CORRESPONDENCE

Rethinking the relationship between nestedness and beta diversity: a comment on Baselga (2010)

ABSTRACT

Baselga [Partitioning the turnover and nestedness components of beta diversity. *Global Ecology and Biogeography*, **19**, 134–143, 2010] proposed pairwise (β_{nes}) and multiple-site (β_{NES}) beta-diversity measures to account for the nestedness component of beta diversity. We used empirical, randomly created and idealized matrices to show that both measures are only partially related to nestedness and do not fit certain fundamental requirements for consideration as true nestedness-resultant dissimilarity measures. Both β_{nes} and β_{NES} are influenced by matrix size and fill, and increase or decrease even when nestedness remains constant. Additionally, we demonstrate that β_{NES} can yield high values even for matrices with no nestedness. We conclude that β_{nes} and β_{NES} are not true measures of the nestedness-resultant dissimilarity between sites. Actually, they quantify how differences in species richness that are not due to species replacement contribute to patterns of beta diversity. Finally, because nestedness is a special case of dissimilarity in species composition due to ordered species loss (or gain), the extent to which differences in species composition is due to nestedness can be measured through an index of nestedness.

INTRODUCTION

Nested subset patterns have been widely reported in both metacommunities and networks of interacting species (Bascompte & Jordano, 2007; Ulrich *et al.*, 2009). A perfectly nested metacommunity is characterized by an ordered sequence of sites in which species-poor assemblages contain a subset of the species occurring in species-rich assemblages. A similar concept applies to species range sizes, such that less widespread species occur in a subset of the sites in which the most common species are found. Thus, if species composition is completely nested, then all sites exhibit different species richnesses and there is no species replacement between sites. Consequently, in a perfectly nested metacommunity, species dissimilarity across sites is only affected by differences in species richness. This means that a portion of the observed beta diversity (the change in species composition across sites) might be attributed to nestedness and the remainder to species replacement. Although these relationships have long been recognized (Simpson, 1943; Harrison *et al.*, 1992; Wright & Reeves, 1992), progress toward an integrated framework has been hindered by differing concepts of beta diversity (Moreno & Rodríguez, 2010; Tuomisto, 2010; Anderson *et al.*, 2011) and a lack of consensus about metrics (Koleff *et al.*, 2003). Recently, Baselga (2010) proposed an approach to distinguishing the contributions of spatial turnover and nestedness to beta-diversity patterns. We report here that Baselga's approach is not satisfactory because the supposed 'nestedness-resultant dissimilarity' does not actually result from and fails to represent the different concepts underlying nestedness.

The framework provided by Baselga (2010) is based on two well-known pairwise dissimilarity measures: Simpson's dissimilarity (see Simpson, 1943 and Lennon *et al.*, 2001) and Sørensen's dissimilarity (Sørensen, 1948). Following Lennon *et al.* (2001) notation, we expressed the matching components for two sites (*i* and *j*) as follows: *a* = number of species occurring in both sites, *b* = number of species occurring in *i* but not in *j*, and *c* = number of species occurring in *j* but not in *i*. Hence, Sørensen (β_{sor}) and Simpson (β_{sim}) dissimilarity indices for two sites can be calculated as follows:

$$\beta_{sor} = \frac{b+c}{2a+b+c} \qquad (1)$$

$$\beta_{sim} = \frac{\min(b,c)}{a+\min(b,c)}. \qquad (2)$$

β_{sor} accounts for the total difference in species composition between two sites (i.e. *b* + *c*), whereas β_{sim} accounts only for the lower component (i.e. $\min(b,c)$). Thus, both β_{sor} and β_{sim} are sensitive to species replacement but only the former is also sensitive to differences in species richness. Another important property is that β_{sor} and β_{sim} will yield the same values both when two sites have the same species richness and when there are no shared species between two sites (see Fig. 1(b) and (c) in Baselga, 2010). Because there is no nestedness between two sites in these situations, Baselga deduced that 'β_{sor} − β_{sim}' would represent a measure of the nestedness component of beta diversity (β_{nes}, according to Baselga's notation).

