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RESEARCH PAPER

CLASSIFICATION OF OPEN HABITATS IN THE PALAEARCTIC

Fine-grain beta diversity in Palaearctic open vegetation: variability within and between biomes and vegetation types

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Abstract

Aims: To quantify how fine-grain (within-plot) beta diversity differs among biomes and vegetation types. **Study area:** 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 spanning broad geographic and ecological gradients. Next, we calculated the slope parameter (*z*-value) of the power-law species–area relationship (SAR) to use as a measure of multiplicative beta diversity. We did this separately for vascular plants, bryophytes and lichens and for the three groups combined (complete vegetation). We then tested whether *z*-values differed between biomes, ecological-physiognomic vegetation types at coarse and fine levels and phytosociological classes. **Results:** We found that *z*-values varied significantly among biomes and vegetation types. The explanatory power of area for species richness was highest for vascular plants, followed by complete vegetation, bryophytes and lichens. Within each species group, the explained variance increased with typological resolution. In vascular plants, adjusted R^2 was 0.14 for biomes, but reached 0.50 for phytosociological

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classes. Among the biomes, mean *z*-values were particularly high in the Subtropics with winter rain (Mediterranean biome) and the Dry tropics and subtropics. Natural grasslands had higher *z*-values than secondary grasslands. Alpine and Mediterranean vegetation types had particularly high *z*-values whereas managed grasslands with benign soil and climate conditions and saline communities were characterised by particularly low *z*-values. **Conclusions:** In this study relating fine-grain beta diversity to typological units, we found distinct patterns. As we explain in a conceptual figure, these can be related to ultimate drivers, such as productivity, stress and disturbance, which can influence *z*-values via multiple pathways. The provided means, medians and quantiles of *z*-values for a wide range of typological entities provide benchmarks for local to continental studies, while calling for additional data from under-represented units.

Syntaxonomic references: Mucina et al. (2016) for classes occurring in Europe; Ermakov (2012) for classes restricted to Asia.

Abbreviations: ANOVA = analysis of variance; EDGG = Eurasian Dry Grassland Group; SAR = species-area relationship.

Keywords

biome, bryophyte, fine-grain beta diversity, GrassPlot, lichen, mean occupancy, Palaearctic grassland, phytosociological class, species–area relationship (SAR), vascular plant, vegetation type, *z*-value

Introduction

The Palaearctic biogeographic realm (*sensu* Olson et al. 2001) is the largest terrestrial realm on Earth, covering more than 52 million square kilometres or approximately 40% of the ice-free terrestrial surface of the globe. Its elevational extent ranges from the lowest (423 m b.s.l.; Dead Sea) to the highest (8,848 m a.s.l.; Mt. Everest) point of the terrestrial surface and is thus exceptionally large. The resulting environmental heterogeneity includes eight of the ten biomes recognised by Bruelheide et al. (2019) and translates into a huge diversity of vegetation types, ranging from single-species stands to those that hold the world records for vascular plant species richness at most grain sizes below 100 m^2 (Wilson et al. 2012; Roleček et al. 2021).

The GrassPlot database (Dengler et al 2018; Biurrun et al. 2019) contains high-quality, multi-scale vegetation-plot data of any type of grasslands and other non-forest habitats of the Palaearctic realm. The selection criteria of GrassPlot include 63% of the habitat diversity of Europe according to a current typology (Janssen et al. 2016), and the fraction probably would be higher for Northern Africa and extra-tropical Asia with their higher fractions of grasslands (Dengler et al. 2020b), tundras, semi-deserts and deserts. Through covering a diverse set of habitat types and providing high-quality data not only for vascular plants, but also for bryophytes and lichens sampled in the same plots, GrassPlot offers a unique framework to analyse plant diversity patterns and their drivers (Biurrun et al. 2021). This is readily evident for species richness, since GrassPlot provides thousands of comprehensively sampled plots at eight standard grain sizes from 0.0001 to 1,000 m^2, together with extensive environmental and structural *in situ* measured variables. However, even more unique is the fact that GrassPlot contains thousands of nested-plot series (see Biurrun et al. 2019), which allow the analysis of small-scale nested species-area relationships (SARs).

A recent study using GrassPlot (Dengler et al. 2020a) found that nested SARs at the mentioned spatial scales can be well described with a power law, $S = c\,A^z$, where S is species richness, A area and c and z modelled parameters (Arrhenius 1921; Dengler 2009). The exponent z only exhibits a small amount of scale dependence (Zhang et al. 2021), meaning that for most purposes it is adequate to assume z to be constant within the range of grain sizes included in GrassPlot. As well as being a parameter of the power-law SAR, the *z*-value, when calculated using nested-plot data, is also a measure of β-diversity (Jurasinski et al. 2009; Dembicz et al. 2021). In fact, the *z*-value measures multiplicative β-diversity, standardized by the grain size ratio (Polyakova et al. 2016; Dembicz et al. 2021). β-diversity quantifies the dissimilarity between local communities and, together with mean α-diversity, makes up the diversity of a larger area (γ-diversity) (Whittaker 1960). Understanding patterns and drivers of β-diversity is thus of high importance both for ecological theory and biological conservation.

According to Storch (2016), *z*-values are closely related to the mean occupancy of species, i.e. the rarer species are in the finest grain size on average, the higher the *z*-values are. Dembicz et al. (2021) analysed which factors influence small-grain *z*-values using the GrassPlot database and found that herb layer cover, elevation, rock and stone cover, latitude and land use had the greatest explanatory power. Based on these findings and mathematical considerations, the authors proposed a conceptual model of how different environmental factors jointly could influence *z*-values by modifying mean occupancy values. We now present a refined version (Figure 1) that summarizes our main hypotheses: While total vegetation cover and similarity of species in adjacent subplots should affect fine-grain *z*-values negatively, mean size of individuals should have a positive influence (Figure 1). Since productivity, stress or disturbance can influence these three variables via multiple pathways, the effects of the former can be amplified or cancelled out (Figure 1).

