

REVIEWS AND
SYNTHESES**Functional diversity: back to basics and looking forward**

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Abstract

Functional diversity is a component of biodiversity that generally concerns the range of things that organisms do in communities and ecosystems. Here, we review how functional diversity can explain and predict the impact of organisms on ecosystems and thereby provide a mechanistic link between the two. Critical points in developing predictive measures of functional diversity are the choice of functional traits with which organisms are distinguished, how the diversity of that trait information is summarized into a measure of functional diversity, and that the measures of functional diversity are validated through quantitative analyses and experimental tests. There is a vast amount of trait information available for plant species and a substantial amount for animals. Choosing which traits to include in a particular measure of functional diversity will depend on the specific aims of a particular study. Quantitative methods for choosing traits and for assigning weighting to traits are being developed, but need much more work before we can be confident about trait choice. The number of ways of measuring functional diversity is growing rapidly. We divide them into four main groups. The first, the number of functional groups or types, has significant problems and researchers are more frequently using measures that do not require species to be grouped. Of these, some measure diversity by summarizing distances between species in trait space, some by estimating the size of the dendrogram required to describe the difference, and some include information about species' abundances. We show some new and important differences between these, as well as what they indicate about the responses of assemblages to loss of individuals. There is good experimental and analytical evidence that functional diversity can provide a link between organisms and ecosystems but greater validation of measures is required. We suggest that non-significant results have a range of alternate explanations that do not necessarily contradict positive effects of functional diversity. Finally, we suggest areas for development of techniques used to measure functional diversity, highlight some exciting questions that are being addressed using ideas about functional diversity, and suggest some directions for novel research.

Keywords

Context dependence, ecosystems, functional classification, indirect use value, phenetics, redundancy, species, species richness, traits.

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INTRODUCTION

Use of the term 'functional diversity' has grown exponentially over the last decade and in 2003–2005 it appeared in the title, abstract or keywords of 238 articles. These include studies of marine, freshwater and terrestrial ecosystems, and span a wide range of taxa from bacteria to bats (Zak *et al.* 1994; Stevens *et al.* 2003). The increase in usage suggests

that the concept of functional diversity is gaining a place of general importance in ecological research (Naeem 2002b). The concept of functional diversity remains, however, rather complex and has been described as 'slippery' (Martinez 1996; Bengtsson 1998; Díaz & Cabido 2001). There are questions about how to define functional diversity, how to measure it, and how to assess its performance. A wide range of definitions exist, such as 'the functional multiplicity

within a community' (Tesfaye *et al.* 2003) and 'the number, type and distribution of functions performed by organisms within an ecosystem' (Díaz & Cabido 2001). But, the term is frequently used without definition or reference to a definition. In 2005, over 50% of published articles with 'functional diversity' in the title, abstract or keywords failed to provide or cite a definition. Rather they appear to rely on an intuitive understanding of its meaning and assume that everyone shares the same understanding.

Functional diversity generally involves understanding communities and ecosystems based on what organisms do, rather than on their evolutionary history. This is a very general definition for functional diversity and an enormous amount of ecological research is relevant. For example, if 'what organisms do' is interpreted as the organisms' phenotype (i.e. a phenotypic trait) then functional diversity equates with phenotypic diversity and the majority of ecological research has touched on this subject. While such generality is acceptable, recent research about the potential consequences of biodiversity for ecosystem processes (Tilman 1999; Chapin *et al.* 2000; Grime 2001; Loreau *et al.* 2001; Hooper *et al.* 2005) has led to a more specific definition: 'the value and range of those species and organismal traits that influence ecosystem functioning' (Tilman 2001). A consequence of this definition, one that pervades this review, is that measuring functional diversity is about measuring functional trait diversity, where functional traits are components of an organism's phenotype that influence ecosystem level processes.

A wide range of important ecological questions can be addressed in terms of functional diversity. There are purely descriptive questions concerning, for example, the nature of latitudinal gradients in functional diversity and whether these differ from what one expects by chance (e.g. Stevens *et al.* 2003). There are questions about the evolutionary and ecological determinants of functional diversity (e.g. Weiher *et al.* 1998). Functional diversity can also address questions about determination of ecosystem level processes (Chapin *et al.* 2000; Díaz & Cabido 2001; Tilman 2001) and is a concept that links species and ecosystems through mechanisms such as resource use complementarity and facilitation. It might thus also be a tool for predicting the functional consequences of biotic change caused by humans (e.g. Chapin *et al.* 2000; Loreau *et al.* 2002). Of the many issues that surround functional diversity, our review centres on how functional diversity influences ecosystem processes, the dynamics of ecosystems, and the stability of ecosystems.

Perhaps because of the importance of these questions, the number of ways to measure functional diversity is increasing rapidly. The measures are not equivalent in the information they contain, differ in how they quantify diversity, and all require quantitative validation. Here we take a step back, to review the basic process of measuring

functional diversity in order that it can be rigorously applied to ecological problems, hopefully with some consistency in the quantitative methods employed. We describe some well known and previously unknown general properties of different measures, highlight their advantages and disadvantages using new models, and suggest directions for future development. Validation of measures will help understand the effects of biodiversity change on ecosystem processes and the natural services they provide humans, and the methods for this are reviewed. Finally, we suggest questions that might lead to significant advances in measuring functional diversity and some ecological questions that might benefit from a more thorough understanding of functional diversity. The biological processes that ultimately govern the distribution and abundance of organisms and traits are not the primary focus of this review.

MEASURING FUNCTIONAL DIVERSITY

Measuring functional diversity requires, ideally, each of the following:

- (1) Appropriate functional information (traits) about organisms to be included in the measure, and irrelevant information to be excluded (what functional traits should be included?).
- (2) Traits to be weighted according to their relative functional importance (Walker *et al.* 1999; Petchey & Gaston 2002a; Roscher *et al.* 2004).
- (3) The statistical measure of trait diversity to have desirable mathematical characteristics (Mason *et al.* 2003; Botta-Dukát 2005; Ricotta 2005). For example, discontinuous vs. continuous measures of diversity.
- (4) The measure to be able to explain and predict variation in ecosystem level processes.

The following sections take each requirement in turn.

Appropriate functional traits

What types of traits?

The broad functional classification scheme used by Naeem (2002a) puts organisms into one of four functional groups based on traits describing how they assimilate energy and carbon. Energy is derived either from processing light (photo) or matter (chemo). Carbon is acquired either from organic (heterotrophy) or inorganic (autotrophy) sources. Plants and animals are photoautotrophs and chemoheterotrophs respectively. Prokaryotes that live at deep sea hydrothermal vents are chemoautotrophs because they use hydrogen sulphide as a source of energy and carbon dioxide as a source of carbon.

