

A comparative evaluation of pairwise nestedness measures

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This paper deals with nestedness measures that are based on pairwise comparisons of sites, evaluates their performance and suggests improvements and generalizations. There are several conceptual and technical criteria to judge their ecological applicability. It is of primary concern whether the measures 1) have a clear mathematical definition, 2) are influenced by the ordering of the data matrix, 3) incorporate similarity alone or similarity together with a dissimilarity component, 4) consider site pairs with identical species number negatively or positively, 5) show sensitivity to small changes in the data, and 6) are not vulnerable to type I and type II error rates. We performed a detailed comparison of the nestedness metric based on overlap and decreasing fill (NODF), the percentage relativized nestedness and the percentage relativized strict nestedness functions (PRN and PRSN, respectively), based on analytical results as well as on artificial and actual examples. We show that NODF is in fact the average Simpson similarity of sites with different species totals, and that its value depends on how the matrix is actually ordered. NODF is modified to always produce the maximum possible result (NODF_{max}), independently of the order of columns and rows. Being based on similarities, NODF and NODF_{max} overemphasize the overlap component of nestedness and underrate richness difference which is also an important constituent of nested pattern in meta-community data. This latter feature is reflected adequately by PRN and PRSN. However, PRSN is similar to NODF and NODF_{max} in sharing the disadvantages that 1) complete agreement and segregation in species composition are not distinguished, 2) a random matrix can have a higher value than truly nested patterns, and 3) they are ill-conditioned statistically. These problems are rooted mostly in that site pairs with tied totals affect the result negatively. We emphasize that PRN is free from these difficulties. PRN, PRSN, and NODF_{max} together with mean Simpson similarity exhibit highly similar statistical performance: they are resistant to type I and type II errors for the less constrained null models, although there are subtle differences depending on matrix fill and algorithm of randomization. The most constrained null model, with all marginal totals fixed, makes all statistics more sensitive to type I errors, although vulnerability depends greatly on matrix fill.

Nestedness is a useful concept in meta-community analysis (Wright et al. 1998, Greve and Shown 2006, Hausdorf and Hennig 2007, Ulrich et al. 2009, Presley et al. 2010) and in studies of bipartite networks (Bascompte et al. 2003, Araujo et al. 2010) to find ecological explanation of structure in presence-absence data. Early methods for the quantification of nestedness produced a single number reflecting some global property of the data matrix (for example, the nestedness temperature, nestedness discrepancy, and the N_c coefficient; Patterson and Atmar 1986, Brualdi and Sanderson 1999, Wright and Reeves 1992, respectively). The N_c index was the first one that operated via pairwise comparisons, being equal to the 'sum of the number of species shared over all pairs of sites' (Wright et al. 1998). To remove matrix-size dependence which characterizes all these methods, Almeida-Neto et al. (2008) proposed a new measure, called the 'nestedness metric based on overlap and decreasing fill' (NODF). In this, pairwise comparisons were relativized using row or column totals and nestedness was expressed as the mean of overlap values calculated for all pairs of sites, species, or

both. Recently, NODF has become one of the most frequently used measures of nestedness (> 3500 hits by Google at 'NODF + nestedness' and 66 citations to Almeida-Neto et al. 2008, in the Web of Science, September 2011). With a different motivation in mind (to simultaneously represent data structure in terms of similarity, beta diversity, nestedness and other ecological phenomena through the simplex method), we proposed two other, closely related formulae for measuring nestedness (Podani and Schmera 2011). In that framework, we used the 'percentage relativized nestedness' (henceforth abbreviated as PRN) and the 'percentage relativized strict nestedness' (PRSN) functions to quantify the relative contribution of nestedness to data structure, also in terms of average pairwise measures. The main novelty was that, in addition to overlap, the PRN and PRSN functions also consider a fraction of dissimilarity (namely, richness difference) as contributor to nestedness pattern in presence-absence data. Thus, there are at least three coefficients of measuring nestedness by means of relativized pairwise coefficients, but the extent to which they agree or differ

is not yet known. A comparative evaluation is thus necessary to reveal their relative merits in view of the conceptual background they are representing. First, we provide a short mathematical description of NODF and propose an order-independent variant of it (NODF_{max}). Then, the performance of these functions is compared with that of PRN and PRSN, based on artificial examples as well as by analytical and statistical evaluation. Our study is completed by actual examples taken from different areas of community ecology. The results allow us to draw conclusions on general features of nestedness coefficients, thus facilitating choice among the increased number of options currently available for ecologists.

Measures

Reformulation of NODF

The NODF measure can be applied to columns (sites) or rows (species) of the data matrix, or both. However, to simplify discussion without losing generality, in this paper we shall deal only with columnwise analyses of nestedness, i.e. with comparisons of sites. NODF is introduced by Almeida-Neto et al. (2008, p. 1229) using column totals, variables indicating whether column totals decrease from left to right, percentage overlap and the degree of paired nestedness to devise the final formula. Full description is not reproduced here; while it is shown below that there is a compact and explicit formula for its calculation.

To facilitate easy comparison, we use the same subscripts as Almeida-Neto et al. (2008) and to clarify the mathematics behind NODF, we rely upon the standard system of abbreviations of the 2 × 2 contingency table generally used for defining pairwise resemblance coefficients in numerical ecology. For a given pair *kl* of sites, *a_{kl}* is the number of species occurring in both sites, *b_{kl}* is the number of species present only in site *k*, and *c_{kl}* is the number of species appearing in site *l* only. Using these symbols, NODF can be written for *n* sites in a concise form as

$$NODF = \frac{100}{\binom{n}{2}} \sum_{k < l} O_{kl}; O_{kl} = \begin{cases} \frac{a_{kl}}{a_{kl} + b_{kl}} & \text{if } b_{kl} > c_{kl} \\ 0 & \text{otherwise} \end{cases} \quad (1)$$

In words, NODF is 100 times the sum of paired overlap values (*O_{kl}*) for which species totals are lower for the second site than for the first, divided by the number of all possible site pairs.

The PRN approach

As mentioned in the Introduction, an alternative view is that both similarity (overlap) and dissimilarity (more precisely, its richness difference component) should influence with equal weight the measurement of nestedness. The following function satisfies this requirement:

$$\bar{N}_{rel} = \frac{1}{\binom{n}{2}} \sum_{k < l} Nrel'_{kl}; Nrel'_{kl} = \begin{cases} \frac{a_{kl} + |b_{kl} - c_{kl}|}{a_{kl} + b_{kl} + c_{kl}} & \text{if } a_{kl} > 0 \\ 0 & \text{otherwise} \end{cases} \quad (2)$$

(mean relativized nestedness, Podani and Schmera 2011). This is based on the decomposition of the total number of species for a given pair of sites (*m* = *a* + *b* + *c*) into three terms, *a*, *|b - c|* and 2min(*b*, *c*). While the first two (overlap and richness difference) contribute to nestedness positively, the third reflects a property that is antithetic to nestedness (Baselga 2010), namely, species replacement. The rationale in making this contrast is that the higher the number of species in site *k* that are replaced by the same number of species in *l*, the larger part of *m* contradicts nestedness. Relativization is achieved by division with *m* and the mean value is obtained for all possible pairs of sites. Then, for easy comparison with NODF, \bar{N}_{rel} is multiplied by 100 to obtain the percentage relativized nestedness (PRN).

