A note on functional diversity measures

Carlo Ricotta*

Department of Plant Biology, University of Rome “La Sapienza”, Piazzale Aldo Moro 5, 00185 Rome, Italy

Received 21 July 2004; accepted 25 February 2005

Summary

Functional diversity (FD) has been seen as the key to understanding ecosystem processes, such as productivity, nutrient cycling and storage, carbon sequestration, and stability to perturbations. Yet it is still unclear how FD should be measured. In this paper, I propose a set of fundamental criteria that a meaningful index of FD should satisfy to reasonably behave in ecological research. If FD is computed from the pairwise functional distances among the species of a given assemblage, the candidate measures should be set monotone, monotone in distance, and should conform to the twinning property. On the other hand, if FD is computed taking into account both the pairwise functional distances among species and their relative abundances, the candidate measure should be concave, thus allowing additive diversity decomposition into $a\cdot b$- and $g$-terms. Conformity to the above requirements may be beneficial for selecting a family of measures that are most appropriate for a correct evaluation of the relations between biological diversity and ecosystem functioning.

© 2005 Gesellschaft für Ökologie. Published by Elsevier GmbH. All rights reserved.

Zusammenfassung

Funktionelle Diversität wurde als ein Schlüssel zum Verständnis von Ökosystemprozessen, wie Produktivität, Nährstoffkreislauf und -speicherung, Kohlenstoffsequestration und Stabilität gegenüber Störung betrachtet. Dennoch ist immer noch unklar, wie funktionelle Diversität gemessen werden sollte. In dieser Veröffentlichung schlage ich eine Anzahl fundamentaler Kriterien vor, die ein bedeutsamer Index der funktionellen Diversität erfüllen sollte, damit er sich in der ökologischen Forschung vernünftig verwenden lässt. Wenn die funktionelle Diversität über die paarweisen funktionellen Distanzen zwischen den Arten einer gegebenen Ansammlung berechnet wird, sollten die in Frage kommenden Maße monotone sein, monotone hinsichtlich der Distance, und sie sollten die ”twinning”-Bedingung (Weitzmann 1992) erfüllen. Auf der anderen Seite, wenn die funktionelle Diversität unter Berücksichtigung sowohl der paarweisen funktionellen Distanzen zwischen den Arten als auch ihren relativen Abundanzen berechnet wird, sollte das in Frage kommende Maß konkav sein, und so die additive Auf trennung der Diversität in $a\cdot b$- und $g$-Größen erlauben. Konformität mit den oben...
Introduction

Functional diversity (FD) has been defined by Tilman (2001) as “those components of biodiversity that influence how an ecosystem operates or functions”. It has been suggested that ecosystems with a greater FD will operate more efficiently in terms of productivity (Tilman et al., 1997), resilience (Nystrom & Folke, 2001), and resistance to invaders (Prieur-Richard & Lavorel, 2000; Dukes, 2001).

In this view, although FD would apparently seem an intuitive and easily studied ecological concept, most of the FD measures used to date fail to estimate the components of biodiversity that influence ecosystem functioning in a satisfactory way, thus rendering the interpretation of results difficult and controversial.

At a first glance, species richness (hereafter SR) or any other traditional diversity measure computed from species relative abundances, such as the Shannon or the Simpson index, may seem a good surrogate measure for FD. The ecological rationale behind such measures is closely related to the observation that, although there is no magic effect of the number of species per se on ecosystem processes, as the number of species increases in ecological communities so does the range of ‘functional space’ occupied by the community (Lawton, Naeem, Thompson, Hector, & Crawley, 1998). Thus, on average and all else being equal, species richer assemblages have greater productivity (Tilman et al., 1997; Pfisterer, Joshi, Schmid, & Fischer, 2004), are more stable to extreme events (Tilman & Downing, 1994), and retain soil nutrients more efficiently (Tilman, Wedin, & Knops, 1996; Tilman et al., 1997).

However, when used to summarize FD, SR implicitly assumes that all species are equally different (Petchey, Hector, & Gaston, 2004), while the way in which differences between species affect diversity-function relationships can be very complex (Lawton et al., 1998), and this is hardly captured by measures such as SR that do not incorporate any information about individual species.