Based on a previous approach used to establish a Simpson extension for mutiple-sites (Baselga *et al.*, 2007), Baselga (2010) proposed a similar extension of the Sørensen measure. For multiple sites, the extensions of the Sørensen and Simpson dissimilarity indices were given by

$$\beta_{sor} = \frac{\left[\sum_{i \neq j} \min(b_{ij}, b_{ji})\right] + \left[\sum_{i \neq j} \max(b_{ij}, b_{ji})\right]}{2\left[\sum_i S_i - S_T\right] + \left[\sum_{i \neq j} \min(b_{ij}, b_{ji})\right] + \left[\sum_{i \neq j} \max(b_{ij}, b_{ji})\right]}, \qquad (3)$$

$$\beta_{sim} = \frac{\sum_{i \neq j} \min(b_{ij}, b_{ji})}{\left[\sum_i S_i - S_T\right] + \left[\sum_{i \neq j} \min(b_{ij}, b_{ji})\right]} \qquad (4)$$
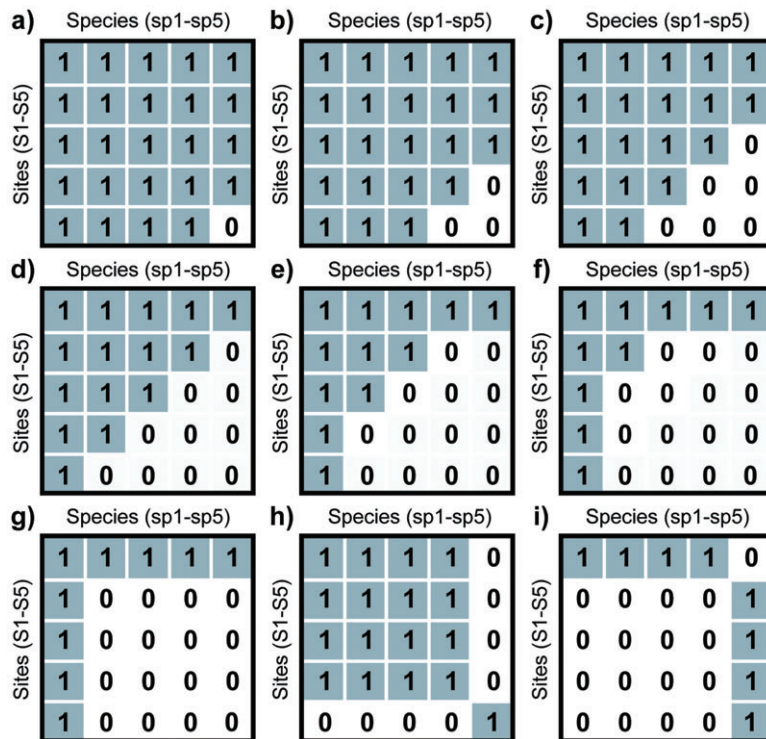
Figure 1 Seven hypothetical nested matrices with decreasing degrees of fill (a–g) and two non-nested matrices (h and i).

where S_i is the total richness at site i, S_T is the regional species richness (gamma diversity), and b_{ij} and b_{ji} represent the number of species exclusive to sites i and j, respectively. Following the same rationale as for the pairwise situation, Baselga (2010) proposed that $\beta_{NES} = \beta_{SOR} - \beta_{SIM}$ would represent a measurement of the dissimilarity that results from nestedness. He pointed out that 'nestedness and dissimilarity due to nestedness are related but different concepts, thus divergences in performance between metrics of nestedness and β_{NES} are consistent with differences between both concepts'.

