

1 **Title**

2 Review and performance evaluation of trait-based between-community dissimilarity measures

3

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10

## 11 **Abstract**

- 12 1. In the recent years a variety of indices have been proposed with the aim of quantifying  
13 functional dissimilarity between communities. These indices follow different  
14 approaches to account for between-species similarities in the calculation of  
15 community dissimilarity, yet they all have been proposed as straightforward tools.
- 16 2. In this paper we reviewed the trait-based dissimilarity indices available in the  
17 literature, contrasted the approaches they follow, and evaluated their performance in  
18 terms of correlation with an underlying environmental gradient using individual-based  
19 community simulations with different gradient lengths. We tested how strongly  
20 dissimilarities calculated by different indices correlate with environmental distances.  
21 Using random forest models we tested the importance of gradient length, the choice of  
22 data type (abundance vs. presence/absence), the transformation of between-species  
23 similarities (linear vs. exponential), and the dissimilarity index in the predicting  
24 correlation value.
- 25 3. We found that many indices behave very similarly and reach high correlation with  
26 environmental distances. There were only a few indices (e.g. Rao's  $D_Q$ , and  
27 representatives of the nearest neighbour approach) which performed regularly poorer  
28 than the others. By far the strongest determinant of correlation with environmental  
29 distance was the gradient length, followed by the data type. The dissimilarity index  
30 and the transformation method seemed not crucial decisions when correlation with an  
31 underlying gradient is to be maximized.
- 32 4. *Synthesis*: We provide a framework of functional dissimilarity indices and discuss the  
33 approaches they follow. Although, these indices are formulated in different ways and  
34 follow different approaches, most of them perform similarly well. At the same time,

35 sample properties (e.g. gradient length) determine the correlation between trait-based  
36 dissimilarity and environmental distance more fundamentally.

37

### 38 **Keywords**

39 beta diversity, dissimilarity index, distance metric, community ecology, functional traits

40

### 41 **Abbreviations**

42 CDF = cumulative distribution function, CWM = community-weighted mean, FDissim =

43 functional dissimilarity, VIS = variable importance score

44

### 45 **Introduction**

46 Understanding and explaining the variation of living communities along dimensions of space

47 and time have been in the focus of ecological research ever since. The widely applied scheme

48 by Whittaker (1960, 1972) to tackle questions of different aspects of community variation

49 divides community diversity into alpha (within-community), beta (between-community) and

50 gamma (across-community) components. It is no exaggeration to say that among these three,

51 beta diversity sparked the most controversy due to the multitude of ways how it can be

52 formulated (Tuomisto 2010a,b, Anderson et al. 2011, Podani & Schmera 2011, Baselga &

53 Leprieur 2015). One of the most popular approaches to beta diversity builds upon

54 quantification of variation between pairs of communities using dissimilarity indices

55 (Anderson et al. 2006, Legendre & De Cáceres 2013, Ricotta 2017). A broad spectrum of

56 such dissimilarity indices are available for many specific purposes providing elementary tools

57 for different fields of ecology and beyond (see reviews by Legendre & Legendre 1998, Podani

58 2000). Nevertheless, choosing from such many options requires a more or less subjective  
59 decision from the researcher which may affect the final result of the analysis. Comparative  
60 reviews of dissimilarity indices (Faith et al. 1987, Koleff et al. 2003) and evaluations of  
61 effects of methodological decisions (Lengyel & Podani 2015) are inevitably helpful in making  
62 these decisions.

63 The most popular, yet not exclusive, interpretations of diversity for long time considered  
64 species as variables which are unrelated with each other. In the last two decades, however, the  
65 functional approach to ecological questions gained unprecedented attention (Díaz & Cabido  
66 2001, McGill et al. 2006). This approach relies on the fact that species are not all maximally  
67 different from each other, rather they can be considered related with respect to similarities in  
68 their traits thought to represent their roles in ecosystems (Violle et al. 2007). The need for  
69 explicitly accounting for between-species relatedness generated a wave of methodological  
70 improvements that introduced new methods in the calculation of diversity. Next to a lively  
71 scientific discussion on how functional alpha diversity can be appropriately quantified (Mason  
72 et al. 2005, Petchey & Gaston 2006, Villéger et al. 2008, Mouchet et al. 2010), suggestions  
73 were made also for the expression of functional beta diversity (Swenson 2011, Botta-Dukát  
74 2018, Chao et al. 2019). Among them, a large variety of indices for calculating dissimilarity  
75 between pairs of communities on the basis of the traits of their species have been proposed  
76 (e.g. Ricotta & Burrascano 2008, Cardoso et al. 2014, Ricotta & Pavoine 2015). Although  
77 these indices have been introduced as straightforward measures for revealing between-  
78 community dissimilarity on the basis of traits, they have very different concepts behind, and  
79 we still lack a comparative review of them.

80 In this paper we aim to provide an overview and a conceptual framework for the pairwise  
81 functional dissimilarity (hereafter called FDissim) measures available in the literature to our  
82 best knowledge. We start with a (1) short overview of the concept and indices of ecological

83 (dis-)similarity without accounting for relatedness of species, then (2) we review and classify  
84 FDissim indices according to their conceptual basis, and (3) we test the performance of  
85 FDissim indices.

86

## 87 **Short overview of taxon-based (dis-)similarity methods**

88 Most FDissim measures are generalizations of simple indices which were originally designed  
89 for expressing dissimilarity based on species composition (that is, omitting similarities  
90 between species). We start the review of trait-based (dis-)similarity measures with a brief  
91 summary of these species-based indices. Then, we present a framework of approaches  
92 including several families of trait-based dissimilarity indices.

### 93 *Species-based indices*

94 Most indices can be written in either similarity ( $s$ ) or dissimilarity ( $d=1-s$ ) form but when we  
95 do not see necessary to specify the form, we call them ‘resemblances’. In the case of  
96 presence/absence data, these indices are based on the well-known  $2 \times 2$  contingency table  
97 whose cells represent the number of species shared (denoted by  $a$ ), as well as the number of  
98 species occurring only in one of the communities ( $b$  and  $c$ ). The fourth cell of the contingency  
99 table quantifying the number of shared absences is disregarded by these indices and rarely  
100 used in ecological analyses (but see Tamás et al. 2001). All these indices agree that they  
101 express similarity as the proportion of shared diversity to total diversity. Hence, all of them  
102 range between 0 and 1. In the case of presence/absence data the number of shared species,  $a$ ,  
103 in the numerator stands for shared diversity for all indices, while the denominators are  
104 different. In the Sørensen index ( $s_S$ ) the denominator is the arithmetic mean of the species  
105 numbers of the two communities, in Ochiai index ( $s_O$ ) it is their geometric mean, in  
106 Kulczynski ( $s_K$ ) it is their harmonic mean, while in Simpson index ( $s_{Si}$ ) it is the richness of the

107 species poorer community. If the two communities are equally species-rich, then these indices  
108 are equal, otherwise  $s_S < s_O < s_K < s_{Si}$ . In the Jaccard index ( $s_J$ ), the denominator is the total  
109 number of species in the two communities, while in Sokal & Sneath index ( $s_{SS}$ ) species  
110 occurring in a single community are taken into account with double weight. There is a direct  
111 and monotonic relationship between Jaccard, Sørensen, and Sokal & Sneath indices (see  
112 Appendix S1). Table 1 summarizes the similarity and dissimilarity forms of the above indices.  
113 For abundance data, the resemblance of two communities is derived from the summation of  
114 species-wise differences, with the simplest interpretation being the Euclidean and the  
115 Manhattan distances, respectively:

116 Eq. 1. 
$$d_{Euclidean} = \sqrt{\sum_{i=1}^{S_{jk}} (x_{ij} - x_{ik})^2}$$

117 Eq. 2. 
$$d_{Manhattan} = \sum_{i=1}^{S_{jk}} |x_{ij} - x_{ik}|$$

118 where  $x_{ij}$  and  $x_{ik}$  are the abundance of species  $i$  in communities  $j$  and  $k$ ,  $S_{jk}$  is the total number  
119 of species in  $j$  and  $k$ . For both indices, the minimum is 0 but the maximum of Euclidean  
120 distance is the square-root of the sum of squared abundances, while for Manhattan distance  
121 the maximum is the sum of abundances. Obviously, their dependence on total abundance  
122 makes these index values difficult to compare across samples; therefore, indices including a  
123 standardization have become more popular in ecological studies. The standardization is  
124 possible in several ways. The first option is to standardize raw species contributions to  
125 between-community dissimilarity ( $x_{ij}-x_{ik}$ ), and then to sum them. Therefore, each species-level  
126 difference in abundance should be divided by a scaling factor in a way that maximal species-  
127 level difference is 1 and this difference is maximal if species present only one of the  
128 compared communities. Summing  $x_{ij}$  and  $x_{ik}$  in the denominator satisfies this requirement and  
129 gives a well-known distance measure, the Canberra index:

130 Eq. 3. 
$$d_{Canberra} = \frac{\sum_{i=1}^{S_{jk}} |x_{ij} - x_{ik}|}{\sum_{i=1}^{S_{jk}} (x_{ij} + x_{ik})}$$

131 However, Canberra index still ranges between 0 and  $S_{jk}$ . According to Ricotta & Podani  
132 (2017), the normalized Canberra index can be derived by unweighted averaging of species  
133 contributions:

134 Eq. 4. 
$$d_{NCanberra} = \frac{1}{S_{jk}} \sum_{i=1}^{S_{jk}} \frac{|x_{ij} - x_{ik}|}{(x_{ij} + x_{ik})}$$

135 Alternatively, species-level differences can be divided by  $\max(x_{ij}, x_{ik})$ . It also results unity, if  
136 species occur only either of the plots. Ricotta & Podani (2017) called this modified Canberra  
137 index, whose normalized version follows:

138 Eq. 5. 
$$d_{NMCanberra} = \frac{1}{S_{jk}} \sum_{i=1}^{S_{jk}} \frac{|x_{ij} - x_{ik}|}{\max(x_{ij}, x_{ik})}$$

139 Calculating from binary data, both normalized Canberra and normalized modified Canberra  
140 result in Jaccard dissimilarity.

141 A different way of standardization is possible if raw species-level differences are summed and  
142 divided by the sum of their theoretical maxima. In this case, the denominator can follow the  
143 logic of Canberra index, thus leading to the Bray-Curtis index:

144 Eq. 6. 
$$d_{BC} = \frac{\sum_{i=1}^{S_{jk}} |x_{ij} - x_{ik}|}{\sum_{i=1}^{S_{jk}} (x_{ij} + x_{ik})}$$

145 Analogously with the normalized modified Canberra index, instead of the sum, the  
146 denominator may contain the maximum of abundance, resulting in the formula known as  
147 Marczewski-Steinhaus index:

148 Eq. 7. 
$$d_{MS} = \frac{\sum_{i=1}^{S_{jk}} |x_{ij} - x_{ik}|}{\sum_{i=1}^{S_{jk}} \max(x_{ij}, x_{ik})}$$

149 Worth to note that Bray-Curtis and Marczewski-Steinhaus indices calculated on  
150 presence/absence data return the values of Sørensen index and Jaccard index in dissimilarity  
151 form, respectively. Moreover, several abundance-based indices can be expressed if we  
152 generalize  $a$ ,  $b$ , and  $c$  quantities used during the definition of indices for presence/absence  
153 data (Tamás et al. 2001).

