Chapter 3
Functional Diversity Indices

Abstract Functional diversity may be summarized using indices based on trait values and species importance in the community, like abundance, cover and biomass. This chapter includes taxonomy of the indices based upon the information they used and the output they offer. For each index we have included its definition, the information needed to estimate it, their statistical and ecological properties, and some reference to explore its application to real cases. To facilitate the comprehension of all indices and diversity measures we used homogeneous notation.

Keywords Single-trait indices · Weighted diversity indices · Multiple-trait indices · Taxonomic biodiversity indices · FDiversity software

3.1 About Functional Diversity Indices and Measures

In this chapter, several indices and their definitions will be introduced. To avoid redundancy, Box 3.1 shows the notation used in this and other chapters. When deviations from this notation occur, it will be made clear in the text. The code name for the indices, as well as the author's reference will be mentioned in each definition. Even though we are focused on functional diversity and functional diversity indices, Sect. 3.2 has a brief presentation and one example of species diversity indices. We include the most commonly used indices and those that are often compared with functional diversity indices.

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Box 3.1: Notation

Variable	Meaning
ij	Used as subscripts to identify species; $i, j = 1, \ldots, \mathrm{S}$
t	Used as subscript to identify traits; $t = 1, \ldots, \mathrm{T}$
S	Number of species
T	Number of traits
$\mathrm{a_i}$	Absolute abundance of the ith species (with units; i.e. $\mathrm{m^2}$ for cover)
$\mathrm{w_i}$	Relative abundance of the ith species; $\mathrm{w_i} = \mathrm{a_i} \Big/ \sum_{i=1}^{S} \mathrm{a_i}$
$\mathrm{x_{ti}}$	tth trait value of ith species; for single-trait indices the subscript t is not necessary

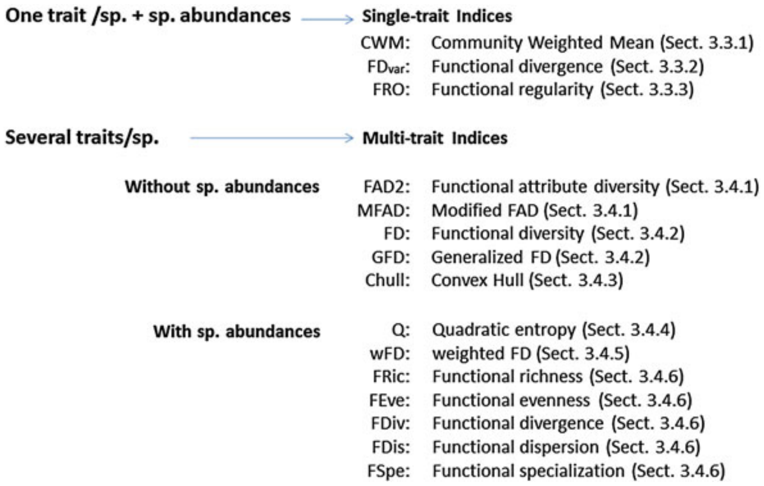

Fig. 3.1 Index classification with reference to sections in this chapter

There are single-trait metrics and indices that include some measurement of abundance to load the contribution of each species to the diversity aspect to be summarized. For example, the community weighted mean (CWM) reflects the functional mean of the trait, the functional divergence (FDvar) reflects the variance of the trait, while the functional regularity index (FRO) measures the functional evenness (Fig. 3.1). The classification criterion in Sects. 3.3 and 3.4 is if the metrics are single-trait or multi-trait. CWM is included as single-trait measure, although there is a fundamental difference between the CWM and the diversity indices: there is not any ecological principle to propose that the CWM of one trait would have any correlation with the functional diversity definition of the community.

Undoubtedly, CWM is a measure that allows knowing the best value to represent the state of a trait in the community; it is a metric of functional composition. Definitions and examples of single-trait indices are presented in Sect. 3.3.

The indices based on multi-trait profiles, may or may not take into account species abundance. In the last decade of the twentieth century, Faith (1996) proposed a functional diversity index based on the application of the index of environmental diversity (ED) to a functional space constructed using phylogenetic information, and Walker et al. (1999) defined a functional diversity index by identifying the number of different combinations of trait values (FAD1). Most of the later approaches are based on dissimilarity among species in trait space, the T-dimensional space defined by the T traits (Fig. 3.1). In Sect. 3.4 we define the indices and present an example. The multi-trait indices that may be estimated without abundance information are based only on presence/absence data; to estimate the other multi-trait indices it is needed to incorporate species abundances. There is some controversy in current literature about how the impact of summarizing functional diversity and its relationship with the variable is used to measure abundance. Posed questions focus on the relative contribution of abundance upon the functional diversity components, like the functional richness, the functional evenness and the functional divergence (Schmera et al. 2009; Poos et al. 2009; Mouchet et al. 2010).

To estimate an index we used abundance-trait profiles corresponding to the species present at the community or assemblage. This profile includes one value for each trait and one value for each variable used to quantify the relative contribution of each species to the pool. At least values of one trait by species are needed to compute single-trait indices and values for two or more traits to compute multi-trait indices. Nevertheless, it is analytically possible to calculate some multi-trait indices with values for only one trait. For example, the FD (Petchey and Gaston 2002) diversity index (Sect. 3.3.1) may be calculating with species values for one trait.

3.2 Species Diversity Indices

Richness (S): richness is the total number of species in a community. It is the most simple biodiversity index and it does not take into account any characteristic of species or their relative abundance. Several estimators to avoid bias due to unseen or unrecorded species are currently used like those proposed by Chao et al. (for details see for example Magurran 2004). In a functional diversity context it is common practice to include enough species to account for near 80% of the abundance (Grime 1998). This approach does not need to adjust observed species number because functional diversity is not affected by rare species.

Shannon Index (H): this index assumes that heterogeneity depends on both, the number of species in a community and their proportional abundances. Conceptually, it is a measure of uncertainty degree related to a random selection of individuals from the community. In a homogeneous community with S species, in which only one is dominant (highly abundant), the uncertainty degree of selecting a given species is lower than if all species would have the same abundance. When species abundances are uneven, the probability that a random individual taken from the population belongs to the dominant species approximates one; conversely, in a heterogeneous community any randomly drawn individual has the same probability (1/S) to belong to any species. The Shannon index is one of the biodiversity measures most widely used.

The Shannon index assumes that individuals are randomly sampled from an "indefinitely large" (i.e., an effectivelly infinite) population. The index also assumes that all species are represented in the sample. It is calculated from the equation (Shannon and Weaver 1949)

$$\mathrm{H} = -\sum_{\mathrm{i}=1}^{\mathrm{S}} \mathrm{w_i} \ln(\mathrm{w_i}).$$

Eveness (*E*): the maximum of Shannon index is attended when all the species has the same relative abundance, and it reduces to

$$\mathrm{H_{max}} = \ln(\mathrm{S}).$$

Based on this maximum it is possible to derive an evenness index, using the maximum as reference for the actual value (Pielou 1975) as the ratio

$$\mathrm{E} = \mathrm{H}/\mathrm{H_{max}},$$

where E is the evenness index.

