

# 1 **Increasing functional and phylogenetic richness of mountaintop flora, despite** 2 **stable taxonomic richness**

3 **Short title:** Multifaceted diversity trends in mountain flora

## 4 **Abstract**

5 **Questions:** Analysing how multiple facets of biodiversity vary across space and time can help to predict  
6 the vulnerability of mountaintop flora to future environmental change. Here we addressed the  
7 following questions: (a) Are elevational patterns of mountaintop plant diversity consistent across  
8 taxonomy, function and phylogeny? (b) How has the taxonomic, functional and phylogenetic diversity  
9 of mountaintop plant communities changed over the past two decades? (c) Is the magnitude of these  
10 temporal trends dependent on elevation?

11 **Location:** Dovrefjell, central Norway

12 **Methods:** The floristic composition of four mountaintops, spread across an elevational gradient from  
13 the tree line to the uppermost margins of vascular plant life, was surveyed every seven years between  
14 2001-2022. Six metrics of taxonomic, functional and phylogenetic richness and differentiation were  
15 calculated for each mountaintop and survey. With these data, we assessed how richness and  
16 differentiation metrics varied over space (across the elevational gradient) and over time (between  
17 surveys).

18 **Results:** All diversity metrics decreased towards higher elevations, except phylogenetic differentiation  
19 which increased significantly by 7% per 100 m elevational gain. Taxonomic richness remained virtually  
20 stable between 2001-2022, while phylogenetic richness increased by 7.5% per decade. Functional  
21 richness also increased, but almost exclusively on the lowest mountaintop by 17% per decade. No  
22 significant temporal trends in taxonomic, functional and phylogenetic differentiation were detected.

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23 Conclusions: Our findings underpin rearrangements in the functional and phylogenetic structure of  
24 mountain plant communities over the past two decades that cannot be predicted from trends in  
25 taxonomic richness alone. This highlights the necessity to look beyond species richness and consider  
26 multiple facets of biodiversity when studying environmental change impacts on mountain biodiversity  
27 and ecosystem functioning.

## 28 **Keywords**

29 Alpine ecosystems, elevational gradient, climate change, community assembly, mountain flora,  
30 multifaceted approach, plant diversity

## 31 **Introduction**

32 Mountain ecosystems harbour a rich and diverse flora, including many endemic and endangered  
33 species (Körner 2004). Mountain plants are generally well adapted to the harsh environmental  
34 conditions of these ecosystems through their small stature and high foliage density allowing them to  
35 engineer a microclimate that differs strongly from the surrounding air temperature (Körner and  
36 Hiltbrunner 2021). Increasing temperatures may create opportunities for warm-adapted species from  
37 lowlands to colonize higher elevations and locally change species compositions (Lenoir et al. 2008,  
38 Pauli et al. 2012, Sandvik and Odland 2013, Lenoir and Svenning 2015, Steinbauer et al. 2018). As these  
39 colonizers build up sufficiently large populations over time, local species losses will likely follow owing  
40 to the competitive replacement of stress-tolerant, cold-adapted mountain plant species by more  
41 vigorous generalists (Alexander et al. 2015). However, many mountain plants are designed to live long  
42 and persist through their clonal growth, belowground storage organs and appropriate seasonal  
43 development (Körner and Hiltbrunner 2021). Besides, they can seek refuge in the myriad of  
44 microhabitats that are present in mountain environments with high topographic heterogeneity  
45 (Opedal et al. 2015, Winkler et al. 2016, Graae et al. 2018, Kulonen et al. 2018).

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46 As a result, native mountain plants are currently still able to coexist with the upward-mowing lowland  
47 species, and many summits across the globe are gaining, rather than losing, plant species over time  
48 (Wipf et al. 2013, Carilla et al. 2018, Steinbauer et al. 2018, Cuesta et al. 2023). Among the newly  
49 arriving species, an overrepresentation of warm-adapted (or, thermophilic) species has been found,  
50 thereby implying gradual thermophilization of mountain plant communities (Gottfried et al. 2012).  
51 Despite the widespread evidence of such trends, several local studies also report stable or decreasing  
52 plant species richness on mountaintops or an absence of thermophilization (see e.g. Vanneste et al.  
53 2017, Hagenberg et al. 2022). Moreover, with time this increase in plant richness is likely a transient  
54 phenomenon that temporarily masks the accumulation of a so-called extinction debt (Dullinger et al.  
55 2012a). In particular, many subnival and nival species are expected to go locally extinct in the decades  
56 to come due to stronger competition with upward moving lowland and alpine species or because they  
57 can no longer expand their habitat ranges and are literally 'pushed off' mountaintops (Geppert et al.  
58 2023). Long-term monitoring programs are thus a powerful method for assessing the vulnerability of  
59 mountain plant communities under future environmental change.

60 Previous studies on mountain plant diversity and its response to climate change predominantly rely  
61 on the richness or abundance of species, i.e. taxonomic diversity (e.g. Klanderud et al. 2003, Pauli et  
62 al. 2012, Steinbauer et al. 2018). Other attributes of biodiversity including the variability in ecological  
63 attributes (functional diversity) and variation in evolutionary history among species (phylogenetic  
64 diversity) are complementary in describing patterns of community assembly and the ecological  
65 consequences of environmental change, but they have been largely ignored (Cadotte et al. 2013).  
66 Within a community, functional diversity encompasses variation in growth form and life-history  
67 strategy among species, and is quantified by the interspecific difference in functional traits (Mason et  
68 al. 2005). Functional traits affect plant fitness and performance via growth, reproduction and survival,  
69 and are thus a key factor determining plant-environment interactions as well as their effect on various  
70 ecosystem properties (Naeem et al. 2012). Communities with higher functional diversity are typically

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71 thought to have higher levels of ecosystem functioning (Lefcheck and Duffy 2015). Moreover, the loss  
72 of species with unique functional traits may have larger impacts on ecosystem function and stability  
73 compared to the disappearance of species with common traits (Mouillot et al. 2014). Phylogenetic  
74 diversity, on the other hand, relates to the difference in evolutionary history and genealogical  
75 relationships among a set of taxa (Faith 1992), and is often measured by the sum of branch lengths in  
76 a phylogenetic tree. Higher phylogenetic diversity within a community is associated with higher levels  
77 of genetic variation, thus promoting the community-level capacity to respond to rapid environmental  
78 change (Cavender-Bares et al. 2009, Faith 2015).

