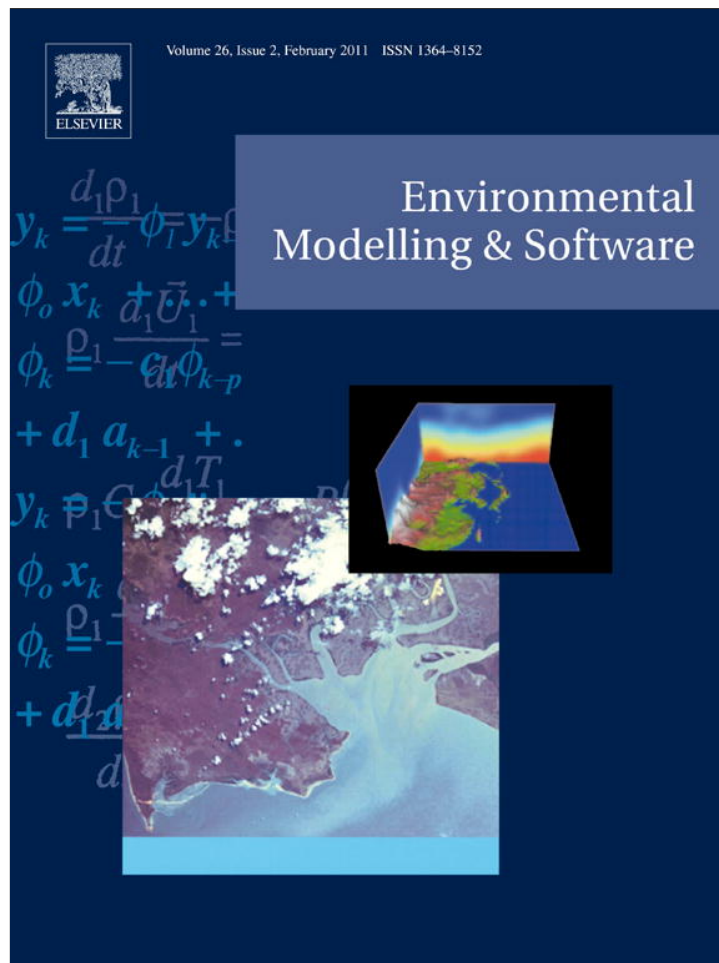


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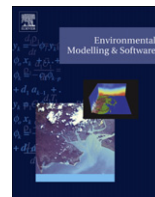
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A straightforward computational approach for measuring nestedness using quantitative matrices

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ABSTRACT

Nestedness has been one of the most reported patterns of species distribution in metacommunities as well as of species interactions in bipartite networks. We propose here a straightforward approach for quantifying nestedness using quantitative instead of presence–absence data. We named our estimator WNODF because it is a simple modification of the nestedness index called NODF. We also introduce the NODF-Program that calculates the above described nestedness metrics as well as metrics for idiosyncratic species and sites. Statistical inference is done through a null model approach, in which the user can choose among five null models commonly used for presence–absence matrices as well as three randomization algorithms for matrices that contain quantitative data. The program performs multiple analyses using many matrices. Finally, the NODF-Program provides four sorting options that, together with the null algorithms, cover a range of possibilities to test hypotheses on the possible mechanisms producing nested patterns. By using a set of model matrices, we showed that WNODF differentiates nested matrices with distinct structures and correctly identifies matrices with no nested pattern as having zero degree of nestedness.

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Software availability

Name of the software: NODF-Program

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Platform: Fortran 95

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1. Introduction

The search for species distribution patterns is a major topic in ecology. It is assumed that widespread patterns in species distribution points to the occurrence of some similar process among diverse ecological systems, allowing the formulation of more general hypotheses. Currently, one of the most frequent and widely

studied patterns related to the distribution of species in metacommunities or along gradients has been the nested subset pattern (Wright et al., 1998; Ulrich and Gotelli, 2007; Ulrich et al., 2009). A consensual definition of nestedness for metacommunities is that it is a community-wide pattern in which assemblages (i.e. islands, local communities or patches) with lower species richness tend to be proper subsets of the species found in the richer assemblages. Hence, nestedness requires a gradient in richness, and nestedness among assemblages with identical richness should not exist (see Almeida-Neto et al., 2008).

