

1 **Disentangling the processes driving plant assemblages in mountain grasslands**
2 **across spatial scales and environmental gradients**

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21 Abstract

22 1. Habitat filtering and limiting similarity are well-documented ecological assembly processes
23 that hierarchically filter species across spatial scales, from a regional pool to local
24 assemblages. However, information on the effects of fine-scale spatial partitioning of
25 species, working as an additional mechanism of coexistence, on community patterns is much
26 scarcer.

27 2. In this study, we quantified the importance of fine-scale spatial partitioning, relative to
28 habitat filtering and limiting similarity in structuring grassland communities in the western
29 Swiss Alps. To do so, 298 vegetation plots (2 m × 2 m) each with five nested subplots (20 cm
30 × 20 cm) were used for trait-based assembly tests (i.e., comparisons with several alternative
31 null expectations), examining the observed plot and subplot level α -diversity (indicating
32 habitat filtering and limiting similarity) and the among-subplot β -diversity of traits (indicating
33 fine-scale spatial partitioning). We further assessed variations in the detected signatures of
34 these assembly processes along a set of environmental gradients.

35 3. We found habitat filtering was the dominating assembly process at the plot level with
36 diminished effect at the subplot level, whereas limiting similarity prevailed at the subplot
37 level with weaker average effect at the plot level. Plot-level limiting similarity was positively
38 correlated with fine-scale partitioning, suggesting that the trait divergence resulted from a
39 combination of competitive exclusion between functionally similar species and
40 environmental micro-heterogeneities. Overall, signatures of assembly processes only
41 marginally changed along environmental gradients, but the observed trends were more
42 prominent at the plot than at the subplot scale.

43 *Synthesis:* Our study emphasises the importance of considering multiple assembly processes
44 and traits simultaneously across spatial scales and environmental gradients to understand
45 the complex drivers of plant community composition.

- 46 **Keywords:** community assembly, environmental gradient, habitat filtering, limiting similarity, niche
- 47 differentiation, spatial partitioning, trait convergence, trait divergence

48 **Introduction**

49 Community assembly is assumed to work as a hierarchy of constraints with potentially varying
50 strengths at different scales (Keddy, 1992; Zobel, 1997; Belyea & Lancaster, 1999; Lortie et al., 2004;
51 McGill, 2010). Community dynamics and structure are therefore the outcome of a succession of
52 filters that limit the set of potentially coexisting species from larger pools. This concept integrates
53 many mechanisms of species coexistence (Chesson, 2000; Barot & Gignoux, 2004; Wilson, 2011).
54 However, empirical investigations addressing actual coexistence in nature have shown little
55 consensus over the years (Miles, Schmidt & Van der Maarel, 1988; Diaz, Cabido & Casanoves, 1998;
56 Firth & Crowe, 2010; Mason, de Bello, Doležal & Lepš, 2011; Götzenberger et al., 2012; Concepción et
57 al., 2017; Conti, de Bello, Lepš, Acosta & Carboni, 2017; Price et al., 2017), despite the prime
58 importance for realistic forecasts of current and future communities (Guisan & Rahbek, 2011;
59 D'Amen, Rahbek, Zimmermann & Guisan, 2017). More research is required to detect and disentangle
60 the signatures of assembly processes based on assemblages observed at different scales.

61

62 When focusing on local plant communities at fine spatial scales (i.e., excluding the roles of
63 phylogeographic and dispersal assembly filters), many studies provide evidence of habitat filtering,
64 an assembly process that allows only the species exhibiting suitable convergent traits to coexist in
65 particular environmental conditions (Watkins & Wilson, 2003; Firth & Crowe, 2010; Chalmandrier et
66 al., 2017; Conti et al., 2017). Although habitat filtering is often implicitly linked to the physical
67 constraints of the environment, the habitat is also defined by its biotic components, including
68 competitors. Therefore, the convergence of traits at the community level may also be driven by the
69 exclusion of weaker competitors by the stronger ones (Bengtsson, Fagerstrom & Rydin, 1994;
70 Chesson, 2000; Mayfield & Levine, 2010; Kunstler et al., 2012). However, when plant competition is
71 at work, the coexistence of species can be empowered by mechanisms that counteract competitive
72 exclusion (Chesson, 2000; Barot & Gignoux, 2004; Wilson, 2011): Opposite to the trait *convergence*

73 caused by habitat filtering, trait *divergence* results from the fact that species must differentiate to
74 compete for different resources (corresponding to different α -niche attributes; Stubbs & Wilson,
75 2004; Wilson & Stubbs, 2012), usually resulting in a range of distinct traits in the community
76 (MacArthur & Levins, 1967; Johansson & Keddy, 1991; Wilson, 2011; D'Andrea & Ostling, 2016). Such
77 trait divergence is therefore expected to limit the trait similarity of coexisting species through α -
78 niche differentiation (Wilson, 2011; Götzenberger et al., 2012). Simultaneous functioning of these
79 counteracting processes (i.e., habitat filtering and limiting similarity) is assumed to be enabled by
80 hierarchical organisation (Weiher & Keddy, 1995; Holdaway & Sparrow, 2006; Bernard-Verdier et al.,
81 2012): abiotic constraints are expected to be more effective at coarser scales than plant interactions,
82 whereas resource competition should mostly work at finer “neighbourhood” scales (Huston, 1999).

83

84 In addition to habitat filtering and limiting similarity, both assuming that communities are spatially
85 homogeneous, assemblages of plant species may be driven by within community spatial partitioning
86 (Amarasekare, 2003). Such processes account for the heterogeneous nature of communities and may
87 be endogenous (e.g., generated by ecology of the plants themselves; Tilman, 1994; Pacala & Levin,
88 1997) or exogenous (e.g., generated by environmental micro-heterogeneities or disturbances; Conti
89 et al., 2017; Price et al., 2017). Spatial partitioning is at the core of several mechanisms promoting
90 species coexistence (Bolker, 2003; Barot & Gignoux, 2004; Adler, Fajardo, Kleinhesselink & Kraft,
91 2013). An example of coexistence mechanisms promoted by endogenous heterogeneity is the
92 competition/colonisation trade-off (Levins & Culver, 1971) in which better colonisers escape
93 competitive exclusion because they can occupy patches that are not yet occupied by the better
94 competitors (e.g., Wildová, Wild & Herben, 2007; Moora, Opik, Zobel & Zobel, 2009). Additionally,
95 environmental heterogeneities are well recognised to develop at a wide range of scales (Levin, 1992),
96 including the very fine ones of the rhizosphere (Raynaud & Leadley, 2004; Scherrer, Schmid & Körner,
97 2011). Although they cannot be considered as a mechanism of coexistence *sensu stricto* (Wilson,
98 2011), such environmental heterogeneities still increase opportunities for species to co-occur.

