



Measuring the contribution of community members to functional diversity

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Although the contribution of community members to functional diversity is a key question of conservation ecology, its measurement and interpretation are rather problematic. In this paper, we suggest a novel method for decomposing functional diversity. To do this we consider functional units (i.e. species or a group of species with identical traits) as the functional building blocks of communities. Then we propose the use of a recently developed measure of functional diversity (called modified functional attribute diversity or MFAD) and suggest additive decomposition of MFAD into functional values contributed by the functional units. We point out that functional values are related to changes in MFAD if the functional unit is removed from the community. This property of decomposition allows the quantification of the contribution of community members to functional diversity. By studying artificial and actual communities we compare the performance of our new method with other recently developed contribution measures, which are based on dendrograms and ordinations. Both theoretical considerations and analyses of artificial and actual data sets suggest that the proposed method of calculating functional values expresses more explicitly the contribution of community members to functional diversity and hereby can be used as a simple, yet efficient method for searching for functional keystones in ecological communities or for quantifying the contribution of community members to functional diversity.

Functional diversity (FD) is generally viewed as one of the key parameters which underpin functioning of ecosystems and communities (Tilman et al. 1997, Petchey and Gaston 2006). Its quantification receives growing interest both in aquatic (Bady et al. 2005, Beche and Resh 2007, Erős et al. 2008) and terrestrial ecology (Mason et al. 2003, Botta-Dukát 2005, Petchey et al. 2007). Several measures have been proposed (Walker 1999, Petchey and Gaston 2002, 2006, Mason et al. 2003, 2005, Botta-Dukát 2005, Mouillot et al. 2005, Schmera et al. 2009, Villéger et al. 2008) and current developments focus mainly on how these measures can be applied and interpreted, with a lively debate on which type of indices is best suitable to such a complex measurement (Ricotta 2005a, 2005b, Mason et al. 2003, Podani and Schmera 2006, 2007, Petchey and Gaston 2002, 2007, Mouchet et al. 2008, Walker et al. 2008, Schmera et al. 2009). The obvious challenge in developing a FD measure is that its mathematical properties might influence answers to fundamental questions of conservation biology (Mason et al. 2003, Mouillot 2005, Ricotta 2005a, 2005b, Villéger et al. 2008, see example in Walker et al. 2008). These include the functional consequences of biotic change caused by humans (Tilman 1999, Chapin et al. 2000, Schwartz et al. 2000, Petchey and Gaston 2006, but see Sivastra and Vellend 2005) and the influences of species loss on ecosystem functioning (Petchey

and Gaston 2002, 2006, Solan et al. 2004, Petchey et al. 2007, Walker et al. 2008). In fact, exact methods are needed for quantifying the contribution of community members to FD in a simple albeit meaningful way.

As an important step in this field, Petchey and Gaston (2002, 2006) examined how species loss influences FD if measured based on dendrograms (dendrogram-based measure, DBM, Petchey and Gaston 2002, see reviews of presence/absence based FD measures in Petchey et al. 2004, Petchey and Gaston 2006, Schmera et al. 2009). They found that species contribute quite differently to the FD of a community (Fig. 4 in Petchey and Gaston 2006). If species contribution is measured by the decrease of FD after species removal (as suggested by Petchey and Gaston 2002) then the contribution of a species to FD can be measured by the branch length connecting the given species to the most similar species in the community. If a species forms a functional unit (FU, sensu Ricotta 2005a) by itself, then it has its own contribution to the FD of the community (as the branch length connecting it to the most similar species is larger than zero, species 2 or 3 in Fig. 1). Contrarywise, if a species forms a functional unit together with other species because they have identical traits (a phenomenon termed as functional redundancy, Petchey et al. 2007, Walker et al. 2008, species 1A or species 1B in Fig. 1), then it has no individual contribution to the FD of the community (as the

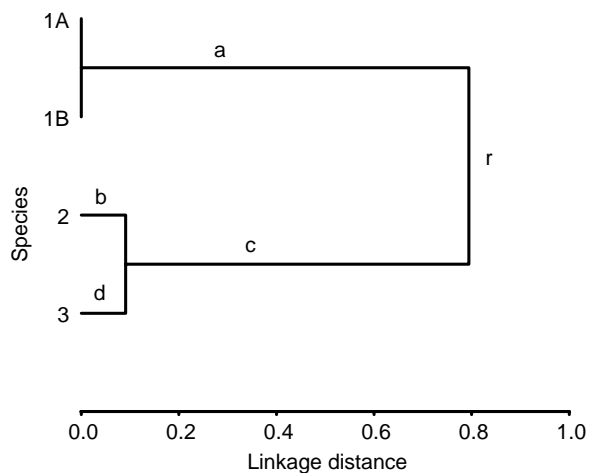


Figure 1. Illustration of how species contribution is measured by dendrogram-based indices of functional diversity. (1A, 1B, 2 and 3 are hypothetical species, from which 1A and 1B have identical trait values thus forming a functional unit). Lower case letters (a, b, c, d) denote dendrogram branches while r shows the position of the root.

branch length connecting this to the most similar species is zero). However, it may not be acceptable intuitively that while a FU itself may have significant contribution to FD of the community (branch a in Fig. 1), the constituting species (1A or 1B) appear to have no contribution if examined separately. In addition, common branches (e.g. branch c in Fig. 1 which links species 2 and 3 to the root of the dendrogram) are not considered in measuring the contribution of species. Consequently, this procedure measures the uniqueness of a species (by depending on how similar it is to the nearest one in the dendrogram, Pavoine et al. 2005) rather than its contribution to FD. Another problem arises when the contributions of several species forming a FU are measured sequentially. In this case, only the species which has been removed the last would have nonzero contribution to FD (after removing species 1A species 1B will have a contribution of branch a). Thus, the rank order of removals influences how the contribution of species to FD is measured. Moreover, a fundamental drawback with the original definition of DBM is that it cannot be applied to species addition, and therefore cannot be adopted to situations in which new species appear in a community (Podani and Schmera 2007), thus making its application to conservation practice rather problematic (Schmera et al. 2009). Finally, ties ('tie' is a standard term in rank statistics to express equality of two or more values) in the dissimilarity matrix and their resolution can strongly influence the shape of the dendrogram (Podani 1989, Backeljau et al. 1996) and in turn the contribution of species. If ties are resolved arbitrarily (this is the most commonly used and often the single option in clustering packages), then species associated with the equal dissimilarity values might have different contributions to FD (Fig. 2C, species 1 and 3). Furthermore, arbitrary resolution will produce different dendrograms depending on the input order of data (Podani 1997). If suboptimal fusion is used, as suggested by Podani (1989) then reversals might appear on the dendrogram (Fig. 2D) thus causing confusion in measuring both branch

lengths and species contributions. The other possibility, multiple fusion (Podani 1989) which amalgamates all objects associated with the given tie into a single cluster may be the only solution to yield an unequivocal result in such situations. Nevertheless, DBM can hardly be considered as an unambiguous measure of species contribution to FD.

