NEW MULTIDIMENSIONAL FUNCTIONAL DIVERSITY INDICES FOR A MULTIFACETED FRAMEWORK IN FUNCTIONAL ECOLOGY

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Abstract. Functional diversity is increasingly identified as an important driver of ecosystem functioning. Various indices have been proposed to measure the functional diversity of a community, but there is still no consensus on which are most suitable. Indeed, none of the existing indices meets all the criteria required for general use. The main criteria are that they must be designed to deal with several traits, take into account abundances, and measure all the facets of functional diversity. Here we propose three indices to quantify each facet of functional diversity for a community with species distributed in a multidimensional functional space: functional richness (volume of the functional space occupied by the community), functional evenness (regularity of the distribution of abundance in this volume), and functional divergence (divergence in the distribution of abundance in this volume). Functional richness is estimated using the existing convex hull volume index. The new functional evenness index is based on the minimum spanning tree which links all the species in the multidimensional functional space. Then this new index quantifies the regularity with which species abundances are distributed along the spanning tree. Functional divergence is measured using a novel index which quantifies how species diverge in their distances (weighted by their abundance) from the center of gravity in the functional space. We show that none of the indices meets all the criteria required for a functional diversity index, but instead we show that the set of three complementary indices meets these criteria. Through simulations of artificial data sets, we demonstrate that functional divergence and functional evenness are independent of species richness and that the three functional diversity indices are independent of each other. Overall, our study suggests that decomposition of functional diversity into its three primary components provides a meaningful framework for its quantification and for the classification of existing functional diversity indices. This decomposition has the potential to shed light on the role of biodiversity on ecosystem functioning and on the influence of biotic and abiotic filters on the structure of species communities. Finally, we propose a general framework for applying these three functional diversity indices.

Key words: competitive filtering; environmental filtering; functional divergence; functional evenness; functional niche; functional richness; functional traits; null model.

INTRODUCTION

The functional diversity of a community has emerged as a facet of biodiversity quantifying the value and range of organismal traits that influence their performance and thus ecosystem functioning (Diaz and Cabido 2001). There is an increasing body of literature demonstrating 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). However, most of this work has used functional-group richness as a surrogate for functional diversity.

Gathering species into groups results in the loss of information and the imposition of a discrete structure on functional differences between species, which are usually continuous (Gitay and Noble 1997, Fonseca and Ganade 2001). Further, most studies using functional groups ignore species abundances, and some species may have a much greater impact on ecosystem functioning because of their greater abundance (Diaz and Cabido 2001). Finally, a functional-group approach may produce different conclusions on the importance of functional diversity for ecosystem functioning depending on the classification method employed (Wright et al. 2006). Thus, there is an urgent need to provide continuous measures of functional diversity that directly use quantitative values for functional traits.

Since 1999, many indices of functional diversity have been published (reviewed in Petchey and Gaston 2006). These indices include a priori classifications (number of functional groups), the sum (FAD; Walker et al. 1999) or

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average (quadratic entropy; Botta-Dukat 2005) of functional distances between species pairs in multivariate functional trait space, distances between species along hierarchical classifications (FD; Petchey and Gaston 2002), and the distribution of abundance along functional trait axes (FDvar; Mason et al. 2003). However, despite the number and variety of these indices, no consensus has arisen on the sensitive question of how to measure functional diversity (Petchey and Gaston 2006). Existing indices have four main limitations:

1) None but FDvar (Mason et al. 2003), the functional regularity index (FRO) of Mouillot et al. (2005), and quadratic entropy (Botta-Dukát 2005) take into account the relative abundance of species. However, as suggested by Grime (1998), the effect of each species has to be weighted according to its abundance in order to reflect its contribution to ecosystem functioning.

2) Some indices are only designed for single-trait approaches (Mason et al. 2005) and as such may give an incomplete image of functional diversity when many traits are used to characterize species functional niches.

3) Some indices are trivially related to species richness, especially the FAD of Walker et al. (1999), where the addition of a new species that is completely identical functionally to another one already in the community causes an augmentation of functional diversity.

4) While indices based on sum of lengths on hierarchical classifications do not take account of abundances, they may deal with many traits simultaneously and are not trivially related to species richness (e.g., the FD index of Petchey and Gaston 2002). Nevertheless, building a classification from the matrix of distances between species pairs leads to a loss of information and modifies the initial interspecific functional distances (as demonstrated by Podani and Schmera [2006]). In other words, a species classification cannot match exactly the relative position of species in a multidimensional functional trait space, and the arbitrary choices in the way of constructing classifications may drastically influence the functional diversity estimation (Podani and Schmera [2007]; but see Petchey and Gaston [2007]).

Recently, Mason et al. (2005) argued that functional diversity cannot be summarized by a single number. Instead they proposed a framework where functional diversity is composed of three independent components—functional richness, functional evenness, and functional divergence—which need to be quantified separately. The interest of splitting functional diversity into three independent components is to provide more detail in examining the mechanisms linking biodiversity to ecosystem functioning. For example, Mason et al. (2008) demonstrated how the primary functional diversity components could be used in combination to test competing hypotheses for species–energy relationships. Moreover, the search for the effects of biotic interactions and environmental filters on biodiversity patterns may benefit from the proposition of such independent

"facets" of functional diversity, since variation in the volume of functional-trait space filled by species does not have the same meaning as a shift in the distribution of abundance within that space. The former may indicate an increasing pressure of environmental filters (Cornwell et al. 2006), while the latter may reveal a shift in the intensity of competitive interactions (Mason et al. 2007, 2008).

However, the indices proposed by Mason et al. (2005) are estimated based on single traits and are not directly transposable for multiple-trait approaches. Here we aim to estimate the three primary components of functional diversity using one existing and two novel indices that are specifically designed to incorporate multiple functional traits. These indices directly measure the distribution of species in multivariate functional trait space and are independent of species richness and each other. We present these indices as general tools for quantifying the functional diversity of any community and propose a practical framework for their application. This framework is based on the use of null models to allow comparison of communities from different species pools and with different species richness. It is hoped this framework will aid in exploring biodiversity–environment–ecosystem functioning relationships in ecology, as well as elucidating processes of community assembly (e.g., Mason et al. 2008).