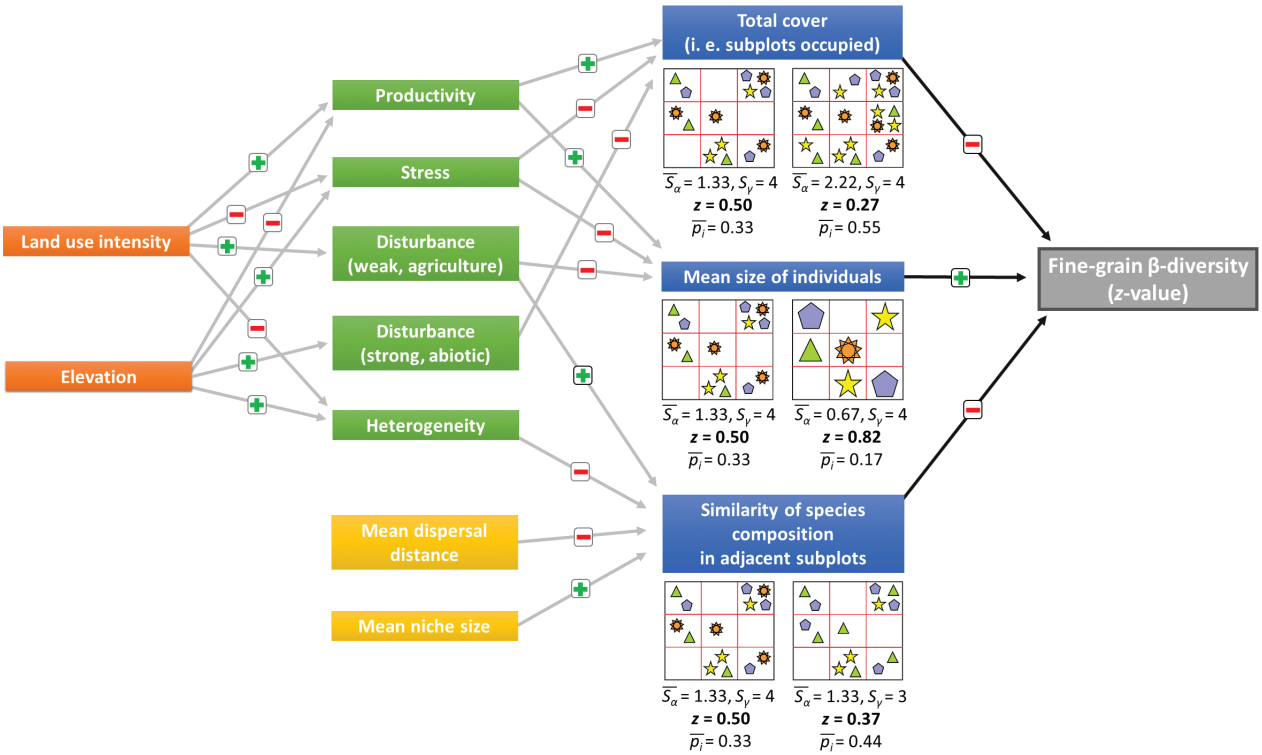

Figure 1. Conceptual figure summarizing our main hypotheses for how different drivers could influence fine-grain β-diversity via changing mean occupancy of species, based on the findings of Dembicz et al. (2021) and ecological theory. Fine-grain β-diversity (and likewise for larger grain sizes) is mathematically 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 are affected by the environmental drivers, productivity, stress, disturbances and heterogeneity (green), as well as the mean traits of the analysed species group, namely dispersal distance and niche size (yellow). 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), could influence fine-grain β-diversity via multiple pathways. 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 values of the respective aspect. The four different symbols represent individuals of four species distributed in a vegetation plot of a total extent of A_γ = 9 and assessed also at a grain size of A_α = 1. Below each community, we provide the corresponding $\overline{S}_\alpha$-, S_γ-, *z*-values as well as the mean occupancies ($\overline{p}_i$). Since $z = \log(S_\gamma/\overline{S}_\alpha) / \log(A_\gamma/A_\alpha)$ and $\overline{p}_i = \overline{S}_\alpha/S_\gamma$, it is obvious that higher $\overline{p}_i$ means lower *z* and vice versa. Influences of one parameter are indicated by the arrows with their + and – symbols; grey arrows correspond 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 +/- symbols along the path. If several paths connect to fine-grain β-diversity, their products should be summed (modified from Dembicz et al. 2021).

Dembicz et al. (2021) analysed the effects of environmental variables, such as climate, soil, topography and land use, on *z*-values, but they did not assess how *z*-values vary across typological units. Here, we address this question, using the same data. For this purpose, we selected three different typologies that are widely used and carry different but complementary information: (a) biomes (reflecting the climax vegetation according to the macroclimate; Schultz 2005; Hunter et al. 2021), (b) ecological-physiognomic vegetation types (at two levels of resolution) and (c) phytosociological classes (reflecting the actual species composition; see Dengler et al. 2008; Mucina et al. 2016). Based on the findings regarding environmental predictors (Dembicz et al. 2021) and our hypotheses on causal pathways (Figure 1), we have the following *a priori* expectations:

1. Among biomes, "Dry tropics and subtropics", "Subtropics with winter rain" and "Alpine" should have particularly high, and "Temperate mid-latitudes" particularly low, *z*-values.
2. Among vegetation types (ecological-physiognomic and phytosociological), those with more closed canopy should have lower *z*-values than those with more open ground; types of secondary grasslands should have lower *z*-values than those of natural grasslands.