Another broad classification of organisms based on resource use is by their trophic position, e.g. herbivores,

primary consumers, secondary consumers and parasites. Such a classification provides a simple measure of functional diversity: the number of trophic groups. Could this number predict ecosystem process rates? At least three lines of evidence suggest not. First, the identity of the trophic groups present (rather than the number of groups) is a critical determinant of ecosystem processes (Hairston & Hairston 1993; Polis & Strong 1996; Downing & Leibold 2002; Holt & Loreau 2002; Paine 2002). Second, experiments show that simultaneous changes in diversity at two trophic levels has complex interactive effects on ecosystem properties (Harte & Kinzig 1993; Schindler *et al.* 1997; Bengtsson 1998; Mikola & Setälä 1998; Mulder *et al.* 1999; Naeem *et al.* 2000; Holt & Loreau 2002; Raffaelli *et al.* 2002; Thébault & Loreau 2003; Petchey *et al.* 2004a, 2006). Third, the biomass of producers in food chains depends on whether there are an odd or an even number of trophic groups, and not the number of trophic groups (Oksanen *et al.* 1981). Consequently, functional diversity might be more usefully focused on the finer functional differences within the broad functional differences described above (Lavorel *et al.* 1997). For example, photoautotrophs all acquire energy and carbon from the sun and CO₂, but they do so in different places (e.g. Berendse 1983) and times (e.g. Stevens & Carson 2001). One could quantify such phenological differences, for example, as the modal time of per cent carbon assimilated. Some chemoheterotrophs are herbivores, others are carnivores; both can be further divided by the size of their prey (e.g. Norberg 2000). This idea of fine functional traits nested within broader functional traits implies a hierarchical functional classification of organisms, just as taxonomic and phylogenetic classifications are. It is at the lower levels of the hierarchy where functional diversity might be best focused rather than the higher levels where species differ fundamentally in their energy source.

The functional differences above mostly concern species' resource use patterns. However, resource use may often be too simplistic as a basis for distinguishing among finer divisions in some functional groups and may be less appropriate for some ecosystem processes. While traits about species' pollinator behaviour sometimes align with resource use patterns, pollinators can be classified by the time of year or the time of day they are active, the morphology of flower they can pollinate, how effectively they pollinate, and so on (e.g. Kremen *et al.* 2002). Toxin degradation (Vinther *et al.* 2003) and bioturbation (Solan *et al.* 2004) may represent patterns of resource use, but may also result from other requirements. For example, bioturbation can result from shelter building. Thus, one could produce a functional classification of organisms based on one set of traits (resource use traits) and another classification with a different set of traits (e.g. pollinator traits) in

mind. The two independently produced classifications would be produced for different reasons and not necessarily correspond well or nest within each other.

Which traits?

The simple answer to which traits to use in functional classifications is all traits that are important for the function of interest and no traits that are functionally uninformative. Consequently, it is again critical to define the function of interest explicitly and in as much detail as possible. Lacking a reason for a classification will obviously make choice of traits very difficult. The more specific the reason the more directed can be selection of appropriate traits.

Specific knowledge about how particular organisms interact with their environment, with each other, and how traits vary over environmental gradients are essential to determine specific traits to use. Knowledge may come from any source, such as expert knowledge, observational studies of how traits are distributed over gradients of environmental variability, experimental studies of interactions between species or theoretical models of communities and ecosystems. A rich and detailed literature about the functionally important plant traits exists. In this, studies of the dominant axes of phenotypic variation across large geographical areas and even globally provide information about the functionally important traits (Grime *et al.* 1997; Ackerly 1999; McIntyre *et al.* 1999; Weiher *et al.* 1999; Westoby *et al.* 2002; Díaz *et al.* 2004; Wright *et al.* 2004). For animals, direct observations of resource use can be made, either by watching them forage (Holmes *et al.* 1979) or gut content analyses (Jaksic & Medel 1990), as well as less direct information, such as dental morphology (Dayan & Simberloff 1994).

One of the potential issues in relying on expert opinion is that the classification becomes subjective and artificial to the extent that two experts in the same system might produce a different classification (Naeem & Wright 2003). Data- and theory-based decisions about the functionally important traits are more preferable, but it seems naïve to assume that they necessarily provide a full set of these (Gitay & Noble 1997; Naeem & Wright 2003). This level of uncertainty about identifying functionally important traits, and excluding functionally unimportant traits, means that functional classifications should be treated at best as hypotheses that need to be tested (see section 'Explaining and predicting ecosystem level processes').

How many traits?

In phenetics (classification of species based on their phenotypes) sufficient traits were included to produce a stable classification: a classification that remains the same if another trait is added (Ehrlich 1964; Sneath & Sokal 1973). It was thought that a minimum of 60 should be used and more if possible. Unfortunately, there was a lack of

empirical or theoretical grounds on which to justify this number (Sneath & Sokal 1973, p. 106).

For functional classifications, there should be no target number of traits, rather the correct number of traits is the number that are functionally important. The number of traits (as well as correlations between them and their relative weighting) can under certain circumstances alter the level of functional redundancy that an assemblage appears to exhibit (Petchey & Gaston 2002a; Rosenfeld 2002). A greater number of traits tends to make for a less redundant assemblage (i.e. functional diversity is sensitive to changes in species richness) and a smaller number a redundant assemblage (i.e. changes in species richness have little effect on functional diversity), making redundancy appear a rather subjective property. However, it is only subjective if the traits used to construct the classification are not well justified through the ecological question and knowledge about the functionally important traits of the species (Walker *et al.* 1999).

Quantitative methods for selecting traits and selecting the appropriate number of traits are in development. These use a unique property of functional diversity: it is a component of biodiversity that has an explicit function. The function is to explain and predict variation in ecosystem level properties. One way to select traits is therefore to pick ones that maximize the explanatory power of functional diversity (e.g. Petchey *et al.* 2004b). This methodology uses experimental manipulations of species richness to identify the functionally important differences between the species and could be applied to other experiments and ecosystems.

Obtaining trait values

How should the functionally important traits be measured? Due to finite resources for research, collecting functional information about organisms involves a tradeoff. One can collect small amounts of very high quality information or large amounts of poorer quality information. High quality information is, for example, direct information about resource use patterns (i.e. a hard trait, Hodgson *et al.* 1999). These are relatively straightforward to document in larger animals through direct observation of feeding behaviour (Holmes *et al.* 1979) or examination of gut contents (Muñoz & Ojeda 1997). They may require greater effort to document for plants (e.g. relative growth rate, Knevel *et al.* 2003), however, and plant ecologists often measure traits that are correlated with hard traits. These so-called soft traits (e.g. tissue density, leaf size and specific leaf area) provide indirect information on functionally important traits. The use of soft traits greatly decreases the amount of effort required to compile functional information, so that data about thousands of plant species can be obtained (e.g. Knevel *et al.* 2003).

A second question is whether to measure values from a single typical individual or average values across many

individuals. If measured, how can variation within a species be included in a classification? The terminal taxa of phenetic and functional classifications are most often species, which forces each to have a single value along each trait dimension. Of course, a great deal of variation occurs within species so that trait values depend on factors such as environment, age and nutritional state. The answer from phenetics is to document all of this variation and include it in the classification. The terminal units of the classification can be age or size classes, for example, and average trait values are calculated within the classes. One could even include intraspecific variation by producing a classification of all the individuals that are measured. Incorporating intraspecific variation into functional classifications and measures of functional diversity has not been adequately addressed and remains a significant challenge.

A third question is in what context should traits be measured. What environmental conditions and geographical locations should be used? How transferable from one context to another are traits? Work on plants suggests that there are globally consistent axes of trait variation. Similarly, body size is thought to be a consistently important trait of animals (and perhaps plants). Whether traits like these can predict how local assemblages respond to changes in biodiversity remains to be seen.

