

Beta diversity for functional ecology

Beta diverzita ve funkční ekologii

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Ricotta C. & Burrascano S. (2008): Beta diversity for functional ecology. – *Preslia* 80: 61–71.

The utility of biodiversity measures that incorporate pairwise species functional differences is becoming increasingly recognized. Functional diversity is regarded as the key for linking community composition to ecosystem processes like productivity, nutrient cycling, carbon sequestration, or stability when subject to perturbations. Therefore, several indices have been proposed to measure the functional diversity of a given species assemblage. The principle behind these measures is that a species assemblage with high functional overlap among species has a lower functional diversity than an assemblage with low functional overlap. On the other hand, the variability in the species functional characters among different species assemblages (i.e., functional beta diversity) has received much less attention. The aim of this paper is thus to discuss a general framework for calculating functional beta diversity from plot-to-plot functional dissimilarity matrices. To illustrate our proposal we use data from two beech forest stands with different management histories in central Italy. The results of our analysis show that, though the two stands are significantly different from one another in terms of their species functional traits, the difference in their functional beta diversity values is only marginally significant. These results are related to the characteristic scale at which ecological variations occur in the two stands.

Keywords: Euclidean distance, functional dissimilarity, multivariate ANOVA, nested sampling design, randomization test

Introduction

Functional diversity (i.e., “those components of biodiversity that influence how an ecosystem operates or functions”, Tilman 2001) is regarded as the key for understanding the effects of community composition on ecosystem functioning (e.g., Lepš et al. 2006, Petchey & Gaston 2006). For this, a number of measures that summarize the functional diversity of a given species assemblage (i.e., local or alpha functional diversity) have been proposed (e.g., Walker et al. 1999, Petchey & Gaston 2002, Botta-Dukát 2005, Mason et al. 2005, Mouillot et al. 2005, Ricotta 2005, de Bello et al. 2006).

These measures are based on the observation that an assemblage with a high functional overlap among species (i.e., an assemblage in which all species are functionally similar) is less functional diverse than an assemblage in which species are less functionally similar. By contrast, the beta component of functional diversity (i.e., the variability in the species functional characters among sampling units in a given area) has received much less attention.

Whittaker (1972) proposed measuring beta diversity (β) as the ratio between regional diversity or gamma diversity (γ) and average alpha diversity ($\bar{\alpha}$) such that $\beta = \gamma / \bar{\alpha}$. For concave diversity indices (i.e., indices for which the total diversity in a pooled set of plots should not be lower than the average diversity within plots), an alternative approach con-

sists in measuring beta diversity with an additive model (Lande 1996, but see Jost 2006, 2007). In this case, $\beta = \gamma - \bar{\alpha}$.

Since Whittaker's seminal work, literally dozens of measures of beta diversity have been proposed. Reviews have been published by Wilson & Shmida (1984), Koleff et al. (2003) and Legendre et al. (2005). All these measures are based solely on species presence and absence data or on species abundances. However, the utility of beta diversity measures that incorporate information about the degree of functional dissimilarity between species assemblages is becoming increasingly recognized.

Pavoine et al. (2004, 2005; see also Ricotta 2005) showed that, if the alpha functional diversity of a set of plots or samples is summarized considering both the species functional characters and their relative abundances, Rao's quadratic diversity (Q) can be used for computing additive beta diversity as $Q_\beta = Q_T - \bar{Q}$, where Q_T is the total (gamma) functional diversity of the pooled set of plots, and \bar{Q} is the average within plot (alpha) functional diversity. The index of Rao for functional diversity can be ultimately applied even if data on species abundances are unknown. In this case, all species within a given plot are treated as equally abundant with single-species relative abundances $p_i = 1/S$, where S is the number of species in the plot. However, Jost (2006, 2007) showed that the diversity indices of the Simpson family, like Rao's Q , suffer from a series of drawbacks that render them inadequate for computing additive beta diversity in a meaningful manner.

