PART 2

Natural science foundations

CHAPTER 4

A functional guide to functional diversity measures

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4.1 Introduction

4.1.1 What is functional diversity and why is it important?

Functional diversity is a component of biodiversity that concerns what organisms do, rather than, for example, their taxonomic identity (Tilman 2001, Naeem and Wright 2003, Hooper *et al.* 2005, Petchey and Gaston 2006). What kinds of resources do organisms exploit, where do they exploit them, and when do they exploit them? Each of these characteristics, and many others, can be a component of functional diversity. Since ecosystem processes ultimately result from the actions of organisms, knowing about these actions and summarizing them in a measure of diversity should inform about ecosystem processes (Tilman 2001, Hooper *et al.* 2005). Therefore, functional diversity has the potential to link morphological, physiological, and phenological variation at the individual level to ecosystem processes and patterns.

One critical reason that functional diversity might link organisms and ecosystems is that it implicitly contains information about how species will compensate for the loss of another. For illustration, consider some species that are functionally rather similar, and some that are rather dissimilar. The similar species each access the same pool of resources. If one of these species is lost, no reduction in the use of that resource pool results, as the other species are present and will accordingly simply increase their use of that same resource. There will also be only a small loss of functional diversity, since the lost species was not very unique in its functional characteristics. If, however, the lost species was quite dissimilar to others in its func-

tional traits, both functional diversity and use of the resource pool will decline in concert. Other changes associated with loss of access to that resource pool might include a reduction in ecosystem processes, such as net primary production.

Another illustration of the interactions that are implicitly represented in measures of functional diversity is that the effect on functional diversity of losing a particular species (or adding a particular species) is context-dependent. The context here is the other species present in the community. In one context, loss of a particular species can have little effect on functional diversity. This would be if the community contains, and continues to contain, functionally similar species to the lost species. If there are no similar species, however, the loss of the same species could have a large effect.

Thus functional diversity is a measure of diversity that implicitly incorporates some mechanisms of ecological interactions between species. In doing so, it provides a general (and yes, assumption-laden) approach for scaling from characteristics of individuals to properties of communities and ecosystems. This makes functional diversity a potentially powerful concept in ecology. At present, much attention is focused on how to measure it, and that is the broad subject of this chapter.

4.1.2 Why not functional group richness?

One method for quantifying functional diversity is to examine the characteristics of some species, and to somehow assign species to functional groups (or guilds) based on these characteristics (Root 1967). This is a popular method, because of the perceived

ease of assigning species groups, and has been used repeatedly in biodiversity-ecosystem function experiments. However, this method has several major drawbacks, all linked to the central issue of how to assign species to groups. The details of the assignment is relatively unimportant here, and methods range from the very subjective to more objective (Holmes *et al.* 1979, Chapin *et al.* 1996, Díaz and Cabido 1997). What is critical here is the decision about how similar species need to be in order to belong to the same functional group, or rather where the boundaries of the groups should be placed. This decision defines the number of functional groups and the average number of species in a functional group. The number of functional groups represented by the species in a local assemblage (functional group richness) is the measure of functional diversity.

The first problem with functional group richness is that any interspecific differences within a group are ignored. This is less of a problem if species form very distinct groups; that is, if species' functional characteristics are distributed discontinuously. However, if variation is more continuous, the amounts of variation that are ignored by functional group richness could be large. Since many important functional traits are continuous, this is a large problem. Even traits which are often considered discontinuous, like N-fixing or not, are in fact continuous at some scale, with the efficiency of nitrogen fixation varying under different soil conditions (Vitousek *et al.* 2002).

The second problem is that the behaviour of functional group richness depends greatly on the number of functional groups that are defined (Petchey & Gaston 2002a, Fonseca and Ganade 2001). Defining many functional groups results in few species per functional group, and strong effects of species richness (and extinctions) on functional diversity, as the number of functional groups begins to approximate the number of species. Defining few functional groups results in many species per functional group, and weak effects of species richness on functional diversity.

Third, no objective method exists for deciding how different species should be in order to belong to different functional groups. Consequently, the number of functional groups, number of species per functional group, and, for example, the effects of species richness and extinction on functional group richness are arbitrary.

Finally, evidence exists that some real assignments of species to functional groups are little better than random assignment of species to groups. In particular, correlations between functional group richness and ecosystem processes in a well-studied grassland plant ecosystem were often higher with random assignment of species groups than the actual grouping used (Petchey 2004, Wright *et al.* 2006).

4.1.3   Non-grouping measures of functional diversity

The recognition that functional group richness is a problematic measure of functional diversity prompted the search for better alternatives. Given some information about what species do, how can one transform this into a measure of the diversity of what the species do? If we record what species do quantitatively, and call this information their traits, or functional traits, then the problem is how to measure the diversity of trait values. Thinking of the species as points in n-dimensional trait space, the question becomes how to measure the diversity of a cloud of points in n-dimensional space.

