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Partitioning of functional diversity reveals the scale and extent of trait convergence and divergence

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Abstract

Questions: Trait differentiation among species occurs at different spatial scales within a region. How does the partitioning of functional diversity help to identify different community assembly mechanisms?

Location: Northeastern Spain.

Methods: Functional diversity can be partitioned into within-community (α) and among-communities (β) components, in analogy to Whittaker's classical α and β species diversity concept. In light of ecological null models, we test and discuss two algorithms as a framework to measure α and β functional diversity (the Rao quadratic entropy index and the variance of trait values). Species and trait (specific leaf area) data from pastures under different climatic conditions in NE Spain are used as a case study.

Results: The proposed indices show different mathematical properties but similarly account for the spatial components of functional diversity. For all vegetation types along the climatic gradient, the observed α functional diversity was lower than expected at random, an observation consistent with the hypothesis of trait convergence resulting from habitat filtering. On the other hand, our data exhibited a remarkably higher functional diversity within communities compared to among communities ($\alpha \gg \beta$). In contrast to the high species turnover, there was a limited functional diversity turnover among communities, and a large part of the trait divergence occurred among coexisting species.

Conclusions: Partitioning functional diversity within and among communities revealed that both trait convergence and divergence occur in the formation of assemblages from the local species pool. A considerable trait convergence exists at the regional scale in spite of changes in species composition, suggesting the existence of ecological redundancy among communities.

Keywords: Alpha and beta diversity; Assembly rules; Biotic and abiotic filtering; Limiting similarity; Niche complementarity; Redundancy.

Introduction

Functional trait diversity (FD, the extent of trait differences in a unit of study; Tilman 2001; Petchey & Gaston 2002; Wilson 2007) is one of the most relevant components of biodiversity affecting ecosystem functioning (Díaz & Cabido 2001; Hooper et al. 2005; Mason et al. 2005; Díaz et al. 2007). Community assembly theory suggests that several forces influence FD, particularly species interactions and habitat filtering (Cornwell et al. 2006; Grime 2006). The relative effects of these processes on trait diversity have traditionally been assessed within communities (Stubbs & Wilson 2004; Fukami et al. 2005; Cornwell et al. 2006; de Bello et al. 2006; Grime 2006; Wilson 2007; Pillar et al. in press), whereas these effects also vary across spatial scales and communities. Community assembly results from forces operating at different spatial scales (Díaz et al. 1998; Pierce et al. 2007) so that trait diversity among species occurs in a given region at different levels, e.g. within community and among communities (MacArthur & Levins 1967; Thompson et al. 1996; Westoby et al. 2002).

The within-community FD describes trait diversity among species coexisting within a given community. Species interactions are supposed to increase the within-community FD, i.e. by limiting the similarity among coexisting species traits (trait divergence; Chesson et al. 2004; Stubbs & Wilson 2004; Hooper et al. 2005). On the other hand, habitat filtering reduces within-community trait differentiation, i.e. by selecting species with shared ecological tolerances from the regional species pool (trait convergence; Weiher & Keddy 1995; Díaz et al. 1998; Garnier et al. 2004; Fukami et al. 2005; Bertiller et al. 2006; Cornwell et al. 2006; Grime 2006). These assembly forces, however, also exert pressure over the among-communities FD, i.e. the trait diversity among species from different communities. Although there have been attempts to calculate among-community components of FD (Westoby et al. 2002), we still need formal frameworks to estimate and assess the relative effects of both within- and among-community trait differentiation.

Understanding spatial patterns of FD is important because it reveals the operation of non-neutral community assembly rules (Weiher & Keddy 1995; Stubbs & Wilson 2004; Cornwell et al. 2006; Mason et al. 2007; Mouillot et al. 2007; Petchey et al. 2007). If local assemblages are composed of random sets of species, their FD values will tend to be distributed according to null models. Nonrandom distributions of species traits indicate that processes such as limiting similarity or environmental filtering structure local assemblages (Mason et al. 2007; Mouillot et al. 2007; Petchey et al. 2007). Therefore, by comparing observed patterns in FD to null expectations, it is possible to test different hypotheses about community assembly that determine trait convergence and divergence among species. Nevertheless, the spatial partitioning of FD is normally not taken into account by such null model approaches. The assessment of within community FD alone only allows for the existence of either trait convergence or trait divergence (see e.g. Fig. 1 in Petchey et al. 2007).

In this paper, we first recall Whittaker's (1975) classical concepts of within- and among-community species diversity and express them in terms of trait diversity. Then, using field data from pastures in NE Spain, we partition both species diversity and FD into different spatial components. We apply two FD algorithms and use null models to compare expected and observed FD partitioning. We conclude that the assessment of trait diversity at different spatial scales, combined with ecological null models, provides a robust framework giving new insights into processes of species assembly and coexistence. In particular, the extent of α and β FD will clarify the relative strength and spatial scale of governing forces for trait convergence and divergence (Grime 2006; Wilson 2007).

