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# Plant spatial patterns and functional traits interaction along a chronosequence of primary succession: evidence from a central Alpine glacier foreland

Tommaso Sitzia, Matteo Dainese, Bertil Krüsi, Duncan McCollin

The main aim of this study was to elucidate the roles of terrain age and spatial self-organisation as drivers of primary succession using high-resolution assessment of plant composition, functional traits and landscape metrics. We sampled 46 plots, 1m x 1m each, distributed along a 15-70 year range of terrain ages on the foreland of the Nardis glacier, located in the southern central Alps of Italy. From existing databases, we selected nine quantitative traits for the 16 plant species present, and we measured a set of seven landscape metrics, which described the spatial arrangement of the plant species patches on the study plots, at a 1cm x 1cm resolution. We applied linear models to study the relationships among plant communities, landscape metrics and terrain age. Furthermore, we used RLQ-analysis to examine trait-spatial configuration relations. To assess the effect of terrain age variation on trait performance, we applied a partial-RLQ analysis approach. Finally, we used the fourth-corner statistic to quantify and test relations between traits, landscape metrics and RLQ axes. Surprisingly, linear models revealed that neither the plant composition nor any of the landscape metrics differed among the three classes of terrain age distinguished, viz. 15-41 y, 41-57 y and 57-66 y, respectively. Further, no correlations were detected between trait patterns and terrain age, however, the floristically defined relevé clusters differed significantly with regard to several landscape metrics and suggestive relationships between increasing patch diversity and traits connected to growth rate were detected. We conclude that (i) terrain age below 70 years is not a good predictor for neither plant composition nor spatial configuration on the studied microhabitat and (ii) the small-scale configuration of the plant species patches correlates with certain functional traits and with plant composition, suggesting species-based spatial self-organisation.

1 **Plant spatial patterns and functional traits interaction along a chronosequence of primary**  
2 **succession: evidence from a central Alpine glacier foreland**

3

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22 plants, terrain age

23

24 Authorship statement

25 TS conceived, designed the study and had the main role in acquisition, analysis and

26 interpretation of data. MD made substantial contribution to acquisition and analysis of data. KB

27 and DM made substantial contribution to analysis and interpretation of data. All authors

28 participated in drafting the article and revising it critically for important intellectual content and

29 gave final approval of the version to be submitted.

30

31

**32 Abstract**

33 The main aim of this study was to elucidate the roles of terrain age and spatial self-organisation  
34 as drivers of primary succession using high-resolution assessment of plant composition,  
35 functional traits and landscape metrics.

36 We sampled 46 plots, 1 m × 1 m each, distributed along a 15-70 year range of terrain ages on the  
37 foreland of the Nardis glacier, located in the southern central Alps of Italy. From existing  
38 databases, we selected nine quantitative traits for the 16 plant species present, and we measured a  
39 set of seven landscape metrics, which described the spatial arrangement of the plant species  
40 patches on the study plots, at a 1 cm × 1 cm resolution. We applied linear models to study the  
41 relationships among plant communities, landscape metrics and terrain age. Furthermore, we used  
42 RLQ-analysis to examine trait-spatial configuration relations. To assess the effect of terrain age  
43 variation on trait performance, we applied a partial-RLQ analysis approach. Finally, we used the  
44 fourth-corner statistic to quantify and test relations between traits, landscape metrics and RLQ  
45 axes.

46 Surprisingly, linear models revealed that neither the plant composition nor any of the landscape  
47 metrics differed among the three classes of terrain age distinguished, viz. 15-41 y, 41-57 y and  
48 57-66 y, respectively. Further, no correlations were detected between trait patterns and terrain  
49 age, however, the floristically defined relevé clusters differed significantly with regard to several  
50 landscape metrics and suggestive relationships between increasing patch diversity and traits  
51 connected to growth rate were detected.

52 We conclude that (i) terrain age below 70 years is not a good predictor for neither plant  
53 composition nor spatial configuration on the studied microhabitat and (ii) the small-scale  
54 configuration of the plant species patches correlates with certain functional traits and with plant  
55 composition, suggesting species-based spatial self-organisation.

56

## 57 Introduction

58 Spatial heterogeneity or pattern in vegetation has long been a subject of debate in ecology (e.g.,  
59 Greig-Smith 1979; Macfadyen 1950). Recently, focus on pattern in vegetation has shifted toward  
60 spatial self-organization, regular pattern formation arising as an emergent property of local  
61 interactions, especially in relatively simple ecosystems such as arid environments and deserts  
62 (Rietkerk and Van de Koppel 2008; Sole and Bascompte 2006). At the local scale, biotic  
63 processes interact with the physical limitations of the environment and where there is a prevalent  
64 forcing factor, such as directional water drainage in peatlands or tidal currents in shallow marine  
65 beds, the interactions between agents may generate striking patterns such as stripes or polygons  
66 (Jiang et al. 2012; Van de Koppel et al. 2012).

67 Glacier forelands are relatively simple environments which have long been the focus for testing  
68 ideas concerning primary succession in ecology. They provide unique opportunities to  
69 investigate successional processes and ecosystem development using chronosequences (see  
70 Matthews 1999 for review). After glacier retreat, vegetation and soils usually develop rapidly  
71 (Chapin et al. 1994), with changes often driven more by allogenic than by autogenic  
72 mechanisms, particularly during the early stages of succession (Matthews and Whittaker 1987).  
73 Classically, vegetation pattern formation on glacier forelands has been related to age since  
74 substrate emergence, i.e. time since deglaciation or terrain age, and has provided rich ground for  
75 debate concerning processes of succession and community development (Cooper 1923; Dolezal  
76 et al. 2008; Fraser 1970; Johnson and Miyanishi 2008).

77 Relationships between the heterogeneity in plant species patches and terrain age on glacier  
78 forelands have received increasing attention since the 1970s. The analysis of vegetation patterns  
79 during primary succession suggested a sequence of wave-like replacements of groups of species,  
80 largely in order of increasing size (Reiners et al. 1971). Matthews and Whittaker (1987) observed  
81 that an early peak in mean diameter of *Poa alpina* and *Oxyria digyna* clumps during succession  
82 is followed by a fast decline (around 50 y terrain age) in development and then in size and cover  
83 values. Shrubs, but also clumps of certain herbaceous species, e.g., *Saxifraga oppositifolia*, have  
84 a tendency to increase in size and number of flowering individuals with increasing terrain age  
85 (Těšitel et al. 2014). However, it has recently been shown that terrain age is not the principal  
86 factor in explaining present-day variation in species composition in glacier forelands, and that  
87 succession rates are not linearly related to time (Rydgren et al. 2014). Species may respond

88 primarily to factors other than time since deglaciation (Matthews and Whittaker 1987; Těšitel et  
89 al. 2014). Amongst these, it has been shown that simple morphological and physiological  
90 attributes (i.e., life-history or functional traits), combined with suitable establishment and  
91 environmental conditions, are the most important drivers of colonization success (Erschbamer et  
92 al. 2008). Therefore, such attributes are often helpful for identifying successional stages  
93 (Erschbamer and Mayer 2011; Schwienbacher et al. 2012). Indeed, the integration between the  
94 available traits database, and databases that combine the abundance of species with  
95 environmental information, can help to identify the traits that respond, influence or interact with  
96 environmental factors and ecological processes (Suding et al. 2008), a major field of functional  
97 ecology. The linkage between plant trait distributions and spatial organization of a landscape has  
98 received some attention (e.g., Deckers et al. 2004; Duflot et al. 2014), but to our knowledge there  
99 are no studies combining plant traits, spatial organization and processes of primary succession in  
100 glacial forelands, at high resolutions.