In a very recent paper, Walker et al. (2008) examined the changes of functional diversity of a bird community from 1969 to 1973. They applied a functional rarefaction technique to correct for sample-size-induced bias in the estimation of functional attribute diversity (FAD, Walker et al. 1999) and DBM, and observed that the rarified species diversity and the rarified FAD of the bird community significantly declined, whereas the rarified DBM did not. They concluded that the decline largely resulted from the loss of redundant species and confirmed this interpretation by applying principal coordinates analysis (PCoA) to the functional trait matrix of the bird community. The arrangement of bird species in the ordination showed that the two least abundant species in 1973 were quite similar to others that had persisted over the study period. However, the first two PCoA axes accounted for 67% of variation between species in the functional trait space (Walker et al. 2008), thus representing the functional organization of the community only roughly. In another paper, Bellwood et al. (2006) used directly the distance of the objects from the centroid of the point scatter, i.e. the origin in centered principal component analysis (PCA) as a trophic specialization measure. Their basic idea was to see how the objects are positioned in the ordination space: those with large scores on important axes contribute more to trophic diversity than objects positioned near the centroid. However, ordination based measures should not be used for quantifying the contribution of community members to FD since the objects at the centroid do not necessarily have zero or close to zero contribution. For instance, Fig. 2E shows that although species 2 is in the centroid of the point scatter (and would be in the origin of centered PCA as well), it has a real contribution to FD of the community. The same is true if PCoA is applied (Fig. 3A–C).

In this paper, we propose a method to quantify the functional value of community members by decomposing FD into additive components. We argue first that FUs should be interpreted as the functional building blocks of communities (Ricotta 2005a, 2005b), thus avoiding arbitrariness of successive species removals in measuring species contributions. Second, we suggest the use of a recently developed measure of functional diversity (MFAD, Schmera et al. 2009). This index, similarly to DBM, is insensitive to species redundancy and applies to both species deletions and additions for which DBM is inadequate (Podani and Schmera 2007, Schmera et al. 2009). Third, we show that decomposing MFAD can be used to measure the functional value of the FUs and prove that functional values are related to the change in FD if the FU is removed from the community. This property of decomposition allows us to provide a meaningful quantification of the contribution of FUs to the FD of the community. Fourth, we provide evidence that the novel decomposition of MFAD presented here expresses more explicitly the contribution of community members to functional diversity

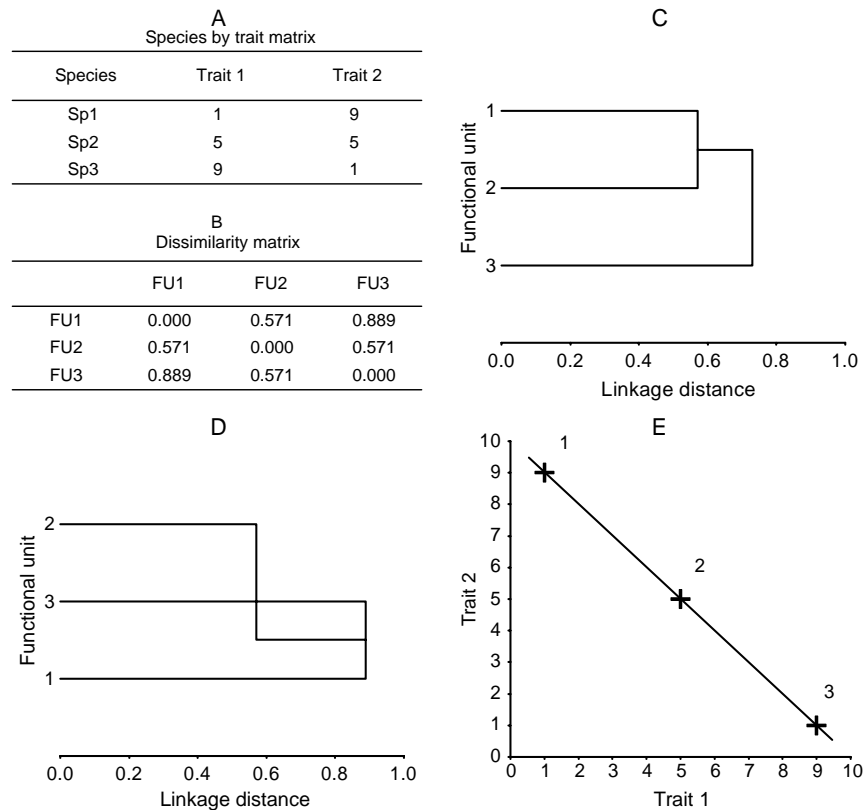


Figure 2. Illustration of how ties in the dissimilarity matrix and their resolution influence the shape of the dendrogram and how an object can be positioned in the centroid of a PCA without having zero contribution to functional diversity. (A) an artificial species by trait matrix, (B) dissimilarity matrix of functional units calculated by the Marczewski–Steinhaus index from the data matrix in (A), (C) dendrogram built from dissimilarity matrix B with UPGMA and arbitrary resolution of ties. Note that the other arbitrary resolution interchanges objects 1 and 3, while the tree remains the same. (D) dendrogram built from dissimilarity matrix B with UPGMA and suboptimal fusion, (E) the two-dimensional coordinate system showing two traits (two axes) and three species (marked by + and labeled as 1, 2 and 3). The position of the species in the coordinate system shows the characteristic value of the species for trait 1 (horizontal axis) and for trait 2 (vertical axis). The line connecting species is the single axis of a principal component analysis (PCA). In this case, species 2 is in the centroid of the PCA and the single axis explains 100% of the variance of the data.

compared to the formerly proposed ordination- or dendrogram-based measures.

measured by affinity values between 0 and 3 (river fishes), and between 0 and 10 (stream caddisflies).

Material and methods

Basic data structure and data sets

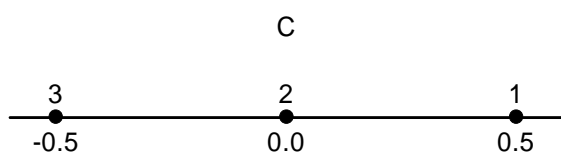
Each community is represented by a species by trait matrix, **A**, with *S* rows and *p* columns. In this, each entry a_{ij} shows the value of species *i* for trait *j*. The value a_{ij} might express real measures (say, size or number) or affinity scores which range from zero to some arbitrary maximum, say 1 or 10. This second data type is termed the fuzzy coding (Chevenet et al. 1994) and is widely used in aquatic ecology (Doledec et al. 2000, Ussegelio-Polatera et al. 2000, Statzner et al. 2001, Santoul et al. 2005, Ilg and Castella 2006, Beche and Resh 2007, Bonada et al. 2007, Erős et al. 2008). Our artificial community data sets are represented by a matrix of three species and two traits (Fig. 2A, 3A). Five actual data sets were analyzed (Table 1). In three of them (insectivorous birds, intertidal fish, predatory vertebrates), the values of species for the functional traits are expressed as percentages. In case of the final two actual data sets, species scores are