One of the first solutions was by Walker *et al.* (1999), followed by Petchey and Gaston's (2002a) use of a method of measuring phylogenetic diversity to solve the problem. Since then, a small industry has sprung up, with frequent critiques, suggestions of new measures, and supposed improvements to old measures (Mason *et al.* 2003, Heemsbergen *et al.* 2004, Botta-Dukát 2005, Mason *et al.* 2005, Mouillot *et al.* 2005a, Pavoine and Doledec 2005, Ricotta 2005a, b, Cornwell *et al.* 2006, Lepš *et al.* 2006, Podani and Schmera 2006, Petchey and Gaston 2007, Fox and Harpole 2008, Mouchet *et al.* 2008, Quintana *et al.* 2008, Walker *et al.* 2008). The impression one might come away with from so much activity in this field is lack of consensus about the most appropriate measure of functional diversity.

The aim of this chapter is to provide a functional guide to functional diversity measurements by two complementary approaches. First, through

illustrations of the uses that functional diversity can be put to: what types of ecological questions can functional diversity help us answer? And second, by showing potential users how to choose among six different measures of functional diversity. Examples show how several of the metrics work (i.e. what they do), in particular how they respond to changes in species richness and species composition, highlighting crucial aspects of the metrics, and how they apply to two simulated datasets. We will also get a sense of where the field needs to go through this analytical review.

4.2   What metrics are out there?

We will focus on six measures of functional diversity.

- Convex hull volume (CHV) (Cornwell *et al.* 2006)
- FD_{var} (Mason *et al.* 2003)
- Functional attribute diversity (FAD) (Walker *et al.* 1999)/Mean dissimilarity (MD) (Heemsbergen *et al.* 2004)
- Rao's quadratic entropy (Q) (Botta-Dukát 2005)
- FD (Petchey and Gaston 2002a)
- Podani and Schmera's modification to FD (here termed FD_{LD}) (Podani and Schmera 2006)

These can be divided among three categories: measures that work on trait values directly (CHV and FD_{var}), measures that work on the distance matrix (FAD/MD and Q), and measures that work on the functional dendrogram (FD and FD_{LD}).

4.2.1   Measures directly using the trait values (CHV and FD_{var})

The convex hull volume (CHV) is the smallest convex shape (set) that can enclose a set of points in n-dimensional space, where each trait provides a new dimension. It was first employed as a measure of the dispersion of species in n-dimensional trait space by Cornwell *et al.* (2006). In one-dimensional space, convex hull volume is the range of the data (maximum value minus the minimum). This measure has only been used for continuous traits.

FD_{var} (Mason *et al.* 2003), when used with a single trait, can be thought of as the sum of squared deviations of species from the weighted mean of the species. It is therefore relatively similar to variance. The weighting of trait values by species can be by abundance, and so gives a measure of functional diversity that can account for differences in abundance between species.

This metric was designed solely to work with single traits, which considerably restricts its utility, but its authors recognized this limitation and suggested averaging for multiple traits. The solution used in the simulations below follows this suggesting and averages FD_{var} values across multiple traits. It is also possible to weight the FD_{var} values for each trait by the degree of statistical independence from other traits, a technique which has been proposed by researchers working on related questions in functional ecology, although not previously for FD_{var}. The notion is to discount traits which are highly correlated with other traits. One formulation of this weighting parameter is $w_t = \frac{1}{2} + \sum_{l=1}^{T}\left(1 - \frac{r_{tl}^2}{2}\right)$, for T traits, considering the relationship between trait t and all other traits l (Kark *et al.* 2002, Mouillot *et al.* 2005c).

4.2.2   Distance-based measures (MD/FAD and Q)

MD (mean dissimilarity) (Heemsbergen *et al.* 2004) and FAD (Functional Attribute Diversity) (Walker *et al.* 1999) are both calculated as the mean distance between species in multivariate space. Note that another distance-based measure is now available (Schmera *et al.* 2009). This requires a decision about the distance measure used: for example, Euclidean, Manhattan, or Gower. Hereafter we use MD to include both MD and FAD.

Q, representing Rao's quadratic entropy, was proposed as a measure of functional diversity by Botta-Dukát (2005). It is the sum, across species pairs, of the product of the distance between the two species in trait space and their two relative abundances. However, other researchers have implemented a modified version of Q, using arbitrary weighting values rather than using relative abundances, which are then modified until the maximum explanatory power for the ecosystem function of interest is achieved (Weigelt *et al.* 2008).

