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

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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.

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

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Authorship statement

TS conceived, designed the study and had the main role in acquisition, analysis and interpretation of data. MD made substantial contribution to acquisition and analysis of data. KB and DM made substantial contribution to analysis and interpretation of data. All authors participated in drafting the article and revising it critically for important intellectual content and gave final approval of the version to be submitted.

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Abstract

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 × 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 1 cm × 1 cm 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.

Introduction

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

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

Relationships between the heterogeneity in plant species patches and terrain age on glacier forelands have received increasing attention since the 1970s. The analysis of vegetation patterns during primary succession suggested a sequence of wave-like replacements of groups of species, largely in order of increasing size (Reiners et al. 1971). Matthews and Whittaker (1987) observed that an early peak in mean diameter of *Poa alpina* and *Oxyria digyna* clumps during succession is followed by a fast decline (around 50 y terrain age) in development and then in size and cover values. Shrubs, but also clumps of certain herbaceous species, e.g., *Saxifraga oppositifolia*, have a tendency to increase in size and number of flowering individuals with increasing terrain age (Těšitel et al. 2014). However, it has recently been shown that terrain age is not the principal factor in explaining present-day variation in species composition in glacier forelands, and that succession rates are not linearly related to time (Rydgren et al. 2014). Species may respond primarily to factors other than time since deglaciation (Matthews and Whittaker 1987; Těšitel et al. 2014). Amongst these, it has been shown that simple morphological and physiological attributes (i.e., life-history or functional traits), combined with suitable establishment and environmental conditions, are the most important drivers of colonization success (Erschbamer et al. 2008). Therefore, such attributes are often helpful for identifying successional stages (Erschbamer and Mayer 2011; Schwienbacher et al. 2012). Indeed, the integration between the available traits database, and databases that combine the abundance of species with environmental information, can help to identify the traits that respond, influence or interact with environmental factors and ecological processes (Suding et al. 2008), a major field of functional ecology. The linkage between plant trait distributions and spatial organization of a landscape has received some attention (e.g., Deckers et al. 2004; Duflot et al. 2014), but to our knowledge there are no studies combining plant traits, spatial organization and processes of primary succession in glacial forelands, at high resolutions.

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

Materials and methods

Study area

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

Data collection

We randomly distributed 46 sampling points in the study area. Using the closest individual method (Krebs 1999), from each of these sampling points, we selected the closest 1m × 1m sample plot, which was (i) safe from landslides and flat (< 5°) and (ii) without any large stones (d > 200 mm). This selection procedure was done to avoid marked differences in site conditions (Vetaas 1997), even if it has not been possible to remove completely a certain variability of texture. Using historical maps and aerial photographs, frontlines of the glacier tongue, i.e. lines of equal terrain age (isochrones), were established for 1945, 1954, 1970, and 1996. Terrain ages (ta) of each sample plot were then classified as follows: (ta_1) between 15 and 41 years (n=11); (ta_2) between 41 and 57 years (n=17); and (ta_3) between 57 and 66 years (n=18) (Fig. 1b). Each plot was subdivided into one hundred 1cm × 1 cm-grid cells. In August 2011, vascular plant species distribution intersecting the central axes of each 1cm × 1cm-cell were then mapped and digitised using ESRI ArcGIS 9.3, yielding for each species the number of 1 cm^2 cells occupied per 1 m^2 (Fig. 2).

