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Global functional variation in alpine vegetation

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Global functional variation in alpine vegetation

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B. J.-A., L. M., R. T. and C. P. C. conceived the study and developed the methodology. P. B., J. D., M. F., A. H., A. Y. K., J. L., N. M., G. P. M., J. N., A. N., R. K. P., G. P., J. Å., P. S., K. V., S. K. W. and E. G. Z. provided the vegetation plot data. F. M. S. and H. B. facilitated access to the sPlot database. R.T. analyzed the data and produced the outputs. R.T and B.J.-A wrote the first manuscript draft. B.J.-A supervised the study. All the authors discussed the methodology and commented on various versions of the manuscript.

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The vegetation plot data is stored and managed by sPlot and the corresponding author and is available upon request. The R code used to carry out the analyses is available at:
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Abstract:

Questions: What is the functional trait variation of vascular plants in alpine areas? How does cross-scale trait variation of alpine vegetation relate to large-scale biogeographic factors? How much do macroclimate and phylogenetic relatedness contribute to explaining the functional variation of alpine plant communities?

Location: Global.

Methods: We compiled a global dataset of alpine vegetation with 5,532 geo-referenced plots, 1,934 species, and six plant functional traits. We used principal component analysis to describe the species' trait space, and trait probability density to assess the functional variation of trait pools and local communities among major habitat types, climatic groups and biogeographic realms. We used multiple regression on distance matrices to model community functional dissimilarity against environmental and phylogenetic dissimilarity.

Results: The first two PCA axes explained 66 % of the species' functional variation and were related to the leaf and stem economic spectra, respectively. Trait pools were largely independent of surrounding habitat types and climate, but with considerable variation among biogeographic realms. A similar pattern emerged at the community level, with a stronger influence of realms on functional variation. Environmental and phylogenetic dissimilarities had a similar influence on community functional dissimilarity, with a negligible effect of geographic distance.

Conclusions: Plant species in alpine areas reflect the global variation of plant function, but with a predominant role of resource-use strategies. Current macroclimate exerts a limited effect on functional pools, mostly acting at the community level in combination with evolutionary imprints of the two global hemispheres. Alpine vegetation is functionally unrelated to the habitats in which it is embedded, supporting its evolutionary distinctiveness from other terrestrial biomes.

Keywords: Global alpine vegetation, functional dissimilarity, trait pools, trait probability density, evolutionary history, macroclimate, phylogenetic dissimilarity, alpine biomes

Introduction

Alpine habitats (i.e. high-elevation habitats above the climatic treeline) cover about 3 % of land outside Antarctica (Körner et al. 2011; Testolin et al. 2020) and represent the only biogeographic unit distributed across all continents and latitudes on both hemispheres (Körner 2003). These habitats support about 10,000 plant species worldwide, many of which are endemics (Körner 2003) and some are global biodiversity hotspots (Myers et al. 2000). Despite the great number of species and its global distribution, alpine vegetation is dominated by few growth forms (i.e. dwarf shrubs, graminoids, herbaceous rosettes and cushions), reflecting functional adaptations to the general characteristics of alpine environments, i.e. low temperatures, short growing season and limited nutrient availability (Körner 1995; Körner 2003; Dolezal et al. 2016; Körner 2019; Stanisci et al. 2020). Yet, to which extent large scale factors shape the spectrum of plant functions across alpine regions remains little understood.

Alpine habitats can be globally differentiated along gradients of seasonality and continentality (Testolin et al. 2020). They are generally considered as ecological units defined by elevation (orobiomes) and nested within different vegetation zones (zonobiomes) that are in turn characterized by distinct plant species pools (Walter & Box 1976; Mucina 2019). Since alpine vegetation is found in regions with different climatic and evolutionary history (Billings 1974), their functional characteristics are influenced by the species pool dominating in that region (Moncrieff et al. 2016; Mucina 2019). Indeed, alpine vegetation shows variation in terms of e.g. abundance of succulents in semi-arid zones, sclerophyllous species in Mediterranean climates, or

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giant rosettes in tropical areas (e.g. *Espletia*, *Lobelia*, and *Dendrosenecio*) However, growth forms might be poor descriptors of plant functioning in tundra vegetation (Thomas et al. 2019) as they still bear a considerable amount of variability in plant characteristics, which can vary widely within a single group (Körner 1995). A more quantitative assessment of plant functioning can be approached by using functional traits (hereafter traits), defined as measurable features affecting the performance of species in their environment (McGill et al. 2006; Garnier et al. 2016). Indeed, a small set of traits can be used to explain different strategies adopted by terrestrial plant species for resources acquisition, growth and reproduction (Grime 1974; Díaz et al. 2016; Bruelheide et al. 2018).

Factors selecting for favorable combinations of traits are generally scale-dependent (Garnier et al. 2016). At large spatial scales, the interplay of different continental processes, mostly driven by macroclimate, determines the current set of functional traits (i.e. the trait pool) that further contributes to define the global biomes (Mucina 2019). Stochastic events and landscape structure limit species dispersal into regional floras (Garnier et al. 2016), that can act as potential sources for new alpine species (Billings 1974). These processes are rooted in the evolutionary history of each region, which is constrained by long-term isolation of major landforms (Chaboureau et al. 2014) and by the phylogenetic origin of the species occurring within each biogeographic realms (Holt et al. 2013; Daru et al. 2017; Daru et al. 2018). At the community scale, trait pools are further constrained by local biotic and abiotic filters that select species assemblages with favorable trait syndromes (Lavorel et al. 1997; Zobel 2016; Mucina 2019). Linking local filtering to evolutionary and biogeographic history remains a major challenge in macroecology and new approaches that incorporate different facets of diversity are

required to understand the patterns and processes regulating plant communities across scales (Pärtel et al. 2016; Ladouceur et al. 2019).

Here, we provide the first cross-scale overview of the functional variation of alpine vegetation and its possible drivers. Specifically, we aim to: 1) describe the trait spectrum of vascular plant species in global alpine ecosystems; 2) assess the trait functional variation of regional pools and local communities among major habitat types, climatic groups and biogeographic realms; 3) estimate the relative contribution of macroclimate and evolutionary history in shaping the functional characteristics of alpine plant communities.

Methods

Study system and data selection

We considered data from alpine vegetation defined as any vascular plant community above the climatic treeline (Körner 2003). In addition to strictly zonal habitats dominated by graminoids, forbs and dwarf shrubs, we included snow-patch plant communities and vegetation on rocks and screes, as they are also found ubiquitously across the alpine vegetation belt. The vegetation-plot data collected by the authors, compiled from the literature, or stored in the sPlot database (v2.1) (Bruehlheide et al. 2019), was first filtered using habitat classifications of the data sources and then further cleaned by excluding plots with tree species or incomplete taxonomic identification. We standardized datasets from different sources by identifying a minimum common set of plot attributes including plot size (i.e. sampled area), elevation, and geographic coordinates. Species names were harmonized using the Taxonomic Name Resolution Service (Boyle et al. 2013) (<http://tnrs.iplantcollaborative.org>) with default settings. Subspecies and varieties were merged at

the species resolution by summing the respective percentage cover values. At this point the dataset consisted of 8,877 plots of alpine vascular vegetation with 5,313 plant species recorded.