79 Although often overlooked, consideration of taxonomic, functional and phylogenetic diversity metrics  
80 in tandem can provide new insights into the rules of community assembly and species coexistence  
81 (Webb et al. 2002, Vamosi et al. 2008, Cavender-Bares et al. 2009, Cadotte et al. 2013). More  
82 specifically, closely related or functionally similar species are more likely to share a niche and compete  
83 for the same resources than distantly related or functionally divergent species. In this scenario, the  
84 likelihood of stable coexistence is thus higher for species with lower trait similarity or phylogenetic  
85 relatedness (leading to community “overdispersion”; Webb et al. 2002). This process of ‘limiting  
86 similarity’ is an important mechanism governing community assembly at fine spatial scales (Cavender-  
87 Bares et al. 2009). At coarser scales, however, environmental filtering organizes communities through  
88 directional selection of species adapted to specific environmental conditions based on similar life-  
89 history strategies or evolutionary histories (leading to community “clustering”; Cornwell et al. 2009,  
90 Laliberte et al. 2014). Alternatively, species-neutral assembly processes such as colonization and local  
91 extirpation could also structure communities in a more stochastic manner (Hubbell 2001).

92 Mountains are characterized by steep environmental gradients over increasing elevation, and these  
93 gradients jointly drive community assembly (Körner et al. 2004, Graham et al. 2014). The mechanisms  
94 that organize communities along elevational gradients are, however, complex and vary depending on  
95 the role of biotic interactions, abiotic filtering and/or dispersal limitations. At low elevations where

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96 abiotic stress is low, interspecific competition is more likely to dominate community assembly,  
97 whereas at higher elevations facilitation (e.g. via nurse plants) and abiotic filtering through  
98 environmental stress will prevail (Callaway et al. 2002), resulting in decreasing species richness  
99 towards higher elevations due to strong environmental filtering associated with lower temperatures  
100 and decreasing resource availability (Bruun et al. 2006). Along with species interactions and  
101 environmental filtering, dispersal limitations of mountain plants also affect community assembly and  
102 local diversity patterns simply because species lack traits that allow them to spread to, germinate and  
103 establish in the harsh climatic conditions and rugged alpine terrain of higher elevations (Klanderud  
104 and Totland 2007). Together these assembly mechanisms may also shape the functional and  
105 phylogenetic structure causing a shift from overdispersed communities at low elevations towards  
106 clustered communities at high elevations, but the generality of such patterns is still under debate (see  
107 e.g. Graham et al. 2014, Montañó-Centellas et al. 2020).

108 Besides, environmental changes over time may alter the relative importance of assembly processes,  
109 and in turn modify elevational patterns in mountain plant diversity. Taxonomic, functional and  
110 phylogenetic diversity metrics can respond differently to environmental changes across space and  
111 time, thereby providing a more mechanistic view on a communities' biodiversity and potential  
112 trajectory of change (Giehl and Jarenkow 2015, Belcik et al. 2020, De Pauw et al. 2021). Indeed, over  
113 time mismatches in the different facets of biodiversity can be expected because they are not likely to  
114 change at a similar rate under environmental stress or disturbance (see Swenson 2011 for a review),  
115 eventually leading to the emergence of functionally or phylogenetically different communities that  
116 cannot be predicted from trends in species richness alone (Monnet et al. 2014, Jarzyna and Jetz 2017).  
117 In fact, the climate-driven upward range expansions of species are presumed to coincide with the  
118 introduction of novel trait expressions for resource use (i.e. increasing functional diversity; Schuchardt  
119 et al. 2023) and the arrival of lowland lineages that temporarily coexist with cold-adapted alpine  
120 specialists already present on mountaintops (i.e. increasing phylogenetic diversity; Harison 2020).

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121 However, in the longer run this state of coexistence is not likely to last, and strong turnover across all  
122 facets of mountaintop biodiversity can be expected once lowland colonizers locally increase their  
123 abundances and gradually outcompete many cold-adapted native species (Nomoto and Alexander  
124 2021, Steinbauer et al. 2022).

125 A multifaceted approach combining different dimensions of biodiversity will help to shed light on the  
126 processes governing community structuring of high-mountain floras as well as their response to  
127 environmental change. However, such studies are still rare (e.g. Tiusanen et al. 2018, Bashirzadeh et  
128 al. 2022), and virtually missing for long temporal scales (across multiple decades). Here we assessed  
129 for the first time how different metrics of taxonomic, functional and phylogenetic diversity of  
130 mountaintop plant communities changed over a period of more than 20 years. We capitalized on  
131 resurvey data of vegetation composition spread across an elevational gradient from the tree line  
132 ecotone to the uppermost limit of vascular plant life in Dovrefjell, Norway. We specifically aimed to  
133 assess whether:

- 134 a) Mountaintop plant communities become increasingly species-poor towards higher elevations,  
135 leading to functional and phylogenetic homogenization. We expect that the filtering effect of  
136 elevation on taxonomic diversity is mirrored in their functional and phylogenetic structure.
- 137 b) Plant diversity on mountaintops has changed over time, not only in terms of species richness  
138 but also across functional and phylogenetic diversity facets. We expect that the immigration  
139 of lowland species has locally increased species diversity on the mountaintops, potentially  
140 filling up previously unoccupied trait space and bringing in new evolutionary lineages.
- 141 c) The magnitude of these temporal changes in mountaintop plant diversity depends on  
142 elevation. We expect the largest effects to be present at low elevations which are strongly  
143 affected by the colonization of novel lowland species, causing significant shifts in the different  
144 facets of biodiversity.

## 145 **Materials and methods**

### 146 **Study area**

147 This study was performed on four summits located in the Dovrefjell-Sunndalsfjella National Park,  
148 Central Norway (Figure 1). The surveys are part of the GLORIA network (Global Observational Research  
149 Initiative in Alpine Environments; [www.gloria.ac.at](http://www.gloria.ac.at)) and are situated along an elevational gradient  
150 from alpine grasslands near the tree line to the uppermost margins of vascular plant distribution (see  
151 Vanneste et al. 2017 and Table S1). The vegetation on the summits ranges from lichen, grass and heath  
152 communities to snow-bed vegetation and barren rock. The tree line in the area is currently positioned  
153 around 1000-1050 m a.s.l. The climate is continental with a mean annual temperature of 1.03 °C and  
154 mean annual precipitation of 442 mm between 2001-2022, and the prevailing wind direction is south-  
155 southwest (measured in Fokstugu weather station at 973 m a.s.l. and 23 km southwest of the study  
156 area). Between 1923-2022, mean annual temperatures at Fokstugu have increased significantly at an  
157 average rate of 0.175 °C per decade, while annual precipitation remained stable despite high  
158 interannual variation (ranging between 288-601 mm) (data extracted from <https://seklima.met.no>;  
159 Figure S1).

