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Disentangling community patterns of nestedness and species co-occurrence

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Two opposing patterns of meta-community organization are nestedness and negative species co-occurrence. Both patterns can be quantified with metrics that are applied to presence-absence matrices and tested with null model analysis. Previous meta-analyses have given conflicting results, with the same set of matrices apparently showing high nestedness (Wright et al. 1998) and negative species co-occurrence (Gotelli and McCabe 2002). We clarified the relationship between nestedness and co-occurrence by creating random matrices, altering them systematically to increase or decrease the degree of nestedness or co-occurrence, and then testing the resulting patterns with null models. Species co-occurrence is related to the degree of nestedness, but the sign of the relationship depends on how the test matrices were created. Low-fill matrices created by simple, uniform sampling generate negative correlations between nestedness and co-occurrence: negative species co-occurrence is associated with disordered matrices. However, high-fill matrices created by passive sampling generate the opposite pattern: negative species co-occurrence is associated with highly nested matrices. The patterns depend on which index of species co-occurrence is used, and they are not symmetric: systematic changes in the co-occurrence structure of a matrix are only weakly associated with changes in the pattern of nestedness. In all analyses, the fixed-fixed null model that preserves matrix row and column totals has lower type I and type II error probabilities than an equiprobable null model that relaxes row and column totals. The latter model is part of the popular nestedness temperature calculator, which detects nestedness too frequently in random matrices (type I statistical error). When compared to a valid null model, a matrix with negative species co-occurrence may be either highly nested or disordered, depending on the biological processes that determine row totals (number of species occurrences) and column totals (number of species per site).

Nestedness and segregated species co-occurrence are two commonly reported meta-community patterns (Leibold and Mikkelson 2002, Almeida-Neto et al. 2007). Both patterns are expressed in a presence-absence matrix, in which each row represents a species, each column represents a site or a sample, and the matrix entries indicate the presence (1) or absence (0) of a particular species in a particular site (McCoy and Heck 1987).

In a nested matrix (Fig. 1A, 1B), species occurrences tend to overlap with one another and share many sites in common. In the extreme case of perfect nestedness, species will overlap maximally in their occurrence, so that the composition of small assemblages is a perfectly nested subset of the composition of larger assemblages. Nestedness was originally attributed to ordered extinction on small islands (Patterson and Atmar 1986), but a pattern of nestedness can also be generated by differential dispersal (Cook and Quinn 1998, Loo et al. 2002, McAbendroth et al. 2005), passive sampling (Andreń 1994, Fischer and Lindenmayer 2002, Higgins et al. 2006), differential habitat quality (Hylander et al. 2005), or nesting of habitats (Hausdorf and Hennig 2003, Wethered and Lawes 2005).

In a segregated species occurrence matrix (Fig. 1C), species tend to occur with one another less frequently. In the case of a perfectly segregated matrix, many species pairs will form perfect “checkerboards” and never co-occur together (Diamond 1975). Many sites will contain unique combinations of species, but some

A

	A	B	C	D	E
1	1	1	1	1	1
2	1	1	1	1	0
3	1	1	1	1	0
4	1	1	1	1	0
5	1	1	1	0	0
6	1	1	1	0	0
7	1	0	0	0	0
8	1	1	0	0	0
9	1	0	0	0	0
10	0	1	0	0	0

B

	A	B	C	D	E
1	1	1	1	1	1
2	1	1	1	1	1
3	1	1	1	1	0
4	0	1	1	1	0
5	1	1	1	0	0
6	1	1	0	1	0
7	1	0	1	0	1
8	0	1	0	0	0
9	1	0	0	0	0
10	1	0	0	0	0

C

	A	B	C	D	E
1	1	1	0	1	1
2	1	0	1	0	1
3	1	0	1	1	0
4	0	1	0	1	1
5	1	1	1	0	0
6	1	0	0	1	0
7	1	0	1	0	0
8	1	1	0	0	0
9	0	1	1	0	0
10	0	1	0	1	0

D

	A	B	C	D	E
1	1	0	1	0	1
2	0	1	0	1	0
3	1	0	1	0	1
4	0	1	0	1	0
5	1	0	1	0	1
6	0	1	0	1	0
7	1	0	1	0	1
8	0	1	0	1	0
9	1	0	1	0	0
10	0	1	0	0	0

