

## Functional diversity measures: an overview of their redundancy and their ability to discriminate community assembly rules

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### Summary

1. Indices quantifying the functional aspect of biodiversity are essential in understanding relationships between biodiversity, ecosystem functioning and environmental constraints. Many indices of functional diversity have been published but we lack consensus about what indices quantify, how redundant they are and which ones are recommended.

2. This study aims to build a typology of functional diversity indices from artificial data sets encompassing various community structures (different assembly rules, various species richness levels) and to identify a set of independent indices able to discriminate community assembly rules.

3. Our results confirm that indices can be divided into three main categories, each of these corresponding to one aspect of functional diversity: functional richness, functional evenness and functional divergence. Most published indices are highly correlated and quantify functional richness while quadratic entropy ( $Q$ ) represents a mix between functional richness and functional divergence. Conversely, two indices (FEve and FDiv respectively quantifying functional evenness and functional divergence) are rather independent to all the others. The power analysis revealed that some indices efficiently detect assembly rules while others performed poorly.

4. To accurately assess functional diversity and establish its relationships with ecosystem functioning and environmental constraints, we recommend investigating each functional component separately with the appropriate index. Guidelines are provided to help choosing appropriate indices given the issue being investigated.

5. This study demonstrates that functional diversity indices have the potential to reveal the processes that structure biological communities. Combined with complementary methods (phylogenetic and taxonomic diversity), the multifaceted framework of functional diversity will help improve our understanding of how biodiversity interacts with ecosystem processes and environmental constraints.

**Key-words:** artificial data, functional divergence, functional diversity measures, functional evenness, functional richness, limiting similarity, motion model, neutrality, niche filtering

### Introduction

Biological diversity, or biodiversity, defined as ‘the variety of life on Earth at all its levels, from genes to ecosystems, and the ecological and evolutionary processes that sustain it’ (Gaston 1996), embraces the diversity of genes, phenotypes, populations, species, communities and ecosystems. As a result, quantifying such a broad concept has proved to be problematic. However, as Purvis & Hector (2000) high-

lighted, ‘We cannot even begin to look at how biodiversity is distributed, or how fast it is disappearing, unless we can put units on it’. Classical biodiversity measurements (species richness or the myriad of diversity indices such as Shannon) have relied on three main assumptions: (i) all species are equal (only relative abundances establish the relative importance of species), (ii) all individuals are equal (whatever their size) and (iii) species abundances have been correctly assessed with appropriate tools and in similar units (Magurran 2005). Yet, species not only offer a wide range of colours or life forms to the Human eye, they are

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also likely to support many goods and services through ecosystem processes (e.g. Díaz *et al.* 2007). Hence, the first assumption of biodiversity measurement is not valid: species are not equal in their effects on ecosystem functioning since their functional traits matter to ecosystem processes.

As early as 1994, Solow & Polasky (1994) suggested that measuring diversity was equal to characterizing the distribution of points in space. Accordingly, measuring functional diversity is quantifying the distribution of functional units in a multidimensional space (Villéger, Mason & Moullot 2008). By analogy with Hutchinson's niche, Rosenfeld (2002) defined functional diversity (i.e. the functional component of biodiversity) as the distribution of species in a functional space whose axes represent functional features. A new generation of measurements has already been proposed to quantify this multidimensional distribution (see Petchey & Gaston 2006 for a review). However, despite the importance of the subject, there is no consensus on how to quantify the functional diversity of a community and relationships between the various indices have not been established. One step further, we still lack a study quantifying the ability of various functional diversity indices to discriminate the processes shaping functional community structures. Mason *et al.* (2005), in suggesting that functional diversity could be divided into three primary components – functional richness, functional divergence and functional evenness –, proposed a definition of functional diversity to guide the conception of new indices and the categorization of existing ones. The three facets are complementary and, taken together, describe the distribution of species and their abundances within the functional space. Functional richness represents the amount of functional space occupied by a species assemblage. Functional evenness corresponds to how regularly species abundances are distributed in the functional space. Finally, functional divergence defines how far high species abundances are from the centre of the functional space. This decomposition of functional diversity reflects complementary characteristics of the distribution of taxa (or individuals) in functional space. Linking indices to a particular functional diversity component could greatly aid ecologists in deciding on a minimum set of indices from the ever increasing range of options. As each component describes an independent aspect of functional diversity, a complete quantification of functional diversity requires at least one index measuring each functional diversity component. Previous works have already categorized functional diversity indices (Petchey, Hector & Gaston 2004; Ricotta 2005; Petchey & Gaston 2006). Among concluding remarks, Petchey & Gaston (2006) emphasized the necessity to determine which functional diversity measure performs best. To achieve this, the explanatory power and their statistical validity have to be well defined. For example, an increase in species richness and/or co-linearity between traits may modify the behaviour of each index (Mouchet *et al.* 2008). Correctly identifying bias in index calculation is crucial to avoid spurious conclusions. Furthermore, no study clearly establishes which measures estimate which facet of functional diversity and several meanings have been attributed to the same index.

For instance, the Rao's quadratic entropy ( $Q$ ) has been labelled a measure of functional diversity (Scherer-Lorenzen *et al.* 2007; Weigelt *et al.* 2008) or functional divergence (Díaz *et al.* 2007). It thus becomes critical to evaluate the possible redundancy or complementarity between these various indices. In other words, do functional diversity indices all quantify the same facet of functional diversity?