If nestedness is understood to exist for unequally rich sites only, then the condition of positive support is further restricted via the mean relativized strict nestedness function given by:

$$\bar{N}'_{rel} = \frac{1}{\binom{n}{2}} \sum_{k < l} Nrel'_{kl}; Nrel'_{kl} = \begin{cases} \frac{a_{kl} + |b_{kl} - c_{kl}|}{a_{kl} + b_{kl} + c_{kl}} & \text{if } a_{kl} > 0 \text{ and } b_{kl} \neq c_{kl} \\ 0 & \text{otherwise} \end{cases} \quad (3)$$

Its value multiplied by 100 gives the percentage relativized strict nestedness (PRSN).

Some basic features of pairwise measures

Dependence on the order of sites

The original description of NODF (see p. 1230 in Almeida-Neto et al. 2008) as well as Eq. 1 implicitly suggest dependence on the ordering of the columns. Consequently, example matrices **A** and **B** given below have drastically different NODF values (100: maximum nestedness vs 0: no nestedness, respectively),

$$\mathbf{A} = \begin{Bmatrix} 1 & 1 & 1 \\ 1 & 1 & 0 \\ 1 & 0 & 0 \end{Bmatrix} \text{ and } \mathbf{B} = \begin{Bmatrix} 1 & 1 & 1 \\ 0 & 1 & 1 \\ 0 & 0 & 1 \end{Bmatrix} \quad (\text{Ex. 1})$$

although they represent the same artificial meta-community. This order-dependence of a nestedness measure might reflect a clear ecological concept (in this case nestedness is interpreted as a gradient analysis, see examples and further references in Lomolino 1996), or might be an undesirable property of the measure (in case of bipartite networks, for instance). To remove the dependence of NODF on the order of sites, Eq. 1 can be modified in the following manner:

$$NODF_{max} = \frac{100}{\binom{n}{2}} \sum_{k < l} Sc_{kl}; Sc_{kl} = \begin{cases} \frac{a_{kl}}{a_{kl} + \min(b_{kl}, c_{kl})} & \text{if } b_{kl} \neq c_{kl} \\ 0 & \text{otherwise} \end{cases} \quad (4)$$

That is, NODF_{max} is 100 times the sum of paired overlap values for which the column totals differ (*Sc*) divided by the number of all possible pairs. The original definition (as reformulated in Eq. 1) gives results identical to those produced by Eq. 4 only if column totals decrease monotonically from left to right. It is easy to see that for any other ordering

the original NODF measure gives lower values, while formula (4) produces unique and maximum value irrespective of how the columns (and rows) of the matrix are presented (order invariance), hence its subscript. In Eq. (4), ordering is ensured implicitly by the $\min(b, c)$ operation in the denominator, which makes pre-ordering unnecessary. Thus, 'DF' in the name of the coefficient seems to reflect 'different fill' rather than 'decreasing fill'. Examination of Eq. 2 and 3 shows immediately that PRN and PRSN are also insensitive to the order of columns, because $Nrel$ and $Nrel'$ are symmetric for b and c .

Similarity vs dissimilarity in quantifying nestedness

Actually, the paired overlap index embedded in Eq. 1 and 4 has long been known in ecology as Simpson similarity [$S = a/(a + \min(b, c))$, Simpson 1943, see also Koleff et al. 2003]. Therefore, 1) NODF is 100 times the mean Simpson similarity of site pairs if column totals decrease strictly monotonically from left to right in the matrix, and 2) $NODF_{max}$ is 100 times the mean Simpson similarity of site pairs if they have unequal column totals. That is, nestedness is inherently equated by similarity. This contradicts the suggestion that beta diversity (i.e. overall dissimilarity) partly reflects nestedness, because these two share a common component (Harrison et al. 1992, Baselga 2010, Schmera and Podani 2011). In contrast to NODF and $NODF_{max}$, PRN and PRSN (Eq. 2–3) express nestedness in terms of similarity and dissimilarity (richness difference) as well. Consequently, as suggested earlier (Podani and Schmera 2011), richness difference ($|b - c|$) may be the joint fraction of beta diversity and nestedness (if $a > 0$ for PRN and if $a > 0$ and $b \neq c$ for PRSN). If one wishes to judge the relative importance of overlap and richness difference influencing the values of PRN and PRSN, the percentages can be decomposed into parts coming from these two sources, allowing a detailed interpretation of results (Podani and Schmera 2011) which is not feasible via the NODF and $NODF_{max}$ approaches.

We demonstrate by examples that whenever the nestedness element of beta diversity is meant, it is understood that nestedness has components other than similarity or overlap. Consider the following two pairs of sites

k	l	k	l	
0	1	0	1	
1	1	1	1	
1	1	1	1	
1	0	1	0	(Ex. 2)
1	0	1	0	
1	0	0	0	
1	0	0	0	

Both pairs contribute equally ($O = S_c = 0.66$) to the sum in Eq. 1 and 4. As a consequence, NODF and $NODF_{max}$ neglect the fact that in the first pair a larger subset of species exhibits nested pattern than in the second, so that in this sense the nestedness value should be larger for the first pair. This difference is caused by species that make the first site pair more dissimilar than the second, so that, as said above, there is a beta diversity component in nestedness which is ignored by NODF and $NODF_{max}$. In contrast, PRN and PRSN do make distinction between these two pairs of sites

with the desired result, because $Nrel = Nrel' = 0.71$ for the first pair, whereas $Nrel = Nrel' = 0.6$ for the second.

The treatment of ties and the concept of perfect nestedness

Although nestedness is often regarded as a straightforward concept, its measurement may follow two distinct lines for site pairs that have identical species totals ('tied sites'). For three pairwise measures (Eq. 1, 3 and 4), the means are calculated such that site pairs which do not satisfy the given condition ($b > c$ or $b \neq c$) contribute by zero to the numerator, while they are still counted in the denominator. Consequently, site pairs with tied column totals are negative contributors to the nestedness value. This implies the understanding that the pairwise nestedness relationship is restricted to a 'poorer' site and a 'richer' one: 'in a nested pattern the species composition of small assemblages is a nested subset of the species composition of large assemblages' (Almeida-Neto et al. 2008, Ulrich et al. 2009). This is not so with Eq. 2 in which tied site pairs contribute positively to the numerator, and therefore to the final mean value. Similarly to PRN, the mean Simpson similarity (\bar{S} , no equation given) also considers tied site pairs positively. Conceptually, these functions view the nestedness relationship symmetrically for tied site pairs. This is consistent with the definition of the Wright and Reeves (1992) N_c measure, which counts 'the number of times a species' presence at a site correctly predicts its presence at equally rich or richer sites' (Wright et al. 1998). (Note that $N_c = \sum_{k < l} a_{kl}$.) For analyzing bipartite networks, Araujo et al. (2010) suggested a measure of nestedness in which tied pairs are also counted positively (see their Fig. 4). Those authors commented that the 'nestedness of a matrix is a measure of how much its elements can be packed without holes' – suggesting agreement with the symmetrical approaches. Also, it is obvious from Definition 1 in Mannila and Terzi (2007) that those authors consider tied site pairs as contributors to full nestedness.

The issue of how tied site pairs are handled includes a problem related to the conceptual definition of nestedness: pairs of sites (and entire communities) are regarded maximally (or perfectly) nested by O , S_c and $Nrel'$ only if they are in a proper (or strict) subset ($A \subset B$) relationship and site pairs with the same species are not nested at all. On the other hand, $Nrel$ and S correspond to the broad-sense subset relationship ($A \subseteq B$), i.e. sites identical in species composition are also considered perfectly nested.