Measuring functional diversity

The method we use here for characterizing FD is described in detail in Schmera et al. (2009) and is reiterated here only briefly. In the first step, species are combined into functional units (FUs) in a way that those species which give completely identical values for all trait variables are considered to represent the same FU. As a result, the number of rows in **A** will be reduced to *N* ($N \leq S$), where *N* is the number of FUs and *S* is the total number of species. In the second step, pairwise dissimilarities (d_{hk} , Fig. 3B) between FUs are calculated using the Marczewski–Steinhaus index (Podani 2000, see also below) to yield the **D** dissimilarity matrix. It is important to note that depending on the quality of the data, other dissimilarity measures might also be useful (for instance the normalized Canberra metric or Gower distance) but they should satisfy the metric axioms (a dissimilarity measure *d* is metric, if $d_{ij} + d_{jk} \geq d_{ik}$ is true for any *i*, *j* and *k* points, Podani 2000) and should range between 0 and 1. In the final step, all pairwise dissimilarities are summed into *d*.. and then

A Species by trait matrix		
Species	Trait 1	Trait 2
Sp1	3	0
Sp2	3	3
Sp3	0	3

B Dissimilarity matrix			
	FU1	FU2	FU3
FU1	0.0	0.5	1.0
FU2	0.5	0.0	0.5
FU3	1.0	0.5	0.0



D

FV of FU_i equals with the total of row i in the dissimilarity matrix divided by the number of FUs. In our example:

$$FV_{FU1} = \frac{0+0.5+1}{3} = 0.5$$

$$FV_{FU2} = \frac{0.5+0+0.5}{3} = 0.33$$

$$FV_{FU3} = \frac{1+0.5+0}{3} = 0.5$$

Figure 3. Illustration of how an object can be positioned in the origin of a PCoA ordination without having zero contribution to the functional diversity and how functional values can be calculated. (A) an artificial species by trait matrix, (B) dissimilarity matrix of functional units calculated by the Marczewski–Steinhaus index, (C) PCoA ordination of functional units based on dissimilarity matrix (B), (D) calculation of functional values of the functional units using dissimilarity matrix (B).

divided by the number of FUs (N) to get the value of functional diversity (MFAD, Schmera et al. 2009):

$$MFAD = \frac{\sum_{h=1}^N \sum_{k=1}^N d_{hk}}{N} = d_{..}/N \quad (1)$$

Decomposing functional diversity into functional values

We know that $d_{..}$ is the sum of $N \times N$ dissimilarity values [$N \times (N-1)$ off diagonal dissimilarities and N zero values in the diagonal of \mathbf{D} , Fig. 3B]. Each row total $d_{h.}$ of \mathbf{D} (representing a FU) is divided by the number of FUs (N) to get the functional value of FU h (FV_h). If the sum of dissimilarity values related to FU h is termed as A_h (FU_h influences both a column and a row in the dissimilarity matrix) then we obtain the following equation:

$$FV_h = \frac{A_h}{2N} = (d_{h.} + d_{.h})/2N \quad (2)$$

Consequently, functional diversity (MFAD) equals the sum of the FVs of the community:

$$MFAD = \sum_{h=1}^N FV_h \quad (3)$$

Effect of functional unit removal/addition to functional diversity

The effect of functional unit h to functional diversity, C_{-h} , expresses how the given FU decreases or increases MFAD if the FU is removed from or added to the community (the minus sign before h shows that FU h is removed from the community). Let $MFAD_{-h}$ be the functional diversity of the same community without the functional unit h . That is,

$$C_{-h} = MFAD - MFAD_{-h} \quad (4)$$

Let A_h be the sum of the dissimilarities which are related to functional unit h (altogether $2 \times (N-1)$ dissimilarity values). We know that we can obtain $MFAD_{-h}$ from the following equation:

Table 1. Information on functional traits, species richness and functional diversity (MFAD) of five actual data sets used in the present paper.

Data set	No. of functional traits	No. of species	No. of functional units	Functional diversity (MFAD)
Insectivorous birds (Holmes et al. 1979)	24	22	22	13.69
Intertidal fishes (Muñoz and Ojeda 1997)	16	13	13	9.48
Predatory vertebrates (Jakšić and Mendel 1990)	15	11	11	8.37
River fishes (species: Schmera et al. 2009 feeding traits: Erős et al. 2008)	4	30	13	6.88
Stream caddisflies (species: Schmera and Erős 2006, feeding traits: Graf et al. 1995)	10	13	9	5.52

$$MFAD_{-h} = \frac{MFAD \times N - A_h}{N - 1} \quad (5)$$

Using Eq. 4 and 5 we obtain

$$C_{-h} = MFAD - \frac{MFAD \times N - A_h}{N - 1}, \text{ and then} \quad (6)$$

$$C_{-h}(N - 1) = MFAD \times N - MFAD - MFAD \times N + A_h \quad (7)$$

which simplifies to

$$C_{-h}(N - 1) = A_h - MFAD \quad (8)$$

By inserting Eq. 2, we have

$$C_{-h}(N - 1) = 2FV_h \times N - MFAD \quad (9)$$

After rearrangements, we get:

$$C_{-h} = \frac{2FV_h \times N - MFAD}{N - 1} \quad (10)$$

This means that by examining the functional diversity (MFAD) of the same community composed by N functional units, the effect of the functional unit h (C_{-h}) depends only on the functional value of the functional unit h (FV_h).

Similarly, if FU_h is added to a community with a functional diversity value MFAD, the new functional value of the community with functional unit h ($MFAD_{+h}$) is:

$$MFAD_{+h} = \frac{MFAD \times N + A_h}{N + 1} \quad (11)$$

And the effect of functional unit h (C_{+h}):

$$C_{+h} = MFAD_{+h} - MFAD \quad (12)$$

Using Eq. 11 and 12 we obtain

$$C_{+h} = \frac{MFAD \times N + A_h}{N + 1} - MFAD \quad (13)$$

After rearrangements, we get

$$C_{+h}(N + 1) = MFAD \times N + A_h - MFAD \times N - MFAD \quad (14)$$

which simplifies to

$$C_{+h} = \frac{A_h - MFAD}{N + 1} \quad (15)$$

This means that if we know MFAD and N of a community and the sum of dissimilarities of the new functional unit to the old community members is also available (this value equals to $A_h/2$), then the effect of the new functional unit can be readily calculated.

