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Pattern detection in null model analysis

Werner Ulrich and Nicholas J. Gotelli

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The identification of distinctive patterns in species x site presence-absence matrices is important for understanding meta-community organisation. We compared the performance of a suite of null models and metrics that have been proposed to measure patterns of segregation, aggregation, nestedness, coherence, and species turnover. We found that any matrix with segregated species pairs can be re-ordered to highlight aggregated pairs, indicating that these seemingly opposite patterns are closely related. Recently proposed classification schemes failed to correctly classify realistic matrices that included multiple co-occurrence structures. We propose using a combination of metrics and decomposing matrix-wide patterns into those of individual pairs of species and sites to pinpoint sources of non-randomness.

Null model analysis has been a popular tool for detecting pattern in binary presence–absence matrices, and previous tests have identified algorithms and metrics that have good statistical properties. However, the behavior of different metrics is often correlated, making it difficult to distinguish different patterns. We compared the performance of a suite of null models and metrics that have been proposed to measure patterns of segregation, aggregation, nestedness, coherence, and species turnover. We found that any matrix with segregated species pairs can be re-ordered to highlight aggregated pairs. As a consequence, the same null model can identify a single matrix as being simultaneously aggregated, segregated or nested. These results cast doubt on previous conclusions of matrix-wide species segregation based on the C-score and the fixed-fixed algorithm. Similarly, we found that recently proposed classification schemes based on patterns of coherence, nestedness, and segregation and aggregation cannot be uniquely distinguished using proposed metrics and null model algorithms. It may be necessary to use a combination of different metrics and to decompose matrix-wide patterns into those of individual pairs of species or pairs of sites to pinpoint the sources of non-randomness.

A major research effort in community ecology has been to infer mechanisms of community organization from patterns in a binary presence–absence matrix. In such a matrix, species are represented by rows, sites are represented by columns, and the entries are the presence or absence of a species in a particular site (McCoy and Heck 1987). Early research (and controversy) focused on the role of interspecific competition in producing checkerboard patterns (Diamond 1975), species segregation (Stone and Roberts 1990), and missing species combinations (Pielou and Pielou 1968). A largely independent focus on species nestedness (Darlington 1957, Patterson and Atmar 1986) emphasized the role of selective, orderly extinction (and immigration) in producing species-poor assemblages whose composition is a perfectly nested subset of more species-rich assemblages.

Leibold and Mikkelson (2002) significantly expanded this framework by proposing tests for additional patterns of Clementsian, Gleasonian, and evenly-spaced gradients. Their method involves re-ordering the rows and columns of a presence–absence matrix by reciprocal averaging to maximize the coherence of species range sizes. A maximally coherent matrix state is one that contains the greatest number of uninterrupted sequences of species occurrences within rows of the re-ordered matrix. In such a re-ordered matrix, 'species turnover' is the replacement of one species by another, and 'boundary clumping' is the extent to which species boundaries are clumped or over-dispersed. Checkerboards, nestedness, Clementsian gradients, Gleasonian gradients, and evenly-spaced gradients are recognized by a combination of patterns of coherence, species turnover, and boundary clumping.

Presley et al. (2010) further expanded Leibold and Mikkelson's (2002) framework, distinguishing among 12 different models based on the combination of boundary clumping and turnover patterns for matrices in which there is positive coherence. They distinguished three types of nested patterns, depending on whether boundary clumping was positive, random, or negative, and they recognized six additional 'quasi-structures' based on weakly positive or negative patterns of species turnover.

The review and decision to publish this paper has been taken by the above noted SE. The decision by the handling SE is shared by a second SE and the EiC.

Both Leibold and Mikkelson (2002) and Presley et al. (2010) also recognized a pattern of 'randomness' which would imply purely stochastic forces in community assembly. This null model represents a ground state against which the other patterns can be meaningfully compared and statistically tested (Gotelli and Graves 1996). Mechanistically, such a null model can be thought of as a stochastic colonization model that excludes species interactions and abiotic forces that structure communities along gradients. Island biogeography models (MacArthur and Wilson 1963), neutral models (Hubbell 2001), and various metacommunity models (Holyoak et al. 2005) can all be interpreted this way. However, estimating the parameters of these models from empirical data has been very challenging (Gotelli and McGill 2006). A more fruitful alternative has been to use a statistical null model, in which an observed presence-absence matrix is reshuffled or randomized in a way that would mimic stochastic assembly of a community without specifying all the details of speciation, colonization, dispersal and extinction (Gotelli and Ulrich 2012).

Null models are always used in conjunction with metrics that quantify the pattern in a presence-absence matrix, usually as a single number. There have been many such measures proposed for quantifying pattern in presence-absence matrices, including metrics of nestedness (Ulrich et al. 2009), species segregation (Stone and Roberts 1990), turnover and β-diversity (Leibold and Mikkelson 2002, Baselga 2010, Tuomisto 2010), coherence (Leibold and Mikkelson 2002), and boundary clumping (Clark and Evans 1954, Hoagland and Collins 1997). Similarly, many algorithms have been proposed for randomizing a presence-absence matrix to mimic a pattern of random community assembly (Gotelli 2000, Ulrich et al. 2009). These algorithms differ in whether the row and column sums of the randomized matrix are treated as fixed, equiprobable, or varying as a function of independently measured properties of sites or species.