The examples that follow clarify the problem of ties and offer examination of the ecological meaningfulness of the results yielded by different functions. Site pair kl will have a zero nestedness value for O , S_c and $Nrel'$ in both of the following cases

k	l	k	l	
1	1	1	0	
1	1	1	0	
1	1	1	0	(Ex. 3)
1	1	0	1	
1	1	0	1	
1	1	0	1	

This may not always be appropriate, however, because these two pairs represent very different ecological and set theoretical

situations. The sites of the first pair are identical in all species and therefore fulfill the subset property of nestedness ($A \subseteq B$). Thus, in Ex. (3) the first pair has a contribution of $Nrel = 1$ (i.e. PRN = 100%), the second $Nrel = 0$ (i.e. PRN = 0%). The same is true for the Simpson index. We note that the left pair has perfect prediction of site presences, and packing is without holes, showing the consistency of PRN and \bar{S} with two other global approaches (N_c and Araujo et al.'s method). Accordingly, the left pair in Ex. 3 is completely nested, as opposed to the right pair. Nevertheless, in calculating NODE, $NODF_{max}$ or PRSN, the latter pair in which we find no species in common, is just as influential as the left one: both are counted only in the denominator. Ecologically, and set-theoretically as well, it is unfortunate that NODE, $NODF_{max}$ and PRSN do not discriminate between cases with complete overlap and complete segregation. In our view, therefore, PRN and mean S handle the problem in an ecologically more meaningful manner.

The meaningfulness problem is illuminated further by the following example, derived by slightly modifying the previous one

$$\begin{array}{cc|cc}
 k & l & k & l \\
 1 & 1 & 1 & 0 \\
 1 & 1 & 1 & 0 \\
 1 & 1 & 1 & 0 \\
 1 & 1 & 1 & 1 \\
 1 & 1 & 0 & 1 \\
 1 & 1 & 0 & 1
 \end{array} \quad (\text{Ex. 4})$$

Here, the situation is perhaps even worse than above: sites in the second pair, which have only one species in common and differ in 5, contribute positively to NODE, $NODF_{max}$ and PRSN ($O = Sc = Nrel' = 0.33$), while the first pair does not ($O = Sc = Nrel' = 0$). Thus, if we insist upon the strict definition of nestedness (i.e. pairwise nestedness is positive only if species totals differ) we obtain a certainly anomalous result. It does not seem ecologically justifiable that any pair of sites can contribute positively to nestedness even though they have only one species in common just because they have different numbers of species, while another pair of sites which contain the same number of species (some or all identical), contributes negatively (being counted in the denominator, while contributing by zero to the numerator). Moreover, the left pair is very close to perfect strict nestedness, because only one '1' must be replaced by '0' to achieve this. On the other hand, that the right pair is not anti-nested (i.e. $a = 0$) is caused only by a single species, further questioning the suggestion that the right pair contributes more to nestedness than the left one. These anomalies are resolved by the $Nrel$ function because it takes the value of 1 for the first pair and 0.33 for the second, so the contributions to PRN are remarkably different and ecologically meaningful.

As a final example demonstrating the tie problem, let us examine another pair of sites with the same number of species (3) such that each site has a single unique species ($a = 2$, $b = 1$, and $c = 1$):

$$\begin{array}{cc}
 k & l \\
 1 & 0 \\
 1 & 1 \\
 1 & 1 \\
 0 & 1
 \end{array} \quad (\text{Ex. 5})$$

For this pair, $O = Sc = Nrel' = 0$, showing that these functions do not check whether nestedness pattern is shown by at least part of the data set. However, even if $b = c$, one might argue that there is a subset of species for which a nested pattern is obvious. It is depicted adequately by $Nrel$, which produces a value of 0.5 for Ex. 5. This considers the overlap fraction positively, implying that presence of 50% of the total number of species is correctly predicted by either site with respect to the other. This is consistent with the view that tied sites can be positive contributors to the overall measure of nestedness, i.e. to PRN.

Sensitivity (or conditioning)

The usual requirement for statistical functions and estimators is that small changes in the data should cause proportionally small changes in the results (well-conditioned measures, Gentle et al. 2004). However, nestedness measures that consider ties negatively are more sensitive to changes in data structure than those accepting tied sites, as the following example illustrates

$$\begin{array}{cc|cc}
 k & l & k & l \\
 0 & 1 & 1 & 1 \\
 1 & 1 & 1 & 1 \\
 1 & 1 & 1 & 1 \\
 1 & 1 & 1 & 1 \\
 1 & 0 & 1 & 0
 \end{array} \quad (\text{Ex. 6})$$

The first pair of sites contributes by 0 to the sum in formulae 1, 2 and 4 because the column totals agree, but when the single 0 value in k is modified to 1 (to obtain the pair on the right), then the contribution will jump to 1 because l is now completely nested in k . That is, O , Sc and $Nrel'$ increase from 0 to 1 abruptly. A practical consequence is that these pairwise measures are too sensitive to sampling error: overlooking a single species in the field can inflate the contribution of a site pair to the final value of the nestedness measure considerably. In other words, O , Sc , $Nrel'$ and, to a smaller extent $NODE$, $NODF_{max}$ and PRSN are ill-conditioned (see also Joppa and Williams 2011, for similar view on NODE). This is not so with $Nrel$, and therefore with PRN, because the above change causes $Nrel$ to increase from 0.6 to 1. We note, however, that sensitiveness upon the change of $a = 0$ to $a > 0$ is approximately the same for all pairwise functions.

Metric?

The full name of NODE is misleading, because in statistical ecology the term 'metric' is normally reserved for a condition that a dissimilarity coefficient satisfies the four metric axioms (Legendre and Legendre 1998, p. 274). By definition, therefore, a similarity measure cannot be a metric. Although more recently the term 'metric' has been widely used in the ecological literature to refer to practically any measure, index, function or a coefficient of something – we strongly advise against this loose usage and recommend retaining its former meaning consistently.

Comparisons

The above examples were selected to emphasize some key features of pairwise nestedness measures. However, to draw

a general and more faithful picture on the performance of these approaches, a detailed comparison is required. Here, we give a mathematical evaluation of some basic properties of Sc , $Nrel$ and $Nrel'$, and then compare the three measures using artificial and actual data more exhaustively, including an extensive randomization experiment for examining the sensitivity of overall measures to type I and type II error rates. Note that we do not examine NODF here, because we do not want to deal with the effect of the order of sites. Computations were performed by the SDRSimplex program (Podani and Schmera 2011), <<http://ramet.elte.hu/~podani>>, whereas randomization tests were done by programs NestRand and NestTest, written by the first author.

Analytical comparison

First of all, we examine in which cases do Sc and $Nrel$, and therefore $NODF_{max}$ and PRN provide identical results. By definition, Sc and $Nrel$ equal zero when $a=0$, which is a universal requirement for nestedness measures (i.e. non-zero overlap). For finding further agreements between these coefficients, we evaluate the case

$$\frac{a}{a + \min(b, c)} = \frac{a + |b - c|}{a + b + c} \quad (5)$$

It is clear from this expression that $Sc = Nrel = 1$ when $\min(b, c) = 0$ because in that case $|b - c| = b + c$. However, we must recall the constraint in Sc that $b \neq c$, which imposes a strong limitation on this equality.

