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Global functional variation in alpine vegetation

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Author's Data Availability Statement:

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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2   **Running title: Alpine functional variation**

3   **Authors:** Riccardo Testolin[1], Carlos P. Carmona[2], Fabio Attorre[1], Peter Borchardt[3], Helge

4   Bruelheide[4,5], Jiri Dolezal[6,7], Manfred Finckh[8], Sylvia Haider[4,5], Andreas Hemp[9], Ute Jandt[4,5],

5   Andrei Yu. Korolyuk[10], Jonathan Lenoir[11], Natalia Makunina[10], George P. Malanson[12], Ladislav

6   Mucina[13], Jalil Noroozi[14], Arkadiusz Nowak[15,16], Robert K. Peet[17], Gwendolyn Peyre[18],

7   Francesco Maria Sabatini[5,4], Jozef Šibík[19], Petr Sklenář[20], Kiril Vassilev[21], Susan K. Wiser[22],

8   Evgeny G. Zibzeev[10], Borja Jiménez-Alfaro[23]

20 **Affiliations:**

10 [1] Department of Environmental Biology, Sapienza University of Rome, Rome, Italy

11 [2] Institute of Ecology and Earth Sciences, University of Tartu, Tartu, Estonia

12 [3] Institute of Geography, CEN – Center for Earth System Research and Sustainability, University

13 of Hamburg, Hamburg, Germany

14 [4] Institute of Biology/Geobotany and Botanical Garden, Martin Luther University Halle-

15 Wittenberg, Halle, Germany

16 [5] German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Leipzig,

17 Germany

18 [6] Institute of Botany of the Czech Academy of Sciences, Průhonice, Czech Republic

19 [7] Department of Botany, Faculty of Science, University of South Bohemia, České Budějovice,

20 Czech Republic

21 [8] Biodiversity, Evolution and Ecology of Plants, Institute of Plant Science and Microbiology,

22 University of Hamburg, Hamburg, Germany

23 [9] Department of Plant Systematics, University of Bayreuth, Bayreuth, Germany

24 [10] Central Siberian Botanical Garden, Siberian Branch, Russian Academy of Sciences,

25 Novosibirsk, Russia

26 [11] UR "Ecologie et Dynamiques des Systèmes Anthropisés" (EDYSAN, UMR 7058 CNRS-

27 UPJV), Université de Picardie Jules Verne, Amiens, France

28 [12] Department of Geographical & Sustainability Sciences, University of Iowa, Iowa City, Iowa,

29 USA

30 [13] Harry Butler Institute, Murdoch University, Perth, Australia

31 [14] Department of Botany and Biodiversity Research, University of Vienna, Vienna, Austria

32 [15] Botanical Garden – Center for Biological Diversity Conservation, Polish Academy of

33 Sciences, Warszawa, Poland

34 [16] Institute of Biology, University of Opole, Opole, Poland

35 [17] Department of Biology, University of North Carolina, Chapel Hill, North Carolina, USA

36 [18] Department of Civil and Environmental Engineering, University of the Andes, Bogota,

37 Colombia

38 [19] Institute of Botany, Plant Science and Biodiversity Centre, Slovak Academy of Sciences,

39 Bratislava, Slovakia

40 [20] Department of Botany, Charles University, Prague, Czech Republic

41 [21] Department of Plant and Fungal Diversity and Resources, Institute of Biodiversity and

42 Ecosystem Research, Bulgarian Academy of Sciences, Sofia, Bulgaria

43 [22] Manaaki Whenua–Landcare Research, Lincoln, New Zealand

44 [23] Research Unit of Biodiversity (CSUC/UO/PA), University of Oviedo, Mieres, Spain

45 **Correspondence:**

46 Riccardo Testolin, Department of Environmental Biology, Sapienza University of Rome, Rome,

47 Italy.

48 Email: riccardo.testolin@uniroma1.it

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57   **Abstract:**

58   **Questions:** What is the functional trait variation of vascular plants in alpine areas? How does

59   cross-scale trait variation of alpine vegetation relate to large-scale biogeographic factors? How

60   much do macroclimate and phylogenetic relatedness contribute to explaining the functional

61   variation of alpine plant communities?

62   **Location:** Global.

63   **Methods:** We compiled a global dataset of alpine vegetation with 5,532 geo-referenced plots,

64   1,934 species, and six plant functional traits. We used principal component analysis to describe

65   the species' trait space, and trait probability density to assess the functional variation of trait

66   pools and local communities among major habitat types, climatic groups and biogeographic

67   realms. We used multiple regression on distance matrices to model community functional

68   dissimilarity against environmental and phylogenetic dissimilarity.

69   **Results:** The first two PCA axes explained 66 % of the species' functional variation and were

70   related to the leaf and stem economic spectra, respectively. Trait pools were largely independent

71   of surrounding habitat types and climate, but with considerable variation among biogeographic

72   realms. A similar pattern emerged at the community level, with a stronger influence of realms on

73   functional variation. Environmental and phylogenetic dissimilarities had a similar influence on

74   community functional dissimilarity, with a negligible effect of geographic distance.

75   **Conclusions:** Plant species in alpine areas reflect the global variation of plant function, but with

76   a predominant role of resource-use strategies. Current macroclimate exerts a limited effect on

77   functional pools, mostly acting at the community level in combination with evolutionary

78   imprints of the two global hemispheres. Alpine vegetation is functionally unrelated to the

79   habitats in which it is embedded, supporting its evolutionary distinctiveness from other terrestrial

80   biomes.

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81 **Keywords:** Global alpine vegetation, functional dissimilarity, trait pools, trait probability

82 density, evolutionary history, macroclimate, phylogenetic dissimilarity, alpine biomes

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Introduction

85 Alpine habitats (i.e. high-elevation habitats above the climatic treeline) cover about 3 % of land

86 outside Antarctica (Körner et al. 2011; Testolin et al. 2020) and represent the only biogeographic

87 unit distributed across all continents and latitudes on both hemispheres (Körner 2003). These

88 habitats support about 10,000 plant species worldwide, many of which are endemics (Körner

89 2003) and some are global biodiversity hotspots (Myers et al. 2000). Despite the great number of

90 species and its global distribution, alpine vegetation is dominated by few growth forms (i.e.

91 dwarf shrubs, graminoids, herbaceous rosettes and cushions), reflecting functional adaptations to

92 the general characteristics of alpine environments, i.e. low temperatures, short growing season

93 and limited nutrient availability (Körner 1995; Körner 2003; Dolezal et al. 2016; Körner 2019;

94 Stanisci et al. 2020). Yet, to which extent large scale factors shape the spectrum of plant

95 functions across alpine regions remains little understood.