101 Recently, the combination of a three-table ordination (RLQ analysis) (Dolédec et al. 1996) and  
102 the fourth-corner, a method to test the direct correlation between a single trait and a single  
103 environmental variable (Legendre et al. 1997), has been proposed to assess trait responses to  
104 environmental variation (Dray et al. 2014). In the present study, we wanted to elucidate how  
105 terrain age affects floristic and life trait composition as well as the spatial configuration of plant  
106 species patches on recently deglaciated microhabitats along a chronosequence of a glacier  
107 foreland in the central Alps. In early successional glacier forelands, plant species tend to form  
108 cushions, tussocks or rosettes separated from each other by bare substrate. In this context we  
109 apply the term “spatial configuration” to the number, size, shape, type and the spatial  
110 arrangement of plant species patches at 1cm<sup>2</sup> resolution on the studied 1m<sup>2</sup> plots (Forman and  
111 Godron 1981). We hypothesised that differences in terrain age would influence the spatial  
112 configuration effect on trait patterning. To test this, we combined ordinary regression and cluster  
113 analysis with the partial RLQ, which subdivides environmental heterogeneity in RLQ analysis  
114 (Wesuls et al. 2012). Using this approach, we added a factor to stratify our samples according to  
115 terrain age. Using this factor as a covariable in the regression and in the partial RLQ analysis,  
116 our main questions were: (1) how does terrain age affect (a) composition, (b) functional trait, and  
117 (c) spatial configuration of plants; and (2) is there evidence for spatial self-organisation or,

118 alternatively, how do landscape metrics correlate with (a) species composition and (b) functional  
119 traits?

## 120 **Materials and methods**

### 121 Study area

122 Field work was performed on the Nardis glacier foreland (46°12'14" N, 10°40'21" E), located in  
123 the Adamello-Presanella group (Rhaetian Alps, southern sector of the Italian Central Alps) on  
124 the southern slope of Presanella Peak (3556 m a.s.l.) (Fig. 1a). The glacier has a surface area of  
125 approximately 1.67 km<sup>2</sup> (SAT 2007) and its tongue extends down to an altitude of 2,720 m a.s.l.  
126 The bedrock consists primarily of acidic granitoid material. The geology is characterized by the  
127 large Adamello–Presanella–Monte Re di Castello batholith (29.4–41 Ma), consisting of tonalite,  
128 an igneous, plutonic intrusive rock. Available climatic data taken from a nearby weather station  
129 (46°25'33" N, 10°41'51" E) located at the same altitude indicate a mean summer temperature of  
130 5.7°C and a mean annual precipitation of 897 mm. The study area where the sampling took place  
131 was approximately 7 hectares in size and corresponded to the zone in front of the glacier tongue,  
132 where the glacier was still present in 1945 (Fig. 1a).

### 133 Data collection

134 We randomly distributed 46 sampling points in the study area. Using the closest individual  
135 method (Krebs 1999), from each of these sampling points, we selected the closest 1m × 1m  
136 sample plot, which was (i) safe from landslides and flat (< 5°) and (ii) without any large stones  
137 (d > 200 mm). This selection procedure was done to avoid marked differences in site conditions  
138 (Vetaas 1997), even if it has not been possible to remove completely a certain variability of  
139 texture. Using historical maps and aerial photographs, frontlines of the glacier tongue, i.e. lines  
140 of equal terrain age (isochrones), were established for 1945, 1954, 1970, and 1996. Terrain ages  
141 (ta) of each sample plot were then classified as follows: (ta<sub>1</sub>) between 15 and 41 years (n=11);  
142 (ta<sub>2</sub>) between 41 and 57 years (n=17); and (ta<sub>3</sub>) between 57 and 66 years (n=18) (Fig. 1b). Each  
143 plot was subdivided into one hundred 1cm × 1cm-grid cells. In August 2011, vascular plant  
144 species distribution intersecting the central axes of each 1cm × 1cm-cell were then mapped and  
145 digitised using ESRI ArcGIS 9.3, yielding for each species the number of 1 cm<sup>2</sup> cells occupied  
146 per 1 m<sup>2</sup> (Fig. 2).

147

### 148 Data analysis

149 Landscape metrics were calculated according to the procedure of Teixido et al. (2007) developed  
150 for quantifying the spatial patterns of landscapes. For each  $1\text{ m} \times 1\text{ m}$ -plot, we calculated eight  
151 indices (Table 1). Calculations were made using the Patch Analyst 5.0 extension for ArcGIS 9.3  
152 (Rempel et al. 2012), adopting a four-neighbour rule to identify the patches. A synthetic  
153 description of each patch metric is reported in Table 1 and further details can be found in  
154 McGarigal and Marks (1994). When available, plant traits were taken from Cerabolini et al.  
155 (2010) and, secondly, from Pierce et al. (2007), Carbognani (2011) and LeBauer et al. (2010).  
156 We did not sample plant traits because this would have been too time-consuming and too  
157 harmful for the vegetation. A brief description of each selected trait is provided in Table 1 (see  
158 also Cornelissen et al. 2003; Gross et al. 2007; Wilson et al. 1999).

159 To verify the absence of marked differences in site conditions among the 46  $1\text{ m} \times 1\text{ m}$ -plots  
160 studied, we assessed the 15th and 85th percentiles of weighted means of selected soil indicator  
161 values according to Landolt et al. (2010). The bio-indicator system of Landolt, developed for  
162 Switzerland, like Ellenberg's analogue for Central Europe (Ellenberg et al. 1991), is based on an  
163 ordinal classification of plants according to the position of their realized ecological niche along  
164 environmental gradients, which can be used as reliable surrogates of field measurements when  
165 the latter are not available (Schaffers and Sýkora 2000).

166 The 46 vegetation relevés were subjected to agglomerative cluster analysis using the Bray–Curtis  
167 coefficient of dissimilarity and Ward's clustering method. Next, ordinary linear models were  
168 applied to verify for differences in landscape metrics between (i) the three classes of terrain age  
169 distinguished, and (ii) the three floristic relevé clusters identified.