Baselga (2010) also mentioned that each of these 'nestedness-dissimilarity' measures 'accounts only for differences in composition due to nestedness'. By deduction, if β_{nes} and β_{NES} are true nestedness-resultant dissimilarity measures, then we can predict that both indices will: (1) increase with increasing nestedness, (2) not vary if nestedness remains constant, and (3) not yield positive values for cases in which there is no nestedness. Along with these three basic requirements, we should also expect strong positive linear relationships between degree of nestedness, β_{nes}, and β_{NES}. Here we also used the index NODF (Almeida-Neto *et al.*, 2008) to measure nestedness.

Following Ulrich & Gotelli (2007a,b) and Almeida-Neto *et al.* (2007, 2008), we used empirical, randomly created and idealized

matrices to evaluate whether β_{nes} and β_{NES} fit the three basic predictions above. The empirical data used were the well-known set of biogeographic presence–absence matrices compiled by Atmar & Patterson (1995). For the randomly created metacommunities, we generated a set of matrices in which occurrence probabilities per cell were drawn from a uniform random distribution (equivalent to the equiprobable row and column null model). We evaluated the effect of matrix size by creating a total of 630 matrices with approximately 50% of fill, with 30 matrices for each of the following dimensions (columns × rows): 5 × 5, 10 × 10, 15 × 15, and so on up to and including 100 × 100. To evaluate Prediction 2, we used perfectly nested matrices (with a fill of approximately 50% and NODF$_{sites}$ = 100) with the same dimensions used to evaluate the effect of size, totalling 20 matrices. Finally, we evaluated Prediction 3 with the idealized matrices illustrated in Fig. 1(h) and 1(i).

Differently from Baselga (2010), here we calculated the NODF index only among sites (hereafter referred to as NODF$_{sites}$) because the focus is on the dissimilarity in species composition. Note that the NODF for columns and rows in Fig. 4 of Baselga (2010) yield the same values because the matrices are squared and the distribution of zeros and ones is symmetrical between both sides of the principal diagonal. Otherwise, NODF for

both columns and rows and NODF for only columns or rows would potentially yield different values.

DO β_{nes} AND β_{NES} INCREASE WITH INCREASING NESTEDNESS?

For the multiple-site measures of beta-diversity (β_{NES}), this question is partially answered by evaluating Baselga (2010). Using a set of hypothetical matrices (illustrated here as Fig. 1a–g), he showed that nestedness degree (NODF$_{sites}$) is at its maximum for intermediate matrix fill and decreases toward both poorly and maximally filled matrices, whereas β_{NES} increases monotonically with decreasing matrix fill. Thus, β_{NES} does not necessarily increase with increasing nestedness because the term $[\Sigma_i S_i - S_T]$ in the denominator of both β_{SOR} and β_{SIM} increases with matrix fill, irrespective of the proportion of joint occurrences. Furthermore, β_{NES} decreases as the matrix fill increases for those cases in which $\min(b, c) = 0$ for all pairs of sites. A similar, though less pronounced, result is obtained when the pairwise measure β_{nes} is used (Fig. 2a). For the identical hypothetical nested matrices, β_{nes} always yields lower values (range: 0.044 to 0.388) than those of β_{NES} (range: 0.095 to 0.667). In addition, there is not necessarily a

monotonic relationship between β_{nes} and β_{NES} (Fig. 2b).

CAN β_{nes} OR β_{NES} YIELD DIFFERENT VALUES FOR MATRICES WITH IDENTICAL NESTEDNESS LEVELS?

