

## Assessing functional diversity: the influence of the number of the functional traits

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Titre (provisoire) :

**Assessing functional diversity: the influence of the number of functional traits**

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Keywords: functional diversity, biological traits, indices' sensitivity, ecosystem monitoring

**Abstract**

Based on a growing corpus of indices, the assessment of the functional diversity has become a central focus in both marine and terrestrial ecology from the last decade. However, the impact of several key-features of the observational protocols on the assessment of functional indices, and then on our perception of functional diversity patterns, is still poorly known. Here, we proposed the first study dealing with the sensitivity of functional diversity indices to the variation of the number of functional traits. We tested the behavior of 6 of the most widely used functional diversity indices on the basis of both simulated and real data sets. We found not solely that the number of functional traits may strongly alter the estimate of the indices considered but it may also lead to conter-intuitive results. The extent and profile of the sensitivity of functional indices to the number of functional traits strongly vary from one index to another. FRic, Q, FDis and FSpe are strongly impacted by the variation in the number of traits contrarily to FEve and FDiv that remain quite stable. Beyond the sensitivity of each index, we also showed that the qualitative or quantitative nature of the traits may also strongly alter the assessment of some indices (through the metric used for computing the functional distance matrix). By pointing out that the variation in both the nature and the number functional traits may impact functional indices in a contrasted manner, we urged the need to take into account this criterion before drawing comparison between empirical studies. In situations where studies

26 do not share the same number of functional traits we suggest to use null models, to overpass  
27 this bias.

28

## 29 **Introduction**

30 Functional diversity, dealing with the value and range of biological traits in ecosystems (Diaz  
31 and Cabido 2001), is becoming a major concept in ecology and ecosystem management in both  
32 terrestrial and marine domains. An increasing body of literature is suggesting that functional  
33 diversity, rather than species diversity, enhances ecosystem functions such as productivity  
34 (Tilman *et al.* 1997; Hooper and Dukes 2004; Petchey *et al.* 2004; Hooper *et al.* 2005),  
35 resilience to perturbations or invasion (Dukes, 2001; Bellwood *et al.* 2004) and regulation in  
36 the flux of matter (Waldbusser *et al.* 2004; Villéger *et al.* 2008). Therefore, it is expected that  
37 functional diversity has the potential to link morphological, physiological, and phenological  
38 variations at the individual level to ecosystem processes and patterns (Petchey, Gorman &  
39 Flynn, 2006). Nowadays, central priorities in ecology is no longer to debate on the need to  
40 involve (or not) functional diversity on studies focused in community ecology but to define  
41 which indices, which functional traits and how many traits must be selected for capturing the  
42 most important aspects of functional diversity (Petchey and Gaston 2006, Villéger *et al.* 2008).  
43 An increasing body of the literature deals with the first issue (Ricotta 2004, Mouchet *et al.*  
44 2010, Schleuter *et al.* 2010). A corpus of indices tends to emerge from these works. They  
45 usually allow to simultaneously taking into count both several functional traits (to fit  
46 Rosenfeld's definition about functional diversity, see Rosenfeld 2002) and species abundance  
47 (or biomass) (to fit "Mass ratio hypothesis", see Grime, 1998). Quadratic entropy (Rao, 1985,  
48 Botta-Dukat, 2005) has been the most widely used diversity index of this kind since several  
49 decades (Pavoine, 2012). Recently, the popularity of other indices, such as those developed in  
50 the frame of the functional space (*e.g.* functional richness, FRic or functional divergence, FDiv,

