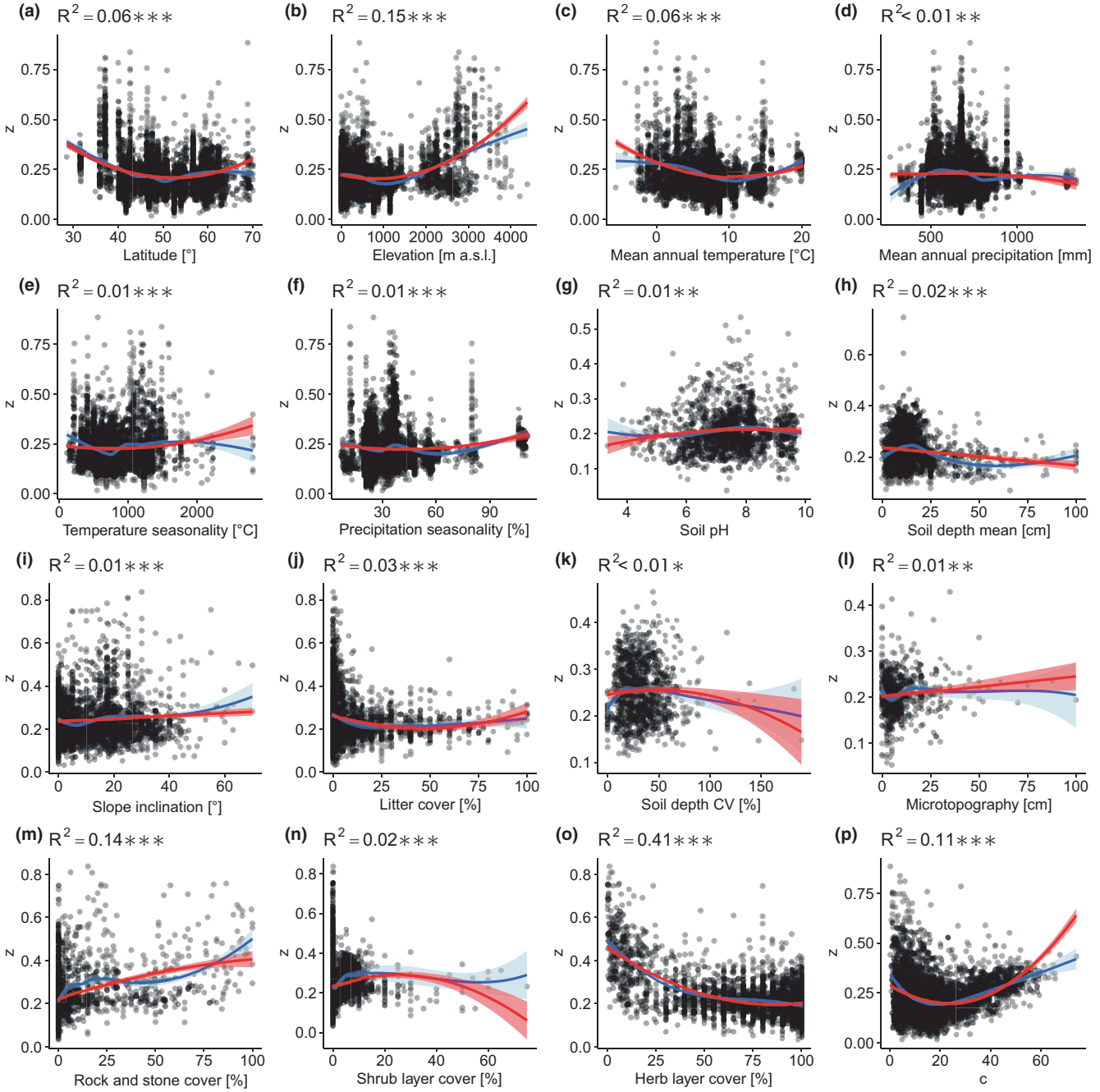


FIGURE 3 *z*-Values for vascular plants (modelled in *S*-space) in relation to: (a) latitude, (b) elevation, (c), mean annual temperature, (d) mean annual precipitation, (e) temperature seasonality, (f) precipitation seasonality, (g) soil pH, (h) soil depth mean, (i) slope inclination, (j) litter cover, (k) soil depth CV, (l) microtopography, (m) rock and stone cover, (n) shrub layer cover, (o) herb layer cover, and (p) *c*-value (= modelled richness at 1 m², as measure of α-diversity). Red lines indicate significant linear, hump-shaped or U-shaped relationships ($p < 0.01$) with confidence intervals, while the blue lines represent local polynomial regression with confidence intervals

