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# A distance-based framework for measuring functional diversity from multiple traits

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**Abstract.** A new framework for measuring functional diversity (FD) from multiple traits has recently been proposed. This framework was mostly limited to quantitative traits without missing values and to situations in which there are more species than traits, although the authors had suggested a way to extend their framework to other trait types. The main purpose of this note is to further develop this suggestion. We describe a highly flexible distance-based framework to measure different facets of FD in multidimensional trait space from any distance or dissimilarity measure, any number of traits, and from different trait types (i.e., quantitative, semi-quantitative, and qualitative). This new approach allows for missing trait values and the weighting of individual traits. We also present a new multidimensional FD index, called functional dispersion (FDis), which is closely related to Rao's quadratic entropy. FDis is the multivariate analogue of the weighted mean absolute deviation (MAD), in which the weights are species relative abundances. For unweighted presence-absence data, FDis can be used for a formal statistical test of differences in FD. We provide the "FD" R language package to easily implement our distance-based FD framework.

**Key words:** functional composition; functional dispersion; functional divergence; functional diversity; functional evenness; functional identity; functional richness; functional trait; multivariate dispersion.

## INTRODUCTION

Functional diversity (FD) is a key driver of ecosystem processes (Hooper et al. 2005), ecosystem resilience to environmental change (Folke et al. 2004), and ecosystem services (Diaz et al. 2007). This has led to the development of several indices for measuring FD (e.g., Petchey and Gaston 2002, Botta-Dukát 2005). Recently, Villéger et al. (2008) have proposed three multidimensional functional diversity (FD) indices for continuous functional traits, each exploring a different aspect of FD: functional richness (FRic), functional evenness (FEve), and functional divergence (FDiv). We fully agree with them that exploring different facets of FD in multidimensional trait space, as they proposed, offers a meaningful framework for measuring FD. That being said, their framework was mostly limited to quantitative traits without missing values and to situations where there are more species than traits, although they had suggested a way to extend their framework to other trait types. The main purpose of this note is to further develop this suggestion, highlighting its strengths and pitfalls.

First, we illustrate how the original framework of Villéger et al. (2008) can be generalized to a highly flexible distance-based framework to measure FD from any distance or dissimilarity measure, any number of traits (including more traits than species), and from different types of traits (i.e., quantitative, semi-quantitative, and/or qualitative), while tolerating missing trait values and allowing the weighting of individual traits. This is a significant improvement over their original framework, which could only deal with quantitative traits, did not allow the use of only one trait or of more traits than species, did not tolerate missing trait values, and did not directly allow the weighting of individual traits.

We also propose a new and intuitive multidimensional FD index, called functional dispersion (FDis), which presents several desirable properties. FDis is the mean distance in multidimensional trait space of individual species to the centroid of all species; it can account for species abundances by shifting the position of the centroid toward the more abundant species and weighting distances of individual species by their relative abundances. FDis is the multivariate analogue of the weighted mean absolute deviation (MAD); this makes the new index unaffected by species richness by construction.

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In order for our distance-based FD framework to be easily implemented, we have developed the “FD” R language package (*available online*)<sup>4</sup> for computing the FRic, FEve, and FDiv indices of Villéger et al. (2008) and our own FDis index under this framework, as well as three other FD indices: the community-level weighted means of trait values (CWM; Lavorel et al. 2008), Rao’s quadratic entropy (Rao 1982, Botta-Dukát 2005), and functional group richness (FGR) based on a posteriori functional classifications (Petchey and Gaston 2006). The flexibility of our distance-based FD framework and its easy implementation in the “FD” package should greatly facilitate the measurement of FD for a wide range of ecological applications.

#### GENERALIZATION TO A FLEXIBLE DISTANCE-BASED FUNCTIONAL DIVERSITY (FD) FRAMEWORK

Villéger et al. (2008) suggested that ordination should be used when there are more traits than species (a situation that cannot be handled by their functional richness [FRic] and functional divergence [FDiv] indices) or when qualitative traits are present. In particular, they proposed to use the principal coordinate analysis (PCoA) axes from a Gower dissimilarity matrix (Gower 1971) among the species as the new traits to compute their FD indices when there are qualitative traits in the original (species  $\times$  trait) matrix. We add that it is also useful when some traits are semi-quantitative, when missing trait values are present, and when individual traits need to be weighted differently, because the Gower dissimilarity index can handle all of these situations (Gower 1971, Legendre and Legendre 1998, Podani 1999).

