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SPECIAL FEATURE: MACROECOLOGY OF VEGETATION

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Global functional variation in alpine vegetation

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Abstract

Questions: What are the functional trade-offs of vascular plant species in global alpine ecosystems? How is functional variation related to vegetation zones, climatic groups and biogeographic realms? What is the relative contribution of macroclimate and evolutionary history in shaping the functional variation of alpine plant communities?

Location: Global.

Methods: We compiled a data set of alpine vegetation with 5,532 geo-referenced plots, 1,933 species and six plant functional traits. We used principal component analysis to quantify functional trade-offs among species and trait probability density to assess the functional dissimilarity of alpine vegetation in different vegetation zones, climatic groups and biogeographic realms. We used multiple regression on distance matrices to model community functional dissimilarity against environmental and phylogenetic dissimilarity, controlling for geographic distance.

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 probability density was largely independent of vegetation zone and macroclimate but differed across biogeographic realms. The same pattern emerged for both species pool and community levels. The effects of environmental and phylogenetic dissimilarities on community functional dissimilarity had similar magnitude, while the effect of geographic distance was negligible.

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 alpine vegetation, mostly acting at the community level in combination with evolutionary history. Global alpine vegetation is functionally unrelated to the vegetation zones in which it is embedded, exhibiting strong functional convergence across regions.

KEYWORDS
alpine biomes, alpine vegetation, evolutionary history, functional convergence, macroclimate, phylogenetic dissimilarity, trait pools, trait probability density

1 | INTRODUCTION

Alpine environments (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 can be found on all continents and at all latitudes (Körner, 2003). These habitats include global biodiversity hotspots (Myers et al., 2000) and support about 10,000 plant species worldwide, many of which are endemics (Körner, 2003). Globally, the vegetation of alpine environments is dominated by few growth forms (e.g. dwarf shrubs, graminoids, herbaceous rosettes and cushions), reflecting functional adaptations to the characteristics of high-mountain ecosystems, such as low temperatures, short growing season and limited nutrient availability (Körner, 1995, 2003, 2020; Dolezal et al., 2016; Stanisci et al., 2020). Some growth forms, however, are more abundant in certain regions (e.g. evergreen dwarf shrubs in boreal ranges, succulents in semi-arid zones, sclerophyllous species in mediterranean-type climates) or are unique to specific areas, such as giant rosettes in tropical mountains (e.g. *Espeletia* and *Dendrosenecio*; Nagy & Grabherr, 2009). Nevertheless, growth forms are poor descriptors of the functional adaptations of alpine vegetation, with several features of alpine plants found to vary widely within a single growth form (Körner, 1995) or showing no variation among different growth forms (Körner et al., 2016).

In alpine environments, plants have adapted to low temperatures and low nutrient supply (Nagy & Grabherr, 2009). In comparison to lowland species, alpine plants are normally shorter, with smaller leaves and lighter seeds (Körner, 2003; Pellissier et al., 2010). These traits increase frost tolerance, photosynthetic efficiency and dispersal success, so they are globally ubiquitous in alpine vegetation (Körner, 2003). Yet, considerable variation remains among species from different alpine regions, e.g., differences in leaf traits (Halloy

& Mark, 1996; Pyankov et al., 1999), suggesting a response to environmental and evolutionary drivers. Most research comparing plants across alpine regions, however, has only focused on individual traits. Assessing how multiple traits vary simultaneously may allow identification of the trade-offs of plant form and function, i.e., the different strategies used by alpine plants for resource acquisition, growth and reproduction (Grime, 1974; Díaz et al., 2016; Bruelheide et al., 2018).

Global alpine areas can be grouped according to their macroclimate (Testolin et al., 2020), and they are linked to different vegetation zones (Walter & Box, 1976) and biomes characterised by their distinct evolutionary history and own species pools (Mucina, 2019). Indeed, present-day alpine floras are the result of upward shifts of species undergoing regional radiations and long-distance migrations associated with the displacement of cold-climate biomes, such as during the Pleistocene glacial cycles (Billings, 1974; Horandl & Emadzade, 2011; Jiménez-Alfaro et al., 2021). The historical legacy of ancestral species, which may have belonged to different vegetation zones and biogeographic realms, together with the environmental filtering of the current macroclimate, have determined the diversity of alpine trait pools, i.e. the total set of plant trait values found in an alpine region today.

Factors selecting for favourable combinations of traits are generally scale-dependent (Garnier et al., 2016). At continental scales, trait pools are defined by the interplay of macroclimate and evolutionary history (Moncrieff et al., 2016; Mucina, 2019), with the latter constrained by the long-term isolation of major land forms (Chaboureau et al., 2014) and by the phylogenetic origin of species occurring in a biogeographic realm (Holt et al., 2013; Daru et al., 2017; Daru et al., 2018). At the scale of local plant communities, trait pools are further constrained by biotic and abiotic filters that select species assemblages with favourable trait syndromes (Lavorel et al., 1997; Zobel, 2016; Mucina, 2019). As a consequence, the trait values in communities might deviate from those of trait pools (Grime, 2006; Marks & Lechowicz, 2006) and may depend on local conditions (e.g. soil properties and topoclimate) rather than macroclimate (Bruelheide et al., 2018). However, considering the varied origin of plants across global alpine environments (Billings, 1974), an evolutionary mark on functionality might still be detectable at the level of communities (Srivastava et al., 2012). 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 patterns and processes across scales (Pärtel et al., 2016; Ladouceur et al., 2019). Disentangling the effect of macroclimate and evolutionary history might therefore open new prospects for understanding, and possibly predicting, biodiversity patterns in alpine regions.