Weighting the traits

A necessary starting point for weighting traits is often standardization of variability across the traits. Combining differences, for example, between organisms' sizes (units of length) with differences in their consumption rates (units of mass per time) requires they be standardized, so that traits have a mean of zero and SD of 1. This creates a starting point that represents a situation where the biological variation within each trait is equally important.

The question of how to weight traits objectively, according to the particular biological question at hand has seldom been addressed in functional classifications. Virtually all standardize the traits for want of any alternative. Yet different weightings can produce very different classifications and have important implications for relationships between taxonomic and functional diversity (Naeem 2002b; Petchey & Gaston 2002a). One example of how to use previous knowledge to assign weightings is given by the classification of plants used in the design of a large-scale manipulation of plant functional richness and species richness (Roscher *et al.* 2004). Here, 12 morphological traits, four phenological traits and one physiological trait were used to divide species among four groups. The different numbers of traits of each type meant that equal weighting would give morphology more influence over the classification than the phenological and physiological traits. To

compensate, and because previous experiments indicate the importance of the physiological trait (nitrogen-fixing ability) it was given double the weight of all other traits. This may not be a perfect solution to weighting traits, but it at least addresses the problem, and justifies the weighting with empirical evidence.

Measuring trait diversity

Discontinuous measures

The number of functional types or groups represented by the species in a local community or assemblage is a common measure of functional diversity. This is obviously the only option when a categorical functional classification is made. For example, when plants are classified into C4 grasses, C3 grasses, N-fixing legumes, and non-N-fixing herbaceous species (Gitay & Noble 1997), the only possible measure of functional diversity is the number of groups present (or that combined with evenness, Stevens *et al.* 2003). The discrete classification of functional traits means that only a discrete measure of functional diversity is possible. In some situations natural variation in functional traits may indeed be categorical (or very clumped), but in most it seems likely that variation is continuous.

Continuous variation among species can, of course, be used to obtain discrete measures of functional diversity. One way to do this is to put the species into groups that are similar in trait values, and to count the number of groups represented in an assemblage. This requires a decision about the amount of difference in the traits that represents functionally significant differences among organisms. Organisms that differ by less than this amount are assigned

to the same group while organisms with greater difference are put in different groups. Grouping species by function produces the commonest measure of functional diversity: functional group/type richness (Martinez 1996; Díaz & Cabido 2001; Tilman 2001; Naeem & Wright 2003). However, dividing species among functional groups may require the largest number of decisions and assumptions of any measure of functional diversity because it can require transformation of continuous data into categorical data (Fig. 1; Table 1). These decisions and assumptions bestow functional group richness with important advantages and disadvantages (Table 1). The most significant disadvantages are perhaps the exclusion of any functional differences that occur between organisms in the same group and the largely arbitrary decision about the extent at which differences are excluded.

Creating functional classifications from species traits that are then split into functional groups has many parallels with phenetics (Ehrlich 1964). The basic method is to obtain information about the traits of organisms, to estimate how similar the organisms are in the values of those traits (calculate a distance matrix), and to construct a classification system that accurately represents all of the pair-wise similarities (most often by hierarchical clustering). While cladistics is now the accepted approach for phylogenetic reconstruction, the methods of phenetics are used in a range of ecological fields that classify organisms according to phenotypic traits. Species' environmental niches have been quantified using the same multivariate statistical methods to classify species (Green 1971), as have functional relationships between species. For example, insectivorous birds (Holmes *et al.* 1979), predatory vertebrates (Jaksic & Medel

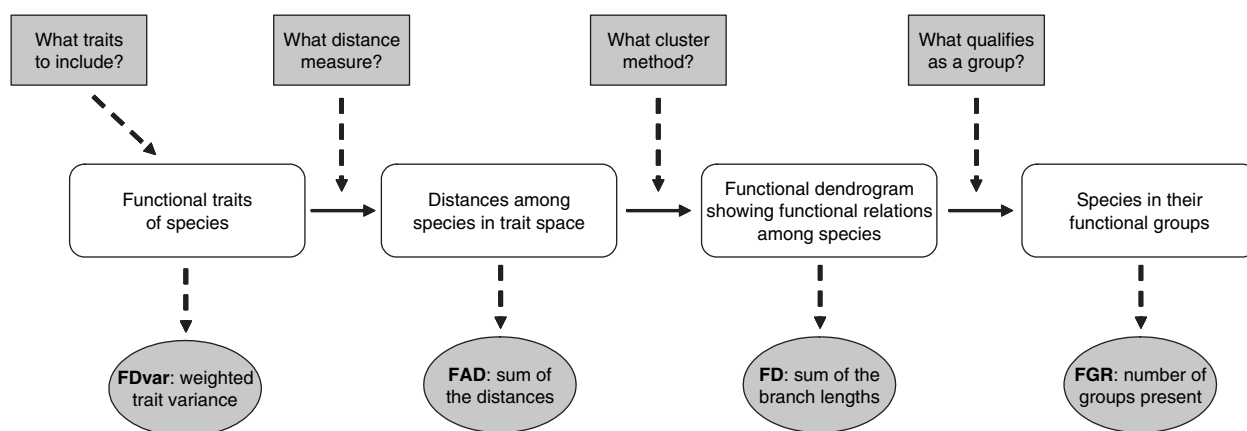


Figure 1 The process of producing a functional classification (unshaded objects) and estimating different measures of functional diversity (shaded ellipses). FDvar (Mason *et al.* 2003); FAD, plant attribute diversity (Walker *et al.* 1999); FD (Petchey & Gaston 2002b); and FGR, functional group richness. Less quantitative approaches implicitly contain all the same steps and decisions. The shaded rectangular boxes represent decisions in the process of making a classification, so that the number of decisions required for each measure increases from left to right.

Table 1 Measure of functional diversity and their attributes

Description	Calculated from distance matrix, hierarchical classification or direct from trait values*	Works with single or multiple traits†	Includes evenness of abundances	Insensitive to species richness <i>per se</i> ‡	Cannot increase if a species is removed or decrease if one is added	Number of assumptions required from Fig. 1
Functional group richness	Hierarchical classification	Multiple	No	Yes	Yes	4
Number of functional groups represented by the species in a community						
Sum of pair-wise distances between species	Distance matrix	Multiple	No	No	No	2
Average pair-wise distances between species	Distance matrix	Multiple	No	Yes	No	2
Sum of branch length of classification	Hierarchical classification	Multiple	No	Yes	Yes	3
Variance of trait values weighted by relative abundance	Trait values	Single	Yes	Yes	Yes	1
Evenness of distances between species and evenness of abundances	Trait values	Single	Yes	Yes	Yes	1
Variance ratio of timing of species' growth	Trait values	Single	No	Yes	No	1
Branch lengths of classification weighted by relative abundance	Distance matrix	Multiple	Yes	Yes	Yes	2

*Whether the measure is calculated directly from the traits of the species, from the distance matrix or from the a hierarchical classification that results from clustering the distance matrix.

†Does the measure work for multiple traits without any extra assumptions.

‡Intuitively, functional diversity should remain constant if a species that is functionally identical to one already present is added.

§Rao (1982), Bady *et al.* (2005) and Botra-Dukát (2005).