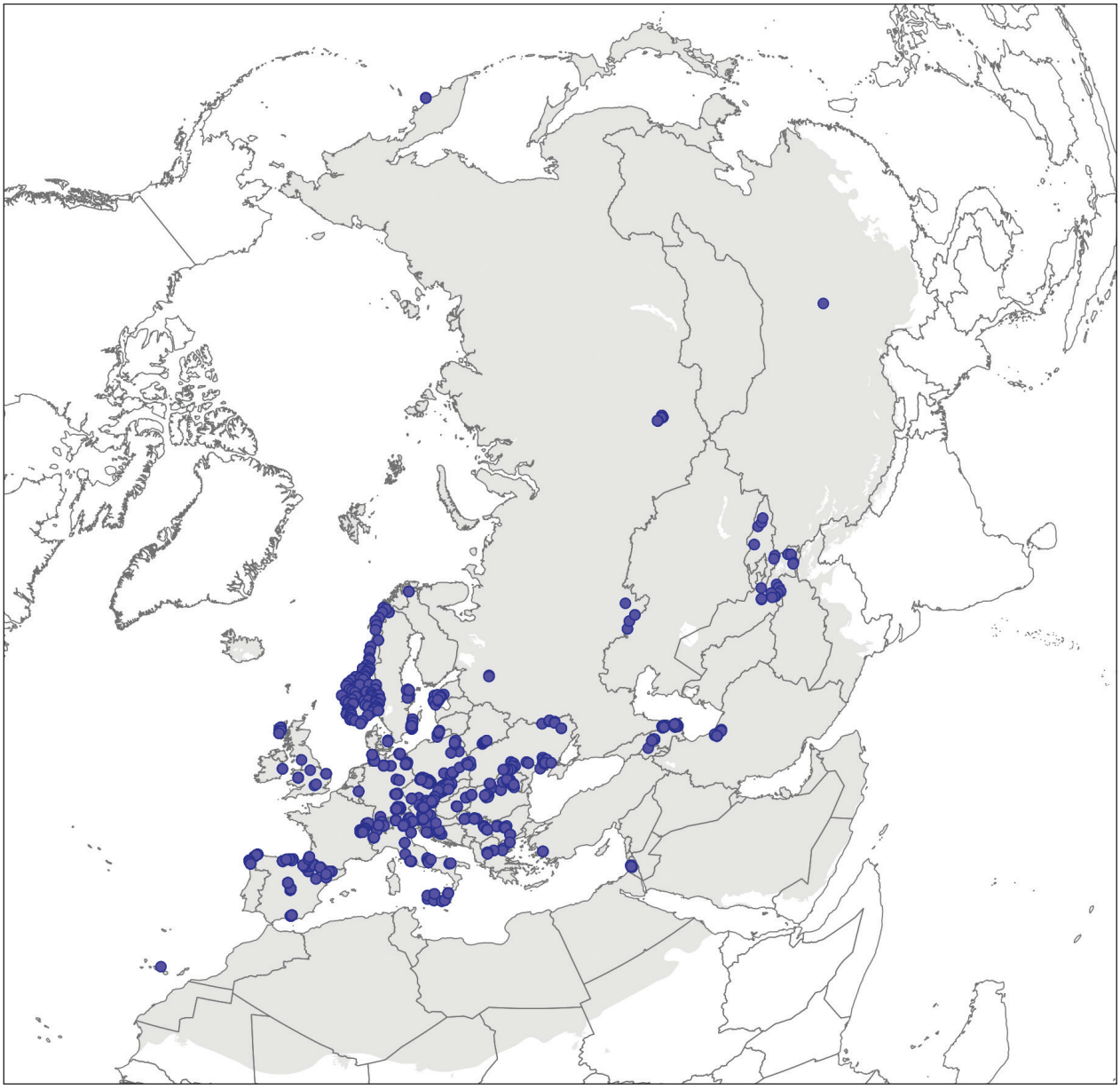

Figure 2. Geographic distribution of the 4,654 nested-plot series used in this study. The grey shading delimits the Palaearctic biogeographic realm.

Beyond testing these expectations, our aim is to provide information on typical *z*-values of biomes and vegetation types. This could help to detect habitat-specific deviations, related for example to anthropogenic disturbances (see, e.g., Tittensor et al. 2007) or invasive species (Powell et al. 2013).

Study area

The geographic scope of GrassPlot and of this study is the whole Palaearctic biogeographic realm. The nested-plot data used cover wide geographic gradients but have the highest density in Europe (Figure 2) with few plots in northern Africa or the eastern half of Asia. They are distributed across 34 different countries, from 28.5° to 70.0° N and 16.2° W to 161.8° E, and cover an elevation gradient from 0 to 4,387 m a.s.l. (Suppl. material 1).

Methods

Vegetation-plot data

We used plot data from the collaborative vegetation-plot database GrassPlot (Dengler et al. 2018; Biurrun et al. 2019; https://edgg.org/databases/GrassPlot). GrassPlot assembles vegetation-plot data from grasslands and other non-forest vegetation types (rocks and screes, deserts, ruderal communities, etc.) from the Palaearctic biogeographic realm. 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 ranging from 0.0001 to 1,024 m²). All series had information on *vascular plant*s, 890 on terricolous (soil-dwelling) *bryophytes*, 894 on terricolous *lichens*, and 862 on all three taxonomic groups (i.e. 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 species groups*.

For those nested-plot series with more than one plot for a certain grain size, we averaged richness values per grain size. Thus, we obtained one single richness value for each grain size within each nested-plot series for each of the sampled species groups.

SAR modelling

We fitted a power function to each dataset (i.e. a species group within a nested-plot series) using the non-transformed "*S*-space" ($S = c\,A^z$) and the "logarithmic *S*-space" ($\log_{10} S = \log_{10} c + z \log_{10} A$) with S = species richness, A = area in m², and c and z the fitted "intercept" and "slope" parameters, respectively. Both approaches are valid, have been widely used in the literature, and have different advantages 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 speaking, fitting in *S*-space gives more weight to a good fit at larger grain sizes, whereas fitting in log *S*-space gives more weight to a good fit at smaller grain sizes and typically reduces heteroscedasticity.