170 To relate plant traits to spatial configuration, taking into account species cover in the plots, we  
171 applied RLQ-analysis, a tool to assess how the environment filters certain species traits (Dolédec  
172 et al. 1996; Dray et al. 2003). The RLQ procedure performs a double inertia analysis of an  
173 environmental-variables-by-samples (R-table) and a species-by-traits (Q-table) matrix, with a  
174 link expressed by a species-cover-by-samples matrix (L-table). RLQ-analysis combines three  
175 unconstrained separate ordinations, correspondence analysis of L-table and centred normed  
176 principal component analyses of Q- and R- tables, to maximise the covariance between  
177 environmental factors and trait data by the use of co-inertia analysis (Bernhardt-Römermann et  
178 al. 2008). Here, we studied the joint structure of three data tables, namely (i) a plot-by-landscape



179 metrics data table (R-table), (ii) a plot-by-species table containing the abundances of the plant  
180 species present in our set of 46 plots (L-table), and (iii) a species-by-trait data table (Q-table).  
181 This RLQ analysis (basic-RLQ) was followed by a partial-RLQ, with the aim of checking the  
182 effect of the covariable terrain age, i.e. to possibly remove the variation related to this factor.  
183 This type of analysis is a special case of RLQ, where the covariable represents a partition of  
184 samples into groups. If the percentage of co-inertia explained by the most representative axis of  
185 partial-RLQ were to be much higher than in the basic-RLQ, this would mean that the influence  
186 of terrain age is relevant. The same approach was followed by Wesuls et al. (2012) to partition  
187 the response of plant traits to grazing-related environmental parameters from other  
188 environmental and temporal variations.

189 A permutation method was used to compare the hypothesis  $H_0: X = 0$  (trait and environment are  
190 unrelated) against  $H_1: X \neq 0$  (trait and environment are related), where  $X$  is the fourth corner, a  
191 trait-by-environment table, whose parameters cross the traits (Q-table) to the environmental  
192 variables (R-table), via the abundance table (L-table) (Legendre et al. 1997). The null hypothesis  
193 consists of three null joint hypotheses: both R and Q are linked to L ( $L \leftrightarrow Q$ ,  $L \leftrightarrow R$ ), only R is  
194 linked to L ( $L \leftrightarrow Q$ ,  $L \leftrightarrow R$ ), only Q is linked to L ( $L \leftrightarrow Q$ ,  $L \leftrightarrow R$ ). The overall null hypothesis is  
195 rejected when both null hypotheses are rejected ( $L \leftrightarrow Q$  and  $L \leftrightarrow R$ ). Dray and Legendre (2008)  
196 proposed to set the alpha argument to  $\alpha = \sqrt{0.05}$ , but recently it has been shown that  $\alpha$  should be  
197 0.05 instead (ter Braak et al. 2012). Given the limited power of this test with few species (ter  
198 Braak et al. 2012), like in the present study, we presented the results according to both the Dray  
199 and Legendre (2008) and the ter Braak et al. (2012) alpha argument settings. A multivariate  
200 permutation test was applied to evaluate the global significance of the traits-spatial configuration  
201 relationships, implemented by the function 'randtest' of the package ade4 (Dray & Dufour 2007).  
202 Next, we tested the associations of spatial configuration and trait variables with the axes of the  
203 basic-RLQ. The strength of the association of landscape metrics and plant traits was measured  
204 with the D2 statistic (Dray et al. 2013). All tests were performed using the combined fourth-  
205 corner statistic (Dray et al. 2013) with 49,999 permutations.

206 All statistical analyses were performed using the open source R software (R Core Team 2013).  
207 We used the library vegan (Oksanen et al. 2011) for the cluster analysis, the library stats (R Core  
208 Team 2013) for the linear regression and the library ade4 (Dray & Dufour 2007) for the RLQ  
209 analysis.

210

211 **Results**

212 The R, L, and Q tables resulting from field surveys and data from existing databases are reported  
213 in the supplementary materials. Based on the Landolt et al. (2010) values within which 80% of  
214 the plots ranged (15th and 85th percentiles reported in parentheses), soils were fairly  
215 homogeneous: moist (3.3-3.5), with a low variable moisture regime (1-1.6), acid to weakly acid  
216 (2.1-3.1), from nutrient-poor to moderately infertile (1.3-2.4), with little or moderate humus  
217 content (1.1-2.7) and moderately drained to sandy (3.3-4.9).

218 We recorded a total of 16 plant species. Three clusters (CLs) resulted from the analysis of the 46  
219 vegetation relevés, characterised by differences in the cover of six plant species (Fig. 3). In the  
220 *Saxifraga*-cluster (CL<sub>1</sub>), *Saxifraga oppositifolia* was much more abundant and *Veronica alpina*  
221 much less than in the other two clusters; while in the *Leucanthemopsis*-cluster (CL<sub>2</sub>),  
222 *Leucanthemopsis alpina* was more abundant. Finally, the *Oxyria*-cluster (CL<sub>3</sub>) was characterised  
223 by relatively high covers of *Oxyria digyna* and *Cardamine resedifolia* (Fig. 3).

224 Linear models showed that the floristically defined relevé clusters differed significantly with  
225 regard to landscape metrics. The Shannon index of diversity (SHDI) and the patch type (=   
226 species) richness (PR) were significantly higher in the *Leucanthemopsis*-cluster (CL<sub>2</sub>) than in the  
227 *Saxifraga*-cluster (CL<sub>3</sub>) and the *Oxyria*-cluster (CL<sub>1</sub>), respectively (Table 2). Also, the mean size  
228 of the vegetation patches (MPS) and total edge (TE) differed significantly among the three relevé  
229 clusters, being greatest in the *Leucanthemopsis*-cluster (CL<sub>1</sub>) and smallest in the *Oxyria*-cluster  
230 (CL<sub>2</sub>). Surprisingly, however, linear models showed that none of the landscape metrics differed  
231 amongst the three classes of terrain age, viz. 15-41 y, 41-57 y and 57-66 y, respectively.

232 The percentages of total co-inertia explained by the first two axes of the basic-RLQ and the  
233 partial-RLQ were 95.5% and 94.2%, respectively. The first axis of the basic-RLQ explained  
234 91.1% co-inertia, while the percentage explained by the first axis of the partial-RLQ was lower  
235 (88.7%), meaning that the spatial configuration gradient along the first axis of the partial-RLQ  
236 was not more pronounced than the basic-RLQ (Table 3). Moreover, the ordination diagrams of  
237 the basic- and partial-RLQ did not show any grouping of plots according to the terrain age factor  
238 (Fig. 4).

239 The test for the model (H<sub>1</sub>: L↔R) showed that the distribution of species with fixed traits was  
240 influenced by the spatial configuration (p = 0.008), while the test for the model (H<sub>1</sub>: L↔Q)

241 showed that species composition of plots with fixed spatial configuration was not influenced by  
242 the species traits ( $p = 0.435$ ). This means that the traits-spatial configuration relationships were  
243 not globally significant.

244 The first basic-RLQ axis was significantly and positively correlated with mean patch size and  
245 negatively to Shannon's diversity (SHDI) and patch richness (PR). The second basic-RLQ axis  
246 was not correlated to any metrics of spatial configuration. Among the plant traits, canopy height  
247 (CH), leaf weight, both dry (LDW) and fresh (LFW), leaf area (LA), and carbon content (LCC)  
248 showed a negative, and leaf dry matter content (LDMC) a positive significant correlation with  
249 the first basic-RLQ axis, while lateral spread (LS) showed a positive and significant correlation  
250 with the second axis (Table 4).