Here, we provide the first overview of the functional variation of alpine vegetation and an attempt to infer possible drivers across spatial scales. Specifically, we aim to: (a) describe the functional trade-offs of vascular plant species in global alpine ecosystems; (b) assess the functional variation of trait pools and local communities among vegetation zones, climatic groups and biogeographic realms; and (c) quantify the relative contribution of macroclimate and evolutionary history in shaping the functional variation of alpine plant communities.

2 | METHODS

2.1 | Study system and data selection

We used data featuring 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 also included snow-patch plant communities and vegetation on rocks and screes, as they are also found ubiquitously across the alpine belt. The plot data collected by the authors, compiled from the literature, or stored in the sPlot database (v2.1; Bruelheide et al., 2019), were first filtered using habitat classifications of the data sources (Appendix S1), and then further reduced by excluding plots with tree species or incomplete taxonomic identification. We standardised data sets from different sources by identifying a minimum common set of plot attributes including plot size, elevation and geographic coordinates. Species names were harmonised using the Taxonomic Name Resolution Service (Boyle et al., 2013; https://tnrs.biendata.org/) with default settings. Species cover values coded with discrete scales were transformed to the mean value of the corresponding percentage interval. Subspecies and varieties were merged at the species resolution by summing the respective percentage cover values. At this point, the data set consisted of 8,419 plots of alpine vascular vegetation with 4,651 plant species recorded.

Each plot was assigned to the vegetation zone dominating the same ecoregion, i.e. montane grasslands and shrublands, temperate broad-leaved and mixed forests, temperate coniferous forests, tropical and subtropical moist broad-leaved forests, and tundra (Olson et al., 2001). These physiognomic types encompassing large areas are presumed to contribute ancestral clades with potential impact on current alpine trait pools. We also assigned the plots to one of three groups summarising the climatic variability of global alpine areas, representing regional alpine biomes in the classification scheme of Testolin et al. (2020): (a) oceanic, characterised by greater precipitation and relative temperature stability; (b) continental, defined by low precipitation and large annual temperature amplitudes; and (c) subtropical, encompassing both tropical and subtropical alpine areas and characterised by low annual precipitation and contrasting diurnal temperature cycles. Single plots falling slightly outside the boundaries of the commonest vegetation zone or climatic group for a given region were manually assigned to those. Finally, each plot was assigned to a biogeographic realm: Afrotropics, Australasia, Nearctic, Neotropics or Palearctic. Each realm represents a broadly defined geographic region characterised by typical flora and fauna and supposed to have a distinct evolutionary history.

For each species, we extracted the gap-filled trait information from the TRY database (v5.0; Shan et al., 2012; Fazayeli et al., 2014; Schrodt et al., 2015; Kattge et al., 2020), provided by the sPlot database as species average values (Bruelheide 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 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 characterise 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 gap-filling process employed hierarchical Bayesian modelling to estimate missing trait values based on other traits available in TRY for individuals of the same species (Schrodt et al., 2015). Only traits of those species having at least one measured trait observation were imputed. Of all species that were selected based on trait data availability, 99% had at least one measurement in TRY for leaf area, 96% for SLA, 98% for LDMC, 97% for leaf N, 91% for plant height and 85% for seed mass. 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 (n = 2,517) were removed. At the community level, we only considered plots with at least 50% cumulative cover of species with trait data. We chose 50% cover as a trade-off between the inclusion of plots for which trait data were scarce vs the representativeness of dominant vegetation in each community. An alternative set of results obtained choosing more conservative thresholds of 75% and 90% cumulative cover of species with trait data (Appendix S2) showed minor differences with the results presented here. The final data set consisted of 5,532 vegetation plots between 0.25 and 400 m^2 in size sampled between 1923 and 2019, with 1,933 species belonging to five vegetation zones, three climatic groups and five biogeographic realms (Figure 1). All the following analyses have been carried out using R 3.6.3 (R Core Team, 2020).

2.2 | Functional trade-offs and variation of trait pools

To analyse the relationships among traits of the plant species in our data set, we performed a principal component analysis (PCA) of the standardised values of the six traits. The loadings of the individual traits were then used to identify the main axes of variation and possible trade-offs of plant strategies (Díaz et al., 2016).