154 Eq. 8. 
$$a' = \sum_{i=1}^{S_{jk}} \min(x_{ij}, x_{ik})$$

155 Eq. 9. 
$$b' = \sum_{i=1}^{S_{jk}} (\max(x_{ij}, x_{ik}) - x_{ij})$$

156 Eq. 10. 
$$c' = \sum_{i=1}^{S_{jk}} (\max(x_{ij}, x_{ik}) - x_{ik})$$

157 Substituting  $a$ ,  $b$  and  $c$  with  $a'$ ,  $b'$  and  $c'$  into the formula of Sørensen index gives Bray-  
158 Curtis, and doing so with Jaccard index results in the Marczewski-Steinhaus. Abundance  
159 versions of all other presence/absence indices can be created in the same manner.

160

### 161 *A classification of FDissim indices*

162 FDissim indices incorporate trait information into the calculation of dissimilarity in different  
163 ways. The simplest solution is when summary statistics or distributions are calculated for the  
164 two communities and a measure of distance or segregation is calculated between them. We  
165 call this the *summary-based class*, and in our review, we include two approaches within this,  
166 the *typical value approach* and the *distribution-based approach*. In the second class we  
167 include indices which utilize a symmetrical species by species (dis-)similarity matrix and link  
168 it directly through matrix operations with the compositional matrix. We call this the  
169 *dissimilarity-based class* which includes the *probabilistic*, the *ordinariness-based*, the  
170 *diversity partitioning*, and the *nearest neighbour approaches*. The third class includes  
171 methods which make use of between-species (dis-)similarities for classification of species;



172 therefore, we call it the *classification-based class*. The classification either transforms the  
173 original structure of the dissimilarity matrix into discrete groups of species which can be used  
174 as functional types, or expresses dissimilarities in a form of a tree-graph where between-  
175 species dissimilarities are organized in an inclusive hierarchy. This is a widespread approach  
176 for accounting for phylogenetic relatedness, since phylogenies are commonly summarized in  
177 the form of cladograms. Such methods heavily rely on the algorithm chosen for the  
178 classification, including the decisions about the number of clusters and the method for  
179 breaking tied values. Examples are provided by Hérault & Honnay (2007), Nipperess et al.  
180 (2010), and Cardoso et al. (2014), while a review is available by Pavoine (2016). As there is  
181 no general recommendation for the classification method, we omit this class from the  
182 framework detailed below and the comparative test. The classification of trait-based  
183 dissimilarity indices and their main properties are summarized on Table 2.

#### 184 *Typical value approach*

185 Indices following this approach represent each community with a typical trait value, and  
186 calculate a distance metric between them. The most commonly applied typical trait value is  
187 the community weighted mean (CWM; Garnier et al. 2004). The rationale behind the CWM  
188 can be linked with the mass ratio hypothesis (Grime 1998) stating that the effect of species on  
189 ecosystem functioning is proportional to their relative abundances. Although, several issues  
190 emerged regarding its limited applicability in statistical inference (Hawkins et al. 2017, Peres-  
191 Neto et al. 2017, Zeleny 2018) and its negligence of within-community variation (Muscarella  
192 & Uriarte 2016), difference in CWM is still considered a reliable indicator of robust changes  
193 in trait composition induced by selective forces like environmental matching or succession  
194 (De Bello et al. 2007, 2013, Kleyer et al. 2012). Ricotta et al. (2015) investigated the  
195 relatedness of the distance between CWMs with the probabilistic approach (see therein) and  
196 showed its applicability on phylogenetic data. Due to its tolerable requirements for

197 computational capacity, Lengyel et al. (2020) used the Euclidean distance between trait  
198 CWMs of phytosociological relevés for the trait-based numerical classification of grasslands  
199 of Poland with a sample size of 6985 sites and 885 species. Another advantage of this method  
200 is its Euclidean property. Besides the community-weighted mean, other typical values, e.g. the  
201 median or the mode, might be considered depending on the scaling of the trait variable and on  
202 specific research aims.

203

#### 204 *Distribution-based approach*

205 Instead of typical values, the distribution of trait values is considered a more reliable  
206 representative of the trait composition and variability of a community. Continuous  
207 distributions can be defined by a density function, while discrete distributions by the  
208 probabilities of the possible values, while both types can be characterized by a cumulative  
209 distribution function (CDF). A useful analogue of the distance between typical values might  
210 be distance between discrete distributions, density functions or CDFs.

211 If data is available on intraspecific trait variation, trait values forms a continuous distribution.  
212 First, separate density functions have to be fitted within each species. Then, density function  
213 of this community-level distribution can be calculated as weighted sum of species level  
214 density functions (Carmona, de Bello, Mason, & Lepš, 2016). If such data is not available, we  
215 can use relative abundances as estimates of probabilities of the corresponding trait values.  
216 Pairs of trait values and their probability form a discrete distribution.

217 Similarity of density functions can be measured by their overlap (see Appendix S2 for  
218 overview of overlap measures). Overlap functions between within-species trait distributions  
219 has already been proved useful in the quantification of between-species niche segregation  
220 (MacArthur & Levins 1967, Mouillot et al. 2005) or trait-based dissimilarity of species (Lepš

221 et al. 2006, De Bello et al. 2013). Nevertheless, they are perfectly applicable to the  
222 community level as well.

223 Gregorius et al. (2003) proposed an index called *delta* for the quantification differences  
224 between discrete trait distributions. Delta is the minimal sum of frequencies shifted from one  
225 trait state to another trait state, weighted by the differences between the respective states.  
226 Minimizing the sum of shifted frequencies is known in linear programming as the  
227 transportation problem (Hitchcock 1941). Due to its relatively high computational demand, it  
228 is unfeasible for large compositional and trait data matrices typically used in ecological  
229 research, therefore, we exclude this index from our comparison.

230 Difference between two CDFs can be calculated at each possible trait values (i.e. not only the  
231 observed ones), then the sum of them can be used as a trait-based dissimilarity measure. In  
232 Appendix S3 we introduce the distance between CDFs in more detail.

233

#### 234 *Maximally distinct communities*

235 Species-based dissimilarities, except Euclidean, Manhattan and (non-normalized) Canberra  
236 distances, equal unity, which is their maximum, when the two compared communities do not  
237 share any species. In this context, we could call such communities maximally distinct.

238 However, when traits are considered, two communities can be similar, even if they do not  
239 share any species. For example, if all species of community *A* is replaced by a similar species  
240 in community *B*, the two communities have no shared species, but from functional point of  
241 view, they are similar. In this context, two communities are maximally distinct, when  
242 similarity of any species from the first community is zero to any species in the other  
243 community. It is a desirable property for a functional similarity index to take the value 0 if  
244 and only if the two compared communities are maximally distinct.

245

246 *Probabilistic approach*

247 This approach can be traced back to the diversity framework proposed by Rao (1982), and  
248 recently extended by Pavoine & Ricotta (2014). Rao's within community diversity is defined  
249 as the expected dissimilarity between two randomly drawn individuals from a single  
250 community:

251 Eq. 11. 
$$Q(\mathbf{p}) = \sum_i \sum_j p_i p_j \delta_{ij}$$

252 where  $p_i$  is the relative abundance of the  $i$ th species in the community and  $\delta_{ij}$  is the  
253 dissimilarity between species  $i$  and  $j$ . This has become a widely used index of functional alpha  
254 diversity (Botta-Dukát 2005). Likewise, a between-community component of diversity,  
255  $Q(\mathbf{p}, \mathbf{q})$ , can be defined as the dissimilarity between two random individuals, each selected  
256 from different communities:

257 Eq. 12. 
$$Q(\mathbf{p}, \mathbf{q}) = \sum_i \sum_j p_i q_j \delta_{ij}$$

258 Between community diversity can be expressed using within community diversity of the two  
259 original communities ( $Q(\mathbf{p})$  and  $Q(\mathbf{q})$ ) and the community with mean relative abundances;  
260  $Q\left(\frac{\mathbf{p}+\mathbf{q}}{2}\right)$ .

261 Eq. 13. 
$$2Q\left(\frac{\mathbf{p}+\mathbf{q}}{2}\right) = 2 \sum_i \sum_j \frac{p_i+q_i}{2} \frac{p_j+q_j}{2} \delta_{ij} = \frac{1}{2} \sum_i \sum_j [p_i p_j + q_i q_j +$$
  
262  $2p_i q_j] \delta_{ij} = \frac{Q(\mathbf{p})+Q(\mathbf{q})}{2} + Q(\mathbf{p}, \mathbf{q})$

263 Subtracting mean within community diversity from the between community diversity leads to  
264 Rao's dissimilarity (also called *DISC*):

265 Eq. 14. 
$$D_Q = \sum_i \sum_j p_i q_j \delta_{ij} - \frac{\sum_i \sum_j p_i p_j \delta_{ij} + \sum_i \sum_j q_i q_j \delta_{ij}}{2} = \sum_i \sum_j p_i q_j \delta_{ij} - \frac{Q(\mathbf{p}) + Q(\mathbf{q})}{2} =$$

266  $2Q\left(\frac{\mathbf{p} + \mathbf{q}}{2}\right) - Q(\mathbf{p}) - Q(\mathbf{q})$

267 where  $p_i$  and  $q_i$  are the relative abundances of species  $i$  in the two communities. Champely  
268 and Chessel (2002) proved that if  $\delta$  has squared Euclidean property, Rao quadratic entropy is  
269 concave function, i.e.  $Q\left(\frac{\mathbf{p} + \mathbf{q}}{2}\right)$  is higher than or equal to mean of  $Q(\mathbf{p})$  and  $Q(\mathbf{q})$ . Thus under  
270 this condition,  $D_Q \geq 0$ . If  $0 \leq \delta_{ij} \leq 1$ ,  $\sum_i \sum_j p_i q_j \delta_{ij}$ , which is the weighted average of  
271 between-species distances, also has to be within this range. Therefore,  $0 \leq D_Q \leq 1$ . However,  
272  $D_Q$  may be much less than 1, even if the two communities are completely distinct, when  $Q(\mathbf{p})$   
273 and  $Q(\mathbf{q})$  are high. Therefore, Pavoine & Ricotta (2014) suggested dividing  $D_Q$  by its  
274 theoretical maximum (see equations 3 and 4 in Pavoine & Ricotta 2014). They recognized  
275 that the resulting indices are representatives of a broader family of indices, hereafter called  
276 *dsimcom*, which are actually the implementations of Rao's between-community and within-  
277 community components of diversity into the similarity formulae designed for  
278 presence/absence data. For this index, it is necessary to introduce the similarity between  
279 species,  $\varepsilon_{ij} = 1 - \delta_{ij}$ . The expected similarity between individuals of different communities,  
280  $A = \sum_i \sum_j p_i q_j \varepsilon_{ij}$  is taken analogous with the shared diversity,  $a$ , according to the parameters  
281 of the similarity indices for presence/absence data disregarding species properties, while the  
282 expected similarities within communities ( $A + B = \sum_i \sum_j p_i p_j \varepsilon_{ij}$  and  $A + C = \sum_i \sum_j q_i q_j \varepsilon_{ij}$ ) are  
283 analogous with the species numbers ( $a + b$ ,  $a + c$ ). In this way, Pavoine & Ricotta (2014)  
284 presented formulae following the Sokal & Sneath, Jaccard, Sørensen, and Ochiai indices.  
285 Additionally, a formula analogous with Whittaker's effective species turnover ( $\beta = \gamma / \alpha - 1$ ;  
286 Whittaker 1972, Tuomisto 2010a) is suggested for two communities, which in similarity form  
287 is shown to be identical with the overlap index of Chiu et al. (2014). In this formulation  
288  $\gamma = A + B + C$  and  $\alpha = (2A + B + C) / 2$ . Pavoine & Ricotta (2014) showed that members of the

289 *dsimcom* family provide meaningful values also if absolute abundances, percentage values or  
290 binary occurrences are used instead of relative abundances.