251 In summary, the first basic-RLQ axis represented a gradient of decreasing diversity as a response  
252 to the presence of larger plant species patches (Fig. 5a). Moreover, as can be seen in Fig. 5b and  
253 Fig. 5c, the first basic-RLQ axis represented a gradient of increasing cover of species with small  
254 and hard leaves, on the right hand side, with high values of leaf dry matter content, like *Sedum*  
255 *alpestre*, to taller species with larger, heavier and softer leaves on the left hand side, like *Luzula*  
256 *alpino-pilosa* and *Oxyria digyna*. The second basic-RLQ axis represented a gradient from plots  
257 characterised by species with low to high competitive clonal ability. For example, *Salix*  
258 *herbacea*, with both clonal and sexual propagation (Reisch et al. 2007) and *Geum reptans*, a  
259 clonal species, obligate outbreeder (Rusterholz et al. 1993) spreading laterally up to 2 m by long  
260 stolons (Stöcklin and Bäumler 1996) were at the top end of the gradient, while *Cerastium*  
261 *uniflorum*, a species with low regeneration ability (Cannone and Gerdol 2003), was at the bottom  
262 end (Fig. 5c).

263 There were eight significant associations between plant traits and landscape metrics. Mean patch  
264 size was negatively correlated with canopy height and positively with leaf dry matter content,  
265 which was also positively correlated to the patch size coefficient of variation. Among the spatial  
266 metrics, the Shannon's index of diversity was the most frequently and positively associated with  
267 plant traits, namely with canopy height, leaf dry and fresh weight, and leaf area. Finally, patch  
268 richness was positively associated with canopy height (Fig. 6). We should stress that the majority  
269 of the tests were significant only when using a significance level of  $\sqrt{0.05}$ .

270

## 271 Discussion

272 Prior work has documented that whilst terrain age may appear to be one of the most obvious  
273 factors affecting plant colonisation processes on glacier forelands (Caccianiga and Andreis  
274 2004), spatial patterns of plant species and their constituent assemblages are often heterogeneous  
275 and complex and not always directly related to the time factor (Burga et al. 2010; Matthews and  
276 Whittaker 1987; Vetaas 1994).

277 In the present study we wanted to elucidate how terrain age affects composition and functional  
278 trait variability as well as the spatial configuration of plant species patches on recently  
279 deglaciaded microhabitats. We applied a grid-sampling technique where the variables of interest  
280 are surveyed on a regular lattice grid at the appropriate scale. This approach, which has many  
281 possible applications, such as habitat suitability assessment (Sitzia et al. 2014a) and trail  
282 alignment (Sitzia et al. 2014b), has been possible since in the type of habitat studied here plant  
283 species form discrete patches in the form of small cushions, tussocks or rosettes separated by  
284 bare substrate.

285 As reported by other authors (Burga et al. 2010) large-scale successional stages, primarily  
286 defined by terrain age, usually contain a wide array of different microhabitats where species  
287 composition is mainly driven by habitat conditions and local disturbances (e.g., floods, rock falls,  
288 and avalanches) more than by time since deglaciation. Whilst large-scale vegetation pattern may  
289 frequently be explained by time since deglaciation, that is not the case at smaller scales, where  
290 the type of microhabitat is often the critical factor. By considering a single type of microhabitat  
291 at the 1m<sup>2</sup> scale in our study (i.e., thereby reducing the confounding effects of local  
292 environmental factors), terrain age turned out to be of little importance with regard to both  
293 species composition and landscape metrics, i.e. size, shape and spatial arrangement of vegetation  
294 patches.

295 At small-scale resolutions (0.5 m × 0.5 m plot and 12.5 cm × 12.5 cm grid), Rydgren et al.  
296 (2014) have also recently confirmed that, with increasing distance from the glacier snout, and  
297 consequently time since deglaciation, terrain age is less important relative to local environmental  
298 variables. During the deglaciation period surveyed here, species richness of the alpine pioneer  
299 zone increased and many species filled their ranges or shifted downward (Cannone and Pignatti  
300 2014) or upward (Walther et al. 2005). Further, resurveys of floristic composition of the  
301 uppermost altitudinal belts have shown significant changes in composition caused by biotic

302 exchange with other plant communities in the same altitudinal belts (Cannone and Pignatti  
303 2014). This is another possible reason for the absence of any effect of terrain age we observed.  
304 Our results place the emphasis on possible relationships between plant traits and landscape  
305 metrics.

306 First, we found that cover of plant species with efficient conservation of nutrients (high LDMC)  
307 (Pierce et al. 2013; Wilson et al. 1999) increased with patch size and its variability. This pattern,  
308 maintained due to processes of intra- and interspecific competition for space and nutrients,  
309 ensured efficient acquisition-conservation trade-offs in plants characterized by slow growth, as in  
310 *Sedum alpestre*. Second, we found that Shannon's diversity increased with increasing cover of  
311 upright-growing plant species, characterised by larger and heavier leaves. A possible explanation  
312 for this lies in the way plants with these traits compete directly and/or indirectly, and how they  
313 modify one another's biotic and abiotic environment, thereby generating a more equitable  
314 distribution of patch sizes, combined with a higher number of species. *Geum reptans* is a long-  
315 lived clonal plant, adaptable in terms of sexual and clonal reproduction (Wepppler et al. 2006) and  
316 strongly rooted, likewise with the second tallest plant *Luzula alpino-pilosa* (Pohl et al. 2011).  
317 According to historical data from similar glacier forelands (Cannone and Pignatti 2014), these  
318 two species are among the few alpine species which have exhibited an increase of coverage in  
319 the last sixty years. Therefore, they must have driven the observed higher Shannon's diversity.  
320 The observed correlation of landscape metrics with species composition together with the  
321 correlations with specific life-form traits seem to indicate some level of life-form or species-  
322 based spatial self-organisation. Self-organization does not of course imply specific causalities  
323 between vegetation patterns and the environment, but is induced by internal variation,  
324 independent of external drivers (Bolliger et al. 2003). The establishment of any particular species  
325 in this microhabitat depends on successful seed establishment which, in turn, is dependent on  
326 random abiotic factors such as wind-aided dispersal and by small-scale variation of the soil  
327 surface characteristics, such as texture, aiding germination. Stochastic factors thus potentially  
328 lead to a high degree of heterogeneity in seedling distribution due to the variability of seed rain,  
329 the soil seed bank, germination, mortality rates of the seedlings as well as other factors  
330 (Erschbamer et al. 2001; Marcante et al. 2009). However, once established, the permanence of  
331 perennial clonal species, such as *Geum reptans*, as well as the cited dynamics in species  
332 composition at uppermost altitudinal belts over the last decades, had a long-lasting effect in

333 terms of the non-linearity of the succession as already demonstrated by other authors, as well as  
334 autogenous spatial patterns, unrelated to the terrain age.

