Rao's quadratic entropy as a measure of functional diversity based on multiple traits

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Abstract

Question: Is Rao's quadratic entropy a suitable measure of functional diversity if several traits are considered?

Methods: It is checked whether Rao's quadratic entropy (FD_Q) satisfies *a priori* criteria suggested by Mason et al. A real data set is used to show that there are often zeros in abundance distributions which maximize functional diversity.

Results and Conclusion: FD_Q fulfils all *a priori* criteria and it surpasses other proposed indices, because it includes species abundances and more than one trait. Therefore, it seems to be an improvement compared to measures of functional diversity that are currently available. An unexpected property of FD_Q is that its value may decrease if species richness increases. The reason is that functional diversity is influenced by both species-abundance based diversity and differences among species. Introduction of a new species into the community increases the species-abundance based diversity, while it may decrease the average dissimilarity among species.

Keywords: Functional diversity; Functional group; Functional redundancy; Trait.

Abbreviation: FD_Q = Functional diversity measured by Rao's quadratic entropy.

Introduction

Traditional ecological diversity indices (see review in e.g. Tóthmérész 1995) summarize information about the relative abundance of species within a community or sample but ignore the degree of difference between species. The biodiversity/ecosystem function debate (e.g. Tilman et al. 1996; Chapin et al. 1997; Aarssen 1997; Huston 1997; Tilman 1997; Wardle 1999, 2001; Loreau et al. 2001; Lepš et al. 2001) highlighted the problems of neglecting species identity. Studies that have jointly addressed species richness, functional richness and functional composition suggest that the importance of functional composition and functional richness tend to be larger than the importance of species richness in influencing ecosystem functions (Díaz & Cabido 2001; Petchey et al. 2004).

Empirical studies often measure functional diversity by the number of functional groups (functional richness), thus they suppose that all differences between groups are equal, and they neglect the differences within groups and abundance of groups (Díaz & Cabido 2001; Mason et al. 2003). The latter problem can be solved by calculating 'traditional' diversity indices from the relative abundance of groups instead of relative abundance of species (e.g. Fekete & Kovács 1978; Lloret & Vilá 2003). Another drawback of this approach is that results strongly depend on the classification of species into groups, and there is no standard method for such a classification (e.g. Jaksic & Medel 1990). Consequently, it seems preferable to calculate functional diversity directly from species characteristics (Mason et al. 2003), but there is no simple standardized index for this purpose.

One possible field, from which such measures can be adopted, is biodiversity estimation for conservation purposes (Petchey & Gaston 2002). In this field numerous methods were developed based on topology (Vane-Wright et al. 1991) and branch length (Faith 1992, 1994) of cladograms or dendrograms, or based on raw (phylo)genetic distances between species (Izsák & Papp 2000; Ricotta 2002, 2004). If these methods are applied to measure functional diversity, taxonomic or (phylo)genetic

differences have to be replaced by differences in characters thought to be of significance in plant growth and ecosystem functions (Petchey & Gaston 2002).

Petchey & Gaston (2002) suggested to use functional diversity (*FD*), the analogue of Faith's (1992, 1994) phylogenetic diversity (*PD*), which measures functional diversity by the summed branch lengths of the dendrogram constructed from functional differences. This method, however, ignores the abundance of species which affects the overall functional diversity (Mason et al. 2003).

Mason et al. (2003) proposed an index of functional diversity, FD_{var}, which is analogous to the evenness index E_{var} of Smith & Wilson (1996). It is essentially the variance in the log-transformed character values weighted by relative abundances. Unfortunately, this index was designed to work with only one character at a time.

I propose an index of functional diversity based on the quadratic entropy of Rao (1982) that incorporates both the relative abundances of species and a measure of the pairwise functional differences between species. Consider an *S*-species community characterized by the relative abundance vector $\mathbf{p} = (p_1, p_2, \ldots, p_s)$ such that