Each plot was then assigned to major habitat types (Olson & Dinerstein 1998; Olson et al. 2001), representing the dominant vegetation of a large geographic area whose species pool could have contributed to that of the alpine belt. Furthermore, we assigned the plots to three different groups summarizing the climatic variability of global alpine areas according to (Testolin et al. 2020): 1) oceanic, characterized by greater precipitation and relative temperature stability, analogous to the oceanic climate of the Köppen-Geiger classification (Köppen 1936); 2) continental, defined by drier conditions and greater yearly temperature differences; 3) subtropical, encompassing both tropical and subtropical alpine areas, and characterized by warmer temperatures with strong daily excursion and low annual precipitation. Single plots falling slightly outside the boundaries of the commonest major habitat type or climatic group for a given region were manually assigned to those. Finally, each plot was assigned to a biogeographic realm (Olson et al. 2001), representing a broad land unit with distinct evolutionary history.

For each species, we linked the gap-filled trait information from the TRY database (v5.0) (Shan et al. 2012; Fazayeli et al. 2014; Schrodtt et al. 2015; Kattge et al. 2020), provided by the sPlot database as species-specific average values (Bruehlheide et al. 2019). We selected six plant functional traits: leaf area (one-sided surface of the fresh leaf), specific leaf area (leaf area per leaf dry mass; SLA), leaf dry matter content (leaf dry mass per leaf fresh mass; LDMC), leaf nitrogen (N) (N per leaf dry mass;), plant height (maximum total height of the plant) and seed mass (dry mass of the seed). We chose these traits because they are commonly used to characterize tundra and alpine vegetation (Bjorkman et al. 2018; Thomas et al. 2019; Liancourt

et al. 2020), and they are fully representative of plant ecological strategies (Díaz et al. 2016). The values of plant height, leaf area and seed mass were $\log_{10}$ -transformed to reduce skewness. Species for which trait information was not available were removed. At the community level, we only considered plots with at least 50 % cover of species with trait data. The final dataset consisted of 5,532 vegetation plots between 0.25 and 400 m² in size sampled between 1923 and 2019, with 1,934 species belonging to five major habitat types, three climatic groups and five biogeographic realms (Figure 1).

Functional spectrum of species pools

All the following analyses have been carried out using R (R Core Team 2020). To analyze the trait space occupied by the species and the relationships among the selected traits, we performed a principal component analysis (PCA) of the standardized values of the six traits. To compare the trait pools of alpine vegetation across major habitat types, climatic groups and biogeographic realms, we used trait probability density, a scale-independent framework that implements the concept of the niche hypervolume while accounting for the probabilistic nature of traits (Carmona et al. 2016). As reliable information on intraspecific variability of the traits was not available across all studied species and for each trait, we estimated it as 50 % of the standard deviation of the species average for each trait (Lamanna et al. 2014). Then, we calculated the single-trait pools as the probability densities for each major habitat type, climatic group and biogeographic realm using the package “TPD” (Carmona 2019), accounting for species frequencies (i.e. the number of plots in each major habitat type, climatic group and biogeographic realm, where a certain species was recorded).

We assessed the functional variation among different groups using kernel density plots and calculating overlap-based pair-wise dissimilarities among trait pools using the “dissim”

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3 194 function of “TPD” package. The significance of the pair-wise dissimilarities was evaluated in a
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5 195 null-modeling framework (Geange et al. 2011; Traba et al. 2017) by pooling the observations
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7 196 from each pair, randomizing the species' labels 999 times while keeping the number of species
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9 197 constant for each group and calculating each time the pair-wise dissimilarity value between the
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11 198 simulated trait probability density. Raw p-values were calculated for each comparison by ranking
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13 199 the empirical dissimilarity value among the simulated ones. The final p-values were computed by
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15 200 applying the Bonferroni correction (Legendre & Legendre 2012). To assess the overall
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17 201 functional variation (among major habitat types, climatic groups and biogeographic realms)
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19 202 while excluding potentially redundant information among the six traits, we also calculated multi-
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23 204 variability (see Results and Discussion), and repeated the same analyses described above for the
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31 206 Functional patterns of communities

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33 207 To analyze the trait patterns across plant communities, we calculated the multi-trait
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35 208 dissimilarities between all vegetation plots as described above, controlling for the relative cover
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37 209 of the species within each plot. The pair-wise dissimilarities were visualized using non-metric
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39 210 multidimensional scaling (NMDS), which allowed comparison of the distribution of plots
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41 211 belonging to different major habitat types, climatic groups and biogeographic realms. The
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43 212 relationship between community dissimilarities and the original traits was assessed by fitting the
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45 213 community weighted means of each trait to the ordination scores with the “envfit” function of
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47 214 the “vegan” package in R (Oksanen et al. 2019). Significant differences among plots belonging
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49 215 to different major habitat types, climatic groups and biogeographic realms were tested using
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51 216 PERMANOVA (Anderson 2001), implemented by the “adonis” function of the R package
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“vegan”, using 999 permutations. Pair-wise tests were performed with the “pairwise.adonis” function of the “pairwiseAdonis” package in R (Martinez Arbizu 2020), applying a Bonferroni correction to the p-values. To assist interpretation of the pair-wise PERMANOVA results, we tested the multivariate homogeneity of group variances with the pair-wise PERMDISP test (Anderson 2006) using the “permutest.betadisper” function of the “vegan” package in R with 999 permutations.

Modeling community dissimilarity

To quantify the relative contribution of climate and evolutionary history in determining functional variation among communities, we modeled plot-level functional dissimilarity as a function of environmental and phylogenetic dissimilarity while controlling for geographic distance. First, we selected the set of species for which both trait and phylogenetic data were available ($n = 1,674$) and further subset the vegetation plots by keeping those with at least 50 % cumulative cover of these species. Thus, we obtained a subset of 5,047 plots and calculated the multi-trait functional dissimilarities between all possible pairs of plots as described above. Then, we built a set of climatic variables known to affect the functionality of vegetation in the alpine belt (Körner 2003; Moser et al. 2005; Nagy & Grabherr 2009) using data from CHELSA at 1 km spatial resolution (Karger et al. 2017). We included the mean temperature, precipitation, growing degree days and mean potential evapotranspiration of the growing season, defined as months with mean temperature above $> 0.9^{\circ}\text{C}$ (Paulsen & Körner 2014). Growing degree days (i.e. the sum of monthly temperatures $> 0.9^{\circ}\text{C}$ multiplied by the total number of days) were calculated using the “growingDegDays” function of the R package “envirem” (Title & Bemmels 2018). Mean potential evapotranspiration of the growing season was estimated with the “hargreaves” function of the R package “SPEI” (Beguería & Vicente-Serrano 2017), using maximum and

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3 240 minimum monthly values of temperature and monthly precipitation. The monthly values of
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5 241 potential evapotranspiration obtained were then averaged across months with mean temperature
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7 242 above 0.9°C. We standardized the four climatic variables and calculated the multivariate
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17 246 function of the R package “picante” (Kembel et al. 2010). To account for the spatial aggregation
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19 247 of plots and unmeasured regional effects on the estimated functional dissimilarity, we calculated
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21 248 the pair-wise geographical distances between plots. Finally, we modeled functional community
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23 249 dissimilarity against these three distanced-based predictors using multiple regression on distance
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26 250 matrices (MRM) with the “lm” function. Despite our measure of functional dissimilarity is
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31 252 turnover (Figure S1), allowing us to treat it as approximately linear (Ferrier et al. 2007).
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33 253 Furthermore, a linear modelling approach allowed us to calculate the adjusted R^2 of all the sub-
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35 254 models necessary to perform variance partitioning (Borcard et al. 1992; Swenson 2014).
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40 256 **Results**