### 335 **Conclusions**

336 Our results confirm that succession and the associated ecological processes on glacier forelands  
337 are highly complex and scale-dependent. At small spatial scales (1 m<sup>2</sup>), constrained by the  
338 limited size of a microhabitat on glacier forelands, studied along a 15-70 year range of time since  
339 deglaciation, we found that (i) plant species cover variability was not related to terrain age but  
340 rather to small differences in topsoil texture or random effects, and (ii) the small-scale  
341 configuration of the plant patches in space (i.e., landscape metrics), were clearly correlated with  
342 plant species composition and, possibly, to specific life-form traits. This, presumably, indicates  
343 some level of life-form, species-based spatial self-organisation. Our study, therefore, indicates  
344 that on the foreland of the Nardis glacier in northern Italy life trait-mediated processes contribute  
345 to small-scale spatial vegetation patterns. Terrain age, by contrast, turned out to be a poor  
346 predictor of (i) species composition, (ii) life-traits and (iii) landscape metrics. Further studies of  
347 this type are recommended at larger spatio-temporal scales.

348

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357



358 **Tables**359 **Table 1**

360 Landscape metrics used to quantify plant patches patterns on a glacier and plant species traits

361 foreland used to correlate them to the physiological characteristics of plant species.

Abbreviation	Unit	Variable name	Description
Landscape metrics			
MPS	cm <sup>2</sup>	Mean patch size	Mean size of all patches
PSCV	%	Patch size coefficient of variation	Variability in patch size relative to mean patch size. PSCV = 0 when all patches are the same size or when there is only 1 patch
TE	cm	Total edge	Total length of edge of all patch boundaries
NP	none	Number of patches	Total number of patches
MSI	none	Mean shape index	Mean shape index of all patches. MSI = 1 when a patch is maximally compact (i.e. a square) and increases without limit as patch shape becomes more irregular (Patton 1975)
SHDI	none	Shannon's diversity index	1 - sum, across all patch types, of the proportional abundance of each patch type multiplied by that proportion. SHDI = 0 when PR = 1 and increases without limit as PR increases and/or the proportional distribution of area among patch types becomes more equitable
PR	none	Patch type richness	Number of different patch types (i.e. plant species)
Functional traits			
CH	mm	Canopy height	Aspects of competitive ability
LDMC	%	Leaf dry matter content	Resistance to physical hazards, long life-span, relative growth rate
LS	cat. (1-6)	Lateral spread	Aspects of competitive ability
LDW	mg	Leaf dry weight	Growth index
SLA	mm <sup>2</sup> mg <sup>-1</sup>	Specific leaf area	Internal resistance to CO <sub>2</sub> movement, nitrogen mass fraction, Rubisco specific activity, relative growth rate
LNC	%	Leaf nitrogen content	Assimilation capacity
LA	mm <sup>2</sup>	Leaf area	Leaf energy and water balance
LFW	mg	Leaf fresh weight	Growth index
LCC	%	Leaf carbon content	Photosynthetic rate

362

363

364 **Table 2**

365 Mean  $\pm$  95% confidence intervals of landscape metrics in relation to terrain age and relevé  
 366 clusters. Terrain age classes: (i)  $ta_1$ , occurring on a terrain ice-free for 15 to 41 years; (ii)  $ta_2$ ,  
 367 occurring on a terrain ice-free for 41 to 57 years; and (iii)  $ta_3$ , occurring on a terrain ice-free for  
 368 57 to 66 years. Relevé clusters: (i) *Saxifraga*-cluster ( $CL_1$ ); (ii) *Leucanthemopsis*-cluster ( $CL_2$ );  
 369 and (iii) *Oxyria*-cluster ( $CL_3$ ). See Table 1 for abbreviations of landscape metrics. *P*-values were  
 370 obtained by ordinary linear models. Statistically significant differences amongst groups are  
 371 indicated in bold.

372

	MPS	PSCV	TE	NP	MSI	SHDI	PR
$ta_1$	59.9 $\pm$ 11.2	177.6 $\pm$ 31.1	1082.0 $\pm$ 114.6	33.9 $\pm$ 2.9	1.39 $\pm$ 0.02	1.26 $\pm$ 0.10	7.18 $\pm$ 0.75
$ta_2$	41.3 $\pm$ 8.6	168.4 $\pm$ 21.0	805.6 $\pm$ 80.8	35 $\pm$ 4.6	1.36 $\pm$ 0.02	1.15 $\pm$ 0.12	5.65 $\pm$ 0.49
$ta_3$	60.6 $\pm$ 11.3	158.9 $\pm$ 20.1	965.1 $\pm$ 67.7	32.5 $\pm$ 2.5	1.41 $\pm$ 0.02	1.12 $\pm$ 0.11	6.11 $\pm$ 0.43
<b>F</b>	1.3	0.17	2.89	0.15	2.31	0.34	2.13
<i>p</i>	0.282	0.841	0.067	0.858	0.111	0.715	0.132
$CL_1$	71.71 $\pm$ 8.35	191.9 $\pm$ 17.13	1068 $\pm$ 60.5	33.55 $\pm$ 3.45	1.397 $\pm$ 0.015	0.919 $\pm$ 0.106	5.75 $\pm$ 0.45
$CL_2$	32.18 $\pm$ 7.74	144.9 $\pm$ 17.06	797 $\pm$ 70.5	36.74 $\pm$ 2.89	1.341 $\pm$ 0.015	1.448 $\pm$ 0.065	6.79 $\pm$ 0.525
$CL_3$	58.05 $\pm$ 18.98	154.9 $\pm$ 57.10	923 $\pm$ 188.5	26.29 $\pm$ 3.99	1.466 $\pm$ 0.032	1.09 $\pm$ 0.139	5.86 $\pm$ 0.62
<b>F</b>	6.266	1.719	4.042	1.677	9.946	10.27	1.488
<i>p</i>	<b>0.004</b>	0.191	<b>0.025</b>	0.199	<b>&lt; 0.001</b>	<b>&lt; 0.001</b>	0.237

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388 **Table 3**

389 Eigenvalues and percentage of variance (%) explained by the first five axes of the basic RLQ  
390 (sum of eigenvalues: 1.395) and the partial RLQ (sum of eigenvalues: 0.958).

391

Axis	Basic RLQ		Partial RLQ	
	Eigenvalue	%	Eigenvalue	%
1	1.272	91.1	0.849	88.7
2	0.061	4.4	0.053	5.5
3	0.036	2.6	0.036	3.8
4	0.019	1.4	0.016	1.7
5	0.005	0.4	0.002	0.2

392

393

394

395 **Table 4**

396 Percentage contribution to total inertia of the basic RLQ and Pearson correlations of spatial  
 397 configuration and plant functional traits with first two basic RLQ axes. Projected inertia by each  
 398 axis is reported in parentheses. Associations significantly correlated with RLQ axis are shown in  
 399 bold ( $p < \sqrt{0.05}$  as proposed by Dray and Legendre (2008) or with an asterisk ( $p < 0.05$ ) as  
 400 proposed by ter Braak et al. (2012).

