

Functional richness, functional evenness and functional divergence: the primary components of functional diversity

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Functional diversity is hypothesised as being beneficial for ecosystem functions, such as productivity and resistance to invasion. However, a precise definition of functional diversity, and hence a framework for its quantification, have proved elusive. We present a definition based on the analogy of the components of species diversity – richness, evenness and divergence. These concepts are applied to functional characters to give three components of functional diversity – functional richness, functional evenness and functional divergence. We demonstrate how each of these components may be calculated. It is hoped that our definition of functional diversity and its components will aid in elucidation of the mechanisms behind diversity/ecosystem-function relationships.

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Functional diversity has been proposed as an important feature of biological assemblages, enabling prediction of the rate and reliability of ecosystem processes (i.e. ecosystem function and ecosystem reliability). This link has been hypothesised for communities of microbes (Griffiths et al. 1997), plants (Tilman et al. 1997, Lavorel and Garnier 2002, Petchey et al. 2004) and animals (Pearson 2001, Bremner et al. 2003). However, there have been few demonstrations of the link, and the interpretation of even those studies has been questioned (Wardle 1999). Testing it will require functional diversity measures to be available, based on a rigorous definition of functional diversity. The various existing definitions do not provide enough detail for deriving functional diversity indices. For example, the widely cited definition of Tilman (2001), of functional diversity as “the value and range of the functional traits of the organisms in a given ecosystem” is sound, but for

the derivation of indices the terms it uses must be exactly defined.

‘Functional diversity’ has been used to describe several different aspects of community or ecosystem structure, such as the variation in the functional characters of plant species (Walker et al. 1999, Petchey and Gaston 2002, Mason et al. 2003), the complexity of food webs (Hulot et al. 2000), and the number of plant functional groups present (Diaz and Cabido 2001). The latter usage seems to have been the most common in community ecology, even though it is not directly related to Tilman’s (2001) definition. Moreover, this usage is problematic if the functional groups are formed subjectively, and even statistical classification may incorporate bias and will necessarily discard information when forming groups. Thus, while the functional group approach has the advantage of speed in application, it is theoretically inferior to the measurement of functional

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diversity on a continuous scale (Fonseca and Ganade 2001).

Several proposed mechanisms behind diversity/ecosystem-function relationships are based on patterns of species distribution in niche/functional space. Niche complementarity has been identified as a possible mechanism linking diversity to ecosystem processes (Tilman et al. 2001, Alder and Bradford 2002, Petchey 2003). One possibility is that the species will differ in resource use, i.e. in alpha niche (Wilson 1999). Then, given an even resource distribution across niche space, higher niche complementarity will allow more complete use of the resources available within a community, thus allowing higher productivity and invasion resistance (Dukes 2001, Petchey 2003). Other functional characters such as drought tolerance may reflect a greater variety of responses to environmental conditions (beta niche), so that niche complementarity may help to buffer ecosystem processes against climatic fluctuations (i.e. increase ecosystem reliability; Tilman 1996, Doak et al. 1998).

The proposed mechanisms linking diversity and ecosystem function via niche complementarity are based on the distribution of species in niche space. Thus, if functional diversity is to be useful in testing these mechanisms, proposed functional diversity indices should directly measure aspects of the distribution of species in niche space. We propose such indices. Our aim is not to justify hypotheses relating diversity to ecosystem function, but to provide means for testing them. It is not possible, or necessarily desirable, to sum up all aspects of functional diversity in a single number (Mouillot et al. 2005). We therefore need to identify the separate components of functional diversity so that possible links between them and ecosystem function can be examined in more detail.

Applying diversity to function

Mouillot et al. (2005) point out that functional diversity can be decomposed into two components – functional evenness and functional richness. This split follows existing definitions of species diversity which may be decomposed into (a) species richness and (b) evenness in species abundance (Purvis and Hector 2000). Two important aspects of this decomposition of species diversity are:

- i) Richness and evenness are orthogonal to each other (i.e. vary independently of each other)
- ii) Richness and evenness relate to the same entities (i.e. to species).

In considering how these concepts might be applied to continuous functional character data we must be careful to follow these criteria.