96 Alpine habitats can be globally differentiated along gradients of seasonality and

97 continentality (Testolin et al. 2020). They are generally considered as ecological units defined by

98 elevation (orobiomes) and nested within different vegetation zones (zonobiomes) that are in turn

99 characterized by distinct plant species pools (Walter & Box 1976; Mucina 2019). Since alpine

100 vegetation is found in regions with different climatic and evolutionary history (Billings 1974),

101 their functional characteristics are influenced by the species pool dominating in that region

102 (Moncrieff et al. 2016; Mucina 2019). Indeed, alpine vegetation shows variation in terms of e.g.

103 abundance of succulents in semi-arid zones, sclerophyllous species in Mediterranean climates, or

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104 giant rosettes in tropical areas (e.g. *Espletia*, *Lobelia,* and *Dendrosenecio*) However, growth

105 forms might be poor descriptors of plant functioning in tundra vegetation (Thomas et al. 2019) as

106 they still bear a considerable amount of variability in plant characteristics, which can vary widely

107 within a single group (Körner 1995). A more quantitative assessment of plant functioning can be

108 approached by using functional traits (hereafter traits), defined as measurable features affecting

109 the performance of species in their environment (McGill et al. 2006; Garnier et al. 2016). Indeed,

110 a small set of traits can be used to explain different strategies adopted by terrestrial plant species

111 for resources acquisition, growth and reproduction (Grime 1974; Díaz et al. 2016; Bruelheide et

112 al. 2018).

113 Factors selecting for favorable combinations of traits are generally scale-dependent

114 (Garnier et al. 2016). At large spatial scales, the interplay of different continental processes,

115 mostly driven by macroclimate, determines the current set of functional traits (i.e. the trait pool)

116 that further contributes to define the global biomes (Mucina 2019). Stochastic events and

117 landscape structure limit species dispersal into regional floras (Garnier et al. 2016), that can act

118 as potential sources for new alpine species (Billings 1974). These processes are rooted in the

119 evolutionary history of each region, which is constrained by long-term isolation of major

120 landforms (Chaboureau et al. 2014) and by the phylogenetic origin of the species occurring

121 within each biogeographic realms (Holt et al. 2013; Daru et al. 2017; Daru et al. 2018). At the

122 community scale, trait pools are further constrained by local biotic and abiotic filters that select

123 species assemblages with favorable trait syndromes (Lavorel et al. 1997; Zobel 2016; Mucina

124 2019). Linking local filtering to evolutionary and biogeographic history remains a major

125 challenge in macroecology and new approaches that incorporate different facets of diversity are

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126 required to understand the patterns and processes regulating plant communities across scales

127 (Pärtel et al. 2016; Ladouceur et al. 2019).

128   Here, we provide the first cross-scale overview of the functional variation of alpine

129 vegetation and its possible drivers. Specifically, we aim to: 1) describe the trait spectrum of

130 vascular plant species in global alpine ecosystems; 2) assess the trait functional variation of

131 regional pools and local communities among major habitat types, climatic groups and

132 biogeographic realms; 3) estimate the relative contribution of macroclimate and evolutionary

133 history in shaping the functional characteristics of alpine plant communities.

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135 **Methods**

136 <u>Study system and data selection</u>

137 We considered data from alpine vegetation defined as any vascular plant community above the

138 climatic treeline (Körner 2003). In addition to strictly zonal habitats dominated by graminoids,

139 forbs and dwarf shrubs, we included snow-patch plant communities and vegetation on rocks and

140 screes, as they are also found ubiquitously across the alpine vegetation belt. The vegetation-plot

141 data collected by the authors, compiled from the literature, or stored in the sPlot database (v2.1)

142 (Bruelheide et al. 2019), was first filtered using habitat classifications of the data sources and

143 then further cleaned by excluding plots with tree species or incomplete taxonomic identification.

144 We standardized datasets from different sources by identifying a minimum common set of plot

145 attributes including plot size (i.e. sampled area), elevation, and geographic coordinates. Species

146 names were harmonized using the Taxonomic Name Resolution Service (Boyle et al. 2013)

147 (http://tnrs.iplantcollaborative.org) with default settings. Subspecies and varieties were merged at

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148 the species resolution by summing the respective percentage cover values. At this point the

149 dataset consisted of 8,877 plots of alpine vascular vegetation with 5,313 plant species recorded.

150 Each plot was then assigned to major habitat types (Olson & Dinerstein 1998; Olson et al.

151 2001), representing the dominant vegetation of a large geographic area whose species pool could

152 have contributed to that of the alpine belt. Furthermore, we assigned the plots to three different

153 groups summarizing the climatic variability of global alpine areas according to (Testolin et al.

154 2020): 1) oceanic, characterized by greater precipitation and relative temperature stability,

155 analogous to the oceanic climate of the Köppen-Geiger classification (Köppen 1936); 2)

156 continental, defined by drier conditions and greater yearly temperature differences; 3)

157 subtropical, encompassing both tropical and subtropical alpine areas, and characterized by

158 warmer temperatures with strong daily excursion and low annual precipitation. Single plots

159 falling slightly outside the boundaries of the commonest major habitat type or climatic group for

160 a given region were manually assigned to those. Finally, each plot was assigned to a

161 biogeographic realm (Olson et al. 2001), representing a broad land unit with distinct evolutionary

162 history.

163 For each species, we linked the gap-filled trait information from the TRY database (v5.0)

164 (Shan et al. 2012; Fazayeli et al. 2014; Schrodt et al. 2015; Kattge et al. 2020), provided by the

165 sPlot database as species-specific average values (Bruelheide et al. 2019). We selected six plant

166 functional traits: leaf area (one-sided surface of the fresh leaf), specific leaf area (leaf area per

167 leaf dry mass; SLA), leaf dry matter content (leaf dry mass per leaf fresh mass; LDMC), leaf

168 nitrogen (N) (N per leaf dry mass;), plant height (maximum total height of the plant) and seed

169 mass (dry mass of the seed). We chose these traits because they are commonly used to

170 characterize tundra and alpine vegetation (Bjorkman et al. 2018; Thomas et al. 2019; Liancourt

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171 et al. 2020), and they are fully representative of plant ecological strategies (Díaz et al. 2016). The

172 values of plant height, leaf area and seed mass were $\log_{10}$-transformed to reduce skewness.

173 Species for which trait information was not available were removed. At the community level, we

174 only considered plots with at least 50 % cover of species with trait data. The final dataset

175 consisted of 5,532 vegetation plots between 0.25 and 400 m^2 in size sampled between 1923 and

176 2019, with 1,934 species belonging to five major habitat types, three climatic groups and five

177 biogeographic realms (Figure 1).

