



Community-level variation in plant functional traits and ecological strategies shapes habitat structure along succession gradients in alpine environment

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Abstract

Plant traits and ecological strategies elucidate various aspects of ecosystem functioning and services. However, the well-recognized trade-offs evident at the species level are not always expected to mirror community-level variation. Here, we investigated, at the regional scale, the community-level trade-offs of three key plant traits representing economics and size spectra (LA—leaf area, LDMC—leaf dry matter content and SLA—specific leaf area) and Grime's CSR (competitive, stress tolerant, ruderal) plant strategies. We compared six siliceous alpine plant communities, also representative of Habitat types of EU Community interest (Habitats Directive, 92/43/EEC), distributed along a succession gradient, using a wide range of phytosociological relevés for which we calculated community weighted mean (CWM) trait values and *C*-, *S*- and *R*-scores. Our aims were to: (1) determine the validity of the plant community global spectrum of trait variation within alpine habitats; (2) investigate the discriminating capacity of plant traits and strategies to identify functional niches of dominance, stress and disturbance along the succession gradient; (3) quantify the variation in community structure (species richness and total species cover) through such functional niches. We observed a clear pattern of community-level trait variation that reflected the plant economics spectrum: from acquisitive and fast-growing characteristics in pioneer succession stages, to conservative and stress-tolerant features toward the succession climax, while the productive niche typical of *C*-selected strategies was scarce. Species richness and total species cover were both greater at intermediate levels of *S*- and *R*-selection gradients, indicating high niche differentiation in habitats characterized by exposure to stress or disturbance. Overall, this study demonstrates that trait trade-offs between communities identified at the global scale can undergo adaptation at the regional scale caused by local environmental conditions and also confirms the applicability of CSR strategies to investigate community-level variation of alpine vegetation.

Keywords Community weighted mean · CSR theory · Functional identity · Functional niche · Habitats directive · Natura 2000

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Introduction

Understanding the forces driving plant community functions has been one of the major goals of vegetation ecology over recent decades. These mechanisms have typically been investigated by analyzing plant functional traits, which are known to provide deeper insights into ecosystem functioning than approaches based solely on species identity (Díaz and Cabido 2001; McGill et al. 2006; Dubuis et al. 2013). Plant functional traits are defined as any morphological, physical or phenological features measurable at the individual level that affect the fitness of the individual (Violle et al. 2007). The main plant trait spectra that have been globally identified represent the trade-offs between resource economics and the

size of plants and their organs (Díaz et al. 2016). Recently, by adopting the mass-ratio hypothesis (i.e., weighting trait values by species abundance; Grime 1998), it was confirmed that half of the global trait variation at the community level reflects such trade-offs (Bruehlheide et al. 2018). Bruehlheide et al. (2018) even stressed that such community trade-offs are weakly associated with climate and soil conditions at the global scale, and that trait combinations are predominantly filtered by local-scale factors. Hence, evaluating the consistency of these global-scale observations in well-defined environments at the regional scale could provide useful elements for the interpretation of trait variation within plant communities.

Many plant traits have a restricted geographic and phylogenetic coverage (Díaz et al. 2016), whereas three leaf traits are applicable to all vascular plant life forms worldwide and represent a wide range of plant functioning: leaf area (LA), determinant of the capacity to intercept light; leaf dry matter content (LDMC), associated with nutrient retention within the plant; specific leaf area (SLA), related to assimilation and growth rates (Garnier et al. 2017). LA is an indicator of the size spectrum, while LDMC and SLA describe opposite extremes of the plant economics spectrum (Díaz et al. 2016). For these reasons, LA, LDMC and SLA are also used to calculate plant CSR (competitive, stress tolerant and ruderal) strategies (Grime 2001), by integrating both plant economics (typical of S to R strategy selection) and plant size (typical of the C strategy) variation spectra in a three-way trade-off in plant functioning (Pierce et al. 2017).

Crucially, C, S and R values are not calculated directly from LA, SLA and LDMC: it is the trade-off between these traits, compared against the global spectrum (position along multivariate axes based on the global ranges of trait values), from which the CSR value is calculated, providing an absolute quantitative comparison with the global flora (Pierce et al. 2017). CSR analysis has allowed strategies to be determined for a wide range of vascular plant species from habitats worldwide, and many examples have been produced using the concepts of interspecific variation and of the ‘strategy of the single species’ (e.g., Cerabolini et al. 2010; Negreiros et al. 2014; Good et al. 2019; Rosenfield et al. 2019). In contrast, an approach involving the ‘community strategy’ or functional signature of the vegetation as a whole is much less evident (Hunt et al. 2004; Ciccarelli 2015; Ricotta et al. 2015; 2016; Cerabolini et al. 2016; Li and Shipley 2017), but could provide key insights into the variability of adaptations within plant communities.

This goal could be achieved, for example, by investigating the functional signature of plants along gradients of vegetation succession, which is an approach often used to gain a better understanding of the variation of plant traits along environmental gradients (Weiher et al. 2011), or to use these to predict community composition (Shipley et al.