Table 4.1   Number of papers citing Walker *et al.* (1999)/Heemsbergen *et al.* (2004) for FAD/MD, Petchey and Gaston (2002a) for FD, Mason *et al.* (2003) for FD_{var}, Botta-Dukát (2005) for Q, Cornwell *et al.* (2006) for CHV and Podani and Schmera (2006) for FD_{LD}. The greater number of citations for FAD/MD and FD are a reflection of the age of the papers.

Theme of paper	Number of citations						
	FAD/MD	FD	FD_{var}	Q	CHV	FD_{LD}	Total[*]
Unrelated studies	96	21	4	1	7	1	124
Use of discrete groupings or standard diversity indices	46	8	1	1	1	0	55
Methods associated with calculating functional diversity	11	11	3	4	0	3	20
New measure of functional diversity	7	11	1	0	0	1	18
Application to empirical data	3	8	4	3	1	0	16
Benefits of looking at functional diversity	9	11	1	1	0	0	15
Pro's and con's of indices	7	7	4	2	0	0	8
Potential use as ecological indicator	1	5	4	0	0	0	6
Total number of times cited	180	82	22	12	9	5	262

[*] There is some overlap in papers cited, so 'Total' refers to the actual number of papers cited under each heading.

Researchers should thus take care when interpreting studies using Q to examine specifically what implementation was used.

4.2.3   Dendrogram-based measures (FD, FD_{LD})

FD (Petchey and Gaston 2002a) is the branch length across the regional functional dendrogram that is required to join the set of species present in an assemblage. The regional functional dendrogram describes the functional relationships among the species in a region, and is constructed from the traits of species. It is important to note that only one dendrogram is constructed: the regional dendrogram (regional because it contains all the species of interest in the study region). The FD of local assemblages is the length of branches required to connect across this regional dendrogram the species in a local assemblage.

In FD_{LD} (Podani and Schmera 2006), each local assemblage has its own dendrogram constructed. This is very different from FD (Petchey and Gaston 2002a), in which only one dendrogram, the regional dendrogram, is constructed. This has no effect on what the measures can be used for. For example, both FD and FD_{LD} can be used to measure the relative functional diversity of local assemblages; both can be used to assess the effect of new species (invaders) on functional diversity.

4.3   Applications of functional diversity

We compiled a list of papers that cite seven of the key functional diversity methods papers: FAD/MD (Walker *et al.* 1999, Heemsbergen *et al.* 2004), FD (Petchey and Gaston 2002a), FD_{var} (Mason *et al.* 2003), Q (Botta-Dukát 2005), CHV (Cornwell *et al.* 2006) and FD_{LD} (Podani and Schmera 2006) from the ISI database. The list of citing papers was examined to see how continuous functional diversity measures are being used (see Table 4.1). Each citing paper was classified into one of eight categories according to their main focus. In total, these seven methods papers were cited by 262 unique papers (FAD 137, MD 45, FD 82, FD_{var} 22, Q 12, CHV 9, FD_{LD} 5).

One striking pattern in papers citing the seven methods papers is the low application to empirical work. Just 16 (out of 262) studies have attempted to apply one of the six functional diversity indices to empirical data. Heemsbergen *et al.* (2004) manipulated the functional dissimilarity of detritivore communities in soil microcosms (measured using MD). They found that functional dissimilarity, and not species number, led to community compositional effects on key ecosystem processes (loss of leaf litter mass and soil respiration). MD was also used to assess the functional similarity of plants in an Australian rangeland community (Walker and Langridge 2002). This

study followed on from the methods used in Walker *et al.* (1999); however, this time they found that the most dominant species in the community were no more dissimilar to each other than to all other species.

FD and MD have been compared to species richness (SR) and functional group richness (FGR) using data from the BIODEPTH experiments (Petchey *et al.* 2004b). Here, it was found that FD and MD had greater explanatory power because they use a much greater amount of trait information and can allow for small differences between species that functional groups ignore. SR, FGR, FD, and MD have also been analyzed for roadside data from Bibury in the UK (Thompson *et al.* 2005). FD has been used to test if functional diversity of exotic mammalian predators leads to extinction of island bird species (Blackburn *et al.* 2005) and if there is a loss in functional diversity of a tropical amphibian community after logging activities (Ernst *et al.* 2006). De Bello *et al.* (2006) used a variation of Q to calculate the functional diversity of plots exposed to various levels of sheep grazing.