MULTIDIMENSIONAL FUNCTIONAL DIVERSITY INDICES

As proposed by Keddy (1992), functional ecologists generally have, for their communities of interest, a matrix with values for selected functional traits for each species. From a geometrical point of view, a species' functional niche may be described by its position in a functional-trait space (Rosenfeld 2002). Assuming that we have T functional-trait values for each species of a given community, the functional-niche space is then the T dimensional space defined by the T axes, each one corresponding to a trait.

We suggest standardizing trait values (mean of 0 and unit variance) so that each trait has the same weight in functional diversity estimation and the units used to measure traits have no influence. The community studied is composed of S species. Any species i has T traits of standardized values ($x_{i1}, x_{i2}, \ldots, x_{iT}$) which are conceived as coordinates in the functional trait space.

When plotting all the S species in a multi-trait space, functional diversity is simply the distribution of species and their abundances in this functional space (Fig. 1a, circles represent species, and diameters are species relative abundances). The indices presented here aim at describing how much space is filled and how the abundance of a community is distributed within this functional space. In the following paragraphs we will keep this general framework of S species plotted in a T dimensional space.

Relative abundances of species are noted ($w_1, w_2, \ldots w_S$), with $\Sigma_{i=1}^{S} w_i = 1$.
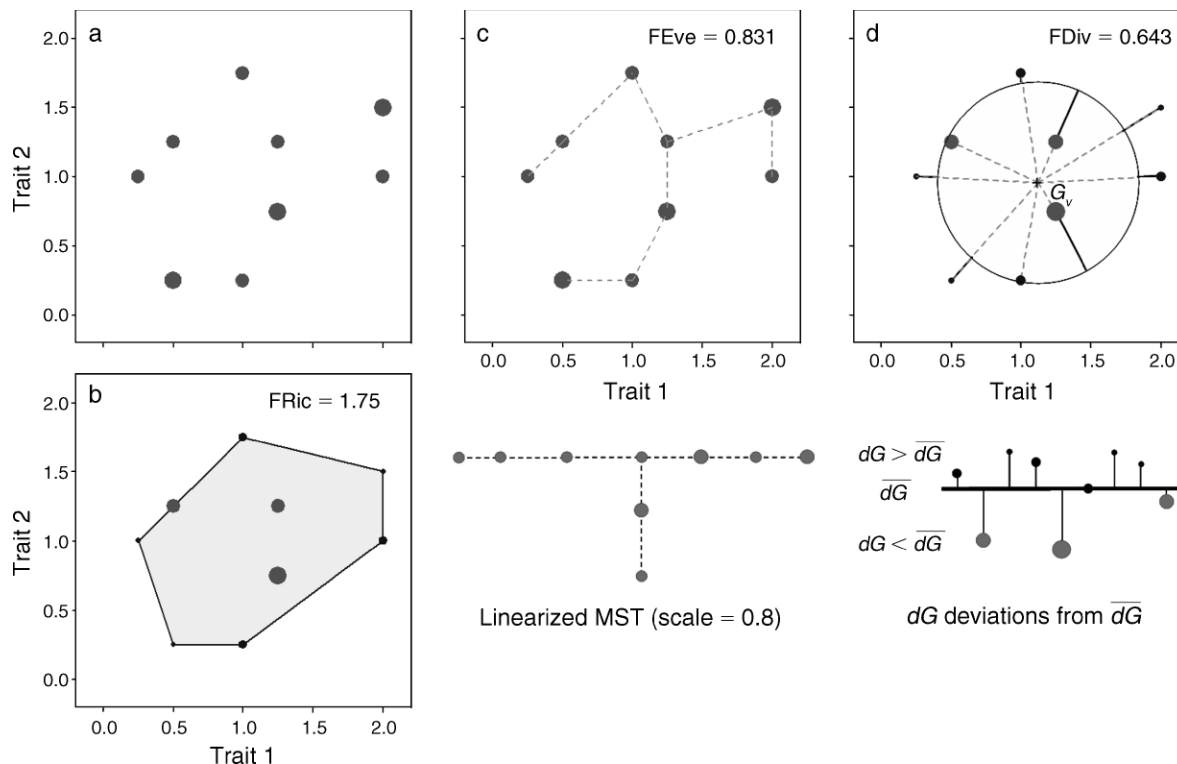
Fig. 1. Estimation of the three functional diversity indices in multidimensional functional space. For simplification, only two traits and nine species are considered. (a) The points are plotted in the space according to the trait values of the corresponding species. Circle diameters are proportional to species abundances. In (b), the convex hull is drawn with a solid black line; the points corresponding to the vertices are black, and the convex hull volume is shaded in gray. The functional richness (FRic) corresponds to this volume. (c) The minimum spanning tree (MST, dashed line) links the points. Functional evenness (FEve) measures the regularity of points along this tree and the regularity in their abundances. For convenience, the tree is plotted stretched under the panel. (d) The position of the center of gravity of the vertices ("G_V," black cross), the distances between it and the points representing the species (gray dashed lines), and the mean distance to the center of gravity (large circle with the black line border). The deviation of the distances from the mean corresponds to the length of the black line linking each point and the large circle with the black line border. This distribution is also represented under the panel. The more the high abundances are greater than the mean, the higher the functional divergence (FDiv).

Following Grime (1998), who underlined the biomass ratio effect, we suggest that good sets of functional diversity indices have to take into account biomass, or at least another estimation of abundance (e.g., number of individuals, percent cover, or density). Indeed, biomass is directly linked to the amount of energy and resources assimilated within a species. Hence, we prefer this measure of abundance even if the indices may incorporate any measure of abundance, since they are based on relative abundances, which are by definition unitless. All of our indices are also suitable for presence/absence data, which is actually a particular case where each species has a relative abundance of $1/S$. We will give a brief description of each primary functional diversity component and outline the indices we propose for their measurement in multivariate functional trait space.