178 <u>Functional spectrum of species pools</u>

179 All the following analyses have been carried out using R (R Core Team 2020). To analyze the

180 trait space occupied by the species and the relationships among the selected traits, we performed

181 a principal component analysis (PCA) of the standardized values of the six traits. To compare the

182 trait pools of alpine vegetation across major habitat types, climatic groups and biogeographic

183 realms, we used trait probability density, a scale-independent framework that implements the

184 concept of the niche hypervolume while accounting for the probabilistic nature of traits

185 (Carmona et al. 2016). As reliable information on intraspecific variability of the traits was not

186 available across all studied species and for each trait, we estimated it as 50 % of the standard

187 deviation of the species average for each trait (Lamanna et al. 2014). Then, we calculated the

188 single-trait pools as the probability densities for each major habitat type, climatic group and

189 biogeographic realm using the package "TPD" (Carmona 2019), accounting for species

190 frequencies (i.e. the number of plots in each major habitat type, climatic group and

191 biogeographic realm, where a certain species was recorded).

192 We assessed the functional variation among different groups using kernel density plots

193 and calculating overlap-based pair-wise dissimilarities among trait pools using the "dissim"

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194   function of "TPD" package. The significance of the pair-wise dissimilarities was evaluated in a

195   null-modeling framework (Geange et al. 2011; Traba et al. 2017) by pooling the observations

196   from each pair, randomizing the species' labels 999 times while keeping the number of species

197   constant for each group and calculating each time the pair-wise dissimilarity value between the

198   simulated trait probability density. Raw p-values were calculated for each comparison by ranking

199   the empirical dissimilarity value among the simulated ones. The final p-values were computed by

200   applying the Bonferroni correction (Legendre & Legendre 2012). To assess the overall

201   functional variation (among major habitat types, climatic groups and biogeographic realms)

202   while excluding potentially redundant information among the six traits, we also calculated multi-

203   trait probability density using the first two PCA axes that incorporated 66 % of the total

204   variability (see Results and Discussion), and repeated the same analyses described above for the

205   single traits.

206   Functional patterns of communities

207   To analyze the trait patterns across plant communities, we calculated the multi-trait

208   dissimilarities between all vegetation plots as described above, controlling for the relative cover

209   of the species within each plot. The pair-wise dissimilarities were visualized using non-metric

210   multidimensional scaling (NMDS), which allowed comparison of the distribution of plots

211   belonging to different major habitat types, climatic groups and biogeographic realms. The

212   relationship between community dissimilarities and the original traits was assessed by fitting the

213   community weighted means of each trait to the ordination scores with the "envfit" function of

214   the "vegan" package in R (Oksanen et al. 2019). Significant differences among plots belonging

215   to different major habitat types, climatic groups and biogeographic realms were tested using

216   PERMANOVA (Anderson 2001), implemented by the "adonis" function of the R package

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217 "vegan", using 999 permutations. Pair-wise tests were performed with the "pairwise.adonis"

218 function of the "pairwiseAdonis" package in R (Martinez Arbizu 2020), applying a Bonferroni

219 correction to the p-values. To assist interpretation of the pair-wise PERMANOVA results, we

220 tested the multivariate homogeneity of group variances with the pair-wise PERMDISP test

221 (Anderson 2006) using the "permutest.betadisper" function of the "vegan" package in R with

222 999 permutations.

223 <u>Modeling community dissimilarity</u>

224 To quantify the relative contribution of climate and evolutionary history in determining

225 functional variation among communities, we modeled plot-level functional dissimilarity as a

226 function of environmental and phylogenetic dissimilarity while controlling for geographic

227 distance. First, we selected the set of species for which both trait and phylogenetic data were

228 available (n = 1,674) and further subset the vegetation plots by keeping those with at least 50 %

229 cumulative cover of these species. Thus, we obtained a subset of 5,047 plots and calculated the

230 multi-trait functional dissimilarities between all possible pairs of plots as described above. Then,

231 we built a set of climatic variables known to affect the functionality of vegetation in the alpine

232 belt (Körner 2003; Moser et al. 2005; Nagy & Grabherr 2009) using data from CHELSA at 1 km

233 spatial resolution (Karger et al. 2017). We included the mean temperature, precipitation, growing

234 degree days and mean potential evapotranspiration of the growing season, defined as months

235 with mean temperature above > 0.9°C (Paulsen & Körner 2014). Growing degree days (i.e. the

236 sum of monthly temperatures > 0.9°C multiplied by the total number of days) were calculated

237 using the "growingDegDays" function of the R package "envirem" (Title & Bemmels 2018).

238 Mean potential evapotranspiration of the growing season was estimated with the "hargreaves"

239 function of the R package "SPEI" (Beguería & Vicente-Serrano 2017), using maximum and

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240 minimum monthly values of temperature and monthly precipitation. The monthly values of

241 potential evapotranspiration obtained were then averaged across months with mean temperature

242 above 0.9°C. We standardized the four climatic variables and calculated the multivariate

243 Euclidean distance among each pair of plots as a measure of environmental dissimilarity. To

244 account for the evolutionary history of plant species in different communities, we also calculated

245 the pair-wise phylogenetic dissimilarity between plots (Ives & Helmus 2010) with the "pcd"

246 function of the R package "picante" (Kembel et al. 2010). To account for the spatial aggregation

247 of plots and unmeasured regional effects on the estimated functional dissimilarity, we calculated

248 the pair-wise geographical distances between plots. Finally, we modeled functional community

249 dissimilarity against these three distanced-based predictors using multiple regression on distance

250 matrices (MRM) with the "lm" function. Despite our measure of functional dissimilarity is

251 constrained between 0 and 1, our dataset mainly encompassed intermediate levels of functional

252 turnover (Figure S1), allowing us to treat it as approximately linear (Ferrier et al. 2007).

253 Furthermore, a linear modelling approach allowed us to calculate the adjusted R^2 of all the sub-

254 models necessary to perform variance partitioning (Borcard et al. 1992; Swenson 2014).

255

Results

257 The PCA of the six trait values at the species level revealed that 66 % of the total trait variation

258 is expressed by the first two PCA axes. The first axis (PC1; 35 % of variation) was mainly

259 related to variations in LDMC, leaf N and SLA, while the second axis (PC2; 31 % of variation)

260 was linked to leaf area, plant height and seed mass (Figure 2, Table S1).

