MACROECOLOGICAL METHODS

Partitioning the turnover and nestedness components of beta diversity

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ABSTRACT

Aim Beta diversity (variation of the species composition of assemblages) may reflect two different phenomena, spatial species turnover and nestedness of assemblages, which result from two antithetic processes, namely species replacement and species loss, respectively. The aim of this paper is to provide a unified framework for the assessment of beta diversity, disentangling the contribution of spatial turnover and nestedness to beta-diversity patterns.

Innovation I derive an additive partitioning of beta diversity that provides the two separate components of spatial turnover and nestedness underlying the total amount of beta diversity. I propose two families of measures of beta diversity for pairwise and multiple-site situations. Each family comprises one measure accounting for all aspects of beta diversity, which is additively decomposed into two measures accounting for the pure spatial turnover and nestedness components, respectively. Finally, I provide a case study using European longhorn beetles to exemplify the relevance of disentangling spatial turnover and nestedness patterns.

Main conclusion Assigning the different beta-diversity patterns to their respective biological phenomena is essential for analysing the causality of the processes underlying biodiversity. Thus, the differentiation of the spatial turnover and nestedness components of beta diversity is crucial for our understanding of central biogeographic, ecological and conservation issues.

Keywords

Beta diversity, Cerambycidae, Europe, nestedness, similarity measures, spatial turnover.

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INTRODUCTION

Although the use of similarity measures to compare the composition of different biotas has a much longer history (e.g. Jaccard, 1912; Simpson, 1943; Sørensen, 1948), the term beta diversity was first introduced by Whittaker (1960) and defined by him as 'the extent of change in community composition' among sites. Beta diversity can be viewed as a measure that compares inventory diversity at two different scales (alpha and gamma diversity). This comparison can be done using the classical multiplicative formulation (beta = gamma/alpha) or using the additive partition of diversity (beta = gamma – alpha), as more recently proposed (Lande, 1996; Veech *et al.*, 2002). However, it was shown by Jost (2007) that the different diversity measures (i.e. richness, entropies) require different partitions (i.e. additive, multiplicative) to produce independent alpha and beta components. In the case of measures of beta diversity based

on species counts, the use of the classical multiplicative partition is mandatory (Baselga, in press), because independence between beta and alpha is a necessary property (Wilson & Shmida, 1984). A second view is to consider beta diversity as a measure of the similarity between sites (Koleff *et al.*, 2003). These approaches have recently been named *proportional diversity* and *differentiation diversity*, respectively (Jurasinski *et al.*, 2009), but this distinction is more formal than conceptual because traditional pairwise similarity indices are monotonic transformations of the multiplicative Whittaker's beta (i.e. gamma/alpha) computed for two sites (Jost, 2007). In other words, *differentiation diversity* measures are, in fact, just special cases of *proportional diversity* measures for *n* = 2. The issue is clearly exemplified by the fact that pairwise similarity indices can be generalized and applied to situations involving multiple sites, with multiple-site similarity measures again being monotonic transformations of Whittaker's beta for any number of sites (Diserud & Ødegaard,
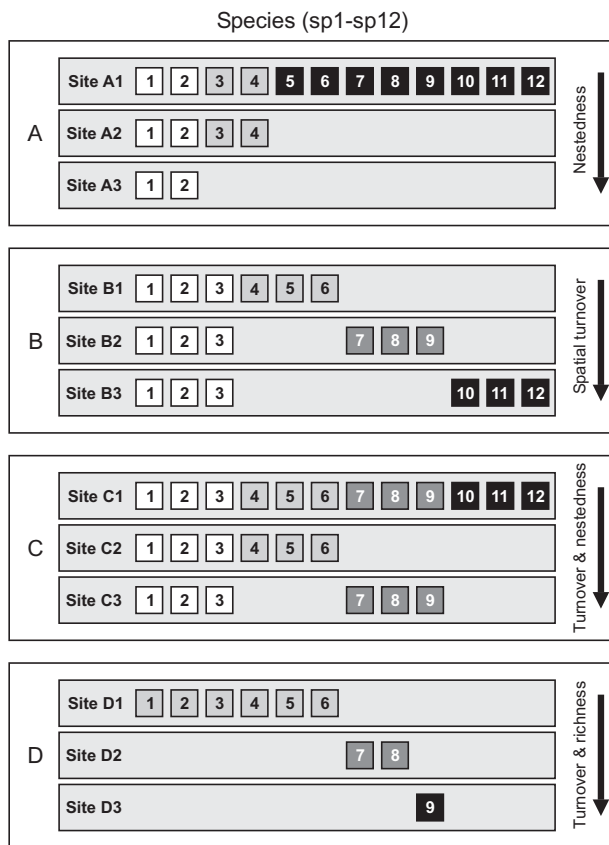
Figure 1 Hypothetical examples involving four islands (A–D) and three sampling sites in each. Biotas of sites A1–A3 are completely nested, because poorer biotas are subsets of richer biotas. Sites B1–B3 have the same richness (six species each) with three species common to all three sites and three species exclusive to each site, i.e. displaying a pattern of spatial turnover. Sites C1–C3 present both patterns, because C2 and C3 are subsets of C1 (nestedness), but some species are replaced between C2 and C3, which are not subsets of each other. Sites D1–D3 present spatial turnover and are obviously not nested, but present differences in richness.

2007). Therefore, these apparently divergent views on beta diversity are actually consistent with a single beta-diversity concept.