Besides quantifying functional diversity, functional diversity measures could close the gap between ecosystem functioning and community ecology. Patterns of functional diversity may reveal species coexistence processes and assembly rules driven by functional traits (Mason *et al.* 2007; Moullot, Mason & Wilson 2007). Niche filtering assumes that coexisting species are more similar to one another than would be expected by chance because environmental conditions act as a filter allowing only a narrow spectrum of traits to persist (Zobel 1997). On the other hand, the competitive exclusion (Hardin 1960) and limiting similarity principles (MacArthur & Levins 1967) assume the stable coexistence of functionally dissimilar species. In addition, neutral theory (Hubbell 2001) posits that species coexist and persist in a system independently of their traits since individuals and species are equivalent. Recent findings suggest that these three mechanisms may co-occur simultaneously and blur the patterns (Helmus *et al.* 2007) or may occur sequentially along environmental gradients (Mason *et al.* 2007). Further, the relative influence of assembly rules depends on the scale of observation (Zobel 1997; Silvertown *et al.* 2006; Kraft *et al.* 2007). Environmental filtering is assumed to be stronger at the regional scale (Díaz, Cabido & Casanoves 1999; Cornwell, Schwillk & Ackerly 2006) whilst species interactions (i.e. competition or limiting similarity) drives local assembly patterns (Cavender-Bares *et al.* 2004; Slingsby & Verboom 2006). Thus the crucial question is no longer which mechanism is valid in ecology but which mechanism has the strongest influence on communities. This latter point needs appropriate tools able to differentiate communities under different assembly rules and the potential of various functional diversity indices is still unknown.

The principal objectives are therefore to set up the typology of existing functional diversity indices and to determine their ability to discriminate assembly processes underlying the functional structure of communities. Ultimately, we aim to provide a guide to use the appropriate functional indices given the issue being investigated.

## Materials and methods

### FUNCTIONAL DIVERSITY MEASURES

One of the first methods proposed to quantify functional diversity relies on the classification of species into various functional groups according to an *a priori* classification (e.g. Hooper & Vitousek 1997; Tilman *et al.* 1997). The number of functional groups is assumed to evaluate species complementarity in resource use (Petchey 2004). However, the choice of functional groups is not based on objective (mathematical or statistical) methods. Indeed, the threshold, from

which functional interspecific dissimilarities are considered to be significant, is an arbitrary decision of the experimenter (Wright *et al.* 2006). This underlines the necessity to work with continuous and objective measurements of functional diversity (Petchey, Hector & Gaston 2004).

The first published index measuring functional diversity in a continuous way, Functional Diversity Attribute (FAD, Walker, Kinzig & Langridge 1999), quantified the sum of all functional pairwise distances between species belonging to the same community. This index evaluates the average functional contribution of each species to the total diversity of a community (Ricotta 2005). In a step forward Petchey & Gaston (2002) proposed the FD index which measures functional diversity from the total branch length linking species belonging to the same community on the functional dendrogram built on the regional pool of species. This latter index has the advantage over the former to be independent of species splitting (i.e. the splitting of one species into two species with similar traits has no effect on the index value). Then, Botta-Dukát (2005) advised the use of Rao's quadratic entropy (following Rao 1982) as a functional diversity measure measuring the mean functional distance between two randomly chosen individuals. Following the functional diversity decomposition of

Mason *et al.* (2005), several measurements have been presented to assess each facet: FDvar (Mason *et al.* 2003), a measurement of the functional divergence (previously proposed as a functional diversity index) and an index of functional richness FR (Mason *et al.* 2005). In parallel, Moullot *et al.* (2005) quantified functional evenness with FRO. FDvar, FR and FRO are all univariate indices (e.g. only one functional trait taken into account). More recently, Villéger, Mason & Moullot (2008) defined multivariate measurements for functional diversity components: FRic (functional richness), FEve (functional evenness) and FDiv (functional divergence). Concurrently, two modified versions of FD and FAD have been proposed, GFD (Mouchet *et al.* 2008) and MFAD (Schmera, Erős & Podani 2009), in order to remove the bias induced by respectively species splitting (Petchey, Hector & Gaston 2004) and the choice of the distance and clustering algorithm (Podani & Schmera 2006). To fit Rosenfeld's definition of functional diversity, we chose to only focus on multivariate measures. In this study, FD, GFD and FRic will be expressed as a proportion of the functional volume occupied by the regional species pool to facilitate their comparison. Descriptions, calculations and references of the eight selected indices FRic, FAD, MFAD, FD, GFD,  $Q$ , FDiv and FEve are presented in Table 1.

**Table 1.** Functional diversity measures

Index		Description	Formula	Based on	Abundance included
Functional Attribute Diversity (Walker, Kinzig & Langridge 1999)	FAD	Sum of pairwise distances between species	$FAD = \sum_{i=1}^S \sum_{j=1}^S d_{ij}$	Distance matrix	No
Modified Functional Attribute Diversity (Schmera, Erős & Podani 2009)	MFAD	Sum of pairwise distances between functional units	$MFAD = \frac{\sum_{i=1}^N \sum_{j=1}^N d_{ij}}{N}$	Distance matrix	No
Functional Diversity (Petchey & Gaston 2002)	FD	Sum of branch length of a functional classification	$FD = i' \cdot h2$	Hierarchical classification	No
Generalized Functional Diversity (Mouchet <i>et al.</i> 2008)	GFD	Sum of branch length of a functional classification	$GFD = i' \cdot h2$	Hierarchical classification	No
Functional Richness (Cornwell, Schwillk & Ackerly 2006; Villéger, Mason & Moullot 2008)	FRic	Convex Hull Volume	Quickhull algorithm	Trait values	No
Rao's quadratic entropy (according to Rao 1982)	$Q$	Sum of pairwise distances between species weighted by relative abundance	$Q = \sum_{i=1}^{S-1} \sum_{j=i+1}^{S-1} d_{ij} p_i p_j$	Distance matrix	Yes
Functional Divergence (Villéger, Mason & Moullot 2008)	FDiv	Species deviance from the mean distance to the centre of gravity weighted by relative abundance	$FDiv = \frac{\Delta d + \overline{dG}}{\Delta  d  + \overline{dG}}$	Trait values	Yes
Functional Evenness (Villéger, Mason & Moullot 2008)	FEve	Sum of MST branch length weighted by relative abundance	$FEve = \frac{\sum_{i=1}^{S-1} \min \left( PEW_i, \frac{1}{S-1} \right) - \frac{1}{S-1}}{1 - \frac{1}{S-1}}$	Trait values	Yes