After the following rearrangements,

$$\frac{a}{a + \min(b, c)} = \frac{a + |b - c|}{a + 2 \min(b, c) + |b - c|} \quad (6)$$

and then

$$a^2 + 2a \min(b, c) + a |b - c| = a^2 + a |b - c| + a \min(b, c) + \min(b, c) |b - c| \quad (7)$$

we obtain

$$a \min(b, c) = |b - c| \min(b, c) \quad (8)$$

which shows clearly that, for any value of $\min(b, c)$, Sc and $Nrel$ are equal if $a = |b - c|$. Thus, the following inequalities also hold:

$$Sc > Nrel \text{ if } a > |b - c| \quad (9)$$

and

$$Sc < Nrel \text{ if } a < |b - c|, \text{ or if } |b - c| = 0, \text{ but } a > 0 \quad (10)$$

Consequently, for data sets in which most pairwise overlaps (a) exceed richness differences ($|b - c|$) the result is that $NODF_{max} > PRN$. For data sets where the opposite is true, i.e. with overall similarity lower than difference, $NODF_{max} < PRN$.

One may also be interested to see how the two indices perform when the components of m are changed, while m is kept constant. In this regard, Sc and $Nrel$ exhibit

similar behavior: if $\min(b, c)$ increases and consequently $|b - c|$ decreases, then both Sc and $Nrel$ decrease! Thus, when there is considerable similarity (but few identity) in species number among the sites, the two functions are expected to give similar results.

The analytical comparison of $NODF_{max}$ and PRSN shows the same result as the comparison of $NODF_{max}$ and PRN with the exception that if $b = 0$ then both functions result in zero. Finally, the analytical comparison of PRN and PRSN shows that they differ only in the richness identity fraction if $b = c$ (Eq. 3).

Artificial data

We selected 8 artificial model matrices of Almeida-Neto et al. (2008, Fig. 1, matrices a–h) and one matrix of Podani and Schmera (2011, Fig. 1, matrix i). For the random matrix (Fig. 1a) we obtain that $PRN = 55\%$, while for the nested matrices with minimum and maximum fill (Fig. 1c–d), $PRN = 100\%$. These are more meaningful scores ecologically than those obtained by $NODF_{max}$ (Table 1). For instance, the random matrix (matrix a) has a higher $NODF_{max}$ value than the nested matrices with minimum (matrix c) and maximum (matrix d) fill. If one wishes to judge the relative importance of overlap and richness difference in shaping these values, the percentages can be decomposed into parts coming from these two sources, allowing a more detailed interpretation of results. For these three example matrices, overlap plus richness difference are $34 + 21\%$, $69 + 31\%$ and $98 + 2\%$, respectively, showing that the relative and absolute importance of overlap increases in that order (Table 1). For perfect nestedness, of course, both $NODF_{max}$ and PRN are maximum, while our approach provides the additional information that richness difference has much higher contribution to nestedness pattern than overlap (Table 1). For model matrices e–i, $NODF_{max}$ is zero, which accords completely with the richness difference component of PRN. However, the overlap component of PRN is positive for the checkerboard, compartment and gradient models, demonstrating that sites with tied species richness are not neglected in case of PRN. As required for a meaningful nestedness index, both $NODF_{max}$ and PRN are zero for the species replacement and anti-nestedness models, because no sites share even a single species. In this case, the PRSN values are close or identical to the $NODF_{max}$ values (Table 1, last column), but this is not always the case, as the actual examples presented below will demonstrate.

Actual data

Inequalities (9–10) allow us to draw some conclusions regarding data structures by examining the plot of $Nrel$ versus Sc for all possible pairs of sites. On the basis of the mathematical reasoning given in Analytical comparison, we can expect that when all points fall above the diagonal line connecting points [0,0] and [1,1] the data set will be dominated by overlaps between pairs of sites. If all points fall below this line, then richness difference becomes the predominating factor in presence/absence pattern. We have

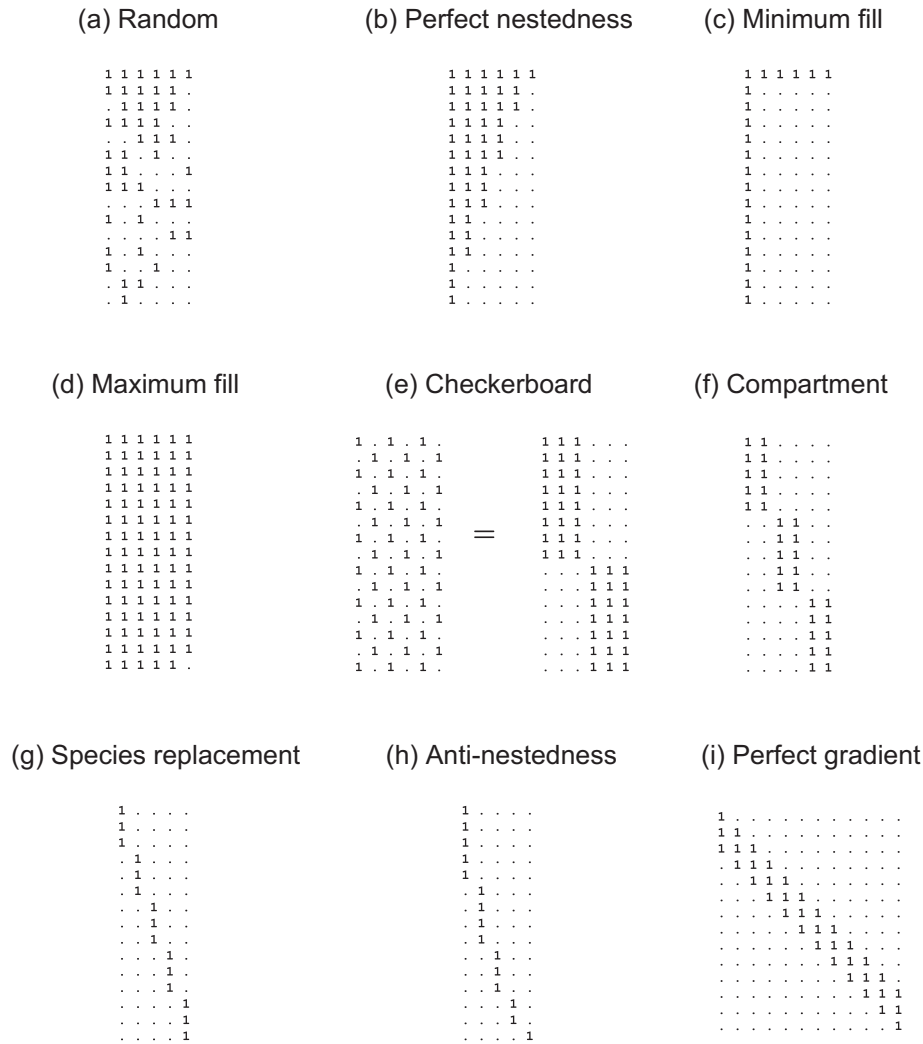


Figure 1. Artificial model matrices of Almeida-Neto et al. (2008, matrices a–h) and Podani and Schmera (2011, matrix i). Names of models as in Podani and Schmera (2011). Note that the checkerboard pattern and the model with two compartments (e) are indistinguishable for order-invariant measures.

selected five radically different actual data sets we used formerly (Podani and Schmera 2011) for demonstrating the decomposition of $a + b + c$ into relative terms. The resulting scatter diagrams are presented in Fig. 2.