### 160 **Vegetation surveys**

161 In all surveys, vascular plant species were recorded during the growing season of 2001, 2008, 2015  
162 and 2022 (see Table S2 for a complete species list). First, the floristic composition of each mountaintop  
163 was characterized by dividing the summit area into eight summit sections: two (an upper and a lower)  
164 sections for each aspect (north, east, south, west). The upper sections are positioned between the  
165 highest summit point (HSP) and the 5-m contour line, while the lower sections were situated between  
166 the 5-m and 10-m contour line. The section corners were carefully relocated during every survey using  
167 GPS points, compass bearings, altimetry and photographic material. In these sections, only presence-  
168 absence of all vascular plant species was recorded. Second, more fine-scale surveys were carried out

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169 in 1 m × 1 m permanent plots, arranged in clusters of four quadrats on every aspect (sixteen plots in  
170 total per summit). In these plots, the percentage cover of all vascular plant species was recorded.  
171 Finally, soil temperatures were recorded at an hourly interval since 2001 on all summits, using  
172 miniature data loggers (TibiT StowAway TBI32 for 2001-2005 and GEO-Precision M-Log5 W for 2005-  
173 2022) installed at 10 cm below the soil surface in every quadrat cluster (see Figure 1 and Pauli et al.  
174 2015). The data collection was performed according to the GLORIA sampling protocol (Pauli et al.  
175 2015), which has been abundantly used to monitor spatial and temporal patterns of mountaintop  
176 plant diversity (see e.g. Pauli et al. 2012, Steinbauer et al. 2018, Galván-Cisneros et al. 2023).

### 177 **Trait data**

178 We selected three key functional traits based on the leaf-height-seed plant ecology strategy scheme:  
179 plant height, seed mass and specific leaf area (SLA) (Westoby et al. 1998). Plant height at maturity is  
180 related to a species' competitive ability and fecundity, while seed mass reflects the trade-off between  
181 dispersal ability and seedling survival (Diaz et al. 2016). Specific leaf area (SLA, leaf area per unit dry  
182 mass) informs on the trade-off between resource acquisition and conservation, and can thus be  
183 related to a plant's ability to respond to opportunities for rapid growth (Wright et al. 2004). Species-  
184 specific trait values were compiled by combining records from the TRY 3.0 database (Kattge et al.  
185 2020) with the Tundra Trait Team database (TTT; Björkman et al. 2018). Trait values were averaged at  
186 the species level, and assumed to be representative for mature and healthy plants grown under  
187 natural conditions within the species distribution range (see Diaz et al. 2022). Plant height, seed mass  
188 and SLA records were available for 94.4%, 87.6% and 86.5% of the species, respectively. Missing trait  
189 values were imputed following Debastiani et al. (2021). This method relies on a random forest  
190 algorithm (*missForest*; Stekhoven and Bühlmann 2012) and incorporates phylogenetic information by  
191 adding phylogenetic eigenvectors to the imputation process. This has shown to be a robust method  
192 for imputation of missing trait values (Penone et al. 2014, Johnson et al. 2021).

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### 193 **Phylogeny and phylogenetic signal**

194 A phylogenetic tree was constructed for all species recorded across the four summits, based on the  
195 megatree of 74,531 seed plant species (Smith and Brown 2018, Yin and Qian 2019) (Figure 1). The  
196 extraction of phylogenetic information was done using the *rtrees* package (Li et al. 2023). Sixteen  
197 species were missing from the megatree but they were grafted and added to the final phylogenetic  
198 tree as a polytomy at the basal node of the most recent common ancestor of the genus in the  
199 megatree. Using the phylogenetic tree, we checked for a phylogenetic signal in the three functional  
200 traits (i.e. whether related species also have more similar traits) with the *phylosig* function in the  
201 *phytools* package (Blomberg et al. 2003). The K-statistic was used to quantify the phylogenetic signal,  
202 with values of  $K > 1$  indicating a strong phylogenetic signal in the trait data (Table S2).

### 203 **Diversity metrics**

204 For each summit section and for every survey, six complementary metrics of alpha diversity were  
205 calculated: one richness-based and one differentiation-based metric derived from taxonomy, function  
206 and phylogeny. Richness metrics were based on counts (e.g. number of species, amount of trait space  
207 occupied by species and number of evolutionary lineages within a community), whereas  
208 differentiation measures represented the pairwise distances among species in a community providing  
209 additional insights in community-level biodiversity (Jurasinski et al. 2009, Roswell et al. 2021). We did  
210 not calculate evenness metrics as only presence-absence data were available for the summit sections.

211 **Taxonomic richness** was quantified by the number of species in each summit section with the *vegan*  
212 package in R (Oksanen et al. 2022). **Functional richness** is defined as the spread of trait values across  
213 species in a community (i.e. occupied trait space), and was computed for each summit section using  
214 the *FD* package (Laliberté and Legendre 2010). First, trait values were standardized to mean zero and  
215 unit variance. Next, a Euclidian distance matrix was calculated based on the pairwise functional  
216 differences among species. To avoid negative eigenvalues, a Cailliez correction was used (Cailliez

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217 1983). The species-species distance matrix was then subject to a principal coordinate analysis (PCoA),  
218 and the resulting PCoA axes were used to compute the functional richness of the plant communities  
219 in each summit section. Functional richness. **Phylogenetic richness** quantifies the number of  
220 evolutionary lineages within a community (Helmus et al. 2007), and was calculated per summit section  
221 using the *pez* package as well as the constructed phylogenetic tree (Pearse et al. 2015). This index is  
222 at its maximum (equal to species richness) when all species in a community are unrelated (that is, a  
223 star phylogeny), and approaches zero when species share large parts of their lineages in the  
224 phylogenetic tree.

225 **Taxonomic, functional and phylogenetic differentiation** were computed for the plant communities  
226 within each summit section using a modified version of Rao's quadratic entropy (RaoQ), hence offering  
227 a common mathematical framework for all three facets of biodiversity and allowing straightforward  
228 comparison between their trends (see Devictor et al. 2010, Monnet et al. 2014):

229 
$$Q = \sum_{i=1}^S \sum_{j=1}^S p_i p_j d_{ij}$$

230 Where  $d_{ij}$  is the distance between species  $i$  and species  $j$ ,  $p_i$  and  $p_j$  are their relative abundances (in  
231 our case, 0/1 for presence-absence data) and  $S$  is the total number of species in each summit section.  
232 For taxonomic differentiation,  $d_{ij} = 1$  was used between each pair of species, and the RaoQ index  
233 was thus reduced to the Gini-Simpson index (Ricotta et al. 2005). For functional and phylogenetic  
234 differentiation, the RaoQ index represented the mean pairwise functional and phylogenetic difference  
235 among species of the plant communities within each summit section, respectively. This index usually  
236 shows lower correlation with species richness (Botta-Dukat 2005, Miller et al. 2017). Means and  
237 standard errors of the six richness and differentiation metrics across the different elevations and  
238 sampling years are given in Figure S2-S4, while pairwise correlations among the diversity metrics are  
239 shown in Figure S5.