2006). The CSR scheme has already been tested in alpine habitats along vegetation primary succession, as well as following zooanthropogenic modifications of climax (i.e., anthropogenic disturbances involving domesticated animals, such as cattle grazing), although only at the species level or at a local scale (Caccianiga et al. 2006; Pierce et al. 2007b; Pierce et al. 2017; Ricotta et al. 2015; 2016). However, the consistency of the CSR scheme at the community level over a regional scale has not yet been tested, despite promising recent results such as those arising from manipulation experiments of herbaceous mesocosms along a gradient of stress and disturbance (Li and Shipley 2017). Thus, it remains crucial to understand patterns of community variation of plant traits and strategies along environmental gradients such as those underpinning vegetation succession.

Mean values of traits and strategies along environmental gradients can be representative of functional niches (Violle et al. 2009; Pierce and Cerabolini 2018), which in turn could be used to investigate community structure, in terms of the mechanisms determining species richness and total species cover. Indeed, even though several phenomena control these two properties in herbaceous vegetation, they can be generalized in the form of the humped-back model of species richness and biomass production (Grime and Pierce 2012). Productive environments favor species that dominate via competitive pre-emption of resources, leading to a reduction of species richness, while stress and disturbance initially stimulate diversity by suppressing potential competitors, but beyond a certain point, only highly specialized organisms can survive, again reducing species richness. Thus, at intermediate productivities, there is a greater range of potential opportunities (Pierce 2014) at which greater variation in functional trait values, CSR strategies and species richness have been demonstrated (Fraser et al. 2015; Cerabolini et al. 2016).

In the present study at the regional scale, we investigated the extent of community-level variation of key plant traits (LA, LDMC and SLA) and Grime’s CRS ecological strategies of six alpine plant communities along a succession gradient. Communities were also representative of three Habitat types of EU Community interest (Habitats Directive, 92/43/EEC): 8110 ‘Siliceous scree of the montane to snow levels (*Androsacetalia alpinae* and *Galeopsetalia ladani*),’ which represents early successional stages; 6150 ‘Siliceous alpine and boreal grasslands’ and 4060 ‘Alpine and Boreal heaths’, respectively, including middle and late successional stages. Specifically, we aimed to:

- (1) Determine whether the functional characterization of alpine plant communities agrees with the major axes of variation within the global spectrum of vegetation communities (Bruehlheide et al. 2018);

- (2) Examine the discriminating capacity of plant traits and strategies at the community level to identify well-defined functional niches involving competition, stress and disturbance along the succession gradients;
- (3) Quantify the changes in communities structure, in terms of species richness (as a proxy of taxonomic diversity) and total species cover (sum of species cover as a proxy of biomass, Ónodi et al. 2017) within the functional niches identifiable along the succession gradient.

Methods

Study area

The vegetation relevés considered in this study were all located in the central-eastern Italian Alps, in the administrative region of Lombardy (Northern Italy), and spanned a surface area of approximately 3300 Km² between latitude 45°35′–46°33′ N and longitude 9°17′–10°33′ E (Fig. 1). In this area, the relevés were distributed within the altitudinal range of the most representative alpine habitats, from approximately 2000 to 3000 m a.s.l. The climate is continental in the internal valleys, with low precipitation mainly concentrated in summer, and sub-Atlantic in the external belts, with slightly higher precipitation and lesser thermal excursions. Despite the scattered presence of carbonate outcrops, geological substrates are mainly metamorphic silicate rocks with gneiss and serpentinite, and alluvial and glacial deposits.

Dataset and traits measurement

We based our analyses on phytosociological relevés representative of the main siliceous alpine plant communities of the study area, available in the Lombardy regional database of plant communities referring to Habitat types of EU Community interest (Annex I of Directive 92/43/EEC) (<http://www.biodiversita.lombardia.it>) (Appendix S1). We selected 382 relevés representative of three Habitat types on alpine silicate substrates (8110 ‘Siliceous scree of the montane to snow levels (*Androsacetalia alpinae* and *Galeopsetalia ladani*)’, 6150 ‘Siliceous alpine and boreal grasslands’, 4060 ‘Alpine and boreal heaths’), divided into six sub-habitats representative of a gradient of vegetation succession, from pioneer to stable and more highly structured plant communities (Table 1), according to Giacomini and Pignatti (1955). We adopted the classification of sub-habitats following the monitoring protocol of Habitat types of Community interest at the regional scale for region Lombardy (Brusa et al. 2017). Specifically, we identified the following sub-habitats: 8110-A ‘Siliceous scree of the montane to snow levels of *Androsacion alpinae*’, 6150-B ‘Siliceous alpine and boreal grasslands of *Salicetalia herbaceae*’, 6150-A ‘Siliceous alpine and boreal grasslands of *Caricetalia curvulae*’ and 4060-A ‘Alpine and Boreal heaths of *Loiseleurio-Vaccinion*’. We further divided sub-habitat 8110-A according to scree stability and the degree of plant colonization: instable screes with early colonization stages (8110-A1), and stable screes with relatively mature succession stages (8110-A2), following Caccianiga and Andreis (2004). Similarly, we divided sub-habitat 6150-A into two subsets depending on

