

# Functional-diversity indices can be driven by methodological choices and species richness

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**Abstract.** Functional diversity is an important concept in community ecology because it captures information on functional traits absent in measures of species diversity. One popular method of measuring functional diversity is the dendrogram-based method, FD. To calculate FD, a variety of methodological choices are required, and it has been debated about whether biological conclusions are sensitive to such choices. We studied the probability that conclusions regarding FD were sensitive, and that patterns in sensitivity were related to alpha and beta components of species richness. We developed a randomization procedure that iteratively calculated FD by assigning species into two assemblages and calculating the probability that the community with higher FD varied across methods. We found evidence of sensitivity in all five communities we examined, ranging from a probability of sensitivity of 0 (no sensitivity) to 0.976 (almost completely sensitive). Variations in these probabilities were driven by differences in alpha diversity between assemblages and not by beta diversity. Importantly, FD was most sensitive when it was most useful (i.e., when differences in alpha diversity were low). We demonstrate that trends in functional-diversity analyses can be largely driven by methodological choices or species richness, rather than functional trait information alone.

**Key words:** biodiversity; community ecology; dendrogram; functional diversity; multivariate analysis; species richness.

## INTRODUCTION

Functional diversity is the amount of inter-specific variation in functional traits in an ecological community. The concept of functional diversity has received considerable attention recently, largely because of the following intuitive argument. Species-diversity indices treat all species identically, whereas functional-diversity indices do not. Therefore, it is reasonable to expect that functional diversity is likely to be more ecologically relevant because species differ from one another in functionally important ways (Petchey and Gaston 2002). For example, several studies have concluded that measures of ecosystem function tend to correlate more strongly with functional-diversity indices than with species-diversity indices (Loreau et al. 2001). These studies have spurred continued interest in developing new and improved functional-diversity indices (Mouchet et al. 2008, Vileger et al. 2008).

Despite the conceptual simplicity of functional diversity, ecologists wishing to measure it must choose from a number of approaches. Mason et al. (2005) developed a typology of functional-diversity indices with three types: functional richness, functional evenness, and functional divergence. This typology is similar in spirit

to the distinction between species richness and evenness in species-diversity studies. For example, functional-richness indices measure the amount of trait space filled by the species in a community, whereas functional-evenness indices measure the evenness in the distribution of abundance in trait space (Mason 2005, Vileger et al. 2008). Using rarefaction techniques, functional richness and evenness can also be thought of as extremes along a gradient of functional-diversity indices (Walker et al. 2008). Rarefaction also makes clear the close relationship between species and functional richness. It is therefore important to ensure that accepted indices of functional richness provide information beyond that of species richness, as data on functional traits can be costly to obtain.

One approach to measuring functional richness, which has shown promise as a predictor of ecosystem function, is the dendrogram-based approach known as “FD” (functional diversity; Petchey and Gaston 2002). This approach consists of measuring functional richness as the total branch length of a dendrogram that clusters species based on the similarity of their functional-trait characteristics. There are numerous methods for constructing a dendrogram; in particular, both a resemblance measure, which measures the difference between species in their functional-trait characteristics, and a clustering algorithm, which specifies the manner in which similar species are grouped together, must be chosen. There is the possibility that ecological conclu-

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sions drawn from an analysis of dendrogram-based functional diversity may be sensitive to the methodological choices that are required for producing a dendrogram. This may be a serious issue given that dendrogram topology may change considerably with changes in the methods used (e.g., Sneath and Sokal 1973, Jackson et al. 1989).

There has been considerable recent debate about the importance of the method of dendrogram construction for the measurement of dendrogram-based functional diversity (Petchey and Gaston 2006, 2007, Podani and Schmera 2006, 2007, Mouchet et al. 2008). To facilitate resolution, we conducted a detailed analysis of the sensitivity of dendrogram-based functional-diversity measures to differences in species richness and methodological choices. For this resolution, we need a quantitative definition of sensitivity. Given a pair of species assemblages and set of dendrogram-construction methods, we make the following definition: conclusions are *insensitive* if all construction methods result in the same assemblage being identified as having higher functional diversity; conclusions are *sensitive* if at least one construction method identifies a different assemblage as having higher functional diversity.