Functional richness

Functional richness represents the amount of functional space filled by the community. For a single-trait approach, the functional richness may be estimated as the difference between the maximum and minimum functional values present in the community (Mason et al. 2005). For multiple-trait studies, functional richness is more challenging to measure, as the index has to estimate the volume filled in the T dimensional space by the community of interest. Recently, Cornwell et al. (2006) proposed the convex hull volume as a measure of the functional space occupied by a community. The convex hull is actually the minimum convex hull which includes all the species considered; the convex hull volume is then the volume inside this hull (Fig. 1b).

Thus, if two species a and b are inside the convex hull volume, whose coordinates (i.e., traits values) are respectively $(x_{a1}, x_{a2}, \ldots x_{aT})$ and $(x_{b1}, x_{b2}, \ldots, x_{bT})$, then any hypothetical species with coordinates $(Kx_{a1} + (1 - K)x_{b1}, Kx_{a2} + (1 - K)x_{b2}, \ldots, Kx_{aT} + (1 - K)x_{bT})$ for $0 \leq K \leq 1$ is also in the convex hull volume. This measure of space occupancy corresponds to a multivariate range. Any species whose trait values are less extreme for all traits than those of the two existing species will be included inside the convex hull volume.

Basically, the convex hull volume algorithm determines the most extreme points (hereafter named vertices, the black circles on Fig. 1b), links them to build the convex hull (lines on Fig. 1b), and finally calculates the volume inside. Therefore, we propose to use the value of the convex hull volume filled by a community as a multidimensional measure of the functional richness (Cornwell et al. 2006, Layman et al. 2007).

We suggest computing the convex hull volume with the Quickhull algorithm (Barber et al. 1996). The number of species must be higher than the number of traits ($S > T$), and the species must not be distributed in a line (in which case the hull volume is zero). The program returns the volume and the identity of the species forming the vertices.

Functional evenness

Functional evenness describes the evenness of abundance distribution in a functional trait space (Mason et al. 2005). The functional regularity index (FRO) has been proposed for the estimation of functional evenness when using a single trait (Mouillot et al. 2005). This index measures both the regularity of spacing between species along a functional trait gradient and evenness in the distribution of abundance across species. FRO takes a value of 1 when the distances between all nearest neighbor species pairs are identical and when all species have the same abundance. Conversely, FRO will approach 0 when some species are tightly packed along the functional axis, with a high proportion of abundance concentrated within a narrow part of the functional-trait gradient. It has the advantage of being independent from species richness, functional richness, and functional divergence. While an extension to multiple trait studies has been proposed for FRO (Mouillot et al. 2005), this method is dependent on ordination techniques and consequently risks the loss of information, especially for traits that are weakly correlated with other traits.

In order to transform species distribution in a T-dimensional functional space to a distribution on a single axis, we choose to use the minimum spanning tree (noted MST hereafter). The MST is the tree that links all the points contained in a T-dimensional space with the minimum sum of branch lengths (Fig. 1d). We compute the MST thanks to the "ape" R-package, which returns the $S - 1$ branches between the S species. By direct analogy to Mouillot et al. (2005), our new functional evenness index measures both the regularity of branch lengths in the MST and evenness in species abundances. As a first step, for each branch l of the MST (dashed line on Fig. 1d), the length is divided by the sum of the abundances of the two species linked by the branch

$$EW_l = \frac{\text{dist}(i,j)}{w_i + w_j}$$

where EW is weighted evenness, dist(i, j) is the Euclidean distance between species i and j, the species

involved is branch l, and w_i is the relative abundance of species i.

Then, for each of these branches, the value of EW_l is divided by the sum of EW values for the MST to obtain the partial weighted evenness (PEW), defined as

$$PEW_l = \frac{EW_l}{\sum_{l=1}^{S-1} EW_l}.$$

In the case of perfect regularity of abundance distribution along the MST, all EW_l will be equal and all PEW_l values will be $1/(S - 1)$. Conversely, when PEW_l values differ among branches, the final index must decrease. To this aim we compared PEW_l values to $1/(S - 1)$. Finally, our functional evenness index is

$$FEve = \frac{\sum_{l=1}^{S-1} \min\left(PEW_l, \frac{1}{S-1}\right) - \frac{1}{S-1}}{1 - \frac{1}{S-1}}.$$

The term $1/(S - 1)$ is subtracted from the numerator and denominator because there is at least one value of PEW_l which is less than or equal to $1/(S - 1)$ whatever S is (see Bulla [1994] for more details about this standardization). Therefore, FEve is not biased by species richness and is constrained between 0 and 1. We obtain 1 when all PEW_l are equal to $1/(S - 1)$. FEve is also independent of the convex hull volume, as it is unitless. We need at least three species to define an MST and then estimate FEve.

Basically, the new index quantifies the regularity with which the functional space is filled by species, weighted by their abundance. FEve decreases either when abundance is less evenly distributed among species or when functional distances among species are less regular (Fig. 2).

Functional divergence

For a single-trait approach, functional divergence represents how abundance is spread along a functional trait axis, within the range occupied by the community (Mason et al. 2005). For instance, divergence is low when the most abundant species have functional traits that are close to the center of the functional trait range. Conversely, when the most abundant species have extreme functional trait values, then divergence is high. In a multivariate context, functional divergence relates to how abundance is distributed within the volume of functional trait space occupied by species (Fig. 1c).