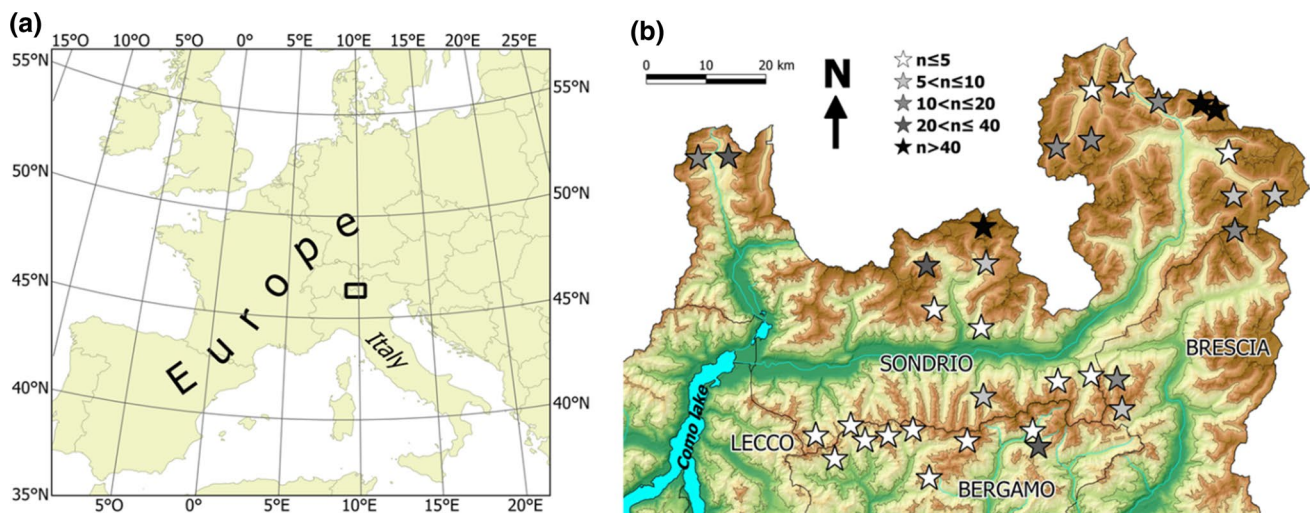


Fig. 1 **a** Location of the study area in the central-eastern Alps within the administrative region of Lombardy (Northern Italy) delimited with a bold black line and **b** density of phytosociological relevés of alpine plant communities analyzed in this study within the georefer-

enced territorial units of the Lombardy regional database of habitats of Community Interest (Annex I of Directive 92/43/EEC) (Brusa et al. 2016)

Table 1 Sub-habitats (i.e., vegetation communities discernible within each Habitat type) analyzed in this study in relation to Habitat types classification (European Commission 2013) and CORINE biotopes (Commission of the European Community 1991)

Habitat code and description	Sub-habitat code	Sub-habitat	Corine biotope	Syntaxa	<i>N</i>	Plot size range (m ²)
8110: Siliceous scree of the montane to snow levels (Androsacetalia alpinae and Galeopsetalia ladani)	8110-A1	Recent and/or disturbed moraines	61.111—Mountain sorrel screes	Androsacetum alpinae	98	6.25–500
			61.112—Rock jasmine screes	Oxyrietum digynae		
	8110-A2	Stabilized moraines	61.113—Alpine wood-rush screes	Luzuletum alpinopilosae Saxifrago bryo-Poetum alpinae	42	6.25–500
6150: Siliceous alpine and boreal grasslands	6150-B	Snowbeds	36.111 Alpine acid snow-patch communities	Polytrichetum sexangularis Salicetum herbaceae	69	1–100
	6150-A1	Microthermal climax grasslands	36.341—Carex curvula grasslands	Caricetum curvulae	89	1–100
	6150-A2	Microthermal grazed grasslands	36.342—Festuca halleri grasslands	Festucetum halleri	51	1–100
4060: Alpine and Boreal heaths	4060-A	Summit heaths on wind-exposed ridges	31.41—Dwarf azalea and Vaccinium heaths	Loiseleurieto-Cetrarietum	33	4–100

The range of the plot size is also reported (minimum and maximum). From top to bottom, the early and late successional stages, respectively. Legend: *N*, numbers of phytosociological relevés of each community

the intensity of the grazing pressure (mainly cattle pasture): low for communities dominated by *Carex curvula* (6150-A1) and high for communities dominated by *Festuca halleri* (6150-A2) (Giacomini and Pignatti 1955; Pierce et al. 2007b). For each plant species listed in the relevés, we collected data of LA, LDMC and SLA from authors' datasets, also available in TRY (Kattge et al. 2020, <https://www.try-db.org>: see datasets n. 227, 228, 229, 371, 372 and related references). Additional data for missing species (27% of all species) were collected in the field, from samples of 5 to 15 fully expanded leaves from different individual adult plants, calculating LA, LDMC and SLA following the standardized methodological protocol for plant traits measurement (Perez-Harguindeguy et al. 2016).

