



Functional imbalance not functional evenness is the third component of community structure

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ABSTRACT

It is generally assumed that functional richness, diversity and evenness are complementary and, taken together, describe different facets of the distribution of species and their abundances in functional space. However, although these three primary components of community structure are commonly accepted by most community ecologists, measures of functional evenness usually fail to properly capture the regularity of species abundances in functional space. In this paper we will use an underexplored decomposition of Rao's index of functional diversity to introduce the notion of functional imbalance, an indicator of the strength of interaction between species abundances and their functional dissimilarities. Functional diversity always increases with increasing functional imbalance. Therefore, functional imbalance seems a more appropriate indicator of this facet of community structure than functional evenness. A worked example aimed at evaluating the influence of grazing on plant community structure showed that all proposed measures of functional imbalance were able to highlight the main functional changes of a dry calcareous grassland in Tuscany (Italy) following grazing exclusion.

1. Introduction

Ecologists have developed a multitude of diversity measures to explore the relationships between community structure and ecosystem functions, such as productivity, carbon storage and cycling, or responses to global changes (Pielou, 1966; Hill, 1973; Peet, 1974; Patil & Taillie, 1982). Although diversity appears as a simple and unambiguous notion, when we look for a suitable numerical definition, we find that no single index adequately summarizes all facets of such a wide-ranging aspect of community structure. Therefore, according to Sarkar & Margules (2002), its measurement remains 'capricious'. Many traditional diversity measures, among which the most popular are the Shannon (1948) entropy and the Simpson (1949) index, are basically measures of uncertainty in predicting the relative abundance of species in a given assemblage. As such, most of them combine in non-standard way the two components of species richness (the number of species in the

assemblage) and their relative abundance distribution (called variously evenness or equitability). High species richness and evenness, which occurs when species tend to be equal or nearly equal in abundance, are both associated to high diversity (Patil & Taillie, 1982). Taken together, these three components of community structure: species richness, evenness and diversity describe different facets of the distribution of species and their abundances (Mouchet et al., 2010).

This classical approach to the quantification of community structure requires a number of assumptions on the data to be analyzed, the foremost of which is that all species are considered equally distinct. Therefore, standard measures of richness, evenness and diversity have to be assessed only based on the number of species and their abundance distribution (Peet, 1974; Mouchet et al., 2010). However, it is well known that the species ecological strategies are related to their functional traits (Díaz & Cabido, 2001). Therefore, the dominant functional traits in plant or animal assemblages usually provide a better ecological

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characterization of the local environmental conditions and ecosystem functioning than the mere occurrence of species. As a result, in the last decades a number of functional diversity measures which incorporate information on functional differences among species have been proposed (Rao, 1982; Walker et al., 1999; Petchey & Gaston, 2002; Mason et al., 2003; Mouillot et al., 2005; Schmera et al., 2009; Laliberté & Legendre, 2010; Guisau & Guisau, 2012; Chao et al., 2014). Such measures are expected to correlate more strongly with ecosystem processes, as species directly or indirectly influence these processes via their traits (Mason & de Bello, 2013).

Like for classical abundance-based measures, Mason et al. (2005) proposed to classify the functional aspects of community structure into three primary components: functional richness, functional divergence and functional evenness. For single traits, Mason et al. (2005) defined these components as “the amount of niche space filled by species in the community” (functional richness), “the evenness of abundance distribution in filled niche space” (functional evenness), and “the degree to which abundance distribution in niche space maximizes divergence in functional characters within the community” (functional divergence). When multiple traits are considered, Villéger et al. (2008) reformulated these concepts as follows: functional richness summarizes the volume of the functional space filled by the community, functional evenness or regularity summarizes how regularly species abundances are distributed in functional space, while functional divergence “relates to how abundance is distributed within the volume of functional trait space occupied by species”.

Tucker et al. (2017) proposed a more specific definition of divergence as the average (abundance-weighted or not) dissimilarity between species. This allowed them to conceptualize the three components richness, evenness and divergence as different aspects of community structure which refer to three complementary questions: How much? How regular? How different? (Tucker et al., 2017). Although Tucker et al. (2017) developed their framework in a phylogenetic context, the same approach can apply to functional data.