In this paper we discuss a general framework for summarizing functional beta diversity from plot-to-plot dissimilarity matrices when data on species relative abundances are missing. For this, we introduce a new plot-to-plot functional dissimilarity measure that uses data on species functional characters and is derived from the taxonomic distance measure of Izsák & Price (2001). Rather than being based on the decomposition of diversity into additive or multiplicative alpha, beta, and gamma components, the proposed approach naturally leads to an ANOVA-like matrix decomposition that is similar to the method used by Ricotta & Marigani (2007). For instance, given two or more sets of plots, overall plot-to-plot functional variability can be partitioned into two complementary components: the functional variability within each set of plots (i.e., functional beta diversity) and the functional variability among the sets of plots. Using this approach, differences in the beta diversity of different sets of plots can be tested as well as differences in the position of sets in multivariate space of functional characters (see Anderson 2001).

Beta diversity and (dis)similarity

Unfortunately, since Whittaker's measure summarizes the beta diversity of a given set of plots with a single scalar, it cannot be used for testing for differences in the variability in the species functional characters among sampling units. As an alternative, we can return to Whittaker's (1972) suggestion that a pairwise plot-to-plot (functional) dissimilarity matrix is per se an expression of beta diversity, such that the mean plot-to-plot dissimilarity may be used as a scalar measure of functional beta differentiation. This method for summarizing beta diversity was thoroughly revised by Legendre et al. (2005) and the reader is referred to this paper for additional details.

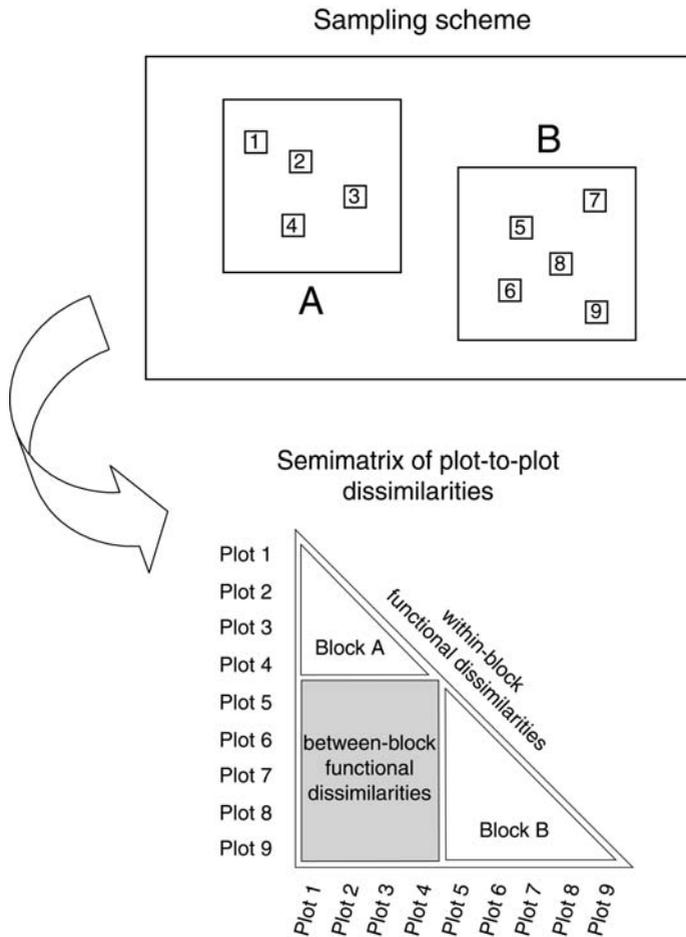


Fig. 1. – Schematic example of a nested sampling design in which two blocks, A and B, are located at random across a given landscape. Within blocks A and B, four and five plots are established, respectively, and a measure of pairwise plot-to-plot functional dissimilarity is computed among all pairs of plots in both blocks. The resulting overall plot-to-plot dissimilarity matrix can thus be partitioned into the plot-to-plot dissimilarities within each block, and the plot-to-plot dissimilarities between blocks.