Data analyses

We determined Grime's CSR (competitive–stress tolerant–ruderal) plant strategies using LA, SLA and LDMC, using the StrateFy CSR classification tool (Pierce et al. 2017). This classification method represents the extent of C-, S- and R-selection using trade-offs between traits (LA, SLA and LDMC), integrated and compared with trade-offs evident globally, hence we tested the functional identity of

sub-habitats using both plant traits and CSR strategies. For each relevé, we estimated the community weighted mean (CWM, i.e., weighting the mean by the relative cover of each species in the relevé) of LA, LDMC and SLA, as well as of C-, S- and R-scores, using the R package 'FD' (Lalibertè et al. 2014). The relative cover of each species in the relevé was obtained converting the ground cover indices (5 = 87.5%, 4 = 62.5%, 3 = 37.5%, 2 = 18.75%, 1 = 6.75%, + = 0.5%, r = 0.1%).

We applied the ANOVA with a Tukey post hoc comparison test to identify significant differences among the CWMs of plant traits and strategies scores between sub-habitats combining the functions 'aov' and 'HSD.test' of R packages 'stats' and 'agricolae', respectively (de Mendiburu 2019). Before running the ANOVA, we checked for normality of functional trait and plant strategy scores by means of the Shapiro–Wilk test and, accordingly, transformed LA and SLA by square root (\sqrt{x}) and logarithmic ($\log[x + 1]$) transformation, respectively, while no transformation was required for LDMC and strategy scores. Then, we identified and removed outlier values by applying the Rosner test to the CWM trait values and plant strategy scores within each sub-habitat, using the R package 'EnvStats' (Millard 2013).

We used the R package ‘*composition*’ (van den Boogaart et al. 2018) to visualize the ternary diagram of CSR strategies; compositional mean and variances of each sub-habitat were calculated using robust estimation. Then, we tested for differences in the CWMs of CSR ternary composition among sub-habitats applying the multivariate analysis of variance (using the ‘*MANOVA*’ function of the R package ‘*stats*’). For this purpose, we transformed the dataset of CSR scores by isometric log-ratio transformation (ILR), which reduced the ternary dataset into a two-dimensional image, in order to account for the compositional data structure (van de Boogaart and Tolosana-Delgado 2013; Dalle Fratte et al. 2019a).

To identify the relationship between species richness and total species cover (sum of all species relative cover per relevé) with the functional niches of dominance, stress and disturbance identifiable along the vegetation succession gradient, we plotted these vs. the CWMs of *C*-, *S*- and *R*-scores, considering all the relevés in all the sub-habitats. We then applied upper boundary regression, which is an extensively used method in ecological studies (Pierce 2014 and references therein) that fits a regression curve to the upper boundary of the dataset. This technique divides the continuous data on the *x*-axis into classes of equal range (known as bins) and fits a regression curve to the highest *y* values within each bin; in this case, the three highest values

present within each 10% bins (of *C*-, *S*- and *R*-scores) were considered. Then, a Lorentzian 3-parameter regression curve was fitted by means of the ‘*nls*’ function of the base R package ‘*stats*’. All the statistical analyses were computed with R software (R Core Team 2019).

Results

Plant traits

The CWMs of LA, LDMC and SLA showed significant differences between sub-habitats, and LDMC and SLA changed consistently along the succession gradient (Fig. 2 and Appendix S2). With regard to LA, grazed grasslands (sub-habitat 6150-A2) exhibited plants with the largest leaves, while dwarf-shrubs heathlands (sub-habitat 4060-A) included plants with the smallest. Leaves were smaller in less stable scree and snowbed sub-habitats (respectively, 8110-A1 and 6150-B), compared to the relatively stable scree and moraines sub-habitat (8110-A2). Both scree and moraine communities (sub-habitats 8110-A1 and 8110-A2) displayed the lowest leaf construction investment (lowest LDMC), while grasslands with low grazing pressure (sub-habitat 6150-A1) and heathlands (sub-habitat 4060-A) exhibited the highest leaf construction investment (highest