The Spatial Components of Species Diversity *sensu* Whittaker

Diversity has been traditionally defined as the variety and abundance of species in a defined unit of space (Magurran 2004). It is measured at various levels of resolution and decomposed into different spatial components highlighting the mechanisms that underlie ecological differentiation and species coexistence (Loreau 2000; Pavoine et al. 2004; de Bello et al. 2007b). The total species diversity in a region (γ diversity) can be partitioned into the within-community diversity (α diversity) and the among-communities diversity (β diversity; Whittaker 1975). This partitioning could be additive (e.g. $\gamma = \alpha + \beta$) or multiplicative ($\gamma = \alpha \times \beta$), depending on models and mathematical indices used (Lande 1996; Loreau 2000; Veech et al. 2002; Ricotta 2005; Jost 2007).

Alpha species diversity has been conventionally expressed as the number of coexisting species within a given community (i.e. species richness), or by composite indices that incorporate the proportion of each species (e.g. Simpson index; Magurran 2004 and references therein). Beta species diversity has been defined as the extent of turnover (or dissimilarity) among communities, i.e. how much diversity is added when pooling different communities together. Several methods for β species diversity measurements have been developed (Magurran 2004). One simple and intuitive formula is based on partitioning the different spatial components of species richness: $\beta = \gamma - \bar{\alpha}$ (Lande 1996; Loreau 2000; Veech et al. 2002; Ricotta 2005), where β is defined as the difference between the total richness in a region (γ) and the average richness within all communities present in that area ($\bar{\alpha}$; see example in Fig. 1). The disadvantage of this approach is that the total regional richness (γ) is often estimated only using a subset of representative communities within the region (Magurran 2004). As a consequence, β and γ increase with the number of sampled units.

Methods to Assess α and β Functional Diversities

Recently, the partitioning of FD into within and among communities (α and β trait diversity) has been proposed in analogy to Whittaker's α and β species diversity (Pavoine et al. 2004; Ricotta 2005). This analogy suggests that α and β FD are calculated for a set of communities in the same way as species diversity. Yet evidence from real communities is scarce, probably because questions on how to define, measure and assess FD variability remain open (Lepš et al. 2006; Petchey & Gaston 2006). Here we discuss two techniques to assess α and β trait diversities for a set of communities: (1) the Rao quadratic entropy index, FD Rao, and (2) an index based on functional trait variance, modified from Mason et al. (2005), FD Mason. These indices, used as an example for a framework of FD partitioning, are among those taking species abundance into account and having larger applicability in FD calculation (Mason et al. 2003, 2005; Lepš et al. 2006; Petchey & Gaston 2006; Lavorel et al. 2008). The framework discussed may be extrapolated and adapted to other indices of functional diversity, including those not considering species abundance (Mason et al. 2007; Petchey et al. 2007). Here, the framework is illustrated using vascular plant data sampled in pastures along a climatic gradient in northeastern Spain (Table 1).

The Rao index

Alpha functional trait diversity

The within-community functional trait diversity (α FD) can be defined as the extent of trait dissimilarity among species in a community (Petchey & Gaston 2002; de Bello et al. 2006). Several indices of within-community FD have been proposed and analysed (Petchey & Gaston 2006 for a review). In particular, the quadratic entropy index of diversity proposed by Rao (1982) has recently been applied to calculate α functional diversity (Pavoine et al. 2004; Ricotta 2005; de Bello et al. 2006). The FD index calculated with Rao's formula is of particular interest because it generalizes the common and intuitive index of the Simpson species diversity (if all the species have different traits, the Rao FD equates to Simpson diversity; see Pavoine et al. 2004; Ricotta 2005; Lepš et al. 2006). Consequently, species and functional diversity could be compared via the Rao index (Pavoine & Dolédec 2005; de Bello et al. 2006).

The Rao index for species diversity represents the probability that two randomly chosen individuals within a community (i.e. α) are from different taxa (Ricotta 2005; Lepš et al. 2006). This means that the Rao index is equal to 1 minus the Simpson dominance index, D (for demonstrations see Botta-Dukat 2005):

$$D = \sum_{i=1}^{S} p_i^2 (1)$$

Table 1. Partitioning of species diversity (using species richness and the Simpson index of species diversity, SD) and functional diversity (using the Rao index, "FD Rao", and the variance approach, "FD Mason") into different spatial components (α, β and γ; % = percentage accounted by α and β over γ). The moisture index for each vegetation belt reflects mean annual precipitation over potential evapotranspiration (P/PET; i.e. higher values indicate more humid conditions).