With this definition, we seek answers to the following questions. First, through a systematic study of previously analyzed data from ecological communities (Petchey and Gaston 2002, 2007, Podani and Schmera 2006): What is the probability that conclusions regarding FD are sensitive to methodological choices? Second: If sensitivity is found to be likely in many communities analyzed, is the probability of sensitivity related to the difference in local species richness (i.e., alpha diversity) between the two assemblages? We hypothesize that the probability of sensitivity should be low when differences in alpha diversity are very high. Intuitively, we expect species richness to drive functional-richness patterns in these cases, no matter how it is measured. This is a null hypothesis; it assumes that functional richness (as measured by FD) does not provide information beyond that provided by species richness. Failure to reject this hypothesis would suggest that FD and alpha diversity are largely redundant, provided that the most species-rich assemblage also tends to have the highest FD. Third: Is the probability of sensitivity related to the amount of species turnover (i.e., beta diversity) between assemblages? As species turnover can be measured in numerous ways, hereafter we use the term “beta diversity” to refer to Lande’s species turnover (Lande 1996). We hypothesize that the probability of sensitivity should be high when beta diversity is low. Low beta diversity indicates that assemblages have similar composition. Therefore, low beta diversity produces conditions under which we intuitively expect small differences in functional diversity. Small differences will presumably be more sensitive to methodological choices. Fourth: Is the probability of sensitivity related to certain types of methodological choices? We hypothesize that conclu-

sions will be more sensitive to the choice of distance measure than to the choice of clustering algorithm, because the distance measure can completely change the order of functional similarity among the species whereas the clustering algorithm is more limited in that it can only alter how groups of species relate to one another in multivariate space. We note that there are reasons to believe that FD will also be quite sensitive to the choice of a clustering algorithm. Indeed, different clustering algorithms can generate quite different tree topologies, which may translate into FD sensitivity. We address these questions by assessing the probability of sensitivity of pairs of randomly drawn sub-assemblages from five ecological communities.

## METHODS

All of our analyses were based on data from ecological communities obtained from the literature. We used the same five data sets used in previous studies of functional diversity (FD) (Petchey and Gaston 2002, 2007, Podani and Schmera 2006). These data sets represent variation in the number (from 13 to 37 species) and type of species, and the number and type of functional traits (from 6 to 27 traits). For example, the three vertebrate data sets use characteristics ranging from foraging behavior to the consumption of prey species as their functional traits (Holmes et al. 1979, Jaksic and Medel 1990, Munoz and Ojeda 1997), whereas the remaining two data sets rely on vegetative characteristics, such as rooting depth and herbivore palatability, of the plants being studied (Golluscio and Sala 1993, Chapin et al. 1996).

Our general approach to assessing the sensitivity of FD to methodological choices was as follows (see Fig. 1 for an example). For each community (i.e., data set), we organized all of the species,  $\gamma$ , into two groups, hereafter referred to as “assemblages.” Let the average species richness over the two assemblages be  $\bar{\alpha}$ . Each species in the community was included in either one of the assemblages or in both. For a given level of beta diversity,  $\beta = \gamma - \bar{\alpha}$ , and difference in alpha diversity between the assemblages,  $\Delta\alpha$ , the total number of unique pairs of assemblages is

$$\Delta\alpha = \frac{\gamma!}{[\gamma - 2\beta]![0.5(2\beta + \Delta\alpha)]![0.5(2\beta - \Delta\alpha)]!} \quad (1)$$

The numerator is the total number of ways that one can order  $\gamma$  species. The three factorials in the denominator are, respectively, the total number of ways that (1) the number of shared species can be ordered, (2) the species that are unique to assemblage 1 (S1) can be ordered, (3) the species that are unique to assemblage 2 (S2) can be ordered (Appendix). In Fig. 1, we give two examples of such orderings when  $\gamma = 11$ ,  $\Delta\alpha = 1$ , and  $\beta = 4.5$ . Note however, that assemblage pairs for which  $(2\beta - \Delta\alpha)$  is an odd number are not possible given the inter-dependencies of these parameters. For each possible combination of  $\beta$  and  $\Delta\alpha$ , we randomly selected 1000 pairs of