As a consequence, there is now a plethora of seemingly reasonable ways to analyze such matrices. Some of these methods can lead to contradictory results when applied to the same data matrix (Gotelli and Ulrich 2012), and very different conclusions when applied to meta-analyses of sets of published data matrices (Wright et al. 1998, Ulrich and Gotelli 2010). However, not all combinations of metrics and null models perform well in practice. Before null models are used to analyze empirical data sets, the performance of candidate randomization algorithms and pattern metrics should be explored with benchmark testing (Gotelli 2001, Gotelli and Ulrich 2012). Such tests evaluate the behavior of null models and their associated metrics by applying them to sets of artificial stochastic matrices that have pre-defined mixtures of deterministic pattern and random associations. Benchmark analysis (Gotelli and Ulrich 2012) can help to identify combinations of null models and metrics that are most powerful for detecting certain kinds of patterns. Benchmark analysis can also steer ecologists away from certain algorithms and indices that lead to frequent rejection of the null hypothesis when applied to simple random matrices (a type I statistical error).

To date, there have been several benchmark analyses of null models for species nestedness (Ulrich and Gotelli

2007a) and species segregation (Gotelli 2001, Ulrich and Gotelli 2007b, 2010), but not for more recently developed metrics of species coherence, turnover, and boundary clumping. Both Leibold and Mikkelson (2002) and Presley et al. (2010) proposed new metrics to be used in combination with existing null model algorithms. They analyzed patterns in artificial matrices exhibiting idealized (extreme) patterns, and they provided examples of different empirical matrices that fit different scenarios in their proposed frameworks. But in neither case have the metrics and null model algorithms been systematically tested against sets of artificial matrices created with varying mixtures of pattern and randomness. Such tests are important not only for finding combinations of metrics and algorithms that have good power for detecting pattern and avoiding type I statistical errors. In previous analyses, many presenceabsence metrics for patterns of nestedness and co-occurrence have exhibited correlated responses when applied to both empirical and artificial data sets, and these correlations are sensitive to how the matrices were constructed as well as to their size, shape, and percent fill. The frameworks proposed by Leibold and Mikkelson (2002), and Presley et al. (2010) implicitly assume that metrics of coherence, turnover, and boundary clumping describe orthogonal, independent properties of matrices. But if the metrics are strongly correlated, some of the proposed cells in their classification frameworks may be redundant or not achievable. Leibold and Mikkelson (2002) recognized this problem and noted that they were able to identify empirical matrices that fit each of the five different scenarios they described.

In this paper, we systematically tested indices of coherence, turnover, and range boundaries proposed by Leibold and Mikkelson (2002) and Presley et al. (2010), as well as some other candidate metrics that might also quantify these kinds of properties. We used these metrics in conjunction with several null model algorithms that have been proposed in previous benchmark tests of nestedness (Ulrich and Gotelli 2007a) and species co-occurrence (Ulrich and Gotelli 2007b). After identifying suitable combinations of metrics and null model algorithms, we tested for patterns of community organization in a meta-analysis of three sets of empirical presence–absence matrices compiled from the published literature and from unpublished sources (Ulrich and Gotelli 2010).

Material and methods

Artificial matrices

In order to understand the behavior of different null model algorithms and algorithms for detecting species turnover, we created two sets of artificial presence–absence matrices with specified amounts of randomness and structure. These matrices differed in their size (number of rows and columns), fraction of the matrix that was filled with species presences, and whether the cells were filled independently, or in a way that reflected specified patterns of species aggregation, segregation, or nestedness. Once these criteria were established, different matrices in each set were created stochastically, to generate variation among matrices of a particular type.

In the construction of these matrices, 'uniform' refers always to placement probabilities drawn from an equiprobable random distribution. 'Exponential' refers to placement probabilities drawn from an exponential random distribution, which was generated from the multiplication of two equiprobable random variables. Both the uniform and exponential distributions will generate variability in row or column totals, but the variability is more extreme with the exponential distribution. This variability reflects the intuition of ecologists that there is heterogeneity among species in their commonness or rarity (the row sums of the matrix), and there is heterogeneity among sites in the number of species they harbor (the column sums of the matrix). This kind of heterogeneity is probably present whether or not species interactions are important, so it is useful to incorporate it in a set of random null matrices for benchmark testing.

