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Running title: Scale-dependence of *z*-values

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Abstract

Questions: Species-area relationships (SARs) are fundamental for understanding biodiversity patterns and are generally well described by a power law with a constant exponent *z*. However, *z*-values sometimes vary across spatial scales. We asked whether there is a general scale dependence of *z*-values at fine spatial grains and which potential drivers influence it.

Location: Palaearctic biogeographic realm.

Methods: We used 6,696 nested-plot series of vascular plants, bryophytes and lichens from the GrassPlot database with two or more grain sizes, ranging from 0.0001 to 1,024 m² and covering diverse open habitats. The plots were recorded with two widespread sampling approaches (rooted presence = species "rooting" inside the plot; shoot presence = species with aerial parts inside). Using GAMs, we tested for scale dependence of *z*-values by evaluating if the *z*-values differ with gran size and tested for differences between the sampling approaches. The response shapes of *z*-values to grain were classified by fitting quadratic GLMs with logit link to each series. We tested whether the grain size where the maximum *z*-value occurred is driven by taxonomic group, biogeographic or ecological variables.

Results: For rooted presence, we found a strong monotonous increase of *z*-values with grain sizes for all grain sizes below 1 m². For shoot presence, the scale dependence was much weaker, with hump-shaped curves prevailing. Among the environmental variables studied, latitude, vegetation type, naturalness and land use had strong effects, with *z*-values of secondary peaking at smaller grain sizes.

Conclusions: The overall weak scale dependence of *z*-values underlines that the power function generally is appropriate to describe SARs within the studied grain sizes in continuous open vegetation, if recorded with the shoot presence method. When clear peaks of *z*-values occur, this can be seen as an expression of granularity of species composition, partly driven by abiotic environment.

Keywords: beta diversity, grassland, GrassPlot, heterogeneity, Palaearctic, power law, rooted presence, scale dependence, shoot presence, species-area relationship, *z*-value, vegetation.

Introduction

Identifying spatio-temporal patterns in biodiversity is a major challenge in macroecology and biogeography (McGill, 2019; O'Sullivan *et al.*, 2019). The spatial scale is of critical importance in studies of components, patterns, and processes of biodiversity (Chase *et al.*, 2018; Schrader *et al.*, 2019). For example, environmental filtering of species, disturbances and biotic interactions drive species richness at fine local scale, while at broader spatial scales the main drivers are speciation, colonization, and extinction dynamics (Shmida and Wilson, 1985; Crawley and Harral, 2001; Drakare *et al.*, 2006). Therefore, when examining the drivers and mechanisms of spatial biodiversity patterns, the scale-sensitivity of these patterns is of paramount importance.

Species-area relationships (SARs), which reflect changes in species richness with increasing grain size (Lawton, 1999; Dengler, 2009), are fundamental in comparing diversity patterns across space (Drakare *et al.*, 2006). SARs are among the most widely documented ecological patterns and have long been regarded as a "genuine law" in ecology (MacArthur and Wilson, 1967; Schoener, 1976; Tjørve *et al.*, 2018). The shapes of SARs have been described by many mathematical models, including the logarithmic model (Gleason, 1922), power law model (Arrhenius, 1921) and more complex models (for reviews, see Dengler, 2009; Tjørve, 2009; Williams *et al.*, 2009). Based on findings of a wide array of studies on SARs of any kind, including in continuous habitats and on islands, the power law model overall performs best (Triantis *et al.*, 2012; Matthews *et al.*, 2016; Dengler *et al.*, 2020). The power law is conventionally expressed as $S = c\,A^z$ (Arrhenius, 1921), which in its logarithmic form becomes $\log S = \log c + z \log A$ (where S is species richness, A is area sampled, and c and z are fitted parameters). The exponent z describes the rate of species accumulation with increasing area, and is a suitable measure of multiplicative beta diversity (Koleff *et al.*, 2003; Sreekar *et al.*, 2018; Dengler *et al.*, 2020; Dembicz *et al.*, subm.).

Given the importance and ubiquity of SARs, many biogeographers and ecologists have analysed *z*-values in detail (Crawley and Harral, 2001; Drakare *et al.*, 2006; Matthews *et al.*, 2019). For example, numerous theoretical models and field experiments have attempted to identify a constant value of *z* for a multitude of different ecosystems and taxa, and have often found values close to 0.25 (Connor and McCoy, 1979; Sugihara, 1980). Other researchers have used the *z*-value as a fruitful approach for studying how different environmental factors affect

SARs (Drakare *et al*., 2006; Patiño *et al*., 2014). Further, studies have examined the variation in *z*-values across spatial and temporal scales, trophic levels and taxonomic groups (Patiño *et al*., 2014; Roslin *et al*., 2014; Fattorini *et al*., 2017; Dembicz *et al*. subm.). However, an extensive review of the literature reveals a lack of consensus regarding the variation in *z*-values of SARs across spatial grains.

Many studies assume that the exponent *z* of the power function (i.e. the slope of the linearized power function) is relatively constant across spatial grains (Drakare *et al.*, 2006; Qiao *et al*., 2012; Dembicz *et al*. subm.). However, some detailed studies have revealed significant changes in *z*-values with grain size (Crawley and Harral, 2001; Fridley *et al*., 2005; Polyakova *et al*., 2016). The concept of 'local *z*' has been proposed to describe such variation of *z*-values with grain size (Williamson, 2003; Dengler, 2009), and can be defined as the local derivative of the SAR between two subsequent grain sizes in double-log space. Using this approach, Crawley and Harral (2001: all vegetation types in a landscape in the United Kingdom), Turtureanu *et al.* (2014: dry grasslands in Romania) and Polyakova *et al.* (2016: dry grasslands in Siberia) found unimodal relationships, i.e. a peak of local *z*-values, albeit at quite different grain sizes. By contrast, Kuzemko *et al.* (2016) and Dembicz *et al.* (2021a) did not find significant scale dependence in dry grasslands of Ukraine and Bulgaria, respectively.

Finally, also methodological issues can influence small-grain *z*-values. There are two contrasting ways how to record a plant species as present in a plot, the any-part system (also called "shoot presence": plants are recorded as present when the vertical projection of any above-ground organ falls inside the plot) and the grid-point system (largely equivalent to "rooted presence": plants are recorded as present when they are attached to the soil surface inside the plot) (Williamson, 2003; Dengler, 2008; Cancellieri *et al.*, 2017). Both methods are widespread in vegetation ecology, but the majority of researchers seems to be unaware of the differences, as reflected by the fact that most studies do not report which of the two methods they applied and standard textbooks like Kent (2012) or van der Maarel and Franklin (2013) do not even mention that these two options have to be considered. However, rooted vs. shoot presence sampling can lead to profound differences in results on α- and β-diversity as well as SAR shapes (Güler *et al.*, 2016; Cancellieri *et al.*, 2017; Dengler *et al.*, 2020). Williamson (2003) demonstrated theoretically that towards fine grain sizes the difference between rooted and shoot sampling will override any ecological or taxonomic driver, with local *z*-values of rooted

presence recording always approaching 1 at very fine scales, while those recorded with shoot presence necessarily approaching 0. Thus, taking into account this methodological aspect is essential if one does not wish to misinterpret a mathematical "constraint" as an ecological process that justifies a new theory, as Plotkin *et al.* (2000) did .

In conclusion, there is scattered evidence that local z-values sometimes show significant scale-dependence, but there is no general picture how prevalent this is and whether and how this scale dependence is related to taxonomic group or to environmental predictors. While it is evident that rooted vs. shoot recording must influence the results, it is unclear below which grain sizes this difference will become noticeable and how strong it will be in relation to other factors. If there should be peaks of local z-values at certain grain sizes this would indicate how spatial heterogeneity of plant communities is organized spatially. As for fine-grain beta diversity in general (Drakare *et al.*, 2006; Dembicz *et al.*, subm.) one should also expect for peak location of local *z*-values to depend on taxonomic group and various environmental factors. Unfortunately, there are so far no comprehensive macroecological studies to examine the prevalence of peaks in local *z*-values and which drivers determine their position.

The present study thus aims at filling this knowledge gap by using 6,696 nested-plot series from the GrassPlot database (Dengler *et al.*, 2018; Biurrun *et al.*, 2019), covering any type of grasslands and other open habitats of the Palaearctic biogeographic realm. In the absence of extensive prior studies it is premature to formulate specific hypotheses. Instead, we conduct an explorative study including a wide range of predictors that often have been shown to be influential on other facets of fine-grain biodiversity, assuming that they also might play a role in scale-dependence of β-diversity. We aimed to answer the following three questions, which, in turn, might contribute to a better understanding on scale-dependence of β-diversity and thus a future formulation of a theory on that topic:

(1) Is there a general pattern of scale dependence of local *z*-values and does it depend on the recording system (shoot vs. rooted presence)?

(2) How does scale dependence differ between taxonomic groups (vascular plants, bryophytes, lichens)?

(3) How does scale dependence vary in relation to broad-scale biogeographic characteristics (latitude, elevation, climate) and fine-scale ecological characteristics (related to the stress-productivity axis, disturbance and heterogeneity)?

Methods

Vegetation-plot data

All plot data used in this paper were taken from the collaborative vegetation-plot database GrassPlot (Dengler *et al.*, 2018; Biurrun *et al*. 2019; https://edgg.org/databases/GrassPlot). The GrassPlot database is a compilation of vegetation-plot data, including methodological, environmental, and structural information, from grasslands and other non-forest vegetation types throughout the Palaearctic biogeographic realm. Requirements for inclusion of the data in the database are precise delineation of plots in the field and sampling with the aim of achieving complete species lists. GrassPlot specifically collects multi-scale datasets from nested-plot sampling schemes (e.g. Dengler *et al.*, 2016) with plot (grain) sizes from 0.0001 m² to 1,024 m².

We extracted all series containing at least two different grain sizes from GrassPlot (v.2.09 in August 2020) to form our dataset, altogether 6,696 series and 177,138 individual plots (Fig. 1). The plots were distributed across 41 countries, from 28° to 70° N and 16° W to 162°E, and covered an elevational gradient from 0 to 5,680 m a.s.l. All series contained information on vascular plants, while 1,260 series contained information on terricolous bryophytes, 1,353 on terricolous lichens, and 1,212 on all three taxonomic groups (complete vegetation).

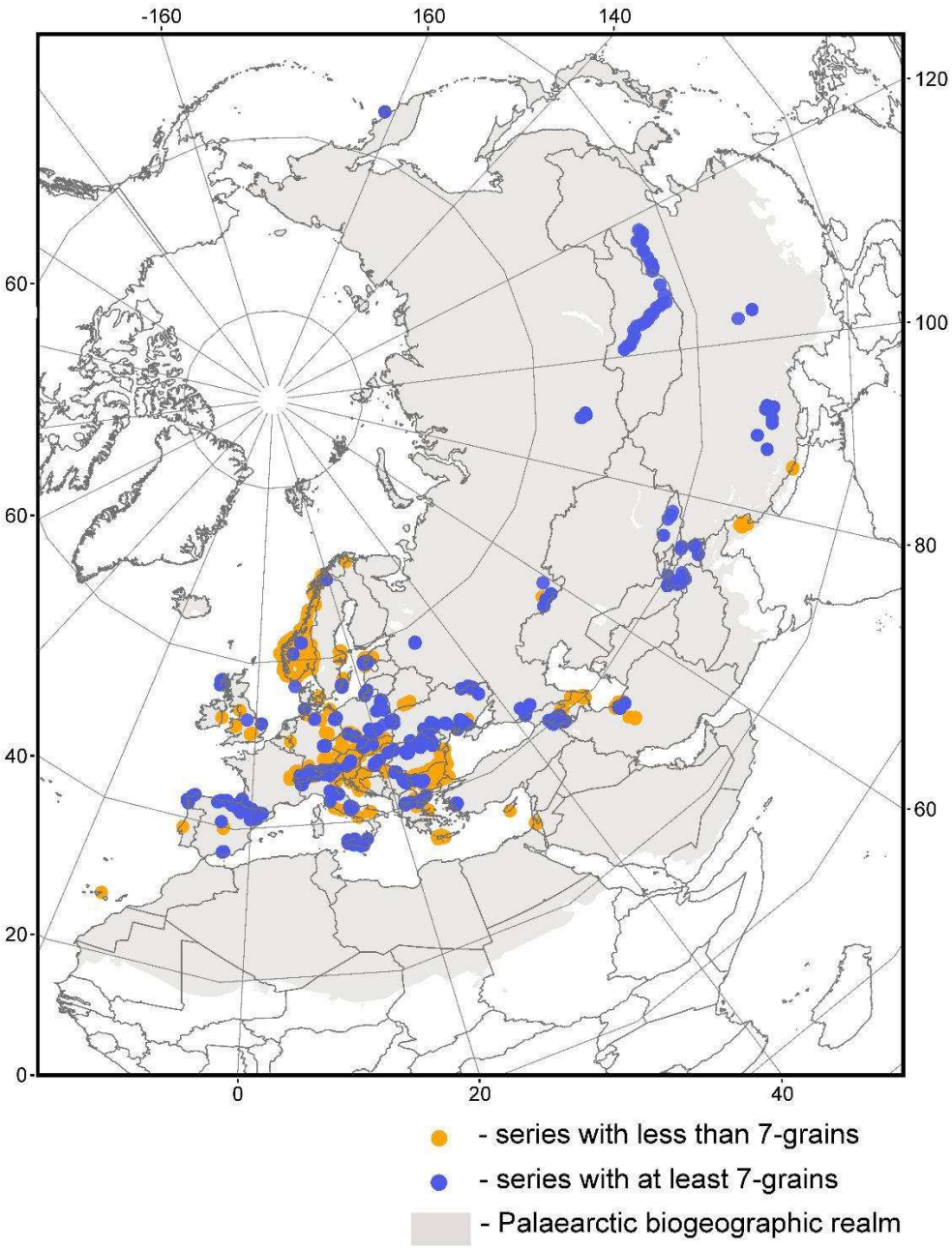

Figure 1. Spatial distribution of the 6,696 series in the Palaearctic biogeographic realm that were analysed in this study.

Calculation of local z-values

We first averaged richness values per grain size for the plot series with more than one plot for a certain grain size. Species richness (*S*) should increase with area (*A*) modelled by the function $S = cA^z$ (Dengler *et al.*, 2020) or its linearized form:

$$logS = zlog\ A + log\ c$$

To account for the possibility that *z*-values can vary between subsequent grain size transitions of a nested-plot series (Crawley and Harral, 2001; Fridley *et al.*, 2005), we calculated local *z* ($z_{i\ to\ i+1}$) (Williamson, 2003) and local grain ($g_{i\ to\ i+1}$) as:

$$z_{i\ to\ i+1} = \frac{log\ S_{i+1} - log\ S_i}{log\ A_{i+1} - log\ A_i}$$

$$g_{i\ to\ i+1} = \frac{log\ A_{i+1} + log\ A_i}{2}$$

where A_i and S_i are the area and the species richness of a particular grain size *i*, respectively. Note that $z_{i\ to\ i+1}$ is not defined if one of the two richness values is 0; thus we excluded such grain size transitions from further analyses. We assigned each local *z* value to the mean of the logarithms of the two successive grain sizes (= logarithm of the geometric mean). In these equations, log denotes base-10 logarithm ($\log_{10}$).

Statistical analyses

All analyses were conducted in R version 4.0.2 (R Development Core Team, 2016).

Overall scale dependence

To analyse the scale dependence of local *z*-values in general, we fitted Generalized Additive (Mixed) Models (GAM(M)s) for $z_{local} = f(g_{local})$ separately for nested plots sampled using two widespread methods of presence recording, i.e. shoot presence and rooted presence. GAMMs were analysed with the R package 'mgcv' with series ID as a random factor. Since the results for GAMs and GAMMs were nearly indistinguishable based on AIC, we report only GAMs in the Results. To avoid overfitting, we paid attention to the number of 'knots' (*k* value) while running GAM(M)s: starting with $k = 0$, we subsequently increased *k* to find the model that best captures the relationship without overfitting based on AIC and shapes of GAM(M)s. We fitted GAM(M)s for all data and after excluding the very few values of $z_{local} > 1$ and $z_{local} < 0$ (for details see Table S1.3). Such values are theoretically impossible if the richness values of the smaller grain sizes are true spatial averages within the area of the largest plot (Williamson, 2003). However, empirically $z_{local} < 0$ can occur if there is no complete nesting and $z_{local} > 1$ when the smaller grain sizes are not sufficiently replicated and their richness values thus biased.

Individual response curves

For subsequent analyses in this study, we only used the theoretically possible values (Williamson, 2003). Since we had a larger proportion of shoot presence data, all subsequent

analyses were conducted for shoot presence data only. Moreover, we restricted ourselves to nested-plot series with at least seven grain sizes with $S > 0$ (i.e. six local *z*-values) to allow for a meaningful assessment of the shape of the scale dependence.

To analyse the patterns of scale dependence of local *z*-values, we fitted to each individual nested-plot series a polynomial GLM with logit link. The underlying model is:

$$y = \frac{1}{1 + exp(b_0 + b_1 x + b_2 x^2)}$$

where x is the local grain size g_{local} and y the predicted local *z*-value. This model has previously been applied to determine the probability of occurrence of a species, in the form of a symmetric Gaussian response curve, based on its presence or absence (binary response) across an environmental gradient (ter Braak and Looman, 1986; Huisman *et al.*, 1993; Oksanen and Minchin, 2002). The same model may be applied to a continuous response in the interval [0, 1], such as local *z*-values. The choice of this simple parametric model against more complex ones (for instance able to fit skewed or bimodal response curves) was justified by the low number of points in each series (typically six grain size transitions for standard GrassPlot series with seven grain sizes). Therefore, we used the three regression coefficients of the model (b_0 = intercept, b_1 = linear term, b_2 = quadratic term) to classify the response curves into four shapes. In case of a hump-shaped response, parameters of the Gaussian function can be retrieved from b_1 and b_2. We identified the location of the optimum as $Opt = -b_1/(2b_2)$. We further quantified $Tol = \frac{1}{\sqrt{-2b_2}}$ as the tolerance of the Gaussian curve, which measures the flattening of the curve (equivalent, in statistical terms, to the variance of a normal distribution). To select hump-shaped and U-shaped curves, we identified series in which *Opt* was within the range of local grain sizes ± 1 order of magnitude. Thus, the shapes of the fitted curves were classified based on the following principles:

Hump-shaped (Gaussian) curves were identified by $Opt \in [min(g_{local}) - 1, max(g_{local}) + 1]$, $Tol > 0$.

U-shaped (inverse Gaussian) curves were identified by $Opt \in [min(g_{local}) - 1, max(g_{local}) + 1]$, $Tol = NA$.

Monotonic decreasing curves were identified by $Opt \notin [min(g_{local}) - 1, max(g_{local}) + 1]$, $b_1 < 0$.

Monotonic increasing curves were identified by $Opt \notin [min(g_{local}) - 1, max(g_{local}) + 1]$, $b_1 > 0$.

Methods for determining peak position

We determined the peak grain size (local grain size where the maximum local z occurred) with two different approaches: (a) we extracted the local grain size corresponding to the maximum *observed* local *z*-value in each series (for explanation, see Fig. S1.1 in Supporting Information); (b) we extracted the local grain size of the maximum *fitted* local *z*-value within the range of local grains ± 1 order of magnitude. In case of fitted hump-shaped curves, we took *Opt* as the position of the peak of the local *z*-value (Fig. S1.1, Table S1.1); for monotonic curves we assigned $min(g_{local}) - 1$ for decreasing curves, $max(g_{local}) + 1$ for increasing curves, and in case of U-shaped curves, we took the local grain one order of magnitude outside the available data for which the higher value was predicted. We labelled the two methods as (a) "observed" and (b) "fitted".

Relating peak position to taxonomic and environmental predictors

We tested how the position of the peaks, either observed or fitted, depended on taxonomic group, biogeographic characteristics and ecological characteristics. For continuous variables, we applied simple linear regressions with both linear and quadratic terms to test their potential influence on the grain size of the peaks for the four taxonomic groups. Best fit was assessed with AIC of the contrasting regression models. For categorical predictors, we applied analysis of variance (ANOVA), followed by Tukey's post-hoc test (R package 'stats').

Since this is the first broad exploratory study on the phenomenon of scale dependence of local *z*-values, we used a wide range of potential predictor variables related to our research questions. They were mostly determined in the field, but some additionally retrieved via the plot coordinates (Table S1.2). For simplicity and following a previous paper using the same dataset (Dembicz *et al.,* subm.), we group them into the following categories, acknowledging that some variables can relate to more than one category: (1) taxonomic group (vascular plants, bryophytes, lichens, and complete vegetation), (2) macroecological characteristics (climate variables, latitude and elevation), (3) ecological characteristics at plot-level, subdivided into those related to (a) productivity, (b) disturbance and (c) heterogeneity, and (4) vegetation

typologies. In the following, we briefly introduce the variables of categories (2) – (4), while details are provided in Table S1.2.

(2) As macroecological variables we used two geographic variables (*latitude* and *elevation*) and four climate variables (*mean annual temperature*, *temperature seasonality*, *mean annual precipitation*, *precipitation seasonality*). *Latitude* and *elevation* with few exceptions were provided by the original dataset collectors, while missing elevation data was derived from digital elevation models GTOPO30 (Danielson and Gesch, 2011) and EU-DEM v.1.1 (2020). QGIS was used to derive climate data from the CHELSA database (Karger *et al.*, 2017), using plot coordinates.

(3a) Here we included variables related to the *stress-productivity gradient* (Grime, 1977; Huston, 2014). As plant cover is one of the main predictors of aboveground biomass (Sanaei *et al.*, 2018), we used *vegetation cover* and *herb layer cover* as rough proxies for productivity and for the competition for light (Grytnes, 2000). Changes in soil properties usually affect vegetation cover and total biomass production (Emiru and Gebrekidan, 2013). We used *soil pH* (assuming maximum productivity at intermediate values) and *mean soil depth* (assuming maximum productivity at high values).

(3b) *Disturbance*, in the sense of removal or destruction of accumulated bio- and necromass is the other main dimension determining species richness and other diversity facets (Grime, 1977; Huston, 2014). Here, we used *litter cover* as a main proxy for the absence of disturbance. We used *slope inclination* (°) as another proxy for disturbance, because erosion increases with increasing slope (Mangeney *et al.*, 2010). As measures of anthropogenic disturbance we included levels of *naturalness* (with five levels) and the presence of *grazing*, *mowing* and *fertilizing* (Table S1.2).

(3c) *Heterogeneity* variables are those that describe the small-scale variability of productivity and/or disturbance, and they are usually determined within the largest or second-largest grain plot of each nested series: *Soil depth CV* (coefficient of variation) indicates the variability of soil depth within a plot. From the perspective of herbaceous vegetation, both *rock and stone cover* and *shrub layer cover* inside the plot can be interpreted as heterogeneity measures, assuming maximum variability in within-plot environmental conditions at intermediate levels.

(4) We tested three *vegetation typologies*: The *biome* represents the climate-driven potential climax vegetation. It was derived via the plot coordinates, using the classification of Bruelheide *et al*. (2019), with six biomes: alpine, boreal, continental (dry mid-latitudes), nemoral (temperate mid-latitudes), mediterranean (subtropics with winter rain), and dry tropics and subtropics. Further, we used a coarser and finer typology of the actual vegetation: vegetation group (six classes) is the coarser level, within which vegetation type (20 classes) is nested. This two-level typology was defined to be applicable across the Palaearctic and accessible with the information provided in the individual datasets. It mainly captures aspects of physiognomy (e.g. dwarf shrubs vs. herbs only), naturalness (natural vs. secondary) and stress factors (e.g. drought, flooding, salinity, cold) (for details, see Biurrun *et al*., 2019).

Results

Pattern of scale dependence of z-values

Local *z*-values revealed scale dependence and differences between the two ways of recording plant presence (Fig. 2, Fig. S2.1). In the case of complete vegetation, local *z*-value reached a shallow maximum for $\log_{10}$ (area) at around -1.5 (corresponding to 0.032 m^2) for shoot presence, while for rooted presence *z*-values started to increase strongly and continuously from around 0 (1 m^2) towards the smallest grain sizes (Fig. 2). For vascular plants, the situation was similar, except that in rooted presence at grain sizes below -2.5 (0.003 m^2) *z*-values decreased again slightly (Fig. S2.1). Whether recorded as shoot presence or rooted presence, bryophytes hardly showed any scale dependence of local *z*-values (Fig. S2.1). For lichens recorded as shoot presence, local *z*-values peaked around -1.75 (0.018 m^2), while they decreased over the studied range for rooted presence (Fig. S2.1). The GAMs conducted with data including theoretically impossible values of local $z > 1$ and local $z < 0$ showed similar patterns (Fig. S2.2). Among the shapes of fitted curves to individual nested-plot series, hump-shapes prevailed for all taxonomic groups (Fig. 3, Table S2.1).