Comparing functional value with other contribution measures

The performance of 3 contribution measures was compared with the FV obtained by the proposed method of diversity decomposition. However, as FV was developed to express the FV of FUs (and not species), all species were first transformed into FUs. This new FU by trait matrix was used as input data in further analyses. The first measure we

used is the distance of the FU from the origin of the functional trait space obtained by principal coordinates analysis (PCoA, Podani 2000), hereafter referred to as distance from the origin and abbreviated as DO. The second one is the contribution of FU calculated using a dendrogram as originally suggested by Petchey and Gaston (2002); hereafter referred to as the original dendrogram construction method (DBM1) and the corresponding contribution measure as CDBM1. The third measure is the modified version of DBM1 (Petchey and Gaston 2006, 2007), hereafter abbreviated as DBM2 and the corresponding contribution measure as CDBM2. The only difference between DBM1 and DBM2 is that in DBM1 the branches connecting the community members should be connected to the root of the dendrogram, whereas in DBM2 they should not (Petchey and Gaston 2006, 2007). In practice, it means that the contribution of FU1 (in Fig. 1) equals to the length of branch a according to DBM1, whereas it equals to the sum of the length of branches a and c according to DBM2.

The similarity between the four contribution measures (FV, DO, CDBM1, CDBM2) is that all of them use the same dissimilarity matrix as input, thus differences between the results reflect only methodological differences. We used the Marczewski–Steinhaus index (Podani 2000) on the functional unit by trait matrix:

$$d_{hk} = \frac{\sum_{i=1}^p |a_{hi} - a_{ki}|}{\sum_{i=1}^p \max\{a_{hi}, a_{ki}\}} \quad (16)$$

where d_{hk} is the dissimilarity between functional units h and k, and a_{hi} is the value of functional unit h on trait i. MFAD and FV values were calculated by an Excel macro, Euclidean distance (Podani 2000) was calculated between the positions of the FUs and the origin of the ordination space as obtained by PCoA. Cluster analysis was performed with Marczewski–Steinhaus index, UPGMA clustering method and arbitrary resolution of ties (Podani 2000). The Pearson correlation coefficient was applied to measure and test the relationship between contribution measures, whereas the t-test for dependent samples (paired t-test) was used to compare contribution values observed by different methods. The dissimilarity matrix, PCoA and cluster analyses were calculated by the SYN-TAX 2000 program package (Podani 2001). The Pearson correlation coefficients and the t-test for dependent samples were computed while the figures were drawn by STATISTICA ver. 6 (Statsoft, Inc. 2003).

Results

The artificial community was used to show how a species by trait matrix (Fig. 3A) can be transformed into the dissimilarity matrix of FUs and how the MFAD of a community can be decomposed into FVs. There are no species identical in functional traits, so each species forms a separate FU. Figure 3B shows the dissimilarity matrix of functional units. We observed the largest dissimilarity value (1.0) between FU1 and FU3 (i.e. species 1 and 3) and the

smallest non-diagonal dissimilarity value (0.5) between FU1 and FU2 (species 1 and 2) and between FU2 and FU3 (species 2 and 3). Diversity decomposition of MFAD into FVs shows that FU1 and FU3 (corresponding to species 1 and 3) have the highest FV, followed by FU2 (Fig. 3D).

We analyzed five actual data sets with different numbers of functional traits and species (Table 1). For instance, the insectivorous bird data set consists of 22 species characterized by 24 functional traits, whereas the river fish data comprise 30 species and four functional traits. In our actual data sets in which the number of functional traits was higher than the number of species in the community each species formed a FU (Table 1: insectivorous birds, intertidal fishes and predatory vertebrates). When the number of functional traits was lower than the number of species then the number of FUs was smaller than the number of species (river fishes and stream caddisflies). In case of river fishes, the 30 species were converted into 13 FUs.

The first two PCoA axes explained on average 60.24% of the variance of the data structure, with the lowest value for predatory vertebrates (48.9%, Fig. 4) and for stream caddisflies with the highest (75.3%, Fig. 8). In four out of the five cases there was significant correlation between the DO values and the FVs, whereas in intertidal fishes (Fig. 6) the correlation was not significant. The minimum DO

values (i.e. the lowest contribution value by a functional unit) varied between 0.039 (river fishes, Fig. 7) and 0.263 (intertidal fishes, Fig. 5), whereas the FUs with the smallest FVs had a range between 0.425 (river fishes, Fig. 7) and 0.687 (predatory vertebrates, Fig. 5). The minimum functional contributions obtained for the DO method and the decomposition of MFAD were significantly different (t-test for dependent samples, $t = -9.191$, $DF = 4$, $p < 0.001$). The two methods identified the same FU as the highest FD contributor in three cases (predatory vertebrates: Fig. 6, river fishes: Fig. 7 and stream caddisflies: Fig. 8), and identified different FUs in the other two cases (insectivorous birds: Fig. 4 and intertidal fishes: Fig. 5). Other differences also occurred. For example, in case of intertidal fishes (Fig. 5) the DO method assessed FU2 as the 8th element in contributing to FD, whereas the decomposition of MFAD ranked it as being the most influential. Another example is that in stream caddisflies (Fig. 8) FU 3 was assessed as the last by the ordination method, whereas according to our method it was the 3rd most important contributor.

Both versions of DBM (CDBM1 and CDBM2) were applied to measure the contribution of FUs to the FD of the community. The two methods produced the same functional contribution value for every FU in case of insectivorous birds and intertidal fishes, whereas the

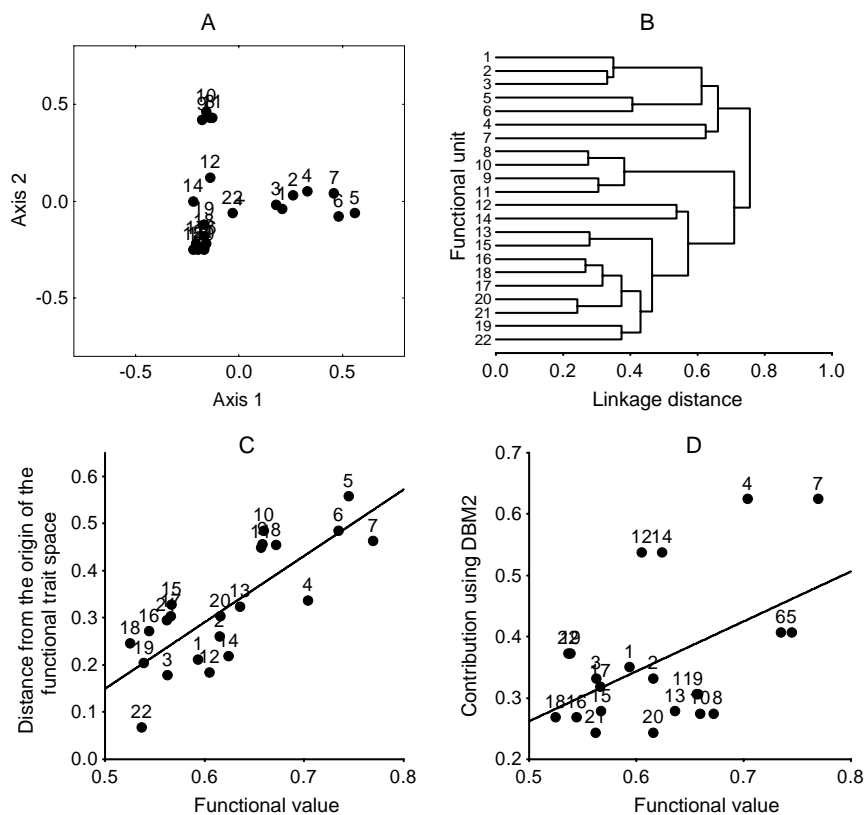


Figure 4. Functional organization of insectivorous birds (Holmes et al. 1979). (A) PCoA ordination of the functional units (+ shows the origin, the first two axes explain a total of 54.9% variance in the data). (B) UPGMA dendrogram of functional units. (C) the relationship between the functional value and the distance from the origin of the ordination space ($r = 0.796$, $p < 0.001$). (D) the relationship between the functional value and CDBM2 ($r = 0.495$, $p = 0.019$).

