Titre (provisoire) :

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

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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

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

Introduction

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

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

Material & Methods

Computation of the selected indices

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

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

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

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

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

Data analyzed

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

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

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

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

- Data used for the direct method (Quantitative traits only)
    - *Simulated data*

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

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

- *Field data*

For the test based on real data, we have used a data set collected in the marine domain. This data set consisted in underwater visual census (UVC) of coral reef fishes in French Polynesia (Kulbicki *et al.* 2010). Sampling was conducted from November to December, in 1995 and 1996, in the central Tuamotu Archipelago on 10 atolls. Fish assemblages were studied using Underwater Visual Census by two divers (Michel Kulbicki and Gerard Mou-Tham, IRD- UR CoReUs). Along each transect, divers notably recorded the species name of each fish encountered, and the number of fish when in school. This set of data contains abundance of 74 fish species (we excluded rare species, *i.e.* with an occurrence inferior to 5% because their functional traits are lesser available). Then, for each species, we have collected three images on FishBase, which is considered as a reference basis for ichthyological studies (http://www.fishbase.org/search.php), in order to calculate the mean value of 9 quantitative functional traits that describe the main ecological functions of fishes (see Appendix A and Villéger *et al.* 2010 for more details on this rationale). For the fauna matrix, we used the total biomass of species to follow the "Mass ratio hypothesis" (Grime 1998). Biomass was deduced from the estimated abundance of fishes, and the formula *Weight (in g) = a*(Lb)* where *a* and *b* 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]: Connaît-on la variance des paramètres a et b ? Cette variabilité des paramètres peut-elle modifier les résultats ?

- Data used for the indirect method (Mix of qualitative and quantitative traits)
  - *Simulated data*

For the simulated data set, we again have simulated 1000 matrices of functional traits crossing 50 species by 15 functional traits being for each, qualitative or qualitative (binomial selection). Quantitative traits were simulated in the same way than for the direct method (see above). For 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 - *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

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

All computations implemented in this study are performed with the R software (R Development Core Team 2012) and notably with the dbFD function (FD package, Laliberté & Shipley, 2011) in which we have included the computation of FSpe.

Results

Whatever we used the direct or indirect methods (and then whatever the nature of the functional traits considered), the FRic index is significantly influenced by the number of traits considered (Friedman test, *p-value* < 0.01 in both cases). FRic shows a nonlinear relation with the number of traits. For quantitative traits (direct method) FRic increases with the number of traits until t=7 or 8 and decreases for a bigger number of traits (cf. Fig. 2a and 2c). When mixing quantitative and qualitative traits (indirect method) FRic also showed an hump-shaped pattern with the real data set, but it reached its maximum value earlier (for t=3, Fig 3c). With both simulated and real data sets, Fric showed a continuous decreasing trend when increasing the number of traits from t=2 (Fig. 3a and 3c). Surprisingly, whatever the direct or indirect method FRic reached values close to 0 when the number of traits increases. This situation is however not observed for the direct method with real data (fig.2c), but it is probably only because the number of functional traits available is not sufficient to obtain this result.

Otherwise, FEve and FDiv are weakly influenced by the number of functional traits whatever 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 3ème 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

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

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

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

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

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

Pavoine and Bonsall (2011) stated that functional divergence can be represented by FDiv, FDis and Q. Regarding FSpe, both our results (correlation FSpe vs FDis and FSpe vs Q near to 1) and its aim (*i.e.* quantifying how apart the species are from the gravity centre, Villéger *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

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