Unfortunately, in spite of the elegance of this approach, in this paper we will first show that measures of functional evenness usually fail to properly capture the regularity of species abundances in functional space. Next, we will use a decomposition of Rao's index of functional diversity proposed by Shimatani (2001) to introduce the notion of functional imbalance, an indicator of the strength of interaction between species abundances and their functional dissimilarities. A worked example on functional changes in plant community structure following grazing exclusion of a dry calcareous grassland in Tuscany (Italy) is then used to show the behavior of three newly proposed imbalance measures in practice. Note that in this paper, the term functional diversity is used as a synonym of functional divergence *sensu* Tucker et al. (2017). By contrast, we will use the term community structure to refer indifferently to any aspect of the species dispersion in (functional) space (see Gregorius & Kosman, 2017).

2. Methods

2.1. A short overview of functional evenness

The degree to which abundances are evenly divided among species is considered a fundamental property of any biological community. Given an assemblage composed of N species with relative abundances p_i ($i = 1, 2, \dots, N$) where $0 < p_i \leq 1$ and $\sum_{i=1}^N p_i = 1$, evenness measures quantify the equality of the relative abundances of the N species.

In ecology, an endless number of evenness measures with a variety of different properties has been proposed (Taillie, 1979; Smith & Wilson, 1996; Ricotta, 2003; Jost, 2010; Tuomisto, 2012; Kvålseth, 2015; Chao & Ricotta, 2019) reflecting a certain degree of disagreement on the concept of evenness itself and its basic properties (Chao & Ricotta, 2019). The main requirement on which all authors agree is probably that

maximum evenness should correspond to an equiprobable species distribution, and the more the relative abundances of species differ the lower the evenness is. Accordingly, most evenness measures are basically normalizations of diversity measures in the range $[0, 1]$ relative to the maximum and minimum possible for a fixed number of species (Jost, 2010).

Pielou's (1966) evenness J , which is by far the most widely used measure of evenness in the ecological literature is shown to be such a measure:

$$J = \frac{\sum_{i=1}^N p_i \log(1/p_i)}{\log N} \quad (1)$$

where $H = \sum_{i=1}^N p_i \log(1/p_i)$ is the well-known Shannon diversity and $\log N$ is the maximum value of H for a given number of species. Accordingly, Pielou's evenness tells us the amount of the Shannon diversity relative to the maximum possible for a given richness, which is obtained if all N species have equal abundance (i.e. if $p_i = p_j = 1/N$ for all $i \neq j$).

Given a square matrix of functional dissimilarities between species d_{ij} ($i, j = 1, 2, \dots, N$) such that $d_{ii} = 0$ and $d_{ij} = d_{ji}$, Villéger et al. (2008) proposed to calculate functional evenness (FEve) based on the minimum spanning tree (MST) which links the N species in multidimensional functional space such that the total length of its $N-1$ branches is minimized. Next, for each branch of the minimum spanning tree, its length d_{ij} is divided by the sum of the abundances of the two species i and j linked by that branch: $d_{ij}/(p_i + p_j)$. Functional evenness is then computed as the regularity with which the quantities $d_{ij}/(p_i + p_j)$ transformed to a finite probability space are distributed along the tree. For details, see Villéger et al. (2008).

Although Villéger et al. (2008) stated that “FEve decreases either when abundance is less evenly distributed among species or when functional distances among species are less regular”, Legras & Gaertner (2018) and Kosman et al. (2021) observed that this is not the case. By definition, FEve is high when the summed abundance of two neighbor species in the MST is proportional to the functional distance between them (length of MST edge): high functional evenness occurs when long edges in the MST are supported by abundant species and short branches by rare species. We can thus claim that FEve does not summarize the regularity of the distribution of functional trait values among species but the consistency between the (ir)regularity of the distribution of functional trait values with that of the abundance value (see Legras & Gaertner, 2018).