## 240 **Statistical analysis**

241 A multilevel modelling approach was adopted to test whether the six richness and differentiation  
242 metrics changed significantly across space (elevational gradient) and time (resurveys). We used  
243 (generalized) linear mixed-effect models (GLMM; Bolker et al. 2009) with the diversity metrics of the  
244 summit sections as response variable and 'elevation' and 'year of sampling' (and their two-way  
245 interaction) as fixed effects. Random intercept terms 'summit' and 'aspect' (nested within 'summit')  
246 were added to account for the hierarchical structure of the dataset and to account for potential spatial  
247 autocorrelation between sections of the same summit and aspect. The models were implemented  
248 using the following syntax:

249 
$$\text{Diversity metric} \sim \text{elevation} + \text{year} + \text{elevation} \times \text{year} + (1|\text{summit}/\text{aspect})$$

250 For taxonomic richness, a Poisson error distribution for count data was applied, while for all other  
251 diversity metrics a Gaussian error distribution was used. All models were built using the *lme4* package  
252 (Bates et al. 2023) with restricted maximum likelihood estimation (REML). Model assumptions were  
253 carefully checked using residual plots. Continuous predictors were scaled to mean zero and unit  
254 variance. P values were obtained from a likelihood-ratio ( $\chi^2$ ) test in the *car* package (Fox and Weisberg  
255 2023), while marginal and conditional  $R^2$  values were calculated with the *MuMin* package following  
256 Nakagawa and Schielzeth (2012). In parallel, we repeated this analysis but with the abundance data  
257 from the 1-m<sup>2</sup> permanent plots on the summits. This alternative analysis was conducted to test the  
258 robustness of our methods, and to assess the potential effect of inclusion of abundances on spatial  
259 and temporal trends in different diversity metrics (see Supplementary Information in Figure S3, Table  
260 S5-S6). All statistical analyses were performed in R 4.2.1 (R Core Team 2023), data manipulation was  
261 achieved with the *dplyr* package (Wickham et al. 2023) and graphs were constructed using the *ggplot2*  
262 package (Wickham 2016).

## 263 **Results**

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264 All diversity metrics in the summit sections decreased significantly towards higher elevations, except  
265 phylogenetic differentiation which increased significantly by approximately 7% per 100 m elevational  
266 gain ( $P < 0.001$ ) (Figure 2, Figure S6-S9, Table S4). For taxonomic richness and differentiation, no  
267 temporal trend between 2001-2022 was detected ( $P = 0.05$  and  $P = 0.417$ , respectively) (Figure 3,  
268 Table S4). From a functional trait perspective, however, richness of the summit sections did show a  
269 significant increase between 2001-2022 ( $P = 0.004$ ), while functional differentiation in the summit  
270 sections did not show any significant temporal pattern ( $P = 0.152$ ) (Figure 3, Table S4). When  
271 accounting for evolutionary history, a significant increase in phylogenetic richness was observed with  
272 an average rate of 7% per decade ( $P = 0.006$ ), while phylogenetic differentiation did not change over  
273 the sampling period ( $P = 0.564$ ) (Figure 3, Table S4). No significant interaction effects between  
274 'elevation' and 'year of sampling' were detected, except for functional richness which increased  
275 predominantly on the lowest summit by almost 17% per decade ( $P = 0.014$ ).

276 We found broadly similar trends for the richness and differentiation metrics when calculated from  
277 abundance data in the 1-m<sup>2</sup> permanent plots on the summits, but also some remarkable differences.  
278 The latter implies that beyond the changes in species identity, changes in species relative abundances  
279 could also drive the observed spatial and temporal trends in the richness and differentiation measures.  
280 However, these plots were much smaller compared to the summit sections and several plots  
281 (especially at higher elevations) did not contain any species. Therefore, we report these results in the  
282 Supplementary Information only (see Table S5).

## 283 Discussion

284 The simultaneous consideration of taxonomic, functional and phylogenetic diversity metrics can  
285 improve our understanding of how plant communities assemble and respond to environmental  
286 changes across space and time. In this observational study, we show that environmental filtering is  
287 the main driver of mountaintop plant diversity across an elevational gradient, causing a significant

288 decline in almost all diversity metrics towards higher elevations. The only exception, however, was  
289 phylogenetic differentiation of the plant communities which increased with elevation – a pattern that  
290 was likely driven by complex evolutionary processes or a shift in interspecific interactions. Over time,  
291 only the functional and phylogenetic richness increased on the mountaintops, while the number of  
292 species remained virtually stable. Colonization by species from the lowlands was counterbalanced by  
293 a gradual loss of resident mountain plants, although novel lowland species still expanded occupied  
294 trait space and added new lineages to the tree of life on the summits. The increase in functional  
295 richness was most apparent at lower elevations, whereas for phylogenetic richness no differences  
296 across summits were detected. In sum, our findings hint on rearrangements in the functional and  
297 phylogenetic structure of mountain plant communities that cannot be predicted from trends in  
298 taxonomic richness alone. However, the generality of such patterns as well as the potential  
299 implications for ecosystem functioning still need to be confirmed using multi-decadal resurvey  
300 datasets from mountain summits across continents.

### 301 **Opposing elevational patterns in taxonomic, functional and phylogenetic diversity**

302 We detected several similarities in the elevational patterns of taxonomic, functional and phylogenetic  
303 diversity of the summit's plant communities. Especially for the richness-based metrics, a sharp decline  
304 towards higher elevations was detected. This trend is unsurprising given that elevation often acts as  
305 an environmental filter that limits species occurrence at high altitudes to species tolerant of the  
306 frequently stringent climatic conditions (Odland and Birks 1999, Körner 2004). Not only temperature  
307 but also water and nutrient availability decreases towards higher elevations, leading to reduced plant  
308 productivity and lower species richness (McCain 2007, McCain and Grytnes 2010). Thus, only species  
309 with specific traits that allow them to tolerate these harsh conditions can survive at higher elevation,  
310 thereby also reducing the trait range of plant communities (de Bello et al. 2013). This is evident in our  
311 results, and was also reported by Asplund et al. (2022) who observed a persistent decrease in  
312 functional trait diversity of vascular plants along a 500-m elevational gradient in southern Norway.