Fig. 1. Four presence–absence matrices with ten species and five sites. In (A) the matrix is highly nested: only two species pairs (10 and 7, 10 and 9) form checkerboard distributions, and species 1 through 9 form a perfectly nested pattern. (B) is the typical product of a passive sampling from a metacommunity having a lognormal species – abundance distribution. (C) is a typical product of a sampling from an equiprobable distribution. The matrix in (D) has nearly the maximum number of checkerboards without any exclusive species combinations. It is highly disordered. Under the fixed – fixed model, the Brualdi and Sanderson nestedness index (BR) does not identify A, B, and C as being nested and does not identify D as being disordered ($Z<2.0$). The co-occurrence indices C-score (CS), number of checkerboard pairs (CH), and number of species combinations (CO) identify matrix C as being segregated (all $Z>10.0$), but matrices (A), (B) and (C) as being random ($-2.0< Z<2.0$). Note that matrix (A) is so highly nested and matrix (D) is so highly segregated that the fixed-fixed model cannot be applied to these extreme cases because there are too few matrix re-arrangements that satisfy the row and column constraints.

combinations will be consistently missing (Pielou and Pielou 1968). Checkerboard distributions and missing species combinations were originally attributed to species interactions (especially competition) or environmental filters, but these same patterns can also be generated by unique habitat associations (Peres-Neto et al. 2001), limited dispersal (Ulrich 2004), and also historical or evolutionary processes that prevent species from co-occurring in the absence of species interactions (Gotelli et al. 1997, Bloch et al. 2007). Patterns of nestedness and species co-occurrence are usually described as deviations from a statistical null model (Gotelli and Graves 1996), in which the pattern in an observed matrix is randomized to mimic the stochastic assembly of a community that is not constrained by species interactions (Gotelli 2001).

Superficially, nestedness and segregated co-occurrence would seem to be describing opposite patterns of community organization (see Leibold and Mikkelson 2002 and Almeida-Neto et al. 2007 for further discussion). However, two empirical meta-analyses of nestedness and co-occurrence in published presence-absence matrices have generated supposedly conflicting results. On the one hand, Wright et al. (1998) found that, by some tests, as many as 70% of their matrices were significantly nested. In contrast, Gotelli and McCabe (2002) used a large subset of these same matrices and found strong evidence for segregated species occurrences: many matrices exhibited more checkerboard species pairs and fewer species combinations than expected by chance. However, these comparisons are complicated by the fact that the two analyses used different null models to test for co-occurrence and nestedness.

In this paper, we systematically explore the relationship between nestedness and species co-occurrence by creating artificial data sets with specified amounts of species segregation, nestedness, or randomness. These matrices were then analyzed with the same set of null models to reveal the expected associations between nestedness and species co-occurrence.

Material and methods

Matrix types

We created two types of random presence-absence matrices (200 matrices each) to study the properties of two randomization algorithms, three measures of co-occurrence, and one measure of nestedness. We created the first type of presence-absence matrices (M_N) by randomly sampling individuals from a metacommunity in which population sizes of the species were distributed according to a lognormal species rank order distribution:

$$S = S_0 e^{[-a(R-R_0)^2]} \tag{1}$$

in which S is the number of species, R is the abundance octave, S_0 is the number of species in the modal octave R_0, and a is the shape-generating parameter. For each matrix, the shape-generating parameter a was sampled randomly from a uniform distribution between 0.1 and 0.5 (a canonical lognormal has $a = 0.2$; May 1975). The size of each matrix was also determined by drawing two integers from a uniform distribution to establish the number of rows ($=m$ species) and the number of columns ($=n$ sites; $3 \le m \le 200$ and $3 \le n \le 50$).

Species numbers per site m_S were also obtained from a uniform random distribution ($3 \leq m_S \leq m$). For each site individuals were then randomly sampled using Eq. 1 until m_S was achieved. This sampling protocol produced matrices that had relatively high matrix fills and were moderately to strongly nested due to passive sampling (Higgins et al. 2006). In the second type of matrix (M_E: again with m species and n sites), species occurrences were assigned equiprobably in the matrix until all rows of the matrix contained at least one species. This type of matrix had a relatively low matrix fill. Both matrix types were designed to cover the range of observed matrices in order to study the behaviour of the co-occurrence and nestedness metrics in dependence on matrix shape and fill.