In metacommunities, maximum (or perfect) nestedness of species composition is achieved when each site contains a subset of those species found in the richer sites. Such a concept is also applied to species incidences (i.e., the number or proportion of local assemblages in which a given species occurs), in which maximum nestedness means that each species is found in a subset of the sites in which those species with higher incidences occur. Nestedness is also a pattern commonly found in bipartite networks of interacting species (Bascompte et al., 2003), chiefly in the non-symbiotic mutualistic ones (Guimarães et al., 2007).

An important step toward our recent understanding of nestedness was the introduction of the matrix temperature concept and

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its associated metric T as well as its companion software (*Nestedness Temperature Calculator*) by Atmar and Patterson (1993). According to them, T was thought to be “at once an empirical measure of the degree of uncertainty in species extinction order and an indication of the relative stability of the constituent populations” (Atmar and Patterson, 1993). However, T does not increase with “extinction disorder”, contradicting the view that matrix temperature is a measure of disorder (see Almeida-Neto et al., 2007). In fact, T is a measure of the symmetry of the distribution of unexpected absences and presences, respectively, on both sides of the perfect nestedness boundary line. Unfortunately, some authors have equated the concept of nestedness with the matrix temperature index and pointed out that nestedness is a measure of order (i.e., the inverse of entropy). Actually, any non-random metacommunity pattern (see examples in Leibold and Mikkelsen, 2002; Hausdorf and Hennig, 2007) is a measure of order, but there is no reason to interpret it as the inverse of noise or temperature.

Previous nestedness indices dealt with presence–absence data only. Recently, Galeano et al. (2009) developed a Weighted-Interaction Nestedness Estimator (hereafter WINE) based on the distance concept peculiar to the temperature index to calculate nestedness over frequency matrices. Their approach is based on Corso et al. (2008); (see also Levartoski et al., 2010) nestedness estimator for presence–absence data, in which a Manhattan distance is calculated from each of the matrix cells containing a link to the cell corresponding to the intersection of the row and columns with the lowest marginal totals. The main difference is that WINE uses a weighted Manhattan distance to account for the frequency data. Like most nestedness estimators, WINE is based on the concepts of unexpected absences and unexpected presences (Patterson and Atmar, 1986; Cutler, 1991). Here we show that because WINE establishes a maximum benchmark according to the empirical data, it does not differentiate nested patterns with maximum or minimum fill from the maximally informative nested pattern (see Atmar and Patterson, 1993; Almeida-Neto et al., 2008). Another property of WINE is that its absolute values (called WIN) cannot be directly compared because they increase with matrix size. To correct for that, Galeano et al. (2009) used the same approach as Wright and Reeves (1992), which is normalizing the index through a randomization procedure. Thus, observed WINE values approach zero when they are close to the mean value of random matrices and approach one when they are close to the maximum nested value for that specific matrix. Then, if the matrix is less nested than the mean value of nestedness of the randomized matrices, WINE will produce negative values (see also Table 2 in Galeano et al., 2009). Such normalization means that WINE is dependent on a specific null model, i.e., its calculation will depend on the choice of a certain randomization algorithm, which entails a choice of a null model.

Galeano et al.'s new estimator is an important initiative and follows a general tendency among ecologists of developing community-wide descriptors for abundance data in metacommunities and interaction networks (Bersier et al., 2002; Banasek-Ritche et al., 2009; Ulrich and Gotelli, in press). On the other hand, WINE is not fully consistent with a simple matrix property derived from the nestedness concept: differences in column (row) totals, i.e., differences in species richness and/or species incidences (see Almeida-Neto et al., 2008, to see similar inconsistencies in presence–absence estimators). The ecological interpretation of this matrix property is maximum heterogeneity in species richness and/or in the incidences of species. For bipartite interaction networks, it means maximum differences in the number of links among the species. A second matrix property derived from the nestedness concept is the maximum overlap of