One complication is finding a method to measure functional divergence that is independent of the volume of functional trait space occupied and the evenness of abundance distribution with that volume. Here we present a novel index to achieve this. Firstly, the coordinates of the center of gravity G_V (g_1, g_2, ... g_T) of the V species forming the vertices of the convex hull are calculated as follows:
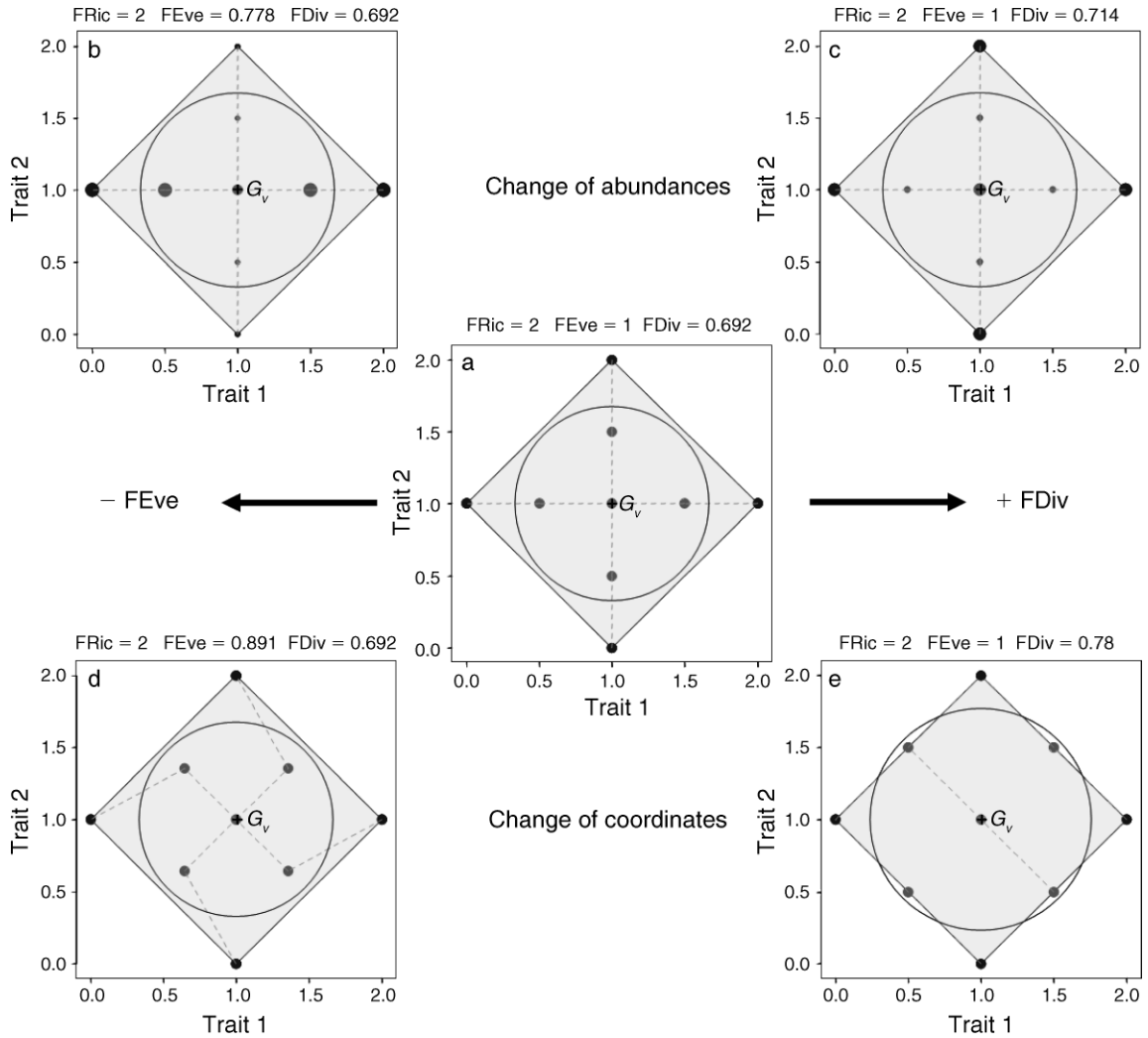
FIG. 2. The center panel (a) is the reference showing that there are nine species and two traits. The figure shows the effect of changes in (d, e) the identities of species and (b, c) their relative abundance on functional divergence (FDiv) and functional evenness (FEve). The key to symbols and lines is the same as for Fig. 1. For simplicity, the coordinates of the extreme points are the same for all the figures, as are functional richness values (FRic) and the shape of the convex hull.

$$g_k = \frac{1}{V} \sum_{i=1}^{V} x_{ik}$$

where x_{ik} is the coordinate of species i on trait k [1, T].

Second, for each of the S species, we calculate the Euclidean distance to this center of gravity:

$$dG_i = \sqrt{\sum_{k=1}^{T} (x_{ik} - g_k)^2}.$$

The mean distance of the S species to the center of gravity ($\overline{dG}$) is then calculated:

$$\overline{dG} = \frac{1}{S} \sum_{i=1}^{S} dG_i.$$

It is important to note that the coordinates of the center of gravity are calculated only on vertices coordinates without taking into account relative abundances; this implies that dG_i and thus $\overline{dG}$ values are only influenced by the shape and the volume of the scatter plot of the S species (Fig. 2).

Then, the sum of abundance-weighted deviances (Δd) and absolute abundance-weighted deviances ($\Delta|d|$) for distances from the center of gravity are calculated across the species:

$$\Delta d = \sum_{i=1}^{S} w_i \times (dG_i - \overline{dG})$$

and

Table 1. Summary of the criteria of Mason et al. (2003) and Ricotta (2005) and properties of our three indices (FRic for functional richness, FDiv for functional divergence, and FEve for functional evenness) for these criteria.