It is not new that beta diversity may reflect two different phenomena: nestedness and spatial turnover (Harrison et al., 1992; Baselga et al., 2007). Nestedness of species assemblages (Fig. 1, island A) occurs when the biotas of sites with smaller numbers of species are subsets of the biotas at richer sites (Wright & Reeves, 1992; Ulrich & Gotelli, 2007), reflecting a non-random process of species loss as a consequence of any factor that promotes the orderly disaggregation of assemblages (Gaston & Blackburn, 2000). Contrary to nestedness, spatial turnover implies the replacement of some species by others (Fig. 1, island B) as a consequence of environmental sorting or spatial and historical constraints (Qian et al., 2005). It should be stressed that although many matrix configurations are possible (Almeida-Neto et al., 2008), all situations in which communities are not

identical can be described with only these two main patterns (turnover and nestedness) or combinations of both, since the only processes needed to generate all the possible patterns are species replacement and species loss (or gain). Note that I use the term 'species loss' just to indicate that some species are absent from some sites, without regard to the underlying mechanism (i.e. extinction, differential dispersal capacity and others; Ulrich et al., 2009). If we are to understand biotic patterns and their causes, patterns which may be revealing different processes must be discerned (Williams et al., 1999) and, in this case, the two processes underlying measures of beta diversity (species loss and species replacement) are not only different but antithetic (Williams, 1996; Gaston & Blackburn, 2000). Therefore, nestedness and species turnover must be disentangled (Baselga, 2007).

The effect of nestedness on similarities between biotas has been known for a long time (Simpson, 1943), preceding the first use of the term 'beta diversity' (Whittaker, 1960), and has subsequently been repeatedly emphasized (Harrison et al., 1992; Koleff et al., 2003; Baselga et al., 2007). To deal with this effect, several measures (Shi, 1993; Williams, 1996; Lennon et al., 2001; Koleff et al., 2003; Baselga et al., 2007) have been developed to compute values of: (1) spatial turnover independent of nestedness, and (2) compositional differences attributable to richness. Among the multiple-site measures intended to account for spatial turnover, β_{-2} (Harrison et al., 1992) and β_{-3} (Williams, 1996) do not provide satisfactory results for certain situations in which both nestedness and spatial turnover are involved (Fig. 1, island C), because both measures would identify these mixed patterns as completely nested ($\beta_{-2} = \beta_{-3} = 0$ in both islands A and C). However, the pairwise Simpson dissimilarity measure (β_{sim}), recovered by Lennon et al. (2001) based on Simpson (1943), and its multiple-site generalization (Baselga et al., 2007) have proved to efficiently discriminate turnover from nestedness ($\beta_{SIM} = 0$ in island A, $\beta_{SIM} = 0.6$ in island B) and mixed situations ($\beta_{SIM} = 0.2$ in island C). The only measure intended to account for differences in richness is β_{gl} (Lennon et al., 2001; Koleff et al., 2003) but it incorporates all richness differences (Fig. 1, island D) and not only those attributable to nestedness (Fig. 1, island A), thereby estimating situations to be equivalent that are in fact very different ($\beta_{gl} = 1.2$ in both islands A and D). In sum, no unified framework exists for measuring beta diversity and partitioning the contributions of spatial turnover and nestedness. Here, I provide such a framework for both pairwise and multiple-site measures, deriving the appropriate indices that partition total beta diversity into two additive components accounting for pure spatial turnover and nestedness. To denote beta-diversity measures I follow the standard notation (β) used by previous authors (i.e. Koleff et al., 2003). Subscripts are used to identify the type of dissimilarity, and I here propose reserving the lower-case letters for the pairwise measures and the upper-case letters for the multiple-site measures (Table 1). Thus, Sørensen pairwise dissimilarity is then β_{sor}, and Simpson-based multiple-site dissimilarity is β_{SIM}, for example. Finally, I provide a simple practical example using European longhorn beetles to show the crucial importance of disentangling spatial turnover and nestedness.

Table 1 Overview of the measures mentioned in this paper, including names, proposed notation, formulas and references. T is the number of sites. See main text for definition of all other variables.