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313 The environmental filter associated with elevation will therefore favour the coexistence of species  
314 with similar traits that allow them to survive in the same habitat (Pavoine et al. 2014). Consequently,  
315 plant communities at higher elevations will be characterized by a more converged trait distribution,  
316 which could result directly from the increased climatic harness or indirectly from lower competition  
317 and increased positive interactions among species (Callaway et al. 2002).

318 Remarkably, phylogenetic differentiation increased significantly with elevation, implying lower  
319 phylogenetic relatedness among species in high-elevation plant communities. Even though few  
320 species are found at higher elevations, they thus represent a comparatively broad range of the  
321 evolutionary tree, thus suggesting the aggregation of phylogenetic lineages in low-elevation plant  
322 communities (near the tree line) and overdispersion in high-elevation plant communities (near the  
323 limits of vascular plant life). This result is somewhat unexpected given that it challenges the  
324 environmental filtering hypothesis on species numbers and functional traits described above. Yet,  
325 previous studies found mixed phylogenetic patterns in mountain plant assemblages across elevational  
326 gradients, ranging from phylogenetic clustering (Bergamin et al. 2021, Galván-Cisneros et al. 2023,  
327 Liang et al. 2023) to overdispersion (Bryant et al. 2008) or even an absence of clear phylogenetic trends  
328 towards higher elevations (Ndribe et al. 2013). Bryant et al. (2008) hypothesised that, in the case of  
329 overdispersion, trait adaptation necessary to cope with the harsh environmental conditions of high  
330 elevations occurs independently in distantly related lineages. This type of convergent evolution has  
331 been observed in alpine plants, and has been used to explain their widespread adaptations to the  
332 stressful conditions at high elevations (e.g. dwarf stature, smaller leaves, high branch density and  
333 specialized morphology such as leafy bracts, wooly coverings and cushion forms; Trewavas 2014,  
334 Zhang et al. 2023). In our study system, plants at the highest summit were indeed mostly species with  
335 a wide elevational distribution range (e.g. *Empetrum nigrum*, *Luzula arcuata*, *Salix herbacea*, etc. occur  
336 across the entire elevational gradient), which are able to tolerate a broad range of temperatures and  
337 could have obtained the ability to tolerate cold temperatures independently throughout their

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338 evolutionary past (Zanne et al. 2018). Alternatively, the observed increase in phylogenetic  
339 overdispersion could result from the shift of competition at low elevations towards facilitation among  
340 species in the high-elevation assemblages. Facilitation is an important driver of plant community  
341 assembly in high-alpine environments where conditions are physically stressful (Callaway et al. 2002),  
342 and has been shown promote phylogenetic differentiation (Valiente-Banuet and Verdú 2007,  
343 Butterfield et al. 2013, Graham et al. 2014, Vega-Álvarez et al. 2019).

344 **Functionally and phylogenetically novel plant communities that cannot be detected from trends in**  
345 **species richness alone**

346 Looking across surveys, the summit's plant communities revealed different temporal trends in  
347 taxonomic, functional and phylogenetic diversity metrics. For instance, taxonomic richness and  
348 differentiation did not increase on the studied mountaintops between 2001-2022. This is in contrast  
349 with many other studies, reporting an increasing plant species richness on European mountaintops  
350 over the past decades because of climate warming (Walter et al. 2005, Holzinger et al. 2008, Pauli et  
351 al. 2012, Wipf et al. 2013, Steinbauer et al. 2018). However, stable species richness was also found by  
352 Hagenberg et al. (2022) over the last two decades in the mountains of northern Sweden. Mountain  
353 ranges at higher latitudes (e.g. Scandinavia) are still strongly influenced by recent glacial retreat since  
354 the last Ice Age, and hence the upward migration of many alpine plants can be delayed by post-glacial  
355 dispersal constraints and slow primary succession (that is, the Holocene migration lag; Dullinger et al.  
356 2012b). On top of that, many alpine plants have very specific substrate requirements (Ellenberg and  
357 Leuschner 2010), and their upward expansion may be hampered by unsuitable bedrock types or  
358 rugged rocky terrain (as, for instance, found on the highest two summits). Nevertheless, several new  
359 species from lower elevations were found on the summits since the first survey in 2001 (e.g.  
360 *Epilobium angustifolium*, *Deschampsia caespitosa*, *Geranium sylvaticum*) but this colonization was at  
361 least partly counterbalanced by the loss of some native alpine specialists (e.g. *Artemisia norvegica*,  
362 *Draba fladnizensis*, *Draba glabella*).

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363 Functional richness of the focal mountaintop communities, on the other hand, did increase over the  
364 20-year monitoring period, indicating that niche space occupied by species in the communities  
365 enlarged over time (Mason et al. 2005). According to Thakur and Chawla (2019), mountaintop plant  
366 communities may show a strong increase in functional richness in the future with higher resource use  
367 and niche differentiation because the filtering effect of low temperature will become less important  
368 in determining their functional composition under climate change. Yet, the significant interaction  
369 between year and elevation revealed that the temporal increase in functional richness was especially  
370 pronounced on the lowest mountaintop, where the environmental filtering effect is already less  
371 important but interspecific competition is a strong driver of plant community assembly (Callaway et  
372 al. 2002). The latter can also promote niche differentiation because it allows species to coexist through  
373 different patterns of resource use, thereby preventing competitive exclusion (Kikvidze et al. 2005,  
374 Zepeda and Martorell 2019). Besides, the lowest summit also received the highest inflow of colonizers  
375 from the tree line ecotone. These newly arriving species are often generalists which typically take up  
376 a larger niche space compared to the native alpine specialists (e.g. colonization by taller growing  
377 species such as *Aconitum septentrionale* or species with high SLA such as *Erigeron* sp., *Trisetum*  
378 *spicatum* and *Deschampsia cespitosa*), hence also promoting functional richness of the local plant  
379 assemblages (Slatyer et al. 2013). This conjecture is further supported by a recent experimental study  
380 from the Swiss and Austrian Alps confirming that future mountain plant communities may exhibit  
381 higher functional richness owing to species turnover and arrival of novel lowland species with trait  
382 expressions for a wider range of resource use which offer competitive advantages over native trait  
383 expressions (e.g. high stature, big and fast-growing leaves or high reproductive output; Schuchardt et  
384 al. 2023). They also predicted that the effects will be largest in the low-alpine zone where upward  
385 moving lowland species are becoming more abundant and are currently filling up free trait niches.