Co-occurrence and nestedness metrics

We used the C-score CS (Stone and Roberts 1990), the checkerboard score CH (Gotelli 2000), and the species combination score CO (Pielou and Pielou 1968) to measure species co-occurrences. The C-score CS_{ij} for species pair ij is defined as:

$$CS_{ij} = (R_i - S)(R_j - S) \qquad (2)$$

where R_i is the row total for species i, R_j is the row total for species j, and S is the number of sites that contain both species. The C-score is calculated for all unique species pairs in the matrix and averaged as an index of community co-occurrence (Stone and Roberts 1990). The larger the CS, the more, on average, species pairs are segregated in their occurrences. The checkerboard score CH is the number of species pairs that never occur together in the same site (“checkerboard pairs” sensu Diamond 1975), and the species combination score CO is a count of the number of species pairs that occur always together (Pielou and Pielou 1968, Gotelli 2000).

We quantified the pattern of nestedness with the discrepancy index BR (Brualdi and Sanderson 1999), which is a count of the number of discrepancies (absences or presences) that must be erased to produce a perfectly nested matrix. The smaller the BR score is, the stronger is the pattern of nestedness. Brualdi and Sanderson (1999) and Ulrich and Gotelli (2007) showed that BR is less prone to type I errors than the popular nestedness temperature measure of Atmar and Patterson (1993, 1995). The Brualdi and Sanderson score is sensitive to the ordering of the rows and columns of the matrix, so all empirical and simulated matrices were ordered by decreasing row and column counts before calculation of BR. None of the other nestedness or co-occurrence indices we analyzed are affected by row and column ordering.

We used two null model algorithms to obtain significance levels for these co-occurrence and nestedness indices. The fixed row – fixed column algorithm (FF) preserves both the row and column totals in the original matrix (Connor and Simberloff 1979, Gotelli 2000) but randomizes the pattern of species co-occurrence. We implemented this null model with a variation of the “sequential swap algorithm” (Manly 1995, Gotelli and Entsminger 2001), in which we sequentially reshuffled 25 000 randomly sampled 2 × 2 submatrices that have the same row and column totals after their elements are swapped. Matrices created this way have the same row and column totals as the original matrix. Each subsequent matrix was created with an additional 5000 swaps. The sequential swap algorithm has been extensively studied in the context of species co-occurrence and nestedness analyses (Gotelli 2000, Simberloff and Zaman 2000, Miklós and Podani 2004, Ulrich 2004, Ulrich and Gotelli 2007). It has a small bias against finding species segregation patterns (Miklós and Podani 2004, Lehsten and Harmand 2006), but has lower type I and type II error probabilities than other randomization algorithms (Gotelli 2000, Gotelli and Entsminger 2001, Ulrich and Gotelli 2007). If matrices are extremely nested (Fig. 1A) or extremely segregated (Fig. 1D), the fixed-fixed model will actually fail because there are few or no matrix re-arrangements that will simultaneously preserve row and column totals. However, if the matrix is not almost perfectly nested or segregated, the fixed-fixed algorithm can generate many random matrices that have identical row and column sums.

The EE algorithm (equiprobable row totals, equiprobable column totals) preserves the total number of species occurrences in the original matrix, but allows both row and column totals to vary freely (Gotelli 2000). This algorithm retains the least of the original matrix structure and is prone to type I errors in both co-occurrence and nestedness analyses (Wright et al. 1998, Gotelli 2000, Ulrich and Gotelli 2007). This algorithm is used in the popular nestedness temperature calculator (Atmar and Patterson 1995), and was used by Wright et al. (1998) in their meta-analysis of nestedness patterns. Although many other null model algorithms are possible for nestedness and co-occurrence analysis (Gotelli 2000, Ulrich and Gotelli 2007), the FF and EE algorithms span the range of possibilities from very conservative to very liberal.