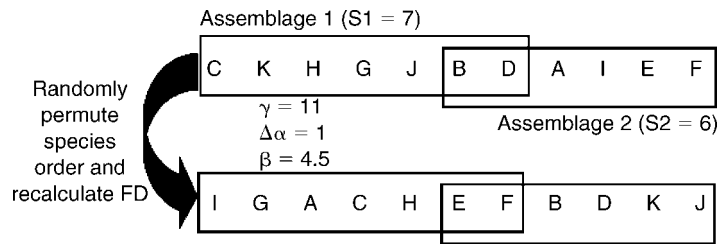


FIG. 1. Measuring the sensitivity of FD (functional diversity) in a hypothetical 11-species community. The procedure consists of randomly dividing the community into two assemblages ( $S_1$ , with seven species, and  $S_2$  with six), noting how FD orders the two assemblages, and assessing the effect of the methodological choices on this order. Each species is represented as a letter, and the assemblages are represented as overlapping rectangles that contain the letters associated with their component species. A new random division can be obtained by leaving the rectangles fixed and permuting the order of species.

assemblages using code programmed in MATLAB version 7.1 (MathWorks 2005). For each of these randomly selected assemblages, we calculated FD based on several different dendrogram-construction methods. FD was considered insensitive to methodological choices for a particular pair of assemblages if the assemblage with the higher FD was the same for all construction methods; FD was otherwise considered sensitive. We then calculated the proportion of the 1000 random iterations that were sensitive. We refer to this proportion as the “probability of sensitivity.” When the probability of sensitivity is high for a particular combination of  $\Delta\alpha$  and  $\beta$ , it is very likely that the conclusions drawn from an FD analysis in this context will be dependent on methodological choices, rather than on the data alone.

In order to calculate FD, two methodological choices must be made. First, a distance (or resemblance) measure must be chosen. Distance measures quantify the difference between two entities based on their characteristics (e.g., species based on their functional traits). There are a large number of resemblance measures from which to choose (Jackson et al. 1989, Legendre and Legendre 1998). We used three distance measures: Euclidean distance as suggested by Holmes et al. (1979); cosine distance; and Gower’s distance, as it allows mixed and missing data types (Gower 1971, Podani 1999, Podani and Schmera 2006, 2007). For Euclidean distance we standardized all trait matrices so that all traits have a mean = 0 and variance = 1 (i.e.,  $z$  scores; Holmes et al. 1979, Petchey and Gaston 2002). We used cosine distance because it more accurately reflects proportional changes in traits whereas the Euclidean distance emphasizes absolute differences. For the Patagonian forb and Arctic vegetation data sets we used only Gower’s distance because these data sets contained missing values and mixed data types; the Euclidean and cosine distances were not appropriate for such data sets (e.g., Podani and Schmera 2006). Second, a clustering algorithm must be chosen. We used three clustering algorithms in our analysis: (1) unweighted pair-group method with arithmetic mean (UPGMA); (2) single linkage (i.e., nearest neighbor); and (3) complete linkage (i.e., maximum or farthest neighbor). These

algorithms represent natural endpoints across a methodological continuum of dendrogram-construction methods, where single linkage lies on one end, complete linkage on the other, and UPGMA lies somewhere in the middle (Podani and Schmera 2006).

We considered several different collections of construction methods because the sensitivity of FD is defined in terms of a particular set of construction methods. For cases where multiple comparisons could be made (e.g., several distance measures), we calculated four separate probabilities of sensitivity: (1) sensitivity with respect to all nine construction methods; (2) sensitivity with respect to the three distance measures with UPGMA clustering (i.e., clustering algorithm is held constant); and (3) sensitivity with respect to the three clustering algorithms with Gower’s distance measure (i.e., distance measure is held constant). In cases where data were deficient and only Gower’s distance could be used, only overall probabilities of sensitivity were calculated. The sensitivity when the clustering algorithm is held constant could be calculated, but these results would be identical to the overall values. Finally, we also calculated probabilities of sensitivity holding other distance measures and clustering algorithms constant and consider pairs of assemblages that do not contain all of the species in the complete data sets. However, we do not present these additional results because they do not alter any of our conclusions.