To compare the trait pools across the vegetation zones, climatic groups and biogeographic realms, we employed trait probability densities, a scale-independent framework that implements the concept of the niche hypervolume while accounting for the probabilistic nature of traits (Carmona et al., 2016). This method requires both the mean and the standard deviation of each trait for all the species. As reliable information on the standard deviations was not available, we assumed it to be constant across species and estimated it as 50% of the standard deviation of all species' mean values for each trait (Lamanna et al., 2014; Carmona, 2019). Then, we calculated the individual trait pools as the probability densities for each vegetation zone, climatic group and biogeographic realm using the R package *TPD* (Carmona, 2019), accounting for species frequencies (i.e. the number of plots in each group where a certain species was recorded). We assessed the functional variation of trait pools using kernel density plots and calculated pair-wise functional dissimilarities among trait pools using the "dissim" function of the *TPD* package. The significance of the pair-wise dissimilarities was evaluated in a null-modelling framework (Geange et al., 2011; Traba et al., 2017) by pooling the observations from each pair, randomising the species' labels 999 times while keeping the number of species constant for each group and ranking the pair-wise dissimilarity values among the simulated trait probability densities. This allowed us to calculate the Bonferroni-corrected p-values for each comparison as:

$$p = \left(1 - \frac{r_{\text{obs}}}{i+1}\right) \times n.$$

where r_{obs} is the rank of the observed dissimilarity value among the simulated ones, i is the number of simulations, and n is the number of pair-wise comparisons (Legendre & Legendre, 2012; Traba et al., 2017). To assess the overall functional variation among vegetation zones, climatic groups and biogeographic realms, while excluding potentially redundant information, we calculated multi-trait probability densities by using the first two axes of the PCA of the six traits and repeated the same analyses described above for individual traits.

2.3 | Functional variation of communities

To analyse the variation in trait values across plant communities, we calculated the multi-trait functional dissimilarities between all vegetation plots as described above, accounting for the cover of the species within each plot. The pair-wise dissimilarities were displayed in the same PCA space as the individual species by calculating the community-weighted means of the first two PCA axes for each plot. This allowed the visualisation of the functional variation of plots belonging to different groups. Significant differences among plots belonging to different vegetation zones, climatic groups and biogeographic realms were tested using PERMANOVA (Anderson, 2001), implemented by the "adonis" function of the R package *vegan* (Oksanen et al., 2019), with 999 permutations.

To quantify the relative contribution of climate and evolutionary history in determining functional variation among communities, we modelled community functional dissimilarity as a function of environmental and phylogenetic dissimilarity while controlling for geographic distance. Phylogenetic data were provided by the sPlot database based on the phylogeny of Qian and Jin (2016). Species present in our data set but missing from this phylogeny were added next to a randomly selected congener, if available (Bruelheide et al., 2019). First, we selected the set of species for which both trait and phylogenetic data were available (n = 1,674) and further took a