291 When  $\varepsilon_{ij}$  contains taxonomical similarities, its off-diagonal elements are 0, and  $A=a$ ,  $B=b$ , and  
292  $C=c$ .

293 Worth to note the inherent link between  $D_Q$  and  $CWMdis$  on the basis of the geometric  
294 interpretation by Pavoine (2012) and Ricotta et al. (2015). Pavoine (2012) showed that if  
295 between-species dissimilarities are in the form  $\delta_{ij}=(d_{ij}^2)/2$  and  $d_{ij}$  is Euclidean embeddable,  $D_Q$   
296 is half the squared Euclidean distance between the centroids of two communities – a function  
297 monotonically related with  $CWMdis$ , the simple Euclidean distance between centroids of  
298 communities. As Ricotta et al. (2015) argue, if species relatedness is only described by a  
299 dissimilarity matrix, which is the common case in phylogenetic analyses, species can be  
300 mapped into a principal coordinate analysis ordination using  $d_{ij}$ . Given the Euclidean  
301 embeddable property of  $d_{ij}$ , this ordination should produce  $S-1$  or fewer ordination axes, all  
302 with positive eigenvalues. Ordination scores for species can be used as traits, and therefore,  
303 centroids of communities, and (squared) Euclidean distances between communities can be  
304 calculated. In the special case when between-species dissimilarities are Euclidean distances,  
305  $D_Q$  must be equal with the Euclidean distance between the weighted averages of traits, that is,  
306  $CWMdis$ .

307 It is also notable that Swenson et al. (2011) and Swenson (2011) use the quantity  $Q(\mathbf{p}, \mathbf{q})$  as a  
308 standalone index of pairwise beta diversity and call it  $D_{pw}$  or “Rao’s  $D$ ”. The latter name is  
309 misleading since Rao (1982) himself noted with  $D_{ij}$  the *DISC* (or  $D_Q$ ) index.  $Q(\mathbf{p}, \mathbf{q})$  measures  
310 dissimilarity between two communities but the dissimilarity of a community from itself is not  
311 zero. Swenson (2011) also presents a standardized version of  $Q(\mathbf{p}, \mathbf{q})$  under the name Rao’s  
312 H. With this formula the dissimilarity of a community to itself is scaled to 1, however, its

313 transformation to a meaningful scale where each community has dissimilarity value zero  
314 towards itself is not elaborated. Due to this drawback, we do not consider these indices in our  
315 review of functional dissimilarity measures.

316 Schmidt et al. (2017) proposed probabilistic indices with weighted and unweighted versions  
317 for expressing community similarity on the basis of taxa interaction networks (called *TINA*,  
318 taxa interaction-adjusted) and phylogenetic relatedness (*PINA*, phylogenetic interaction-  
319 adjusted). *TINA* and *PINA* differ only in what type of data the interaction matrix contains.  
320 Notably, the functional formula of weighted *TINA* is identical with the Ochiai version of  
321 *dsimcom*. However, the unweighted *TINA*, abbreviated *TU*, is not a special case of *TINA*,  
322 which we consider an inconsistency. Therefore, we did not include *TU* as a separate index.

323

#### 324 *Ordinariness-based approach*

325 With respect to functional alpha diversity, Leinster & Cobbold (2012) introduced the concept  
326 of species ordinariness defined as the weighted sum of relative abundances of species similar  
327 to a focal species within the same community, or in other words, the expected similarity of an  
328 individual of the focal species and an individual chosen randomly from the same community.

329 According to Ricotta & Pavoine (2015) it is straightforward to replace abundances with  
330 ordinariness values in the species-based (dis-)similarity indices. Following this concept,  
331 Ricotta & Pavoine (2015) introduced a new family of trait-based similarity measures called  
332 *dissABC*. *dissABC* applies the schemes of Jaccard, Sørensen, Ochiai, Kulczynski, Sokal &  
333 Sneath, and Simpson indices. Either relative or absolute abundances can be chosen as input  
334 values. Species ordinariness values can be calculated either with respect to the pooled species  
335 list of the two communities under comparison, or to the total species list of the data matrix.

336 For species-based analyses, Ricotta & Podani (2017) suggested a general formula of distance  
337 measures in which community dissimilarity is calculated by the weighted averaging of  
338 species-level differences in abundance. From this formula, a normalized Canberra distance,  
339 Bray-Curtis distance, Marczewski-Steinhaus index, and an evenness-based dissimilarity index  
340 (Ricotta 2018) can be derived. According to Pavoine & Ricotta (2019), replacing species  
341 abundances with species ordinariness values, a meaningful dissimilarity index can be  
342 designed, which is called *generalized\_TradiDiss*. Additionally, this index contains a factor  
343 which weights the contribution of each species to the overall dissimilarity between the two  
344 communities. This weight can be set to give even weight to all species or to weigh them  
345 proportionally to their relative abundance in the pooled communities.

346

#### 347 *Diversity partitioning approach*

348 Following the work of Hill (1973), a community with *diversity of order  $q$ ,  ${}^qD$* , is as diverse as  
349 a theoretical community containing  ${}^qD$  equally abundant species. The order of diversity,  $q$ ,  
350 expresses the weight given to differences in species abundance,  $q = 0$  representing the  
351 presence/absence case,  $q = \infty$  considering only the relative abundance of the most abundant  
352 species in the community. Without accounting for interspecific similarities, there is emerging  
353 consensus that using effective numbers (also called number of equivalents) is a  
354 straightforward way for partitioning diversity into within-community (alpha), between-  
355 community (beta) and across-community (gamma) components (Jost 2007). Of these three,  
356 the between-community component, beta diversity, can be interpreted as a form of  
357 dissimilarity when applied for two communities (Ricotta 2017). Beta diversity can be derived  
358 from alpha and gamma diversity in a multiplicative (beta = gamma/alpha) or an additive way  
359 (beta = gamma – alpha). Jost (2007) and Chao et al. (2012) argued that multiplicative beta  
360 diversity is a useful way for quantifying community differentiation; however, due to its



361 scaling between 1 and  $N$  ( $N$  being the number of communities) it is not comparable across  
362 samples containing different numbers of communities. To remove this dependence, they offer  
363 three solutions with which the value of multiplicative beta can be normed. Although, for  
364 pairwise comparisons,  $N$  is always 2, it seems straightforward to follow these  
365 recommendations, since the scaling between 0 and 1 has several advantages, and most other  
366 indices also share this property. The rescaling formulae of Chao et al. (2012) embody  
367 different concepts of community (dis-)similarity, which together we call the family of  
368 *multiplicative beta indices*. The first formula is the relative turnover rate per community,  
369 which is a linear transformation of beta to the normed scale.

370 Eq. 15. 
$$\beta_{turnover}\langle q \rangle = ({}^q\beta - 1)/(N - 1)$$

371 Here 0 means identical species composition, while 1 indicates totally distinct communities. In  
372 the pairwise comparison ( $N = 2$ ),  $\beta_{turnover}\langle q \rangle = {}^q\beta - 1$ .

373 The second index measures homogeneity, and is a linear transformation of the inverse of beta.  
374 With respect to the fact that the complement term of homogeneity is heterogeneity, we call its  
375 dissimilarity form  $\beta_{heterogeneity}$ :

376 Eq. 16. 
$$\beta_{heterogeneity}\langle q \rangle = 1 - \left( \frac{1}{{}^q\beta} - \frac{1}{N} \right) / \left( 1 - \frac{1}{N} \right)$$

377 When  $N = 2$ ,  $\beta_{het}\langle q \rangle = 2 - 2/{}^q\beta$ . With  $q = 0$  (presence/absence case) the index is identical with  
378 Jaccard index, while with  $q = \infty$  (abundance case) it is the Morisita & Horn index.

379 The third index measures overlap between communities, whose counterpart is segregation,  
380 thus we call it  $\beta_{segr}$ :

381 Eq. 17. 
$$\beta_{segregation}\langle q \rangle = 1 - \left[ \left( \frac{1}{{}^q\beta} \right)^{q-1} - \left( \frac{1}{N} \right)^{q-1} \right] / \left[ 1 - \left( \frac{1}{N} \right)^{q-1} \right]$$

382 With  $q = 0$ ,  $\beta_{segregation}\langle q \rangle = \beta_{turnover}\langle q \rangle$ , and both gives the Sørensen index.

383 According to Leinster & Cobbold (2012), it is possible to implement species similarities in the  
384 calculation of effective numbers. This way, the meaning of  ${}^qD^Z$ , is the diversity of a  
385 theoretical community with  ${}^qD^Z$  *equally abundant* and *maximally different* species. Hence,  
386 both unevenness in the abundance structure and the between-species similarities decrease the  
387 value of effective species number. Due to measuring diversity in effective numbers, it is  
388 possible to partition diversity into alpha, beta, and gamma fractions (Leinster & Cobbold  
389 2012; Botta-Dukát 2018) in the multiplicative way. Then, this multiplicative beta can be  
390 rescaled using the formulae proposed by Chao et al. (2012). These indices behave consistently  
391 only if abundances are taken into account as relative abundances.

392

### 393 *Nearest neighbour approach*

394 The earliest representatives of this family were shown by Clarke & Warwick (1998) and Izsák  
395 & Prince (2001), then Ricotta & Burrascano (2008), and Ricotta & Bacaro (2010; see  $D_{CW}$   
396 and  $D_{IP}$  indices). Later Ricotta et al. (2016) introduced a new, general family called *PADDis*.  
397 All these indices were primarily defined for presence-absence data type. The approach is  
398 based on a re-definition of the  $b$  and  $c$  quantities of the  $2 \times 2$  contingency table. Looking at  
399 species as maximally different, and taking  $X$  and  $Y$  the two communities under comparison,  $b$   
400 can be viewed as the total uniqueness of community  $X$ . The uniqueness of a single species in  
401  $X$  is 1 if it is absent in  $Y$ , otherwise it is 0. Therefore,  $b$  is the sum of species uniqueness  
402 values. However, from a functional perspective, the uniqueness of a species present only in  $X$   
403 should be between 0 and 1 if it is absent in  $Y$  but a similar species present there. Therefore, it  
404 is possible to define the analogue of  $b$  which accounts for similarities between species:

405 Eq. 18. 
$$B = \sum_{i \in X} (1 - \max_{j \in Y} \varepsilon_{ij}) = S_x - \sum_{i \in X} \max_{j \in Y} \varepsilon_{ij}$$

406 The same logic applies for  $c$ , which is the uniqueness of community  $Y$ , where  $C$  expresses the  
407 degree of uniqueness:

408 Eq. 19. 
$$C = \sum_{i \in Y} (1 - \max_{j \in X} \varepsilon_{ij}) = S_Y - \sum_{i \in Y} \max_{j \in X} \varepsilon_{ij}$$

409 Ricotta et al. (2016) define the  $A$  quantify as follows:

410 Eq. 20. 
$$A = a + (b - B) + (c - C)$$

411 Having  $A$ ,  $B$ , and  $C$  defined as analogues of  $a$ ,  $b$ , and  $c$ , it is now possible to design trait-based  
412 similarity measures following the logics of Jaccard, Sørensen, Sokal & Sneath, Kulczynski,  
413 Ochiai and Simpson indices. It is notable that Ricotta et al. (2016) define  $A$  as a quantity that  
414 ensures the components  $B$  and  $C$  to add up to  $a + b + c$  but with no explicit biological  
415 interpretation. Notably,  $D_{IP}$  and  $D_{CW}$  are identical with the Sørensen and Kulczynski forms of  
416 *PADDis*. The generalization of  $D_{IP}$  and  $D_{CW}$  to relative abundances,  $D_{CW}(Q)$ , was also derived  
417 by Ricotta & Bacaro (2010). For these two versions, it is not necessary to explicitly define the  
418  $A$  component. Using the relationships between Jaccard, Sørensen, Kulczynski, Ochiai and  
419 Sokal & Sneath indices, from  $D_{CW}(Q)$  it is theoretically possible to derive the extension of  
420 *PADDis* to relative abundances; however, the biological interpretation of  $A$  remains dubious  
421 in this framework.