386 In accordance with functional richness, phylogenetic richness also increased between 2001-2022 but  
387 no interaction between year and elevation was found indicating that the increase was uniform across

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388 the four summits. Most likely, the new colonizers have added more phylogenetic diversity to the  
389 summit's plant communities than was lost with the local extirpation of native alpine species. This is  
390 possible through immigration of lowland clades that are not yet present on the summits (e.g. *Primula*  
391 *stricta* and *P. scandinavica* were recorded for the first time in 2022 and added a new branch to the  
392 phylogenetic tree), particularly if these clades are also distant relatives that increase the local pool of  
393 lineages (see also Swenson et al. 2006). Meanwhile, the few alpine specialists that were lost from the  
394 summit's communities likely belong to clades that are sister to other clades with lower extinction risk  
395 and still persist on the summits (e.g. *Astragalus norvegicus* was lost, but the sister species *A. alpinus*  
396 and *A. frigidus* remained present throughout the surveys). Despite the increase in phylogenetic  
397 richness over time, no temporal trend in phylogenetic differentiation of the summit's assemblages  
398 could be found. This implies that, while the number of phylogenetic lineages increased over time  
399 owing to immigration of lowland species, phylogenetic distances among species in the mountaintop  
400 communities remained virtually unchanged. Over time, immigration thus brings new lineages into the  
401 communities through the introduction of phylogenetically distinct species, but this process does not  
402 seem to affect the communities' overall evolutionary relatedness.

#### 403 **Implications for mountain biodiversity and ecosystem functioning**

404 Our study was unique in that we quantified shifts in mountaintop plant diversity across space and time  
405 using a multifaceted approach based on taxonomy, function and phylogeny. Hence, we were able to  
406 highlight the importance of looking beyond taxonomic diversity and including functional and  
407 phylogenetic diversity approaches to better understand plant community assembly and responses to  
408 environmental change on mountaintops. In particular, our results emphasize that future  
409 environmental changes may give rise to novel plant communities on mountaintops with different  
410 functional and phylogenetic properties. It is possible that the observed widespread trends in species  
411 richness (e.g. Pauli et al. 2012, Steinbauer et al. 2018) mask more complex, and currently unrevealed,  
412 trends in functional and phylogenetic diversity. Upward-moving lowland species are currently still

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413 present with low abundances and mostly coexist with native alpine species, potentially leading to a  
414 transient state of increased functional and phylogenetic richness. However, the competitive potential  
415 of lowland species is strong (Schuchardt et al. 2023), and further increases in their abundance can be  
416 expected as well as gradual losses of native species. More studies exploring the taxonomic, functional  
417 and phylogenetic turnover in mountain plant communities along multidecadal time series and across  
418 larger spatial scales are essential to confirm the generality of these trends. Additionally, these studies  
419 may help to shed light on the vulnerability of mountaintop biodiversity to future environmental  
420 change and the potential implications for mountain ecosystem stability and functioning.

### 421 **Critical viewpoints and avenues for future research**

422 While our study provides valuable insights into the mechanisms driving changes in mountaintop plant  
423 diversity across space and time, it should be noted that all diversity metrics were based on presence-  
424 absence data given that our summit-wide plots were too large to accurately estimate plant covers.  
425 This type of data may only capture part of the changes and, to some extent, give contradictory results  
426 because species density dynamics are so far overlooked. We therefore advise future studies to also  
427 use relative abundance data in summit-wide resurveys, and assess how community-level shifts in  
428 abundance and dominance of species on mountaintops affect local plant diversity trends beyond the  
429 loss of native and colonization of lowland species. To illustrate, our additional analysis using relative  
430 abundance data from the 1-m<sup>2</sup> permanent plots already hints on the importance of species density  
431 shifts in shaping mountaintop plant communities across space and time. Yet, these plots were too  
432 small to capture the species pool of an entire summit and several plots on the higher summits did not  
433 contain any plant species at all, making it virtually impossible to discern reliable spatial and temporal  
434 trends at these small spatial scales.

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436 We are grateful to Rozália E. Kapás and Hanne T. Petlund for their assistance in the fieldwork, and to  
437 the GLORIA coordination office for assistance with data quality checks and taxonomic standardization.

#### 438 **Data availability**

439 The data is owned by the GLORIA coordination office and can be obtained upon request via  
440 [gloria.office@boku.ac.at](mailto:gloria.office@boku.ac.at). All code needed to reproduce the analyses and figures is available on Github  
441 (<https://github.com/to-vanneste/Diversity-Dovrefjell.git>).

