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On two dissimilarity-based measures of functional beta diversity

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Abstract. In this paper, we propose two related versions of a dissimilarity-based measure of functional beta diversity, together with the associated tests for differences in beta diversity among different groups of samples. Both measures are based on the optimal functional matching between the species in two samples. As such, they are tightly connected to Hurlbert’s seminal work on encounter-based diversity measures. The behavior of the proposed measures is illustrated with one worked example on the functional turnover of Alpine species along a successional gradient. Results show that both measures proved able to detect the functional turnover of vegetation along the chronosequence. The method, for which we provide a simple R function, further allows to evaluate the functional contribution of single sampling units to the overall beta diversity of any kind of species assemblages.

Keywords: Algorithmic measure; Assignment problem; Functional dissimilarity; Optimization process; Randomization test.

1. Introduction

Beta diversity measures the variability in species composition among a set of sampling units and is considered to be a key signature of the ecological processes that make species assemblages more or less similar to one another (Anderson et al. 2011; Bennet and Gilbert 2016). Since the pioneering work by Whittaker (1972), there have been intense discussions on how to measure beta diversity and how to test for differences in beta diversity among different groups of samples. For reviews, see e.g. Lande (1996), Koleff et al. (2003), Anderson et al. (2006, 2011), Jost (2007), Tuomisto (2010a, 2010b), Chase et al. (2011), Chao and Chiu (2016), Legendre and De Cáceres (2013), Ricotta (2017), Chao and Ricotta (2019) and references therein.

Irrespective of how beta diversity is measured, an important requisite for diversity measures is their ecological interpretability. According to the seminal paper of Stuart Hurlbert (1971), meaningful diversity indices should have a straightforward biological interpretation: “We therefore can muddle along with a plethora of indices, each supported by at least one person’s intuition and a few recommended by fashion, or we can sharpen our thoughts and rephrase our questions in terms of biologically meaningful properties [...]” (Hurlbert 1971 p. 579).

Among these properties, the probability of intra- and interspecific encounters is a variable of interest, as it is directly related to the potential ecological interactions among all individuals and species in the community (Hurlbert 1971; Patil and Tailie 1982). This encounter-based approach is

45 even more important for functional diversity where, unlike for classical diversity measures, the
46 species are not considered equally dissimilar from each other. In a sense, dealing with functional
47 diversity measures, the potential amount of ecological interactions among different individuals is
48 ideally related to their functional resemblance.

49 In this paper, we thus propose two different versions of a dissimilarity-related index of functional
50 beta diversity, together with the associated tests for differences among different groups of samples.
51 Both indices are based on the optimal functional matching between the species in two samples. As
52 such, they are tightly connected to Hurlbert's encounter-based approach.

53

54 **2. A dissimilarity-based index of functional beta diversity**

55 Given a set of N samples, let p_{jk} be the relative abundance of species $j=1,2,\dots,S$ in sample
56 $k=1,2,\dots,N$ such that $0 \leq p_{jk} \leq 1$ and $\sum_j^S p_{jk} = 1$. The information on the species functional
57 organization within samples is usually represented by a symmetric $S \times S$ matrix of pairwise
58 functional dissimilarities d_{ij} between species i and j in the range $[0,1]$ (with $d_{ij} = d_{ji}$ and $d_{ii} = 0$)
59 which represent the multivariate differences in the character states among the S species.

60 To calculate a dissimilarity-based index of functional beta diversity, the first step consists in
61 calculating the pairwise functional dissimilarity D_{hk} between any pair of samples h and k . To this
62 end, Ricotta et al. (2021a) first used an algorithmic measure originally developed by Kosman
63 (1996) and Gregorius et al. (2003) to calculate genetic distances between populations. The measure
64 is based on the optimal matching between the species abundances in h and k so as to minimize the
65 overall functional dissimilarity between both samples.

66 The dissimilarity index D_{hk} is calculated as follows: given two samples h and k , with n
67 individuals in both samples, each individual in h is matched to an individual in k in order to get n
68 pairs that minimize the sum of functional dissimilarities between the individuals in each pair
69 (Kosman & Leonard, 2007). The pairs are built such that all individuals in both samples are used
70 only once. The overall functional dissimilarity between the two samples is then obtained as the
71 mean dissimilarity between each pair of individuals (i.e. by dividing the sum of functional
72 dissimilarities by the n pairs of individuals). However, since the number of individuals in h and k is
73 generally not the same, to get a complete matching between the samples, this procedure is usually
74 performed on the species relative abundances in both samples. The algorithmic dissimilarity D_{hk}
75 can be thus interpreted as the minimum cost per individual needed to change the character states of
76 the species in sample h to the states of the species in k (Gregorius et al. 2003).