422

## 423 **Methods**

424 The performance of FDissim indices can be reliably tested on data sets with known  
425 background processes driving community assembly which is hardly possible to satisfy with  
426 real data. Therefore, we compared the performance of FDissim indices using simulated data  
427 sets. The data sets were generated using the *comm.simul* function of the *comsimitv* R package  
428 (Botta-Dukát & Czúcz 2016, Botta-Dukát 2020). This function follows an individual-based

429 model for a meta-community comprising  $N$  communities and a regional pool of  $S$  species.  
430 Local communities include  $J$  individuals, and are distributed equidistantly along a continuous  
431 environmental gradient (with gradient values between 0 and 1). Each individual possesses  
432 three traits: an ‘environmental’, a ‘competitive’ trait, and a neutral trait, all ranging on [0; 1].  
433 Intraspecific variation in trait values is neglected in the simulation, that is, individuals  
434 belonging to the same species are identical. The environmental trait defines the optimum of  
435 the species along the environmental gradient. The closer the position of a community along  
436 the environmental gradient to the environmental trait value of a species, the more suitable it is  
437 for that species:

438 Eq. 21. 
$$\textit{suitability} = \frac{(\textit{environment} - \textit{environmental trait})^2}{\sigma}$$

439 where  $\sigma$  (sigma) is adjustable so as to change the niche width of the species, and hence, the  
440 length of the gradient (see later). The competitive trait represents the resource acquisition  
441 strategy of the individual. The more similar the latter value between two individuals, the  
442 higher the competition is between them, which means that intraspecific competition is the  
443 strongest. The neutral trait has no effect on community assembly, thus it is not considered in  
444 our study. The simulation starts with the random assignment of all individuals of all  
445 communities to species. The second step is a ‘disturbance’ event, when one individual ‘dies’  
446 in each community. This individual is to be replaced by an offspring of other individuals  
447 within the same community or those of other communities. Each individual produces one  
448 offspring or does not reproduce. Probability of reproduction depends on the strength of  
449 competition. The offspring remains in the same community or randomly disperses into any of  
450 the other communities. Finally, the dead individual is replaced by one new individual from  
451 the seeds produced and dispersed. The probability that an individual of a certain species  
452 replaces the dead individual is defined by the number of seeds of that species and the

453 suitability of the habitat. Steps between the disturbance event and the establishment of a new  
454 individual constitute a single 'generation'. Community composition is evaluated after lot of  
455 generations. The strength of the environmental filtering can be adjusted by the sigma  
456 parameter, respectively. When sigma is 0, all species are maximally specialist, which means  
457 that they can occur only at the optimum point of the gradient (that is, at the exact value for the  
458 environmental trait). If sigma is infinity, species are maximally generalist and all points along  
459 the environmental gradient are equally suitable for them. Therefore, sigma is the parameter  
460 which defines the suitability of each point of the gradient for each species based on its  
461 distance from the respective optima. We generated data sets with sigma values 0.01, 0.1, 0.25,  
462 0.5, 1 and 5 in order to simulate situations with different strength of environmental filtering.  
463 The number of communities was 30, each community comprised 200 individuals, the number  
464 of species in the species pool was 300, the simulation iterated for 100 generations, and we  
465 allowed no intraspecific trait variation. For all the other parameters, we used the default  
466 options.

467 However, it needed further explanation what real situations the six simulated levels of  
468 environmental filtering represent. To provide a reference and assist interpretation, we  
469 calculated two species-based beta-diversity measures, the multiplicative beta (Whittaker  
470 1960) and the gradient length of the first axis of a detrended correspondence analysis (DCA)  
471 ordination (Hill & Gauch 1980; Appendix S5, Fig. S5.1). The former gives the number of  
472 distinct communities present in the total species pool of the gradient, while the latter is  
473 minimal number of average niche breadths (also called turnover units) necessary for covering  
474 the total gradient length. Moreover, we plotted the abundance of species in the sample units  
475 along the gradient as a visual tool for assessing gradient length (Appendix S5, Fig. S5.2). All  
476 these methods indicated that with sigma = 0.01 the gradient is extremely long: there are more  
477 than 10 distinct communities and near 20 turnover units along the gradient. Samples with such

478 high beta diversity are very rare and special in real ecological research; therefore, findings  
479 from simulations with  $\sigma = 0.01$  are mostly of theoretical importance. Beta diversity  
480 values from  $\sigma = 0.1$  to  $\sigma = 1$  are more similar to real study situations, hence they  
481 should be more relevant for practice. At  $\sigma = 5$ , environmental filtering is practically not  
482 operating, between-community variation is driven by interspecific relations and chance.

483 We calculated between-species dissimilarities as the Gower distance between their  
484 environmental trait values which in this case equals the Euclidean distance scaled to [0; 1].  
485 These distances had to be transformed to similarities according to the requirements of the  
486 FDissim indices. Several formulae are available with which it is possible; however, they may  
487 assume different functional relationships between similarity and distance. One of such  
488 formulae we used is the linear transformation according to *Similarity = 1 - Distance*. Besides  
489 this, we also used *Similarity =  $e^{-u \times Distance}$*  which supposes a curvilinear function between  
490 similarity and distance (Leinster & Cobbold 2012). With this exponential formula, it is  
491 possible to weight the importance of small Gower distances between species relative to large  
492 distances. With changing the parameter  $u$  it is possible to adjust how steeply similarity  
493 decreases with increasing distance. We set  $u = 10$  which leads to a relatively steep decline.  
494 Although, after this transformation the minimal value for similarity is higher than zero, we  
495 considered it negligibly low ( $e^{-10} \approx 0.000045$ ) so we did not apply the transformation proposed  
496 by Botta-Dukát (2018). For all FDissim indices where it was necessary we used the similarity  
497 matrix or a dissimilarity matrix calculated as *Dissimilarity = 1 - Similarity* as input. The  
498 dissimilarity matrix is identical with the Gower distance matrix if the similarities were  
499 calculated in a linear way, but in the other case, it keeps the exponential relationship between  
500 distance and (dis-)similarity.

501 Dissimilarity matrices were calculated for the four community data sets with different sigma  
502 values, with the two functions transforming Gower distances, and across a broad range of

503 available FDissim indices. For indices where absolute or relative abundances could have been  
504 taken into account, we opted for relative abundance for the sake of better comparability. With  
505 *generalized\_Traddiss*, we calculated the ‘even’ and the ‘uneven’ weighting versions. The  
506 entire analysis was run with abundance and presence/absence data. Some FDissim indices are  
507 only suitable for binary data, thus the number of indices applied for relative abundance and  
508 binary data were 25 and 31, respectively. In cases of indices handling both data types, we  
509 used exactly the same version of the index as with abundance data, hence communities with  
510 different numbers of species were given equal weight due to division by community totals.  
511 Additionally, dissimilarity matrices were also calculated using the Bray-Curtis index (for  
512 binary data: Sørensen index in dissimilarity form) to provide a contrast against the case  
513 disregarding between-species dissimilarities.

514 Then for each dissimilarity matrices, we conducted two types of analyses. Firstly, we  
515 compared how strongly the dissimilarity indices correlate with the environmental distance  
516 using Kendall tau rank correlation. This gives an estimate of how well a dissimilarity index  
517 reveals the monotonic relationship between trait composition of local communities and the  
518 environmental gradient. We visually assessed the shape of relationship between dissimilarity  
519 and environmental distance in the case of lowest sigma (i.e., longest gradient) when the  
520 distortion of linear relationship between the two is supposed to be the strongest. Then, to  
521 disentangle the effects of different methodological decisions and the sigma parameter on the  
522 correlation between FDissim indices and environmental distance we calculated a random  
523 forest model. In this model the dependent variable was the Kendall tau correlation coefficient,  
524 while the independent variables were the sigma, the data type (abundance vs.  
525 presence/absence), the transformation method for Gower distances (linear vs. exponential),  
526 and the FDissim method. Within approaches FDissim methods often strongly correlated that  
527 resulted in very similar Kendall’s tau values. Therefore, only the Sørensen/Bray-Curtis

528 versions of *dsimcom*, *dissABC*, *PADDis/D<sub>CW</sub>*, *generalized\_Tradiidiss* with uneven weights, as  
529 well as  $\beta_{turnover}$ , *CWMdis*, and the *CDFdis* were included into this analysis. Variable  
530 importance scores (VIS) in the random forest were estimated by the permutation approach  
531 based on mean decrease in log-likelihood using the *varimp* function of the *partykit* package.  
532 The effects of the model terms were also illustrated by heat-maps.

533 All statistical analyses were done in R (R Core Team 2019) using the *FD* (Laliberté &  
534 Legendre 2010, Laliberté et al. 2014), *adiv* (Pavoine 2020a,b), *comsimitv* (Botta-Dukát 2020),  
535 *vegan* (Oksanen et al. 2019), *DescTools* (Signorell et al. 2020), *partykit* (Hothorn et al. 2006,  
536 Strobl et al. 2007, Strobl et al. 2008, Hothorn & Zeileis 2015) packages.

## 537 **Results**

538 Kendall tau correlation coefficients decreased as the strength of environmental filtering  
539 decreased (that is, with increasing sigma) in all examined cases. For *FD* indices which  
540 handled both data types, presence/absence data resulted in lower correlations than abundance  
541 data for all indices. For most indices, this difference was highest at intermediate values for  
542 sigma. These trends were consistent between the linear and the exponential transformations.  
543 Correlations for all indices at all sigma values with linear transformation are shown in Table 3  
544 for abundances data and in Table 4 for presence/absence data.

545 In most simulation scenarios, the *FD* indices correlated more strongly with the  
546 environmental gradient than the species-based Bray-Curtis index. However, in several  
547 occasions, indices belonging to the nearest neighbour family performed poorer than the  
548 species-based dissimilarity. Notably, at the highest sigma and with presence/absence data, all  
549 indices showed correlation near to zero but among them the Bray-Curtis index had the highest  
550 correlation with environmental distance.



551 As expected, we found perfect rank correlations among Jaccard, Sørensen, Sokal-Sneath and  
552 Whittaker's beta versions of *dsimcom*, among Jaccard, Sørensen and Sokal-Sneath forms of  
553 *dissABC*, between  $D_{IP}$  and Sørensen form of *PADDis* (only for presence-absence data),  
554 between  $D_{CW}$  and Kulczynski form of *PADDis* (only for presence-absence data), and between  
555  $D_{IP}$  and  $D_{CW}$  (for abundance data type).