401

<b>Variables</b>	<b>Contribution to total inertia [%]</b>	<b>Axis 1 (91.2%)</b>	<b>Axis 2 (4.4%)</b>
<i>Spatial configuration</i>			
MPS	24.5	<b>0.28</b>	0.10
PSCV	13.67	0.21	0.02
NP	1.86	-0.09	-0.06
TE	3.16	0.06	0.05
MSI	2.75	0.05	0.02
SHDI	46.07	<b>-0.40</b>	0.09
PR	7.99	<b>-0.16</b>	0.05
<i>Plant traits</i>			
CH	20.02	<b>-0.35 *</b>	0.02
LDMC	20.17	<b>0.34 *</b>	0.10
LS	4.15	0.09	<b>0.16</b>
LDW	8.84	<b>-0.22</b>	0.04
SLA	5.73	-0.17	-0.04
LNC	8.3	-0.21	-0.03
LA	13.33	<b>-0.28</b>	0.05
LFW	9.06	<b>-0.22</b>	0.09
LCC	10.4	<b>-0.23</b>	-0.06

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405 **Figure captions**

406 **Fig. 1** (a) Location of the study area (triangle), (b) image of the glacier foreland in 2011, and (c)  
407 a map of how the glacier have retreated from 1945 (more external isochrones) to 2006 (date of  
408 the digital terrain model used as a base map), with the position of the 46 1m × 1m-plots studied  
409 (black dots). Coordinates are reported according to the geographic coordinate system ETRS 89 /  
410 UTM zone 32N (EPSG: 25832).

411

412 **Fig. 2** Schematic representation of the plant species survey. To each 1 m<sup>2</sup> sampling plot (a) a  
413 virtual 1 cm-grid is superimposed (b) to produce the final species-patch map (c).

414

415 **Fig. 3** Change in cover [cm<sup>2</sup> / m<sup>2</sup>] of (a) *Cardamine resedifolia*, (b) *Leucanthemopsis alpina*, (c)  
416 *Oxyria digyna*, (d) *Saxifraga bryoides*, (e) *Saxifraga oppositifolia*, (f) *Veronica alpina*, among  
417 the three relevé clusters (1: *Saxifraga*-cluster, CL<sub>1</sub>; 2: *Leucanthemopsis*-cluster, CL<sub>2</sub>; 3: *Oxyria*-  
418 cluster, CL<sub>3</sub>). F and p-values were obtained by linear ordinary models.

419

420 **Fig. 4**

421 Sample scores (46 vegetation plots) of the first two axes of the basic-RLQ (left plot) and the  
422 partial-RLQ (right plot). The symbols show the terrain age classes of the sample plots (ta<sub>1</sub> =  
423 square, ta<sub>2</sub> = triangle, ta<sub>3</sub> = circle). The basic- and the partial-RLQ eigenvalues are reported in  
424 Table 4. The values of d give the grid size.

425

426 **Fig. 5**

427 Ordination diagrams of the first two axes of the RLQ-analysis displaying the (a) landscape  
428 metrics scores, (b) plant trait scores, (c) species scores. Abbreviations for landscape metrics,  
429 terrain ages and relevé clusters are reported in Table 1 and 2. Abbreviations for species: CarRes,  
430 *Cardamine resedifolia*; CerUni, *Cerastium uniflorum*; GeuRep, *Geum reptans*; HieAlp,  
431 *Hieracium alpinum*; LeuAlp, *Leucanthemopsis alpina*; LuzAlp, *Luzula alpino-pilosa*; OxyDig,  
432 *Oxyria digyna*; PoaAlp, *Poa alpina*; RanGla, *Ranunculus glacialis*; SalHer, *Salix herbacea*;  
433 SaxBry, *Saxifraga bryoides*; SaxOpp, *Saxifraga oppositifolia*; SedAlp, *Sedum alpestre*; VerAlp,  
434 *Veronica alpina*. *Adenostyles leucophylla* was not reported to avoid excessive gathering of

435 points; its position would be outside the plot, in the upper part of the second (upper-right)  
436 quadrant. The values of  $d$  give the grid size.

437

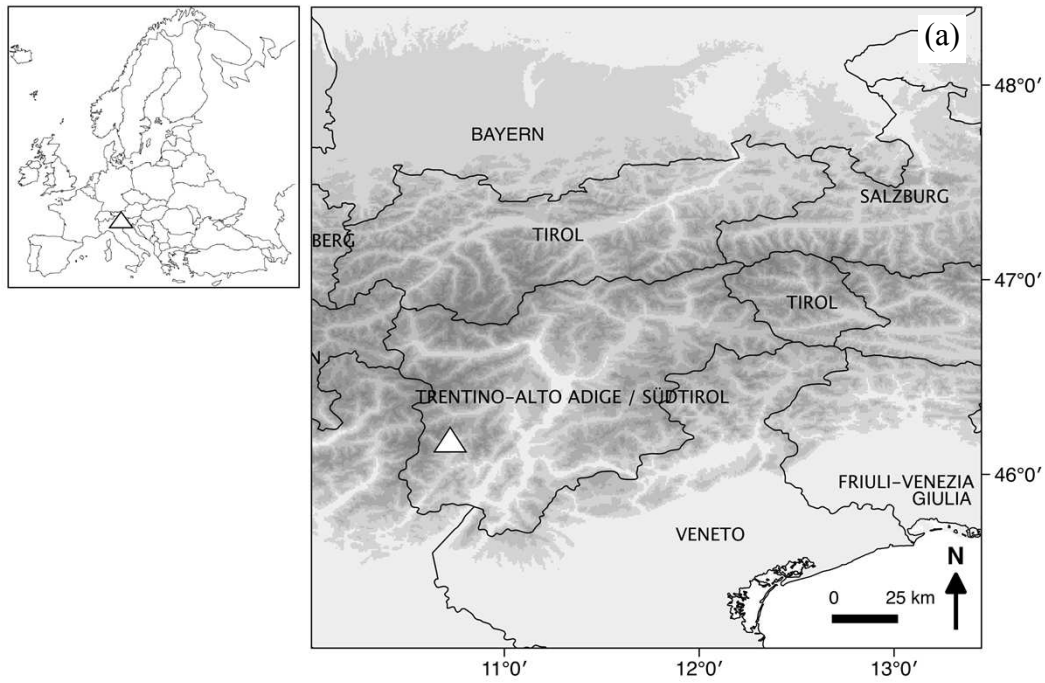
438 **Fig. 6**

439 Schematic representation of the association between individual plant traits and landscape  
440 metrics. Grey cells correspond to negative significant relationships while black cells correspond  
441 to positive significant relationships. The strength of the association was measured with the D2  
442 statistic and tested through a fourth-corner analysis (Dray et al. 2013). P-values were corrected  
443 by a sequential procedure (49,999 repetitions) which leads to significant associations if the  
444 maximum p-value was lower than  $\alpha = \sqrt{0.05}$  as proposed by Dray and Legendre (2008).