$$\sum_{i=1}^{S} p_i = 1. \tag{1a}$$

Rao (1982) defined quadratic entropy as

$$FD_Q = \sum_{i=1}^{S-1} \sum_{j=i+1}^{S} d_{ij} p_i p_i \tag{1b}$$

where d_{ij} is the difference between the *i*-th and *j*-th species ($d_{ij} = d_{ji}$ and $d_{ii} = 0$) and FD_Q expresses the average difference between two randomly selected individuals with replacements. d_{ij} values can be defined arbitrarily – with the restriction that $d_{ij} = d_{ji}$ and $d_{ii} = 0$ – or calculated by any distance function (see e.g. Legendre & Legendre 1998; Podani 2000) considering one or more characters of species. It is easily shown that if $d_{ij} = 1$ for all $i \neq j$, FD_Q reduces to the Simpson diversity index (meaning the complement of the original Simpson dominance index):

$$1 - \sum_{i=1}^{s} p_i^2 \tag{2}$$

There are many difference functions in the ecological literature (see e.g. Legendre & Legendre 1998; Podani 2000) which could be applied to measure functional differences. The following questions must be considered when we choose a distance measure:
• In which scale are the traits measured?
• Is standardization of character values desirable or not?
• Is log-transformation of character values possible and meaningful or not?

• Are correlations among descriptors taken into account?

Functional attributes are generally measured in nominal (i.e. unordered categories) or ratio scale (i.e. quantitative traits). If all traits are unordered categorical, I suggest to use the complement of the simple matching coefficient (Podani 2000).

$$d_{ij} = \frac{u_{ij}}{n} \tag{3}$$

where: n = total number of traits considered, u_{ij} = number of traits with different values in species *i* and *j*. Standardization and transformation procedures are meaningless in the case of categorical data. At this scale there is no distance measure that takes into account correlations among traits.

Many distance functions have been developed to compare quantitative data (see e.g. Legendre & Legendre 1998; Podani 2000), but most of them were designed to deal with species abundances. Here it is suggested to use Euclidean distance divided by the number of traits:

$$d_{ij} = \frac{1}{n} \sum_{k=1}^{n} \left(X_{ik} - X_{jk} \right)^2 \tag{4}$$

and mean character difference:

$$d_{ij} = \frac{1}{n} \sum_{k=1}^{n} \left| X_{ik} - X_{jk} \right| \tag{5}$$

where: n = the number of traits considered, X_{ik} = value of trait *k* in species *i*.

The mean character difference assigns a smaller relative importance to the largest differences than Euclidean distance does. Through the division by the number of traits considered FD_Q is not affected by the number of traits directly.

Prior to the calculation of the distances, values can be standardized by the standard deviation or by the range of traits. Here, standardization by range is preferred, because in that case the empirical maximum value of the distance functions is 1. If we want to compare communities, the same standardization has to be used for the whole data set. It means that if we include a new community into the comparison, actual standard deviation and range values will be changed, therefore the previously calculated FD_Q values have to be recalculated. Therefore it is suggested to standardize by the theoretical range (if this is known), instead of the actual one.

After standardization all traits have the same weight, which can be undesirable in some cases. On the other hand, as a result of the standardization, FD_Q is unaffected by the units in which the character is measured. If there are no negative values, it can also be achieved by

log-transformation.

The above-mentioned distance functions do not take into account the correlations between traits. It follows that if two or more traits are related to the same functional attribute, this attribute receives more importance than others. We can solve this problem by using Mahalanobis generalized distance:

$$d_{ij} = \sum_{k=1}^{n} \sum_{l=1}^{n} w_{kl} \left(X_{ik} - X_{jk} \right) \left(X_{il} - X_{jl} \right) \qquad (5)$$

where: w_{kl} = elements of inverse of variance-covariance matrix of traits.

The Mahalanobis generalized distance automatically standardizes the traits by their standard deviation. Since the variance-covariance matrix is calculated from the actual data, this measure changes if new communities are included in the comparison; hence FD_Q values have to be recalculated. This is a reason for preferring the exclusion of strongly correlated traits instead of using the Mahalanobis generalized distance.

If we want to consider categorical and quantitative traits simultaneously, we have to use distance functions for mixed data. Gower (1971) proposed a dissimilarity measure which allows the simultaneous appearance of presence/absence, unordered categorical and quantitative variables, while missing scores are also tolerated. Podani (1999) developed an extension in order to consider ordered categorical variables as well. If all traits are unordered categorical, Gower's dissimilarity is equal to the complement of the simple matching coefficient (see above). If all traits are quantitative, it is equal to the mean character difference (see above) calculated after standardization by range. If both types of traits occur in the data set, at first distances are calculated for the two types separately, and then the distance is calculated as the mean weighted by the number of traits belonging to the two types.