Dissimilarity measure	Notation	Formula	References
Pair-wise measures			
Sørensen pairwise dissimilarity	β_{sor}	$\dfrac{b+c}{2a+b+c}$	Sørensen (1948), Koleff *et al.* (2003)
Simpson pairwise dissimilarity	β_{sim}	$\dfrac{\min(b,c)}{a+\min(b,c)}$	Simpson (1943), Lennon *et al.* (2001), Koleff *et al.* (2003)
Nestedness-resultant dissimilarity	β_{nes}	$\dfrac{\max(b,c)-\min(b,c)}{2a+\min(b,c)+\max(b,c)}\times\dfrac{a}{a+\min(b,c)}$	This paper
Lennon richness-based dissimilarity	β_{gl}	$\dfrac{2[\max(b,c)-\min(b,c)]}{2a+\max(b,c)+\min(b,c)}$	Lennon *et al.* (2001), Koleff *et al.* (2003)
Multiple-site measures			
Whittaker's beta	β_W	$\dfrac{S_T}{\sum_i S_i/T}$	Whittaker (1960)
Harrison multiple-site dissimilarity	β_{-1}	$\dfrac{\beta_W-1}{T-1}$	Harrison *et al.* (1992)
Diserud-Ødegaard multiple-site similarity	$1-\beta_{-1}$	$1-\beta_{-1}=\dfrac{T-\beta_W}{T-1}$	Diserud & Ødegaard (2007)
Harrison multiple-site turnover measure	β_{-2}	$\dfrac{\dfrac{S_T}{\max(S_i)}-1}{T-1}$	Harrison *et al.* (1992)
Williams multiple-site turnover measure	β_{-3}	$1-\dfrac{\max(S_i)}{S_T}$	Williams (1996)
Sørensen-based multiple-site dissimilarity	β_{SOR}	$\dfrac{\left[\sum_{i<j}\min(b_{ij},b_{ji})\right]+\left[\sum_{i<j}\max(b_{ij},b_{ji})\right]}{2\left[\sum_i S_i-S_T\right]+\left[\sum_{i<j}\min(b_{ij},b_{ji})\right]+\left[\sum_{i<j}\max(b_{ij},b_{ji})\right]}$	This paper
Simpson-based multiple-site dissimilarity	β_{SIM}	$\dfrac{\left[\sum_{i<j}\min(b_{ij},b_{ji})\right]}{\left[\sum_i S_i-S_T\right]+\left[\sum_{i<j}\min(b_{ij},b_{ji})\right]}$	This paper
Nestedness-resultant multiple-site dissimilarity	β_{NES}	$\dfrac{\left[\sum_{i<j}\max(b_{ij},b_{ji})\right]-\left[\sum_{i<j}\min(b_{ij},b_{ji})\right]}{2\left[\sum_i S_i-S_T\right]+\left[\sum_{i<j}\min(b_{ij},b_{ji})\right]+\left[\sum_{i<j}\max(b_{ij},b_{ji})\right]}\times\dfrac{\sum_i S_i-S_T}{\left[\sum_i S_i-S_T\right]+\left[\sum_{i<j}\min(b_{ij},b_{ji})\right]}$	This paper

INNOVATION

The simplest case: pairwise dissimilarities

The Sørensen dissimilarity index (β_{sor}) is one of the most used measures due to its dependence on the proportion of species shared between two communities and its linear relationship with Whittaker's beta (Diserud & Ødegaard, 2007). The Sørensen dissimilarity index (β_{sor}) is formulated as:

$$\beta_{sor}=\frac{b+c}{2a+b+c}, \tag{1}$$

where *a* is the number of species common to both sites, *b* is the number of species that occur in the first site but not in the second and *c* is the number of species that occur in the second site but not in the first. It is well known that this measure incorporates both true spatial turnover and differences in richness (Koleff *et al.*, 2003).

To describe spatial turnover without the influence of richness gradients, the Simpson dissimilarity index (β_{sim}) was first proposed by Simpson (1943) and later recovered by Lennon *et al.* (2001):
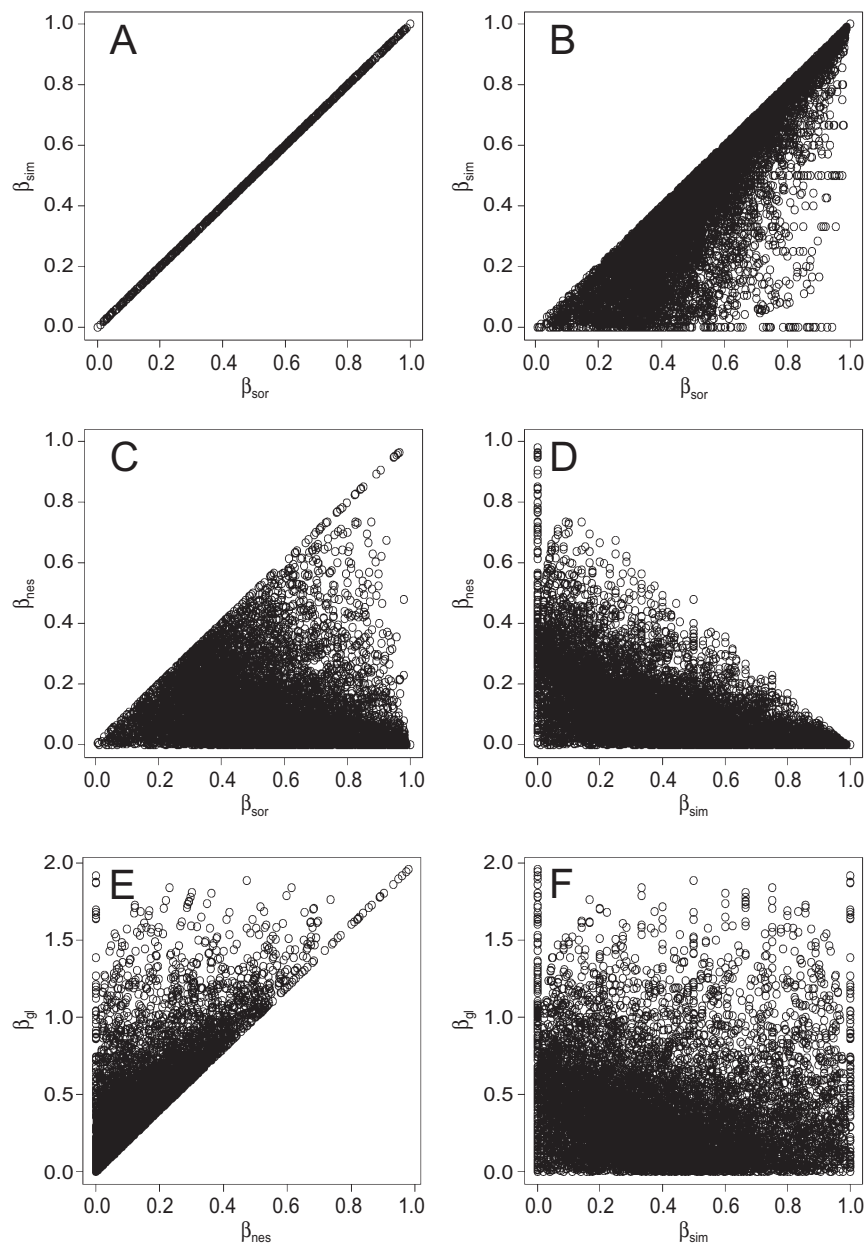
$$\beta_{sim}=\frac{\min(b,c)}{a+\min(b,c)}, \tag{2}$$