Regions (5 vegetation belts)	Species diversity				Functional diversity			
	no. sp.	%	SD	%	Rao	%	Mason	%
γ total all regions	134	100	0.98	100	0.76	100	37.21	100
$\bar{\alpha}$ within sites	25.9	19.3	0.92	93.5	0.68	90.0	31.35	84.3
β among sites	108.1	80.7	0.06	6.5	0.08	10.0	5.86	15.7
Veg. belt 1 (moist. index = 0.39)								
γ total region	46	100	0.94	100	0.72	100	29.32	100
$\bar{\alpha}$ within sites	15.9	34.5	0.89	94.5	0.68	94.7	27.62	94.2
β among sites	30.1	65.5	0.05	5.5	0.04	5.3	1.70	5.8
Veg. belt 2 (moist. index = 0.50)								
γ total region	65	100	0.96	100	0.72	100	63.34	100
$\bar{\alpha}$ within sites	21	32.3	0.89	93.1	0.64	89.3	56.04	88.5
β among sites	44	67.7	0.07	6.9	0.08	10.7	7.30	11.5
Veg. belt 3 (moist. index = 0.72)								
γ total region	74	100	0.96	100	0.71	100	19.79	100
$\bar{\alpha}$ within sites	28.8	39.0	0.93	96.1	0.68	95.3	19.15	96.8
β among sites	45.1	61.0	0.04	3.9	0.03	4.7	0.64	3.2
Veg. belt 4 (moist. index = 1.34)								
γ total region	78	100	0.97	100	0.73	100	24.74	100
$\bar{\alpha}$ within sites	30.3	38.8	0.94	96.4	0.69	94.0	23.29	94.1
β among sites	47.7	61.2	0.03	3.6	0.04	6.0	1.45	5.9
Veg. belt 5 (moist. index = 2.05)								
γ total region	53	100	0.97	100	0.74	100	31.92	100
$\bar{\alpha}$ within sites	30.3	57.2	0.94	97.7	0.72	97.6	30.67	96.1
β among sites	22.7	42.7	0.02	2.3	0.02	2.4	1.25	3.9

where p_i is the proportion of the ith species in a community (i.e. sample) and s is the number of species in the community (species richness).

If we calculate FD, the Rao index indicates the expectation of trait dissimilarity between two randomly chosen individuals in a community (Ricotta 2005; Lepš et al. 2006). If d_{ij} is the dissimilarity between each pair of species i and j, the FD calculated with the Rao index gives:

$$\alpha FD = \sum_{i=1}^{s}\sum_{j=1}^{s} d_{ij}p_ip_j (2)$$

Therefore, FD is the sum of the trait dissimilarity among all possible pairs of species, weighted by the product of the species relative abundance. By considering species abundance, the index gives highest importance to the dissimilarity between dominant species (de Bello et al. 2007a). There are several possible ways to calculate d_{ij} depending on the type of data and traits available (Mouillot et al. 2005; Ricotta 2005; Lepš et al. 2006); d_{ij} usually varies from 0 (species i and j totally overlap in their traits) to 1 (species i and j differ totally in their traits). For example, for a single categorical trait (e.g. legumes versus no legumes), $d_{ij} = 1$ indicates pairs of species from different categories, while for species sharing the same category $d_{ij} = 0$.

For quantitative traits, various dissimilarity measures have been suggested (Mouillot et al. 2005; Ricotta 2005; Lepš et al. 2006). Here we use $d_{ij} = 1 - O$, where O is the overlap of the trait value distribution between species (which takes into account the within-species trait variability). To calculate the trait value distribution, we used the average and standard deviation of the trait values measured for each species in the field, and calculated the overlap assuming normal distribution of trait values (see e.g. Fig. 3 in Lepš et al. 2006). The dissimilarity (and consequently the FD index) can be applied for single and multiple traits (de Bello et al. 2006; Lepš et al. 2006). The way in which dissimilarity is calculated is one of the most important methodological decisions affecting the behaviour of FD.