1990) and fish (Muñoz & Ojeda 1997) have each been classified by using the multivariate methods of phenetics (the groups are called guilds, Simberloff & Dayan 1991). Division of plant species among groups with similar effects on ecosystem properties (functional effect types) or similar responses to environmental change (functional response types) has also been accomplished using multivariate methods (Chapin *et al.* 1996; Gitay & Noble 1997; Lavorel *et al.* 1997; Westoby & Leishman 1997; Roscher *et al.* 2005).

Continuous measures

When quantitative information about the functional traits of species is used to produce functional classifications, functional diversity can be estimated without dividing species among functional groups. Essentially, this amounts to measuring the spread of points (species) in n -dimensional trait space, in a way that meets expectations about how measures of functional diversity should behave. For example, one might expect that addition of a non-unique species leaves functional diversity unchanged and that addition of a novel species will always increase functional diversity (e.g. Mason *et al.* 2003; Moullot *et al.* 2005). Continuous measures have advantages over group-based measures of diversity, as has been detailed in previous articles (Bengtsson 1998; Díaz & Cabido 2001; Hooper *et al.* 2002; Petchey & Gaston 2002a; Naeem & Wright 2003). The advantages are all derived from the fundamental difference between group-based measures and non-group measures: the former assume that the pair-wise distances between species are binary (two species are either the same or different), whereas the latter allow the pair-wise distances to vary continuously (similarity or dissimilarity is a continuum).

One disadvantage of continuous measures is the seemingly infinite number of ways in which these pair-wise distances can be summarized. At present there are at least six different measures of functional diversity that make a continuous estimate of the amount of variation in the traits of species (Walker *et al.* 1999; Petchey & Gaston 2002b; Mason *et al.* 2003; Heemsbergen *et al.* 2004; Botta-Dukát 2005; Moullot *et al.* 2005; Ricotta 2005), although the analogous problem of how to summarize the extent of genetic differences among organisms provides many more options (e.g. Mallet 1996). No doubt the number will continue to increase. One way to distinguish among the measures is by how they respond to loss of species, addition of species or for those that include abundances, changes in species abundances. Rather than simply repeat or review the analyses of previous authors (Mason *et al.* 2003; Botta-Dukát 2005; Moullot *et al.* 2005; Ricotta 2005) the following three sections categorize existing continuous measures and discuss some of the most important characteristics, some of which are new observations.

Average pair-wise distance

Imagine that species are points in n -dimensional space (where n is the number of traits) and that a line joins each pair of species. If there are s species there are $(s^2 - s)/2$ lines and the lengths of these lines are the pair-wise distances between species (Fig. 2). Several measures of functional diversity are summaries of these pair-wise distances. For example, functional attribute diversity (Walker *et al.* 1999) is their sum, while another measure is their mean (Heemsbergen *et al.* 2004). A recently proposed measure, Rao's quadratic entropy (Rao 1982; Bady *et al.* 2005; Botta-Dukát 2005; Ricotta 2005) is similar, except it is able to include the abundances of species (see Section 4.3.3). A significant advantage of measures based on pair-wise distances is the large amount of study they have received (Rao 1982; Weitzman 1992; Champely & Chessel 2002) and their relative mathematical simplicity. They do not, for example, require as many assumptions as do measures that include hierarchical clustering (Fig. 1).

Summaries of pair-wise distances appear, however, to have two less than desirable properties. The first is mathematical (Ricotta 2005). Intuitively, addition of a species to a community or an assemblage should either increase functional diversity (if the species is in some

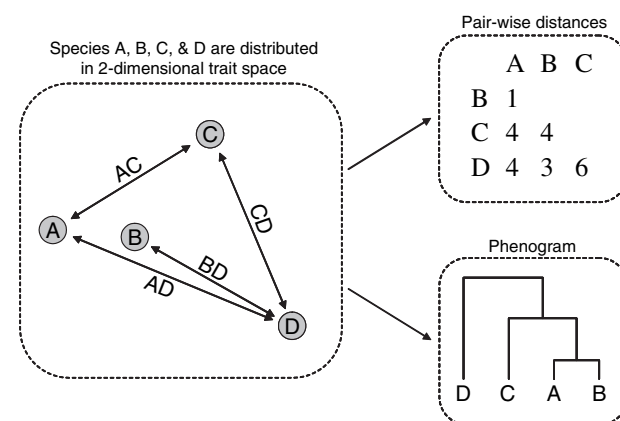


Figure 2 Measuring functional diversity is a problem of how to measure the amount of variation represented by a set of points in multivariate space, for example, species A, B, C and D in the left-most dashed box. The arrows between the species (shaded circles) represent four of the six pair-wise distances. All six pair-wise distances are given in the matrix in the upper-right dashed box. Pair-wise distances are used directly by some measures of functional diversity (Table 1). The phenogram in the lower-right dashed box is a hierarchical description of the distances between species. Some measures of functional diversity work directly on this phenogram (Table 1). In these examples, the distance metric (i.e. Euclidean, Manhattan and Jaccard) is arbitrary, as is the clustering method (e.g. average linkage and minimum linkage) that produced the phenogram.

manner different from those already present) or leave functional diversity unchanged (if the species is identical to one already present) (Solow *et al.* 1993). It is difficult to argue that adding a species will decrease functional diversity (so long as evenness is ignored). However, the mean of the pair-wise distances can easily decrease if a species is added to an assemblage. Figure 2 illustrates how this can happen. A community that contains species A, C and D can be represented by three pair-wise distances (AC, AD and CD), the mean of which in this case is $(4 + 4 + 6)/3 = 4.7$. Adding species B adds three new pair-wise distances (only BD is illustrated), each of which is quite short. The mean pair-wise distance is now 3.7.

Simulations of both mean dissimilarity (Heemsbergen *et al.* 2004) and Rao's Q (assuming identical abundances of all species) confirm that according to these measures, the least speciose community can have greatest functional diversity (Fig. 3). Simulated trajectories of loss of functional diversity caused by extinctions similarly show that an extinction can increase functional diversity (Fig. 3). This seems counterintuitive.

The second and more subtle property of summaries of pair-wise distances is that they treat the pair-wise distances as independent. For example, consider in Fig. 2 that the distance between A and D (AD) is four units, and the distance between BD is three units. Taking the mean pair-wise distances as a measure of functional diversity assumes these two distances are independent. In fact, the short distance AB suggests that some of the biological differences represented by AD are common to those represented by BD. Treating these two differences independently may represent a kind of double counting of biological differences between species and cause an inflated measure of functional diversity. Whether this holds for a variety of distance/dissimilarity measures (e.g. Euclidean, Marczewski–Steinhaus and Bray–Curtis) remains to be proved.