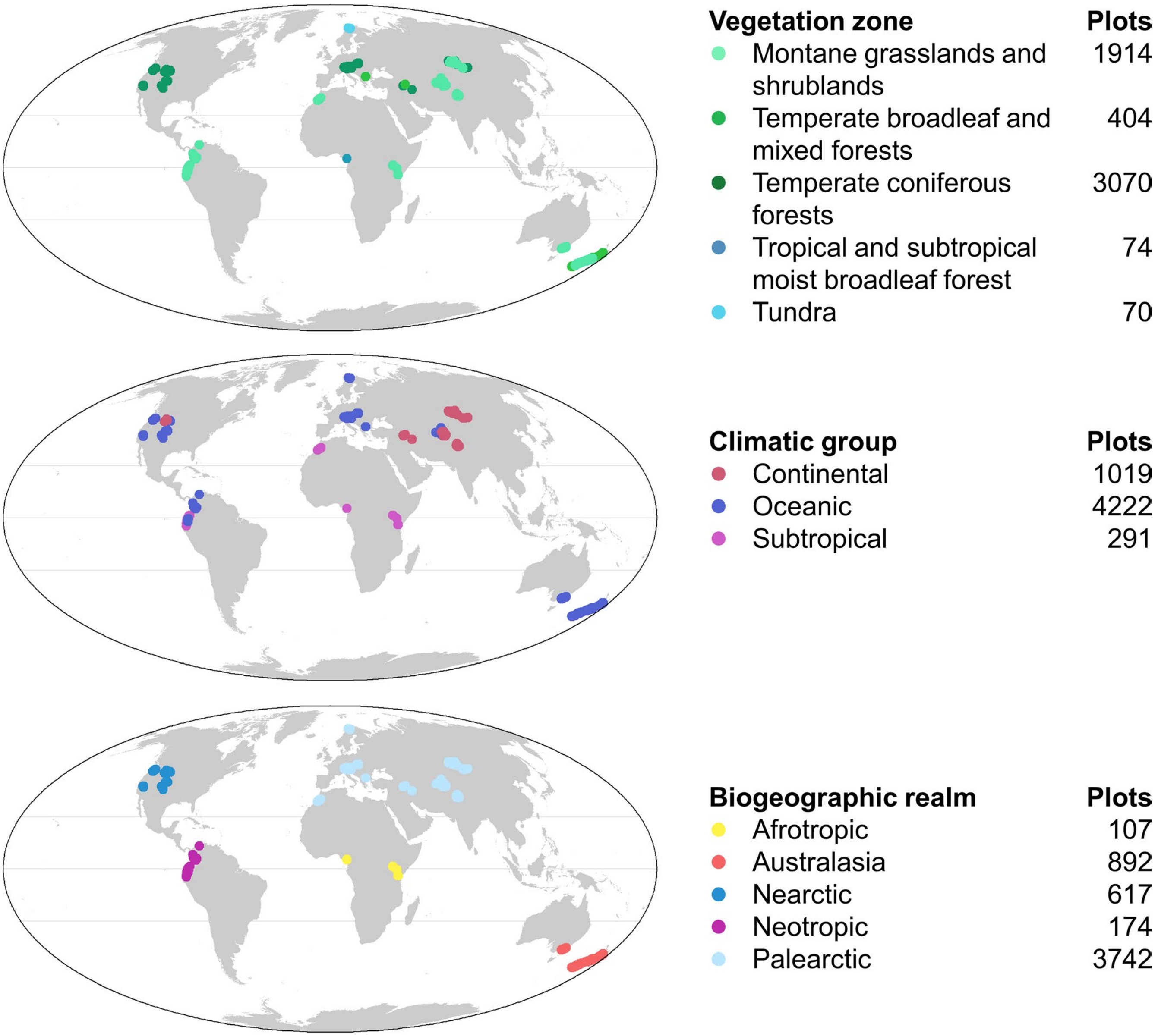

FIGURE 1 Spatial distribution of 5,532 alpine vegetation plots across vegetation zones, climatic groups and biogeographic realms

subset of 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. We also performed alternative selections of plots with 75% and 90% cumulative cover of species with trait and phylogenetic data to assess the effect of a more conservative cumulative cover threshold on the model results (Appendix S2). Then, we built a set of climatic variables known to affect alpine vegetation (Körner, 2003; Moser et al., 2005; Nagy & Grabherr, 2009) using data from the CHELSA bioclimatic database at ~1-km spatial resolution (Karger et al., 2017). The included variables were mean temperature, precipitation, growing degree days and mean potential evapotranspiration. Each variable was calculated within the time frame of the growing season, defined as days with mean temperature > 0.9°C (Paulsen & Körner, 2014). Growing degree days (i.e. the sum of monthly temperatures > 0.9°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 minimum monthly values of temperature and monthly precipitation. The monthly values of potential evapotranspiration obtained were then averaged across months with mean temperature above 0.9°C. We standardised the four climatic variables and calculated the Euclidean distance among each pair of plots as a measure of environmental dissimilarity.

To account for the evolutionary history of plant species in different communities, we also calculated the pair-wise phylogenetic dissimilarity between plots (Ives & Helmus, 2010) with the "pcd" function of the R package *picante* (Kembel et al., 2010). To account for the spatial aggregation of plots and unmeasured regional effects on the estimated functional dissimilarity, we calculated the pair-wise geographical distances between plots. Finally, we modelled functional community dissimilarity against these three distanced-based predictors using multiple regression on distance matrices (MRM) with the "lm" function. Despite our measure of functional dissimilarity is constrained between 0 and 1, our data set mainly encompassed intermediate levels of functional turnover (Appendix S1), allowing us to treat it as approximately linear (Ferrier et al., 2007). Further, a linear modelling approach allowed us to calculate the adjusted R^2 of all the sub-models necessary to perform variance partitioning (Borcard et al., 1992; Swenson, 2014).

3 | RESULTS

The first two PCA axes accounted for 66% of the total trait variation among species. The other axes explained less variation than expected by chance and were not considered further. The first axis (PC1; 35% of variation) was mainly related to variations in LDMC, leaf N and SLA, while the second axis (PC2; 31% of variation) was linked to leaf area, plant height and seed mass (Figure 2, Appendix S1).

When focusing on the level of vegetation zones, we observed negligible differences in trait probability density and low functional dissimilarity among trait pools. The only exception was the alpine vegetation related to tropical and subtropical moist broadleaved forests, which exhibited slightly greater plant height values compared to other vegetation zones (Figure 3; Appendix S1).

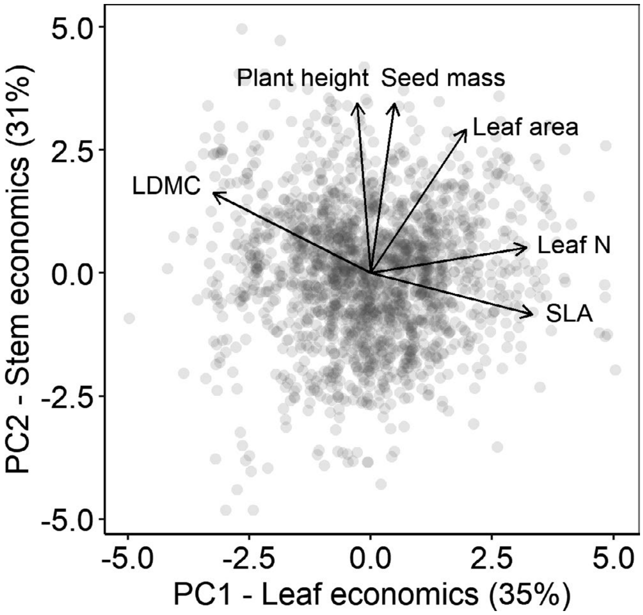

FIGURE 2 Functional variation of 1,933 vascular plant species in global alpine areas along the first two principal components of six traits representing main functional trade-offs. LDMC, leaf dry matter content; SLA, specific leaf area

Among climatic groups, subtropical alpine areas also exhibited greater plant height values when compared to oceanic and continental ones, with minor variation in the distribution of other traits (Figure 3; Appendix S1). However, we observed considerable variability in trait probability density among biogeographic realms. The alpine vegetation of the Australasian and Neotropical realms had lower SLA compared to that of the others and similar values of plant height to the Afrotropics, which were greater than those of the Palearctic and Nearctic. As for leaf area and seed mass, the Neotropics generally showed higher values compared to the Palearctic and Nearctic, which in turn presented higher leaf N and lower LDMC than Australasia (Figure 3; Appendix S1). Multi-trait patterns seemingly reflected those observed at the single trait level. Among vegetation zones 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 Neotropics and Australasia, with the Afrotropical pool taking an intermediate position between the two groups.