Here, it is worth mentioning that this dissimilarity-based approach also leads to a straightforward ANOVA-like model of hierarchical decomposition of overall plot-to-plot functional variability at different scales.

For instance, imagine that the vegetation of a given region is sampled according to the nested sampling design of Fig. 1 (see also Ricotta & Marignani 2007): first, Q blocks of a given size are located at random (or according to any other sampling scheme) across the study area. Within each block, a given number of plots, which can vary from block to block, is established and the species presence and absence scores in each plot are recorded along with a list of selected species functional characters.

Next, from the functional characters of the species within each plot, a measure of pairwise plot-to-plot functional dissimilarity is computed among all pairs of plots (see below for a worked example). The resulting overall plot-to-plot dissimilarity matrix can thus be partitioned into the plot-to-plot dissimilarities within each block and the plot-to-plot dissimilarities among all blocks. Accordingly, the overall plot-to-plot dissimilarity matrix represents the variability in the species functional organization at different hierarchical levels within a nested sampling design. This way of partitioning functional plot-to-plot dissimilarities within a nested sampling hierarchy is flexible in that spatial heterogeneity in species functional characters within a given region can be partitioned along a nested sampling hierarchy on the basis of any categorical factor, such as habitat, land use, land management or soil type.

Also, the proposed matrix decomposition constitutes the basic data architecture to test for differences in beta diversity among different sets of plots and for differences in the position of sets in multivariate space of functional characters.

Illustrative example

Study area and sampling methods

To illustrate the proposed calculation of beta diversity from functional dissimilarity matrices we used data from two beech forests with different management histories located in Abruzzo (central Italy). We compared the functional characters of the understorey vegetation of an old-growth forest stand located in Vallone Cervara (41°49'N, 13°43'E) with a similar beech forest, managed as high forest, located in Vallone Ciafassa (41°48'N, 13°41'E). According to Piovesan et al. (2005), the old-growth stand has not been managed for at least a hundred years.

Both forest stands are on north-facing slopes on Cretaceous limestones at an altitude of 1600–1850 m. The climate is temperate with an average annual temperature of about 10.6 °C and average annual rainfall of 1035 mm.

Within each stand, the presence and absence scores of all understorey vascular plants were sampled within nine quadrats of 20 × 20 m in size, located at random across the stand. To identify as many species as possible and to include species with different phenology, the quadrats were sampled at different times (May, June and July 2006) during the growing season.

Description of the functional dissimilarity measure

For all species of both forest stands we computed a pairwise species dissimilarity matrix based on eight widely used functional traits (see Smith et al. 1997 and references therein). Since the species' dispersal and colonization ability, together with the occurrence of many microhabitats, are among the most important factors maintaining local species diversity in old-growth forests (Nilsson et al. 1995, Vellend et al. 2000, Norden & Appelqvist 2001), most of these traits are related to the species' vegetative characteristics and dispersal ability (see Table 1). Ferns were included with wind-pollinated plants since the dispersal of spores that ensures genetic mixing is primarily through wind and no association with pollinating insects is expected.

Table 1. – Description of the plant functional traits used in this study.

Functional trait	Data type	Attribute
Life form	Nominal	Chamaephyte; hemicryptophyte; geophyte; therophyte; nanophanerophyte
Dispersal mode	Nominal	Anemochorous; endozoochorous; epizoochorous; low-distance dispersal; non specialized
Seed persistence in soil	Nominal	Persistent; non persistent
CSR strategy	Nominal	Competitor; stress-tolerant; ruderal
Maximum height	Ordinal	(1) < 20 cm; (2) 20–50 cm; (3) 50–100 cm; (4) > 100 cm
Propagule size (maximum length)	Ordinal	(1) < 0.5 mm; (2) 0.5–2.0 mm; (3) 2.1–5.0 mm; (4) 5.1–10.0 mm; (5) > 10 mm
Propagule shape (length/breadth ratio)	Ordinal	(1) < 1.5; (2) 1.6–2.5; (3) > 2.5
Start of the flowering season	Quantitative	Month

Functional traits are typically not homogeneous in measurement scale, as a combination of possible data types (nominal, ordinal, and ratio; see e.g. Podani 2005, Ricotta & Avena 2006) is usually used simultaneously. Accordingly, a meaningful dissimilarity measure is needed that is suitable for use with a mixture of measurement scales. Also, species \times traits matrices often contain missing data, e.g. when information on a given trait for a given species is lacking or when it does not make sense to define a functional trait for some species, like seed weight for ferns.