That being said, Villéger et al. (2008) did not provide any details on how this approach should be implemented. We believe that this is needed in order to better highlight its strengths and pitfalls. This is especially relevant given that the situations already listed here (i.e., presence of qualitative and semi-quantitative traits, and/or missing values) are likely to be common in functional trait data sets. For example, about one-third of all plant functional traits from the standard list of Cornelissen et al. (2003) are qualitative or semi-quantitative.

The original FD framework of Villéger et al. (2008) can actually be generalized to a flexible distance-based FD framework in which (1) any appropriate distance measure of choice is computed from the (species  $\times$  trait) matrix, (2) this distance matrix is analyzed through PCoA, and (3) the resulting PCoA axes are used as the new traits to compute the FD indices. In that view, the original approach of Villéger et al. (2008) simply represents the particular case where all traits are quantitative and where the Euclidean distance is used.

To be fair to them, our distance-based framework is in line with what they proposed, i.e., to use the (standardized) traits directly to compute FD if all traits are quantitative, or to use the PCoA axes of a Gower dissimilarity matrix if some traits are qualitative (in the Gower dissimilarity, quantitative traits are ranged in the [0–1] interval instead of being standardized). We simply highlight that any distance measure can actually be used, not only the Euclidean distance or the Gower dissimilarity. Although we contend that one of these two measures (Euclidean and Gower) will be appropriate in many situations, other measures may be preferred for particular applications. For example, other dissimilarity measures can accommodate different types of variables and missing values (Estabrook and Rogers 1966, Pavoine et al. 2009).

Such a distance-based framework is not new for the analysis of ecological data. For example, the use of PCoA axes as variables has already been presented in the context of multivariate analysis of variance (Legendre and Anderson 1999) and general discriminant analysis (Anderson and Robinson 2003). This previous work has pointed out an important issue that needs to be considered when using that approach, but which Villéger et al. (2008) have not mentioned: what should we do if PCoA returns negative eigenvalues? Indeed, some distance matrices will not allow the distance relationships among the objects to be fully represented in a Euclidean space (Gower 1982). This problem can result from the use of a semimetric or nonmetric distance measure or from the presence of missing values (Legendre and Legendre 1998); it can even arise with most of the metric distance measures (Gower 1982). In all these cases, PCoA can return negative eigenvalues. The corresponding PCoA axes are not real, and therefore cannot be used as traits to compute FD. If one ignores these imaginary axes and uses only the ones with positive eigenvalues, not all the variation of the original trait data is represented, leading to biased estimates of FD.

Three correction methods are available (Legendre and Legendre 1998). The first two consist of adding the smallest possible constant to either the distances (Cailliez 1983) or the squared distances (Lingoes 1971, Gower and Legendre 1986) so that all negative eigenvalues are eliminated. The third one, which does not work for all coefficients, consists of taking the square root of the distances (see Legendre and Legendre 1998: Table 7.2). More details on these corrections methods can be found in Legendre and Anderson (1999).

Another potential pitfall regarding the use of PCoA axes as traits concerns the standardization of traits. Villéger et al. (2008) suggested standardizing traits in order to make them dimensionally homogeneous and to put equal weight to each trait in the estimation of FD.

<sup>4</sup> (<http://cran.r-project.org/web/packages/FD>)

This is a sensible suggestion given that we rarely know a priori if some traits are more important than others. As such, the R code that they provided (*available online*)<sup>5</sup> to compute their FD indices automatically standardizes each trait, without allowing the user to choose otherwise. However, it is crucial that the PCoA axes are not standardized prior to the estimation of FD. In a distance-based approach, if traits are to be standardized, this needs to be done prior to computing the (species  $\times$  species) distance matrix. PCoA axes are scaled to lengths equal to the square roots of their eigenvalues, or in other words to variances equal to the PCoA eigenvalues divided by  $(n - 1)$ : the first axis always represents the largest proportion of variation, while the additional axes represent progressively smaller amounts of variation. Therefore, standardizing the PCoA axes prior to the estimation of FD would give equal weight to each PCoA axis, which in turn would distort trait space, leading to incorrect estimates of FD. It would be unfair to blame Villéger et al. (2008) for this potential pitfall, as they never mentioned whether PCoA axes should be standardized or not when they are to be used as traits. However, we believe that their silence on the issue, coupled with the fact that their code automatically standardizes traits before computing their FD indices, could have led users to miscalculate FD. Our new “FD” package (*available online*; see footnote 4) avoids this potential pitfall.