Therefore, it might be reasonable to substitute SR with measures of FD that summarize the extent of functional differences in a species pool (Hooper, 1998; Fonseca & Ganade, 2001; Naeem & Wright, 2003).

In this paper, I propose a set of basic criteria that an index of FD should satisfy to reasonably quantify resource use complementarity and thereby explain ecosystem functioning. Unlike Mason, MacGillivray, Steel, and Wilson (2003) that developed ten empirical criteria against which the performance of an index can be tested a posteriori, this attempt of defining general criteria for FD measures relies on the axiomatic work of Rao (1986) and Solow and Polasky (1994). Hence, it enables the a priori construction of FD measures with the required features.

A first set of requirements for functional diversity measures

A common measure of FD is the number of functional groups represented by the species in a given assemblage. The categorization of species into functional groups can be done by simply assigning each species found in the assemblage to a given a priori defined functional group (Hector et al., 1999), or by standard multivariate clustering methods (Gitay & Noble, 1997; Deckers, Verheyen, Hermy, & Muys, 2004; Roscher et al., 2004).

To cluster species into functional groups, first, a set of functional traits thought to be of significance for ecosystem functioning is measured for each species obtaining an $S \times \tau$ matrix of $\tau$ functional traits measured on $S$ species (Petchey & Gaston, 2002). Next, the trait matrix is converted into a distance matrix $D$ the elements $d_{ij}$ of which embody the functional distances between the $i$th and the $j$th species such that $d_{ii} = 0$ and $d_{ij} = d_{ji}$ for any $i \neq j$. Finally, the distance matrix is clustered with standard multivariate methods to separate species from different functional groups.

Of the problems associated with assigning species to groups, perhaps the least tractable are that (i) the result can depend on the number and type of functional characters that are measured, and this is basically a subjective decision which depends partly on the objective of the study (Diaz & Cabido, 1997; Pillar, 1999; Fonseca & Ganade, 2001), and (ii) the conclusions on FD will often depend on the
arbitrary scale at which differences between species qualify as functionally significant, or, in other words, on how many groups are used (Petchey & Gaston, 2002).

An additional drawback of this way of measuring FD is that it assumes that species within groups or clusters are functionally identical and that all species pairs drawn from different groups are equally different (Lawton & Brown, 1993; Petchey et al., 2004).

Apart from functional group richness (FR), there are, however, additional methods for summarizing the extent of species functional differences. For example, Walker, Kinzig, and Langridge (1999) proposed an index termed ‘Functional Attribute Diversity’ (FAD) aimed at estimating the dispersion of species in trait space as the sum of the pairwise species distances in $\Delta$:

$$\text{FAD} = \sum_{i<j \in \Delta} d_{ij}.$$  \hfill (1)

Also, Petchey and Gaston (2002) proposed a new index of FD, which is computed as the total branch length of the functional dendrogram that results from clustering the species in trait space.

Regardless of the proposed index, in most cases the information available for computing the FD of a given species assemblage is the set of pairwise species functional distances $d_{ij}$ of $\Delta$. In this case, Solow and Polasky (1994) advocate a set of natural requirements that such diversity measures should satisfy. First, diversity should not be decreased by the addition of a new species to a given species set $A$. Formally, let $A$ and $B$ designate two species assemblages and let $\delta$ denote a diversity index. If $B$ is a subset of $A$, written $B \subset A$, then $\delta(B) \leq \delta(A)$. This property is called ‘set monotonicity’. Next, diversity should not be increased by the addition of a species that is functionally identical to a species already in the set. Weitzman (1992) referred to this as ‘twinning’.

This second requirement is more controversial. For instance, as stressed by Lawton et al. (1998), because no two plant species have identical functional niches, adding a new species to a given species set should necessarily increase FD. If the functional differences between the species already in the set and the new species are large, the increase will be large; if these differences are small, the increase will be small, though still positive. However, in the presence of two species that are very close from a functional viewpoint, such as two microspecies of Hieracium or Taraxacum, it may happen that the selected functional characters are unable to capture these minor functional differences. In this case, $d_{ij} = 0$, and the corresponding distance matrix contains two identical rows and columns (see species C and D in Table 1).