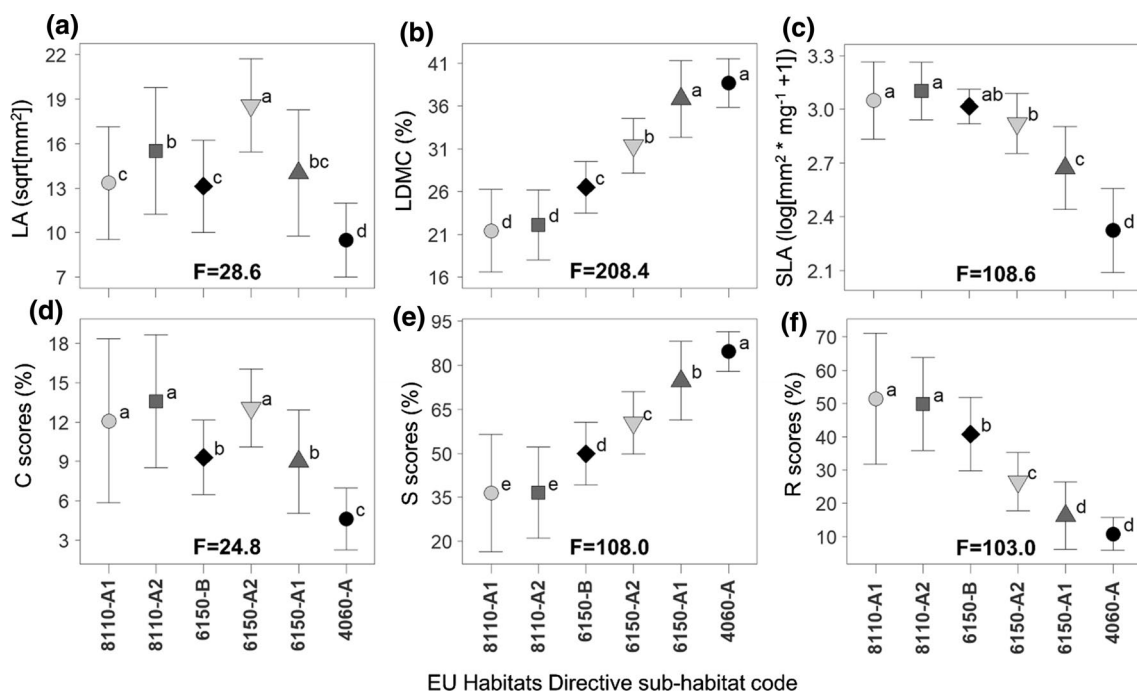


Fig. 2 Mean values and standard deviation of community weighted means (CWMs) of **a** leaf area (LA), **b** leaf dry matter content (LDMC), **c** specific leaf area (SLA), **d** *C*-strategy scores, **e** *S*-strategy scores, and **f** *R*-strategy scores for each sub-habitat (i.e., vegeta-

tion communities discernible within each Habitat type, see Table 1). Small letters indicate the results of the post hoc comparisons. Results of the ANOVA are also shown below each plot, indicating *F*-values; *p* values are always < 0.001

LDMC). The snowbed sub-habitat (6150-B) exhibited intermediate values of LDMC, being significantly higher than screes and moraines and, simultaneously, lower than the other two grassland and heathland sub-habitats. LDMC was higher in communities with low grazing pressure (sub-habitat 6150-A1) and lower with intense grazing pressure (sub-habitat 6150-A2).

SLA exhibited the opposite pattern to LDMC along the succession gradient. Both scree and moraine communities (sub-habitats 8110-A1 and 8110-A2) exhibited the most acquisitive leaves (highest mean values of SLA), opposed to heathlands (sub-habitat 4060-A) which showed the most conservative leaves (lowest mean values of SLA). Snowbeds (6150-B) showed intermediate SLA values between pioneers and the other grassland communities. SLA was higher in communities that were subject to grazing (sub-habitat 6150-A2) and lower where the grazing pressure was less intense (sub-habitat 6150-A1).

Plant strategies

All the sub-habitats significantly differed in terms of CWM *C*-, *S*- and *R*-scores (Fig. 2 and Appendix S3); however, they showed a clear pattern only along *S*- and *R*- gradients. *C*-selection was the less discriminative; nonetheless, significant differences were still present. The most competitive communities (highest *C*-scores) were early succession stages and grazed grasslands, whereas summit heathlands of wind-exposed ridges (sub-habitat 4060-A) were the less competitive (lowest *C*-scores).

Dwarf shrublands sub-habitats (4060-A) were also the most stress tolerant (highest *S*-scores), in contrast to scree and moraine communities (sub-habitats 8110-A1 and 8110-A2) which showed the lowest degree of *S*-selection. Grasslands with intense grazing pressure (sub-habitat 6150-A2) showed intermediate values of *S*-scores, being significantly higher than both scree and snowbed sub-habitats, and lower than grasslands with low grazing pressure and heathlands.

The pattern of *R*-selection opposed that for *S*-selection. Scree and moraine communities (sub-habitats 8110-A1, 8110-A2) were the most ruderal (highest values of *R*-scores) and heathlands (sub-habitat 4060-A) the less ruderal (lowest values of *R*-scores). Among grasslands, snowbeds showed the highest values of *R*-scores, while high grazing pressure (sub-habitat 6150-A2) was reflected in higher *R*-scores.

The sub-habitats differed significantly in terms of CSR ternary space occupation (Pillai = 0.61; $F = 32.8$; $p < 0.001$) and showed a robust variation along the succession gradient related to either unproductive niches (*S*-selection) or niches characterized by frequent disturbances to individuals (*R*-selection) (Fig. 3). Specifically, pioneer communities (sub-habitats 8110-A1 and 8110-A2) were placed toward the *R*-corner and displayed the highest variance, while at

the other extreme of the succession gradient, heathlands (sub-habitat 4060-A) were located closer to the *S* corner and showed the lowest variance. Among grasslands, that with the lowest grazing pressure (sub-habitat 6150-A1) exhibited a functional signature similar to that of heathlands, while snowbeds (6150-B) exhibited a signature closer to that of scree and moraine communities and showed a lower variance (Appendix S4).