Data analysis

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

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

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

To relate plant traits to spatial configuration, taking into account species cover in the plots, we applied RLQ-analysis, a tool to assess how the environment filters certain species traits (Dolédec et al. 1996; Dray et al. 2003). The RLQ procedure performs a double inertia analysis of an environmental-variables-by-samples (R-table) and a species-by-traits (Q-table) matrix, with a link expressed by a species-cover-by-samples matrix (L-table). RLQ-analysis combines three unconstrained separate ordinations, correspondence analysis of L-table and centred normed principal component analyses of Q- and R- tables, to maximise the covariance between environmental factors and trait data by the use of co-inertia analysis (Bernhardt-Römermann et al. 2008). Here, we studied the joint structure of three data tables, namely (i) a plot-by-landscape metrics data table (R-table), (ii) a plot-by-species table containing the abundances of the plant species present in our set of 46 plots (L-table), and (iii) a species-by-trait data table (Q-table). This RLQ analysis (basic-RLQ) was followed by a partial-RLQ, with the aim of checking the effect of the covariable terrain age, i.e. to possibly remove the variation related to this factor. This type of analysis is a special case of RLQ, where the covariable represents a partition of samples into groups. If the percentage of co-inertia explained by the most representative axis of partial-RLQ were to be much higher than in the basic-RLQ, this would mean that the influence of terrain age is relevant. The same approach was followed by Wesuls et al. (2012) to partition the response of plant traits to grazing-related environmental parameters from other environmental and temporal variations.

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

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

Results

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

We recorded a total of 16 plant species. Three clusters (CLs) resulted from the analysis of the 46 vegetation relevés, characterised by differences in the cover of six plant species (Fig. 3). In the *Saxifraga*-cluster (CL_1), *Saxifraga oppositifolia* was much more abundant and *Veronica alpina* much less than in the other two clusters; while in the *Leucanthemopsis*-cluster (CL_2), *Leucanthemopsis alpina* was more abundant. Finally, the *Oxyria*-cluster (CL_3) was characterised by relatively high covers of *Oxyria digyna* and *Cardamine resedifolia* (Fig. 3).

Linear models showed that the floristically defined relevé clusters differed significantly with regard to landscape metrics. The Shannon index of diversity (SHDI) and the patch type (= species) richness (PR) were significantly higher in the *Leucanthemopsis*-cluster (CL_2) than in the *Saxifraga*-cluster (CL_3) and the *Oxyria*-cluster (CL_1), respectively (Table 2). Also, the mean size of the vegetation patches (MPS) and total edge (TE) differed significantly among the three relevé clusters, being greatest in the *Leucanthemopsis*-cluster (CL_1) and smallest in the *Oxyria*-cluster (CL_2). Surprisingly, however, linear models showed that none of the landscape metrics differed amongst the three classes of terrain age, viz. 15-41 y, 41-57 y and 57-66 y, respectively.

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

The test for the model (H_1: L↔R) showed that the distribution of species with fixed traits was influenced by the spatial configuration ($p = 0.008$), while the test for the model (H_1: L↔Q) showed that species composition of plots with fixed spatial configuration was not influenced by the species traits (p = 0.435). This means that the traits-spatial configuration relationships were not globally significant.

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

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

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

Discussion

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

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

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

At small-scale resolutions (0.5 m × 0.5 m plot and 12.5 cm × 12.5 cm grid), Rydgren et al. (2014) have also recently confirmed that, with increasing distance from the glacier snout, and consequently time since deglaciation, terrain age is less important relative to local environmental variables. During the deglaciation period surveyed here, species richness of the alpine pioneer zone increased and many species filled their ranges or shifted downward (Cannone and Pignatti 2014) or upward (Walther et al. 2005). Further, resurveys of floristic composition of the uppermost altitudinal belts have shown significant changes in composition caused by biotic exchange with other plant communities in the same altitudinal belts (Cannone and Pignatti 2014). This is another possible reason for the absence of any effect of terrain age we observed. Our results place the emphasis on possible relationships between plant traits and landscape metrics.

First, we found that cover of plant species with efficient conservation of nutrients (high LDMC) (Pierce et al. 2013; Wilson et al. 1999) increased with patch size and its variability. This pattern, maintained due to processes of intra- and interspecific competition for space and nutrients, ensured efficient acquisition-conservation trade-offs in plants characterized by slow growth, as in *Sedum alpestre*. Second, we found that Shannon's diversity increased with increasing cover of upright-growing plant species, characterised by larger and heavier leaves. A possible explanation for this lies in the way plants with these traits compete directly and/or indirectly, and how they modify one another's biotic and abiotic environment, thereby generating a more equitable distribution of patch sizes, combined with a higher number of species. *Geum reptans* is a long-lived clonal plant, adaptable in terms of sexual and clonal reproduction (Weppler et al. 2006) and strongly rooted, likewise with the second tallest plant *Luzula alpino-pilosa* (Pohl et al. 2011). According to historical data from similar glacier forelands (Cannone and Pignatti 2014), these two species are among the few alpine species which have exhibited an increase of coverage in the last sixty years. Therefore, they must have driven the observed higher Shannon's diversity.