The points are most scattered for the heterogeneous data set of floating mat plants (Tatár 2002). For a given value of Sc , there is a wide range of $Nrel$ values, which is especially striking for $Sc = 0$. For the meadow sites (Mueller-Dombois and Ellenberg 1974), most points form a narrow cloud, with the few exceptions representing site pairs that have the same species totals (similarly to the previous example). The point cloud is above the diagonal line reflecting that overlap exceeds richness differences, i.e. Sc is higher than $Nrel$. The situation is the opposite for the Colorado fish metacommunity (Smith 1978): $Nrel$ is higher than Sc in many cases, and most points are positioned below the diagonal line. The Channel Islands bird example (Diamond and Jones 1980) illustrates a balanced situation, the point cloud deviates from the diagonal approximately equally on both sides. Finally, for the desert fish data (known to have

the highest degree of nestedness in ecology, Kodric-Brown and Brown 1993), we obtain only three points (not shown graphically). For three pairs of sites, $Sc = 0.0$ and $Nrel = 0.6$, while for 305 pairs $Sc = Nrel = 1$, and for 70 pairs $Sc = 0$ while $Nrel = 1$. That is, 73 points are on the bottom line, because part of the nestedness pattern is explained by tied sites disregarded by Sc . The difference between $Nrel$ and $Nrel'$ is that $Nrel' = 0$ for the points where $Nrel > 0$ and $Sc = 0$. Graphically it involves movement of all points at $Sc = 0$ to the origin in the $Nrel$ vs Sc plot, whereas the other points remain unchanged. Consequently the behaviour of $Nrel'$ is more similar to $NODF_{max}$ than that of $Nrel$.

Qualitative assessment of the $Nrel$ vs Sc plots may be supplemented by examining means and contributions. Whereas the joint distributions of Sc and $Nrel$ differ considerably, the means and percentages show less discrepancy (Table 2), with some still obvious trends. $PRN > NODF_{max}$ when richness difference (part of beta diversity) is much higher than overlaps (Colorado fish). $NODF_{max} > PRN$ when overlaps exceed more than four times richness differences

Table 1. Comparison of $NODF_{max}$ percentage relativized nestedness and its components (PRN = percentage overlap (similarity) + percentage richness difference, with $a > 0$) for artificial model matrices shown in Fig. 1.

Matrix	$NODF_{max}$	Richness			
		Overlap %	difference %	PRN	PRSN
(a) Random (with 50% fill)	45*	34	21	55	46
(b) Perfect nestedness	100	38	62	100	100
(c) Nestedness with minimum fill	33	69	31	100	33
(d) Nestedness with maximum fill	33	98	2	100	33
(e) Checkerboard	0	40	0	40	0
(f) Compartment	0	20	0	20	0
(g) Species replacement	0	0	0	0	0
(h) Anti-nestedness	0	0	0	0	0
(i) Gradient	0	11	0	11	0

*In Almeida-Neto et al. (2008, Table 2) $NODF = 49$ is given. This is a wrong result; that $NODF = 45$ is confirmed by the ANINHADO program (Guimaraes and Guimaraes 2006).

(meadow). When richness differences and overlaps (similarity) are almost equal, $NODF_{max}$ and PRN are also similar (Channel Islands birds). However, closeness in overlap and difference components does not always lead to similar $NODF_{max}$ and PRN values. As the floating mat plants example demonstrates, large deviation in one direction may be compensated for by more, closely positioned points on the other side of the diagonal, resulting in similar percentages. Yet, the two statistics differ in more than 5 units. The very highly nested desert fish data have only a marginally higher $NODF_{max}$ value than the Colorado fish data (80.7 vs 79.4), while the difference is more pronounced if measured by PRN (99.7 vs 81.9). This dataset is made perfectly nested by changing a single zero value to 1, which is better reflected by the score of 99.7 than by 81.9. For the readers' information, Table 2 includes the PRSN values as well, showing that difference from PRN is usually negligible, with the exception of the desert fish example in which only 6 species occur.

Sensitivity to type I and type II error rates

Following the guidelines given by Gotelli (2000), we used a 'noise test' to examine the sensitivity of nestedness measures to type I and type II error rates. We started with a perfectly nested (i.e. structured) matrix and then gradually perturbed it to obtain increasingly random matrices. A nestedness measure, which is vulnerable to type II error, does not detect significant nestedness even if there is only little randomness in the data, so the curve of right tail probabilities (p) versus noise level (x) start to increase too early. Conversely, a nestedness measure is prone to type I errors if significant nestedness is indicated even when a matrix is greatly randomized, which is reflected by the very low slope of the p-x curve. Thus, plotting right tail probabilities versus the noise level by which a fully nested matrix is perturbed is useful to draw conclusions on both types of errors simultaneously (Fig. 5 in Gotelli 2000).

The errors were estimated in the following manner. We considered four nestedness indices (PRN, PRSN, $NODF_{max}$, mean Simpson), whereas the original $NODF$ was not included because its order dependence would require an additional randomization strategy complicating the study unnecessarily. For each index, we used 4 randomization strategies disregarding degenerate matrices that potentially occur during simulations (i.e. those with zero column or row totals): 1) full randomization by maintaining the number of presences in the data, 2) randomization by keeping species (row) totals fixed, 3) randomization by keeping site (column) totals fixed, and 4) randomization such that both column and row totals (i.e. all marginal totals) are fixed. We assumed that test results depend on how the matrix is saturated with presences, so we decided to use three different matrices: low fill (32%), medium fill (53%) and high fill (73%, Fig. 3, top row). Each model matrix was perturbed step-by-step to obtain test matrices. In case of the full randomization model, 20 pairs of randomly chosen values in the matrix were interchanged in each step. For the fixed row total model, two values were swapped in every row, whereas in case of the fixed column total model, two random values were transposed in every column of the matrix in each step. For the fixed row and column totals null model, the test matrices were created in the same way as for the fixed row total model, because fully nested matrices lack checkerboard submatrices without which perturbation by the swapping method cannot be launched. (Note that Gotelli 2000, used fixed row totals for perturbation to create test matrices for all types of null models.) That is, since matrix size is 20×20 , every step involves 20 elementary changing operations for all the four strategies. Complete randomness is achieved after approximately 20 steps (400 interchanges) but we run the analysis up to $x = 50$ steps.

Each test matrix was subjected to further randomization to obtain the reference distribution of the four nestedness statistics. We did 999 complete randomizations of the test matrix, from which we calculated the right tail probabilities that the random values exceeded the actual statistic for the test matrix. Each randomization was achieved through Markov Chain Monte Carlo (MCMC) simulation involving the same type of rearrangement that we used to create the test matrices themselves, except for the fixed row-fixed column total model in which we used the trial swap method (Miklós and Podani 2004) to ensure equiprobability distribution of all possible matrices. Burn-in was 1000, whereas sampling was made from the MCMC sequence at 1000-step intervals, which ensures adequate mixing because matrix size is 400. MCMC was run until 1000 values were obtained which offers a sufficiently good estimation of the sampling distribution of the four statistics for each noise level, null model and each value of fill.