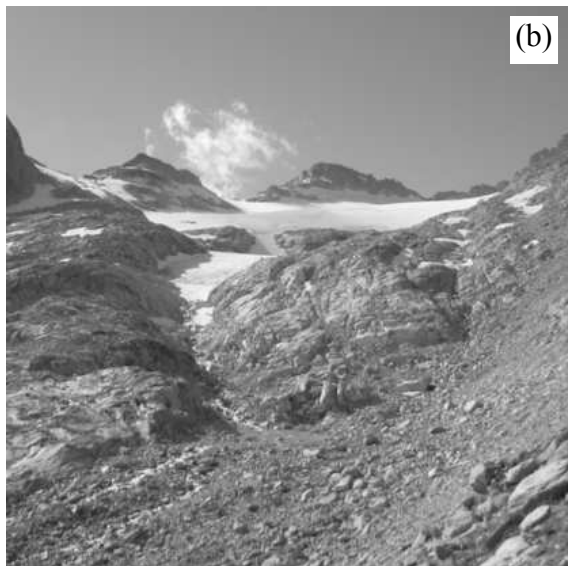
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446 **Figures**

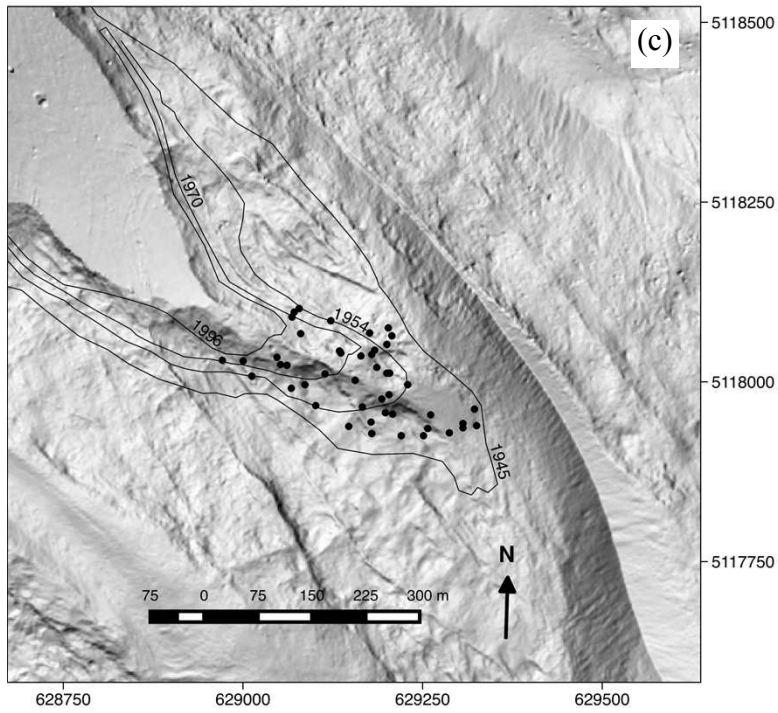
447 Fig. 1



448



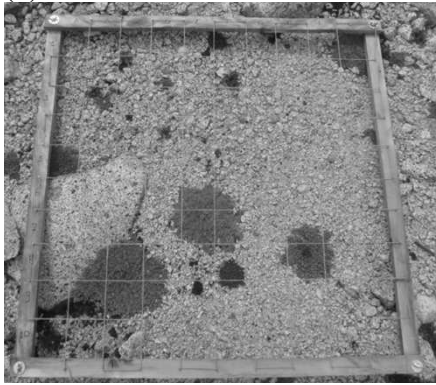
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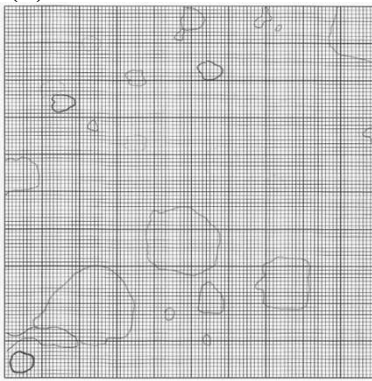
450  
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454 Fig. 2

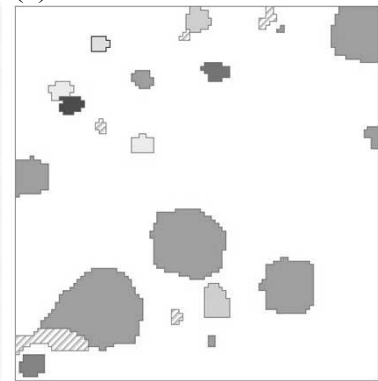
455 (a)



(b)



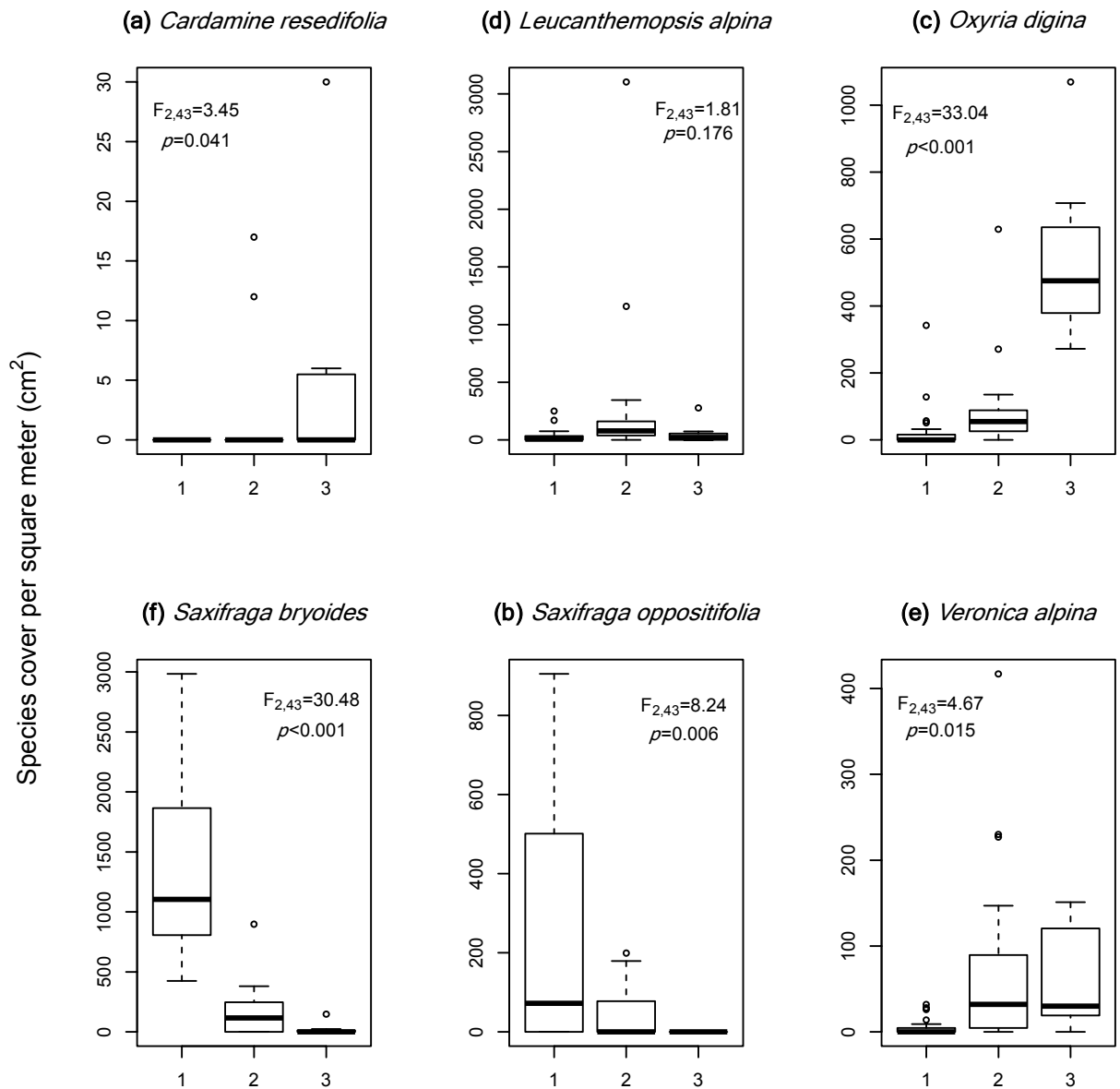
(c)