99 Combined endogenous and exogenous fine-scale spatial heterogeneities are expected to segregate
100 plant functional syndromes leading to fine-scale spatial niche partitioning (Amarasekare, 2003; Conti
101 et al., 2017; Price et al., 2017).

102
103 Whereas the roles of different assembly processes are expected to vary in relation to spatial scale,
104 they may also vary along environmental gradients (Mason et al., 2011; Carboni et al., 2014; Mudrak
105 et al., 2016; Chalmandrier et al., 2017; Bowman & Swatling-Holcomb, 2018). Based on the
106 hypotheses related to stress gradients, abiotic constraints would be expected to be decisive for co-
107 occurrences under harsh environmental conditions, such as in cold and dry areas, whereas
108 competition would define species assemblages in more productive habitats (Louthan, Doak & Angert,
109 2015). Conversely, the role of spatial partitioning should be emphasised in environments prone to
110 patchiness in vegetation and spatial heterogeneity (Amarasekare, 2003; Stark, Lehman, Crawford,
111 Enquist & Blonder, 2017). Variations in importance of different assembly processes along
112 environmental gradients demonstrate that interpretations derived from one habitat cannot
113 necessarily be generalised to communities elsewhere. Thus, quantifying the role of different
114 assembly processes across different spatial scales and along environmental gradients is essential for
115 better understanding community assembly (Weiher et al., 2011; Conti et al., 2017).

116
117 In this study, we aimed to disentangle the signatures of different processes defining local plant
118 assemblies (summarised in Table 1) across spatial scales (plots of 2 m × 2 m and subplots of 20 cm ×
119 20 cm) and environmental gradients. Our analyses were based on a nested sampling design to record
120 the within-community heterogeneity of vegetation (Fig. 1), including information on plant functional
121 traits combined with environmental data in abiotic habitats. We applied different null models for
122 trait reshuffling to assess the importance of habitat filtering (interpreted from trait convergence) and
123 limiting similarity (interpreted from trait divergence) at two different spatial scales (i.e., plot and

124 subplot level) and spatial partitioning among subplots (i.e., interpreted from β -diversity of traits
125 within each plot). We further assessed the variations in the investigated assembly processes along
126 environmental gradients.

127 **Materials and Methods**

128 *Data collection*

129 The study area covers approximately 700 km² of a mountain region located in the western Swiss Alps
130 (46°23' N, 7°05' E). This region is characterised by a large elevation gradient with strong variation in
131 climatic, edaphic and land use factors. A set of 298 plots of 2 m × 2 m, each with five nested subplots
132 of 20 cm × 20 cm, were distributed across non-forested areas within the study area from 820 to 3045
133 m a.s.l. according to a stratified-random sampling (using elevation, slope and aspect as strata)
134 designed to evenly cover the range of grassland habitat conditions (Fig. 1). At the 2 m plot scale, the
135 cover of different plant species was estimated as modified ordinal classes (Braun-Blanquet, 1964),
136 which were then subsequently converted to percentage cover values: 0 = absent; r = 0.01 %; + = 0.2
137 %; 1 = 3 %; 2 = 15 %; 3 = 37.5 %; 4 = 62.5 %, 5 = 87.5 % (Pottier et al., 2013). At the 20 cm subplot
138 level, the percentage cover of species was visually estimated in the field. All the field data were
139 collected during the peak vegetation period between June and August 2009, starting from lower
140 elevation sites and moving to higher elevation sites.

141

142 Plant trait information was collected from a previous study (Dubuis et al. 2013) for the 244 most
143 frequent and locally abundant species (of 722 vascular plant species recorded in total). Four traits
144 associated with the performance of plant species during the persistence phase of their life cycle
145 (Westoby, Falster, Moles, Vesk & Wright, 2002; Wright et al., 2004) were measured (hereafter,
146 growth traits): average vegetation height (VH in cm), which is associated with the ability of a plant to
147 compete for light, and specific leaf area (SLA in mm² mg⁻¹), leaf dry matter content (LDMC in mg mg⁻¹)
148 and leaf nitrogen content (LNC in % of dry leaf mass), which indicate the resource-use strategy of a
149 species (Wilson, Thompson & Hodgson, 1999; Reich, 2014). These traits were measured for 4 to 20
150 individuals (generally 10) per species within the study area, evenly distributed within the bioclimatic

151 ranges of the species as defined in Pottier et al. (2013). Trait measurements followed the basic
152 recommendations of Cornelissen et al. (2003) and are detailed in Dubuis et al. (2013). For the details
153 on trait data, see Supplementary material Appendix 1 Fig. A1.

154
155 For the trait-based detection of assembly processes, we discarded the plots in which trait-assigned
156 species accounted for less than 80 % of the relative vegetation cover resulting in 269 plots for the
157 final analyses. With the threshold of 80 %, most of the plots were retained for the analyses (e.g., a 95
158 % threshold would have retained only 147 plots).

159
160 The spatial variation of different assembly processes was examined against the environmental
161 conditions of each plot. Based on preliminary analyses, elevation (m a.s.l.), growing degree-days
162 (GDD; average of 1961-1990 with a 0 °C threshold), moisture index over the growing season (average
163 values of 1961-1990 from June to August) and topographic position (positive values express convex
164 topographies such as ridges, peaks, and exposed sites, whereas negative values indicate concave
165 surfaces such as valley bottoms or lower ends of slopes) were chosen as the most influential
166 predictors (see Supplementary material Appendix 1 Fig. A2). These variables were extracted from
167 digital maps at a 25 m × 25 m resolution following Zimmermann and Roberts (2001).

168 169 *Detecting the signatures of assembly processes*

170 The detection of assembly processes was based on a trait-based approach and the comparison of
171 observed patterns against patterns derived from null models. All analyses were conducted in R 3.4.1
172 (R Core Team, 2017; see Appendix 4 for details of the packages and functions used).

173

174 Habitat filtering and limiting similarity were tracked at both plot and subplot levels to examine scale
175 dependency of these processes. Habitat filtering was inferred in the case of convergence of growth
176 traits in which observed within-plot (or within-subplot) functional diversity was lower than that
177 expected under null assembly. Correspondingly, limiting similarity was inferred in the case of
178 divergence of growth traits in which observed within-plot (or within-subplot) functional diversity was
179 greater than that expected under null assembly. Fine-scale spatial partitioning was inferred from
180 spatial segregation of growth traits among subplots within each plot in which the β -component of
181 functional diversity was greater than that under a null assembly. We measured plot and subplot
182 functional diversity using a modified version of the α -Rao quadratic entropy index following de Bello,
183 Lavergne, Meynard, Lepš and Thuiller (2010). This metric is based on the functional dissimilarity
184 among species weighted by their abundance. The β -component of functional diversity within each
185 plot was measured with the β -Rao quadratic entropy index (de Bello et al., 2010).

