Quantifying and interpreting functional diversity of natural communities: practical considerations matter

Kvantifikace a interpretace funkční diverzity ekologických společenstev: důležitost praktických hledisek

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Dedicated to Marcel Rejmánek

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Lepš J., de Bello F., Lavorel S. & Berman S. (2006): Quantifying and interpreting functional diversity of natural communities: practical considerations matter. – Preslia 78: 481–501 .

Quantifying the functional diversity in ecological communities is very promising for both studying the response of diversity to environmental gradients and the effects of diversity on ecosystem functioning (i.e. in "biodiversity experiments"). In our view, the Rao coefficient is a good candidate for an efficient functional diversity index. It is, in fact, a generalization of the Simpson's index of diversity and it can be used with various measures of dissimilarity between species (both those based on a single trait and those based on several traits). However, when intending to quantify the functional diversity, we have to make various methodological decisions such as how many and which traits to use, how to weight them, how to combine traits that are measured at different scales and how to quantify the species' relative abundances in a community. Here we discuss these issues with examples from real plant communities and argue that diversity within a single trait is often the most ecologically relevant information. When using indices based on many traits, we plead for careful a priori selection of ecologically relevant traits, although other options are also feasible. When combining many traits, often with different scales, methods considering the extent of species overlap in trait space can be applied for both the qualitative and quantitative traits. Another possibility proposed here is to decompose the variability of a trait in a community according to the relative effect of among- and within-species differentiation (with the latter not considered by current indices of functional diversity), in a way analogical to decomposition of Sum of squares in ANOVA. Further, we show why the functional diversity is more tightly related to species diversity (measured by Simpson index) when biomass is used as a measure of population abundance, in comparison with frequency. Finally, the general expectation is that functional diversity can be a better predictor of ecosystem functioning than the number of species or the number of functional groups. However, we demonstrate that some of the expectations might be overrated – in particular, the "sampling effect" in biodiversity experiments is not avoided when functional diversity is used as a predictor.

Keywords: biodiversity index, functional trait, grasslands, intraspecific and interspecific diversity, PCA, Rao index, resource use efficiency, sampling effect, SLA, stable isotope

Introduction

Biological diversity has puzzled ecologists for centuries (e.g. Darwin 1859, Rejmánek et al. 2004). "How are so many species able to coexist?" or "How is the ecosystem functioning affected by its diversity?" are examples of questions that ecologists have been asking for a long time. However, the first step in answering such questions is the quantification of diversity. Originally, species diversity – simply the number of coexisting species, or measured by compound indices that incorporate relative proportions of individual species – has been used as the main quantification of biodiversity (Magurran 2004). In the late 1960s and the 1970s, for example, virtually no community study could be done without calculating the Shannon H' or Simpson dominance/diversity indices (i.e. indices reflecting both the number of species and their proportions).

Nevertheless, mechanistic models (verbal or mathematical) concerning the functional consequences of diversity have been based on the fact that species differ from each other (and thus function differently; MacArthur 1955). Similarly, the importance of the differences among species for maintaining species coexistence was explicitly expressed by the concept of limiting similarity (MacArthur & Levins 1967). Ecologists have thus progressively realized that species differ from each other in terms of some traits (Díaz & Cabido 2001) and thus that the effect of ecological diversity might be based on the "extent of trait dissimilarity among species in a community" (or functional diversity; Tilman 2001, Petchey & Gaston 2002). Traditionally, species diversity has been considered a surrogate for functional diversity in most studies linking biodiversity to ecosystem functioning (Díaz & Cabido 2001; Loreau et al. 2003). However, some pairs of species are very similar to each other, while some are very different. Consequently, the relationship between species diversity and functional diversity is expected to be positive (Petchey & Gaston 2002) but not necessarily very tight (Díaz & Cabido 2001, Petchey & Gaston 2006).

Recently, several methods have been described and discussed on how to calculate the functional diversity (Mason et al. 2003, 2005, Botta-Dukát 2005, Ricotta 2005, Petchey & Gaston 2006, de Bello et al. 2006). Among these, the Rao coefficient is gaining currency as a good candidate as an efficient functional diversity index, because it is a generalization of the Simpson's index of diversity, it is easy intuitively understandable, and it can be used with various measures of dissimilarity between species (both those based on a single trait, and those based on many traits; Ricotta 2005, Petchey & Gaston 2006). Whatever index is applied, however, there are some crucial questions and decisions that have to be faced in order to quantify the functional differences among species. Some of these points have been already discussed by previous theoretical analyses (Mason et al. 2003, Petchey & Gaston 2002, Botta-Dukát 2005, Ricotta 2005). Nevertheless, several other aspects remain unclear or unresolved. The first aim of this paper is thus to focus on the most recent issues that might be of interest for scientists that aim to calculate functional diversity. In particular, functional differences among species must always be quantified on the basis of some species traits. This raises the important methodological question of how many and which traits to use, how to weight them, how to combine them (with different scales) and how to quantify species relative abundance in a community. These issues are here discussed with examples from plant communities that we have studied recently.

Another present limitation of the indices of functional diversity relates to the fact that they use fixed values of traits per species (i.e. by using the average of the trait values from the literature or data bases), to calculate the extent of trait dissimilarity in a community. Nevertheless, (at least some) traits are highly variable within a species (e.g. Al Haj Khaled et al. 2005, Petrů et al. 2006). Thus, the second aim of this paper is to propose a way to take into account the relative contribution of intraspecific trait variability (i.e. within species) to functional diversity of a community, and thus to account for this component of functional diversity not yet resolved by the current available measurements (Petchey & Gaston 2006).

Finally, we believe that functional diversity is an important property of a community. In our view, its use both as (i) a response to environmental variables and as (ii) a predictor of community function will bring new insights into the mechanisms of community functioning. Plant functional traits have been proposed since the 1990s as tools to progress in our understanding of the response of community composition to changing environmental conditions, and of the effects of these changes on ecosystem functioning (see review by Lavorel et al. 2006). Most studies of community response to date have focussed on responses of individual species (de Bello et al. 2005) or of community-level traits ("aggregated traits" sensu Garnier et al. 2004). Few studies have attempted to link these two levels of responses (but see McIntyre & Lavorel 2001), although the use of traits and their distributions within communities has been recognized as a promising mean in understanding mechanisms of community assembly in order to predict community dynamics (Díaz et al. 1999, McGill et al. 2006). Such a pursuit would require using both aggregated traits and at least a description of functional diversity (S. Lavorel et al., submitted). At the same time, various studies concerning the mechanisms of ecosystem functioning are now intending to use the measure of functional diversity (which may be as simple as the functional richness, i.e. the number of functional groups) as a predictor, i.e. studying the effects of species diversity on given ecosystem functions (Diaz & Cabido 2001, Petchey & Gaston 2006, Wright et al. 2006). Few recent studies have also related ecosystem processes to aggregated traits (Garnier et al. 2004, Quétier et al. 2006). Nevertheless, we also caution that some expectations on the use of functional diversity as a predictor of ecosystem functioning might be exaggerated, as not all problems concerning the relationship between diversity and ecosystem functioning will be resolved by functional diversity indices. As an example, the claim of Petchey & Gaston (2006) that the manipulation of functional diversity when keeping the number of species constant will overcome the sampling effect in biodiversity experiments seems to be somehow overoptimistic. We will demonstrate this by reconsidering the Ecotron experiment (Naeem et al. 1994) together with its critique (Huston 1997) from the point of view of functional diversity.