To fit the power model in log *S*-space, we used linear regression and the standard 'lm' function in R. The fitting in *S*-space followed the approach of Dengler et al. (2020a; see also Matthews et al. 2019). We applied non-linear regression using the 'mle2' function in the 'bbmle' R package (Bolker and R Core Team 2017). Starting parameter values were derived from 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 $S = 0$ (Dengler et al. 2020a). For both the *S*-space and log *S*-space fitted models, we obtained the *z*-values for further analyses.

Analyses of the *z*-values

We excluded nested-plot series with zero reported species for the investigated species 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). The latter was true for 0.01% of all series across the four species groups in log *S*-space and 0.25% in *S*-space. Consequently, for log *S*-space we obtained *z*-values for 4,570 series for vascular plants, 719 for bryophytes, 417 for lichens and 862 for complete vegetation, while for *S*-space we estimated *z*-values for 4,554 series for vascular plants, 716 for bryophytes, 400 for lichens and 862 for the complete vegetation. Note that in some cases taxonomic groups were searched for but did not occur; therefore, the number of series for complete vegetation is higher than the numbers for bryophytes or lichens.

We tested how the modelled *z*-values depended on biome and vegetation types of three different typologies. First, as a biome typology, we used the ecozones of Schultz (2005) with additional separation of an Alpine biome (Körner et al. 2017) – as implemented by Bruelheide et al. (2019). Further, we used the coarse and fine vegetation typology of GrassPlot (Biurrun et al. 2019), which is mainly based on ecological and physiognomic criteria (for details see Suppl. material 2). Lastly, we used the phytosociological classes. Plots were assigned to classes based on the information provided by data contributors, as well as by expert judgement based on floristic composition. Classes occurring in Europe were named after Mucina et al. (2016), classes restricted to Asia according to Ermakov (2012).

As the visual inspection of the boxplots did not yield severe violations of the assumptions of linear models (see Quinn and Keough 2002), we applied analyses of variance (ANOVAs) with the 'aov' function (R package 'stats'), followed by Tukey's HSD *post hoc* test using the functions 'TukeyHSD' (R package 'stats') and 'multcompLetters4' (R package 'multcompView'; Graves et al. 2019) to produce a letter-based representation of all-pairwise group comparisons. For the ANOVAs, we excluded some categories that had very few observations only (see details below).

For visualisation of the distribution of the observed values, we used violin plots, a method of plotting numeric data that is a hybrid of boxplots and kernel density plots, able to identify multimodality (R package 'ggplot2'; Thrun et al. 2020). The scale of the violin plots was set to "width".

To avoid strong unequal sample sizes and heterogeneous variances among categories when comparing taxa, which could make *F*-tests unreliable, we restricted comparisons to biomes, vegetation types and phytosociological classes represented in complete vegetation by at least ten nested-plot series. All computations were performed with R 4.1.1 (R Core Team 2021).

Results

As the results were qualitatively similar for log *S*-space and *S*-space, and as we had slightly more replicates for log *S*-space, we present the results from the ANOVAs and violin plots only for log *S*-space in the main text. Descriptive statistics (number of replicates, means, medians, 10% and 90% quantiles) for both spaces are provided in Suppl. material 3.

Vascular plants

The mean and median *z*-values of most biomes and vegetation types were around 0.25, although the range was

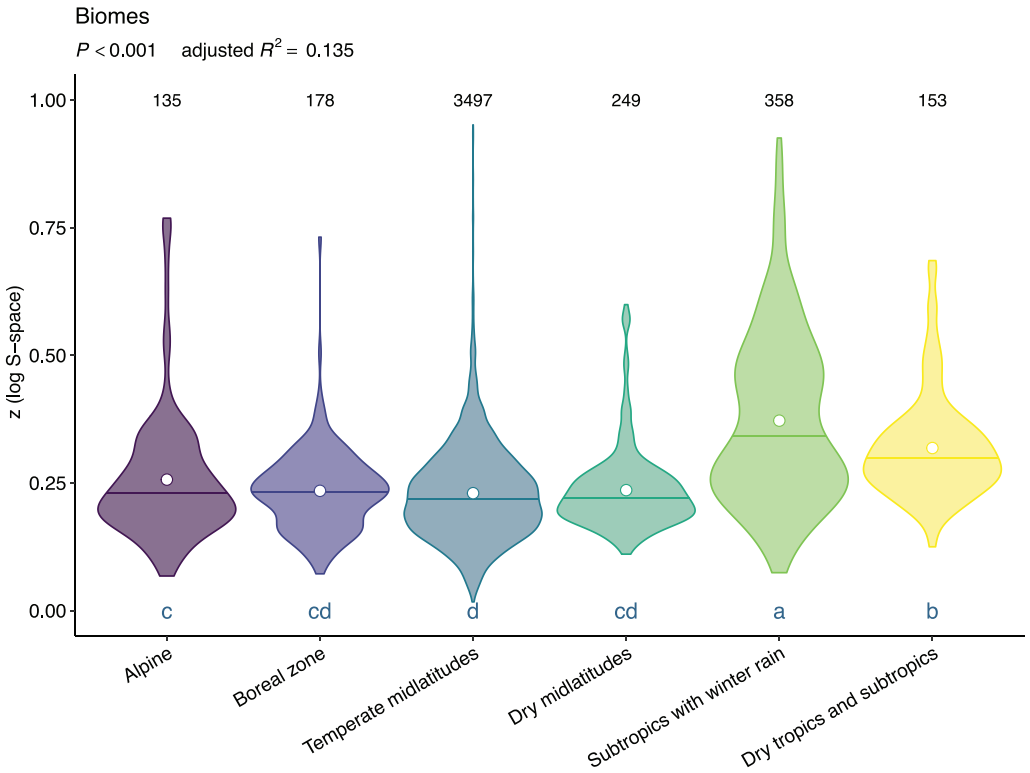

Figure 3. Comparison of fine-grain *z*-values of vascular plants between the biomes included in GrassPlot with suitable data. The biomes are sorted in descending order of latitude and elevation. The circles represent the means, the horizontal lines the medians and the letters homogeneous groups according to Tukey's HSD post hoc test following a significant ANOVA (in decreasing order). Numbers at the top of the violin plots indicate the number of nested-plot series in each biome.