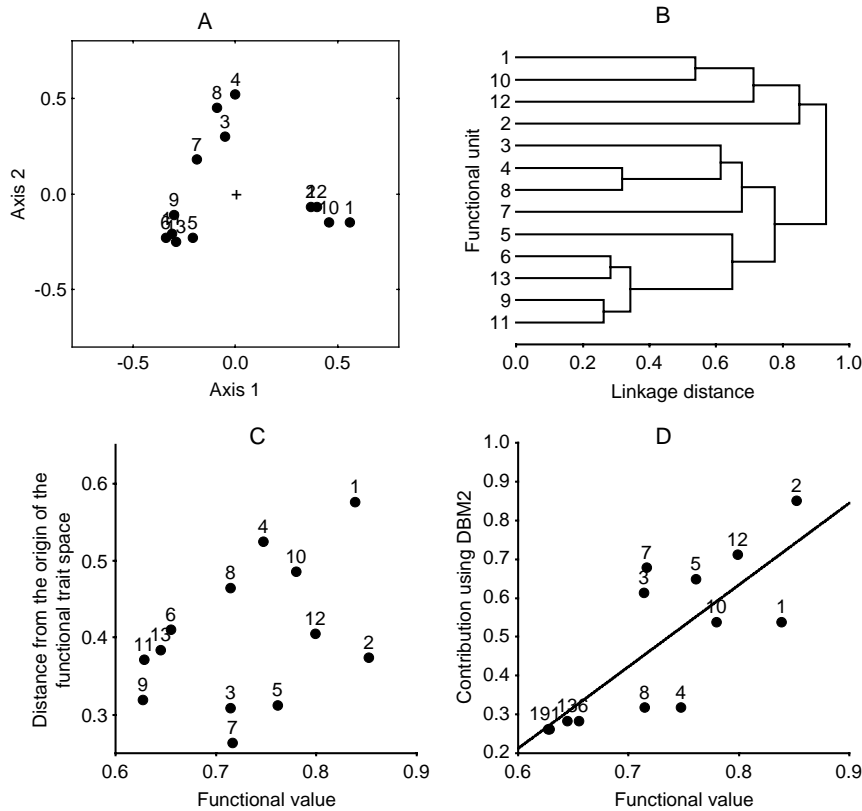


Figure 5. Functional organization of intertidal fishes (Muñoz and Ojeda 1997). (A) PCoA ordination of the functional units (+ shows the origin, the first two axes account for 55.0% variance). (B) dendrogram of functional units. (C) the relationship between the functional value and the distance from the origin of the ordination space ($r = 0.405$, $p = 0.169$). (D) the relationship between the functional value and CDBM2 ($r = 0.781$, $p = 0.002$).

contribution of FU9 in predatory vertebrates, the contribution of FU3 in river fishes and finally the contribution of FU2 in stream caddisflies were different (not shown). In two cases with CDBM2, the most contributive FUs reached a value higher than 1.0 (FU9 in predatory invertebrates, Fig. 6 and FU3 in river fishes, Fig. 7). Nevertheless, correlations between CDBM1 and CDBM2 were always very strong and highly significant ($r \geq 0.994$, $p < 0.001$).

In many cases, CDBM2 values were equal (for instance, for FU2 and FU3 in the insectivorous birds data, see Fig. 4, but many other examples exist, see Fig. 4–8). Although the correlation between FVs and CDBM2 was always positive and significant ($0.495 \leq r \leq 0.912$, and $0.042 \leq p < 0.001$), we observed several disagreements between the two methods. For instance, the contribution values of FUs 12 and 14 in insectivorous birds were highly overestimated using DBM2 compared to the decomposition of MFAD (Fig. 4). In contrast, the contribution values of FUs 4 and 1 in stream caddisflies were highly underestimated using DBM2 compared to the decomposition of MFAD (Fig. 8).

Finally, when the contribution values of FUs were compared using DO and DBM2 methods, then their relationship was significant only in one (river fishes, $R = 0.74$, $p = 0.004$) out of five cases ($p > 0.25$ in the other four examples).

Discussion

Although FD is regarded as a key factor in understanding the link between ecosystem function and biodiversity (Tilman et al. 1997), its measurement poses a number of problems some of them still unresolved (Ricotta 2005a, 2005b). In the present paper, we proposed a method to calculate the contribution of community members to functional diversity and compared it with other measures using actual data sets. Although the same dissimilarity matrix of community members was used as input for all methods; functional contribution values estimated by the different methods produced contrasting results in many cases. This observation emphasizes the importance of carefully selecting the method for the calculation of functional diversity of communities and the contribution of community members to it.

The first two PCoA axes in our actual data sets were not always sufficient to visualize the functional organization of the community completely (i.e. the dissimilarity relationships of functional units). The distance from the origin of the functional trait space expresses how far is the given community member from the centre of the point scatter of the community in potentially more than two dimensions (Fig. 3C) and is a generally accepted measure of

