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# 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.

**Keywords:** Community structure; Diversity decomposition; Functional regularity; Functional space; Rao's quadratic diversity.

## 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 & Tailie, 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

46 Shannon (1948) entropy and the Simpson (1949) index, are basically measures of uncertainty in  
47 predicting the relative abundance of species in a given assemblage. As such, most of them combine  
48 in non-standard way the two components of species richness (the number of species in the  
49 assemblage) and their relative abundance distribution (called variously evenness or equitability).  
50 High species richness and evenness, which occurs when species tend to be equal or nearly equal in  
51 abundance, are both associated to high diversity (Patil & Taillie, 1982). Taken together, these three  
52 components of community structure: species richness, evenness and diversity describe different  
53 facets of the distribution of species and their abundances (Mouchet et al., 2010).

54 This classical approach to the quantification of community structure requires a number of  
55 assumptions on the data to be analyzed, the foremost of which is that all species are considered  
56 equally distinct. Therefore, standard measures of richness, evenness and diversity have to be  
57 assessed only based on the number of species and their abundance distribution (Peet, 1974;  
58 Mouchet et al., 2010). However, it is well known that the species ecological strategies are related to  
59 their functional traits (Díaz & Cabido, 2001). Therefore, the dominant functional traits in plant or  
60 animal assemblages usually provide a better ecological characterization of the local environmental  
61 conditions and ecosystem functioning than the mere occurrence of species. As a result, in the last  
62 decades a number of functional diversity measures which incorporate information on functional  
63 differences among species have been proposed (Rao, 1982; Walker et al., 1999; Petchey & Gaston,  
64 2002; Mason et al., 2003; Mouillot et al., 2005; Schmera et al., 2009; Laliberté & Legendre, 2010;  
65 Guiasu & Guiasu, 2012; Chao et al., 2014). Such measures are expected to correlate more strongly  
66 with ecosystem processes, as species directly or indirectly influence these processes via their traits  
67 (Mason & de Bello, 2013).

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

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

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

97

## 98 **2. Methods**

### 99 **2.1. A short overview of functional evenness**

100 The degree to which abundances are evenly divided among species is considered a fundamental  
101 property of any biological community. Given an assemblage composed of  $N$  species with relative  
102 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  
103 equality of the relative abundances of the  $N$  species.

104 In ecology, an endless number of evenness measures with a variety of different properties has  
105 been proposed (Taillie, 1979; Smith & Wilson, 1996; Ricotta, 2003; Jost, 2010; Tuomisto, 2012;  
106 Kvålseth, 2015; Chao & Ricotta, 2019) reflecting a certain degree of disagreement on the concept  
107 of evenness itself and its basic properties (Chao & Ricotta, 2019). The main requirement on which  
108 all authors agree is probably that maximum evenness should correspond to an equiprobable species  
109 distribution, and the more the relative abundances of species differ the lower the evenness is.  
110 Accordingly, most evenness measures are basically normalizations of diversity measures in the  
111 range  $[0, 1]$  relative to the maximum and minimum possible for a fixed number of species (Jost,  
112 2010).

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

115

$$116 \quad J = \frac{\sum_{i=1}^N p_i \log(1/p_i)}{\log N} \quad (1)$$

117

118 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  
119 of  $H$  for a given number of species. Accordingly, Pielou's evenness tells us the amount of the  
120 Shannon diversity relative to the maximum possible for a given richness, which is obtained if all  $N$   
121 species have equal abundance (i.e. if  $p_i = p_j = 1/N$  for all  $i \neq j$ ).

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

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

139 Alternative measures of functional evenness based on different combinations of species  
140 abundances and interspecies dissimilarities can be found in Mouillot et al. (2005), Ricotta et al.  
141 (2014), Tucker et al. (2017), or Kosman et al. (2021). However, there are at least two good reasons  
142 for considering functional evenness not fully appropriate for describing the regularity of species  
143 abundances in functional space:

144

145 1. Irrespective of how functional evenness is calculated, increasing the regularity of species  
146 abundances and/or dissimilarities does not automatically increase functional diversity (Ricotta et al.,  
147 2021). Therefore, the traditional assumption that diversity is maximized for a perfectly regular  
148 distribution of species abundances and dissimilarities (or for a combination of both of them) does  
149 not necessarily hold for functional diversity measures (Pavoine & Bonsall, 2009).