The summed length across dendrograms

A quite different approach to using pair-wise distances was inspired by the field of evolutionary biology, where the total length of an evolutionary tree is used as a measure of

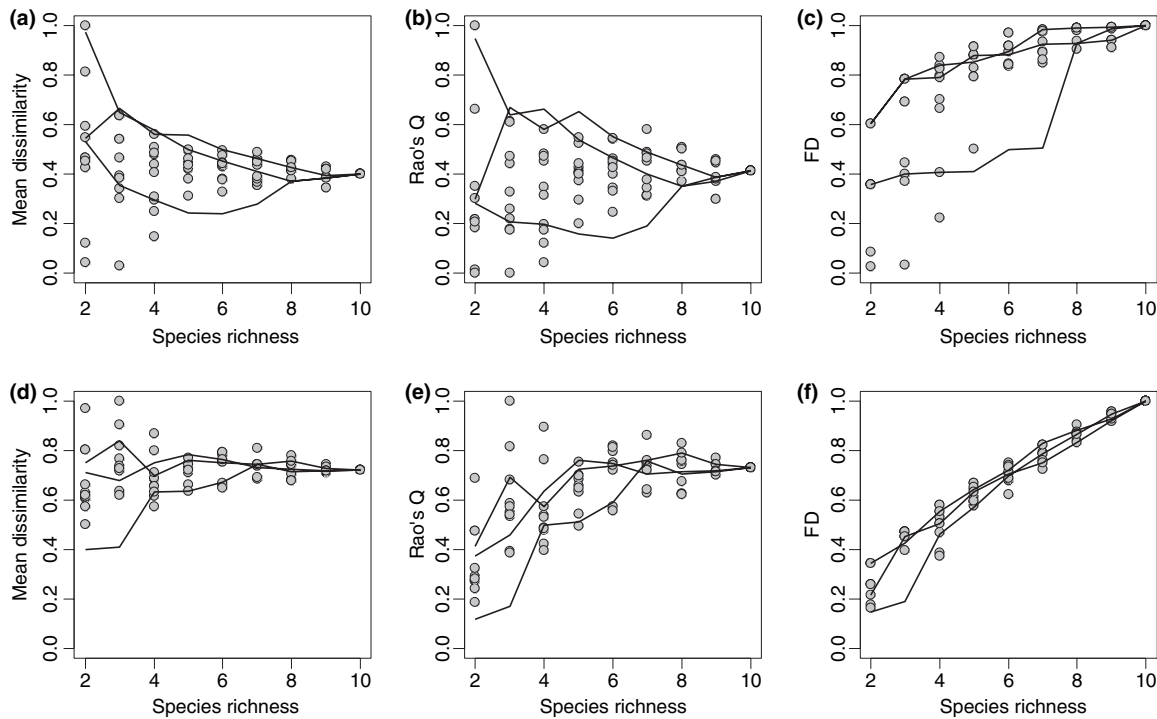


Figure 3 The behaviour of three measures of functional diversity along a species richness gradient. (a,d) Mean dissimilarity (Heemsbergen *et al.* 2004); (b,e) Rao's Q (Rao 1982; Bady *et al.* 2005; Botta-Dukát 2005); and (c,f) FD (Petchey & Gaston 2002b). Each circle shows the value of functional diversity (*y*-axis) for the level of richness indicated on the *x*-axis, for 10 combination of species or all possible combinations if that was < 10; (a–c) are when species have one trait, the value of which is a random normal deviate; (d–f) are when each species has five traits and the values of which are random normal deviates. Lines show the change in functional diversity caused by sequential addition (left to right) or removal (right to left) of species to/from communities. Each of the three lines shows a different order of addition/removal. All measures are standardized to the interval [0,1].

phylogenetic diversity or the evolutionary history represented by a set of species (May 1990; Vane-Wright *et al.* 1991; Faith 1992). An analogous measure of functional diversity is the total branch length of a functional dendrogram (Petchey & Gaston 2002b). Using a dendrogram requires more decisions, for example, about linkage method and distance measure in the hierarchical clustering, and these represent a disadvantage over pair-wise distance-based measures (Fig. 1). However, when measured as total branch length, functional diversity cannot decrease if a species is added to a community, cannot increase if a species is removed (Fig. 3), and remains unchanged if a species is added or lost that is identical to one already present. These are all intuitively logical changes in response to species richness.

Using the dendrogram also accounts for potential non-independence in the source of differences between species. In Fig. 2, much of the distances AD and BD are shared across the dendrogram and this shared distance only contributes once to the total branch length. This avoidance of double counting differences between species is a significant advantage of measures of functional diversity that are based on the dendrogram of functional relationships.

Here, we suggest a minor improvement on the previously proposed measure (Petchey & Gaston 2002b): that the total branch length be that required to connect all the species, but not connect them to the root of the dendrogram. The total branch length of a speciose assemblage will usually contain branches down to the root, so the change has no effect. It does have effect at low levels of species richness, where the path across the dendrogram required to join the species does not necessarily include the root. This improvement does not change the conclusions in previously published papers about the qualitative behaviour of FD (e.g. Petchey & Gaston 2002b), but it will be worth investigating its significance for quantitative analyses (e.g. Petchey *et al.* 2004b).

A disadvantage of using dendrograms is that they assume hierarchical or close to hierarchical functional variation among organisms. It is unclear, however, how well hierarchies can describe the functional differences among species. Consider, for example, the traits 'feeding at night' and 'feeding during the day', and the resources small vertebrates, small invertebrates and large invertebrates. If species that feed at night only eat small organisms and ones that feed during the day only eat large ones, then type of organism is completely nested within feeding period (night or day) and the differences can be accurately described by a hierarchy. If, however, some species that feed at night specialize on small vertebrates and some specialize on small invertebrates, and day feeders also specialize on either of the two small resource types, resource type is not nested within

feeding time. Here the functional differences are less well represented by a hierarchy.

In reality one might argue that the suite of invertebrate prey may overlap little between night and day, making a more hierarchical pattern of variation. One method for checking the extent to which functional variation is hierarchical is to correlate the phenetic distances (pair-wise distances across the dendrogram) with the pair-wise distances in the distance matrix used to construct the dendrogram (this is often called the cophenetic correlation). This correlation can be maximized by selecting the distance measure and clustering algorithm that minimizes the difference between trait distances and phenetic distances (Sokal & Sneath 1973; Blackburn *et al.* 2005). When performed for mammalian predators that have invaded oceanic islands the cophenetic correlation was 0.88, indicating that a hierarchy produces a reasonable representation of natural variation. Maximizing this correlation, even in the absence of questions about a hierarchy, will ensure that branch lengths are most biologically meaningful, in that they best match the biological differences measured among the organisms.

Including evenness

Just as measures of species diversity can include the evenness in which abundances or biomass are distributed among species (e.g. the Shannon diversity index), so can measures of functional diversity (Rao 1982; Mason *et al.* 2003; Bady *et al.* 2005; Botta-Dukát 2005; Mason *et al.* 2005; Mouillot *et al.* 2005; Pavoine & Doledec 2005). Indeed, the idea that an assemblage of 10 species that is dominated by one is less diverse than an assemblage with 10 equally represented species is intuitively appealing (Purvis & Hector 2000). The same argument applies to measures of functional diversity: an assemblage may be more diverse if distinct trait values are represented by similar numbers of individuals than if the vast majority of individuals exhibit the same trait value (Mouillot *et al.* 2005). This idea is supported by theoretical models and empirical evidence that evenness of abundances influences ecosystem level processes independently of species richness (Nijs & Roy 2000; Polley *et al.* 2003; Dangles & Malmqvist 2004).