Recently (2007–2008), the number of papers incorporating these continuous measures of functional diversity into empirical studies has notably risen. This is perhaps a sign that they are being increasingly recognized as a useful way to examine applied questions. Schamp *et al.* (2008) used CHV as one of six metrics to estimate the dispersion of traits (biomass, height, and seed mass) in their target plant community. Epps *et al.* (2007) used Q to calculate the chemical diversity of litter and foliar mixtures. They then examined the relationship between species richness and chemical diversity using published data from temperate and tropical forest systems. Jiang *et al.* (2007) compared the effects of plant functional diversity (measured using FD_{var}) on community productivity and soil water content in an experiment on artificial plant communities. Mason *et al.* (2007, 2008) examined the functional diversity of French lake communities using FD_{var} as a measure of functional divergence. Mouillot *et al.* (2007) used both FD and FD_{var} to determine whether assembly rules in lagoon fish communities are driven by functional traits and to seek relationships between functional diversity of fish and environmental gradients. FD has also

been used to calculate the functional diversity of zooplankton in Canadian lakes (Barnett and Beisner 2007), applied to long-term avian distribution datasets (Petchey *et al.* 2007), and used to determine the functional significance of forest diversity in a long term biodiversity experiment (Scherer-Lorenzen *et al.* 2007b).

Another subset of citing papers consider the pros and cons of these functional diversity indices. Petchey and Gaston (2006) provide a review of the most popular functional diversity measures in BEF (Biodiversity-Ecosystem Functioning) research, some of which are evaluated by Ricotta (2005a). Podani and Schmera (2006) review dendrogram-based measures of functional diversity. Mason *et al.* (2003) highlight that FD does not account for species abundance, and claim incorrectly that it is a simple surrogate for SR. They acknowledge the shortcomings of FD_{var} in only accounting for one character at a time. Botta-Dukát (2005) suggests that Q is the best alternative as it uses both species abundance and pairwise functional differences between species, a view echoed by other authors (Lepš *et al.* 2006). It has been proposed that functional diversity can be split into functional richness, evenness, and divergence (Mason *et al.* 2005). Here, FD can be considered a measure of functional richness, while FD_{var} and Q can be considered measures of functional divergence. A functional diversity framework for BEF research has also been suggested, based around use of response and effect traits (Lavorel and Garnier 2002, Naeem and Wright 2003).

There still appears to be a sizeable portion of studies that make use of functional group richness, despite this method being discouraged in many of the continuous functional diversity papers. This is particularly true of older studies (2000–2003) that cite Walker *et al.* (1999). This is unsurprising given that, at this stage, continuous measures of functional diversity were not yet widely recognized. For example, Allen *et al.* (2003), Anderson *et al.* (2000), Davic (2003), Decocq and Hermy (2003), Hector *et al.* (2000), Lepš *et al.* (2001), Lloret and Vila (2003), Ni (2003), and Richardson *et al.* (2002) all used discrete functional groups or plant functional types as measures of functional diversity. More recently, trophic groupings have been empirically shown to

be inappropriate for grassland species (Heisse *et al.* 2007), arable plants (Hawes *et al.* 2005), lake-dwelling shredders (Bjelke and Herrmann 2005), and larval anuran predators (Chalcraft and Resetarits 2003).

Discrete functional groupings continue to be employed in studies of functional diversity. For example, Berg *et al.* (2004), Bret-Harte *et al.* (2004), Chu *et al.* (2006), Dimitrakopoulos *et al.* (2006), Downing (2005), Fischer *et al.* (2007), Krab *et al.* (2008), Micheli and Halpern (2005), Moretti (2006), and Zavaleta and Hulvey (2007) all used trophic groups, functional groups or grass/forb/legume classifications. In many cases, the use of discrete functional groupings seems to be a result of the difficulty in applying trait-based functional diversity measures to real systems. The large amounts of data collection necessary for appropriate trait clustering may prove impractical for many studies. Additionally, there may be a perception that the subjectivity surrounding the choice and number of traits makes continuous measures as arbitrary as discrete measures of functional diversity. This point is further highlighted by the number of authors that have used variations of the main continuous functional diversity measures (Roscher *et al.* 2004, Fukami *et al.* 2005, Pavoine and Doledec 2005) or proposed additional functional diversity indices (Dumay *et al.* 2004, Ricotta 2004, Bady *et al.* 2005, Mouillot *et al.* 2005a, Thuiller *et al.* 2006a).

In spite of this apparent reluctance to embrace continuous measures of functional diversity in empirical BEF studies, there seems to be an increasing appreciation for the benefits of these measures over discrete functional groupings. A bootstrap analysis on empirical data from the BIODEPTH experiments shows that FGR has relatively poor power for explaining variation in an ecosystem process (Petchey 2004). Naeem and Wright (2003), Jax (2005), Ricotta (2005a) and Bulling *et al.* (2006) have all recommended the use of functional diversity for advancing the understanding of how biodiversity affects ecosystem functioning, rather than focusing just on species diversity. There has been a call for studies of parasite biodiversity to look to taxonomic and functional diversity for patterns and processes that

have escaped notice to date (Poulin 2004). Attempts have also been made to encourage phytoplankton ecologists to make use of the new methods for studying functional diversity in lakes (Weithoff 2003). This could be important for BEF research given the short generation times associated with phytoplankton, allowing true succession to take place in one season. Finally, it has been demonstrated that even for species-rich systems like coral reefs, a single functionally important family, parrotfish, are the only creatures carrying out significant bioerosion, a major reef process (Bellwood *et al.* 2003). Without attempting to quantify the functional diversity of ecosystems and the consequences of loss of that diversity in an appropriate way, we are in danger of overlooking a crucial aspect of BEF relationships.

