1   **Title**

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

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Abstract

1. In the recent years a variety of indices have been proposed with the aim of quantifying functional dissimilarity between communities. These indices follow different approaches to account for between-species similarities in the calculation of community dissimilarity, yet they all have been proposed as straightforward tools.

2. In this paper we reviewed the trait-based dissimilarity indices available in the literature, contrasted the approaches they follow, and evaluated their performance in terms of correlation with an underlying environmental gradient using individual-based community simulations with different gradient lengths. We tested how strongly dissimilarities calculated by different indices correlate with environmental distances. Using random forest models we tested the importance of gradient length, the choice of data type (abundance vs. presence/absence), the transformation of between-species similarities (linear vs. exponential), and the dissimilarity index in the predicting correlation value.

3. We found that many indices behave very similarly and reach high correlation with environmental distances. There were only a few indices (e.g. Rao's D_Q, and representatives of the nearest neighbour approach) which performed regularly poorer than the others. By far the strongest determinant of correlation with environmental distance was the gradient length, followed by the data type. The dissimilarity index and the transformation method seemed not crucial decisions when correlation with an underlying gradient is to be maximized.

4. *Synthesis*: We provide a framework of functional dissimilarity indices and discuss the approaches they follow. Although, these indices are formulated in different ways and 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

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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 2×2 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. $$d_{Canberra} = \sum_{i=1}^{S_{jk}} \frac{|x_{ij} - x_{ik}|}{(x_{ij} + x_{ik})}$$

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

7

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

252   where p_i is the relative abundance of the *i*th species in the community and δ_{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. $\qquad Q(\mathbf{p}, \mathbf{q}) = \sum_i \sum_j p_i q_j \delta_{ij}$

258   Between community diversity can be expressed using within community diversity of the two

259   original communities (Q(**p**) and Q(**q**)) and the community with mean relative abundances;

260    $Q\left(\frac{\mathbf{p}+\mathbf{q}}{2}\right)$.

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

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 δ 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, ε_{ij}=1- δ_{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

13

289   *dsimcom* family provide meaningful values also if absolute abundances, percentage values or

290   binary occurrences are used instead of relative abundances.

291   When ε_{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), $\beta_{turnover}(q) = \,^q\beta$ - 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. $$\beta_{heterogeneity}\langle q \rangle = 1 - \left(\frac{1}{\,^q\beta} - \frac{1}{N}\right)\bigg/\left(1 - \frac{1}{N}\right)$$

377   When N = 2, $\beta_{het}(q) = 2-2/\,^q\beta$. 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 β_{segr}:

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

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

17

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 $^qD^{\mathbf{Z}}$, is the diversity of a

385   theoretical community with $^qD^{\mathbf{Z}}$ *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 2×2 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. $$B = \sum_{i \in X}\left(1 - \max_{j \in Y} \varepsilon_{ij}\right) = S_x - \sum_{i \in X} \max_{j \in Y} \varepsilon_{ij}$$

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. $C = \sum_{i \in Y}\left(1 - \max_{j \in X} \varepsilon_{ij}\right) = S_y - \sum_{i \in Y} \max_{j \in X} \varepsilon_{ij}$

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

439   where σ (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

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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

22

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_Tradidiss*, 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

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528 versions of *dsimcom*, *dissABC*, *PADDis*/D_{CW}, *generalized_Tradidiss* 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.

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 FDissim 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 FDissim 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_Tradidiss* 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_Tradidiss*. 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

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576 patterns were the relatively poor performance of the *PADDis*/D_{CW} 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

26

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

601 indices.

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_{IP}, D_{CW} 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

29

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 comsimitv R package. Own functions for functional

741   dissimilarity indices are made available through the Zenodo public repository:

742   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

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

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 tpye			R function
				A	R	P/A	
Summary-based	*Typical value*	*CWM-based*	Ricotta et al. (2015)	X	X	X	FD:::functcomp
	Distribution-based	*CDF-based*	Appendix S3	X	X	X	our new functions, see Data availability
Direct dissimilarity	*Probabilistic*	*DISC/D_Q*	Rao 1982, Pavoine & Ricotta (2014)	X	X	X	adiv::SQ
		dsimcom	Pavoine & Ricotta (2014)	X	X	X	adiv:::dsimcom
	Ordinariness-based	*dissABC*	Pavoine & Ricotta (2015)	X	X	X	adiv:::dissABC
		generalized_Tradidiss	Pavoine & Ricotta (2019)	X	X		adiv:::generalized_Tradidiss
	Diversity	*multiplicative beta*	Chao et al. (2012)		X		our new functions, see Data

44

	partitioning						availability
	Nearest neighbour	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
		PADDis	Ricotta et al. (2016)			X	adiv:::PADDis
Classification-based	not discussed	not discussed	Hérault & Honnay (2007), Nipperess et al. (2010), Cardoso et al. (2014), Pavoine (2016)				