#### WEIGHTING THE TRAITS

Villéger et al. (2008) have suggested standardizing all traits to mean 0 and unit variance to give the same weight to each trait in functional diversity (FD) estimation. As mentioned previously, this is justified by the fact that we rarely know a priori which traits are the most important. Nonetheless, weighting of individual traits can be a useful tool for FD estimation and has been identified as an important area for future FD research (Petchey and Gaston 2006). The Gower dissimilarity index can be programmed to provide different weightings to descriptors of mixed types, as suggested by Legendre and Legendre (1998). Our “FD” package (see footnote 4) includes the “gowdis” function to compute the Gower dissimilarity coefficient, with options to assign different weights to individual descriptors and to treat semi-quantitative variables as described by Podani (1999). This coefficient is the default used in the “dbFD” function of the “FD” package to measure FD under our distance-based framework when some traits are semi-quantitative and/or qualitative, or when weights are specified.

There is at least one obvious case where different weightings would be required for adequately estimating FD. When, for a given qualitative trait (e.g., for flowering plants, pollinator type), an individual species

can have more than one attribute (e.g., bees, flies, moths), this trait is typically reclassified into as many binary (0, 1) variables as there are individual attributes for that trait (e.g., bee pollinated, fly pollinated, moth pollinated). However, doing so artificially increases the weight given to that trait relative to other traits. A sensible solution is to give a weight  $w_i = x_i/b_i$  to each binary variable required to reclassify the trait, where  $x_i$  is the original weight given to trait  $i$ , and  $b_i$  is the number of binary variables required to re-code trait  $i$ .

#### FUNCTIONAL DISPERSION

One very intuitive measure of functional diversity (FD) for a community of  $S$  species on which  $T$  quantitative traits were measured is the dispersion (i.e., spread) of the  $S$  species in the  $T$ -dimensional space. In univariate statistics, dispersion can be estimated by measures such as the mean absolute deviation, the sum of squared deviations from the mean (SS), the variance, the standard deviation, or the range, among others. Villéger et al. (2008) proposed a valuable framework to explore distinct facets of FD, but only their functional richness (FRic) index can estimate the dispersion of species in trait space. It does so through the volume of the minimum convex hull that includes all species, which itself is a multivariate analogue of the range. Although FRic is clearly useful, it is well known that the range is not a reliable estimator of dispersion because it is highly sensitive to outliers. In addition, FRic cannot integrate information on relative abundances. Consequently, rare species with extreme trait values will greatly inflate FRic. This may or may not be a desirable property, depending on the application. On the other hand, the functional evenness (FEve) and functional divergence (FDiv) indices of Villéger et al. (2008) are interesting and can take into account the relative abundances of the species, but they do not estimate the dispersion of species in trait space. Indeed, they focus on the distribution of species within the convex hull independently of its actual volume (see Appendix A). Hence the development of a reliable estimate of functional dispersion that could also consider species relative abundances would be useful.

We suggest using multivariate dispersion (Anderson et al. 2006) as a multidimensional index of functional dispersion (FDis). In that view, FDis is the mean distance of individual species to the centroid of all species in the community (Fig. 1a). Details on how to compute multivariate dispersions in PCoA space from any distance or dissimilarity measure and how to correct for negative eigenvalues are given by Anderson (2006). FDis can account for relative abundances by computing the weighted centroid of the  $\mathbf{X} = [x_{ij}]$  (species  $\times$  trait) matrix in the following way:

$$\mathbf{c} = [c_i] = \frac{\sum a_j x_{ij}}{\sum a_j}$$

<sup>5</sup> (<http://www.ecolag.univ-montp2.fr/software>)