51 see Villéger *et al.* 2008), has strongly increased (*e.g.* Villéger *et al.* 2010; Gerisch *et al.* 2012).  
52 However, the sensitivity of index estimates to the variation of several key-features in the  
53 observation protocols has still been poorly studied. For instance, none studies has investigated  
54 the sensitivity of functional indices to the variation in the number of functional traits considered.  
55 Historically, an incomplete knowledge on the biology and ecology of organisms strongly  
56 limited the ability to obtain accurate data on a given functional trait simultaneously for all  
57 species belonging to a community (Villéger, 2008). In such a context, the optimal number of  
58 traits to consider was not a matter of priority interest. However, the improvement of both data  
59 collection processes and general knowledge on the biology and ecology of species nowadays  
60 has enhanced the possibility of taking into account multiple functional traits in numerous fields.  
61 As a consequence, the number of diversity studies based on several functional traits has strongly  
62 increased in recent years for many taxa, in both marine (*e.g.* Villéger *et al.* 2010, Parravicini *et*  
63 *al.* 2014; D'agata *et al.* 2014) and terrestrial ecosystems (*e.g.* Gerisch *et al.* 2012; Janecek *et al.*  
64 2013; Mazel *et al.* 2014). In this context, we proposed the first study focused on the sensitivity  
65 of functional diversity indices to the variation in the number of functional traits considered. We  
66 investigated this issue on the basis of a set of indices that are usually considered as among the  
67 most promising indices with the view of assessing and monitoring functional diversity in both  
68 marine and terrestrial ecosystems (*e.g.* Bellwood *et al.* 2006; Villéger *et al.* 2010; Mouillot *et*  
69 *al.* 2011; Pakeman *et al.* 2013; Carboni *et al.* 2013; Stuart-Smith *et al.* 2013; Buisson *et al.*  
70 2013; Janecek *et al.* 2013; D'agata *et al.* 2014; Parravicini *et al.* 2014). In particular, we address  
71 the following questions: (1) To which degree and how is each index affected by the number of  
72 traits considered?, (2) Is the influence of the number of traits in the assessment of functional  
73 diversity similar whatever the index used?, (3) Does the sensitivity of each index to the number  
74 of traits vary according to the nature of functional traits (quantitative vs qualitative)?

75

76

77 **Material & Methods**

78

79 **Computation of the selected indices**

80 The six indices tested in this paper include the three indices developed by Villéger *et al.*  
81 2008 (functional richness FRic, functional evenness FEve, functional divergence FDiv),  
82 functional dispersion FDis (Laliberté & Legendre, 2010), quadratic entropy of Rao Q (Botta-  
83 Dukat 2005) and functional specialization FSpe (Villéger *et al.* 2010) (see table X for a short  
84 description of each index). The method involved for computing these indices differs according  
85 to the nature (quantitative or qualitative) of the functional traits used for characterizing the  
86 species (Laliberté & Legendre, 2010).

87

88 If all studied traits are quantitative and no value is missing, indices are directly computed  
89 through their mathematical formula (hereafter called "direct method"). For indices related to  
90 the functional space concept (*i.e.* FRic, FEve and FDiv), the T trait values for each species are  
91 then used as T coordinates for projecting each species in the functional space (Villéger *et al.*  
92 2008). For the three other indices (*i.e.* FDis, Q and FSpe), they are directly computed using  
93 Euclidean distance.

94

95 Conversely, if all traits are either qualitative or represent a mix of both qualitative and  
96 quantitative variables, or if they are missing values, none of the 6 indices considered can be  
97 directly computed through a direct method. Indeed, regarding FRic, FEve and FDiv, species  
98 cannot be projected according to their values in qualitative functional traits in a relevant  
99 manner. Similarly, for FDis, Q and FSpe, Euclidean distance cannot be used on qualitative data.  
100 In these cases, authors have to carry out an alternative method (hereafter called "indirect

101 method”), which differs according to the indices considered. Regarding FDis, Q and FSpe, the  
102 indirect method consists in using the Gower distance rather than the Euclidean distance  
103 (Laliberté & Legendre, 2010; Podani 2006). Regarding FRic, FEve and FDiv, the problem is  
104 solved by carrying out a factorial analysis (a PCoA based on Gower distance for the  
105 dissimilarity matrix) on the functional traits matrix (Laliberté & Legendre, 2010). Factorial  
106 coordinate’s matrix can be then used for projecting species on the functional space (see figure  
107 X for a comparison between direct and indirect methods). The number of axes conserved for  
108 the computation of functional indices after the factorial analyses is equivalent to the number of  
109 functional traits considered (and therefore, it is the number of traits of the functional space). In  
110 this way, the number of dimensions of the functional space for the indirect method is the same  
111 as for the direct method. Indeed, FRic being sensitive to the number of dimensions of the  
112 functional space (Podani 2006), keeping the same dimensions for the both methods allows us  
113 thus to overcome this potential bias.