the non-empty cells. The ecological interpretation of this property is maximum similarity in species composition given differences in species richness or maximum co-occurrence among species given differences in species incidences. These two simple properties are the necessary and sufficient conditions for a perfect nested pattern based on presence–absence data. We define nestedness for quantitative matrices as a special case of nestedness in which the two previously cited conditions are satisfied together with a third property: that all 2×2 submatrices follow the form: $\begin{pmatrix} a & b \\ c & d \end{pmatrix}$; ($a > b$, $a > c$, $d < b$, $d < c$). Note that rows and columns of these submatrices do not have to be adjacent. Thus, in metacommunities a perfect nestedness for quantitative matrices occurs when a perfectly nested pattern for presence–absence data also shows a pattern in which (1) all populations making up any local assemblage have lower abundances than their conspecific populations in richer assemblages, and (2) all co-occurring species have distinct abundances, with their within-community abundance orders being positively related to their between-community incidences. If only condition (1) is satisfied ($a > b$, $a \leq c$, $d \geq b$, $d < c$), then we have a perfect nested pattern only in species composition. Similarly, if only condition (2) is satisfied ($a \leq b$, $a > c$, $d < b$, $d \geq c$), then we have perfect nestedness only in species incidences.

We propose a straightforward approach to quantifying nestedness using quantitative (instead of presence–absence) data that is fully consistent with our general definition of nestedness and with predictions derived from the nestedness concept. Our quantitative estimator is a simple modification of the NODF index (Almeida-Neto et al., 2008), which we call WNODF (Weighted Nestedness metric based on Overlap and Decreasing Fill). To permit the measurement of nestedness according to any sequence of columns and/or rows, NODF and WNODF quantify whether a given sequence of columns (rows) shows decreasing marginal totals (i.e., incidences or richness). By using this sequential approach, we can quantify nestedness according to any criterion or gradient related to species or sites. We also introduce a new software program to the nestedness index proposed here: the NODF-Program. This software permits the easy quantification of both WNODF and NODF as well as two other established estimators for incidence data, T and discrepancy (Brualdi and Sanderson, 1999).

2. The NODF index for abundance data: WNODF

Given a matrix with n columns and m rows, let F refer to the number of cells with non-zero values for any column c_i or row r_i , where i indicates column or row position and c_1 and r_1 correspond to the upper left corner of the matrix. Thus, the paired nestedness between any pair of columns c_i and c_j ($j > i$) will be greater than zero only if $F(c_i) > F(c_j)$. For any pair of columns in which $F(c_i) \leq F(c_j)$, the paired nestedness will be zero. Then, the weighted value of paired nestedness for any pair of columns is calculated as the percentage of cells in c_j that have lower values than cells of the same row in c_i . Then, we can calculate a mean nestedness value for all pairs of columns as:

$$\text{WNODF}_c = 100 \sum_{i=1}^{n-1} \sum_{j=i+1}^n \frac{k_{ij}}{N_j} \quad (1)$$

where k_{ij} denotes the number of cells with lower values in c_j and N_j is the total number of non-empty cells in c_j . Likewise, for any pair of rows r_i and r_j ($j > i$), there can be a paired nestedness higher than zero only if $F(r_i) > F(r_j)$. Similarly, the paired nestedness between any pair of columns will be zero if $F(r_i) \leq F(r_j)$. Following the same simple procedure used for columns, the value of weighted paired

nestedness for any pair of rows is calculated as the percentage of cells in r_j that have lower values than those cells in r_i located in the same column positions.