There is an ongoing debate regarding a standard procedure for calculating FD. Petchey and Gaston (2002) based their measure of FD on a dendrogram derived from a data set that included all species that were of interest (i.e., the entire community). For an assemblage that does not contain all of the species in the entire community, FD is measured as the total branch length of the dendrogram minus the branch lengths of the species that are not included in the assemblage (see Petchey and Gaston [2002, 2007] for more details). We refer to this approach as the “Petchey-Gaston (PG) method.” Alternatively, Podani and Schmera (2006) suggested that FD should be calculated as the total branch length of a dendrogram that is unique to each assemblage, i.e., recalculated from the reduced data set.

TABLE 1. The maximum probability of FD (functional diversity) sensitivity for five communities previously used to examine FD (Podani and Schmera [PS] 2006, Petchey and Gaston [PG] 2007), together with the number of species and the number of combinations of  $\Delta\alpha$  and  $\beta$ .

Community	No. species	Maximum probability of sensitivity		Number of combinations of $\Delta\alpha$ and $\beta$	Data sources†
		PS	PG		
Insectivorous birds	22	0.818	0.497	134	(A) Holmes et al. (1979)
Intertidal fish	13	0.976	0.366	46	(B) Munoz and Ojeda (1997)
Predatory vertebrates	11	0.610	0.594	32	(C) Jaksic and Medel (1990)
Patagonian forbs	24	0.364	0.196	159	(D) Golluscio and Sala (1993)
Arctic vegetation	37	0.244	0.142	370	(E) Chapin et al. (1996)

† Parenthetical capital letters are used to identify which data sources are used in Figs. 2 and 3.

We refer to this measure as the “PS (Podani-Schmera) method.” As this debate remains unresolved, we tested whether FD was sensitive using both methods. To calculate FD using the PG method, we calculated a species-by-branch matrix and a vector of branch lengths for the complete community using the code of Petchey and Gaston (2002) for the R programming language (R 2.7.0; R Development Core Team 2008). We then used this code to calculate FD using the PG method for each assemblage (see Petchey and Gaston [2002] for more details). We repeated this approach for each of the nine construction methods (i.e., three distance measures for each of the three clustering algorithms). To calculate dendrograms using the PS method, we calculated unique dendrograms for all assemblages and construction methods. We used MATLAB version 7.1 (MathWorks 2005) to calculate the sum of dendrogram lengths for each assemblage and construction method.

To display all of these results, we constructed image plots with the R programming language. Image plots can be used to show how a variable changes over a two-dimensional grid. The shading of each square on the grid represents the value of the variable at that grid location. In our case, the variable of interest is the probability of sensitivity and the grid is defined by beta diversity,  $\beta$ , and the difference in alpha diversity,  $\Delta\alpha$ , between the two assemblages. However, only certain combinations of  $\beta$  and  $\Delta\alpha$  are possible. For example, for an 11-species community it is not possible to create two assemblages such that  $\beta = 6$ ,  $\Delta\alpha = 3$ , and all of the species are in at least one of the two assemblages. Therefore, for identification purposes, these impossible grid locations are plotted in white whereas all other levels of sensitivity are some shade of grey. Higher levels of sensitivity are represented by darker shades of grey. This results in a checkerboard pattern. However, it is important to keep in mind that the checkerboard pattern is solely an artifact of the impossibility of certain combinations of  $\beta$  and  $\Delta\alpha$ .

## RESULTS

We identified numerous cases for which FD (functional diversity) had a high probability of sensitivity across all communities; that is, it is easy to find cases for which conclusions derived from FD analyses will be

driven primarily by methodological choices. In the worst-case scenario, FD sensitivity reached probabilities of 0.976 using the PS (Podani-Schmera) method and 0.594 using the PG (Petchey-Gaston) method (Table 1). Variation in the probabilities of sensitivity was largely driven by variation in alpha diversity, with the highest probabilities of sensitivity found when assemblages were similar in alpha diversity (Figs. 2 and 3). In every case where the probability of sensitivity was 0, FD was larger for the assemblage with more species; this result indicates that FD and alpha diversity lead to identical conclusions about the diversity of assemblages in these cases. Therefore, our hypothesis concerning the relationship between alpha diversity and probability of sensitivity is consistent with our results. Contrary to our hypothesis, there were no consistent patterns in the relationship between beta diversity and probability of sensitivity (Figs. 2 and 3).