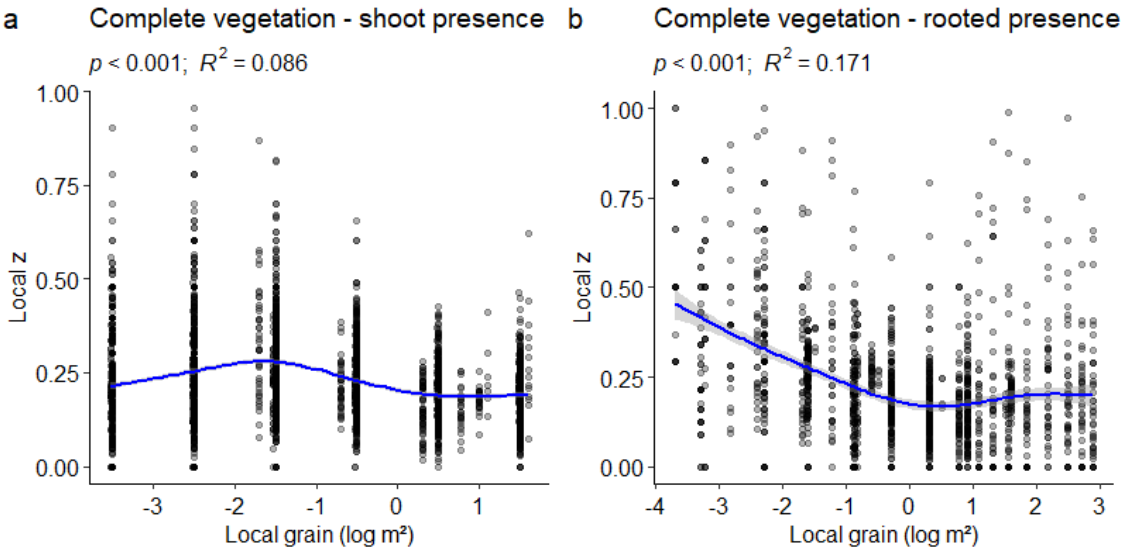

Figure 2. Generalized additive models (GAMs) with 95% confidence intervals (pale blue) for the effect of local grain (on log scale) on local *z*-value for complete vegetation, in plot series using two different ways of recording species occurrence: a) shoot presence and b) rooted presence.

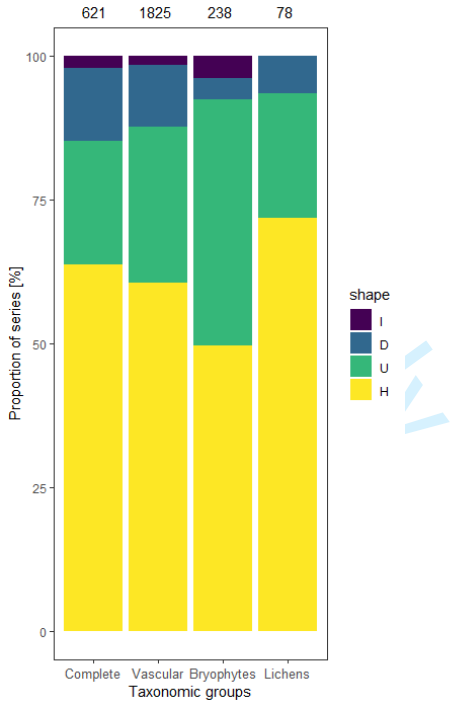

Figure 3. Comparison of the four shapes of fitted curves (hump-shaped (H), U-shaped (U), monotonic decreasing (D), and monotonic increasing (I)) for the complete vegetation and for the taxonomic groups vascular plants, bryophytes, and lichens (series with at least seven grain sizes). Values on top of bars are the number of nested-plot series analyzed.

Taxonomic groups

The observed peak grain sizes did not differ significantly among taxonomic groups (ANOVA; p = 0.119). Mean peak locations were between -1.55 and -1.38, i.e. 0.03-0.04 m² (Fig. S2.3). The only discernible difference was that peak position in the case of bryophytes was more variable than for the other two taxonomic groups. By contrast, the fitted peak grain size differed significantly among taxonomic groups (ANOVA with Tukey's HSD test) (Fig. S2.3). Here, the highest fitted peak grain was found for bryophytes (0.06 m²), followed by lichens (0.05 m²) and vascular plants (0.02 m²).

Observed vs. fitted peaks

We conducted all following analyses for the observed and the fitted peak grain size. As the results were similar, we present only those for observed peaks in the main text, while those for fitted peaks are provided in Supporting Information (Figs. S2.9–S2.12, S2.14, S2.19–S2.22, S2.24, S2.26, S2.31–S2.34).

Macroecological characteristics

For vascular plants, the observed peak grain size showed a significant U-shaped relationship with latitude (minimum at around 47° N) and an initially flat then increasing relationship with elevation (Fig. 4; see Fig. S2.4 for a map). Also the relationship with mean annual temperature was u-shaped (Fig. 4), while the other macroecological variables only had low explanatory power (Fig. S2.5). Observed peak grain size was not explained by macroecological variables in the case of bryophytes (Fig. S2.6), whereas for lichens it showed a unimodal relationship with latitude and elevation, but a u-shaped relationship with precipitation seasonality (Fig. S2.7). Complete vegetation behaved similarly to vascular plants in the case of elevation (u-shaped to increasing), but showed the opposite pattern (slightly unimodal for latitude and mean annual precipitation (Fig. S2.8).

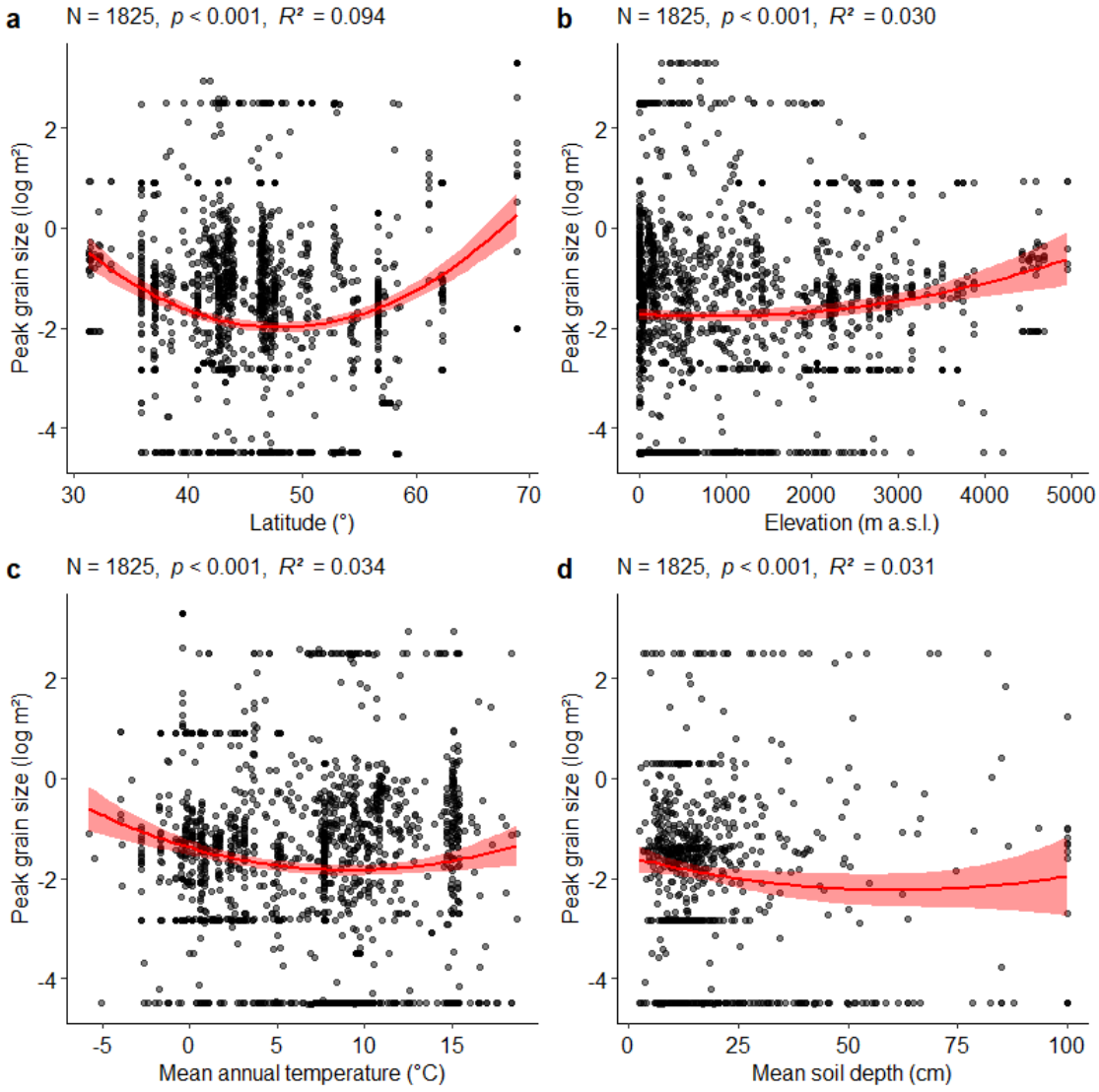

Figure 4. Differences in observed peak grain size (local grain size where the maximum local z occurred) of vascular plants depending on predictor variables. Red lines indicate quadratic relationships ($p < 0.05$) with confidence intervals.

Ecological characteristics related to productivity

From the variables related to the stress-productivity gradient, in vascular plants only mean soil depth had an explanatory power above 3% (u-shaped relationship; Fig. 4) while all others had low explanatory power or were insignificant (Fig. S2.5). The pattern was similar but weaker for complete vegetation (Fig. S2.8), while no relationships for any of the tested variables occurred in bryophytes and lichens (Figs. S2.6–S2.7).

Ecological characteristics related to disturbance

Observed peak grain size of vascular plants and bryophytes increased monotonically with litter cover (Figs. S2.5–S2.6), while there was no relationship for lichens and complete vegetation (Figs. S2.7–S2.8). Slope inclination did not show a pattern for any of the four groups (Figs. S2.5–S2.8).

For vascular plants, observed peak grain size was highest in unused natural grasslands and lowest in semi-intensified secondary grasslands (Fig. 5). Also for complete vegetation there was a tendency of decreasing peak grain size with decreasing naturalness, while for bryophytes there were no differences at all and lichens had a significantly higher peak grain size in extensively managed natural grasslands compared to both unmanaged natural grasslands and semi-natural secondary grasslands (Fig. S2.13). In vascular plants any management consistently decreased peak grain size (Fig. S2.15), but the effect was most pronounced in the case of mowing with a decrease by about one order of magnitude and an explained variance of 3.8% (Fig. 6). While in complete vegetation three of the five management categories also led to a decrease in peak grain size (albeit with very low explained variance; Fig. S2.18), there was no effect in the case of bryophytes (Fig. S2.16) and even an increase for two categories in the case of lichens (Fig. S2.17).

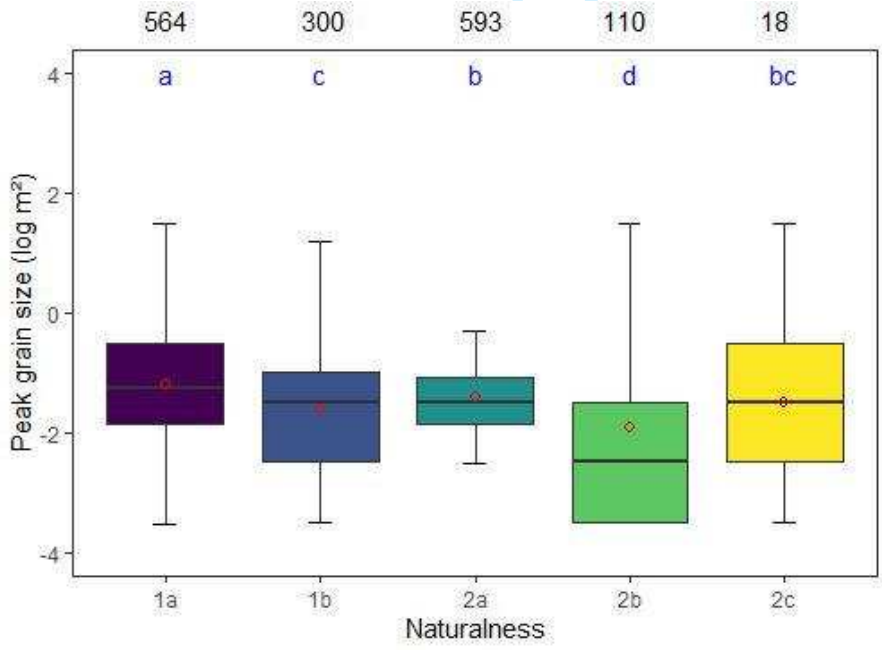

Figure 5. Differences of the observed peak grain size (local grain size where the maximum local z occurred) for vascular plants between the five levels of naturalness present in this study (no series for 1c – natural

grasslands, overused): 1 – natural grasslands (1a – not managed, 1b – extensively managed); 2 – secondary grasslands (2a – semi-natural, 2b – semi-intensified, 2c – intensified) (p < 0.001; $R^2_{adj.}$ = 0.028). Blue lowercase letters indicate homogeneous groups (p < 0.05) as tested with Tukey's post-hoc test ANOVA, the figures on top indicate the numbers of data. Box and whisker plots represent the median and quartiles while the red dots represent the mean values.

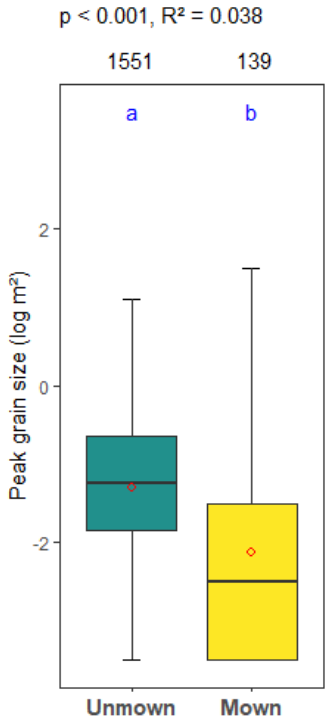

Figure 6. Effect of mowing on observed peak grain size (local grain size where the maximum local z occurred) for vascular plants (p < 0.001; R^2 = 0.038). Box and whisker plots represent the median and quartiles while the red dots represent the mean values for each management type.

Ecological characteristics related to heterogeneity

We found minimal to no influence of our heterogeneity-related variables on observed peak position in any of the taxonomic groups (Figs. S2.5–S2.8).

Vegetation typologies

Considering biomes (i.e. broad-scale potential/climax vegetation), for vascular plants the nemoral biome had the lowest peak grain sizes, the alpine, boreal and dry tropics and subtropics biomes the highest and the continental biome and the subtropics with winter rain intermediate peak grain sizes (Fig. S2.23). By contrast for bryophytes and lichens there was no significant pattern and for complete vegetation it was very weak (Fig. S2.23).

Among all predictors, in vascular plants the actual vegetation type had the highest predictive power for peak grain size, 13.8% at the fine level (Fig. S2.27) and 6.8% at the coarse level (Fig. 7). Peak grain size was particularly high in all types of dwarf shrublands and particularly low in secondary grasslands and alpine deserts (Figs. 7, S2.27). There was no effect of vegetation type in the case of bryophytes and lichens and only a weak effect in complete vegetation (Figs. S2.25, S2.28–S2.30).

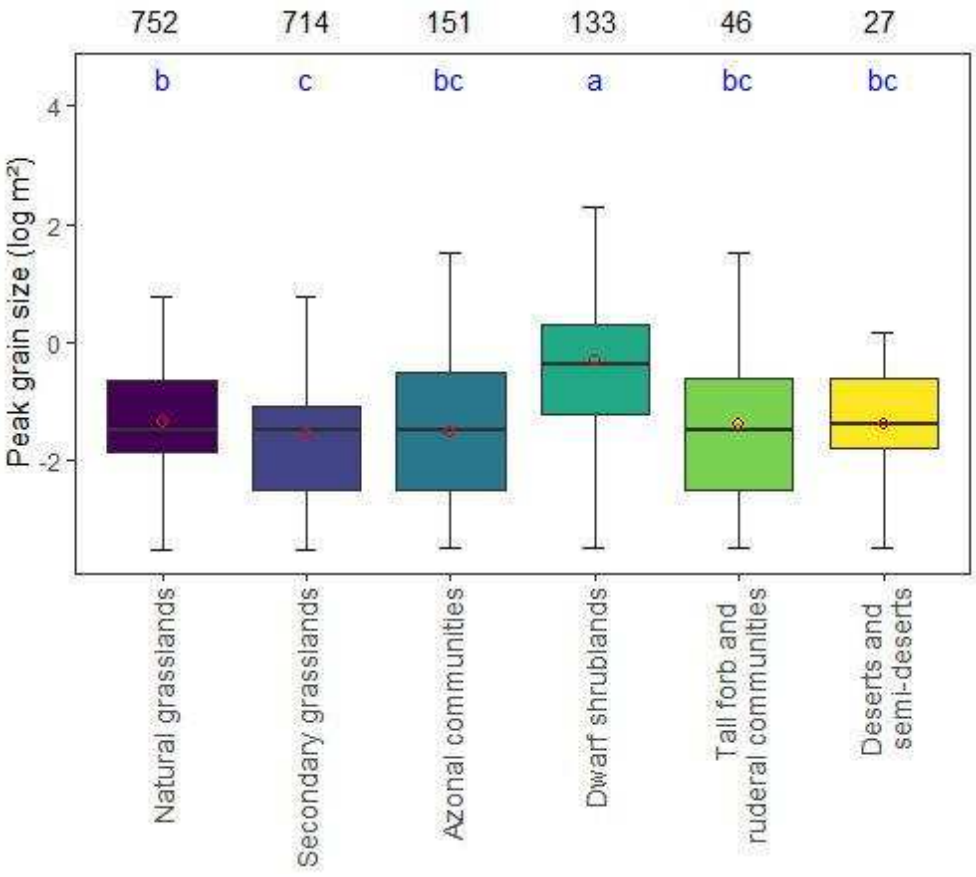

Figure 7. Differences in the observed peak grain size (local grain size where the maximum local *z* occurred) between the six main vegetation types for the vascular plants ($p < 0.001$, $R^2_{adj.} = 0.068$). A common blue lower-case letter between two boxes indicates homogeneous groups as tested with Tukey's post-hoc test with ANOVA ($p < 0.05$), the figures on top indicate the numbers of data. Box and whisker plots represent the median and quartiles while the red dots represent the mean values for each vegetation type at coarse level.

Explanatory power of different predictors

Overall, for vascular plants, the highest proportion of variance in the observed peak grain size was explained by vegetation types at fine level (0.138), followed by latitude (0.094), vegetation types at coarse level (0.068), mowing (0.038) biomes (0.031) and naturalness

(0.028). The explanatory power of the bivariate regressions for the fitted peaks on average was lower than for the observed peaks. For bryophytes, lichens and complete vegetation, there were much fewer significant relationships and they generally were also weaker.

Discussion

Differences between records of shoot and rooted presence

At fine grain sizes, the scale dependence of local *z*-values differed depending on whether plants were recorded with shoot presence or rooted presence. These differences were best visible for our big datasets of complete vegetation and vascular plants and somehow less pronounced in our smaller (and thus potentially less balanced) datasets of bryophytes and lichens. In all four groups, *z*-values of rooted presence recorded data started to increase more or less monotonously below a threshold somewhere between 1 and 10 m², while for shoot presence there was either a shallow peak around 0.01 m² or no systematic scale dependence. This is in agreement with Williamson (2003) who demonstrated mathematically that *z*-values at very small grain sizes must approach a value of zero in the case of the "any-part system" and a value of one in the case of the "grid-point system". His "any-part system" is equivalent to shoot presence, while his "grid-point system" is very similar to rooted presence in our study (for details, see Dengler, 2008). These deviations from the "normal" shape of the species-area relationships to the far left of the graph are "mathematical artefacts" caused by the way in which plant presence is recorded, and thus should not be interpreted ecologically. For a tree-only dataset of a tropical rainforest recorded with the grid-point system, Williamson (2003) found that local *z*-values started to increase from below approx. 10^5 m² (10 ha) and reached one at around 1 m². For the non-forest communities in our study, we found that for complete vegetation the increase in *z*-values started below approx. 1 m², and values reached nearly 0.5 at 1 cm². The diverging peak positions can easily be explained by the size difference in the organisms studied (herbs, dwarf shrubs, bryophytes and lichens vs. tropical trees). We did not actually reach a local *z*-value close to one, possibly because our smallest grain size was not small enough and because rooted presence is similar, but not identical, to the grid-point system. For the any-part (shoot presence) system, Williamson (2003) predicted a decrease in local *z*-values at small grain sizes towards zero. We found no indication of this effect, since at the smallest grain size we still had a mean local z-value of around 0.22, which was only slightly different from the overall average. This apparent deviation from the theoretical pattern can be

explained: in a species-area study in dry grasslands with grain sizes down to 1 mm², Dengler *et al*. (2004) observed "flattening" of the species-area curves towards small grain sizes, equivalent to a decrease in local *z* towards zero, but only at grain sizes smaller than 1 cm².

Overall scale dependence of local z-values

When removing the strong methodological effect of rooted presence sampling and concentrating on shoot presence data, we found only a weak overall scale dependence of local *z*-values for vascular plants and complete vegetation (8.6% and 10.8% explained variance, respectively). For lichens, the effect was slightly stronger (13.1%), while local *z*-values of bryophytes hardly showed any systematic scale dependence (1.9%). These relatively weak effects when combining all nested-plot series could either mean that the scale dependence in individual nested-plot series is also low or that it is stronger, but the shape of the response varies idiosyncratically among the series. Our shape analysis of the fitted response curves of local *z*-values vs. local grain revealed a prevalence of hump-shaped curves (Fig. 3), meaning a peak within the observed range of areas, irrespective of taxonomic group. As for most of the nested-plot series we had only six grain size transitions, we could not conduct a meaningful test on statistical superiority of quadratic vs. linear vs. no scale dependence. Thus, we have to acknowledge that among the four distinguished response types of Figure 3 an unknown fraction of a fifth type of "no significant scale dependence" is hidden, so the prevalence of hump-shaped curves is probably lower than Figure 3 suggests. This coincides with the fact that two studies that analyzed relatively small regional subsets of the GrassPlot data did not either find a significant scale dependence (Kuzemko *et al.*, 2016; Dembicz *et al.*, 2021a). However, as already the combined data of all nested-plot series (Fig. 2, Fig. S2.1) show clear peaks for complete vegetation, vascular plants and lichens, it is evident that among those nested plots that actually show a scale dependence, unimodal relationships with peaks inside the fitted range will prevail.

Position and meaning of peaks

Assuming a unimodal response, we found that peak grain generally varied across the whole analyzed grain size range (Figs. 2). For all three groups as well as for complete vegetation it was around -1.6 to -1.4, corresponding to 0.03–0.04 m², in the analyses of individual nested-plot series. This coincides to the overall peaks derived for all grain-size transitions with the

GAMs, except for bryophytes that did not show any peak there (which corresponds to a much larger variability of the peak location for bryophytes than for the two other taxonomic groups in case of the series-based analyses). Not to find any systematic difference in the peak location of the three contrasting taxonomic groups was unexpected as both their sizes and their spatial distribution patterns seem to be quite different. However, it might be that our prior assumption that bryophytes and lichens are smaller than vascular plants is not necessarily true in the two-dimensional projection to the ground which is quantified with shoot presence. Indeed, there are also quite extensive thalli of some carpet-forming mosses or reindeer lichens.

The mean peak positions found in this study for vascular plants and complete vegetation (mostly 0.01 – 0.1 m²) are quite similar to those reported for Palaearctic grasslands in regional studies (Turtureanu *et al.*, 2014; Polyakova *et al.*, 2016). In contrast, Crawley & Harral (2001) found a very different peak (at around 40,000 m²) in a study of species richness of vascular plants in a landscape in England including a wide range of different habitats (grasslands, forest patches, riparian vegetation, heathlands, etc.). The much larger peak grain size probably reflects the granularity of habitats in the British landscape, inducing a steep increase of species-richness when new habitats with ecologically different species are included in the samples. By contrast, the data in GrassPlot refer to the internal organization of plant communities within 100 m² (or rarely up to 1024 m²) of a patch selected in most of the cases for relative homogeneity (Dengler *et al*., 2018; Biurrun *et al*. 2019).