77 Finding the optimal matching between the species abundances in h and k is known as the
 78 assignment problem, a special type of linear programming or linear optimization problem (Dantzig
 79 and Thapa 1997). Dealing with species relative abundances, the functional dissimilarity between
 80 samples h and k can be formulated as (Gregorius et al., 2003):

81

$$82 \quad D_{hk} = \min_{\pi} \sum_i^S \sum_j^S d_{ij} \times \pi(i, j) \quad (1)$$

83

84 where $\pi(i, j)$ is the relative abundance of species i in sample h that is matched with species j in
 85 sample k . Since D_{hk} is essentially a mean dissimilarity between matched pairs of individuals, if the
 86 functional dissimilarity d_{ij} between each pair of individuals is in the range $[0, 1]$, the resulting
 87 mean dissimilarity also ranges between 0 and 1. Kosman (2014) further showed that if all species in
 88 h and k are considered maximally dissimilar from each other (i.e. if $d_{ij} = 1$ for all species i in sample
 89 h and species j in sample k), D_{hk} will be equal to $D_{hk} = \frac{1}{2} \sum_{i,j}^S |p_{ih} - p_{jk}|$.

90 A simple way to generalize D_{hk} to more than two samples, which is usually adopted in
 91 community ecology for calculating the beta diversity of a set of N samples (but see e.g. Diserud and
 92 Ødegaard 2007), consists in calculating the mean value of D_{hk} for all possible pairs of samples:

93

$$94 \quad \beta_N = \frac{\sum_{k>h}^N D_{hk}}{N(N-1)/2} \quad (2)$$

95

96 Once beta diversity has been calculated, the next step is how to test for differences in beta
 97 diversity among different groups of samples. To this end, Anderson (2006) proposed a multivariate
 98 analogue of Levene's (1960) test, which is directly connected to the way β_N is calculated. The test
 99 can be considered in two steps: first, starting from the functional dissimilarities between all pairs of
 100 sampling units D_{kn} , the dissimilarity D_k of each individual sample from its group centroid in
 101 multivariate space is calculated according to McArdle and Anderson (2001). Next, the average of
 102 these dissimilarities among groups is compared using ANOVA. A P -value can be then obtained
 103 with either the traditional tables on F -distribution or by using a permutation procedure (Anderson
 104 2006).

105 A drawback of this method is that the dissimilarity of individual samples from the group centroid
 106 depends on the number of samples in each group. Take for example a group composed of five

107 maximally dissimilar samples, i.e. with $D_{hk} = 1$ for all $h \neq k$. In this case, the dissimilarity $D_{k\cdot}$ of
 108 each individual sample from its group centroid is equal to $D_{k\cdot} = 0.632$. By contrast, for ten
 109 maximally dissimilar samples, $D_{k\cdot} = 0.671$ (for details, see Anderson 2006). Accordingly, this test
 110 works correctly only with fully balanced designs with the same number of samples in each group.

111 To overcome this problem, a possible solution may consist in substituting $D_{k\cdot}$ with the mean
 112 dissimilarity of each individual sample k from all other $N - 1$ samples in the same group:

$$114 \quad D_{\bar{k}} = \frac{\sum_{h \neq k}^N D_{hk}}{N - 1} \quad (3)$$

115
 116 The same approach was used by Violle et al. (2017) and Kosman et al. (2019) to calculate the
 117 mean distance in trait space of a species to all other species in a community. The main advantage of
 118 $D_{\bar{k}}$ over $D_{k\cdot}$ is that $D_{\bar{k}}$ is not influenced by the number of samples in each group. Like for the
 119 Anderson (2006) test, the average of these dissimilarities among groups can be then compared using
 120 standard ANOVA (see the example in Appendix 1).