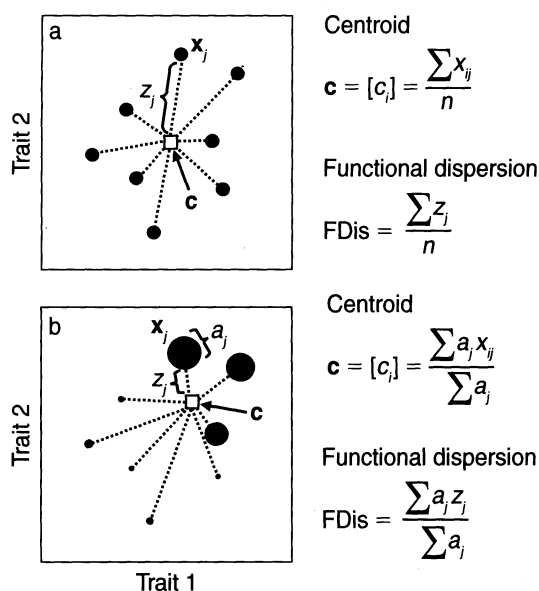


FIG. 1. An example showing how functional dispersion (FDis) is computed. The  $n$  individual species in a two-dimensional trait space are represented by black circles whose sizes are proportional to their abundances. Vector  $\mathbf{x}_j$  represents the position of species  $j$ , vector  $\mathbf{c}$  is the centroid of the  $n$  species (white square),  $z_j$  is the distance of species  $j$  to centroid  $\mathbf{c}$ , and  $a_j$  is the abundance of species  $j$ . In panel (a), all species have equal abundances (i.e., presence-absence data). In that case,  $\mathbf{c} = [c_i]$ , where  $c_i$  is the mean value of trait  $i$ , and FDis is the mean of distances  $z$  of individual species to  $\mathbf{c}$ . In panel (b), species have different abundances. In that case, the position of  $\mathbf{c}$  is weighted by the species relative abundances, such that it shifts toward the more abundant species. Individual distances  $z$  of species to  $\mathbf{c}$  are weighted by their relative abundances to compute FDis.

where  $\mathbf{c}$  is the weighted centroid in the  $i$ -dimensional space,  $a_j$  the abundance of species  $j$ , and  $x_{ij}$  the attribute of species  $j$  for trait  $i$  (Fig. 1b). This implies that traits are quantitative, but we described in the *Generalization to a flexible distance-based functional diversity (FD) framework* section how other trait types (i.e., semi-quantitative, qualitative) can be handled as well through principal coordinate analysis (PCoA). FDis, the weighted mean distance  $\bar{z}$  to the weighted centroid  $\mathbf{c}$ , is then computed as

$$\text{FDis} = \frac{\sum a_j z_j}{\sum a_j}$$

where  $a_j$  is the abundance of species  $j$  and  $z_j$  is the distance of species  $j$  to the weighted centroid  $\mathbf{c}$ .

These two modifications over Anderson's (2006) procedure essentially shift the position of the centroid toward the more abundant species and weigh distances of individual species to this weighted centroid by their relative abundances (Fig. 1b). When all species have equal abundances (i.e., presence-absence data; Fig. 1a), FDis is simply the unweighted mean distance to the

centroid as originally described by Anderson (2006). FDis has no upper limit and requires at least two species to be computed. For communities composed of only one species, we suggest that FDis should be 0.

We ran simulations to compare FDis to the FD indices of Villéger et al. (2008) and to Rao's quadratic entropy  $Q$  (Rao 1982, Botta-Dukát 2005, Ricotta 2005), a popular multidimensional FD index that is conceptually similar to FDis and can also account for species relative abundances. To do so, we created 20 000 artificial communities of 5–100 species drawn from a common pool of 500 species via the "simul.dbFD" function of our "FD" package. Values for three functional traits were generated following a normal distribution. Relative abundances were generated from a lognormal distribution. FDis was moderately positively related to FRic ( $r = 0.425$ , Fig. 2a) and FDiv ( $r = 0.475$ , Fig. 2b), and weakly with FEve ( $r = 0.214$ , Fig. 2c). On the other hand, FDis showed a strong positive linear relationship with Rao's  $Q$  ( $r = 0.966$ , Fig. 2d). Both FDis and Rao's  $Q$  were little influenced by species richness (FDis,  $r = 0.274$ , Fig. 2e; Rao's  $Q$ ,  $r = 0.264$ , Fig. 2f). For completeness, we repeated our simulations with presence-absence data (Appendix B). Results were very similar, with the exception that FDiv and FEve were less associated with FDis ( $r = 0.110$  and  $r = 0.131$ , respectively).