261   When looking at the habitat types dominating the regions in which alpine vegetation is

262 embedded, we observed negligible differences in trait probability density and low functional

263 dissimilarity among trait pools. The only exception was represented by alpine vegetation of

264 tropical and subtropical moist broadleaf forests, which exhibited slightly greater plant height

265 values compared to other groups (Figure 3; Table S2). Similarly, among climatic groups,

266 subtropical alpine areas exhibited greater plant height values compare to oceanic and continental

267 ones, with minor variation in the distribution of other traits (Figure 3; Table S3). As for

268 biogeographic realms, we observed considerable variability in trait probability density. The

269 alpine vegetation of Australasia and Neotropic presented lower SLA compared to that of other

270 biogeographic realms and similar values of plant height to the Afrotropic and Neotropic, which

271 are both greater than those of the Palearctic and Nearctic. As for leaf area and seed mass, the

272 Neotropics generally showed greater values compared to the Palearctic and Nearctic, which in

273 turn presented greater leaf N and lower LDMC than Australasia (Figure 3; Table S4). Multi-trait

274 patterns seemingly reflected those observed at the single trait level. Among major habitat types

275 and climatic groups, multi-trait functional dissimilarities were not significant or very modest

276 (Table 1). Conversely, among biogeographic realms, Palearctic and Nearctic were similar to one

277 another and differentiated from Neotropic and Australasia, with the Afrotropic pool lying in

278 between.

279   The NMDS of multi-trait dissimilarities among alpine plant communities revealed no

280 distinct patterns between different major habitat types or climatic groups (Figure 4). Indeed, at

281 the community level, major habitat types explained 11 % of the total variance in multi-trait

282 dissimilarities ($R^2 = 0.11$, p = 0.001) and pair-wise comparisons identified only small differences

283 among major habitat types, which are probably due to differences in multivariate dispersions

284 (Table S5). Similarly, climatic groups explained 5 % of the variance ($R^2 = 0.05$, p = 0.001), with

285 negligible differences emerging from pair-wise comparisons (Table S6). On the other hand, the

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286 NMDS of functional dissimilarities among alpine plant communities showed distinct patterns

287 among biogeographic realms (Figure 4), with Palearctic, Nearctic and Afrotropic communities

288 occupying large part of the community variation space, whereas Neotropic assemblages occupied

289 the portion characterized by greater plant height leaf area and seed mass. Australasian plots

290 represented a separate entity, mainly defined by larger values of LDMC and smaller SLA and

291 leaf N. Biogeographic realms explained 19 % of the total variance ($R^2 = 0.19$, $p = 0.001$), mainly

292 ascribable to the Australasian communities (Table S7).

293 Finally, the MRM model fit on a subset of plots (with available phylogenetic

294 information) explained 16.6 % of the variance in community dissimilarities. Environmental and

295 phylogenetic dissimilarities both explained 6.2 % of the variance individually, while 4 % was

296 shared between the two. Geographic distance exhibited a marginal effect, explaining only 0.3 %

297 of the variance (Figure 5).

298

299 **Discussion**

300 <u>Functional trait spectrum of alpine plants</u>

301 Alpine plant species are strongly differentiated based on their resource-use strategies and,

302 secondarily, plant height. We selected six traits relevant to resources use, growth and

303 reproduction, and used PCA to describe the trait spectrum of 1,934 vascular plant species in

304 global alpine ecosystems. The first axis of trait variation (PC1) reflected different strategies in

305 terms of returns on investments of nutrients and dry mass in leaves, i.e. the leaf economics

306 spectrum (Wright et al. 2004). The second axis (PC2) represented the stem economics spectrum

307 (Baraloto et al. 2010) and, to some extent, the colonization versus exploitation continuum

308 defined by seed mass (Díaz et al. 2016). These results are in line with previous analyses of alpine

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309   and tundra vascular plants (Dolezal et al. 2016; Thomas et al. 2019) and are consistent with the

310   global spectrum of plant form and function (Díaz et al. 2016). The resource-use strategy reflects

311   the absence of trees and tall shrubs in alpine vegetation, and the general abundance of prostrate

312   species which are mainly differentiated by local conditions. Indeed, the small size allows alpine

313   plants to respond more closely to the buffered microclimate conditions near the ground (Geiger

314   et al. 2003), thus being decoupled from the fluctuations of the macroenvironment (Körner et al.

315   1989; Körner 2003). Along the first axis of functional trait variation, leaf construction costs of

316   alpine plants tend to vary depending on local temperature, frost stress and exposure to light

317   (Körner et al. 1989), hence the greater variation of related traits (Stanisci et al. 2020). In contrast,

318   the second axis showed a more complex variation of traits, with a predominant role of plant

319   height and seed mass. Although such variation can be also related to environmental constrains,

320   these traits are expected to vary little within regional alpine species pools (Ladouceur et al.

321   2019), thus they may be also linked to macroecological differences across regional floras.

322   <u>Variation of alpine trait pools</u>

323   Trait pools of alpine plants were largely independent of habitat types dominating at the regional

324   level, suggesting that alpine vegetation is functionally similar across region, regardless of the

325   different floras in which they are embedded. This reflects the overall convergence of growth

326   forms in alpine vegetation (Körner 2003; Aubert et al. 2014; Körner 2019), resulting from the

327   adaptative response to similar ecological conditions (Givnish 2010; Horandl & Emadzade 2011;

328   Hughes & Atchison 2015; Givnish 2016). Moreover, this finding contrasts with the general view

329   of alpine areas as elevational orobiomes that should not be considered independently of the

330   zonobiomes they originate from (Walter & Box 1976), and supports the distinction of alpine

331   ecosystems from other terrestrial biomes (Testolin et al. 2020). Trait pools were also convergent

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332   with respect to climatic groups, indicating that large-scale macroclimatic patterns above the

333   treeline have moderate effects on functional features of alpine vegetation, which is consistent

334   with the similar patterns of primary productivity found in global alpine areas (Testolin et al.

335   2020).

336   We found a stronger degree of trait pool divergence across biogeographic realms. This

337   could be expected as functional differences might emerge in otherwise structurally similar plant

338   groups when these are compared across evolutionarily distinct areas (Alvarado-Cárdenas et al.

339   2013). Specifically, we observed a distinction between the trait pools of the Holarctic realm, as

340   opposed to the Neotropic and Australasia. The trait pool in the Afrotropic realm lied in between.

