

REPORT

## Functional diversity (FD), species richness and community composition

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### Abstract

Functional diversity is an important component of biodiversity, yet in comparison to taxonomic diversity, methods of quantifying functional diversity are less well developed. Here, we propose a means for quantifying functional diversity that may be particularly useful for determining how functional diversity is related to ecosystem functioning. This measure of functional diversity “FD” is defined as the total branch length of a functional dendrogram. Various characteristics of FD make it preferable to other measures of functional diversity, such as the number of functional groups in a community. Simulating species’ trait values illustrates how the relative importance of richness and composition for FD depends on the effective dimensionality of the trait space in which species separate. Fewer dimensions increase the importance of community composition and functional redundancy. More dimensions increase the importance of species richness and decreases functional redundancy. Clumping of species in trait space increases the relative importance of community composition. Five natural communities show remarkably similar relationships between FD and species richness.

### Keywords

Clustering, community composition, FD, functional dendrogram, functional diversity, functional groups, functional redundancy, species identity, species richness, traits.

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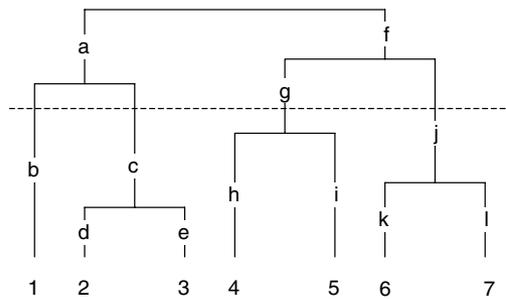
### INTRODUCTION

Functional diversity, the extent of functional differences among the species in a community (Tilman 2001), is an important determinant of ecosystem processes (Loreau 1998; Chapin *et al.* 2000; Tilman 2000; Díaz & Cabido 2001; Loreau *et al.* 2001). A common measure of functional diversity is the number of functional groups represented by the species in a community (Naeem & Li 1997; Hooper 1998; Hector *et al.* 1999; Rastetter *et al.* 1999; Fonseca & Ganade 2001; Tilman 2001; Tilman *et al.* 2001). Of the problems associated with assigning species to groups (Schulze & Mooney 1993; Lavorel *et al.* 1997) perhaps least tractable is the arbitrary scale at which differences between species qualify as functionally significant (Simberloff & Dayan 1991; Vitousek & Hooper 1993; Root 2001). There is no simple, satisfactory, or standardized measure of functional diversity (Díaz & Cabido 2001; Tilman 2001).

Here we present a measure of functional diversity that permits quantification of functional diversity in a manner similar to one method by which taxonomic diversity is quantified. We call it FD because of strong links with PD,

an accepted measure of phylogenetic diversity (May 1990; Vane-Wright *et al.* 1991; Faith 1992, 1994; Williams *et al.* 1994) (but see Clarke & Warwick 1998; Warwick & Clarke 1998). FD is the total branch length of the functional dendrogram (Fig. 1) that is often used in multivariate approaches to dividing species among functional groups (Körner 1993; Chapin *et al.* 1996; Díaz & Cabido 1997; Lavorel *et al.* 1997) and guilds (Terborgh & Robinson 1986; Hawkins & MacMahon 1989; Simberloff & Dayan 1991).

As a measure of functional diversity, FD has some notable properties. It measures the extent of complementarity among species’ trait values (in the same way as PD is directly related to uniquely evolved characters among species) by estimating the dispersion of species in trait space. We use Williams’s (2001) general definition of complementarity throughout this article: “Complementarity is a property of sets of objects that exists when at least some of the objects [traits] in one set [species] differ from the objects [traits] in another set [species].” For example, greater differences between species’ trait values represent greater trait complementarity and larger FD. This  $t$ -dimensional trait dispersion is a measure of the phenotypic diversity that is



**Figure 1** An example functional dendrogram of the relations between species 1–7. The dendrogram has been “cut” by the dashed line at an arbitrary level to assign species to four functional groups: {1}, {2, 3}, {4, 5}, {6, 7}. The total branch length (FD) for species 1–7 is the total length of branches *a–l*. The branch length remaining after species 6 and 7 are lost is the length of branches *a–i* (branches *j*, *k*, and *l* lost). Horizontal lines on this dendrogram do not contribute to FD.

recognized as an important community property (Loreau & Behera 1999; Loreau 2000; Norberg *et al.* 2001).

Second, FD measures diversity at all hierarchical scales simultaneously by avoiding any decision about the ecological significance of differences among species. FD includes the small functional differences between species ignored by functional groups *and* the large functional differences that might delineate these groups. For example, variation between genotypes, populations, species, and genera are all potentially included in FD. This property of FD is vital because no obvious or objective scale exists for dividing species among functional groups and guilds (Simberloff & Dayan 1991; Vitousek & Hooper 1993). Third, FD is a continuous rather than categorical measure and, hence, can avoid arbitrary delineation of continuous variation into categorical groups that often occurs when assigning species to functional groups.