121

122 **3. A second index of beta diversity**

123 A second method for deriving a measure of multiple-site functional dissimilarity among
 124 sampling units may consist in calculating the dissimilarity of Kosman (1996) and Gregorius et al.
 125 (2003) $D_{k\eta}$ between the species relative abundances in sample k and the species relative
 126 abundances in an hypothetical complementary sample η . This complementary sample is obtained by
 127 pooling together the species relative abundances of all $N - 1$ samples that are different from k such
 128 that the relative abundance of species j in η is calculated as:

129

$$130 \quad p_{j\eta} = \frac{\sum_{h \neq k}^N p_{jh}}{N - 1} \quad (4)$$

131

132 According to this leave-one-out approach, η can be interpreted as the compositional centroid of
 133 the $N - 1$ samples that differ from k in Euclidean space (see Champely and Chessel 2002). A
 134 multiple-site measure of beta diversity can be then obtained by taking the mean of the
 135 dissimilarities $D_{k\eta}$ over the N samples:

136

137
$$\beta_{\eta} = \frac{\sum_k^N D_{k\eta}}{N} \quad (5)$$

138

139 If beta diversity is calculated according to Eq. 5, a test for differences in beta diversity among
140 different groups of samples can be then performed in the usual way, by comparing the mean values
141 of $D_{k\eta}$ within each group with ANOVA.

142

143 **4. Worked example**

144 **4.1. Data**

145 To illustrate the behavior of the proposed measures, we used a data set of Alpine vegetation
146 sampled by Caccianiga et al. (2006) along a primary succession at the foreland of the Rutor Glacier
147 (Northern Italy). The data set has been already used in previous studies on community structure and
148 diversity (Ricotta et al., 2016; Ricotta et al., 2020) and is composed of 45 species in 59 plots of
149 approximately 25 m². All data are available in Ricotta et al. (2016, Appendix S2). The species
150 abundances in each plot were measured with a five-point ordinal scale transformed to ranks. The
151 plots were classified into three successional stages based on the age of the glacial deposits: early-
152 successional stage (17 plots), mid-successional stage (MSS; 32 plots), and late-successional stage
153 (10 plots).

154 For all 45 species sampled at the three successional stages, we used six quantitative traits that are
155 related to their successional status along the primary succession: canopy height (CH; mm), leaf dry
156 mass content (LDMC; %), leaf dry weight (LDW; mg), specific leaf area (SLA; mm² × mg⁻¹), leaf
157 nitrogen content (LNC; %), and leaf carbon content (LCC; %). All traits can be found in Caccianiga
158 et al. (2006, Table 2).

159 First, we used the Euclidean distance to compute a matrix of pairwise functional distances
160 between the 45 species from the six functional traits. For this purpose, all trait values for the 45
161 species were standardized to zero mean and unit standard deviation. The output functional distances
162 were then scaled in the range [0,1] by dividing each distance by the maximum value in the
163 distance matrix.

164 Using the algorithmic approach of Kosman (1996) and Gregorius et al. (2003), we next
165 calculated the beta diversity components (i.e. dissimilarities) $D_{\bar{k}}$ and $D_{k\eta}$ for each sample in each
166 successional stage. All calculations were performed with a new R script (available in the electronic
167 Appendix 1 and 2 of this paper) that modifies the R function `dislptransport` in Ricotta et al.
168 (2021, Appendix S3). We finally tested for differences in beta diversity among the three
169 successional stages by comparing the average of these dissimilarities among groups with ANOVA.

170 P-values were obtained by using a permutation procedure. Among the many available permutation
171 procedures in ANOVA designs (Anderson and Ter Braak 2003; Anderson 2004), we used the
172 simplest approach, which consists in permuting individual observation units among the three
173 successional stages of the Rutor chronosequence. To this end, we reshuffled $17+32+10=59$
174 observed dissimilarities $D_{\bar{k}}$ and $D_{k\eta}$ into random groups of 17, 32, and 10 units, respectively (9999
175 permutations) and recalculated the F-values for each permutation. The same permutation procedure,
176 was then used to perform a post-hoc pairwise t-test with Holm correction of the values of $D_{\bar{k}}$ and
177 $D_{k\eta}$ between the three successional stages.

178

179 **4.2. Results**

180 The results of the permutational ANOVA on the values of $D_{\bar{k}}$ and $D_{k\eta}$ among the three
181 successional stages were in both cases highly significant ($F(D_{\bar{k}})=71.56$, $p < 0.001$ and
182 $F(D_{k\eta})=18.91$, $p < 0.001$). For both dissimilarity coefficients $D_{\bar{k}}$ and $D_{k\eta}$, the within-group
183 dispersion (or beta diversity) progressively decreased along the primary succession (Figure 1). As
184 shown by Caccianiga et al. (2006) and Ricotta et al. (2016), the significantly higher beta diversity of
185 the early-successional samples may be due to the random dispersal mechanisms that drive the
186 colonization of the moraine ridges in the first successional stages (abiotic filter). In contrast, the
187 lower beta diversity of the mid- and late successional samples is associated to a lower level of
188 stochasticity in the colonization process of the later successional stages and hence to an increased
189 level of functional homogeneity among different sampling units (biotic filter).