Figure 2 Relative performance of β_{sor}, β_{sim}, β_{nes} and β_{gl} under situations of equal (a) and unequal richness (b–f). Simulations were performed in R, taking random values of a, *b* and *c* matching components from uniform distributions between 1 and 100, where *a* is the number of species common to both sites, *b* is the number of species that occur in the first site but not in the second and *c* is the number of species that occur in the second site but not in the first. Under conditions of equal richness, *b* and *c* are always equal, so $\beta_{sor} = \beta_{sim}$ and $\beta_{nes} = 0$. Under conditions of unequal richness, *b* and *c* can take different values, so β_{sim} and β_{nes} randomly vary between β_{sor} and 0, but are mutually dependent as $\beta_{sor} = \beta_{sim} + \beta_{nes}$. The new measure β_{nes} is only slightly related to β_{gl} because the former accounts only for differences in composition due to nestedness, whereas the latter accounts for any difference in richness (as island D in Fig. 1, for example).

where *a*, *b*, *c* are the same variables as defined for Sørensen dissimilarity. When both localities have the same number of species *b* and *c* must be equal, thus β_{sor} and β_{sim} are also equal because $b/(a + b) = 2b/(2a + 2b)$ (as also empirically shown in Fig. 2a). It is also obvious that any dissimilarity between two localities with the same number of species is completely due to spatial turnover because nestedness cannot occur. When both

sites have different number of species, *b* and *c* are different, thus β_{sor} and β_{sim} are also different (as shown in Fig. 2b). Since β_{sor} and β_{sim} are equal in the absence of nestedness, their difference is a measure of the nestedness component of beta diversity. Therefore, I here introduce the nestedness-resultant dissimilarity (β_{nes}) which is derived using basic operations on fractions, and formulated as

$$\beta_{nes} = \beta_{sor} - \beta_{sim} = \frac{b+c}{2a+b+c} - \frac{\min(b,c)}{a+\min(b,c)}$$

$$= \frac{\max(b,c) - \min(b,c)}{2a+\min(b,c)+\max(b,c)} \times \frac{a}{a+\min(b,c)}. \quad (3)$$

It should be noted that the first term of the product is very similar to β_{gl} (Lennon *et al.*, 2001; Koleff *et al.*, 2003), a measure of differences in richness, but in this case this term is multiplied by the second term, which is Simpson similarity (i.e. similarity independent of richness differences = $1 - \beta_{sim}$). This product is needed to separate differences in richness caused by nestedness from other differences in richness: for example, two completely different communities (sharing no species, i.e. $1 - \beta_{sim} = 0$) may have a different number of species, but they are obviously not nested (Fig. 1, island D). In this way, β_{nes} yields the nestedness component of beta diversity, instead of any difference on richness, as β_{gl} does (Fig. 2c–f). Therefore we have a dissimilarity measure accounting for all aspects of beta diversity (β_{sor}) that can be partitioned into two additive components accounting for pure spatial turnover (β_{sim}) and nestedness (β_{nes}):

$$\beta_{sor} = \beta_{sim} + \beta_{nes} \quad (4)$$

Multiple-site dissimilarities

The same additive partition can be conducted for multiple-site dissimilarity measures, but only if multiple-site indices are formulated in terms of matching components as pairwise measures. Otherwise, nestedness and turnover cannot be separated and measures do not perform well in all situations. This is the case for β_{-2} (Harrison *et al.*, 1992) and β_{-3} (Williams, 1996). None of these measures are exact turnover partitions of β_{-1} (Harrison *et al.*, 1992), which is a transformation of Whittaker's beta to be bounded between 0 and 1 (i.e. the Sørensen dissimilarity equivalent for more than two sites). The same occurs with the Diserud–Ødegaard multiple-site similarity, which is, in fact, the same measure as β_{-1} but expressed as a similarity (i.e. Diserud–Ødegaard = $1 - \beta_{-1}$). Therefore, it is necessary to adopt the approach suggested in Baselga *et al.* (2007) and build multiple-site equivalents of the matching components (*a*, *b*, *c*). In the cited paper, an index accounting just for the species turnover component was proposed, but the same procedure can be followed to formulate an index accounting for both species turnover and nestedness derived from the pairwise Sørensen dissimilarity:

$$\beta_{SOR} = \frac{\left[\sum_{i<j}\min(b_{ij},b_{ji})\right] + \left[\sum_{i<j}\max(b_{ij},b_{ji})\right]}{2\left[\sum_i S_i - S_T\right] + \left[\sum_{i<j}\min(b_{ij},b_{ji})\right] + \left[\sum_{i<j}\max(b_{ij},b_{ji})\right]}, \quad (5)$$

where S_i is the total number of species in site i, S_T is the total number of species in all sites considered together and b_{ij}, b_{ji} are the number of species exclusive to sites i and j, respectively,

when compared by pairs. Thus, $\left[\sum_{i<j}\min(b_{ij},b_{ji})\right]$ and $\left[\sum_{i<j}\max(b_{ij},b_{ji})\right]$ are the multiple-site analogues of the *b* and *c* matching components of pairwise measures, respectively, and $\left[\sum_i S_i - S_T\right]$ is the analogue of the *a*-component.