What is the meaning of such a peak in the relationship of local *z*-values vs. local grain? A peak refers to a local maximum in the rate of species accumulation, i.e. it indicates a spatial grain (sampling unit size) where more new species appear in a sampling unit than expected from the overall "global" *z*-value of the power law SAR. These irregularities in the rate of species accumulation reflect variability of species occupancy due to differences of abundances and the spatial heterogeneity of vegetation. Let us consider that a plant community is composed of "granules" or floristically rather homogenous patches: increasing the recording area within a granule would lead to a slow increase in richness, while moving from one "granule" to another would give a steep increase. If granules show a wide variation in their sizes, then likely no or only a weak peak is found, while a strong prevalence of a certain granule size should cause a visible peak in the curve. The smaller the "granules", the finer the spatial grain where the position of the maximum local *z*- value appears. Theoretically, there could also

be multiple peaks if there are two or more nested granule sizes (cf. the concepts of hierarchical patch dynamics; Kotliar and Wiens, 1990; Wu and Loucks, 1995). Unfortunately, the limited number of grain-size transitions in our dataset (mostly only six) did not allow us to detect such multiple peaks. Generally, the peaks observed were not very pronounced and their position varied, indicating a high idiosyncrasy in granule-size distributions in vegetation. Knowledge on peak grain size can be useful to explore the relationship between β-diversity and the environmental drivers shaping the compositional heterogeneity at different spatial scales.

Drivers of the peak position

Among the predictors studied for vascular plants, vegetation type had the relatively strongest effect, with dwarf shrublands having particularly high peak grain sizes and secondary grasslands particularly low ones. This makes sense given that heathlands have dwarf shrubs as main structural elements, whose size is larger on average than that of herbs, while secondary grasslands are subject to some type of management/land use, which might reduce the average size of plant individuals and thus granules. This interpretation coincides with the fact that also naturalness and land management were among the variables with relatively strong impact. Generally, peak position decreased from natural to secondary grasslands and within each of the two groups with increasing land use intensity – with the exception of intensively used secondary grasslands, for which, however only a very small locally clustered sample was available. Any type of land management (mowing, burning, livestock grazing, fertilization) decreased the peak grain size, but the effect of mowing was strongest. This could be explained by the fact that mowing is the less discriminant land use (i.e. all the stems of all species are cut). Generally, management prevents litter accumulation and limits growth of the strongest competitors, thus maintaining species coexistence through reducing competition and increasing availability of establishment microsites (Tilman, 1994; Questad and Foster, 2008), so (particularly with the shoot presence approach) the smaller “spatial granules” can hold more species, thus lead to fine “granule” and cause a *z*-value peak at smaller grains.

Among the biogeographic variables, latitude showed the strongest effect on observed peak position (9.4% explained variance), with a U-shaped response and a minimum at around 47° N (Fig. 4). This was also reflected in the comparison of biomes, where we found a minimum of the peak position in the nemoral biome and particularly high values in the alpine, boreal and dry subtropical biomes (Fig. 7). The fact that local z-values peak at particularly fine grain sizes

for plots from between 45 and 50 °N latitude and/or the nemoral biome might not be a consequence of latitude/biome *per se*, but of higher land use intensity driven by the rather benign environment of this latitude/biome. Interestingly, in the same region also the total *z*-values (i.e. assuming a constant *z*) were lowest, as Dembicz *et al*. (subm.) found and attributed this to the same likely reason.

Conclusions and outlook

The overall weak scale dependence of local *z*-values within the range 0.0001–1024 m² questions the widespread search for SAR models that are more complicated than the power function (see reviews by Tjørve, 2003; 2009). Instead it supports conclusions of two previous GrassPlot publications (Dengler *et al.*, 2020; Dembicz *et al.*, subm.) that: (i) the power function is an appropriate model to describe SARs at these scales in continuous vegetation in open habitats; and (ii) deviations from the "perfect" power law are relatively minor and inconsistent. Thus, for most purposes one can safely assume a constant *z*-value across the grain sizes studied here. However, this is only true if species richness is recorded with the shoot presence method, as for data recorded with the rooted presence method we found significant deviations from the power law below 1 m², i.e. strongly increasing *z*-values. This finding matches the theory and suggests that shoot presence recording is preferable when studying SARs, as this permits a focus on ecological determinants of curve shapes by reducing distortion by mathematical artifacts.

We consider SARs within the grain size range analyzed here to be mainly an expression of granularity of species composition, which in turn is partly driven by granularity of the abiotic environment, and partly by the growth form of the dominant species. If granule sizes vary over a large range, constant *z*-values (no scale dependence of local *z*-value) should be expected, while a prevalence of a particular granule size should lead to a peak of local *z*-values vs. grain size. Scale dependence of local *z*-values appears to be mainly locally driven and highly idiosyncratic. Of the few macroecological patterns that emerged, the responses to latitude (possibly also related to land use), naturalness, and land use were most prominent. We propose a mechanism explaining the effect of land use on decreasing peak *z*-value position, but this should be tested experimentally. To explore the topic further, we also recommend conducting simulation studies using artificial communities with varying granularity and species-abundance

distribution to understand more mechanistically how these parameters shape the details of SARs.

Acknowledgements

We would like to thank the hundreds of colleagues who obtained high-quality plant diversity data from across the Palaearctic and contributed them to GrassPlot.

Author contributions

J.De. conceived the idea of the study and led together with I.B., I.D. and R.P. the compilation and harmonisation of the data, which were contributed by most of the authors. J.Z. and F.G. conducted the statistical analyses with support from J.De., R.J. , K.V.M. and S.W., while J.Z. and J.De. led the writing, with major inputs from F.G., S.B., J.M.A., and J.-A.G., I.D. and D.V. prepared the maps and all co-authors revised 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 2.09. 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. Methodological details

Appendix S2. Additional detailed results

Supporting Information to the paper Zhang, J. *et al.* Scale dependence of species-area relationships is widespread but generally weak in Palaearctic grasslands *Journal of Vegetation Science.*

Appendix S1. Methodological details.

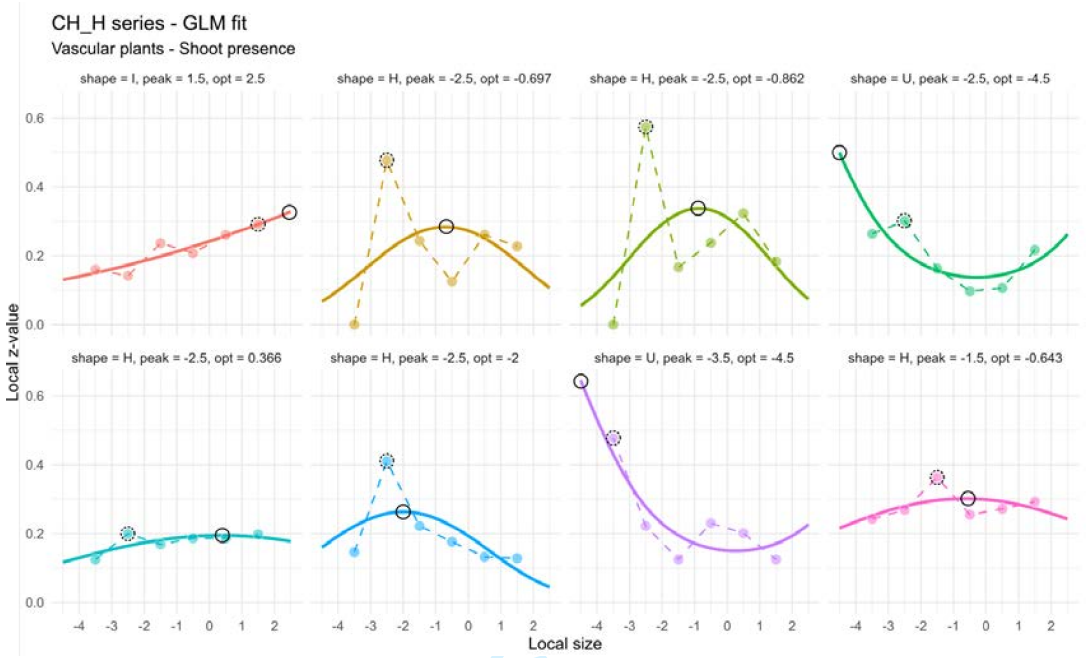

Figure S1.1. Actual local *z*-values and fitted Gaussian curves for the dataset CH_H series from GrassPlot (subalpine and alpine habitats in Grisons, Switzerland, sampled by J. Dengler and colleagues). The shape of each individual curve and the maximum *z* value are determined in the interval of the observed local scale ± 1. H: hump-shaped (Gaussian); U: U-shaped (inverse Gaussian); I: monotonic increasing; peak (dotted circle): actual local scale of the maximum local *z*-value; opt (plain circle): local scale of the maximum fitted local *z*-value.

Table S1.1. The curve parameters with peak recognition for the eight nested-plot series in CH_H (see Fig. S1.1). Peak_act: actual local grain of the maximum observed local *z*-value; Peak_mod: local grain of the maximum fitted local *z*-value.

SeriesID	Shape	Peak_act	Peak_mod	b0	b1	b2	Opt	Tol	Max
CH_H_N001_100	I	1.5	2.5	-1.145	0.169	0.000	-203.636	NA	0.000
CH_H_N002_100	H	-2.5	-0.697	-0.984	-0.164	-0.118	-0.697	2.059	0.284
CH_H_N003_100	H	-2.5	-0.862	-0.797	-0.283	-0.164	-0.862	1.745	0.337
CH_H_N004_100	U	-2.5	-4.5	-1.828	0.059	0.103	-0.285	NA	0.137
CH_H_N005_100	H	-2.5	0.366	-1.424	0.019	-0.025	0.366	4.440	0.195
CH_H_N006_100	H	-2.5	-1.997	-1.431	-0.403	-0.101	-1.997	2.226	0.263
CH_H_N007_100	U	-3.5	-4.5	-1.733	-0.054	0.103	0.263	NA	0.149
CH_H_N008_100	H	-1.5	-0.643	-0.855	-0.039	-0.030	-0.643	4.077	0.301

Table S1.2. Predictor variables used to explain the position of the peak local *z*-value, grouped into four broad categories.

Predictor variables [with units]	Type	Explanation	Source(s)
1. Taxonomic group			
Taxonomic group	Categorical	Vascular plants, bryophytes, lichens, and complete vegetation (all groups sampled simultaneously)	GrassPlot (Dengler *et al.*, 2018)
2. Biogeographic characteristics			
Latitude [°]	Metric		GrassPlot (Dengler *et al.*, 2018)
Elevation [m a.s.l.]	Metric		GrassPlot (Dengler *et al.*, 2018)
Mean annual temperature [°C]	Metric	-	CHELSA (Karger *et al.*, 2017)
Mean annual precipitation [mm]	Metric	-	CHELSA (Karger *et al.*, 2017)
Temperature seasonality [°C]	Metric	Temperature variation over a given year (or averaged years) based on the standard deviation (variation) of monthly temperature averages	CHELSA (Karger *et al.*, 2017)
Precipitation seasonality [%]	Metric	Measure of the variation in monthly precipitation totals over the course of the year	CHELSA (Karger *et al.*, 2017)
3. Ecological (site) characteristics			
3.1 Productivity			
Soil pH	Metric	In upper soil layer, measured in H2O	GrassPlot (Dengler *et al.*, 2018)
Soil depth mean [cm]	Metric	Mean of five random measurements within a plot	GrassPlot (Dengler *et al.*, 2018)
Vegetation cover [%]	Metric	Estimated in the field	GrassPlot (Dengler *et al.*, 2018)
Herb layer cover [%]	Metric	Estimated in the field	GrassPlot (Dengler *et al.*, 2018)
3.2 Disturbance			
Slope inclination [°]	Metric	Measured in the field	GrassPlot (Dengler *et al.*, 2018)
Litter cover [%]	Metric	Estimated in the field	GrassPlot (Dengler *et al.*, 2018)
Naturalness - at fine level	Categorical	no series for 1c – natural grasslands, overused): 1 – natural grasslands (1a – not managed, 1b – extensively managed); 2 – anthropogenic grasslands (2a – semi-natural, 2b – semi-intensified, 2c - intensified	GrassPlot (Dengler *et al.*, 2018)
Livestock grazing	Binary	Grazed vs. not grazed grassland	GrassPlot (Dengler *et al.*, 2018)
Mowing	Binary	Mown vs. not mown grassland	GrassPlot (Dengler *et al.*, 2018)
Burning	Binary	Burnt vs. unburnt grassland	GrassPlot (Dengler *et al.*, 2018)
Fertilization	Binary	Fertilized vs. unfertilized grassland	GrassPlot (Dengler *et al.*, 2018)
Managed	Binary	Managed vs. not managed	GrassPlot (Dengler *et al.*, 2018)
3.3 Heterogeneity			
Soil depth CV [cm]	Metric	Standard deviation of five random measurements	GrassPlot (Dengler *et al.*, 2018)
Rock and stone cover [%]	Metric	Estimated in the field as independent from vegetation cover and adding up to 100% with cover of gravel and fine soil	GrassPlot (Dengler *et al.*, 2018)

Predictor variables [with units]	Type	Explanation	Source(s)
Shrub layer cover [%]	Metric	Estimated in the field	GrassPlot (Dengler *et al.*, 2018)
4. Vegetation typology			
Biome	Categorical	Six biomes represented in the analyzed, among nine types distinguished in GrassPlot (as shown in Fig. S2.4) according to a recent classification by Bruelheide et al. (2019, based on Schultz, 2005 and Körner *et al*., 2017), for details see Biurrun *et al*. (2019)	GrassPlot (Dengler *et al.*, 2018)
Vegetation group	Categorical	Six groups, for the details see Biurrun et al. 2019	GrassPlot (Dengler *et al.*, 2018)
Vegetation type	Categorical	20 vegetation types represented in the analysed data , among 22 types distinguished in GrassPlot (see Biurrun *et al*., 2019)	GrassPlot (Dengler *et al.*, 2018)

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Table S1.3. Numbers of plots and series for all data and theoretically possible values of local $0 \leq z \leq 1$ used in the analysis. Number of plots, grain size transitions/pairs and nested plot series with at least seven grain sizes, local *z*-values were > 1 or < 0.

Recording method	Shoot presence					Root presence					Total				
Data category	Plot	grain size transitions/pairs	Number of Local z <0	Number of Local z >1	nested plot series with at least 7 grain sizes	Plot	grain size transitions/pairs	Number of Local z <0	Number of Local z >1	nested plot series with at least 7 grain sizes	Plot	grain size transitions/pairs	Number of Local z <0	Number of Local z >1	nested plot series with at least 7 grain sizes
Vascular plants	154942	22698	292	166	2114	21642	6137	13	27	275	177138	29276	317	196	2442
Bryophytes	11605	2651	6	5	500	4126	1423	50	25	119	15797	4109	57	30	622
Lichens	17896	1289	4	3	291	4126	694	5	10	71	22061	2000	10	13	364
Complete vegetation	11410	4179	9	2	636	4126	1610	6	15	130	15602	5845	15	17	772

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Appendix S2. Additional detailed results.

Table S2.1. Shapes of fitted curves.

Taxonomic group	Total series	Shape	Number of series	Percent (%)
Complete vegetation	621	Hump-shaped (H)	396	64
		U-shaped (U)	133	21
		Decreasing (D)	79	13
		Increasing (I)	13	2
Vascular plants	1825	Hump-shaped (H)	1105	61
		U-shaped (U)	497	27
		Decreasing (D)	194	11
		Increasing (I)	29	1
Bryophytes	238	Hump-shaped (H)	118	50
		U-shaped (U)	102	42
		Decreasing (D)	9	4
		Increasing (I)	9	4
Lichens	78	Hump-shaped (H)	56	72
		U-shaped (U)	17	22
		Decreasing (D)	5	6
		Increasing (I)	0	0

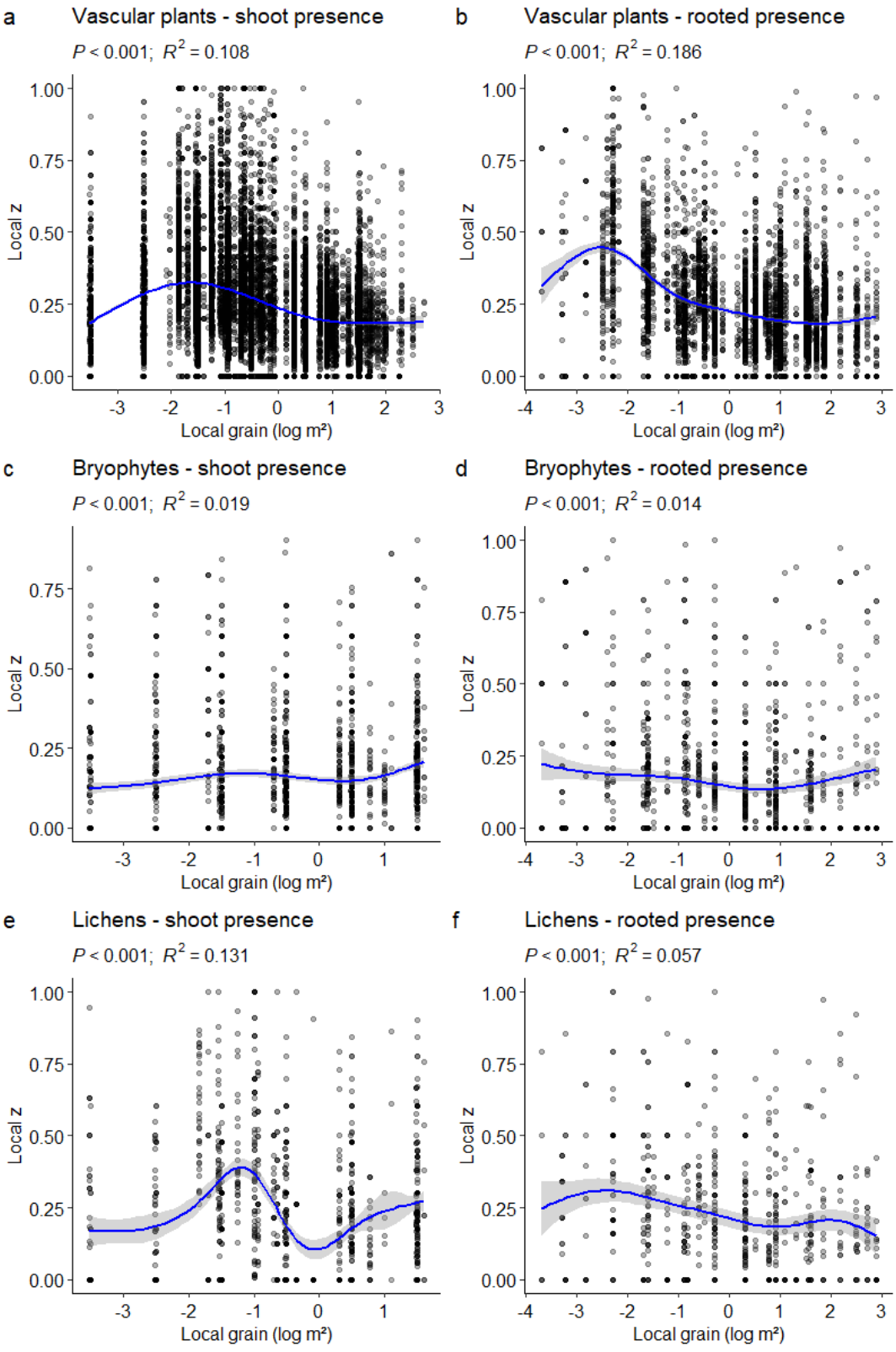

Figure S2.1. Generalized additive models (GAMs) of the effect of local grain on local *z* for (a, b) vascular plants, (c, d) bryophytes, and (e, f) lichens, with data obtained using two different ways of recording plants: (a, c, e) shoot presence and (b, d, f) rooted presence (excluding theoretically impossible values of local $z > 1$ or < 0).

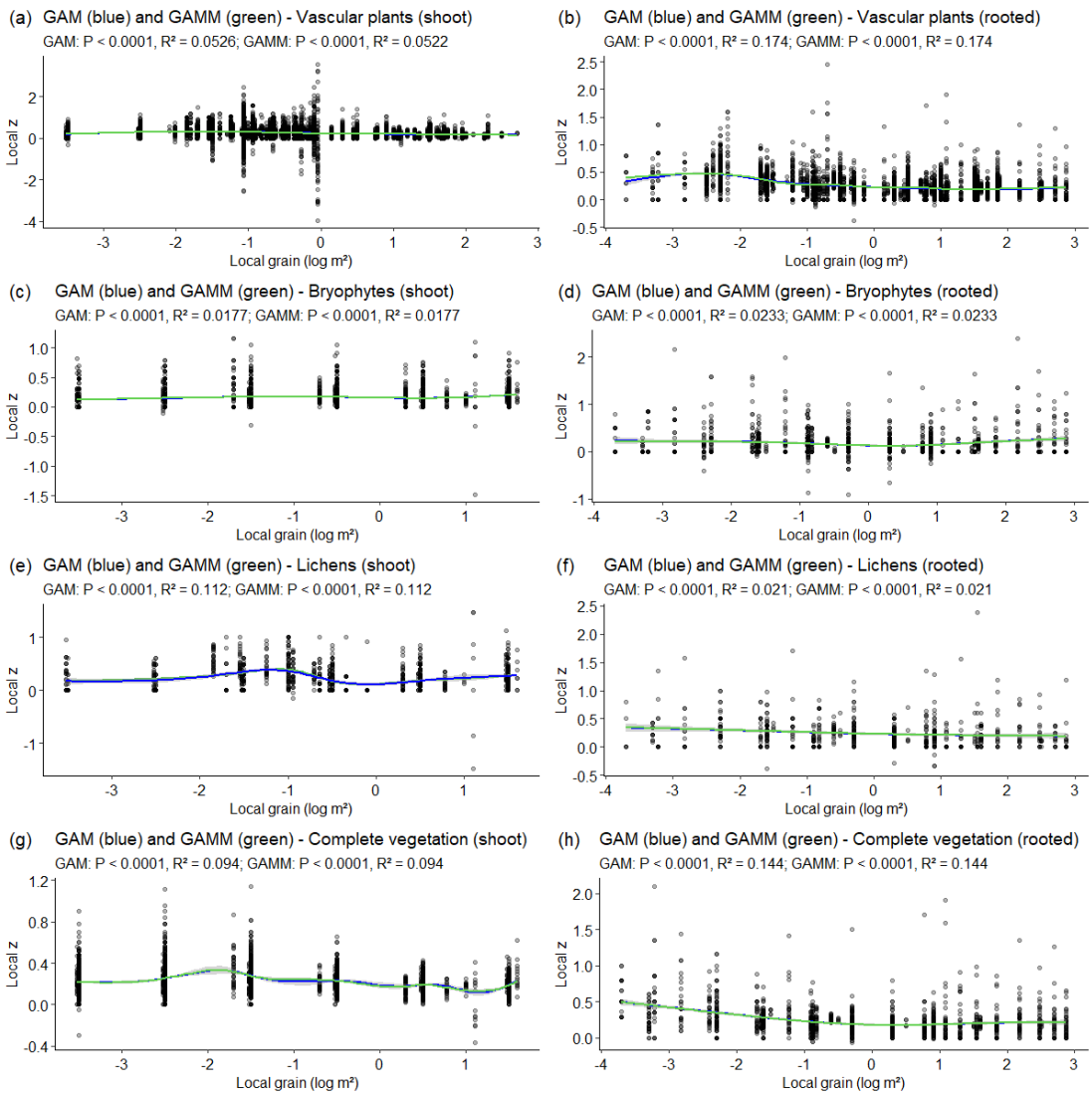

Figure S2.2. Generalized additive models (GAMs) and generalized additive mixed models (GAMMs) of the effect of local grain on local z for (a,b) vascular plants, (c,d) bryophytes, (e,f) lichens, and (g,h) with data obtained using two different ways of recording plants: (a,c,e,g) shoot presence and (b,d, f,h) root presence (with all data).