Beta functional trait diversity

Recently, Pavoine et al. (2004), Pavoine & Dolédec (2005) and Ricotta (2005) have proposed partitioning of FD into different spatial components with the Rao index. With different mathematical approaches, they proposed calculation of the β (among-communities) and γ (regional) components of trait diversity, similar to Whittaker's additive approach (γ = α + β; Veech et al. 2002). This allows the partitioning of the total functional diversity in a way analogous to the decomposition of the sum of squares in ANOVA (Pavoine et al. 2004; Ricotta & Marignani 2007). Such partitioning of diversity can also be used to compare various diversity components simultaneously (e.g. genetic, phylogenetic, taxonomic and functional, depending on the information used to define d_{ij}; Pavoine et al. 2004; Hardy & Senterre 2007). Similar to the decomposition of sum of squares in ANOVA, the method can be applied at multiple scales (e.g. to hierarchical structured data or, possibly, to factorial designs; Pavoine & Dolédec 2005). With the Rao approach, β FD reflects how much new functional diversity is gained when pooling different communities together (Fig. 1). In particular, β Rao FD is the difference between γ (the expectation of dissimilarity of two random individuals in the whole region) and $\bar{\alpha}$ (the expected dissimilarity of two individuals within communities).

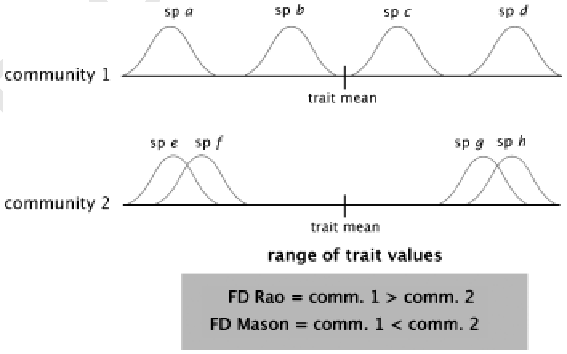

Fig. 1. Comparison of FD values in two hypothetical communities with four species and with different trait value overlaps among species (curves = trait value distribution for each species; bigger curve intersection = greater overlap). Two indices are presented: the FD Rao index (which calculates the dissimilarity between all pairs of species), and the FD Mason (sums the species trait deviation with respect to the community trait mean). Community 1 has a more even trait value distribution, i.e. with smaller trait overlap. Community 2 has a higher trait overlap among species (e.g. two herbs, species *e* and *f*, and two trees, species *g* and *h*, with height as a trait; i.e. theoretical lower niche complementarity). The two FD indices can lead to different results: the FD Mason is higher in community 2 (the sum of deviation of species mean trait is higher than in community 1), but the FD Rao is lower (increased overlap, for example between species *e* and *f*). Note that this difference is valid when the trait dissimilarity in the Rao index is based on the overlap of trait value distribution.

Rao index application

The approach of calculating different spatial components of FD with the Rao index is appealing and relatively easy to use. To calculate different spatial components of FD it is necessary to follow three steps: (1) calculate the α FD for every community; (2) calculate the γ (regional) FD; and then (3) the β FD is defined by $\beta = \gamma - \bar{\alpha}$. To calculate the γ FD (i.e. step 2), it is necessary to treat the study region as a single sample (being the proportion of species occurring in the region equal to the average over all sampling points; Fig. 1):

$$\gamma FD = \sum_{i=1}^{s}\sum_{j=1}^{s} d_{ij} P_i P_j (3)$$

where

$$P_i = \sum_{c=1}^{n} p_{ic}/n (4)$$

c is the number of sampling points (1 to n) in the region, and S is the number of species in the region. In order to calculate FD for a given sample, it is essential to have two matrices of data: one containing species abundances (or presence/absence) in different communities (i.e. the sampling points) and another containing the traits of each species. Algorithms and examples to calculate FD are available, e.g. at http://botanika.bf.jcu.cz/suspa/FunctDiv.php. The calculation of α, β and γ species diversity could be similarly considered using the Simpson index, i.e. following the above-mentioned steps (1–3), where only the species by samples matrix is necessary.

The Mason index

Another well-known index of FD is the index of functional divergence that was originally proposed by Mason et al. (2003, 2005) for α FD. This intuitive approach considers the α FD as the variance of species traits within a community (i.e. their deviation from the community mean). Two communities might have a similar mean trait value but a different deviation from this mean (practically, this can be seen as the error bars shown around the community mean trait value). In particular, the α functional trait diversity could be defined as:

$$\alpha FD = \sum_{i=1}^{S} p_i (x_i - \bar{x})^2, (5)$$

where p_i is the proportion of the ith species, s is the number of species in the community (species richness), x_i is the mean trait value of the ith species, and $\bar{x}$ is the community mean (or aggregated mean value, see also Fig. 1) calculated as:

$$\bar{x} = \sum_{i=1}^{s} p_i x_i (6)$$

This α functional diversity represents the overall variance of a given trait in a community. Note that the index in formula (3) is modified with respect to Mason et al. (2003, 2005), i.e. without the original transformation proposed by the authors (Lepš et al. 2006). Following the same approach, β functional diversity is defined as:

$$\beta FD = \sum_{c=1}^{n} \frac{1}{n} (\bar{x}_c - \bar{x}_{region})^2 (7)$$

where n is the number of communities (samples) in the region, x_c is the average of the cth community ($c = 1,2,\ldots,n$) and x_{region} is the overall mean across all communities in a region. With this formula, the β functional diversity represents the increase in variance resulting from pooling different communities together.