Other studies that cite these key functional diversity methods papers discuss the use of traits (Cornelissen *et al.* 2003, Norberg 2004, Poff *et al.* 2006, Barnett *et al.* 2007) and species abundances (de Bello *et al.* 2007, Lavorel *et al.* 2008) in quantifying functional diversity. There is also a significant body of work that recommends the use of functional diversity as an ecological indicator in environmental impact assessment (Bady *et al.* 2005, Heino 2005, Mouillot *et al.* 2005b, Dierssen 2006, Henle *et al.* 2006, Mouillot *et al.* 2006). Here, in the presence of increased environmental stress, the range of functional attributes is likely to be narrow as only the most adapted species survive, with the niche filtering concept suggesting that surviving species will share many biological characteristics (Franzén 2004, Statzner and Moss 2004).

4.4 Differences between measures. Effects of species richness on functional diversity

4.4.1 Background

Biodiversity can affect ecosystem processes by a variety of routes (Tilman 1999b, Chapin *et al.* 2000c). As biodiversity changes, so does composition and richness. For example, an invasion adds a novel species with a novel identity, thereby changing composition; it also increases species

richness by one. During the late 1990s and into the first decade of the twenty-first century an acrimonious debate flared around these effects (Loreau *et al.* 2001). Which was more important: the effects of the identity of a novel species, or the effects of having one more species (Loreau *et al.* 2001)?

Experimental and theoretical results suggested that both can be important in different situations (Hooper and Vitousek 1997, Huston 1997, Tilman 1997). One investigation focused on the effects of species richness and composition on functional diversity (Petchey and Gaston 2002a). When is functional diversity affected strongly by species richness, and when strongly by species composition? Since functional diversity should relate with ecosystem processes, the answer to this question also informs about the relative importance of species richness and composition for ecosystem processes.

Since the then-dominant measure of functional diversity, namely functional group richness, was problematic for answering questions about the importance of species richness, Petchey and Gaston (2002a) developed a continuous measure (FD – see above). Results of this and a related study (Petchey and Gaston 2002b) indicated that the effective dimensionality of trait space determined the relative importance of species richness and composition. The effects of species richness were strongest in high dimensional space; the effects of composition dominated in low dimensional space.

The effective dimensionality of trait space results from the number of traits used to measure functional diversity and the correlation (or lack thereof) between them. Many uncorrelated traits means high effective dimensionality, while many correlated traits or few traits (regardless of correlation) means low effective dimensionality.

Thus the nature of the variation among species was critically important for understanding patterns of functional diversity. Furthermore, Petchey and Gaston (2002a) found that this conclusion was robust to details of how their functional dendrogram was constructed. Here, we extend Petchey and Gaston's simulations and ask how robust is their conclusion in the face of variation in how functional diversity is measured.

4.4.2   Methods

A collection of local assemblages varying in species composition and richness were simulated. The species richness gradient, from six to 20 species, was constructed by randomly selecting species from a regional species pool containing 20 species. At each species richness level there were up to five distinct communities, each containing a different random composition of species. Obviously, there was only one composition possible for the 20 species community, and some random draws within a richness level may have contained the same set of species. Five sets of assemblages that each represented an extinction trajectory from 20 to six species were also constructed. These trajectories are useful to know how loss (or gain) of a species can affect a functional diversity measure.

The functional diversity of each local community was calculated by the methods described in Section 2 (CHV, FD_{var}, MD, Q, FD, FD_{LD}). Simulations and measurements of all measures of functional diversity were made in R (R Development Core Team 2008). Where required, distances were Euclidean and the clustering algorithm was UPGMA. Contact OLP for R script to calculate the measures of functional diversity, including convex hull volume.

Calculating convex hull volume is complex (Cornwell *et al.* 2006). In the R library *geometry* (Grasman and Gramacy 2008) the function *convhulln* interfaces the Qhull library (Barber *et al.* 1996). For one dimensional data (one trait) we made CHV the range of the data (maximum value minus the minimum value). CHV requires that the number of species is greater than the number of traits, since each species is a vertex in the convex hull, hence the lowest richness in the simulations was six species.

We made two separate sets of simulations. In one, species differed in only one trait, and in the other they differed in five traits. Trait values were drawn from a normal distribution with a mean of zero and standard deviation of one. When there were five traits, there were no correlations between them.