Probability values and standardized effect sizes

Significance levels of the nestedness and co-occurrence metrics were in all cases obtained from the lower and upper 95% confidence limits of the respective null model distributions. We counted the number of simulations for which BR, CS, CH and CO had observed values above or below the respective 95%

confidence limits of the null model distributions EE and FF. We also calculated a standardized effect size (SES) to quantify the direction and degree of deviation from the null model. SES is a Z-transformed score $[Z = (x - \mu)/\sigma]$ (x = observed index value, μ = mean and σ = the standard deviation of the 100 index values from the simulated matrices). SES values below -2.0 or above 2.0 indicate approximate statistical significance at the 5% error level (two-tailed test). All null models and nestedness indices were calculated with the software applications Nestedness (Ulrich 2006a), Matrix (Ulrich 2006b), Cooc (Ulrich 2007) and with EcoSim 7.72 (Gotelli and Entsminger 2006).

Diagnostic tests

In a first series of tests we wanted to evaluate the importance of nestedness to co-occurrence patterns. Therefore, we artificially increased or decreased the degree of nestedness in the set of M_N and M_E matrices to achieve a small and medium degree of nestedness. Because the results of null model analyses are sensitive to changes in row and column totals of the matrix (and therefore matrix fill; Gotelli 2000), we used the FF algorithm to derive from each matrix new matrices with increased and decreased nestedness that preserved the row and column totals of each test matrix: After each swap, we measured BR and retained the new matrix if it had the desired increase or decrease in nestedness, carrying out between two and 10 times the number of swaps as the matrix fill level. These alterations created a new set of matrices derived from the original M_N and M_E matrices that had increased or decreased levels of nestedness as measured by BR but did not change matrix properties that might influence the metrics. We then used the null model analysis to measure the pattern of co-occurrence in this expanded set of matrices. This analysis reveals the effects of nestedness on the pattern of species co-occurrence in a series of increasingly structured matrices. In a second series of tests, we reversed the procedure, this time increasing or decreasing the degree of co-occurrence as measured by the CS score and then tracing the respective changes in BR, CH, and CO.

Results

Unmodified matrices

The equiprobable null model (EE) identified nearly all of the M_N matrices as being significantly nested (Table 1, 2). It further pointed to highly non-random species co-occurrences when measured by CS and CO. This null model also identified 77 of the 400 original M_E matrices (19%) as being disordered (Table 1 and 2 combined). For the M_E matrices, more than half of the CS scores and about half of the CO scores were beyond the respective 95% confidence limits, indicating species segregation (Table 1, 2).

In contrast to these results for the EE algorithm, the fixed – fixed algorithm (FF) identified more than 95% of the M_N and M_E matrices as being not significantly nested (Table 1, 2). There was a slight bias for the CS index applied to the unmodified M_N matrices: 44 of the original 400 M_N matrices (11%, Table 1, 2 combined) indicated species segregation, whereas only 10 (2.5%) should have been found by chance. CH and CO performed better and identified less than 8% of the 400 matrices as having non-random co-occurrences.

Modified matrices

In the case of the M_N matrices with increasing levels of nestedness, BR and CS were negatively correlated ($r = -0.55$, $p < 0.0001$): matrices with high levels of nestedness (low values of BR) also displayed high levels of species segregation (high values of CS). Of the 124 matrices of Fig. 2A with BR > 2.0, CS was in 35 cases < -2.0 (28%). Of the 142 matrices with BR < -2.0, CS was in 84 cases > 2.0 (59%). BR and CO were less negatively correlated ($r = -0.26$, $p < 0.0001$), and BR and CH appeared to be independent ($r = 0.006$, $p > 0.5$). These effects are also mirrored in the number of significant matrices in the groups with increased or decreased nestedness (Table 1).

For the M_E matrices, in contrast, we found a positive correlation between BR and CS (Fig. 2B; $r = 0.56$, $p < 0.0001$): matrices with high levels of nestedness (low values of BR) displayed low levels of species segregation (low values of CS). BR and CO were positively correlated ($r = 0.33$; $p < 0.0001$) and BR and CH were negatively correlated ($r = -0.21$, $p < 0.0001$). CS was positively correlated with matrix fill (Fig. 3A), although there is considerable scatter in the relationship. The metrics returned 36 of 147 M_N matrices with a fill > 0.5 (24.5%) to have $Z > 2.0$. At low matrix fill this correlation vanished. Matrix size also influenced the performance of CS. 20.2% of the matrices with mn > 2500 had CS > 2.0, but only 5.8% of the matrices with mn < 2500 (Fig. 3B) did so. BR, CH, and CO, in turn, were not significantly correlated with matrix fill and size (not shown).