$d_{ij}$ : dissimilarity between species (or functional unit)  $i$  and  $j$ .  $S$ : the total species richness.  $N$ : the total number of functional units.  $p_i$ : relative abundance of species  $i$ .  $x$ : trait value.  $dG$ : mean distance to the centre of gravity.  $\Delta d$ : sum of abundance-weighted deviances.  $\Delta |d|$ : absolute abundance-weighted deviances from the centre of gravity.  $PEW$ : partial weighted evenness.  $i'$ : branch presence/absence row vector.  $h2$ : branch length vector.

GFD, FD and FRic were expressed as the proportion of occupied space (i.e. the local community) compared to the maximal volume (i.e. the regional pool).

## THEORETICAL DATASETS

To investigate the behaviour of indices in a realistic framework, we created artificial data exhibiting patterns displayed by real communities. Artificial data have the benefit of allowing control over community parameters. In this dataset, we manipulated species richness and community structure through three community assembly schemes: habitat (or niche) filtering (van der Valk 1981; Keddy 1992), limiting similarity (MacArthur & Levins 1967) and neutral assembly (Hubbell 2001). To simulate the functional structure of species in the regional pool, we used a modelling approach proposed by Kraft *et al.* (2007). This conceptual framework is based on evolutionary models incorporating the Brownian motion model of trait evolution, which is extensively used in literature and includes assembly processes in the generation of more realistic artificial data. Initially, the Brownian motion model was developed to reproduce the random movement of microscopic particles, immersed in a liquid or gas affected by thermal noise, whose total displacement is drawn from a normal distribution centred around 0 (Felsenstein 1985). Brownian models assume a constant rate of evolution of trait while species evolve independently from each other. Consequently some species may be characterized by similar trait attributes. This model of trait evolution predicts that phylogenetically closely related species should be functionally more similar to each other.

Following Kraft *et al.*'s (2007) procedure, a primary set of a thousand species  $\times$  traits matrices (each representing an artificial regional pool of 150 species characterized by five traits) was simulated under the assumption of a Brownian motion model without any assumption concerning assembly rule. From each of the one thousand regional pools, ten local communities (having from 10 to 100 species with an interval of 10) were then produced using each assembly rule algorithm following the framework of Kraft *et al.* (2007). The niche filtering algorithm was based on the distance between species functional attributes and the optimum defined for each functional trait (at a given species richness, the furthest species from the optimum were eliminated). Limiting similarity assumes that there is a limit to how similar two co-existing species can be in their niches. Consequently, one of the nearest neighbours in each pair of species was removed until the desired species richness was achieved. The neutral assembly algorithm randomly subsampled, without replacement, communities from the regional pool. Algorithms used to simulate each process are extreme relative to what would be observed in nature where each process can act simultaneously generating some blurring effects.

One step further than Kraft *et al.*'s design, we allocated species abundances according to each assembly rule to complete simulation of the three assembly processes. To fit realistic sampling distributions, species abundances were generated using a log-normal distribution (a common pattern in nature, Preston 1948) then standardised to relative abundances. In the niche filtering context, the nearer a species was to the optimum trait values, the greater its abundance. For limiting similarity, abundance decreased with increasing similarity (decreasing functional distance) between all co-occurring species. In the random scenario, abundances were randomly distributed.

## TYPOLOGY OF THE FUNCTIONAL DIVERSITY INDICES

Each index of functional diversity was calculated for the one thousand artificial communities corresponding to each of the three assembly processes and each of the ten species richness levels, aggregating 240 000 values (N.B.: here, the large number of values renders *P*-values uninformative since statistical tests will have a very strong power).

Relationships between each pair of functional diversity measures were investigated using the Spearman coefficient of correlation. Additionally, a typology of all indices was carried out on the matrix crossing functional diversity measures (variables) and communities (objects) using a principal component analysis (PCA). To support the classification of indices into groups using the PCA axes, we applied a K-means partition (Legendre & Legendre 1998) based on index coordinates on the main PCA axes (i.e. those with an eigenvalue higher or equal to 1). For each number of groups, the Calinski-Harabasz criterion was computed. This criterion uses the Variance Ratio Criterion, which is analogous to *F*-Statistics, to minimize the within-group sum of squares and maximize the between-group sum of squares. The partition yielding the highest Calinski-Harabasz value (corresponding to the set of most compact groups) was retained for the final typology (Legendre & Legendre 1998).