556 Dissimilarity indices showed various shapes of relationship with environmental distance  
557 (Appendix S4). At strongest environmental filtering, all FDissim indices had dissimilarity  
558 values near zero at minimal environmental distance, only the species-based Bray-Curtis which  
559 had dissimilarity was near 0.4 at the smallest environmental distances. In case of linear  
560 transformation of Gower distances and presence/absence data, approximately linear  
561 relationship was found for *CWMdis*, *CDFdis*,  $D_Q$ , Sørensen and Ochiai forms of *dsimcom*,  
562 Jaccard form of *dissABC*, Marczewski-Steinhaus form of *generalized\_Tradiidiss* with both  
563 weighting versions,  $\beta_{heterogeneity}$  and  $\beta_{segregation}$ ; although, most other indices showed only a  
564 small degree of distortion of linear function (Figure S4.1). Exponential relationship was found  
565 for the evenness-based (PE) form of *generalized\_Tradiidiss*. Notably, the taxon-based Bray-  
566 Curtis index had the steepest asymptotic function among all. In case of exponential  
567 transformation all other indices relying on between-species dissimilarities showed an  
568 asymptotic curve (Figure S4.2).

569 In the random forest, niche width (that is, sigma) acquired by far the highest variable  
570 importance score (VIS=0.114). The less important variables were the data type (VIS=0.0176),  
571 the dissimilarity method (VIS=0.0037) and the transformation (VIS=-0.00001). The heat map  
572 (Figure 1) also revealed a strong decrease in correlation along increasing sigma. It is also  
573 clearly shown that in most cases abundance data resulted in significantly higher correlation  
574 than presence/absence. The difference between linear and exponential transformation methods  
575 was not always visible. Regarding variation between dissimilarity indices, the most striking

576 patterns were the relatively poor performance of the *PADDis/D<sub>CW</sub>* indices. All but the latter  
577 index combined with abundance data and linear transformation of dissimilarities lead to the  
578 highest correlation with environmental distance.

579

## 580 **Discussion**

### 581 *General patterns in the correlation with environmental distance*

582 We ran different simulation scenarios with varying strength of environmental filtering. We  
583 expected that the correlation between FDissim indices and environmental distance to be the  
584 highest when the environmental filtering is the strongest, and the correlation to become  
585 neutral when environmental filtering is not effective. When environmental filtering was  
586 strongest (that is, minimal overlap of species niches along the environmental gradient), all  
587 FDissim indices correlated highly with the environmental gradient. As expected, correlation  
588 between trait dissimilarity and environmental distance decreased as filtering weakened,  
589 moreover, differences between families of indices became more apparent. This result suggests  
590 that all tested methods are able to reveal the strong environmental filtering processes.

591 As the contribution of competitive exclusion and stochastic processes approach or override  
592 environmental filtering, the correlation between FDissim indices and the background gradient  
593 becomes weaker. This decrease itself is not a drawback of the FDissim methods, rather it is a  
594 consequence of our study design, since we applied a series of scenarios where the effect of  
595 niche filtering was decaying. However, we think that the degree of the decrease reflects the  
596 sensitivity of the FDissim indices to the underlying trait-environmental relationship. Indices,  
597 which showed high correlation with environmental distance, could be capable of revealing the  
598 environmental signal even when it is weak. Actually, in our tests, most indices reached  
599 similarly high correlation, and there were only a few combinations of simulation parameters

600 which resulted in a decreased correlation with environmental distance for some dissimilarity  
601 indices.

602 *Determinants of the correlation based on the random forest model*

603 The random forest model revealed that the effect of gradient length is the most important  
604 determinant of the correlation between dissimilarity and environmental distance, while  
605 methodological decisions had much lower variable importance. These observations suggest  
606 that the absolute value of the correlation between dissimilarity and environmental distance is  
607 primarily dependent on the sample in hand, and can be influenced by methodological  
608 decisions to a limited extent.

609 Correlations were stronger with abundance than with presence/absence data. This finding is at  
610 least partly attributable to our simulation design where community composition was driven by  
611 individual-based processes: birth, fitness difference, reproduction, and death. As a result,  
612 species relative abundances had to be proportional with their environmental suitability in the  
613 local community. Transforming such data to binary scale loses meaningful information and  
614 weakens the correlation between dissimilarity in trait composition and environmental  
615 background. In cases when presences and absences of species respond more robustly to the  
616 main environmental gradient, while relative abundances change stochastically, or abundance  
617 estimations are inaccurate, the binary data type might be more straightforward.

618 Transforming between-species dissimilarities has a potential to conform distributional  
619 requirements, to approximate expert intuitions about relatedness of species or to customize  
620 sensitivity to functional difference with respect to specific research aims. For most indices  
621 across the tested range of gradient length and data type, the exponential transformation  
622 resulted a somewhat lower correlation than with linear transformation. More insight is  
623 provided by examining the shape of the relationships besides the pure correlation value. After

624 linear transformation of Gower distances, most dissimilarity indices showed a linear or  
625 slightly curved function along environmental distance; although the scatter of the evenness-  
626 based *generalized\_TradiDiss* differed considerably from the straight line towards an  
627 exponentially increasing one. After exponential transformation of between-species trait  
628 dissimilarities, all indices in the direct dissimilarity-based class showed a rather steeply  
629 increasing asymptotic function. This result suggests that with the exponential transformation  
630 of between-species dissimilarities, it is possible to make FDissim indices more sensitive to  
631 smaller differences in functional composition. Certainly, summary-based indices (*CWMDis*,  
632 *CDFdis*) are not affected by this transformation, since they are not based on between-species  
633 dissimilarities.

#### 634 *Comparison of taxon-based vs. trait-based dissimilarity*

635 The basic assumption of functional ecology is that the traits of individuals should be in closer  
636 relationship with ecological properties than their taxonomical status. Following this argument,  
637 we expected that trait-based dissimilarity measures correlate more strongly with the  
638 environmental background than species-based indices. In contrast, higher correlation of  
639 species-based dissimilarity than trait-based dissimilarity indicates loss of information with the  
640 introduction of between-species similarity – which is non-sensual since our data was  
641 simulated in a way to possess a strong pattern in trait-environment relationship. We used the  
642 Sørensen/Bray-Curtis index in a dissimilarity form as a reference method representing  
643 species-based dissimilarity calculations disregarding traits. Our expectation was fulfilled by  
644 all indices with the exception of the members of the nearest neighbour family (*D<sub>IP</sub>*, *D<sub>CW</sub>* and  
645 *PADDis*). We suspect two potential reasons behind the low performance of these latter groups  
646 of indices. The first one is the improper scaling factor used for standardizing the ‘operational  
647 part’ of the indices (see the description in of the *PADDis* family and the discussion about it  
648 under the paragraph “Within-family variation of indices”). Second, these indices rely on the

649 quantities of minimally different species in the two communities under comparison. However,  
650 the minimum is a less robust descriptor of any sample distribution because of its dependency  
651 on sampling error; therefore, it might provide a poor representation of total community  
652 dissimilarity.

653 Although, we did not include dissimilarity values at exactly zero distance, the y-intercept (also  
654 called ‘nugget’) of the dissimilarity vs. environmental distance functions can be extrapolated  
655 with negligible error (Fortin & Dale 2005). Brownstein et al. (2012) argued that the nugget of  
656 the distance decay relationship is a direct estimate of the amount of chance in the variation  
657 between local communities. In this respect worth noting is that the nugget with species-based  
658 Bray-Curtis index was near 0.4, while with all trait-based indices the nugget was near zero.  
659 This suggests that without accounting for species similarities, environmental distance between  
660 communities can be overestimated due to similar species replacing each other.

#### 661 *Within-family variation of indices*

662 The perfect correlation between Jaccard, Sørensen and Sokal-Sneath forms of *dsimcom* and  
663 *dissABC* families was expected, since the original, taxon-based Jaccard, Sørensen and Sokal-  
664 Sneath indices are algebraically related, too (Janson & Vegelius 1981). However, for *PADDis*  
665 Jaccard, Sørensen and Sokal-Sneath forms showed correlation below 1. At this family, the *B*  
666 and *C* components of the 2×2 contingency table are defined as measurable quantities with  
667 clear interpretation: the sum of species uniqueness values within each community. The total  
668 diversity ( $A+B+C$ ) is defined to be equal with the species richness of the pooled pair of  
669 communities ( $a+b+c$ ), and the quantity *A* is derived by subtracting ( $B+C$ ) from it. With this  
670 definition, *A* remains a virtual quantity with no biological interpretation. In *PADDis* indices,  
671 trait-based quantities *B* and *C* appear in the numerator (the ‘operational part’ sensu Ricotta et  
672 al. 2016) of the indices, while in the denominators (i.e., in the ‘scaling factor’) the taxon-  
673 based quantities, *a*, *b* and *c* are used. We argue that the inconsistent behaviour of *PADDis* is

674 due to the application of taxon-based quantities for scaling factors of trait-based operational  
675 parts. At the same time, we acknowledge that we either see no obvious solution to define total  
676 diversity or shared diversity according to the uniqueness-based idea behind *PADDis* in a more  
677 realistic way. In the *generalized\_TradiDiss* family, the trait-based analogue of Bray-Curtis  
678 index can be achieved by calculating generalized Canberra distance with uneven weighting of  
679 species. We expected this to be perfectly correlated with Marczewski-Steinhaus form of  
680 *generalized\_TradiDiss* index with uneven weighting, since Bray-Curtis and Marczewski-  
681 Steinhaus indices are the abundance forms of Sørensen and Jaccard indices, respectively.  
682 However, the correlation between them was lower. In the *generalized\_TradiDiss* family,  
683 between-community dissimilarity is calculated as weighted sum a standardized differences in  
684 species ordinariness values. Species ordinariness is calculated on the basis of species  
685 abundance and trait values; however, weights used for adjusting species-level contributions  
686 are derived solely from abundances. Therefore, *generalized\_TradiDiss* also follows a ‘hybrid’  
687 approach in accounting for taxon-based vs. trait-based information. We argue that this is the  
688 reason why the algebraic relationships between the original Sørensen and Jaccard indices does  
689 not apply to its Sørensen/Bray-Curtis-type and Jaccard/Marczewski-Steinhaus-type forms. To  
690 sum up, we point to our observation that Jaccard, Sørensen and Sokal-Sneath forms of certain  
691 families of indices do not satisfy the algebraic relationships they supposed to, opening space  
692 for potential confusion. These algebraic relations hold only if *A*, *B* and *C* quantities are  
693 explicitly and consistently defined.

694 Families of *FDissim* indices combine abundance difference of species between plots and  
695 interspecific trait differences in a unique way, while indices belonging to the same family  
696 differ in how they relate this amount of ‘unshared’ variation (summarized as the *b* and *c*  
697 portions of the contingency table) to the shared (*a*) variation. Some indices are able to handle  
698 abundances either as absolute or relative abundance (e.g. *dsimcom*, *generalized\_TradiDiss*,

699 *dissABC*), while others divide absolute abundances by their sum over the respective  
700 community, thus they work only with relative abundances. When indices in the former group  
701 are set to consider absolute abundances, they become sensitive to variation in the summed  
702 abundances of the communities under comparison. To place our tests on a common ground,  
703 we simulated communities with equal total number of individuals, and set all indices, where  
704 relevant, to work with relative abundances. Hence, we removed the effect of differences in  
705 total abundance. The constant number of individuals might have increased the similarity  
706 between FDissim indices belonging to the same family and the correlation with the  
707 environmental gradient. The sum of abundances, let them be measured on any quantitative  
708 scale, may vary considerably in real study situations due to aggregated distribution of  
709 individuals or uneven sampling effort. Therefore, our findings are more likely valid for  
710 settings when the sum of abundances are relatively stable, e.g. when sampling effort is  
711 controlled and individuals are dispersed evenly, or when abundances are recorded on  
712 percentage scale.