relationship with *soil depth* (Figure 3, Appendix S4). By contrast, *z*-values of bryophytes and lichens were not related to *soil depth* (Appendix S4). *Fertilized* grasslands had significantly lower *z*-values in vascular plants than *unfertilized* ones (mean values: 0.15 vs 0.23; Appendix S4; no significant patterns in the other groups due to the low number of replicates). For vascular plants, *z*-values had a strongly decreasing and slightly U-shaped relationship with *herb layer cover* (Figure 3), while the relationship was insignificant for bryophytes, increasing for lichens and hump-shaped for complete vegetation (Appendix S4).

Across all taxonomic groups, *z*-values were positively related to *slope inclination* (Figure 3, Appendix S4). However, the smoothed curve for vascular plants shows that in the flattest areas (slope inclination <7°), the relationship was negative (Figure 3). The *z*-values

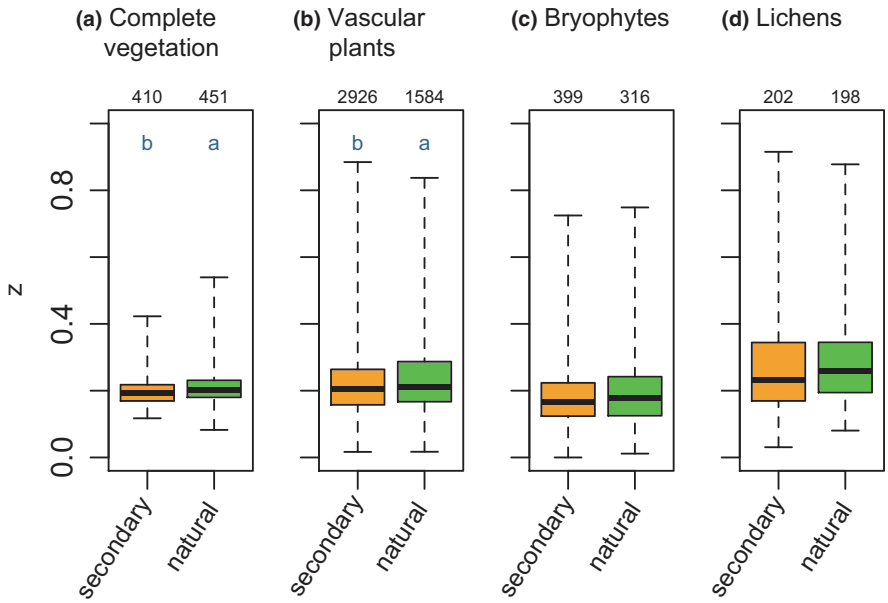


FIGURE 4 Differences of *z*-values (modelled in *S*-space) between secondary and natural grasslands for the four taxonomic groups: (a) complete vegetation, (b) vascular plants, (c) bryophytes, and (d) lichens. The numbers on top indicate the numbers of nested-plot series used, while different letters indicate significant differences between the groups