As mentioned before, a multiple-site similarity measure accounting only for species turnover is already known (Baselga *et al.*, 2007), and β_{SIM} is just its complement:

$$\beta_{SIM} = \frac{\left[\sum_{i<j}\min(b_{ij},b_{ji})\right]}{\left[\sum_i S_i - S_T\right] + \left[\sum_{i<j}\min(b_{ij},b_{ji})\right]}. \quad (6)$$

The multiple-site dissimilarity accounting only for nestedness can just be derived by simple subtraction:

$$\beta_{NES} = \beta_{SOR} - \beta_{SIM}$$

$$= \frac{\left[\sum_{i<j}\min(b_{ij},b_{ji})\right] + \left[\sum_{i<j}\max(b_{ij},b_{ji})\right]}{2\left[\sum_i S_i - S_T\right] + \left[\sum_{i<j}\min(b_{ij},b_{ji})\right] + \left[\sum_{i<j}\max(b_{ij},b_{ji})\right]}$$

$$- \frac{\left[\sum_{i<j}\min(b_{ij},b_{ji})\right]}{\left[\sum_i S_i - S_T\right] + \left[\sum_{i<j}\min(b_{ij},b_{ji})\right]}$$

$$= \frac{\left[\sum_{i<j}\max(b_{ij},b_{ji})\right] - \left[\sum_{i<j}\min(b_{ij},b_{ji})\right]}{2\left[\sum_i S_i - S_T\right] + \left[\sum_{i<j}\min(b_{ij},b_{ji})\right] + \left[\sum_{i<j}\max(b_{ij},b_{ji})\right]}$$

$$\times \frac{\sum_i S_i - S_T}{\left[\sum_i S_i - S_T\right] + \left[\sum_{i<j}\min(b_{ij},b_{ji})\right]}. \quad (7)$$

Performance of multiple-site measures

As shown before, the *a*-component analogue for the multiple-site measures is very simply computed, while still accounting for the different degrees of overlap derived from species shared by more than two sites, because it is derived using the inclusion–exclusion principle (Erickson, 1996) to substitute the term $\left[\sum_{i<j}a_{ij} - \sum_{i<j<k}a_{ijk} + \sum_{i<j<k<l}a_{ijkl} - \ldots\right]$ by $\left[\sum_i S_i - S_T\right]$ as first proposed by Diserud & Ødegaard (2007). In contrast, the *b*- and *c*-component analogues cannot be simplified in that form while maintaining comparisons among more than three sites because of the need to separate the maximum and minimum values. For this reason, the *b*- and *c*-component analogues are computed only for pairs of sites because doing the contrary would imply severe computational difficulties in the generalization of indices
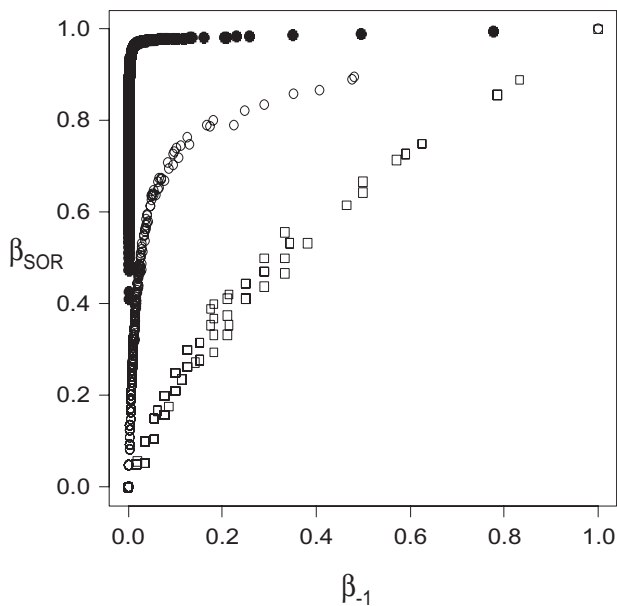
Figure 3 Relationship of β_{SOR} and β_{-1} in situations involving different numbers of sites (squares, $n = 3$; empty circles, $n = 10$; solid circles, $n = 100$). Simulations were performed in R, with random presence–absence tables being built with 10 species and n sites.

for situations involving any number of sites. Doing this simplification, the multiple-site nature of the measures is not compromised, since the a-component analogue accounts for the information on species shared by more than two sites, but, as a consequence, measures are dependent on the number of sites (n), i.e. β_{SOR} is a transformation of Whittaker's beta and β_{-1}, but the shape of the relationship depends on n (Fig. 3). Therefore, it is essential that comparisons between multiple-site measures, as proposed in this paper, should always be conducted among areas with equal numbers, or a very similar number, of sites. In the real world, we could be interested in comparing multiple-site dissimilarity values of regions including different numbers of sites, so a simple procedure for handling datasets with a different number of cases is provided using an empirical dataset (see below).