Simpson Index (*D*): Simpson index of biodiversity equals the probability of drawing without replacement two individuals of different species from a given collection. There is more than one form to express the index. The expression widely used offers the index as a measure of dominance

$$\mathrm{D} = 1 - \sum_{\mathrm{i}=1}^{\mathrm{S}} \mathrm{w_i^2},$$

where $\mathrm{w_i^2}$ is the squared of the proportion of the *i*th species (Simpson 1949).

3.3 Single-Trait Metrics and Indices: Properties and Estimation

3.3.1 Community Weighted Mean

Community weighted mean (CWM) is a good indicator to represent the expected functional value of one trait in a random community sample. Also defined as aggregate values of plant traits by Garnier et al. (2004) it is extensively used as community weighted mean (Díaz et al. 2007; Lavorel et al. 2008). As CWM is based on single-trait, each trait has its CWM value in the assemblage. To calculate it we need one trait value to represent each species, so if we have 10 species and we want to calculate CWM of specific leaf area (SLA) we need 10 SLA's values (x_i in Box 3.1). We also need one variable representing the contribution of each species to the community. Suppose that for each species we have evaluated the cover in square meters (a_i in Box 3.1) then we may express the cover in relative form (w_i in Box 3.1). The community weighted mean is

$$\mathrm{CWM} = \sum_{i=1}^{S} w_i \, x_i . \tag{3.1}$$

It is strongly recommend following standard protocols to assign trait values to species (Cornelissen et al. 2003). Depending on the trait variability it could be necessary to measure 5–10 representative individual for each species. After having the data set for the whole community the mean value for continuous variables or median for discrete ones may represent each species in the index calculation. There are several categories already defined in the literature for particular traits like flammability (Cornelissen et al. 2003; Jaureguiberry et al. 2011), or nodule type for nitrogen-fixing species (Cornelissen et al. 2003).

To apply the formula (3.1) to the example in Box 3.2 we have to calculate the relative contribution of each species from the cover data in its original scale divided by the total coverage, in this case it is 10,042 m^2, doing so we obtained the values of the relative cover column. Having all the data in the appropriate scale, we multiply each SLA value by the corresponding relative value and sum all results to obtain the CWM. In the example its value is 19.01 $mm^2\ g^{-1}$. This value is greater than the arithmetic mean (18.26 $mm^2\ g^{-1}$) because it incorporates a loaded factor that in this case favors the *sp2* and *sp8* with greater SLA values. To summarize community performance related to ecosystem processes the CWM represents the best single value to link with other variables and look for relationships with a given ecosystem service.

Box 3.2: Trait profiles for ten species used to estimate CWM

Species	SLA (mm^2g^{-1})	Cover (m^2)	Relative cover	Species	SLA (mm^2g^{-1})	Cover (m^2)	Relative cover
sp1	19.30	245	0.0235	sp6	13.81	312	0.0300
sp2	19.53	2540	0.2439	sp7	9.94	780	0.0749
sp3	15.64	34	0.0033	sp8	21.93	3545	0.3405
sp4	18.44	2045	0.1964	sp9	31.65	108	0.0104
sp5	17.37	35	0.0034	sp10	14.98	768	0.0738

3.3.2 Functional Divergence

Functional divergence index (FD_{var}) is essentially the variance in the attribute values of the species present at a site, with the squared residuals weighted by the abundance of the species involved (Mason et al. 2003). It is defined as

$$FD_{var} = \frac{2}{\pi} \arctan(5V) \tag{3.2}$$

where 5 is a scaling factor used to define the index over a range of 0–1; V is the weighted variance of trait X, expressed as:

$$V = \sum_{i=1}^{S} w_i \left(\ln x_i - \overline{\ln x}\right)^2. \tag{3.3}$$

This index considers one trait at a time and used the relative abundance of each species (w_i) to load its contribution to the variability in the community (Box 3.1). The mean of $\ln x_i$ is weighted by the abundance as

$$\overline{\ln x} = \sum_{i=1}^{S} w_i \ln x_i. \tag{3.4}$$

Using data from Box 3.2 the FDvar is 0.15 and this index has no units because the trait values, originally expressed in squared millimeters of leaf area divided by dry weight in grams has been transformed to a logarithm scale and expressed in the range zero–one. So this value of 0.15 corresponds to a small variability for SLA. If we interchange in Box 3.2 the cover of species *sp7* and *sp8* but keeping the SLA values and recalculate the FDvar, we obtain FDvar = 0.30. This is twice the first estimation, and it is the consequence of assigning a cover of 3,545 m^2 to *sp7* with SLA = 9.94 $mm^2\ g^{-1}$ (one of the smallest values for SLA). The variability of this trait increases due to that more abundant species now bear the more extreme values for SLA (9.94, 19.53 and 18.44 $mm^2\ g^{-1}$).

This index has also been defined to handle more than one value of the trait by species (Mason et al. 2003) using the character values (x_i) and the abundance of these values in all the species of the community. For this functional divergence formulation the sum is over the total possible values of the trait under consideration.

3.3.3 Functional Regularity

Functional regularity index (FRO) has been defined for one trait with only one value of the trait by species, like the mean or the median. FRO was introduced to capture a neglected aspect of functional diversity as is the regularity or evenness of the trait values in the observed range (Mouillot et al. 2005). As the other single-trait indices it also used the relative abundance of each species. The procedure to calculate the index needs to sort the observations. It is as follows: (a) the species are ranked by increasing values of the trait (x_i); (b) we calculate the weighted difference $\left(EW_{i,i+1}\right)$ of trait values of two consecutive species loaded by the abundance difference as

$$EW_{i,i+1} = \frac{|x_{i+1} - x_i|}{|w_{i+1} + w_i|} \tag{3.5}$$

where w_i is the relative abundance of the ordered *i*th species; (c) with these values, we calculate the percentage of the weighted difference ($PEW_{i,i+1}$) in trait values for the pair of species as

$$PEW_{i,i+1} = \frac{EW_{i,i+1}}{\sum_{i=1}^{S-1} EW_{i,i+1}}; \tag{3.6}$$

and (d) the FRO index results from the summation of all $S - 1$ pair comparison, choosing the minimum between the percentage of the weighted difference and the equally probable space $1/(S - 1)$

$$FRO = \sum_{i=1}^{S-1} \min\left(PEW_{i,i+1}, \frac{1}{S-1}\right). \tag{3.7}$$

The maximum of FRO is obtained when each pair of nearest neighbors equals $1/(S - 1)$ and each species has the same abundance, case of maximum functional regularity and $FRO = 1$. In all other cases FRO is less than one; and quantifies how the observed community differs from other communities with the same richness, where all species have the same abundance, and its trait values are regularly distributed resembling to the outcome of the uniform probability distribution.