The strong positive correlation between FDis and Rao's  $Q$  was expected given that both indices aim at estimating the dispersion of species in trait space, weighted by their relative abundances. However, they do so differently. When abundances are frequencies (i.e., counts of individuals), Rao's  $Q$  expresses the mean distance between two randomly selected individuals (Botta-Dukát 2005). On the other hand, FDis is the weighted mean distance of individual species to their weighted centroid, where weights are their relative abundances (Fig. 1); this is the multivariate analogue of the weighted mean absolute deviation (MAD). Although both indices are clearly associated, one potential advantage of FDis over Rao's  $Q$  is that in the unweighted case (i.e., with presence-absence data), it opens possibilities for formal statistical tests for differences in FD between two or more communities through a distance-based test for homogeneity of multivariate dispersions (Anderson 2006), which itself is a multivariate extension of Levene's (1960) test on absolute deviations.

FDis is, by construction, unaffected by species richness, can be computed from any distance or dissimilarity measure (Anderson et al. 2006), can handle any number and type of traits (including more traits than species), is not strongly influenced by outliers, and can take into account species relative abundances. FDis also satisfies all criteria but the first one (i.e., to be constrained between 0 and 1 for convenience) of Mason et al. (2003) if traits are standardized prior to its computation (see Appendix C). FDis does not satisfy