Finally, we can calculate the mean paired nestedness for the $n(n-1)/2$ pairs of columns as well as for the $m(m-1)/2$ pairs of rows. Equivalent to the NODF index for presence–absence matrices (Almeida-Neto et al., 2008), WNODF can be calculated as:

$$\text{WNODF} = \frac{2(\text{WNODFc} + \text{WNODFr})}{m(m-1) + n(n-1)} \quad (2)$$

3. Idiosyncrasy

Atmar and Patterson (1993) termed species that decrease the matrix-wide nestedness “idiosyncratic”. One goal of nestedness analysis has always been to identify such “deviating” species that run counter to the ecological and geographic gradients of species occurrences and cause a nested subset pattern (Ulrich et al., 2009). Previous idiosyncrasy analyses have been performed using solely the temperature concept because the *Nestedness Temperature Calculator* by Atmar and Patterson (1995) was the only software that allowed this type of analysis.

We introduce indices for idiosyncratic species and sites based on WNODF and the discrepancy index of Brualdi and Sanderson (1999). In the case of WNODF, we define species or site idiosyncrasy as the number of paired cells for each column or row, where $F(c_j) > F(c_i)$ ($i < j$) and where the cells in c_j (r_j) have higher values than those cells in c_i (r_i). Indices are normalized by dividing the count by the number of incidences of the respective row or column. Note that this definition is also applicable to incidence matrices.

For the discrepancy-based index, we use the minimum number of incidences (separately calculated for rows and columns) that have to be shifted within rows (columns) to achieve the maximum nestedness possible for a given matrix (Ulrich and Gotelli, 2007). We define the discrepancy-based degree of idiosyncrasy as the number of these necessary shifts for each column and row divided by the total number of incidences in the respective row or column.

Note that the power to detect idiosyncrasy depends on the number of incidences per row or column. Power is highest at intermediate number of occurrences. Note further that the power of statistical inference depends on the null model. Null models that do not preserve row and column totals differ in null spaces from the original row/column. In most cases the null space is wider and therefore the power to detect idiosyncrasy is reduced.

4. Program description

We introduced the FORTRAN 95 software named NODF-Program, which calculates the abovementioned nestedness estimators for abundance data as well as the original NODF for presence–absence data (Almeida-Neto et al., 2008). To allow comparison, the NODF-Program also calculates two commonly used nestedness indices for presence–absence matrices: (1) Brualdi and Sanderson's (1999) discrepancy in the modification of Ulrich and Gotelli (2007) and (2) the modified temperature score (Atmar and Patterson, 1993; Ulrich and Gotelli, 2007). The program accepts standard space-delimited text file matrices, with sites in columns and species in rows (the Ecosim format, Gotelli and Entsminger, 2006). Multiple analyses using many matrices are possible and require an additional file containing the file names.

Statistical inference is performed using a null model approach (Gotelli, 2000, 2001; Ulrich and Gotelli, 2007). The user can choose between five null models commonly used with presence–absence matrices (the fixed row and column totals constraint model; the

equiprobable row and fixed column totals constraint model; the fixed row totals and equiprobable column constraint model, and the equiprobable row/column null model, cf. Gotelli, 2000, and Ulrich et al., 2009, for detailed descriptions). The fifth null model resamples the matrix that is proportional to the observed row and column marginal totals until the observed number of incidences is achieved (Connor and Simberloff, 1979). In the case of the fixed row–fixed column constraint model randomization is done with the independent swap algorithm (Gotelli, 2000) using $10nm$ swaps, where n and m are the numbers of rows and columns, respectively. Even for moderately sized matrices (80 species, 40 sites), the number of swaps exceeds the 30,000 swaps recommended by Hausdorf and Hennig (2007) for large matrices.

For the study of matrices that contain quantitative data, we use three recently developed randomization algorithms (Ulrich and Gotelli, in press). These models start with a cleared matrix and place individuals into the matrix cells using three different constraints:

- 1) rc assigns individuals to matrix cells proportional to observed row and column abundance totals until, for each row and column, total abundances are reached.
- 2) aa resamples the matrix proportional to observed row and column abundance totals until the matrix-wide number of individuals is reached. In a few cases, this algorithm generates matrices with empty rows (species) or columns (sites).
- 3) ss resamples the matrix proportional to observed row and column abundance totals until the matrix-wide number of species is reached. In a few cases, this algorithm generates matrices with empty columns (sites).