The decomposition of Mouillot et al. (2005) was limited to situations where each species is characterised by a single (e.g. mean or median) functional character value. However, in the real world species have a frequency distribution across niche space, reflecting the range of resources that the species is able to use (Fig. 1). In addition, within-population genotypic variation, phenotypic plasticity (resulting from local environmental heterogeneity; Kark et al. 2002), character shifts after local interspecific interactions (Schluter 2000, Day and Young 2004), and ontogenetic differences (Kramer and Bryant 1995) affect the type of resources that individuals (or individual organs, for plants) are able to utilise (Bolnick 2001, Via 2004). Using these distributions in niche space we may be able to gain a more accurate picture of the resources collectively available to the species within a community. The number of measurements required is large, but not impossible as can be seen in the study of Stubbs and Wilson (2004), where 23 functional characters were measured with estimates of intraspecific variation for each.

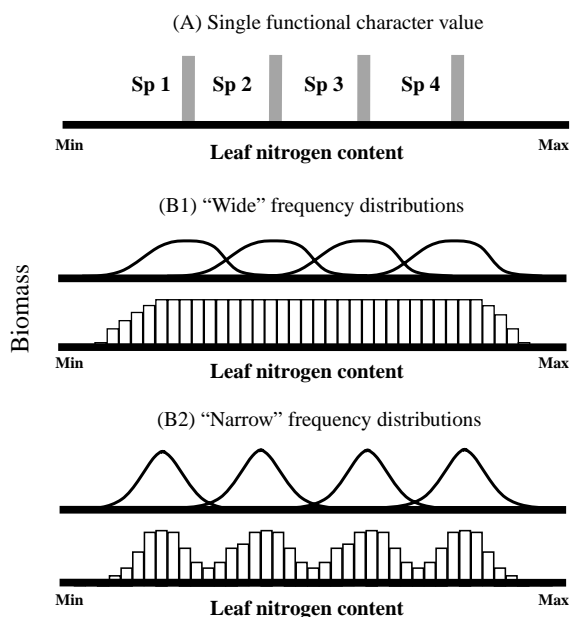


Fig. 1. Functional character values vs frequency distributions in niche space. The vertical axes represent abundance (e.g. biomass). The bell-shaped curves indicate the distribution of the abundance of individual species in niche space (e.g. leaf nitrogen content). The histograms indicate the summed abundance of the species occurring in each functional character category (i.e. equal-width sections of the functional character range). The diagrams of species frequency distributions in niche space show that the use of single character values (A) may not be able to distinguish between communities which differ in how the abundance of species is distributed in niche space. For this, the distribution of character values is required (B): in the first community (B1) biomass is more evenly distributed in niche space than in the second community (B2).

We identify two aspects of species frequency distributions in niche space that are analogous to species richness and species evenness (Fig. 2). Firstly, the amount of niche space occupied by the species within a community may be used as a richness measure – functional richness – since it is independent of abundance (i.e. a section of niche space is considered to be occupied even if only very little abundance occurs within it, in the same way that a species counts towards species richness even if it occurs in a very small amount). Secondly, the evenness of the distribution of abundance in niche space may be used as an evenness measure – functional evenness – since it is orthogonal to functional richness. Functional richness and functional evenness both relate to the same entities – niche space or sections of niche space (see ‘Measuring the components of functional diversity’). Functional evenness applies only to the distribution of abundance in occupied niche space, just as species evenness applies only to the abundances of the species that are present.

The overall divergence between the species within a community has received increasing attention as a component of biodiversity in the last decade (Diaz and Cabido 2001). It has been measured in a variety of ways, such as taxonomic distinctness (Clarke and Warwick 2001), genetic variation (Shimatani 2001), functional complexity (Petchey and Gaston 2002) and ‘functional diversity’ (Walker et al. 1999, Mason et al. 2003). Of these only the FD_{var} of Mason et al. (2003) is both directly related to how spread-out or how clumped the species are in niche space and weighted by abundance

(see the comment on the FD index of Petchey and Gaston 2002 and the $FAD2$ of Walker et al. 1999 in the section below on ‘Other present and future measures of functional diversity’). The limitation of FD_{var} is that, although it may provide a useful means for testing proposed mechanisms behind diversity/ecosystem-function relationships, it is based for each functional character on a single value for each species, rather than the species’ frequency distributions (Fig. 1). Consequently, FD_{var} gives only an approximation of species distributions in niche space and, in turn, their collective use of resources. However, the degree to which the distribution of species abundances in niche space maximises total community variation in functional characters may be used as a divergence measure – functional divergence (Fig. 3). This is orthogonal to functional richness and functional evenness, and takes account of the frequency distributions of species through niche space.