## PERFORMANCE OF THE INDICES

We examined the influence of two major parameters on multivariate functional diversity indices: species richness and community assembly rules. The relationship of each measure of functional diversity with those parameters was explored using a two factors ANOVA on the mean value of each index for every richness level and assembly rule. Finally, a performance test, based on a statistical power analysis (type II error), was conducted for each index in order to evaluate its ability to detect non-random patterns shaping functional community structures. To this aim, for a given level of species richness, the distribution of index values calculated under the limiting similarity hypothesis on one side, the niche filtering one on the other side, was compared to the distribution of index values calculated in the random scenario (here, our null hypothesis). More precisely, we calculated the statistical power as the proportion of index values obtained under an assembly rule (limiting similarity or niche filtering) that produced significant results in the predicted direction (alternative hypothesis), i.e. the ability to detect an ongoing effect. We used type I error at  $P = 0.05$  for all tests.

## Results

## PARTITIONING FUNCTIONAL DIVERSITY INDICES

Spearman correlations between functional diversity measures (Table 2) revealed a high correlation between FRic, FAD, MFAD, GFD and FD (coefficient values ranged from 0.769 to 0.999). As expected, GFD and FD on one hand, MFAD and FAD on the other hand, are highly associated (Spearman coefficients of 0.999 and 0.986 respectively). FEve was weakly correlated to other measures (see Table 2 for details). Finally, FDiv was essentially related to *Q* ( $r_{Q-FDiv} = 0.833$ ) which is also correlated to FRic ( $r_{Q-FRic} = 0.695$ ).

The first three axes of the PCA carried out on the eight indices, accounted for 95.28% of total inertia (Fig. 1). The K-means classification confirmed the classification of indices into four groups (optimal Calinski-Harabasz criterion = 114.55). The first group gathered MFAD, FAD, FD and GFD. The second group was composed of *Q* and FDiv while FRic and FEve represented the third and the fourth group respectively. The K-means classification is well illustrated by PCA plot based on the first and third axes (lower part of

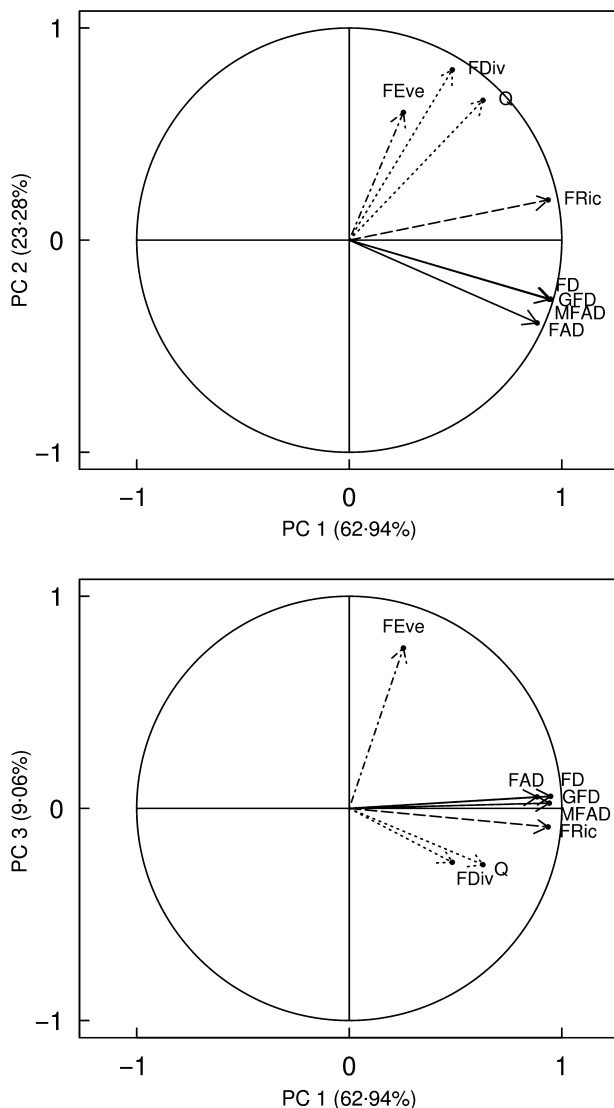


**Table 2.** Spearman correlation coefficients between functional diversity measures

	FAD	MFAD	FD	GFD	FRic	<i>Q</i>	FDiv	FEve
FAD	1	***	***	***	***	***	***	NS
MFAD	0.986	1	***	***	***	***	***	***
FD	0.975	0.965	1	***	***	***	***	***
GFD	0.975	0.965	0.999	1	***	***	***	***
FRic	0.769	0.819	0.864	0.863	1	***	***	***
<i>Q</i>	0.299	0.426	0.367	0.367	0.695	1	***	***
FDiv	0.099	0.197	0.237	0.236	0.621	0.833	1	***
FEve	-0.001	0.053	0.067	0.067	0.285	0.373	0.405	1

The correlation coefficients are evaluated on 30 000 artificial species communities, characterized by three assembly patterns, scattered into ten species richness levels.

NS, non significant; \* $P < 0.05$ ; \*\* $P < 0.01$ ; \*\*\* $P < 0.001$ .



**Fig. 1.** Principal Component Analysis carried out on the on artificial species communities, characterized by three assembly patterns, scattered into ten species richness levels (10, 20, 30, 40, 50, 60, 70, 80, 90, 100 sp). The eight functional diversity indices are represented in the three axes volume. Several variable vectors are superimposed because the corresponding indices are very close on PCA plans (i.e. FD, GFD and MFAD on plan 1–2 and FD and GFD on plan 1–3). K-means groups (Calinski-Harabasz criterion of 114.55) are disentangled using the line types.