Criteria	FRic	FEve	FDiv
Positive values†	yes	yes	yes
Be constrained to a 0–1 range (for convenience) and use that range well‡		yes	yes
Be unaffected by the units in which the abundance is measured†	yes	yes	yes
Reflect the contribution of each species in proportion to its abundance†		yes	yes
Be unaffected by the units in which the character is measured†		yes	yes
Reflect the range of character values present†	yes		
Be unaffected by the number of species†		yes	yes
Be unaffected when a species is split in two species with the same traits values and the same total abundance†	yes		yes
Set monotonicity (a subset of a community is less diverse that this community)‡	yes		
Concavity (a set of communities is in mean less diverse than the aggregated pool)‡	yes		

Note: Empty cells did not meet the criteria of that particular index.
† These criteria are from Ricotta (2005).
‡ These criteria are from Mason et al. (2003).

$$\Delta|d| = \sum_{i=1}^{S} w_i \times |dG_i - \overline{dG}|.$$

Functional divergence may then be calculated as

$$\text{FDiv} = \frac{\Delta d + \overline{dG}}{\Delta|d| + \overline{dG}}.$$

Values of dG_i are Euclidean distances and thus are positive or null, hence Δd is bounded between $\overline{dG}$ and $\Delta|d|$. Therefore, addition of $\overline{dG}$ to the numerator and denominator ensures that the index ranges between 0 and 1. The index approaches 0 when highly abundant species are very close to the center of gravity relative to rare species (Δd is negative and tends to $-\overline{dG}$), and it approaches unity when highly abundant species are very distant from the center of gravity relative to rare species (Δd is positive and tends to $\Delta|d|$; see Fig. 2 for illustration).

For presence/absence data, functional divergence is the highest if all the species are on the convex hull and at equal distance to its center of gravity (i.e., if the center of gravity of the convex hull is also a center of symmetry of the functional space). This condition is actually true whatever the relative abundances of species.

Given that the distances considered in the formula are those from the center of gravity of the vertices, functional divergence is a priori independent from the shape and the volume of the convex hull and so from the functional richness index. A script (R statistical language [R development Core Team 2007]) to compute the three indices is *available online*.[4]

ASSESSING THE VALIDITY OF THE INDICES

Some authors have proposed criteria that functional diversity indices have to match (Mason et al. 2003, Ricotta et al. 2005, Petchey and Gaston 2006). From these published criteria we selected 10 that appear relevant for a multidimensional approach (and which

[4] ⟨http://www.ecolag.univ-montp2.fr/software/⟩

are not contradictory). We do not expect that each of our three indices matches each criterion but rather that the ensemble of indices does (Table 1).

First, our three indices are positive, and the higher they are, the higher the component of functional diversity they quantify is. Functional divergence (FDiv) and functional evenness (FEve) are strictly constrained between 0 and 1. Functional richness has no upper limit because it quantifies an absolute volume filled, which depends partly on the number of traits and on their unit. However, functional richness values may be constrained between 0 and 1 via standardization by the global hull volume (e.g., the volume occupied by all species considered in a particular study, as proposed for the FR_i index of Mason et al. 2005). The three indices are independent of the unit used to measure species abundances. Indeed, functional richness is, by construction, independent of species abundances while functional divergence and functional evenness take into account species relative abundances, which are unitless. Functional divergence and functional evenness both reflect the distribution of species abundances in functional space, and thus the contribution of each species to functional divergence and functional evenness is proportional to its abundance.

Functional richness is the only index that reflects the range of the trait values and thus, as expected, is affected by the unit of the traits (Fig. 3). However, as noted previously, this may be accounted through standardization by the maximum possible hull volume. The three indices are not affected by a translation or a rotation of the functional space of reference (Fig. 3).

To test whether our indices match the criteria of independence with species richness and whether our indices are independent from each other, we generated artificial communities. The number of traits was fixed to three. Coordinates of the species for each axis were generated using a uniform distribution (i.e., all values had equal chance of being selected) within a range of 10. Seven species richness values were considered (10, 15, 20, 25, 30, 35, and 40). Species abundances were generated

FRic = 2 FEve = 1 FDiv = 0.692

Enlargement

Rotation

Translation

FRic = 8 FEve = 1 FDiv = 0.692

FRic = 2 FEve = 1 FDiv = 0.692
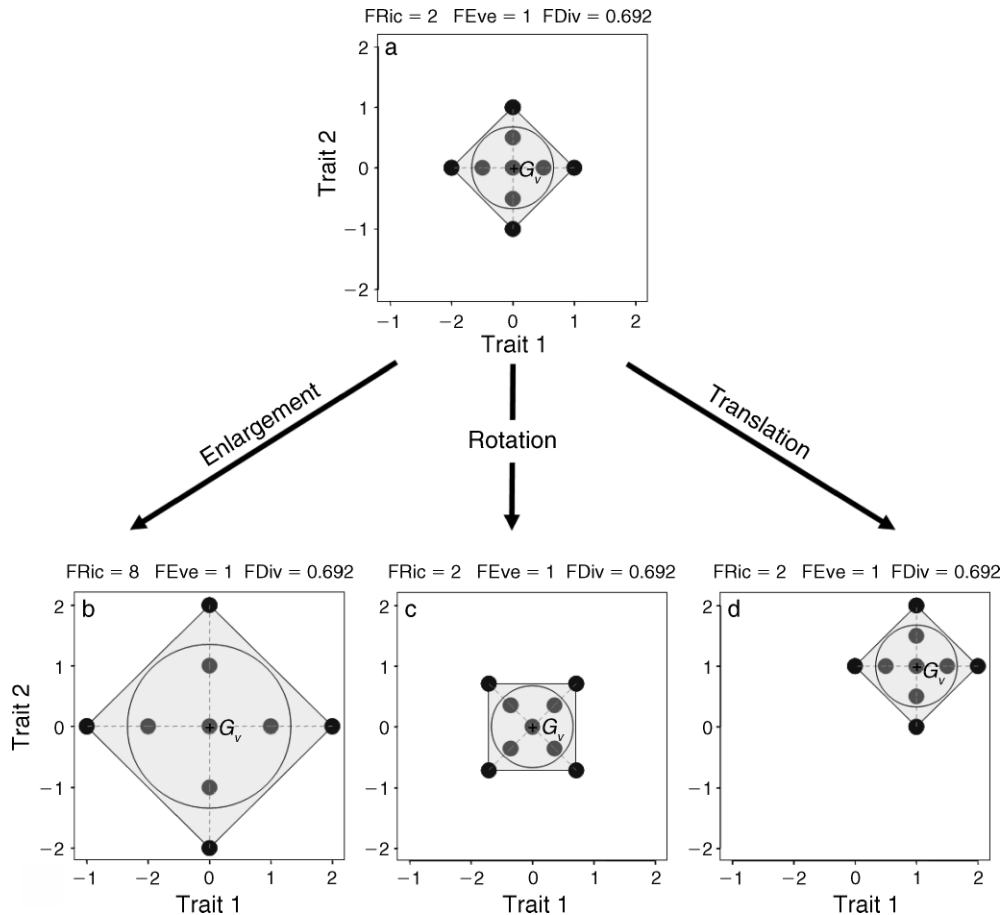
FRic = 2 FEve = 1 FDiv = 0.692