Perhaps the simplest approach to incorporating information about species abundances into a measure of functional diversity is to again use a summary of the pair-wise distances between objects. Instead of the objects being the species, the objects are individuals or units of biomass, and the mean distance is calculated across all the objects. If two species contribute the vast majority of individuals or biomass to a community, the distance between these two species will dominate the value of functional diversity. Rao's quadratic entropy can be thought of as the mean distance between

individuals (Rao 1982; Bady *et al.* 2005; Botta-Dukát 2005; Ricotta 2005).

One consequence of measures of functional diversity that include evenness is that a re-evaluation of terminology is required. Perhaps functional 'diversity' should be reserved for measures that include evenness, whereas measures that do not account for evenness should be called functional 'richness'. This would make their meanings analogous to species diversity and species richness. We would, however, certainly suggest that authors make a clear statement about whether they include abundances or not, rather than rely on the assumption of any convention.

Challenges with measures of diversity that include evenness occur because one has to decide how to weight the contribution of richness relative to the contribution of evenness (Hurlbert 1971). One weighting can make an assemblage appear more diverse than another, while another weighting gives the opposite impression. A similar problem is that two assemblages could differ in diversity for several reasons: they differ only in species richness, they differ only in evenness or they differ in both. Exactly the same phenomenon occurs when the evenness of species abundances is incorporated into measures of functional diversity. Furthermore, because functional diversity is a link between species traits and ecosystem processes, including evenness in its measurement forces an assumption about the relative importance for ecosystem processes of variation in traits among species and variation in their abundances. Just how important is richness relative to the evenness of abundances remains unknown (Moullot *et al.* 2005).

Moullot *et al.* (2005) include a second aspect of evenness in their measure of functional regularity: how evenly trait values are distributed along the trait axis. An assemblage with clumps of trait values would be less regular than one with evenly spaced trait values. This type of evenness is incorporated with evenness in abundances to produce a measure of functional regularity (Moullot *et al.* 2005).

Loss of individuals and functional diversity

How might measures of functional diversity that include abundances alter our perception of how species loss affects functional diversity (Petchey & Gaston 2002a)? Here we synthesize evenness-based measures with loss of individuals (a process that eventually leads to loss of species) to provide some preliminary answers. The assemblages are all simulated (random trait values for species and random starting abundances). The results depend on two factors: the order in which individuals are lost and the correlation between abundance and functional distances. For the first, individuals are either lost at random, are lost from less abundant species more frequently than by chance (a more plausible scenario) or are lost from more abundant species less frequently than by chance (the less plausible scenario). For

the second factor, there is either no relationship between functional similarity and abundance, the most functionally dissimilar species are the most abundant (Sugihara *et al.* 2003) or the most functionally dissimilar are the least abundant (less plausible).

Simulated loss of individuals across the nine possible combinations of scenarios shows quite different patterns of loss of functional diversity (Fig. 4). When functionally dissimilar species are more abundant (middle row), loss of individuals often increases functional diversity (Rao's Q) and sometimes leads to species poor assemblages with very high functional diversity (because very dissimilar species remain). The lack of a relationship between abundance and functional distances (top row) and the less plausible scenario of functionally unique species being less abundant (bottom row) both result in decreases in functional diversity as individuals are removed, more often than not. Different scenarios of loss of individuals (differences between columns) appear to have weaker and less systematic effects on the loss of functional diversity. It appears that the most plausible scenarios (middle row, columns 1 and 3) do not show the most rapid loss of functional diversity (either Rao's Q or FD), suggesting that the organization of functional dissimilarities and abundances (e.g. Sugihara *et al.* 2003) may buffer functional diversity against the impacts of species loss. However, investigation of patterns and scenarios of real assemblages are needed.

Explaining and predicting ecosystem level processes

Existing evidence

Theoretical models of assemblages composed of a single trophic level confirm the potential for a mechanistic link between species and ecosystem processes (Hooper *et al.* 2002). Models typically assume that functional diversity equates to resource use complementarity so that differences in how species gain resources is the variation represented by functional diversity (Tilman *et al.* 1997; Loreau 1998; Diaz & Cabido 2001). The models predict that greater resource use complementarity leads to more complete and/or efficient use of resources and consequently, greater productivity (e.g. primary productivity if plants are the single trophic level). However, the relative importance of functional diversity is reduced if variation in diversity is accompanied by other factors that affect ecosystem processes, such as changes in resource levels that occur over large spatial scales (Wardle *et al.* 1997b; Loreau 2000; Fridley 2002). Consequently, the explanatory and predictive power of functional diversity is likely greatest when traits about resource use differences among species are used and at relatively local spatial scales.

The vast majority of empirical tests of whether functional diversity informs about ecosystem level functioning use an