114 Hereafter, we have simultaneously computed each of the 6 indexes considered on the  
115 basis of these two categories of methods (direct and indirect) in order to assess if the sensitivity  
116 of the indices to the variation in the number of traits may differ according to the nature of  
117 functional traits considered.

118

#### 119 **Data analyzed**

120 The influence of the variation of the number of traits on the values of functional diversity  
121 indices by both the direct and indirect methods has been carried out through tests based on two  
122 types of data: simulated data and field data issued from coral reef ecosystems.

123 The comparison of results issued from both simulated and field data allowed us to have a more  
124 complete view of indices behavior. More precisely, field data allow enabled us to ensure that  
125 simulations properly reflect the structure of natural communities while simulated data allow us

126 to assess that the choice of a natural community's example issued from field data is not a  
127 particular case in his community's structure.

128 Field data allow us to analyze a particular community and the functional diversity indices  
129 provide the functional characteristic of this chosen community. These data also illustrate the  
130 effects of the number of traits on indices in a real situation. However, the number of traits in  
131 field data is not always sufficient. Moreover, the distribution of a trait values in a real  
132 community is not always easy to capture since it would require a large number of samples, and  
133 this distribution is important in studies on index behavior for statistical reasons. Consequently,  
134 simulated data allow thus to complete and measure the generality of the results obtained with  
135 field data. We argue that the combination of both sets of data provide a more complete view of  
136 the behavior of indices.

- 138 • Data used for the direct method (Quantitative traits only)
  - 139 ○ *Simulated data*

140 For the test based on simulated data, we have simulated 1000 matrices of functional  
141 traits ("functional matrix" in the figure 1) crossing 50 species by 15 functional traits. The  
142 number of functional traits investigated was selected on the basis of a non-exhaustive review  
143 of the literature using functional traits in both marine and terrestrial ecosystems (32  
144 publications). We found that authors incorporated  $15 \pm 6$  (mean  $\pm$  sd) functional traits.

145 The traits values for each species were obtained by random selection in the normal distribution  
146 (see more details on this rationale in Kraft *et al.* 2008 and Mouchet *et al.* 2010). The number of  
147 species functionally different was 50 whatever the number of traits considered. Otherwise, 1000  
148 fauna/floristic matrices (abundances matrices) were simulated by random selection in the log  
149 normal distribution. Each abundance matrix have 1 row and 50 columns in order to simulate  
150 the result of a sample of 50 species on a single site.

**Commenté [MZ1]:** merci à JCP d' améliorer facilement ce petit paragraphe justifiant la double approche (data réelles et simulées)

**Mis en forme :** Surlignage

**Mis en forme :** Surlignage

**Commenté [P2]:** Je propose qq chose comme ça, mais c'est difficile de faire mieux que l'original JCG...  
A prendre, à discuter, ou à laisser...

**Mis en forme :** Police :Non Gras

**Commenté [P3]:** Quels paramètres ont été choisis (moyenne, variance) ? Est-ce que ce sont les mêmes que pour les données réelles ? Les données réelles suivent-elles une loi normale ? Sinon, pourrait-on essayer d'autres lois ?