Because it relies on a functional dendrogram, FD shares a number of properties in common with multivariate approaches to functional grouping of species. First, that all and only the traits that are related to the ecosystem process of interest are used. For example, one might not include flower colour in an attempt to quantify diversity that is important for biomass productivity. Second, variation within each trait is typically standardized, so that variation within one trait has equal influence on the measure of diversity as variation in any other trait. Trait standardization probably results from little available information about the relative importance of different traits; there is no reason why traits cannot or should not be weighted differently for the purpose of calculating FD (or assigning species to functional groups). Here, we only use traits that were considered important by the authors of primary literature sources and weight traits

equally in the absence of any information on the relative importance of different traits. The implications of both assumptions are addressed in the Discussion.

Also in common with multivariate approaches to functional grouping, FD may appear similar to phenetics: grouping organisms on the basis of observed physical similarities using primarily multivariate methods (Sokal & Sneath 1963). There are at least three important distinctions, however. First, phenetics focuses on morphological traits, whereas functional traits are used for functional groupings and to calculate FD. For example, proportions of different prey types exploited is often used in functional classifications (e.g. Muñoz & Ojeda 1997). Second, functionally motivated methods need not assume a single correct functional dendrogram, whereas phenetics, to some extent, aims to elucidate the single correct evolutionary relationship among species. For example, different weightings of functional traits will produce different functional dendrograms, none of which are, a priori, correct or incorrect. Third, the emphasis of FD should be on using the total branch length of a functional dendrogram to measure functional diversity, rather than the particular analytical methods used to produce the functional dendrogram.

Here, we describe how to calculate FD from species' traits and show how it associates with species richness and community composition. This differs from studies of the effects of species richness and composition on niche filling (Tilman *et al.* 1997; Díaz & Cabido 2001) because we use species traits to estimate functional diversity (niche filling). As well as simulating different extents and patterns of trait complementarity among species, we also test how species richness, community composition, and functional diversity are related in five natural communities.

## METHODS

### Calculating FD

There are four steps to calculating FD: (1) obtaining a trait matrix, (2) converting the trait matrix into a distance matrix, (3) clustering of the distance matrix to produce a dendrogram, and (4) calculating the total branch length of the dendrogram. The first three steps are standard multivariate methods (see Pielou (1984), whose notation we follow, for an accessible account of these methods) that have been used widely to divide species among functional groups and guilds. The fourth step is accomplished by simple matrix manipulation (see Pielou 1984). A more detailed description follows; other papers provide similar methods for calculating PD (Faith 1992, 1994; Rodrigues & Gaston 2002).

The trait matrix  $\mathcal{J}$  contains values  $(x_{s,t})$  of trait  $t$  of species  $s$ .

$$S = \begin{pmatrix} x_{1,1} & x_{1,2} & x_{1,3} & \dots & x_{1,t} \\ x_{2,1} & x_{2,2} & x_{2,3} & \dots & x_{2,t} \\ x_{3,1} & x_{3,2} & x_{3,3} & \dots & x_{3,t} \\ \dots & \dots & \dots & \dots & \dots \\ x_{s,1} & x_{s,2} & x_{s,3} & \dots & x_{s,t} \end{pmatrix}$$

Traits must be linked to the function(s) of interest (Leishman & Westoby 1992; Chapin *et al.* 1996; Díaz & Cabido 1997; Fonseca & Ganade 2001). For example, rooting depth, maximum growth rate, and leaf nitrogen concentration are important components of plant functional diversity when primary production is the process of interest. In contrast, functional diversity of vertebrate consumers is probably linked to the range of prey species consumed. Here, traits can be a prey species, and values are the number or proportion of that prey in the species' diet. Traits can be continuous (e.g. leaf nitrogen concentration) or binary variables (e.g. C<sub>4</sub> or C<sub>3</sub> metabolic pathway). Categorical variables can be included (e.g. degree of mesophytism; Golluscio & Sala 1993) though they will be less meaningful if they possess no intrinsic rank. We followed the usual protocol of standardizing the trait matrix so that values of all traits have a mean = 0 and variance = 1 (e.g. Holmes *et al.* 1979; Jaksic & Medel 1990; Golluscio & Sala 1993; Chapin *et al.* 1996; Muñoz & Ojeda 1997).