For the FF model, the increase or decrease in nestedness affected the matrix patterns measured by CS, whereas the CH and CO results were largely unaffected (Table 1). Under this null model, CS identified 36 of the 200 (18%) M_N matrices with a highly increased degree of nestedness as being segregated. For the set of matrices with decreased

Table 1. Numbers of scores of BR, CS, CH, and CO below or above the 95% confidence limits of matrices with small and medium increases (IN I and IN II)) or decreases (DN I and DN II) in the degree of nestedness. Manipulated scores are marked in grey. For each test, there were 200 matrices created.

Metacommunity	Null model	Matrix type	95% confidence limits BR		CS		CH		CO	
			Below	Above	Below	Above	Below	Above	Below	Above
Lognormal	Fixed-fixed	Original	2	7	7	18	0	16	2	8
M_N		IN I	35	0	2	28	1	10	0	13
		IN II	107	0	1	36	2	5	0	13
		DN I	0	51	19	8	1	3	3	2
		DN II	0	121	32	2	0	1	2	4
	Equiprobable	Original	194	0	195	1	38	58	0	154
		IN I	196	1	196	1	40	57	0	148
		IN II	196	0	197	1	41	50	0	148
		DN I	195	0	197	1	41	55	0	153
		DN II	192	2	197	1	42	48	0	141
Equal	Fixed-fixed	Original	2	2	4	0	1	3	3	1
M_E		IN I	18	0	11	0	0	3	6	0
		IN II	68	0	18	0	0	12	3	1
		DN I	0	21	0	7	4	5	2	12
		DN II	0	54	0	23	6	3	1	12
	Equiprobable	Original	1	35	1	135	11	2	92	0
		IN I	3	10	0	125	10	3	99	1
		IN II	8	6	0	125	13	2	99	1
		DN I	1	86	1	133	11	3	90	3
		DN II	0	113	0	135	13	2	86	1

Table 2. Numbers of scores of BR, CS, CH, and CO below or above the 95% confidence limits of matrices with small and medium increases (IN I and IN II)) or decreases (DN I and DN II) in species co-occurrence. Manipulated scores are marked in grey. For each test, there were 200 matrices created.

Metacommunity	Null model	Matrix type	95% confidence limits							
			BR		CS		CH		CO	
			Below	Above	Below	Above	Below	Above	Below	Above
Lognormal M_N	Fixed-fixed	Original	4	5	5	26	0	13	1	11
		IC I	3	14	46	1	0	5	6	4
		IC II	0	18	117	0	0	2	8	4
		DC I	14	4	1	73	0	13	1	19
		DC II	10	3	0	131	0	12	1	15
	Equiprobable	Original	196	0	197	0	50	52	0	143
		IC I	196	0	198	0	57	43	0	144
		IC II	195	1	197	0	59	42	0	146
		DC I	198	0	196	1	55	48	0	144
		DC II	197	0	196	1	54	51	0	144
Equal M_E	Fixed-fixed	Original	2	2	5	7	5	0	0	5
		IC I	5	1	30	1	1	0	9	1
		IC II	10	1	73	0	0	2	16	1
		DC I	2	4	0	24	1	3	0	16
		DC II	1	7	0	70	1	7	0	27
	Equiprobable	Original	2	43	1	124	11	4	90	3
		IC I	1	30	3	116	14	1	99	2
		IC II	3	22	4	113	5	4	104	3
		DC I	0	44	0	134	9	7	82	3
		DC II	0	58	1	139	15	6	74	9