The observed correlation of landscape metrics with species composition together with the correlations with specific life-form traits seem to indicate some level of life-form or species-based spatial self-organisation. Self-organization does not of course imply specific causalities between vegetation patterns and the environment, but is induced by internal variation, independent of external drivers (Bolliger et al. 2003). The establishment of any particular species in this microhabitat depends on successful seed establishment which, in turn, is dependent on random abiotic factors such as wind-aided dispersal and by small-scale variation of the soil surface characteristics, such as texture, aiding germination. Stochastic factors thus potentially lead to a high degree of heterogeneity in seedling distribution due to the variability of seed rain, the soil seed bank, germination, mortality rates of the seedlings as well as other factors (Erschbamer et al. 2001; Marcante et al. 2009). However, once established, the permanence of perennial clonal species, such as *Geum reptans*, as well as the cited dynamics in species composition at uppermost altitudinal belts over the last decades, had a long-lasting effect in terms of the non-linearity of the succession as already demonstrated by other authors, as well as autogenous spatial patterns, unrelated to the terrain age.

Conclusions

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

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Tables

Table 1

Landscape metrics used to quantify plant patches patterns on a glacier and plant species traits foreland used to correlate them to the physiological characteristics of plant species.

Abbreviation	Unit	Variable name	Description
Landscape metrics			
MPS	cm^2	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^2mg^{-1}	Specific leaf area	Internal resistance to CO_2 movement, nitrogen mass fraction, Rubisco specific activity, relative growth rate
LNC	%	Leaf nitrogen content	Assimilation capacity
LA	mm^2	Leaf area	Leaf energy and water balance
LFW	mg	Leaf fresh weight	Growth index
LCC	%	Leaf carbon content	Photosynthetic rate

Table 2

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

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

Table 3

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

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

Table 4

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

Variables	**Contribution to total inertia [%]**	**Axis 1 (91.2%)**	**Axis 2 (4.4%)**
Spatial configuration			
MPS	24.5	**0.28**	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	**-0.40**	0.09
PR	7.99	**-0.16**	0.05
Plant traits			
CH	20.02	**-0.35** *	0.02
LDMC	20.17	**0.34** *	0.10
LS	4.15	0.09	**0.16**
LDW	8.84	**-0.22**	0.04
SLA	5.73	-0.17	-0.04
LNC	8.3	-0.21	-0.03
LA	13.33	**-0.28**	0.05
LFW	9.06	**-0.22**	0.09
LCC	10.4	**-0.23**	-0.06

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Figure captions

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

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

Fig. 3 Change in cover [cm^2 / m^2] of (a) *Cardamine resedifolia*, (b) *Leucanthemopsis alpina*, (c) *Oxyria digyna*, (d) *Saxifraga bryoides*, (e) *Saxifraga oppositifolia*, (f) *Veronica alpina,* among the three relevé clusters (1: *Saxifraga*-cluster, CL_1; 2: *Leucanthemopsis*-cluster, CL_2; 3: *Oxyria*-cluster, CL_3). F and *p*-values were obtained by linear ordinary models.

Fig. 4

Sample scores (46 vegetation plots) of the first two axes of the basic-RLQ (left plot) and the partial-RLQ (right plot). The symbols show the terrain age classes of the sample plots (ta_1 = square, ta_2 = triangle, ta_3 = circle). The basic- and the partial-RLQ eigenvalues are reported in Table 4. The values of d give the grid size.