Steps in calculating functional diversity

The Rao coefficient presents several desirable properties for describing the functional diversity (FD) of a community (see Ricotta 2005, Botta-Dukát 2005). In fact, it is a generalized form of the Simpson index of diversity. If proportion of i-th species in a community is p_i and dissimilarity of species i and j is d_{ij}, the Rao coefficient has the form:

$$FD = \sum_{i=1}^{s} \sum_{j=1}^{s} d_{ij} p_i p_j$$

where s is the number of species in the community; $d_{ii} = 0$, i.e. dissimilarity of each species to itself is zero. If $p_{ij} = 1$ for any pair of species (so each pair of species is completely different), then FD is the Simpson index of diversity expressed as 1 minus Simpson index of dominance D, i.e. $1 - \sum_{i-1}^{s} p_i^2$ (see e.g. Botta-Dukát 2005 for details).

The Rao coefficient is very flexible, and can be used with various dissimilarity measures (for example, Shimatani 2001 used it with taxonomic dissimilarity, asymmetrical measures can be also used, etc.). The main methodological decisions are mainly how to measure the species dissimilarity, and how to characterize the proportion of a species in the community. The same decisions, however, have to be made even if we decide for other indices of functional diversity.

Selection of traits

The functional dissimilarity among species has to be based on a set of species traits. This raises the question of which traits should be considered. It is a general custom to speak about "functional diversity". The functioning of individual species is determined mainly by their ability to capture and conserve resources, or to withstand the pressure of competitors, environmental stress etc. (Grime 2001). However, direct measurements of these "hard traits" are usually not available for many species. Instead, we usually have available easily measurable (often morphological) traits "soft traits", and use them as a surrogate (see the discussion on the value of soft and hard traits in Weiher et al. 1999 and McIntyre et al. 1999). In plant species for example, the specific leaf area (SLA) is a good surrogate for the plant ability to use light efficiently while plant height is an indirect characteristic of the ability to compete for light (Weiher et al. 1999, Grime 2001, Westoby et al. 2002). Consequently, interpretations of functional diversity should take into account that, depending on the availability of trait values for species, we often have access only to structural diversity and expect that it characterizes the interspecific differentiation in the functioning. Often, for example, below-ground processes are ignored, although it is hoped that they may either be approached through relatively easily accessible traits (e.g. rooting depth), or somehow associated with "soft" aboveground traits (Cornelissen et al. 2001, Craine et al. 2005).

Besides this general issue, several specific methodological decisions on the selection of species' traits need to be considered prior to the calculation of functional diversity. At first we need to decide how many traits to use, i.e. whether it is better to use a single trait or to combine several traits. This issue will depend greatly on the ecological question to be answered. Different properties and constraints of single- vs. multi-trait indices of FD may also need to be considered (S. Lavorel et al., submitted).

In many cases, information on diversification based on single traits might be the ecologically most important. For instance, a mature forest community is clearly highly diverse in terms of plant height, whereas it will be probably very uniform in types of seed banks of individual species (the vast majority of species have no or at best a transient seed banks; Grime 2001). In contrast, a pasture is much less diversified in height, but the variability in seed bank types among species will be higher (Grime 2001). Consequently, determining in which individual traits a community is diversified and in which it is rather uniform might be crucial for suggesting the mechanisms of species coexistence, as well as the effects of species diversity on ecosystem functioning. Critically, under some circumstances, diversity in a well-targeted trait might be a better predictor of community behaviour than some functional diversity based on the combination of not very relevant traits. Recently Petchey et al. (2004) and Wright et al. (2006) demonstrated that using a priori functional groups based on life forms, or measures of functional diversity based on a list of easily available traits failed to capture effects of changed community composition on aboveground biomass productivity. This conclusion may not be surprising in the view that specific traits rather than life forms determine productivity and other biogeochemical functions (e.g. Chapin 2003, Garnier et al. 2004, Quétier et al. 2006). For example, we can expect that diversity in the soil seed bank type will be more important for the community recovery after a disturbance (see e.g. Lavorel et al. 1994) than functional diversity based on a set of vegetative traits with no direct relation to the process of recovery. This stresses that the selection of traits needs to be made depending on the ecosystem function of interest (Petchey & Gaston 2006).

Alternatively, we might choose to apply a measure of functional diversity based on the combination of a set of specifically selected traits, such as those that incorporate different ecological strategies (e.g. Grime 2001, Westoby 1998) or ad hoc defined response groups. The characterization of functional diversity in terms of several traits could be applied also when we know that various traits exert a combined effect on some specific ecosystem functioning of interest. For instance if we are interested in the diversity of regeneration traits such as seed number, seed size, type of seed bank, plant phenology etc. In general, whenever we decide to use multiple traits, we face (at least) three important problems that have to be solved: (1) how many and which traits to use and whether all the traits will have the same weight (and, if not, how to weight them), (2) how to combine them (with different scales) and (3) how to evaluate species' abundances (for indices of functional diversity that take them into account; Petchey & Gaston 2006). These three issues will be discussed in detail in the following sections.

Number and weighting of traits

It is very likely that the first filter determining the traits than can be used to calculate the functional diversity will be determined, in practice, by the availability of trait values. In first instance it should be noted that it would not be wise to use a trait only because its values are available. In plant studies, for example, the traits related to some morphological structures (as leaves or seeds) are often available, because they are relatively easy to measure, and together provide proxies for a specific function (e.g. specific leaf area and leaf nitrogen content for photosynthetic rate; Wright et al. 2004). It is thus common to measure several traits for a given structure, but we should be aware that these traits are also often consistently correlated (Garnier et al. 2004). The trait information within some plant characteristics (e.g. leaves) might therefore be, to a certain extent, redundant when aiming to describe functional diversity.

The case of correlated traits has also no simple solution. There are, for example, some pairs of trait values that are highly correlated by their very nature (e.g. seed volume and seed mass), because they relate to the same character (and the tight correlation corresponds to the trivial fact that seed size measured by volume or mass varies over several orders of magnitude, whereas the specific mass varies much less), and thus one of them is clearly redundant. If we use both of them, the seed size will get the double weight in calculations of FD indices. In fact, the value of the FD calculated using the Rao index in terms on some sets of traits is equal to the average of the FD calculated for single traits. For example, FD calculated by combining 4 plant traits is the average of the FD calculated for each single trait (Fig. 1).