Multi-trait dissimilarities of alpine plant communities revealed distinct patterns among biogeographic realms (Figure 4), with Australasian, Afrotropical and Neotropical plots characterised by larger values of LDMC and smaller SLA and leaf N. PERMANOVA showed that biogeographic realm explained 19% of the functional variation ($R^2 = 0.19$, $p = 0.001$), vegetation zones explained 11% ($R^2 = 0.11$, $p = 0.001$) and climatic groups explained 5% ($R^2 = 0.05$, $p = 0.001$). The same patterns emerged when considering more conservative thresholds of cumulative cover of species with trait data (Appendix S2).

Finally, the MRM model fit on a subset of plots with available phylogenetic information explained 16.6% of the communities' functional dissimilarity. Environmental and phylogenetic dissimilarities both explained 6.2% individually, while 4% was shared between the two of them. Geographic distance exhibited a marginal effect, explaining only 0.3% (Figure 5). Again, adopting more conservative thresholds of cumulative cover of species with trait and phylogenetic data did not significantly affect the results (Appendix 2).

4 | DISCUSSION

4.1 | Functional trade-offs of alpine plant species

We selected six traits linked to resource use, growth and reproduction of plants and used PCA to describe the functional trade-offs of 1,933 vascular plant species in global alpine ecosystems. PC1 differentiated strategies in terms of investments of nutrients and dry mass in leaves and hence the leaf economics spectrum (Wright et al., 2004). This spectrum discriminates between species, those with high leaf construction costs (high LDMC, low SLA) and low leaf nutrient concentrations (low leaf N) related to slower vegetative development rates vs fast-growing species with high leaf nutrient concentration and cheaper construction costs that promote