The above procedure was repeated 100 times for every combination of null model, fill value and nestedness index, and the results were averaged for each value of x for each combination (Fig. 3). It strikes the eye immediately that the four measures behave almost indistinguishably in cases of the less constrained models (the first 3 null models \times 3 fill values). The shape of the curves is also fairly similar in these cases suggesting that, on average, all measures have fairly similar statistical properties. Low slope at the beginning,

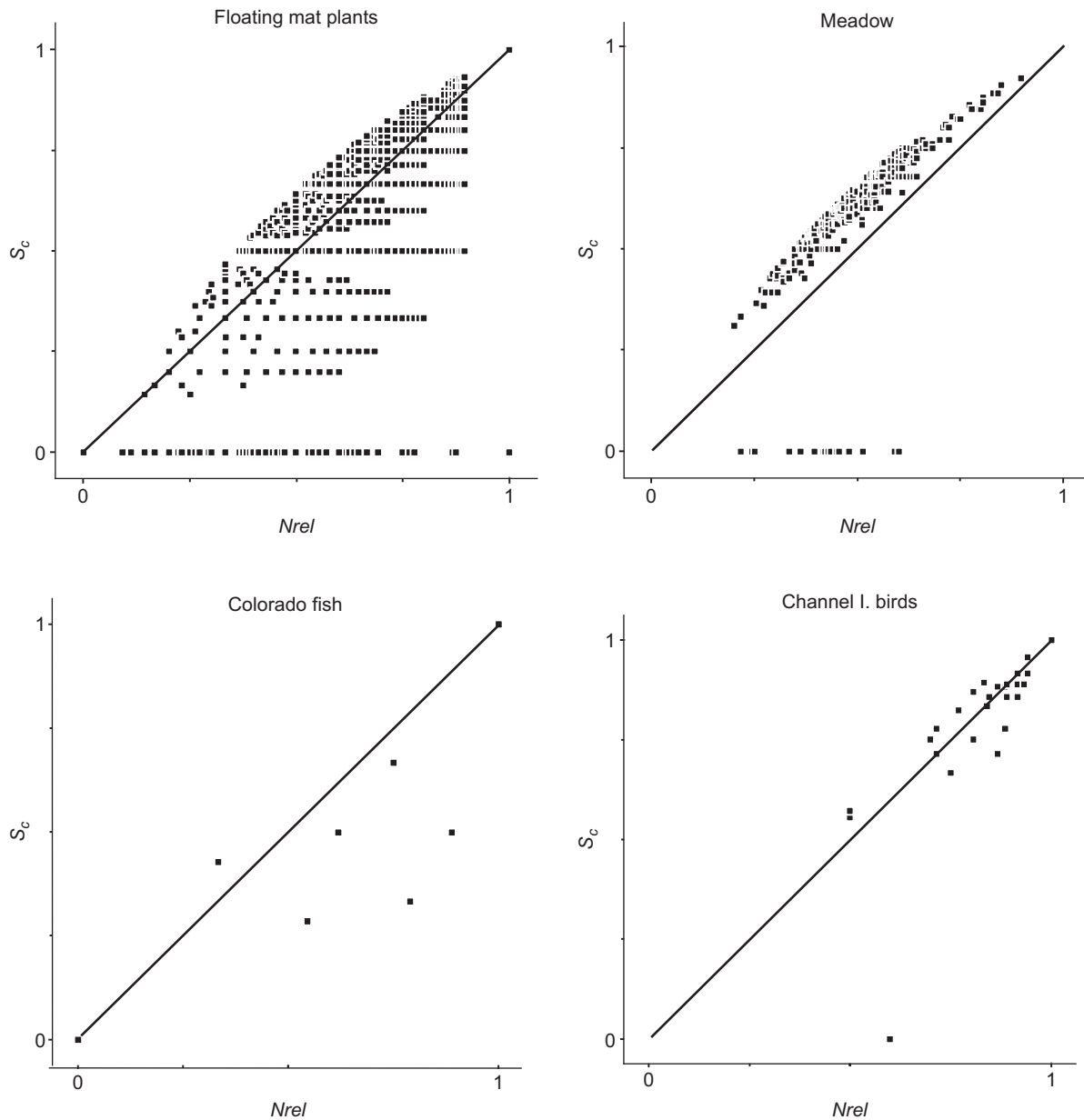


Figure 2. Relationship between N_{rel} and S_c for four actual data sets. Diagonal lines connect points [0,0] and [1,1] to enhance interpretation. The axes are not centered to the origin in order to make points at $S_c = 0$ visible.

dramatic increase afterwards, and then leveling off after fair randomness is achieved indicate that the measures are not susceptible to type I and type II errors (see the ideal curve in Gotelli 2000, his Fig. 5). Nevertheless, there are subtle differences that deserve our attention. Of the nine cases, the fixed column total model for the high-fill data (Fig. 3)

exceeds the conventional $p = 0.05$ level the earliest, after five steps. This means that under the corresponding null model (site totals are constant) the chance for committing type II error is the highest for dense data matrices. In the other cases, $x > 10$ steps were needed to leave the $p \leq 0.05$ zone, suggesting higher statistical power (i.e. much lower

Table 2. Comparison of $NODF_{max}$, PRN, PRSN and the mean Simpson index for five actual data sets, showing the two additive components of PRN (overlap and richness difference) as well.

Meta-community	$NODF_{max}$	Overlap %	Richness difference %	PRN	PRSN	Mean Simpson
Floating mat plants	58.7	31.2	32.9	64.1	61.7	0.620
Meadow	58.0	41.4	8.6	50.0	47.4	0.617
Colorado fish	51.4	12.8	46.7	59.5	59.5	0.514
Channel I. birds	79.4	40.1	41.8	81.9	79.7	0.821
Desert fish	80.7	54.8	44.9	99.7	80.7	0.998