Fig. 5

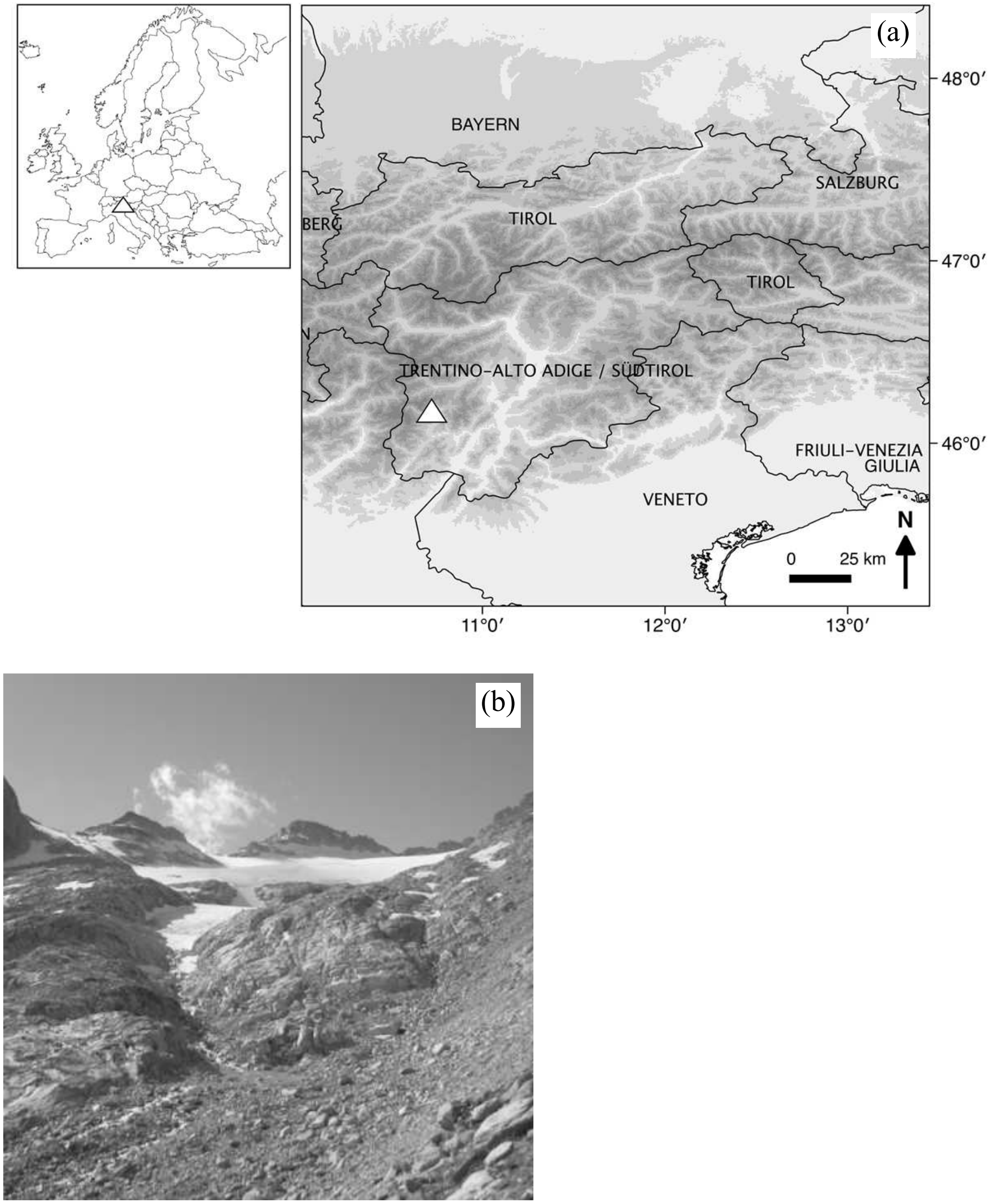
Ordination diagrams of the first two axes of the RLQ-analysis displaying the (a) landscape metrics scores, (b) plant trait scores, (c) species scores. Abbreviations for landscape metrics, terrain ages and relevé clusters are reported in Table 1 and 2. Abbreviations for species: CarRes, *Cardamine resedifolia*; CerUni, *Cerastium uniflorum*; GeuRep, *Geum reptans*; HieAlp, *Hieracium alpinum*; LeuAlp, *Leucanthemopsis alpina*; LuzAlp, *Luzula alpino-pilosa*; OxyDig, *Oxyria digyna*; PoaAlp, *Poa alpina*; RanGla, *Ranunculus glacialis*; SalHer, *Salix herbacea*; SaxBry, *Saxifraga bryoides*; SaxOpp, *Saxifraga oppositifolia*; SedAlp, *Sedum alpestre*; VerAlp, *Veronica alpina*. *Adenostyles leucophylla* was not reported to avoid excessive gathering of points; its position would be outside the plot, in the upper part of the second (upper-right) quadrant. The values of d give the grid size.