Using the data of Box 3.2 we obtained a $FRO = 0.39$ (Fig. 3.2a), approximately one third of a community where the ten species have equal abundance and its trait values are uniformly distributed in the range of SLA (9.94 to 31.65 $mm^2\ g^{-1}$). Suppose that due to human modification or to environmental process the relative abundance of each species is near 0.10 (Fig. 3.2b). In this case the FRO increase to 0.60. FRO may also increase if the trait values are more evenly distributed. If we interchange abundance of species *sp7* and *sp8*, and also between *sp9* and *sp10*, we obtained $FRO = 0.47$ (Fig. 3.2c).

All these changes in FRO have happened with the same set of trait values, but with modifying the matching between trait value and the relative abundance. The index may also be affected by changes in the trait values. For example, if the species *sp1*, *sp5* and *sp10* change their values to 29.30, 27.37 and 24.98 $mm^2\ g^{-1}$, the FRO with the observed abundance would be 0.65; and if we considered all species with the same abundance it would be 0.89, closer to one, due to a very uniformly distribution of equally abundance trait values (Fig. 3.2d).

Even though FRO is defined for one trait at a time, the authors (Mouillot et al. 2005) suggested two options to extend the index to multiple traits. One is to estimate FRO for each trait and then take the mean value to represent the

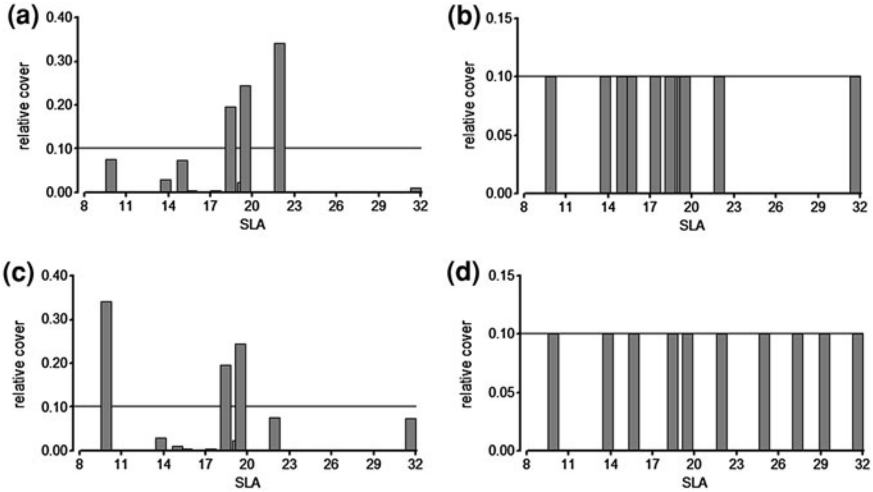

Fig. 3.2 Relative abundance for specific leaf area (SLA) trait values of species in Box 3.2. **a** Original data, corresponding to FRO = 0.39; **b** species with the same abundance (relative cover 0.10), corresponding to a FRO = 0.60; **c** interchange abundance values between sp7 and sp8, and between sp9 and sp10, corresponding to FRO = 0.47; **d** change the SLA values of sp1, sp5 and sp10 to 29.30, 27.37 and 24.98 mm^2g^{-1} with the same species abundance (0.10), corresponding to a FRO = 0.89. Note y-axis scale in **a** and **c** is different from y-axis scale in **b** and **d**. Horizontal line is at relative cover 0.10 in the four plots

community; this mean value may be weighted by trait importance if desirable. The second one is to compute a Principal Component Analysis on the S × T matrix and use the principal components to compute T values of FRO and then sum using eigenvalues or standard deviation of eigenvectors as weights to compute the overall functional regularity (OFRO)

$$\mathrm{OFRO} = \sum_{t=1}^{T} \mathrm{SD}_t \times \mathrm{FRO}_t,$$

where SD_t the standard deviation and FRO_t the functional regularity for each principal component.

3.4 Multi-Trait Indices: Properties and Estimation

3.4.1 Functional Attribute Diversity

The index FAD (Functional Attribute Diversity, Walker et al. 1999; Walker and Langridge 2002) has two expressions. FAD1 is the number of different attribute combinations that occur in the community and it is always less than or equal to richness. When traits are in a continuous scale it always coincides with richness and its use is not recommended. When the traits are categorical, with few levels it may resume a crude functional richness; even though, there are more appropriate functional indices as further described.

The second expression (FAD2) is the sum of the standardized distance between all pairs of species in the trait space. The authors recommend expressing the trait values in a five-point scale. As an ecological distance (ED), they use the Euclidean distance between two species. The sum over all pairs of species gives the FAD2. The ecological distance between species ‘i’ and ‘j’ may be expressed as (Eq. 1a, from Walker et al. 1999)

$$\mathrm{ED_{ij}} = \sqrt{\sum_{t=1}^{T} \left(x_{tj} - x_{ti}\right)^2}$$

where T is the total number of attributes, and x_{ti} and x_{tj} are the values of the *t*th trait of species ‘i’ and ‘j’. Using $\mathrm{ED_{ij}}$, which is the Euclidean distance between two species, FAD2 is defined as

$$\mathrm{FAD2} = \sum_{i=1}^{S} \sum_{j>1}^{S} \mathrm{ED_{ij}}$$

in a community with S species.

In an attempt to make FAD2 comparable among communities with different number of species, the authors propose to standardize the index dividing by the number of interspecies comparisons. With S species the total number of distances among a pair of species is $S \times (S - 1)/2$, and the index for each community to be compared may be transformed to comparable scales using

$$\mathrm{FAD2_{(Z)}} = \frac{\mathrm{FAD2}}{S(S-1)/2},$$

being $\mathrm{FAD2_{(Z)}}$, the standardize expression.

MFAD is another modified version of FAD2 proposed by Schmera et al. (2009) to overcome the violation of monotonicity criteria. For a given assemblage with S species and T traits they first defined the so called functional units. The number of functional units results from combining the species with exactly the same trait profiles into only one functional unit. The number of entities in the data matrix will be reduced from S to N ($N \leq S$), and dimensions of the distance matrix will be reduced from $S \times S$ to $N \times N$. N itself is a measure of functional richness, already proposed by Walker et al. (1999) as FAD1.

To calculate MFAD, the dissimilarity metric must be defined in the range [0; 1], and the authors proposed the use of the Marczewski-Steinhaus index (Marczewski and Steinhaus 1958) or a distance defined in the same interval, like Gower distance (Gower 1971). The index is estimated as:

$$\mathrm{MFAD} = \frac{\sum_{i=1}^{N} \sum_{j>1}^{N} d_{ij}}{N},$$

where d_{ij} is the dissimilarity between functional units 'i' and 'j', and N is the number of functional units.