<table>
<thead>
<tr>
<th>$A$</th>
<th>$B$</th>
<th>$C$</th>
<th>$D$</th>
<th>$E$</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>0</td>
<td>20</td>
<td>50</td>
<td>50</td>
</tr>
<tr>
<td>B</td>
<td>20</td>
<td>0</td>
<td>30</td>
<td>30</td>
</tr>
<tr>
<td>C</td>
<td>50</td>
<td>30</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>D</td>
<td>50</td>
<td>30</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>E</td>
<td>60</td>
<td>40</td>
<td>10</td>
<td>10</td>
</tr>
</tbody>
</table>

Since species C is functionally identical to species D, the corresponding rows and columns contain the same values. Adding up the pairwise species distances in $\Delta$, we obtain $\text{FAD} = 600$.

A third requirement set out by Solow and Polasky (1994) is that diversity should not be decreased by an arbitrary increase in the distances between species. That is, for a one-to-one mapping of the species assemblage $B$ onto $A$ such that $d_{ij}(B) \leq d_{ij}(A)$ with at least one strict inequality, then $\delta(B) \leq \delta(A)$. This property is called ‘monotonicity in distance’. In its very essence this property requires that if the units in which some species’ functional traits are measured change (for example from centimeter to millimeter, or from kilogram to gram) such that the resulting pairwise species distances increase, the corresponding FD measure should change accordingly.

A stronger version of this property was advocated by Mason et al. (2003), who require that diversity should be unaffected by the units in which the functional traits are measured. Nonetheless, even the weaker requirement of monotonicity in distance extremely narrows the search for sensible measures of FD, such that virtually none of the FD measures used to date in the ecological practice possess all required properties.

While FR with a priori defined functional groups trivially satisfies all above requirements (Table 1), FAD does not conform to the twinning requirement and increases with the addition of a species that is functionally identical to a species already in the set.

To partially solve this drawback, it may be wise to introduce an additional constraint: that, in the presence of two or more species with identical functional traits, FAD is computed from a reduced distance matrix $\Delta'$, in which functionally identical species are grouped into one single ‘functional species’ (see Table 2). The rationale behind this aggregation is that the number of taxonomic
species itself is not relevant to FD unless these species possess distinct functional traits.

Still, a possible drawback of FAD is that the index is not smoothly increasing when species are added. For example, imagine a set of species in which species \( j \) is functionally far from all the others. Adding a new species that is functionally very close to species \( j \) will increase FAD by a lot, even though the traits of the additional species are similar to those of species \( j \). In a sense, this implies a weighting for the evenness of the distribution of species in the multidimensional trait space. Whether this is a problem or not depends on the specific application of the index.

An alternative way for summarizing FD from the elements \( d_{ij} \) of \( D \) consists in measuring the average contribution of any ‘functional species’ to total community diversity. This may be adequately summarized as

\[
D = \frac{1}{S} \sum_{i,j} \frac{d_{\text{max}}}{d_{\text{min}}},
\]

where \( d_{\text{max}} \) is the maximum distance in \( A' \) (i.e., in graph-theoretical terms, the diameter of \( A' \)), and \( d_{\text{min}} \) is the nearest-neighbour distance of the functional species \( j \) (i.e., the minimum non-zero distance in the \( j \)th row or column of \( A' \)). To render \( D \) independent of SR, the summation term in Eq. (2) is multiplied by \( 1/S \), where \( S \) is the number of ‘functional species’ in the assemblage. Unfortunately, \( D \) is not monotone in distance. One additional drawback of this measure is that it is unaffected by changes in the intermediate pairwise distances. That is, it does not show appropriately how species are distributed in the multidimensional trait space.

Two additional diversity measures that conform to all the above requirements were proposed by Weitzman (1992) and Solow and Polasky (1994). However, due to their complexity, both measures had no big impact on subsequent studies on community functioning.