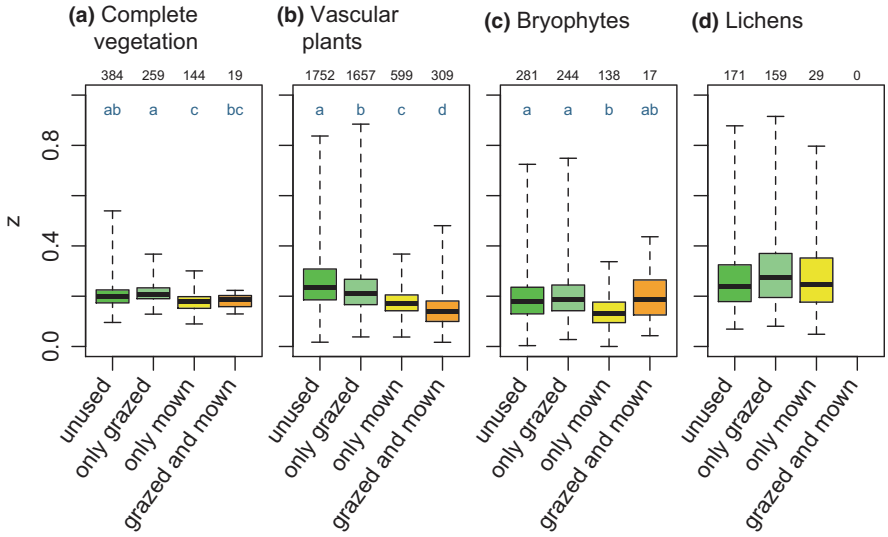


FIGURE 5 Effect of grazing and mowing on *z*-values (modelled in *S*-space) for the four taxonomic groups: (a) complete vegetation, (b) vascular plants, (c) bryophytes, and (d) lichens. The figures on top indicate the numbers of nested-plot series used, while different letters indicate significant differences among groups according to the post hoc test

of vascular plants had a U-shaped relationship with *litter cover*, with a strongly negative influence of this factor in the range from 0% to 20% indicated by the smoothing function (Figure 3). There was a similar U-shaped relationship for bryophytes, increasing from 20% cover (Appendix S4), while the relationship was positive for lichens and complete vegetation (Appendix S4). *Natural grasslands* had significantly higher *z*-values than secondary ones for vascular plants and complete vegetation (Figure 4). Moreover, for vascular plants, there was a strong and consistent decrease in *z*-values with increasing land use intensity both within the natural and the secondary grasslands (Appendix S4). The *z*-values of vascular plants were clearly influenced by *livestock grazing* and *mowing*, with the highest values found in unused grasslands, followed by only grazed and only mown grasslands and finally those subject to both management techniques (Figure 5). For the two other taxonomic groups and the complete vegetation, the patterns were less pronounced, but with a tendency toward higher *z*-values in grazed-only grasslands (Figure 5). For *burning*, we did not find an effect on *z*-values, except in bryophytes where unburned grasslands had significantly lower values than burned ones (Appendix S4).

Soil depth CV had a weak hump-shaped effect for *z*-values of vascular plants, but a positive one on those of complete vegetation (Figure 3, Appendix S4). *Microtopography* was a positive predictor for *z*-values of vascular plants and complete vegetation, while for bryophytes the relationship was slightly hump-shaped, and for lichens, it was non-significant (Figure 3, Appendix S4). For vascular plants, bryophytes and complete vegetation, *z*-values increased monotonically with *rock and stone cover*, while there was no relationship for lichens (Figure 3, Appendix S4). For vascular plants and bryophytes, *z*-values had a hump-shaped relationship with shrub cover, while for lichens and complete vegetation it was positive (Figure 3, Appendix S4).

3.4 | α-diversity

The z-values exhibited a strong relationship with the *c-values of the power model*, i.e. the modelled richness at 1 m². For vascular plants, bryophytes and lichens individually, the relationship was U-shaped with minima around 20 species for vascular plants and about 10 species for each of the non-vascular groups (Figure 3, Appendix S4). By contrast, for complete vegetation, the relationship was linear negative (Appendix S4).

3.5 | Explanatory power of the different predictors

Overall, the explanatory power of the bivariate models was relatively low, with R^2_{adj} ranging from <0.01 to 0.41 (Appendix S6). The mean predictive power of the 16 bivariate regressions was 0.07 for vascular plants, 0.02 for bryophytes, 0.02 for lichens and 0.03 for complete vegetation (Figure 3, Appendix S4). The highest explained variance of *z*-values of vascular plants was found for herb layer cover ($R^2_{adj} = 0.41$), followed by naturalness at the fine level (0.18), elevation (0.15), rock and stone cover as well as grazing and mowing (both 0.14) and the *c*-value (0.11). The variable with the highest R^2_{adj} value for bryophyte and lichen *z*-values was the *c*-value ($R^2_{adj} = 0.08$ and 0.16, respectively), while all other predictors had $R^2_{adj} < 0.06$ (Appendix S6). The variables with the highest R^2_{adj} for complete vegetation were soil depth CV ($R^2_{adj} = 0.10$), followed by inclination and grazing/mowing (both 0.06).