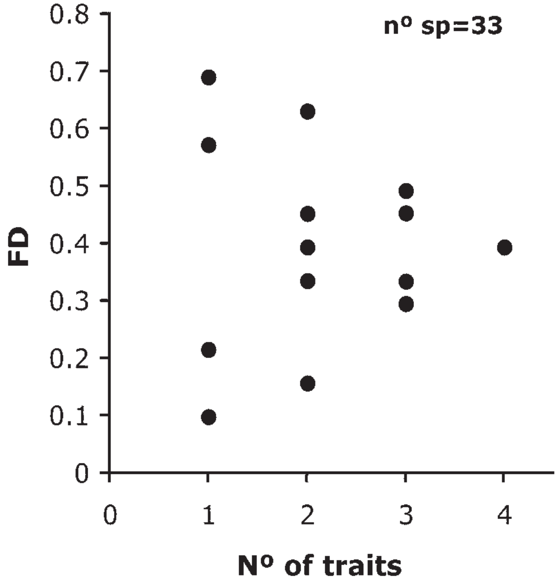

Fig. 1. – Possible functional diversity (FD) values when using 4 traits (the ones in bold from the example in Fig. 2: SLA, δ^{13}C, leguminose, leaf length-size) in different combinations (1 trait = single FD values; 2 traits = combining all possible combinations of two traits; 3 traits = combining all possible combinations of three traits; 4 traits = index calculates including all 4 measurements). Data from plot with 33 species from a rangeland in NE Spain. The FD for a given combination of traits is the average of single trait FD measurements. Note that the FD of single traits for a community can be rather variable, see also Fig. 4.

As an alternative to dropping some traits completely (because considered redundant), we could also opt for "softer" solutions, such as the differential weighting of the traits or the calculation of an overall functional diversity for some plant feature (i.e. functional diversity for leaves traits). Generally the down-weighting of some traits responds to the fact that we either consider they are less relevant to ecological functioning or because they are correlated with other traits in the data set. The weighting according to the "relevance" for ecological functioning does not have necessarily to be completely subjective – it can be, for example, based on the fact that some traits exhibit a lack of response to some environmental or management gradients (e.g. the degree of responsiveness can be quantified and used as a weight of a trait). However, in this case, we should be aware that the functional diversity of a community would be dependent on the context of the study (i.e. the environmental gradient considered).

It is generally possible to use some algorithm for down-weighting highly correlated traits (e.g. based on covariance, as suggested by Botta-Dukát 2005). Then, however, we should decide whether the correlation (or covariance) should be weighted by species abundance, and whether this should be correlated within a community for which we calculate the functional diversity (in this case, the trait weights will differ within the study), or within the whole data set (in this case, the value of FD will be context dependent). Last but not least, should there be some irrelevant traits in the data set, they will probably be independent of others, and consequently, might achieve the highest weight. None of these problems should be unsurpassable, yet we should be aware of them.

Then it should also be considered that some pairs of traits will be correlated in most data sets, but their ecological meaning can be also functionally distinct. For example the seed size and the number of seeds are usually negatively correlated because of the trade-off in investment into sexual reproduction, but not so closely, because the total investment into reproduction varies among species, and ecologically, each of them reflects a different feature of ecological behaviour. Also, for various reasons, in some particular data sets it might happen that ecologically unrelated traits can be correlated. Direct inspection of the correlation matrix might be a good solution. A fast overview of the correlation among species traits in a database can be graphically achieved by a Principal Components Analysis (PCA, see Lepš & Šmilauer 2003). It should be noted that if the axes of a PCA are given equal weight, they could theoretically be used also to simultaneously solve the problems of both correlated traits and their overweighting in FD.

In the graphs obtained by a PCA the angle between a pair of arrows representing two traits indicates the magnitude of their correlation. This can be observed in the example in Fig. 2, showing the correlation of several traits at species level (134 species) and the correlation of traits and FD (calculated for single traits) at the community level (60 plots along a climatic gradient in NE Spain; see de Bello et al. 2005 for sites description). Among leaf traits, we noted a negative correlation between leaf $\delta^{13}C$ (carbon 13 stable isotope ratio) and SLA ($r = -0.52$ at species level and $r = -0.70$ at the community level; Pearson correlation), reflecting the general trade-off between assimilation and conservation of resources (Díaz et al. 2004). However, the functional diversity calculated for the two individual traits (i.e. FD for SLA and $\delta^{13}C$) were negatively (albeit slightly) correlated ($r = -0.26$). This indicates that the FD diversity indices calculated from correlated traits are not necessarily redundant, if traits reflect different functions. In general the correlation of FD measurements might be independent of the correlation of traits (for example the functional diversity calculated for leaf size showed a correlation to FD SLA, even if SLA and leaf size were not correlated at the species level; Fig. 1a). The low correlations among FD measurements indicate that the selected traits reflect independent components of functional differentiation and features of ecological behaviour. In this way, the FD calculated for a given community could be quite different depending on the trait, or on the particular combination of traits, considered (Fig. 1; note that the averaging FD indices concerning leaf characteristic in this graph can be also considered a way to weigh them into a single FD measurement concerning leaves traits).

In the above paragraphs, the problem of correlated traits in the calculations of FD was analysed and some possible solutions discussed. We nevertheless recommend, as a better approach, to start with an a priori idea, i.e. which traits should be relevant for ecosystem functioning or that capture the various axes in the differentiation among species. The LHS system of Westoby (1998) might be a good example of this, with SLA, height, and seed mass being relevant descriptors that capture basic processes in plant functioning. These three traits may then be used as the base for our calculations. Sandra Lavorel et al. (submitted) showed that Rao's functional diversity coefficient, calculated using the three LHS traits, captured adequately variation in community composition in response to grassland management along a continental scale gradient in aridity. They concluded that, in this case, these traits and their combination may be adequate to reflect community responses to the associated environmental gradients. Alternatively, it is also possible to decide that each of the basic features (i.e. Leaf, Height, Seed), can be better characterized by more than one