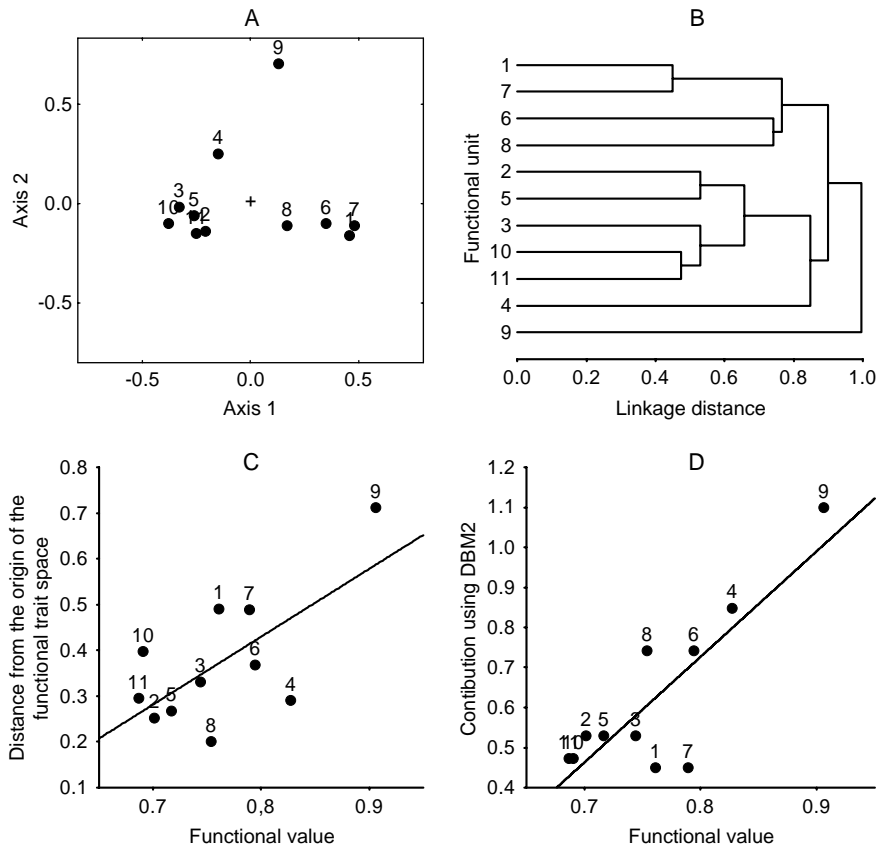


Figure 6. Functional organization of predatory vertebrates (Jaksić and Mendel 1990). (A) PCoA ordination of the functional units (+ shows the origin, the first two axes explain 48.9% of the variance). (B) dendrogram of functional units. (C) the relationship between the functional value and the distance from the origin of the ordination space ($r=0.672$, $p=0.023$). (D) the relationship between the functional value and CDBM2 ($r=0.835$, $p=0.001$).

conservation value, called as typicalness (Eyre and Rushton 1989). However, we point out that distance from the origin cannot be used as a contribution measure because community members positioned close to the origin do not necessarily have zero or close to zero contribution to FD. Distances of FUs close to the origin showed significantly lower contributions than the FVs calculated for the same FUs and some disagreements were observed between the contribution values of FUs using ordination and the decomposition of MFAD (for instance, FU3 in stream caddisflies). Admittedly, in four out of the five actual data sets we examined here the correlation between typicalness and FV was significant, showing that in most cases functionally typical community members (low distance from the origin of the functional trait space) are low contributors (low FV) to the FD of the community. Thus, the results are equivocal so distances from the origin of the functional trait space are not recommended for general use.

The improved version of the dendrogram-based measure (Petchey and Gaston 2006, 2007; DBM2 in this paper) provided in many cases equal contributions to several pairs of FUs. However, as we have shown this can be an artefact due to the dendrogram construction options. Another problem with CDBM2 is that it measures by definition the linkage distance of the community member to the most similar community member in the dendrogram. This

explains why species forming functional units by other species (Fig. 1) have zero contribution to the FD of the community. However, the analysis of stream caddisflies showed (Fig. 8) that this way of calculation does not necessarily express our intuitive definition of functional contribution. FUs 1 and 4, for example, are linked at a linkage distance of 0.2 to each other showing that both of these FUs have low uniqueness (Pavoine et al. 2005) in this community. However, the common branch of these two FUs is linked at a very high linkage distance to the other FUs, suggesting that in contrast to their low uniqueness value, their contribution to the FD of the community is not negligible. Unfortunately, the recently existing contribution measures using dendrograms (using both DBM1 and DBM2) cannot quantify this phenomenon, even if it is clearly shown by the dendrogram. Another undesirable property of CDBM2 is that even if the dissimilarity index producing the dissimilarity matrix varied between 0 and 1, its value lies between 0 and 2.

Theoretical considerations and analyses of actual data showed that the novel method of assessing functional value of community members has several advantages. First, in agreement with Ricotta (2005a), we consider FUs as the functional building blocks of communities. If a FU is composed by several species, then the 'true' functional value of these species should be expressed together, rather

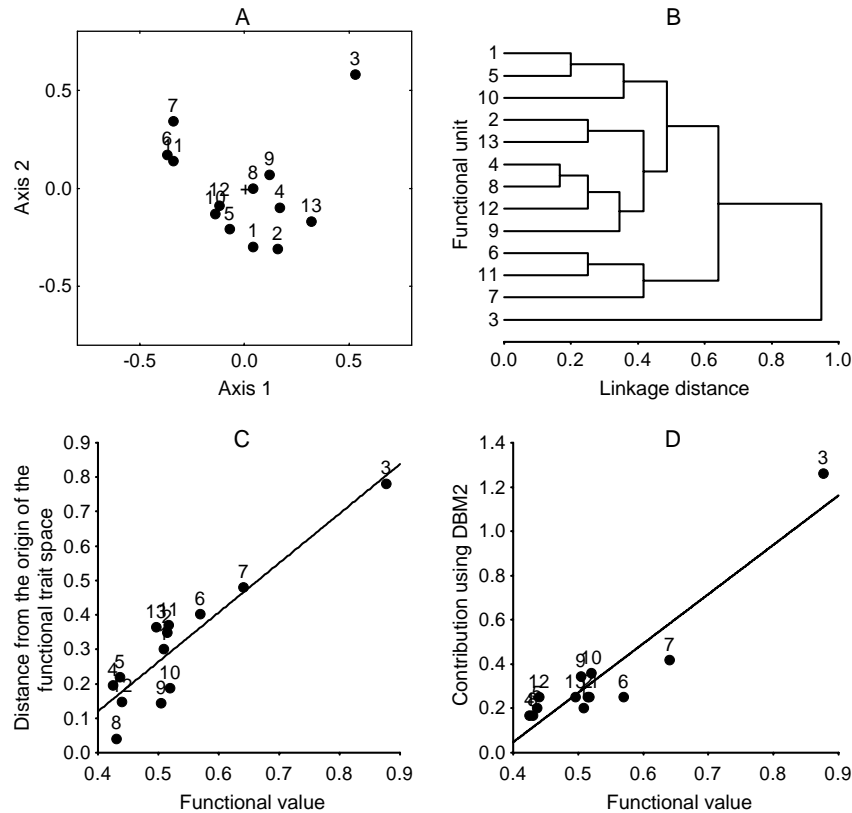


Figure 7. Functional organization of river fishes (species list: Schmera et al. 2009, feeding traits of the species: Erős et al. 2008). (A) PCoA ordination of the functional units (+ shows the origin, the first two axes explain 67.1% of variance). (B) dendrogram of functional units. (C) the relationship between the functional value and the distance from the origin of the ordination space ($r=0.913$, $p < 0.001$). (D) the relationship between the functional value and CDBM2 ($r=0.934$, $p < 0.001$).

than individually. If intrinsic redundancy is a common phenomenon of communities, then random removal of a species will have relatively little effect on FD (Petchey et al. 2007). However, this change depends on the number of species forming a FU as well as on the FV of this functional unit. Second, using the method of additive decomposition of MFAD, the FVs of functional units can be exactly calculated in such a way that the sum of FVs equals to MFAD, and the FVs are related to the change in MFAD if the given FU is removed from the community. These properties of decomposition allow meaningful quantification of the contribution of FUs to the functional diversity of the community, avoiding the disadvantages associated with traditional methods such as DBM (which measure uniqueness rather than functional contribution, cannot handle properly equal values and species addition) or principal coordinates analysis (which measures functional typicalness rather than contribution).