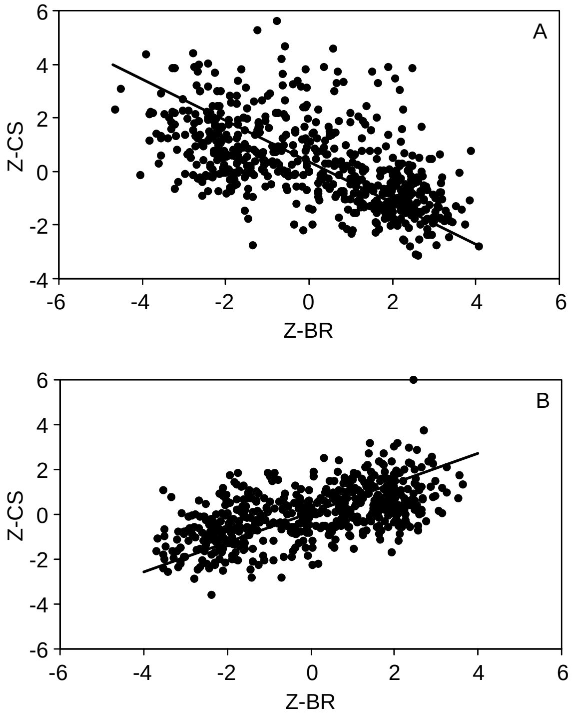

Fig. 2. Dependence of the C-score co-occurrence index (CS) on the Brualdi and Sanderson nestedness index (BR). In both cases, the patterns are measured as standardized Z-scores. 200 initial matrices were created in each case, and then the degree of nestedness was artificially increased (200 matrices) or decreased (200 matrices) by sequential swapping of submatrices. (A) 200 initial matrices created by passive sampling (M_N) from a log-normal species abundance distribution. (B) 200 initial matrices created by simple sampling (M_E) from uniform distributions of species and site occurrences. (A) $R^2 = 0.30$; $p < 0.0001$. (reduced major axis regression $CS = -0.77\ BR + 0.36$. (B) $R^2 = 0.32$; $p < 0.0001$; $CS = 0.08 + 0.66\ BR$.

nestedness, 12% had CS scores smaller than expected by chance. In contrast, CH and CO were largely unaffected by the changes in nestedness. Between 0.5 and 10% of the matrices fell beyond the 95% confidence limits of the null model. The equiprobable null model, in turn, was insensitive to changes in nestedness while pointing to high degrees of non-random co-occurrences (CS, CH and CO) irrespective to the degree of nestedness.

The increase or decrease in species co-occurrence (measured by CS) had little effect on the performance of BR (Table 2). Between 2 and 10% of the matrices were identified as being significantly nested or disordered. For the M_N matrices, BR and CS were negatively correlated, and for the M_E matrices BR and CS were positively correlated (Table 2).

Discussion

Fig. 2A and 2B clarify the general relationships that are to be expected between nestedness and species co-occurrence. In the simplest and most general case (Fig. 2B), we created random matrices by sampling from row and column distributions that were uniform. For this set of matrices, high levels of nestedness are associated with low levels of species segregation, which matches our intuition about how these two metrics should behave. However, if random matrices are created by sampling from log-normal species abundance distributions, the relationship reverses (Fig. 2A), and matrices with high levels of nestedness are associated with high levels of species segregation. This counterintuitive behaviour might point to some shortcomings in our understanding of co-occurrence within a presence-absence matrix. Leibold and Mikkelson (2002) analyze a broader range of patterns, and distinguish between patterns of coherence, species turnover, and boundary clumping in presence-absence matrices. They and Almeida-Neto et al. (2007) argue for a negative correlation between the degrees of nestedness and species segregation. However, our results show that this relationship depends on the way the matrix was constructed (particularly on matrix fill).

The analyses presented here support previous studies (Gotelli 2000, Ulrich and Gotelli 2007) suggesting that the fixed-fixed model is superior to the equiprobable model for both nestedness and co-occurrence analyses. Our results also corroborate recent critiques of the equiprobable model by Fischer and Lindenmayer (2002), Rodríguez-Gironés and Santamaría (2006) and Ulrich and Gotelli (2007), who all found that this model is prone to sampling artefacts.

Although the fixed-fixed model has good statistical properties when tested with most kinds of random matrices, there is a slight bias towards detecting segregated co-occurrence with the C-score and the fixed-fixed model at high values of matrix fill (Fig. 3A) and size (Fig. 3B). The CS metric should be used with care for large matrices (nm >2500) and/or matrices that are highly filled (>50%). In these cases the more conservative CH and CO metrics appeared to be more appropriate. However, Gotelli and McCabe (2002) did not find an effect of matrix fill in their meta-analysis of co-occurrence patterns, although matrix size was weakly correlated with effect size.