341   This pattern likely reflects different evolutionary histories and adaptations of alpine vegetation in

342   the Northern and Southern Hemispheres (Billings 1974). Indeed, much of the ancestral alpine

343   vascular flora originated during the Miocene (23-5 Ma) from Arcto-Tertiary and Antarcto-

344   Tertiary floras through upward migration and evolution of lowland taxa (Billings 1974). As a

345   consequence, Holarctic alpine vegetation shares many species with the Arctic (Billings 1974)

346   and has major links with Afrotropic alpine species (Linder 2014; Carbutt & Edwards 2015). In

347   contrast, a large part of Neotropic alpine plants originated locally through migration and

348   adaptation of Neotropical lowland species (Sklenář et al. 2011), some of which contributed also

349   to Afrotropic lineages (Linder 2014). Finally, the functional similarity of Neotropics and

350   Australasia probably derived from both migration (Raven & Axelrod 1972) and convergent

351   evolution during the Pliocene (5 Ma) and the Pleistocene (2.5 Ma), when further mountain uplift

352   and repeated glaciations induced the diversification of the respective alpine floras (McGlone et

353   al. 2001; Winkworth et al. 2005; Sklenář et al. 2011; Madriñán et al. 2013).

354   Functional patterns of alpine communities

355 At the community level, the NMDS showed the same functional continua as the one detected by

356 the PCA at the species level, revealing the analogy between present-day community assembly

357 and individual species' evolutionary histories (Bruelheide et al. 2018). We did not observe strong

358 differentiation between plots belonging to different major habitat types or climatic groups, while

359 biogeographic realms exhibited greater discriminatory power as they did for trait pools. We

360 found that Australasian communities form a self-standing group characterized by conservative

361 leaves with high construction costs. This is in agreement with the scarcity of cushion plants and

362 the relative abundance of sclerophyllous dwarf shrubs in the Australasian alpine flora, when

363 compared to other global alpine regions (Ballantyne & Pickering 2015).

364   The functional distinctness of Australasian alpine communities from Holarctic and Tropical

365 ones also reflects the differences in trait pools between the two Hemispheres and the long time

366 isolation (45 – 49 Ma) of Australasia from other biogeographic realms of Gondwanan origin

367 (Raven & Axelrod 1972). Holarctic and Tropical communities, however, were not as

368 functionally distinct as their trait pools, indicating that other processes apart from evolutionary

369 history are involved at the local scale. Indeed, although our model highlighted the presence of a

370 phylogenetic signal on functional dissimilarity, environmental dissimilarity explained an equal

371 amount of variance (Figure 5). This is coherent with the process of niche conservatism in highly

372 heterogeneous areas where the retention of the ancestral niche characteristics could lead to both

373 conservatism and divergence of the realized niche (i.e. the functional characteristics) (Pyron et

374 al. 2015). Nevertheless, the negligible effect of geographic distance and the large amount of

375 unexplained variance point to fine-scale environmental factors (e.g. microclimate), disturbance

376 and biotic interactions as the main drivers of community trait composition in alpine ecosystems

377 (Grime 2006; Dolezal et al. 2019). In other words, the combination of phylogenetic constrains

378 and within-region climatic variation seem to be major drivers of the functional trait variation

379 observed in alpine plant communities.

380 <u>Basic assumptions</u>

381 Even if we used the largest dataset of alpine vegetation ever collected, our study does not come

382 without uncertainties. When comparing functional dissimilarities across geographical units and

383 spatial scales, for instance, we presumed that the species for which trait data were available were

384 also representative of the dominant vegetation in our study areas. For several tropical species,

385 however, such data were not available, and we had to remove a large number of plots in Africa

386 and South America. Although we recognize that this could have led to the exclusion of peculiar

387 combinations of traits and that even rare species can drive trait divergence among communities

388 at the regional scale (Richardson et al. 2012), this is probably less relevant at the global level.

389 We also note that our dataset encompassed vegetation plots of very different sizes (0.25 - 400

390 m^2). As species richness generally increases with area (Lomolino 2000), larger plots might be

391 functionally richer than smaller ones (Smith et al. 2013; Wang et al. 2013), biasing the

392 comparison among plots of different sizes. However, when accounting for specie abundances –

393 or, in our case, cover – the relationship between functional diversity and plot size tends to

394 weaken or disappear as a consequence of species dominance and functional redundancy

395 (Karadimou et al. 2016). Therefore, as the trait probability density framework accounts for the

396 distribution of trait values in plant communities, plot size likely had a minor effect in the

397 estimation of functional dissimilarity among alpine communities. Although we collected most of

398 the vegetation plot data currently available on alpine vegetation, much effort will be needed in

399 the future to collect data with a consistent sampling protocol, including functional traits and a

400 proper representativity of species and vegetation types from disparate global regions.

Conclusions

This study demonstrates how the functional adaptations of alpine plants relate to the global

variation of plant form and function. Specifically, we highlighted how the trait pools of current

alpine vegetation are scarcely related to lowland floras and macroclimatic patterns, while they

still carry the evolutionary signature inherited by their Laurasian and Gondwanan ancestors. In

combination with climatic factors, this evolutionary mark still determines variation in functional

traits at the community level. Yet, we admit that other regional factors not accounted for in this

study (e.g. soil properties, topoclimatic gradients) are likely influencing functional traits of

alpine vegetation at large spatial scales. In general, we found alpine vegetation to be globally

comparable in terms of functional diversity and related macroecological drivers. This finding

might contribute to the identification of alpine biomes in the context of global vegetation

zonation, with a special attention to the habitats above the treeline. In this respect, future work

should be oriented toward the inclusion of trait data from tropical and subtropical species

currently underrepresented in global datasets, as well as fine-scale environmental characteristics.

426 **Author contributions:** B. J.-A., L. M., R. T. and C. P. C. conceived the study and developed the

427 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.

428 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.

429 facilitated access to the sPlot database. R.T. analyzed the data and produced the outputs. R.T and

430 B.J.-A wrote the first manuscript draft. B.J.-A supervised the study. All the authors discussed the

431 methodology and commented on various versions of the manuscript.

432 **Data availability:** The vegetation plot data is stored and managed by sPlot and the

433 corresponding author and is available upon request. The R code used to carry out the analyses is

434 available at: https://figshare.com/s/c2c0ad45f6f1cd3d1689.