Decisions about distance measures were more important than decisions about clustering algorithms. For example, when UPGMA clustering was kept constant and only distance measures were compared, FD was more sensitive than when Gower's distance was held constant and clustering methods were compared (Figs. 2 and 3). These results were not altered by the distance measure held constant (e.g., Euclidean, cosine or Gower's) or by the clustering algorithm held constant (e.g., UPGMA, single linkage and complete linkage), and so we only present the results for holding constant Gower's distance and UPGMA, respectively (Fig. 2).

There are some additional trends worth mentioning. The PG method of FD calculation led to lower probabilities of sensitivity than the PS method in all cases (Figs. 2 and 3, Table 1). Also, where greater numbers of dendrogram-construction methods are compared, the probabilities of sensitivity increase. For example, compare the overall probabilities (nine construction methods) with the probabilities obtained by holding the clustering method at UPGMA (three construction methods) (Fig. 2). This difference makes intuitive sense because as one considers more construction methods, it becomes more likely to find a method that leads to different conclusions regarding the ranking of the assemblages in terms of FD.

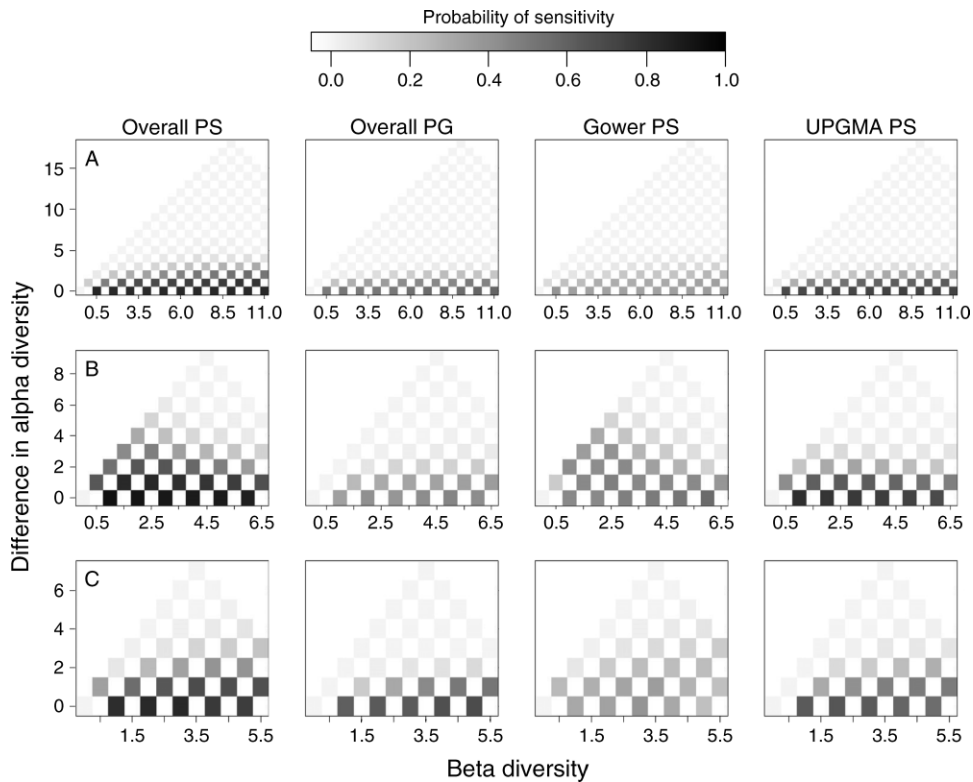


FIG. 2. The effect of alpha and beta diversity on the probability that FD is sensitive to dendrogram construction methods for three communities crossed with four sets of construction methods. Darker shading represents a higher probability of sensitivity. Data sources are given in Table 1. Each column is for a different set of construction methods. For the first two left-hand columns, overall PS and PG, all nine methods of dendrogram construction (three distance measures times three clustering algorithms) were used with the PS (Podani-Schmera) and PG (Petchey-Gaston) methods, respectively. For the right-hand two columns, all three clustering algorithms with the PS method were used with Gower's distance and UPGMA (unweighted pair-group method with arithmetic mean) held constant, respectively.