Again, the answer is given in Fig. 4 of Baselga (2010). Three pairs of matrices (here, Fig. 1a and g, b and f, c and e) have the same $NODF_{sites}$ values but showed distinct values for both β_{nes} and β_{NES}. For instance, matrices (a) and (g), both with $NODF_{sites} = 40$, have 'nestedness-dissimilarity' values ranging from 0.044 (a) to 0.267 (g) and 0.095 (a) to 0.667 (g) for β_{nes} and β_{NES}, respectively. These nested matrices with the same NODF values can have more than one degree of β_{nes} or β_{NES} because they differ in the degree of fill. Another undesirable situation may occur when either β_{nes} or β_{NES} yields more than one value for perfectly nested matrices ($NODF_{sites} = 100$). If these beta-diversity measures truly quantify the extent to which nestedness contributes to overall beta diversity, both β_{nes} and β_{NES} should remain constant for matrices with maximum nestedness levels because the contribution of nestedness is at its maximum. To examine whether perfectly nested matrices have distinct values of β_{nes} and β_{NES}, we used a set of squared matrices with $NODF_{sites} = 100$ but with distinct sizes (from 25 to 10,000 cells). We found that β_{nes} and β_{NES} increase with matrix size, even in situations in which the level of nestedness is at its maximum (Fig. 3a, b). β_{nes} showed a constant but very small increase, with values ranging from 0.357 to 0.384 (Fig. 3a). However, β_{NES} values ranged from 0.500 to 0.944 from the smallest to the largest matrix (Fig. 3b), which means that β_{NES} detects higher contributions of nestedness to beta diversity for larger matrices. For β_{NES}, the reason for the matrix-size dependence is that, in nested matrices, the term $\Sigma_{i \neq j} \max(b_{ij}, b_{ji})$ increases faster than the term $[\Sigma_i S_i - S_T]$. The increase in β_{nes} occurs because for a pair of nested sites, $\max(b_{ij}, b_{ji})$ increases with increasing absolute difference in species. In this case, an increase in the number of sites indicates the inclusion of richer sites that contribute more to overall $\beta_{sor} = \beta_{nes}$.

To examine whether β_{nes} and β_{NES} increase with increasing matrix size irrespective of matrix structure, we used a set of randomly created matrices with fill close to 50% and of the same sizes as described above (from 25 to 10,000 cells). Interestingly, the result was
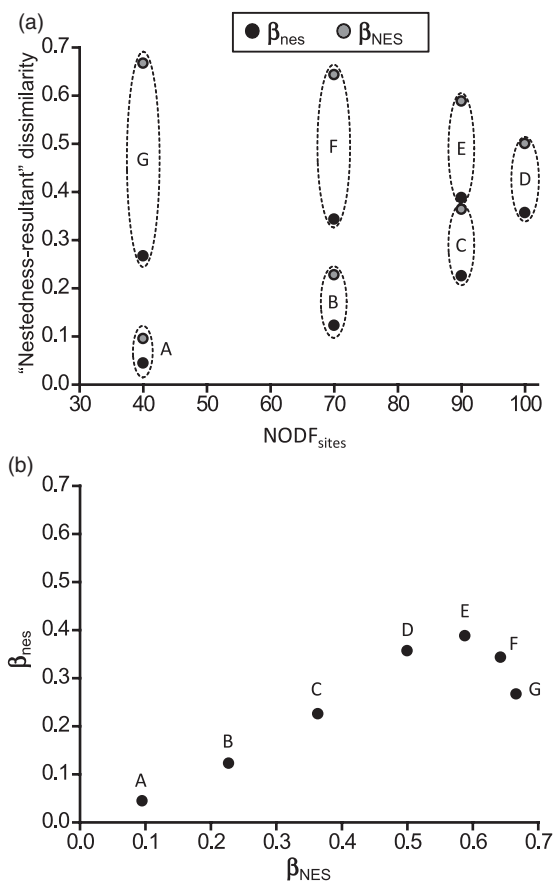
opposite to that found for perfectly nested matrices: both β_{nes} and β_{NES} decreased with increasing matrix size for these randomly created matrices (Fig. 3c and d). Almeida-Neto *et al.* (2008) showed that there is no consistent variation in nestedness with increasing matrix size. Therefore, increasing or decreasing values of β_{nes} and β_{NES} with matrix size produce the false impression that nestedness is contributing more or less, respectively, to overall beta diversity.