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644

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	$\mathbf{0.27^{**}}$
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	$\mathbf{0.24^{**}}$
Temperate broadleaf and mixed forests - Tropical and subtropical moist broadleaf forests	$\mathbf{0.34^{*}}$
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	$\mathbf{0.19^{**}}$
Continental - Subtropical	$\mathbf{0.22^{*}}$
Oceanic - Subtropical	$\mathbf{0.31^{**}}$
Biogeographic realms	
Afrotropic - Australasia	0.40^{ns}
Afrotropic - Nearctic	0.26^{ns}
Afrotropic - Neotropic	0.29^{ns}
Afrotropic - Palearctic	0.23^{ns}
Australasia - Nearctic	$\mathbf{0.47^{**}}$
Australasia - Neotropic	0.36^{ns}
Australasia - Palearctic	$\mathbf{0.45^{**}}$
Nearctic - Neotropic	$\mathbf{0.43^{**}}$
Nearctic - Palearctic	0.13^{ns}
Neotropic - Palearctic	$\mathbf{0.41^{**}}$

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650 **Figures**
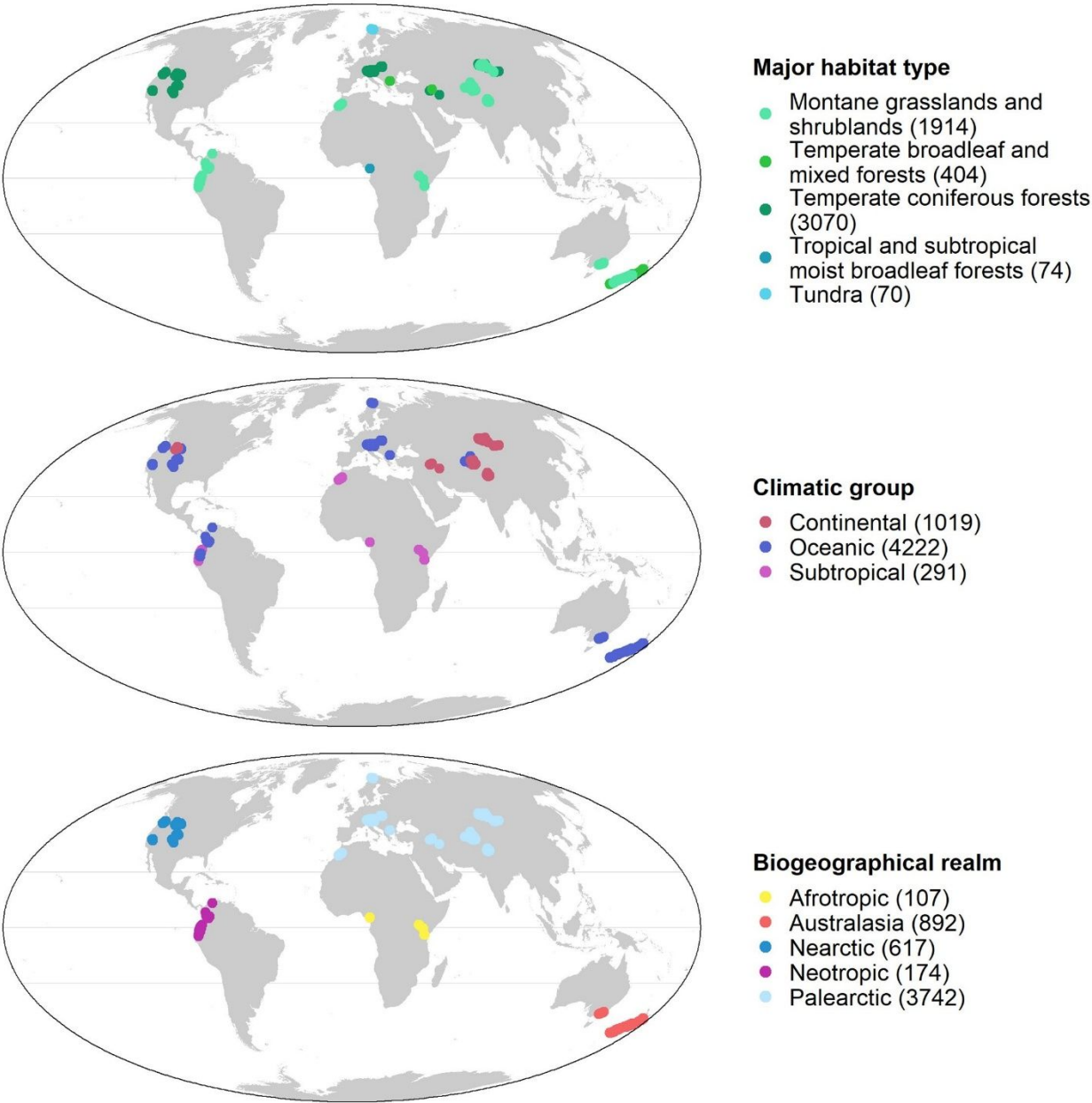
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652 **Figure 1.** Spatial distribution of 5,532 alpine vegetation plots across major habitat types, climatic
653 groups and biogeographic realms. The numbers of plots in each group are reported in brackets.

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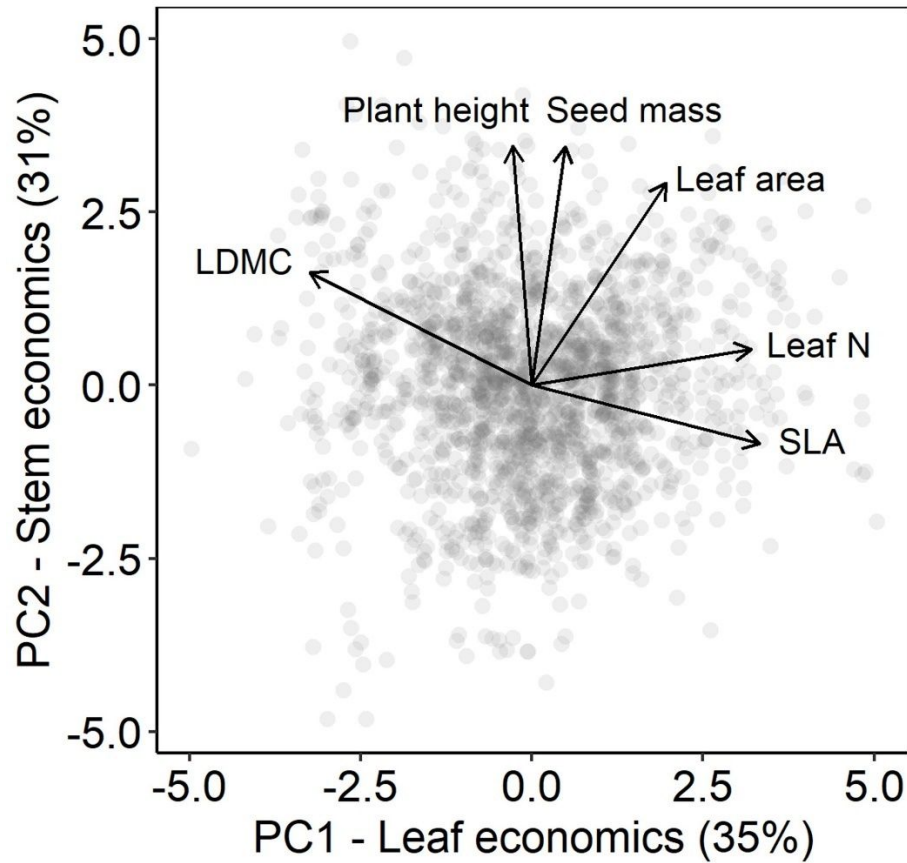
Figure 2. Functional trait space of 1934 alpine vascular plant species along the first two principal components of six functional traits. SLA = Specific leaf area; LDMC = Leaf dry matter content.