from 0.15 to 0.50 (Figures 3–6). However, in most of the typological units, there was a large variation, with extreme values sometimes almost covering the entire theoretically possible range from 0 to 1 (Figures 3–6). Despite this variation, for each of the four typologies there were distinct groups that differed significantly in their mean *z*-values (Figures 3–6). The explanatory power of the typologies was relatively low for biomes and coarse-level vegetation types ($R^2 = 0.14$), intermediate for fine-level vegetation types ($R^2 = 0.36$) and high for phytosociological classes ($R^2 = 0.50$).

Among the biomes, the Temperate midlatitudes had the lowest mean *z*-value, but were hardly different from Alpine, Boreal zone and Dry midlatitudes (Figure 3). By contrast, the vegetation of the Dry tropics and subtropics, and particularly the Subtropics with winter rain, had clearly higher *z*-values (Figure 3). Among the coarse-level vegetation types, natural grasslands had clearly the highest mean *z*-values, followed by dwarf shrublands, whereas azonal communities had the lowest values (Figure 4). Among the fine-level vegetation types, Mediterranean grasslands, alpine grasslands and garrigues and thorn-cushion communities had particularly high *z*-values, while saline communities and saline steppes and semi-deserts had particularly low values (Figure 5). Among the phytosociological classes, the Mediterranean class *Stipo-Trachynietea* and the high-elevation classes *Festucetea indigestae* and *Carici-Kobresietea* had particularly high *z*-values, followed by *Juncetea trifidi* and *Sedo-Scleranthetea*, while the saline classes *Festuco-Puccinellietea* and *Juncetea maritimi*, as well as the mesic secondary grassland classes *Molinio-Arrhenatheretea* and *Nardetea strictae*, had particularly low *z*-values (Figure 6).

The four species groups in comparison

For all four vegetation typologies considered, the explained variance was highest for vascular plants, followed by complete vegetation, whereas it was relatively low in bryophytes and lowest in lichens (Suppl. material 4: Figures S4.1–S4.4). For the four biomes with sufficient data, the pattern was similar among all four species groups with the Subtropics with winter rain always being in the group of highest *z*-values (Suppl. material 4: Figure S4.1). For coarse-level vegetation types, vascular plants, bryophytes and complete vegetation showed a similar pattern of decreasing *z*-values from natural grasslands via secondary grasslands to azonal communities, whereas the three other categories (with much fewer observations) were at an intermediate position (Suppl. material 4: Figure S4.2). By contrast, lichens did not differ significantly in their mean *z*-values among coarse-level veg-

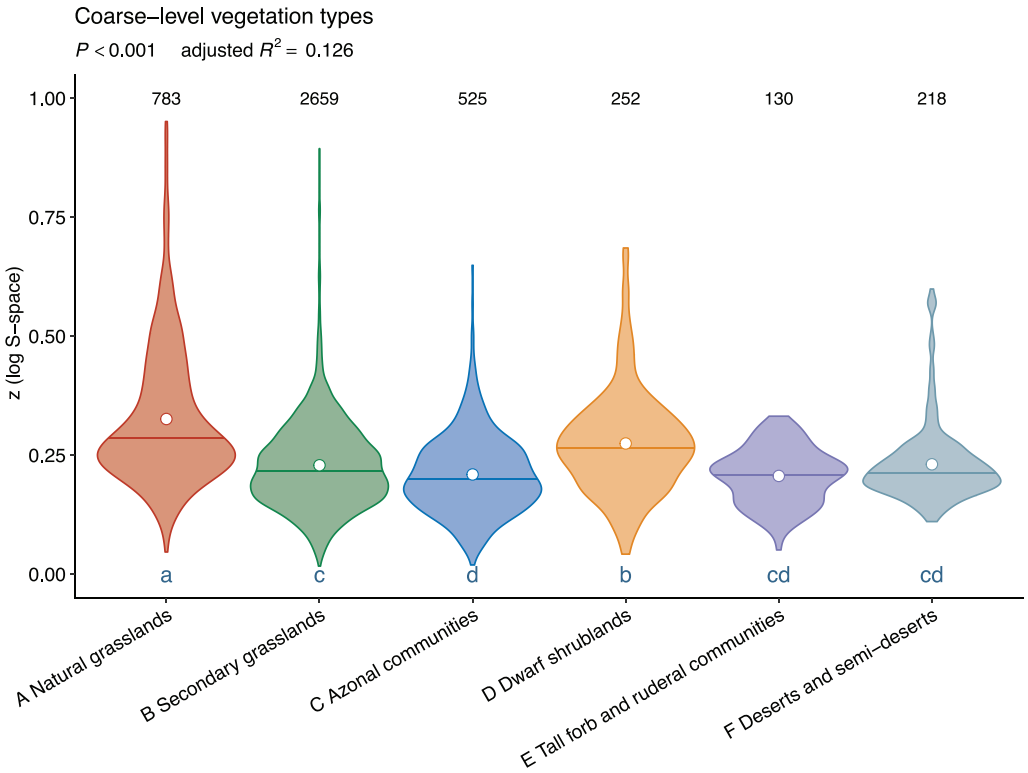

Figure 4. Comparison of fine-grain *z*-values of vascular plants between the six coarse-level vegetation types distinguished in GrassPlot. The circles represent the means, the horizontal lines the medians and the letters homogeneous groups according to Tukey's HSD post hoc test following a significant ANOVA (in decreasing order). Numbers at the top of the violin plots indicate the number of nested-plot series in each coarse-level vegetation type.