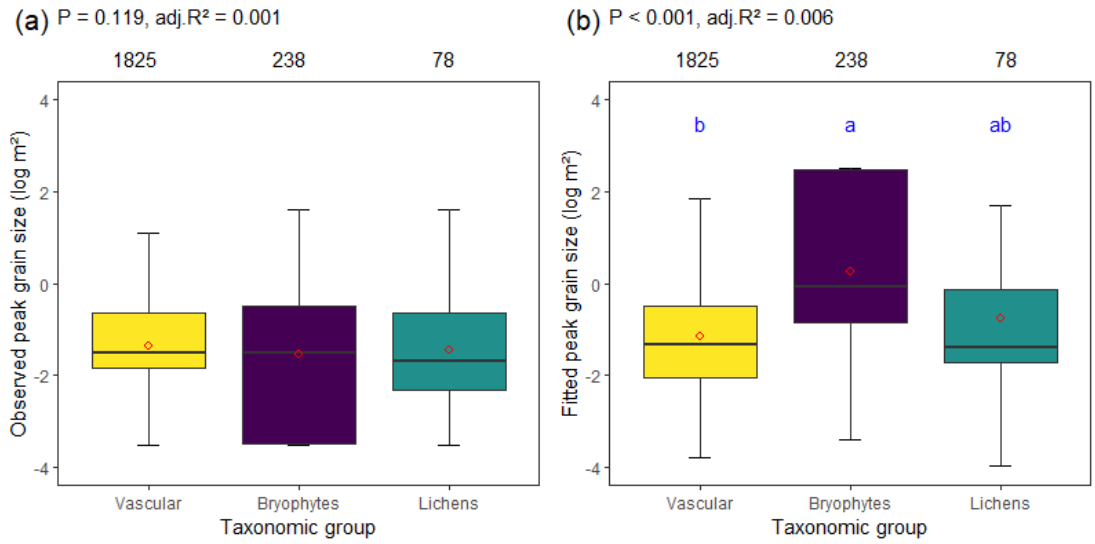

Figure S2.3. Differences in observed peak grain size (a) and fitted peak grain size (b) among taxonomic groups recorded by shoot presence. Blue lowercase letters indicate homogeneous groups ($P < 0.05$) according to Tukey's post-hoc tests.

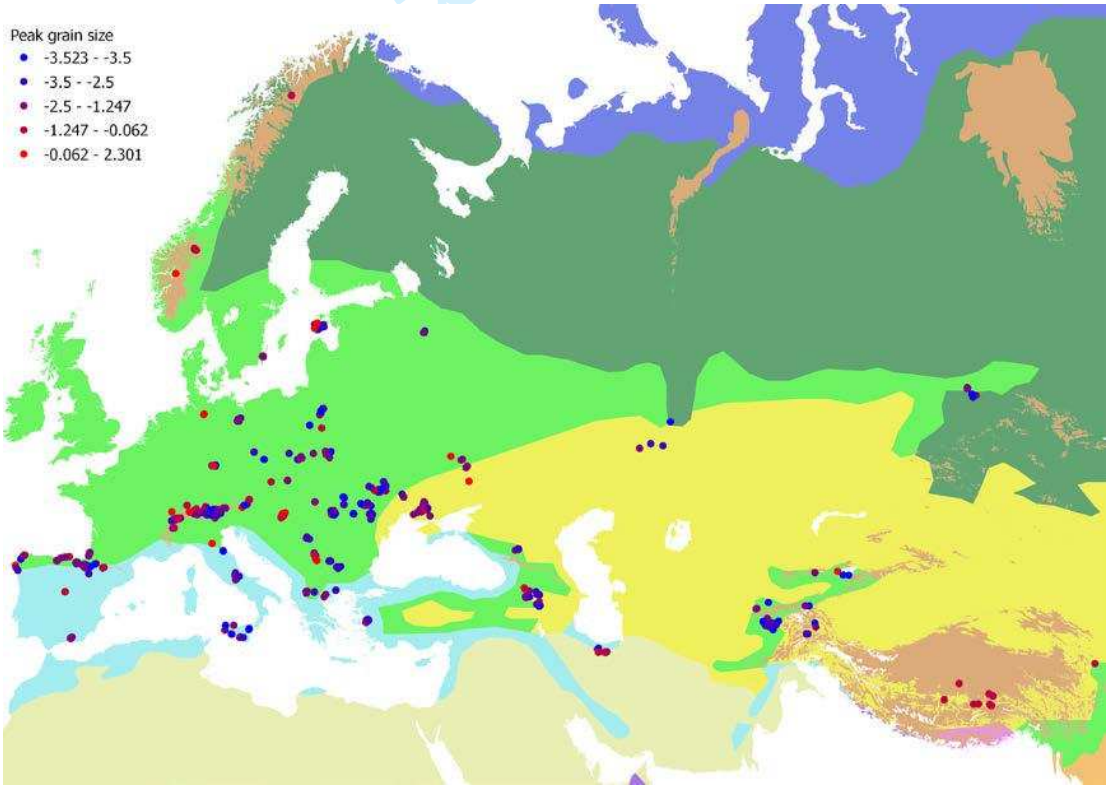

Figure S2.4. Spatial distribution of the grain sizes of observed peak for vascular plants. The values are given as $\log_{10}$ of area in m². The colours of the background refer to the biomes distinguished in GrassPlot.

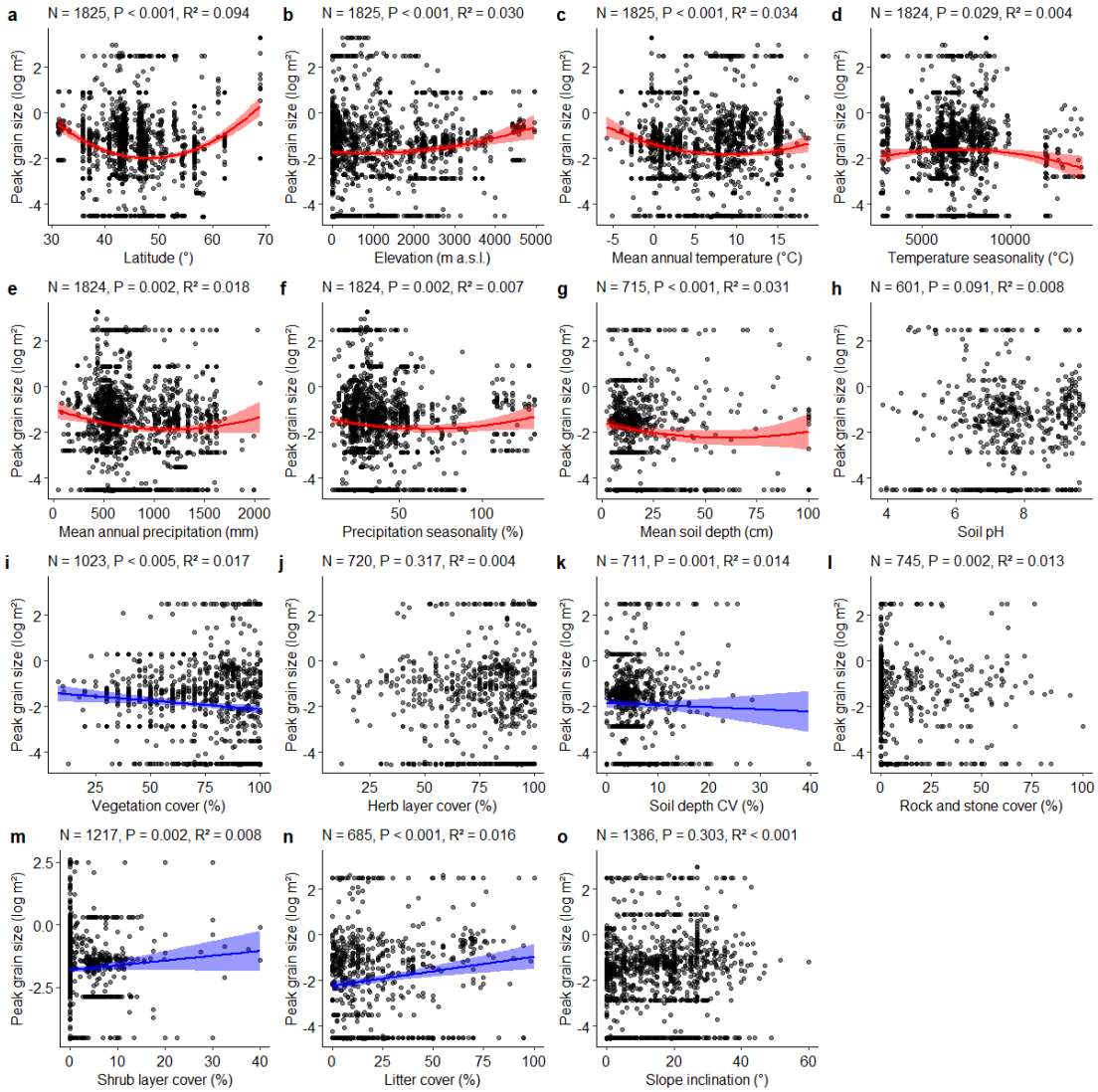

Figure S2.5. Differences in observed peak grain size (local grain size where the maximum local *z* occurred) of vascular plants (R^2<0.02) depending on predictor variables. Blue lines indicate significant linear relationships (p < 0.05) with confidence intervals, red lines represent quadratic relationships (p < 0.05) with confidence intervals.

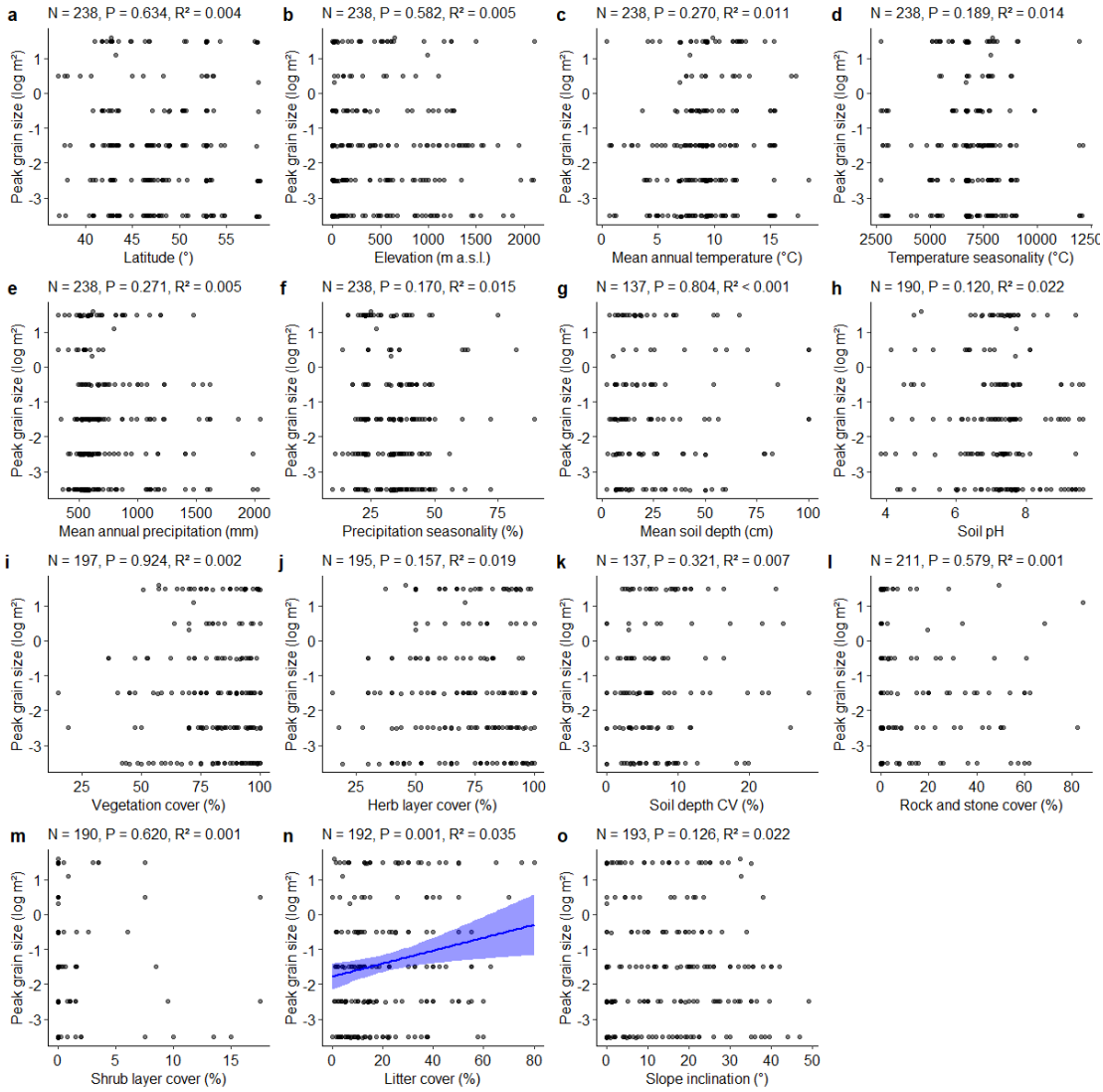

Figure S2.6. Differences in observed peak grain size (local grain size where the maximum local *z* occurred) of bryophytes depending on predictor variables. Blue lines indicate significant linear relationships ($p < 0.05$) with confidence intervals, red lines represent quadratic relationships ($p < 0.05$) with confidence intervals.

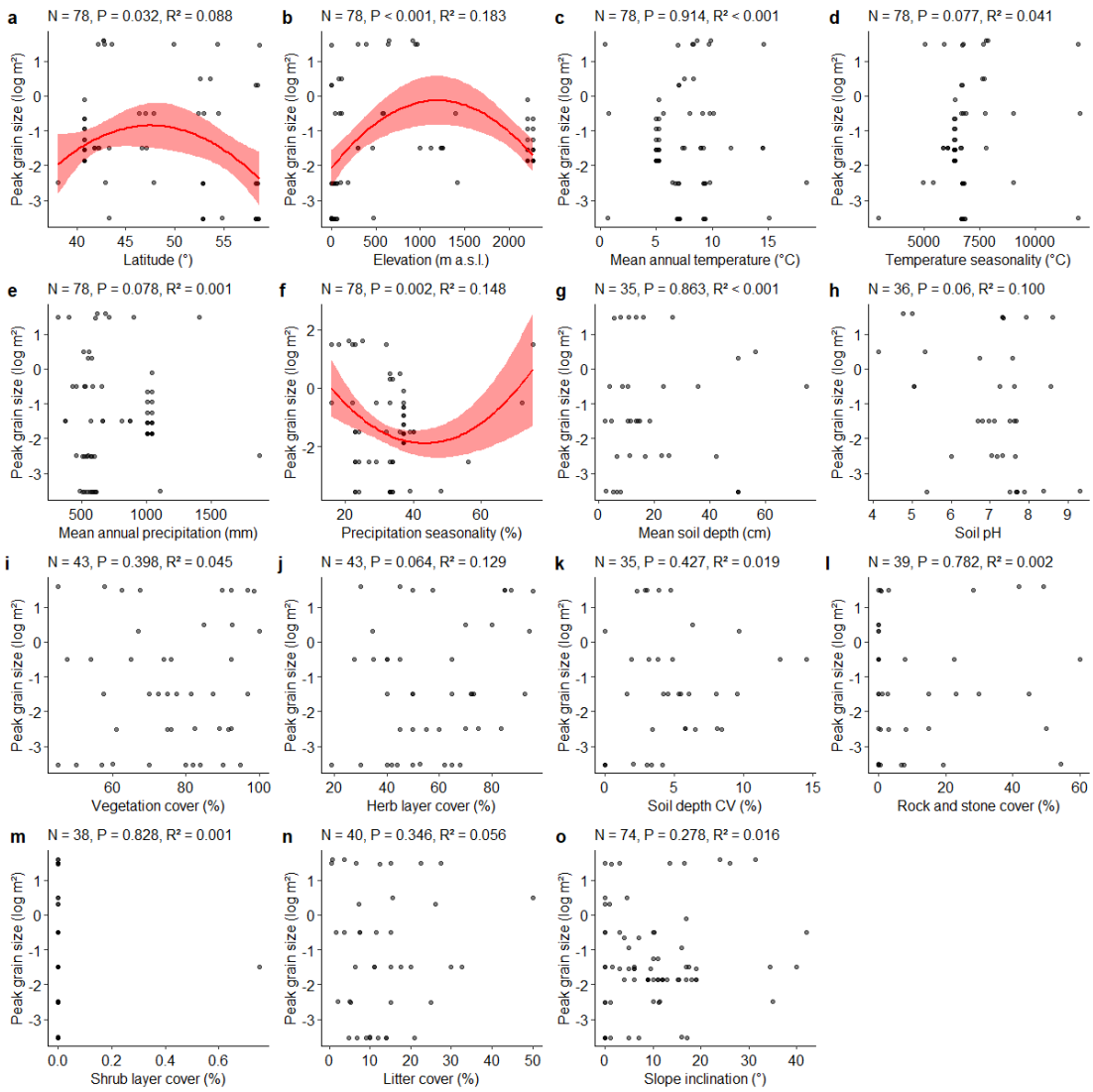

Figure S2.7. Differences in observed peak grain size (local grain size where the maximum local *z* occurred) of lichens depending on predictor variables. Blue lines indicate significant linear relationships ($p < 0.05$) with confidence intervals, Red lines represent quadratic relationships ($p < 0.05$) with confidence intervals.

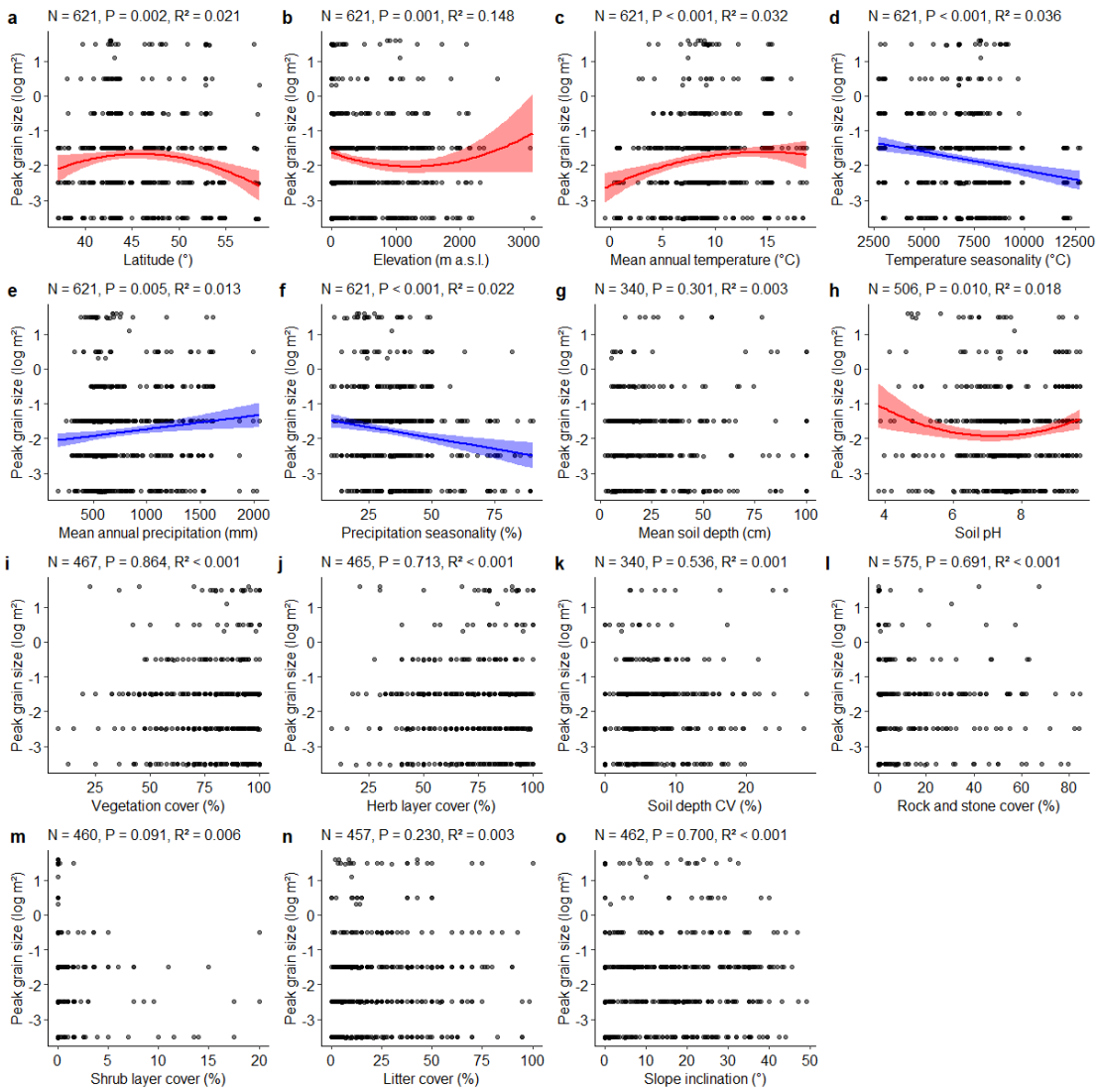

Figure S2.8. Differences in observed peak grain size (local grain size where the maximum local *z* occurred) of complete vegetation depending on predictor variables. Blue lines indicate significant linear relationships ($p < 0.05$) with confidence intervals; red lines represent quadratic relationships ($p < 0.05$) with confidence intervals.

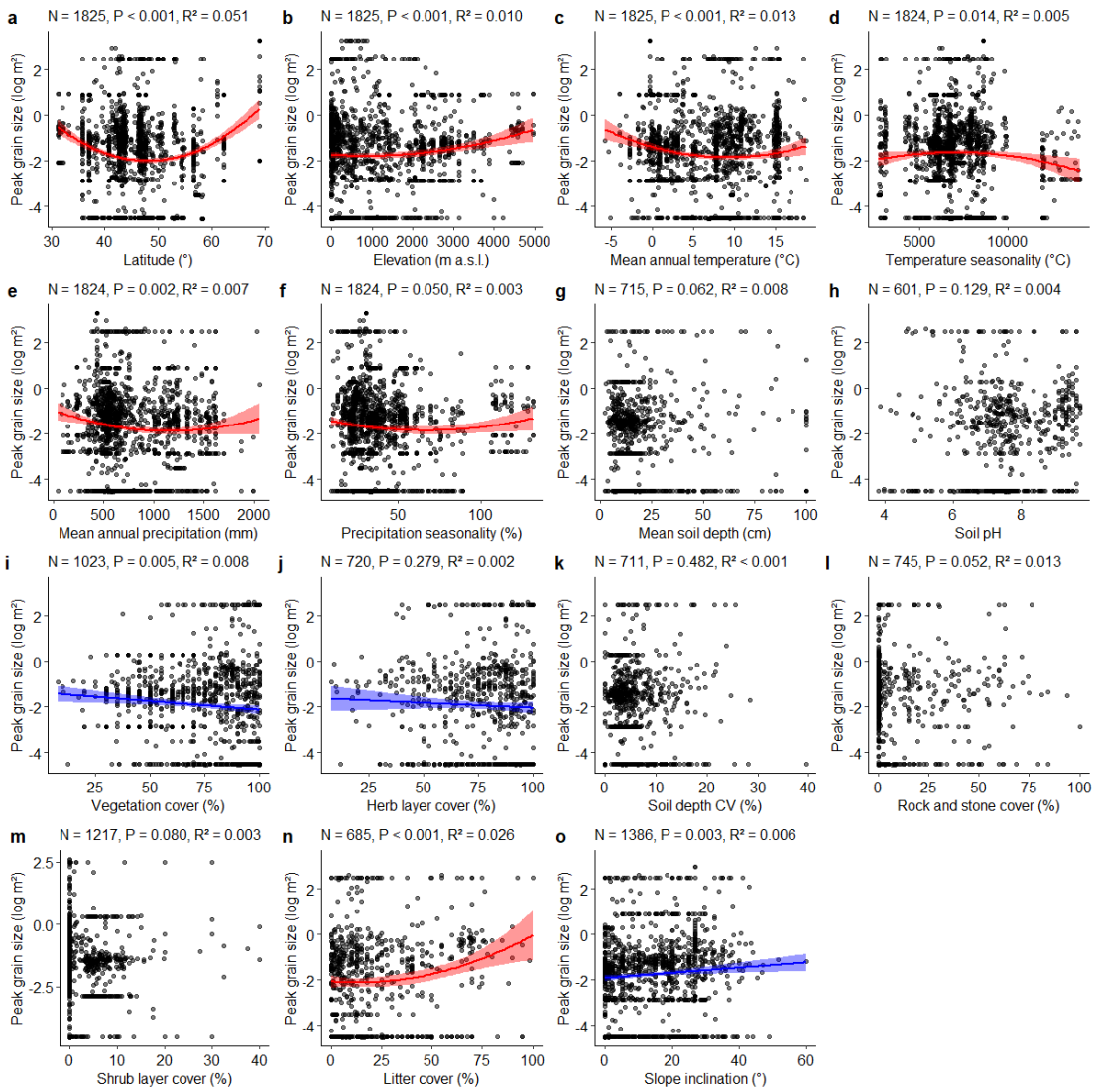

Figure S2.9. Differences in fitted peak grain size (local grain size where the maximum local z was predicted) for vascular plants depending on predictor variables. Blue lines indicate significant linear relationships ($p < 0.05$) with confidence intervals; red lines represent quadratic relationships ($p < 0.05$) with confidence intervals.