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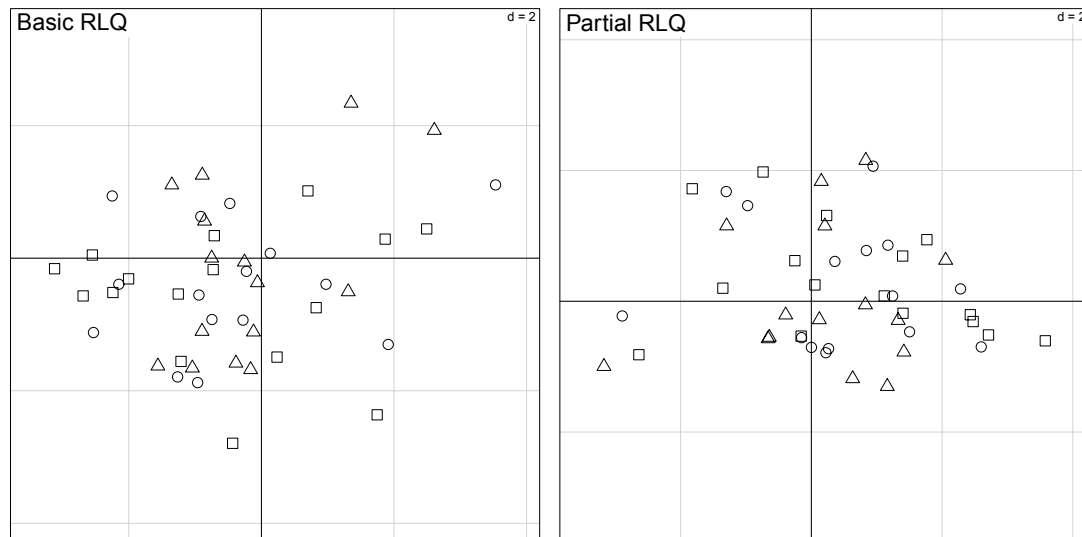


458 Fig. 3

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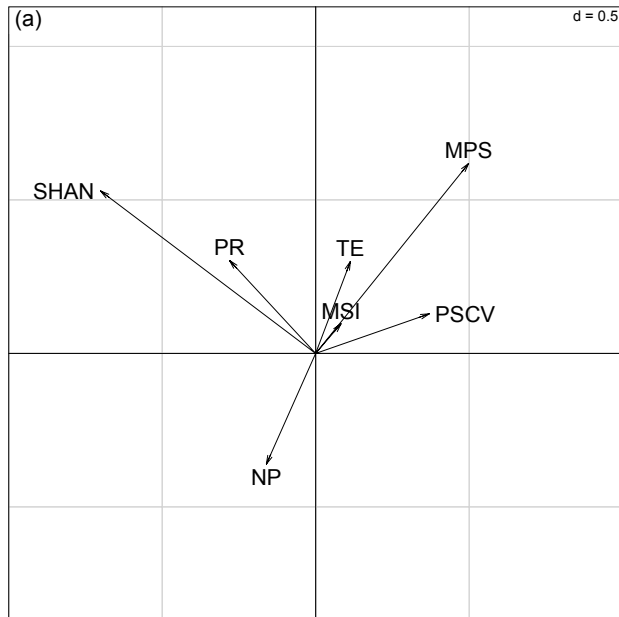
462 Fig. 4



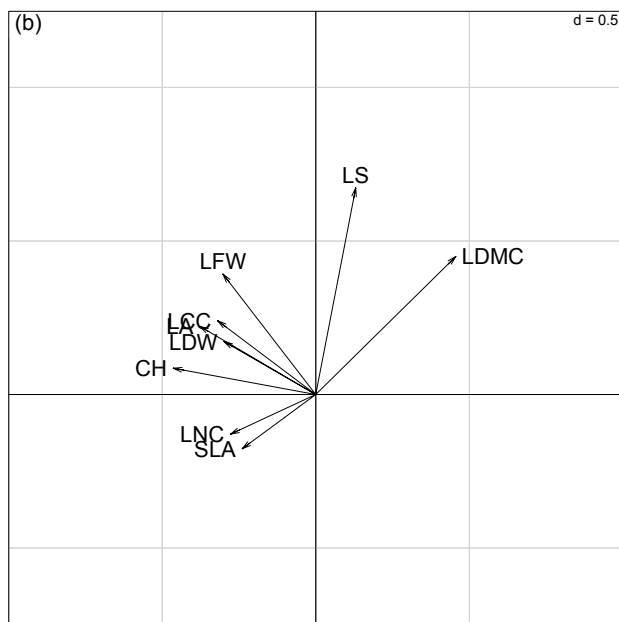
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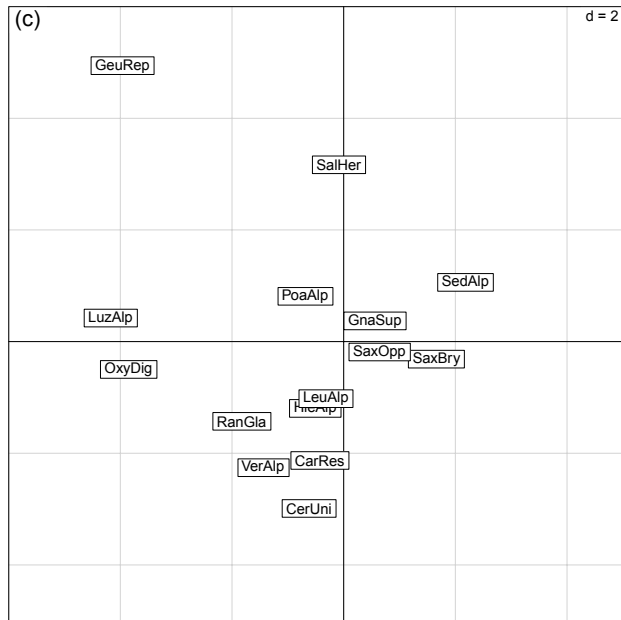
465 Fig. 5



466



467



468

469

470 Fig. 6

	MPS	PSCV	TE	NP	MSI	SHDI	PR
CH							
LDMC							
LS							
LDW							
SLA							
LNC							
LA							
LFW							
LCC							

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