etation types (Suppl. material 4: Figure S4.2). Likewise, for fine-level vegetation types, the patterns for complete vegetation, vascular plants and bryophytes were similar, with Mediterranean and rocky grasslands having the highest *z*-values (Suppl. material 4: Figure S4.3). Finally, when analysing the phytosociological classes, across all four species groups, the *Sedo-Scleranthetea* had the highest *z*-values (sometimes together with other classes), whereas *Molinio-Arrhenatheretea*, *Nardetea strictae* and *Scheuchzerio-Caricetea* had particularly low *z*-values (Suppl. material 4: Figure S4.4).

Discussion

Overall patterns

Similar to previous studies, we found large variation in *z*-values within most of the typological units considered (Schmiedel et al. 2010; Dengler et al. 2012; Pedashenko et al. 2013). Whereas the only two previous studies that to our knowledge tested for differences in fine-grain *z*-values between vegetation types had not reported any significant differences (Dengler et al. 2012; Pedashenko et al. 2013), we found highly significant differences, which in the case of vascular plants explained more than half of the overall variance. These contrasting results can be attributed to (i) our much larger sample size, which allowed for detection of differences despite the strong variation within typological units, and (ii) our more diverse array of phytosociological classes, thus longer gradients. By contrast, the former study that compared *z*-values between biomes had also found significant differences (Schmiedel et al. 2010).

Second, we found that the explained variance increased the finer resolved our typology was: while biomes explained only around 14% of the variance, phytosociological classes accounted for more than 50%. This finding is not surprising and mainly reflects that our typological units are meaningful entities that differ in their vegetation patterns as well as their average productivity, stress and disturbance (see Dengler et al. 2008; De Cáceres et al. 2015), all of which affect *z*-values (see Figure 1). The relatively small amount of variance explained by biome indicates that, for *z*-values, macroclimate is less important than local conditions, such as soil and water conditions, as well as disturbance regimes due to management.

Third, we found a clear decrease in explained variance (or in other words, in distinctness of the patterns) from vascular plants via complete vegetation to bryophytes and lichens. This is consistent with findings of two previous GrassPlot studies that looked at other aspects of fine-grain *z*-values (Dembicz et al. 2021; Zhang et al. 2021). Partially, this might be explained by the fact that, due to the generally low replication of smaller plots within a nested plot series

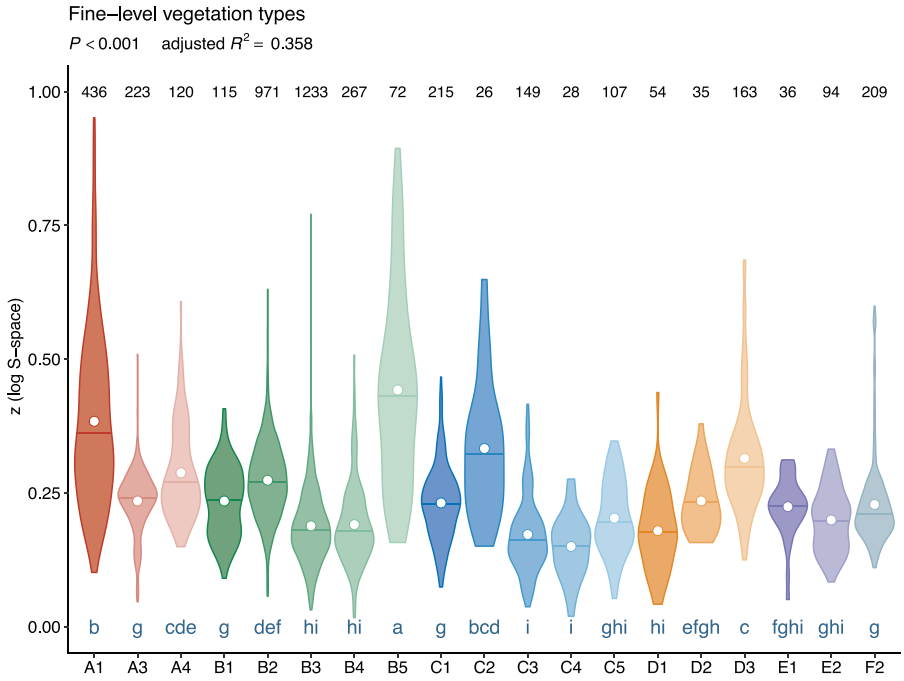

Figure 5. Comparison of fine-grain *z*-values of vascular plants between those fine-level vegetation types distinguished in GrassPlot that were represented by at least 10 observations. A1 = alpine grasslands, A3 = xeric grasslands and steppes, A4 = rocky grasslands, B1 = sandy dry grasslands, B2 = meso-xeric grasslands, B3 = mesic grasslands, B4 = wet grasslands, B5 = Mediterranean grasslands, C1 = dunes, C2 = rocks and screes, C3 = saline communities, C4 = saline steppes and semi-deserts, C5 = wetlands, D1 = lowland heathlands, D2 = arctic-alpine heathlands, D3 = garrigues and thorn-cushion communities, E1 = tall forb communities, E2 = ruderal communities, F2 = cold deserts and semi-deserts. The circles represent the means, the horizontal lines the medians and the letters homogeneous groups according to Tukey's HSD post hoc test following a significant ANOVA (in decreasing order). Numbers at the top of the violin plots indicate the number of nested-plot series in each fine-level vegetation type.