MFAD measures the dispersion of species in the trait space in comparable scales if the set of traits are the same. So it provides a simple numerical tool to compare several communities. Several authors have claimed that its contribution to functional diversity approach is not significant due to high correlation with richness (Mouchet et al. 2010; Pavoine and Bonsall 2011).

3.4.2 Functional Diversity Based on Dendrograms

There is a family of functional diversity indices based on dendrograms. The first one was proposed by Petchey and Gaston (2002) and has been used in functional ecology as 'the' index. Even a decade later this index and its code name FD is one of the most used in applied functional ecology. Several adjustments have emerged from scientific controversy between Petchey and Gaston (2002, 2006, 2007) and Podani and Schmera (2006, 2007); others from the inclusion of abundance to weight the relative contribution of each branch tree to the index (wFD, Pla et al. 2008; Casanoves et al. 2008, 2011).

FD is the total length of the branches of the dendrogram constructed from information on species functional traits (Petchey and Gaston 2002). Different measures of dissimilarities, and different strategies used to define the dendrogram lead to different values of FD. As in the hierarchical clustering algorithm several linking strategies can be used and the number of distance measurement can be calculated to quantify the distance between species, Mouchet et al. (2008) have proposed iteratively select the best combination of linkage and distance to reproduce the original distance between the species pool. The selection is based on the cophenetic correlation and the index is known as generalized-FD (GFD).

The first definition of FD (Petchey and Gaston 2002) proposed to make a single dendrogram for the so-called 'regional community', with all the species that have been observed in any sample of the study area. Based on this maximum value for FD, any particular sample of the study area will have its own FD resulting from the sum of branch length of the species present at the considered sample, required to connect these species to the root of the dendrogram. This expression was criticized because the index does not equal zero when only one species is present. It is zero only when no species is present (Podani and Schmera 2006).

These authors have proposed to recalculate the dendrogram for each sample, but in doing so the desirable property of 'set monotonicity' does not hold. That is, the index may be greater for a community after one (or more) species is lost; and conversely the FD may be smaller for a community which has gained one or more species.

The second definition of FD as the sum of lengths of all branches of the dendrogram made by Petchey and Gaston (2006) addresses the lack of monotonicity that arises when using a particular dendrogram for each sample as Podani and Schmera had proposed. To calculate FD in each sample of the community, this version of FD sums the lengths of the branches on the dendrogram needed to connect the present species, no including the length of the branch to get to the root (Petchey and Gaston 2007).

Both versions of the FD are based on a single trait value per species. However, it is possible to incorporate intraspecific variability in the estimation when trait values are available at individual level. This functional diversity index incorporates intraspecific variability and it is less correlated with richness (iFD, Cianciaruso et al. 2009). The authors claim that important ecosystem processes operate at individual level, like competition for resources, niche occupancy and so natural selection. A particular value taken by the trait is an attribute of the individual; within a species the trait may show different attributes along environmental gradients or through time, or among different land use practices.

One way to avoid subjectivity in the selection of the distance measurement and the linkage strategy is to compare the ultrametric matrix computed to make the dendrogram with the distance matrix calculate from the functional trait profiles. Even though, no clustering procedure perfectly fits data distribution in multidimensional space. Mouchet et al. (2008) propose a systematic procedure to calculate combinations of distances (Euclidean and Gower) and several cluster linkages: single linkage, complete linkage, UPGMA (unweighted pair group method using arithmetic averages), WPGMA (weighted pair group method using arithmetic averages), UPGMC (unweighted pair group centroid method), WPGMC (weighted pair group centroid method) and Ward’s method; and then, build the consensus tree that optimally represents the clustering methods.

This index is called Generalized FD (GFD) and the selection of the best combination is based on the comparison between dissimilarity matrix and cophenetic matrix. The cophenetic matrix is an S × S symmetrical matrix that quantifies the distance between species in the dendrogram. The less difference between the corresponding elements of these two matrices, the better the cluster procedure resembles the diversity in trait space. The authors used the cophenetic correlation (Pearson correlation computed from pairs of distances) to select the combination that best fits. If the cophenetic correlation is large, the distance portrayed in the dendrogram is a good representation of distances between species, in the trait space. R script may be downloaded from Ecolag author’s site (http://www.ecolag.univ-montp2.fr) and FDiversity software also calculates it from the same information used for the other functional diversity indices.

Further discussion about dissimilarity measurements, cluster strategies and comparison among communities can be found in Petchey et al. (2004) and Petchey and Gaston (2007), the response of Podani and Schmera (2007) and Poos et al. (2009).

FDiversity team[1] (Pla et al. 2008; Casanoves et al. 2011) proposed using abundance to quantify species contribution to the community when a hierarchical clustering approach is used for functional diversity (wFD, Sect. 3.4.5).

3.4.3 Convex Hull Hyper-Volume

The dispersion of species in the trait space is a crude multivariate representation of the functional diversity in a community. Cornwell et al. (2006) proposed to synthesize this dispersion by quantifying the best shape hyper-volume with an appropriated volume model. Among the candidates are hyper-cube or hyper-sphere models, but these do not reduce the amount of empty space. A better option is to use the convex hull, defined as the smallest convex set enclosing the points (Barber et al. 1996).

A convex hull hyper-volume (CHull) in a multivariate space is defined, based on the irregular form yielded by species occupancy in the trait space. Taking two species from one community, any third species with traits inside the range of traits is included in the CHull. If only two traits are involved, the CHull may be represented with a surface in 2D (Fig. 3.3a–c); when there are three traits the CHull is a volume in 3D (Fig. 3.3d), and with four or more traits CHull is a hypervolume. The convex hull is a multivariate measure of the range of trait space (trait values that may be found in a given assemblage). The sequence from Fig. 3.3a–c shows increasing trait ranges; the three graphs have the same units because the trait values were standardized to have zero mean and unit variance. T3, the third trait has the widest range, so the combination T3–T2 has the highest surface, all expressed in standard deviations from the corresponding mean.

3.4.4 Quadratic Entropy

Functional diversity may be expressed as the average of the species differences when some measurement of pairwise differences between species and relative frequency data are available. The index proposed by Rao (1982) is derived from entropy theory and is expressed as a quadratic form using the matrix of distances among species and the vector of relative abundance of species. To compute the index it is necessary to calculate the Euclidean distance between species in the trait space as

$$d_{ij} = \sum_{t=1}^{T} \left(x_{tj} - x_{ti}\right)^2$$

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[1] FDiversity team is integrated by the authors of this book and is the developer team of FDiversity, statistical software to calculate functional diversity with extended capabilities (Di Rienzo et al. 2008).