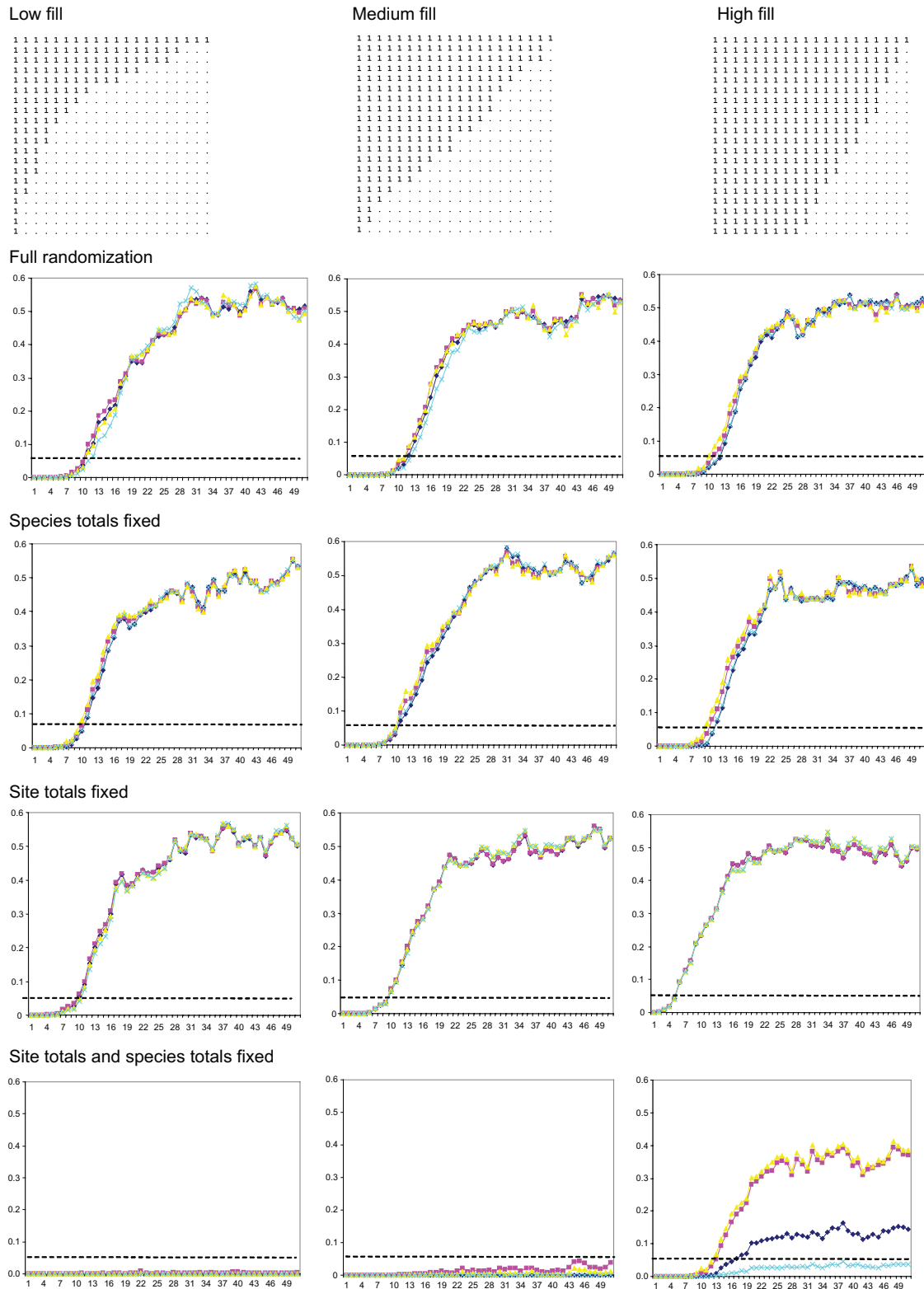


Figure 3. ‘Noise tests’ of four nestedness measures based on three different nestedness patterns (20 species by 20 sites data matrices) and four null models. The x-axis (0 to 50) is the noise level applied to obtain test matrices: $20 \times$ is the number of value pairs transposed in the matrix in full randomization, and x is the number of value pairs transposed within each row (species totals fixed) and each column (site totals fixed) in the second two cases, respectively. For the fourth model, with all marginal totals fixed, perturbation was achieved in the same way as for the fixed species total model. The y axis is the tail probability (p value) obtained from 999 randomizations, with the 0.05 level indicated by a dashed line. Each point is the average of 100 independent runs. The differences between the nestedness measures are so small that the corresponding symbols are hard to distinguish in all but one panels (diamonds: PRN, squares: PRSN, triangles: $NODF_{max}$, X: mean Simpson index).

probability of type II error). The best overall statistical performance is detected for the full randomization model and the matrix with medium fill: here we see the steepest increments at intermediate values of x , that is, the best realization of the ideal curve. Upon scrutiny of figures enlarged, we can also see that for full randomization and the model with species totals fixed, the curves of PRSN and NODF_{\max} run slightly below the curve of the other two functions until complete randomness is achieved. These demonstrate that functions excluding tied site totals are sensitive a little bit more to type I errors (and less prone to type II errors) than those considering tied sites. In other words, on average a little more random matrices are considered by PRSN and NODF_{\max} significantly nested than by PRN and mean Simpson. However, when simulations are constrained so as to keep site totals fixed, no such differences can be revealed.

The most constrained null model, with all marginal totals fixed, provides different results (Fig. 3, bottom panels). For the matrix with low fill, all measures remain much below the $p = 0.05$ level over the entire range of noise, which is indicative of high type I error. The situation is similar for the matrix with medium fill, because only a slight increase of tail probabilities is achieved up to the 50th step. The results are somewhat closer to those of the less constrained models for the matrix with high fill: the two statistics which disregard tied sites (PRSN and NODF_{\max}) perform fairly well because these show the same trend after 10 steps as for the less constrained models. PRN is more vulnerable to type I error and therefore has more power, whereas the mean Simpson index remains below the $p = 0.05$ level, still indicating significant difference even though the other three statistics fall inside the acceptance region.

The present study is completed by the significance tests of data matrices used in this paper as well as those in Podani and Schmera (2011). We use the same procedure as above, i.e. the observed statistics are compared with 999 simulated values. For the small random data set (Fig. 1a), all models and all measures suggest acceptance of the null hypothesis (non-nestedness), such that right tail probabilities were the highest for NODF_{\max} ($p > 0.53$) and the lowest for PRN ($p > 0.26$). For the five actual data sets used in this paper (Colorado fish, meadow, floating mat plants, Channel Island birds and desert fish), all models and all the four measures suggest rejection of the null hypothesis, i.e. all these matrices exhibit nestedness pattern significantly different from random (usually, $p < 0.01$). This suggests that an average PRN value of 50% or higher (Table 2) is a rough indication of significant nestedness by itself at the conventional p value of 0.05, and that further distinction between significant cases would require several orders of magnitude more randomizations than used in this paper (i.e. 10 million randomizations would be necessary to get better estimates of p).

To illustrate how nestedness tests are influenced by an ecological process, we use the islet arthropod data of Rey (1981) who recorded the fauna at irregular intervals for a year to monitor the recolonization of islets after defaunization by insecticides. We took the data from the 10th, 13th, 20th and 53rd weeks after treatment and found that the resulting trends are quite clearly visible in the simplex diagrams (Podani and Schmera 2011). If we now focus our interest on testing only the nestedness pattern, we obtain the

results summarized in Table 3. There is considerable agreement among functions, and a somewhat weaker agreement among the null models. At the first two dates, the faunistic pattern is significantly non-nested, while in case of the third date all but one models allow detecting significant deviation towards nestedness ($p < 0.05$), the exception being the fixed site totals model. By the last date, i.e. one year after treatment, the distributional pattern of arthropods is unequivocally more nested than randomly expected. That is, as far as departure towards nestedness is concerned, recolonization of the island is successful.

Discussion

Nestedness measures may be categorized in several ways, which is helpful for the ecologist when selecting among the various possibilities. Technically, global indices derive a single value directly from the data (e.g. nestedness temperature), whereas measures in the other group operate via calculating pairwise functions. In this paper, interest was focused on the properties of the latter group (Fig. 4). We did not examine N_c because of its dependence on matrix size, a problem solved by using relativized pairwise measures and their means. NODF is the only function that depends on the arrangement of columns in the data matrix. Therefore, we recommend its use only if there is some a priori ordering information on sites (e.g. a well-defined ecological gradient, or a biogeographical sequence such as a set of islands increasing in size, see examples in Lomolino 1996) which must be kept fixed when evaluating nestedness (Almeida-Neto et al. 2008, p. 1230). Otherwise, we suggest a modification of this function which always produces the maximum, and therefore a unique value (NODF_{\max}), demonstrating that pairwise analysis does allow order-invariant solutions for the quantification of nestedness. The other three measures (PRN, PRSN

Table 3. Right tail probabilities for four nestedness measures in case of four actual data sets representing stages of insect recolonization on an island (Rey 1981), with four null models (from top to bottom for each data set: full randomization, randomizing with fixed species totals, randomizing fixed site totals, and randomization with all marginal totals fixed). Each probability value is based on 999 randomizations of the data matrix by MCMC with sampling interval 2.5 times the size of the matrix (no. of species by no. of sites, in brackets). Values significant at $p = 0.05$ are shown in bold.