Alternative measures of functional evenness based on different combinations of species abundances and interspecies dissimilarities can be found in Mouillot et al. (2005), Ricotta et al. (2014), Tucker et al. (2017), or Kosman et al. (2021). However, there are at least two good reasons for considering functional evenness not fully appropriate for describing the regularity of species abundances in functional space:

1. Irrespective of how functional evenness is calculated, increasing the regularity of species abundances and/or dissimilarities does not automatically increase functional diversity (Ricotta et al., 2021). Therefore, the traditional assumption that diversity is maximized for a perfectly regular distribution of species abundances and dissimilarities (or for a combination of both of them) does not necessarily hold for functional diversity measures (Pavoine & Bonsall, 2009).
2. Like for classical evenness, the concept of functional evenness has been defined in many different and sometimes conflicting ways. Therefore, in the ecological literature, there is a general inconsistency and lack of justification as to whether functional evenness should be high if either species abundances or functional dissimilarities are even (as originally proposed by Mason et al., 2005), if abundances and functional dissimilarities are positively linked so

that the values of $d_{ij}/(p_i + p_j)$ are even (as in Villéger et al., 2008), or, on the contrary, if abundances and functional dissimilarities are negatively linked, as in Ricotta et al. (2014) and Kosman et al. (2021).

Accordingly, the notion of functional evenness fails to appropriately capture the homogeneity of species abundances and the regularity of interspecies distances (Legras & Gaertner, 2018). In the following paragraphs, in the wake of Shimatani (2001) and Pavoine et al. (2013), we will show that functional imbalance may represent a more appropriate indicator of the (ir)regularity in the distribution of species abundance in functional trait space.

2.2. Introducing functional imbalance

Rao (1982) first proposed a diversity index which incorporates a measure of the pairwise (functional) differences between species. This index, which is usually called quadratic diversity Q , is defined as the expected dissimilarity between two individuals drawn at random with replacement from the assemblage:

$$Q = \sum_{i,j=1}^N p_i p_j d_{ij} \quad (2)$$

As such, it is a suitable index of functional divergence *sensu* Tucker et al. (2017). For simplicity, in this paper we assume that the interspecies dissimilarities d_{ij} in Eq. (2) are bounded in the range [0, 1]. The properties of quadratic diversity have been studied extensively by many previous authors (Shimatani, 2001; Champely & Chessel, 2002; Rao, 2010; Pavoine, 2012). A relevant point here is that if all species in the assemblage are treated as maximally dissimilar from each other (i.e. $d_{ij} = 1$ for any $i \neq j$), quadratic diversity reduces to the classical (abundance-only) Simpson diversity $S = 1 - \sum_{i=1}^N p_i^2 = 2 \sum_{i>j}^N p_i \times p_j$.

Shimatani (2001) further showed that Rao's quadratic diversity can be decomposed as.

$$Q = S \times \bar{d}_{ij} + B \quad (3)$$

where S is the Simpson diversity, \bar{d}_{ij} is the mean dissimilarity between all species in the assemblage $\bar{d}_{ij} = \frac{1}{N(N-1)/2} \sum_{i>j}^N d_{ij}$, and B is a covariance-like (im)balance factor between the abundances of species pairs $p_i \times p_j$ and their functional dissimilarities d_{ij} : $B = 2 \sum_{i>j}^N (d_{ij} - \bar{d}_{ij}) (p_i \times p_j - \frac{S}{N(N-1)})$.

B is positive if the functional dissimilarities are positively correlated to species abundances such that the highest values of d_{ij} mainly correspond to the highest values of $p_i \times p_j$. In the opposite case, B is negative if the values of d_{ij} are negatively correlated to the values of $p_i \times p_j$.

Rao's index thus depends on species diversity, on interspecies functional dissimilarities and on the interaction between species abundances and dissimilarities (B) such that for fixed values of S and \bar{d}_{ij} quadratic diversity increases if dominant species are functionally distant and less abundant species are close to each other (Shimatani, 2001; Pavoine et al., 2013). Hence, unlike for classical measures for which diversity increases with increasing evenness, functional diversity increases with increasing 'functional imbalance'. In other words, functional diversity is high if the distribution of species abundances positively correlates with that of functional distances. By contrast, functional diversity is low if the distribution of species abundances negatively correlates with that of functional distances.