We constructed two types of random matrices (M_{fixed size} and $M_{\text{fixed fill}}$). We generated these matrix types to span the range of empirical matrices that are typically generated by field ecologists who sample replicated assemblages at local and regional spatial scales. The M_{fixed size} matrices all had m = 50 rows and n = 50 columns. The proportion of cells in each matrix that was filled with 1 s was chosen from a random uniform distribution with limits of 0.1 and 0.9. In contrast, the $M_{\text{fixed fill}}$ matrices were all filled with a fixed proportion of 0.4, but the number of rows and the number of columns for each matrix was determined by a draw of two random uniform numbers (m = 10 to 100 rows and n = 10 to 100 columns). For both matrix types, we generated 100 matrices each using nine different placement algorithms (Table 1; Supplementary material Appendix A1 contains examples of each matrix type):

- 1. Uniform-uniform random matrices. We filled the matrix cells randomly and independently until the desired matrix fill was reached (uniform uniform random matrices). The probability of placing an occurrence in cell c_{ij} of the matrix was the product of two probabilities, each drawn from uniform random distribution, that specified placement in row *i*, column *j*. This matrix type represents random colonization in which all species are approximately equal in occurrence frequency, and all sites are approximately equal in suitability to be colonized.
- 2. Exponential-exponential random matrices. We filled the matrix cells randomly and independently until the

Table 1. Summary of nine different algorithms used to generate a suite of artificial matrices for testing null model algorithms and indices of community structure.

| Algorithm | Heterogeneity among species | Heterogeneity among sites | Initially hypothesized association patterns |
|-----------|-----------------------------|------------------------------|---|
| 1 | no | no | none |
| 2 | yes | yes | none |
| 3 | yes | no | none |
| 4 | no | no | segregation |
| 5 | no | no | aggregation |
| 6 | yes | yes | segregation |
| 7 | no | no | compartmentalized |
| 8 | yes | yes | nested |
| 9 | yes | yes | turnover |
| | | | |

desired matrix fill was reached. The probability of placing an occurrence in cell c_{ij} of the matrix was the product of two probabilities, each drawn from a random exponential random distribution, that specified placement in row *i*, column *j*. This matrix type represents random colonization in which species differ greatly in occurrence frequency, and sites differ greatly in their suitability. The algorithm generates highly nested matrices.

- 3. *Exponential-uniform random matrices*. We filled the matrix cells randomly and independently until the desired matrix fill was reached. The probability of placing an occurrence in cell c_{ij} of the matrix was the product of two probabilities, one drawn from an exponential distribution that specified the probability of placement in row *i*, and one drawn from a uniform distribution that specified the probability of placement in column *j*. This matrix type represents random colonization in which species differ greatly in their occurrence frequency, but all sites are approximately equal in their suitability.
- 4. Uniform-uniform segregated matrices. We randomly selected two rows (uniform distribution) and two columns (uniform distribution) and filled the four cells with a 2×2 checkerboard submatrix {{1,0},{0,1}}. We randomly selected additional pairs of rows and columns until the desired matrix fill was reached. This matrix type represents a pattern of species segregation in which all species are approximately equal in occurrence frequency, and all sites are approximately equal in suitability, but each species is part of a pair in which the pair members exclude one another in a classic checkerboard distribution. Note that, with this algorithm, each species forms a perfect checkerboard unit with one other species, but occurrence patterns should be random within the remaining S 2 species pairs of which it is a member.
- 5. Uniform-uniform aggregated matrices. We randomly selected two rows (uniform distribution) and two columns (uniform distribution) and filled the four cells with a 2×2 aggregated submatrix {{1,1},{1,1}} until the desired matrix fill was reached. This matrix type represents a pattern of species aggregation in which all species are approximately equal in occurrence frequency, and all sites are approximately equal in suitability, but each species is a member of a pair that tends to occur in an aggregated distribution. Similar to algorithm no. 4, each species belongs to one such aggregated pair, but its occurrence should be random with respect to the remaining S 2 species pairs in which it is a member.
- 6. Exponential-exponential segregated matrices. We randomly selected two rows (exponential distribution) and two columns (exponential distribution) and filled the four cells with 2×2 checkerboard submatrices {{1,0},{0,1}} until the desired matrix fill was reached. This matrix type represents a pattern of species segregation in which species differ greatly in their occurrence frequency, and sites differ greatly in their suitability, but species within individual pairs tend to exclude one another in a classic checkerboard distribution.
- 7. Uniform-uniform compartmentalized matrices. We sequentially filled the matrix with completely filled rectangular submatrices until the desired matrix fill was reached. At each step, the number of rows and columns

in the submatrix was determined by drawing a random uniform integer between 2 and m/2 and n/2, respectively (compartmented matrices). This matrix type represents a pattern in which there are aggregated submatrices of species and sites in which occurrence is clustered.

