Quantifying the extent of plant functional specialization using Grime's CSR strategies

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ABSTRACT

Specialization refers to a species adaptation to a restricted range of environmental conditions. While generalist species are able to exploit a wide variety of resources in a broad range of habitats, specialist species tend to have narrower niche breadths. From an evolutionary perspective, specialization is the result of a functional syndrome in which a suite of traits covary to allow the effective exploitation of specific resources. Accordingly, the measurement of specialization should be based on a multi-trait approach. In plant ecology, a well-known classification of the adaptive strategies of plants is Grime's competitor, stress tolerator, ruderal (CSR) theory in which the three principal strategies represent relatively easily measurable trait combinations from the global spectrum of plant form and function arising under conditions of competition, abiotic restriction to growth or periodic disturbance, respectively. In this paper, we thus introduce a method to summarize the functional specialization of plant species and communities by applying inequality measures to Grime's CSR strategies. The general idea is that a plant species that can be exclusively assigned to one CSR strategy can be considered a specialist (as it adopts only one adaptive strategy to access resources), while species that share functional characteristics of multiple CSR strategies can be considered more generalist. The behavior of the proposed measures is shown with one case study on the functional changes of six Alpine vegetation types ordered along a gradient, from pioneer to more stable communities.

1. Introduction

Specialization refers to a species adaptation to an increasingly narrower niche breadth. Generalist species are able to persist in a broad range of habitats exploiting a wide variety of resources, whereas specialist species are adapted to a restricted range of environmental conditions (Devictor et al., 2010; Carboni et al., 2016; Morelli et al., 2019). Accordingly, specialist species with narrow environmental tolerance and limited resource exploitation are commonly more prone to extinction and more negatively impacted by perturbations than generalists (McKinney and Lockwood, 1999; Bergamini et al., 2009; Colles et al., 2009; Clavel et al., 2011; Bowler et al., 2019; Benedetti et al., 2022). Likewise, communities and ecosystems that host many specialist species can be expected to be particularly sensitive to on-going

environmental changes (Carboni et al., 2016). Measuring the level of specialization of a given species or assemblage is thus an important step to effectively identify their degree of vulnerability to global change.

The first measures of specialization were usually based on a simple Boolean distinction between specialist and generalist species relative to the species affinity for a specific land use or habitat type (e.g. Gregory et al., 2005). More recently, several continuous measures of habitat specialization have been developed (e.g. Devictor et al., 2010; Poisot et al., 2012). Since generalist species tend to colonize a wider range of habitats with more variable environmental conditions compared to specialist species, one line of attack to summarize specialization consists in measuring the variability in environmental conditions across the sites in which a species occurs (Clavero and Brotons, 2010). For example, the Species Specialization Index (SSI; Julliard et al., 2006) and its successive

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variations quantify habitat specificity based on the frequency of occurrence of a given focal species among habitat classes (Devictor et al., 2008; Clavel et al., 2011; Larsen et al., 2011; O'Reilly et al., 2022).

A second approach to quantify specialization reflects the species response to environmental heterogeneity in terms of species turnover (Fridley et al., 2007). Being adapted to a wider range of environmental conditions, generalist species should have a relatively high rate of species turnover across the sites in which they occur. That is, generalist species are expected to co-occur with a relatively high number of species with different ecological features, whereas specialists should consistently co-occur with a more limited set of ecologically more homogeneous species. Accordingly, species turnover rates indirectly mirror the species' response to environmental heterogeneity (Carboni et al., 2016).

Morelli et al. (2019) further proposed a general measure of specialization that summarizes the habitat specialization of bird species by applying the Gini index of inequality to the Boolean degree of association (scored as 0 or 1) of a given focal species to different habitat types. According to this proposal, habitat specialization varies from 0 for a species that occurs in all habitat types to 1 for a species associated with a single habitat type. Since specialization is generally considered a multidimensional concept (Devictor et al., 2010; Benedetti et al., 2022), Morelli et al. (2019) applied the same specialization index to four additional sets of categorical variables related to diet, foraging behavior, foraging substrate, and nesting site characteristics. For example, diet specialism varied from 0 for a species that uses all diet types to 1 for a species associated with a single type of diet (out of 9 types, incl. leaves, fruits, seeds, arthropods, etc., constituting at least 10% of the diet).