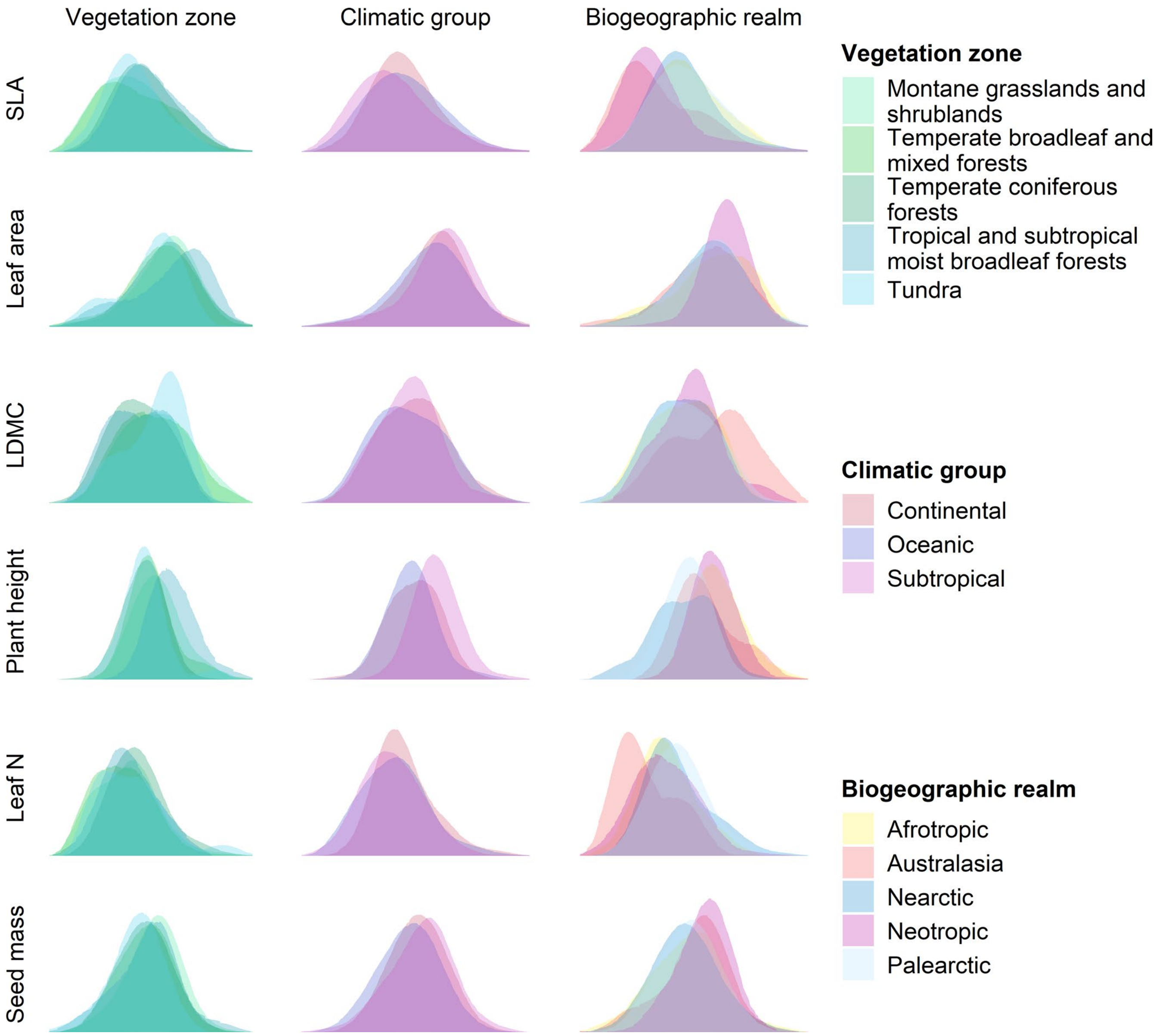

FIGURE 3 Kernel density plots of alpine trait pools estimated using trait probability density for six individual plant traits among vegetation zones, climatic groups and biogeographic realms. LDMC, leaf dry matter content; SLA, specific leaf area

a quick return of the investments in nutrients and carbon (Wright et al., 2004). PC2 reflected differences in plant size, conforming to the stem economics spectrum (Baraloto et al., 2010) that separates taller plants able to carry larger leaves and seeds (large plant height, leaf area and seed mass) from smaller plants. These results agree with previous analyses of alpine and tundra vascular plants (Dolezal et al., 2016; Thomas et al., 2019) and are consistent with directions of variation in the global spectrum of plant form and function (Díaz et al., 2016). Nevertheless, the predominance of variation in resource use strategies rather than size 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. Small size allows alpine plants to respond to and modify the microclimate near the ground (Geiger et al., 2003) by accumulating heat under the leaf canopy regardless of fluctuations of the macroenvironment (Körner et al., 1989; Körner, 2003). Additionally, the main variation observed along PC1 could be explained by the greater variability of leaf construction costs of alpine plants, which depend on local temperature, frost stress and prolonged exposure to light (Körner et al., 1989). Any of these may vary widely even within a single mountain range, hence the greater variation of the related traits (Stanisci et al., 2020).

4.2 | Variation of alpine trait pools

Trait pools of alpine plants were largely independent of the vegetation zone, suggesting that alpine vegetation is functionally different

TABLE 1 Multi-trait pair-wise dissimilarities (Diss) of alpine vegetation between vegetation zones, climatic groups and biogeographic realms. Significant dissimilarities ($p < 0.05$) are in bold

	Diss
Vegetation zones	
Montane grasslands and shrublands–Temperate broad-leaved and mixed forests	0.16^{ns}
Montane grasslands and shrublands–Temperate coniferous forests	**0.27****
Montane grasslands and shrublands–Tropical and subtropical moist broad-leaved forests	0.29^{ns}
Montane grasslands and shrublands–Tundra	0.27^{ns}
Temperate broad-leaved and mixed forests–Temperate coniferous forests	**0.24****
Temperate broad-leaved and mixed forests–Tropical and subtropical moist broad-leaved forests	**0.34***
Temperate broad-leaved and mixed forests–Tundra	0.23^{ns}
Temperate coniferous forests–Tropical and subtropical moist broad-leaved forests	0.28^{ns}
Temperate coniferous forests–Tundra	0.25^{ns}
Tropical and subtropical moist broad-leaved 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****

Significance codes: ***, $p < 0.001$; **, $p < 0.01$; *, $p < 0.05$; ns, $p \geq 0.05$.

from the surrounding flora in which it is embedded. Thus, the convergence of growth forms that characterises alpine vegetation (Körner, 2003, 2020; Aubert et al., 2014) follows adaptation to similar ecological conditions (Givnish, 2010, 2016; Horandl & Emadzade, 2011; Hughes & Atchison, 2015). This finding contrasts with the view of alpine areas as elevational "orobiomes" closely related to the "zonobiomes" they originate from (Walter & Box, 1976) but agrees with the distinction of alpine ecosystems from other terrestrial biomes (Testolin et al., 2020). Trait pools were also convergent among climatic groups, indicating that macroclimatic differences above the treeline have little influence on the functional features of alpine vegetation, which is consistent with the similar patterns of primary productivity found across global alpine biomes (Testolin et al., 2020).

However, we observed some divergence of trait pools across biogeographic realms. Such functional differences might emerge even among structurally similar plant groups when these are compared across areas with distinct evolutionary histories (Alvarado-Cárdenas et al., 2013). Specifically, we observed a distinction between the trait pool of the Holarctic realm and those of the Neotropics and Australasia, while the trait pool of the Afrotropical realm occupied an intermediate position. 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). Consequently, Holarctic alpine vegetation shares many species with the Arctic (Billings, 1974) and has major links with Afrotropical alpine species (Linder, 2014; Carbutt & Edwards, 2015). In contrast, a large part of Neotropical alpine plants originated locally through migration and adaptation of Neotropical lowland species (Sklenář et al., 2011), some of which also contributed to Afrotropical lineages (Linder, 2014). Finally, the functional similarity of the 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 led to the diversification of the respective alpine floras (McGlone & Heenan., 2001; Winkworth et al., 2005; Sklenář et al., 2011; Madriñán et al., 2013).