We thus arrive at an overall definition of functional diversity as: the distribution of the species and abundance of a community in niche space, including:

- the amount of niche space filled by species in the community (functional richness)
- the evenness of abundance distribution in filled niche space (functional evenness) and
- the degree to which abundance distribution in niche space maximises divergence in functional characters within the community (functional divergence).

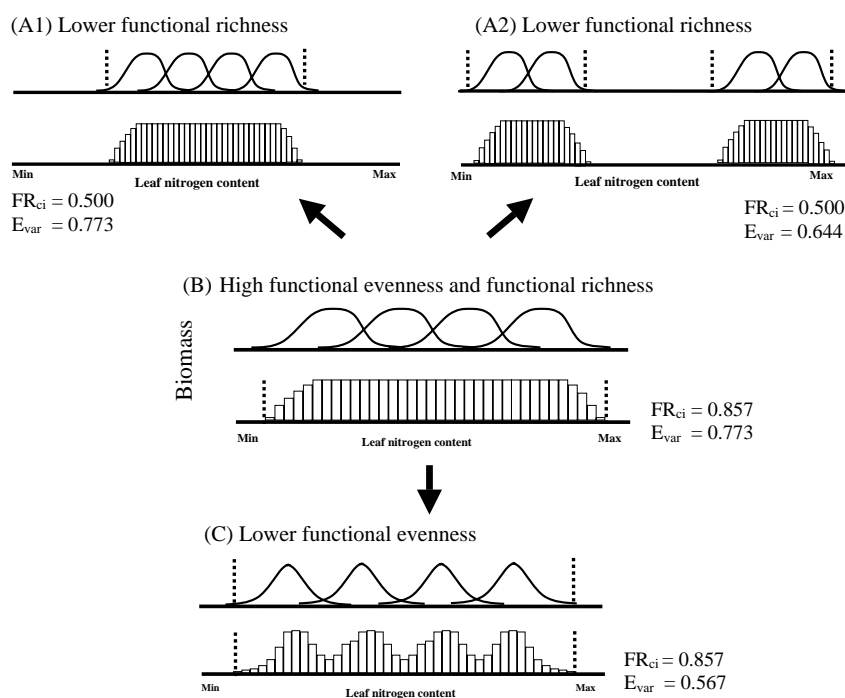


Fig. 2. Functional richness and functional evenness. The vertical axes represent abundance (e.g. biomass). The bell-shaped curves indicate the distribution of the abundance of individual species in niche space. The histograms indicate the summed abundance of the species occurring in each functional character category (i.e. equal-width sections of the functional character range). The vertical dotted lines indicate the amount of niche space filled by the species together. Functional richness can decrease without a change in functional evenness if the evenness of abundance within the niche space is unchanged (going from B to A1). Similarly, functional evenness can decrease without a change in functional richness if the amount of niche space filled is unchanged (going from B to C).

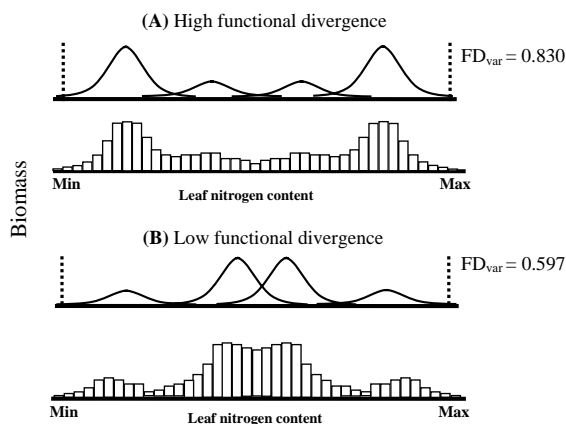


Fig. 3. Functional divergence. As in Fig. 2 the bell-shaped curves show the distribution of species abundance (e.g. biomass) in niche space (e.g. leaf nitrogen content) while the histograms show the summed abundance of the species present in each category. The vertical dotted lines indicate the amount of niche space filled by the species. (A) A community with relatively high functional divergence, with the most abundant species occurring at the extremities of the functional character range. (B) A community with relatively low functional divergence, with the most abundant species occurring towards the centre of the functional character range. Functional divergence can change without a change in either functional richness or functional evenness (going between A and B).

Measuring the components of functional diversity

Indices are required for quantifying these three components of functional diversity for characters measured on continuous scales. Any such index must be intrinsically independent of species richness and species evenness, and all those we present are. Initially, we deal only with individual characters (i.e. univariate niche space), which is a useful initial approach for determining whether any particular character is especially related to ecosystem function. Consideration is given later to measuring functional diversity for multiple characters.