Therefore, Podani & Schmera (2006) suggest the use of Gower's (1971) formula modified by Podani (1999) to allow the inclusion of ordinal variables in the data and group average clustering (UPGMA) as a standard combination of techniques for calculating pairwise species functional distances. For instance, Gower's formula applies to a mixture of different measurement scales and accommodates missing data. It is therefore well suited for calculating dissimilarities based on species functional traits.

The Gower dissimilarity between two objects (species) i and j is (Gower 1971; modified by Podani 1999):

$$d_{ij} = \frac{\sum_{k=1}^K w_{kij} \cdot \delta_{kij}}{\sum_{k=1}^K w_{kij}} \quad (1)$$

where K is the number of variables (functional characters), δ_{kij} is a measure of discordance between species i and j for variable k , and the Boolean weight $w_{kij} = 0$ if the value of variable k for species i is missing.

For mixed data, the definition of δ_{kij} depends on the measurement scale of the different functional characters. For nominal variables, if $x_{ki} \neq x_{kj}$, $\delta_{kij} = 1$, where x_{ki} is the raw data score for species i and variable k ; otherwise, if $x_{ki} = x_{kj}$, $\delta_{kij} = 0$. For ratio-scale variables, $\delta_{kij} = |x_{ki} - x_{kj}| / [\max\{x_k\} - \min\{x_k\}]$.

Finally, for ordinal variables, all scores, x_{ki} , are converted into ranks r_{ki} . That is, given a set of values for variable k , all values are numbered by consecutive integers (i.e., the smallest value gets rank 1, the next one rank 2, and so on) or by their means if equal values

are present in the original data (so-called ties). Ranks represent therefore the underlying order of the original values. Next, pairwise species discordance for variable k is defined as $\delta_{kij} = |r_{ki} - r_{kj}| / [\max\{r_i\} - \min\{r_i\}]$. For additional details see Podani (1999) and Podani & Schmera (2006).

In Gower's measure, all discordance values between nominal, ordinal and ratio scale variables are measured within the range $[0, 1]$, so that all functional traits are weighted in the same way when calculating dissimilarity. The range of dissimilarities takes also values from 0 to 1; thus Gower's measure conforms to the requirement of Mason et al. (2005) that functional diversity should not be influenced by the number of traits (see Podani & Schmera 2006).

Using Gower's formula, pairwise species dissimilarities were thus computed with the SYN-TAX 2000 program package (Podani 2001). Next, expanding on Izsák & Price (2001; see also Bacaro et al. 2007), a measure of plot-to-plot functional dissimilarity (FD) for all plots sampled at both study sites was calculated as the average minimum functional dissimilarity between any two species in different plots.

Specifically, given two plots, A and B, the average minimum functional dissimilarity (FD) between plots A and B is computed as:

$$FD = \frac{\sum_i d_{iB} + \sum_j d_{jA}}{S_A + S_B} \quad (2)$$

where d_{iB} is the minimum Gower's functional dissimilarity between species i in plot A and all species at plot B, d_{jA} is the minimum functional dissimilarity between species j in plot B and all species in plot A, and S_A and S_B are the number of species at plots A and B, respectively. FD is thus an inverse measure of the average functional overlap between each species in the first plot and its "functional nearest neighbour" in the second plot, and vice versa. High values of FD denote low average functional overlap between plots, while low values of FD imply high average functional overlap.