The Gini coefficient is one of the many well-known indices that have been used for more than fifty years to quantify the evenness or unevenness of the distribution of plant species abundances within communities (Chao and Ricotta, 2019). Therefore, in vegetation science, the extension of evenness indices to the measurement of the species degree of specialization has great potential to develop an ecological indicator of specialization that is not severely affected by local environmental conditions.

Specialization, seen through the lens of evolutionary theory, should be evident as particular phenotypes with extreme phenotypic characteristics. Quantification and analysis of phenotypic traits, and thus the extent of adaptive specialization, is thus an area of overlap between evolutionary and ecological theory, with ecology providing methodologies for measuring 'functional traits' (i.e. phenotypic characters that affect survival). A further concept common to both evolutionary and ecological theory is that of suites of traits acting together to influence survival, and of trade-offs between these sets of traits acting during local adaptation: these evolutionary concepts can be summarized and quantified by ecological adaptive strategy schemes (Grime, 2001). Indeed, Grime's (1977; 2001) competitor, stress tolerator, ruderal (CSR) theory aims to explain the principle adaptive responses of plants and the variation in plant function between extreme functional types (see also Grime and Pierce, 2012). According to the CSR scheme, competitors (C) are species of stable and productive habitats that invest resources in relatively rapid and continued growth of large individuals which allows for resource preemption. Stress-tolerators (S) are adapted to conditions of variable productivity in which extensive reserve tissues buffer metabolic rates from environmental variability. Ruderals (R) invest a large proportion of resources in propagules, from which the population can regenerate despite repeated disturbances (Grime, 1977; Pierce et al., 2017). Based on Grime's CSR theory, the adaptive functional strategies of vascular plants can be thus compared within and between communities by means of ternary diagrams.

Variation in CSR strategies mirrors trade-offs in the world-wide leaf economics spectrum and the leaf size spectrum (i.e. the global spectrum of plant form and function, *sensu* Díaz et al., 2016). Accordingly, Pierce et al. (2017) developed a CSR-classification method by which the trade-offs between a few easily determined leaf traits in both functional spectra are used to assign species a position in the triangular space of CSR strategies. Very high values of specific leaf area (SLA) and leaf dry matter content (LDMC) reflect both extremes of fast and slow leaf economics, respectively. At the same time, orthogonal to the leaf economics spectrum, leaf area (LA) is associated with the species' ability to intercept light and hence also with plant and seed size (Cerabolini et al., 2010; Pierce et al., 2012; 2013; 2014; Díaz et al., 2016).

The aim of this paper is thus to propose a method to quantify the functional specialization of plant species and communities applying evenness-like measures to Grime's (1974) CSR strategies. The general idea is that a plant species that can be exclusively assigned to one CSR strategy can be considered a specialist (as it adopts only one adaptive strategy to access resources), while species that share functional characteristics of multiple CSR strategies can be considered more generalist. As a case study, we used historical data on Alpine vegetation belonging to six different successional stages ordered along a gradient, from pioneer to more stable communities. As specialization is generally associated with stability, particularly in extreme environments such as cold alpine habitats (Boulangeat et al., 2012), we hypothesize that the shift toward more mature and stable communities is characterized by increasing specialization (i.e. species tend to occupy more extreme regions of the CSR triangle).

2. Data

The dataset was compiled by Zanzottera et al. (2020) and consists of 382 phytosociological relevés (i.e. plant community plots of variable size and shape with abundance data for all recorded species, which we now refer to as plots) available in the biodiversity database of the administrative region of Lombardy, Northern Italy (http://www.biodiversita.lombardia.it). The plots are representative of the main siliceous plant communities in the central-eastern Italian Alps and were distributed within the altitudinal range of the most typical Alpine habitats, from approximately 2000 m to 3000 m a.s.l. Geological substrates and moraine deposits mainly consist of metamorphic silicate rocks with gneiss and serpentine. The climate is mainly continental or subcontinental with low annual precipitation, mostly concentrated in the summer.