Note however that in Eq. (3) Shimatani's covariance-like imbalance factor B represents the excess of diversity between Rao's Q and the product of the Simpson diversity and mean species dissimilarity $S \times \bar{d}_{ij}$. As such, the values of B are not free to vary independently, but are constrained by the values of $S \times \bar{d}_{ij}$. Due to this dependence, it is not possible to compare the imbalance of communities with different values

of $S \times \bar{d}_{ij}$ (see Jost, 2007; Chao et al., 2012). Therefore, some kind of standardization should be performed to get a relative measure of imbalance that is independent of the other components of Rao's diversity. In the next paragraphs we will thus present three standardized measures of functional imbalance that allow us to measure the sign and strength of the interaction between species abundances and their functional dissimilarities in a more appropriate way.

A first application of the Shimatani decomposition was used by Sol et al. (2020) to explore the impact of urbanization on avian functional diversity. To facilitate the interpretation of the imbalance factor, Sol et al. (2020) transformed B to a correlation coefficient:

$$Cor_B = \frac{cov(d_{ij}, p_i p_j)}{\sqrt{var(d_{ij}) var(p_i p_j)}} \quad (4)$$

where $var(d_{ij})$ is the variance of the species functional dissimilarities d_{ij} for all $i \neq j$, $var(p_i p_j)$ is the variance of the product of the relative abundance of species i and j : $p_i \times p_j$ for all $i \neq j$, and $cov(d_{ij}, p_i p_j)$ is the covariance between d_{ij} and $p_i \times p_j$. For additional details on the calculation of Cor_B , see Appendix 1 (Supporting information).

Two additional measures of functional imbalance are based on two distinct transformations of Rao's quadratic diversity. In the first case, functional imbalance can be summarized as standardized effect size (SES; Collyer et al., 2022):

$$SES_B = \frac{Obs(Q) - Mean(Q)}{SD(Q)} \quad (5)$$

where $Obs(Q)$ is the observed value of Rao's quadratic diversity for a given assemblage, $Mean(Q)$ is the mean of the null distribution of Q in random assemblages obtained by permuting the relative abundances p_i among the N species (thus varying only the balance factor B and keeping S and \bar{d}_{ij} unchanged), and $SD(Q)$ is the standard deviation of the null distribution. SES_B thus represents a measure of functional imbalance or irregularity in the distribution of species abundances in functional space which is expressed as the departure of the observed functional diversity from the mean of the null distribution in standard deviation units (Gotelli & McCabe, 2002).

Finally, to measure functional imbalance, we can also use a normalized version of Q obtained as:

$$Q_B = \frac{Obs(Q) - Min(Q)}{Max(Q) - Min(Q)} \quad (6)$$

where like for SES_B , $Min(Q)$ and $Max(Q)$ are the minimum and maximum values that quadratic diversity can assume by permuting the relative abundances p_i among the N species, and leaving everything else unchanged (i.e. S and \bar{d}_{ij} do not vary with permutation). This latter measure of functional imbalance is obtained by normalizing a measure of diversity in the unit range, thus providing some sort of formal and conceptual continuity between classical (un)evenness and functional imbalance.

3. Worked example

3.1. Data and methods

We conducted our study in a seminatural grassland located close to the summit of Monte Labbro, Tuscany (Italy), a predominantly calcareous massif of 1193 m on the Uccellina-Monte Amiata ridge. The area has been grazed for centuries, mostly by sheep, with human traces dating back to the Bronze Age. From the 1960s onwards, the grazing pressure decreased, triggering the secondary succession of semi-natural grasslands into increasingly dense scrublands with *Prunus spinosa*, *Rubus ulmifolius* and *Cytisus scoparius* (Maccherini et al., 2007). From late

summer 2000 to early spring 2001, the area was subjected to a restoration project, which involved the cutting of shrubs on overgrown grasslands (see Maccherini et al., 2018). In 2001, we planned a before-after-control-impact (BACI) study to evaluate the influence of grazing and sowing of native species on grassland restoration. We located the experimental plots in a cleared overgrown pasture (before cutting, *Prunus spinosa* covered 80%), grazed by donkeys, which were reintroduced into the area few years before restoration management; the site is occasionally grazed by sheep, hares and cattle.