150

151 2. Like for classical evenness, the concept of functional evenness has been defined in many  
152 different and sometimes conflicting ways. Therefore, in the ecological literature, there is a general  
153 inconsistency and lack of justification as to whether functional evenness should be high if either  
154 species abundances or functional dissimilarities are even (as originally proposed by Mason et al.,  
155 2005), if abundances and functional dissimilarities are positively linked so that the values of  
156  $d_{ij}/(p_i + p_j)$  are even (as in Villéger et al., 2008), or, on the contrary, if abundances and functional  
157 dissimilarities are negatively linked, as in Ricotta et al. (2014) and Kosman et al. (2021).

158

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

164

## 165 **2.2. Introducing functional imbalance**

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

170

$$171 \quad Q = \sum_{i,j=1}^N p_i p_j d_{ij} \quad (2)$$

172

173 As such, it is a suitable index of functional divergence *sensu* Tucker et al. (2017). For simplicity,  
174 in this paper we assume that the interspecies dissimilarities  $d_{ij}$  in Eq. (2) are bounded in the range  
175 [0, 1]. The properties of quadratic diversity have been studied extensively by many previous authors  
176 (Shimatani, 2001; Champely & Chessel, 2002; Rao, 2010; Pavoine, 2012). A relevant point here is  
177 that if all species in the assemblage are treated as maximally dissimilar from each other (i.e.  $d_{ij} = 1$

178 for any  $i \neq j$ ), quadratic diversity reduces to the classical (abundance-only) Simpson diversity

$$179 \quad S = 1 - \sum_{i=1}^N p_i^2 = 2 \sum_{i>j}^N p_i \times p_j.$$

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

181

$$182 \quad Q = S \times \bar{d}_{ij} + B \tag{3}$$

183

184 where  $S$  is the Simpson diversity,  $\bar{d}_{ij}$  is the mean dissimilarity between all species in the

185 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

186 abundances of species pairs  $p_i \times p_j$  and their functional dissimilarities  $d_{ij}$ :

$$187 \quad B = 2 \sum_{i>j}^N (d_{ij} - \bar{d}_{ij}) \left( p_i \times p_j - \frac{S}{N(N-1)} \right).$$

188  $B$  is positive if the functional dissimilarities are positively correlated to species abundances such

189 that the highest values of  $d_{ij}$  mainly correspond to the highest values of  $p_i \times p_j$ . In the opposite

190 case,  $B$  is negative if the values of  $d_{ij}$  are negatively correlated to the values of  $p_i \times p_j$ .

191 Rao's index thus depends on species diversity, on interspecies functional dissimilarities and on

192 the interaction between species abundances and dissimilarities ( $B$ ) such that for fixed values of  $S$

193 and  $\bar{d}_{ij}$  quadratic diversity increases if dominant species are functionally distant and less abundant

194 species are close to each other (Shimatani, 2001; Pavoine et al., 2013). Hence, unlike for classical

195 measures for which diversity increases with increasing evenness, functional diversity increases with

196 increasing 'functional imbalance'. In other words, functional diversity is high if the distribution of

197 species abundances positively correlates with that of functional distances. By contrast, functional

198 diversity is low if the distribution of species abundances negatively correlates with that of

199 functional distances.

200 Note however that in Eq. (3) Shimatani's covariance-like imbalance factor  $B$  represents the

201 excess of diversity between Rao's  $Q$  and the product of the Simpson diversity and mean species

202 dissimilarity  $S \times \bar{d}_{ij}$ . As such, the values of  $B$  are not free to vary independently, but are constrained

203 by the values of  $S \times \bar{d}_{ij}$ . Due to this dependence, it is not possible to compare the imbalance of

204 communities with different values of  $S \times \bar{d}_{ij}$  (see Jost, 2007; Chao et al., 2012). Therefore, some

205 kind of standardization should be performed to get a relative measure of imbalance that is

206 independent of the other components of Rao's diversity. In the next paragraphs we will thus present

207 three standardized measures of functional imbalance that allow us to measure the sign and strength

208 of the interaction between species abundances and their functional dissimilarities in a more  
209 appropriate way.