Finally, as regards FR obtained from multivariate clustering procedures, since adding a species to a given trait matrix may change the structure of the corresponding functional dendrogram, this measure is generally not set monotone.

A simple counterexample showing that the index FR may violate set monotonicity can be constructed as follows. Table 3 shows a distance matrix containing the pairwise species distances (the same as in Table 2) among four species A, B, C, and D. The distances are selected such that the four species can be embedded in a one-dimensional Euclidean space without distortion.

Applying a single-link clustering method to the pairwise species distances of Table 3, the dendrogram of Fig. 1 is obtained. Adding species E, to the species set \{A, B, C, D\}, a second distance matrix is obtained (see Table 4). Applying the same clustering method to the pairwise distances of Table 4, results in the dendrogram of Fig. 2. If both dendrograms are cut at an a priori defined arbitrary level \( d > 20 \), adding species E to the species set \{A, B, C, D\}, reduces the number of functional groups from 2 to 1.

By contrast, although FR and FD are both obtained from clustering the species in trait space, testing FD against set monotonicity is not as simple as for FR. To calculate the FD of a set of species and a subset thereof, Petchey and Gaston (2002) suggest to calculate the dendrogram of the larger set of species. The FD of the set is the sum of the branch lengths of this dendrogram, while the FD of the subset is the sum of the branch lengths required to connect these species to the root of the dendrogram (for details, see Petchey & Gaston, 2002).

Hence, since species are removed or added from the dendrogram which describes all species in the set, and are not directly removed or added to the trait matrix, FD may be considered set monotone in the inverse sense. That is, FD cannot increase by subtracting a species from a given species set. In a sense, FD seems more adequate for quantifying the loss of ecosystem functioning.

<table>
<thead>
<tr>
<th>A</th>
<th>B</th>
<th>{C, D}</th>
<th>E</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>0</td>
<td>20</td>
<td>50</td>
</tr>
<tr>
<td>B</td>
<td>20</td>
<td>0</td>
<td>30</td>
</tr>
<tr>
<td>{C, D}</td>
<td>50</td>
<td>30</td>
<td>0</td>
</tr>
<tr>
<td>E</td>
<td>60</td>
<td>40</td>
<td>10</td>
</tr>
</tbody>
</table>
that is caused by a species extinction, than for comparing the FD of different species assemblages. Notice that a similar procedure was proposed by Webb (2000) for computing the taxonomic diversity of a given species assemblage and of a subset thereof from the topology of the corresponding cladogram.

This unconventional way of measuring FD is obtained at the cost of another shortcoming of FD. For instance, although all species are represented as dimensionless points in the multivariate trait space, according to the definition of Petchey and Gaston (2002), there is no fixed minimum value for single-species communities.

A second set of requirements for functional diversity measures

A problem with the proposal of quantifying diversity directly from the functional distance matrix is that these indices do not take into account the abundance of each species. However, often some species are much more important than others in the control of ecosystem processes because of their greater abundance (Diaz & Cabido, 2001).

Imagine a plant community or sample composed of $S$ species, where $p_j$ is the relative abundance of the $j$th species ($j = 1, 2, \ldots, S$) such that $0 \leq p_j \leq 1$ and $\sum_{j=1}^S p_j = 1$.

Rao (1986) provided two rules needed to characterize a measure of diversity. The first one is that it must be non-negative. The second one concerns concavity. Using Whittaker’s (1960, 1972) traditional definition of species diversity, this means that the total diversity in a pooled set of communities, that is its $\gamma$-diversity, exceeds (or equals) the average $\alpha$-diversity within communities.