We established a randomized block design with four blocks and four 3 × 5 m experimental plots in each block stratified on elevation. Individual plots in each block were randomly assigned to one of four treatments: no grazing or sowing; sowing without grazing; grazing without sowing; sowing and grazing. Ungrazed plots have been fenced off to protect them from livestock in spring 2002; sowing was carried out in October 2001. In previous studies, a very small effect of sowing compared to grazing was observed for this experiment (Maccherini & Santi, 2012; Maccherini et al., 2018). Given the reduced significance of sowing, in this paper, only the grazing factor was considered. During the project, one ungrazed plots was excluded from analysis.

In late June 2019, the cover of all vascular plant species within each 1 × 2 m subplot at the center of the experimental plots was estimated using a point quadrant method with a density of 100 pins/m² (Moore & Chapman, 1986). All species touched by each pin were recorded so that the total species cover within each 1 × 2 m subplot can exceed 200 pins. Species present in a plot but not touched by any pin were recorded with an arbitrary cover of 0.5 pins. All species abundance data are available in Appendix 2.

A set of functional traits was measured for the most abundant species in both treatments (8 grazed plots and 7 ungrazed plots). Collectively, these species account for ~ 70% of the total cover in each treatment. According to Grime's (1998) mass-ratio hypothesis, these species are expected to make a substantial contribution to community structure and functioning.

The following six leaf functional traits were measured (mean of three replicates for each species in each treatment): specific leaf area (SLA, mm²/mg), leaf dry matter content (LDMC, mg/g), nitrogen and carbon content (N% and C%) and nitrogen and carbon stable isotope composition (δ¹⁵N and δ¹³C, ‰). Stable isotope composition is calculated as the ratio of the rarest to commonest (heavy to light) isotope of carbon and nitrogen relative to an international accepted reference standard. For additional details, see Dawson et al. (2002).

The selected traits are usually associated with the leaf economics spectrum (Wright et al., 2004), reflecting a possible trade-off between fast-growing acquisitive species versus slow-growing, more conservative species. Specifically, SLA and LDMC are considered soft morpho-anatomical traits correlated with relative growth rate, photosynthetic rate, and nutrient concentration. Higher SLA values are correlated with lower leaf span and higher photosynthetic rate. LDMC is related to the density of leaves; it has been demonstrated to scale negatively with the potential growth rate and positively with leaf lifespan (Cornelissen et al., 2003). N% and C% are considered as a proxy of photosynthetic rate, while δ¹³C reflects the photosynthetic water use efficiency (i.e., the amount of water used by plants per unit of plant material produced), with lower values reflecting a greater stomatal aperture. Finally, in sites that receive a high input of nitrogen from animals, δ¹⁵N can be used to trace the organic N enrichment within the plant community (Dawson et al., 2002).

All traits were normalized to the unit range by their minimum and maximum values. To visualize plot-level differences in community functioning between the two treatments, we calculated the community-weighted mean values (CWM) of each trait at each plot: $CWM = \sum_{i=1}^N p_i \times T_{ir}$, where T_{ir} is the normalized value of trait T for species i in treatment r . We next applied a principal component analysis (PCA) on the CWM values of all grazed and ungrazed plots. From the normalized

trait values (available in Appendix 2), we calculated a matrix of functional Euclidean distances between all pairs of species within each treatment. These distances were then linearly rescaled by dividing each distance by the maximum value found in both matrices. We then used the scaled functional distances and the species relative abundances in each plot to calculate Cor_B , SES_B and Q_B . All calculations were performed with a new R function available in an Electronic Appendix to this paper (see Supplementary data, Appendix 3). Starting from version 2.1.2, the R function will be also available in package *adiv* (Pavoine, 2020): <https://cran.r-project.org/web/packages/adiv/index.html>.

The values of Q_B were estimated based on 10,000 random permutations, which is a manageable subset of the total number of $N!$ possible permutations. Additional work is ongoing to find an analytical or algorithmic solution to the exact calculation of Q_B . The calculation of SES_B was performed using the same number of permutations used for Q_B . For each plot, we also calculated species richness, the Rao quadratic diversity and its basic components S and \bar{d}_{ij} (see Eq. (3)), together with a traditional (abundance-only) index of evenness explicitly developed for the Simpson diversity (see Smith & Wilson, 1996):

$$E = \frac{1 - \sum_{i=1}^N p_i^2}{1 - 1/N} = \frac{S}{1 - 1/N} \quad (7)$$

Like Pielou's evenness, this index tells us the amount of Simpson's diversity relative to the maximum possible for a given species richness.