Classical nestedness analysis requires the matrix to be sorted according to species richness. However, in gradient analysis, the user often wishes to sort the data in another way. The above defined abundance-based nestedness indices require additional sorting according to column and row abundance totals. The NODF-program provides four sorting options: according to row/column species richness, row/column abundance totals, and a double sorting where the matrix is first sorted according to row/column species richness and then rows and columns of equal species richness are further sorted according to abundance totals. In a fourth option, the matrix can be left unsorted.

Observed degrees of nestedness are compared to the distribution of the nestedness scores obtained from the null model matrices (the number of matrices is user-defined, with a default of 1000). Statistical inference is based on the lower and upper 95% confidence limits of the null distribution.

The program output contains summary data about the matrix (number of species, number of sites, matrix fill and number of occurrences). For each index observed and expected, raw scores are given, as well as the standard deviations of the expected scores, the Z-transformed scores ($Z = (\text{observed score} - \text{expected score}) / \text{StdDev}_{\text{exp}}$) and the associated probability level for the standard normal distribution. Also given are the skewness, the upper and lower 95% confidence limits and probability levels obtained from the null distribution.

Lastly, the user can choose the estimator of idiosyncrasy. The output contains the degree of idiosyncrasy for each column and row together with probability levels and lower and upper 95% confidence limits of the null distribution.

5. Consistency with the nestedness concept

Similar to the approach of Almeida-Neto et al. (2008), we evaluated whether WNODF and WIN were consistent with the

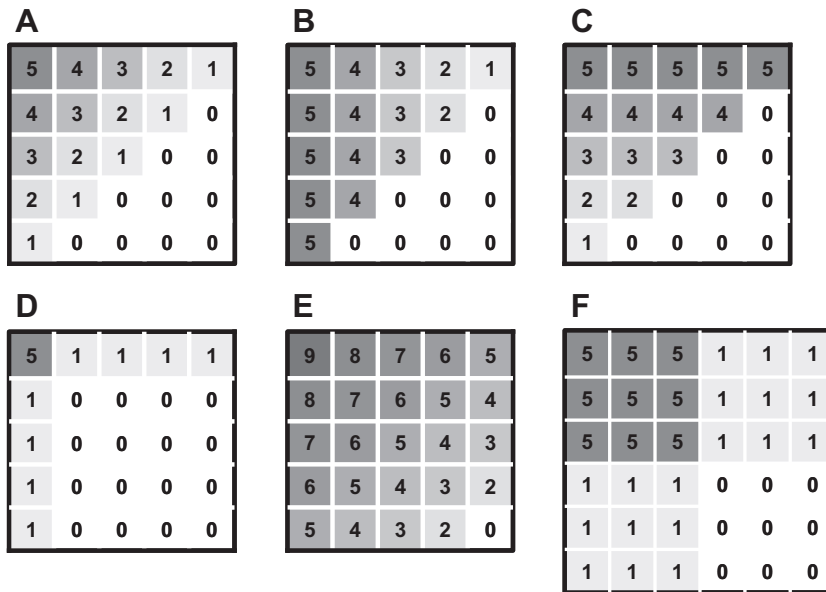


Fig. 1. Matrix representations of six idealized structures with some level of nestedness among columns and/or rows (i.e., degree of nestedness > 0). A: perfect nestedness; B: perfect nestedness among columns; C: perfect nestedness among rows; D: minimally filled nested matrix; E: maximally filled nested matrix; F: core-periphery pattern. See “Consistency with the nestedness concept” for further details.

usual ecological concept of nestedness by using model matrices. First, the ecological meaning of nestedness does not depend on the kind of data used (presence–absence or quantitative data). Hence, for metacommunities, nestedness is basically a pattern of species incidence and/or species composition regardless of whether quantitative data are used. Thus, the information that an index using quantitative data adds is whether the nested pattern for presence–absence data conforms to a pattern in which the populations making up smaller local assemblages have lower abundances than their conspecifics populations occurring in richer assemblages.