The plots belong to six Alpine successional stages on silicate substrates, from pioneer to more highly structured communities: vegetation of recent and disturbed moraines (8110-A1; 98 plots), vegetation of stabilized moraines (8110-A2; 42 plots), vegetation of Alpine snowbeds (6150-B; 69 plots), microthermal grazed grasslands dominated by *Festuca halleri* (6150-A2; 51 plots), microthermal climax grasslands dominated by *Carex curvula* (6150-A1; 89 plots), Alpine summit heaths (4060-A; 33 plots). Nomenclature follows the classification of EU habitats of Community interest (European Commission, 2013) and Zanzottera et al. (2020).

Species abundances within plots were estimated visually in the field with a Braun-Blanquet (BB) seven-point ordinal scale. Prior to analysis, the BB scores were converted to percentage values by using the mean values of the interval cover classes: r = 0.1%, + = 0.5%, 1 = 6.75%, 2 = 18.75%, 3 = 37.5%, 4 = 62.5%, 5 = 87.5% (Zanzottera et al., 2020). The precision level obtained with this transformation is generally considered adequate for the information provided by the BB scale (see e.g. van der Maarel, 1979). Note that other transformations, such as the conversion of the BB scores to ranks (van der Maarel, 1979; 2007) did not significantly change the sign and strength of our results.

3. Methods

3.1. CSR strategies

According to Morelli et al. (2019), evenness-based measures of specialization provide information on species adaptations to environmental conditions. However, the identification of traits representing the relevant dimensions of environmental space remains challenging (Reif

et al., 2016). As emphasized by Devictor et al. (2010), specialization can be seen as a functional syndrome in which several traits covary to affect the species fitness and survival, thus allowing the effective exploitation of particular resources. Therefore, measures of functional specialization should be related to multiple trait dimensions (Morelli et al., 2019; Benedetti et al., 2022).

The CSR classification method of Pierce et al. (2017) assigns continuous percentage values of each strategy axis (C, S, R) realized by a focal plant species based on the trade-off between the leaf traits LA, SLA and LDMC, compared to their global range of values. Although LA, SLA and LDMC cannot represent all factors that affect plant functioning, the three leaf traits are related to a broader spectrum of whole-plant, leaf and reproductive traits. Accordingly, the method is generally applicable to vascular plants, thus allowing for general conclusions and global comparisons (Pierce et al., 2017).

For all plant species sampled along the successional gradient, the values of LA (mm^2), LDMC (%) and SLA (mm^2/mg) were collected by Zanzottera et al. (2020). Next, the StrateFy classification tool of Pierce et al. (2017) was used to classify the species according to Grime's CSR functional strategies with fuzzy coded values ranging from 0 to 1 such that $C + S + R = 1$ (Chevenet et al., 1994).

3.2. Species-level and community-level specialization

Following Morelli et al. (2019), we calculated the degree of specialization for each species in the dataset by applying an index of inequality or concentration (i.e. the opposite of evenness) to their CSR values. Among the many dozens of concentration measures available in the ecologist's toolbox, we used the complement of the evenness index of Williams (see Kvålseth, 2015). Let C_j, S_j, and R_j be the proportions of Grime's C, S, and R strategies for species j (with $C_j + S_j + R_j = 1$) and $P_j = (C_j, S_j, R_j)$ be the distribution of the actual CSR scores for species j. Further, let $P_1 = (1/3, 1/3, 1/3)$ and $P_0 = (1, 0, 0)$ be the most extreme distributions for a three-class classification, respectively. P_1 would correspond to a maximally generalist species for which $C_j = S_j = R_j = 1/3$, while P_0 represents a specialist species associated with a single CSR strategy. The Williams concentration is expressed as the Euclidean distance $d(P_j, P_1)$ between the actual CSR proportions P_j and the most even distribution P_1 normalized by the distance between the most extreme distributions P_1 and P_0. This is the distance for which $d(P_j, P_0)$ is expected to take on its extremal values (Kvålseth, 2015), such that the index of specialization becomes:

$$\sigma_j = \frac{d(P_j, P_1)}{d(P_0, P_1)} \tag{1}$$

The values of σ_j range from zero to one. For a given species, specialization is maximal if the corresponding point falls close to any of the corners of the CSR triangle, which refers to a situation where the value of a CSR strategy is one and the other two values are zero. Specialization progressively decreases as the point approaches the centroid of the triangle, which corresponds to an even distribution of the CSR strategies.