FIG. 3. Properties of the three functional diversity indices (FRic for functional richness, FDiv for functional divergence, and FEve for functional evenness). Two traits (axes) and nine species (points) with equal abundances are considered for graphical commodity. The key to the symbols and lines is the same as for Fig. 1. Panel (a) is the community of reference. Two communities with (c) a rotation or with (d) a translation between them have similar functional richness, functional evenness, and functional divergence. However, (b) two communities having the same shape but different sizes have similar functional evenness and functional divergence while having different functional richness values.

using a uniform distribution within a range of 100 and then standardized to relative abundances. One hundred replicates (coordinates and abundances) were generated using R software for each of these seven cases. The three indices were computed for these 700 data sets. Pearson's coefficients of correlation between each index and species richness and between the three indices were then tested.

Our simulations using artificial data sets showed clearly that functional richness and species richness are strongly and positively related ($r = 0.872$, $P < 0.001$; Fig. 4a). As expected from the sampling effect, it is more likely to obtain a larger hull volume with more species in the community. However, for a given T-dimensional functional space, the maximal convex hull is obtained with 2^T species whose coordinates are a combination of the extreme values on each axis. In other words, in such a given Euclidian space, the maximal volume given the ranges on the axes is a hypervolume with all its angles

square. For example, with a three-dimensional space, the maximum convex hull volume is obtained with at least eight points constituting a cube. It is impossible to fill the whole available space with fewer than eight species. This property means that for communities with species richness less than 2^T, observed functional richness values are not comparable. Practically, to avoid this bias, the number of species must increase exponentially with the number of traits in comparative studies. Cornwell et al. (2006) do not explicitly point out this bias in their study, but they overcome it using a randomization procedure allowing the observed functional richness value to be compared with that expected at random for the species richness level of the community. This limit partly explains the positive correlation between the convex hull volume index and species richness, the shape of the relation depending on the number of traits, and on their correlations.
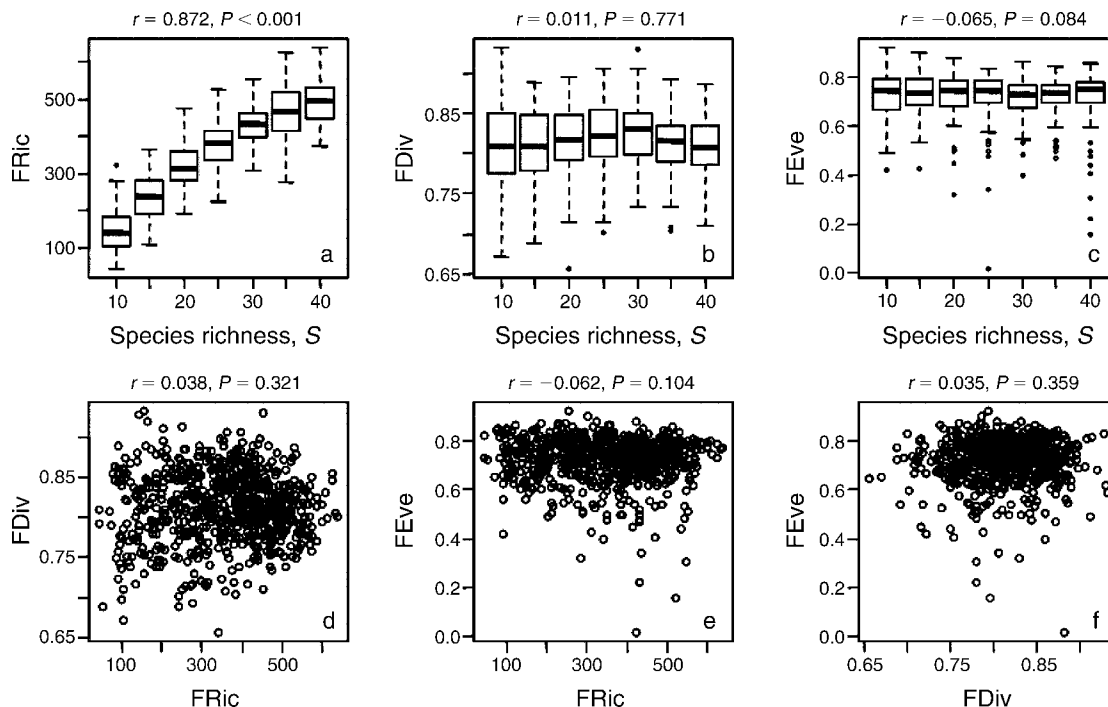
FIG. 4. Properties of the three functional diversity indices for artificial communities. Three traits were considered, and both the coordinates and the abundances of the species were generated under a uniform law (with respective range of 10 and 100). Seven species richness levels (S) were considered. Each species richness level was replicated 100 times. For each community, functional richness (FRic), functional divergence (FDiv), and functional evenness (FEve) were estimated. The first three panels (a, b, c) show the relations between each index and species richness. The three last panels (d, e, f) present the correlations between the three indices. Pearson's coefficients of correlation and levels of significance are given above the panels. FRic is the only index correlated to species richness. The three indices are independent of each other.