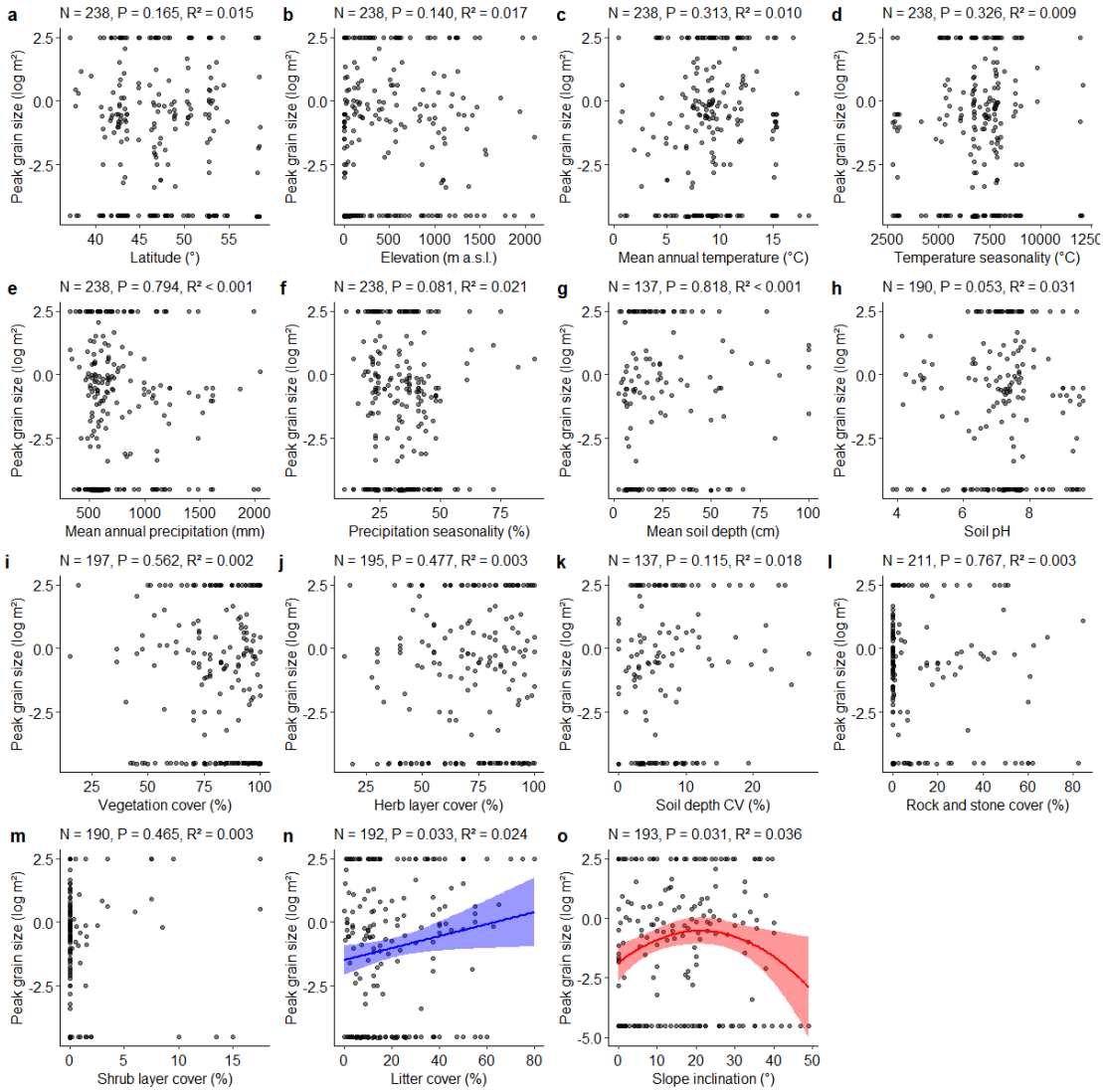

Figure S2.10. Differences in fitted peak grain size (local grain size where the maximum local *z* was predicted) for bryophytes depending on predictor variables. Blue lines indicate significant linear relationships ($p < 0.05$) with confidence intervals; red lines represent quadratic relationships ($p < 0.05$) with confidence intervals.

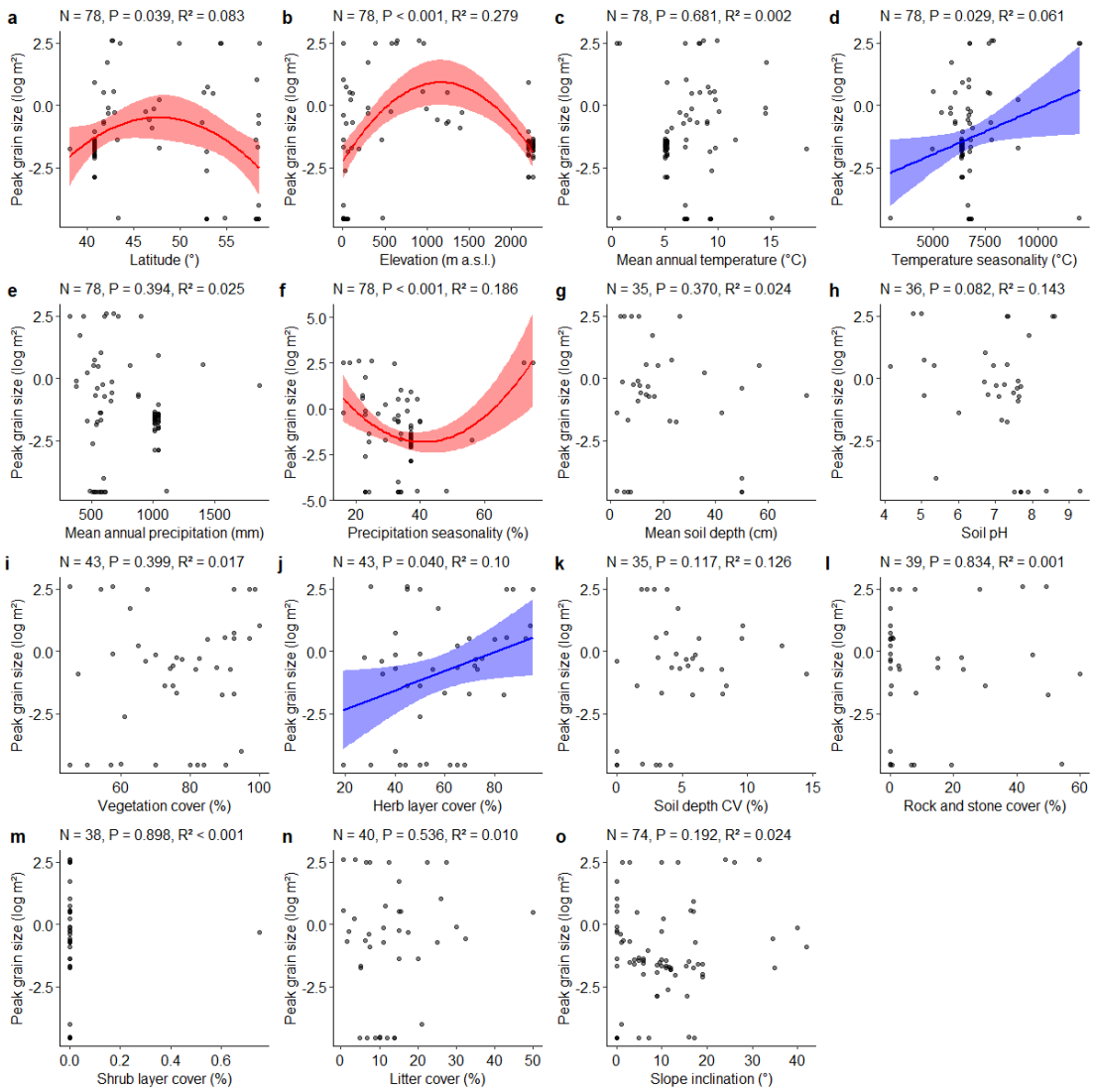

Figure S2.11. Differences in fitted peak grain size (local grain size where the maximum local *z* was predicted) for lichens depending on predictor variables. Blue lines indicate significant linear relationships ($p < 0.05$) with confidence intervals; red lines represent quadratic relationships ($p < 0.05$) with confidence intervals.

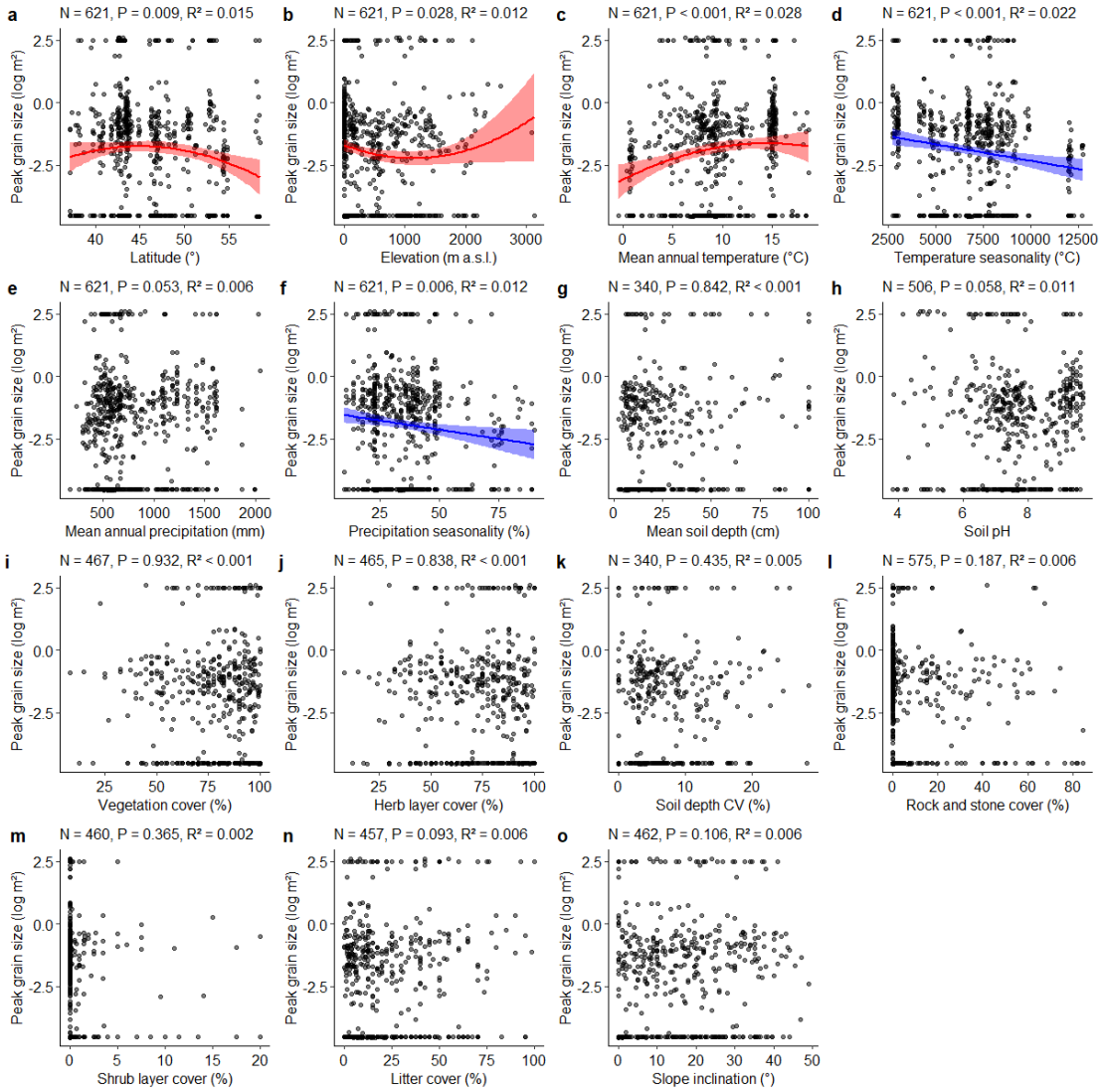

Figure S2.12. Differences in fitted peak grain size (local grain size where the maximum local *z* was predicted) for complete vegetation depending on predictor variables. Blue lines indicate significant linear relationships ($p < 0.05$) with confidence intervals; red lines represent quadratic relationships ($p < 0.05$) with confidence intervals.

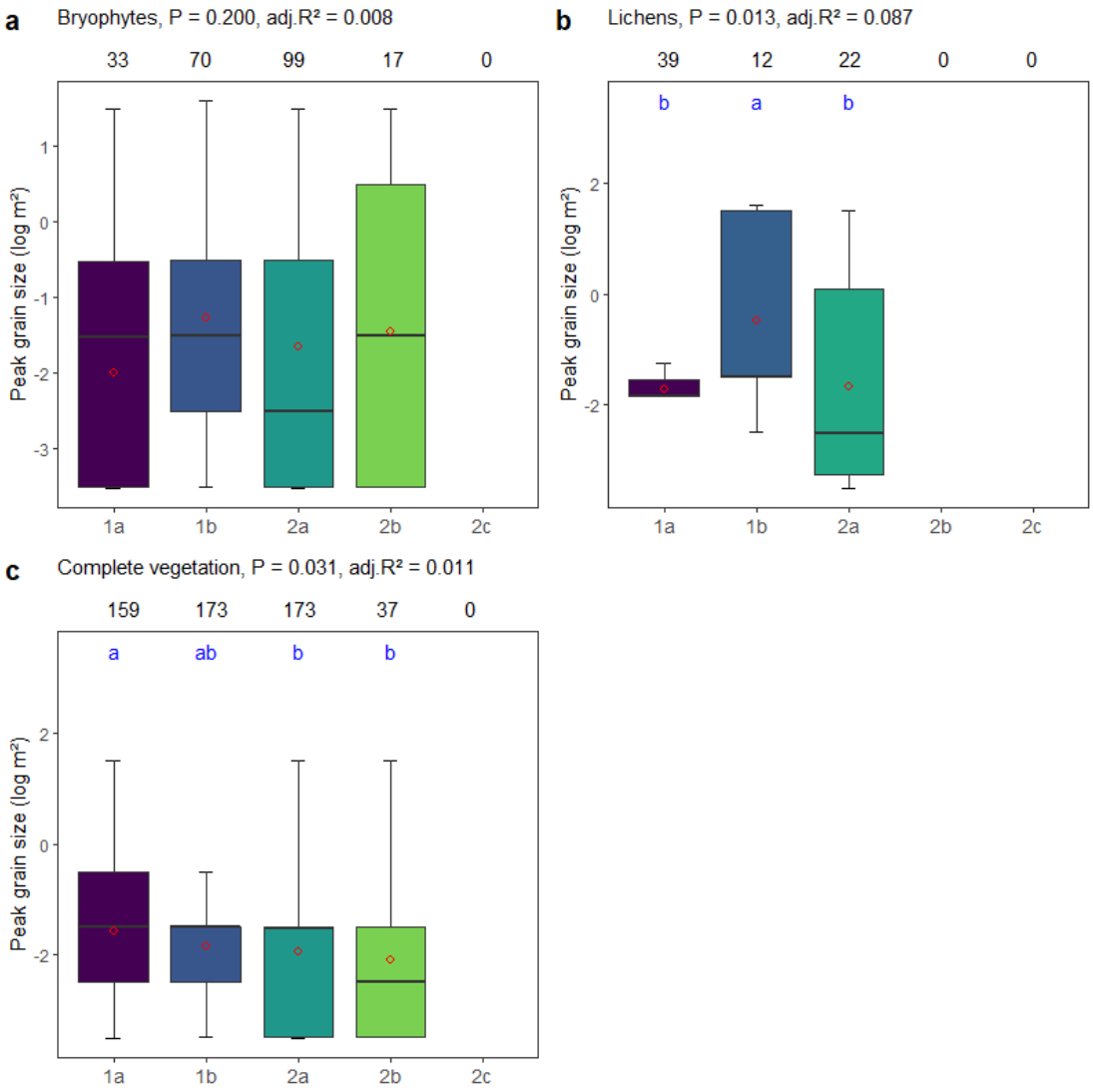

Figure S2.13. Comparison of observed peak grain size (local grain size where the maximum local z occurred) at the five levels of naturalness present in this study (no series for 1c – natural grasslands, overused): 1 – natural grasslands (1a – not managed, 1b – extensively managed); 2 – secondary grasslands (2a – semi-natural, 2b – semi-intensified, 2c – intensified). Blue lowercase letters indicate homogeneous groups ($P < 0.05$) as tested with Tukey's post-hoc test ANOVA, the figures on top indicate the sample size. Box and whisker plots represent the median and +- 1.5 IQR (interquartile range) while the red dots represent the mean values for each naturalness.

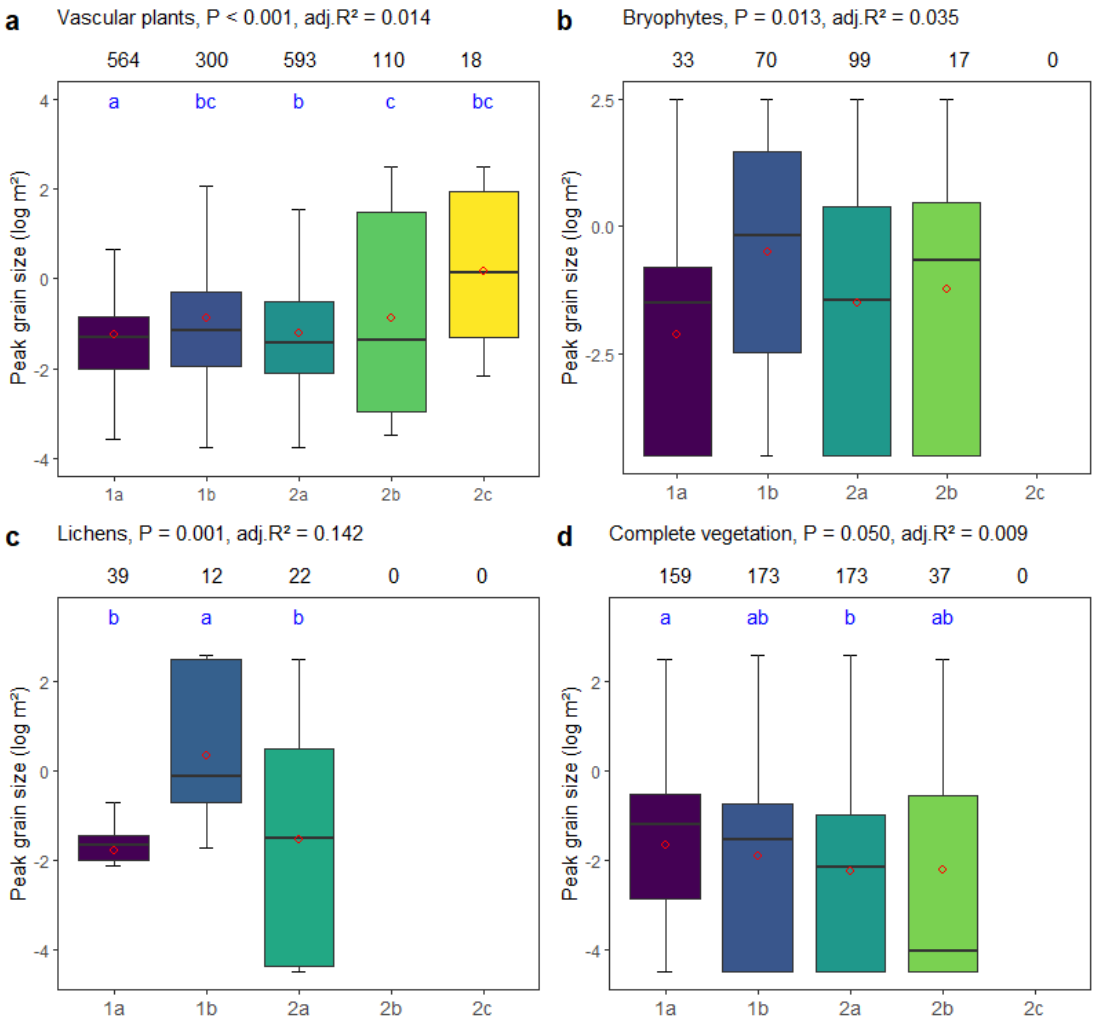

Figure S2.14. Comparison of fitted peak grain size (local grain size where the maximum local *z* was predicted) for a) vascular plants, b) bryophytes, c) lichens, d) complete vegetation in the five levels of naturalness considered in the study (no series for 1c – natural grasslands, overused): 1 – natural grasslands (1a – not managed, 1b – extensively managed); 2 – secondary grasslands (2a – semi-natural, 2b – semi-intensified, 2c – intensified). Blue lowercase letters indicate homogeneous groups ($p < 0.05$) as tested with Tukey's post-hoc test with ANOVA.

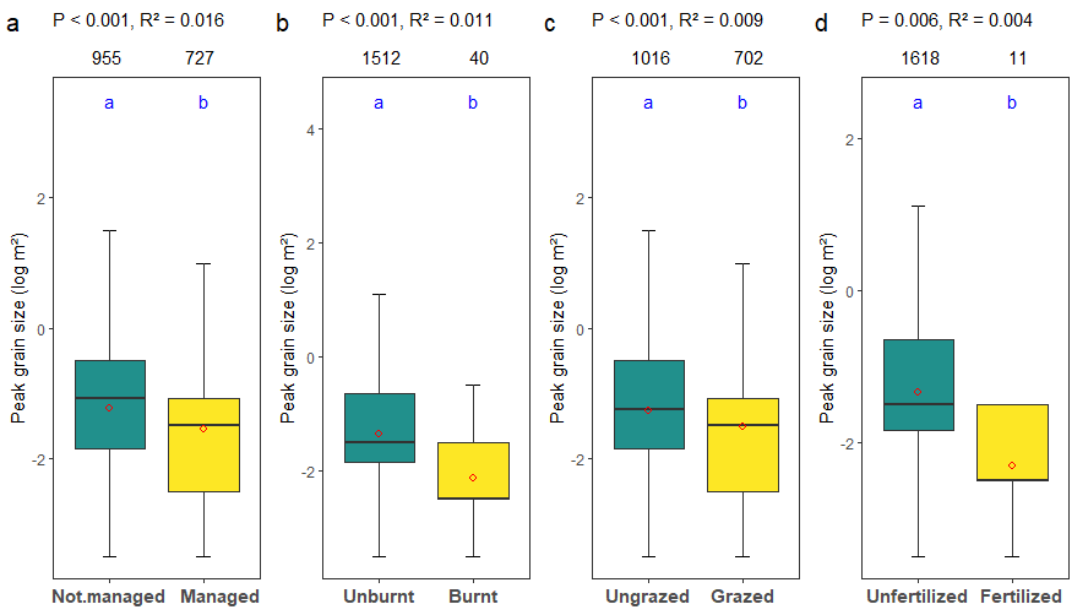

Figure S2.15. Comparison of effect of land use on observed peak grain size (local grain size where the maximum local z occurred) for vascular plants.