Notice that since Gower's measure of pairwise species dissimilarity varies from 0 to 1, from Eq. (2) it follows that FD also varies in the range $[0, 1]$. Notice also that in principle, the dissimilarities d_{iB} and d_{jA} could be weighted by the species relative abundances in each plot, p_i and p_j to obtain an extension of Eq. (2) suitable for quantitative data (C. Ricotta, unpublished):

$$FD_{(Q)} = \frac{1}{2} \left(\sum_i p_i \cdot d_{iB} + \sum_j p_j \cdot d_{jA} \right) \quad (3)$$

Statistical tests

Once a species dissimilarity matrix is compiled for all pairwise plot-to-plot distances, it is possible to test for differences in beta diversity among different set of plots.

For this, Anderson (2006) proposed that beta diversity be measured as the average dissimilarity of individual plots from their group centroid in multivariate space. Differences in beta diversity among different groups of plots can then be tested using a test for homo-

geneity of multivariate dispersions that is basically a multivariate extension of Levene's test (Levene 1960).

The core of Anderson's proposal is the calculation of an F-statistic to compare the average distance of observation units from their group centroid; a P-value may be obtained by permuting least squares residuals among the set of plots. Though the test can be based on any dissimilarity index, a major difficulty occurs when computing the group centroids for dissimilarity measures that are not Euclidean embeddable (see Gower & Legendre 1986).

For Euclidean distances, the centroid can be simply computed as the arithmetic mean for each variable in the multi-species space. However, most dissimilarity measures widely used in ecology, like the Jaccard or Bray-Curtis dissimilarity, are not Euclidean embeddable (see Gower & Legendre 1986, Legendre & Gallagher 2001). In this case, the computation of the centroid is much more difficult, and principal coordinate ordination (Gower 1966) is needed to place the observations into a Euclidean space that preserves the original dissimilarities among them. For instance, the Euclidean distance between two observations in the principal coordinate space is equal to the original dissimilarity value between both observations using the chosen dissimilarity index on the original variables (Gower 1966, Legendre & Legendre 1998). For more details on this test and the underlying calculations see Anderson (2006).

The Anderson (2006) test for homogeneity of multivariate dispersions tells us if the sets of plots analyzed differ in their beta diversity values (i.e., if the beta diversity of one set of plots is significantly different from the beta diversity of the other sets of plots); however, it does not test for differences in the position of sets in multivariate space of functional characters. That is, it does not tell us if the sets of plots significantly differ in their functional characters. For this purpose a different test is needed.

This second test, which represents a multivariate extension of traditional analysis of variance (ANOVA), is a test of the significant difference between two or more groups, based on any distance measure (see Anderson 2001, McArdle & Anderson 2001). In analogy with ANOVA, this test calculates an F-value by dividing the variance of all the distances between observations that do not occur in the same group by the variance of all the distances between observations that occur in the same group. A P-value is then computed by permutation of group membership (i.e., by appropriately shuffling the rows and columns of the corresponding dissimilarity matrix).

Based on the pairwise plot-to-plot functional dissimilarity matrix, differences in beta diversity among the plots of both forest stands were tested with the program PERMDISP (Anderson 2004; freely available at: <http://www.stat.auckland.ac.nz/~mja/Programs.htm>). The same matrix was used to test for differences in the position of both sets of plots in multivariate space of functional characters. In this case, permutation was performed with PAST (Hammer et al. 2001), for which free software is available on the internet (<http://folk.uio.no/ohammer/past>).

Results

Differences in the beta diversity of both forest types were tested using 999 permutations of least squares residuals. The results show only marginal evidence of significant changes in beta diversity between the unmanaged and managed forest ($F = 5.181$, $P = 0.103$). At the same time, a test of the null hypothesis of no difference in the position of both sets of plots