- 8. Proportional-proportional nested matrices. As in algorithm no. 2, we filled the matrix cells randomly and independently until the desired matrix fill was reached. The probability of placing an occurrence in cell c_{ij} of the matrix was specified from two exponential random distributions. After sorting the matrix according to row and column totals, we randomly introduced a small number (5 to 10% of matrix fill) of unexpected absences in the upper left region of the matrix and a few unexpected presences in the lower right region of the matrix. Except for random placement, and the introduction of a small number of unexpected absences and presences, matrices generated this way should be strongly nested.
- 9. Normal-uniform turnover matrices. We filled the matrix until the desired fill was reached. The placement probabilities for columns were drawn from a uniform distribution. The placement probabilities for rows were drawn from a normal distribution with the mean centered at the corresponding diagonal cell of the matrix. This algorithm generates a pattern in which there is turnover of species across sites, expressed as a concentration of presences along a diagonal band when the matrix is ordered by reciprocal averaging (Leibold and Mikkelson 2002).

In summary (Table 1), our set of artificial matrices include three algorithms in which species colonization is independent, but there are varying degrees of heterogeneity in species occurrences and site suitability (1, 2, 3), two algorithms which should generate segregated pairs of species (4, 6), and one algorithm each that should generate matrices that are aggregated (5), compartmentalized (7), nested (8), and exhibit turnover (9). Thus, our 1800 artificial matrices, with varying degrees of randomness and structure, were constructed to test the performance of different metrics and different null model algorithms. Examples of each matrix type are contained in Supplementary material Appendix A1.

Empirical matrices

We analyzed three collections of empirical matrices that have previously been studied in species co-occurrence analysis (Wright et al. 1998, Ulrich and Gotelli 2007a, b, 2010). The first is the set of 288 biogeographic presence– absence matrices compiled by Atmar and Patterson (1995). The second is a set of 147 abundance matrices contained in Supplement A of Ulrich and Gotelli (2010). The third is a set of 36 interaction matrices (species × species) that includes abundance data from the NCEAS database (< www.nceas. ucsb.edu/interactionweb/html/datasets.html#anemone_ fish >). In total, we analyzed 471 empirical species × sites matrices. We classified these matrices as large scale (landscape to continental), small scale (local to landscape), and interaction matrices. Additionally, we sorted the matrices of the first two sets into eight taxonomic groups (fishes, herptiles [Amphibia and Reptilia], mammals, birds, insects, other invertebrates, plants, and protozoa).

Metrics

We considered a set of 13 possible metrics (Table 2) that potentially can detect patterns of species segregation (4a, 4b, 4c, 12), species aggregation (4a, 5, 8, 9, 10, 12, 13), nestedness (1, 2, 3), turnover (6), range coherence (7), and clustering of species' range boundaries (11). Some metrics of species segregation, aggregation, and compositional dissimilarity (4, 5, 12, 13) do not depend on the ordering of the rows and columns of the matrix. Metrics of nestedness (1, 2, 3)are calculated from matrices that have been arranged in order of decreasing row and columns sums. Metrics of turnover (6), range coherence (7), clustering (11), and some metrics of species aggregation (4b, 8, 9, 10), and species segregation (4c) are calculated from a matrix that is ordered on the basis of reciprocal averaging (correspondence analysis). Following the proposal of Leibold and Mikkelson (2002), the first axis from a correspondence analysis orders the rows and columns of a presence-absence matrix in a way that maximizes uninterrupted strings of presences (coherence) in both the rows and columns of the matrix. Soerensen's and Simpson's indices have recently been proposed for use as metrics of species turnover and nestedness (Baselga 2010, Podani and Schmera 2011, but see Almeida-Neto et al. 2012). However, the indices are calculated using the row and column sums of a presenceabsence matrix. We did not consider these indices, because we wanted to compare all indices with a fixed - fixed null model, which preserves row and column sums, and has performed well in previous analyses of species co-occurrence (Gotelli 2000) and nestedness (Ulrich and Gotelli 2007a).

Metrics independent of matrix sorting

We estimated matrix wide species segregation by the *C*-score (Stone and Roberts 1990) that is a normalized count of the number of checkerboard submatrices ({{1,0},{0,1}} or {{0,1},{1,0}}). The original normalization of the *C*-score was an average calculated over the number of species pairs (Stone and Roberts 1990). This normalization causes the raw *C*-score to be positively correlated with the number of sites (Ulrich and Gotelli 2007b). An additional scaling should therefore also account for the number of site combinations [n(n-1)/2]. We hence use a modified *C*-score of the form

$$C - score = \frac{4\sum_{i,j} \begin{pmatrix} 1 & \dots & 0 \\ \dots & \dots & \dots \\ 0 & \dots & 1 \end{pmatrix}}{mn(m-1)(n-1)} (1)$$

$$= \frac{4\sum_{i,j} (N_i - N_{ij})(N_j - N_{ij})}{mn(m-1)(n-1)}$$

where N_i and N_j denote total number of occurrences of species *i* and *j* and N_{ij} is the number of joint occurrences.