Species richness and total species cover within the functional niches along the succession gradient

Since the productive niche (*C*-corner) was scarcely represented within the analyzed communities, we fitted the regression curves only along the gradients of increasing CWMs of *S*- and *R*-strategy scores, which reflect the functional niches occupied by species in these habitats (Fig. 4). Species richness and total species cover displayed significant intermediate peaks along both *S*- and *R*-score gradients.

Along the *S*-selection gradient, or what can be interpreted as a ‘productivity niche gradient’, the highest values of species richness and total species cover were exhibited by alpine siliceous grasslands (EU Habitat type 6150), specifically by the grassland sub-habitat characterized by high grazing pressure (6150-A2), at intermediate values of *S*-selection (a range of between 40 and 60% CWM *S*-score). Species richness diminished toward both the lowest and the highest values of the *S*-selection gradient, following an almost unimodal symmetrical distribution.

Species richness and total species cover followed a positive unimodal asymmetrical distribution along the *R*-selection gradient. Indeed, they exhibited an intermediate peak at low values of the ‘disturbance niches’ gradient (a range of between 20 and 30% of *R*-scores), in correspondence of grasslands with high grazing pressure.

Discussion

This study provides an overview of how CWMs of plant traits and CSR ecological strategies are selected within alpine plant communities and indicate the type and range of realized niches occupied along a succession gradient. This regional-scale analysis of the community-level variation of plant functional traits and ecological strategies implements, and also validates, the recent observation of global-scale trade-offs that modulate trait combinations (plant height and resource acquisitiveness), not only between species (Díaz et al. 2016) but also between plant communities (Bruehlheide et al. 2018). However, within alpine plant communities, size variation is scarcely evident, probably because these communities are characterized by a simple vertical structure

Fig. 3 Community weighted means (CWMs) of each sub-habitat (i.e., vegetation communities discernible within each Habitat type, see Table 1) represented within the CSR strategy triangle displaying their means and variances

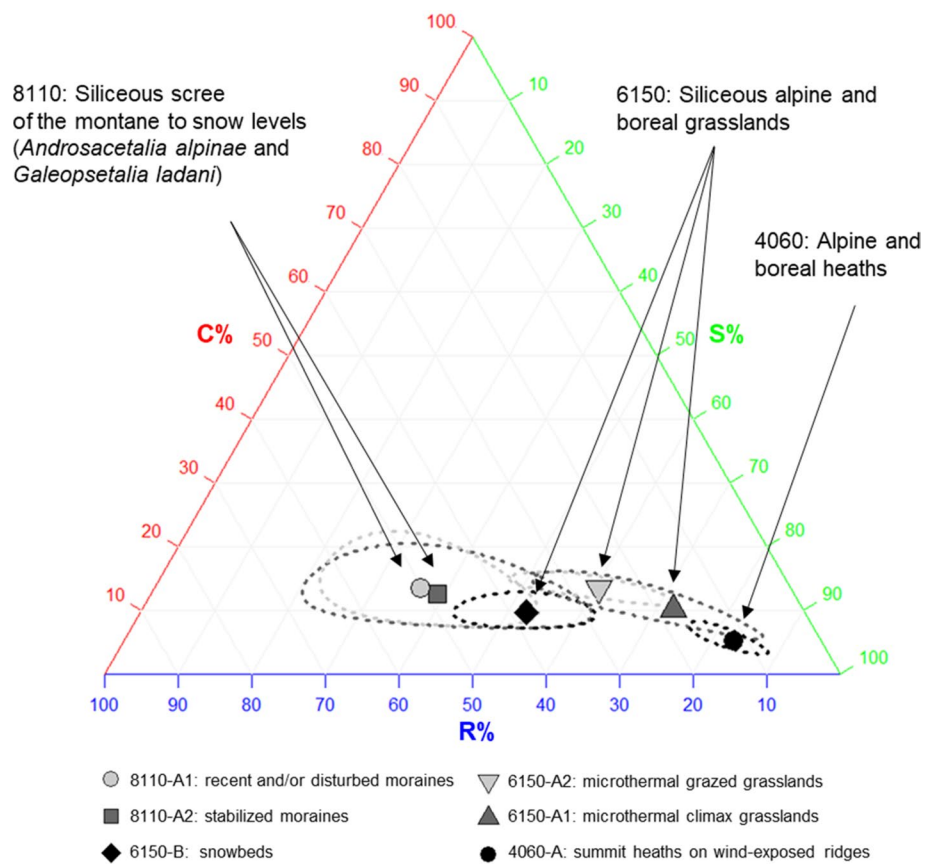
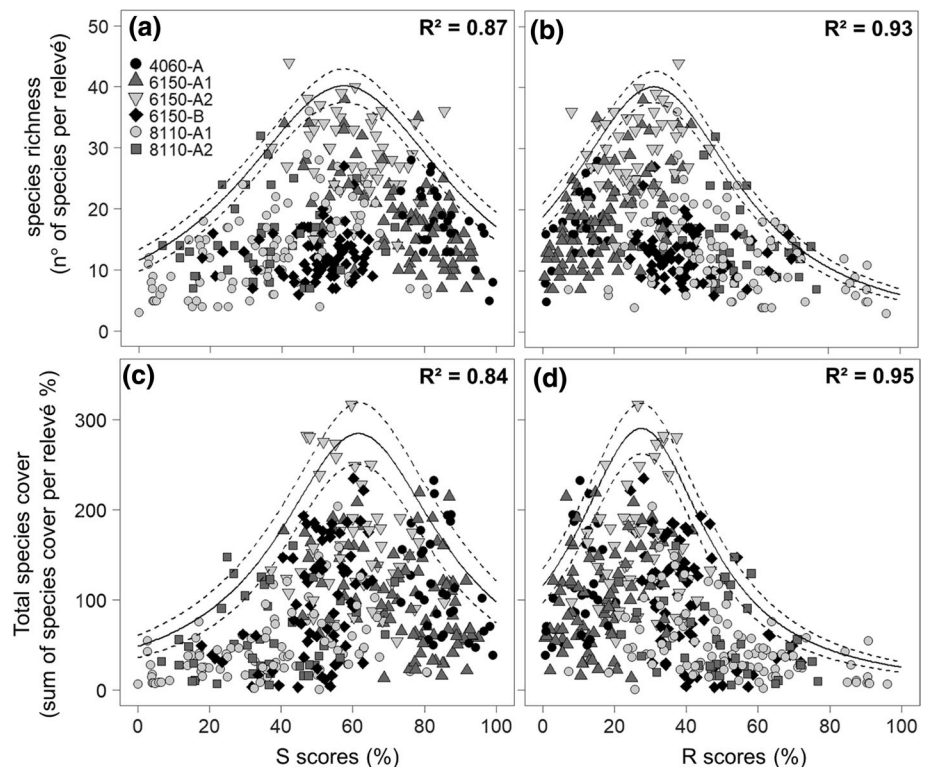