4.4.3   Results

The effect of trait number (one versus five) was consistent across all six diversity measures. Increasing the number of traits caused a greater
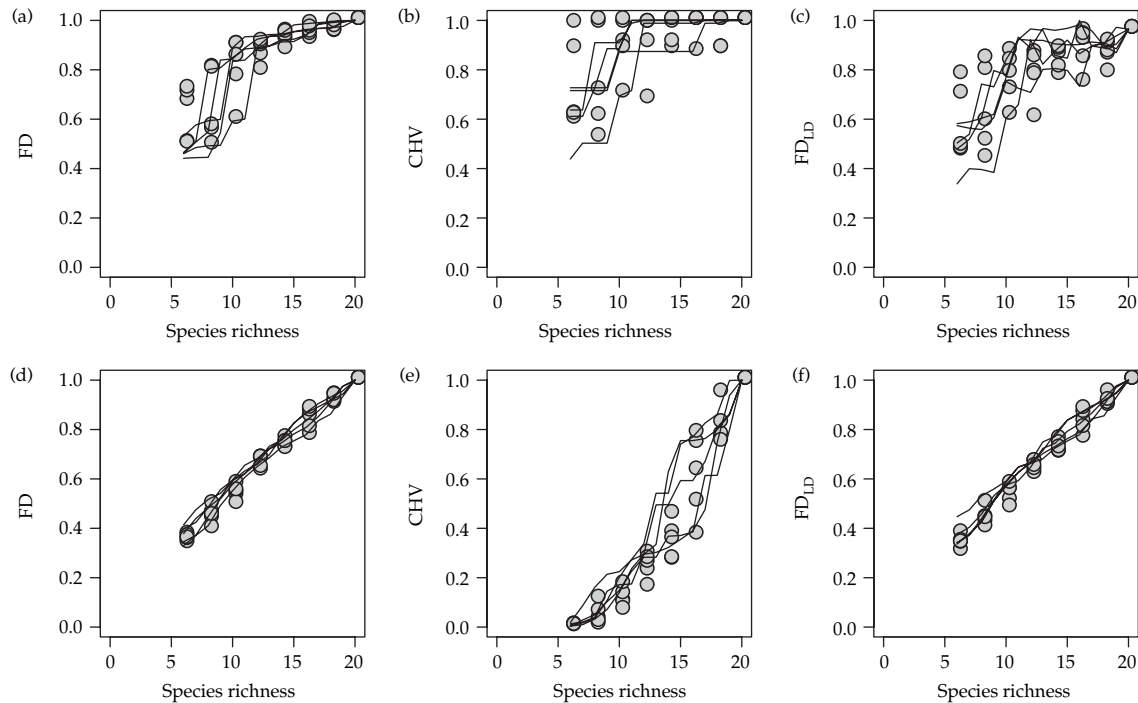
Figure 4.1   Simulated relationships between three measures of functional diversity (FD, CHV, FD$_{LD}$; see Section 4.4 for explanation) when species in the regional pool differ in one trait dimension (top row) or five trait dimensions (bottom row). At each richness level there are five different communities (filled circles), each a random draw of species from the regional pool. There are also five extinction trajectories, from 20 species to six species, shown by unbroken lines.

effect of species richness on functional diversity values, and a weaker effect of species composition. The effect was clearest for FD, CHV, and FD$_{LD}$ (Fig. 4.1), and was also present for MD, Q, and FD$_{var}$ (Fig. 4.2). With one trait, values of functional diversity varied greatly within a level of species richness (panels (a), (b), and (c) in Figs. 4.1 and 4.2); there was much reduced variation with five traits (panels (d), (e), and (f) in Figs. 4.1 and 4.2). Similarly, with one trait, different sequences of species loss had very different effects on the loss of functional diversity. With five traits, loss of functional diversity was more similar among different sequences of species loss.

The general relationship between species richness and functional diversity differed greatly among the six measures. Three (FD, CHV, and FD$_{LD}$) exhibited an overall positive relationship with species richness (Fig. 4.1). Two (MD and Q) exhibited little relationship with species richness,

and one (FD$_{var}$) appeared to show a negative relationship (Fig. 4.2).

Effects of species loss differed qualitatively between the six measures. Two (FD and CHV) either decreased or remained the same when a species was lost (Fig. 4.1). The other four (FD$_{LD}$, MD, Q, FD$_{var}$) decreased, increased, or remained unchanged (Figs. 4.1 and 4.2).