| Tabl | e 2. | Summary | ∕ of | 15 | inc | lices | for | co-occurre | nce an | alysis | used | in | this | pap | oer. |
|------|------|---------|------|----|-----|-------|-----|------------|--------|--------|------|----|------|-----|------|
|------|------|---------|------|----|-----|-------|-----|------------|--------|--------|------|----|------|-----|------|

| Index | Name | Description | Matrix ordering | Pattern | Reference |
|-------|----------------------------|---|--------------------------|---|--------------------------------------|
| 1 | NODF | normalized count of species overlap along the gradient of decreasing species richness of sites and species | row and column totals | nestedness | Almeida-Neto et al. 2008 |
| 2 | BR | normalized count of shifts in occurrences to get a perfectly nested matrix | row and column totals | nestedness | Brualdi and Sanderson 1999 |
| 3 | BR _{turn} | normalized count of shifts in occurrences to get a perfectly nested matrix | reciprocal averaging | nestedness | this work |
| 4a | modified <i>C-score</i> | normalized number of 2×2 checkerboard units | unordered | aggregation/ segregation | Stone and Roberts 1990, this work |
| 4b | C _{Turn} | normalized number of 2×2 checkerboard units with occurrences in the turnover region of the sorted matrix | reciprocal averaging | segregation | this work |
| 4c | C _{Seg} | normalized number of 2×2 checkerboard units with occurrences not in the turnover region of the sorted matrix | reciprocal averaging | segregation | this work |
| 5 | Clumping | normalized number of clumped 2×2 submatrices | unordered | aggregation | this work |
| 6 | R ² | rank correlation of row and column position for occupied cells in an ordered matrix | reciprocal averaging | turnover | this work |
| 7 | EmAbs | number of embedded absences within rows | reciprocal averaging | range coherence | Presley et al. 2010 |
| 8 | NND | average nearest neighbor distance of occupied cells | reciprocal averaging | aggregation (low values) | Clark and Evans 1954 |
| 9 | JoinOcc | number of occupied adjacent grid cells | reciprocal averaging | aggregation | Moran 1948 |
| 10 | Block | blocked quadrat variance | reciprocal averaging | aggregation | Hill 1973 |
| 11 | Morista | relative abundance distribution of range boundaries among sites | reciprocal averaging | clustering of species range boundaries | Hoagland and Collins 1997 |
| 12 | Chao | relative abundance distribution among sites | unordered | segregation | Chao et al. 2008 |
| 13 | Togetherness | normalized number of paired 2 × 2 submatrices (togetherness score) | unordered | aggregation | Stone and Roberts 1992, this work |

Chao et al. (2008) extended the Morisita index of similarity for two communities to a matrix-wide metric for n communities of the form

$$Chao = \sum_{i}^{m} \frac{\left[\left(\sum_{j=1}^{n} p_{ij} \right)^{2} - \sum_{j=1}^{n} \left(p_{ij} \right)^{2} \right]}{(n-1) \sum_{j=1}^{n} \left(p_{ij} \right)^{2}}$$
(2)

where p_{ij} is the relative abundance of species *i* in site *j*. Low values of *Chao* indicate dissimilarity of species relative abundance distribution among sites, which can be interpreted as a measure of negative covariance in relative abundances. The metric is independent of the ordering of the matrix.

A simple metric for aggregation that is independent of matrix order is a count of the total number of 2×2 submatrices of the form {{1,1},{1,1}}. The *Clumping* metric is therefore the aggregation equivalent to the *C*-score. As in the case of the *C*-score we calculate *Clumping* in the normalized form divided by the total number of 2×2 submatrices [mn (m-1) (n-1)/4].

The togetherness score (*Tog*) of Stone and Roberts (1992) is a complement of the *C*-score and defined from 2×2 submatrices of the form {{1,0},{1,0}} or {{0,1},{0,1}}. The metric *Tog* is a count of the total number of these submatrices. It is standardized with regard to matrix size by

$$Tog = \frac{4\sum_{i,j} \begin{pmatrix} 1 & \dots & 0 \\ \dots & \dots & \dots \\ 1 & \dots & 0 \end{pmatrix}}{mn(m-1)(n-1)} (3)$$
$$= \frac{4\sum_{i,j} N_{ij}(n-N_i-N_j+N_{ij})}{mn(m-1)(n-1)}$$

Tog can range from 0.0 to 1.0, with high values of *Tog* indicating positive species association. We note that *Tog* differs from the previous metrics in that it is column centered and scores of a matrix and its transpose differ.

Metric depending of matrix sorting

With perfect spatial turnover, species occurrences should be concentrated along the diagonal of the matrix after ordination by reciprocal averaging (Leibold and Mikkelson 2002). Such a matrix can be subdivided into a nearly completely filled region (AT, area of turnover) and two empty regions (AC, areas of co-occurrence) (Fig. 1, 2: maximum species turnover). The area of AT equals the matrix fill defined as fill = w*S, where S is the number of species and w is the width of this sub-region of the matrix. For calculations, all cells that were intersected by the margins of the filled region were included in the ATregion.