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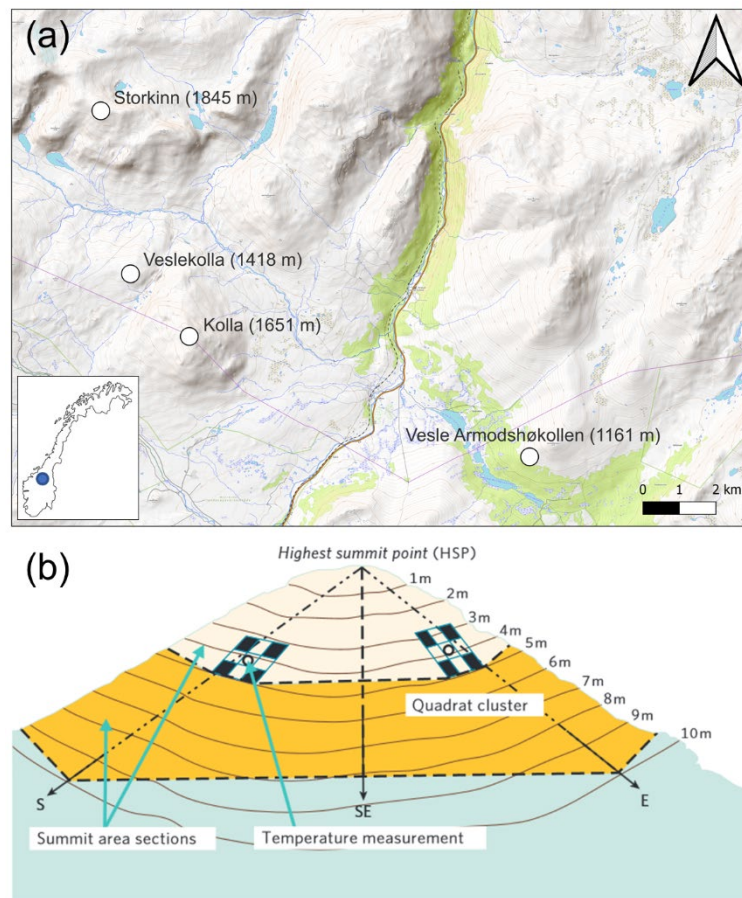
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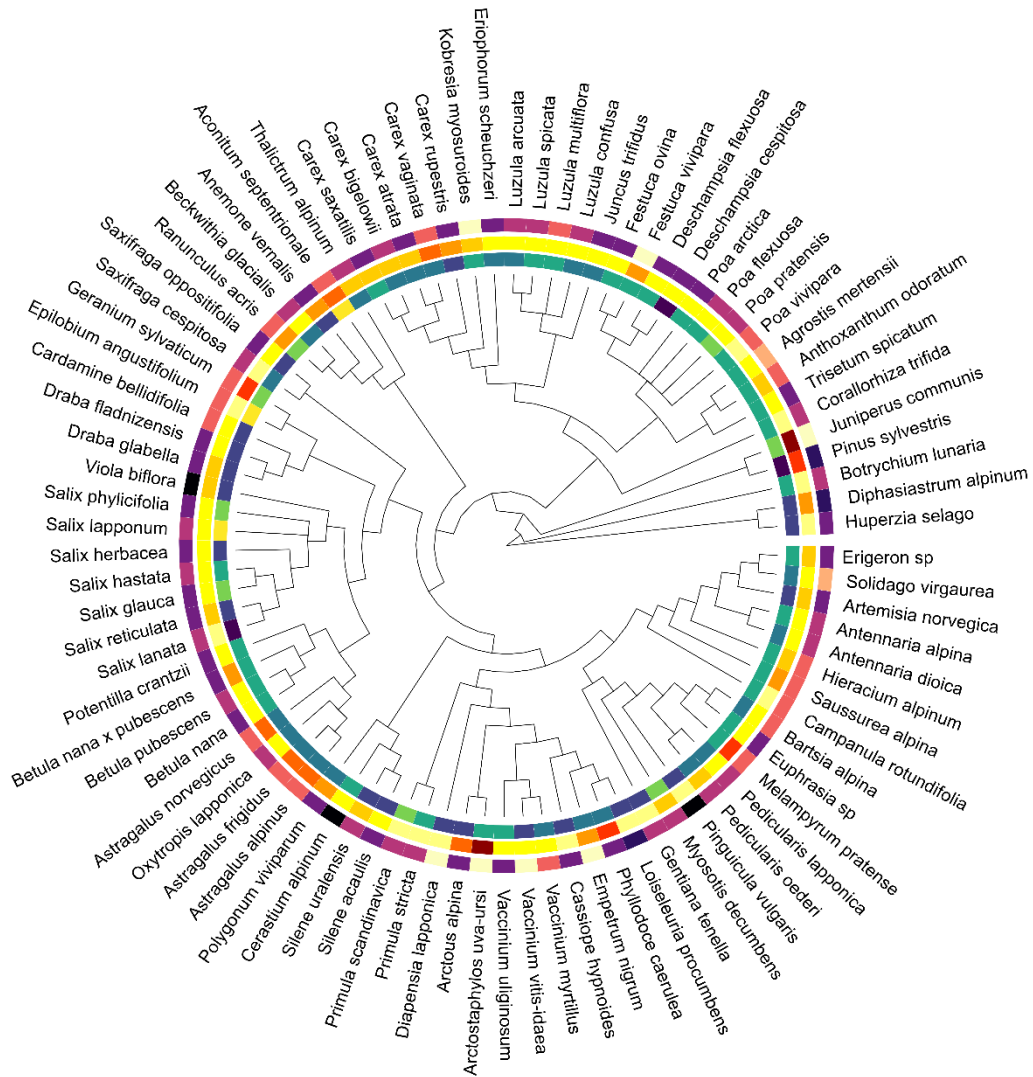


702

703 **Figure 1.** (a) Geographical location of the study site. Within the framework of the GLORIA network (<https://gloria.ac.at>), four  
 704 summits were selected representing an elevational gradient from alpine grasslands near the tree line up to the upper margins  
 705 of vascular plant life. The summits are located in the Dovrefjell-Sunndalsfjella National Park, Central Norway. (b) Each  
 706 monitoring site consists of eight summit area sections: two sections (an upper and a lower) for each aspect (north, east,  
 707 south, west). The upper sections were positioned between the highest summit point (HSP) and the 5-m contour line, while  
 708 the lower sections were situated between the 5-m and 10-m contour line. In each section, the occurrence of all vascular  
 709 plant species was recorded during the growing season of 2001, 2008, 2015 and 2022. In addition, more fine-scale surveys  
 710 were carried out in 1 m × 1 m permanent plots, arranged in clusters of four quadrats on every aspect (sixteen plots in total  
 711 per summit). In these plots, the percentage cover of all vascular plant species was recorded. Finally, soil temperatures were  
 712 recorded at an hourly interval starting in 2001 on all summits, using miniature data loggers (GEO-Precision M-Log5 W logger)  
 713 installed at 10 cm below the soil surface in every quadrat cluster. This figure was adapted from Pauli et al. 2015.

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714

Plant Height (m) >0.75 0.05-0.1 0.2-0.5 0-0.05 0.1-0.2 0.5-0.75 Seed Mass (mg) 0-0.1 0.1-0.5 0.5-1 1-2 2-4 4-8 >8 SLA (mm<sup>2</sup>/mg) >30 10-15 20-25 0-5 15-20 25-30 5-10

715

**Figure 2.** Phylogenetic tree of all vascular plant species recorded in the summit sections of the four GLOBIA mountaintops at