For all measures, the significance of differences between both treatments (grazed and ungrazed) was tested with ANOVA. P-values were obtained by 10,000 random permutations of individual plots within the treatments.

3.2. Results

As expected, grazing has had a profound impact on community structure and functioning. Grazing disturbance acts as a filter, selecting for a higher number of ruderal species with more acquisitive, fast-growing strategies. In contrast, ungrazed plots host less rich and diverse communities, mainly composed of species with more conservative and slow-growing strategies.

As shown by the PCA biplot in Fig. 1, species in grazed plots exhibit on average higher values of SLA and lower LDMC, suggesting that these communities host species positioned on the acquisitive side of the leaf economics spectrum, minimizing leaf construction and maintenance costs while maximizing the capacity to acquire resources and proliferate rapidly (Díaz et al., 2016).

In this study, acquisitive species are mainly perennial and annual forbs (e.g. *Teucrium chamaedrys*, *Orlaya grandiflora* and *Xeranthemum cylindraceum*) and N-fixer species, such as *Trifolium incarnatum*, which survives predominantly under grazing conditions. These species have a competitive advantage in grazed areas because of their capacity to acquire nutrients more rapidly and regrow after disturbance, generally displaying a higher resilience after stressful events (Herrero-Jáuregui and Oesterheld, 2018; Busch et al., 2019; Ladouceur et al., 2019).

Species in ungrazed plots show a shift toward more conservative growth strategies. Such species invest more resources in developing durable leaves (higher LDMC) being at the same time more resistant to drought stress at the cost of reduced photosynthetic rate (lower %N) and carbon fixation (higher δ¹³C values). Due to the high input of nitrogen from animals, grazed plots also exhibited higher values of δ¹⁵N than ungrazed plots.

In terms of diversity, ungrazed plots show a tendency towards a progressive decrease of all its components, such as species richness, Simpson's diversity and evenness, mean functional dissimilarity, Rao's quadratic diversity and all measures of functional imbalance Cor_B , SES_B and Q_B (Table 1). Hence, although the values of Cor_B are always negative denoting an overall negative correlation in both treatments between species abundances and their functional dissimilarities, in ungrazed

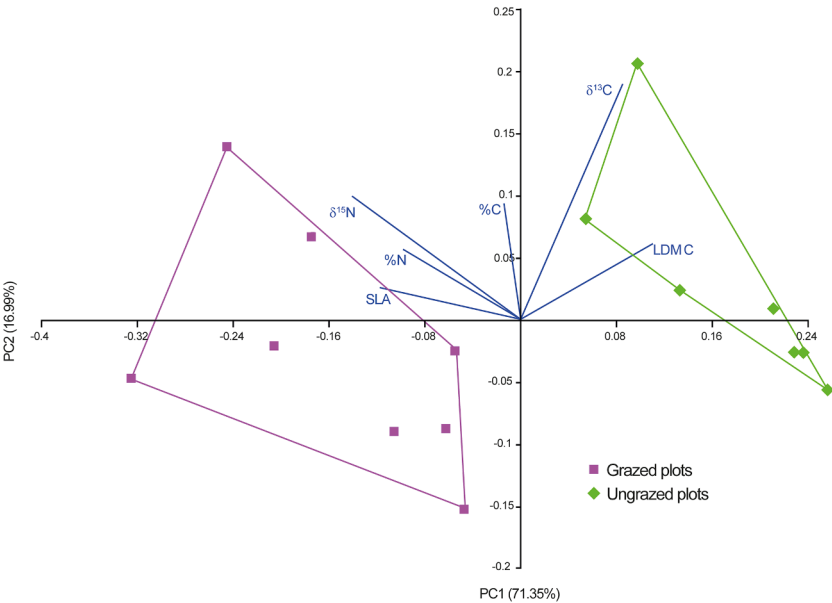


Table 1
Mean (SD) values of individual plots within each treatment (grazed and ungrazed) for species richness N , Simpson's diversity S and evenness E , Rao's quadratic diversity Q , mean functional dissimilarity \bar{d}_{ij} , and functional imbalance Cor_B , SES_B and Q_B . Pairwise comparisons of index differences between the two treatments were performed with ANOVA. P-values were obtained by randomly permuting individual plots within the treatments (10000 permutations). Asterisks indicate significant values: * $p < 0.05$, ** $p < 0.01$.