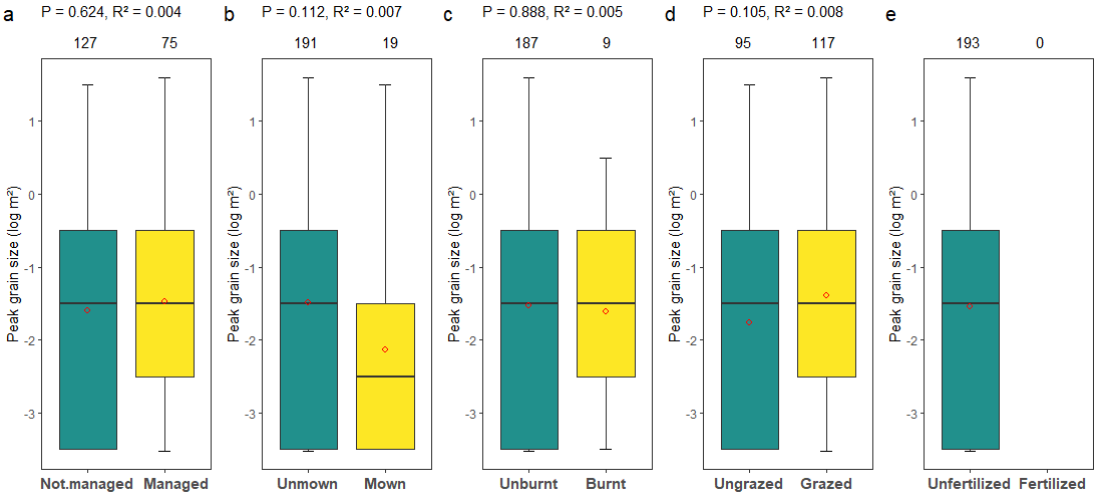

Figure S2.16. Comparison of effect of land use on observed peak grain size (local grain size where the maximum local z occurred) for bryophytes.

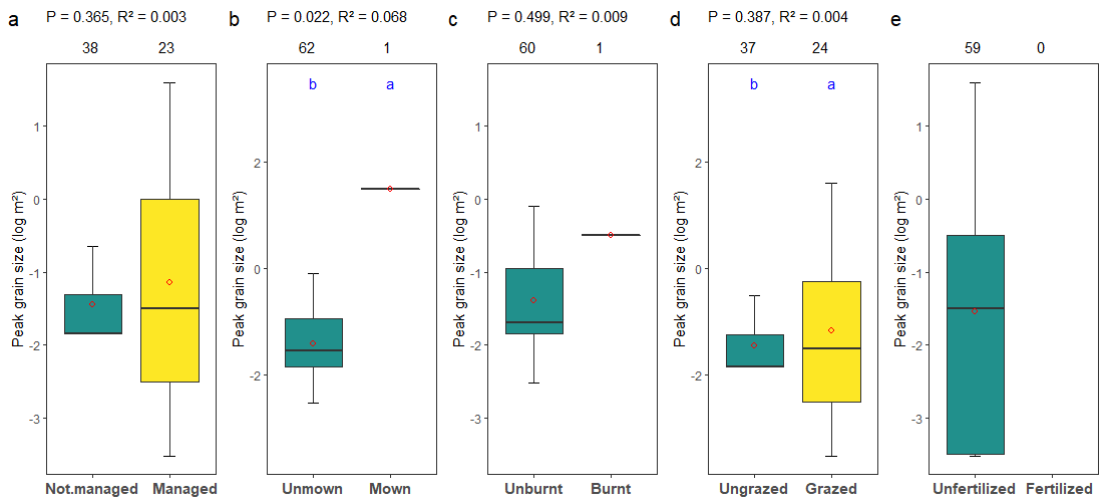

Figure S2.17. Comparison of effect of land use on observed peak grain size (local grain size where the maximum local z occurred) for lichens.

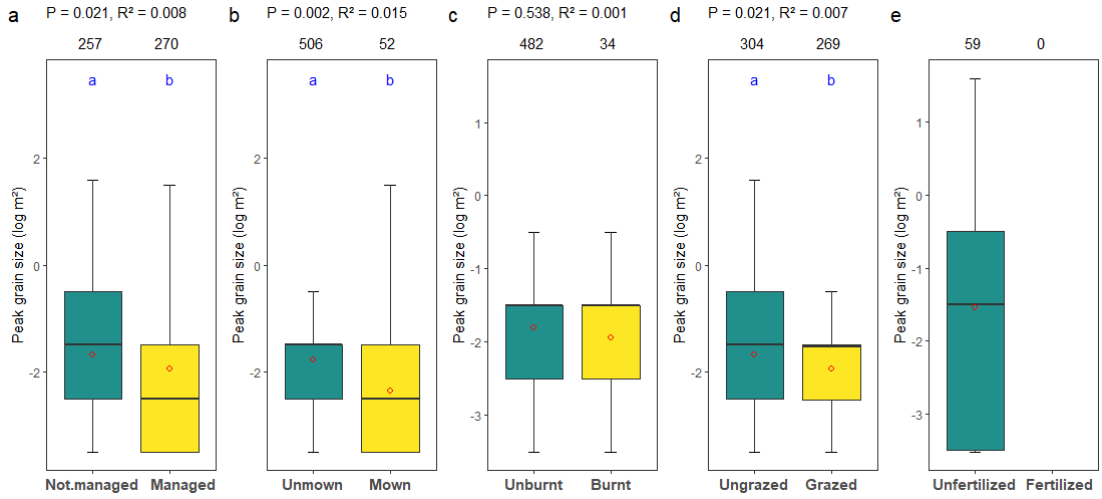

Figure S2.18. Comparison of effect of land use on observed peak grain size (local grain size where the maximum local z occurred) for complete vegetation.

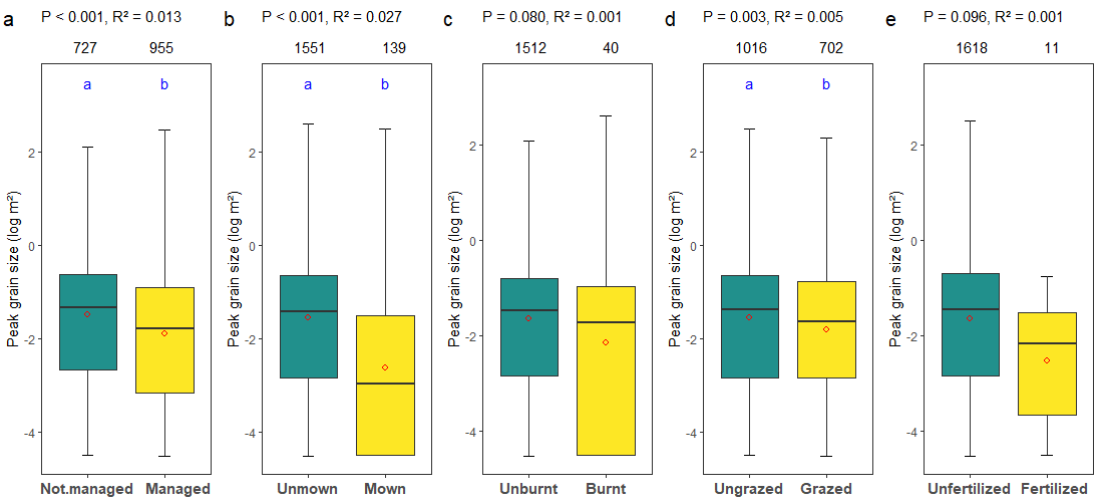

Figure S2.19. Comparison of effect of land use on fitted peak grain size (local grain size where the maximum local z was predicted) for vascular plants.

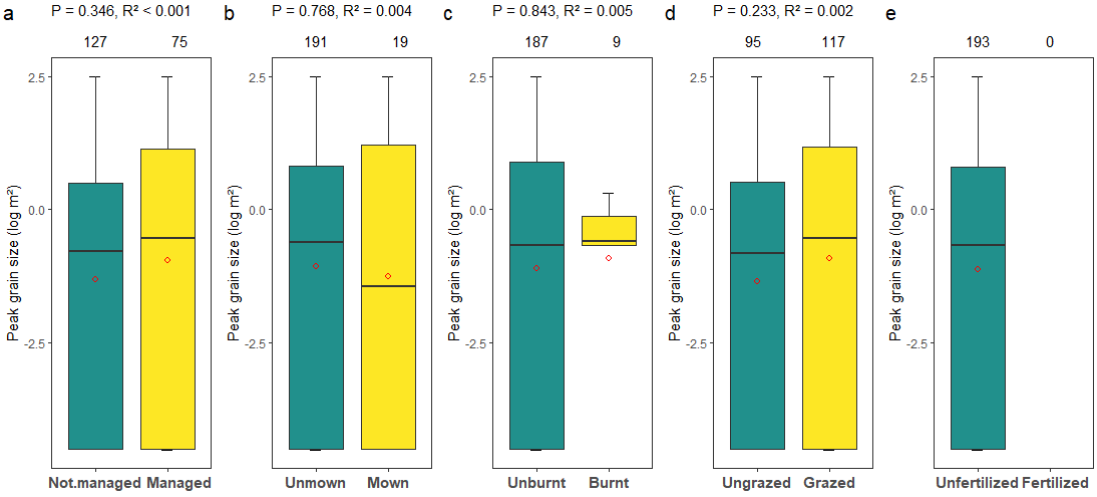

Figure S2.20. Comparison of effect of land use on fitted peak grain size (local grain size where the maximum local z was predicted) for bryophytes.

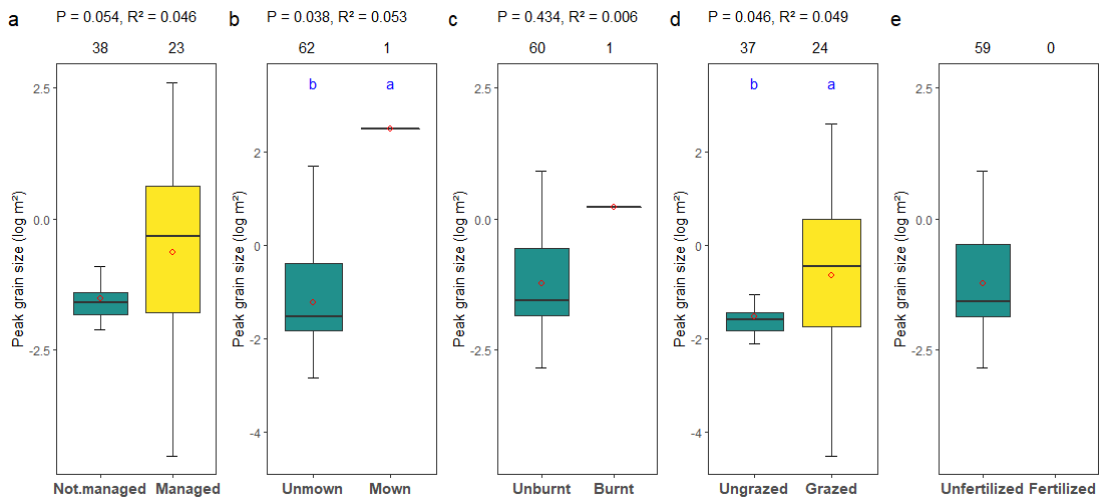

Figure S2.21. Comparison of effect of land use on fitted peak grain size (local grain size where the maximum local z was predicted) for lichens.

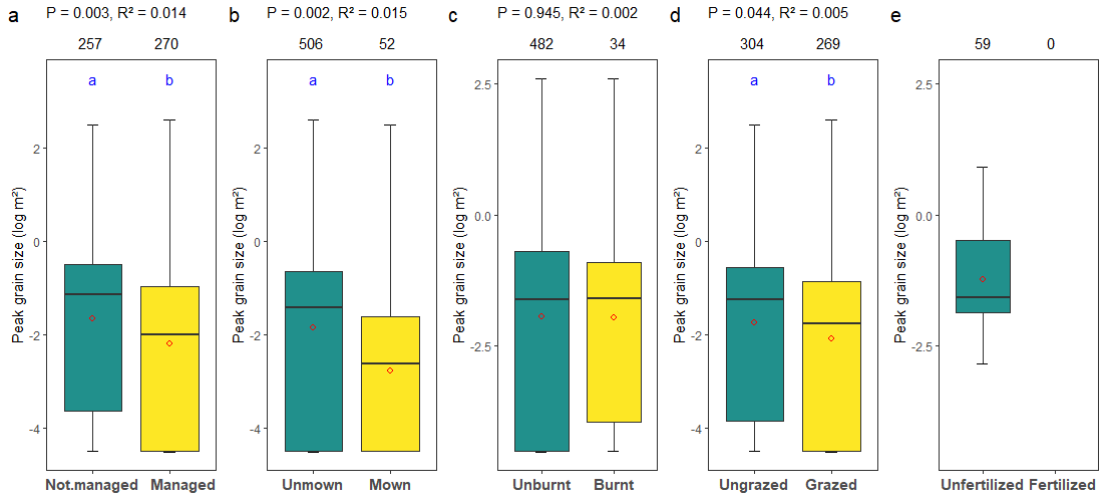

Figure S2.22. Comparison of effect of land use on fitted peak grain size (local grain size where the maximum local z was predicted) for complete vegetation.

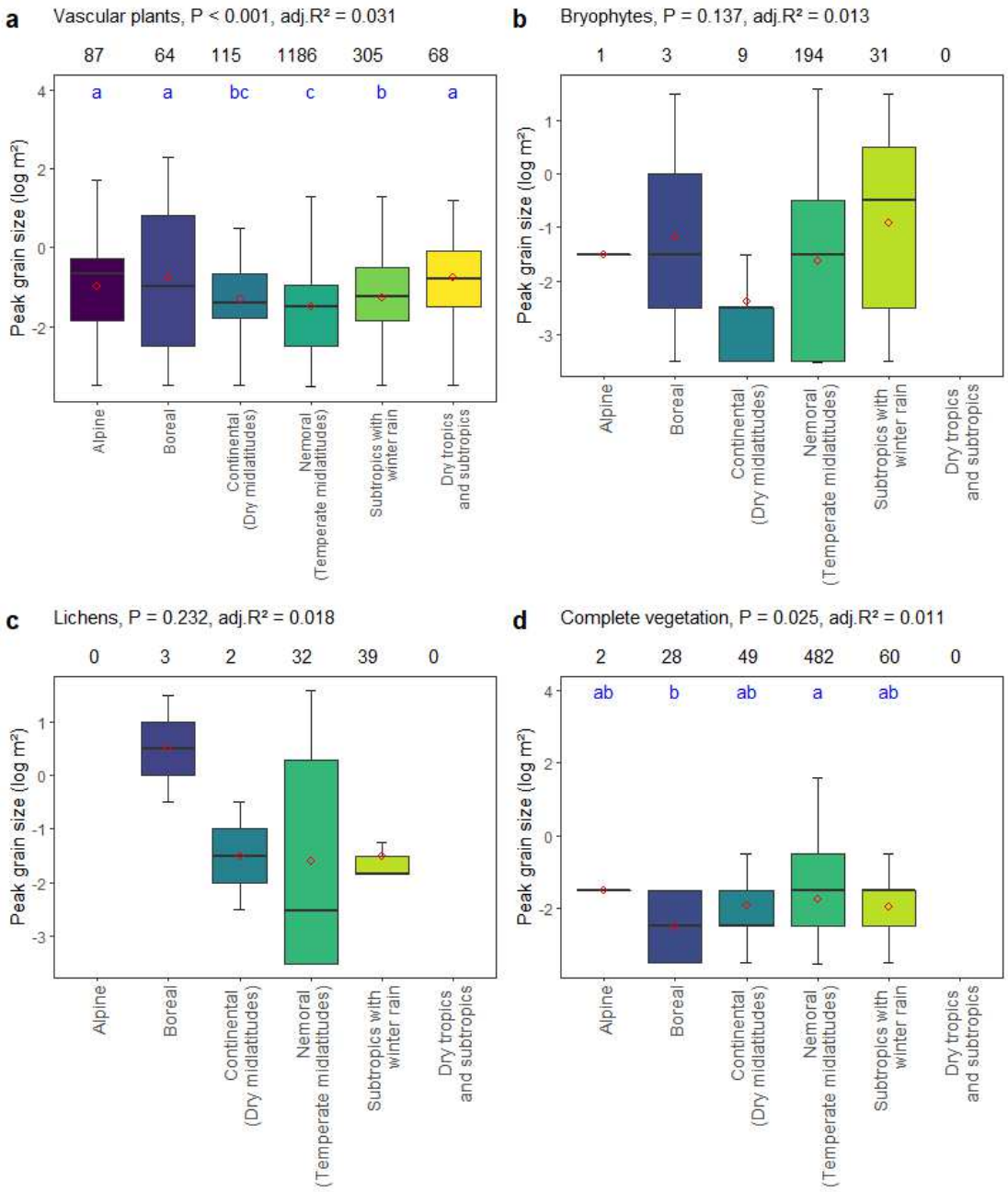

Figure S2.23. Comparison of observed peak grain size (local grain size where the maximum local z occurred) for a) vascular plants, b) bryophytes, c) lichens, d) complete vegetation between the six biomes considered in this study. A common blue lower-case letter between two boxes indicates homogeneous groups as tested with Tukey's post-hoc test with ANOVA ($P < 0.05$), the figures on top indicate the numbers of data. Box and whisker plots represent the median and quartiles while the red dots represent the mean values for each biome.

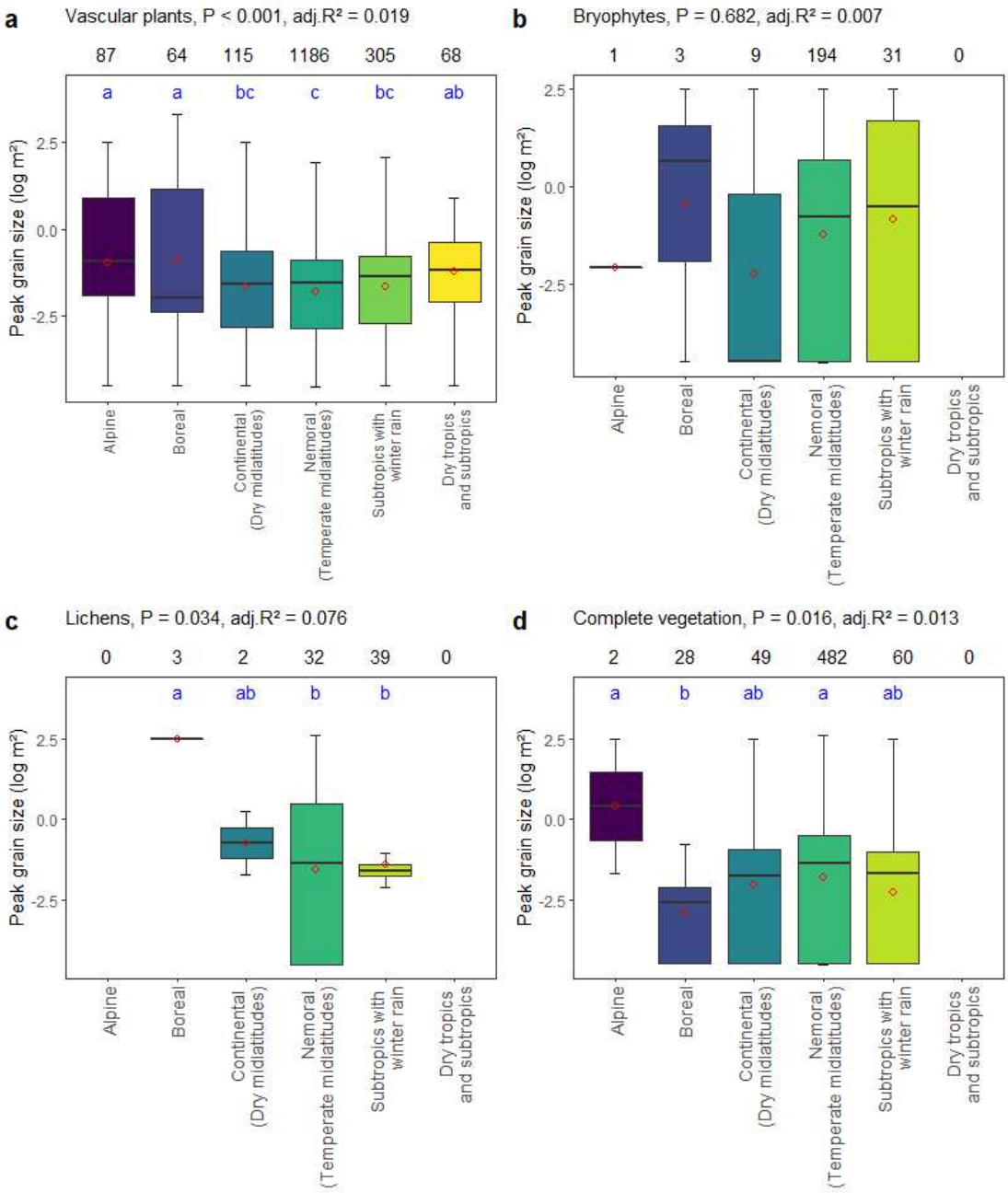

Figure S2.24. Comparison of fitted peak grain size (local grain size where the maximum local z was predicted) for a) vascular plants, b) bryophytes, c) lichens, d) complete vegetation between the six biomes considered in the study. A common blue lower-case letter between two boxes indicates homogeneous groups as tested with Tukey's post-hoc test with ANOVA ($P < 0.05$), the figures on top indicate the numbers of data. Box and whisker plots represent the median and quartiles while the red dots represent the mean values for each biome.

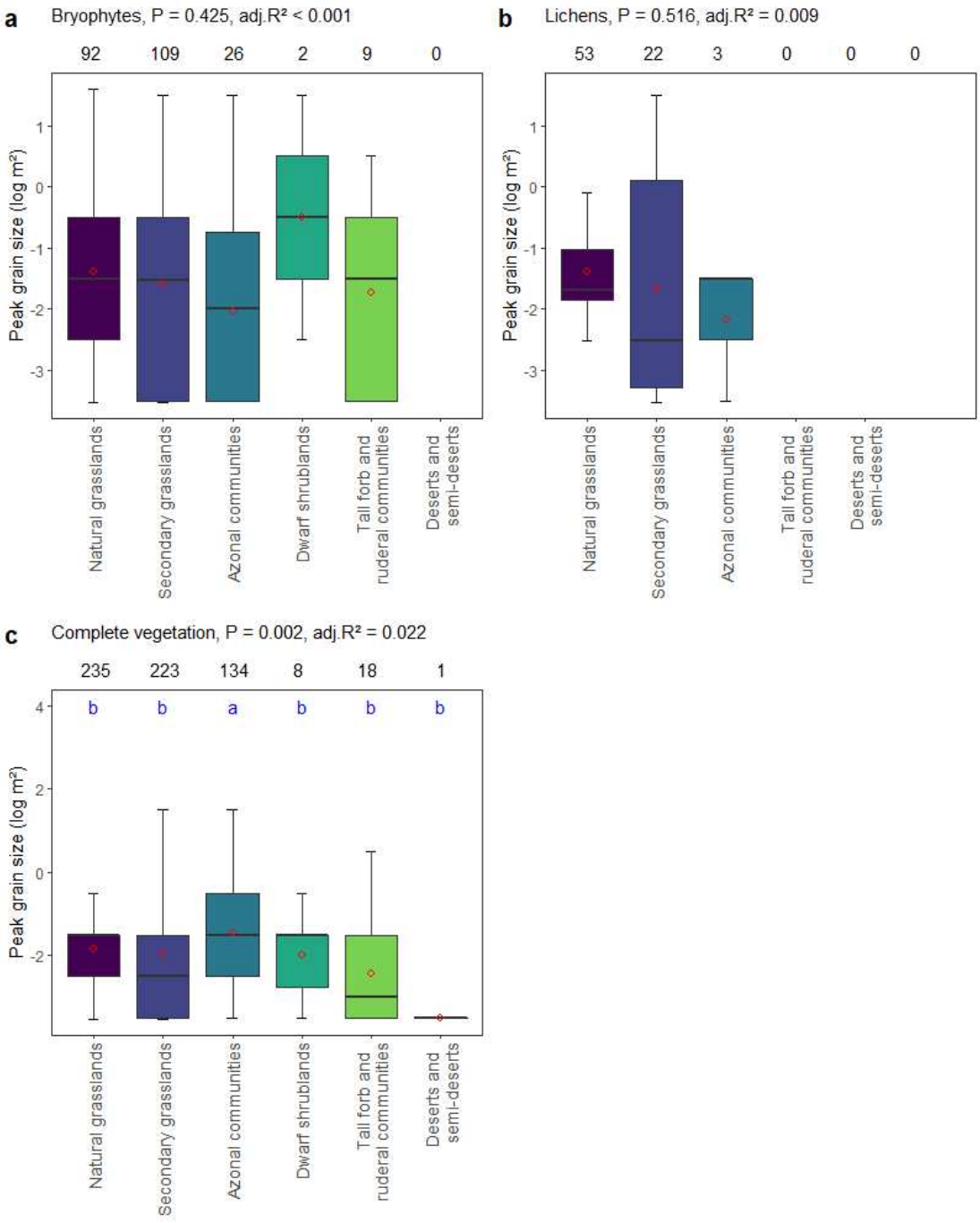

Figure S2.25. Comparison of observed peak grain size (local grain size where the maximum local z was predicted) for a) bryophytes, b) lichens, c) complete vegetation between the six vegetation types at coarse level considered in this study. A common blue lower-case letter between two boxes indicates homogeneous groups as tested with Tukey's post-hoc test with ANOVA ($p<0.05$). Box and whisker plots represent the median and quartiles while the red dots represent the mean values for each vegetation type at coarse level.