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43 257 The PCA of the six trait values at the species level revealed that 66 % of the total trait variation
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45 258 is expressed by the first two PCA axes. The first axis (PC1; 35 % of variation) was mainly
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47 259 related to variations in LDMC, leaf N and SLA, while the second axis (PC2; 31 % of variation)
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50 260 was linked to leaf area, plant height and seed mass (Figure 2, Table S1).
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52 261 When looking at the habitat types dominating the regions in which alpine vegetation is
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55 262 embedded, we observed negligible differences in trait probability density and low functional
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dissimilarity among trait pools. The only exception was represented by alpine vegetation of tropical and subtropical moist broadleaf forests, which exhibited slightly greater plant height values compared to other groups (Figure 3; Table S2). Similarly, among climatic groups, subtropical alpine areas exhibited greater plant height values compared to oceanic and continental ones, with minor variation in the distribution of other traits (Figure 3; Table S3). As for biogeographic realms, we observed considerable variability in trait probability density. The alpine vegetation of Australasia and Neotropic presented lower SLA compared to that of other biogeographic realms and similar values of plant height to the Afrotropic and Neotropic, which are both greater than those of the Palearctic and Nearctic. As for leaf area and seed mass, the Neotropics generally showed greater values compared to the Palearctic and Nearctic, which in turn presented greater leaf N and lower LDMC than Australasia (Figure 3; Table S4). Multi-trait patterns seemingly reflected those observed at the single trait level. Among major habitat types and climatic groups, multi-trait functional dissimilarities were not significant or very modest (Table 1). Conversely, among biogeographic realms, Palearctic and Nearctic were similar to one another and differentiated from Neotropic and Australasia, with the Afrotropic pool lying in between.

The NMDS of multi-trait dissimilarities among alpine plant communities revealed no distinct patterns between different major habitat types or climatic groups (Figure 4). Indeed, at the community level, major habitat types explained 11 % of the total variance in multi-trait dissimilarities ($R^2 = 0.11$, $p = 0.001$) and pair-wise comparisons identified only small differences among major habitat types, which are probably due to differences in multivariate dispersions (Table S5). Similarly, climatic groups explained 5 % of the variance ($R^2 = 0.05$, $p = 0.001$), with negligible differences emerging from pair-wise comparisons (Table S6). On the other hand, the

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3 286 NMDS of functional dissimilarities among alpine plant communities showed distinct patterns
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5 287 among biogeographic realms (Figure 4), with Palearctic, Nearctic and Afrotropic communities
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7 288 occupying large part of the community variation space, whereas Neotropic assemblages occupied
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9 289 the portion characterized by greater plant height leaf area and seed mass. Australasian plots
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11 290 represented a separate entity, mainly defined by larger values of LDMC and smaller SLA and
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13 291 leaf N. Biogeographic realms explained 19 % of the total variance ($R^2 = 0.19$, $p = 0.001$), mainly
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15 292 ascribable to the Australasian communities (Table S7).
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19 293 Finally, the MRM model fit on a subset of plots (with available phylogenetic
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21 294 information) explained 16.6 % of the variance in community dissimilarities. Environmental and
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23 295 phylogenetic dissimilarities both explained 6.2 % of the variance individually, while 4 % was
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25 296 shared between the two. Geographic distance exhibited a marginal effect, explaining only 0.3 %
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27 297 of the variance (Figure 5).
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33 299 **Discussion**
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35 300 Functional trait spectrum of alpine plants
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37 301 Alpine plant species are strongly differentiated based on their resource-use strategies and,
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39 302 secondarily, plant height. We selected six traits relevant to resources use, growth and
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41 303 reproduction, and used PCA to describe the trait spectrum of 1,934 vascular plant species in
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43 304 global alpine ecosystems. The first axis of trait variation (PC1) reflected different strategies in
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45 305 terms of returns on investments of nutrients and dry mass in leaves, i.e. the leaf economics
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47 306 spectrum (Wright et al. 2004). The second axis (PC2) represented the stem economics spectrum
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49 307 (Baraloto et al. 2010) and, to some extent, the colonization versus exploitation continuum
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51 308 defined by seed mass (Díaz et al. 2016). These results are in line with previous analyses of alpine
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and tundra vascular plants (Dolezal et al. 2016; Thomas et al. 2019) and are consistent with the global spectrum of plant form and function (Díaz et al. 2016). The resource-use strategy reflects the absence of trees and tall shrubs in alpine vegetation, and the general abundance of prostrate species which are mainly differentiated by local conditions. Indeed, the small size allows alpine plants to respond more closely to the buffered microclimate conditions near the ground (Geiger et al. 2003), thus being decoupled from the fluctuations of the macroenvironment (Körner et al. 1989; Körner 2003). Along the first axis of functional trait variation, leaf construction costs of alpine plants tend to vary depending on local temperature, frost stress and exposure to light (Körner et al. 1989), hence the greater variation of related traits (Stanisci et al. 2020). In contrast, the second axis showed a more complex variation of traits, with a predominant role of plant height and seed mass. Although such variation can be also related to environmental constraints, these traits are expected to vary little within regional alpine species pools (Ladouceur et al. 2019), thus they may be also linked to macroecological differences across regional floras.

Variation of alpine trait pools

Trait pools of alpine plants were largely independent of habitat types dominating at the regional level, suggesting that alpine vegetation is functionally similar across region, regardless of the different floras in which they are embedded. This reflects the overall convergence of growth forms in alpine vegetation (Körner 2003; Aubert et al. 2014; Körner 2019), resulting from the adaptative response to similar ecological conditions (Givnish 2010; Horandl & Emadzade 2011; Hughes & Atchison 2015; Givnish 2016). Moreover, this finding contrasts with the general view of alpine areas as elevational orobiomes that should not be considered independently of the zonobiomes they originate from (Walter & Box 1976), and supports the distinction of alpine ecosystems from other terrestrial biomes (Testolin et al. 2020). Trait pools were also convergent

with respect to climatic groups, indicating that large-scale macroclimatic patterns above the treeline have moderate effects on functional features of alpine vegetation, which is consistent with the similar patterns of primary productivity found in global alpine areas (Testolin et al. 2020).