To assess differences in Grime's functional strategies along the vegetation succession, we first calculated the average proportion of CSR strategies in each plot. This is the mean of single species-level CSR scores weighted by the relative abundance of each species in plot k (Garnier et al., 2004):

$$\overline{C}_{jk} = \sum_{j=1}^{N} p_{jk} \times C_j \tag{2a}$$

$$\overline{S}_{jk} = \sum_{j=1}^{N} p_{jk} \times S_j \tag{2b}$$

$$\overline{R}_{jk} = \sum_{j=1}^{N} p_{jk} \times R_j \tag{2c}$$

where p_{jk} is the relative abundance of species $j (j = 1, 2, ..., N)$ in plot k such that $0 < p_{jk} < 1$ and $\sum_{j=1}^{N} p_{jk} = 1$. This yields the average distribution of the CSR scores for plot k: $P_k = (\overline{C}_{jk}, \overline{S}_{jk}, \overline{R}_{jk})$.

$\overline{C}_{jk}$, $\overline{S}_{jk}$, and $\overline{R}_{jk}$ are community-aggregated functional parameters *sensu* Violle et al. (2007). From a mathematical viewpoint, they represent the expected values of a trait if we randomly select an individual from the community. As such, $P_k = (\overline{C}_{jk}, \overline{S}_{jk}, \overline{R}_{jk})$ represents a simple summary statistic of the pool of local strategies within a given community that can be used to summarize community-level functional responses to environmental drivers (Gaüzère et al., 2019).

From the mean plot-level CSR strategies, we next calculated the community-level specialization of each plot σ_k

$$\sigma_k = \frac{d(P_k, P_1)}{d(P_0, P_1)} \tag{3}$$

A key property of the proposed specialization index is that, due to the convexity of the function in Eq. (1) for a constant three-class classification, for a given plot k the community-level specialization σ_k calculated from the $\overline{C}_{jk}$, $\overline{S}_{jk}$, and $\overline{R}_{jk}$ values is always lower than the corresponding mean of the species-level specialization values σ_j weighted by their relative abundances p_{jk}:

$$\overline{\sigma}_{jk} = \sum_{j=1}^{N} \sigma_j \times p_{jk} \tag{4}$$

such that

$$\sigma_k \leqslant \overline{\sigma}_{jk} \tag{5}$$

That is, by averaging the species CSR strategies, specialization is decreased (proof in the electronic Supplementary Material of this paper, Appendix 1).

Like classical diversity measures that can be partitioned into alpha, beta and gamma components (Whittaker 1972), this 'dilution effect' allows specialization to be decomposed into community-level specialization σ_k, mean species-level specialization $\overline{\sigma}_{jk}$ and the normalized excess of $\overline{\sigma}_{jk}$ with respect to σ_k that we will call CSR variability σ_{vark}:

$$\sigma_{vark} = \frac{\overline{\sigma}_{jk} - \sigma_k}{\overline{\sigma}_{jk}} \tag{6}$$

The values of σ_{vark} range from zero to one and represent the extent of strategy variation. That is, the variability of the CSR strategies of single species within a given plot k. If all species in plot k have the same CSR values, $\overline{\sigma}_{jk} = \sigma_k$ and hence $\sigma_{vark} = 0$. On the contrary, σ_{vark} progressively increases as individual species assume increasingly different CSR values, and complement each other in their strategies.

For each plot, the values of σ_k, $\overline{\sigma}_{jk}$ and σ_{vark} were calculated with a new R function available in the electronic Supplementary Material (Appendix 2). To visualize the ternary diagram of CSR strategies of the different plots, we used the R package 'composition' (van den Boogaart et al., 2018). We then tested for significant differences in the CSR ternary composition among the different vegetation types with distance-based multivariate ANOVA (Anderson, 2001). To this end, we used the R package 'PERMANOVA' (Vicente-Gonzalez and Vicente-Villardon, 2021). P-values were obtained by 9999 random permutations of individual plots among the successional stages. In order to account for the constant sum constraint of the CSR ternary diagram, we calculated pairwise dissimilarities between plots with the Bray and Curtis (1957) dissimilarity. This is a set-theoretical measure which is extensively used in multivariate analysis to summarize compositional differences between plots in terms of a Venn-diagram (Cross and Sudkamp, 2010;

Roberts, 2017). Finally, we separately tested for pairwise differences in the values of σ_k, $\overline{\sigma}_{jk}$, σ_{vark} and single C, S and R strategies among the six selected successional stages with standard univariate ANOVA and 9999 random permutations.