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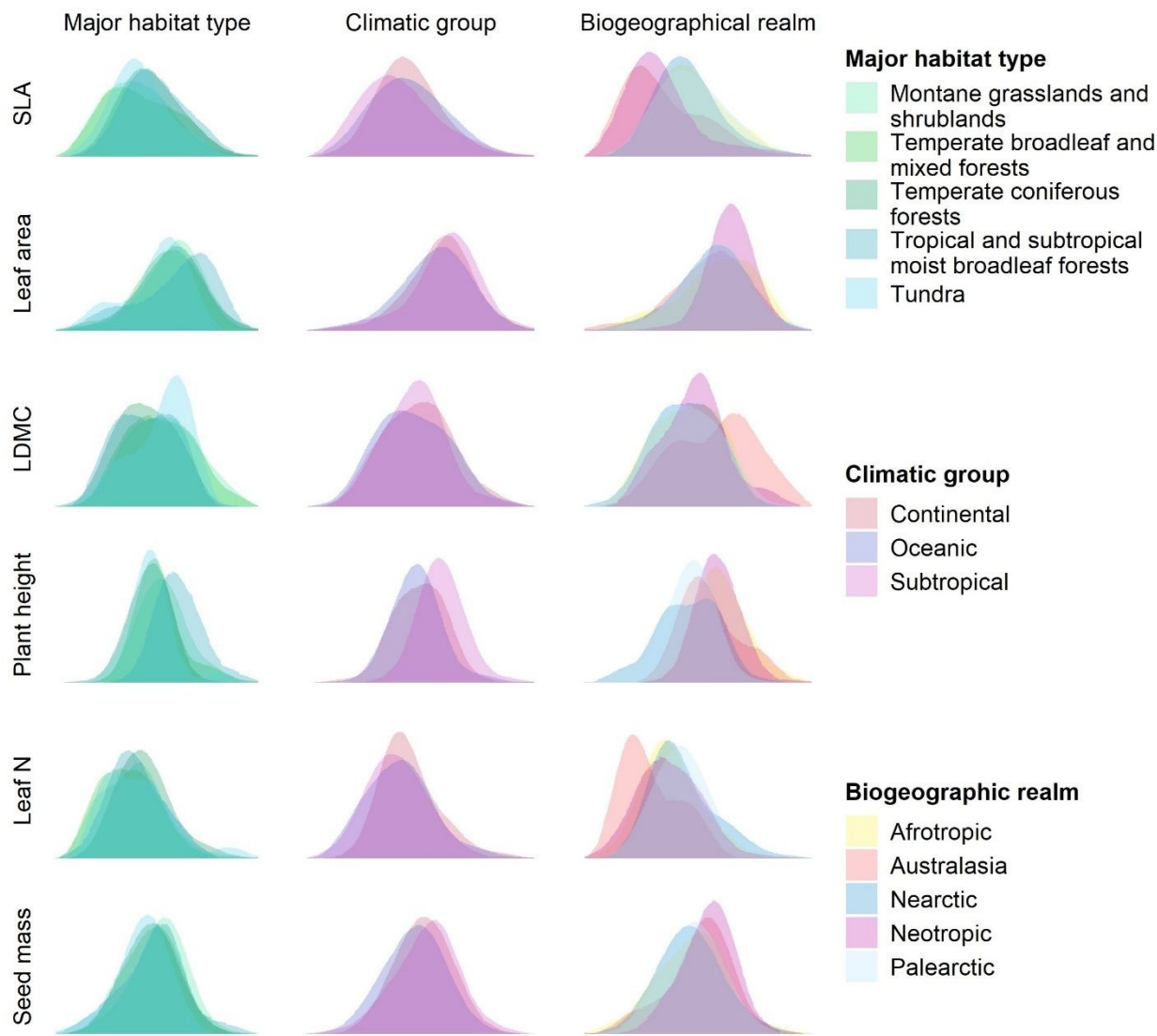
Figure 3. Kernel density plots of trait pools estimated using trait probability density for six individual plant functional traits among habitat types, climatic groups and biogeographic realms. SLA = Specific leaf area; LDMC = Leaf dry matter content.

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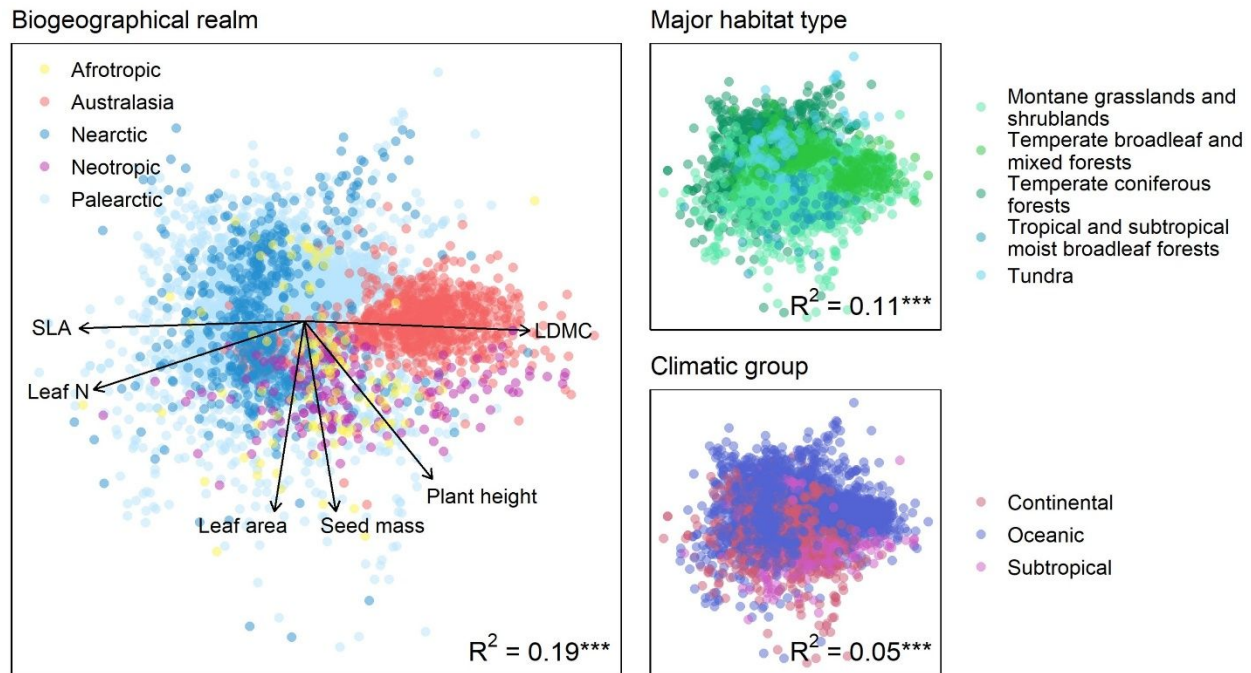
Figure 4. Non-metric multidimensional scaling (NMDS) of alpine vegetation plots based on
multi-trait functional dissimilarity, calculated using the first two principal components of six
plant functional traits. The points represent the single vegetation plots. The colors represent
major habitat types, 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 ≥ 0.05.