Functional richness

Low functional richness (Fig. 2) indicates that some of the resources (alpha niches) potentially available to the community are unused. This will reduce productivity (Petchey 2003). If the functional character represents environmental tolerances (beta niches) lower functional richness implies that under some environmental conditions, species to take advantage of the conditions will be missing, giving reduced buffering against environmental fluctuations (Tilman 1996). Invasion resistance may also be lower, since there will be gaps in niche space which an invader can exploit (Dukes 2001).

The measurement of functional richness depends on knowing the distribution of the abundance of each

species through niche space (Fig. 2). Measurements for each character from several individuals of each species are required to describe the distribution. If an asymptotic distribution such as the normal is fitted, a cut-off point must be chosen below which niche space is considered as empty. For animal populations this would probably be a single individual, but for plants a more arbitrary cut-off would be needed.

The amount of niche space filled for a character, calculated as above, must be standardised to enable comparison of different characters. If the absolute range of a character is known (e.g. the percentage of biomass allocated to root must be in the range 0 to 100), the amount of niche space filled for the character would be expressed as a proportion of it:

$$FR_{ci} = \frac{SF_{ci}}{R_c} \quad (1)$$

where FR_{ci} = the functional richness of functional character c in community i ,

SF_{ci} = the niche space filled by the species within the community,

R_c = the absolute range of the character.

If the absolute range of a character is not known, R_c may be taken as the largest range in the set of communities being studied which will make the calculations consistent within the study, or it may be taken as the range of values reported in the literature.

On occasion it may prove impractical to obtain enough replicates to accurately define the frequency distribution of species in niche space (Fig. 2). In such cases the distance between the minimum and maximum of the mean (or median) values for the species may be used as a surrogate for functional richness. However, if some sections of niche space are not occupied (Fig. 2, A2), the estimate will be inflated, and invalid.

Examples of communities where functional richness is higher ($FR_{ci}=0.857$) and lower ($FR_{ci}=0.500$) can be seen in Fig. 2. Functional richness can either remain unchanged or increase as species richness increases (Petchey and Gaston 2002). Thus it has no a priori relationship with species richness, nor does it with species evenness, it is orthogonal to them.

Functional evenness

Functional evenness may be seen as the degree to which the biomass of a community is distributed in niche space to allow effective utilisation of the entire range of resources available to it (i.e. within the niche space it encompasses). Assuming resource availability is even throughout niche space, lower functional evenness indicates that some parts of niche space, whilst occupied, are under-utilised. This will tend to decrease productivity and reliability, and increase opportunity for invaders.

As with functional richness, direct measurement of functional evenness requires knowledge of the distribution of the abundance of each species throughout niche space (i.e. measurements from several individuals of each species for each character). It also requires nomination of a cut-off point below which community abundance is considered negligible, since the calculation is made only over occupied niche space. Functional evenness can be measured directly by dividing the occupied niche space into many (i.e. >100) narrow categories (Fig. 3), and applying an evenness index to the abundance contained within each character category (e.g. the indices recommended in Smith and Wilson 1996 and Mouillot and Wilson 2002). The use of such a large number of categories will minimise the loss of information, thus avoiding some of the problems associated with the functional group approach. As the species evenness indices recommended by Smith and Wilson (1996) and Mouillot and Wilson (2002) are independent of species richness, they will also be independent of the number of functional character categories used. Thus, there is no bias associated with the number of categories chosen: use of too few will result in some loss of information, but the error could give higher or lower functional evenness.

If information on the frequency distributions of individual species in niche space is not available, functional evenness may be approximated by applying an index that measures both the evenness of spacing between species means or medians in niche space and evenness of species abundances, e.g. the FRO index of Mouillot et al. 2005.

Using E_{var} (Smith and Wilson 1996), functional evenness is higher for the community depicted in Fig. 2A1 and 2B ($E_{\text{var}}=0.773$) than for Fig. 2C ($E_{\text{var}}=0.567$) (only 39 categories were used, for clarity of display). This measure has no a priori relationship with functional richness. Therefore, if a relation occurs it will be an ecological feature, not a mathematical artefact.

Functional divergence

High functional divergence indicates a high degree of niche differentiation, and thus low resource competition. Thus communities with high functional divergence may have increased ecosystem function as a result of more efficient resource use.