186

187 We considered five different representations of trait diversity: one multidimensional space
188 considering the four growth traits simultaneously (multidimensional space combining all growth
189 traits, CGT), and four one-dimensional spaces each consisting of one separate growth trait. All traits
190 were log transformed and standardised (for details, see Supplementary material Appendix 1 Fig. A1).

191

192 A critical aspect of testing for assembly processes is the use of an appropriate null model that focuses
193 only on the ecological mechanisms under study (Harvey, Colwell, Silvertown & May, 1983; Gotelli &
194 Ulrich, 2012; Götzenberger et al., 2016). Detecting habitat filtering or limiting similarity requires
195 testing whether the trait values of species make a difference in terms of community structuring. In
196 this respect, we built null models in which trait values of a species were reshuffled as a unit (i.e., all
197 traits of one species, hereafter called trait unit) among species to prevent unrealistic/unobserved
198 combinations of traits and to preserve fundamental trade-offs between traits (Mouillot, Mason &

199 Wilson, 2007; Hardy, 2008). With this approach, the species abundance patterns and species richness
200 of plots and subplots were fixed, as were the species frequencies among the plots and subplots.
201 Therefore, this reshuffling procedure also fixed the frequency of the functional syndromes over the
202 study area. The range of trait units considered for this reshuffling procedure differed when seeking
203 the signature of habitat filtering or limiting similarity. Whereas the tests of habitat filtering
204 considered the total range of trait units (i.e., based on all species recorded in the study area) at the
205 plot level and the local range of trait units (i.e., based on all species recorded in a plot) at the subplot
206 level, the tests of limiting similarity were based on a restricted range of trait unit values. For limiting
207 similarity, only trait units falling into the observed range of trait values were considered, which
208 allowed detection of limiting similarity independent of habitat filtering (Bernard-Verdier et al., 2012).
209 For example, if the observed range of vegetation height in a plot or a subplot was 10-50 cm, only trait
210 values of the total (for plot level analysis) or local plot range (for subplot analysis) between 10 and 50
211 cm were considered. Using different species pool sources for trait units, habitat filtering and limiting
212 similarity could be detected for a given plot/subplot simultaneously.

213

214 An additional question is whether the reshuffling of trait units among species should be free or
215 constrained allowing only the trait units of species with similar abundances (i.e., vegetation cover) to
216 be reshuffled. To test whether reshuffling had any effect on our results, we ran three different null-
217 models for habitat filtering, limiting similarity and fine-scale spatial partitioning: (1) model allowing
218 trait units to be reshuffled freely independent of abundances; (2) model only allowing trait units to
219 be reshuffled within predefined abundance classes (see Appendix 2 for more details; Hardy, 2008;
220 Wilson & Stubbs, 2012); and (3) model constraining the reshuffling by weights according to the
221 differences in abundance between species (i.e., reshuffling between two species with similar
222 abundances is much more likely than between species with highly different abundances; see
223 Appendix 3 for more details). Because the results of these three null models were similar, we only

224 report the results for the first one here. Detailed descriptions and all results of the other two null
 225 models can be found in Appendices 2 and 3.

226

227 The null models were run 10,000 times for each test. Based on our null models, we then calculated
 228 the standard effect size (SES) of α -Rao or β -Rao for each plot and subplot as

$$229 \quad SES_{Rao} = (Rao_{plot} - \mu_{Rao_{nm}}) / \sigma_{Rao_{nm}}$$

230 where Rao_{plot} is the observed α -/ β -Rao and $\mu_{Rao_{nm}}$ is the mean and $\sigma_{Rao_{nm}}$ is the standard deviation
 231 of α -/ β -Rao of the null model simulations. With negative SES of α -Rao for the habitat filtering test,
 232 the functional diversity was lower than that expected under the null assembly (i.e., signal of habitat
 233 filtering). Conversely, positive SES of α -Rao for the limiting similarity test indicated that the functional
 234 diversity was higher than that expected under the null assembly (i.e., signal of limiting similarity).
 235 Positive SES of β -Rao for the spatial partitioning test indicated that plant traits were spatially
 236 segregated among subplots within a plot.

237

238 To test whether an overall effect of habitat filtering or limiting similarity occurred at the plot and
 239 subplot levels, and whether the effect was significantly different between these spatial scales, we
 240 used a Wilcoxon test comparing α -Rao at the plot level and the mean α -Rao at the subplot level (i.e.,
 241 the mean of the five subplots nested within a plot). To test for an overall effect of fine-scale
 242 partitioning, we used a Wilcoxon test of the β -Rao among subplots.

243

244 *Analysing changes in assembly processes along environmental gradients*

245 To explore potential changes in the strength of habitat filtering and limiting similarity (at the plot and
 246 subplot levels) and spatial partitioning processes (among subplots) along environmental gradients
 247 (elevation, GDD, moisture index, topographic position), generalised linear models (GLM) for the SES

248 (plot/subplot α -Rao, subplot β -Rao) of growth traits were fitted. Because we were not interested in
249 building a single meaningful and accurate statistical model per assembly process but in interpreting
250 the variation along environmental gradients, we fitted one model for each assembly process and
251 environmental factor. Environmental factors were provided to the models as second order
252 polynomials, and the optimal model was selected based on stepwise AIC. Because all of the strong
253 environmental gradients in the study area were highly correlated with elevation (Pearson
254 correlations: GDD = -0.99, moisture index = 0.88 and topographic position = 0.59; see Supplementary
255 material Appendix 1 Fig. A2 for details), only the results for elevation as the principal stress gradient
256 are reported in the main manuscript.

257 **Results**

258 *The relative importance of assembly processes*

259 The mean SES of α -Rao with total trait range reshuffling was significantly lower than zero at the plot
260 level ($p < 0.01$, Wilcoxon test) for all growth traits except LDMC, but not at the subplot level (Fig. 2).
261 This result indicated the predominance of habitat filtering at the coarse spatial scale of 4 m². The
262 mean SES of α -Rao with restricted trait range reshuffling was significantly greater than zero for all
263 growth traits (except VH at the plot level) at both spatial scales ($p < 0.01$, Wilcoxon test) but was
264 significantly higher at the subplot level ($p < 0.01$, Wilcoxon test), indicating the predominance of
265 limiting similarity at the fine spatial scale of 0.04 m² (Fig. 2). Trait convergence from the total range
266 of trait values was strongest for VH and LNC, whereas trait divergence with trait reshuffling restricted
267 to the observed range of the local plot/subplot was strongest for SLA and LDMC. Based on
268 comparison of SES of α -Rao values with total and restricted trait range reshuffling, habitat filtering
269 and limiting similarity at the plot level were negatively linked, indicating that these two processes
270 acted as opposing forces (i.e., plots with strong habitat filtering showed weak limiting similarity, and
271 plots with weak habitat filtering showed strong limiting similarity; $R^2 \approx 0.8$; Fig. 3), despite the
272 independent null-tests. These functional patterns were not related to plot species richness (Fig. 3).