190 Note that, since $D_{\bar{k}}$ is essentially an average dissimilarity between pair of samples, while $D_{k\eta}$ is
191 the dissimilarity between a given sample k and a complementary sample η that is obtained by
192 pooling together the species relative abundances of all samples that are different from k , the values
193 of $D_{k\eta}$ are generally lower than the values of $D_{\bar{k}}$ (see e.g. Figure 1).

194

195 **5. Discussion**

196 In this paper we proposed two measures of functional beta diversity, β_N and β_η which originate
197 from Whittaker's (1972) suggestion that beta can be summarized from a dissimilarity coefficient
198 between pairs of samples (see also Chao and Chiu 2016). The proposed measures are tightly
199 connected to each other to the point that both of them can be considered '*variazioni sul tema*' of the
200 same approach. In particular, $D_{k\eta}$ represents the dissimilarity of sample k from the pooled set of
201 species in the $N-1$ samples that differ from k . Therefore, this index, together with the

202 corresponding beta diversity β_η , is directly related to the notion of originality (or distinctiveness,
203 Pavoine et al. 2017). A sample is functionally original if its functional characteristics are rare in the
204 pooled set of samples. The index is also related to the notion of the complementarity of a sample
205 compared to a reference set of samples: complementarity being the gain in biodiversity units
206 provided by adding an area (or sample) to a set of areas (samples) (Faith et al. 2004). These two
207 notions (originality and complementarity) are used in conservation biology to identify sites with
208 distinct species/functional/phylogenetic composition (and thus sites for which conservation actions
209 should be a priority because of their distinct composition) (e.g. Mishler et al. 2014).

210 From the perspective of conservation biology, Kosman et al. (2019) recently proposed an
211 additional indicator for estimating functional differences among samples: functional uniqueness, or
212 singularity. Based on this approach, a sample that is on average quite distant from most samples but
213 functionally similar to another sample has a lower conservation priority compared to a sample with
214 the same average distance to other samples but without a close neighbor in functional space. To
215 summarize this property, Violle et al. (2017) calculated the minimum pairwise distance between a
216 focal sample and all other samples, while the singularity measure of Kosman et al. (2019) is based
217 on variation in distances of the focal sample to all other samples, not just the nearest neighbor in
218 trait space. Nonetheless, irrespective of how singularity is calculated, it can be easily derived from
219 the distances D_{hk} in Eq. 1.

220 Unlike the vast majority of functional dissimilarity measures used in community ecology, the
221 algorithmic index of Kosman (1996) and Gregorius et al. (2003), is not based on the excess of
222 among-sample diversity compared to within-sample diversity (e.g. Chao et al. 2014; Chiu and Chao
223 2014; Pavoine and Ricotta 2014). Therefore, it is very flexible as it can be based on any between-
224 species dissimilarity measure of choice without restrictions on their geometrical properties (see e.g.
225 Pavoine and Ricotta 2014). Also, the index of Kosman (1996) and Gregorius et al. (2003) satisfies
226 an important requisite for functional dissimilarity measures which requires that dissimilarity
227 remains unchanged if a given species j is replaced by two functionally identical species with the
228 same total abundance of j . For mathematical details, see Leinster and Cobbold (2012); Pavoine and
229 Ricotta (2019). From an ecological viewpoint, this means that the measures that conform to this
230 requisite summarize the functional dissimilarity among samples irrespective of the identity of the
231 species that support these functions. Accordingly, this algorithmic dissimilarity is closer to the
232 essence of functional dissimilarity than the measures that do not conform to this requisite.

233 Regarding the test for differences in functional beta diversity among different groups of samples,
234 the principle is the same as that of Anderson (2006). However, the values of $D_{\bar{k}}$ and $D_{k\eta}$ are not
235 influenced by the number of samples in each group. In addition, we do not need to calculate the

236 functional centroid of each group, and this renders the test much easier to perform, especially if the
237 dissimilarities D_{hk} and $D_{k\eta}$ are not embeddable in Euclidean space without distortion (for details,
238 see McArdle and Anderson 2001).

239 Nonetheless, alongside the pros, there are also a few potential cons for this test: like for the
240 Anderson test, the values of $D_{\bar{k}}$ and $D_{k\eta}$ are not fully independent of each other. This is because,
241 for a given sample k the quantity $D_{\bar{k}}$ ($D_{k\eta}$) is obtained by averaging all dissimilarities D_{hk} (all
242 species relative abundances p_{jh}) over all $N-1$ samples that are different from k (see Eq. 3 and 4,
243 respectively). This nonindependence may become relevant for small numbers of samples such that
244 in the most critical situation of $N=2$, the values of $D_{\bar{k}}$ and $D_{k\eta}$ are identical for both samples.