Relationship between β_{NES} and nestedness measures

It should be stressed that β_{NES} is rooted in the framework of beta-diversity analyses and intended to account for the patterns of beta diversity caused by nestedness. In other words, it is not a measure of nestedness in absolute terms but a measure of the dissimilarity of communities due to the effect of nestedness patterns. Many measures of nestedness are available, diverging in the different philosophies behind each metric (Ulrich *et al.*, 2009). It was recently shown by Almeida-Neto *et al.* (2008) that most of these metrics tend to measure some degree of nestedness even in matrices with a complete absence of nestedness. The cited authors proposed a measure of nestedness, NODF

(nestedness metric based on overlap and decreasing fill), that accurately identifies these cases as not nested. In this sense, NODF and β_{NES} are similar in that both measures yield zero values when no nestedness patters are present. However, NODF yields its maximum value (perfect nestedness) for intermediate values of filling and symmetrically decreases to both extremes of filling because, in these cases, more sites have exactly the same composition (Fig. 4). On the contrary, β_{NES} reflects the increasing dissimilarity between nested communities produced by the increasing differences in the number of species. In all cases included in Fig. 4, beta diversity is completely due to nestedness but β_{NES} accurately identifies island G as having higher beta diversity than island A. In summary, nestedness and *dissimilarity due to nestedness* are related but different concepts, thus divergences in performance between NODF and β_{NES} are consistent with differences between both concepts.

A real example: nestedness and spatial turnover in European longhorn beetles

Partition of the nestedness and turnover components of beta diversity is essential, because confusing two antithetic processes in a single pattern could lead to flawed conclusions. Here, I use the European longhorn beetle fauna (Coleoptera: Cerambycidae) to exemplify the implications of discerning nestedness and spatial turnover patterns. Details on these data were fully described in a previous paper (Baselga, 2008), but basically they consist of country-level inventories with presence–absence data (Danilevsky, 2007). In order to test for the existence of latitudinal patterns of beta diversity, as could be expected by the biogeographic history of Europe, I have split the data into two groups: northern European countries, with mean latitude higher than 48° ($n = 19$) and southern European countries ($n = 15$). The same two groups of inventories were used in Baselga *et al.* (2007), although here I discarded the inventories of European Turkey, Crimea and Moldova from the southern group to better exemplify how to handle datasets with different numbers of cases when computing multiple-site dissimilarities. All analyses were carried out in R (R Development Core Team, 2006), using the functions 'beta-multi.R' (see Appendix S1 in Supporting Information) and 'beta-pairwise.R' (Appendix S2). The file 'beta-multi.R' includes the functions to compute multiple-site dissimilarities β_{SOR}, β_{SIM} and β_{NES}, called beta.SOR(x), beta.SIM(x) and beta.NES(x), respectively, where x is a data frame in which sites are rows and species are columns. The file 'beta-pairwise.R' includes the functions to compute distance matrices using pairwise dissimilarities β_{sor}, β_{sim} and β_{nes}, called beta.sor(x), beta.sim(x) and beta.nes(x), respectively. For the two large areas (northern versus southern Europe) I first assessed the overall multiple-site dissimilarity, considering the total beta diversity (β_{SOR}), as well as the spatial turnover (β_{SIM}) and nestedness (β_{NES}) components, and then compared the patterns between northern and southern Europe. To make comparable dissimilarities computed for sets with different number of sites (19 vs. 15), β-values for northern Europe were com-
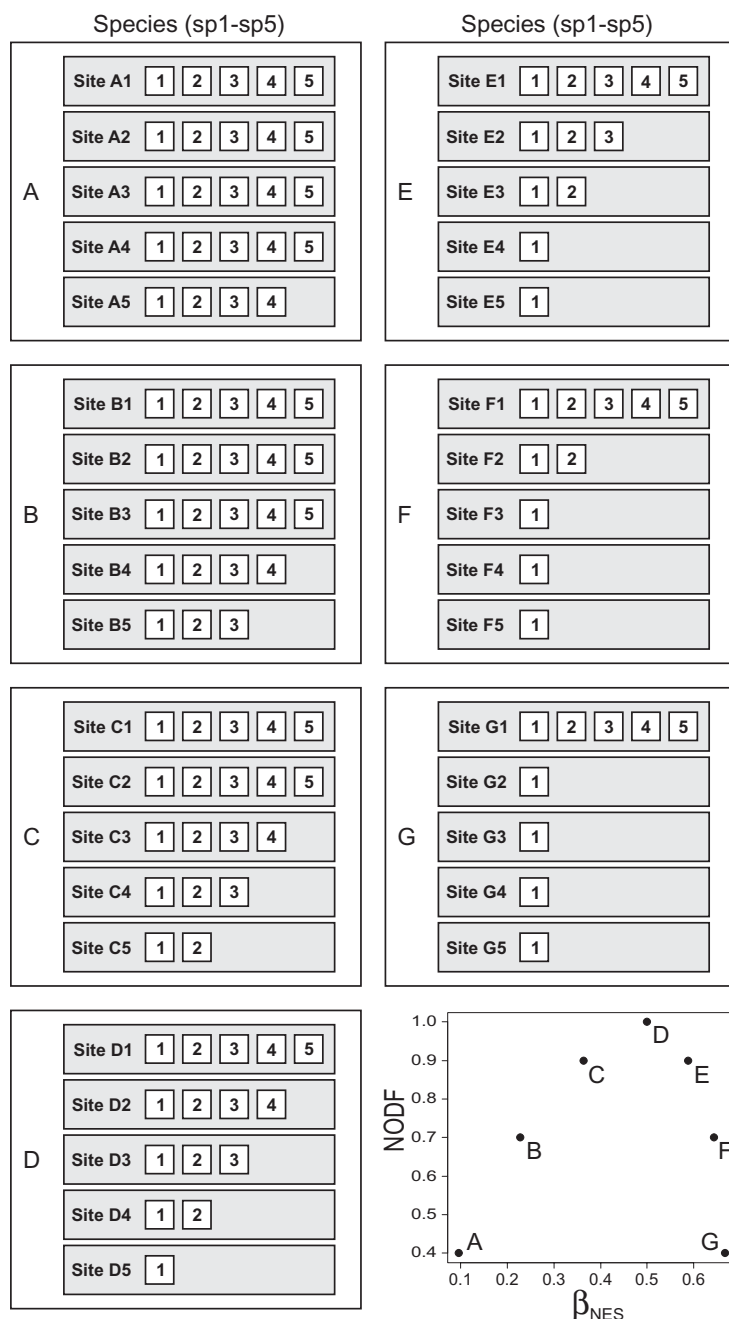
Figure 4 Hypothetical examples involving seven islands (A–G) and five sampling sites in each. All islands show nestedness patterns, but differ in the degree of filling. Also, beta diversity is completely due to nestedness in all islands as no species turnover exists between any of the sites. NODF (nestedness metric based on overlap and decreasing fill) considers island D as perfectly nested (NODF = 1) and symmetrically decreases towards both extremes of maximum and minimum filling. However, β_{NES} increases continually from islands A to G because it measures dissimilarity between communities due to nestedness. This behaviour of β_{NES} is consistent with the fact that beta diversity (the ratio between gamma and mean alpha) increases from A to G.