Mason et al. (2003) composed a list of *a priori* criteria that should be satisfied by a functional diversity index. The first aim of this paper is to show that the quadratic entropy satisfies these criteria. In addition, this paper demonstrates some properties of quadratic entropy in the case that multiple traits are considered.

Material and Methods

To check if the criteria proposed by Mason et al. (2003) are fulfilled, I used their numerical examples (Table 1 in Mason et al. 2003) with a slight modification (Table 1). Numerical examples consider only one trait, because if criteria are fulfilled in this case, they are fulfilled if more than one trait is used. The reason is that distance function proposed above, first calculate differ-

ences trait-by-trait and then sum them. Thus FD_Q is equal to the average functional diversities calculated from the traits one by one.

Since these criteria concern quantitative traits, distances between species were calculated by mean character difference. In order to illustrate effects of data transformation, three types of data were used, raw data, data standardized by range and log-transformed data.

Shimatani's (2001) theorem was used to investigate whether FD_Q is sensitive to the correlation among traits or whether it is affected by the univariate trait distributions only.

Contrary to the traditional species-abundance diversity, functional diversity does not increase automatically if species richness increases (Izsák & Szeidl 2002). To demonstrate this, seven qualitative traits (biomass production, height, rooting depth, leaf longevity, SLA, leaf N content, leaf width) of 28 vascular plants were used from a data set used by Chapin et al. (1996). Distances between species were calculated by mean character differences. The dendrogram resulting from single linkage classification (Podani 2000) was used to illustrate differences between species. The relative abundance vector resulting in a maximal FD_Q was calculated by optimization. These relative abundances will be called here 'optimal' relative abundances. The calculation was done by the quasi-Newton method implemented in the Quattro Pro 6.02 programme using different species pools: all of the 28 species, and different combinations of 27 species from this pool. Results for the latter type will be shown by means of two examples: the species pool excluding *Vaccinium uliginosum* and the species pool excluding *Rubus chamaemorus*, respectively.

Results

Conformity to prior criteria

Numerical examples in Table 1 show that criteria 2-5 and 8-9 were met, irrespective of the data transformation. Criterion 9 is essential for any functional diversity index, therefore its formal proof is elaborated in App. 1. Criterion 6 is met, only if standardization or log-transformation are applied. Criterion 7 is not satisfied if log-transformation is applied. However, the meaning of 'values that are equally extreme' is ambiguous. In the numerical example, two values are equally extreme, if they equally differ from the mean of the values. In the original table of Mason et al. (2003), two values are equally extreme, if their logarithms are equally different from the mean of the log-transformed values. With this definition, criterion 7 would have been satisfied by only FD_Q calculated after the log-transformation.

The numerical example suggests that FD_Q does not

satisfy the first criterion, i.e. its minimum is zero, but its maximum is not one. If the applied distance function ranges between zero and one, FD_Q ranges between zero (when all species functionally equivalent) and Simpson diversity (when all species are maximally different from each other, i.e. $d_{ij} = 1$ for all $i \neq j$). If there are more than two species, all pairwise differences are maximal only if the traits being considered are categorical. The simple matching coefficient ranges between zero and one, thus

if differences between species are calculated by this form, the maximum of FD_Q is the Simpson diversity. The maximum of Simpson diversity is $(1 - 1/S)$ where S is the number of species. Thus, in this case the potential maximum FD_Q value depends on the number of functionally different species, and it asymptotically converges to 1 if number of maximally different species approaches infinite. So, in this case FD_Q asymptotically satisfies criterion 1.

Table 1. Nine criteria (according to Mason et al. 2003) for an index of functional diversity, with tests using artificial data sets, A and B. Three functional diversity values correspond to the three distance functions applied: mean character difference without any transformation, mean character difference after standardization by range, and mean character difference after log-transformation, respectively. To meet the criterion, the diversity of community A should be lower than that of community B, or equal, as indicated. OK √ = the criterion was met.