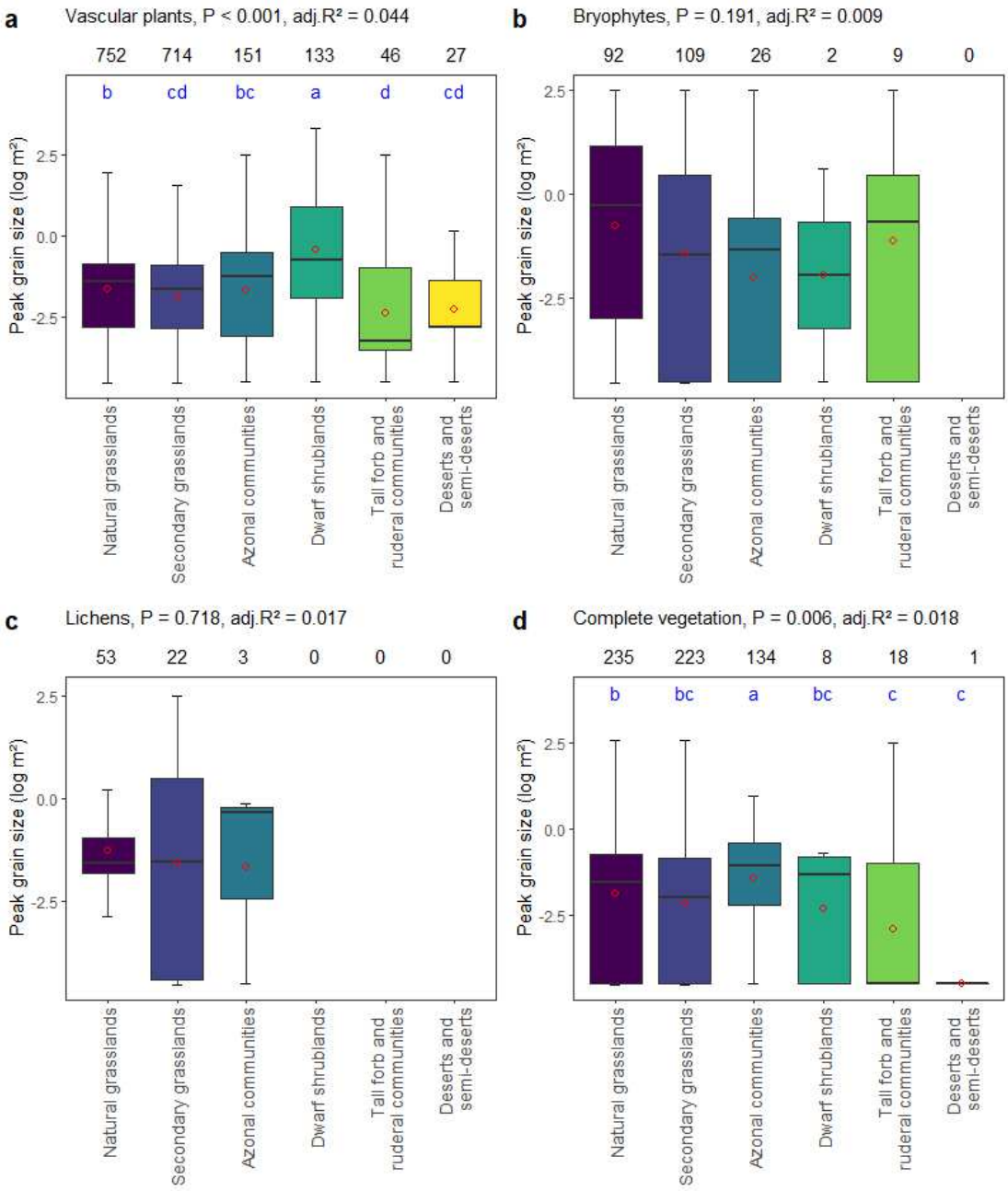

Figure S2.26. Comparison of fitted peak grain size (local grain size where the maximum local z was predicted) for a) vascular plants, b) bryophytes, c) lichens, d) complete vegetation between the six vegetation types at coarse level considered in this study. A common blue lower-case letter between two boxes indicates homogeneous groups as tested with Tukey's post-hoc test with ANOVA ($p < 0.05$). Box and whisker plots represent the median and quartiles while the red dots represent the mean values for each vegetation type at coarse level.

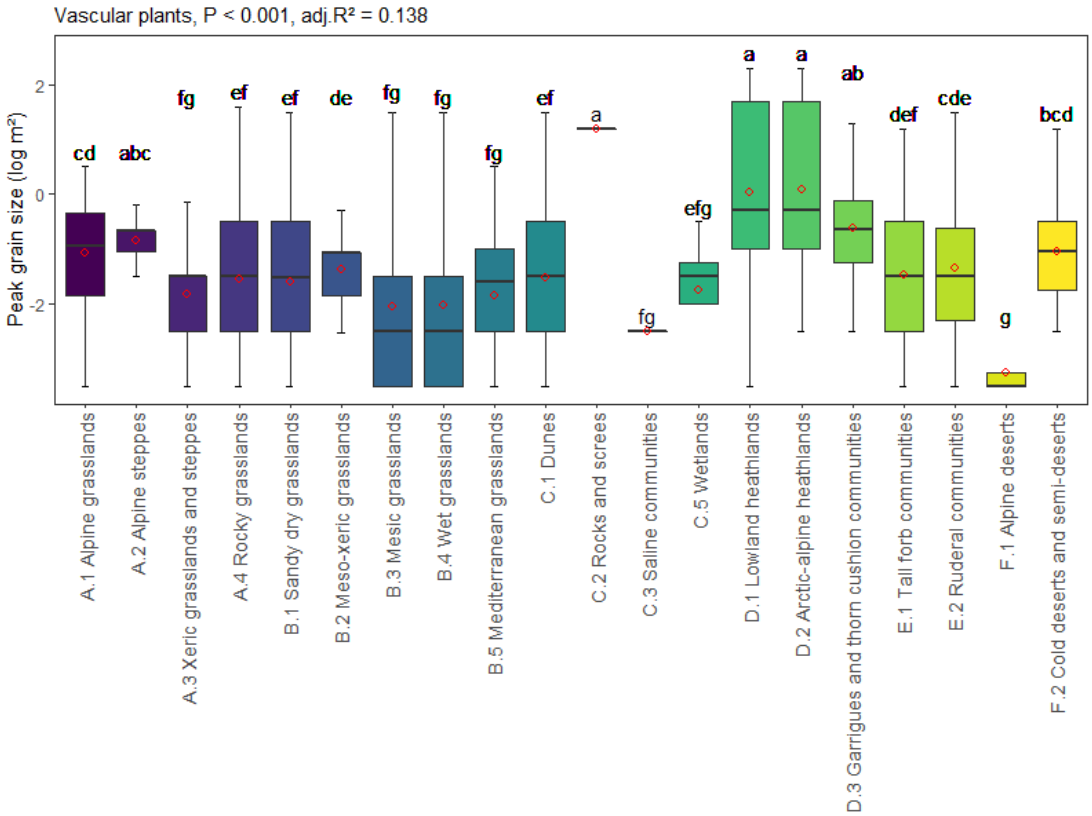

Figure S2.27. Comparison of observed peak grain size (local grain size where the maximum local z occurred) for vascular plants between the vegetation types at fine level considered in this study. A common lower-case letter between two boxes indicates homogeneous groups as tested with Tukey's post-hoc test with ANOVA (p <0 .05). Box and whisker plots represent the median and quartiles while the red dots represent the mean values for each vegetation type at fine levels.

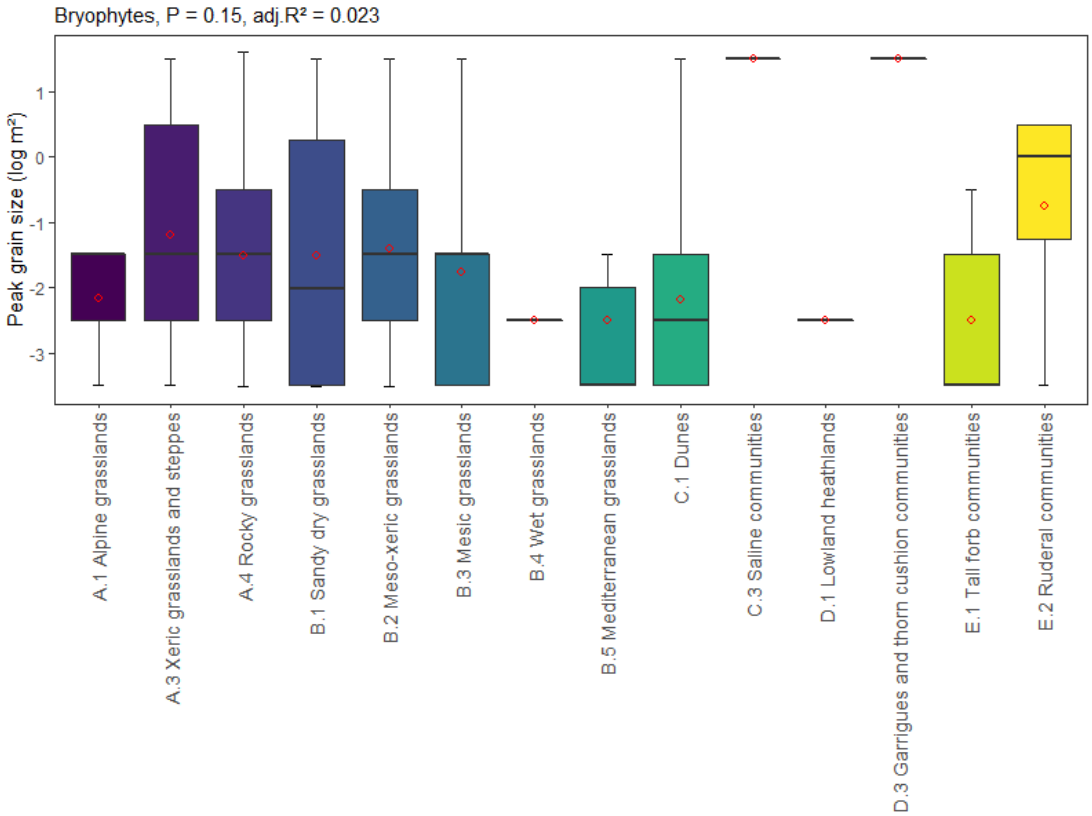

Figure S2.28. Comparison of observed peak grain size (local grain size where the maximum local *z* occurred) for bryophytes between the vegetation types at fine level considered in this study. Box and whisker plots represent the median and quartiles while the red dots represent the mean values for each vegetation type at fine levels.

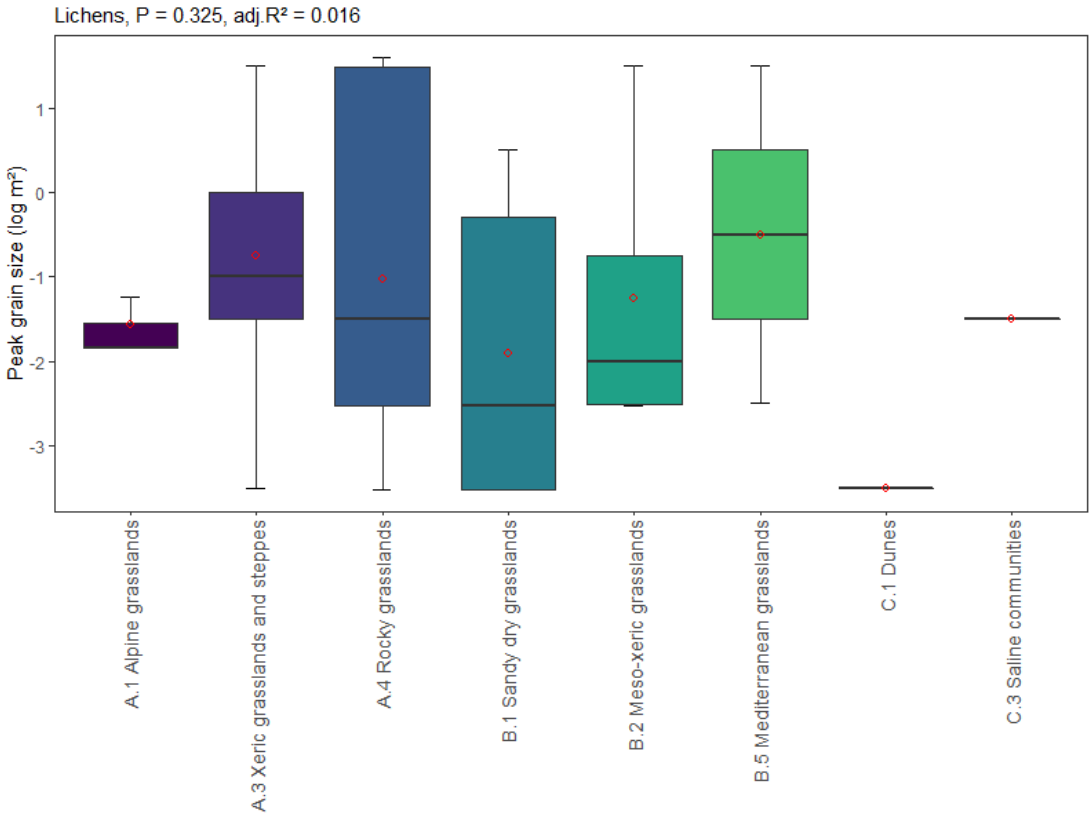

Figure S2.29. Comparison of observed peak grain size (local grain size where the maximum local *z* occurred) for lichens between the vegetation types at fine level considered in this study. Box-and-whisker plots represent the median and quartiles while the red dots represent the mean values for each vegetation type at fine levels.

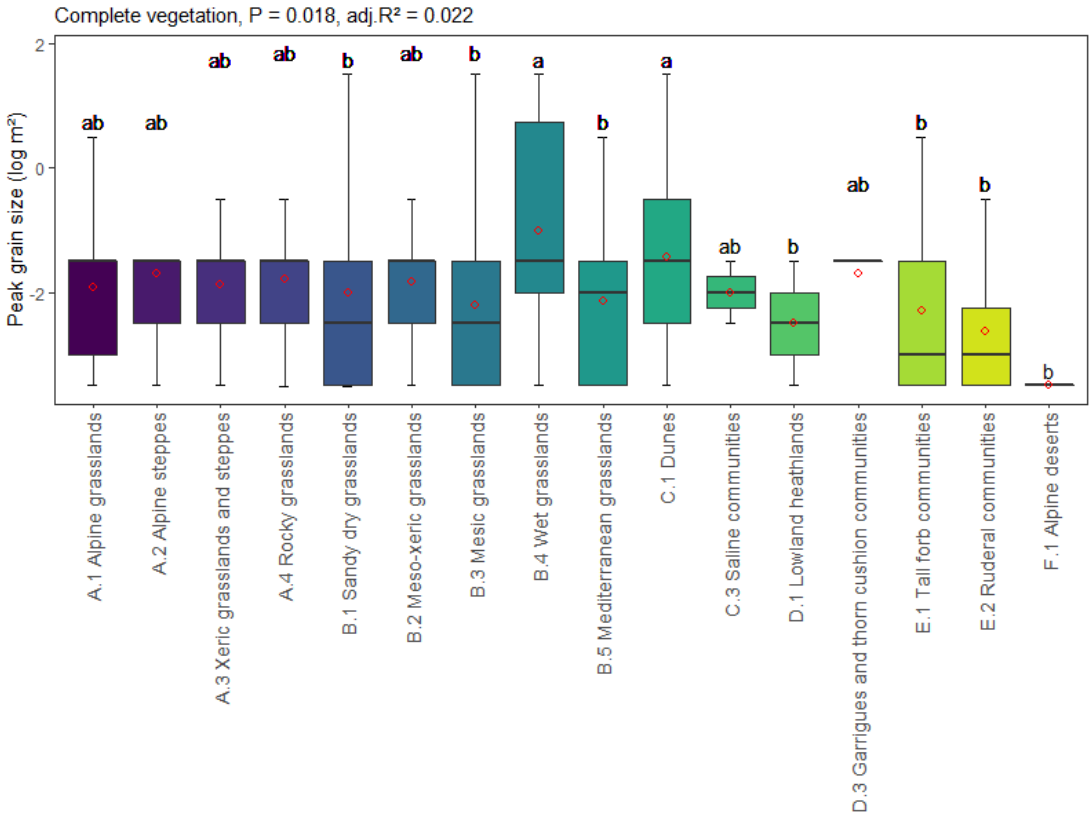

Figure S2.30. Comparison of observed peak grain size (local grain size where the maximum local z occurred) for complete vegetation between the vegetation types at fine level considered in this study. A common lower-case letter between two boxes indicates homogeneous groups as tested with Tukey's post-hoc test with ANOVA ($p < 0.05$). Box and whisker plots represent the median and quartiles while the red dots represent the mean values for each vegetation type at fine levels.

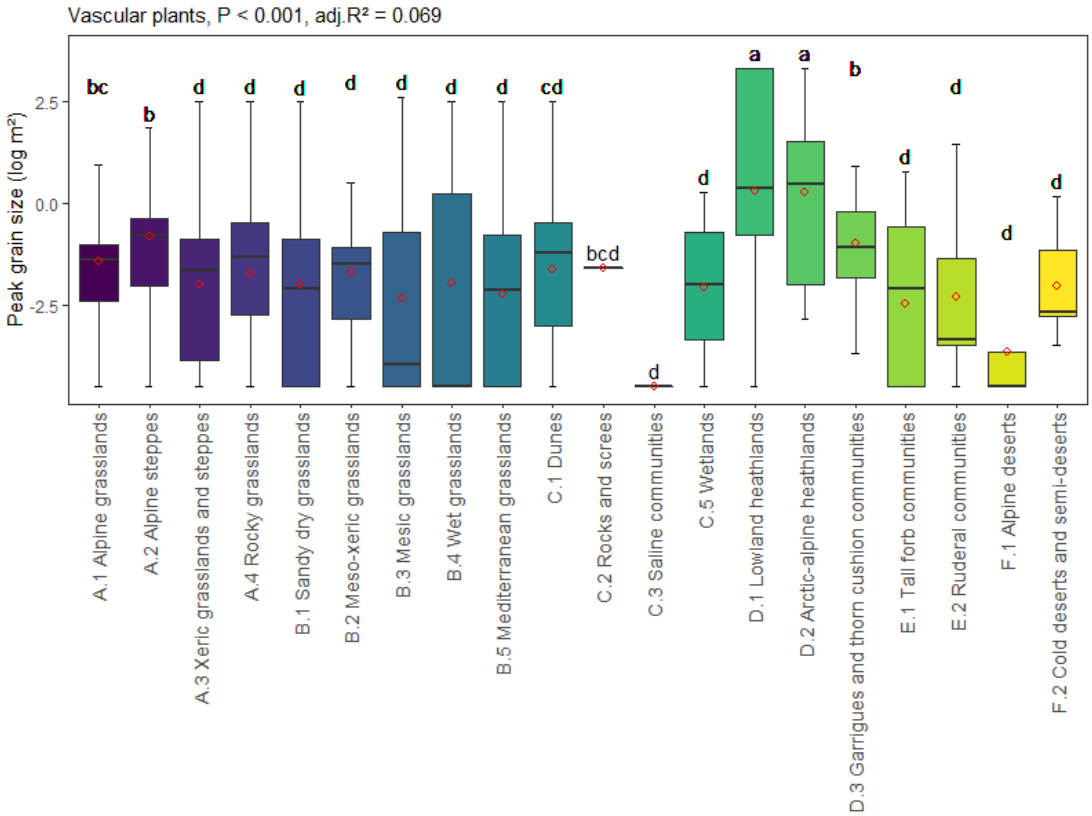

Figure S2.31. Comparison of fitted peak grain size (local grain size where the maximum local z was predicted) for vascular plants between the vegetation types at fine level considered in this study. A common lower-case letter between two boxes indicates homogeneous groups as tested with Tukey's post-hoc test with ANOVA ($p < 0.05$). Box and whisker plots represent the median and quartiles while the red dots represent the mean values for each vegetation type at fine levels.

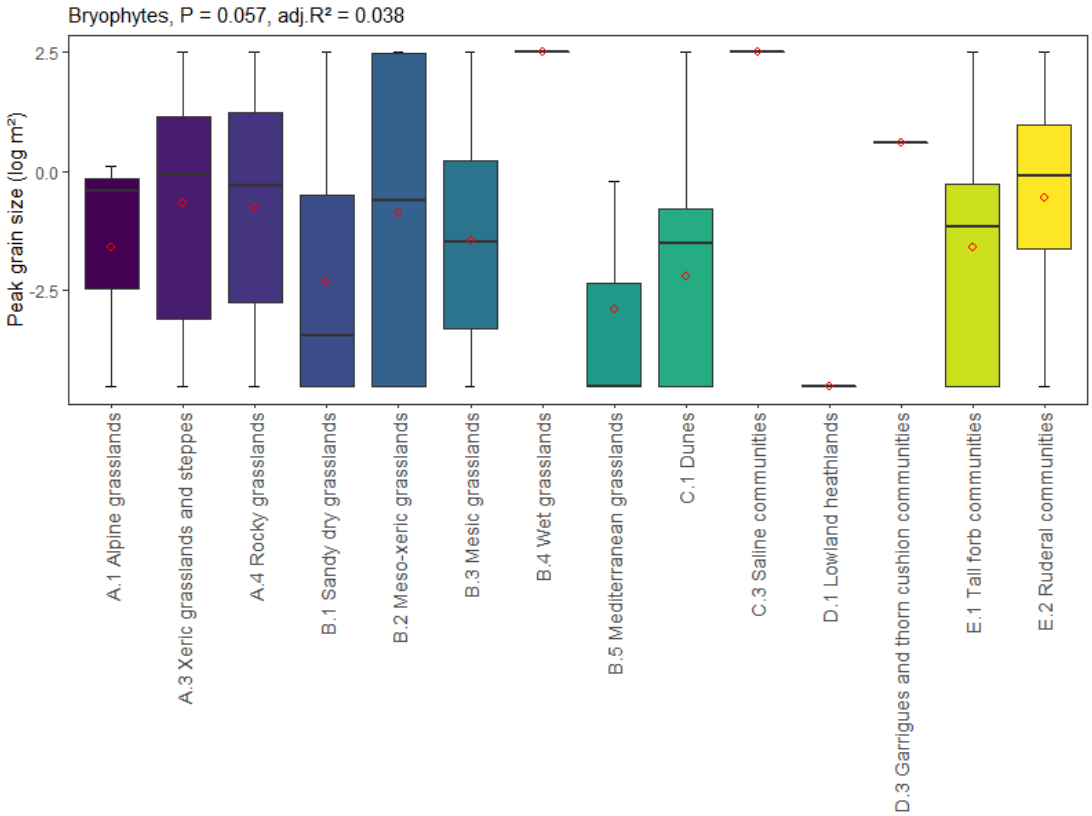

Figure S2.32. Comparison of fitted peak grain size (local grain size where the maximum local z was predicted) for bryophytes between the vegetation types at fine level considered in this study. Box and whisker plots represent the median and quartiles while the red dots represent the mean values for each vegetation type at fine levels.