Fig. 6

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

Figures

Fig. 1



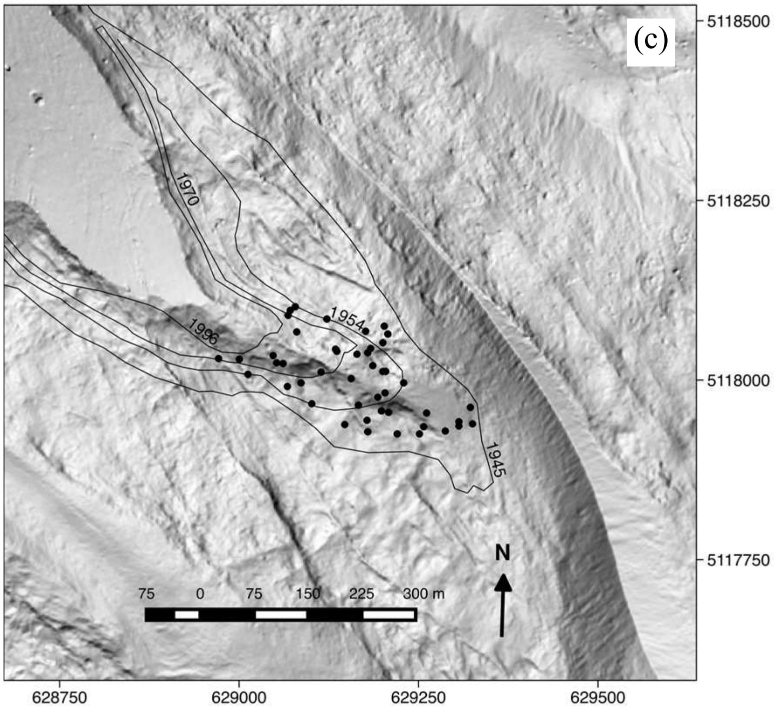

(c)
1970
1954
1996
1945
5118500
5118250
5118000
5117750
628750
629000
629250
629500
75 0 75 150 225 300 m
N