	Grazed plots (8 plots)	Ungrazed plots (7 plots)
N^*	17.25 (2.727)	12.857 (2.748)
S^{**}	0.849 (0.033)	0.651 (0.131)
E^{**}	0.902 (0.032)	0.707 (0.140)
Q^{**}	0.369 (0.019)	0.217 (0.053)
\bar{d}_{ij}^{**}	0.444 (0.015)	0.415 (0.016)
Cor_B^{**}	-0.026 (0.066)	-0.167 (0.093)
SES_B^{**}	-0.228 (0.547)	-1.153 (0.434)
Q_B^{**}	0.465 (0.093)	0.221 (0.096)

plots dominant species are on average more functionally similar to each other compared to grazed plots. Likewise, the negative values of the SES_B index imply that the observed values of Rao's Q are generally lower than the null expectation in random assemblages, thus showing again that in both treatments dominant species tend to be more functionally similar to each other compared to less abundant ones.

The higher functional homogenization of ungrazed plots is due to the increasing dominance of *Bromus erectus* and the encroachment of functionally similar shrubs along the secondary succession. In contrast, in grazed plots, selective grazing and the patchy concentration of nutrients due to animal manure give rise to contrasting microsites which host an increased number of functionally diverse grazing-adapted species with different life histories (Pierce et al., 2007; Maccherini & Santi, 2012). Such higher spatial and temporal turnover in species composition reduces species dominance increasing at the same time functional imbalance.

4. Discussion

It is generally agreed that the (ir)regularity of the distribution of species abundances in functional space is a relevant component of the relationship between community composition and functioning (Mouillot et al., 2005; Mouchet et al., 2010). In this paper, we showed that

Fig. 1. Biplot of the principal component analysis of 15 vegetation plots from a calcareous grassland in Tuscany (Italy) characterized by the community-weighted mean values (CWM) of six functional traits (SLA, LDMC, %C, %N, $\delta^{13}C$, $\delta^{15}N$). Convex hulls indicate groups of grazed and ungrazed plots. Numbers in brackets are the amount of variance associated with each principal component. Vectors represent the direction and the strength of the correlation between explanatory variables and the first two principal components.

functional imbalance is a more appropriate indicator of this facet of community structure than previous measures of functional evenness. We thus proposed three new measures which allow us to compare the strength of interaction between species abundances and their functional dissimilarities among communities with different species richness, abundance and dissimilarity distribution. Unlike most previous measures of functional evenness, for Cor_B , SES_B and Q_B functional diversity always increases with functional imbalance. That is, with the positive link between dissimilarity and abundance.

As shown by our results, all proposed measures of functional imbalance were able to highlight the main changes in community structure following grazing exclusion of a dry calcareous grassland in Tuscany. Hence, looking simultaneously at various facets of functional diversity, it is possible to recognize not only whether two communities are functionally different, but also why they are different. That is, which components take on higher/lower values in community A than in community B. This allows us to investigate in deeper detail the functional processes that shape community structure.

Functional diversity increases when species abundance and dissimilarity are positively linked. This is because if functional differences among dominant species are high, the abundance-weighted variability in functional trait values is also high (e.g. Kondratyeva et al., 2019). On the other hand, the high amount of functional redundancy in a community where abundant species are more similar to each other reduces functional diversity. We have thus proposed an approach based on a covariance-like measure of functional imbalance which allows to distinguish positive links between species abundance and functional dissimilarity (where functional diversity is high) from negative links (where functional diversity is low). While it is generally assumed that functional differences among dominant species can have beneficial effects on ecosystem properties (Grime, 1998), negative links between abundance and functional dissimilarity usually reflect evenness in the species contribution to certain ecological functions within ecosystem (Hillebrand et al., 2008; Ricotta et al., 2014). Indeed a rare species might contribute disproportionately of its abundance to functional diversity and ecosystem processes if it has distinct functional traits (Dee et al., 2019). Both scenarios are thus worth studying and our framework allows to distinguish between them.