273

274 Overall, SES of β -Rao among subplots did not deviate from zero (Fig. 2). However, 3.3 to 10.3 %
275 (depending on the studied trait) of the plots showed much greater β -Rao than that expected under
276 null assembly, indicating that fine-scale spatial partitioning was a relevant process in our study area.
277 Most importantly, SES β -Rao among subplots was significantly positively correlated with plot level
278 SES α -Rao with restricted trait range reshuffling (Fig. 4), indicating strong connection of limiting
279 similarity at the plot level with within plot (i.e., among subplots) spatial partitioning. Neither process
280 was linked to species richness of a plot (Fig. 4).

281

282 *Assembly processes along environmental gradients*

283 Of the four growth traits (i.e., community weighted mean of the plots), only vegetative height ($R^2 =$
284 0.6) and SLA ($R^2 = 0.42$) varied with elevation, whereas LNC and LDMC were largely independent of
285 elevation ($R^2 < 0.15$; Fig. 5). Overall, the explanatory power of environmental gradients (i.e.,
286 elevation) for SES α -Rao with total trait range reshuffling (i.e., habitat filtering; $R^2 = 0.05-0.26$) and
287 with restricted trait range reshuffling (i.e., limiting similarity; $R^2 = 0.02-0.17$) at the plot level was
288 weak and negligible at the subplot level ($R^2 < 0.04$; Fig. 5; for more detailed results on the other
289 environmental gradients, see Supplementary material Appendix 1 Fig. A3). Our results for the CGT
290 (combined growth traits) showed that habitat filtering was strongest in productive low elevation
291 habitats; whereas limiting similarity was strongest in cold climates at high elevations. These signals
292 were mostly driven by only two traits, with habitat filtering by SLA ($R^2 = 0.26$) and limiting similarity
293 by VH ($R^2 = 0.17$). Nevertheless, habitat filtering for VH remained the strongest assembly process
294 observed, although the importance was relatively constant with elevation (Fig. 5). Fine-scale spatial
295 partitioning did not show any significant signal along environmental gradients ($R^2 < 0.02$; Fig. 5 and
296 Supplementary material Appendix 1 Fig. A3).

297 **Discussion**

298 *Variations of assembly processes with scale and traits*

299 Our study revealed the signatures of several assembly processes across different spatial scales, with
300 habitat filtering (interpreted from trait convergence) the dominant effect at the large scale (i.e.,
301 among plots) and limiting similarity (interpreted from trait divergence) the dominant effect at the
302 fine scale (i.e., within a plot). Consistent with the literature (Weiher & Keddy, 1995; Holdaway &
303 Sparrow, 2006, Götzenberger et al., 2012), we found a strong overall signal of habitat filtering for
304 three of four growth traits (not LDMC) at the plot level and no or only a weak signal at the subplot
305 level. In contrast to habitat filtering, limiting similarity was detected at both spatial scales with
306 stronger effects for all growth traits at the subplot level.

307

308 At the subplot scale (0.04 m²), limiting similarity acting at the neighbourhood scale within
309 herbaceous plant communities was the dominant assembly process indicating species competition at
310 fine scales (van der Maarel & Sykes, 1993; Purves & Law, 2002; Reitalu et al., 2008). However, we
311 also detected trait divergence at the plot scale indicating that competition effects might act not only
312 at centimetre but also at metre scales in grassland communities. Additionally, the plot level trait
313 divergence could result from spatial partitioning processes. This interpretation was indeed supported
314 by the positive correlation between plot level limiting similarity and spatial partitioning, which is a
315 pattern that was also found in a recent study conducted by Conti et al. (2017). Consequently, similar
316 to Mayfield and Levine (2010), who demonstrated that trait convergence could be due to different
317 mechanisms, our results indicated that trait divergence could also be due to different mechanisms
318 operating at different scales.

319

320 Despite the positive relationship between plot level trait divergence and SES of β -Rao, we detected
321 fine-scale spatial partitioning of plant functional traits less frequently than habitat filtering and

322 limiting similarity. Nevertheless, even if the size of our plots (4 m²) was sufficiently small to assume
323 spatial homogeneity of the investigated environmental factors, we might still encounter either
324 biologically generated micro-heterogeneities (e.g., very short-distance dispersal and vegetative
325 reproduction) or fine-scale patchiness in other environmental factors (e.g., edaphic factors, spatially
326 restricted disturbances). The observed spatial partitioning further suggests that the metacommunity
327 concept should be accounted for at very fine scales in future studies (e.g., Kneitel & Chase, 2004;
328 Leibold et al., 2004; Alexander et al., 2012; Laliberté, Norton, Scott & Mason, 2013). This could be
329 accomplished, for example, by combining our approach based on β -diversity patterns and fine-scale
330 measurements of the physical environment (Conti et al., 2017; Stark et al., 2017) with spatially
331 explicit tests (Siefert 2012).

332

333 Additionally, our results revealed that assembly processes worked on different traits with habitat
334 filtering mostly observed for VH and LNC and limiting similarity for SLA and LDMC. These results
335 corroborated the observation of a strong decrease in VH with elevation: apart from the length of the
336 growing season, fertilised lowland grasslands select tall species able to compete for light, whereas
337 alpine/nival landscapes select strongly for small stature plants with thermic decoupling from
338 atmospheric conditions (Körner, 2003). LNC varied across habitats depending on environmental
339 conditions, with plants with high LNC selected for at high elevations in natural environments (Han,
340 Fang, Reich, Ian Woodward & Wang, 2011). We also found high LNC values at low elevations,
341 presumably related to farming-based fertilisation. By contrast, SLA and LDMC are mostly associated
342 with the ability to compete for nutrients (Wilson et al., 1999) and therefore are expected to show
343 trait divergence (i.e., limiting similarity).

344

345 Here, we only used four growth traits, but other traits are also expected to show strong patterns of
346 habitat filtering (e.g., leaf form or anatomy, flower pollination, diaspore morphology; Pellissier,

347 Fournier, Guisan & Vittoz, 2010) or limiting similarity (e.g., root depth; Cornwell & Ackerly, 2009).
348 Indeed, recent studies concentrating on functional diversity reveal a tendency to combine traits into
349 one functional space (e.g., in multi-traits; Cornwell, Schwilk & Ackerly, 2006; Laughlin, 2014;
350 Carmona, de Bello, Mason & Leps, 2016). However, with this approach, or by concentrating only on
351 one or few traits, important mechanisms depicting trait patterns to underlying assembly processes
352 can be hidden (Mason et al., 2011; Conti et al., 2017). To discriminate between different sources of
353 fine-scale spatial partitioning, one should consider more traits related to plant regenerative
354 strategies and ability to pre-empt or explore space. In perennial grasslands in which regeneration is
355 mostly vegetative, a signature of fine-scale spatial partitioning could therefore be detected by trait
356 divergence of clonal traits/syndromes (Moora et al., 2009; Pottier & Evette, 2011; Klimešová &
357 Herben, 2015).