#### DISCUSSION

Our results demonstrate that FD (functional diversity) is sensitive to choices of distance measure and clustering algorithm in many cases. The major factor contributing to a high probability of sensitivity is low variation in alpha diversity between the assemblages being compared. By contrast, beta diversity between assemblages was a very poor predictor of sensitivity. This did not support our initial hypothesis that lower beta diversity (i.e., higher redundancy between traits across assemblages) would lead to a higher probability of sensitivity. The consistency and severity of our results suggest that this sensitivity is not likely to be unique to the examples we present. Indeed, we did not actively search for atypical data to support our position; we merely used the same data that have been used consistently by investigators when evaluating FD (Petchey and Gaston 2002, 2007, Podani and Schmera 2006).

If our results are so clear, why did others (e.g., Petchey and Gaston 2007) conclude that decisions regarding methodological choices have only a minor effect on FD, especially given that they used the same

data that we use here? There are two possible reasons for this discrepancy. First, to evaluate sensitivity, previous studies have shown that FD calculated using Gower's distance was strongly collinear with FD calculated using the Euclidean distance across many functional-trait matrices (Petchey and Gaston 2007). However, these trait matrices differed widely in number of species. In our analysis, we demonstrate that FD becomes more sensitive as variation in alpha diversity becomes small. Therefore, in the light of our new work, it is not surprising that others have found low sensitivity to methodological choices; in their case, our results strongly suggest that variation in FD was being driven largely by differences in alpha diversity, no matter what methodological choices were made. Second, we compared more distance measures than previously investigated (Petchey and Gaston 2007, Podani and Schmera 2007). We feel this is a more appropriate comparison as there are a large number of distance measures in the multivariate literature deemed to be appropriate. Additionally, when we restricted our analysis to comparing only Gower's distance and Euclidean distance (with PG dendrogram construction and UPGMA held constant), we found that rates of sensitivity remained high when

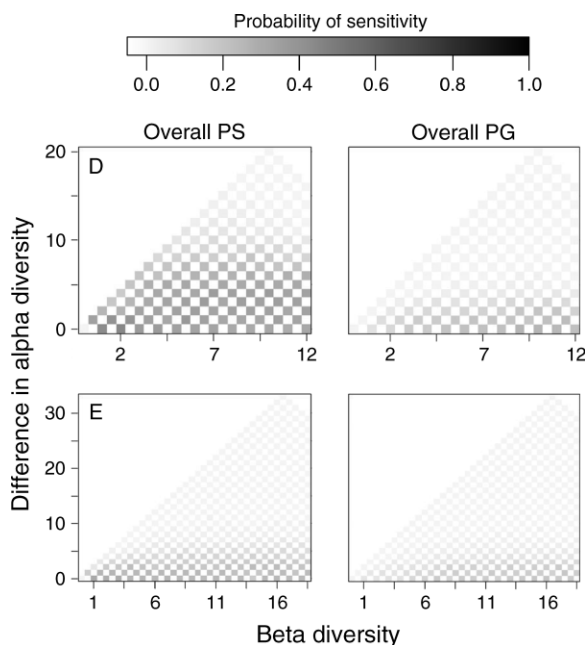


FIG. 3. The effect of alpha and beta diversity on the probability that FD is sensitive to dendrogram-construction methods for two communities crossed with two methods of FD calculation. Darker shading represents a higher probability of sensitivity. Data sources are as given in Table 1. For these communities, only Gower's distance could be calculated, and so only three construction methods could be compared, corresponding to the three clustering algorithms. Each column is for a different method of FD calculation. The first is for the PS method, and the second is for the PG method.

differences in alpha diversity were low (maximum probability of sensitivity: 0.260 for the bird data, 0.162 for the fish data, and 0.319 for the mammal data). Thus, FD did not provide much additional information in this case, beyond that provided by alpha diversity.