Fig. 2

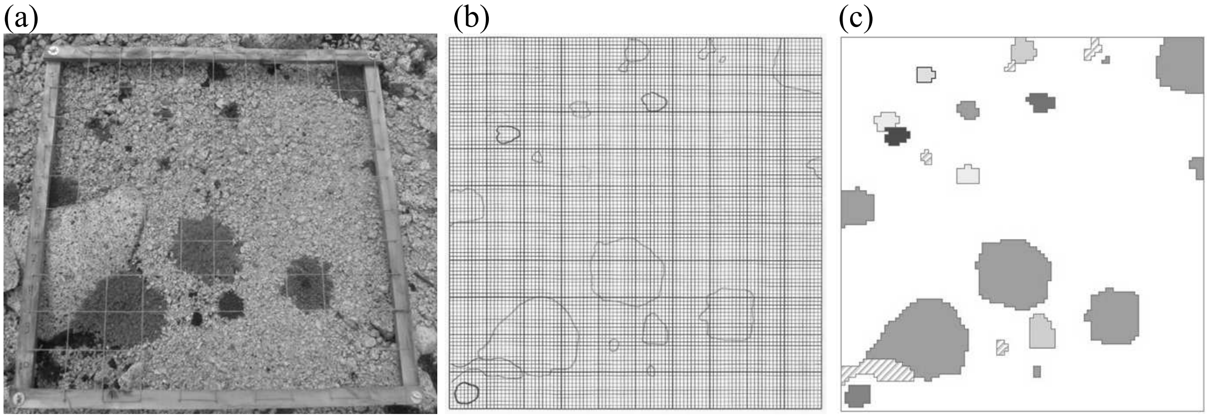


Fig. 3

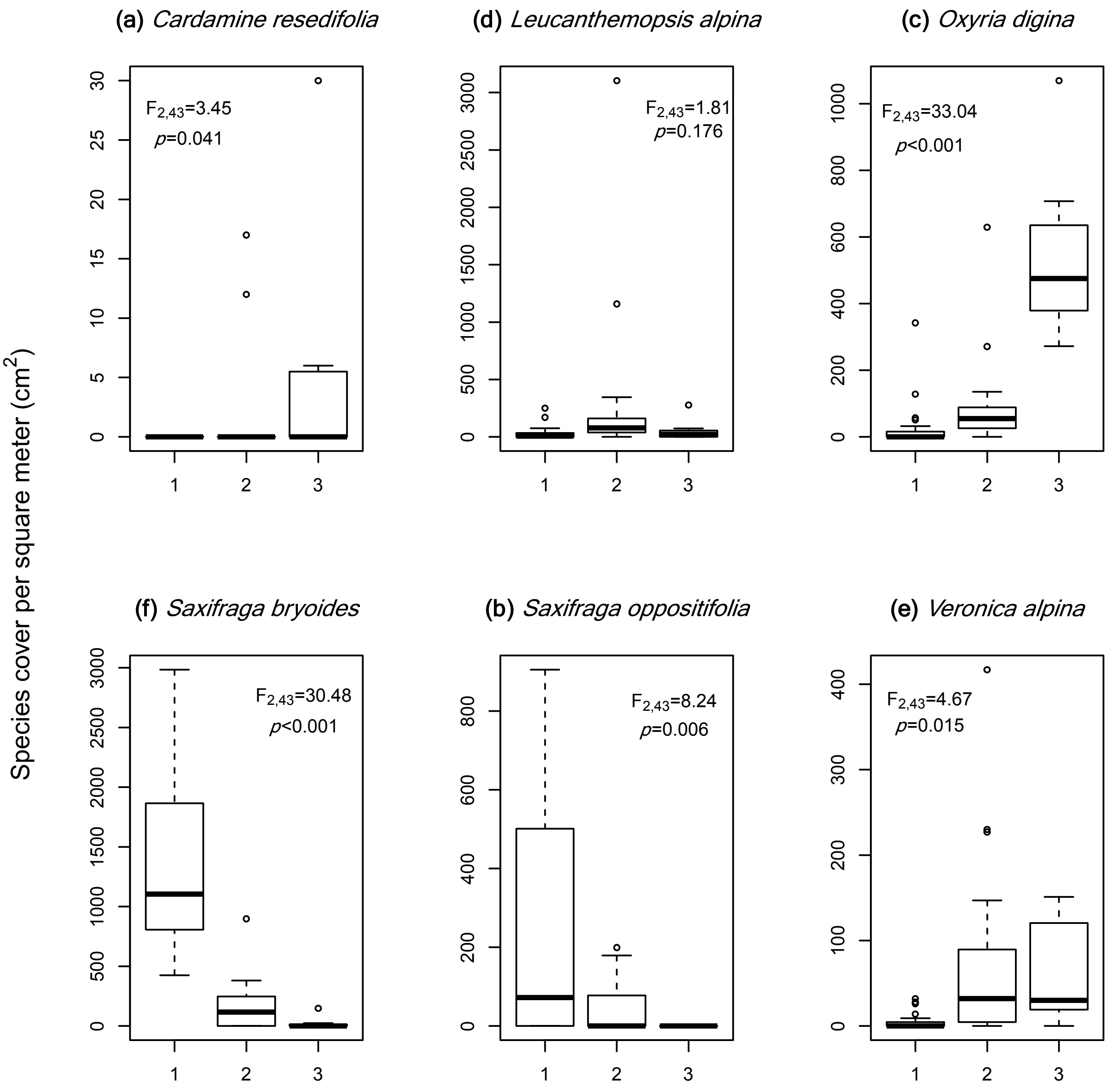

(a) Cardamine resedifolia
F2,43=3.45
p=0.041
(d) Leucanthemopsis alpina
F2,43=1.81
p=0.176
(c) Oxyria digina
F2,43=33.04
p<0.001
(f) Saxifraga bryoides
F2,43=30.48
p<0.001
(b) Saxifraga oppositifolia
F2,43=8.24
p=0.006
(e) Veronica alpina
F2,43=4.67
p=0.015
Species cover per square meter (cm2)
1
2
3