### 713 *Limitations of our study*

714 In our study, we simulated a research situation in a simplistic way. We applied only one  
715 environmental gradient which operated as an environmental filter driving convergence on a  
716 single trait. Besides this, we applied another trait which was constantly affected by a low level  
717 of competitive exclusion. These two traits were uncorrelated. Nevertheless, there was some  
718 effect of random drift on community composition due to the probabilistic components of the  
719 simulation algorithm. We varied the strength of environmental filtering thus it had different  
720 relative contribution compared with competitive exclusion and stochasticity. In real research  
721 situations local trait composition is influenced by a wide range of processes, including several  
722 abiotic and biotic filters acting simultaneously. Unless they are manipulated as parts of an  
723 experimental system, the full set of such filters are usually unknown for the researchers. The

724 multiplicity of filters may reduce the ability of FDissim indices in recovering trait-  
725 environment relationships. Further research should clarify how increasing complexity of the  
726 sample affects the behaviour of FDissim indices.

727

## 728 **Conclusions**

729 Considering the diversity of concepts they are built upon, FDissim indices showed  
730 unexpectedly low variation in performance. CWMdis, dsimcom, generalized\_TradiDiss  
731 acquired the highest correlation with environmental distance in all simulation scenarios,  
732 therefore they seem to be equally suitable for quantifying pairwise beta diversity based on  
733 traits. Nevertheless, the most important determinant of the matching between trait-based  
734 dissimilarity and environmental distance is the length of the trait gradient. Besides this, the  
735 data type (presence/absence vs. abundance) also affected the correlation more strongly than  
736 the choice of FDissim method. Extending the comparative tests of FDissim measure to more  
737 complex gradients and real data sets could offer further insight into their behaviour.

738

## 739 **Data availability**

740 Simulated data was generated using the comsimtv R package. Own functions for functional  
741 dissimilarity indices are made available through the Zenodo public repository:  
742 [10.5281/zenodo.4323590](https://doi.org/10.5281/zenodo.4323590).

743

## 744 **Author contributions**

745 A.L. designed and carried out the analysis, lead writing, Z.B.D. discussed the concept and the  
746 results, wrote parts of and commented on the manuscript.



747

748 **References**

- 749 Anderson, M. J., Crist, T. O., Chase, J. M., Vellend, M., Inouye, B. D., Freestone, A. L.,  
750 Sanders, N. J., Cornell, H. V., Comita, L. S., Davies, K. F., Harrison, S. P., Kraft, N. J. B.,  
751 Stegen, J. C. & Swenson, N. G. (2011). Navigating the multiple meanings of  $\beta$  diversity: a  
752 roadmap for the practicing ecologist. *Ecology Letters*, 14(1), 19-28. doi:10.1111/j.1461-  
753 0248.2010.01552.x
- 754 Anderson, M. J., Ellingsen, K. E. & McArdle, B. H. (2006). Multivariate dispersion as a  
755 measure of beta diversity. *Ecology Letters*, 9(6), 683-693. doi:10.1111/j.1461-  
756 0248.2006.00926.x
- 757 Baselga, A. & Leprieur, F. (2015). Comparing methods to separate components of beta  
758 diversity. *Methods in Ecology and Evolution*, 6: 1069-1079. doi:10.1111/2041-210X.12388
- 759 Botta-Dukát, Z. & Czúcz, B. (2016). Testing the ability of functional diversity indices to  
760 detect trait convergence and divergence using individual-based simulation. *Methods in*  
761 *Ecology and Evolution*, 7, 114-126. <https://doi.org/10.1111/2041-210X.12450>
- 762 Botta-Dukát, Z. (2005). Rao's quadratic entropy as a measure of functional diversity based  
763 on multiple traits. *Journal of Vegetation Science*, 16, 533-540. [https://doi.org/10.1111/j.1654-  
764 1103.2005.tb02393.x](https://doi.org/10.1111/j.1654-1103.2005.tb02393.x)
- 765 Botta-Dukát, Z. (2018). The generalized replication principle and the partitioning of  
766 functional diversity into independent alpha and beta components. *Ecography*, 41: 40-50.  
767 doi:10.1111/ecog.02009
- 768 Botta-Dukat, Z. (2020). *comsimitv*: Flexible Framework for Simulating Community  
769 Assembly. R package version 0.1.4. <https://CRAN.R-project.org/package=comsimitv>

- 770 Brownstein, G., Steel, J.B., Porter, S., Gray, A., Wilson, C., Wilson, P.G. & Wilson, J. B.  
771 (2012). Chance in plant communities: a new approach to its measurement using the nugget  
772 from spatial autocorrelation. *Journal of Ecology*, 100, 987-996.  
773 <https://doi.org/10.1111/j.1365-2745.2012.01973.x>
- 774 Cardoso, P., Rigal, F., Carvalho, J.C., Fortelius, M., Borges, P.A.V., Podani, J. & Schmera, D.  
775 (2014). Partitioning taxon, phylogenetic and functional beta diversity into replacement and  
776 richness difference components. *Journal of Biogeography*, 41, 749-761.  
777 doi:10.1111/jbi.12239
- 778 Carmona, C. P., de Bello, F., Mason, N. W. H., Lepš, J. (2016). Traits without borders:  
779 Integrating functional diversity across scales. *Trends in Ecology and Evolution* 31(5), 382-  
780 394. doi: 10.1016/j.tree.2016.02.003
- 781 Champely, S., Chessel, D. (2002). Measuring biological diversity using Euclidean metrics.  
782 *Environmental and Ecological Statistics* 9, 167–177.  
783 <https://doi.org/10.1023/A:1015170104476>
- 784 Chao, A., Chiu, C. and Hsieh, T.C. (2012). Proposing a resolution to debates on diversity  
785 partitioning. *Ecology*, 93, 2037-2051. <https://doi.org/10.1890/11-1817.1>
- 786 Chao, A., Chiu, C.-H., Villéger, S., Sun, I.-F., Thorn, S., Lin, Y.-C., Chiang, J.-M., &  
787 Sherwin, W. B. (2019). An attribute  $\alpha$  diversity approach to functional diversity, functional  
788 beta diversity, and related (dis)similarity measures. *Ecological Monographs*, 89(2), e01343.  
789 10.1002/ecm.1343
- 790 Chiu, C.-H., Jost, L. & Chao, A. (2014). Phylogenetic beta diversity, similarity, and  
791 differentiation measures based on Hill numbers. *Ecological Monographs*, 84(1), 21-44.

- 792 Clarke, K.R. & Warwick, R.M. (1993). Quantifying structural redundancy in ecological  
793 communities. *Oecologia*, 113(2), 278-289.
- 794 De Bello, F., Carmona, C.P., Mason, N.W.H., Sebastià, M. T. and Lepš, J. (2013). Which  
795 trait dissimilarity for functional diversity: trait means or trait overlap? *Journal of Vegetation*  
796 *Science*, 24, 807-819. doi:10.1111/jvs.12008
- 797 De Bello, F., Lepš, J., Lavorel, S., & Moretti, M. (2007). Importance of species abundance for  
798 assessment of trait composition: an example based on pollinator communities. *Community*  
799 *Ecology*, 8(2), 163–170. <https://doi.org/10.1556/ComEc.8.2007.2.3>
- 800 Díaz, S., & Cabido, M. (2001). Vive la différence: plant functional diversity matters to  
801 ecosystem processes. *Trends in Ecology and Evolution*, 16(11), 646–655.  
802 [https://doi.org/10.1016/S0169-5347\(01\)02283-2](https://doi.org/10.1016/S0169-5347(01)02283-2)
- 803 Faith, D. P., Minchin, P. R. & Belbin, L. (1987). Compositional dissimilarity as a robust  
804 measure of ecological distance. *Vegetatio* 69, 57-68.
- 805 Fortin, M. J. & Dale, M.R.T. (2005). *Spatial Data Analysis: a Guide for Ecologists*.  
806 Cambridge University Press, Cambridge.
- 807 Garnier, E., Cortez, J., Billès, G., Navas, M., Roumet, C., Debussche, M., Laurent, G.,  
808 Blanchard, A., Aubry, D., Bellmann, A., Neill, C. & Toussaint, J. (2004). Plant functional  
809 markers capture ecosystem properties during secondary succession. *Ecology*, 85, 2630-2637.  
810 doi:10.1890/03-0799
- 811 Gregorius, H. R., Gillet, E.M. & Ziehe, M. (2003). Measuring Differences of Trait  
812 Distributions Between Populations. *Biometrical Journal*, 45, 959-973.  
813 <https://doi.org/10.1002/bimj.200390063>

- 814 Grime, J. P. (1998). Benefits of plant diversity to ecosystems: immediate, filter and founder  
815 effects. *Journal of Ecology*, 86, 902–910.
- 816 Hawkins, B.A., Leroy, B., Rodríguez, M.Á., Singer, A., Vilela, B., Villalobos, F., Wang, X.  
817 & Zelený, D. (2017). Structural bias in aggregated species-level variables driven by repeated  
818 species co-occurrences: a pervasive problem in community and assemblage data. *Journal of*  
819 *Biogeography*, 44, 1199-1211.
- 820 Héroult, B., & Honnay, O. (2007). Using life-history traits to achieve a functional  
821 classification of habitats. *Applied Vegetation Science*, 10(1), 73–80.  
822 <https://doi.org/10.1111/j.1654-109X.2007.tb00505.x>
- 823 Hill, M. O. & Gauch, H. G. (1980). Detrended Correspondence Analysis: An Improved  
824 Ordination Technique. *Vegetatio*, 42, 47–58.
- 825 Hill, M. O. (1973). Diversity and evenness: a unifying notation and its consequences.  
826 *Ecology*, 54(2), 427–432.
- 827 Hitchcock, F.L. (1941). Distribution of a product from several sources to numerous localities.  
828 *Journal of Mathematical Physics*, 20: 224-230.
- 829 Hothorn, T., Hornik, K., Van de Wiel, M. A. & Zeileis, A. (2006). A Lego System for  
830 Conditional Inference. *The American Statistician*, 60(3), 257–263.
- 831 Hothorn, T., Zeileis, A. (2015). partykit: A Modular Toolkit for Recursive Partytioning in R.  
832 *Journal of Machine Learning Research*, 16, 3905-3909. URL  
833 <http://jmlr.org/papers/v16/hothorn15a.html>
- 834 Izsák, C., & Price, R. G. (2001). Measuring b-diversity using a taxonomic similarity index,  
835 and its relation to spatial scale. *Marine Ecology Progress Series* 215, 69–77.