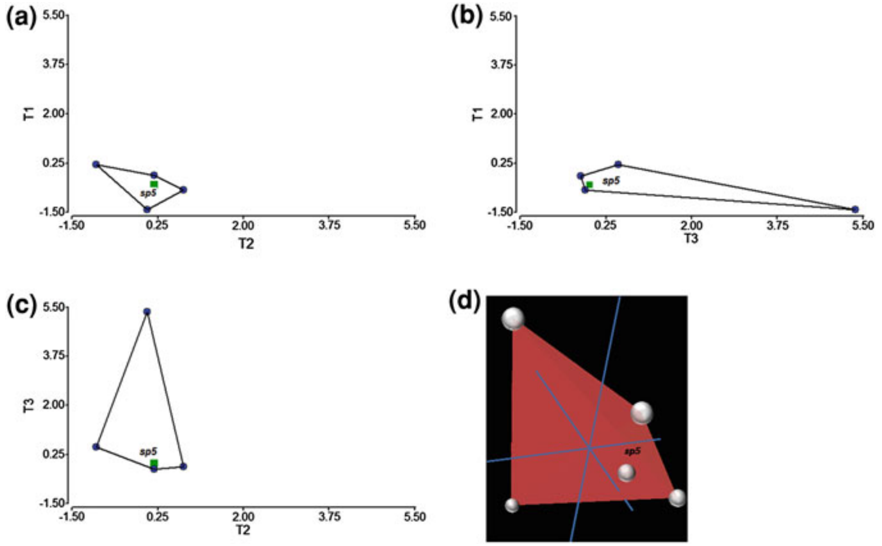


Fig. 3.3 Convex hull (CHull) in two and three dimensions. The data are for three traits and five species; **a** surface delimited by the outer species in plane T1-T2 (CHull = 1.140), **b** surface in plane T1-T3 (CHull = 2.941), **c** surface in plane T3-T2 (CHull = 4.947), **d** volume in the three dimensional space T1-T2-T3 (CHull = 0.462); sp5 has intermediate trait values and it is identify within the surfaces and also within the volume. Data are standardized and CHull values showed at the top of each graph. A similar limit for x–y axes of the first three graphs allows visual comparison among CHull values. Trait values were standardized by trait

and estimate Rao index as (Rao 1982)

$$\mathrm{Rao} = \sum\nolimits_{i=1}^{S-1} \sum\nolimits_{j>1}^{S} d_{ij}\, w_i w_j = \frac{1}{2}\mathbf{w}'\,\mathbf{D}\,\mathbf{w}$$

where d_{ij} is the distance between species ‘i’ and ‘j’. In matrix notation, **D** is a distance matrix with elements d_{ij}, and **w** is a column vector with the relative abundances.

Botta-Dukát (2005) has suggested using Euclidean distance divided by the number of traits used to define it. To be compared, functional diversity indices has to be evaluated over the same set of traits, so all the distances are calculated over the same number of traits and this adjustment has no effect for comparison among samples or communities. The new expression is the original divided by a constant.

The Rao index may also be seen as the expected value of the conflict among species (Ricotta and Szeidl 2006). As the species abundances are expressed as relative values, it sums to one $\sum\nolimits_{i=1}^{S} w_i = 1$ and the frequency of any species may be expressed as $1 - \sum\nolimits_{j \neq i}^{S} w_j$. So, the conflict between species ‘i’ and the remaining $(C_d(w_i))$ may be express as

$$C_d(w_i) = \sum_{j \neq i}^{S} d_{ij} w_j .$$

The functional diversity is then

$$\mathrm{Rao} = \sum_{i=1}^{S} w_i\, C_d(w_i) = \sum_{i=1}^{S} w_i \left[\sum_{j \neq i}^{S} d_{ij}\, w_j \right],$$

the second summation equals $\sum_{j=1}^{S} d_{ij}\, w_i$, since the distance of a species with itself is zero, $d_{ii} = d_{jj} = 0$. This expression proves that the Rao index is also a measure of the conflict among species (Ricota and Szeidl 2006).

The unbiased estimator of Rao when the abundance of species is expressed as number of individuals is

$$\hat{\mathrm{Rao}} = \frac{n}{n-1} 2 \sum_{i>j}^{S} d_{ij} \frac{n_i n_j}{n^2}, \quad \hat{\mathrm{Rao}} = 2 \sum_{i>j}^{S} d_{ij} \frac{n_i n_j}{n(n-1)},$$

where n_i is the number of individuals of species ‘i’ and $n = \sum_{i=1}^{S} n_i$ is the total number of individuals. If the sample is big enough the correction term $n/(n-1)$ is almost one and the index may be calculated without correction. The variance of $\hat{\mathrm{Rao}}$ may be estimated as (Shimatani 2001)

$$\mathrm{Var}(\hat{\mathrm{Rao}}) = \frac{4}{S(S-1)} \left\{ \begin{array}{l} (3-2S) \left(2 \sum_{i>j}^{S} d_{ij} \frac{n_i n_j}{n^2} \right)^2 + \\ \qquad + (S-2) \sum_{i,j,k}^{S} d_{ij} d_{ik} \frac{n_i n_j n_k}{n^2} + \sum_{i>j}^{S} d_{ij} \frac{n_i n_j}{n^2} \end{array} \right\}.$$

The variance is useful with large samples and when differences between communities have to be tested based on one sample for each community. The distribution model for Rao index is not known and depends on the distance measure thus, non parametric estimation may be preferred to build confidence intervals and to test hypothesis.

Useful information may be extracted from the symmetric matrix $Q = \mathrm{diag}(\mathbf{w})\mathbf{D}(\mathrm{diag})\mathbf{w}$, where ‘diag’ states for diagonal matrix with relative abundances of each species. This matrix has dimension $S \times S$ and its *ij*th element is $q_{ij} = d_{ij}\, w_i w_j$, its main diagonal is zero, and it is known as the species contribution matrix. The absolute species contribution for each species may be evaluated summing along the columns of the contribution matrix, and a relative expression of this contribution is obtained dividing these values by $2 \times$Rao index (Box 3.3). The reference must be twice the index because each distance, between two species, counts twice, one when sum is over the column for the first one of the pair and the other when the sum is over the second.

Box 3.3: Distance matrix and abundance vector used to estimate Rao index

$$\mathrm{X} = \begin{array}{cccc} t_1 & t_2 & t_3 & \\ 0.20 & -1.00 & 0.51 & \mathit{sp1} \\ -1.41 & 0.03 & 5.35 & \mathit{sp2} \\ -0.20 & 0.18 & -0.27 & \mathit{sp3} \\ -0.70 & 0.77 & -0.18 & \mathit{sp4} \\ -0.52 & 0.18 & -0.08 & \mathit{sp5} \end{array}$$

X is the data matrix with 3 columns, one for each trait; and 5 rows, one for each species. The trait values has been standardize (see Box 4.1 for details).

$$\mathrm{A} = \left[70 \quad 27 \quad 1 \quad 140 \quad 17 \right]$$

A is the vector of observed frequencies.

$$\mathbf{w} = [0.274509\ 0.105882\ 0.003922\ 0.549020\ 0.066667]$$

W is the vector of relative frequencies.