We found a stronger degree of trait pool divergence across biogeographic realms. This could be expected as functional differences might emerge in otherwise structurally similar plant groups when these are compared across evolutionarily distinct areas (Alvarado-Cárdenas et al. 2013). Specifically, we observed a distinction between the trait pools of the Holarctic realm, as opposed to the Neotropic and Australasia. The trait pool in the Afrotropic realm lied in between. This pattern likely reflects different evolutionary histories and adaptations of alpine vegetation in the Northern and Southern Hemispheres (Billings 1974). Indeed, much of the ancestral alpine vascular flora originated during the Miocene (23-5 Ma) from Arcto-Tertiary and Antarcto-Tertiary floras through upward migration and evolution of lowland taxa (Billings 1974). As a consequence, Holarctic alpine vegetation shares many species with the Arctic (Billings 1974) and has major links with Afrotropic alpine species (Linder 2014; Carbutt & Edwards 2015). In contrast, a large part of Neotropic alpine plants originated locally through migration and adaptation of Neotropical lowland species (Sklenář et al. 2011), some of which contributed also to Afrotropic lineages (Linder 2014). Finally, the functional similarity of Neotropics and Australasia probably derived from both migration (Raven & Axelrod 1972) and convergent evolution during the Pliocene (5 Ma) and the Pleistocene (2.5 Ma), when further mountain uplift and repeated glaciations induced the diversification of the respective alpine floras (McGlone et al. 2001; Winkworth et al. 2005; Sklenář et al. 2011; Madriñán et al. 2013).

Functional patterns of alpine communities

At the community level, the NMDS showed the same functional continua as the one detected by the PCA at the species level, revealing the analogy between present-day community assembly and individual species' evolutionary histories (Bruehlheide et al. 2018). We did not observe strong differentiation between plots belonging to different major habitat types or climatic groups, while biogeographic realms exhibited greater discriminatory power as they did for trait pools. We found that Australasian communities form a self-standing group characterized by conservative leaves with high construction costs. This is in agreement with the scarcity of cushion plants and the relative abundance of sclerophyllous dwarf shrubs in the Australasian alpine flora, when compared to other global alpine regions (Ballantyne & Pickering 2015).

The functional distinctness of Australasian alpine communities from Holarctic and Tropical ones also reflects the differences in trait pools between the two Hemispheres and the long time isolation (45 – 49 Ma) of Australasia from other biogeographic realms of Gondwanan origin (Raven & Axelrod 1972). Holarctic and Tropical communities, however, were not as functionally distinct as their trait pools, indicating that other processes apart from evolutionary history are involved at the local scale. Indeed, although our model highlighted the presence of a phylogenetic signal on functional dissimilarity, environmental dissimilarity explained an equal amount of variance (Figure 5). This is coherent with the process of niche conservatism in highly heterogeneous areas where the retention of the ancestral niche characteristics could lead to both conservatism and divergence of the realized niche (i.e. the functional characteristics) (Pyron et al. 2015). Nevertheless, the negligible effect of geographic distance and the large amount of unexplained variance point to fine-scale environmental factors (e.g. microclimate), disturbance and biotic interactions as the main drivers of community trait composition in alpine ecosystems (Grime 2006; Dolezal et al. 2019). In other words, the combination of phylogenetic constraints

and within-region climatic variation seem to be major drivers of the functional trait variation observed in alpine plant communities.

Basic assumptions

Even if we used the largest dataset of alpine vegetation ever collected, our study does not come without uncertainties. When comparing functional dissimilarities across geographical units and spatial scales, for instance, we presumed that the species for which trait data were available were also representative of the dominant vegetation in our study areas. For several tropical species, however, such data were not available, and we had to remove a large number of plots in Africa and South America. Although we recognize that this could have led to the exclusion of peculiar combinations of traits and that even rare species can drive trait divergence among communities at the regional scale (Richardson et al. 2012), this is probably less relevant at the global level. We also note that our dataset encompassed vegetation plots of very different sizes (0.25 - 400 m²). As species richness generally increases with area (Lomolino 2000), larger plots might be functionally richer than smaller ones (Smith et al. 2013; Wang et al. 2013), biasing the comparison among plots of different sizes. However, when accounting for specie abundances – or, in our case, cover – the relationship between functional diversity and plot size tends to weaken or disappear as a consequence of species dominance and functional redundancy (Karadimou et al. 2016). Therefore, as the trait probability density framework accounts for the distribution of trait values in plant communities, plot size likely had a minor effect in the estimation of functional dissimilarity among alpine communities. Although we collected most of the vegetation plot data currently available on alpine vegetation, much effort will be needed in the future to collect data with a consistent sampling protocol, including functional traits and a proper representativity of species and vegetation types from disparate global regions.

401 **Conclusions**

402 This study demonstrates how the functional adaptations of alpine plants relate to the global
403 variation of plant form and function. Specifically, we highlighted how the trait pools of current
404 alpine vegetation are scarcely related to lowland floras and macroclimatic patterns, while they
405 still carry the evolutionary signature inherited by their Laurasian and Gondwanan ancestors. In
406 combination with climatic factors, this evolutionary mark still determines variation in functional
407 traits at the community level. Yet, we admit that other regional factors not accounted for in this
408 study (e.g. soil properties, topoclimatic gradients) are likely influencing functional traits of
409 alpine vegetation at large spatial scales. In general, we found alpine vegetation to be globally
410 comparable in terms of functional diversity and related macroecological drivers. This finding
411 might contribute to the identification of alpine biomes in the context of global vegetation
412 zonation, with a special attention to the habitats above the treeline. In this respect, future work
413 should be oriented toward the inclusion of trait data from tropical and subtropical species
414 currently underrepresented in global datasets, as well as fine-scale environmental characteristics.

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Author contributions: B. J.-A., L. M., R. T. and C. P. C. conceived the study and developed the methodology. P. B., J. D., M. F., A. H., A. Y. K., J. L., N. M., G. P. M., J. N., A. N., R. K. P., G. P., J. Š., P. S., K. V., S. K. W. and E. G. Z. provided the vegetation plot data. F. M. S. and H. B. facilitated access to the sPlot database. R.T. analyzed the data and produced the outputs. R.T and B.J.-A wrote the first manuscript draft. B.J.-A supervised the study. All the authors discussed the methodology and commented on various versions of the manuscript.

Data availability: The vegetation plot data is stored and managed by sPlot and the corresponding author and is available upon request. The R code used to carry out the analyses is available at: <https://figshare.com/s/c2c0ad45f6f1cd3d1689>.