Figure 1. Ordinated example matrix with raw scores of the 14 metrics used in this study (Table 2). AT and AC: matrix areas used for calculating the C_{Turn} (AT) and the C_{Segr} (AC) scores, respectively.

Based on this spatial partitioning of the ordered matrix, the global *C-score* C_{total} can be decomposed into three components. The first component C_{Turn} is calculated for those checkerboard pairs for which both occurrences fall within *AT*. C_{Turn} measures the part of segregation that stems from species turnover. The second component C_{Segr} is calculated only for those occurrences that fall outside AT (AC in Fig. 2). C_{Segr} measures the part of segregation that does not stem from species turnover. The third component C_{Mixed} is calculated for checkerboards for which one



Figure 2. Six theoretical presence–absence matrices showing different degrees of co-occurrence. Left side: raw matrix; right side: ordinated matrix (order reversed for the compartmented matrix).



Figure 3. A perfectly nested matrix remains nested with reversed ordering of either species or sites after reciprocal averaging.

occurrences is within AT and the other is within AC. C_{Mixed} is calculated as the remaining fraction:

$$C_{Mixed} = C_{total} - C_{Turn} - C_{Segr}$$
⁽⁴⁾

In a matrix ordinated by reciprocal averaging, the position of the non-empty cells is specified by the row and column numbers. We calculated the coefficient of correlation r of the row and column numbers of non-empty cells. In this context, r^2 is an index of how orderly the pattern is of the non-empty cells along the matrix diagonal. The index will be nearly 1.0 when the matrix has maximum coherence in combination with high turnover, and will be lower if the matrix has less structure. We compared the observed r^2 with the r^2 calculated for the randomized matrices, which were also ordinated by reciprocal averaging.

Presley et al. (2010) proposed a count of the number of embedded absences *EmbAbs* within rows in the ordinated matrix as a metric of coherence of species range sizes (Leibold and Mikkelson 2002), with low numbers of embedded absences with respect to the null distribution indicating strong matrix-wide coherence (Fig. 3). We normalized *EmbAbs* by dividing it by the matrix fill. As in the case of *Tog*, *EmbAbs* scores differ from those calculated after matrix transposition.

Hoagland and Collins (1997) proposed to use the Morisita index to assess clumping of species range boundaries in an ordinated matrix. *Morisita* is calculated as

$$Morisita = n \sum_{i=1}^{n} \frac{k_i}{N} \frac{k_i - 1}{N - 1}$$
(5)

where k_i denotes the number of starting and stopping boundaries at site *i*. *N* is the total number of starting and stopping boundaries and equals therefore two times the number of species. Large values of *Morisita* denote clustered boundaries of species occurrence.

To quantify patterns of species aggregation, we used a common member of the Clark and Evans (1954) nearestneighbor class of metrics for spatial aggregation o the form

$$NND = \frac{\sum_{i=1}^{m} \sum_{j=1}^{n} d_{ij}^{2}}{2 \ fill}$$
(6)

where d_{ij} is the distance to the nearest neighbor (= occupied cell) in the ordinated matrix for each species occurrence

and *fill* is the total number of occurrences. Small values of NND indicate an aggregated pattern.

The join-count statistic (Moran 1948) is similar to the nearest neighbour method and uses sums of entries of all occupied cells in the vicinity of a given focal cell (Cliff and Ord 1973). We used the presence–absence version *JoinOcc* of this metric and counted the occurrences within a 3×3 quadrate surrounding each occupied cell in the matrix.

$$JoinOcc = \frac{\sum_{i=2}^{m-1} \sum_{j=2}^{n-1} \sum_{i=i-1}^{i-1} \sum_{j=j-1}^{j=j+1} x_{ij} x_{i_1 j_1}}{\sum_{i=1}^{m} \sum_{j=1}^{n} x_{ij}}$$
(7)

where x_{ij} and x_{i1j1} denote abundances (presence–absence) in cells (i,j) and (i1,j1) and the denominator is the total abundance in the matrix. High values of *JoinOcc* denote an aggregated pattern.

Blocked quadrate variances (Hill 1973, Dale 1999) are a diverse group of metrics that use the variances of contiguous submatrices of similar or differing size to infer nonrandom structure. We used a blocked quadrate variance index of the following form:

$$Block = \frac{\sum_{i=1}^{m-3} \sum_{j=1}^{n-3} [(x_{ij} - x_{i+2,j+2})^2 + (x_{ij} - x_{i,j+2})^2 + (x_{ij} - x_{i+2,j})^2]}{8L}$$
(8)

where x_{ij} denotes the sum of entries of the 2×2 submatrices $(x_{ij}, x_{i+1,j}, x_{i,j+1}, x_{i+1,j+1})$ and L = 3(m-3)(n-3) is the total number of summands. High values of *Block* indicate species aggregation.