We assessed whether both estimators quantify nestedness in six model matrices with distinct nested structures with abundance

data: (1) Perfect nestedness; (2) Perfect nestedness among columns, in which there is decreasing abundance from left to right but identical abundances from top to bottom; (3) Perfect nestedness among rows, in which there is decreasing abundance from top to bottom but identical abundances from left to right; (4) Minimally filled nested matrix, in which there is only one fully filled column and one fully filled row; (5) Maximally filled nested matrix, in which only the cell located in the bottom right corner is not filled, and (6) the Core-periphery pattern, in which there is a core of species with higher incidences and abundances and a core of sites with higher richness and abundances (Fig. 1A–F). Although all of these model matrices have at least some degree of nestedness, they represent distinct structures and an appropriate estimator should

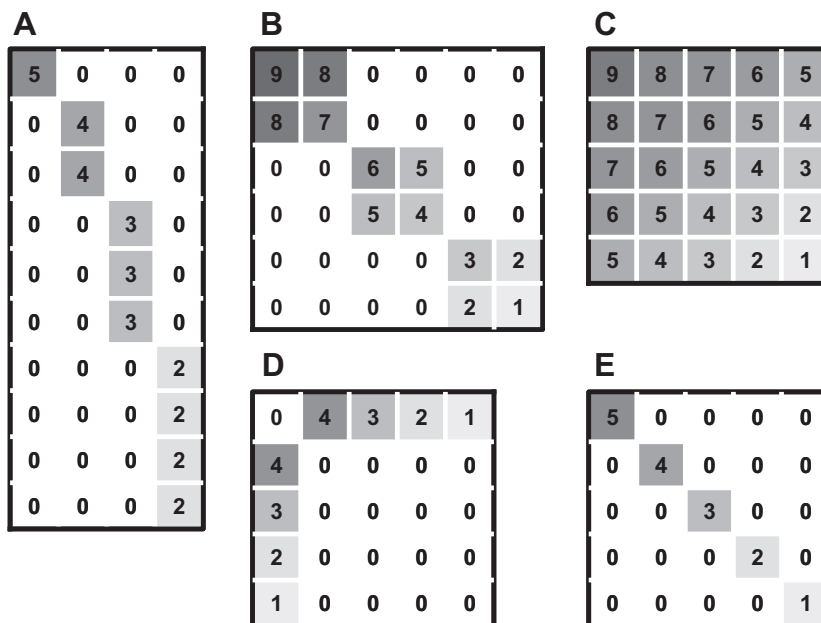


Fig. 2. Matrix representations of five idealized structures with no nestedness among columns and rows (i.e., degree of nestedness = 0). A: non-inclusive subsets; B: compartmented model; C: full matrix; D: equal richness pattern; E: beta-diversity model.

Table 1

Nestedness analysis of quantitative model matrices using WINE and WNODF. The “nested matrices” represent cases in which the degree of nestedness should be higher than zero, whereas the “non-nested matrices” are cases in which there should be no nestedness. η : WINE estimator and its associated Z-scores. Obs: observed WNODF value. Z-scores are based on a null model that constrains matrix fill, retains the distribution of number of events in links but not constraining marginal totals. Z-values in bold indicate significant nestedness values according to null model aa ($\alpha = 5\%$). In the case of WNODF double sided 95% confidence limits (CL) of the null model distribution are also given (not available for η). Prior to analysis the null model matrices were double sorted according to marginal richness and abundance totals.