Similar to Rao's index, this approach can also be used to decompose diversity as for the sum of squares in ANOVAs. A disadvantage of using Mason's FD approach is that the trait diversity is calculated only using the species trait mean values. Consequently, the within-species variability for a trait is not accounted for (Mouillot et al. 2005; Lepš et al. 2006) and, therefore, it cannot consider the possible overlap between pairs of species (as with d calculated using species overlap in the Rao index; Fig. 1). This latter characteristic could lead to different results and information between FD Rao and FD Mason (note that if trait overlap is not taken into account in the calculation of trait dissimilarity, the two indices give similar results because of similar mathematical formulations; not shown). For example, the FD Mason has high values when species have very different traits from the community mean, even if some species have overlapping traits between them (Fig. 1, community 2; e.g. a community with two tree species and two herbaceous species, with height as a trait). The latter is a case in which FD Rao will have low values because some pairs of species overlap in their traits (resulting in a more realistic estimate of niche space occupied).

Case study

We sampled 60 plant communities from pastures along an altitudinal and climatic gradient in

NE Spain. The samples (100 m^2 each) were distributed across five vegetation belts along the gradient (12 samples per region in a factorial design, see de Bello et al. 2006, 2007b for details). Species frequency was recorded as presence/absence in 100×1 m^2 quadrats for each sample. Data was used to calculate: (1) species diversity using the Whittaker additive approach, (2) Simpson species diversity and FD with the Rao index and (3) following Mason's approach (Table 1).

The species included in the case study were the most frequent (and consequently the most dominant) vascular plant species found along the gradient (134 species of the total 404 found in the study, representing on average $>74\%$ of the total vegetation composition for each sample). The turnover of these species among communities thus reflects replacement of the most abundant species. For this example, we considered specific leaf area (SLA) as a single trait to calculate FD. This trait is of particular relevance because it mirrors a fundamental axis of differentiation among species (Díaz et al. 2004), from more "acquisitive" (higher SLA, rapid acquisition of resources) to more "conservative" (lower SLA, conservation of resources within protected tissues) strategies. SLA was measured for all the 134 most abundant species (with a minimum of five individuals × two leaves per species). The mean and standard deviation for the SLA values for each species were used to calculate species overlap for the Rao index (details in Lepš et al. 2006).

Null models

Randomization tests were applied to calculate "null" distributions of species composition (i.e. on the species × plot matrix) and both indices of functional diversity. This was done by applying the trial swap method of Miklos & Podani (2004), which satisfies requirements for equi-distribution in the randomization. For this method, we used the *commsimulator* function implemented in the *vegan* library (http://cc.oulu.fi/~jarioksa/softhelp/vegan.html) in the R software (R Development Core Team 2007). Reshuffling the species × plot matrices was done with three constraints, i.e. while keeping (1) the same number of species (species richness) per plot in the permuted and observed data, (2) the same number of total species occurrences per region (i.e. number of plots where the species occur in a region), and (3) the total abundance of species in a region constant (i.e. the sum of the number of quadrats occupied in all plots).

The first two constraints are usually applied in the case of swap methods (Miklos & Podani 2004); however, we considered it equally important to also keep the total abundance of each species constant (constraint no. 3), since species abundances in a region are likely to be related to species functional traits. As the trial swap was initially proposed for species occurrence data only (i.e. presence/absence), randomizations were first done on presence/absence (while respecting the first two constraints). Then, the total abundance of a given species within a region was shuffled among all plots where the species was present in the randomized matrices (R script available on request).

For each region (12 plots each), we re-sampled species composition 999 times and calculated FD indices (FD Rao and FD Mason) for each new matrix. The test of significance of observed versus expected values provides a test of the hypothesis that observed functional diversity partitioning differs from that expected at random. This, in turn, provides evidence for the effect of different assembly mechanisms in the biological communities under study.

Results

Species diversity

Our data show a substantial mismatch between partitioning (i) the species richness and (ii) the Simpson index (left section in Table 1). The β Simpson index is much lower than the β species richness (over γ). The β Simpson diversity index (or SD) accounted for 6.5% of the diversity in whole region and ranged from 2.3% and 6.9% within each vegetation belt, while the β species richness accounted for around 80% diversity over the whole region and ranged between 42.7% and 67.7% within each belt (Table 1). This result (and similarly Pavoine & Dolédec 2005) indicates that the β species richness and the β Simpson diversity indices measure noticeably different properties in species turnover among communities.