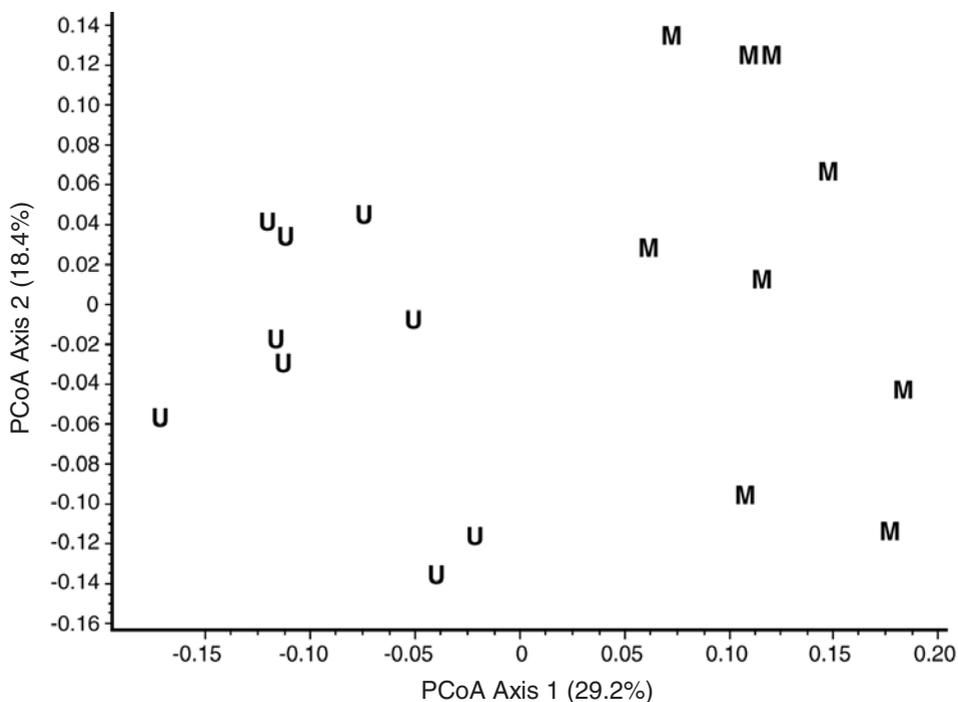


Fig. 2. – Ordination plot of the first two axes of a principal coordinate analysis (PCoA) using the functional dissimilarity matrix for the forest stands analyzed. Managed plots are denoted by M; unmanaged plots are denoted by U. Numbers in brackets are the percentage of variance associated with each principal coordinate axis. Average distances from group centroids in the principal coordinate space (i.e., functional beta diversity) for managed and unmanaged plots are 0.449 and 0.308, respectively.

in multivariate space of functional characters gave an observed F-value of 10.634. When the observed F-value is compared with the distribution found for this value and 999 alternative F-values obtained by randomly reallocating the plots to both groups, the most extreme level of significance possible $P = 0.001$ (i.e., 1 in 1000) was obtained.

Figure 2 shows a plot of the first two axes of a principal coordinate ordination from the functional dissimilarity matrix. Figure 2 provides strong visual support for a difference in the location of both sets of plots in ordination space. By contrast, there seems to be little evidence for differences in the dispersion of both groups in ordination space.

Discussion

Functional ecology is entering a crucial phase in the development and refining of adequate measures of functional diversity. In this, beta diversity has played a key role in identifying the spatial component of ecosystem functioning. For this purpose, the spatial variability in species richness and their relative abundances, which constitute the core of traditional beta diversity measures needs to be accompanied by a measure of the variability of the species

functional characters at different scales of observation, from the local to the landscape level.

In this paper, we combine a matrix of S species presences and absences $\times N$ plots with a matrix of S species $\times K$ functional characters to obtain an $N \times N$ quadratic matrix of pairwise plot-to-plot average minimum functional dissimilarity. The resulting $N \times N$ quadratic matrix can be used to measure different aspects of species functional heterogeneity or beta diversity in a very flexible and powerful manner.

As for the worked example, the observed difference in the position of both sets of plots in multivariate functional space is related to differences in ecological conditions in the two stands. The unmanaged plots are dominated by interior forest species with low dispersal ability due to large seeds with low persistence in soil (see Thompson et al. 1998). By contrast, in the managed plots the understorey species are usually stress-tolerant perennials with bulbs or rhizomes or possess small seeds that persist in the soil. Moreover, in good agreement with a recent study of Liira et al. (2007), which found that old-growth forests have on average a denser understorey and herb layer than managed forests, the unmanaged plots are characterized by the presence of understorey species of larger size.