- 836 Janson, S. & J. Vegelius (1981). Measures of ecological association. *Oecologia*, 49(3), 371-  
837 376.
- 838 Jost, L. (2007). Partitioning diversity into independent alpha and beta components. *Ecology*,  
839 88, 2427–2439.
- 840 Kleyer, M., Dray, S., Bello, F., Lepš, J., Pakeman, R.J., Strauss, B., Thuiller, W. & Lavorel,  
841 S. (2012). Assessing species and community functional responses to environmental gradients:  
842 which multivariate methods? *Journal of Vegetation Science*, 23, 805-821. doi:10.1111/j.1654-  
843 1103.2012.01402.x: 1199–1211.
- 844 Koleff, P., Gaston, K. J. & Lennon, J. J. (2003). Measuring beta diversity for presence–  
845 absence data. *Journal of Animal Ecology*, 72, 367-382. doi:10.1046/j.1365-  
846 2656.2003.00710.x
- 847 Laliberté, E. & P. Legendre (2010). A distance-based framework for measuring functional  
848 diversity from multiple traits. *Ecology*, 91, 299-305.
- 849 Laliberté, E., Legendre, P., & Shipley, B. (2014). FD: measuring functional diversity from  
850 multiple traits, and other tools for functional ecology. R package version 1.0-12.
- 851 Legendre, P. & Legendre, L. (1998) *Numerical ecology*. Elsevier, Amsterdam, NL
- 852 Legendre, P., De Cáceres, M. (2013). Beta diversity as the variance of community data:  
853 dissimilarity coefficients and partitioning. *Ecology Letters* 16, 951–963
- 854 Leinster, T. & Cobbold, C.A. (2012). Measuring diversity: the importance of species  
855 similarity. *Ecology*, 93, 477-489. doi:10.1890/10-2402.1
- 856 Lengyel, A. & Podani, J. (2015). Assessing the relative importance of methodological  
857 decisions in classifications of vegetation data. *Journal of Vegetation Science*, 26, 804-815.  
858 doi:10.1111/jvs.12268

- 859 Lengyel, A., Swacha, G., Botta-Dukát, Z. & Kacki, Z. (2020). Trait-based numerical  
860 classification of mesic and wet grasslands in Poland. *Journal of Vegetation Science*, 31, 319–  
861 330. <https://doi.org/10.1111/jvs.12850>
- 862 Lepš, J., de Bello, F., Lavorel, S. & Berman, S. (2006). Quantifying and interpreting  
863 functional diversity of natural communities: practical considerations matter. *Preslia*, 78, 481–  
864 501.
- 865 MacArthur, R., Levins, R. (1967). Limiting similarity convergence and divergence of  
866 coexisting species. *American Naturalist*, 101, 377–387.
- 867 Mason, N. W. H., Mouillot, D., Lee, W. G. & Wilson, J. B. (2005). Functional richness,  
868 functional evenness and functional divergence: the primary components of functional  
869 diversity. *Oikos*, 111, 112-118. doi:10.1111/j.0030-1299.2005.13886.x
- 870 McGill, B., Enquist, B. J., Weiher, E., Westoby, M. (2006). Rebuilding community ecology  
871 from functional traits. *Trends in Ecology and Evolution* 21(4), 178-185.
- 872 Mouchet, M.A., Villéger, S., Mason, N.W.H. and Mouillot, D. (2010). Functional diversity  
873 measures: an overview of their redundancy and their ability to discriminate community  
874 assembly rules. *Functional Ecology*, 24, 867-876. doi:10.1111/j.1365-2435.2010.01695.x
- 875 Mouillot, D., Stubbs, W., Faure, M., Dumay, O., Tomasini, J.A., Wilson, J.B. & Chi, T.D.  
876 (2005). Niche overlap estimates based on quantitative functional traits: a new family of  
877 non-parametric indices. *Oecologia*, 145, 345–353.
- 878 Muscarella, R. & Uriarte, M. (2016). Do community-weighted mean functional traits reflect  
879 optimal strategies? *Proceedings of the Royal Society B*, 283, 20152434.  
880 <https://doi.org/10.1098/rspb.2015.2434>

- 881 Nipperess, D.A., Faith, D.P. & Barton, K. (2010), Resemblance in phylogenetic diversity  
882 among ecological assemblages. *Journal of Vegetation Science*, 21, 809-820.  
883 doi:10.1111/j.1654-1103.2010.01192.x
- 884 Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Peter R.  
885 Minchin, P. R., O'Hara, R. B., Simpson, G. L., Solymos, P., Stevens, M. H. M., Szoecs, E. &  
886 Wagner, H. (2019). *vegan: Community Ecology Package*. R package version 2.5-6.  
887 <https://CRAN.R-project.org/package=vegan>
- 888 Pavoine, S. & Ricotta, C. (2014). Functional and phylogenetic similarity among communities.  
889 *Methods in Ecology and Evolution*, 5, 666--675.
- 890 Pavoine, S. & Ricotta, C. (2019). Measuring functional dissimilarity among plots: Adapting  
891 old methods to new questions. *Ecological Indicators*, 97, 67-72.
- 892 Pavoine, S. (2012). Clarifying and developing analyses of biodiversity: towards a  
893 generalisation of current approaches. *Methods in Ecology and Evolution*, 3, 509-518.  
894 doi:10.1111/j.2041-210X.2011.00181.x
- 895 Pavoine, S. (2016). A guide through a family of phylogenetic dissimilarity measures among  
896 sites. *Oikos*, 125, 1719-1732. doi:10.1111/oik.03262
- 897 Pavoine, S. (2020). *adiv: An R package to analyse biodiversity in ecology*. *Methods in*  
898 *Ecology and Evolution*, 11, 1106– 1112. <https://doi.org/10.1111/2041-210X>.
- 899 Peres-Neto, P.R., Dray, S. & ter Braak, C.J.F. (2017). Linking trait variation to the  
900 environment: critical issues with community-weighted mean correlation resolved by the  
901 fourth-corner approach. *Ecography*, 40, 806-816.
- 902 Petchey, O. L. & Gaston, K. J. (2006). Functional diversity: back to basics and looking  
903 forward. *Ecology Letters*, 9, 741-758. doi:10.1111/j.1461-0248.2006.00924.x

- 904 Podani, J. & Schmera, D. (2011). A new conceptual and methodological framework for  
905 exploring and explaining pattern in presence – absence data. *Oikos*, 120, 1625-1638.  
906 doi:10.1111/j.1600-0706.2011.19451.x
- 907 Podani, J. (2000). Introduction to the exploration of multivariate biological data. Backhuys,  
908 Leiden, NL.
- 909 R Core Team (2019). R: A language and environment for statistical computing. R Foundation  
910 for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>.
- 911 Rao, C. R. (1982). Diversity and dissimilarity coefficients: a unified approach. *Theoretical*  
912 *Population Biology*, 21, 24-43.
- 913 Ricotta C. & Burrascano S. (2008). Beta diversity for functional ecology. *Preslia*, 80, 61–71.
- 914 Ricotta, C. & G. Bacaro. (2010). On plot-to-plot dissimilarity measures based on species  
915 functional traits. *Community Ecology*, 11, 113–119.
- 916 Ricotta, C. & J. Podani. (2017). On some properties of the Bray-Curtis dissimilarity and their  
917 ecological meaning. *Ecological Complexity*, 31, 201–205.
- 918 Ricotta, C. & Pavoine, S. (2015). Measuring similarity among plots including similarity  
919 among species: an extension of traditional approaches. *Journal of Vegetation Science*, 26,  
920 1061-1067. doi:10.1111/jvs.12329
- 921 Ricotta, C. (2017). Of beta diversity, variance, evenness, and dissimilarity. *Ecology and*  
922 *Evolution* 7, 4835– 4843. <https://doi.org/10.1002/ece3.2980>
- 923 Ricotta, C. (2018). A family of (dis)similarity measures based on evenness and its relationship  
924 with beta diversity. *Ecological Complexity*, 34, 69-73. DOI: 10.1016/j.ecocom.2018.03.002



- 925 Ricotta, C., Bacaro, G., Caccianiga, M., Cerabolini, B.E.L. & Moretti, M. (2015). A classical  
926 measure of phylogenetic dissimilarity and its relationship with beta diversity. *Basic and*  
927 *Applied Ecology* 16(1), 10-18. <https://doi.org/10.1016/j.baae.2014.10.003>
- 928 Ricotta, C., Podani, J., Pavoine, S. (2016). A family of functional dissimilarity measures for  
929 presence and absence data. *Ecology and Evolution*, 6, 5383–5389. DOI: 10.1002/ece3.2214
- 930 Schmidt, T., Matias Rodrigues, J. & von Mering, C. (2017). A family of interaction-adjusted  
931 indices of community similarity. *ISME Journal* 11, 791–807.  
932 <https://doi.org/10.1038/ismej.2016.139>
- 933 Signorell, A. et mult. al. (2020). DescTools: Tools for descriptive statistics. R package version  
934 0.99.38.
- 935 Strobl, C., Boulesteix, A.L., Kneib, T., Augustin, T. & Zeileis, A. (2008). Conditional  
936 Variable Importance for Random Forests. *BMC Bioinformatics*, 9(307).  
937 <http://www.biomedcentral.com/1471-2105/9/307>
- 938 Strobl, C., Boulesteix, A.L., Zeileis, A. & Hothorn, T. (2007). Bias in Random Forest  
939 Variable Importance Measures: Illustrations, Sources and a Solution. *BMC Bioinformatics*, 8,  
940 25. <http://www.biomedcentral.com/1471-2105/8/25>
- 941 Swenson N. G., Anglada-Cordero P. & Barone J. A. (2011). Deterministic tropical tree  
942 community turnover: evidence from patterns of functional beta diversity along an elevational  
943 gradient. *Proceedings of the Royal Society B*, 278, 877–884.
- 944 Swenson, N. G. (2011). Phylogenetic Beta Diversity Metrics, Trait Evolution and Inferring  
945 the Functional Beta Diversity of Communities. *PLoS ONE* 6(6), e21264.  
946 <https://doi.org/10.1371/journal.pone.0021264>

- 947 Tamás, J., Podani, J. & Csontos, P. (2001). An extension of presence/absence coefficients to  
948 abundance data: a new look at absence. *Journal of Vegetation Science*, 12, 401-410.  
949 doi:10.2307/3236854
- 950 Tuomisto, H. (2010a). A diversity of beta diversities: straightening up a concept gone awry.  
951 Part 1. Defining beta diversity as a function of alpha and gamma diversity. *Ecography*, 33, 2-  
952 22. doi:10.1111/j.1600-0587.2009.05880.x
- 953 Tuomisto, H. (2010b). A diversity of beta diversities: straightening up a concept gone awry.  
954 Part 2. Quantifying beta diversity and related phenomena. *Ecography*, 33, 23-45.  
955 doi:10.1111/j.1600-0587.2009.06148.x
- 956 Villéger, S., Mason, N.W.H. & Mouillot, D. (2008). New multidimensional functional  
957 diversity indices for a multifaceted framework in functional ecology. *Ecology*, 89, 2290-2301.  
958 doi:10.1890/07-1206.1
- 959 Violle, C., Navas, M. L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I. & Garnier, E.  
960 (2007). Let the concept of trait be functional! *Oikos*, 116, 882-892. doi:10.1111/j.0030-  
961 1299.2007.15559.x
- 962 Whittaker, R. H. (1960). Vegetation of the Siskiyou Mountains, Oregon and California.  
963 *Ecological Monographs*, 30, 280–338.
- 964 Whittaker, R. H. (1972). Evolution and measurement of species diversity. *Taxon*, 21, 213-  
965 251. doi:10.2307/1218190
- 966 Zelený, D. (2018). Which results of the standard test for community weighted mean approach  
967 are too optimistic? *Journal of Vegetation Science* 29, 953-966.
- 968

969 **Tables and Figures**

970

971 Table 1. Similarity and dissimilarity forms of resemblance indices for presence-absence data

972

Name of the index	Similarity version	Dissimilarity version
Sørensen	$s_S = \frac{2a}{2a + b + c} = \frac{a}{(S_j + S_k)/2}$	$d_S = \frac{b + c}{2a + b + c} = \frac{b + c}{S_j + S_k}$
Ochiai	$s_O = \frac{a}{\sqrt{(a + b)(a + c)}} = \frac{a}{\sqrt{S_j S_k}}$	$d_O = \frac{b + c}{\sqrt{S_j S_k}}$
Kulczynski	$s_K = \frac{1}{2} \left( \frac{a}{a + b} + \frac{a}{a + c} \right) = \frac{a}{2/(1/S_j + 1/S_k)}$	$d_K = \frac{1}{2} \left( \frac{b}{a + b} + \frac{c}{a + c} \right) = \frac{1}{2} \left( \frac{b}{S_j} + \frac{c}{S_k} \right)$
Simpson	$s_{Si} = \frac{a}{a + \min(b, c)} = \frac{a}{\min(S_j, S_k)}$	$d_{Si} = \frac{b + c}{\min(S_j, S_k)}$
Jaccard	$s_J = \frac{a}{a + b + c} = \frac{a}{S_{jk}}$	$d_J = \frac{b + c}{a + b + c} = \frac{b + c}{S_{jk}}$
Sokal & Sneath	$s_{SS} = \frac{a}{a + 2(b + c)}$	$d_{SS} = \frac{2(b + c)}{a + 2(b + c)}$

973

974

975 Table 2. Classification of trait-based dissimilarity indices. In columns of input data type X-es indicate, if abundance (A), relative abundance (R),  
 976 and presence-absence data can be used as input.