4 | DISCUSSION

4.1 | Explanatory power

Although many of the tested variables, representing both biogeographical and local habitat characteristics, were significant, the explanatory power of these bivariate models was low, with only few variables exceeding 10% explained variance. This is in striking contrast to macroecological studies of coarse-grain α- and β-diversity, which often find R^2_{adj} values above 50% with only one or a few predictors (Pinto-Ledezma et al., 2018). There are only few large-extent, fine-grain studies in macroecology (Beck et al., 2012), and thus few examples of how much explained variance one can expect. Bruelheide et al. (2018), in a global study of community-weighted means of traits, found that none of 30 tested environmental variables explained more than 10% of the total variance, and all 30 together only 10.8%. Reasons for the relatively low explained variance in fine-grain macroecological studies include the possible effects of other unmeasured factors, such as legacy effects, influences of the surroundings, and interspecific interactions, and a spatial mismatch between the environmental predictors (mostly derived from coarse- or at best medium-grain global databases) and the fine-grain biodiversity response variables. In this respect, analyses based on GrassPlot have the advantage that, unlike those in Bruelheide et al. (2018; based on sPlot), they contain numerous well-curated in-situ determined predictor variables (soil, microtopography, heterogeneity, land use, vegetation structure), which coincides with the relatively higher explained variance in our case. However, for climatic variables, we also had to rely on coarser-grain data, despite it being known that temperature can strongly vary across short distances, particularly in mountains (Opedal et al., 2015). As we tested numerous variables that cover a wide range of different aspects, including many that typically yield high explanatory power for different facets of biodiversity, both in classical macroecological (large extent, coarse grain) and vegetation ecological (small extent, fine grain) studies, we doubt that other variables individually would yield much higher R^2 values. Rather, we assume that relatively low explained variance will be a typical outcome of large-extent, fine-grain studies.

4.2 | Mechanisms driving variation in *z*-values

The relationships between β-diversity and a wide range of predictor variables at any grain size are interpretable through the influence of these variables on mean occupancy, which determines β-diversity (Storch, 2016). At fine spatial scales one can decompose the spatial arrangement of plant communities into three different aspects that together make up mean occupancy: (a) total cover; (b) mean size of individuals; and (c) similarity of species composition between adjacent subplots. While the relationships between these three aspects and mean occupancy are mathematically self-evident (right part of Figure 6, Appendix S7), the open question prior to our study was how various environmental drivers or species properties would influence one or several of these aspects. Inspired by our findings and theoretical considerations, we have developed a conceptual model (Figure 6), which is able to explain some surprising outcomes of our study. For example, variables could have no or very weak effects when positive and negative influences on mean occupancy cancel themselves out, while some "aggregated" variables could have unexpectedly strong effects when they influence mean occupancy consistently via more than one pathway. While the left and middle parts of Figure 6 are consistent with our findings, they should be seen as a set of testable hypotheses. In the following we will discuss our individual findings in this framework.

4.3 | Taxonomic groups

The *z*-values differed significantly among taxonomic groups (lichens > vascular plants > bryophytes). A study at much coarser grain sizes (regional to continental) by Patiño et al. (2014) found similar *z*-values of 0.18 and 0.21 for the two lineages of bryophytes (i.e. liverworts and mosses) and 0.21 and 0.33 for the two lineages of vascular plants (i.e. pteridophytes and spermatophytes). Patiño et al. (2014) attributed the flatter SARs of liverworts, mosses and