Fig. 4 Upper boundary regression of species richness (a, b) and total species cover (c, d) of sub-habitats (i.e., vegetation communities discernible within each EU Habitat type, see Table 1) along the gradient of increasing community weighted means (CWMs) of *S* (a, c) and *R* (b, d) strategy scores. Lines represent the Lorentzian 3-parameter regression curve (continuous line) and its 95% confidence interval (dotted line). The significance of the fitting of the upper boundary regression curve is also shown in each plot, indicating R^2 values; p values are always < 0.0001



with species belonging mostly to the herbaceous-shrubby layer (Thomas et al. 2020). Nonetheless, we found evidence that local-scale factors underpinning the vegetation succession gradient select trait combinations at the community level (Bruehlheide et al. 2018), which are strongly reflected also within the framework of Grime's CSR strategy theory (Grime 2001; Grime and Pierce 2012).

The restriction of trait variability to a subset of those available in the regional species pool (i.e., functional convergence; Grime 2006) is typical of habitats of low temperatures (De Bello et al. 2013, Rosbakh et al. 2015; Wright et al. 2017; Thomas et al. 2020), such as those of high altitudes. However, the CWMs of traits relevant to the leaf economics spectrum (LDMC and SLA; Wright et al. 2004; Reich 2014) changed consistently with variations of the local environmental conditions underpinned by the succession gradient. Confirming previous observations (Grime 2001; Díaz et al. 2004; Gobbi et al. 2010; Li et al. 2017), communities from pioneer succession stages (scree, moraines and glacier forelands) are characterized by rapidly growing species (high SLA and low LDMC) that are replaced, as the succession goes on, by species with low relative growth rates and conservative–exploitative tendencies (low SLA and high LDMC).

However, such differences along succession gradients are almost never linked to just one environmental factor, but rather to their interactions. For instance, instable and stable scree sub-habitats showed similar CWMs of traits related to the leaf economics spectrum among them, almost comparable to snowbed communities (particularly SLA), highlighting the striking relationships between scree habitats and short growing seasons, because of the late snow melting in snowbeds, as also found in local-scale studies (Choler 2005). Considering that SLA is negatively related to leaf lifespan and positively related to relative growth rate (Reich 2014; Wright et al. 2004), to overcome this 'time constraint' for seasonal growth, these habitats select species with trait attributes that optimize carbon acquisition: fast-growing and low-cost leaves with short lifespan and high SLA (see also Kudo et al. 1999). Similar convergence also for LA due to late snow melting could be expected (Venn et al. 2011). However, among these three sub-habitats, LA increased with the greatest substrate stability (sub-habitat 8110-A2), possibly indicating a lower constrained allocation of resources favored by more stable substrates. We also observed the opposite trend in microthermal grasslands related to the effects of grazing pressure (Pierce et al. 2007b), which were characterized by fast-growing and acquisitive species. This may seem to contrast the expectation that communities exposed to high grazing pressure should develop resistance to herbivory by selecting species with tougher leaves (Pellissier et al. 2018). Despite this, grazing generates local disturbance due to cattle trampling and increases soil nutrient

content and nutrient 'patchiness' (Peco et al. 2017), favoring exploitative species with greater colonization ability and faster growth rates (Niu et al. 2015).