The distance matrix **D** is derived from the trait matrix. It contains the pair-wise distances ( $d_{ij}$ ) between species  $i$  and  $j$  in  $t$ -dimensional trait space and is symmetric about the zero diagonal. Functional attribute diversity (Walker *et al.* 1999) is the sum of the elements of **D**.

$$D = \begin{pmatrix} 0 & d_{1,2} & d_{1,3} & \dots & d_{1,s} \\ d_{2,1} & 0 & d_{2,3} & \dots & d_{2,s} \\ d_{3,1} & d_{3,2} & 0 & \dots & d_{3,s} \\ \dots & \dots & \dots & 0 & \dots \\ d_{s,1} & d_{s,2} & d_{s,3} & \dots & 0 \end{pmatrix}$$

Hierarchical clustering of the distance matrix produces the functional dendrogram (e.g. Fig. 1). This dendrogram can be expressed by a species-branch matrix **H1** and a branch-length row vector **h2'** (Rodrigues & Gaston 2002). The elements of **H1** indicate if the pathway from base to tip of the dendrogram for species  $s$  includes branch  $b$  ( $b_{s,b} = 1$ ) or not ( $b_{s,b} = 0$ ). The elements in **h2'** are the length  $l_b$  of branch  $b$ .

$$H1 = \begin{pmatrix} b_{1,1} & b_{1,2} & b_{1,3} & \dots & b_{1,b} \\ b_{2,1} & b_{2,2} & b_{2,3} & \dots & b_{2,b} \\ b_{3,1} & b_{3,2} & b_{3,3} & \dots & b_{3,b} \\ \dots & \dots & \dots & \dots & \dots \\ b_{s,1} & b_{s,2} & b_{s,3} & \dots & b_{s,b} \end{pmatrix}, h2' = (l_1 \ l_2 \ l_3 \ \dots \ l_b)$$

The branch presence/absence vector  $i'$  is the row vector of column sums of matrix **H1** converted to a 0/1 vector ( $i' = 0/1(\text{column sums}(\mathbf{H1}))$ ). FD is the total branch length

of the functional dendrogram – the product of the branch presence/absence row vector  $i'$  and the transposed branch-length vector (**h2**) (FD =  $i' \cdot h2$ ). The FD of a subset of species is calculated by removing rows from **H1** to create sub(**H1**) and hence sub( $i'$ ). Zero values in sub( $i'$ ) represent the branches unique to the absent species (Fig. 1). Here, FD = sub( $i'$ )**h2**. This definition of FD (and similarly PD) includes the length of basal branches common to all species (Rodrigues & Gaston 2002), unlike the original definition of PD (Faith 1992). Advantages of including common basal branches include preventing FD = 0 for single-species communities, so that FD = 0 is reserved for communities without any species (other differences and advantages are discussed elsewhere; Rodrigues & Gaston 2002).

Various distance measures and clustering techniques exist (Pielou 1984). Here, Euclidean distance and the unweighted pair-group clustering method using arithmetic averages (UPGMA) produced the distance matrix and functional dendrogram, respectively, in all our analyses. The qualitative relations between FD, species richness, and community composition presented here are robust to changes in the distance metric (Euclidean or Pianka's niche overlap; Pianka 1973) and the clustering method (UPGMA, single linkage, or complete linkage).

### Simulated effects of species richness and composition on FD

Different patterns and extents of trait complementarity among species illustrate how species richness and community composition influence FD. Three simulated trait matrix structures cover a wide range of trait complementarity among species.

Trait matrix **A<sub>t</sub>** contains  $s$  species and  $t$  traits. The elements of **A<sub>t</sub>** are drawn randomly from a normal distribution with mean = 0 and variance = 1 (normal[0, 1]). Randomly assigning trait values ensures that covariance between traits is zero and, hence, varying the number of traits varies the number of dimensions that separate the species in trait space.

Trait matrices **B<sub>f</sub>** and **C** contain one trait, perhaps because there is one dominant axis of variation among species (this would also occur with  $t$  perfectly correlated traits). Values in trait matrix **B<sub>f</sub>** are normal[ $x_i$ , 1] for species  $i$ . This produces functionally similar clumps of species (broadly similar to functional groups), with the mean of the functional clumps at  $x_i$ . Varying the number  $f$  of values that  $x_i$  can take varies the number of functional clumps along the resource axis. If  $f = 2$ , for example, species separate into two clumps in trait space. If  $f = 1$  or  $f \gg s$  there is no functional clumping of species. Values in trait matrix **C** are all the same, so that all species are identical.

## Case studies

Five case studies were selected to cover a wide range of taxa and traits; for each study the trait matrix was derived from the primary literature source (Table 1). The taxa were plants in two studies, birds, fish, and predatory vertebrates. The traits ranged from physiological properties (e.g. leaf N, P uptake; Chapin *et al.* 1996) to prey consumed (e.g. by percentage of all the prey consumed by a species; Muñoz & Ojeda 1997) to feeding behaviour (e.g. by percentage of total time spent feeding; Holmes *et al.* 1979). The original publications of the case studies divided plants among functional groups and animals among guilds, though there may be little to distinguish them in reality (e.g. Simberloff & Dayan 1991; Allison *et al.* 1996; Vitousek *et al.* 1996).