The β Simpson index shows increases in the probability that two species will be from different taxa when communities are pooled. Hence, when α Simpson species diversity is high, β diversity is low whatever the extent of the turnover of species (Jost 2007). High α Simpson species diversity implies a strong probability that individuals in a community are different. Therefore, it is likely that this probability cannot increase more by increasing the number of samples and pooling communities with very different compositions. As a result, the β Simpson will be low even if there is high turnover of species. Our data, with communities having high values of α Simpson diversity, represent an example of such a situation (Table 1); since the least abundant species along the gradient were not considered, high β species richness reflects a high turnover of the most abundant species. This indicates that the β Simpson index does not specifically focus on the turnover in species composition and that caution is needed in its comparison with other indices of diversity, e.g. species richness and FD. The limitation of comparing the β Simpson diversity with the β richness can be resolved by applying the correction proposed by Jost (2007) to the Simpson index (i.e. $\beta = (\gamma - \alpha)/(1 - \alpha)$). After correction, β Simpson values from our data approached β richness values (after correction β Simpson = 75% of the diversity in the whole region, instead of 6.5% obtained without correction).

Functional diversity

Comparing FD Rao with FD Mason produced very similar results in partitioning the spatial components of functional diversity (right section in Table 1). In the whole region and within each vegetation belt, the proportions of α and β FD accounted for were similar with both methods (Table 1). β FD Rao accounted for 10% diversity over the whole region and ranged between 2.4% and 10.7% within each vegetation belt, while β FD Mason accounted for 15.7% diversity over the whole region and ranged between 3.9% and 11.5% within each belt (Table 1). In our data set, the absolute values of γ FD showed the most notable difference between the two methods: it was rather stable across vegetation belts with Rao's index while it showed marked differences with FD Mason, probably because one index was scaled between 0 and 1 while the other was not. In all vegetation belts considered, and irrespective of the FD index, the observed α FD was lower than expected at random, while, as a result, the observed β FD was higher than expected at random (Fig. 3). These trends were more pronounced at the regional scale, i.e. taking into account species turnover along the climatic gradient (Fig. 3). Finally, β FD Rao was remarkably higher than α FD Rao even when applying a correction similar to that proposed by Jost (2007) for Simpson diversity (after correction β FD Rao = 25% for the whole region; potentially, the same correction could also be applied to the Rao index, l. Jost et al. pers. comm.).

Discussion

Irrespective of the FD index used, we observed strong patterns highlighting different community assembly mechanisms. First, the observed α functional diversity was lower than expected by chance (i.e. α FD observed $<$α FD expected), an observation consistent with the hypothesis of trait convergence resulting from habitat filtering (Cornwell et al. 2006; Mason et al. 2007; Mouillot et al. 2007; Petchey et al. 2007). A lower observed versus expected FD should indicate that environmental filters constrain coexisting species to share some similar traits, i.e. by selecting species with similar ecological tolerances from the regional species pool (Díaz et al. 1998; Grime 2006; Garnier et al. 2007). Although other explanations exist (Petchey et al. 2007), environmental filtering produces communities with higher similarity than expected at random, thus resulting in a functional redundancy of species traits within communities (see also Cornwell et al. 2006). As a consequence of such filtering, the among-community trait differentiation was higher than expected at random (i.e. β FD observed $>$β FD expected), indicating that the environment selects for species with different traits better adapted to different habitats (Weiher & Keddy 1995).

Second, we observed a remarkably higher FD for within communities compared to among communities (α FD $\gg$ β FD; Table 1 and Fig. 3). This suggests that differences in traits among species within a habitat can be as great as trait differences across the full range of an environmental gradient (Fonseca et al. 2000), probably resulting in a modest shift in single plant trait values along environmental gradients (Wright et al. 2004). Previous studies (Westoby et al. 2002; Pavoine & Dolédec 2005) support our observations and suggest that among-communities differentiation for particular traits can be relatively small compared with processes acting at local scales (within community). Consistent with our data, results from very large data sets indicate that much of the total leaf economy variation occurs among coexisting species (Wright et al. 2004). This is an important biological pattern, which suggests that the functional differentiation among species is associated with species coexistence, a result consistent with the hypothesis of limiting similarity mechanisms (MacArthur & Levins 1967; Stubbs & Wilson 2004; Hooper et al. 2005; Wilson 2007). In our data set, in particular, the coexistence of species of different growth forms in the same habitats (de Bello et al. 2006) likely underlies the coexistence of species with different SLA (Wright et al. 2004; Bertiller et al. 2006) because trait convergence within a given growth form is expected (McIntyre et al. 1999).