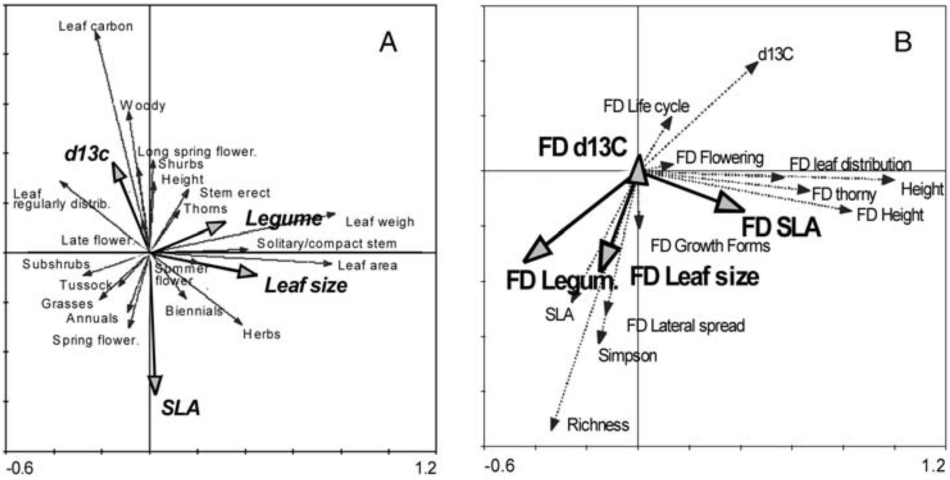

Fig. 2. – The correlation among traits and functional diversity (FD) measurements (for single traits) can be observed at both species (A: species × traits) and community level (B: plot × traits and FD), by the calculation of PCAs. The correlation at species trait level do not necessarily imply correlated FD measurements at the community level. Data from species (134) and communities (60) along a climatic gradient in NE Spain. The traits used in the Fig. 1 have been highlighted. (d13C = δ^{13}C stable isotope ratio).

trait (for example, leaves by SLA, shape, and total leaf area or size; height will have a single measure, and sexual reproduction will be characterized by seed mass and number). Then we can down-weight the individual traits in a way that each of the L, H and S will have the same total weight (i.e. weight of each trait will be 1/number of traits in respective group; e.g. Fig. 1, for some leaf traits).

Combining traits: overcoming differences in scale

To combine a set of the traits into a common index of functional diversity, we need at first to get the traits on a comparable scale. This means, for example, that we need a procedure that makes it possible to compare the difference among quantitative species traits, e.g. in traits such as plant height, in seed weight, SLA, time of flowering and type of pollination. This task has been often solved in numerical multivariate methods (Lepš & Šmilauer 2003), where the two common solutions are transformation (i.e. an algebraic function of initial value, independent of any other value in the data set) and standardization (a function, relating the value to other values in the data set).

Probably, the simplest solution could be the log transformation (which is used, e.g. in Mason et al. 2003, but similarly can be used in measures of interspecific difference for the Rao index). This option is highly intuitive and appealing for traits related to "size" – by log transformation, multiplicativity is converted to additivity: if a size of a trait of species A is twice that of species B, then the difference in logarithm will be the same, regardless of the absolute values. For example, average height of one and two meters will provide the same difference as 20 cm and 40 cm, which seems to be ecologically interpretable. Also, all the variables will be measured on a scale of orders over which they vary (if the common logarithm is used, then the range or standard deviation of log-transformed data provides a good idea over how many orders of magnitude the variable ranges).

However, it should be noted that this approach has important limitations. The use of the logarithm implies that the trait values must be positive. Some even stronger restrictions apply. Generally, the log transformation is useful to standardize data on the ratio scale (see e.g. Zar 1996 for the definition of ratio and interval scales – only for data on ratio scale is it meaningful to say that one value is x-times greater than the other one; after the log transformation, the values that differ by x-times have the same difference). The requirement that the values must all be positive forms also a difficulty when zero signifies the absence of a given traits. For example, the amount of latex could be quantified, with zero meaning its absence. The log transformation cannot then be used without using further "ad hoc" adjustment (as adding some arbitrary constant to the original value), which distorts the transformation of multiplicativity into additivity. Log transformation is generally not useful for data on an interval scale (including data on a circular scale), even in situations where the actual data do not contain zeros and negative values. Consequently, log transformation should not be used, e.g. for phenological data (as, e.g. Julian day of onset of flowering), or for stable isotopes ratios (e.g. $\delta^{13}C$, $\delta^{15}N$). For example, if the log transformation is used for the phenology characterized by the Julian day, then one week difference in early spring would signify much more than one week in late autumn. If, for any reason, we decide to start the year at the summer solstice, then one week difference in autumn would signify much more than one week in spring.

The log transformation converts the multiplicative nature of the data on a ratio scale into additivity. Nevertheless, this does not mean that it put different variables on a comparable scale. The individual variables can be scaled according to the linear dimension of plants (e.g. plant height), according to area (leaf area) or according to volume (typically biomass of a plant, or seed mass). By their nature (allometric relations among various characteristics), the area is a quadratic, and volume a cubic function of linear dimensions. Thus, if the linear dimension varies over an order of magnitude, the area is expected to vary over two orders, and volume or mass over three orders. Consequently, if seed size is characterized by seed linear dimension, then its variability will be much less than when characterized by seed mass. The simplest correction is to transform the relationships, where known a priori, to isometric relationships (e.g. dividing log volume by 3); unfortunately, for most of the traits the relationships are not known a priori – at least not exactly. The allometric equations differ among species, and do not follow exactly the "theoretical values" (Whittaker et al. 1974).

Several alternatives to the log transformation are possible. The most frequently used one is to standardize each variable to its Z-score, i.e., each variable would be transformed by

$$Z = \frac{x - \bar{x}}{s_x}$$

i.e., we first subtract the common mean and then divide by standard deviation s_x of the variable in the whole set of species. On should be aware, however, that this transformation is context dependent (mean and standard deviation are calculated in the data set) – functional diversity of each community would then depend on the complete set of species used in the whole study.

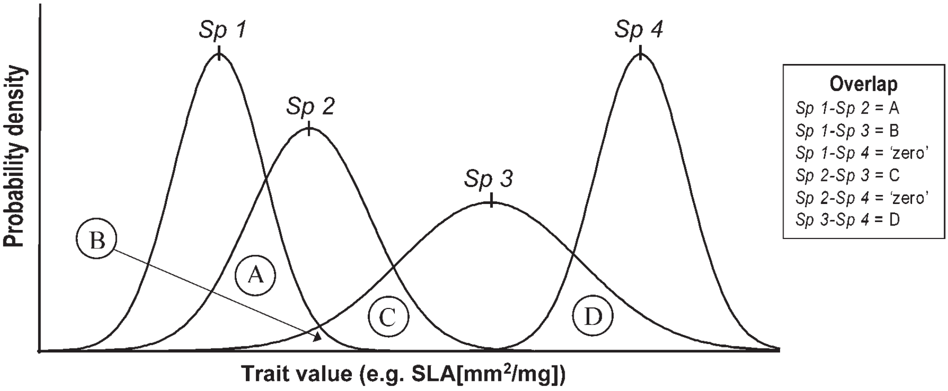

Fig. 3. – Schematic representation of the meaning of species overlap (*O*) based on their probability density (this can be estimated by knowing for example the mean trait value and its standard deviation). Note that the area below the curve is always unity by definition, so that 1-*O* corresponds for each species to the part not shared with the compared species. Using the normal approximation, the overlap is always positive, but for very different species, the values are so small that can be practically considered zero. Also note that with roughly constant variability, the more the mean differ, the smaller overlap.