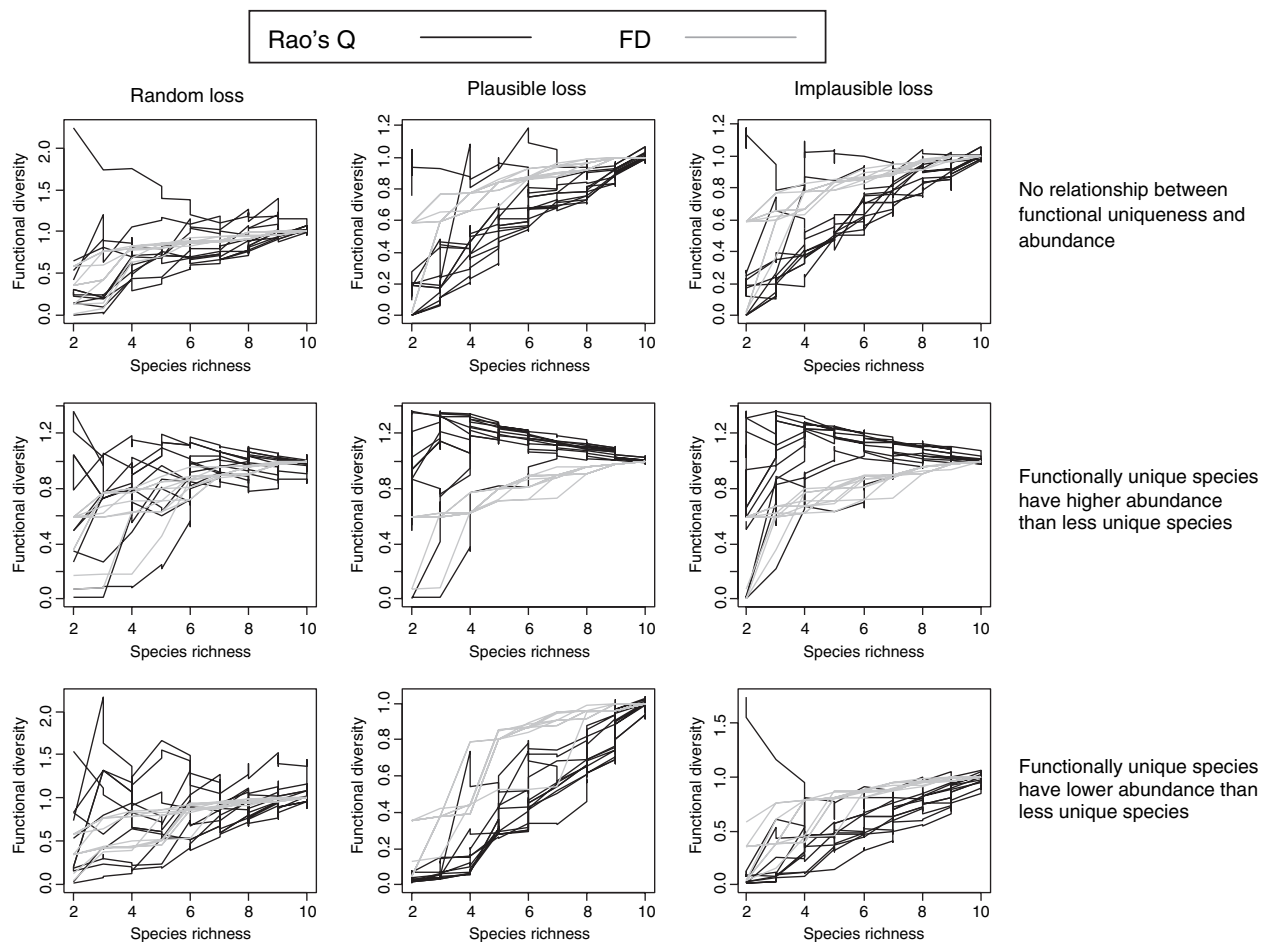


Figure 4 Trajectories of species loss and functional diversity change caused by sequential loss of individuals from simulated assemblages (black lines, Rao's Q: quadratic entropy; grey lines, FD: Petchey & Gaston 2002b). The assemblages start with 10 species whose abundances are random log-normal deviates [mean $\log(\text{abundance}) = 2$, standard deviation $\log(\text{abundance}) = 1$]. Individuals are removed and lines show the resultant trajectory of loss of species and change in functional diversity. There are three scenarios of loss of individuals (in the three columns) and assemblages are structured in three different ways (in the three rows). The first column is when individuals are lost from assemblages at random. The second is when individuals are disproportionately lost from rare species (a more plausible scenario). The third column is when individuals are disproportionately lost from abundant species (a less plausible scenario). The first row is when abundance is not related to functional distance. The second row is when species more distant from others in functional space are more abundant (e.g. Sugihara *et al.* 2003). The third row is when species more distant from others in functional space are less abundant. Vertical parts of the trajectories of Rao's Q occur because changes in relative abundance distributions changes functional diversity without changing species richness.

priori functional classification to produce functional groups. The number of functional groups in experimental assemblages is then manipulated (either by assembling communities or by removing species from existing communities) while all other variables should be controlled (Allison 1999; Schmid *et al.* 2002; Díaz *et al.* 2003). This includes either experimental and/or statistical control of variation in the number of species, because variation in species richness results in hidden treatments that greatly complicate the interpretation of outcomes (Huston 1997; Grime 1998). If

functional diversity links species and ecosystems, a significant relationship between the functional diversity of an experimental assemblage and ecosystem level processes is predicted. However, significant questions exist about how to test whether *a priori* functional classifications explain significant variation in experiments. Two detailed analyses of the explanatory power of *a priori* functional classifications (e.g. grass, forb and legume) show that it is often less than when species are assigned to groups entirely randomly (Petchey 2004; Wright *et al.* 2006). Much of the explanatory

power of *a priori* functional groups may derive from grouping *per se*, rather than which species go into which group (Petchey 2004).

Earlier experiments are summarized by Díaz & Cabido (2001), where functional diversity had significant effects on ecosystem properties in 10 of 28 experiments with plants. More recent experiments using plants may provide stronger evidence of the importance of functional diversity (Symstad *et al.* 1998; Spehn *et al.* 2000; Reich *et al.* 2001; Tilman *et al.* 2001; Dimitrakopoulos & Schmid 2004; Hooper & Dukes 2004). Additionally, functional similarity (which may be different from functional diversity) appears to affect the rate of ecosystem processes performed by assemblages of soil macrofauna (Heemsbergen *et al.* 2004), and the diversity of prey sizes can affect ecosystem level properties in aquatic communities (Norberg 2000).

A refinement of the question of how functional diversity links organismal traits and ecosystem processes is what is the predicted form of the relationship between functional diversity and ecosystem functioning. The relationship between taxonomic diversity and ecosystem level processes can have several potential forms (Schulze & Mooney 1993). For example, a saturating relationship between the two indicates a redundant assemblage that will become less redundant and lose functional capacity as species are lost. Other hypotheses are of linear, sigmoidal or idiosyncratic relationships. However, no hypotheses have yet addressed the shape of the relationship between functional diversity and ecosystem functioning. One possibility is that a unit increase in the range of resource types used by organisms will cause a unit increase in productivity, so that a linear

relationship between functional diversity and ecosystem functioning is predicted (Fig. 5). This linear relationship implies nothing about the shape of the relationship between taxonomic diversity and functional diversity (Naeem & Wright 2003) or between taxonomic diversity and ecosystem functioning. It is simply a proposed constraint on the function that transforms functional diversity into levels of ecosystem processes (see Fig. 5).

Interpreting non-significant results

What should be concluded from the many examples of no relationship between functional diversity and an ecosystem level process (Dukes 2001; Díaz & Cabido 2001; Stevens & Carson 2001)? One or all of several explanations can be proposed. First, inappropriate information might have been used to construct the classification (i.e. the functional groups are incorrect or the traits are functionally unimportant). In our experience, this is the most common interpretation of the absence of a significant result. Second, the measure of functional diversity might be inappropriate. Third, both the classification and measure are appropriate, but other ecological factors may be more important than functional diversity. Fourth, the experiment may have insufficient statistical power. Finally, it is possible that functional diversity has no effect. The majority of studies examining ecosystem effects of functional diversity fail to distinguish among these alternatives. Accepting the third explanation, if the first two are rejected, implies that functional diversity is a weak explanatory variable and that focusing attention on other determinants of ecosystem

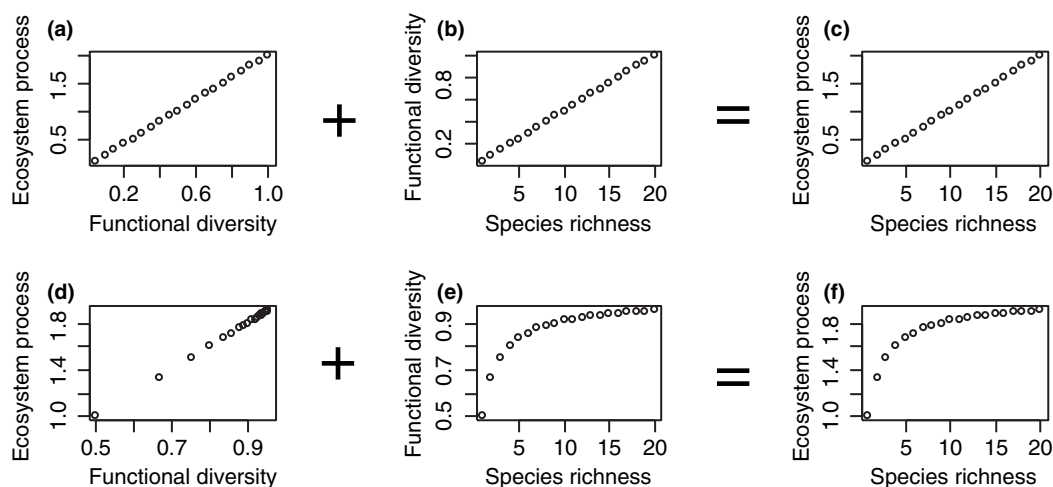


Figure 5 Notional relationships between species richness, functional diversity and ecosystem functioning. The two rows represent two independent sets of relationships. Both rows adhere to a linear relationship between ecosystem process and functional diversity (a,d) without constraining the form of the relationship between ecosystem functioning and species richness (c,f), which is defined by the relationship between species richness and functional diversity (b,e).

processes is important. Rejecting the first four would imply that there is no functional effect of biodiversity.