716

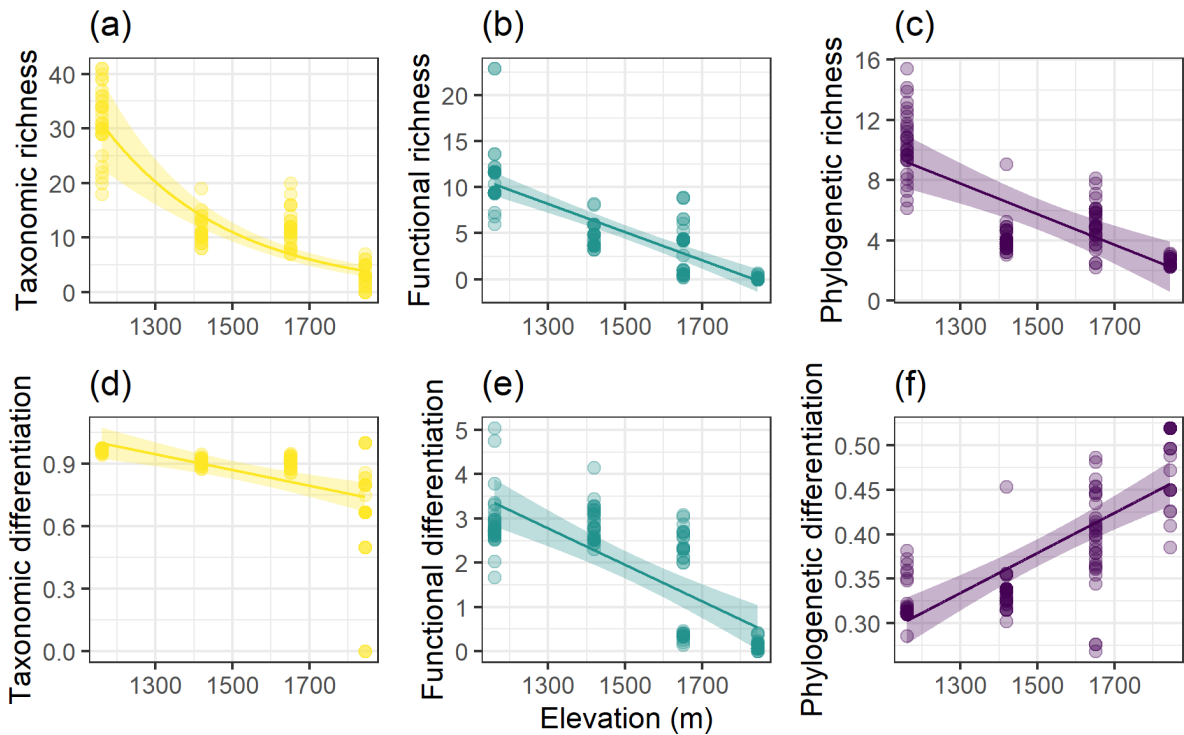
Dovrefjell, central Norway between 2001-2022. The tree was visualized with the *ggtree* and *gheatmap* package in R (Yu et

717

al. 2017). Functional trait values are shown with a color scale around the tree, with plant height (m) in the inner circle, seed

718

mass (mg) in the middle circle and specific leaf area (SLA; mm<sup>2</sup>/mg) in the outer circle.

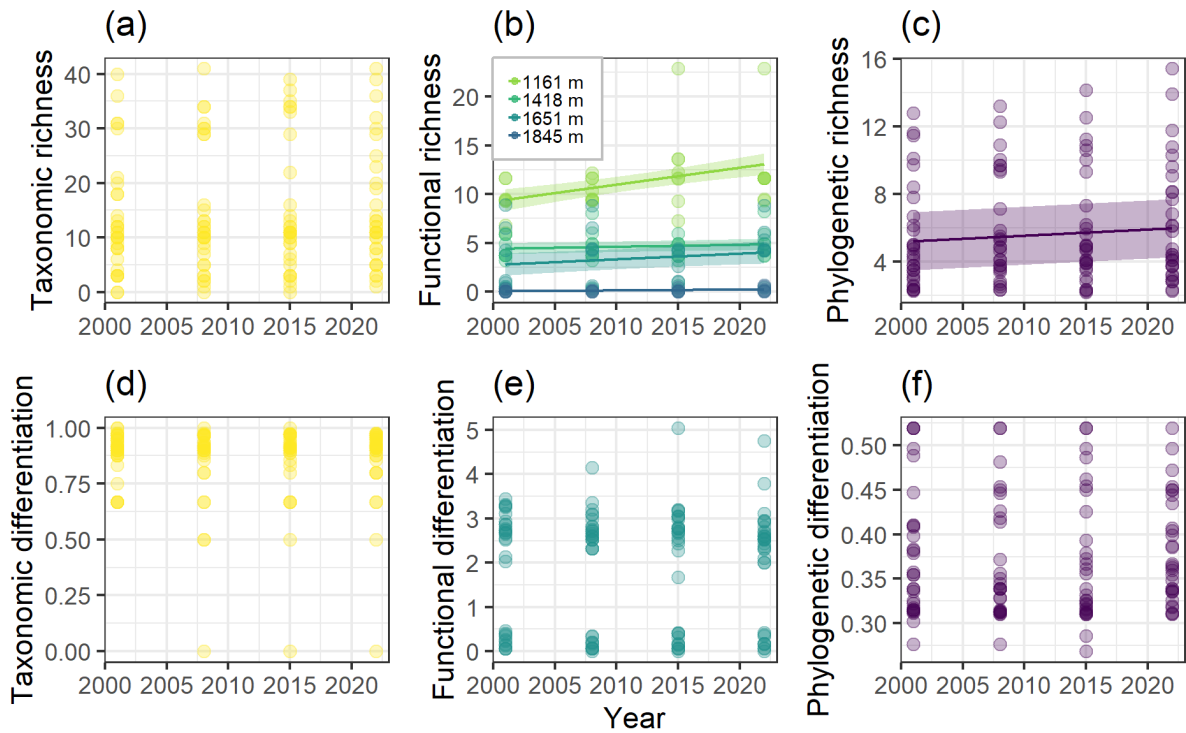


719

720 **Figure 3.** Elevational patterns in (a) taxonomic richness, (b) functional richness, (c) phylogenetic richness, (d) taxonomic  
 721 differentiation, (e) functional differentiation, and (f) phylogenetic differentiation. Lines and shading show model predictions  
 722 and 95% confidence intervals for significant parameter estimates based on (generalized) linear mixed-effect models,  
 723 respectively. For taxonomic richness, a Poisson error distribution was applied, while for the other diversity metrics a Gaussian  
 724 error distribution was used. Transparency of points was added for clarity; darker areas thus indicate overlapping data points.

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725

726 **Figure 4.** Temporal patterns in (a) taxonomic richness, (b) functional richness, (c) phylogenetic richness, (d) taxonomic  
 727 differentiation, (e) functional differentiation, and (f) phylogenetic differentiation. Lines and shading show model predictions  
 728 and 95% confidence intervals for significant parameter estimates based on (generalized) linear mixed-effect models,  
 729 respectively. For taxonomic richness, a Poisson error distribution was applied, while for the other diversity metrics a Gaussian  
 730 error distribution was used. Transparency of points was added for clarity; darker areas thus indicate overlapping data points.  
 731 For functional richness, a significant interaction effect between year and elevation was found. Hence, the temporal trend  
 732 was plotted for each elevation separately.

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