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

213

$$214 \quad Cor_B = \frac{\text{cov}(d_{ij}, p_i p_j)}{\sqrt{\text{var}(d_{ij}) \text{var}(p_i p_j)}} \quad (4)$$

215

216 where  $\text{var}(d_{ij})$  is the variance of the species functional dissimilarities  $d_{ij}$  for all  $i \neq j$ ,  $\text{var}(p_i p_j)$   
217 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  
218  $\text{cov}(d_{ij}, p_i p_j)$  is the covariance between  $d_{ij}$  and  $p_i \times p_j$ . For additional details on the calculation of  
219  $Cor_B$ , see Appendix 1 (Supporting information).

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

223

$$224 \quad SES_B = \frac{Obs(Q) - Mean(Q)}{SD(Q)} \quad (5)$$

225

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

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

234

$$235 \quad Q_B = \frac{Obs(Q) - Min(Q)}{Max(Q) - Min(Q)} \quad (6)$$

236



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

243

### 244 **3. Worked example**

#### 245 **3.1. Data and methods**

246 We conducted our study in a seminatural grassland located close to the summit of Monte Labbro,  
247 Tuscany (Italy), a predominantly calcareous massif of 1193m on the Uccellina-Monte Amiata ridge.  
248 The area has been grazed for centuries, mostly by sheep, with human traces dating back to the  
249 Bronze Age. From the 1960s onwards, the grazing pressure decreased, triggering the secondary  
250 succession of semi-natural grasslands into increasingly dense scrublands with *Prunus spinosa*,  
251 *Rubus ulmifolius* and *Cytisus scoparius* (Maccherini et al., 2007). From late summer 2000 to early  
252 spring 2001, the area was subjected to a restoration project, which involved the cutting of shrubs on  
253 overgrown grasslands (see Maccherini et al., 2018). In 2001, we planned a before-after-control-  
254 impact (BACI) study to evaluate the influence of grazing and sowing of native species on grassland  
255 restoration. We located the experimental plots in a cleared overgrown pasture (before cutting,  
256 *Prunus spinosa* covered 80%), grazed by donkeys, which were reintroduced into the area few years  
257 before restoration management; the site is occasionally grazed by sheep, hares and cattle.

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

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

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

276 The following six leaf functional traits were measured (mean of three replicates for each species  
277 in each treatment): specific leaf area (SLA, mm<sup>2</sup>/mg), leaf dry matter content (LDMC, mg/g),  
278 nitrogen and carbon content (N% and C%) and nitrogen and carbon stable isotope composition  
279 ( $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$ , ‰). Stable isotope composition is calculated as the ratio of the rarest to commonest  
280 (heavy to light) isotope of carbon and nitrogen relative to an international accepted reference  
281 standard. For additional details, see Dawson et al. (2002).

282 The selected traits are usually associated with the leaf economics spectrum (Wright et al., 2004),  
283 reflecting a possible trade-off between fast-growing acquisitive species versus slow-growing, more  
284 conservative species. Specifically, SLA and LDMC are considered soft morpho-anatomical traits  
285 correlated with relative growth rate, photosynthetic rate, and nutrient concentration. Higher SLA  
286 values are correlated with lower leaf span and higher photosynthetic rate. LDMC is related to the  
287 density of leaves; it has been demonstrated to scale negatively with the potential growth rate and  
288 positively with leaf lifespan (Cornelissen et al., 2003). N% and C% are considered as a proxy of  
289 photosynthetic rate, while  $\delta^{13}\text{C}$  reflects the photosynthetic water use efficiency (i.e., the amount of  
290 water used by plants per unit of plant material produced), with lower values reflecting a greater  
291 stomatal aperture. Finally, in sites that receive a high input of nitrogen from animals,  $\delta^{15}\text{N}$  can be  
292 used to trace the organic N enrichment within the plant community (Dawson et al., 2002).