Fig. 1): FRic is gathered with FD, GFD, FAD and MFAD while FEve is independent of FDiv and *Q*.

#### PROPERTIES OF FUNCTIONAL DIVERSITY INDICES

The two factors ANOVA segregated the functional diversity indices into two groups according to the relative magnitude of *F*-values: indices mainly influenced by species richness (i.e. FAD, MFAD, FD and GFD) and indices mostly affected by assembly rules (i.e. FRic, *Q*, FDiv and FEve) (Table 3). Furthermore, FAD, MFAD, FD, GFD and FRic values monotonically increased with species richness whatever the underlying assembly rule (Fig. 2). Conversely, FDiv, *Q* and FEve indices exhibited a weak relationship with species richness.

#### PERFORMANCE OF FUNCTIONAL DIVERSITY INDICES

Overall the power analysis revealed that GFD, FD, FRic and FDiv had a high power to detect both assembly rules (limiting similarity and niche filtering), particularly for species richness levels higher than 30 species. For communities with a lower richness (10 species), FRic is the best performing index whatever the underlying assembly rule.

FAD, MFAD, *Q* and FEve were more able to detect niche filtering patterns than limiting similarity patterns for which

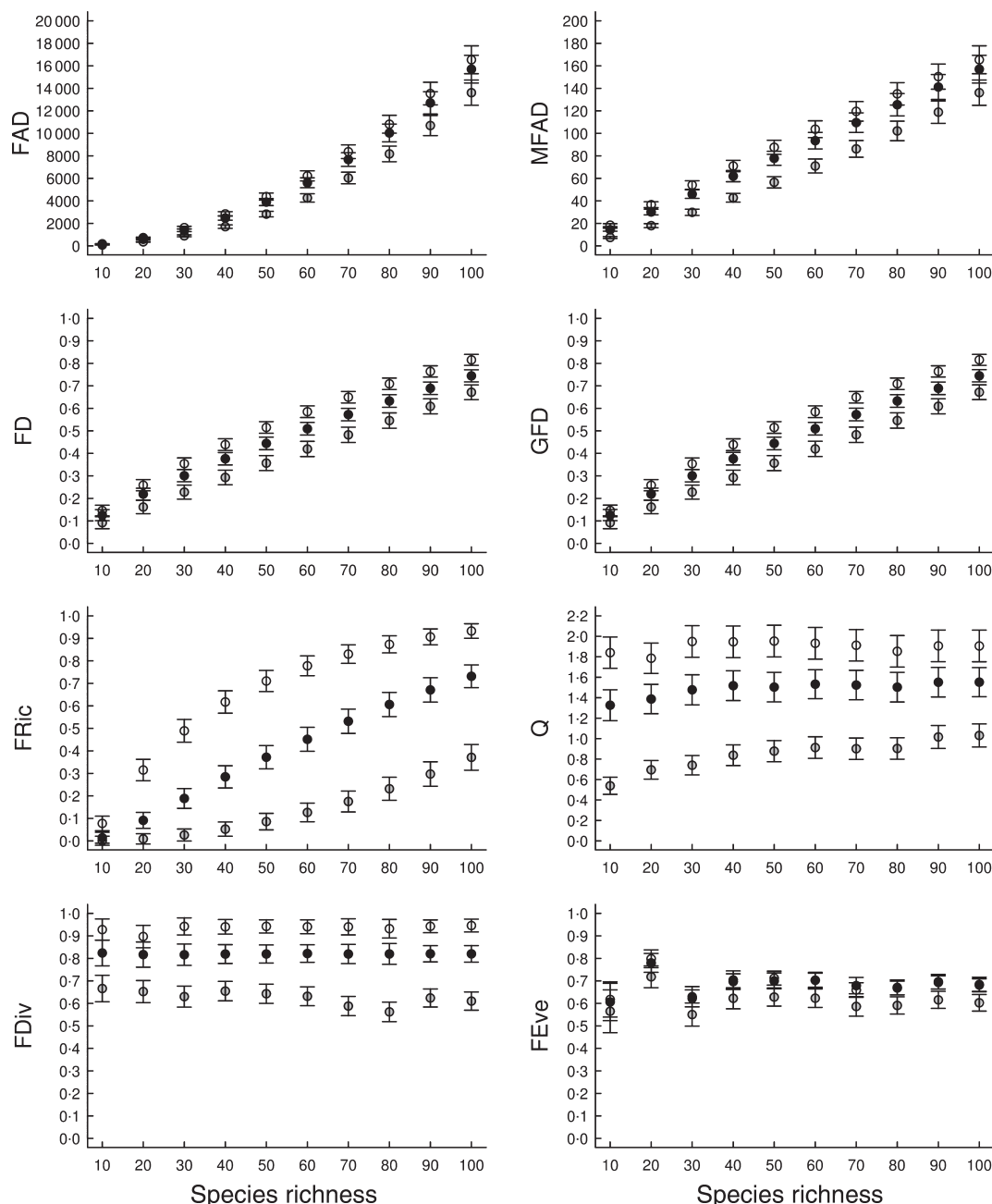
**Table 3.** Effects (*F*-statistic) of assembly rules and species richness on functional index values tested by a two factors ANOVA

Factors	Assembly rules	Species richness	Assembly rules: Species richness
d.f.	2	9	18
FAD	394.33	<b>2456.13</b>	610.37
MFAD	378.83	<b>2091.91</b>	483.8
FD	153465.8	<b>415917.5</b>	1077.3
GFD	151014.1	<b>410205.5</b>	1053.0
FRic	<b>269668.9</b>	55623.9	4015.5
<i>Q</i>	<b>52560.03</b>	405.37	87.23
FDiv	<b>113939.3</b>	157.27	209.49
FEve	<b>6346.7</b>	2290.06	22.81

The main factor is in bold.