## RESULTS

### Simulated effects of species richness and composition on FD

The number of traits  $t$  in the trait matrix  $A_n$ , and hence the dimensionality of trait space, determines the shape of the relationship between FD and species richness. A scattered saturating relationship transforms into a tight linear one as the number of traits increases from 1 to  $s$  (Fig. 2).

The saturating relationship between FD and species richness (Fig. 2a), with scatter among communities that contain equal numbers of species, occurs when few traits separate species. Both the scatter and saturation occur because traits of some pairs of species complement each other, whereas those of other pairs of species do not (distances between species in trait space range widely from 0 upwards; Fig. 3a). The scatter among communities with equal numbers of species results from compositional

differences. For example, a five-species community could contain five very similar species (low FD) or five very different ones (high FD). The relationship saturates, indicating redundancy in species' contributions to FD, because the chance of adding a species with particularly unique/complementary traits decreases as the number of species increases.

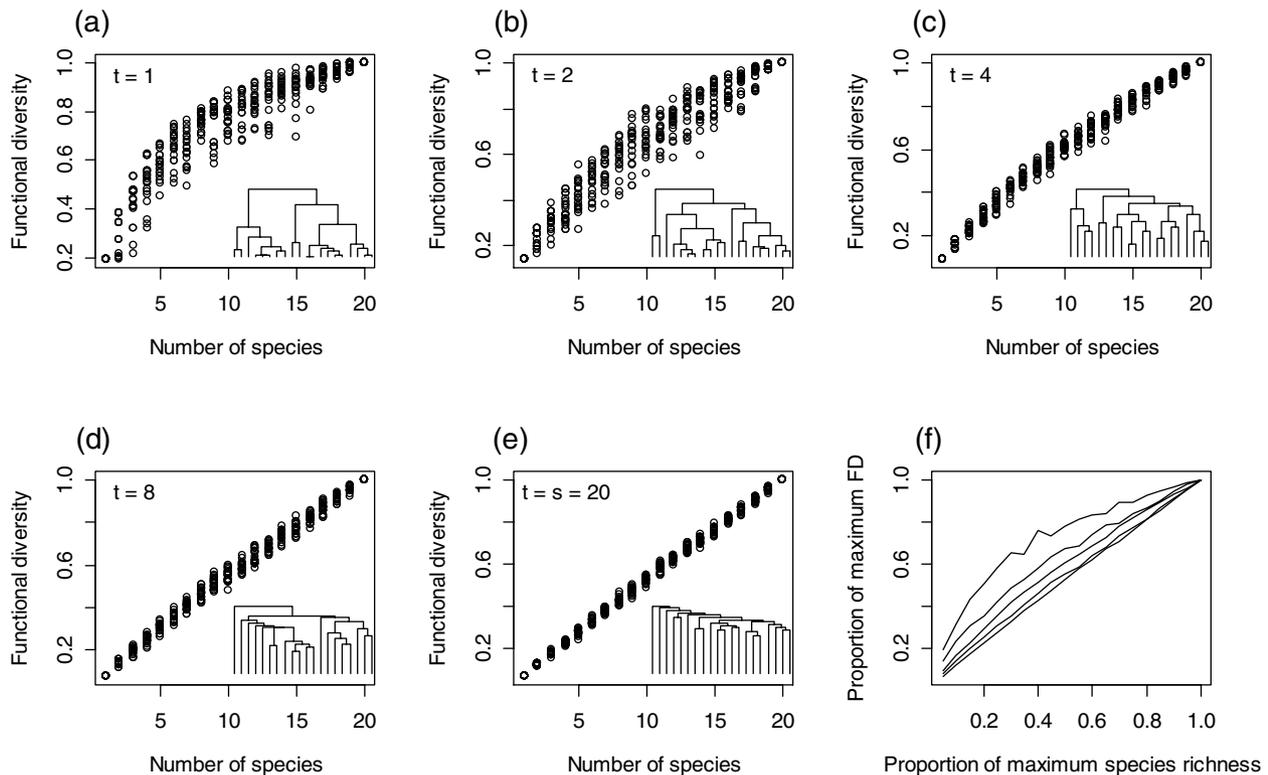
The occurrence of several traits results in a tight linear relationship between FD and the number of species in a community (Fig. 2e). Both the linear relationship and low scatter occur because traits of all species are equally complementary (all values in the distance matrix are quite similar; Fig. 3a). Here, addition of any one species to a community causes a similar increase in FD to that caused by adding any other species. Low variation around the linear trend indicates that community composition, or species identity plays little role in determining FD and that there is little or no redundancy in species' contributions to FD.