**Mis en forme :** Surlignage

**Mis en forme :** Surlignage

**Mis en forme :** Surlignage

**Commenté [P4]:** Même genre de questions...

151           ○ *Field data*

152 For the test based on real data, we have used a data set collected in the marine domain. This  
153 data set consisted in underwater visual census (UVC) of coral reef fishes in French Polynesia  
154 (Kulbicki *et al.* 2010). Sampling was conducted from November to December, in 1995 and  
155 1996, in the central Tuamotu Archipelago on 10 atolls. Fish assemblages were studied using  
156 Underwater Visual Census by two divers (Michel Kulbicki and Gerard Mou-Tham, IRD- UR  
157 CoReUs). Along each transect, divers notably recorded the species name of each fish  
158 encountered, and the number of fish when in school. This set of data contains abundance of 74  
159 fish species (we excluded rare species, *i.e.* with an occurrence inferior to 5% because their  
160 functional traits are lesser available). Then, for each species, we have collected three images on  
161 FishBase, which is considered as a reference basis for ichthyological studies  
162 (<http://www.fishbase.org/search.php>), in order to calculate the mean value of 9 quantitative  
163 functional traits that describe the main ecological functions of fishes (see Appendix A and  
164 Villéger *et al.* 2010 for more details on this rationale). For the fauna matrix, we used the total  
165 biomass of species to follow the “Mass ratio hypothesis” (Grime 1998). Biomass was deduced  
166 from the estimated abundance of fishes, and the formula  $Weight\ (in\ g) = a*(Lb)$  where  $a$  and  $b$   
167 are constants obtained on FishBase and  $L$  the length of fish in centimeters unit.

Commenté [P5]: JCG ne plonge-t-il plus ?

Mis en forme : Surlignage

Commenté [P6]: Connait-on la variance des paramètres  $a$  et  $b$  ? Cette variabilité des paramètres peut-elle modifier les résultats ?

- 169 • Data used for the indirect method (Mix of qualitative and quantitative traits)

170           ○ *Simulated data*

171 For the simulated data set, we again have simulated 1000 matrices of functional traits crossing  
172 50 species by 15 functional traits being for each, qualitative or quantitative (binomial selection).

173 Quantitative traits were simulated in the same way than for the direct method (see above). For  
174 each qualitative trait, we have randomly selected, for each species, one modality among four

Mis en forme : Surlignage

Commenté [P7]:  
Combien de traits qualitatifs sur les 15 simulés ? Ont-ils été mélangés avec les autres ou mis à la fin ? Je pense qu'il faudrait le préciser.

Mis en forme : Surlignage



175 Fauna/floristic matrices (abundances matrices) were simulated by random selection in the log  
176 normal distribution.

177           o *Field data*

178 For the field data set, we have used the same data set as for the direct method (*i.e.* UVC of reef  
179 coral fishes in French Polynesia), and we still worked on 9 functional traits. However, we  
180 considered a different set of functional traits in order to mix qualitative and quantitative traits.  
181 These functional traits (diet, level in water column, home range, schooling, activity, behavior,  
182 crypticity, trophic level and adult average size). These functional traits have been selected  
183 because they are often used in the studies focusing on the functional diversity of fishes (*e.g.*  
184 Lamouroux *et al.* 2002 ; Olden *et al.* 2006 ; Claudet *et al.* 2010 ; Villéger *et al.* 2011 ; Villéger  
185 *et al.* 2013). Used in combination they are supposed to describe the main facets of fish ecology  
186 (Guillemot *et al.* 2011 ; Parravicini *et al.* 2014). One of these 9 functional traits, is quantitative  
187 (mean size), while the other ones are qualitative. Finally, we obtained a functional matrix  
188 crossing 74 species by 9 functional traits. For the fauna matrix, we used the same matrix of  
189 biomass that previously described with the direct method (see above). Then, we make  
190 resampling (1000 bootstraps) on the functional matrix (selection is realized with no replacing)  
191 and we computed, for each bootstrap, the six functional diversity indices.

192  
193           For both methods (direct and indirect) and, for each type of data (field and simulated  
194 data), we have computed indices, by bootstrapping (1000 iterations), varying the number of  
195 traits from 2 to 9 (for the field data set) or 15 functional traits (for the simulated data). FRic and  
196 FDiv being not calculable for a single trait, all computations start from two traits (see Villéger  
197 *et al.* 2008 for more details about this property). Moreover, for all tests, the number of functional  
198 units (*i.e.* the number of species sharing a specific combination of traits) is kept relatively stable

199 during the increase of number of functional traits (some indices being sensitive to this  
200 parameter, Mouchet *et al.* 2008).

201

202 All computations implemented in this study are performed with the R software (R Development  
203 Core Team 2012) and notably with the dbFD function (FD package, Laliberté & Shipley, 2011)  
204 in which we have included the computation of FS<sub>pe</sub>.