“:” represents the interaction between factors.

All *P*-values associated are very highly significant.



**Fig. 2.** Functional diversity indices as a function of species richness for three community assembly rules: limiting similarity (open circles), filtering (gray circles) and random assembly (black circles). Each circle shows the mean value and the corresponding standard deviation of each functional diversity measures (y-axis) for the level of richness indicated on the x-axis. GFD, FD and FRic are standardized to the interval [0, 1].

power values are lower than 40% whatever the richness values (Fig. 3). However, FAD and MFAD performed poorly for higher richness values (> 50 species) while FEve performed poorly for lower richness values (< 40 species).

## Discussion

### FACETS OF FUNCTIONAL DIVERSITY

Functional diversity components (richness, divergence, evenness) were already presented in a univariate framework

(Mason *et al.* 2005; Moullot *et al.* 2005). But our comparison of existing indices based on simulated communities proves that functional diversity measures actually measure different facets of functional diversity while some indices are highly redundant. According to our results, measures of functional diversity can be scattered into four groups all related to the three orthogonal functional components previously described.

The first component of functional diversity, functional richness, is characterized by indices from two K-means groups: FAD, MFAD, FD, GFD and FRic. As functional

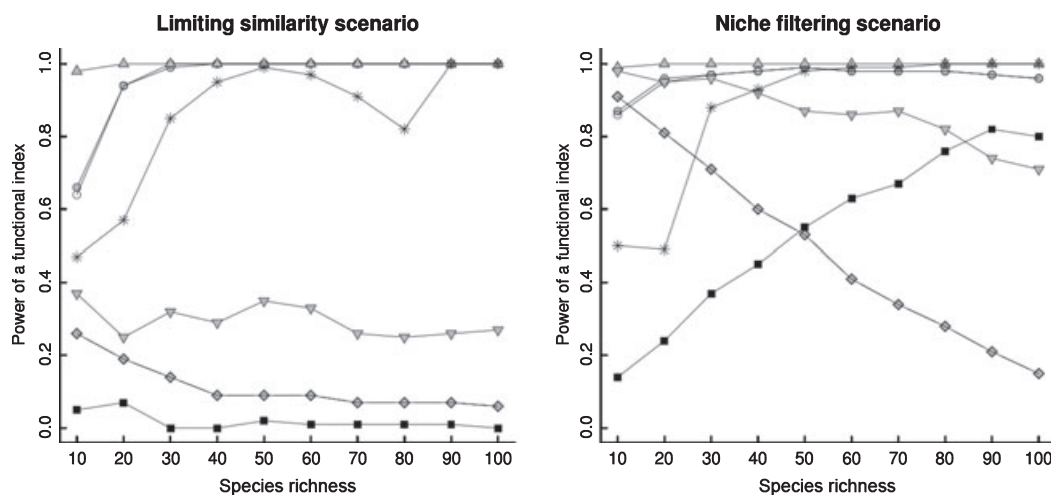


Fig. 3. Power of functional diversity indices to detect assembly patterns occurring in communities. The power values are expressed as Type II error. (The functional measures are represented by the following symbols: ● GFD, ○ FD, ◆ FAD, ◇ MFAD, ▲ FRic, ▼  $Q$ , \* FDiv, ■ FEve).

richness corresponds to the volume of functional space occupied by species (abundance is not involved), only FRic measures this volume directly while distance-based (FAD and MFAD) and dendrogram-based (FD and GFD) indices provide an indirect estimate of this volume. On one hand, FAD, FD and their sister indices measure the sum of distances (in the space or along the tree) involving all the species. On the other hand, FRic only takes into account the species with the most extreme trait values forming the vertices of the convex hull. FRic is distinguished from the others on K-means partition because it ignores the potential functional variation within the convex hull while the other functional richness measures do not.

The second of these components (functional divergence) is represented by FDiv and, to a less extent,  $Q$ . FDiv measures how abundances tend to be on the outer margins of the functional space while controlling for functional richness (Villéger, Mason & Moullot 2008). High levels of functional divergence will be associated to a high degree of niche differentiation among species within communities: the most abundant species are very dissimilar and weakly compete.  $Q$  is the only functional diversity measure that is not clearly related to one of the functional diversity components. In fact,  $Q$  is not merely a measure of functional divergence even if it is gathered with FDiv on PCA. The correlation between FDiv and  $Q$  is explained by Champely & Chessel (2002) who emphasized that, in an Euclidean space, Rao's quadratic entropy is the 'weighted average of the square distances between the underlying Euclidean representation of  $D$  [a distance matrix] and the corresponding centre of gravity'. Weigelt *et al.* (2008) characterized Rao's quadratic entropy  $Q$  as 'a continuous measure of functional diversity including information about the evenness of the distribution of functional traits within a community'. Besides, Scherer-Lorenzen *et al.* (2007) found a strong correlation between FD and  $Q$  (Pearson correlation coefficient of 0.73). Here we demonstrate that  $Q$  is not fully associated to either of the two components described previously. Indeed, both PCA and Spearman correlation coefficient

prove that  $Q$  embraces two components: functional richness and divergence.  $Q$  depends both on the range of functional space occupied and on the similarity between species with the highest abundances. Consequently, for a given functional richness, a community with a high  $Q$  will tend to have a high FDiv (the reciprocal is not true). Similarly, for a given distribution of abundances among species, a community with a higher functional richness (FRic) will have a higher  $Q$ .