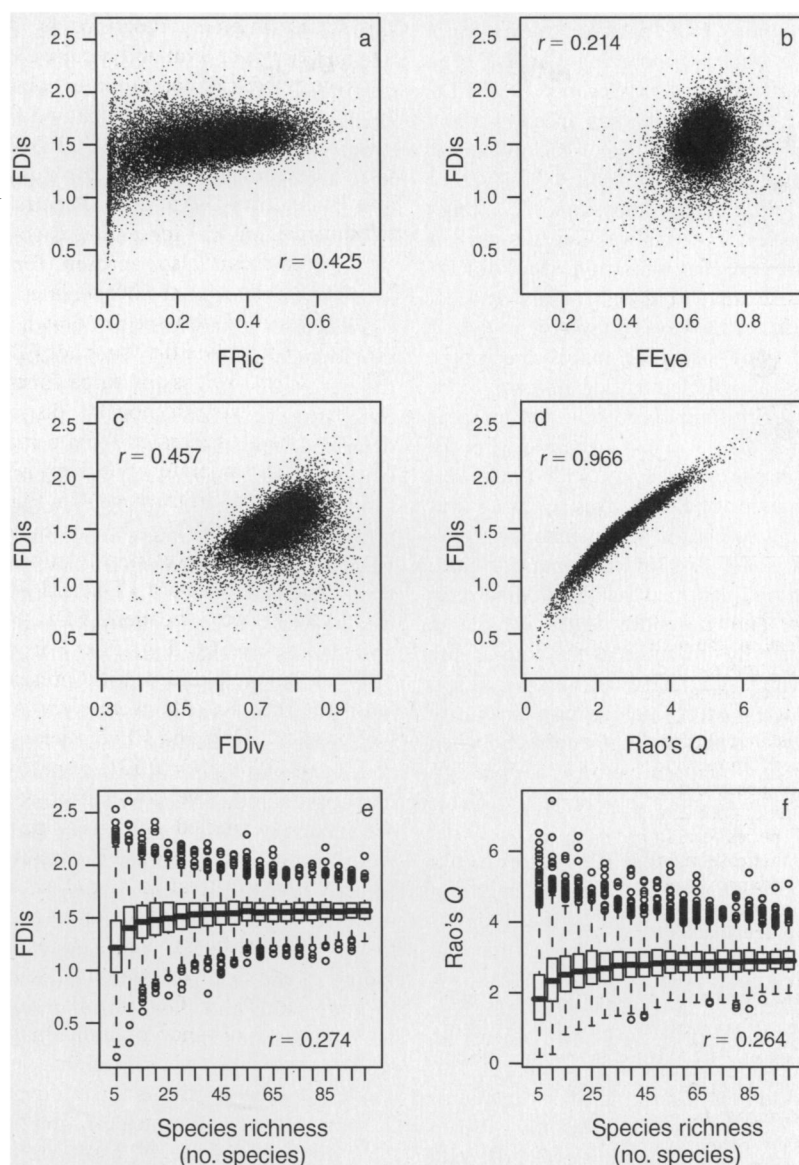


FIG. 2. Simulation results (20 000 communities) showing (a) the relationships between FRic and FDis, (b) FDiv and FDis, (c) FEve and FDis, (d) Rao's  $Q$  and FDis, (e) species richness and FDis, and (f) species richness and Rao's  $Q$ .

the set monotonicity criterion (i.e., a subset of a community should be no more diverse than the whole community) of Ricotta (2005) because removing species that are close to the centroid effectively increases the dispersion of species in trait space. This represents an interesting ecological signal, not a methodological artifact. In our simulations (Fig. 2), FDis satisfied the set concavity criterion of Ricotta (2005), since the total  $\gamma$  diversity of the pooled set of communities was greater ( $FDis_{\gamma} = 1.584$ ) than the mean  $\alpha$ -diversity of all communities ( $FDis_{\alpha} = 1.519$ ). Further investigation is required to confirm whether this property can be generalized.

#### BRIDGING THE GAP BETWEEN THEORY AND PRACTICE

For a functional diversity (FD) framework to be most useful it has to be easily implemented by ecologists, if possible with freely available software. As such, we applaud the efforts made by Villéger et al. (2008) to provide the code to compute their FD indices in the freely available R language environment (R Development Core Team 2009). Likewise, we provide the "FD" R package (see footnote 4) to easily implement our distance-based FD framework. Our "FD" package includes numerous elements of flexibility (see Appendix D). First, whereas the "F\_RED" function of Villéger et al. (2008) only allowed quantitative traits to be used, the

“dbFD” function of our “FD” package allows for a wide range of input options, including the use of a (species  $\times$  species) distance matrix. Second, “F<sub>RED</sub>” did not allow the use of more traits than species for any of the three FD indices it returned. For FRic and FDiv, this was supported by the fact that no convex hull can be computed when there are more dimensions (i.e., traits) than points (i.e., species), but this was unnecessary for FEve, which does not have that limitation. Our “dbFD” function can deal with any number of traits. Indeed, more traits than species can always be used for FDis and FEve. For FRic and FDiv, when the goal is to compare several communities, this problem is elegantly solved by selecting a subset of principal coordinate analysis (PCoA) axes such that  $T = S_{\min} - 1$ , where  $S_{\min}$  is the number of species in the community with the fewest species and  $T$  the number of PCoA axes to be used as traits. However, doing so entails dimensionality reduction, which implies some loss of information. Such information loss can be quantified via the  $R^2$ -like ratio in PCoA (Legendre and Legendre 1998). Third, in “dbFD,” FRic is generally measured as the convex hull volume, but when there is only one quantitative trait it is measured as the range. For a single semi-quantitative trait, FRic is the range of the ranks. Conversely, when only qualitative and semi-quantitative traits are present, FRic is measured as the number of unique trait-value combinations in a community.