However, larger α FD values relative to β FD in observed and expected data (Fig. 2) could also result from a mathematical artifact rather than from a reflection of community assembly processes linked to trait divergence. Yet, the null algorithm applied does not assume α and β FD vary independently (i.e. they are complementary). Indeed, if α FD is larger in the null model than in the observed data, β FD is necessarily smaller. Consequently, larger α than β FD values in both observed and expected data should result from the null model formulation, in which species richness per plot, species frequencies and total abundance of species in a region are similar in the permuted and observed data. Under these

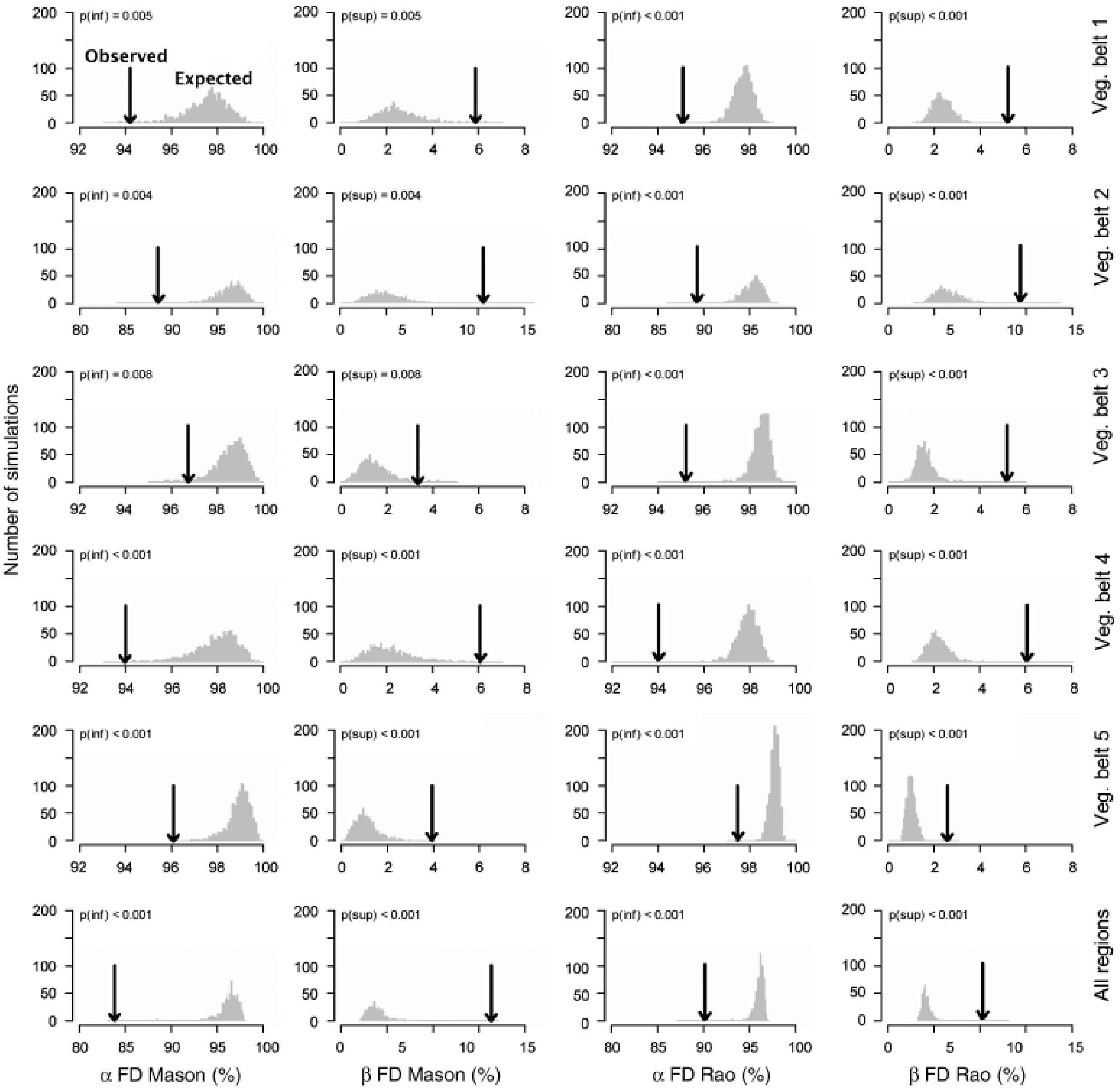

Fig. 2. Different partitioning of functional diversity in observed (black arrows) versus expected data resulting from null species distribution with 999 randomizations (grey bars). The comparison is shown for each of the different vegetation belts considered, from drier (above) to more humid (below) conditions, and for two functional diversity indices (left FD Mason, right FD Rao). Values of functional diversity for within communities (α) and among communities (β) reflect the percentage accounted for over the regional functional diversity (γ). A test of significance of observed versus expected values is shown for each panel.

circumstances, the observed α is smaller than that expected under the null model, and we ascribe this to environmental filtering.