205

206

207

## 208 **Results**

209 Whatever we used the direct or indirect methods (and then whatever the nature of the functional  
210 traits considered), the FRic index is significantly influenced by the number of traits considered  
211 (Friedman test, *p*-value < 0.01 in both cases). FRic shows a nonlinear relation with the number  
212 of traits. For quantitative traits (direct method) FRic increases with the number of traits until  
213  $t=7$  or 8 and decreases for a bigger number of traits (cf. Fig. 2a and 2c). When mixing  
214 quantitative and qualitative traits (indirect method) FRic also showed an hump-shaped pattern  
215 with the real data set, but it reached its maximum value earlier (for  $t=3$ , Fig 3c). With both  
216 simulated and real data sets, FRic showed a continuous decreasing trend when increasing the  
217 number of traits from  $t=2$  (Fig. 3a and 3c). Surprisingly, whatever the direct or indirect method

218 FRic reached values close to 0 when the number of traits increases. This situation is however  
219 not observed for the direct method with real data (fig.2c), but it is probably only because the  
220 number of functional traits available is not sufficient to obtain this result.

221

222 Otherwise, FE<sub>ve</sub> and FDiv are weakly influenced by the number of functional traits whatever  
223 the method and the nature of the traits (cf. Fig.2a, Fig.2c, Fig.3a, and Fig.3c). The most

Mis en forme : Surlignage

Commenté [P8]: Une hypothèse d'explication (H1) : ne peut-on pas supposer qu'en augmentant le nombre de traits étudiés dans une communauté, on prend le risque d'avoir plus de redondances fonctionnelles entre les différentes espèces ?

Lorsqu'on a deux traits, on a un convexe dans le plan fonctionnel. Supposons le assez grand pour que sa surface indique une grande diversité fonctionnelle. Si on ajoute un 3<sup>ème</sup> trait, on a un simplexe (volume) dans un espace fonctionnel à 3 axes. Si la « hauteur » de ce simplexe est faible, le volume sera alors petit, même si la surface projetée en dimension 2 était grande...

Dans ce cas, le max obtenu dans les résultats donnerait une idée du nombre de traits à prendre en compte pour cet indice.

Bien sûr, l'explication sur le défaut de l'algorithme de calcul est tout à fait valable, n'y aurait-il pas un autre algorithme pour vérifier ? (je me renseigne de mon côté)

Mis en forme : Surlignage

224 important variations (while limited) occurred for FEve for the real data with the indirect method  
225 (cf. Fig 3c), but it is very stable with the simulated data (Fig 3a). In short, whatever the nature  
226 of the traits, estimate variations of these two indices according to the number of traits are very  
227 weak and sometimes negligible.

228  
229 Functional dispersion (FDis) and functional specialization (FSpe) are highly correlated ( $r=0.99$   
230 or  $r=0.98$  according to method, Pearson's correlation, Table ??) and they are both greatly  
231 influenced by the number of functional traits with the direct method (*i.e.* when using only  
232 quantitative traits, Fig. 2b and Fig. 2d). Both real data and simulated data provide the same  
233 pattern : FDis and FSpe strongly increased with the number of traits. FDis and FSpe are also  
234 strongly correlated with the quadratic entropy of Rao ( $r=0.98/0.97$  and  $r=0.97/0.97$  respectively,  
235 Table ??), which is, by consequence, also highly influenced by the number of functional traits  
236 with the direct method. In contrast, with the indirect method (*i.e.* utilization of Gower's  
237 distance), these three indices are not (simulated data, Fig 3a) or weakly (real data, Fig 3d)  
238 influenced by the number of traits (Fig 3b et Fig3d). For the real data set, this weak relationship  
239 is particularly true when simultaneously considering more than 3 or 4 traits (Fig.3d).