358

359 Although null model approaches are widely used and tested in studies of community assembly, their
360 outcomes, similar to any other observational method, do not imply causation. The ecological
361 interpretation that trait convergence is driven by habitat filtering and that divergence results from
362 competition is certainly an over-simplification (HilleRisLambers, Adler, Harpole, Levine & Mayfield,
363 2012). For example, competitive exclusion can also result in trait convergence, by clustering species
364 of similar competitive ability (similar height, shade tolerance, or other competition related traits;
365 Chesson, 2000; Mayfield & Levine, 2010; Herben & Goldberg, 2014). Although we attributed some of
366 the changes in functional diversity to such processes, overall, the exclusion of weaker competitors
367 was unlikely: SES values for all traits were higher at the subplot level than those at the plot level. If
368 competitor exclusion was effective at the subplot scale, the opposite should be observed.

369

370 For community assembly studies that compare observed trait diversity patterns with randomised
371 ones, another concern is that simultaneously acting processes may lead to random patterns, which

372 could mask the processes that create opposing patterns (e.g., trait convergence vs. divergence)
373 (HilleRisLambers et al., 2012; Götzenberger et al., 2016). Nonetheless, the deviation of SES value
374 distributions from 0 to either positive or negative values can at least indicate the prevailing process
375 acting for a given trait at a given scale. Moreover, in this study, we particularly addressed the
376 simultaneously acting processes of habitat filtering and limiting similarity using different species
377 pools over which trait data were randomised (Figures 3 and 4, see also de Bello et al., 2012).
378 Although such an approach still relies on the assumption that habitat filtering and limiting similarity
379 can be interpreted from convergence and divergence, an indication of those sites in which
380 simultaneous processes are potentially at play is nevertheless provided.

381

382 Despite the limitations of the null model and more generally of the empirical-approach, our study
383 supports the conclusion of Münkemüller et al. (2012) that the inference of assembly processes from
384 diversity patterns is more relevant when based on a set of criteria rather than on a unique one.
385 Münkemüller et al. (2012) combined α - and β -indices for taxonomic, functional and phylogenetic
386 diversity metrics. Here, we further highlighted the importance of combining several species pool
387 definitions and tests of assembly rules at nested scales.

388

389 *Variations of assembly processes along environmental gradients*

390 Although we found a strong influence of elevation on the mean trait values themselves (i.e., VH and
391 SLA), the strength of the processes creating different trait dispersion patterns only varied marginally
392 with elevation. VH showed the strongest overall signal of habitat filtering but was relatively constant
393 across elevation ($R^2 = 0.07$). This result indicated that a strong selection for VH (trait convergence)
394 occurred at both high and low elevations, but for opposite sizes (i.e., small at high elevation, tall at
395 low elevation). Dominance of the best competitors for light in productive habitats is often reported
396 (Perronne, Munoz, Borgy, Reboud & Gaba, 2017), and the advantage of short stature in the

397 alpine/nival belt (high elevation) to allow thermic decoupling from atmospheric conditions is well
398 documented (Körner, 2003). For SLA, the primary influence of elevation on habitat filtering was for
399 selecting high SLA species towards lower elevations and low SLA species towards higher elevations.
400 At low elevation, the detected pattern was most likely not a direct effect of the physical environment
401 but an indirect effect of favourable conditions in productive habitats favouring species with quick
402 growth and high SLAs (e.g., *Crepis biennis*, *Holcus lanatus*; de Bello et al., 2013). This trait
403 convergence due to biotic interactions (i.e., competitive exclusion of weaker traits; Chesson, 2000;
404 Mayfield & Levine, 2010) might also explain why we observed less habitat filtering at higher than at
405 lower elevations (see also Mudrak et al., 2016). This finding further highlights the difficulty of null
406 model approaches to distinguish trait convergence resulting from abiotic (i.e., physiological limits)
407 and biotic (i.e., competitive exclusion) habitat filtering, because both processes might work
408 simultaneously and on the same traits (HilleRisLambers et al., 2012).

409
410 The signal of limiting similarity was only weakly linked to elevation with the strongest effect visible
411 on SLA and VH for which limiting similarity increased with elevation. This result is apparently
412 contradictory to the stress-gradient hypothesis, which predicts an increase in limiting similarity in
413 productive lowlands in which plant competition is expected to be more intense (Bertness & Callaway,
414 1994; He, Bertness & Altieri, 2013; Chamberlain, Bronstein & Rudgers, 2014; Chalmandrier et al.,
415 2017). An alternative interpretation, as presented above, is that the observed patterns of trait
416 divergence at the plot level were linked to habitat heterogeneity within plots rather than the direct
417 effects of competition-driven limiting similarity. With increasing elevation, the plots (4 m²) were
418 likely to become environmentally more heterogeneous (soil depth, percentage of rock cover) leading
419 to the coexistence of species with varying SLA and VH, such as cushion plants, succulents (on rocks)
420 and grasses. Nevertheless, spatial partitioning did not vary significantly with any of the
421 environmental factors tested. This suggested that fine-scale partitioning might result from a variety
422 of mechanisms (endogenous/exogenous heterogeneity) that did not necessarily respond similarly to

423 environmental variations, or that the analyses and underlying data could not capture the true drivers
424 of spatial partitioning within the communities.

425

426 Our findings support the general view that topo-climatic conditions act as strong drivers of
427 community assemblages in a mountain range, such as the one studied here, with implications for
428 spatial modelling of plant species assemblages (Guisan & Rahbek, 2011; D'Amen et al., 2015; D'Amen
429 et al., 2017; D'Amen et al., 2018). However, mountain grasslands are often used as grazing grounds
430 for livestock, with intensity varying in relation to elevation. In previous studies, added fertilisation
431 and mowing has led to observed trait convergence and divergence depending on the attribute
432 examined and the type/intensity of treatment (Mason et al., 2011; Bloor & Pottier, 2014; Louault et
433 al., 2017). Therefore, further investigations of assembly processes in mountain grasslands should also
434 integrate descriptors of land management.