The preceding discussion leads to the following important conclusion regarding FD. FD is most sensitive to methodological choices when it genuinely provides new information beyond that provided by alpha diversity. This is because conditions under which FD is sensitive coincide with relatively little variation in alpha diversity between assemblages. Thus, in these cases FD could potentially provide useful information about the differences between the assemblages and ecosystem function. Unfortunately it is precisely in these cases, where FD would genuinely be useful, that it is expected to be highly sensitive to the choice of a distance measure or clustering algorithm. On the other hand, FD is not sensitive to methodological choices, in those cases when it provides very little information beyond that already provided by species richness (alpha diversity). This is because, when FD is insensitive, our results show that alpha diversity is largely redundant with FD no matter what methodological choices are made. Newer approaches to measuring functional richness (e.g., convex hull volume or consensus dendrograms) have

been proposed that may reduce the subjectivity of multivariate decisions (Cornwell et al. 2006, Mouchet et al. 2008, Villegger et al. 2008); however, decisions are still required that may alter results (e.g., trait scaling and transformations or what to include in the consensus). Further research into understanding these methodological choices will likely enhance our ability to measure functional richness. Here we wish to raise awareness about the importance of species richness and methodological choices for calculating functional richness, and identify cases for which sensitivity is likely to be an issue.

What can be done to minimize the impact of sensitivity? One simple approach could be to analyze data from ecological communities using several different construction methods to ensure that sensitivity is not an issue. However, if sensitivity is an issue, a decision must be made. Our results suggest potential approaches for reducing the probability of sensitivity. First, we found that probabilities of sensitivity were systematically lower for the PG (Pechey-Gaston) method of FD calculation than for the PS (Podani-Schmera) method. Therefore, one might be tempted to recommend the PG method for general use. There is an important issue with this recommendation however. The PG method assumes that the entire community is known, whereas the PS method does not. In a recent paper (Walker et al. 2008), we emphasized the importance of assuming that there may be species in the community that are undiscovered or undetected in the study area when estimating FD from field data. In some cases, this might not be a problem. For example, Barnett et al. (2007) have recently published a list of species to be used in studies of FD in zooplankton communities. However, in the vast majority of cases, there will typically be a high degree of uncertainty about the composition of the entire community. The PG method does not provide the same estimate as the PS method for a subset of the community. Given that the PS method provides the correct dendrogram length for that particular subset, as it is based on a distance matrix constructed from this subset, such differences between the methods remain a concern. Therefore, even though the PS method is more sensitive than the PG method, we recommend the PS method for general use and the PG method when the species list for the entire community is known.

Second, we found that FD is much more sensitive to the choice of a distance measure than to the choice of a clustering algorithm. Therefore, one might be tempted to simply adopt a particular distance measure as a standard. However, FD is not completely insensitive to the choice of clustering algorithm (e.g., range in maximum probability of sensitivity across communities: 0.137 to 0.260 for PG method and 0.248 to 0.364 for PS method). Furthermore, the choice of a distance measure must be made very carefully. We are skeptical that a single distance measure can be found that is justifiable in all situations; indeed, the history of multivariate statistics teaches us that there is no distance measure

that can be uniformly recommended in all cases (Sneath and Sokal 1973, Legendre and Legendre 1998).

To calculate functional richness, a method for quantifying inter-specific differences in functional traits is required. In cases where there is only one trait of interest, simple approaches such as the weighted-trait variation (FDVar; Mason et al. 2005) may be appropriate. However, the flexibility to use more than one trait is often required to understand even simple natural systems (Villegger et al. 2008). Unfortunately in these multivariate situations, complications arise as researchers have to make several key decisions during data analysis (e.g., choice of a distance measure, clustering algorithm, data transformations, scaling). Ideally, these decisions should have minimal impact on scientific conclusions. Here we demonstrate that, in the case of the popular index of functional richness, FD, decisions inherent in multivariate analyses can drastically alter conclusions of functional diversity and that sensitivity in FD is highest when differences in alpha diversity are low. These results suggest that, in cases where information captured by dendrogram-based functional diversity would be most useful, it is redundant with alpha diversity.

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#### APPENDIX

Derivation of Equation 1 (*Ecological Archives* E090-025-A1).