Fig. 4

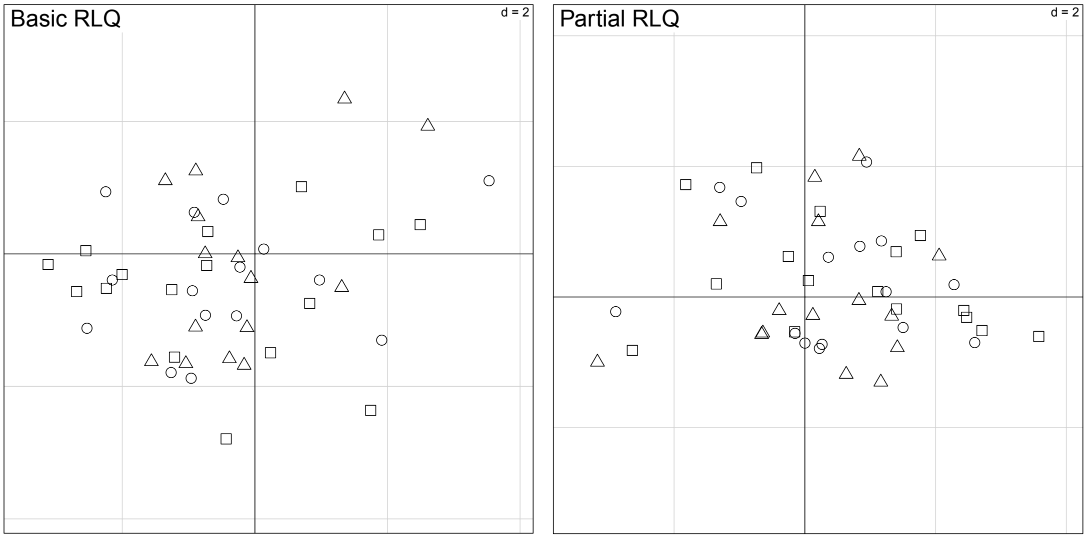
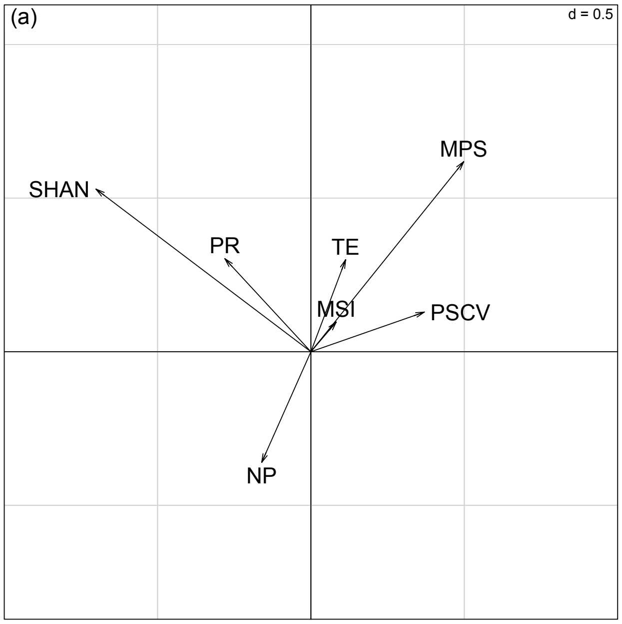
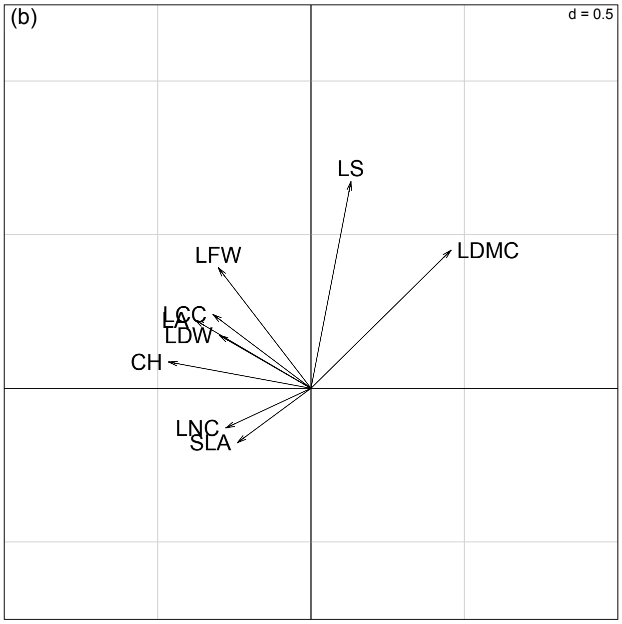