435 **Conclusions**

436 The dominating assembly process at the coarse scale across elevation was habitat filtering,
437 particularly for VH, selecting for small plants at high and tall plants at low elevation sites. Limiting
438 similarity was detected at plot and subplot levels, particularly for resource-acquisition traits (SLA and
439 LDMC), but was stronger and dominating at the subplot level. Plot level trait divergence occurred
440 particularly at high elevations, presumably indicating spatial partitioning rather than limiting
441 similarity as the underlying mechanism. Our findings suggest that approaches studying and modelling
442 assembly processes, such as stacked species distribution models (S-SDMs; Dubuis et al. 2011) or
443 mechanistic models of community assembly (Shipley, Vile & Garnier 2006, Demalach, Zaady, Weiner
444 & Kadmon 2016, Lohier, Jabot, Weigelt, Schmid, B. & Deffuant 2016), should consider the interaction
445 of biotic and abiotic factors along environmental gradients, particularly when examining
446 communities at fine spatial scales. Further, the detection of spatial partitioning in this study calls for
447 high-resolution abiotic data to allow understanding and forecasting of community and biodiversity
448 patterns at fine scales. Overall, our study highlights the importance of analysing the roles of several
449 assembly processes simultaneously across different spatial scales and in combination with abiotic
450 gradients to allow a deeper understanding of the complex interaction of abiotic and biotic drivers
451 shaping natural grassland communities.

452

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460

461 AG and JP, with LG and MZ, conceived the initial idea. AG, ALD, LP, JP and PV led the collection of the
462 data. JP and DS analysed the data. HM, DS and JP led the writing, with all authors contributing and
463 helping in interpreting the results.

464

465 **Data accessibility**

466 All species, environmental and trait data are available from the Dryad Digital Repository:
467 <https://doi.org/10.5061/dryad.2dq836f> (Guisan et al., 2018).

468

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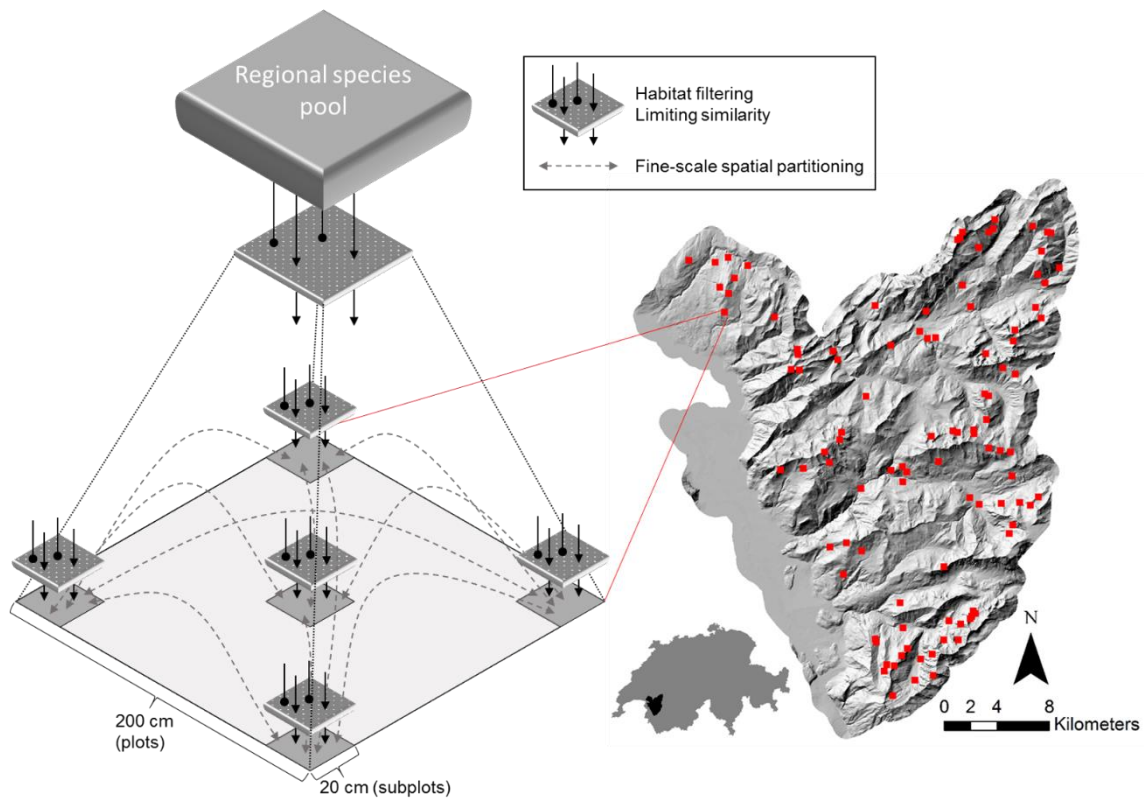
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- 741 Zobel, M. (1997). The relative of species pools in determining plant species richness: An alternative
742 explanation of species coexistence? *Trends in Ecology & Evolution*, 12(7), 266-9.
- 743

744 Table 1. List of the plant assembly processes that are hypothesised to drive community patterns. In
 745 this study, the coarse scale level refers to plots of 4 m² and the fine scale level to “subplots” each of
 746 0.04 m² nested within the 4 m² plots (see Fig. 1). VH = vegetation height, SLA = specific leaf area,
 747 LDMC = leaf dry matter content, LNC = leaf nitrogen content, CGT = multidimensional space
 748 combining all growth traits.

Assembly hypothesis	Short explanation of the underlying mechanisms	Expected pattern	Metric	Scale	Trait space(s) considered
Habitat filtering	Only species sharing similar adaptation to cope with prevailing environmental conditions can co-occur.	Trait convergence	SES of α -Rao	Within plot and within subplot	No restriction of the total trait space of the study area is used. VH, SLA, LDMC, LNC and CGT
Limiting similarity	Species show limiting similarity (i.e., α -niche differentiation = differences in the traits related to the ways the species compete for a common resource) to coexist.	Trait divergence	SES of α -Rao	Within plot and within subplot	Restricted to the trait range of the plot/subplot VH, SLA, LDMC, LNC and CGT
Fine-scale spatial partitioning	Species coexist at the plot level because they segregate in space due to endogenous or exogenous spatial heterogeneity	Segregation of traits among subplots within a plot	SES of β -Rao	Among subplots of each plot	Restricted to the trait values measured for the species recorded in each plot VH, SLA, LDMC, LNC and CGT