Indeed, equal numbers of species and traits and an identity (diagonals = 1, off-diagonals = 0) trait matrix results in identical distances among all species pairs and zero effect of community composition on FD. Here, adding any species to a community causes exactly the same increase in FD as adding any other species. Replacing one species in a community with any other species will have no effect on FD. In contrast, functional attribute diversity (Walker *et al.* 1999) is not a linear function of species richness with an identity trait matrix (here, functional attribute diversity =  $\sqrt{2} * (s^2 - s)/2$  (Fig. 3b). This difference represents a significant advantage of FD over functional attribute diversity.

Manipulating the number of functional clumps  $f$  alters the distribution of FD among communities that contain equal numbers of species (Fig. 4). If there are few functional clumps ( $f = 3, 4, 6$ ; Fig. 4) compared to the maximum number of species ( $s = 20$ ) discontinuous distributions of FD appear as horizontal strata in Fig. 4(a)–(d). In Fig. 4(b),

**Table 1** The case studies for which relationships between FD and species richness were calculated

Taxonomic range	No. of species ( $s$ ) and traits ( $t$ )	Type of trait	Reference
1. Insectivorous birds	$s = 22$ $t = 27$	24 were percentage utilization of foraging behaviour, live weight, mean(foraging height), SD(foraging height)	(Holmes <i>et al.</i> 1979)
2. Arctic vegetation	$s = 37$ $t = 21$	Large variety, e.g., height, leaf N, herbivore palatability, northern limit	(Chapin <i>et al.</i> 1996)
3. Predatory vertebrates	$s = 11$ $t = 15$	Consumption of different prey species	(Jaksić & Medel 1990)
4. Patagonian forbs	$s = 24$ $t = 6$	Max. root depth, max. sprouting depth, max. distance between shoots, mesophytic degree, month of pre-emergence growth, month of post-flowering dormancy	(Golluscio & Sala 1993)
5. Rocky intertidal fish	$s = 13$ $t = 16$	Consumption of different prey species	(Muñoz & Ojeda 1997)



**Figure 2** Effects of the number of traits  $t$  that vary among species (the number of traits in matrix  $A_t$ ) on the relationships between FD and species richness. (a–e)  $t = 1, 2, 4, 8, 20$ , respectively, for 20 random draws of species at each richness level from the same functional dendrogram. FD was standardized to vary between 1 and 0. (f) Means of the 20 random draws for each of (a–e) plotted on standardized axes (highest to lowest lines are for  $t = 1, 2, 4, 8, 20$ , respectively). There was one functional dendrogram for each of (a–e), though numerous simulations of different functional dendrograms for the same number of traits show qualitatively identical results.

the four strata result from the four combinations of three functional clumps that result in very different FD. Increasing the number of functional clumps ( $f=10$ ) relative to the maximum number of species produces a more continuous distribution of FD among communities with equal numbers of species (tending towards the qualitative patterns for one clump; Fig. 2a). A special case of  $B_f$  occurs where trait values are normal $[x_i, 0]$  and  $1 > f > s$ . Here, functional clumps contain identical species and the functional dendrogram is not fully resolved (Fig. 4a). This relationship would also result if functional group (conventional definition) membership was used as the only trait differing among species.

Identical species (represented in matrix  $C$ ) is the only scenario in which increasing the number of species is not associated with any change in FD (not shown in a figure).

### Case studies

The relationship between FD and species richness was similar among the case studies despite the wide range of taxa and trait types (Fig. 5). Qualitatively, the relationships seem close to the most linear relationship in Fig. 1. There may be

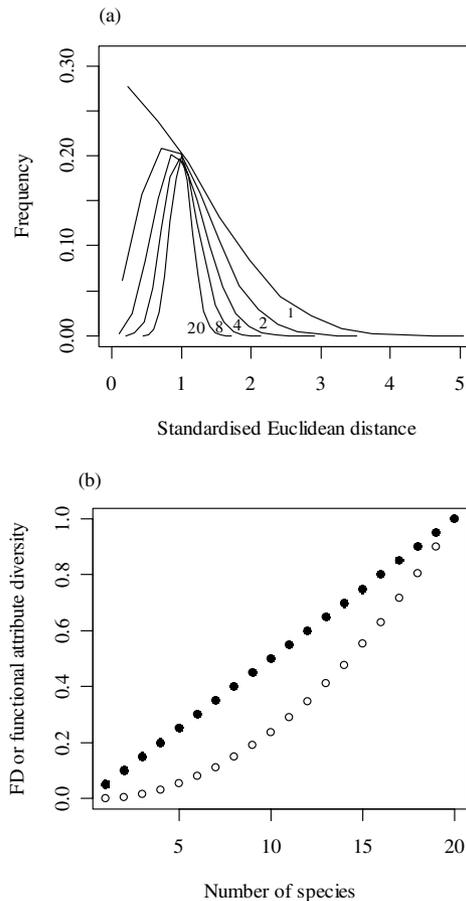
slightly more or less scatter and saturation in some case studies relative to others (contrast Fig. 5a,e). There was a lack of obvious horizontal strata in these empirical relations between FD and species richness.