With this data the distance matrix D may be calculated using the Euclidean distance

```
              sp1       sp2       sp3       sp4       sp5
       sp1   0.0000   27.0786    2.1608    4.4190    2.2589
       sp2  27.0786    0.0000   33.0710   31.6326   30.2995
  D =  sp3   2.1608   33.0710    0.0000    0.6062    0.1385
       sp4   4.4190   31.6326    0.6062    0.0000    0.3905
       sp5   2.2589   30.2995    0.1385    0.3905    0.0000
```

Each element of the contribution matrix Q may be calculated multiplying the distance between two species by the corresponding relative frequencies. For examples, for the first element of the second column the value 0.7871 was obtained as

$$q_{12} = 27.0786 \times 0.274509 \times 0.105882.$$

```
                          sp1    sp2    sp3    sp4    sp5
                    sp1  0.0000 0.7871 0.0023 0.6660 0.0413
                    sp2  0.7871 0.0000 0.0137 1.8389 0.2139
                Q = sp3  0.0023 0.0137 0.0000 0.0013 0.0000
                    sp4  0.6660 1.8389 0.0013 0.0000 0.0143
                    sp5  0.0413 0.2139 0.0000 0.0143 0.0000

                  Total  1.4967 2.8546 0.0173 2.5205 0.2695
      Contribution (%)     20.9   39.9    0.2   35.2    3.8
```

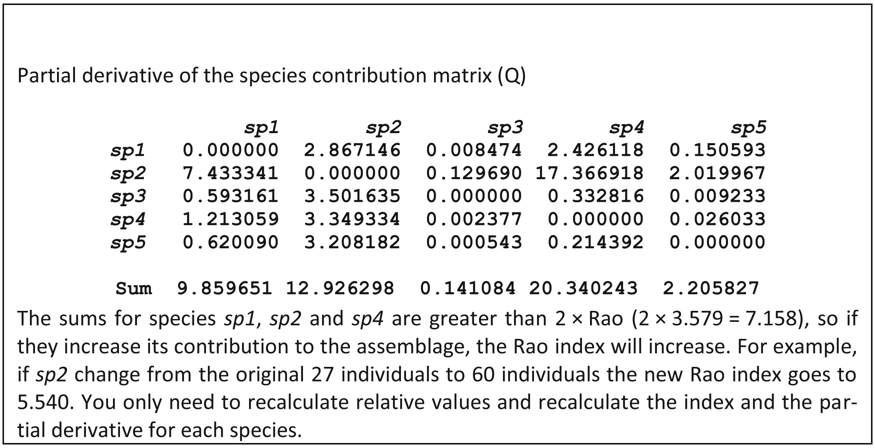
Two species (*sp2* and *sp4*) have high contribution, other two has very low contribution (*sp3* and *sp5*) and *sp1* has a medium contribution to the functional diversity.

Both, absolute and relative contributions of each species are highly related to abundance. To explore the effect of species contribution upon the index, the partial derivative of the species contribution matrix (Q) with respect to the *i*th species contribution (n_j) may be computed as

$$\partial Q / \partial n_j = \frac{2}{n} \left(\sum_{i=1}^{S} d_{ij} \frac{n_i}{n} - \mathrm{Rao} \right).$$

If $\sum_{i=1}^{S} d_{ij} n_i \big/ n$ is greater than Q, a small increment of species 'j' increases the Rao diversity index (Shimatani 1999). This is because the first term is the average distance from an individual of species 'j' to all the others (see numerical example in Box 3.4), and the second term is the average distance over all the pairs; so, if the species 'j', has a greater average and its frequency increases, the overall average increases accordingly. On the other hand, if a species with very small contribution increases its relative abundance the index may decrease due to a negative difference between the species average distance and the overall average distance that is the Rao index.

Box 3.4: Species relative abundance changes affect the Rao index



Partial derivative of the species contribution matrix (Q)

```
             sp1       sp2       sp3       sp4       sp5
sp1     0.000000  2.867146  0.008474  2.426118  0.150593
sp2     7.433341  0.000000  0.129690 17.366918  2.019967
sp3     0.593161  3.501635  0.000000  0.332816  0.009233
sp4     1.213059  3.349334  0.002377  0.000000  0.026033
sp5     0.620090  3.208182  0.000543  0.214392  0.000000

Sum    9.859651 12.926298  0.141084 20.340243  2.205827
```

The sums for species *sp1*, *sp2* and *sp4* are greater than 2 × Rao (2 × 3.579 = 7.158), so if they increase its contribution to the assemblage, the Rao index will increase. For example, if *sp2* change from the original 27 individuals to 60 individuals the new Rao index goes to 5.540. You only need to recalculate relative values and recalculate the index and the partial derivative for each species.

The partial derivative is useful for understanding graphics of changes in diversity when one species is virtually removed from the assemblage. The index may increase or decrease in relation to the average distance of the removed species with the overall average distance.

The expression of quadratic entropy as an absolute value is not useful when the comparisons have to be done between communities with very different numbers of species or when different sets of traits were used to define the distance matrix. To get a relative expression the maximum has to be estimated from the data. The distance matrix does not depend on the abundance of species and is fixed for a given set of species, but changes in the relative abundance of these species may lead to the maximum diversity index (Rao_{max}). There are two types of abundance vectors that define two subclasses of maximum: (a) weak maximization, when some of the w_i abundances that maximize Rao_{max} are zero; and (b) strong maximization, when all the w_i values that maximize Rao_{max} are positives.

The maximization process relies on the dissimilarity matrix and on any ultrametric matrix that belongs to the strong subclass (Pavoine et al. 2005). The drawback arising from having only some species to maximize the Rao's quadratic index when dissimilarity between species are based on functional traits is the absence of distance measures that guaranty the ultrametric condition and then ecological meaningful expression of the functional diversity using relative Rao index. Taxonomic or phylogenic dissimilarity trees may have ultrametric distances and give a maximum value of Rao that relies on total abundance distributed among all the species presents.

In the *ade4* software, also available as an R library, the sentence 'divc' may be used to calculate this index. The algorithm return Rao when absolute value is required (scale = FALSE), and the relative value (scale = TRUE) in the range [0, 1] when scaling is required. With FDiversity software both expressions may be obtained simultaneously.