These results are even more evident from the analyses of Grime's CSR plant strategies, which highlighted the ruderal to stress-tolerant gradient along the succession (Fig. 3). This strategy spectrum suggests that niche segregation and coexistence within alpine plant communities are mediated by a strong functional divergence with response to differential local stress and disturbance (see also Pierce et al. 2007b). The strong ruderal characteristics (rapid completion of the life cycle and selection of regenerative traits) exhibited by scree and snowbed sub-habitats are a response to their exposure to disturbance, which in alpine habitats is mainly represented by geomorphological and seasonal-climatic factors. Our results support the hypothesis that continued physical disturbance has a relevant role in the initial stages of primary succession (Matthews 1992; Caccianiga and Andreis 2004; Caccianiga et al. 2006; Ricotta et al. 2015; 2016; Pierce et al. 2017). Conversely, toward the late succession stages, climax grasslands and shrubland sub-habitats showed strong selection toward stress-tolerant characteristics, i.e., low productivity and conservative adaptations, typical of harsh niches. Generally, in the alpine context, seasonal variation and disturbance are marked and the period suitable for growth is often short, leading to a high survival risk for many species which must invest in defensive adaptations against such situations rather than in improving their competitive ability (Gobbi et al. 2010).

The functional convergence toward stress-tolerant strategies in mature communities demonstrates that alpine plant communities do not include productive niches that select for competitive strategies (Fig. 3). Competition is generally assumed to be more prominent at low elevations and at sites with low abiotic stress (Choler et al. 2001; Callaway et al. 2002), while it diminishes with altitude and relatively stressful physical conditions. However, the presence of this empty niche also suggests some possible future scenarios emerging from climate change. In particular, a warmer climate with longer growing season, as expected in the European Alps in future decades (Kovats et al. 2014; EEA 2017), could expose these habitats to the intrusion of new competitor species from lower altitudes or even exotic flora (Thuiller et al. 2008; Bjorkman et al. 2018; Dalle Fratte et al. 2019a, b). This scenario would result in shifting dominances of species within communities and in the formation of novel species assemblages and thus will modify ecological networks altering ecosystem processes (Walther 2010).

We found robust evidence at the regional scale that CSR theory is a powerful tool to investigate the functional niches available within communities (response to abiotic factors as mediated by CWMs of CSR strategies) and their structure (species richness and total species cover), refining similar

observations that can be obtained using species plant traits trade-offs (Violle and Jiang 2009). Species richness and total species cover exhibited a unimodal distribution curve along both gradients of productivity (*S*-scores) and disturbance (*R*-scores) (Fig. 4), with microthermal grasslands mainly ordinated at the peak of the curve. In particular, grazed grasslands represented the sub-habitat with the highest species richness and total species cover. Indeed, although herbivory is a supplementary source of disturbance, it imposes strong selection on plant communities, suppressing potential dominant species and favoring diversity by allowing a larger number of subordinate species to coexist (Pierce et al. 2007a, b; Cerabolini et al. 2016).

It is widely recognized that the pattern between community diversity and disturbance is well predicted by a unimodal curve, according to the humped-back model (Grime 1973). Here, we confirm that in alpine context this pattern is highly consistent also in terms of the total species cover; in fact, its maximum corresponds with that of species richness along the same gradient. This may seem in conflict with the humped-back curve of biodiversity and biomass (e.g., Pierce 2014; Fraser et al. 2015; Cerabolini et al. 2016). However, as the competitive strategy is not represented in alpine ecosystems, the right-hand flank of the humped-back model is not well represented (the side related to the competitive niche, Grime and Pierce 2012) and high species richness corresponds to the highest biomass production. While an increase in stress or disturbance drives an homogeneous selection toward high niche differentiation, their weakening leads to differential increase in species richness and biomass along *S*- and *R*-scores (respectively, symmetrical and positive asymmetrically distributed). Distinct processes thus operate along the two gradients, specifically, the faster increase in species diversity and biomass with decreasing stress agrees with the stress gradient hypothesis (Maestre et al. 2009; Malkinson and Tielbörger 2010), which suggests that facilitation is more common in conditions of high abiotic stress.

Conclusions

This study demonstrated that alpine communities are strongly selected in terms of the economics spectrum, but the stable, productive niche typical of *C*-selected strategies is scarcely represented, suggesting that trade-offs between communities at the global scale can experience adaptations at the regional scale caused by local environmental conditions. Moreover, Grime's CSR strategies allowed a more precise functional interpretation of alpine vegetation along the succession gradient compared to single plant traits, allowing the identification of realized functional niches within alpine communities. Our results proved these relationships to be robust over a regional scale, and not only at a local scale

as for previous studies, thus that they provide a legitimate general representation of siliceous alpine vegetation.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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