For diversity measures that are computed from species relative abundances, imagine a pooled set of $K$ samples in which $p_{jn}$ is the relative abundance of the $j$th species in the $n$th sample ($n = 1, 2, \ldots, K$) and $w_n$ is the weight associated with the $n$-th sample such that $\sum_{n=1}^K w_n = 1$. Next, let $\gamma$ be the total diversity of the pooled set of samples computed using the weighted species relative abundances within the samples $\tilde{p}_j = \sum_{n=1}^K w_n p_{jn}$. For a concave diversity index we

Table 4. Hypothetical distance matrix $D$ obtained by adding species $E$, to the species set $\{A, B, C, D\}$

<table>
<thead>
<tr>
<th></th>
<th>A</th>
<th>B</th>
<th>C</th>
<th>D</th>
<th>E</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>0</td>
<td>20</td>
<td>50</td>
<td>60</td>
<td>32</td>
</tr>
<tr>
<td>B</td>
<td>20</td>
<td>0</td>
<td>30</td>
<td>40</td>
<td>12</td>
</tr>
<tr>
<td>C</td>
<td>50</td>
<td>30</td>
<td>0</td>
<td>10</td>
<td>18</td>
</tr>
<tr>
<td>D</td>
<td>60</td>
<td>40</td>
<td>10</td>
<td>0</td>
<td>28</td>
</tr>
<tr>
<td>E</td>
<td>32</td>
<td>12</td>
<td>18</td>
<td>28</td>
<td>0</td>
</tr>
</tbody>
</table>
obtain (Lande, 1996):

\[ \gamma = \sum_{n=1}^{K} w_n x_n, \]  

where the equality holds for identical samples (i.e., if \( m = n \) for all sample pairs \( m, n = 1, 2, \ldots, K \)) and \( x_n \) is the species diversity within the \( n \)th sample. The weights \( w_n \) associated with the different samples may be equal (i.e., \( w_n = 1/K \)), or may reflect properties as diverse as their size, their conservation value, etc.

From Eq. (3) it follows that, for a diversity index that is concave, the total species diversity \( \gamma \) of the pooled set of samples can be additively partitioned into two non-negative components: average within-sample diversity \( \bar{x} = \sum_{n=1}^{K} w_n x_n \), and between-sample diversity or \( \beta \)-diversity, such that

\[ \beta = \gamma - \sum_{n=1}^{K} w_n x_n = \gamma - \bar{x}. \]  

Violation of Eq. (3) would imply the non-interpretable result of a negative diversity among samples. In concrete terms, this property means that diversity increases by mixing different species assemblages (Pavoine, Dufour, & Chessel, 2004). So, the requirement of concavity is the analogue of set monotonicity for measures that are computed from species relative abundances.

In contrast to Whittaker’s (1972) multiplicative model of diversity in which \( \beta = \gamma / \bar{x} \), according to the additive model of Eq. (4), all diversity components are expressed in the same units so that they can be directly compared (Veech, Summerville, Crist, & Gering, 2002; Ricotta, 2003). To the best of my knowledge, a concave diversity measure that incorporates both the abundances of species and their pairwise functional distances has never been applied in the ecological practice.

For instance, Mason et al. (2003) proposed an index of FD – FD\(_{\text{avg}}\) that is essentially the variance in the character values of the species of a given assemblage, with the squared residuals weighted by the abundance of the species involved. However, the proposed index, being designed to work only with a single functional character at a time, is very far from a genuine multivariate measure of FD. It remains unclear how different characters should be compared (see Mason et al., 2003).

By contrast, in the framework of taxonomic diversity, a number of authors (e.g., Izsák & Papp, 1995, 2000; Warwick & Clarke, 1995, 1998; Clarke & Warwick, 1998; Shimatani, 2001) used an index of diversity similar or identical to Rao’s quadratic entropy (see below) that incorporates both species’ relative abundances and a measure of their pairwise taxonomic distances. Unfortunately, these papers have mostly been overlooked in FD research.

Interestingly, any FD measure that satisfies set-monotonicity can be decomposed into additive \( \alpha \)-, \( \beta \)- and \( \gamma \)-terms. For instance, for an index of FD that is computed from the elements \( d_{ij} \) of \( \Delta \) without incorporating species relative abundances, the definition of set monotonicity implies that \( \delta(A) \leq \delta(A \cup B) \), where the symbol \( \cup \) denotes the union of \( A \) and \( B \). Therefore, \( w_A \delta(A) + w_B \delta(B) \leq \delta(B \cup A) \), such that all FD measures that conform to the requirements proposed by Solow and Polasky (1994) do also conform to Rao’s (1986) axioms.