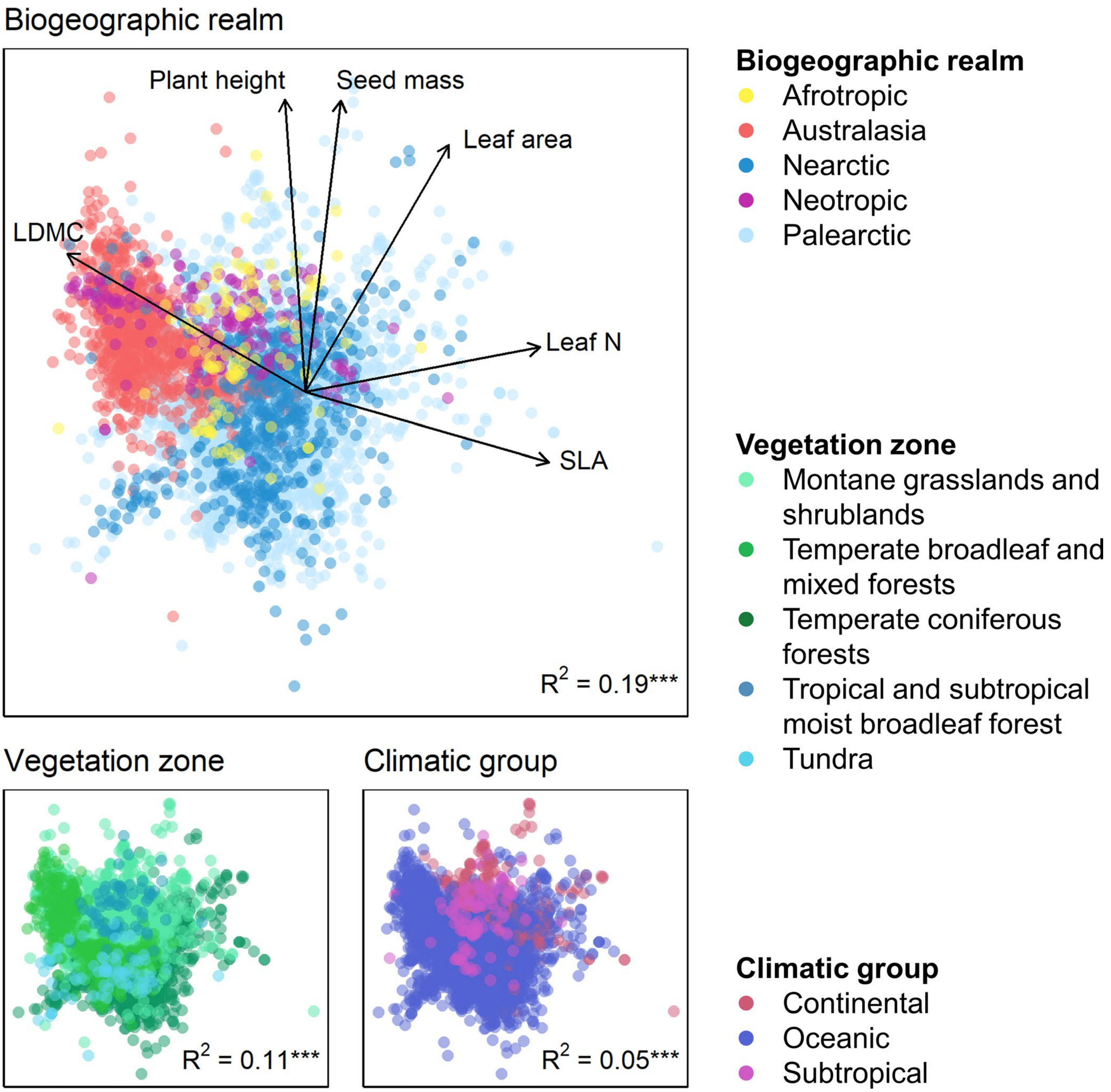

FIGURE 4 Functional variation of alpine plant communities. Each dot represents a vegetation plot, whose position is based on community-weighted means of the first two axes of a principal components analysis PCA of six functional traits. The arrows represent the trait loadings on the PCA axes. The total variance of community dissimilarity explained by the groups (PERMANOVA) is reported in the bottom-right corner of each graph. LDMC, leaf dry matter content; SLA, specific leaf area. Significance codes: ***, $p < 0.001$; **, $p < 0.01$; *, $p < 0.05$; ns, $p \geq 0.05$

4.3 | Functional variation of alpine communities

Communities were not functionally distinct among vegetation zones or climatic groups, while biogeographic realms exhibited greater discriminatory power, as they did for the trait pools. Australasian communities form an isolated group characterised by leaves with high construction costs, which agrees with the greater abundance of sclerophyllous dwarf shrubs in the Australasian alpine flora relative to other global alpine regions (Ballantyne & Pickering, 2015). The functional distinctness of Australasian alpine communities from Holarctic and tropical ones may also reflect differences in trait pools between the two hemispheres and could be related to the long-time isolation (45 – 49 Ma) of Australasian landforms 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 regional evolutionary history are involved at the local scale. Indeed, although our model highlighted the presence of a phylogenetic signal in functional