Compared to Cor_B , which is expressed as a standard correlation coefficient in the range [-1, 1] between the product of species abundances $p_i \times p_j$ and their functional dissimilarities d_{ij} , SES_B and Q_B are normalized locally: that is, by keeping species abundances and interspecies

dissimilarities unchanged and modifying only the interaction between them. Alternative ways for normalizing Rao with different biological meanings were studied e.g. by Pavoine & Bonsall (2009) or Ricotta et al. (2016), and the interested reader is addressed to these papers for additional details.

This permutation procedure allows SES_B and Q_B to be independent of the other components of Rao's diversity S and \bar{d}_{ij} . Here, independence or unrelatedness *sensu* Chao et al. (2012) means that knowing the values of S and \bar{d}_{ij} would put no mathematical constraints on the range of values that the imbalance factor can take. In particular, Chao & Chiu (2016) proposed an intuitive condition to assure the unrelatedness of two measures: the range of values that a measure of functional imbalance can take should be a fixed interval (usually in the range 0–1) regardless of the values of S and \bar{d}_{ij} . While SES_B quantifies functional imbalance in standard deviation units, the index Q_B conforms to this requirement. This ensures that the same magnitude of functional imbalance quantifies the same degree of irregularity of species abundance distribution in functional space, even if the assemblages differ in their diversity or dissimilarity structure (see Chao & Ricotta, 2019). Note that our proposal of calculating functional imbalance by normalizing an index of functional diversity is not confined to the Rao quadratic diversity. Rather, the same approach can be generalized to virtually any functional diversity index that is based on a combination of species abundances and their functional dissimilarities simply by permuting the relative abundances p_i among the N species. The interpretation of the results will then depend case by case on the index formulation.

An important limitation of Q_B is that to the best of our knowledge, the index calculation is computationally extremely intensive and, by using permutations, we will get rather crude estimates of $Min(Q)$ and $Max(Q)$. Nonetheless, even if suboptimal, the results of Q_B are coherent, both in sign and strength, with those obtained with Cor_B and SES_B . Therefore, it seems that the speed of current digital devices allows us to approximate the problem in a sufficiently short time to make this kind of measures operational for the analysis of community structure.

In recent years there has been a renewed interest in a series of algorithmic measures of diversity and dissimilarity (e.g. Weitzman, 1992; Kosman, 1996) that could not be extensively used at the time of their proposal due to a lack of computing power. Thanks to their flexibility, these algorithmic measures could give new impulse to biodiversity theory from new perspectives and with new assumptions. Another field where advanced computational methods will possibly give new impulse to diversity analysis is the choice of an appropriate set of traits that maximize their association to the ecological process of interest (de Bello et al., 2021). As highlighted by Lavorel et al. (2008), the relevant traits for ecosystem functioning depend case by case on the analyzed process. In principle, increasing the dimensionality of functional spaces by the progressive use of a higher number of traits may lead to a stronger relationships between community structure and ecosystem functioning. However, such artificially enlarged functional spaces do not necessarily have a direct biological relationship to the ecological property of interest. Therefore, we need to select a suitable set of traits that are actually relevant for the property that we are attempting to estimate. We believe that advanced machine learning methods and artificial intelligence (Lucas, 2020) will greatly contribute to the construction of such 'tailored' functional spaces (Ricotta et al., 2021).

To conclude, Cor_B , SES_B and Q_B constitute the vehicle for measuring functional imbalance. However, like for any other ecological problem, the way to go (i.e. how many and which traits to use, how to code them and the method for computing interspecies dissimilarities) should be assessed case by case based on the specific question at hand. We thus hope, this work will help to build an increasingly conscious approach to the summarization of the many different facets of functional diversity and their relationship with ecosystem functioning.

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CRediT authorship contribution statement

Carlo Ricotta: Conceptualization, Methodology, Data analysis, Writing – original draft. **Giovanni Bacaro:** Data collection, Data analysis, Writing – review & editing. **Simona Maccherini:** Data collection, Data analysis, Writing – review & editing. **Sandrine Pavoine:** Methodology, Software, Data analysis, Writing – review & editing.

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.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecolind.2022.109035>.

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