A method for calculating functional divergence was presented by Mason et al. (2003) based on an abundance-weighted sum of squares. It uses the mean character value for each of the species in a community. If enough values are available for each species to describe the distribution of individuals of each species in niche space, functional divergence could be calculated using the character values and abundances of the N functional

character categories (where N = 100) in place of species character and abundance values (Fig. 3):

$$FD_{\text{var}} = 2/\pi \arctan \left[5 \times \sum_{i=1}^N [(\ln C_i - \overline{\ln x})^2 \times A_i] \right] \quad (2)$$

where FD_{var} = the functional divergence across functional character categories,

C_i = the character value for the i th functional character category,

A_i = the proportional abundance of the i th functional character category,

$\overline{\ln x}$ = the abundance-weighted mean of the natural logarithm of character values for the categories. That is, the sum of category proportional abundances multiplied by the natural logarithm of category character values.

The arc tangent is taken of the abundance-weighted sum of squares for the categories, and multiplied by $2/\pi$ so that the index is constrained to vary between 0 and 1. The inclusion of the value 5 allows a more even use of the 0 to 1 scale, e.g. giving FD_{var} of 0.830 for Fig. 3a and 0.597 for Fig. 3b. This measure has no a priori relationship with species richness, species evenness, functional richness or functional evenness.

Other present and future measures of functional diversity

Index FAD2 of Walker et al. (1999) measures the functional divergence of a community using multiple characters, by summing the squared Euclidian distance between all possible species pairs in niche space. However, Mason et al. (2003) outlined several problems with this index, especially when including abundance. For example, FAD2 gives a different result if a single species is split into two functionally identical species with the same total abundance between them as the initial species. This is important when considering microspecies (e.g. in genera such as *Hieracium* or *Taraxacum*), since such species might easily be lumped together in field sampling and thus yield a different result in FAD2 than if they were identified correctly. In fact, such microspecies not only look almost identical, functionally they are effectively identical. In addition to the concerns of Mason et al. (2003), FAD2 does not control for species richness or the number of functional characters used: as either increases, FAD2 will also tend to increase. To satisfy the condition of orthogonality, functional diversity should not vary systematically with species richness, and surely the number of functional characters measured should not bias a community's functional diversity in a known direction!

A method for calculating functional complexity, 'FD', was presented by Petchey and Gaston (2002). Using our conceptual framework, this index may be viewed as a multivariate measure of functional richness. In practice,

their method gives results for functional complexity that are highly correlated with species richness, though this effect will be reduced when the characters are less correlated (O. Petchey, pers. comm.). This index is not affected by the splitting of a species into two functionally identical species with the same total abundance, and thus appears fairly robust. Since Petchey and Gaston (2002) used Euclidean distance, their FD index will be influenced by the number of functional characters used in the same way as FAD2.

Shimatani (2001) demonstrated that the quadratic entropy index of Rao (1982) may be used as a measure of taxonomic and genetic diversity. It is a small step to apply this index as a measure of functional diversity, by using some multivariate distance measure, such as Euclidean distance, to calculate the distance between species in niche space. Following our conceptual framework, such an index might be viewed as a multivariate measure of functional divergence. This index would not be affected by the splitting of a species into two functionally identical species with the same total abundance between them.

Another method for measuring functional divergence in multi-dimensional niche space is to take the mean across the characters measured of values for a single-character index such as the FD_{var} of Mason et al. (2003).

In measuring functional diversity using multiple characters, one must be careful that the functional characters included are not trivially correlated (e.g. leaf thickness and specific leaf area will tend to be negatively correlated as they are dependent on the same aspect of leaf morphology), as the use of such trivially correlated characters may result in spuriously high or low values of functional diversity.

Another aspect of species distribution in niche space is interspecific overlap in niche space. However, we see this as an aspect of functional redundancy rather than of functional diversity, relevant to questions of the functional impairment of an ecosystem after species loss (Rosenfeld 2002), with the added complication that for true redundancy there should be full overlap in alpha niche but not in beta niche (Wilson 1999). Niche overlap also has the drawback that it requires species to be identified correctly, which is difficult for cryptic species. Indeed, the whole concept of functional diversity is to replace taxonomic species with functional richness and functional evenness, which also happen to avoid this problem.

Conclusions

We have demonstrated that functional diversity comprises three major components: functional richness, functional evenness and functional divergence. Each of these can be calculated relatively simply by ecologists

from any background. Use of these three components will eliminate much of the confusion currently surrounding the measurement of functional diversity, and will aid ecologists in examining the mechanisms behind diversity/ecosystem-function relations.

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