4. Results

The ternary diagram in Fig. 1 shows the mean CSR strategies of the different vegetation types. The mean CSR strategies for all plots of the six Alpine vegetation types are available in the electronic Supplementary Material (Appendix 3), together with the corresponding values of plot-level specialization σ_k, mean species-level specialization $\overline{\sigma}_{jk}$ and the extent of strategy variation σ_{vark}.

From a functional perspective, all vegetation types except the early successional stages (habitat 8110-A1 and 8110-A2) showed significant differences in their CSR strategies (Fig. 1 and Table 1). This variation along the successional gradient was mostly reflected by a progressive substitution of acquisitive and ruderal species by more conservative and stress-tolerant ones along the R-S axis. Pioneer moraine communities (8110-A1 and 8110-A2) were closer to the R-corner of the ternary diagram, whereas more mature and stable communities, such as climax grasslands (6150-A1) and heathlands (4060-A) were located toward the S-corner. Among the grassland plant communities, the CSR strategies of the Alpine snowbeds (6150-B) showed higher similarity to the moraine communities, while grazed grasslands (6150-A2) are functionally closer to the more mature and stable communities. In contrast, the presence of productive habitats that host C-selected species is much more limited. Nonetheless, significant differences in the abundance of competitor species are also present with early successional stages being the most competitive habitat types and late-successional stages the least competitive ones (Tables 1 and 2).

This strategy variation along the successional stages occurred alongside a progressive increase of plot-level specialization σ_k and mean species-level specialization $\overline{\sigma}_{jk}$, and a corresponding decrease in functional variability σ_{vark} (Fig. 1 and Table 2). Pioneer plant communities (8110-A1 and 8110-A2) and Alpine snowbeds (6150-B) which are subjected to more random dispersal processes showed the lowest degree of species-level and plot-level specialization and the highest degree of

Fig. 1. Mean plot-level CSR strategies for the six Alpine vegetation types used in this study. 8110-A1: recent and disturbed moraines (mean of 98 plots), 8110-A2: stabilized moraines (42 plots), 6150-B: Alpine snowbeds (69 plots), 6150-A1: microthermal climax grasslands dominated by *Carex curvula* (89 plots), 6150-A2: microthermal grazed grasslands dominated by *Festuca halleri* (51 plots), 4060-A: Alpine summit heaths (33 plots). The size of the symbols is proportional to the mean values of σ_k (main diagram), and σ_{vark} (top right inset) shown in Table 2.

Table 1

Results of the PERMANOVA test for pairwise differences in plot-level CSR strategies among the selected vegetation types (Bray-Curtis dissimilarity, 9999 permutations). The p-values of the pairwise comparisons between vegetation types are shown without adjustment for multiple testing (overall F = 173.8, p = 0.0001). 8110-A1: recent and disturbed moraines, 8110-A2: stabilized moraines, 6150-B: Alpine snowbeds, 6150-A1: microthermal climax grasslands dominated by *Carex curvula*, 6150-A2: microthermal grazed grasslands dominated by *Festuca halleri*, 4060-A: Alpine summit heaths.