Our data, as in other studies (Fonseca et al. 2000; Westoby et al. 2002; Wright et al. 2004), demonstrate the biological importance of trait differentiation among coexisting species. Since species adapt to a given habitat through a combination of traits resulting in a number of viable arrangements, the within-habitat differentiation for particular traits is accompanied by allometric changes and/or trade-offs with other traits (Westoby et al. 2002). Therefore, new mathematical tools are needed specifically to test how such within-habitat differentiation occurs compared to that among habitats. In particular, the inherent dependence of FD β on FD α could be avoided by developing a similar correction to that proposed by Jost (2007) for the Simpson index (L. Jost et al. pers. comm.). In this direction, also, different null models could be applicable: randomizations of only species traits (Cornwell et al. 2006), less constrained species randomizations (Petchey et al. 2007), or assessments of trait allometric relationships in random versus observed data. Each approach might be tested with both simulated and real data, to evaluate whether null models can be applied to the partitioning of functional diversity at different spatial scales. Yet, assembly rules often assume lower interspecific than intraspecific competition. As a result, the null models might also require information on numbers of individuals and their randomization.

Third, the modest turnover of FD among communities contrasts with the high turnover of species among habitats (Whittaker 1975; Fig. 3). Our data, and those in Pavoine & Dolédec (2005), show a much more marked turnover in species (as β species richness) than in functional trait diversity among communities (β FD). Here, with SLA as an example, little functional differentiation occurred among communities over the whole gradient (β FD around 10–15%), although most of the differentiation in species richness occurred at that level (β species richness around 80%). The steep change in species turnover in this case (Table 1, de Bello et al. 2007b) was not caused by the replacement of rare or minor species, since we considered only the most abundant species along the gradient. Therefore, our data represent an indication of the contrasting turnover of species versus FD among communities. This result implies that a high replacement in species composition (taxonomical turnover) might result in a rather stable functional assemblage for certain traits (low functional turnover; e.g. Fukami et al. 2005), suggesting the existence of ecological redundancy among communities (Petchey et al. 2007). Certainly, more research is needed to assess whether this pattern is maintained for different traits and for indices of FD based on multiple traits.

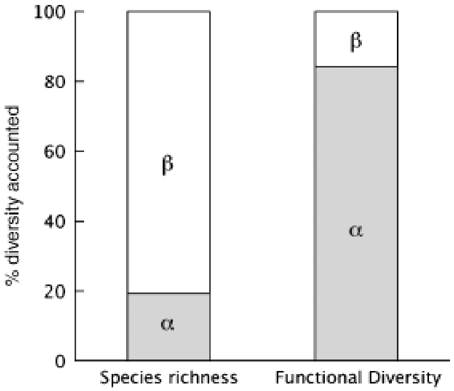

Fig. 3. Contrasting partitioning of diversity of species richness (i.e. first column in Table 1) versus functional diversity (based on the FD Mason, i.e. last column of Table 1) into α ("within-community") and β ("among-communities") components over all locations considered.

Ideally, to compare species and functional diversity partitioning, Rao's index should be applied to both, because the FD Rao is a generalization of the Simpson index of species diversity. Unfortunately, we showed that, due to its formulation, the Rao index for species diversity (i.e. the Simpson index) does not point specifically towards the turnover of species among communities. Therefore, for this purpose, FD could only be compared with other indices of diversity (e.g. species richness; Fig. 3), while remaining aware that different indices give different mathematical and conceptual information. Such comparisons leave open questions as to how much a different turnover in species and functional diversity depends on different methods of calculation or on different biological patterns.

To conclude, we believe that partitioning of functional diversity at different spatial scales can offer new insights into the mechanisms driving trait convergence and divergence and, therefore, the assembly and coexistence of species in biological communities. Partitioning functional diversity within and among communities reveals that both trait convergence and divergence might occur in the formation of assemblages from the local species pool. In particular, while several proofs of trait convergence resulting from habitat filtering have been provided previously (Cornwell et al. 2006; Mason et al. 2007; Mouillot et al. 2007; Petchey et al. 2007), similar proofs of the importance of limiting similarity mechanisms mostly remain overlooked (Wilson 2007; Pillar et al. in press). The assessment of the spatial components of functional diversity, and particularly along environmental gradients, can certainly offer valuable tools to address these questions and evaluate trait convergence and divergence for different traits, organisms and community types.

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