293 All traits were normalized to the unit range by their minimum and maximum values. To visualize  
294 plot-level differences in community functioning between the two treatments, we calculated the  
295 community-weighted mean values (CWM) of each trait at each plot:  $CWM = \sum_{i=1}^N p_i \times T_{i\tau}$ , where  
296  $T_{i\tau}$  is the normalized value of trait  $T$  for species  $i$  in treatment  $\tau$ . We next applied a principal  
297 component analysis (PCA) on the CWM values of all grazed and ungrazed plots. From the  
298 normalized trait values (available in Appendix 2), we calculated a matrix of functional Euclidean  
299 distances between all pairs of species within each treatment. These distances were then linearly  
300 rescaled by dividing each distance by the maximum value found in both matrices. We then used the  
301 scaled functional distances and the species relative abundances in each plot to calculate  $Cor_B$ ,  
302  $SES_B$  and  $Q_B$ . All calculations were performed with a new R function available in an electronic  
303 appendix to this paper (see Supplementary data, Appendix 3). Starting from version 2.1.2, the R  
304 function will be also available in package *adiv* (Pavoine, 2020): [https://cran.r-](https://cran.r-project.org/web/packages/adiv/index.html)  
305 [project.org/web/packages/adiv/index.html](https://cran.r-project.org/web/packages/adiv/index.html).

306 The values of  $Q_B$  were estimated based on 10000 random permutations, which is a manageable  
307 subset of the total number of  $N!$  possible permutations. Additional work is ongoing to find an  
308 analytical or algorithmic solution to the exact calculation of  $Q_B$ . The calculation of  $SES_B$  was  
309 performed using the same number of permutations used for  $Q_B$ . For each plot, we also calculated  
310 species richness, the Rao quadratic diversity and its basic components  $S$  and  $\bar{d}_{ij}$  (see Eq. 3),  
311 together with a traditional (abundance-only) index of evenness explicitly developed for the Simpson  
312 diversity (see Smith & Wilson, 1996):

$$314 \quad E = \frac{1 - \sum_{i=1}^N p_i^2}{1 - 1/N} = \frac{S}{1 - 1/N} \quad (7)$$

315  
316 Like Pielou's evenness, this index tells us the amount of Simpson's diversity relative to the  
317 maximum possible for a given species richness.

318 For all measures, the significance of differences between both treatments (grazed and ungrazed)  
319 was tested with ANOVA. P-values were obtained by 10000 random permutations of individual  
320 plots within the treatments.

### 321 322 **3.2. Results**

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

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

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

337 Species in ungrazed plots show a shift toward more conservative growth strategies. Such species  
338 invest more resources in developing durable leaves (higher LDMC) being at the same time more

339 resistant to drought stress at the cost of reduced photosynthetic rate (lower %N) and carbon fixation  
340 (higher  $\delta^{13}\text{C}$  values). Due to the high input of nitrogen from animals, grazed plots also exhibited  
341 higher values of  $\delta^{15}\text{N}$  than ungrazed plots.

342 In terms of diversity, ungrazed plots show a tendency towards a progressive decrease of all its  
343 components, such as species richness, Simpson's diversity and evenness, mean functional  
344 dissimilarity, Rao's quadratic diversity and all measures of functional imbalance  $Cor_B$ ,  $SES_B$  and  
345  $Q_B$  (Table 1). Hence, although the values of  $Cor_B$  are always negative denoting an overall negative  
346 correlation in both treatments between species abundances and their functional dissimilarities, in  
347 ungrazed plots dominant species are on average more functionally similar to each other compared to  
348 grazed plots. Likewise, the negative values of the  $SES_B$  index imply that the observed values of  
349 Rao's  $Q$  are generally lower than the null expectation in random assemblages, thus showing again  
350 that in both treatments dominant species tend to be more functionally similar to each other  
351 compared to less abundant ones.

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

359

#### 360 **4. Discussion**

361 It is generally agreed that the (ir)regularity of the distribution of species abundances in functional  
362 space is a relevant component of the relationship between community composition and functioning  
363 (Mouillot et al., 2005; Mouchet et al., 2010). In this paper, we showed that functional imbalance is a  
364 more appropriate indicator of this facet of community structure than previous measures of  
365 functional evenness. We thus proposed three new measures which allow us to compare the strength  
366 of interaction between species abundances and their functional dissimilarities among communities  
367 with different species richness, abundance and dissimilarity distribution. Unlike most previous  
368 measures of functional evenness, for  $Cor_B$ ,  $SES_B$  and  $Q_B$  functional diversity always increases with  
369 functional imbalance. That is, with the positive link between dissimilarity and abundance.

370 As shown by our results, all proposed measures of functional imbalance were able to highlight  
371 the main changes in community structure following grazing exclusion of a dry calcareous grassland  
372 in Tuscany. Hence, looking simultaneously at various facets of functional diversity, it is possible to

373 recognize not only whether two communities are functionally different, but also why they are  
374 different. That is, which components take on higher/lower values in community A than in  
375 community B. This allows us to investigate in deeper detail the functional processes that shape  
376 community structure.