4.4.4   Conclusions

The effect of number of traits on the relative importance of species richness and composition (Petchey and Gaston 2002a), appears robust to different measures of functional diversity. Therefore, to understand the effects of richness and composition, the choice of which traits to include in measures of functional diversity is obviously critical. The choice of which functional diversity measure to use with this question is less important. This
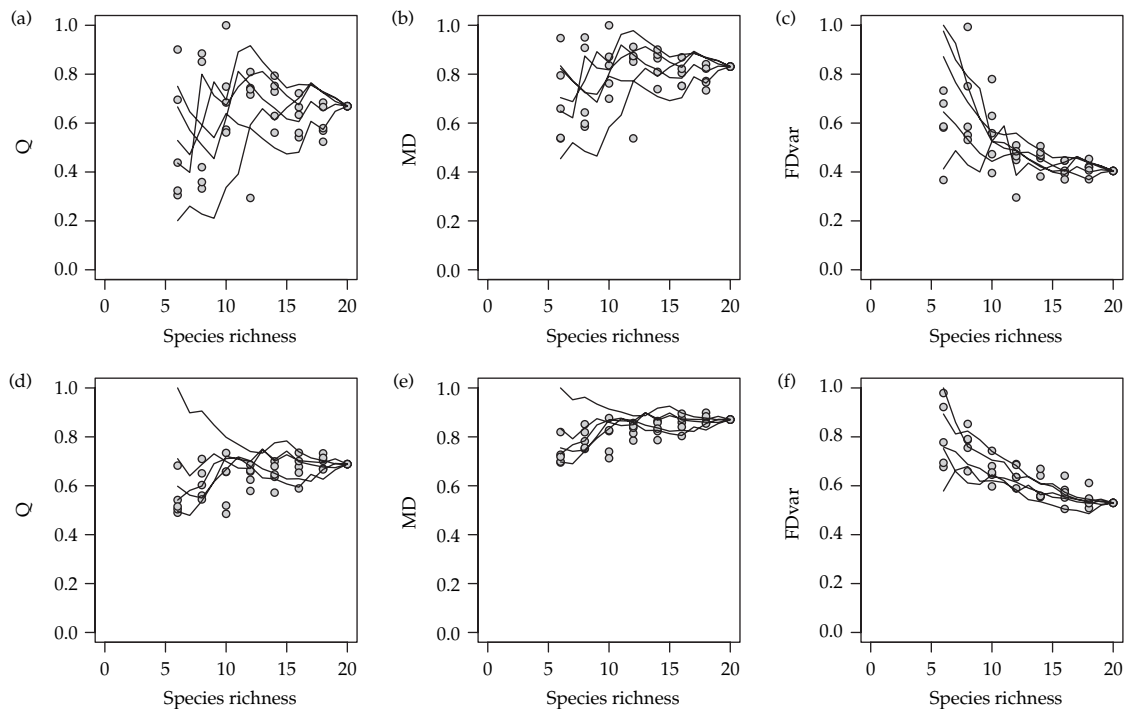
Figure 4.2   Simulated relationships between three measures of functional diversity (Q, MD, FD$_{var}$; see Section 4.4 for explanation) when species in the regional pool differ in one trait dimension (top row) or five trait dimensions (bottom row). All other details are the same as in Fig. 4.1.

reinforces previous findings (e.g. Petchey and Gaston 2002a) that details of the functional diversity measure (such as distance measure and clustering method) may have little importance relative to choosing appropriate sets of traits.

The qualitative effect of species richness on functional diversity does, however, differ between diversity measures. For example, FD, CHV, and FD$_{LD}$ generally increase with increases in species richness, while the others (MD, Q, FDvar) do not. This broad difference results from the fact that loss of a species can cause increases in some measures of functional diversity (MD, Q, FDvar), but cannot cause an increase in other measures (FD, CHV). FD$_{LD}$ can increase, but only rarely and by small amounts (Figs. 4.1(c) and (f)). Should a measure of functional diversity be able to increase when an extinction occurs? Should a measure be able to decrease when a species is added?

Suggestions that the answer to the last two questions is 'no' mean that a positive relationship is correct (Ricotta 2005a); only FD and CHV meet this criteria. However, others suggest that measures of functional diversity should not be closely correlated with species richness, or even that functional diversity should be independent of species richness (e.g. Mason *et al.* 2003). It remains unclear, however, how to reconcile these ideas with the suggestions that increases (or decreases) in species richness cannot cause a decrease or (increase) in functional diversity. Furthermore, there may be multiple 'facets' to functional diversity that are not included in our analyses. For example, how regularly are species distributed in trait space, and the regularity of the distribution of species abundances in trait space (Villéger *et al.* 2008). Indeed, adding species abundances to measures of functional diversity greatly increases the complexity of measurement.