Vegetation type	8110-A1	8110-A2	6150-B	6150-A2	6150-A1	4060-A
8110-A1		p = 0.3857	p = 0.0001	p = 0.0001	p = 0.0001	p = 0.0001
8110-A2	F = 0.8		p = 0.0001	p = 0.0001	p = 0.0001	p = 0.0001
6150-B	F = 25.1	F = 25.7		p = 0.0001	p = 0.0001	p = 0.0001
6150-A2	F = 163.2	F = 125.8	F = 84.7		p = 0.0002	p = 0.0001
6150-A1	F = 411.4	F = 279.6	F = 227.1	F = 19.9		p = 0.0001
4060-A	F = 429.5	F = 399.1	F = 366.8	F = 88.5	F = 27.1	

Table 2

Mean (SD) values of plot-level specialization σ_k, mean species-level specialization $\overline{\sigma}_{jk}$, extent of strategy variation σ_{vark} and single C, S and R strategies in each vegetation type. For each indicator, numbers followed by the same letter do not differ significantly at $p < 0.01$. Pairwise differences between vegetation types were tested with standard ANOVA and 9999 permutations of individual plots between vegetation types.

	Vegetation type					
	8110-A1	8110-A2	6150-B	6150-A2	6150-A1	4060-A
C	0.166 (0.040)[a]	0.182 (0.031)[a]	0.123 (0.043)[b,c]	0.136 (0.031)[b]	0.110 (0.034)[c]	0.064 (0.018)
S	0.342 (0.117)[a]	0.320 (0.134)[a]	0.446 (0.096)	0.627 (0.117)	0.723 (0.120)	0.836 (0.044)
R	0.493 (0.120)[a]	0.499 (0.123)[a]	0.431 (0.098)	0.237 (0.096)	0.167 (0.091)	0.100 (0.036)
σ_k	0.336 (0.110)[a]	0.337 (0.113)[a]	0.352 (0.083)[a]	0.466 (0.144)	0.594 (0.165)	0.756 (0.065)
$\overline{\sigma}_{jk}$	0.593 (0.080)[a]	0.582 (0.071)[a]	0.510 (0.108)	0.640 (0.099)	0.738 (0.104)	0.847 (0.048)
σ_{vark}	0.442 (0.133)[a]	0.424 (0.162)[a]	0.301 (0.132)[b]	0.286 (0.138)[b]	0.211 (0.137)	0.108 (0.053)

within-plot functional variability/diversity. At the other extreme of the successional gradient, climax grasslands (6150-A1) and heathlands (4060-A) showed the highest degrees of specialization and the lowest functional variability, meaning that the strong functional convergence toward stress-tolerant strategies of mature vegetation, such as low productivity and conservative adaptations goes together with an increased 'internal homogeneity' in terms of the species CSR strategies (Ricotta et al., 2016; Zanzottera et al., 2020). Not surprisingly, grazing has a strong impact on community structure promoting the assemblage of functionally diverse communities (Ricotta et al., 2022). In grazed grasslands, the moderate disturbance combined with an increase in nutrient supply related to the presence of cattle tends to increase the functional diversity of plants (Dalle Fratte et al., 2022). Therefore, despite a different position along the S-R axis, grazed grasslands (6150-A2) showed a relatively high extent of strategy variation similar to that of less mature vegetation, such as snowbeds (6150-B).

5. Discussion

In this paper, we introduced a method to assess the degree of functional specialization of plant species and communities, which is based on the application of Williams inequality index to Grime's CSR strategies.
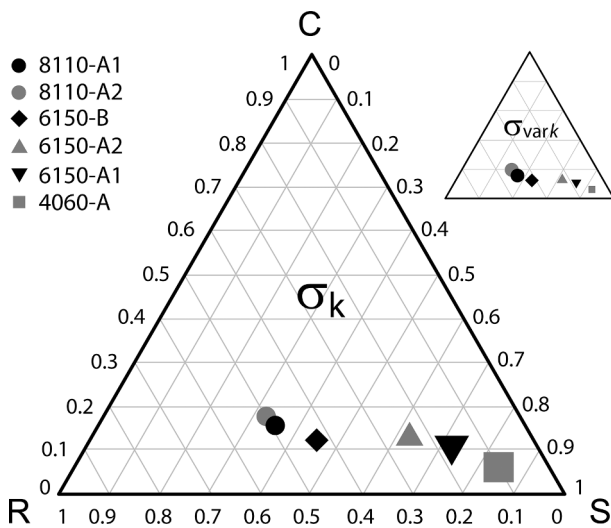
Since CSR strategies mirror the trade-offs between the main spectra of adaptive plant traits, such as plant size and resource economics (Pierce et al., 2017), the proposed method is directly related to the most prominent aspects of plant functional variation worldwide.