The last of these components, functional evenness, is represented only by FEve. FEve measures the regularity of the distribution of abundance in functional space. FEve will be maximized by an even distribution of both species and abundances in the functional space. FEve values will be lower when some parts of the functional space are empty while others are densely populated.

No one functional diversity measure encapsulates the three facets simultaneously. Therefore, investigation of the relationships between environment, functional diversity and ecosystem functioning must consider the three independent components of functional diversity (see Villéger, Mason & Moullot 2008 for a complete framework).

#### HOW DO FUNCTIONAL DIVERSITY MEASURES RESPOND TO SPECIES RICHNESS AND ASSEMBLY RULES?

Limiting similarity favours functional dissimilarity (thus complementarity) among species within a community (Moullot, Mason & Wilson 2007). Niche filtering rather postulates the exclusion of species with traits poorly adapted to the ecosystem, yielding communities with similar species (redundancy) (Cornwell, Schilke & Ackerly 2006). Both processes impact the functional diversity components through the distribution of species (and their abundances) in the functional space defined by the corresponding functional traits. Accordingly, 'limiting similarity' yielded the highest functional diversity values and 'niche filtering', the lowest, while communities constructed with neutral assembly ('random')

had intermediate values (Fig. 2). Besides the impact of assembly rules, functional diversity values may also be influenced by species richness. For instance, FD (or GFD) values increased with species richness while FEve showed a more even distribution of values along the species richness axis (Fig. 2). Therefore, assembly rules and species richness impacts on functional measures had to be established to accurately interpret index values variation.

FAD, MFAD, FD and GFD are principally driven by species richness (Table 3). They generally increase linearly with increasing species richness (Fig. 2). In fact, the probability of occupying a broader functional space increases with the number of species by sampling effect (i.e. with the increasing probability to include species with a combination of extreme trait values). In the case of FAD, the addition of a species is always accompanied by the addition of new pairwise distances, whatever the degree of functional redundancy with the species already present in the community. This dependency to 'species split' is the main concern about the use of FAD (Petchey & Gaston 2006). This drawback is partially solved by MFAD. MFAD is calculated on functional units: two functionally redundant species are considered as one (Ricotta 2005; Schmera, Erös & Podani 2009). Unfortunately, when continuous and quantitative trait data are considered, no species is entirely redundant with another, so the functional unit is no longer relevant and species splitting remains problematic. In both cases MFAD and FAD increase exponentially with species richness, indicating that these indices are highly sensitive to species richness and do not correctly translate the degree of redundancy among species or traits. Conversely, GFD and FD are not sensitive to species splitting. However, they also are strongly influenced by species richness. In fact, adding a species to a regional pool adds branch lengths to the regional pool tree. Thus, the total branch length increases (unless it is perfectly redundant with a species already present in the regional pool) and functional richness is related to species richness. Functional richness measures that are less closely linked to species richness should be preferred. Alternatively, information independent from species richness is obtained when using null models (Petchey *et al.* 2007) or when using residuals of the linear regression between FD and species richness (Moullot, Dumay & Tomasini 2007) to generate expected values of functional richness for different levels of species richness.

FRic, FEve, FDiv and  $Q$  are much more sensitive to community assembly rules than species richness (Table 3). Unlike other functional richness measures, FRic does not take into account pairwise distances or branch lengths between species but the vertices of the convex hull. Even if FRic increases monotonically with species richness, it is more influenced by assembly rules (Fig. 2). Our results suggest that FRic more accurately represents the change in functional space dimensionality caused by community structure (for instance, changes in either the number of axes or the association between them). Contrarily, FEve, FDiv and  $Q$  are less dependent on the dimensionality of functional space and then more influenced by assembly rules. As  $Q$  quantifies both the distribution of functional units in functional space and the volume occupied in the functional space, it is logical that it is more sensitive to species richness than FDiv. Functional divergence and evenness measures, respectively FDiv and FEve, are only weakly sensitive to species richness according to their construction (Villéger, Mason & Moullot 2008). Functional evenness and divergence, through FEve and FDiv, quantify the distribution of functional units in functional space whatever the number of dimensions of the functional niche.

However, the sensitivity of an measure to assembly rules rather than species richness is not consistent with its ability to accurately discriminate assembly rules underlying community structure. The power analysis deserves to be discussed for two separate cases: indices including abundances or not. Indeed, biomass distribution can emphasize or understate functional relationships between species or units but is also affected by assembly rules. For presence/absence indices (GFD, FD and FRic), we obtained an overall high ability to successfully discriminate assembly rules with power values between 64 and 100% whatever species richness values. Yet FRic consistently reaches the highest power values especially for richness levels lower than 30 species which are commonly encountered in natural communities. For indices considering abundances (FAD, MFAD,  $Q$ , FDiv and FEve), the discrimination power is more variable. Overall, FDiv performs best while  $Q$ , FAD, MFAD and FEve poorly discriminate limiting similarly from a neutral process whatever the species richness. FEve is quite sensitive to niche filtering but hardly distinguishes limiting similarity from random assembly. Even if species were regularly distributed in the functional space, the log-normal distribution of abundances (i.e. few common species with a skewed tail of rare species) led to an uneven repartition of abundances. The highest level of evenness, FEve, would be expected when both species and their abundance are regularly distributed. It could be the case in competition (or limiting similarity) context where abundances are more evenly distributed than following a log-normal distribution curve. FEve could also discriminate between assembly algorithms when niche space is constant across all three assembly patterns (Mason *et al.* 2008).