Why do some measures behave very differently from others? Consider the idea of the species in an assemblage forming a cloud of data in

n-dimensional trait space. FD and CHV are intuitively similar, and both measure, in some broad sense, the volume of trait space that is represented by the data cloud. As they both measure volume (in some sense), adding a species cannot cause a decrease, and removing a species cannot cause an increase. They do, however, differ in the sense that volume is measured. CHV is the minimum (convex) volume that includes all the species (points in the data cloud). Whether any species, or how many species, occupy the space inside the convex hull has no effect on CHV. This is clear in Fig. 4.1(b), where loss (or addition) of species often has no effect on CHV. Furthermore, CHV is influenced perhaps more than other measures by the most extreme (i.e. minimum and maximum) trait values, since these, by definition, determine the volume. In contrast, FD measures, in a sense, a combination of the size of the data cloud, and how filled in is the data cloud. That is, FD is affected both by the range of trait values present, and by the different species that might occur within the range. (FD_{LD} is in these respects similar to FD and CHV.)

MD, Q, and FD_{var} are also intuitively similar to each other. These each represent, in some sense, the average distance between species in n-dimensional space. Here, adding a species that lies close to several other species can decrease the average distance, or increase it if the new species is distant from most others. Conversely, removing a species that lies close to other species will likely increase the average distance.

4.5 Discussion

4.5.1 Which measure?

First, this question is secondary to that of which traits to include (Naeem and Wright 2003, Lepš et al. 2006, Petchey and Gaston 2006). Indeed, the question of what qualifies as a 'functional trait' may be complex and hierarchical (Violle et al. 2007). The measure can be less important than the traits included (Figs. 4.1 and 4.2), and this phenomenon is probably quite general. A consequence is that we risk focusing too much effort on the rather 'easy' practice of inventing new measures and modifying old ones (as demonstrated by the high proportion

of new measures of functional diversity in Table 4.1), and far too little effort thinking about which traits to include. What traits of plants are important determinants of biomass production (Díaz and Cabido 1997)? What traits of stream invertebrates are important determinants of leaf litter breakdown (Jonsson and Malmqvist 2000)? To stand any chance of measuring functional diversity correctly, these questions (and those about the traits of other organisms) must be answered. Which traits to include is a great challenge – 'great' in the sense that it gives a reason and opportunity to spend time learning more about what the organisms in ecosystems do.

If we are confident that we have the functionally important traits, only then can we ask 'which measure?' There certainly isn't one answer to this question, but here are some thoughts on how to decide. First, decide if you (i.e. your ecological question) need a measure of functional diversity that includes evenness in relative abundances of species (Q and FD_{var}) (Ricotta 2007). In doing so, note that a 'yes' answer means that addition of a species can decrease functional diversity and loss of a species can increase it (Figs. 4.1 and 4.2, panels (d) and (e)). If you need a measure that does not include species' relative abundances, and does not allow addition (or loss) of species to decrease (or increase) functional diversity, then FD or CHV are appropriate. If you need a measure that incorporates how much of a range of trait space is filled choose FD; otherwise CHV is likely sufficient.

If you can't make up your mind about any of these questions, or are curious, see how the answer to your particular question depends on the measure (as in Section 4.4). You may find, as here, that the choice of measure is less important than which traits are included in the measure.

4.5.2 Conclusions

What is the significance of this enormous activity in developing metrics for the quantification of functional diversity? Functional diversity is a vital component of research about the functional consequences of biodiversity (Biodiversity-Ecosystem Functioning, or BEF research). Indeed, the

Millennium Ecosystem Assessment concluded that species *per se* is less important than what the species do. Arguably this knowledge was implicit in the design of some of the earliest biodiversity experiments. For example, Naeem *et al.* (1994) chose for the Ecotron experiments a functionally balanced set of plant species. Consequently, the ecosystem services that humans rely upon are more likely related with the functional diversity of organisms, rather than taxonomic or phylogenetic diversity. The examples in Section 4.3 provide some empirical evidence for this. The explosion of different measures may represent the recognized importance of creating an accurate and predictive measure. It has always been clear that we first need to know which traits are important for each ecosystem service we might choose to focus on. Our analyses in Section 4.4 show that the choice of traits may hold more sway than the choice of a functional diversity index. The conclusion must therefore be that understanding species' natural histories (traits) and how these interact with their environment is a prerequisite for functional diversity to be a concept that can lead to management and conservation of ecosystem services.

Other important challenges remain. The data demands of including intraspecific variability in measures of functional diversity (Cianciaruso *et al.* 2009). It seems clear, however, that variation among the individuals in a species could have important effects on community and ecosystem processes (e.g. Pachepsky *et al.* 2007). Another challenge is how to estimate total functional diversity from a sample. Rarefaction methods can be applied to functional diversity measures and have potential (e.g. Walker *et al.* 2008). Perhaps most importantly, we need to carry out experiments that test the assumptions and predictions of functional diversity. The knowledge from these will help us understand the broad ecological questions to which functional diversity can make a significant contribution.

4.6 Acknowledgements