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645 **Tables**

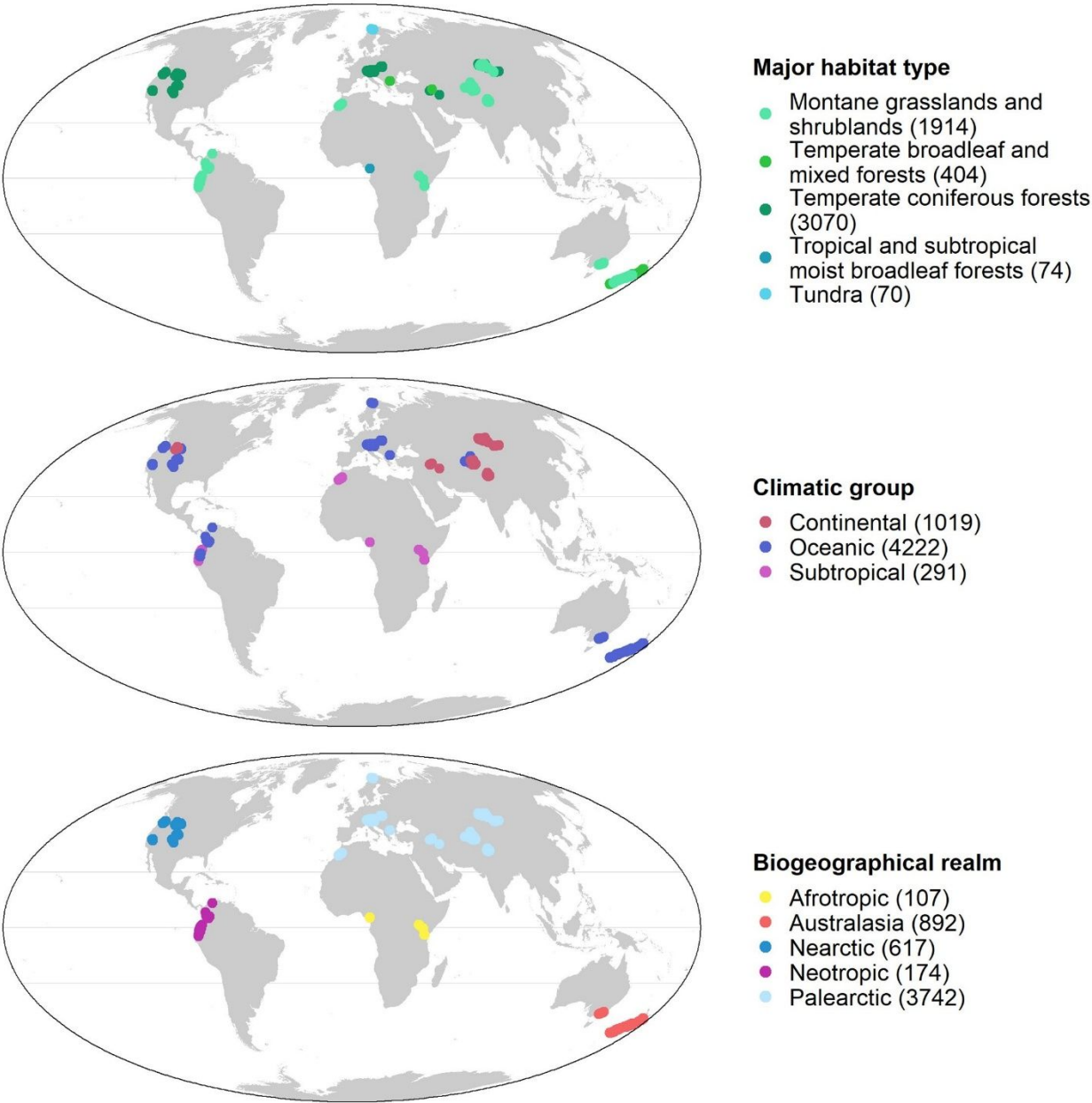
646 **Table 1.** Multi-trait pair-wise dissimilarities (Diss) of alpine vegetation between major habitat
 647 types of surrounding areas, climatic groups and biogeographic realms. Significant dissimilarities
 648 ($P < 0.05$) are in bold. Significance codes: ***: $p < 0.001$; **: $p < 0.01$; *: $p < 0.05$; ns: $p \geq 0.05$.

	Diss
Major habitat types	
Montane grasslands and shrublands - Temperate broadleaf and mixed forests	0.16 ^{ns}
Montane grasslands and shrublands - Temperate coniferous forests	0.27**
Montane grasslands and shrublands - Tropical and subtropical moist broadleaf forests	0.29 ^{ns}
Montane grasslands and shrublands - Tundra	0.27 ^{ns}
Temperate broadleaf and mixed forests - Temperate coniferous forests	0.24**
Temperate broadleaf and mixed forests - Tropical and subtropical moist broadleaf forests	0.34*
Temperate broadleaf and mixed forests - Tundra	0.23 ^{ns}
Temperate coniferous forests - Tropical and subtropical moist broadleaf forests	0.28 ^{ns}
Temperate coniferous forests - Tundra	0.25 ^{ns}
Tropical and subtropical moist broadleaf forests - Tundra	0.38 ^{ns}
Climatic groups	
Continental - Oceanic	0.19**
Continental - Subtropical	0.22*
Oceanic - Subtropical	0.31**
Biogeographic realms	
Afrotropic - Australasia	0.40 ^{ns}
Afrotropic - Nearctic	0.26 ^{ns}
Afrotropic - Neotropic	0.29 ^{ns}
Afrotropic - Palearctic	0.23 ^{ns}
Australasia - Nearctic	0.47**
Australasia - Neotropic	0.36 ^{ns}
Australasia - Palearctic	0.45**
Nearctic - Neotropic	0.43**
Nearctic - Palearctic	0.13 ^{ns}
Neotropic - Palearctic	0.41**

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650 **Figures**



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652 **Figure 1.** Spatial distribution of 5,532 alpine vegetation plots across major habitat types, climatic

653 groups and biogeographic realms. The numbers of plots in each group are reported in brackets.

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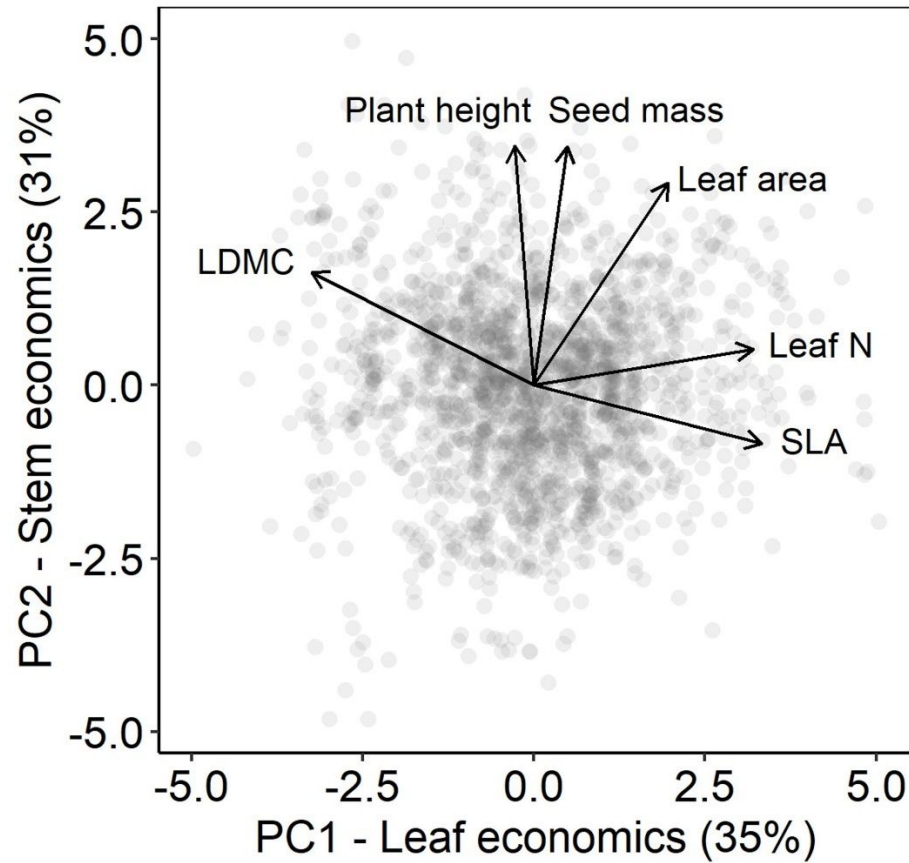


Figure 2. Functional trait space of 1934 alpine vascular plant species along the first two principal components of six functional traits. SLA = Specific leaf area; LDMC = Leaf dry matter content.