DO β_{nes} AND β_{NES} DETECT NESTEDNESS FOR CASES IN WHICH THERE IS NO NESTEDNESS?

Baselga (2010) stated that 'NODF and β_{NES} are similar in that both measures yield zero values when no nestedness patterns are present'. To verify this statement, we used two hypothetical non-nested matrices (i.e. with $NODF_{sites} = 0$) with five sites and five species. In the first matrix, the richest site harboured four species, and the four other sites had only a single species that did not occur in the richest

site (Fig. 1h). In the second example, we included four sites with the same four species and a single site with an endemic species (Fig. 1i). We found that Baselga's statement above is true for β_{nes} but not for β_{NES}. For both non-nested matrices $\beta_{SOR} = 0.769$ and $\beta_{SIM} = 0.571$, so that $\beta_{NES} = 0.198$. Furthermore, depending on the matrix size and arrangement, β_{NES} can yield values higher than 0.5. For instance, extending Fig. 1(h) to 500 species in the richest site and 500 sites with the same single species absent from the richest site, the values of dissimilarity are $\beta_{SOR} \cong 1.0$ and $\beta_{SIM} = 0.333$ so that $\beta_{NES} = 0.667$. Although these are only hypothetical examples, they clearly illustrate that β_{NES} is not necessarily zero when there is no nestedness.

DO β_{nes} AND β_{NES} SHOW STRONG POSITIVE RELATIONSHIPS WITH NESTEDNESS?

We used empirical presence–absence data compiled by Atmar & Patterson (1995) to answer this question. We found moderate to
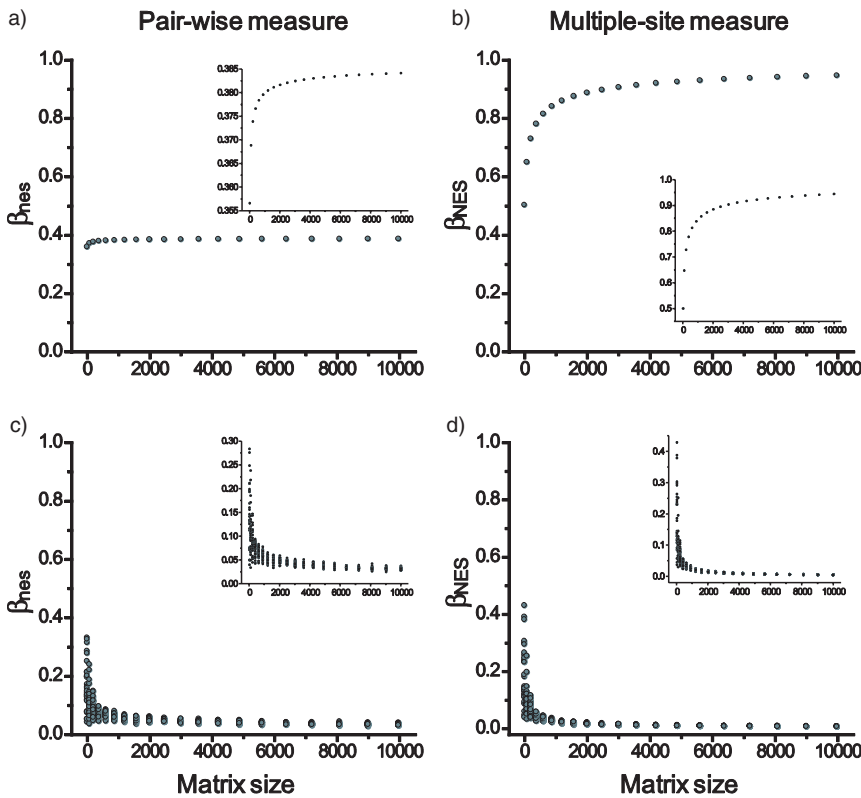

Figure 2 (a) Relationships of nestedness degree ($NODF_{sites}$) with the pairwise (β_{nes}) and the multiple-site (β_{NES}) measures of beta-diversity. (b) The relationship between β_{nes} and β_{NES} for the nested hypothetical examples showed in Figure 1.