Another possibility would be to relate the variation to the potential range of trait values (a similar method was suggested by Mason et al. 2005). However, even this possibility is affected by subjective decisions. For example, the weight of plant height differentiation would change dramatically whether we decide to include all the vegetation including woody species (and the upper limit of the range will be in tens of meters), or just to restrict the analysis to herbaceous vegetation. The intermediate choice is the measured range, which is less subjective but more context-dependent.

The last possibility which we propose here, is based on the concept that differences in trait values among species are usually understood as a proxy for niche differentiation, i.e. as a mean of differential way of resource use (Mason et al. 2005). Because all the trait values vary within a population, the more similar the trait values of two species are, the higher the proportion of the populations might be expected to overlap. From this point of view, the magnitude of the difference might be scaled by the within-population variation. If we look at the functional meaning of the difference, we might be interested in how much the two species overlap (Fig. 3). If we know the probability density functions of the two species, their overlap *O* can be calculated as

$$O = \int_{-\infty}^{+\infty} \min\left\{ f(species1),\ f(species2) \right\}$$

where *f*(*species*) is a probability density function for the trait value for given species. In most cases, the limits can be narrower – just for feasible values of the traits. The probability density function is usually unknown, but the mean and standard deviation trait values are usually available and can be used for its estimation. Then, using the normal approximation is a good way to calculate the actual values (in the case that the trait distribution is known to be highly positively skewed, approximation by the lognormal distribution or prior log transformation could be a reasonable solution). O ranges from 0 (the two species do not overlap at all) to 1 (the two species are identical). Consequently, $1-O$ is a measure of dissimilarity, scaled against between zero and one. The advantage of this approach is that it does not require any further assumptions of the possible range of values of traits, and can be used for any quantitative variable, regardless of the scale, thus offering a solution for the problem of the combination of traits with different scales.

Also, an analogous approach can be used for qualitative variables, both when crisp or fuzzy classifications are used. In the case of crisp classification (i.e. each species belongs to a single category, e.g. is either C3 or C4 plant) the overlap is 1 in the case where they belong to the same category, and 0 if they belong to different categories. If the fuzzy classification is used (the species usually, say from 80%, behaves as a tree, but occasionally, 20%, as a shrub), the data are usually coded as so called dummy or indicator variables (as in de Bello et al. 2005), with M_j being species membership in the j-th category (i.e., for the species in the above example, $M_{\text{tree}} = 0.8$, $M_{\text{shrub}} = 0.2$). In the case of crisp classification, the same approach can be used, except the values can be either 0 or 1 only. The overlap for the trait is then

$$O = \sum_{j=1}^{n} \min\left(M_{species\ 1,j}, M_{species\ 2,j}\right)$$

Again, the species dissimilarity can be calculated as $1\text{-}O$. If this dissimilarity is based on a crisp classification (i.e. could be either 0 or 1), and used for calculation of the Rao coefficient, the resulting value is the Simpson coefficient calculated on the proportions of individual groups. The advantage of the approach is for each trait, the O has the same meaning – i.e. the overlap between the two species. It makes it possible to reasonably combine the traits – the multi-trait dissimilarity can be calculated as average overlap over the traits used. As it closely resembles the simple matching coefficient, we call this value matching dissimilarity MD:

$$MD = 1 - \frac{\sum_{i=1}^{k} O_i}{k}$$

where k is the number of studied traits, and O_i is the overlap in the i-th trait.

Weighting species dissimilarities: frequency vs. biomass data

As emphasized above, the trait selection, and indeed the choice of the type of index to apply to address a question about the role of functional diversity need to be tailored to the ecological question at hand. Some indices, as the Rao index, take into account species abundance in the quantification of functional diversity, i.e. by weighting the pair-wise species dissimilarity in the trait space by the product of relative abundances of the two species. This gives a differential weight to the traits of more dominant and/or less abundant species, as species abundance is affecting various components of ecosystem functioning (Petchey & Gaston 2006).

The indices that take into account species relative abundance behave differently from indices based solely on species list (see Petchey & Gaston 2006, de Bello et al. 2006). We believe that the former are more informative and only those are discussed in this paper.

There are three common ways to quantify the relative abundance of species in communities: counts of individuals (population density), frequency or cover estimates, and biomass. The frequency is strongly affected by the size of basic sampling units and for the point quadrats, the frequency is an estimate of cover. Each of these can be more or less relevant to some specific processes. Population density may be most relevant when addressing demographic processes, such as recruitment or dispersal. Frequency may be best used to account for competition (e.g. asymmetric competition for light). Biomass is recommended when attempting to link ecosystem processes such as primary productivity, decomposition or soil resource use to plant traits (Garnier et al. 2004). It is well known to field ecologists that these quantities are not equivalent. In vegetation studies, they are in particular affected by species canopy architecture and dry matter content. An important difference between biomass- and frequency-based calculations of relative abundances is that evenness in the former is usually lower than in the latter (usually much lower when the frequency is based on large basic sampling units). It is hence not uncommon for 5–10 species, if not fewer, to make up the majority of the biomass (e.g. 80%), while a larger number of species (10–20) may be needed to achieve the same threshold on a frequency basis (particularly when using relatively large basic sampling units). Similarly, the biomass values vary over several orders of magnitude among species, whereas the cover varies less and frequency even less.

The way of quantifying species' relative abundances has important consequences for calculations of compound diversity indices. In fact, when calculating the Simpson diversity using biomass, the index value will be mostly affected by proportions of dominants, and will vary over a wide range of values. The values of Simpson diversity calculated on the basis of frequency will depend more on the total number of species and their proportions, and the index values will vary much less. Then, the Simpson index is the upper limit of the Rao index. As a consequence, the Rao index calculated on the basis of biomass will be much more affected by this limitation and consequently tightly correlated with Simpson index, than when using the frequency. Pakeman & Quested (2006) demonstrated that considering only the most dominant species did not affect the calculation of community aggregated means for adult traits associated with biogeochemistry, thereby confirming the finding by Garnier et al. (2004) that it was possible to capture changes in major ecosystem properties along a successional gradient even using the traits of the two most dominant species. On the other hand, when considering regeneration traits, which often have a greater variability within a single community, it was no longer possible to apply the 80% rule to capture community-level properties adequately.