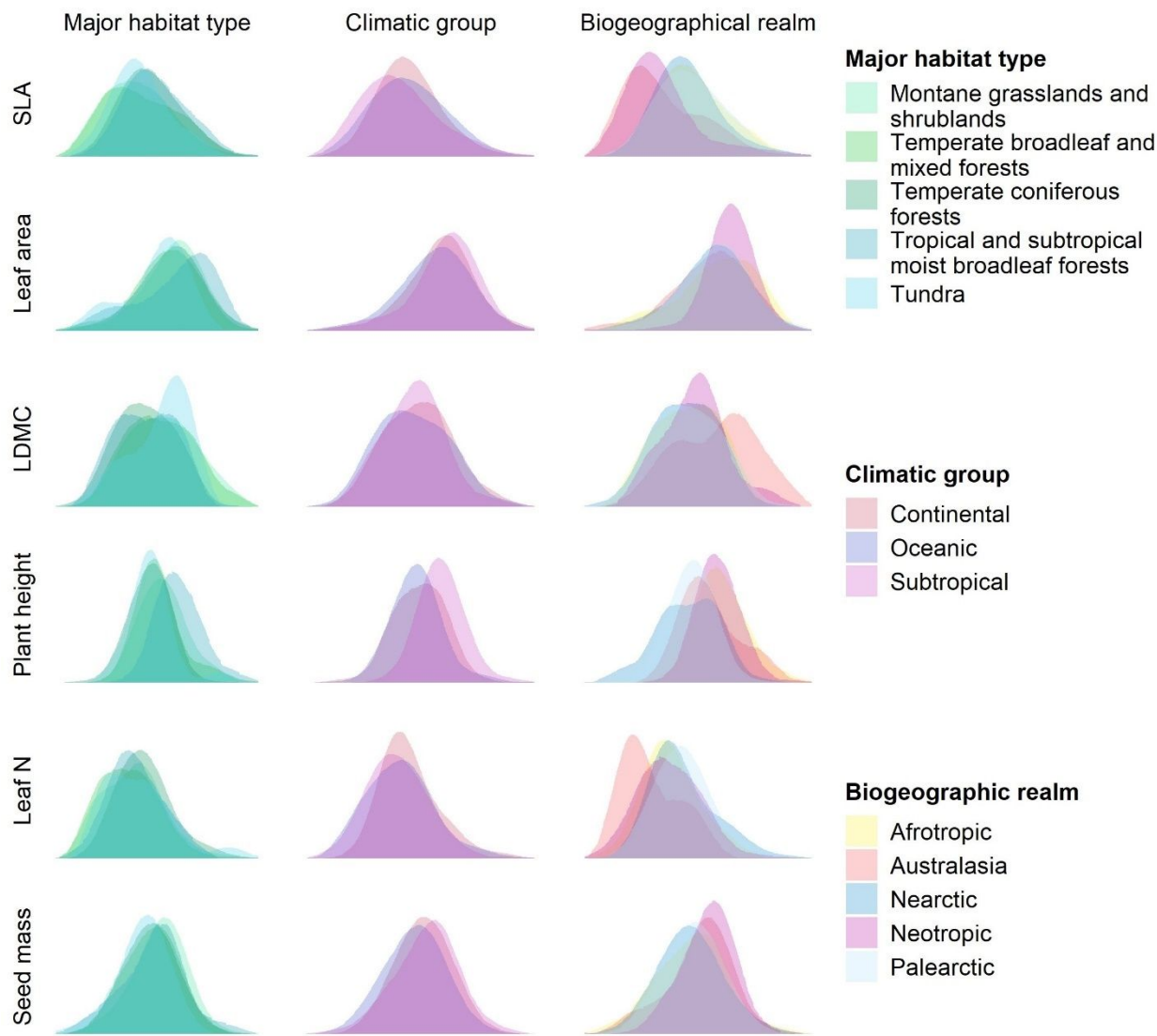


Figure 3. Kernel density plots of trait pools estimated using trait probability density for six individual plant functional traits among habitat types, climatic groups and biogeographic realms. SLA = Specific leaf area; LDMC = Leaf dry matter content.

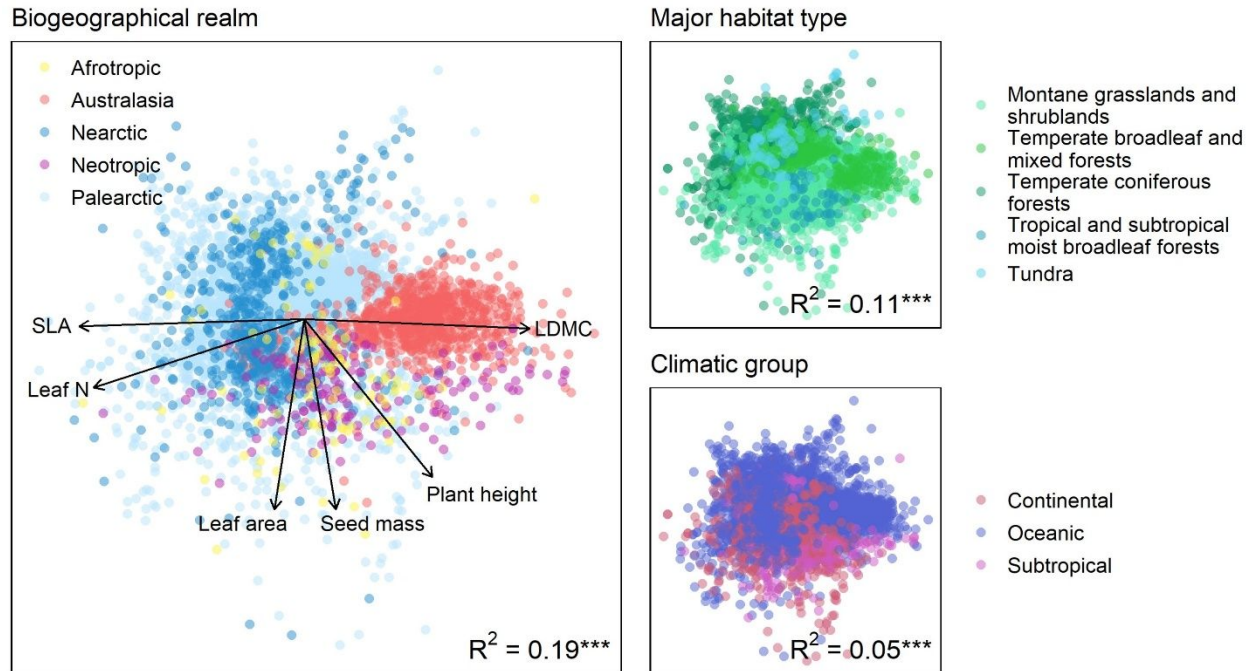


Figure 4. Non-metric multidimensional scaling (NMDS) of alpine vegetation plots based on multi-trait functional dissimilarity, calculated using the first two principal components of six plant functional traits. The points represent the single vegetation plots. The colors represent major habitat types, climatic groups and biogeographic realms. The arrows represent the correlation of the individual functional traits with the NMDS scores and are based on the community weighted means of each trait. The total variance explained by the groups is reported in the bottom-right corner of each graph. SLA = Specific leaf area; LDMC = Leaf dry matter content. Significance codes: ***: $p < 0.001$; **: $p < 0.01$; *: $p < 0.05$; ns: $p \geq 0.05$.