Pattern	Matrix	WINE		WNODF								
		η	Z-value	Whole matrix			Columns only			Rows only		
				Obs	Z-value	95% CL	Obs	Z-value	95% CL	Obs	Z-value	95% CL
Nested ^a	Perfect (Fig. 1A)	1.02	3.80	100	3.99	9.3–67.4	100	3.20	6.5–78.9	100	3.24	15.2–81.5
	Among columns only (Fig. 1B)	0.91	3.19	50	0.50	16.6–67.8	100	2.98	16.7–78.0	0	–2.81	6.8–66.7
	Among rows only (Fig. 1C)	0.91	3.22	50	0.70	17.3–64.1	0	–2.37	5.1–65.7	100	3.58	23.9–71.9
	Minimally filled (Fig. 1D)	1.00	4.50	40	2.14	0.6–36.3	40	1.55	1.1–48.1	40	1.82	1.3–40.3
	Maximally filled (Fig. 1E)	0.40	1.67	40	1.21	0–52.5	40	1.05	0–54.7	40	1.14	0–54.3
Non-nested	Core-periphery (Fig. 1F)	0.92	4.43	60	0.83	28.7–71.4	60	0.64	26.4–75.4	60	0.48	22.9–75.7
	Non-inclusive subsets (Fig. 2A)	0.73	2.71	0	–2.41	3.1–23.5	0	–1.80	2.1–34.6	0	–2.34	3.4–24.4
	Compartmented (Fig. 2B)	–0.42	–2.14	0	–4.30	20.2–58.2	0	–3.71	18.1–67.8	0	–3.95	18.0–59.2
	Full matrix (Fig. 2C)	0.01	0.06	0	–0.89	0–49.5	0	–0.91	0–57.2	0	–0.89	0–47.5
	Equal richness (Fig. 2D)	1.24	4.40	0	–2.35	3.3–46.7	0	–1.79	3.2–67.1	0	–2.23	3.8–54.8
	Beta-diversity (Fig. 2E)	0.27	0.12	0	–1.68	0.6–31.4	0	–1.40	0.2–37.9	0	–1.45	0.3–36.1

^a The “nested matrices” are not necessarily significantly nested because significance depends on the choice of the null model.

be able to differentiate these models according to their different levels of nestedness.

Then, we used five model matrices (Fig. 2A–E) in which no degree of nestedness should be found given the definition of a nested pattern. For these model matrices, a suitable index should produce zero values because they represent a complete lack of nestedness. The non-nested models are: (1) Non-inclusive subsets, based on the “anti-nested” model proposed by Poulin and Guégan (2000), in which there is decreasing fill among all column pairs (see Almeida-Neto et al., 2007); (2) Compartmented model, constituted here by three subsets; (3) Full matrix, where all species occur in all sites and, consequently, all sites have identical richness; (4) Equal richness, in which all but one species occur in only one site and all but one site have only one species, and (5) Beta-diversity, a model in which there is no overlap between columns. For convenience and to allow illustration, we used small matrices, but the results do not qualitatively differ from those obtained using larger matrices.

Table 1 shows that both WNODF and WINE correctly identified some degree of nestedness for all “nested” matrices. However, WINE inflated the values of nestedness for most nested models and was unable to differentiate between very distinct nested patterns (see, for example, Fig. 1A and D; Table 1). On the other hand, WNODF correctly calculated distinct nested values for these matrices, distinguishing the perfect nested pattern from the others. In addition, WNODF can be calculated for columns or rows only, differentiating whether and how sites and species contribute to the overall pattern.

Based on the very concept of nestedness, there is no nested pattern if all species have the same incidence and all sites have the same richness. Likewise, there should be no nestedness if there is no overlap among species ranges or no species that is found in at least two sites. However, WINE produced positive and even significant nested values for matrices with no co-occurrence among species and/or for matrices with sites of identical richness (Table 1). Because WNODF is directly based on overlap and decreasing fill, it correctly identified all of these matrices as having no nested structure, i.e., degree of nestedness = 0.

We conclude that WNODF is a suitable and versatile index to measure the degree of nestedness for quantitative data. The values calculated through WNODF are always a fraction of the degree of the nestedness measured by NODF for presence–absence data. The difference between both nestedness indices expresses how much of the nestedness in incidence and/or species composition resembles

a gradient of abundances. Regarding the recent estimator proposed by Galeano et al. (2009), we do not recommend its use as a direct measure of nestedness. On the other hand, WINE can be used in the context of matrix temperature, i.e., “at once an empirical measure of the degree of uncertainty in species extinction order and an indication of the relative stability of the constituent populations”, according to Atmar and Patterson (1993).

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