240

241

## 242 **Discussion**

243 Following the concept of Ludwig and Reynolds (1998), Mouillot *et al.* (2005) and  
244 Mason *et al.* (2005) shown that functional diversity could be split into three major components:  
245 functional richness, functional evenness and functional divergence. Later, Villéger *et al.* (2008)  
246 and Laliberté *et al.* (2010) translated these three components in indices: functional richness was  
247 characterized by FRic, functional evenness by FEve and functional divergence by FDiv and  
248 FDis. Q has been also considered as an index describing the functional divergence component

249 notably because of its strong correlation with FDis (Mouchet *et al.* 2008 and Pavoine & Bonsall  
250 2011). More generally, several authors stressed the importance of defining indices able to  
251 properly characterise each of these three components in order to have a complete view of  
252 functional diversity in ecosystems (Mason *et al.* 2005, Mouillot *et al.* 2005). The results of the  
253 present study directly contribute to this important issue.

254 First, in the recent literature, determination of functional richness on a continuous scale  
255 is mainly (if not exclusively) assessed through a single index: FRic. FRic index is defined as  
256 the amount of functional space occupied by the functional units (species sharing the same values  
257 of functional traits) of a community (Mason *et al.* 2005; Villéger *et al.* 2008).

258 Our study pointed out a strong and non-linear relationship between functional richness  
259 (FRic) and the number of functional traits. Moreover, we showed that this index takes values  
260 near to zero when the number of functional traits increases beyond a threshold. This is clearly  
261 a non-intuitive result, notably because the number of functional units did not decrease with the  
262 increase in the number of traits. By definition, FRic is supposed to be close to zero when the  
263 community is either poor in functional units or when all functional units of the community are  
264 functionally very similar. However, here we showed that this index could be near to zero even  
265 if none of these two situations occurred (*cf.* Fig. 2a and 3a). FRic requires the computation of a  
266 complex algorithm (the “convex hull volume”). Podani (2009) evidenced a drawback of this  
267 algorithm. This author demonstrated that the convex hull volume takes values near to zero when  
268 individual trait ranges are wide (Podani, 2009). Our results suggest that this algorithm could be  
269 also not well adapted for computing a volume when the numbers of dimensions (here the  
270 number of traits) is too high. These results tend to be supported by the fact that FRic does not take  
271 values near to zero (and not decreased) when the number of functional traits is high and when  
272 the number of axes is kept constant and small (*e.g.* 3 axes, see Fig. S1).

Mis en forme : Surlignage

Commenté [P9]: A revoir éventuellement avec l'hypothèse précédente.

Mis en forme : Surlignage

273 Moreover, FRic suffer from several other drawbacks. First, it doesn't take into account  
274 the number of functional units present in the functional space. For instance, an ecosystem with  
275 only 5 functional units representing 5 vertices would have the same value of FRic than an  
276 ecosystem with 20 functional units if they share the same 5 vertices. Intuitively an ecosystem  
277 with 20 functional units should be more resistant and more resilient than another ecosystem  
278 with only 5 functional units (Diaz and Cabido 2001). Otherwise, FRic doesn't include the  
279 species abundance that is not in accordance with one of Ricotta's criteria (Ricotta *et al.* 2005,  
280 Villéger *et al.* 2008). Indeed, for FRic, an ecosystem where vertices are represented by a single  
281 individual has the same value of FRic than an ecosystem where each vertex is represented by  
282 numerous individuals. For all of these reasons assessing the resistance or resilience of  
283 ecosystem on the single basis of FRic index is not relevant (Podani, 2009). In short, the high  
284 sensitivity of FRic to the variation in the number of traits and its counter-intuitive behavior  
285 when the number of traits increases, evidenced additional problems that call into questions its  
286 use in functional diversity studies, particularly for studies working with multiple traits.

287  
288 Conversely, we found that functional evenness (represented here by FEve, Villéger *et*  
289 *al.* 2008) is only weakly influenced by the number of functional traits whatever the method  
290 used. In addition to the fact that FEve is not influenced by the species richness (Mouchet *et al.*  
291 2008), our results strongly support its use for assessing the evenness component of the  
292 functional diversity.