We used NODF (nestedness based on overlap and decreasing fill, Almeida-Neto et al. 2008) and discrepancy BR (Brualdi and Sanderson 1999) to estimate the degree of nestedness. For this analysis, matrices were sorted according to row/columns totals. If a perfectly nested matrix is ordinated by reciprocal averaging, it retains its nested structure, but with a reversed ordering of either rows or columns (Fig. 3). Thus we tested whether the appropriately rescaled metric BR (termed BR_{turn}) also works using ordinated matrices.

In all cases, random expectations were obtained from 1000 null matrices each that were either randomized using a null model that retains row and column totals (fixed – fixed null model, FF) or a null model that assigned occurrences equiprobably random to matrix cells (equiprobable – euqiprobable null model, EE). Randomization of the fixed – fixed null model was done with the independent swap algorithm (Gotelli and Entsminger 2003) using 10*n*mswaps for each randomized matrix. Statistical significances came from the respective tail distributions at the twosided 5% error level. Additionally we calculated Z-transformed scores (Z = Obs - Exp)/StDev_{Exp}; Obs and Exp: observed and expected scores, StDev_{Exp}; standard deviation of expectation). Z-scores should have values below -1.96and above +1.96 at the two-sided 5% error level under the assumption that the respective null distribution is approximately normal.

Results

Metric and null model performance on random matrices

Regardless of the null model used, all of the metrics had a low frequency of rejection (type I error) when tested against random-uniform matrices (first row in Table 3 and 4). However, if the null model was EE (Table 3), all of the metrics had high frequencies of rejection when tested against random matrices with heterogeneous row and/or column totals (exponential-exponential random and exponentialuniform random). If the null model was FF (Table 4), type I errors were again low for exponential-exponential random matrices, but somewhat elevated for exponentialuniform random matrices. For this type of random matrix, the BR, Morisita, and NND indices performed best, and Clumping performed the worst (Table 4). When used with FF C-score and Togetherness identified all matrices in an identical manner. Regardless of whether the pattern was random, segregated, or aggregated both indices were consistently in the upper tail of the null distribution (Table 4).

Overall, *FF* controlled best for type I errors in purely random matrices with heterogeneous row and column totals. There was little difference in performance on matrices of fixed size (upper panel, Table 3 and 4) versus fixed fill (lower panel, Table 3 and 4). Because of the consistently poor performance of *EE* on random matrices, we restrict the description of results for structured matrices to tests with *FF*.

Metric performance on segregated matrices

For uniformly and exponentially segregated matrices, three metrics that are independent of matrix sorting (*C-score, Togetherness* and *Clumping*) had the best power for detecting non-randomness regardless of the type of null model (Table 3, 4). However, *Clumping* detected at least 62% of the uniformly segregated and turnover matrices as being aggregated while *C-score* and *Togetherness* always performedidentically. For the fixed-size matrices, *C-score* and *Togetherness* were less powerful at detecting non-randomness when the patterns were created by inserting segregated elements into a random matrix with exponential row and column totals (exponential segregated). In this case, the *Clumping* and *Chao* indices had better power. With the exception of *BR*, *BR_{turn}*, and *NND*, all metrics had very good power to detect turnover matrices as being non-random. With these matrices, C_{Turn} and R^2 performed equally well.

Metric performance on aggregated matrices

C-score, Togetherness, Clumping and R^2 detected at least 76% of the aggregated matrices as being non-random. (Table 4), whereas the other metrics performed much worse. For the nested matrices, the *C-score* identified all but one of the simulated matrices as non-random, but *Chao*, R^2 , EmbAbs and JoinOcc also performed well for fixed size matrices. For fixed fill matrices, C-score, Togetherness, Clumping, Chao, C_{Segr} , R^2 , BR, EmbAbs and JoinOcc were all equally powerful in detecting pattern. BR_{turn}, C_{Segr}, Morisita, NND and Block detected less than 50% of the aggregated matrices (Table 4, Supplementary material Appendix A1) as being non-random. NODF performed worse than BR in detecting a nested pattern. In the fixed fill matrices with an intermediate fill of 40%, NODF correctly detected 73% of the nested matrices (fixed - fixed null model), but detected only 35% of the nested fixed size matrices (Table 4). This difference shows the low power of NODF at high or low matrix fill. Compartmentalized matrices were detected most frequently by the C-score, Togetherness, Clumping, C_{Turn} and NODF, with minor differences between fixed fill and fixed size matrices. R^2 and, to a lesser degree, C_{Turn} identified most aggregated matrices as having significant turnover (Table 4).

The exponential – exponential algorithm produced highly nested and therefore aggregated matrices. Such a matrix structure leaves a too low effective sample space for the FF null model and consequently FF was not able to detect this pattern (Table 4).

Correlations among metrics

When tested against the set of all 1800 artificial matrices, many of the 15 indices were highly correlated in their performance (Z-scores), particularly for *EE* (Table 5, upper panel). The strongest positive correlations were between *BR* and *Clumping* (r = 0.98) and between *BR* and *EmbAbs* (r = 0.86). The strongest negative correlations were between *EmbAbs* and *JoinOcc* (r = -0.97) and between *C-score* and *Clumping* (-0.96). Of the 105 pairwise correlations among the indices, 28 had correlations > [0.7].