245 Even more importantly, the randomization process associated to this test, while being
246 statistically sound, has only little biological foundation. Beta diversity describes the spatial
247 variability in species composition and is considered to be a key signature of a number of community
248 assembly processes, such as dispersal, habitat filtering, intra- and inter-specific competition, or the
249 species responses to environmental conditions (Bennet and Gilbert 2016). Therefore, while the
250 permutation of the dissimilarities $D_{\bar{k}}$ and $D_{k\eta}$ among sampling units has no clear biological
251 meaning, a biologically sound null model should provide some indication on whether differences in
252 beta diversity among groups of samples are actually related to deterministic assembly processes that
253 deviate from stochastic patterns of species co-occurrence (Chase et al. 2011). This may be achieved,
254 for example, by restricted permutation of species occurrences among the samples in each group.
255 However, to construct an adequate randomization test that correctly addresses the ecological
256 questions under study without confounding within group heterogeneity with between group
257 heterogeneity, some additional work is needed. In the meantime, the tests described in this paper
258 may represent an acceptable, though ecologically imperfect solution to the problem.

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355 **Supplementary Material**

356 **Appendix 1.** R scripts and examples for the calculation of the two functional beta diversity measures
 357 proposed in this paper

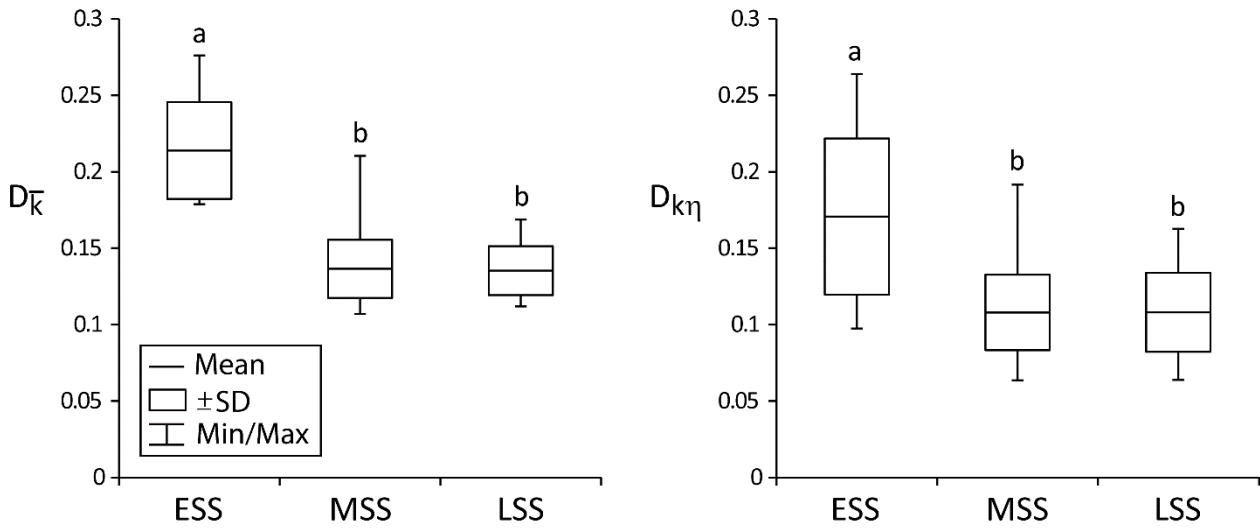
358 **Appendix 2.** R scripts in text format

359 **Author contributions.** CR conceived the idea; CR, EK and SP developed the methodology; MC and
360 BC collected the data; all authors analyzed the data; CR took the lead in writing the main text. SP
361 wrote the R script. All authors revised the manuscript critically and approved the final version.

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

365
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367 **Figure 1.** Box plots of the beta diversity components (dissimilarity coefficients) $D_{\bar{k}}$ and $D_{k\eta}$ for the
 368 three successional stages of the Alpine vegetation of the Rutor glacier. ESS = early-successional
 369 stage; MSS = mid-successional stage; LSS = late-successional stage. Different letters a and b
 370 indicate significantly different distributions at $p < 0.001$ for $D_{\bar{k}}$ and $p < 0.01$ for $D_{k\eta}$
 371 (permutational t-test with Holm adjustment for multiple tests based on 9999 randomizations).
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