We thus explored here the response of functional plant diversity to the use of frequency- vs. biomass-based relative abundances, using a floristic and trait data set describing changes in functional composition across 15 plots representing 5 levels of management in subalpine grasslands, in the Lautaret area in the French central Alps (Quétier et al. 2006). Species relative frequencies were calculated based on a point quadrat survey of species frequencies using three 10 m lines per 30 × 30 m plot, with intercepts every 20 cm. The relative frequency for each species in a plot was calculated as the number of hits for that species over the total number of hits for the plot. Relative biomass values were estimated by hand sorting of species from a biomass sample of 1 m^2 in each plot. Species relative frequencies and relative biomass values within each plot were correlated ($R^2 = 0.50$, $P < 0.001$), as were species ranks (Spearman correlation $R^2 = 0.36$, $P < 0.001$), with as expected a skew in biomass rank-

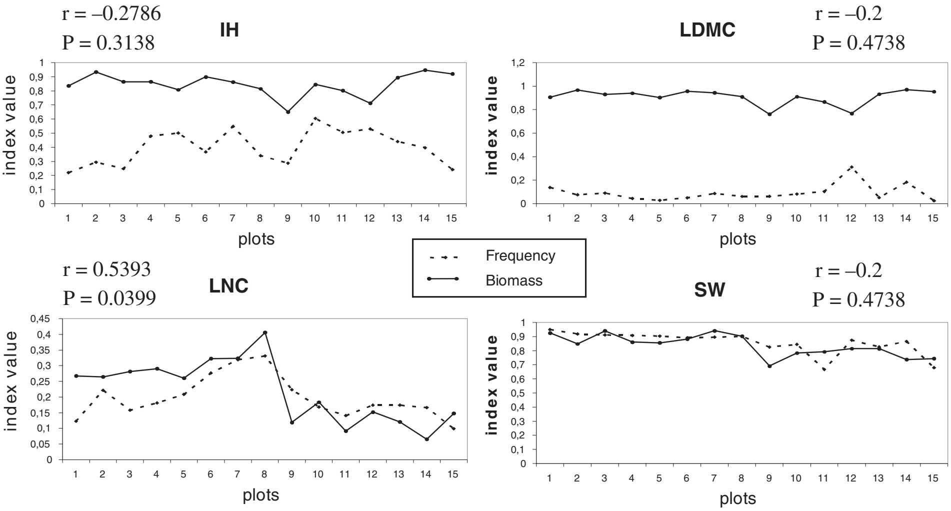

Fig. 4. – Variations in functional diversity, calculated using Mason's (2002) functional divergence index (FDiv) using either frequency vs. biomass as an estimate of species relative abundance. Values of FDiv have been calculated for inflorescence height (IH), leaf dry matter content (LDMC), leaf nitrogen content (LNC) and seed weight (SW) and compared for 15 grassland plots from the Lautaret field site in the French central Alps (see Quétier et al. 2006). The three consecutive plots (i.e. 1–3, 4–6, etc.) are managed in identical way. Correlation coefficients between values calculated on the basis of biomass and frequency and their significance are indicated.

ings towards grasses. Functional divergence (FDiv; Mason et al. 2003) was calculated using either relative frequency or relative biomass (as an abundance weighting) and for several single traits: reproductive height, leaf dry matter content (LDMC), leaf nitrogen content (LNC) and seed weight. The FDiv calculated with frequency and biomass were not correlated for reproductive height nor for LDMC (though a negative trend was observed for the latter) while a weak positive correlation was observed for LNC and seed weight (Fig. 4). These results confirm that the selection of the way the species abundance is estimated has important effects on the measurements of functional diversity.

For LDMC, the low correlation between estimates of FDiv with frequency vs. biomass may be explained by the weight of grasses in the calculations, which have a greater LDMC as a group than dicots (Cruz et al. 2002) and therefore are over-represented in biomass-based vs. frequency-based relative abundances. The frequency-based FDiv for LDMC of the whole community was, in fact, better correlated with FDiv of dicots ($P = 0.091$, marginally significant) than FDiv of grasses ($P = 0.739$). These results also confirms that phylogenetic constrains have important functional consequences in species' adaptations (de Bello et al. 2005). Consequently, the skew of relative abundances towards grasses when using biomass instead of frequency resulted in poor correlation between the two measures. Conversely, because frequency-based FDiv for LNC of the whole community was positively correlated with FDiv of grasses ($P = 0.048$) frequency- and biomass-based calculations of FDiv for this trait were correlated. The same reasoning could not apply to the other traits, which had a more even distribution across life forms. Finally, for the four traits considered, differences in FDiv across management levels were generally less significant when using biomass- than frequency-based weights (data not presented).

The among- and within-species extent of trait dissimilarity

The quantification of the functional diversity of a community, as seen in the above sections, takes specifically into account the dissimilarity in the trait space among species. The within species differentiation is either ignored (as e.g. in the Mason et al. 2003), or is used as a "yardstick" to scale interspecific differences (as in the case of calculating overlap of the probability density functions; Fig. 3).

This within species differentiation in some circumstances might be very relevant for the functioning of the ecosystem (Booth & Grime 2003, Fischer et al. 2004, Madritch & Hunter 2003). For example, in a forest, there might be important differences in the immediate functioning of adult individuals vs. juvenile individuals within the same species, i.e. in their photosynthesis, use of water, nutrients, etc. (Cornelissen et al. 2003a). Further, within the same community, some individuals of the same species can have different growth rates depending on the identity of their neighbour or the particular microclimate where they grow (Pugnaire et al. 2004). Also, some species are able to produce seeds of various sizes (heterocarpy), where the variability (with the corresponding functional consequences) can be considerable, comparable with differences among species.

In general, thus, the extent of trait variation (dissimilarity) in a community might be determined more by either an "among-species trait differentiation" or by a "within-species differentiation". As an example, a similar extent of trait variation (e.g. for height as a trait) in two communities might be affected in a different proportion by the among- and the within-species trait variation (Fig. 5). Let us consider the among species trait variation in a community. This can be characterized by the variance of species trait values weighted by the species relative abundance (this is analogical to FDiv of Mason et al. 2003, without the non-linear transformation used by the original authors to get the coefficient to the interval between zero and one; both, non-transformed or log transformed values can be used, depending on the nature of the trait). This characteristic takes into account the average trait value per species, so it characterizes only the variability among species, and consequently it will be called *Among* here.

$$Among = \sum_i p_i \left(x_1 - \bar{x}\right)^2$$

where p_i is the proportion of i-th species, x_i is the mean trait value of i-th species and x is the grand mean (or aggregated mean value as defined in the above sections), calculated as:

$$\bar{x} = \sum_i p_i \, x_i$$

Let's consider now the within-trait variation. If we have available a proper estimate of the within species variability of the trait, then we can characterize the within-species variability (called *Within* here) by the weighted average of within-species variances (s_i^2):

$$Within = \sum_i p_i \, s_i^2$$

Then the extent of trait variation (called *Total* here) can depend in the different proportion on either the *Within* or the *Among* trait differentiation. This approach can be compared with the ordinary one-way ANOVA as there is clear correspondence with sum of squares,