## DISCUSSION

This study demonstrates the utility of FD as a measure of functional diversity. It measures the extent of trait complementarity among species; it measures diversity across all scales simultaneously; and it is a continuous measure of the natural variation among species. FD is an amalgam of the diversity caused by species richness, number of functional groups, community composition, and species identity. Here, investigations of how species richness and community composition affect FD provide several novel and intuitive insights.

### Simulated effects of species richness and composition on FD

Relationships between functional diversity/ecosystem functioning and species richness depend on the distribution of



**Figure 3** (a) The distribution of distances between species in trait space ( $d_{ij}$ ) when different numbers of traits  $t$  are included in the trait matrix  $A_t$  (numbers by the curves indicate the number of traits). Distances between species  $i$  and  $j$  were calculated 20 000 times for each number of traits  $t$  using  $d_{ij} = \sqrt{\sum_t (\text{normal}[0,1] - \text{normal}[0,1])^2}$ , and were standardized by the mean distance for each value of  $t$  (b) Relationship between FD and species richness (filled circles) and functional attribute diversity (Walker *et al.* 1999) and species richness (open circles) for an identity trait matrix. Here, distance between all pairs of species are identical and a linear relationship between diversity and species richness is expected.

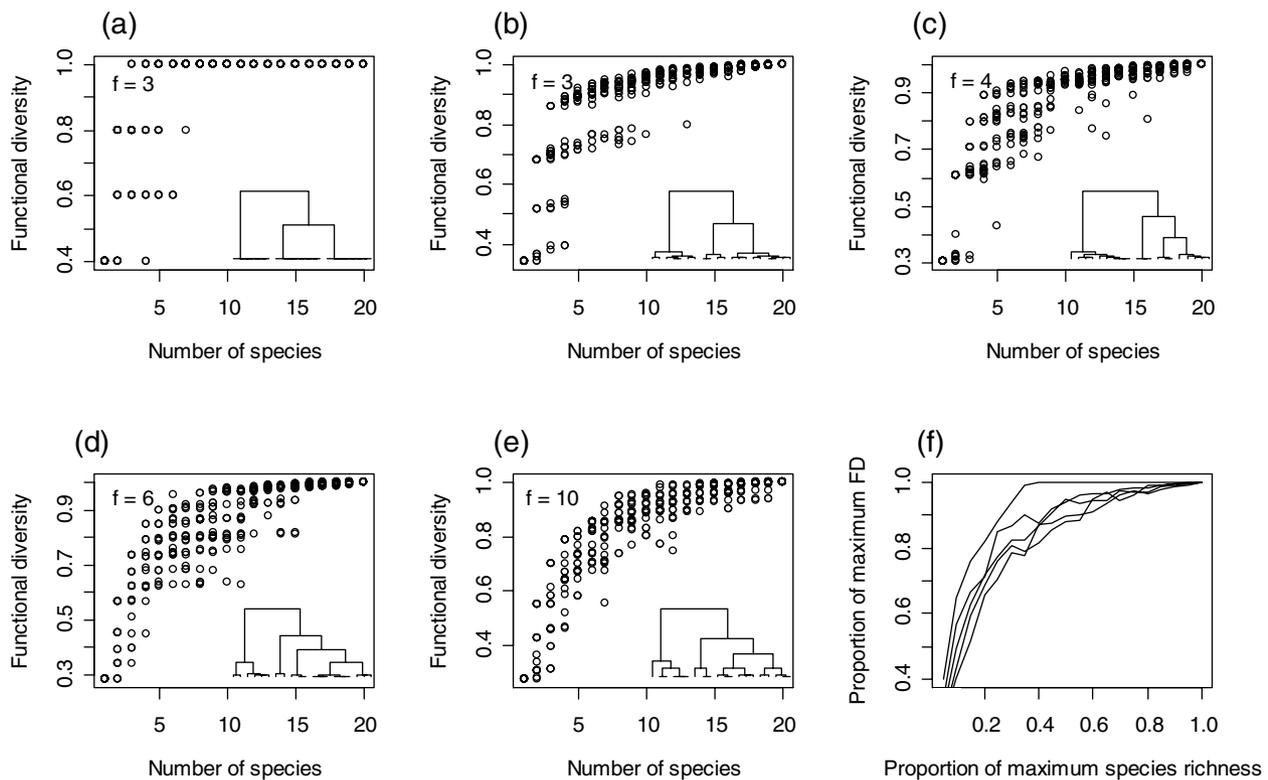
trait complementarity among species (Sala *et al.* 1996; Tilman *et al.* 1997; Díaz & Cabido 2001), as well as the presence of ecological engineers (Lawton & Jones 1995) and keystone species (Bond 1993). Species richness is strongly associated with functional diversity when species' traits are equally complementary. Variation in community composition is associated with variation in functional diversity when species' traits are more or less complementary to each other. As well as showing this in a single conceptual framework, our simulations reveal that the *effective* dimensionality of trait space alters the distribution of trait complementarity among species (Fig. 3a), controls the relative importance of species

richness and community composition (Fig. 6), and determines the extent of the redundancy in species contributions to FD.