Class	Approach	Family	References	Input Data			R function
				A	R	P/A	
<i>Summary-based</i>	<i>Typical value</i>	<i>CWM-based</i>	Ricotta et al. (2015)	X	X	X	FD:::functcomp
	<i>Distribution-based</i>	<i>CDF-based</i>	Appendix S3	X	X	X	our new functions, see Data availability
<i>Direct dissimilarity</i>	<i>Probabilistic</i>	<i>DISC/D<sub>Q</sub></i>	Rao 1982, Pavoine & Ricotta (2014)	X	X	X	adiv:::SQ
		<i>dsimcom</i>	Pavoine & Ricotta (2014)	X	X	X	adiv:::dsimcom
	<i>Ordinariness-based</i>	<i>dissABC</i>	Pavoine & Ricotta (2015)	X	X	X	adiv:::dissABC
		<i>generalized_Tradiidiss</i>	Pavoine & Ricotta (2019)	X	X		adiv:::generalized_Tradiidiss
	<i>Diversity</i>	<i>multiplicative beta</i>	Chao et al. (2012)		X		our new functions, see Data

	<i>partitioning</i>						availability
	<i>Nearest neighbour</i>	$D_{CW}, D_{CW}(Q)$	Clarke & Warwick (1998), Ricotta & Bacaro (2010)		X	X	our new functions, see Data availability
		$D_{IP}$	Izsák & Prince (2001), Ricotta & Bacaro (2010)		X	X	our new functions, see Data availability
		<i>PADDis</i>	Ricotta et al. (2016)			X	adiv:::PADDis
<i>Classification-based</i>	not discussed	not discussed	Hérault & Honnay (2007), Nipperess et al. (2010), Cardoso et al. (2014), Pavoine (2016)				

978 Table 3. Kendall tau correlations between environmental distance and the functional  
 979 dissimilarity measures at different values of sigma and with abundance data type

	<b>Sigma=0.01</b>	<b>Sigma=0.1</b>	<b>Sigma=0.25</b>	<b>Sigma=0.5</b>	<b>Sigma=1</b>	<b>Sigma=5</b>
<i>CWMdis</i>	0.974	0.905	0.846	0.828	0.649	0.251
<i>CDFdis</i>	0.974	0.904	0.845	0.83	0.646	0.255
<i>D(Q)</i>	0.974	0.912	0.832	0.828	0.637	0.243
<i>dsimcom.SS</i>	0.974	0.911	0.832	0.829	0.638	0.243
<i>dsimcom.Jac</i>	0.974	0.911	0.832	0.829	0.638	0.243
<i>dsimcom.Sor</i>	0.974	0.911	0.832	0.829	0.638	0.243
<i>dsimcom.Och</i>	0.974	0.911	0.832	0.829	0.639	0.243
<i>dsimcom.Beta</i>	0.974	0.911	0.832	0.829	0.638	0.243
<i>dissABC.Jac</i>	0.967	0.899	0.82	0.813	0.617	0.243
<i>dissABC.Sor</i>	0.967	0.899	0.82	0.813	0.617	0.243
<i>dissABC.SS</i>	0.967	0.899	0.82	0.813	0.617	0.243
<i>dissABC.Och</i>	0.968	0.899	0.819	0.814	0.618	0.243
<i>dissABC.Kul</i>	0.968	0.898	0.819	0.814	0.619	0.243
<i>dissABC.Si</i>	0.954	0.867	0.789	0.791	0.616	0.243
<i>Tradidiss.GC.even</i>	0.974	0.908	0.816	0.829	0.626	0.245
<i>Tradidiss.MS.even</i>	0.974	0.908	0.814	0.828	0.623	0.243
<i>Tradidiss.PE.even</i>	0.974	0.907	0.828	0.831	0.639	0.25
<i>Tradidiss.GC.uneven</i>	0.967	0.901	0.827	0.815	0.622	0.244
<i>Tradidiss.MS.uneven</i>	0.966	0.899	0.823	0.813	0.618	0.243
<i>Tradidiss.PE.uneven</i>	0.969	0.905	0.837	0.821	0.637	0.249
$\beta_{turnover}$	0.974	0.911	0.837	0.829	0.641	0.251
$\beta_{heterogeneity}$	0.974	0.911	0.837	0.829	0.641	0.251
$\beta_{segregation}$	0.974	0.911	0.837	0.829	0.641	0.251

$D_{IP}$	0.923	0.778	0.68	0.565	0.338	0.034
$D_{CW}$	0.923	0.778	0.68	0.565	0.338	0.034
<i>Bray-Curtis (species-based)</i>	0.711	0.832	0.778	0.678	0.455	0.086

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982 Table 4. Kendall tau correlations between environmental distance and the functional  
 983 dissimilarity measures at different values of sigma and with presence/absence data type

	<b>Sigma=0.01</b>	<b>Sigma=0.1</b>	<b>Sigma=0.25</b>	<b>Sigma=0.5</b>	<b>Sigma=1</b>	<b>Sigma=5</b>
<i>CWMdis</i>	0.944	0.818	0.691	0.568	0.353	0.014
<i>CDFdis</i>	0.943	0.820	0.700	0.594	0.306	-0.001
<i>D(Q)</i>	0.941	0.818	0.701	0.59	0.313	-0.003
<i>dsimcom.SS</i>	0.944	0.821	0.705	0.593	0.316	-0.003
<i>dsimcom.Jac</i>	0.944	0.821	0.705	0.593	0.316	-0.003
<i>dsimcom.Sor</i>	0.944	0.821	0.705	0.593	0.316	-0.003
<i>dsimcom.Och</i>	0.944	0.822	0.707	0.592	0.323	0.000
<i>dsimcom.Beta</i>	0.944	0.821	0.705	0.593	0.316	-0.003
<i>dissABC.Jac</i>	0.946	0.819	0.704	0.592	0.292	-0.006
<i>dissABC.Sor</i>	0.946	0.819	0.704	0.592	0.292	-0.006
<i>dissABC.SS</i>	0.946	0.819	0.704	0.592	0.292	-0.006
<i>dissABC.Och</i>	0.946	0.819	0.704	0.591	0.293	-0.006
<i>dissABC.Kul</i>	0.946	0.819	0.704	0.591	0.294	-0.006
<i>dissABC.Si</i>	0.939	0.835	0.701	0.556	0.324	0.019
<i>Tradidiss.GC.even</i>	0.945	0.820	0.707	0.593	0.305	-0.005
<i>Tradidiss.MS.even</i>	0.945	0.819	0.707	0.592	0.304	-0.005
<i>Tradidiss.PE.even</i>	0.947	0.821	0.704	0.595	0.323	-0.002
<i>Tradidiss.GC.uneven</i>	0.946	0.819	0.702	0.592	0.308	-0.006
<i>Tradidiss.MS.uneven</i>	0.946	0.819	0.703	0.592	0.307	-0.006
<i>Tradidiss.PE.uneven</i>	0.947	0.820	0.698	0.593	0.326	-0.003
$\beta_{turnover}$	0.943	0.817	0.699	0.585	0.331	-0.003
$\beta_{heterogeneity}$	0.943	0.817	0.699	0.585	0.331	-0.003
$\beta_{segregation}$	0.943	0.817	0.699	0.585	0.331	-0.003

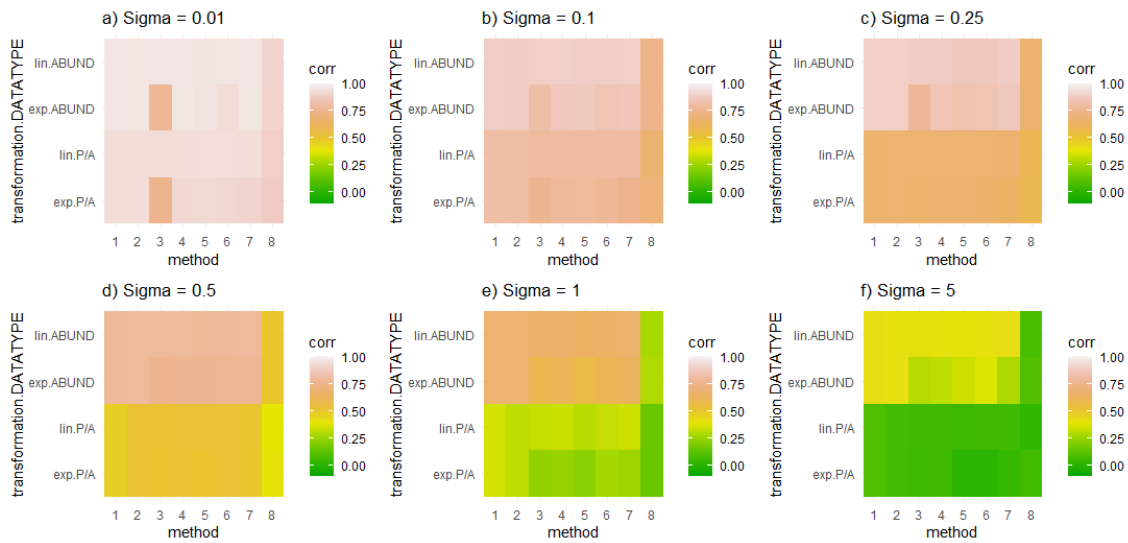


<i>D<sub>IP</sub></i>	0.905	0.696	0.597	0.435	0.158	-0.017
<i>D<sub>CW</sub></i>	0.904	0.694	0.593	0.431	0.160	-0.017
<i>PADDis.Jac</i>	0.904	0.679	0.575	0.418	0.154	-0.025
<i>PADDis.Sor</i>	0.905	0.696	0.597	0.435	0.158	-0.017
<i>PADDis.SS</i>	0.902	0.662	0.546	0.396	0.144	-0.034
<i>PADDis.Och</i>	0.904	0.697	0.596	0.436	0.159	-0.017
<i>PADDis.Simp</i>	0.881	0.620	0.474	0.343	0.158	0.030
<i>PADDis.Kul</i>	0.904	0.694	0.593	0.431	0.160	-0.017
<i>Sørensen (species-based)</i>	0.698	0.724	0.606	0.415	0.127	0.048

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986 Figure 1. Heat maps showing the interactive effects of niche width (sigma), transformation of  
987 between-species dissimilarities (lin = linear, exp = exponential), data type (ABUND =  
988 abundance, P/A = presence/absence), and dissimilarity index (1 – *CWMDis*, 2 – *CDFdis*, 3 –  
989  $D_Q$ , 4 – *dsimcom*/Sørensen, 5 – *dissABC*/Sørensen, 6 – *generalized\_Tradiidiss*/generalized  
990 Canberra, uneven weighting, 7 –  $\beta_{turnovers}$ , 8 –  $D_{CW}$ ) on the correlation with environmental  
991 distance



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