977

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

	Sigma=0.01	Sigma=0.1	Sigma=0.25	Sigma=0.5	Sigma=1	Sigma=5
CWMdis	0.974	0.905	0.846	0.828	0.649	0.251
CDFdis	0.974	0.904	0.845	0.83	0.646	0.255
D(Q)	0.974	0.912	0.832	0.828	0.637	0.243
dsimcom.SS	0.974	0.911	0.832	0.829	0.638	0.243
dsimcom.Jac	0.974	0.911	0.832	0.829	0.638	0.243
dsimcom.Sor	0.974	0.911	0.832	0.829	0.638	0.243
dsimcom.Och	0.974	0.911	0.832	0.829	0.639	0.243
dsimcom.Beta	0.974	0.911	0.832	0.829	0.638	0.243
dissABC.Jac	0.967	0.899	0.82	0.813	0.617	0.243
dissABC.Sor	0.967	0.899	0.82	0.813	0.617	0.243
dissABC.SS	0.967	0.899	0.82	0.813	0.617	0.243
dissABC.Och	0.968	0.899	0.819	0.814	0.618	0.243
dissABC.Kul	0.968	0.898	0.819	0.814	0.619	0.243
dissABC.Si	0.954	0.867	0.789	0.791	0.616	0.243
Tradidiss.GC.even	0.974	0.908	0.816	0.829	0.626	0.245
Tradidiss.MS.even	0.974	0.908	0.814	0.828	0.623	0.243
Tradidiss.PE.even	0.974	0.907	0.828	0.831	0.639	0.25
Tradidiss.GC.uneven	0.967	0.901	0.827	0.815	0.622	0.244
Tradidiss.MS.uneven	0.966	0.899	0.823	0.813	0.618	0.243
Tradidiss.PE.uneven	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
Bray-Curtis (species-based)	0.711	0.832	0.778	0.678	0.455	0.086

980

981

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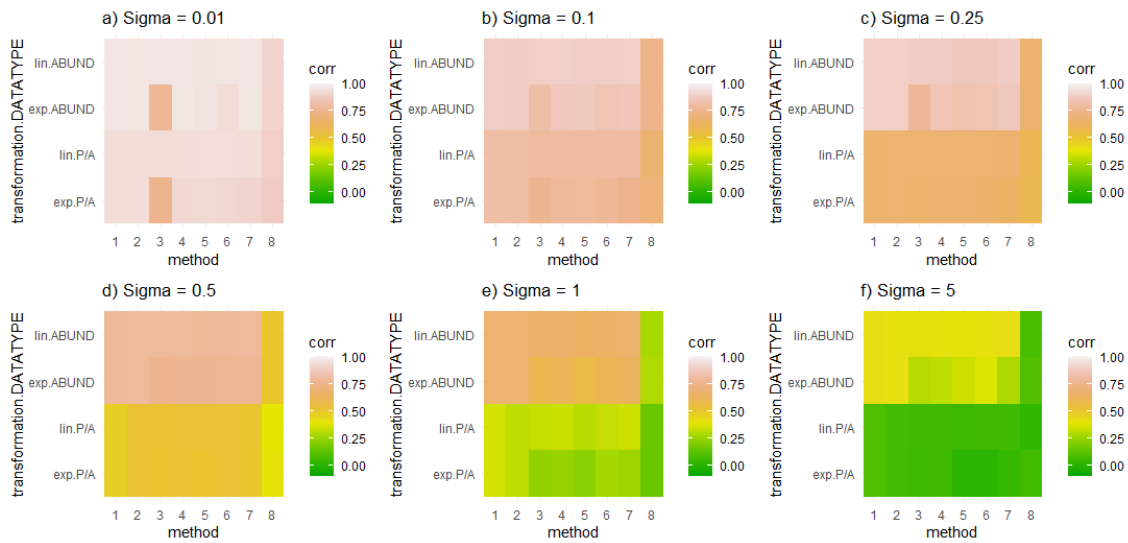
	Sigma=0.01	Sigma=0.1	Sigma=0.25	Sigma=0.5	Sigma=1	Sigma=5
CWMdis	0.944	0.818	0.691	0.568	0.353	0.014
CDFdis	0.943	0.820	0.700	0.594	0.306	-0.001
D(Q)	0.941	0.818	0.701	0.59	0.313	-0.003
dsimcom.SS	0.944	0.821	0.705	0.593	0.316	-0.003
dsimcom.Jac	0.944	0.821	0.705	0.593	0.316	-0.003
dsimcom.Sor	0.944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

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

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985

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_Tradidiss*/generalized

990 Canberra, uneven weighting, 7 – $\beta_{turnover}$, 8 – D_{CW}) on the correlation with environmental

991 distance

992