Three factors independently influence the effective dimensionality of trait space, and hence the relative importance of species richness and composition for FD. Increasing (or decreasing) the number of traits included in the trait matrix will increase (or decrease) the effective dimensionality of trait space. Increasing (or decreasing) the absolute correlation between traits will decrease (or increase) the effective dimensionality of trait space. Weighting traits very differently (or more equally) will also reduce (or increase) the effective dimensionality of trait space. We chose to manipulate the effective dimensionality of trait space in our simulations by varying the number of uncorrelated traits, though we have produced qualitatively identical results through varying the correlation between traits and differential weighting of traits.

Fewer effective trait dimensions increases the relative importance of species identity by making some species very similar and others very different; increasing the number of effective trait dimensions allows all species to differ similarly (Fig. 3a). A single trait axis will always cause strong effects of community composition (species identity) regardless of how species distribute on that axis; some species are close on the trait axis while others are distant. This may be the case in recent experimental manipulations of species richness and functional diversity (Tilman 1997; Spehn *et al.* 2000; Schmid *et al.* 2001). Clumping of species along the trait axis or the existence of strong functional types results in species that are either very similar or differ greatly, further increasing the influence of community composition on FD. For example, communities containing species with very complementary traits have greater FD than communities species with similar traits, independent of the number of species in the communities. Similarly, replacing one of the species in a community with another species may or may not affect FD – the identity of the species is important.

Trait space with many effective dimensions allows all species to be equally similar (and dissimilar). This decreases the importance of species identity not because all species are very similar, but because species are similarly different. As mentioned, high effective dimensionality of trait space may result from the inclusion of many traits in an analysis. This will occur when many traits were measured because they were all considered functionally important. Many traits may also be included in analyses when there is simultaneous interest in multiple ecosystem processes. For example, there may be a suite of, say, five traits important for biomass production and a suite of five traits associated with decomposition rate. Here, measures of FD relevant to either biomass production or decomposition rates will contain five traits and emphasize effects of community composition. Measures of FD relevant to both processes



**Figure 4** Effects of functional clumping  $f$  in trait values (in matrix  $B_f$ ) on the relationships between FD and species richness. The number of clumps along a resource use axis is an analogue of the number of functional groups in a community. (a–e)  $f = 3, 3, 4, 6,$  and  $10$ , respectively, for 20 random draws of species at each species richness level. In (a) all species within a clump are identical; in (b) species differ slightly within clumps. (f) Means of the 20 random draws for each of (a–e) plotted on standardized axes. The four horizontal strata in (b) result from the four combinations of functional clumps that result in very different FD: lowest = {A}, {B}, {C}; low = {B,C}; high = {A,B}, {A,C}; highest = {A,B,C}. FD was standardized to vary between 1 and 0.