Fig. 5


(a)
d = 0.5
MPS
SHAN
PR
TE
MSI
PSCV
NP


(b)
d = 0.5
LS
LDMC
LFW
LCC
LA
LDW
CH
LNC
SLA

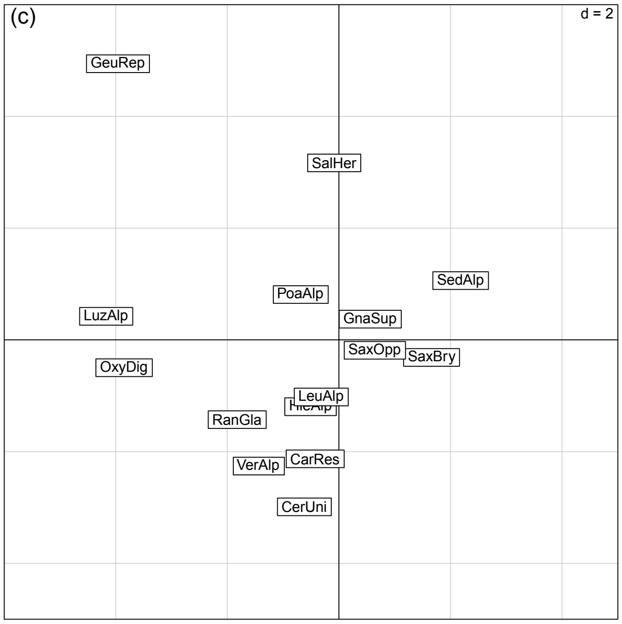
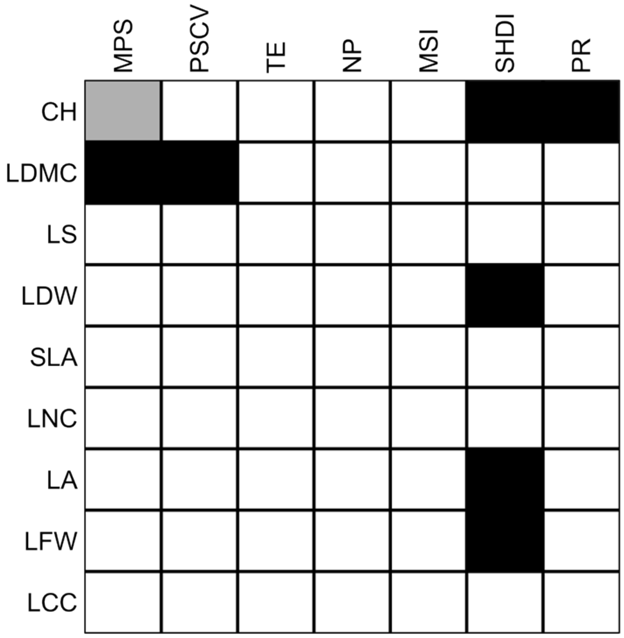

(c)
d = 2
GeuRep
SalHer
SedAlp
PoaAlp
LuzAlp
GnaSup
SaxOpp
SaxBry
OxyDig
LeuAlp
RanGla
CarRes
VerAlp
CerUni

Fig. 6



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

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