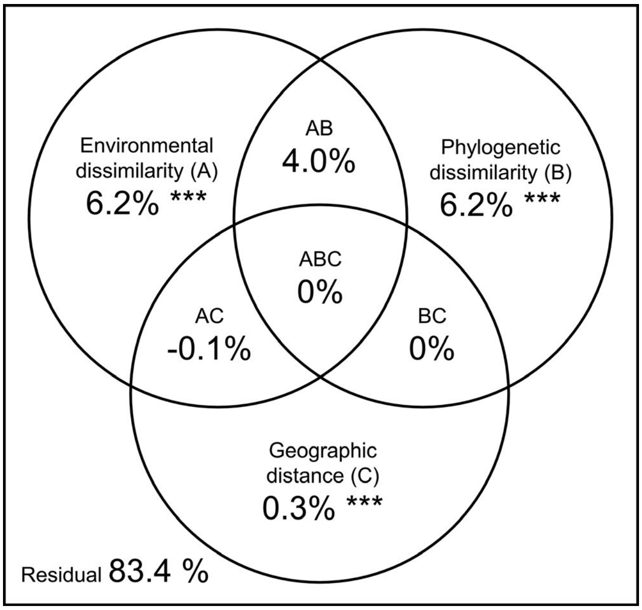

FIGURE 5 Venn diagram of multi-trait functional dissimilarity of alpine vegetation communities displaying variance partitioning among environmental dissimilarity (a), phylogenetic dissimilarity (b), and geographic distance (c). Significance codes: ***, $p < 0.001$; **, $p < 0.01$; *, $p < 0.05$; ns, $p \geq 0.05$

dissimilarity, environmental dissimilarity explained an equal amount of variance. This is consistent 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 realised 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. soil properties and topoclimate), disturbance and biotic interactions as the main drivers of community trait composition in alpine ecosystems (Grime, 2006; Dolezal et al., 2019).

4.4 | Assumptions and caveats

Even though we used the largest data set of alpine vegetation ever collected, our study does not come without uncertainties. First, many mountain regions, including outstanding centres of alpine plant diversity such as the Himalayas and Hengduan Mountains (Favre et al., 2015; Xing & Ree, 2017; Muellner-Riehl et al., 2019; Ding et al., 2020), were not represented in our data set, preventing us from providing a complete global picture of alpine plant functional variation. Still, our plots encompass alpine vegetation in six continents from boreal to tropical latitudes, allowing meaningful global comparisons that could be further refined by the future inclusion of additional alpine regions, especially in the tropical and subtropical belts. Second, when comparing functional dissimilarities across geographical units and spatial scales, 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 exclude many plots in Africa and South America. Although we recognise that this could have led to the exclusion of unusual 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. Third, we note that our data set encompasses vegetation plots of very different sizes (0.25–400 m^2). 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. However, when accounting for species abundances — or, in our case, cover — the relationship between functional diversity indices and plot size tends to weaken or disappear because 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 plot data in alpine vegetation currently available, much effort is still needed to collect data with a consistent sampling protocol, including functional traits and a proper representation of species and vegetation types from disparate global regions.

5 | CONCLUSIONS

This study provides the first overview of the global functional trait variation in alpine vegetation. While alpine species exhibit the same trade-offs observed in vascular plants globally, the absence of trees in alpine ecosystems leads to a greater variety of traits related to resource use strategies rather than size. We found that alpine vegetation is scarcely related to the vegetation zones in which it is embedded and is largely independent of macroclimatic patterns, at least for the traits analysed in this study. However, evolutionary history seemingly affected current trait pools, and phylogenetic constraints and macroclimate equally determine the functional dissimilarity of communities. Overall, our results indicate a strong functional convergence of adult plant traits in global alpine vegetation, with implications at both regional and community level. This finding agrees with the functional convergence observed for regeneration traits in alpine plants across continents (Fernández-Pascual et al., 2020), further supporting a distinct delineation of alpine ecosystems in the context of the global biomes. Yet, other factors not accounted for in this study (e.g. soil properties, topoclimatic gradients) are likely influencing functional traits of alpine vegetation locally. In this respect, future work should be oriented toward the inclusion of additional fine-scale environmental characteristics, as well as trait data from tropical and subtropical species currently underrepresented in global data sets.

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AUTHOR CONTRIBUTIONS

BJ-A, LM, RT and CPC conceived the study and developed the methodology. PB, JD, MF, AH, AYK, JL, NM, GPM, JN, AN, RKP, GP, JŠ, PS, KV, RV, SKW and EGZ provided the vegetation plot data. FMS and HB facilitated access to the sPlot database. RT analysed the data and produced the outputs. RT and BJ-A wrote the first manuscript draft. BJ-A supervised the study. All the authors discussed the methodology and commented on various versions of the manuscript.

DATA AVAILABILITY STATEMENT

The vegetation plot data are stored and managed by sPlot and the corresponding author and are available upon request. The R code used to carry out the analyses is available at: https://dx.doi.org/10.6084/m9.figshare.14040152

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SUPPORTING INFORMATION

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

Appendix S1. Supporting information of alpine vegetation plot data selection and analysis

Appendix S2. Sensitivity analysis of results to different cumulative cover thresholds of species with trait and phylogenetic data

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