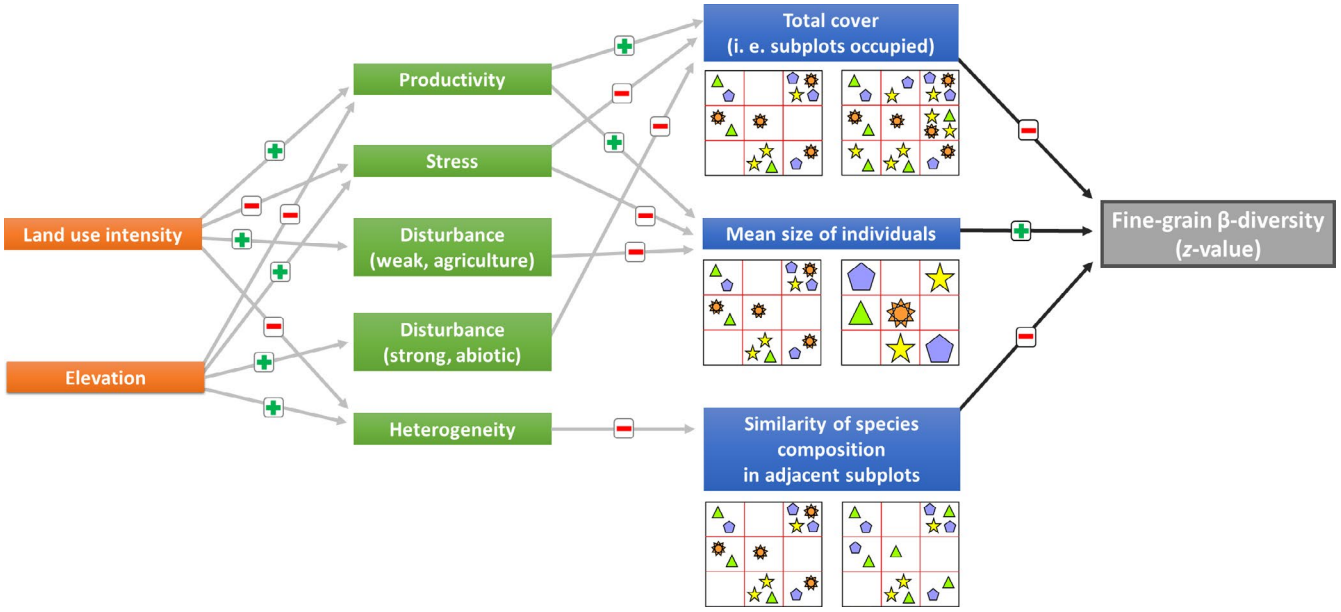


FIGURE 6 Conceptual figure summarizing our hypotheses how different drivers could influence fine-grain β-diversity via changing mean occupancy of species, based on the findings of our study and theoretical considerations. Fine-grain β-diversity (and likewise for larger grain sizes) is mathematically linked to mean occupancy, which can be decomposed into (i) total cover; (ii) mean size of individuals; and (iii) similarity of species composition between adjacent subplots. These three aspects of mean occupancy again are affected by the environmental drivers: productivity, stress, disturbances as well as heterogeneity (green). Note that disturbance can have contrasting effects depending on its type and intensity. To the very left we exemplify how two aggregated environmental parameters, land use intensity and elevation (orange), via multiple pathways could influence fine-grain β-diversity. What we mean with the three aspects that make up mean occupancy is illustrated with a pair of figures showing to the left a situation with low and to the right with high value of the respective aspect. The four different symbols represent individuals of four species distributed in a vegetation plot of a total extent of $A_\gamma = 9$ and assessed also at a grain size of $A_\alpha = 1$. Influences of one parameter are indicated by the arrows with their + and − symbols, with grey arrows corresponding to ecological hypotheses and black arrows to strict mathematical relationships. We did not aim to display all possible relationships in this figure, but concentrated on those that we consider most important. The expected effect of a certain driver or aggregated environmental parameter on fine-grain β-diversity can be estimated by multiplying the +/-

pteridophytes to their higher long-distance dispersal capabilities via spores compared to spermatophytes via seeds or other much heavier diaspores. Dispersal limitation might also play a role at short distances, particularly when considering that the majority of vascular plants are spreading clonally. While our small-grain *z*-values for bryophytes (0.19) were similar to the coarse-grain values of Patiño et al. (2014), those for vascular plants (0.23) were much lower than their coarse-grain results for spermatophytes (the dominant group of vascular plants: 0.33). We are not aware of any coarse-grain study of SARs of lichens, but since they are also mainly distributed via spores or small vegetative diaspores, one should assume low *z*-values similar to those of bryophytes and pteridophytes. The finding that lichens show the highest fine-grain *z*-values (0.28) among the three taxa is probably because they are mostly restricted to a few microhabitats with reduced competition by vascular plants and bryophytes, typically around rock outcrops or on shallow, open soil (i.e. in patches with strong abiotic stress). In such microhabitats, not only one but a whole array of lichen species can occur, leading to a steep SAR (i.e. high *z*-value). We thus hypothesize that the two main traits influencing fine-grain β-diversity of species groups are their mean dispersal distance and their mean niche breadth (Appendix S7).

4.4 | Biogeographic characteristics

Among the climate variables, mean annual temperature had the strongest influence on *z*-values with a U-shaped relationship. This could indicate that environmental stress leads to higher *z*-values. At the low end of the gradient, coldness would directly represent the stress, while at the high end drought effects might be the stress factor. By contrast, *z*-values showed only very weak relationships with the other three climatic factors, which highlights that there might not be a direct relationship between macroclimate and fine-grain *z*-values.