Several functional diversity measures currently available are very different from those we discussed here regarding formalism and conceptual background. For instance, certain indices consider species abundances (Rao 1982, Bady et al. 2005, Botta-Dukát 2005, Erős et al. 2008, Villéger et al. 2008) and some of these estimate not only species abundance but also the value of functional trait of the species in the field (Mason et al. 2003, 2005, Mouillot et al. 2005, 2007, Lavorel et al. 2008). We do not want to generate here a debate on the relative merits of the various

methods, but call attention to the complex nature of functional diversity assessment and related techniques such as decomposition of functional diversity.

Measuring functional contribution of community members receives increasing attention in biodiversity research, especially if ecosystem services are considered (Mouillot et al. 2008). For instance, according to a predictive model on marine invertebrate communities, decrease of species richness reduced the depth of bioturbation (a primary determinant of sediment oxygen concentration which influences the biomass of organisms and the rate of organic matter decomposition), but the magnitude of reduction depends on how the functional contribution of individual species co-vary with the risk of extinction (Solan et al. 2004). Similarly, field observations suggest (Ernest et al. 2006) that environmental impact strongly influences the FD of communities, whereas their species richness is not necessarily affected. It is clear from these results that removing species with high functional contribution might strongly influence ecosystem services. Finally, conservation practice requires information on whether protected areas maintain only species rich communities or preserve original ecosystem services (Mouillot et al. 2008). All of these studies confirm our view that reliable assessments of how community members contribute to the FD of a community should be integral part of conservation studies.

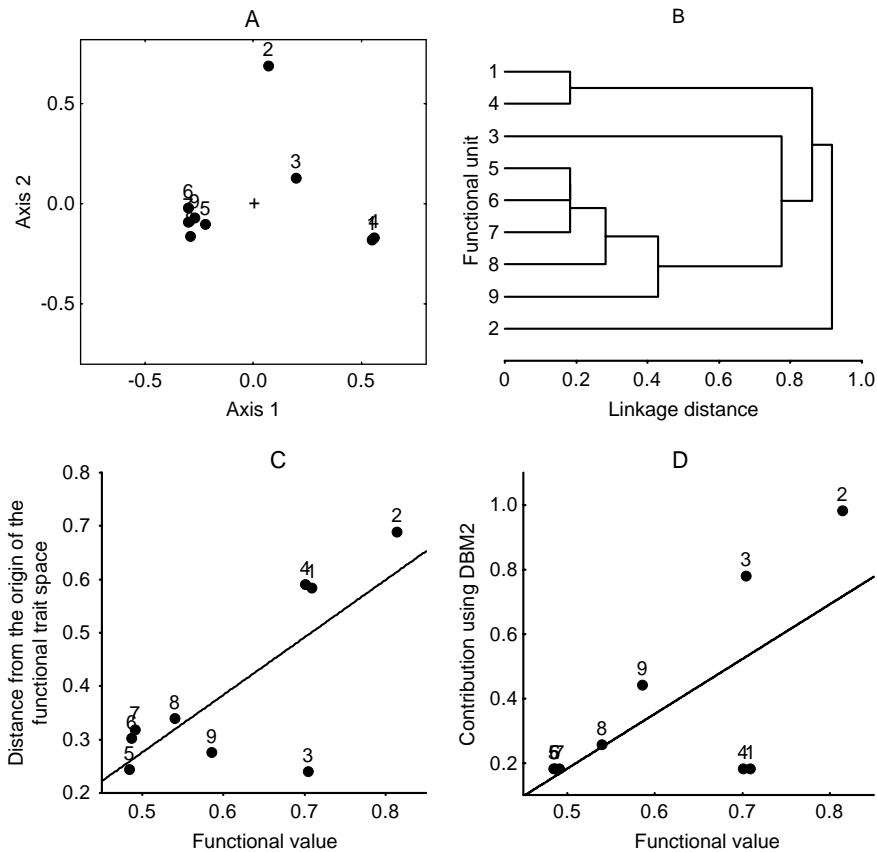


Figure 8. Functional organization of stream caddisflies (species list: Schmera et al. 2009, feeding traits of the species: Graf et al. 1995). (A) PCoA ordination of the functional units (+ shows the origin, the first two axes explain 75.3% variance). (B) dendrogram of the functional units. (C) the relationship between the functional value and the distance from the origin of the ordination space ($r=0.759$, $p=0.018$). (D) the relationship between the functional value and CDBM2 ($r=0.685$, $p=0.042$).

In summary, this study provides a new mathematical tool to calculate the functional values of functional units, which are interpreted as the building blocks of communities. This novel method is ideal for identifying functional keystones of the community and can also be used in association with phylogenetic diversity and phylogenetic contribution measures (reviewed by Schweiger et al. 2008).

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References

Backeljau, T. et al. 1996. Multiple UPGMA and neighboring trees and performance of some computer packages. – *Mol. Biol. Evol.* 13: 309–313.

Bady, P. et al. 2005. Use of invertebrate traits for the monitoring of European large rivers: the effects of sampling effort on genus richness and functional diversity. – *Freshwater Biol.* 50: 159–173.

Beche, L. A. and Resh, V. H. 2007. Biological trait diversity of benthic macroinvertebrates in California Mediterranean-

climate streams: long-term annual variability and trait diversity patterns. – *Fundam. Appl. Limnol.* 169: 1–23.

Bellwood, D. R. et al. 2006. Functional versatility supports coral reef biodiversity. – *Proc. R. Soc. Lond. B* 273: 101–107.

Bonada, N. et al. 2007. Taxonomic and biological trait differences of stream macroinvertebrate communities between Mediterranean and temperate regions: implications for future climatic scenarios. – *Global Change Biol.* 13: 1658–1671.

Botta-Dukát, Z. 2005. Rao's quadratic entropy as a measure of functional diversity based on multiple traits. – *J. Veg. Sci.* 16: 533–540.

Chapin, F. S. et al. 2000. Consequence of changing biodiversity. – *Nature* 405: 234–242.

Chevenet, F. et al. 1994. A fuzzy coding approach for the analysis of long-term ecological data. – *Freshwater Biol.* 31: 295–309.

Doledec, S. et al. 2000. Accurate description of the abundance of taxa and their biological traits in stream invertebrate communities: effect of taxonomic and spatial resolution. – *Arch. Hydrobiol.* 148: 25–43.