#### WHICH FUNCTIONAL DIVERSITY MEASURE TO USE?

First of all, the choice of indices depends on the questions being raised and the study context. Here we propose a guideline, following our results, concerning two issues: the influence of biodiversity on ecosystem functioning which is mainly investigated with controlled communities in experiments and the elucidation of processes governing biodiversity patterns at local, regional and continental scales. For the former issue, the crucial question is no longer whether species richness influences ecosystem processes such as productivity or resilience but which facet of biodiversity has the strongest influence on ecosystem processes and in which environmental conditions (Cadotte *et al.* 2009). For instance, Villéger *et al.* (2010) demonstrated how habitat degradation differentially impacts each of the three components of functional diversity



with a loss of functional divergence while species richness increases. To test the effect of a set of biodiversity facets on ecosystem functioning ecologists usually rely on regression methods (e.g. Cadotte *et al.* 2009). However multicollinearity among explanatory variables is known to generate spurious results with interpretable coefficients since effects cannot be unambiguously segregated (Mac Nally 2002). Thus there is a need to consider independent facets of functional diversity to correctly assess effects of the diversity of traits on ecosystem processes. To this aim, we suggest to use a combination of three indices: one for each facet. FRic, FDiv and FEve seem to constitute a relevant combination since (i) these indices were built to be complementary (Villéger, Mason & Moullot 2008), (ii)  $Q$  is not independent from functional richness and (iii) GFD or FD need a cluster analysis which has some methodological problems and which loses information by reducing the dimensionality of the functional space (Mouchet *et al.* 2008). Nonetheless, in the case where the number of species in experiments is too small compared to the number of traits (richness higher than  $2^T$  with  $T$  being the number of traits), FRic, FEve and FDiv are no longer relevant. We suggest either to compute an ordination method (e.g. PCA) to reduce the number of traits or to use a combination composed of GFD and  $Q$  which are weakly correlated (0.367) but which miss the functional evenness component.

Concerning the second issue, the ability of functional diversity indices to reveal assembly rules underlying community structure, we differentiate indices taking into account abundances and the others relying only on presence/absence data. For the latter (GFD, FD and FRic), the power analysis shows that the three indices are able to efficiently differentiate assembly rules whatever species richness (Fig. 3). However we suggest using FRic for low richness values (10 species) instead of dendrogram-based indices while the choice of FD and GFD would be justified when the number of species is less than the number of traits (Villéger, Mason & Moullot 2008). GFD has the advantage over FD (i) to propose the 'best' dendrogram to represent the species in a reduced functional space (the one with less distortion) and (ii) to cope with categorical and/or quantitative traits with missing data. Although calculating FDiv or FEve on presence-absence data is possible, the abundance contribution to functional diversity will be missing, so abundance data are always preferable for these indices. When abundance data are available our results unambiguously suggest using FDiv which is the only index taking into account species abundances with a power value higher than 47% whatever the assembly rule or the richness value. Other indices poorly perform to either discriminate the limiting similarity process from a neutral process or when species richness is high ( $> 60$ ).

As FAD and MFAD are sensitive to the splitting and do not quantify any original functional diversity facet, we do not suggest their use for any purpose.

Last of all, as  $Q$  summarizes both functional richness and divergence, values should be interpreted with this in mind. Consequently, interpretation of relationships between  $Q$  and ecosystem or assembly processes will be complicated.

Yet, indices combining functional diversity components (like  $Q$ ) can be useful and must not be systematically avoided. Indeed,  $Q$  is the only concave abundance-weighted measure allowing a decomposition of the quadratic entropy into alpha-, beta- and gamma-diversities (Villéger & Moullot 2008).

Guidelines provided in this study rely on well defined artificial datasets. In the field, multiple factors may influence the functional structure of communities. Discriminating assembly rules of real communities from different environments and with varying species richness could be less straightforward. However, Mason *et al.* (2008) demonstrated that functional diversity indices may reveal changes in community assembly processes along an environmental gradient, suggesting that these indices may be robust in the face of complex processes structuring communities.

## Conclusion

In the study of relationships connecting functional diversity, community ecology and ecosystem processes, it is crucial to measure each of the complementary components with an appropriate index. Having established a set of appropriate indices, comparing the observed behaviour of each functional diversity index to that expected at random would be of great interest in testing whether communities are dominated by a particular assembly process. Significant departure from random expectation might indicate either that limiting similarity (index values higher than expected by chance, e.g. Cornwell, Schilck & Ackerly 2006) or niche filtering (index values lower than expected by chance) is the dominant process. However, assembly processes can interact to give a complex pattern or even a neutral one (Helmus *et al.* 2007). Therefore, investigating community structure with complementary methods such as phylogenetic relatedness (Webb 2000; Webb *et al.* 2002) through co-occurrence patterns (Cavender-Bares *et al.* 2004) or abundance distribution (Anderson, Lachance & Starmer 2004) appears indispensable to avoid spurious conclusions.

Considering both a multifaceted framework and assembly processes would allow more accurate predictive models and tools in the comprehension of how community structure is related to ecosystem functioning and opens new fields of research. Specifically, it provides a clear framework for addressing questions such as how environmental constraints influence functional diversity and how the three components of functional diversity interact with ecosystem processes such as the productivity, resilience or resistance to invasion.

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