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

391 Compared to  $Cor_B$ , which is expressed as a standard correlation coefficient in the range [-1, 1]  
392 between the product of species abundances  $p_i \times p_j$  and their functional dissimilarities  $d_{ij}$ ,  $SES_B$   
393 and  $Q_B$  are normalized locally: that is, by keeping species abundances and interspecies  
394 dissimilarities unchanged and modifying only the interaction between them. Alternative ways for  
395 normalizing Rao with different biological meanings were studied e.g. by Pavoine & Bonsall (2009)  
396 or Ricotta et al. (2016), and the interested reader is addressed to these papers for additional details.

397 This permutation procedure allows  $SES_B$  and  $Q_B$  to be independent of the other components of  
398 Rao's diversity  $S$  and  $\bar{d}_{ij}$ . Here, independence or unrelatedness *sensu* Chao et al. (2012) means that  
399 knowing the values of  $S$  and  $\bar{d}_{ij}$  would put no mathematical constraints on the range of values that  
400 the imbalance factor can take. In particular, Chao & Chiu (2016) proposed an intuitive condition to  
401 assure the unrelatedness of two measures: the range of values that a measure of functional  
402 imbalance can take should be a fixed interval (usually in the range 0–1) regardless of the values of  $S$   
403 and  $\bar{d}_{ij}$ . While  $SES_B$  quantifies functional imbalance in standard deviation units, the index  $Q_B$   
404 conforms to this requirement. This ensures that the same magnitude of functional imbalance  
405 quantifies the same degree of irregularity of species abundance distribution in functional space,

406 even if the assemblages differ in their diversity or dissimilarity structure (see Chao & Ricotta,  
407 2019). Note that our proposal of calculating functional imbalance by normalizing an index of  
408 functional diversity is not confined to the Rao quadratic diversity. Rather, the same approach can be  
409 generalized to virtually any functional diversity index that is based on a combination of species  
410 abundances and their functional dissimilarities simply by permuting the relative abundances  $p_i$   
411 among the  $N$  species. The interpretation of the results will then depend case by case on the index  
412 formulation.

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

419 In recent years there has been a renewed interest in a series of algorithmic measures of diversity  
420 and dissimilarity (e.g. Weitzman, 1992; Kosman, 1996) that could not be extensively used at the  
421 time of their proposal due to a lack of computing power. Thanks to their flexibility, these  
422 algorithmic measures could give new impulse to biodiversity theory from new perspectives and  
423 with new assumptions. Another field where advanced computational methods will possibly give  
424 new impulse to diversity analysis is the choice of an appropriate set of traits that maximize their  
425 association to the ecological process of interest (de Bello et al., 2021). As highlighted by Lavorel et  
426 al. (2008), the relevant traits for ecosystem functioning depend case by case on the analyzed  
427 process. In principle, increasing the dimensionality of functional spaces by the progressive use of a  
428 higher number of traits may lead to a stronger relationships between community structure and  
429 ecosystem functioning. However, such artificially enlarged functional spaces do not necessarily  
430 have a direct biological relationship to the ecological property of interest. Therefore, we need to  
431 select a suitable set of traits that are actually relevant for the property that we are attempting to  
432 estimate. We believe that advanced machine learning methods and artificial intelligence (Lucas,  
433 2020) will greatly contribute to the construction of such ‘tailored’ functional spaces (Ricotta et al.,  
434 2021).

435 To conclude,  $Cor_B$ ,  $SES_B$  and  $Q_B$  constitute the vehicle for measuring functional imbalance.  
436 However, like for any other ecological problem, the way to go (i.e. how many and which traits to  
437 use, how to code them and the method for computing interspecies dissimilarities) should be  
438 assessed case by case based on the specific question at hand. We thus hope, this work will help to

439 build an increasingly conscious approach to the summarization of the many different facets of  
440 functional diversity and their relationship with ecosystem functioning.

441

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445

446 **Credit authorship contribution statement**

447 CR: Conceptualization; Methodology; Data analysis; Writing – original draft. GB: Data collection;  
448 Data analysis; Writing - review & editing. SM: Data collection; Data analysis; Writing - review &  
449 editing. SP: Methodology; Software; Data analysis; Writing - review & editing.