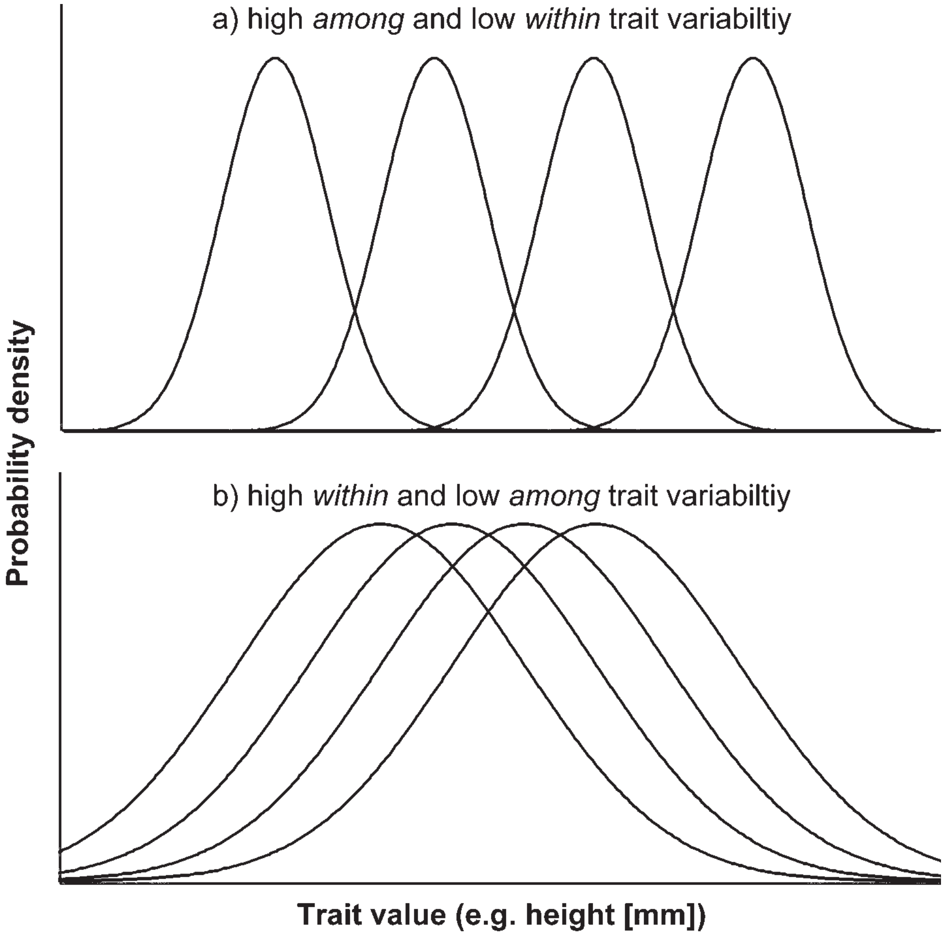

Fig. 5. – Schematic representation of the probability density functions in two hypothetical communities with a similar extent of *total* trait variability. In one case (a) the community shows high *among*– and low *within*-species trait variability components and in the other (b) low *among*– and high *within*-species trait variability components. For simplicity, the relative abundances of species are not displayed.

i.e. between or groups some of squares corresponds to *Between,* within or residual sum of squares corresponds to *Within.* Analogically to the total sum of squares (which is in ANOVA sum of group and error sum of squares), also here we can characterize the total variability in a trait by

$$Total = Between + Within$$

In this way the extent of functional differentiation in a community can be partitioned into the relative effect of these two components. It should be noted that because we use the proportions p which sum up to one, the values of *Between*, *Within* and *Total* are not dependent on the number of observations (as the sum of squares in ANOVA, where they are weighted by number of observations). Moreover, they are good estimates of variances of mean trait values among the species, mean variance within the species, and variance of the trait within a community.

We should also be aware that, in most cases, the selection of individuals is not a random sample, and does not aim to cover the whole variability within a population. In fact, the standardized protocols of trait sampling often suggest considering only the adult not damaged individuals in optimal growing conditions (Cornellisen et al. 2003b). This may often result in a sampling bias caused by the fact that the field workers tend to preferentially collect or measure the most visible (and often bigger) individuals within a species (S. Gaucherand & S. Lavorel, unpublished). Consequently, the FD quantified in this way (i.e. without proper random selection of individuals) might lead to serious underestimation of the *Within* component of trait variability.

Overcoming the sampling effect problem in biodiversity experiments

The newly emerging possibilities for the use of functional diversity measures are considered very promising for biodiversity experiments (Petchey & Gaston 2006). In biodiversity experiments, species richness is manipulated and the ecosystem functioning (often characterized as simply as the total standing biomass taken to reflect productivity) is measured as a response. The design and interpretation of biodiversity experiments has been widely disputed (e.g. Lepš 2004). One of the disputed problems is the sampling effect (Huston 1997). It has been argued that that the use of FD indices might solve this problem. In particular, Petchey & Gaston (2006) claimed that “experiments that manipulate trait distributions in local assemblages will provide understanding of the mechanisms that link species and ecosystems that cannot be gained through manipulations of species richness. Partly this is because they more directly address the mechanisms behind diversity effects and partly because they can be performed while species richness is held constant and sampling effects are eliminated.” Although the manipulation of functional diversity brings new insights and can overcome some of problems of biodiversity experiments, we believe that the problems analogical to the sampling effect could remain unresolved.

The “classical” sampling effect is based on the fact that the higher the species number in the assemblage, the higher the probability that a species able “to do the job” (a species that by its presence or absence drives the output in ecosystem functioning) is included. In the most often used species number–productivity relationships, the species able “to do the job” is usually the most productive one, which finally prevails in the assemblage. When (at least one of) such species is present, the productivity of a mixture is higher. For example, Huston (1997) re-analysing the Ecotron experiment of Naeem et al. (1994) have demonstrated that the potential plant height could be a good indicator of species potential productivity, and that the tremendous effect of medium diversity in this experiment was probably the effect of including *Chenopodium album* L. – the tallest species of the “medium diversity” mixture, so, in a sense, the species with the most extreme value of the important trait. If the species composition at each diversity level is a random selection (or some regular selection with representation of the species equal in all the diversity levels), then the probability of including such a species increases with the number of species in a mixture – which is the basis of the sampling effect.