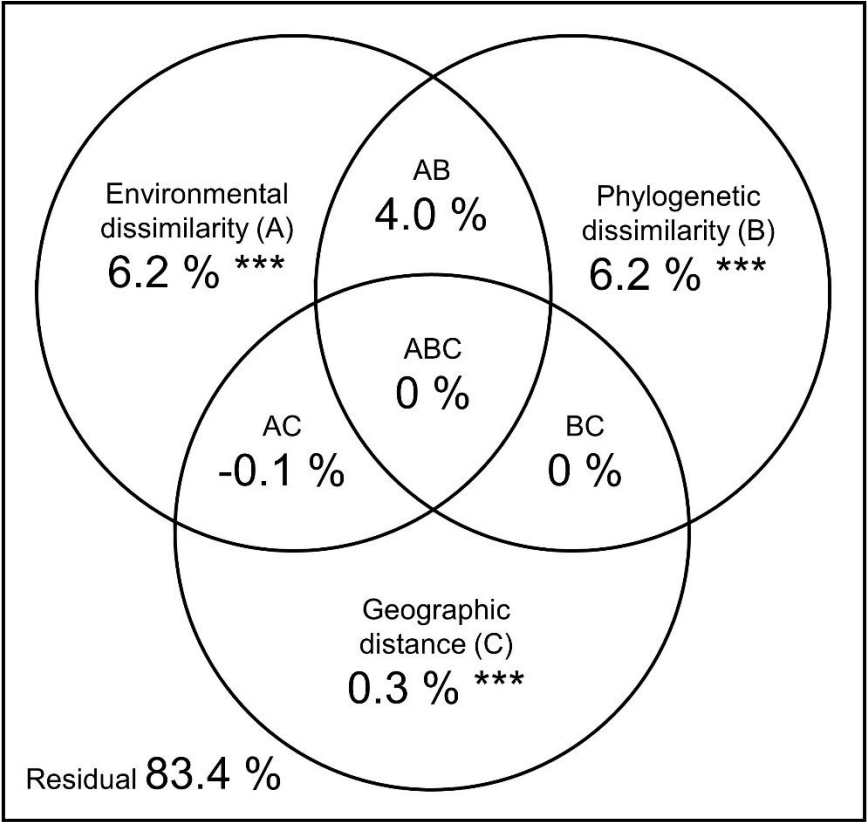


Figure 5. Venn diagram of multi-trait functional dissimilarity of alpine vegetation communities displaying variance partitioning among environmental dissimilarity (A), phylogenetic dissimilarity (B), and geographic distance (C) predictor matrices. Significance codes: ***: $p < 0.001$; **: $p < 0.01$; *: $p < 0.05$; ns: $p \geq 0.05$.

Supporting Information for “Global functional variation in alpine vegetation”**Table S1.** Correlations of single traits with the first two PCA axes. SLA = Specific leaf area; LDMC = Leaf dry matter content.

Traits	PC1	PC2
SLA	0.55	-0.14
Leaf area	0.33	0.49
LDMC	-0.54	0.27
Plant height	-0.05	0.58
Leaf N	0.53	0.09
Seed mass	0.08	0.57

Table S2. Pair-wise dissimilarity of alpine vegetation trait pools between major habitat types for 6 plant functional traits. SLA = Specific leaf area; LDMC = Leaf dry matter content. Significance codes: ***: $p < 0.001$; **: $p < 0.01$; *: $p < 0.05$; ns: $p \geq 0.05$.

Major habitat types	SLA	Leaf area	LDMC	Plant height	Leaf N	Seed mass
Montane grasslands and shrublands - Temperate broadleaf and mixed forests	0.08 ^{ns}	0.09 ^{ns}	0.04 ^{ns}	0.12 ^{ns}	0.06 ^{ns}	0.13 [*]
Montane grasslands and shrublands - Temperate coniferous forests	0.18 ^{**}	0.05 ^{ns}	0.19 ^{**}	0.20 ^{**}	0.15 ^{**}	0.15 ^{**}
Montane grasslands and shrublands - Tropical and subtropical moist broadleaf forests	0.23 [*]	0.20 ^{**}	0.17 ^{ns}	0.25 ^{**}	0.10 ^{ns}	0.10 ^{ns}
Montane grasslands and shrublands - Tundra	0.11 ^{ns}	0.19 ^{**}	0.17 ^{ns}	0.24 ^{**}	0.09 ^{ns}	0.25 ^{**}
Temperate broadleaf and mixed forests - Temperate coniferous forests	0.17 ^{**}	0.05 ^{ns}	0.16 ^{**}	0.10 ^{ns}	0.21 ^{**}	0.04 ^{ns}
Temperate broadleaf and mixed forests - Tropical and subtropical moist broadleaf forests	0.21 ^{ns}	0.22 ^{ns}	0.15 ^{ns}	0.36 ^{**}	0.12 ^{ns}	0.09 ^{ns}
Temperate broadleaf and mixed forests - Tundra	0.16 ^{ns}	0.12 ^{ns}	0.17 ^{ns}	0.13 ^{ns}	0.09 ^{ns}	0.13 ^{ns}
Temperate coniferous forests - Tropical and subtropical moist broadleaf forests	0.06 ^{ns}	0.20 ^{ns}	0.06 ^{ns}	0.45 ^{**}	0.12 ^{ns}	0.11 ^{ns}
Temperate coniferous forests - Tundra	0.15 ^{ns}	0.16 ^{ns}	0.24 ^{**}	0.08 ^{ns}	0.17 ^{**}	0.10 ^{ns}
Tropical and subtropical moist broadleaf forests - Tundra	0.21 ^{ns}	0.30 ^{ns}	0.22 ^{ns}	0.48 ^{**}	0.11 ^{ns}	0.18 ^{ns}

Table S3. Pair-wise dissimilarity of alpine vegetation trait pools between climatic groups for 6 plant functional traits. SLA = Specific leaf area; LDMC = Leaf dry matter content. Significance codes: ***: $p < 0.001$; **: $p < 0.01$; *: $p < 0.05$; ns: $p \geq 0.05$.

Climatic groups	SLA	Leaf area	LDMC	Plant height	Leaf N	Seed mass
Continental - Oceanic	0.10**	0.07 ^{ns}	0.07 ^{ns}	0.09 ^{ns}	0.14**	0.11**
Continental - Subtropical	0.17**	0.09 ^{ns}	0.08 ^{ns}	0.31**	0.16**	0.08 ^{ns}
Oceanic - Subtropical	0.12 ^{ns}	0.14 ^{ns}	0.11 ^{ns}	0.39**	0.05 ^{ns}	0.16**

Table S4. Pair-wise dissimilarity of alpine vegetation trait pools between biogeographic realms for 6 plant functional traits. SLA = Specific leaf area; LDMC = Leaf dry matter content. Significance codes: ***: $p < 0.001$; **: $p < 0.01$; *: $p < 0.05$; ns: $p \geq 0.05$.