Figure 3 Variation in the pairwise (β_{nes}) and the multiple-site (β_{NES}) measures of beta-diversity with increasing matrix size for perfectly nested matrices (a and b) and for randomly created matrices with fill close to 50% (c and d). Inset graphs show the same relationships, but with smaller ranges in the Y-axis to facilitate the interpretation of trends.
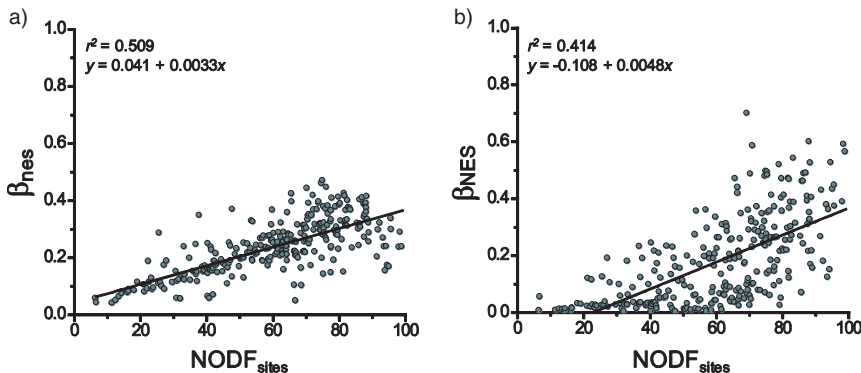

Figure 4 Linear regressions of degree of nestedness (measured by $NODF_{sites}$) against the pairwise (β_{nes} in a) and the multiple-site (β_{NES} in b) measures of beta-diversity for 288 presence–absence matrices of the dataset of Atmar & Patterson (1995).

strong positive correlations between β_{nes} and $NODF_{sites}$ ($r_{Pearson} = 0.713$) and between β_{NES} and $NODF_{sites}$ ($r_{Pearson} = 0.643$) (Fig. 4a, b). However, such linear relationships with $NODF_{sites}$ explained at most 50% of the variation between these measures of beta diversity (Fig. 4a, b). In addition, the variation of β_{NES} with $NODF_{sites}$ is better described as a bounded relationship in which the range of variation in β_{NES} increases at higher levels of nestedness (Fig. 4b).

We then performed multiple linear regressions using $NODF_{sites}$, matrix fill (%) and log-transformed matrix size as independent variables to scrutinize their relative contributions to the values of both β_{nes} and β_{NES}. For β_{nes}, we found a negligible effect of matrix

size, a small but significant negative effect of degree of filling, and a strong positive influence of $NODF_{sites}$ (Table 1). Nestedness level was also the main predictor of β_{NES}, but we found a significant negative effect of matrix size, stronger than the negative influence of matrix fill. $NODF_{sites}$ was relatively less important for β_{NES} compared with β_{nes}, even considering the possible confounding effects of matrix size and fill.

NESTEDNESS VERSUS DIFFERENCES IN SPECIES RICHNESS

We have provided sound arguments for avoiding using Baselga's (2010) approach to

quantify the extent to which dissimilarity in species composition results from nestedness. We showed that neither β_{nes} nor β_{NES} satisfied some fundamental requirements: (1) increasing with increasing nestedness, (2) not varying when nestedness remains constant, and (3) not yielding positive values for cases in which there is no nestedness. A simple reason for why both measures fail is that they take into account absolute differences in species richness between pairs of sites (β_{nes}) or among multiple sites (β_{NES}). Similar to β_{sim} and β_{SIM}, $NODF_{sites}$ is invariant with regard to differences in richness when $\min(b, c) = 0$, but it results in maximum nestedness values when $nx_i > nx_j$ or in zero values if $nx_i \leq nx_j$. Hence, if we have $a = 5$, $b = 1$ and $c = 0$ for a

Table 1 Multiple regression models to explain the variance in the pairwise (β_{nes}) and the multiple-site (β_{NES}) measures of beta-diversity from nestedness degree (NODF$_{sites}$), log-transformed matrix size (= species × sites) and matrix fill (%) for 288 biogeographical presence–absence matrices (Atmar & Patterson, 1995).