The values obtained with artificial communities showed that functional divergence and functional evenness are independent from species richness (Fig. 4b, c). These two indices are also independent from functional richness (Fig. 4d, e) and each other (Fig. 4f).

Two of the three indices satisfied the modified twinning criterion proposed by Mason et al. (2003), that diversity is not affected when a species is replaced by two species with the same trait values and the same total abundance. If the species is a vertex, the convex hull volume algorithm will consider only one of the two twins as a vertex and thus the convex hull, and so the richness will not be modified. Similarly, the position of the center of gravity of the vertices will not be affected. Moreover, the Δd and $\Delta|d|$ of the FDiv computation will be unchanged by the fact that the abundance is split between two entities having the same position. On the contrary, the evenness index does not satisfy this criterion. If a species is split into two species identical for all traits and which share the initial abundance, the regularity of trait values will be changed, as there are now two species at the same place in the functional space. It is not a bias of our index but is inherent to our definition of functional evenness. This would only be problematic when it is difficult to identify species with

certainty or where taxonomic opinion differs as to whether a subspecific taxon should be treated as a separate species. Thus, we believe that the latter point, indices independent from species richness, is far more important in the ecological context.

Functional richness is the only index in accordance with the monotonicity criterion proposed by Ricotta et al. (2005). Indeed, the functional-richness value of a subset of species cannot be superior to the functional-richness value of the whole set. Functional divergence and functional evenness do not match this criterion, as the addition of species can decrease functional divergence (a new abundant species close to the center of gravity of the functional space) and functional evenness (a new species close to an abundant species), because these indices consider relative abundances.

Similarly, functional richness is the only index to respect the concavity criterion, for the same reason as for the monotonicity criterion. By contrast, indices of divergence and evenness are not additive, which means that the divergence (or the evenness) of two communities is not linked to the mean of the two index values but depends on the characteristics of the new constructed community (species traits and relative abundances).
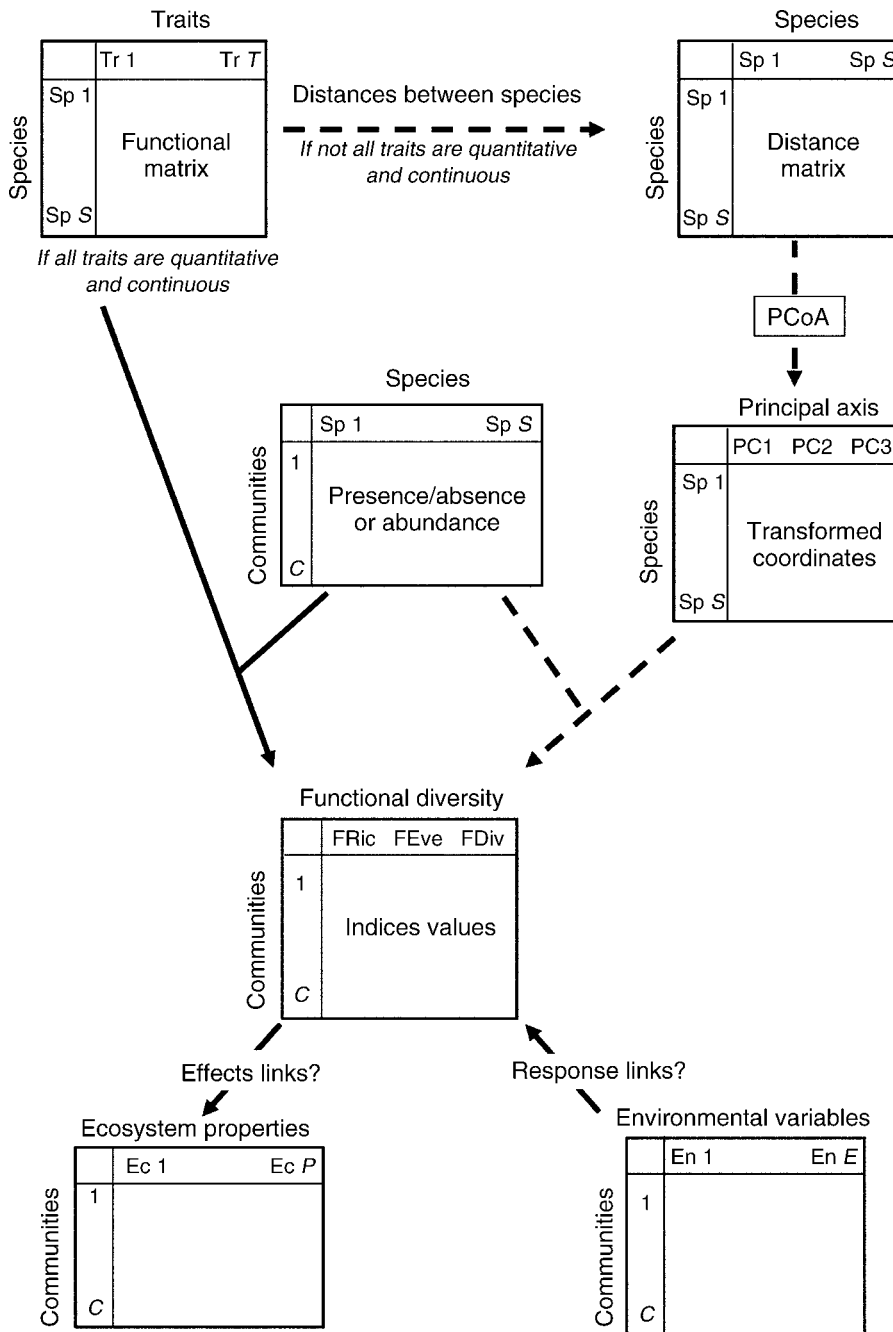
Fig. 5. General framework to study the effect of environmental conditions on functional diversity or the effect of functional diversity on ecosystem properties.