3.4.5 *Extended FD*

The FD proposed by Petchey and Gaston (2006) is based on a dissimilarity matrix computed with one mean value by trait and species and no importance measure to weigh the species abundance in the community. It is possible to load each entry of this dissimilarity matrix with a relative measure of abundance (frequency, coverage, biomass, basal area, or other) before performing the dendrogram. If d_{ij} denotes the dissimilarity measurement between species 'i' and 'j', and w_i and w_j denote the relative abundance of each species, the weighted FD (wFD) is computed from a matrix with entries $d'_{ij} = d_{ij}\left(\sqrt{w_i w_j}\right)$. The resulting weighted dissimilarity matrix is symmetric with zeros in the diagonal. The wFD is computed as the total branch length of the functional dendrogram derived from this symmetric matrix (Pla et al. 2008, Casanoves et al. 2008, 2011). The scaled form of wFD multiplies the sum by the total number of species to put it in the same metric as FD.

As in the FD case, the dendrogram may be computed only with the set of species present in each plot (wFDp plot based), or may be derived from one dendrogram including the species community pool (wFDc community based). With equi-abundance wFD equals FD. In case study 1 in Sect. 4.2 we compare FD and wFD to show how changes in these indices can be used to explore the relationship between functional diversity and changes in abundance and trait values.

3.4.6 *Functional Richness, Evenness, Divergence and Dispersion*

Villéger et al. (2008) argued that functional diversity cannot be summarized by a single number because it has to include components of richness, evenness and divergence taken into account the trait values and their abundance. They proposed a framework where functional diversity comprises three components: functional richness, functional evenness, and functional divergence. The three independent components provide more detail in examining the mechanisms linking biodiversity to ecosystem functioning. Mason et al. (2005) were one of the first to call the attention about the importance of these three facets of functional diversity to understand its relationship with ecosystem processes and ecosystem services. Villéger et al. defined FRic (functional richness), FEve (functional evenness) and FDiv (functional divergence) using multiple traits.

To complement these three measurements of functional component Villéger et al. (2010) have proposed an index of functional specialization (FSpe) that quantify the relative positions of species respect to the gravity center calculated from the regional pool of species. The index is based on Bellwood et al. (2006) relative distance of a species from the centroid of the principal component space account for at least 85% of the variability observed.

Functional richness (*FRic*): FRic represents the trait space filled by the community. In the one trait case it is represented by the range (maximum–minimum), but with more than one trait it is represented by the volume filled by the community in the trait space. The procedure is like the convex hull hyper-volume (Cornwell et al. 2006). The algorithm identifies the extreme species and then estimates the volume in the trait space. It is recommended to standardize the traits to avoid scale effects. To calculate FRic the number of species must be greater than the number of traits and the species must not relay on a line. The maximum value of FRic in a T dimensional trait space is attained when 2^T species have a combination of extreme trait values.

An option to estimate FRic when the number of species is less than the number of traits is to synthesize the trait space using a multivariate technic to reduce the dimensions. If all the traits are in a quantitative scale principal component analysis may be applied and the resulted component used as new ‘trait synthesis’. The number of components retained depends on the proportion of variability explained and are limited to the number of species minus one. With categorical or nominal traits the reduction may be derived using principal coordinate analysis (also known as classical multidimensional scaling) and retained the appropriate coordinate values. In the R-scrip of FD-library written by Laliberté and Legendre (2010) to perform this calculation, this procedure is used by default. In FDiversity, there are two separate indices, one for Convex Hull (equal to FRic when $S > T$, and no values when $S \leq T$ or at least two species are distributed in a line) and other for FRic calculated using linear combination of traits resulted from ordination technics.

Functional evenness (*FEve*): FEve measures the regularity of spacing between species in the trait space as did the univariate FRO and also the evenness in the distribution of the species abundance. The authors do not use the overall FRO proposed by Mouillot et al. (2005, see Sect. 3.3.3) because the method depends on ordination techniques and some information may be lost. Villéger et al. (2008)

used the minimum spanning tree (MST) to transform a multidimensional space to a distribution on a single axis. The MST links points in the T-dimensional space with the minimum sum of branch lengths. As in FRO this new functional evenness index measures both the regularity of branch lengths in the MST and the evenness in species abundances. There are a total of $S - 1$ branches in the MST of S species and each of the b branch length is divided by the sum of the abundances of the species linked

$$\mathrm{EW_b} = \frac{\mathrm{d}_{\mathrm{ij}}}{\mathrm{w_i} + \mathrm{w_j}},$$

where $\mathrm{EW_b}$ is the weighted evenness, $\mathrm{d_{ij}}$ is the Euclidean distance between species i and j, those involved in the branch b, and $\mathrm{w_i}$ and $\mathrm{w_j}$ are the relative abundance of these species.

In case of perfect regularity of abundance all weighted evenness would be equal, but otherwise it is useful to compute the partial weighted evenness $\mathrm{PEW_b}$ dividing by the sum of the $\mathrm{EW_b}$ across the $S - 1$ branches

$$\mathrm{PEW_b} = \frac{\mathrm{EW_b}}{\sum_{\mathrm{b}=1}^{\mathrm{S}-1} \mathrm{EW_b}}.$$

When the $\mathrm{PEW_b}$ value differs among branches, the final index will decrease. To quantified the discrepancy they compared $\mathrm{PEW_b}$ with $1/(S - 1)$, the index is

$$\mathrm{FEve} = \frac{\sum_{\mathrm{b}=1}^{\mathrm{S}-1} \min\left(\mathrm{PWE_b}, \frac{1}{\mathrm{S}-1}\right) - \frac{1}{\mathrm{S}-1}}{1 - \frac{1}{\mathrm{S}-1}}$$

with an standardization similar to that suggested by Bulla (1994).

This index does not correlate with species richness and ranges from 0, complete unevenness, to 1, complete evenness and it is independent of the convex hull. At least three species have to be present in the sample to enable the calculation because at least three points are needed to define the MST, no matter the number of traits. The index value decreases when relative abundance of species is less evenly distributed and when distances among species are irregular.

Functional divergence (*FDiv*): FDiv quantify how the trait values are spread along the range of a trait space. For only one trait Mason et al. (2003) have defined $\mathrm{FD_{var}}$ (see Sect. 3.3.2) but when there are more than one trait the linear range is replace by a multidimensional range, like the convex hull. So functional divergence is related to how abundance is distributed within the volume of functional trait space. The first step in index calculation is defining the gravity center of the V species that form the vertices of the convex hull $\mathrm{G_v} = \{\mathrm{g_1}, \mathrm{g_2}, \ldots, \mathrm{g_T}\}$, being

$$\mathrm{g_t} = \frac{1}{\mathrm{V}} \sum_{\mathrm{i} \in \mathrm{Sv}}^{\mathrm{V}} \mathrm{x_{ti}}$$

where Sv is the subset of all the V species forming the vertices of the convex hull, x_{ti} is the coordinate (trait value) of species 'i' on the 't' trait, T is the total number of traits, and g_t is the coordinate of the gravity center for trait 't'. Knowing the coordinate of gravity center, we compute Euclidean distance of each species from this point as

$$dG_i = \sqrt{\sum_{t=1}^{T} (x_{ti} - g_t)^2}$$

and the mean distance $\overline{dG}$ of the S species to the gravity center is

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

These distances are computed only with trait values and do not include the species abundance, so they reflect the shape and the volume of the convex hull. To take the abundance into account it is necessary to compute the abundance-weighted deviances (Δd) and the absolute abundance-weighted deviances ($\Delta|d|$) as

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

and

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

being w_i the relative abundance of species 'i'. The functional divergence index is then

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

Adding $\overline{dG}$ to the numerator and denominator makes that the index belongs to interval 0 to 1, because dG_i are Euclidean distance and so are positive or zero, thus Δd is bounded between $\overline{dG}$ and $\Delta|d|$.