puted using a resampling procedure, taking 100 random samples of 15 inventories and computing the average β (see R script in Appendix S3). In a second analysis, I assessed the increase of biotic dissimilarity with geographic distance (equivalent to the distance decay of similarity), as computed with the total beta diversity (β_{sor}), as well as with the turnover (β_{sim}) and nestedness (β_{nes}) measures. Since the lack of independence of observations (distances) precludes the test for significance by means of traditional regression procedures, significance of the Pearson correlations was computed by means of Mantel permutation tests using the vegan package (Oksanen *et al.*, 2007) in R (R Development Core Team, 2006). To

compare the intercepts and slopes yielded by the different dissimilarity indices, the frequency distributions of the parameters were estimated by bootstrapping in order to detect significant differences between measures. A frequency distribution of 1000 slopes and intercepts was retrieved by bootstrapping, using the boot package (Canty & Ripley, 2008). When assessing the significance of one parameter being larger in one region than in the other, the probability of obtaining the opposite result by chance was empirically computed by comparing the estimated distributions of parameters.

In the case of multiple-site dissimilarities, the estimated overall beta diversity was very similar for northern (β_{SOR} = 0.71)
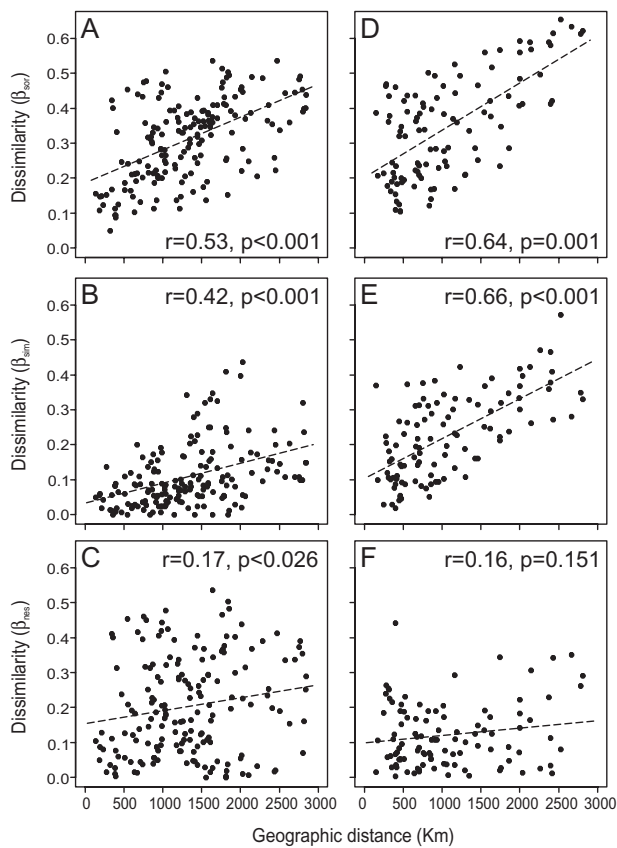
Figure 5 Relationship between faunal dissimilarity (β_{sor}, β_{sim} and β_{nes}) and geographic distances in northern (a–c) and southern Europe (d–f). Pearson correlation (*r*) and significance (*P* computed using Mantel tests) are shown. See the main text for differences among intercept and slope values between the two regions.

and southern Europe ($\beta_{SOR} = 0.74$). We could thus have concluded that beta diversity is quite similar in both areas. However, when this overall beta diversity is partitioned into its turnover and nestedness components, it remains clear that processes underlying these beta-diversity values are clearly different: in northern Europe both spatial turnover and nestedness contribute strongly and similarly to beta diversity ($\beta_{SIM} = 0.40$, $\beta_{NES} = 0.31$), whereas in southern Europe spatial turnover is responsible for most of the beta diversity ($\beta_{SIM} = 0.61$, $\beta_{NES} = 0.13$). In other words, beta-diversity patterns in northern Europe are the result of both species replacement between regions and species loss towards the north (Baselga, 2008), whereas beta-diversity patterns in southern Europe are almost completely caused by species replacement only.