Testing the first explanation implies that the functional classification may be wrong, because the traits are wrong (Hooper *et al.* 2002; Petchey *et al.* 2004b). One logical implication is that the performance of the candidate classification be tested against random classifications, rather than using standard parametric tests of statistical significance (Petchey 2004). Another consequence of accepting that a functional classification is inappropriate is the temptation to produce different classifications based on different functional traits until one that explains variation in ecosystem functioning is found. Unfortunately, this is problematic because it makes functional diversity impossible to falsify. A safer and perhaps more appropriate response is that the information used to construct the classification was based on best available information about the particular system. Either we know too little about the system reliably to identify the functional traits of species and should study it more or other factors play a dominant and overwhelming role in determining ecosystem level processes (Wardle *et al.* 1997a,b; Grime 1998; Fridley 2001).

Testing the second explanation can be accomplished by comparing the properties and explanatory power of different measures of functional diversity (Table 2). Presumably a measure that distorts the functional differences expressed by the organisms will provide lower explanatory and predictive power than a measure that accurately represents the differences. For example, one expects greater explanatory power if the measure is independent of species richness (Table 2) and this is confirmed by quantitative analyses (Petchey *et al.* 2004b). However, there have been very few tests of the relative power of different measures of functional diversity and none of the power of measures of functional diversity that include information about relative abundance distributions.

CONCLUDING REMARKS

Functional diversity is a powerful, important component of biodiversity, but as the above review shows, it is also rather complex. It is clear that a variety of definitions are available. We focus mainly on that which relates the functional traits of organisms to ecosystem level properties. This leads us to conclude that trait choice is critical, that much information exists about what traits are functionally important, and that it should be possible quantitatively to validate these in experiments. Independent of trait choice, functional diversity is being measured in an increasing number of ways and the literature contains some very involved statistical and mathematical discussions of these measures. No doubt

these will continue and more measures will be proposed. However, here we have pointed out some broad differences between measures that have not previously been observed. These mean that there are gross differences in how the measures respond to species loss, for example, and may provide criteria for assessing which measures are more appropriate. Such assessments should also be based on the predictive power of different measures (Petchey *et al.* 2004b). There is no 'perfect' measure of functional diversity, nor is there likely to be. We need to think hard about what we expect of one (e.g. Mason *et al.* 2003), assess how it performs (Petchey *et al.* 2004b) and design it accordingly. The following questions might guide future research.

What experiments do we need?

Bespoke experiments that manipulate trait distributions in local assemblages will provide understanding of the mechanisms that link species and ecosystems that cannot be gained through manipulations of species richness. Partly this is because they more directly address the mechanisms behind diversity effects and partly because they can be performed while species richness is held constant and sampling effects are eliminated (Huston 1997). Experiments that manipulate whether a functionally distinct species is common or rare will help understand the relative importance of functional differences and relative abundances.

What organisms should we focus on?

Perhaps the greatest research challenge is to integrate the science reviewed above with that of microbial ecology and environmental microbiology. The genetic and metabolic diversity of micro-organisms is vast compared with that of larger organisms (Pace 1997). Understanding how all organisms contribute to ecosystem processes, regardless of their size, will benefit by transferring concepts and ideas between traditionally distinct fields and ultimately lead to a more unified and complete understanding of biological influences on ecosystem processes (Horner-Devine *et al.* 2003).

Can we include intraspecific variation in measures of functional diversity?

Individuals within species differ, sometimes just as much as the differences between species. None of the methods for estimating functional diversity give a clear method for incorporating this level of biological diversity. Is there a way of measuring functional diversity that is free of taxonomic scale?

Is it possible to incorporate evenness into dendrogram-based measures?

Currently, only measures based on pair-wise distances between species include abundances, yet these have some undesirable properties. Measures based on the length of a dendrogram do not yet incorporate species abundances. A measure that combines the two could include the best properties of both approaches.

Which measures of functional diversity perform the best?

There has been very little quantitative work on the relative explanatory power of different measures of functional diversity (e.g. Petchey *et al.* 2004b). Fair quantitative comparisons will provide an objective method to assess different measures.

Can the role of facilitation between species be incorporated into functional diversity measures?

At present, functional diversity measures cannot adequately account for facilitative interactions. At present, all the measures account for the amount of difference between species' traits, and not facilitative interactions between specific combinations of traits that can be important determinants of ecosystem processes (Cardinale *et al.* 2002).

Is there a role of functional diversity for understanding other ecosystem processes?

We have mostly focused on understanding the impacts of functional differences in resource use requirements on ecosystem processes, but difference in other traits, such as pollinator types and resistance to invasion, could be used to explain and predict changes in the ecosystem processes that these drive.

In addition to these seven largely methodological questions are a range of questions about understanding the drivers of how functional diversity varies through time and space, including human impacts. While all these questions have been addressed to some extent, they certainly represent opportunities for new and important research.

What are the ecological and evolutionary drivers of functional diversity?

Phylogenetically conserved functional differences would suggest a strong impact of evolutionary process on patterns of functional diversity. Dominance of ecological processes, such as character displacement, environmental filtering, and assembly rules (Weiher *et al.* 1998; Lavorel & Garnier 2002; Hooper *et al.* 2005) would lead to a weaker impact of

phylogeny on community structure and ecosystem functioning. Understanding how the two map could be important in studies of phylogenetic impacts on community structure (e.g. Losos 1996; Webb *et al.* 2002; McClain *et al.* 2004).

How does functional diversity vary through time and space?

Knowledge about such variation in functional diversity is generally very sparse (e.g. Bremner *et al.* 2003; Stevens *et al.* 2003). Coverage of species composition and trait information about plants is sufficient for a global map of plant functional diversity, as well as detailed accounts of changes in functional diversity over recent and geological time spans (Beerling & Woodward 2001).

How are humans impacting functional diversity?

We know a little about how extinctions might impact functional diversity (Petchey & Gaston 2002a) and the positive effects on functional diversity of establishing marine reserves (Micheli & Halpern 2005). Studying the consequences of human actions should be a priority. The simulation study of how loss of individuals impacts functional diversity (see Section 4.3.2.4) could be repeated for real assemblages.

Can functional diversity information help prioritize conservation efforts?

A species that contributes a large amount of functional diversity may be considered more valuable than one that contributes less (Walker 1992; Fonseca & Ganade 2001). However, much research and a good deal of caution is recommended. The highly context-dependent nature of functional diversity may make it difficult to generalize any conclusions about species' values. A species may have high indirect use value in one context, but low in another.

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