Our results help to interpret the previous meta-analyses of Wright et al. (1998) and Gotelli and McCabe (2002). The most important difference between these studies is that the Wright et al. (1998) study found that nestedness was widespread when tested with the nestedness temperature calculator. However, both the metric and the randomization algorithm in the nestedness calculator have since been shown to be

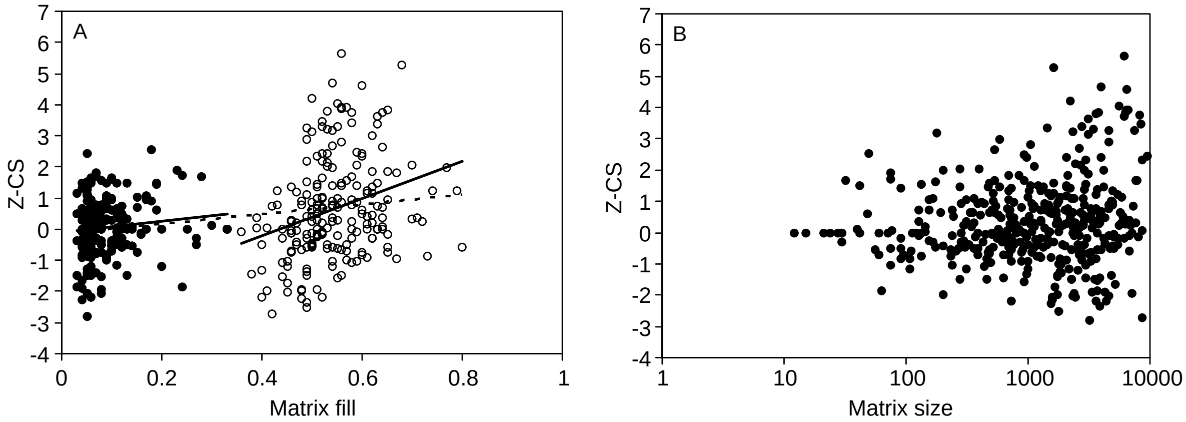

Fig. 3. Dependence of the co-occurrence index C-score (measured by standardized Z-scores) on matrix fill (A) and matrix size = m species × n sites (B) for matrices with comparably low (the M_E matrices, full dots) and high (the M_N matrices, open dots) matrix fill. The dashed line in A gives the ordinary least squares regression slope ($r^2 = 0.07$, $p < 0.0001$) for the entire data set, the solid lines in (A) give the respective regressions for the M_E (left data cluster: $r^2 = 0.001$, $p = 0.09$) and M_N matrices (right data cluster: $r^2 = 0.08$, $p < 0.0001$). Of the 276 matrices in (B) with mn < 2500 only 5.8% had Z(CS) > 2.0, of the 124 remaining larger matrices 20.2% had Z(CS) > 2.0.

vulnerable to type I errors (rejecting the null hypothesis too frequently; Fischer and Lindenmayer 2002, Rodríguez-Gironés and Santamaría 2006). In a recent publication (Ulrich and Gotelli 2007), we re-analyzed the data matrices compiled by Wright et al. (1998) with the fixed-fixed model and the Brualdi and Sanderson index. Only 11% of the matrices were revealed to be nested, and the true frequency of nestedness probably lies between 10 and 40% (Ulrich and Gotelli 2007) in contrast to the frequency of 70% reported by Wright et al. (1998), who used the EE algorithm and the nestedness temperature measure.

But the results of the current study show that, even with an appropriate fixed-fixed null model, some matrices may simultaneously display patterns of both nestedness and species segregation. As in a Sudoku puzzle, the fixed-fixed model introduces interesting internal constraints on matrix structure, so that the relationship between nestedness and co-occurrence will depend on how the marginal totals for the matrices are generated. As Stone and Roberts (1992) pointed out, the fixed-fixed constraint ensures that for a matrix with species segregation, at least some species pairs must also be aggregated in their occurrence. Depending on the pattern in the row and column totals, this constraint in the fixed-fixed model may generate matrices that are simultaneously nested and segregated. These results are also consistent with a wider range of potential patterns of coherence, species turnover, and boundary clumping that can be described for presence-absence matrices (Leibold and Mikkelson 2002, Almeida-Neto et al. 2007). Null model tests can and should be used to establish patterns in species occurrence data (Gotelli 2001), but further analyses may be required to tease apart mechanisms such as species interactions, habitat segregation, dispersal limitations, passive sampling, and ordered extinctions.

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