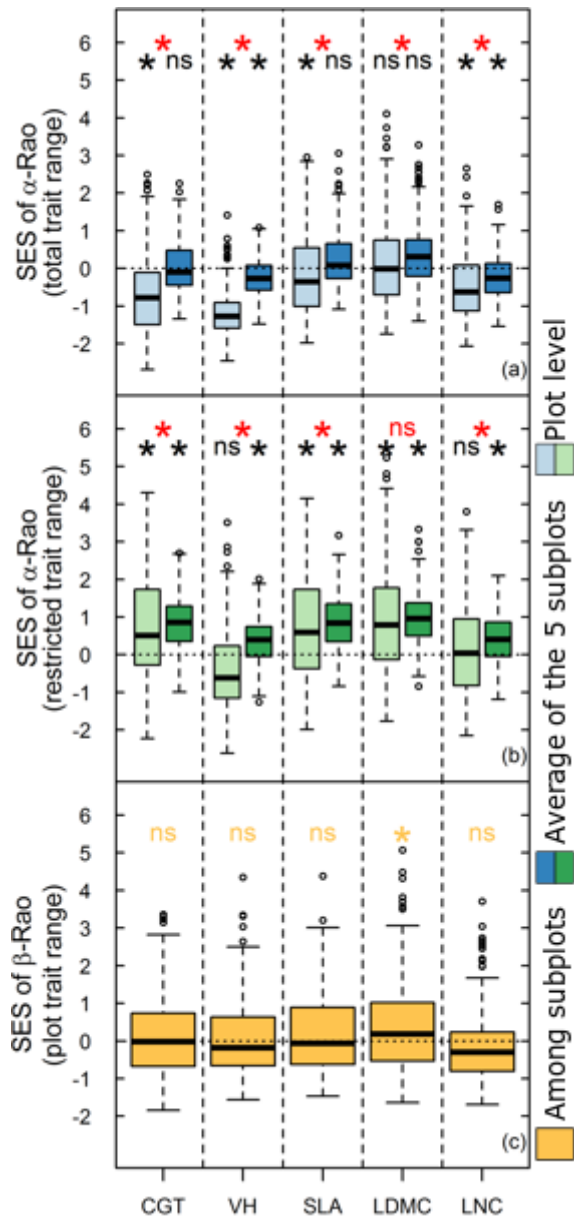
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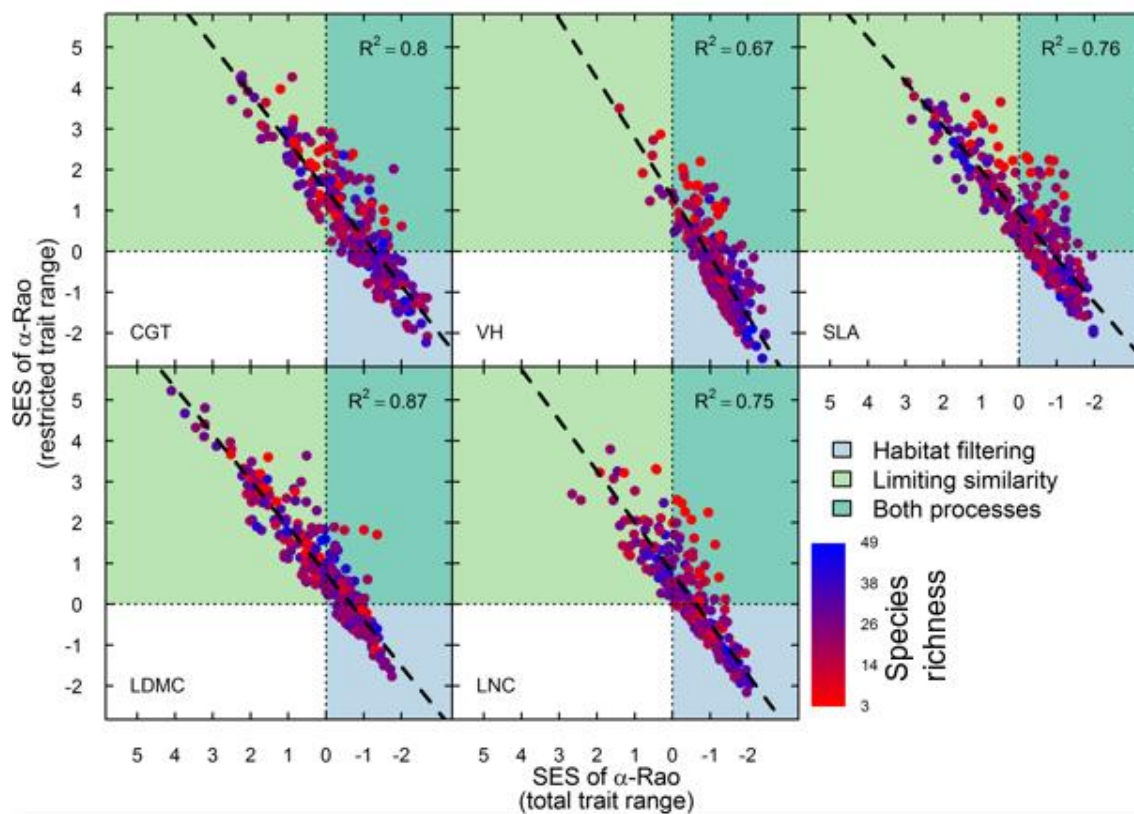
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752 Figure 1. The general framework of the study was based on a nested sampling design to test for the
 753 signatures of different assembly processes. Habitat filtering and limiting similarity were analysed at
 754 two scales (2×2 m plots and 20×20 cm subplots) using null model approaches to compare observed
 755 trait structure with null expectations. The among subplots spatial partitioning process was analysed
 756 in each plot using a null model designed to test for spatial segregation of plant functional traits or
 757 syndromes.