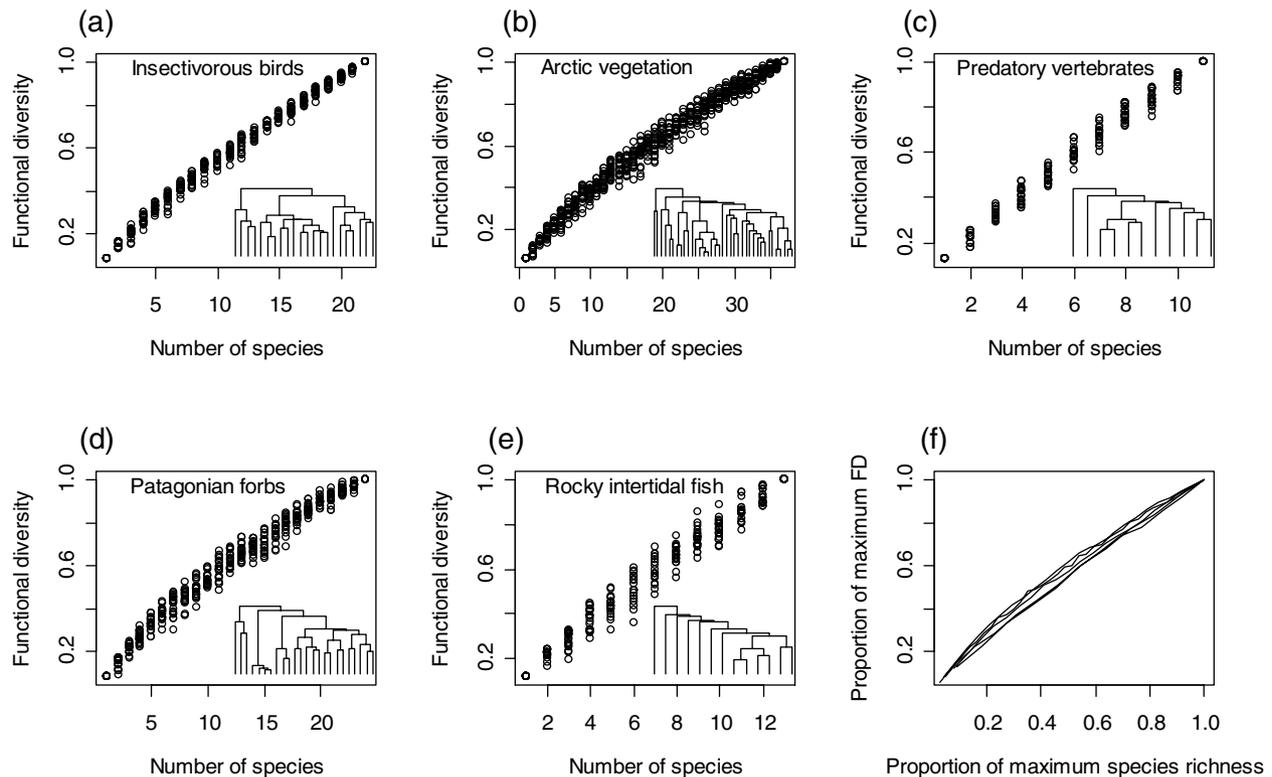
simultaneously will contain 10 traits and species richness will be more important for functional diversity. This idea is similar to the hypothesis that many species are required for many ecosystem processes because different species are important for different processes at different times (Walker *et al.* 1999; Yachi & Loreau 1999).

Including all and only the functionally significant traits will be critical for calculating a value of FD that predicts ecosystem functioning well, just as including functionally significant traits is essential in methods for identifying functional groups (Leishman & Westoby 1992; Díaz & Cabido 1997; Fonseca & Ganade 2001). Different traits may be important for different ecosystem functions and, hence, many traits may be important when all aspects of ecosystem functioning are considered. Here, the effect of species richness on FD will dominate over that of species composition.

### Case studies

The five real communities for which trait matrices were investigated covered a wide range of taxa and traits. Yet

the five curves in Fig. 5 do not obviously separate the two plant and three animal studies. They are all relatively linear, suggesting separation of species in multidimensional niche space, dominant effects of species richness, and little redundancy in species' contributions to FD. Similarly, none of the real relationships show any evidence of the horizontal strata that can occur when species clump strongly in trait space (contrast Fig. 5 with Fig. 4a–d). The linearity, similarity, and lack of horizontal strata in these empirical relationships between FD and species richness may result from several factors. Our simulations and discussion so far focus upon the influence of including several traits in the trait matrix and that these traits are uncorrelated. Equal weighting of the traits may also contribute to the result. If in reality some traits are more important for determining ecosystem functioning than others then they should be given greater weighting in the trait matrix. Differential weighting of traits will decrease the effective dimensionality of trait space and increase the relative importance of species composition. Decisions about which traits to include and how to weight those



**Figure 5** Relationships between FD and species richness for (a–e) five empirical studies of species' trait values. There were 20 random draws of species at each level of species richness. (a) Insectivorous birds (b) arctic vegetation (c) predatory vertebrates (d) Patagonian forbs, and (e) rocky intertidal fish. FD was standardized to vary between 1 and 0. (f) Mean relations between FD and number of species on standardized axis.

traits must be addressed by experts in particular communities and should be verified experimentally.

Theory and experiments reveal that resource use complementarity is one process that links biodiversity and ecosystem functioning (e.g. Hooper 1998; Loreau 1998; Hector *et al.* 1999; Norberg 2000). In the plant case studies, FD measures the extent of complementarity among species in morphological and ecophysiological trait space. In the animal studies, FD measures the extent complementarity in resource use space. Clearly then, FD measures the source of this link – resource partitioning – in the animal case studies. In the plant case studies, however, FD measures resource use complementarity indirectly by assuming that traits relate to resource capture differences among species. Empirical investigations of the ecosystem level consequences of FD, that is, the explanatory capabilities of FD, deserve the same attention as our exploration of the species level causes of functional diversity. This should include determination of which traits need to be included in trait matrices and the relative importance of the different traits.

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