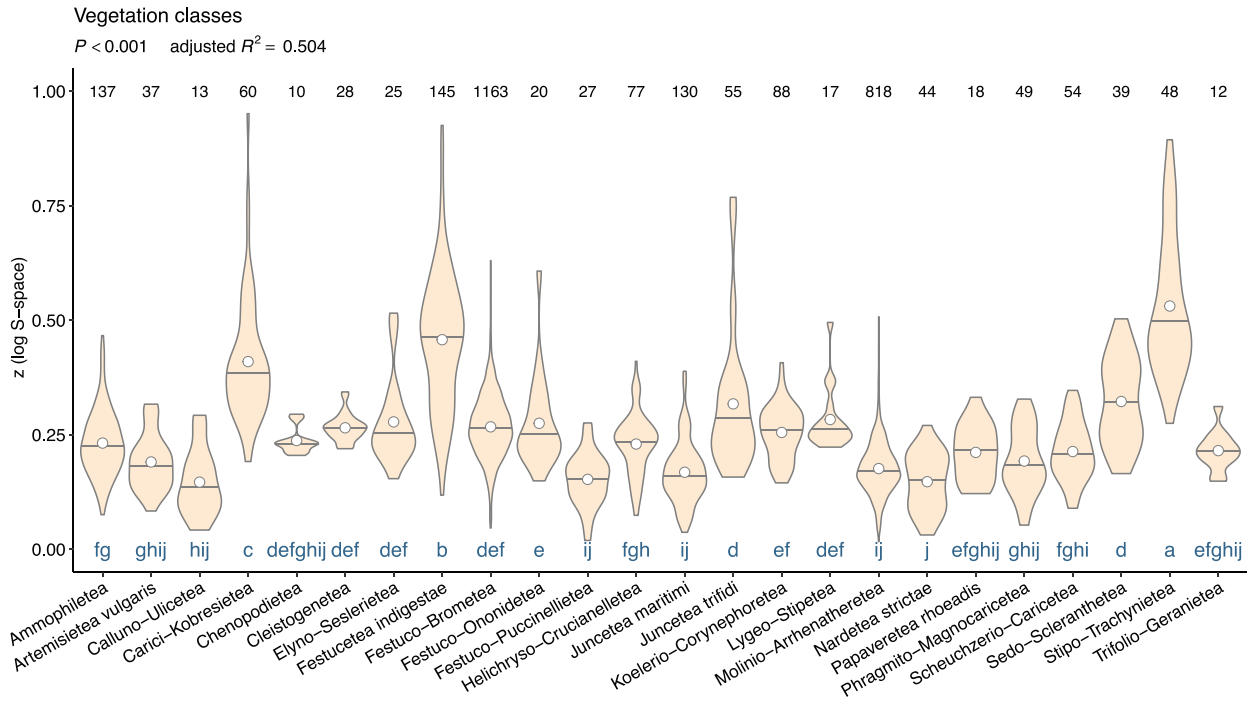

Figure 6. Comparison of fine-grain *z*-values of vascular plants between those phytosociological classes that were represented by at least 10 observations. The circles represent the means, the horizontal lines the medians and the letters homogeneous groups according to Tukey's HSD post hoc test following a significant ANOVA (in decreasing order). Numbers at the top of the violin plots indicate the number of nested-plot series in each phytosociological class.

(typically only two replicates), there were often mean richness values of zero reported for bryophytes or lichens in the smaller plots, while in reality the mean values always must be above zero. This leads to an interpretation of no difference in the SARs within these taxa, which might not have been the case with more replicates, given that we could have then established different mean richness values between 0 and 1 for the different grain sizes. On the other hand, an ecological reason for the lower explained variance might be that the spatial distribution of non-vascular species is more dependent on micro-structures than on the vegetation type.

Entities with high and low fine-grain *z*-values

The two subtropical biomes (Subtropics with winter rain, Dry tropics and subtropics) had clearly higher *z*-values than the rest, which is consistent with the increase in *z*-values from 50 °N southward reported by Dembicz et al. (2021). However, we did not find the (moderate) poleward increase (Dembicz et al. 2021), which might be due to the fact that a large fraction of our Boreal series was from the southern border of the Boreal zone and we did not have a sufficient number of Arctic series to include them. Dembicz et al. (2021) also reported a strong increase in *z*-values with elevation, whereas in our study the Alpine biome did not have higher *z*-values than the Boreal zone or the Dry midlatitudes, and only slightly higher values compared to the Temperate midlatitudes. This discrepancy points to the fact that mainly non-climatic factors (such as increased small-scale heterogeneity) are responsible for higher *z*-values at higher elevation, and thus a climatically defined "Alpine" biome (as used here, based on the definition of Körner et al. 2017) might not stand out as much as an alternative definition based on plots above 2,000 or 3,000 m a.s.l. (see Dembicz et al. 2021). Our results are similar to Schmiedel et al. (2010) who compared fine-grain *z*-values of biomes in Southern Africa. They found the by far highest values in the "Namib Desert" followed by the "Succulent Karoo", both belonging to the Dry tropics and subtropics. At much larger grain sizes (1 to 1,000,000 km^2), Gerstner et al. (2014) also compared *z*-values of vascular plants among biomes. Among the biomes common to their and our study, they had particularly high values for "Mediterranean forests, woodlands, and scrub or sclerophyll forests" (0.280), medium for "Montane grasslands and shrublands" (0.215) and "Deserts and xeric shrublands" (0.205), low for "Temperate broadleaf and mixed forests" (0.161) and "Temperate grasslands, savannas, and shrublands" (0.144) and very low for "Boreal forest/taiga" (0.078). While the absolute numbers are lower, the ranking of biomes is relatively similar to ours (see Figure 3) – despite the many orders of difference in grain size, which makes it unlikely that the same drivers are relevant (see Shmida and Wilson 1985 for α-diversity).