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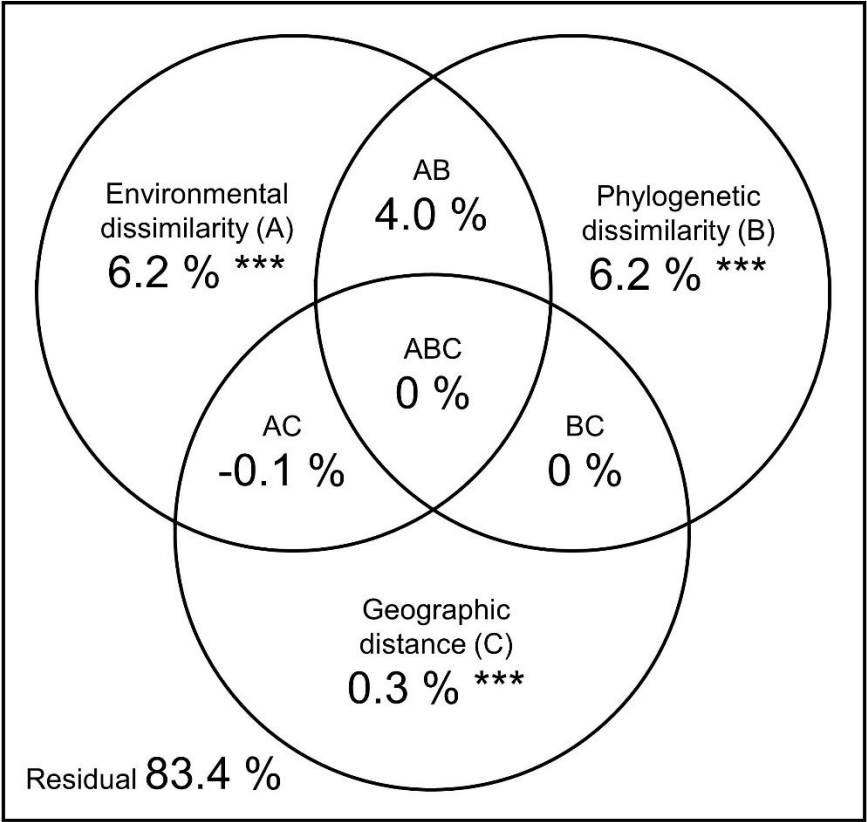
Figure 5. Venn diagram of multi-trait functional dissimilarity of alpine vegetation communities displaying variance partitioning among environmental dissimilarity (A), phylogenetic dissimilarity (B), and geographic distance (C) predictor matrices. Significance codes: ***: $p<0.001$; **: $p< 0.01$; *: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

31

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 ≥ 0.05.

	PERMANOVA		PERMDISP
Major habitat types	**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. 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: $p \geq 0.05$.

	PERMANOVA		PERMDISP
Climatic groups	**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

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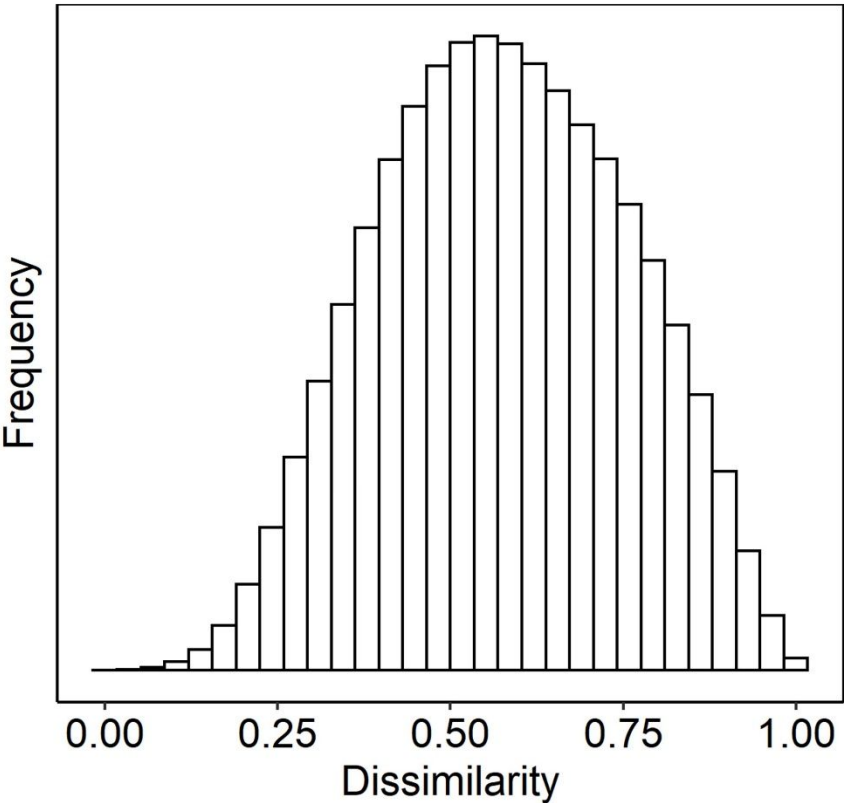51
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Figure S1. Distribution of multi-trait pair-wise functional dissimilarity values among alpine vegetation plots.