Dependent variable Explanatory variables	Standardized coefficient	P	r^2	Adjusted r^2
β_{nes}	Overall $F = 154.1$, $P < 0.001$, $R^2 = 61.9\%$			
Matrix size	−0.038	0.388	0.010	0.003
Matrix fill	−0.439	< 0.001	0.087	0.186
NODF$_{sites}$	0.980	< 0.001	0.526	0.580
β_{NES}	Overall $F = 124.0$, $P < 0.001$, $R^2 = 56.7\%$			
Matrix size	−0.460	< 0.001	0.027	0.258
Matrix fill	−0.244	< 0.001	0.087	0.058
NODF$_{sites}$	0.798	< 0.001	0.348	0.446

given pair of sites and $a' = 5$, $b' = 50$ and $c' = 0$ for another pair, the value of NODF$_{sites}$ remains constant (NODF$_{sites} = 100$), but $\beta_{nes} = \beta_{sor} = \beta_{SOR} = \beta_{NES}$ yields 0.091 for the first pair and 0.833 for the second.

The approach of Baselga (2010) is in fact a measure (β_{nes} or β_{NES}) of the contribution of richness differences to overall beta diversity rather than of nestedness-resultant dissimilarity. The extent to which nestedness contributes to beta-diversity patterns can be calculated using NODF$_{sites}$ or another appropriate nestedness metric. As can be easily seen, for those cases in which $a + b \neq a + c$, NODF$_{sites}$ and the Simpson similarity index between two sites yield the same values (see Lennon *et al.*, 2001). Thus, the paired nestedness between two sites with different species richness can be formulated as:

$$\text{NODF}_{sites} = \text{Simpson's similarity}$$
$$= \frac{a}{a + \min(b,c)}. \quad (5)$$

However, to allow for the evaluation of different mechanisms, nestedness is frequently calculated following a given ordering of sites according to some sorting criteria such as species richness, island size or isolation, whereas the Simpson similarity index does not depend on the order of sites.

GENERAL RECOMMENDATIONS

The study of species diversity, nestedness and species co-occurrence is replete with papers that introduce new metrics (cf. the reviews of Lande, 1996; Ulrich & Gotelli, 2007a,b; Ulrich *et al.*, 2009). The history of nestedness metrics is emblematic of the ongoing discussion about the frequency and causes of nested subset patterns based on inappropriate metrics and statistical testing (Ulrich &

Gotelli, 2007a; Almeida-Neto *et al.*, 2008; Ulrich *et al.*, 2009). Recently, a number of critical reviews of metrics and null hypotheses have appeared that have used extensive testing with simulated and empirical ecological matrices (Ulrich & Gotelli, 2007a,b, 2010; Almeida-Neto *et al.*, 2008; Gotelli & Ulrich, 2010; Almeida-Neto & Ulrich, 2011) to clarify the behaviour of co-occurrence and nestedness metrics.

The concept of nestedness and the hypotheses used to explain this pattern are much more related to 'directional turnover in community structure' (see Anderson *et al.*, 2011) than to non-directional variations in community structure. The new approach proposed by Baselga (2010) may be useful for determining how differences in species richness that are not due to species replacement contribute to patterns of beta-diversity along spatial, temporal or environmental gradients. However, Baselga's approach is not suited to quantifying nestedness-resultant dissimilarity. Because nestedness is a special case of dissimilarity in species composition due to ordered species loss (or gain), the extent to which differences in species composition is due to nestedness can be quantified through an index of nestedness.

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