Biogeographic realms	SLA	Leaf area	LDMC	Plant height	Leaf N	Seed mass
Afrotropic - Australasia	0.36*	0.11 ^{ns}	0.31 ^{ns}	0.23 ^{ns}	0.31 ^{ns}	0.14 ^{ns}
Afrotropic - Nearctic	0.06 ^{ns}	0.12 ^{ns}	0.04 ^{ns}	0.41**	0.11 ^{ns}	0.07 ^{ns}
Afrotropic - Neotropic	0.40**	0.25 ^{ns}	0.13 ^{ns}	0.07 ^{ns}	0.08 ^{ns}	0.23 ^{ns}
Afrotropic - Palearctic	0.03 ^{ns}	0.12 ^{ns}	0.04 ^{ns}	0.43**	0.18**	0.07 ^{ns}
Australasia - Nearctic	0.34**	0.04 ^{ns}	0.33**	0.24**	0.40**	0.19 ^{ns}
Australasia - Neotropic	0.13 ^{ns}	0.27**	0.30 ^{ns}	0.25**	0.27 ^{ns}	0.12 ^{ns}
Australasia - Palearctic	0.34**	0.05 ^{ns}	0.30**	0.22**	0.43**	0.16**
Nearctic - Neotropic	0.36**	0.26**	0.12 ^{ns}	0.40**	0.14 ^{ns}	0.27**
Nearctic - Palearctic	0.07 ^{ns}	0.02 ^{ns}	0.03 ^{ns}	0.17*	0.09 ^{ns}	0.06 ^{ns}
Neotropic - Palearctic	0.38**	0.25**	0.13 ^{ns}	0.41**	0.18**	0.22**

Table S5. Output of the pair-wise PERMANOVA and PERMDISP tests on multi-trait dissimilarities among alpine vegetation plots belonging to different major habitat types. R^2 values indicate the magnitude of the multivariate differences. Significant PERMDISP tests indicate absence of homogeneity in multivariate dispersions. Significance codes: ***: $p < 0.001$; **: $p < 0.01$; *: $p < 0.05$; ns: $p \geq 0.05$.

Major habitat types	PERMANOVA		PERMDISP
	F Model	R^2	p
Montane grasslands and shrublands - Temperate broadleaf and mixed forests	60.22	0.03*	***
Montane grasslands and shrublands - Temperate coniferous forests	656.69	0.12*	***
Montane grasslands and shrublands - Tropical and subtropical moist broadleaf forests	8.54	0.004*	ns
Montane grasslands and shrublands - Tundra	17.87	0.01*	ns
Temperate broadleaf and mixed forests - Temperate coniferous forests	215.80	0.06*	*
Temperate broadleaf and mixed forests - Tropical and subtropical moist broadleaf forests	26.81	0.05*	ns
Temperate broadleaf and mixed forests - Tundra	15.61	0.03*	*
Temperate coniferous forests - Tropical and subtropical moist broadleaf forests	71.80	0.02*	**
Temperate coniferous forests - Tundra	21.34	0.01*	*
Tropical and subtropical moist broadleaf forests - Tundra	19.52	0.12*	ns

Table S6. Output of the pair-wise PERMANOVA and PERMDISP tests on multi-trait dissimilarities among alpine vegetation plots belonging to different climatic groups. R² values indicate the magnitude of the multivariate differences. Significant PERMDISP tests indicate absence of homogeneity in multivariate dispersions. Significance codes: ***: p<0.001; **: p<0.01; *: p<0.05; ns: p ≥ 0.05.

Climatic groups	PERMANOVA		PERMDISP
	F Model	R ²	p
Continental - Oceanic	156.19	0.03**	***
Continental - Subtropical	86.20	0.06**	***
Oceanic - Subtropical	110.18	0.02**	ns

Table S7. Output of the pair-wise PERMANOVA and PERMDISP tests on multi-trait dissimilarities among alpine vegetation plots belonging to different climatic groups. R^2 values indicate the magnitude of the multivariate differences. Significant PERMDISP tests indicate absence of homogeneity in multivariate dispersions. Significance codes: ***: $p < 0.001$; **: $p < 0.01$; *: $p < 0.05$; ns: $p \geq 0.05$.

Biogeographic realms	PERMANOVA		PERMDISP
	F Model	R^2	Disp
Afrotropic - Australasia	98.95	0.09*	***
Afrotropic - Nearctic	33.78	0.04*	*
Afrotropic - Neotropic	12.50	0.04*	**
Afrotropic - Palearctic	53.13	0.01*	***
Australasia - Nearctic	806.15	0.35*	***
Australasia - Neotropic	130.72	0.11*	***
Australasia - Palearctic	1385.37	0.23*	***
Nearctic - Neotropic	127.52	0.14*	ns
Nearctic - Palearctic	81.10	0.02*	***
Neotropic - Palearctic	180.46	0.04*	ns

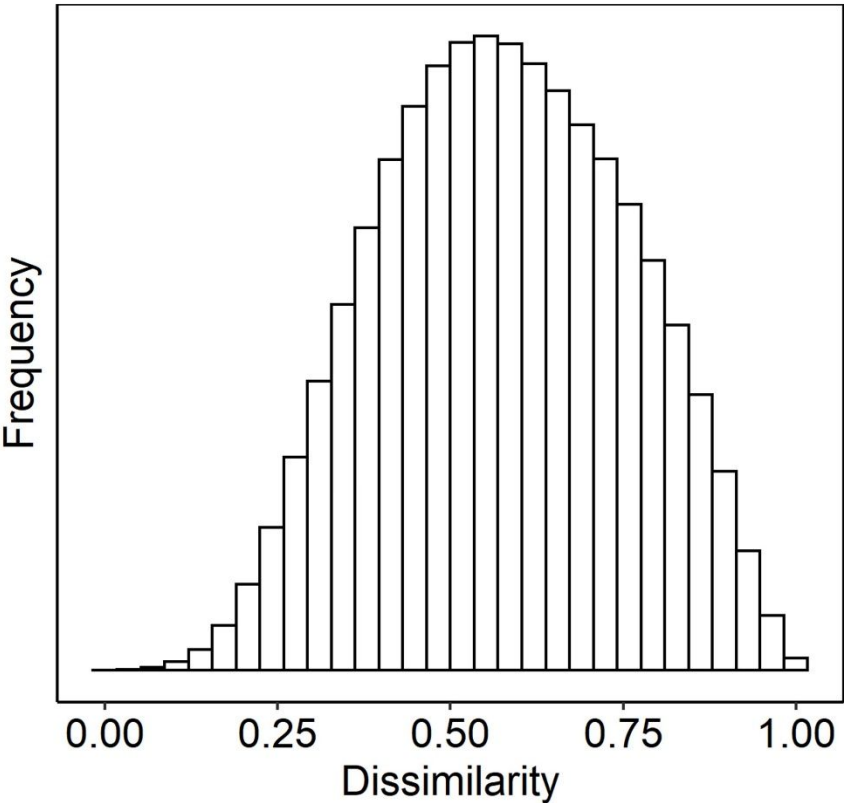


Figure S1. Distribution of multi-trait pair-wise functional dissimilarity values among alpine vegetation plots.