Criterion		Character	Abundance	FD_Q		Character	Abundance	FD_Q	OK?
1: Is constrained to a 0-1 range	**A**	1.0	10	0.000	**B**	0.00001	10	37.624	
(for convenience) and use that	**0**	1.0	10	0.000	**close to 1**	0.01	10	0.376	
range well		1.0	10	0.000		1.0	10	6.620	
		1.0	10			100.0	10		
2: Reflects the range of character	**A**	2.0	1	2.500	**B**	0.1	1	38.588	√
values present, since that is the	**lower**	4.0	1	0.025	**higher**	1.0	1	0.386	√ [1]
point of the index	**diversity**	6.0	1	0.571	**diversity**	10.0	1	2.878	√
		8.0	1			100.0	1		
3: Reflects the contribution of	**A**	0.1	1	5.396	**B**	0.1	10	38.588	√
each species in proportion to its	**lower**	1.0	100	0.054	**higher**	1.0	10	0.386	√
abundance: a community is not	**diversity**	10.0	100	1.197	**diversity**	10.0	10	2.878	√
functionally diverse if all species		100.0	1			100.0	10		
with extreme character values are									
present in very minor amounts									
4: Decrease when the abundance	**A**	0.1	0.1	16.244	**B**	0.1	1	16.365	√
of a minor species with an	**lower**	1.0	10	0.163	**higher**	1.0	10	0.164	√
extreme character value	**diversity**	10.0	100	0.453	**diversity**	10.0	100	0.463	√
decreases		100.0	1000			100.0	1000		
5: Does not change much when	**A**	0.1	0.000001	16.365	**B**			16.365	√
a species present in minute	**equal**	1.0	10	0.162		1.0	10	0.162	√
amounts disappears	**diversity**	10.0	100	0.463		10.0	100	0.463	√
		100.0	1000			100.0	1000		
6: Is unaffected by the units in	**A**	0.1	1	16.365	**B**	0.001	1	0.164	
which the *character* is measured.	**equal**	1.0	10	0.164		0.01	10	0.164	√
This is essential for any character	**diversity**	10.0	100	0.463		0.1	100	0.463	√
that could be measured on more than		100.0	1000			1.0	1000		
one scale (e.g. mm, cm or m)[2]									
7: Is symmetrical with regard to	**A**	2	1	0.403	**B**	8	1	0.403	√
small and large values that are	**equal**	4	10	0.067		6	10	0.067	√
equally far from the mean[3]	**diversity**	6	100	0.061		4	100	0.133	
		8	1000			2	1000		
8: Is unaffected by the units in	**A**	0.1	1	16.365	**B**	0.1	100	16.365	√
which the *abundance* is measured. It	**equal**	1.0	10	0.164		1.0	1000	0.164	√
is unacceptable to have the index	**diversity**	10.0	100	0.463		10.0	10000	0.463	√
value dependent on the unit chosen[4].		100.0	1000			100.0	100000		
9[5]: Is unaffected when a species is	**A**	0.1	1	16.365	**B**	0.1	1	16.365	√
split in two (i.e. replaced by two with	**equal**	1.0	10	0.164		1.0	10	0.164	√
the same character value, with the	**diversity**	10.0	100	0.463		10.0	100	0.463	√
same total abundance), because		100.0	1000			100.0	500		
taxonomic species itself is not						100.0	500		
relevant for functional diversity[5]									

[1] This criterion is satisfied only if characters were standardized with the same range in both communities; [2] It is satisfied due to standardization of characters; [3] This criterion and the corresponding numerical example are slightly modified; [4] This is satisfied due to using relative abundances; [5] Criteria 9 and 10 of Mason et al. (2003) correspond to the same principle, therefore they are merged here.