293  
294 Pavoine and Bonsall (2011) stated that functional divergence can be represented by  
295 FDiv, FDis and Q. Regarding FSpe, both our results (correlation FSpe vs FDis and FSpe vs Q  
296 near to 1) and its aim (*i.e.* quantifying how apart the species are from the gravity centre, Villéger  
297 *et al.* 2010, Pla *et al.* 2012), suggested that this index could also be used for assessing functional

**Commenté [JG10]:** Je ne suis pas du tout certain qu'on laisse ce qui est surligné en jaune dans ce papier. A discuter...

**Commenté [P11]:** Je comprends la réticence à laisser ce paragraphe tel quel mais il me semble qu'il contient une idée intéressante qui devrait être mentionnée je pense :  
La redondance fonctionnelle est importante pour la résilience même si l'indice FRic ne la capture pas.

298 divergence. For this facet, our work has demonstrated that quadratic entropy of Rao (Q),  
299 functional dispersion (FDis) and functional specialization (FSpe) were positively and highly  
300 correlated with the number of functional traits when catching functional aspects exclusively on  
301 the basis of a set of quantitative traits (*cf.* Fig 2). As a consequence the level of functional  
302 diversity assessed on the basis of these indices is strongly impacted by the number of traits  
303 studied when considering quantitative traits only while the situation is different when using a  
304 mix of qualitative and quantitative traits. A part of this drawback is probably, linked to the  
305 difference in the metric used for computing the functional distance in both cases. Indeed, several  
306 authors showed that the Euclidean distance (used for computing the functional distance matrix  
307 with quantitative traits) is positively correlated with the number of functional traits (see Mason  
308 *et al.* 2005, Podani & Schmera 2006 or Mason *et al.* 2007). While Q, FDis and FSpe are, by  
309 mathematical construction, proportional to this distance (*cf.* Table X), the relation observed  
310 between each of them and the number of functional traits is probably due to this property. The  
311 greater stability of Q, FDis and FSpe we observed when using indirect methods (based on  
312 Gower's distance instead of the Euclidean distance) highly support this hypothesis. Conversely  
313 to the Euclidean distance, Gower's distance is not influenced by the number of functional traits  
314 (because it is weighted by the sum of the distance between two species per functional trait; see  
315 Podani & Schmera 2009 for more details about this standardization).

316         Among the indices studied, FDiv represents a particular case notably in the sense that it  
317 is not directly proportional to the distance between species (see its mathematical formula, Table  
318 ? ). By consequence, the metric used does not influence assessments of this index. In addition,  
319 we found that FDiv is weakly impacted by the number of traits. Thus, we recommend the use  
320 of FDiv index to estimate the divergence facet of functional diversity.

321

322 In conclusion, we showed that the number of functional traits may have an important  
323 impact on the estimation of functional indices values and that this impact differs according to  
324 the indices chosen. Moreover, the nature of functional traits influences also the indices values  
325 (through the metric used to compute indices). Thus, these significant and sometimes important  
326 variations in diversity estimates may have strong impact on our perception of diversity patterns  
327 and of its role in ecosystem functioning. This drawback might have a particularly strong impact  
328 on results issued from meta-analyses based on the empirical comparison of previous studies  
329 that do not share the same number of traits. This sensitivity is important to point out notably in  
330 the actual context where an increasing number of meta-analyses dealing with functional  
331 diversity are carried out (*e.g.* Buisson *et al.* 2013, Stuart-Smith *et al.* 2013, D'agata *et al.* 2014,  
332 Parravacini *et al.* 2014, Mazel *et al.* 2014, Mouillot *et al.* 2014). A solution to avoid this bias  
333 might be to compare beforehand the value of each index to null models respecting the same  
334 conditions that those used to compute indices (*e.g.* same number of functional traits, same  
335 method). A similar approach (*i.e.* use of null models) has been recommended by several authors  
336 (*cf.* Mason *et al.* 2007; Mason *et al.* 2008 ; Villéger *et al.* 2008 or also Villéger *et al.* 2010) to  
337 overpass the sensibility of these indices to the variation of species richness (Mouchet *et al.*  
338 2010). Here, our results highlight the need to extend this approach not only for studies having  
339 different specific richness but also with the view to compare studies that have not the same  
340 number of functional traits.

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