Second, natural grasslands had systematically higher *z*-values than secondary grasslands. This corroborates the previously reported clear negative effects of land use intensity on *z*-values (Dembicz et al. 2021). At the lower typological level, the three units with particularly high z-values were Alpine grasslands, Mediterranean grasslands and garrigues and thorn-cushion communities. This outstanding position of two Mediterranean units and one Alpine unit is consistent with the extraordinary fine-grain β-diversity found for the Subtropics with winter rain (above) and for natural habitats combined with high elevation (Dembicz et al. 2021). The same pattern is reflected in the phytosociological classes where three of the five units with the highest *z*-values were natural grasslands above the timberline, one unit belonged to Mediterranean grasslands and one unit to temperate rocky outcrop communities, the latter two with rather open vegetation structure.

Reasons for variation in *z*-values

Nested-plot *z*-values are mathematically closely linked to mean occupancy (Storch 2016; Dembicz et al. 2021). Therefore, factors that increase mean occupancy at fine grains will decrease fine-grain *z*-values and vice versa (see Figure 1). Following Dembicz et al. (2021), we argue that there are three main factors that have a direct (mathematical) relationship with *z*-values (Figure 1). All other things being equal, *z*-values will increase with decreasing total cover, higher dissimilarity in species composition between adjacent patches and increasing mean size of plant individuals. These direct factors are influenced in different ways by various drivers, like disturbance and stress. In particular, disturbance can have opposing effects on *z*-values depending on the intensity (Figure 1). While disturbance as a result of agricultural land use (e.g., mowing or moderate grazing) will normally decrease *z*-values, more extreme disturbance (e.g., fire, flooding) might increase *z*-values (Figure 1). The reason for this assumption is that "proper" grassland management is conducted in a way that vegetation cover is not decreased (Dembicz et al. 2021).

Our findings with regard to the different typological entities fit well into the hypothetical schema of Figure 1. Just like Dembicz et al. (2021), we confirm the negative impact of typical grassland management on fine-grain β-diversity by demonstrating that *z*-values were systematically lower in secondary than in natural grasslands. We also confirm that, at the typological level, more stressful habitats, in particular those where the stress leads to a more open vegetation structure (i.e. lower total cover), typically have higher *z*-values, which is particularly true for Alpine and Mediterranean habitats. On the other hand, vegetation types with benign conditions, and thus high cover, combined with the effects of agricultural disturbances that reduce the mean size of individuals and homogenize the vegetation, like *Molinio-Arrhenatheretea* and *Nardetea strictae*, have rather low *z*-values. However, saline communities as well as saline steppes and semi-deserts, had even lower mean *z*-values. In relation to Figure 1 this was, at first glance, rather unexpected as these communities can be considered among the most stressed vegetation types included in the study, typically also having a very open vegetation structure. However, in these extreme cases, other factors may be relevant that are not reflected

in Figure 1. For example, the extreme stress might filter the species pool so strongly that there are simply no additional species available that could grow in the large plot, thus limiting the slope of the SAR from the upper end.

Conclusions and outlook

This is the most comprehensive study to date that relates fine-grain β-diversity as measured using *z*-values to different vegetation typologies. We thus complement the recent study of Dembicz et al. (2021) who related nested-plot *z*-values to a wide range of environmental predictors, and demonstrated that *z*-values are a useful measure of multiplicative β-diversity as they are independent from the ratio of areas at the α- and γ-level. This characteristic was particularly useful in our case given that the sizes of the smallest and biggest plots varied substantially across series.

We found that despite important variation, there are clear differences in mean *z*-values among typological units. While there is not a single reason for low or high *z*-values, the values themselves can still be used as informative tools to assess the influence of certain drivers, particularly land-use intensity (see also Tittensor et al. 2007; Dembicz et al. 2021) and biotic invasions (Powell et al. 2013). Our results, broken down into different typologies (Suppl. material 3), provide a set of "benchmarks", which future local- oro continental-scale studies in Palaearctic open habitats can utilise, in a similar way to the α-diversity benchmarks provided in the GrassPlot Diversity Explorer (https://edgg.org/index.php/databases/GrasslandDiversityExplorer; Biurrun et al. 2021). For the missing or less represented units, Suppl. material 3 can be understood as a call to collect such nested-plot data, preferentially using the EDGG standard (Dengler et al. 2016), and contribute them to the collaborative GrassPlot database (Dengler et al. 2018; Biurrun et al. 2019) so that we can draw an even more complete picture in the future.

Data availability

The vegetation-plot data used are stored in and available from the GrassPlot database (https://edgg.org/databases/GrassPlot; Dengler et al. 2018) under version number 2.04 (20 March 2020).

Author contributions

J.D. initiated the data collection and, together with I.D. and S.B., conceived the idea for this paper. Most authors contributed data. J.D. served as custodian and I.B. as database manager of the GrassPlot database. F.G., M.J.S. and T.J.M. conducted the statistical analyses, while I.D. and J.D. led the writing. All authors checked, improved and approved the manuscript.

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Supplementary material

Supplementary material 1
Nested-plot datasets used in this study and their sources
Link: https://doi.org/10.3897/VCS/2021/77193.suppl1

Supplementary material 2
Overview of the coarse- and fine-level vegetation typology used in GrassPlot (including a few categories without nested-plot series in the current study)
Link: https://doi.org/10.3897/VCS/2021/77193.suppl2

Supplementary material 3
Descriptive statistics of *z*-values per typological unit for the four species groups and the two *S*-spaces
Link: https://doi.org/10.3897/VCS/2021/77193.suppl3

Supplementary material 4
Results in log *S*-space for the four species groups
Link: https://doi.org/10.3897/VCS/2021/77193.suppl4