We added other multidimensional FD indices in our “FD” package. The community-level weighted means of trait values (CWM) is a direct extension of the “biomass ratio hypothesis” (Grime 1998) and represents functional composition (sometimes called functional identity). Because functional composition has been shown to be a key driver of ecosystem processes (e.g., Mokany et al. 2008), we felt that the inclusion of CWM was important. CWM can be multidimensional, as it is a vector containing as many elements as there are traits. When the goal is to compare several communities, PCoA axes could be computed from the CWM data, using an appropriate distance measure, and these axes could be used as an index of functional composition. As previously mentioned, correction for negative eigenvalues may be necessary. Multivariate analyses could then be used to compare functional composition between groups of communities (e.g., Legendre and Anderson 1999) or to carry out spatial analysis of functional diversity (Legendre et al. 2005). As far as we know, CWM has been used strictly for quantitative traits, but our “FD” package extends it to qualitative and semi-quantitative traits. Another addition is functional group richness (FGR), which is computed from an a posteriori classification of species based on their functional traits (i.e., the “data-defined” approach of Gitay and Noble [1997]). This differs from commonly used a priori classifications such as  $C_4$  grasses,  $C_3$  grasses, or legumes

(e.g., Tilman et al. 1997), which generally follow a “deductive approach” (Gitay and Noble 1997). FGR computed from a priori functional classifications has been shown to be a poor predictor of ecosystem processes (Wright et al. 2006, Mokany et al. 2008), yet it is unclear whether this also applies to a posteriori classifications. It may turn out to be so, in which case FGR could still be useful for descriptive purposes.

#### CONCLUSION

Villéger et al. (2008) have set the stage well for the development of a multidimensional and multifaceted framework for functional ecology. The purpose of this note was to improve their framework. First, we described how the approach of Villéger et al. (2008) could be generalized to a flexible distance-based functional diversity (FD) framework. Second, we presented a new FD index, functional dispersion (FDis). FDis is the weighted mean distance in multidimensional trait space of individual species to the weighted centroid of all species, where weights correspond to the relative abundances of the species. Finally, we provided the “FD” R language package (see footnote 4) to easily implement our distance-based FD framework. We believe that our distance-based FD framework and our code represent significant improvements over the original approach described by Villéger et al. (2008), yet we see it simply as a second step and believe that our contribution can certainly be improved upon in the future. We will welcome suggestions to make our distance-based FD framework, and its implementation in our “FD” package, even more useful and flexible. Doing so will help in increasing the ability of ecologists to understand and predict the functional consequences of human-induced changes in biodiversity, a major contemporary goal for ecology.

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#### LITERATURE CITED

- Anderson, M. J. 2006. Distance-based tests for homogeneity of multivariate dispersions. *Biometrics* 62:245–253.
- Anderson, M. J., K. E. Ellingsen, and B. H. McArdle. 2006. Multivariate dispersion as a measure of beta diversity. *Ecology Letters* 9:683–693.
- Anderson, M. J., and J. Robinson. 2003. Generalised discriminant analysis based on distances. *Australian and New Zealand Journal of Statistics* 45:301–318.
- Botta-Dukát, Z. 2005. Rao’s quadratic entropy as a measure of functional diversity based on multiple traits. *Journal of Vegetation Science* 16:533–540.
- Cailliez, F. 1983. The analytical solution of the additive constant problem. *Psychometrika* 48:305–310.