Functional dispersion (*FDis*): Functional dispersion (FDis) is a multi-dimensional index based on multi-trait dispersion (Laliberté and Legendre 2010). FDis is the average distance of individual species to the centroid of all species in the community trait space taken into account the relative abundances of species by computing the weighted centroid. It is calculated from the 'species × trait' matrix as

$$\mathbf{c} = \{c_1, c_2, \ldots, c_T\}$$

where the vector **c** has the coordinates of the weighted centroid in the T-dimensional space, and c_t for $t = 1, \ldots, T$, is estimated for each dimension (trait) as

$$c_t = \sum_{i=1}^{S} w_i \, x_{ti}$$

being w_i the relative abundance of species 'i', and x_{ti} the value of the 't' attribute of species 'i'. This formulation implies that $x_{(.)}$ represent a quantitative trait, but the authors generalize the distance measure to include semi-quantitative and qualitative traits through principal coordinate analysis (PCoA).

FDis, the weighted average distance $\bar{z}$ from each species to the weighted centroid **c**, is then computed as

$$\mathrm{FDis} = \sum_{i=1}^{S} w_i \, z_i$$

where w_i is the abundance of species 'i' and z_i is the distance of species 'i' to the weighted centroid **c**. This procedure essentially shift the position of the centroid towards the more abundant species and weigh distances of individual species to this weighted centroid by their relative abundances. It has been suggested that communities with only one species should have FDis = 0, but there is no upper limit for this index.

Functional specialization (*FSpe*): Functional specialization is defined using the multidimensional trait space of the regional pool of species and quantifying how apart the species are from the gravity center. To estimate the index for each plot the distance is loaded by the relative contribution of each species.

The first step in index calculation is defining the gravity center of the S species in the T-dimensional space of the traits $G = \{g_1, g_2, \ldots, g_T\}$, being

$$g_t = \frac{1}{S} \sum_{i=1}^{S} x_{ti}$$

where x_{ti} is the coordinate (trait value) of species 'i' on the 't' trait, T is the total number of traits, and g_t is the coordinate of the gravity center for trait 't'. Knowing the coordinate of gravity center, we compute Euclidean distance of each species from this point as

$$dG_i = \sqrt{\sum_{i=1}^{S} (x_{ti} - g_t)^2}.$$

If the traits are standardized the gravity center has coordinates (0, …, 0). The FSpe is computed at plot level (or local level) as the weighted sum of the dG_i of species present at the plot using its relative abundance (w_i) to load

$$\mathrm{FSpe} = \sum_{i \in \mathrm{plot}}^{S} (dG_i \times w_i).$$

3.5 Ability of Indices to Detect some Ecological Processes

The assembly process is one of the ecological mechanisms that model the way how species coexist in a community. Even though the set of species that form a given community depends on available species, it is also strongly affected by the main assembly process that operates during early stages. The pattern generated combine environmental stress and biological competition that operates on interactions among species and between species and the environmental conditions. The combination may affect morphological, physiological and functional properties that characterize the species in the community. These properties can be grouped to associate with an environmental ecological service or process. Several authors have studied patterns of assembling species assuming that the traits are phylogenetically conserved (Kraft et al. 2007; Mouchet et al. 2010): limiting similarity (MacArthur and Levins 1967) to produce a uniform dispersion of traits values (Stubbs and Wilson 2004), habitat filtering (Zobel 1997) to produce cluster of traits values (Perez-Neto 2004) and neutral assembly (Gotelli and Graves 1996) to produce random scattering.

The functional diversity indices have different abilities to reflect these processes, and their dependence on species richness varies. Ideally, functional diversity indices have to be able to reflect other aspect of community than crude richness in order to be useful to link trait expression to functional performance. Changes in trait community weighted mean may be used to associate community function to a given ecological services; for example, wood density (wd) is associate to carbon sequestration: as wd-CWM increases the expected amount of carbon sequestered in vegetal tissues increases. Shifts in CWM for key traits may be combining with functional diversity indices to trace changes in community succession, for example restoration after fire events (Ricotta and Moretti 2011).

Mouchet et al. (2010) examined the performance of several functional diversity indices using increasing richness (from 10 to 100 species with intervals of 10) and simulation data set using three assembly processes (limiting similarity, environmental filtering and neutral or random). They compared five indices that do not include abundance (FAD2, MFAD, FD, GFD and FRic) and three indices including abundance (Rao, FDiv and FEve). Spearman correlation coefficient was not significant between FEve and FAD2, among the others the correlations were highly significant. Using this set of indices the authors identified four groups of indices related to the three orthogonal functional components.

The functional components (Villéger et al. 2008) have also been referred as facets of functional diversity in the single-trait approach (Mason et al. 2005) and have to be interpreted as properties emerging of the set of species in a given community. The facets or components of functional diversity are not associated to species, it is not the sum of species attributes. They are community characteristics that depend on the interaction among species, and between species pool and the environment. The main facets or components of functional diversity are: functional richness, functional evenness and functional divergence.

The four groups were identified using the algorithm K-means based on principal component axes calculated with indices values in the communities. Two of these groups were identified with functional richness and include FAD2, MFAD, FD, GFD and FRic. The functional divergence is associated with FDiv and also with Rao, and functional evenness is associated with FEve.

The ability of indices to differentiate assembly processes showed that FRic, FEve, FDiv and Rao are much more sensitive than FAD2, MFAD, FD and GFD. Indices with values higher than expected by chance are associated to limiting similarity and with values lower than expected by chance are associated to environmental filtering. Whichever the index selected, relationship of functional diversity to community assemblage processes has to be investigated comparing the observed value with that expected by random. When no evidence is found to reject the random process, both environmental filtering and the competition may be operated sequentially or simultaneously. The best subset of indices includes FRic, FEve and FDiv because each is able to reflect one component of functional diversity. We have to mention that in this work FDis, the one proposed by Laliberté and Legendre (2010) to complement the other three was not included; neither the FSpe proposed by Villéger et al. (2010).

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