Sampling date	PRN	PRSN	NODF_{\max}	Mean Simpson
Week 10 (6 × 25)	0.375	0.422	0.622	0.637
	0.280	0.294	0.409	0.377
	0.266	0.276	0.507	0.495
	0.345	0.349	0.497	0.525
Week 13 (6 × 27)	0.387	0.574	0.577	0.134
	0.539	0.710	0.832	0.363
	0.088	0.340	0.375	0.066
	0.388	0.558	0.576	0.135
Week 20 (6 × 33)	0.007	0.006	0.010	0.018
	0.013	0.011	0.007	0.013
	0.142	0.142	0.124	0.124
	0.005	0.003	0.008	0.017
Week 53 (6 × 33)	0.001	0.001	0.001	0.001
	0.008	0.011	0.014	0.007
	0.002	0.002	0.002	0.002
	0.001	0.003	0.002	0.001

and the mean of Simpson index) are also independent of matrix ordering. We think that it is important both theoretically and practically to have order-invariant measures, because our attention can be focused on true community properties unaffected by the manner the data are presented before calculations, which is often a technical issue and does not reflect any genuine ecological relationship. Order invariance appears an especially useful property whenever bipartite networks are evaluated for nestedness (Bascompte et al. 2003) because in these cases no external criteria for ordering are available, yet in these cases NODF has been used extensively (Fortuna et al. 2010).

Our comparative analysis disclosed a conceptual controversy existing in the literature of nestedness, namely, whether site pairs with tied column totals are considered negatively or positively and, consequently, perfect nestedness should be interpreted as a proper subset or as a broad subset relationship. Several global measures such as the nestedness temperature are influenced as much as different permutations of sites with tied totals produce different results (Roberge et al. 2009), a minor aspect of order dependence discussed above. Whether or not to ignore ties appears very critical in pairwise comparisons. The original NODF, $NODF_{max}$ as well as PRSN consider tied pairs as negative contributors to nestedness (Fig. 4). The problem with these functions is that they are relatively sensitive to minor changes in the data and the results may be at variance with intuitive expectations of the ecologist (e.g. in the treatment of fully identical and fully segregated site pairs with equal richness). Users should keep these considerations in mind when selecting any of these methods. We argue that measures are well-conditioned and results are more interpretable ecologically when tied pairs are counted positively, i.e. nestedness is understood in a less restrictive manner. This is achieved by *Nrel* and the derived PRN function or the mean of the original Simpson similarity index: these consider site pairs with identical species totals positively, no matter whether $b = c > 0$ or $b = c = 0$. We note only that change from *Sc* to *S* means that all points in the *Nrel* vs *Sc* plot at *Sc* = 0 move up to positions determined by the corresponding $S = a/(a + b)$ value, thus $\bar{S} \geq NODF_{max}$.

As a relaxation of the dilemma over this issue, we have demonstrated (Podani and Schmera 2011, Table 2) that the broad and strict versions of the percentage relativized nestedness measure (PRN and PRSN, respectively) provide only marginally different results when applied to actual data sets, especially if the number of species is large. It means that the dispute over including or excluding tied sites in pairwise comparisons is often without practical relevance.

A more critical conceptual issue concerns which features of presence-absence pattern should be incorporated in the nestedness measure. $NODF$ and $NODF_{max}$, being derived from the Simpson similarity coefficient, overemphasize the overlap component of nestedness and underrate the beta diversity component (Fig. 4). While the use of $NODF$ solves certain statistical problems detected for global indices (Almeida-Neto et al. 2008), the implicit restriction to similarity has not yet received sufficient attention. For the PRN (percentage relativized nestedness) function (Podani and Schmera 2011), richness difference – a fraction of beta diversity – is also considered as a direct indicator of nestedness pattern, which agrees well with the observation of many ecologists that only the species replacement component of beta diversity is antagonistic to nestedness. Not surprisingly, then, the performance of conditional similarity (*Sc*) and relativized nestedness (*Nrel*) functions may differ remarkably, depending on internal data structure. Theory suggests and examples demonstrate that fair agreement between them is expected when richness differences are minor; otherwise discrepancy may be substantial. The observation that $NODF_{max}$ and PRN do not contradict radically each other probably comes from the fact that calculating arithmetic averages of the constituting *Sc* and *Nrel* functions diminishes differences in other distributional properties of these statistics.

There is a current trend to incorporate null models and permutation tests into newly developed measurement techniques in statistical ecology. As our study shows, the examination of the behaviour of new methods based on some example situations should complement more sophisticated simulation studies. Without doing so, widespread application of measures and their statistical tests may lead to false or

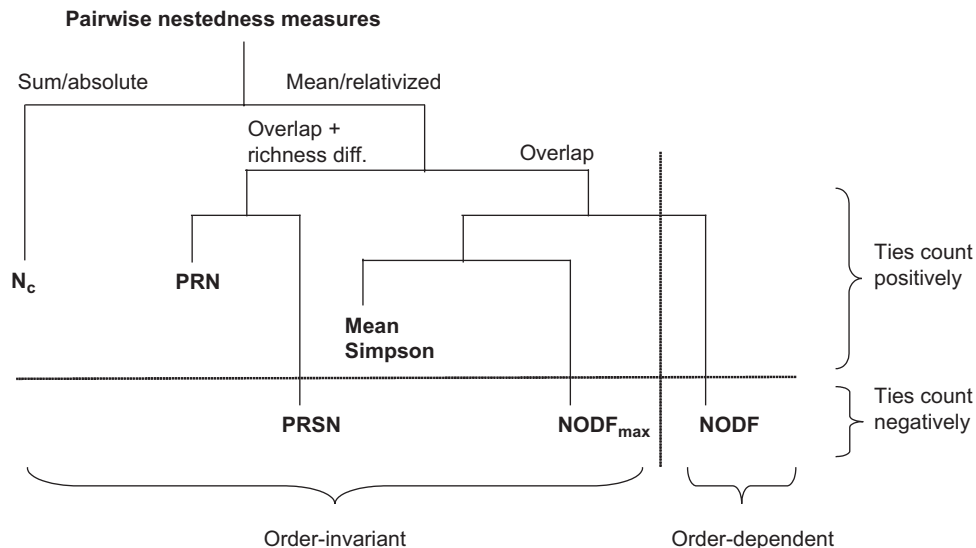


Figure 4. A tree-like summary of conceptual and technical issues to be considered when selecting pairwise measures of nestedness.

unsubstantiated conclusions. The simulations revealed that statistical testing of nestedness pattern via pairwise measures is practically free from type I and type II errors for the less constrained null models. The exceptions are matrices with high fill in cases when site totals are fixed during randomizations. Jonsson (2001) suggests not to use the fixed site totals model in nestedness tests anyway. The randomization model with all marginal totals fixed has completely different statistical properties. For low and medium fill, type I error is very high, whereas this error decreases as matrix fill increases. Then, for high matrix fill, the differences between statistics become more substantial than above: PRSN and NODF_{max} outperform PRN and especially mean Simpson. In actual situations examined in this paper, differences between null models and observed measures did not influence the conclusions (except for the arthropod data in week 20). The practical consequence is that there is a set of measures with high statistical power for nestedness analysis, which is not so with some global indices of nestedness (Jonsson 2001, Almeida-Neto et al. 2008) and with measures of species co-occurrence patterns (Gotelli 2000) whose results depend much more on the underlying null models.

According to Ulrich et al. (2009), NODF has the appealing feature that total nestedness can be decomposed into contributions by columns and rows in the data. However, PRN and PRSN can also be extended easily to this direction, by calculating the weighted average of PRN_{cols} and PRN_{rows} (and PRSN_{cols} and PRSN_{rows}, respectively). In our view, therefore, the PRN measure satisfies all requirements for being an ecologically meaningful and interpretable statistical function for measuring nestedness. Further advantage of PRN is its compatibility with the conceptual and methodological framework we proposed (Podani and Schmera 2011) for elucidating pattern in presence-absence data. The so-called SDR simplex approach is suitable to analyzing the relative weight of nestedness, beta diversity, and other features in shaping (meta-)community assembly both graphically and numerically.

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