In summary, our set of three indices meets all the criteria required for functional diversity measures. The three indices are actually complementary. Moreover, functional divergence and evenness are independent from species richness, which allows comparison of communities with different species richness without bias. Similarly, their independence from functional richness allows for testing of differences in functional divergence or evenness with different functional richness values.

FROM THEORY TO PRACTICE

Generally, data sets contain two to four of the following matrices in Fig. 5: (1) a functional trait matrix (with values for each of the S species, for each of the T-functional traits), (2) an "abundance pattern" matrix

(with the abundances of each species in the C communities), (3) an "environmental" matrix (with values for each of the E environmental variables in each community), and (4) an "ecosystem properties" matrix (with values for each of the P ecosystem properties such as productivity, flux of nutrients, or resistance to perturbation in each of the communities). The main limiting factor is that functional traits have to be the same for the communities to be compared. This emphasizes the need for consensual lists of traits for each type of organism (plant, terrestrial animal, fishes, microorganisms).

Moreover, as underlined by Petchey and Gaston (2006), the a priori selection of traits is often critical. The main problems concern the number of traits and their identity. Indeed, the number of traits is linked to the amount of work needed to measure them on each species, but also to the functions that are quantified. The choice of the traits has to be led by the need to describe each function as well as possible while avoiding redundancy (i.e., trivial correlations) between them. In particular, when using functional traits derived from other traits (e.g., ratios), original traits should not be used in calculating functional diversity since the original and derived traits may be trivially related. If traits are carefully selected, then any correlation between traits in the species–trait matrix may be considered a relevant aspect of species distribution in functional trait space. For example, the competitive, stress tolerant, and ruderal strategy (CSR) theory of Grime (1974, 2001) shows that correlations between traits that have no a priori link reveal major trends in plant functional strategy. More generally, correlations between traits may highlight patterns of species aggregation in a functional space where species separate into functional groups, whereas this may not be evident when functional traits are not correlated. Using ordination axes in calculating functional diversity will obscure these correlations. Ordinations also risk the loss of information, since the ordination axes can only capture a proportion of the variation in functional trait values across species. In summary, if functional traits are selected so that trivial correlations are avoided, any correlation between traits will represent a relevant aspect of species distribution in functional-trait space, and there will be no need to apply ordination techniques to obtain orthogonal axes. However, we may encounter constraints in the data which imply the use of ordination techniques, such as the use of too many traits compared to species number or the use of categorical data.

All of our indices are designed to quantify functional diversity using continuous traits. However, as exposed by Podani and Schmera (2006), ecological variables and, in particular, functional traits are sometimes qualitative either categorical (type of photosynthesis, ability to sprout after fire) or circular (time of reproduction). To overcome this problem, we propose to estimate a distance matrix using distances such the Gower distance which allows mixing qualitative and quantitative traits (Podani and Schmera 2006). In this case, a Principal Coordinates Analysis (PCoA) may be used to represent species distribution in a multidimensional functional space. PCoA works on distance matrix and its outputs are similar to those obtained from PCA (Legendre and Legendre 1998), i.e., the coordinates of species in a Euclidean functional space with reduced uncorrelated dimensions. Another particular case is the use of presence/absence data. Then, functional divergence and functional evenness have a different meaning in the sense that they would quantify the relative position of species within the functional space instead of the distribution of abundance.

However, we believe that in order to compare functional diversity values among communities with different species richness and different regional species pools, the best way is to consider observed values relative to those expected at random. Expected values may be obtained using a matrix swap randomization (Manly 1995) that maintains species richness of communities and the frequency of occurrence of species in randomized matrices. In fact, such a correction when comparing functional diversity of different local communities is necessary for all indices, since species functional traits in the pool will constrain the range of functional-diversity values possible. Methodologies for comparing observed functional diversity values to those expected by chance were provided in Mason et al. (2007, 2008).

The primary components of functional diversity identified by Mason et al. (2005) have aided us in finding a set of orthogonal multivariate functional diversity indices to give a comprehensive framework for the quantification of functional diversity in multidimensional functional trait space. It is possible that this framework does not capture all aspects of functional diversity, but it remains the sole available method for classifying functional diversity indices by the aspect of species distribution in functional trait space that they measure (cf. the classification system employed by Petchey and Gaston 2006). In helping to decide on a set of orthogonal indices, the primary functional diversity components aid the application of functional diversity indices in elucidation patterns and processes in ecological communities.

Functional diversity may act either as (1) an indicator of the processes governing community assembly (e.g., environmental and competitive filtering; Cornwell et al. 2006) and the impact of perturbations (e.g., climate change, fire, grazing or overfishing) and environmental gradients on community structure (e.g., Mouillot et al. 2007), or (2) an indicator of ecosystem functions such as productivity, resilience, and nutrient cycling (e.g., Petchey et al. 2004). Concurrent examination of functional diversity indices representing separate primary components increases the detail with which we may examine a variety of hypotheses relating to these dual

roles of functional diversity. For example, Mason et al. (2008) found that functional evenness, compared to that expected at random, increased linearly with mean annual temperature and species richness in French lacustrine fish communities, while functional richness and functional divergence showed asymptotic relationships in both cases. These results, considered together, suggest that increased niche specialization (as opposed to an increase in the volume of niche space occupied) with increasing temperature allowed more species to coexist in high-energy communities. Similarly, an orthogonal set of indices might allow comparison of evidence for increased niche specialization or occupied niche volume as mechanisms for increased productivity or resilience. Using this approach, functional diversity indices may in effect be used to test not only whether niche complementarity enhances ecosystem function, but which type of complementarity enhances ecosystem function the most.

Until now, such an approach has been constrained to the use of univariate functional diversity indices. The three indices we propose here allow the implementation of the primary functional diversity components in multiple dimensions. They provide independent information about the position and relative abundances of species in a multidimensional functional space. Therefore, we believe that these new indices may help in the exploration of biodiversity–environment–ecosystem functioning relationships in ecology.

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