Effects of the correlation between traits

Shimatani (2001) showed that Rao's quadratic entropy is based on three factors: species diversity (Simpson index), species distinctness and a balance factor, as follows: FD_Q = SpDiv * SpDis + BaFac. Species distinctness is the mean functional distance between species (mean of the non-diagonal elements of the distance matrix). The balance factor is the covariance between the $p_i p_j$ and d_{ij} values multiplied by $S(S–1)/2$.
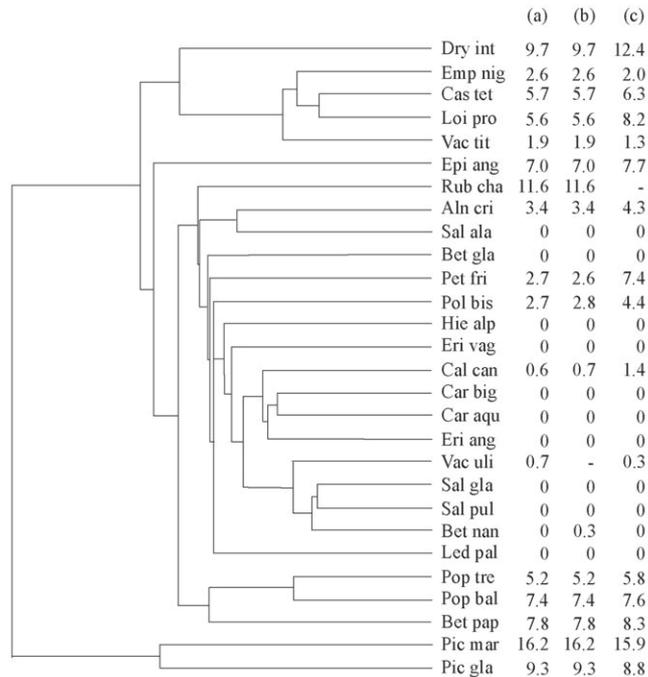
Species diversity is mathematically independent from the representation of traits. If the distance functions proposed above (except Mahalanobis generalized distance) are used, species distinctness depends only on the univariate trait distribution, and only the balance factor is affected by the correlation among traits. If all species have the same abundance, the balance factor is zero. Thus, in this special case, FD_Q is not sensitive to correlation among traits, but otherwise it is.

When is FD_Q maximal?

Fig. 1 shows a dendrogram of 28 species, and optimal relative abundance vectors (i.e. relative abundances that results in a maximal value for FD_Q), if the whole species pool is considered, and if one species (*Vaccinium uliginosum* and *Rubus chamaemorus*, respectively) were excluded. First, it should be mentioned that there are zero values in optimal vectors, and often there are species similar to them with non-zero optimal relative abundance. For example, *Salix alaxensis* has zero optimal relative abundance, while optimal relative abundance of the similar *Alnus crispa* is 3.4%. On the other hand, species dissimilar to all other species (they are represented by isolated branches of the dendrogram) often have high optimal relative abundance.

If one species is removed from the species pool, it may affect optimal relative abundance of the similar species only. For example, after removing *Vaccinium uliginosum*, optimal relative abundance of *Betula nana* is increased, while other values do not change considerably. But removing one species (mainly if it is represented by isolated branches of the dendrogram) may result in many positive and negative changes in the optimal relative abundance values (e.g. removing *Rubus chamaemorus* in this example).

	(a)	(b)	(c)
Dry int	9.7	9.7	12.4
Emp nig	2.6	2.6	2.0
Cas tet	5.7	5.7	6.3
Loi pro	5.6	5.6	8.2
Vac tit	1.9	1.9	1.3
Epi ang	7.0	7.0	7.7
Rub cha	11.6	11.6	-
Aln cri	3.4	3.4	4.3
Sal ala	0	0	0
Bet gla	0	0	0
Pet fri	2.7	2.6	7.4
Pol bis	2.7	2.8	4.4
Hie alp	0	0	0
Eri vag	0	0	0
Cal can	0.6	0.7	1.4
Car big	0	0	0
Car aqu	0	0	0
Eri ang	0	0	0
Vac uli	0.7	-	0.3
Sal gla	0	0	0
Sal pul	0	0	0
Bet nan	0	0.3	0
Led pal	0	0	0
Pop tre	5.2	5.2	5.8
Pop bal	7.4	7.4	7.6
Bet pap	7.8	7.8	8.3
Pic mar	16.2	16.2	15.9
Pic gla	9.3	9.3	8.8

Fig. 1. Average linkage dendrogram for 28 species based on mean character differences demonstrating functional similarities among species. The three columns present abundance vectors that maximize FD_Q; (a) All species included, (b) *Vaccinum uliginosum* excluded, (c) *Rubus chamaemorus* excluded. Species are:

Aln cri = *Alnus crispa*	Bet gla = *Betula glandulosa*	Bet nan = *B. nana*	Bet pap = *B. papyrifera*
Cal can = *Calamagrostis canadensis*	Car aqu = *Carex aquatilis*	Car big = *C. bigelowii*	Cas tet = *Cassiope tetragona*
Dry int = *Dryas integrifolia*	Emp nig = *Empetrum nigrum*[1]	Epi ang = *Epilobium angustifolium*	Eri ang = *Eriophorum angustifolium*
Eri vag = *Eriophorum vaginatum*[2]	Hie alp = *Hierochloe alpina*	Led pal = *Ledum palustre*[3]	Loi pro = *Loiseleuria procumbens*
Pet fri = *Petasites frigidus*	Pic gla = *Picea glauca*	Pic mar = *P. mariana*	Pol bis = *Polygonum bistorta*[4]
Pop bal = *Populus balsamifera*	Pop tre = *Populus tremuloides*	Rub cha = *Rubus chamaemorus*	Sal ala = *Salix alaxensis*
Sal gla = *Salix glauca*	Sal pul = *Salix pulchra*	Vac uli = *Vaccinium uliginosum*	Vac vit = *V. vitis-idaea*

[1] ssp. *hermaphroditum*; [2] ssp. *spissum*; [3] *ssp. decumbens*; [4] ssp. *plumosum*.

Discussion

Conformity to prior criteria

The index of functional diversity (FD_Q) proposed here satisfies most of the *a priori* criteria and it can combine several characters. Thus, it seems to represent the best solution so far for measuring functional diversity. An additional advantage of FD_Q is that if relative abundance is calculated from the number of individuals, it has a clear meaning; i.e. it is the mean functional dissimilarity between two randomly selected individuals. Of course, FD_Q can be calculated even if abundance is measured by other methods (e.g. cover estimation, harvesting biomass etc.). In these cases FD_Q is a measure of functional diversity without the above-mentioned direct interpretation.

The only comparable index proposed, that of Mason et al. (2003), is designed to work with one character at a time. Other proposed measures of functional diversity do not consider within-group differences among species (e.g. Lloret & Vilá 2003) or species abundance (e.g. Petchey & Gaston 2002). The bias caused by neglecting within group differences was discussed in detail by Petchey & Gaston (2002) and Mason et al. (2003). Neglecting the abundance of functional types causes an over-estimation of functional diversity, because it is equivalent to supposing that all functional types are equally abundant.

Except for the rare situation that all species are equally abundant, FD_Q is affected not only by the univariate trait distributions, but also by the covariance between traits. In my opinion it is a desirable property. However, a less desirable consequence is that if many traits are linked to the same ecosystem function (e.g. resource capture or regeneration after fire), this function is overemphasized. Although this problem can be solved by using the Mahalanobis generalized distance, it may result in another problem due to the inherent standardization (see above). That is why this distance function is not recommended. Instead, we should make a careful selection of traits based on the results of preliminary studies of the relationship between traits and ecosystem functions (cf. Díaz et al. 2004).

Choosing a distance function is a significant decision in the use of FD_Q. If only categorical traits are considered, a simple matching coefficient seems to be a reliable distance function. If only quantitative traits are considered, we should not use raw data because in this case FD_Q is affected by the units in which the character is measured. Standardization by range or standard deviation solves this problem. All traits will then have the same weight (which may be advantageous or disadvantageous), and FD_Q values depend on the other communities involved in the comparison. Log-transformed data are also unaffected by units, while free from the above-mentioned disadvantage of standardization. Therefore it seems to be the best solution, if there are no negative values (if there are zero values, a very small constant has to be added to all values). If categorical and qualitative traits are considered in the same analysis, the number of potential distance functions is strongly limited. Development of a new function more flexible than the Gower distance would be effective.

The *a priori* criteria published by Mason et al. (2003) are a milestone in the development of functional diversity measures. Although these criteria were formulated for the situation when only one trait is considered, any measure of functional diversity to be developed in the future has to satisfy these criteria. If more than one trait is considered, there may be further *a priori* criteria. Unfortunately, if the number of traits considered increases from one to two, the complexity of the system increases considerably. We will have to obtain experience with FD_Q, before we can develop further criteria.

Species richness, species abundances and functional diversity

The results presented here demonstrate that the relative abundance vector that maximizes FD_Q may contain zero values. This property of quadratic entropy was discussed in detail by Izsák & Szeidl (2002) in the context of genetic diversity. The most interesting consequence of this property is that an increase in species richness may result in a decrease of functional diversity. This seems to be contra-intuitive. But we should consider that functional diversity is influenced both by the species-abundance based diversity and by differences among species. Introduction of new species into the community will increase the species-abundance diversity, but it may decrease the average dissimilarity among species. Consequently, functional diversity may increase or decrease.