Ernest, R. et al. 2006. Diversity erosion beyond the species level: dramatic loss of functional diversity after selective logging in two tropical amphibian communities. – *Biol. Conserv.* 133: 143–155.

Erős, T. et al. 2008. Comparison of fish assemblage diversity in natural and artificial rip-rap habitats in the littoral zone of a large river (River Danube, Hungary). – *Int. Rev. Hydrobiol.* 93: 88–105.

Eyre, M. D. and Rushton, S. P. 1989. Qualification of conservation criteria using invertebrates. – *J. Appl. Ecol.* 26: 159–171.

- Graf, W. et al. 1995. Trichoptera. – In: Moog, O. (ed.), *Fauna aquatica Austriaca – a comprehensive species inventory of Austrian aquatic organisms with ecological notes*. Federal Ministry for Agriculture and Forestry, Wasserwirtschaftskataster Vienna.
- Holmes, R. T. et al. 1979. Guild structure of the Hubbard Brook bird community: a multivariate approach. – *Ecology* 60: 512–520.
- Ilg, C. and Castella, E. 2006. Patterns of macroinvertebrate traits along three glacial stream continuums. – *Freshwater Biol.* 51: 840–853.
- Jaksić, F. M. and Mendel, R. G. 1990. Objective recognition of guilds: testing for statistically significant species clusters. – *Oecologia* 82: 87–92.
- Lavorel, S. et al. 2008. Assessing functional diversity in the field – methodology matters! – *Funct. Ecol.* 22: 134–147.
- Mason, N. W. H. et al. 2003. An index of functional diversity. – *J. Veg. Sci.* 14: 571–578.
- Mason, N. W. H. et al. 2005. Functional richness, functional evenness and functional divergence: the primary components of functional diversity. – *Oikos* 111: 112–118.
- Mouchet, M. et al. 2008. Towards a consensus for calculating dendrogram-based functional diversity indices. – *Oikos* 117: 794–800.
- Mouillot, D. et al. 2005. Functional regularity: a neglected aspect of functional diversity. – *Oecologia* 142: 353–359.
- Mouillot, D. et al. 2007. Is the abundance of the species determined by their functional traits? A new method with a test using plant communities. – *Oecologia* 152: 729–737.
- Mouillot, D. et al. 2008. Do we protect originality in protected areas? A new index and an application to the Bonifacio Strait Natural Reserve. – *Biol. Conserv.* 141: 1569–1580.
- Muñoz, A. A. and Ojeda, F. P. 1997. Feeding guild structure of a rocky intertidal fish assemblage in central Chile. – *Environ. Biol. Fishes* 49: 471–479.
- Pavoine, S. et al. 2005. Is the originality of a species measurable? – *Ecol. Lett.* 8: 579–586.
- Petchey, O. L. and Gaston, K. J. 2002. Functional diversity (FD), species richness and community composition. – *Ecol. Lett.* 5: 402–411.
- Petchey, O. L. and Gaston, K. J. 2006. Functional diversity: back to basics and looking forward. – *Ecol. Lett.* 9: 741–758.
- Petchey, O. L. and Gaston, K. J. 2007. Dendrograms and measuring functional diversity. – *Oikos* 116: 1422–1426.
- Petchey, O. L. et al. 2004. How do different measures of functional diversity perform? – *Ecology* 85: 847–857.
- Petchey, O. L. et al. 2007. Low functional diversity and no redundancy in British avian assemblages. – *J. Anim. Ecol.* 76: 977–985.
- Podani, J. 1989. A method for generating consensus partitions and its application to community classification. – *Coenoses* 4: 1–10.
- Podani, J. 1997. On the sensitivity of ordination and classification methods to variation in the input order of data. – *J. Veg. Sci.* 8: 153–156.
- Podani, J. 2000. Introduction to the exploration of multivariate biological data. – Backhuys.
- Podani, J. 2001. SYNTAX 2000. Computer programs for data analysis in ecology and systematics. User's manual. – Scientia, Budapest.
- Podani, J. and Schmera, D. 2006. On dendrogram-based measures of functional diversity. – *Oikos* 115: 179–185.
- Podani, J. and Schmera, D. 2007. How should a dendrogram-based measure of functional diversity function. A rejoinder to Petchey and Gaston. – *Oikos* 116: 1427–1430.
- Rao, C. R. 1982. Diversity and dissimilarity coefficients: a unified approach. – *Theor. Popul. Biol.* 21: 24–43.
- Ricotta, C. 2005a. A note on functional diversity measures. – *Basic Appl. Ecol.* 6: 479–486.
- Ricotta, C. 2005b. Through the jungle of biological diversity. – *Acta Biotheor.* 53: 29–38.
- Santoul, F. et al. 2005. Spatial patterns of the biological traits of freshwater fish communities in S.W. France. – *J. Fish Biol.* 66: 301–314.
- Schmera, D. and Erős, T. 2006. Estimating sample representativeness in a survey of stream caddisfly fauna. – *Ann. Limnol. Int. J. Limnol.* 42: 181–187.
- Schmera, D. et al. 2009. A measure for assessing functional diversity in ecological communities. – *Aquat. Ecol.* 43: 157–167.
- Schwartz, M. W. et al. 2000. Linking biodiversity to ecosystem function: implication for conservation ecology. – *Oecologia* 122: 297–305.
- Schweiger, O. et al. 2008. A comparative test of phylogenetic diversity indices. – *Oecologia* 157: 485–495.
- Sivastra, D. S. and Vellend, M. 2005. Biodiversity-ecosystem function research: is it relevant to conservation? – *Annu. Rev. Ecol. Evol. Syst.* 36: 267–294.
- Solan, M. et al. 2004. Extinction and ecosystem function in marine benthos. – *Science* 306: 1177–1180.
- Statzner, B. et al. 2001. Perspectives for biomonitoring at large spatial scales: a unified measure for the functional composition of invertebrate communities in European running waters. – *Basic Appl. Ecol.* 2: 73–85.
- Tilman, D. 1999. The ecological consequences of changes in biodiversity: a search for general principles. – *Ecology* 80: 1455–1474.
- Tilman, D. et al. 1997. The influence of functional diversity and composition on ecosystem processes. – *Science* 277: 1300–1302.
- Usseglio-Polatera, P. et al. 2000. Biological and ecological traits of benthic freshwater macroinvertebrates: relationships and definition of groups with similar traits. – *Freshwater Biol.* 43: 175–205.
- Villéger, S. et al. 2008. New multidimensional functional diversity indices for a multifaceted framework in functional ecology. – *Ecology* 89: 2290–2301.
- Walker, B. et al. 1999. Plant attribute diversity, resilience, and ecosystem function: the nature and significance of dominant and minor species. – *Ecosystems* 2: 95–113.
- Walker, S. C. et al. 2008. Functional rarefaction: estimating functional diversity from field data. – *Oikos* 117: 286–296.