The assessment of the increase of dissimilarity with geographic distance using pairwise measures, yielded similar results (Fig. 5). The increase of faunal dissimilarity with geographic distance is estimated to be similar in northern (intercept = 0.186, slope = 9.43×10^{-5}) and southern Europe (intercept = 0.202, slope = 1.35×10^{-4}) by β_{sor} (Fig. 5a,d). Inter-

cepts are not significantly different ($P = 0.288$), but the slope is significantly higher in southern Europe ($P = 0.021$). Nevertheless, this pattern is not easily interpretable because it reflects the combined effects of spatial turnover and nestedness. When these components are differentiated, it becomes clear that spatial turnover (Fig. 5b,e) is higher in southern (intercept = 0.103, slope = 1.14×10^{-4}) than in northern Europe (intercept = 0.032, slope = 5.70×10^{-5}; both intercepts and slopes differ at $P < 0.001$), whereas nestedness (Fig. 5c,f) is higher in northern (intercept = 0.153, slope = 3.73×10^{-5}) than in southern Europe (intercept = 0.100, slope = 2.11×10^{-5}). In the latter comparison, slopes are not significantly different ($P = 0.247$), while the intercept is significantly higher in northern Europe ($P = 0.034$). It should be noted that the intercept and slope values yielded by β_{sor} are exactly the sum of intercept and slope values yielded by β_{sim} and β_{nes}, respectively.

The relevance of disentangling nestedness from turnover

The simple example presented above is neither a detailed analysis of beta-diversity patterns nor a comprehensive assessment of the processes underlying the patterns. However, it brings attention to the need for partitioning beta diversity into its spatial turnover and nestedness components in order to discern the antithetic processes underlying beta diversity. In the case of European longhorn beetles, the finding that beta diversity is similar in northern and southern Europe is misleading, as the underlying patterns and processes are quite different. In southern Europe beta diversity is caused by spatial turnover, reflecting the high proportion of endemics present in this region (Baselga, 2008), whereas in northern Europe beta diversity is partially caused by spatial turnover but also by nestedness, reflecting the ordered loss of species to the north (Baselga, 2008). These patterns are not likely to be an exception, but are probably the rule for many taxa which have higher values of richness and endemism in southern Europe, for example trees (Svenning & Skov, 2007b) or herptiles (Araújo *et al.*, 2008). Of course, no generalization can be made about the causes of nestedness or spatial turnover, but the biological implications of species loss or species replacement are always completely different. In the case of Europe, the effect of glaciations is a firm candidate for explaining such differences between regions. Northern biotas are the result of post-glacial recolonization processes (Hewitt, 1999) and nestedness patterns point out the relevance of dispersal limitation in structuring these assemblages (Svenning & Skov, 2007a), since southern species are not replaced by northern ones but disappear progressively to the north. In contrast, southern regions acted as Pleistocene glacial refugia, conserving the palaeoendemic species that disappeared from the north during glaciations and being also centres of speciation (Ribera & Vogler, 2004). Thus, no patterns of nestedness are found in southern Europe, and assemblages are structured by spatial turnover processes probably linked to the isolation of biotas in different refugia during glaciations and the related speciation events.

CONCLUSION

The differentiation of the spatial turnover and nestedness components of beta diversity is crucial for improving our understanding of central biogeographic, ecological and conservation issues. From its origin, biogeography has dealt with the definition of borders between biogeographic regions, based on patterns of biotic replacement. Impoverished zones must be distinguished from replacement zones, because each case can be generated by different historical or environmental factors (Williams *et al.*, 1999). For example, spatial turnover patterns suggest the existence of 'any barrier or selective differentiation between the faunas', whereas nestedness patterns do not, as pointed out early on by Simpson (1943, note 5). In ecology, assigning the different beta-diversity patterns to their respective biological phenomena is essential to analyse the causality of the processes underlying biodiversity. Patterns of beta diversity have been attributed either to environmentally deterministic processes or to dispersal limitation and other historical effects (Nekola & White, 1999; Condit *et al.*, 2002; Duivenvoorden *et al.*, 2002; Tuomisto *et al.*, 2003; Qian *et al.*, 2005), but clear inference on the processes involved is prohibited by the mixing of the antithetic processes of species loss and species replacement in standard beta-diversity measures. For conservation purposes the distinction is essential, because nestedness and spatial turnover patterns also require antithetic conservation strategies (Wright & Reeves, 1992). The former would permit the prioritization of just a small number of the richest sites, whereas the latter would require devoting conservation efforts to a large number of different sites, not necessarily the richest ones. Finally, even the estimates of global biodiversity could be compromised by the measure used to assess beta diversity, which is a key step in the extrapolation of global figures of richness (Erwin, 1982; Odegaard, 2000; Novotny *et al.*, 2007), because confounding subsets of richest biotas (nestedness) as if they actually were different biotas (turnover) would cause overestimations of global diversity.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 R function 'beta-multi.R'.

Appendix S2 R function 'beta-pairwise.R'.

Appendix S3 R scripts for the case study using European longhorn beetles.

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BIOSKETCH

Andrés Baselga is interested in the integration of several biodiversity-related disciplines as a way to search for robust hypotheses for the causes of biodiversity. These include an accurate knowledge of biodiversity (taxonomy) and its spatial (biogeography), temporal (phylogeny) and environmental (macroecology) dimensions. He is especially interested in the integration of beta-diversity patterns in the central debate about large-scale gradients of biodiversity.

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