The minima of the U-shaped relationships of *z*-values of vascular plants, bryophytes and complete vegetation with latitude were around 50–55°N. This finding differs substantially from the strong negative relationship known for coarse-grain β-diversity in plants (Qian & Ricklefs, 2007; Qian, 2009) as well as across taxa and scales (meta-analysis by Drakare et al., 2006). Qiao et al. (2012), using nested plots from forests in China, found a negative relationship between *z*-values and latitude for all vascular plants, trees and shrubs, but not for herbaceous plants. The difference between our results and the two studies (Drakare et al., 2006; Qiao et al. 2012) could stem from the different ranges in latitude (Drakare et al., 2006:

0–60°; Qiao et al., 2012: 19–52° vs 35–70° in the present study). The poleward decrease until ca. 50–55° is consistent across all three studies, while the increase from the minimum towards the Arctic was missed by the other studies because their gradients did not extend so far poleward. Moreover, specifically for grasslands, higher land use intensity in the temperate zone (mainly between 45° N and 50° N) could have contributed to the reduced *z*-values there (see below).

We found an increase in fine-grain β-diversity of vascular plants and bryophytes with elevation, which contrasts with Moradi et al. (2020) for grasslands in Iran (2,000–4,500 m a.s.l.), Kraft et al. (2011) for forests in Ecuador (400–2300 m a.s.l.; only trees) and Qiao et al. (2012) for forests in China (300–3,150 m a.s.l.), who found decreasing *z*-values. However, it is in agreement with findings for *z*-values of vascular plants in the Karoo, South Africa (290–1800 m a.s.l.; van der Merwe & van Rooyen, 2011). We assume that the increasing fine-grain β-diversity with elevation can be explained by (a) the increased harshness of the climate with increasing elevation and resulting stress for plants, possibly impacting spatial patterns of plants (see above for latitude); (b) an increased role of facilitation leading also to clustered distributions of species (Anthelme et al., 2014); (c) higher species turnover at small distances in an increasingly rugged topography and thus stronger small-scale gradients of soil conditions, water availability and microclimate, which are generally much more pronounced at higher elevations (Körner, 2003); and (d) as for latitude, the natural patterns possibly being amplified by higher land use intensities at lower elevations.

4.5 | Stress–productivity

For vascular plants, the relationship with fertilization, soil depth mean and herb layer cover can be interpreted as a decrease in fine-grain β-diversity with higher productivity. A decrease in β-diversity means an increase in mean occupancy (Storch, 2016; Figure 6), which can happen either if all species become more frequent or if the rarest species are dropped out from the community due to asymmetric competition. Indeed, Filibeck et al. (2019) found that fine-grain *z*-values in Italian limestone grasslands were negatively correlated with soil depth, as deep-soil sites were colonized by competitive and patch-forming species, curtailing composition heterogeneity. In addition, Chiarucci et al. (2006) found a negative relationship between *z*-values and grassland productivity in Italy and Germany. By contrast, DeMalach et al. (2019), studying drylands worldwide with a different measure of β-diversity, found the opposite pattern, i.e. increasing β-diversity with higher cover. This discrepancy is hard to explain, but our data set is much more comprehensive in environmental space and numbers; thus we trust that our findings are more general. Finally, we only found a minimal effect of productivity-related predictors on the *z*-values of bryophytes and lichens. A possible explanation could be that the direct effects of productivity are counteracted by the opposing effects of increased herb layer cover, which increases the stress for bryophytes through lower light availability.

4.6 | Disturbance

We found that natural grasslands had higher fine-grain β-diversity than secondary grasslands whose existence depends on anthropogenic biomass removal. For vascular plants, grazing and mowing both affected *z*-values negatively, but more strongly for mowing. Thus, we conclude that land use by humans on average reduces fine-grain β-diversity in open vegetation. It is understandable that mowing particularly strongly decreases *z*-values as it removes above-ground biomass non-selectively, thus reduces interspecific competition (Wilson et al., 2012), thereby increasing stand homogeneity. Besides actual disturbance effects, livestock grazing can create some heterogeneity in comparison to meadows, e.g. due to selective feeding, the heterogeneous trampling intensity and patchy distribution of excrements (Gillet et al., 2010; Tälle et al., 2016). While land use parameters yielded R^2_{adj} values of up to 0.20, the explained variances of our two other measures related to disturbance, slope inclination and litter cover were 0.03 or less, indicating that agricultural disturbances have a different influence on *z*-values than abiotic disturbances.