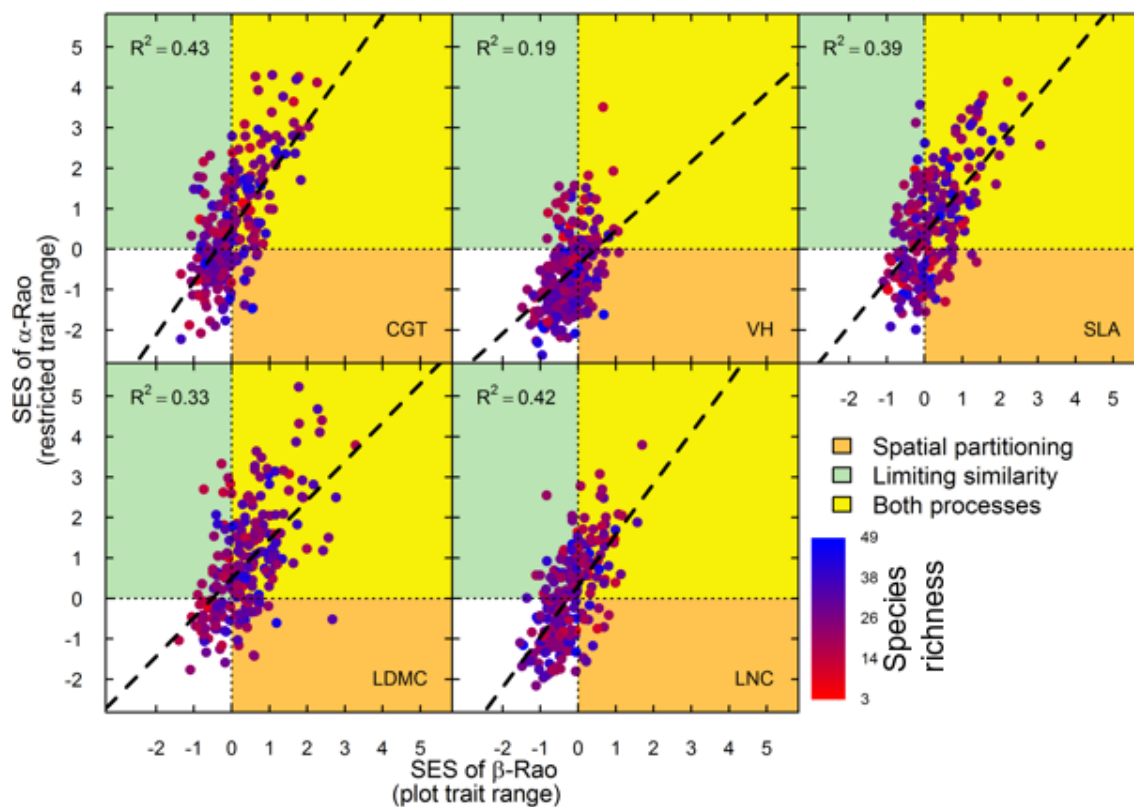
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759 Figure 2. Distribution of SES of α -Rao at the plot level and average (of the five subplots) α -Rao at the
 760 subplot level for (a) total trait range (indicating habitat filtering) and (b) restricted trait range
 761 (indicating limiting similarity). (c) Distribution of SES of β -Rao among subplots (indicating fine-scale
 762 spatial partitioning). Black asterisks above a boxplot mark significant ($p < 0.01$) differences from zero,
 763 and red asterisks mark significant differences ($p < 0.01$) between plot and subplot level α -Rao. The
 764 boxes span from the 25th to the 75th percentile, and the whiskers indicate ± 2 SD. CGT=
 765 multidimensional space combining all growth traits, VH = Vegetation height, SLA = Specific leaf area,
 766 LDMC = Leaf dry matter content, LNC = Leaf nitrogen content, ns = Non significant.



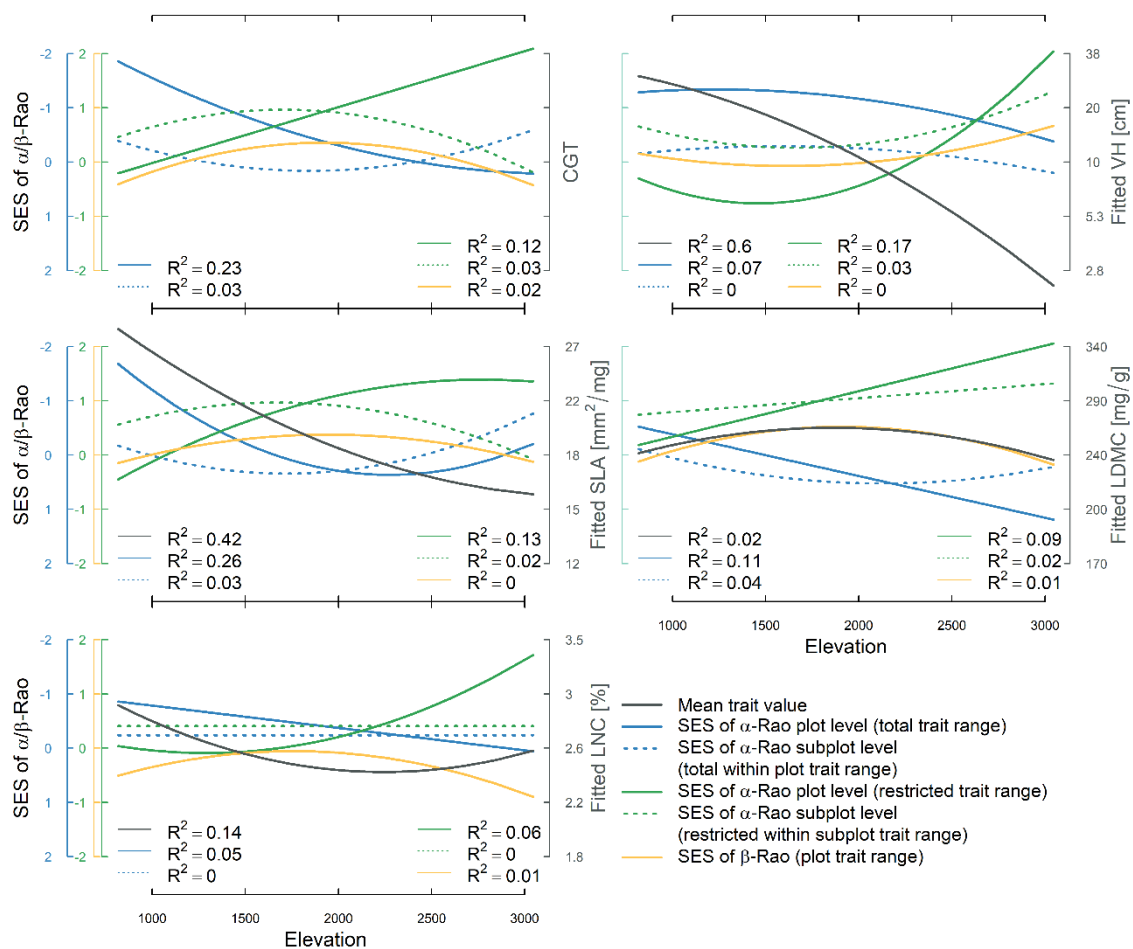
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768 Figure 3. Correlation of strength of limiting similarity and habitat filtering measured by SES of α -Rao
 769 at the plot level. Different coloured areas indicate the dominant assembly process, and the colour
 770 gradient (red to blue) indicates the species richness of the plots. Please note that the x-axis (habitat
 771 filtering) is inverted, i.e., increasing effect to the right. See Fig. 2 for abbreviations.



772

773 Figure 4. Correlation of strength of limiting similarity and spatial partitioning measured by SES of α -
 774 Rao at the plot level and SES of β -Rao among subplots. Different coloured areas indicate the
 775 dominant assembly process, and the colour gradient (red to blue) indicates the species richness of
 776 the plots. See Fig. 2 for abbreviations.



777

778 Figure 5. Generalised linear models fitted for different traits, habitat filtering, limiting similarity and
 779 spatial partitioning along the elevation gradient. Models were fitted as second-degree polynomials
 780 with stepwise AIC to select the best model. Please note that the y-axis for habitat filtering is inverted.
 781 See Fig. 2 for abbreviations.