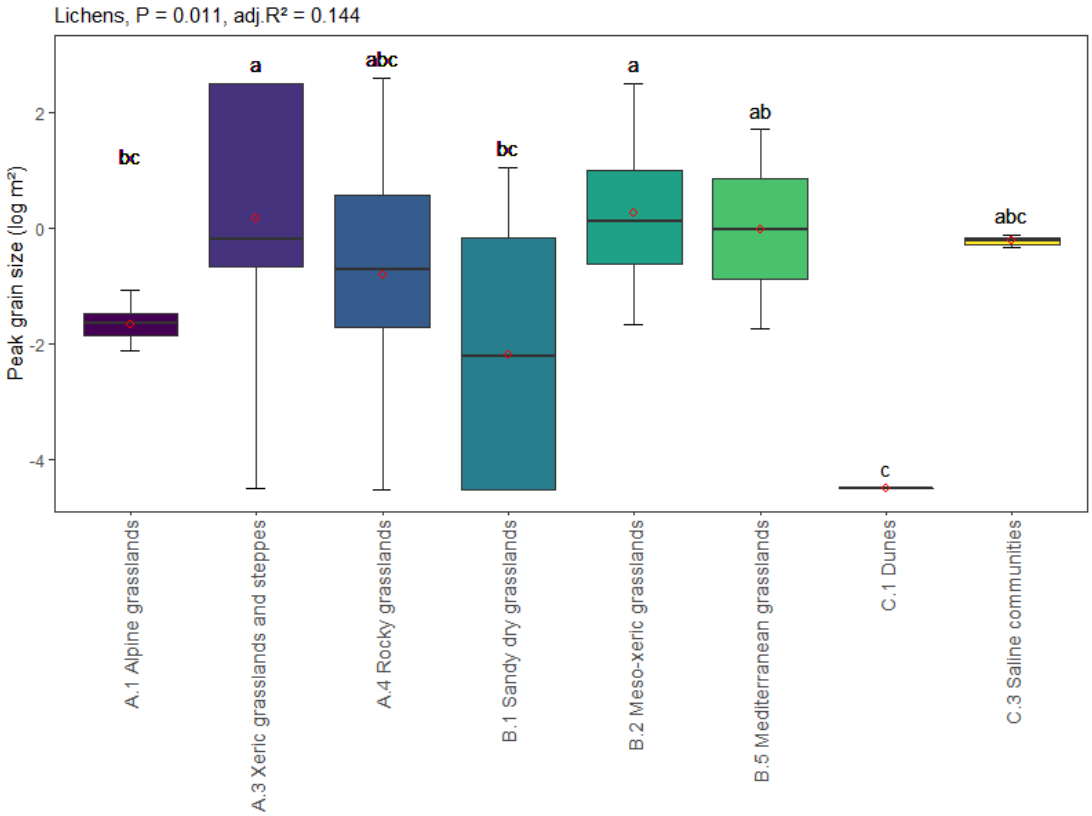

Figure S2.33. Comparison of fitted peak grain size (local grain size where the maximum local z was predicted) for lichens between the vegetation types at fine level considered in this study. A common lower-case letter between two boxes indicates homogeneous groups as tested with Tukey's post-hoc test with ANOVA ($p < 0.05$). Box and whisker plots represent the median and quartiles while the red dots represent the mean values for each vegetation type at fine levels.

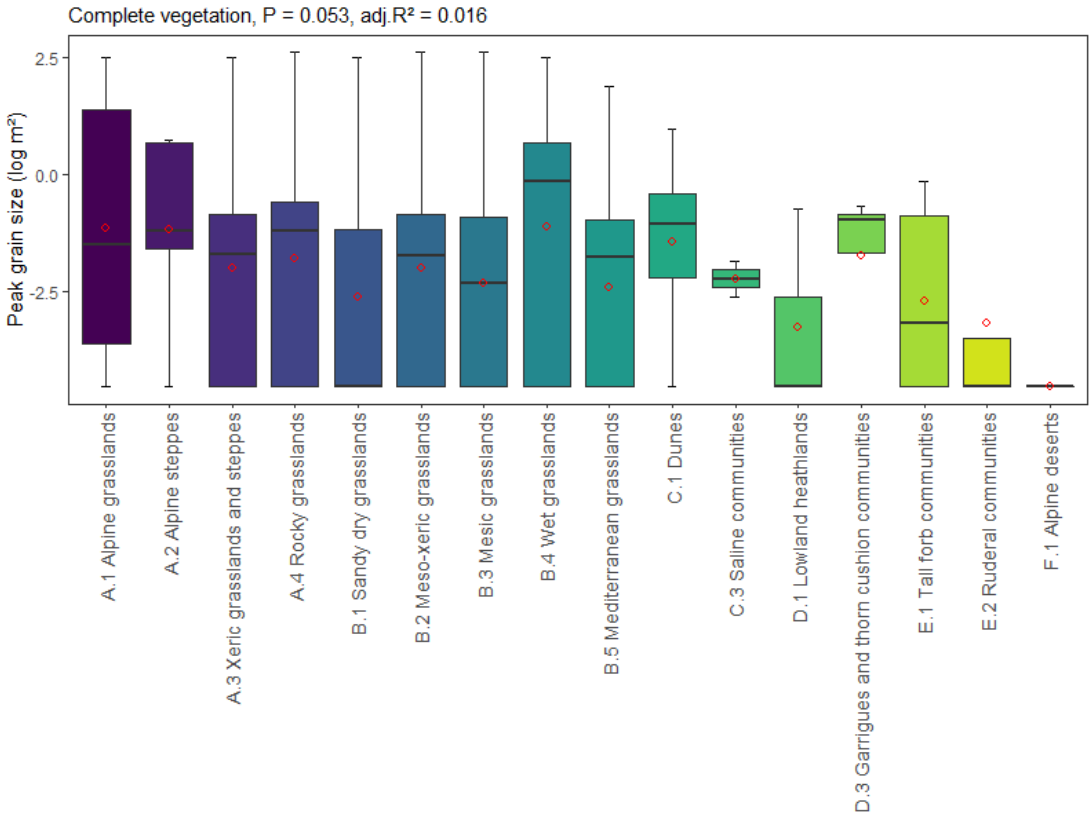

Figure S2.34. Comparison of fitted peak grain size (local grain size where the maximum local z was predicted) for complete vegetation between the vegetation types at fine level considered in this study. A common lower-case letter between two boxes indicates homogeneous groups as tested with Tukey's post-hoc test with ANOVA ($p < 0.05$). Box and whisker plots represent the median and quartiles while the red dots represent the mean values for each vegetation type at fine levels.

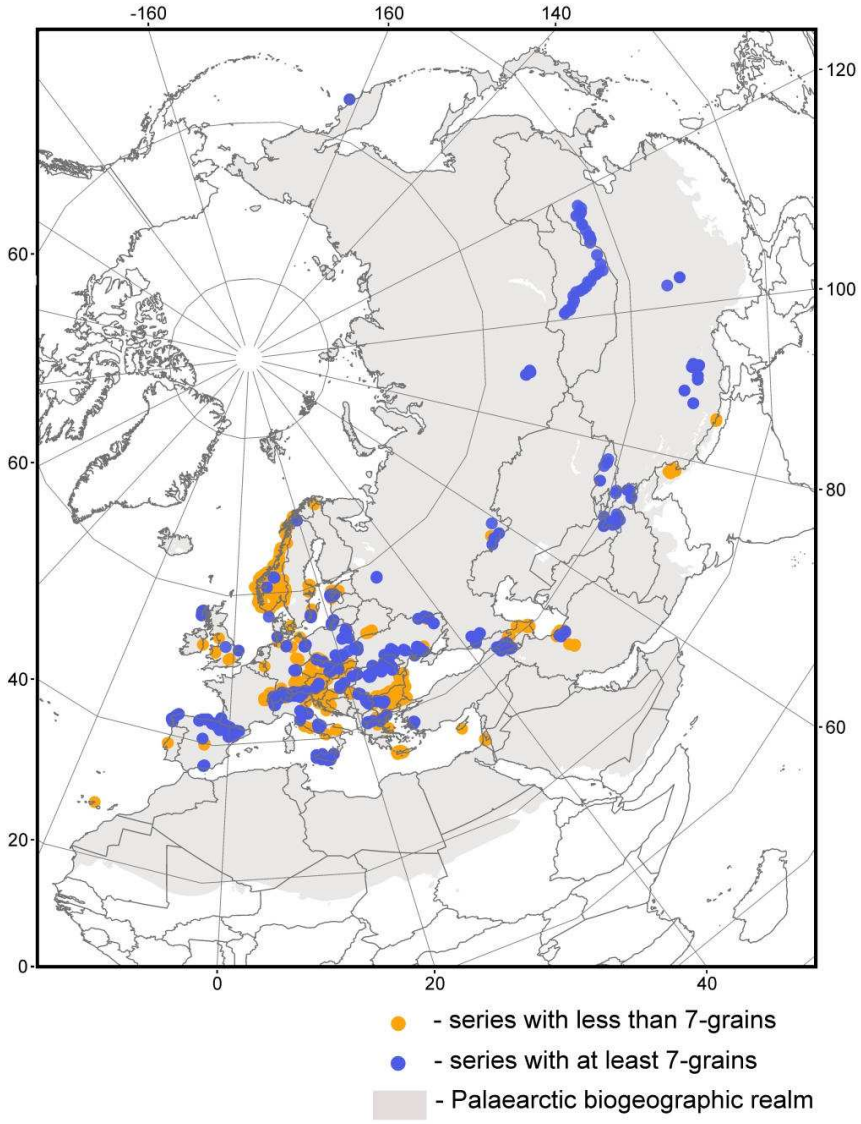

Figure 1. Spatial distribution of the 6,696 series in the Palaearctic biogeographic realm that were analysed in this study.

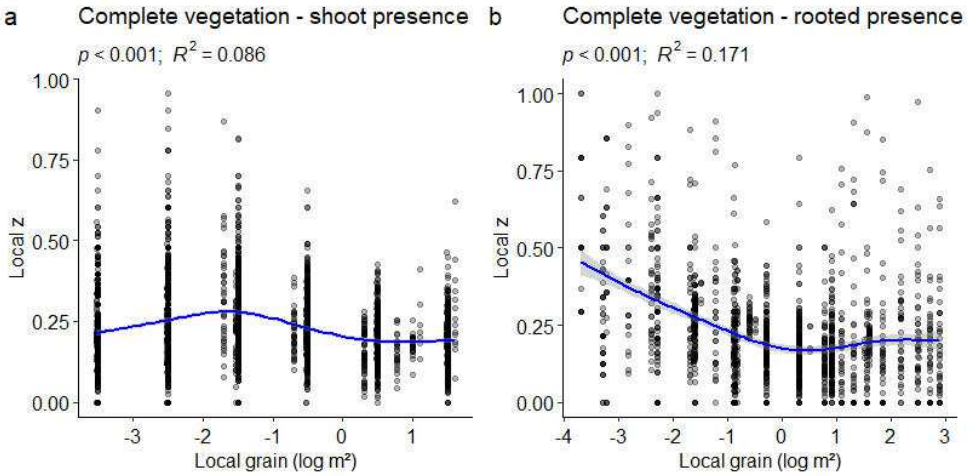

Figure 2. Generalized additive models (GAMs) with 95% confidence intervals (pale blue) for the effect of local grain (on log scale) on local z-value for complete vegetation, in plot series using two different ways of recording species occurrence: a) shoot presence and b) rooted presence.

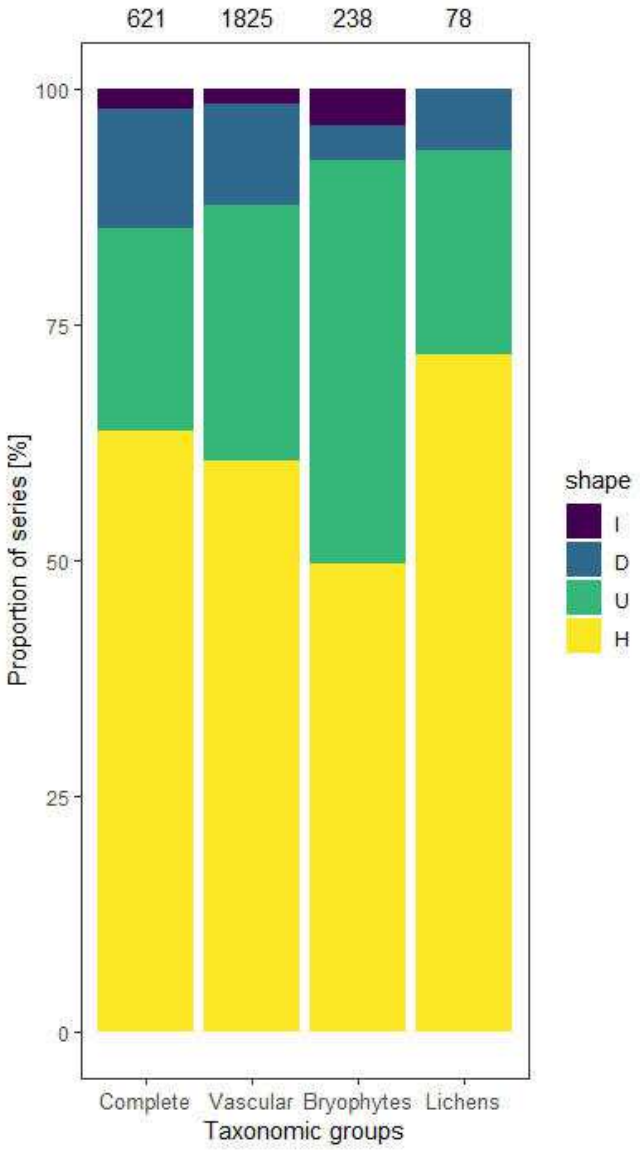

Figure 3. Comparison of the four shapes of fitted curves (hump-shaped (H), U-shaped (U), monotonic decreasing (D), and monotonic increasing (I)) for the complete vegetation and for the taxonomic groups vascular plants, bryophytes, and lichens (series with at least seven grain sizes). Values on top of bars are the number of nested-plot series analyzed.

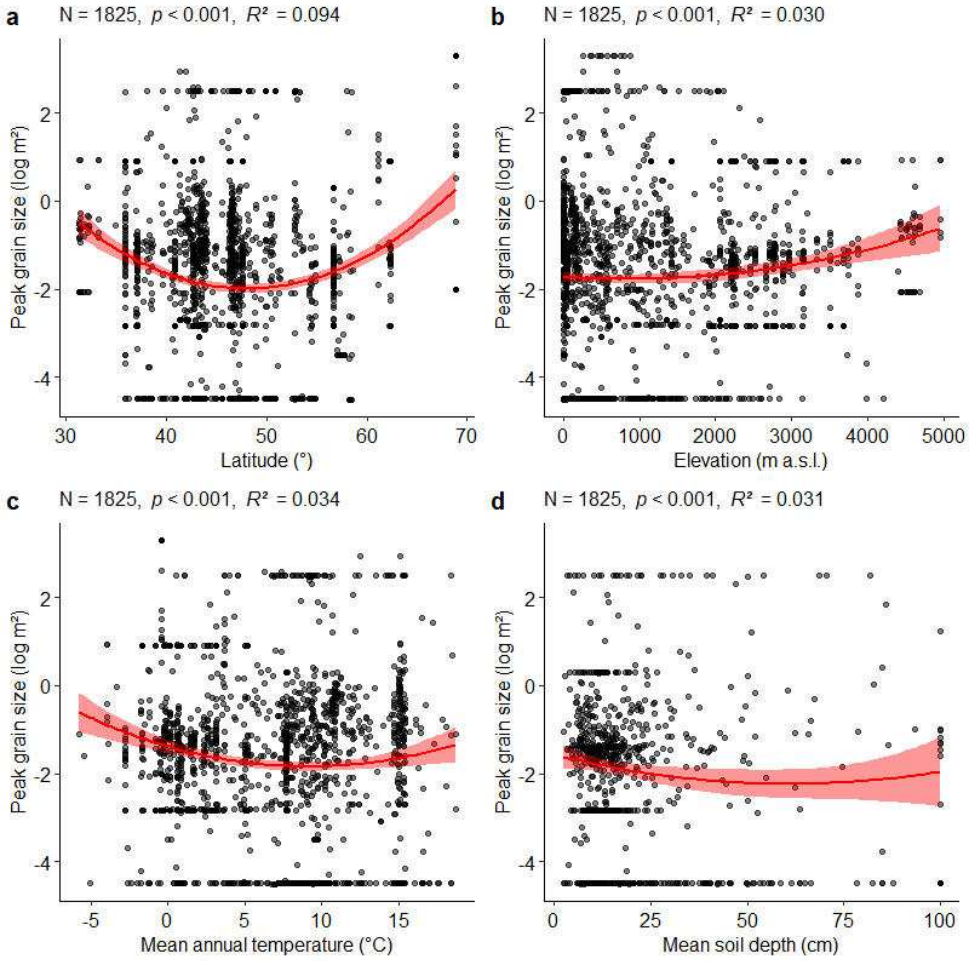

Figure 4. Differences in observed peak grain size (local grain size where the maximum local z occurred) of vascular plants depending on predictor variables. Red lines indicate quadratic relationships ($p < 0.05$) with confidence intervals.

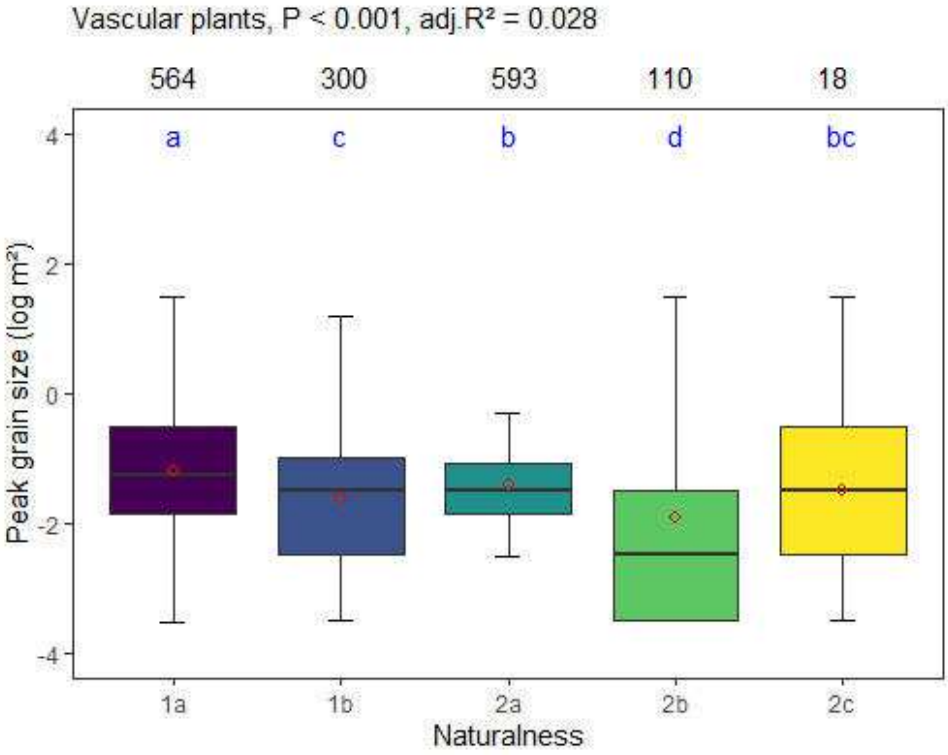

Figure 5. Differences of the observed peak grain size (local grain size where the maximum local z occurred) for vascular plants between the five levels of naturalness present in this study (no series for 1c – natural grasslands, overused): 1 – natural grasslands (1a – not managed, 1b – extensively managed); 2 – secondary grasslands (2a – semi-natural, 2b – semi-intensified, 2c – intensified) ($p < 0.001$; $R^2_{adj.} = 0.028$). Blue lowercase letters indicate homogeneous groups ($p < 0.05$) as tested with Tukey's post-hoc test ANOVA, the figures on top indicate the numbers of data. Box and whisker plots represent the median and quartiles while the red dots represent the mean values.

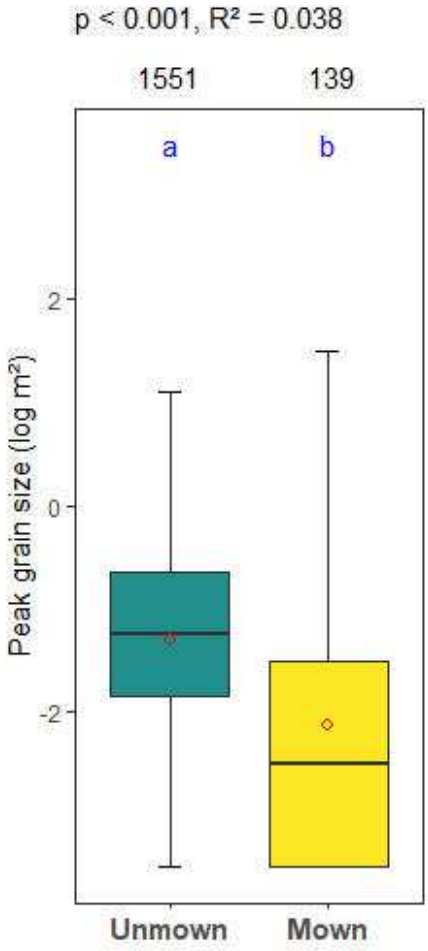

Figure 6. Effect of mowing on observed peak grain size (local grain size where the maximum local z occurred) for vascular plants ($p < 0.001$; $R^2 = 0.038$). Box and whisker plots represent the median and quartiles while the red dots represent the mean values for each management type.

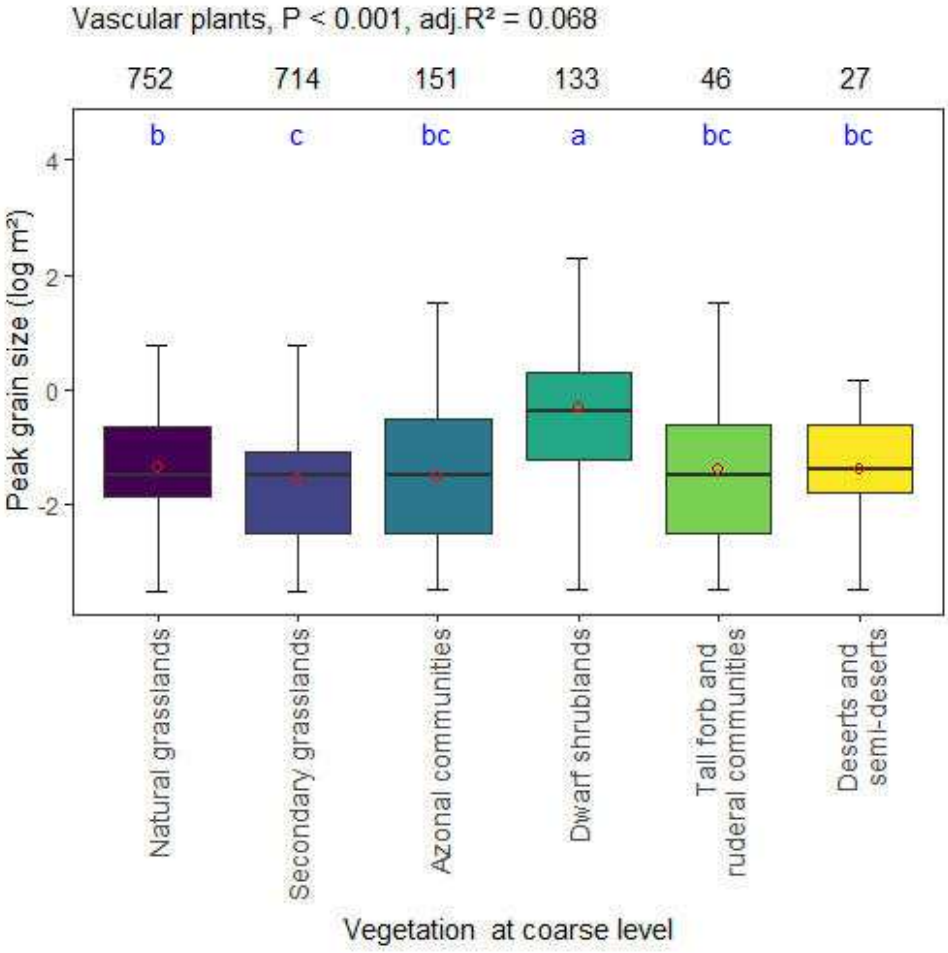

Figure 7. Differences in the observed peak grain size (local grain size where the maximum local z occurred) between the six main vegetation types for the vascular plants ($p < 0.001$, $R^2adj. = 0.068$). A common blue lower-case letter between two boxes indicates homogeneous groups as tested with Tukey's post-hoc test with ANOVA ($p < 0.05$), the figures on top indicate the numbers of data. Box and whisker plots represent the median and quartiles while the red dots represent the mean values for each vegetation type at coarse level.