From a biological viewpoint, we observed a distinct pattern of community-level strategy variation that mirrors relevant changes in the plant economics spectrum: the vegetation of the early successional stages is characterized by fast-growing acquisitive species that are progressively replaced by conservative species with stress-tolerant characteristics in the late successional stages (Caccianiga et al., 2006; Gobbi et al., 2010; Zanzottera et al., 2020; Verrall et al., 2022). The absence of significant variation along the leaf size spectrum is typical of low temperature habitats (Thomas et al., 2020). Competitive strategies are usually assumed to be more widespread at sites with lower abiotic stress (Choler et al., 2001; Caccianiga et al., 2006; Zanzottera et al., 2020). In agreement with our hypothesis, the higher extent of CSR strategy variation of the early-successional stages is possibly related to the random dispersal mechanisms that drive the colonization of the pioneer communities, whereas the increased functional homogeneity of the more mature and stable communities may be associated to a lower level of stochasticity in the colonization process of the later successional stages (Caccianiga et al., 2006; Ricotta et al., 2016).

From a more 'technical' perspective, an important requisite for the proposed specialization index is that it conforms to the value-validity property. This property has been introduced by Kvålseth (2015) and allows a measure not only to rank different species (or communities) according to their degree of specialization, but also to rank the differences between any two pairs of species. A similar criterion proposed by Molinari (1989) that an acceptable index of concentration or unevenness should meet is that for a two-class classification, it should keep a linear relationship between minimum and maximum concentration. Allow that a measure of concentration ranges from zero when concentration is minimum to unity when concentration is maximum. For a fuzzy-coded classification composed of only two classes, A and B, we would assign a concentration value equal to one to the case where $A_j = 1$ and $B_j = 1 - A_j = 0$. In contrast, we would assign a concentration value equal to zero to the case where $A_j = B_j = 0.5$. According to Molinari (1989), an ideal concentration measure should have a linear response from minimum to maximum concentration (see e.g. Smith and Wilson, 1996, Fig. 2). Then, for the distribution $A_j = 0.75$, $B_j = 0.25$ which is intermediate between the extreme cases $A_j = 1$, $B_j = 0$ and $A_j = B_j = 0.5$, the index takes on the intermediate concentration value of 0.5. It is easily shown that the specialization index σ_j in Eq. (1) conforms to this requirement. Therefore, unlike most concentration measures for which only 'larger than' comparisons may be valid, the values of σ_j can be used as valid indicators of the true extent of specialization from a data set. For details, see Molinari (1989) and Kvålseth (2015).

A relevant outcome of our approach is that it immediately leads to a direct relationship between σ_{vark} and functional diversity. As stated by Gregorius and Kosman (2017), functional diversity focuses on the assessment of (functional) differences between species. According to this definition, σ_{vark} is thus a suitable measure of community-level functional diversity that can be used to assess the extent of variation of CSR strategies at different scales along a nested sampling design.

Imagine that the vegetation of a certain area is sampled according to a nested design in which Q blocks are located across the study area. Within each block, a given number of plots is established and the species abundances in each plot are recorded along with their CSR strategies. From the species CSR strategies within each plot, a measure of plot-level CSR functional variation σ_{vark} can be computed according to Eq. (6). Likewise, a measure of within-block functional variation can be computed as the normalized excess of mean plot-level specialization $\overline{\sigma}_{kq}$ within block $q = 1, 2, ..., Q$ with respect to the corresponding block-level specialization σ_q calculated from the mean plot-level CSR scores within each block ($\overline{C}_{kq}$, $\overline{S}_{kq}$ and $\overline{R}_{kq}$), and so on along a nested sampling

hierarchy. This hierarchical structure of CSR variability can be then related to any scale-dependent environmental factor, such as climate, topography, land use or soil characteristics (Ricotta and Marignani, 2007) thus allowing the role of environmental drivers in shaping the functional structure of plant communities to be explored. To conclude, we hope that our proposal will help to quantify key aspects of community structure, such as functional specialization and the extent of its variation.

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Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The data and code used in this study are made available in the Supplementary Material to this paper

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2023.110066.

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