- Cornelissen, J. H. C., S. Lavorel, E. Garnier, S. Díaz, N. Buchmann, D. E. Gurvich, P. B. Reich, H. ter Steege, H. D. Morgan, M. G. A. van der Heijden, J. G. Pausas, and H. Poorter. 2003. A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Australian Journal of Botany* 51:335–380.
- Díaz, S., S. Lavorel, F. de Bello, F. Quétier, K. Grigulis, and T. M. Robson. 2007. Incorporating plant functional diversity effects in ecosystem service assessments. *Proceedings of the National Academy of Sciences (USA)* 104:20684–20689.
- Estabrook, G. F., and D. J. Rogers. 1966. A general method of taxonomic description for a computed similarity measure. *BioScience* 16:789–793.
- Folke, C., S. Carpenter, B. Walker, M. Scheffer, T. Elmqvist, L. Gunderson, and C. S. Holling. 2004. Regime shifts, resilience, and biodiversity in ecosystem management. *Annual Review of Ecology, Evolution, and Systematics* 35:557–581.
- Gitay, H., and I. R. Noble. 1997. What are functional types and how should we seek them? Pages 3–19 in T. M. Smith, H. H. Shugart, and F. I. Woodward, editors. *Plant functional types: their relevance to ecosystem properties and global change*. Cambridge University Press, Cambridge, UK.
- Gower, J. C. 1971. A general coefficient of similarity and some of its properties. *Biometrics* 27:857–871.
- Gower, J. C. 1982. Euclidean distance geometry. *Mathematical Scientist* 7:1–14.
- Gower, J. C., and P. Legendre. 1986. Metric and Euclidean properties of dissimilarity coefficients. *Journal of Classification* 3:5–48.
- Grime, J. P. 1998. Benefits of plant diversity to ecosystems: immediate, filter and founder effects. *Journal of Ecology* 86: 902–910.
- Hooper, D. U., et al. 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs* 75:3–35.
- Lavorel, S., K. Grigulis, S. McIntyre, N. S. G. Williams, D. Garden, J. Dorrough, S. Berman, F. Quétier, A. Thébault, and A. Bonis. 2008. Assessing functional diversity in the field—methodology matters! *Functional Ecology* 22:134–147.
- Legendre, P., and M. J. Anderson. 1999. Distance-based redundancy analysis: testing multispecies responses in multifactorial ecological experiments. *Ecological Monographs* 69:1–24.
- Legendre, P., D. Borcard, and P. Peres-Neto. 2005. Analyzing beta diversity: partitioning the spatial variation of community composition data. *Ecological Monographs* 75:435–450.
- Legendre, P., and L. Legendre. 1998. *Numerical ecology*. Second English edition. Elsevier Science, Amsterdam, The Netherlands.
- Levene, H. 1960. Robust tests for equality of variances. Pages 278–292 in S. G. Olkin, W. Hoeffding, W. G. Madow, and H. B. Mann, editors. *Contributions to probability and statistics*. Stanford University Press, California, USA.
- Lingoes, J. C. 1971. Some boundary conditions for a monotone analysis of symmetric matrices. *Psychometrika* 36:195–203.
- Mason, N. W. H., K. MacGillivray, J. B. Steel, and J. B. Wilson. 2003. An index of functional diversity. *Journal of Vegetation Science* 14:571–578.
- Mokany, K., J. Ash, and S. Roxburgh. 2008. Functional identity is more important than diversity in influencing ecosystem processes in a temperate native grassland. *Journal of Ecology* 96:884–893.
- Pavoine, S., J. Vallet, A. Dufour, S. Gachet, and H. Daniel. 2009. On the challenge of treating various types of variables: application for improving the measurement of functional diversity. *Oikos* 118:391–402.
- Petchey, O. L., and K. J. Gaston. 2002. Functional diversity (FD), species richness and community composition. *Ecology Letters* 5:402–411.
- Petchey, O. L., and K. J. Gaston. 2006. Functional diversity: back to basics and looking forward. *Ecology Letters* 9:741–758.
- Podani, J. 1999. Extending Gower's general coefficient of similarity to ordinal characters. *Taxon* 48:331–340.
- R Development Core Team. 2009. *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. (<http://www.R-project.org>)
- Rao, C. R. 1982. Diversity and dissimilarity coefficients—a unified approach. *Theoretical Population Biology* 21:24–43.
- Ricotta, C. 2005. A note on functional diversity measures. *Basic and Applied Ecology* 6:479–486.
- Tilman, D., J. Knops, D. Wedin, P. Reich, M. Ritchie, and E. Siemann. 1997. The influence of functional diversity and composition on ecosystem processes. *Science* 277:1300–1302.
- Villéger, S., N. W. H. Mason, and D. Mouillot. 2008. New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology* 89:2290–2301.
- Wright, J. P., S. Naeem, A. Hector, C. Lehman, P. B. Reich, B. Schmid, and D. Tilman. 2006. Conventional functional classification schemes underestimate the relationship with ecosystem functioning. *Ecology Letters* 9:111–120.

#### APPENDIX A

A figure showing that FDiv and FEve do not estimate functional dispersion (*Ecological Archives* E091-022-A1).

#### APPENDIX B

Simulation results with presence-absence data (*Ecological Archives* E091-022-A2).

#### APPENDIX C

A list of criteria for functional diversity indices tested on FDis (*Ecological Archives* E091-022-A3).

#### APPENDIX D

A table listing the main features of the “dbFD” function (*Ecological Archives* E091-022-A4).