To bridge the gap between diversity measures that are computed from species relative abundances and diversity measures that are computed from inter-species distances, Rao (1982) proposed an index termed quadratic entropy (Q) as

\[ Q = \sum_{i=1}^{S} \sum_{j=1}^{S} d_{ij} p_i p_j, \]  

where \( d_{ij} \) is the distance between the \( i \)th and the \( j \)th species in the community and \( Q \) expresses the average distance between two randomly selected individuals. It is easily shown that for \( d_{ij} = \text{constant for all} \ i \neq j \), \( Q \) reduces to \( d_{ij}D \), where \( D \) is the Simpson index \( 1 - \sum_{j=1}^{S} p_j^2 \). Also, if all species are equally abundant (i.e., \( p_j = 1/S \)) and the inter-species distances \( d_{ij} \) are constructed using an \( S \times \tau \) matrix of \( \tau \) functional traits, \( Q \) can be written in the form: \( \text{FAD}/S^2 \) (see Izsák & Papp, 2000; Ricotta, 2002).

Therefore, \( Q \) allows measuring the diversity of a given community combining the species’ relative abundances with the biological information about the functional dissimilarity between the species.

As any diversity index that is computed from species relative abundances, \( Q \) does not satisfy set monotonicity. However, under some circumstances, the quadratic diversity is concave and can be decomposed into additive \( \alpha \)-, \( \beta \)- and \( \gamma \)-terms. For instance, if the species distance matrix \( \Delta \) is Euclidean, then \( Q \) is concave (Champely & Chessel, 2002). More specifically, a matrix \( \Delta(S \times S) \) of distances is said to be Euclidean if and only if \( S \) points can be embedded in an Euclidean space such that the Euclidean distance between \( S_i \) and \( S_j \) is \( d_{ij} \) for mathematical details, see Gower & Legendre, 1986). Consequently, if the inter-species distances \( d_{ij} \) are Euclidean, the resulting FD measure can be additively decomposed into \( \alpha \)-, \( \beta \)- and \( \gamma \)-diversities as shown by Eq. (4).
Conclusion

Expanding on Rao (1986) and Solow and Polasky (1994), I suggested some general criteria that an index should meet to adequately summarize FD. These criteria are not univocal, but vary depending on how FD is computed. If the index is computed from a functional trait matrix ignoring the species relative abundances, it should be set monotone, monotone in distance, and should conform to the twinning property. By contrast, if FD is summarized combining species relative abundances with pair-wise species distances, it should be concave, thus allowing additive diversity decomposition into $\alpha$, $\beta$, and $\gamma$-terms. In both cases, the measures obtained conform to the additive diversity model of Eq. (4).

As any general statistical model, the additive partitioning of diversity makes no assumption about the processes that determine the observed diversity patterns, but provides a useful basis for investigating and understanding them.

As stressed by a number of authors (e.g., Loreau, 2000; Wagner, Wildi, & Ewald, 2000; Veech et al., 2002), additive diversity decomposition is flexible in that $\gamma$-diversity can be partitioned along a nested sampling hierarchy on the basis of any categorical factor, such as habitat, resource availability or soil type. Of course, this is not to say that the proposed criteria will result in a single, agreed-upon measure of FD. Summarizing a large multivariate data set such as a trait matrix into a single diversity figure inevitably results in some loss of information. Therefore, a perfect FD measure does not exist.

Since different diversity measures have been defined based on distinct objectives and motivations, their mathematical formulation can be expected to influence the sign and strength of their connection with the functioning and organization of biological communities. Consequently, a clear understanding of the mathematics that reside behind diversity measures is not a sterile academic exercise, but an essential part of ecological research. From this perspective, conformity to the additive partitioning model can be considered a very general requirement for FD measures that may be beneficial for selecting (or developing) a family of indices that are most appropriate for quantifying the relations between biological diversity and ecosystem functioning.

References