4.7 | Heterogeneity

Assuming that heterogeneity increases *z*-values, we expected larger *z*-values to be associated with high soil depth CV, high microtopography, intermediate rock and stone cover and intermediate shrub cover. However, we mostly found very weak or no effects, with explained variances of 0.02 or less, which contrasts with some geographically or ecologically narrower studies (Harner & Harper, 1976; Polyakova et al., 2016). Only rock and stone cover had a moderate effect in the case of vascular plants ($R^2_{adj} = 0.14$) and complete vegetation (0.05), but, contrary to our assumption, we found the highest *z*-values at close to 100% rocks and stones. This is logical due to the negative relationship between z-values and mean occupancy: the less space is available for plants to grow inside a plot, the lower the mean occupancy and logically, but counter-intuitively, the higher the *z*-value.

4.8 | α-Diversity

The *z*-values showed an unexpected U-shaped relationship with the *c*-values (except for complete vegetation). This second parameter of the power function represents the intercept in the log–log representation or, in other words, the species richness at the unit area (in our case: 1 m²), which one could call α-diversity. If the total species richness of whole plots ("γ-diversity") was constant, a higher value of the slope parameter would necessarily lead to a lower intercept, so that the relationship between *z* and *c* would be negative. Since γ-diversity varies considerably across the Palaearctic, more complex patterns are possible. While moderately species-rich plots located in suboptimal/stressful conditions indeed had the expected negative relationship between *z* and *c*, there were some plots characterized by both high *c* and z, which means that these plots must also

have exceptionally high total richness. This indicates that the most species-rich plots are characterized by a prevalence of subordinate species with low mean occupancy. Our finding contrasts with the strong negative relationships between *z* and *c* recently reported for island SARs of archipelagos across the globe (Matthews et al., 2019b), where γ-diversity also varied substantially. The reason for the discrepancy is unknown, but it could be related to the differences in scale and SAR type.

4.9 | Conclusions and outlook

While, before our study, there was only scattered and inconclusive knowledge and hardly any theory about drivers of fine-grain *z*-values, our comprehensive study has now enabled us to propose a theory consisting of a set of hypotheses that are in agreement with our findings (Figure 6, Appendix S7). In the future, the validity of these hypotheses should be tested with observational or, even better, experimental studies. While our findings partly concur with those from coarse-grain β-diversity studies, we found substantial differences for biogeographic variables. Whereas coarse-grain β-diversity typically declines with elevation (Tello et al., 2015; Sabatini et al., 2018) and latitude (Qian & Ricklefs, 2007; Qian, 2009), fine-grain β-diversity increased monotonously with elevation and showed a U-shaped relationship with latitude. Similar scale dependence of drivers is well known for α-diversity (Field et al., 2009; Siefert et al., 2012). It will be interesting to determine at which grain size the positive effect of elevation on fine-grain β-diversity turns into a negative effect.

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AUTHOR CONTRIBUTIONS

JDe conceived the idea of this paper and initiated the data collection. Most authors contributed data, while JDe served as custodian and IB as database manager of the GrassPlot database. MJS and TJM conducted the statistical analyses, ID and JDe led the writing. All authors checked, improved and approved the manuscript.

DATA AVAILABILITY STATEMENT

The data used in this paper are derived from the collaborative vegetation-plot database GrassPlot (Dengler et al., 2018; Biurrun et al., 2019), version 2.02. They can be requested from GrassPlot with a project proposal following the GrassPlot Bylaws (see https://edgg.org/databases/GrassPlot).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

Appendix S1. Summary of previous findings for fine-grain β-diversity (z-values) in relationship to the predictors analysed in our study

Appendix S2. Additional information on the origin of the analysed nested-plot series

Appendix S3. Detailed overview of the considered predictor variables

Appendix S4. Additional results in *S*-space

Appendix S5. Analyses of z-values modelled in log *S* -space

Appendix S6. The numeric outputs of all analyses in *S* -space and log *S* -space

Appendix S7. Conceptual figure illustrating how different drivers could influence fine-grain β-diversity (expanded version)

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