Petchey & Gaston (2002) found a strong positive correlation between species richness and values of their functional diversity index (FD) in real and simulated communities. This is a consequence of the definition of FD, i.e. the summed branch lengths of the dendrogram of species based on functional differences. Entering new species into the community increases the number of branches, and consequently increases FD.

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App. 1. Proof of the relative independence of FD_Q.

FD_Q will remain the same when a species is split into two subunits, i.e. replaced by two units with the same character values and with the same total abundance.

Definitions:
Consider an *N*-species community characterized by the relative abundance vector $\mathbf{p} = (p_1, p_2, \ldots, p_N)$ such that $0 \le p_1 \le 1$ and

$\sum_{i=1}^{N} p_i = 1$. Let d_{ij} be the functional dissimilarity between *i*-th species and *j*-th species.

Let $FD_Q(\mathbf{p}) = \sum_{i=1}^{N}\sum_{j=1}^{N} d_{ij} p_i p_j$ be the functional diversity of this community.

Let us split the *k*-th species in two. The relative abundance vector of this community is $\mathbf{q} = (q_1, q_2, \ldots, q_N, q_{N+1})$, where $q_i = p_i$, $\forall i \ne k$ and $i \ne N+1$, and $q_k + q_{N+1} = p_k$. The functional dissimilarities between species remain unchanged, and $d_{ik} = d_{iN+1}$.

Theorem: $FD_Q(\mathbf{p}) = FD_Q(\mathbf{q})$.

Proof:

$$FD_Q(\mathbf{q}) = \sum_{i=1}^{N+1}\sum_{j=1}^{N+1} d_{ij} q_i q_j = \sum_{i=1}^{k-1}\sum_{j=1}^{k-1} d_{ij} q_i q_j + \sum_{i=k+1}^{N}\sum_{j=k+1}^{N} d_{ij} q_i q_j + 2 q_k \sum_{i=1}^{N} d_{ik} q_i + 2 q_{N+1} \sum_{i=1}^{N+1} d_{iN+1} q_i$$

Since $q_i = p_i \ \forall i \ne k$ and $i \ne N+1$,

$$\sum_{i=1}^{k-1}\sum_{j=1}^{k-1} d_{ij} q_i q_j + \sum_{i=k+1}^{N}\sum_{j=k+1}^{N} d_{ij} q_i q_j = \sum_{i=1}^{k-1}\sum_{j=1}^{k-1} d_{ij} p_i p_j + \sum_{i=k+1}^{N}\sum_{j=k+1}^{N} d_{ij} p_i p_j$$

$$\sum_{i=1}^{N} d_{ik} q_i = \sum_{i=1}^{N+1} d_{iN+1} q_i, \text{ because } d_{ik} = d_{iN+1}.$$

Thus,

$$FD_Q(\mathbf{q}) = \sum_{i=1}^{k-1}\sum_{j=1}^{k-1} d_{ij} p_i p_j + \sum_{i=k+1}^{N}\sum_{j=k+1}^{N} d_{ij} p_i p_j + 2(q_k + q_{N+1})\sum_{i=1}^{N+1} d_{ik} q_i = \sum_{i=1}^{k-1}\sum_{j=1}^{k-1} d_{ij} p_i p_j + \sum_{i=k+1}^{N}\sum_{j=k+1}^{N} d_{ij} p_i p_j + 2 p_k \sum_{i=1}^{N+1} d_{ik} q_i$$

Since $d_{kk} = 0$ and $d_{kN+1} = 0$, $p_k \sum_{i=1}^{N+1} d_{ik} q_i = p_k \sum_{i=1}^{N} d_{ik} p_i$.

That is,

$$FD_Q(\mathbf{q}) = \sum_{i=1}^{k-1}\sum_{j=1}^{k-1} d_{ij} p_i p_j + \sum_{i=k+1}^{N}\sum_{j=k+1}^{N} d_{ij} p_i p_j + p_k \sum_{i=1}^{N} d_{ik} p_i + p_k \sum_{j=1}^{N} d_{kj} p_j = \sum_{i=1}^{N}\sum_{j=1}^{N} d_{ij} p_i p_j = FD_Q(\mathbf{p}) .$$