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## 623 **Supporting Information**

### 624 **Appendix 1**

625 Detailed explanation of the calculation of the correlation coefficient between the species  
626 abundances and their functional dissimilarities.

### 627 **Appendix 2**

628 Functional traits and abundances of the species sampled in the grazed and ungrazed plots used in  
629 the worked example.

### 630 **Appendix 3**

631 R function for the calculation of the functional imbalance measures  $Cor_B$ ,  $SES_B$  and  $Q_B$ .

632 **Table 1**

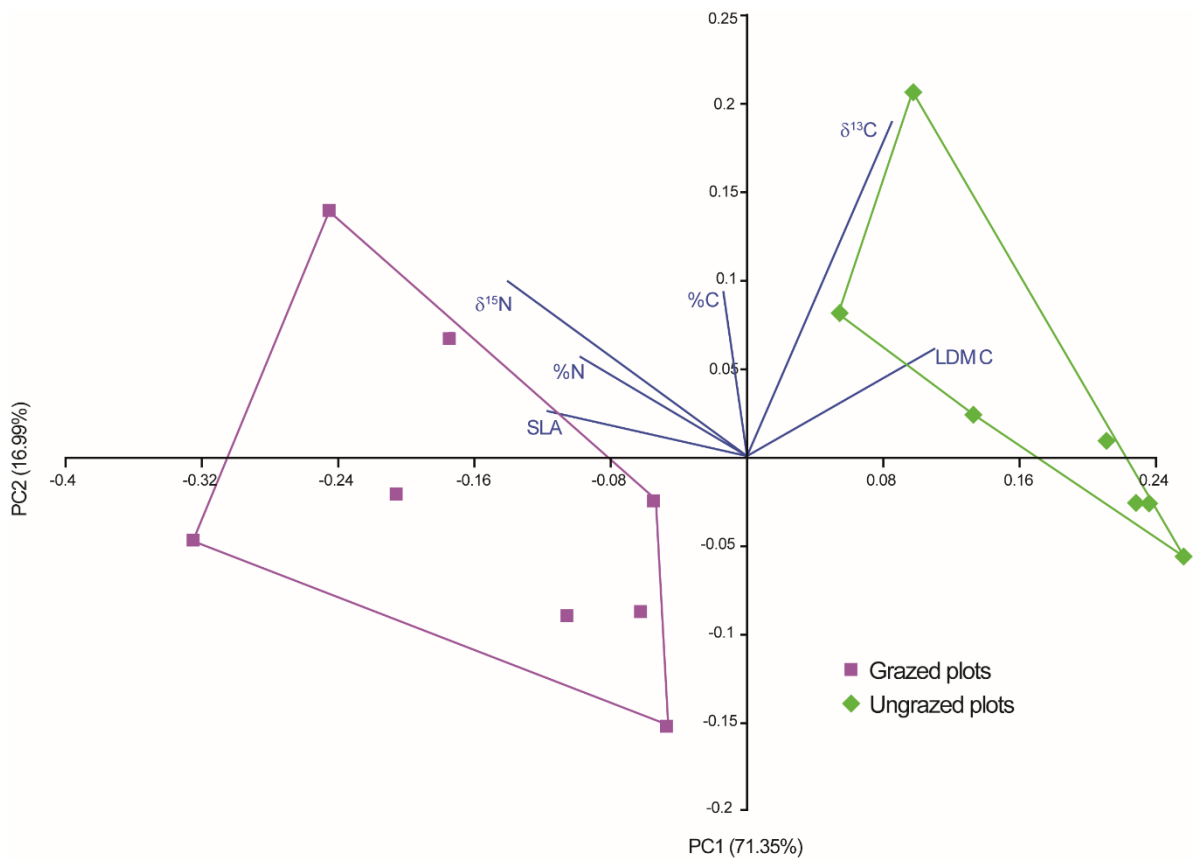
633 Mean (SD) values of individual plots within each treatment (grazed and ungrazed) for species  
 634 richness  $N$ , Simpson's diversity  $S$  and evenness  $E$ , Rao's quadratic diversity  $Q$ , mean functional  
 635 dissimilarity  $\bar{d}_{ij}$ , and functional imbalance  $Cor_B$ ,  $SES_B$  and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

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	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)
$d_{ij}^{**}$	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)

644

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



657