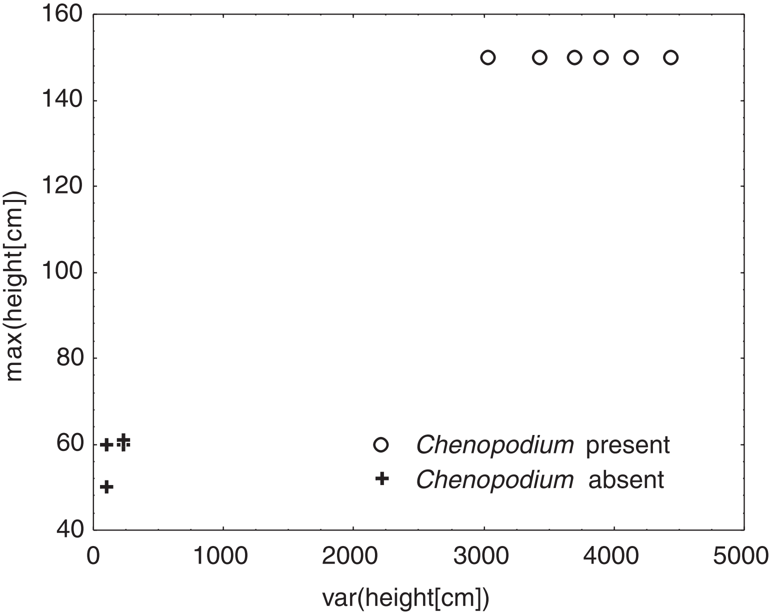

Fig. 6. – Relationship between maximum height and variance in height in the three-species assemblages formed as all the possible three-species combinations from the five species used in medium diversity mixtures in the Ecotron experiment (Naeem et al. 1994). The mixtures containing *Chenopodium album* have higher height variability, but also the highest potential height (and so they are expected to have higher productivity).

Nevertheless, even the use of functional diversity might not overcome the sampling effect, as including the "extreme" type usually also enhances the functional diversity. If the extreme type really means better functioning of the assemblage, then we are getting situation very similar to the sampling effect in the biodiversity experiments. Let us consider, as an example, in a "classical" diversity–productivity experiment, where the number of species is held constant, and only species composition (and, in this way also the "functional diversity") is manipulated. Let us consider the variance of a trait as a measure of functional diversity, and take, for simplicity, a single trait, i.e. plant height. We have taken the five species used in the "medium diversity" of the original Ecotron experiment (Naeem et al. 1994, typical species maximum from local flora, cited according to Huston 1997 in cm given in parentheses): *Senecio vulgaris* L. (30), *Stellaria media* (L.) Vill. (50), *Chenopodium album* (150), *Spergula arvensis* L. (40), *Cardamine hirsuta* L. (60). Then we selected the three species mixtures out of this pool (there are ten possible species combination). We can see that there is a highly positive relationship between the variance of height and maximum height; also, the communities containing *Chenopodium album* have much higher variance (Fig. 6). Similarly, there will be positive relationship between maximum height and average of distances between species, and assemblages with *Chenopodium* will have higher average distances between species than the other assemblages. The relationships will be less pronounced, if the distribution of heights is less positively skewed, but even in this case, the assemblages containing the highest species would have on average higher FD, and similarly, there will be positive relationship between the FD and height of the highest species (the character of the relationship in Fig. 6 does not change, if we use the log transformed heights – i.e. using a form of Mason et al. 2003; data not shown). We can reasonably expect that the productivity of a species (within a given growth form) will be positively correlated with its maximum height. Further, we can expect that the mixtures (when grown in productive environment) will be dominated by the tallest species (in particular by *Chenopodium album*, when the species is present). As a result, we will very probably get a positive relationship between FD (whatever index we will use for its calculation) and productivity, caused by mechanism very analogical to the sampling effect. Consequently, even if we consider the FD an important and useful characteristic of a community, more relevant than the plain number of species, its use does not necessarily solve all the problems. Sampling effect in biodiversity experiments is one of those, and remains unresolved.

Conclusions

The quantification and interpretation of functional diversity must take into account various important methodological issues. If several species traits are intended to be included into a single FD index, we recommend that traits are selected a priori; i.e. which traits should be relevant for ecosystem functioning or that capture the various axes in the differentiation among species. Then several criteria should also be met (having traits on a comparable scale, making clear if species abundance is considered and in which terms, e.g. frequency or biomass, screening of trait and FD measurements correlations). In many cases, using FD indices per single trait could be more meaningful and useful in assessing specific ecological questions than aggregating traits in a single index. Various solutions to the problems of FD quantification were developed in the text, as the possibility to use the probability density curves of species traits to account for species dissimilarities (1 – overlap). This approach can be further extended to the quantification of the intraspecific trait differentiation in a community, not yet considered by previous indices.

Acknowledgements

The research was supported by the EU VISTA project (EVK-2002-00356), the Czech Ministry of Education projects MS 6007665801 and LC 06073, and the project DIVHERBE from the French ACI-ECOGER programme. We are grateful for constructive comments by Mike Palmer.

Souhrn

Kvantifikace funkční diverzity ekologických společenstev je velmi slibným novým přístupem jak ve studiu odpovědi diverzity na gradienty prostředí, tak při studiu vlivu diverzity na funkci ekosystémů (v tzv. biodiverzitních experimentech). Podle našeho názoru je Raův (Rao) koeficient vhodným kandidátem pro měření funkční diverzity. Tento koeficient je zobecněním Simpsonova koeficientu diverzity a může být použit s různými měrami nepodobnosti druhů (jak s měrami založenými na jedné, tak na mnoha charakteristikách sledovaných druhů). Při praktickém výpočtu musíme udělat několik rozhodnutí o konkrétních metodách – především jak mnoho a které charakteristiky použijeme, jak je budeme vážit, jak budeme kombinovat charakteristiky měřené na různých stupnicích a jak kvantifikovat relativní abundanci jednotlivých druhů. Na reálných příkladech ukazujeme, že diverzita založená na jednotlivých charakteristikách často poskytuje ekologicky smysluplné výsledky. Při užití indexů založených na více charakteristikách preferujeme použití omezeného počtu předem vybraných ekologicky důležitých vlastností, i když nevylučujeme jiné přístupy. Při kombinaci různých charakteristik měřených na různých

stupnicích doporučujeme novou metodu založenou na překryvu jednotlivých charakteristik – tato metoda může být použita jak pro kvantitativní, tak pro kvalitativní charakteristiky. Dále navrhujeme novou metodu, kde variabilita znaku ve společenstvu je rozkládána na část způsobenou variabilitou mezi druhy a na část danou variabilitou znaku uvnitř druhů; tato metoda je analogická rozkladu součtu čtverců v analýze variance. Dále ukazujeme, proč bývá index funkční diverzity těsněji korelován se Simpsonovým indexem druhové diverzity při užití biomasy než při užití frekvence.

Obecně se předpokládá, že funkční diverzita může být lepším prediktorem funkce ekosystému než pouhý počet funkčních skupin. I když je tento předpoklad reálný, nevyřeší užití indexů funkční diverzity všechny problémy – ukazujeme například, že tzv. “sampling effect” v biodiverzitních experimentech nebude vyloučen, ani pokud budou indexy funkční diverzity použity jako prediktor.

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Received 2 August 2006
Revision received 26 September 2006
Accepted 1 October 2006

Erratum:

Lepš J., de Bello F., Lavorel S. & Berman S. (2006): Quantifying and interpreting functional diversity of natural communities: practical considerations matter. – Preslia 78: 481–501.

The phrase in the third line from the bottom on p. 483
“If $p_{ij} = 1$ for any pair of species…” should read correctly “If $d_{ij} = 1$ for any pair of species…”