Looking at differences in the within-stand plot-to-plot functional variability or beta diversity of both forests, Fig. 2 shows that the managed forest has a slightly higher (though only very marginally significant) functional beta diversity compared to the unmanaged forest. For instance, the average distance from the group centroid in the principal coordinate space for the managed and unmanaged plots is 0.449 and 0.308, respectively.

This small difference in the multivariate dispersion of functional characters within both forest stands can be explained by the different scale at which the disturbance regimes affect the forest spatial variability. In the unmanaged stand, except for catastrophic events, natural disturbance operates at a small-scale and is staggered-over-time in the different forest patches. Therefore, the unmanaged forest can be viewed as a mosaic representing a spatial match to the forest cycle over time. The smallest patches of this mosaic are the ones taken up by the gap and innovation phases, as they have the size of the canopy of a single tree (Emborg et al. 2000).

It is noteworthy that the gap and innovation phases are the ones in which significant changes in ecological conditions occur, i.e., great variation in light intensity at the forest floor (Emborg 1998). Therefore, the functional variability within the unmanaged stand is due to the presence of different microhabitats that determine variations in forest floor microclimatic conditions, including a wide range of different soil temperatures, light, water and nutrient availability (Ritter & Vesterdal 2006). The plant species related to these variations are scattered through the forest stand; as they occur in gaps of different age, they can survive after gap closure, depending on their ecological plasticity.

By contrast, the managed stand is subject to a more homogeneous human-induced disturbance that operates at the stand scale; therefore, in this case the within-stand functional variability is related to environmental conditions varying gradually across the stand, such as soil depth or moisture. Accordingly, at our scale of analysis, plot-to-plot functional variability in the managed stand is slightly higher than that in the unmanaged stand. Nonetheless, as both stands maintain a relatively dense forest structure with a high diversity of species and life forms, the observed differences in functional beta diversity are only marginally significant.

Interestingly, testing for differences in the beta diversity of both stands using the traditional F-distribution instead of permutation methods suggests that the observed value is significantly large at the $P = 0.037$ level. That is, there seems to be strong evidence for a difference in the variability of the species functional characters among sampling units. However, as individual distances from group centroids are not independent observations, the degrees of freedom in the classical parametric test are greatly inflated such that the significant result of this test is just the consequence of highly inflated degrees of freedom. In conclusions, it is hoped that the proposed framework for summarizing functional beta diversity may help ecologists to understand the spatially-explicit relations between species variability and ecosystem functioning at various scales.

Souhrn

Míry biodiverzity zahrnující funkční rozdíly mezi dvojicemi druhů jsou stále více používány. Funkční diverzita je klíčem k propojení složení společenstva s ekosystémovými procesy, jako jsou produktivita, koloběh živin, sekvestrace uhlíku či stabilita vůči perturbacím. Bylo navrženo několik indexů měřících funkční diverzitu daného souboru druhů, založených na předpokladu, že soubor druhů s velkými překryvy funkčních vlastností má menší funkční diverzitu než soubor s malými překryvy. Naproti tomu variabilita ve funkčních vlastnostech druhů mezi různými soubory druhů (tedy funkční beta diverzita) byla mnohem méně studována. Cílem práce je proto vytvořit a diskutovat obecný rámec pro výpočet funkční beta diverzity, založený na maticích funkční nepodobnosti mezi plochami. Návrh je ilustrován pomocí dat ze dvou bukových lesů ve střední Itálii, lišících se historií obhospodařování. Výsledky analýzy ukazují, že i když se oba porosty průkazně liší ve funkčních vlastnostech přítomných druhů, rozdíl ve funkční beta diverzitě je na hranici průkaznosti. Výsledek je ovlivněn měřtkem, na kterém se ve studovaných lesích projevuje ekologická variabilita.

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Received 12 October 2007
Revision received 24 January 2008
Accepted 29 January 2008