For *FF*, there were only 13 such correlations (Table 5, lower panel). The largest positive correlations were between R^2 and *JoinOcc* (r=0.94), and between *C-score* and *Togetherness* (r=0.80). The largest negative correlations were between *JoinOcc* and *EmbAbs* (r=-0.90) and between R^2 and *EmbAbs* (-0.89). Although they should identify opposite patterns, there was a positive correlation (r=0.55) between *C-score* and *Clumping*. *Z*-scores of *Chao*, *NND* and *Morisita* were only weakly correlated with other metrics (Table 5), particularly with those designed to detect aggregation. These metrics and the also weak performing *Block* metric are not considered further.

Performance of metrics on idealized matrices

Seven indices (*Clumping*, *C*-score, C_{Segr} , C_{Turn} , *EmbAbs*, R^2 and *NODF*) were used to test for patterns in the six

Table 3. Numbers of matrices (100 matrices each of nine types and two size/fill options as described in the methods section) that were detected by 15 different metrics as having scores significantly higher (score above the upper 95% confidence limit, UCL) or lower (score below the lower 95% confidence limit, LCL) than expected from the distribution of scores of the equiprobable – equiprobable null model.

| | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 |
|--------------|--------------------------------|-------|---------------------|--------|-------------|----------|---------|---------|---------------------|------------|-------|-------------------|----------|--|---------|----------|-------|---------------------|----------------------|-------|--------|--------|----------|---------|----------|---------|-----------|--------|---------|---|
| | | | Metric | indepe | ndent of | row/colu | umn sor | ting | | | | 0 | rdinatio | c | | | Sorti | ng acco colum | rding to n totals | row/ | | | Metric c | lepende | nt on ro | //colum | nn sortir | 50 | | |
| Matrix | | C-sc | ore | Toget | ther | Clump | ing | Сһас | | C_{Turn} | | C _{Segr} | | BR_{turn} | | R^{2} | NC | DF | В | R | Blo | ck | EmbAı | bs | JoinOco | ~ | Aorisita | | DNN | |
| pattern | Matrix type | > UCL | <pre>CCL </pre> | > UCL | <lcl></lcl> | > UCL < | | ^ NCL < | <pre>CCL ></pre> | NCL < | 1< 10 | J> J) | CL > Ui | CL <lc< td=""><td>:L > UC</td><td>101 > 10</td><td>- NCL</td><td><pre>> CCL</pre></td><td>> UCL</td><td>< LCL</td><td>> UCL</td><td>< TCL</td><td>> ∩CL</td><td>< TCL ></td><td>nct <</td><td>-CL > L</td><td>ICL < L0</td><td>CL > U</td><td>CL < LC</td><td></td></lc<> | :L > UC | 101 > 10 | - NCL | <pre>> CCL</pre> | > UCL | < LCL | > UCL | < TCL | > ∩CL | < TCL > | nct < | -CL > L | ICL < L0 | CL > U | CL < LC | |
| Fixed size | matrices | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Random | Uniform random | 2 | 2 | ŝ | 4 | e | 9 | 3 | 4 | 1 | 5 0 | 5 | 0 | -0 | 4 | 0 | 2 | -0 | 2 | 5 | 2 | | | 0 | 2 | 4 | 2 | 4 | 4 | |
| | Exponential-exponential random | 0 | 100 | 0 | 100 | 100 | 0 | 100 | 0 | - | 34 (| 0 10 | 0 62 | 34 | 0 | 86 | 93 | L) | 0 | 100 | 11 | 59 | 0 | 100 | 88 | 2 | 0 | 23 | ~ | |
| | Exponential-uniform random | 0 | 100 | 100 | 0 | 100 | 0 | 6 | 87 | 0 | 00 | 0 10 | 0 60 | 16 | 69 | 24 | 100 | 0 | 0 | 100 | 16 | 79 | 0 | 100 | 98 | 0 7 | 4 | 41 | 26 | |
| Segregatec | Uniform segregated | 69 | 0 | | | 0 | 43 | 0 | 2 | 20 (| 0 2. | 3 0 | 0 | 0 | 55 | 0 | 0 | 68 | 51 | 0 | 4 | 4 | 3 | 2 | 2 | 2 | 2 | 2 | ŝ | |
| | Exponential segregated | 0 | 89 | 29 | 2 | 79 | 0 | | 79 | 0 4 | 12 (|) 5! | 5 | 10 | 0 | 37 | 56 | 0 | 0 | 56 | 14 | - | 0 | 55 | 46 | 1 | 2 5 | 0 | 10 | |
| | Turnover | 0 | 94 | 0 | 74 | 100 | 0 | 87 | 0 | 81 1 | 8 | 10 | 0 73 | 13 | 100 | 0 | 87 | 0 | 0 | 95 | 0 | 66 | 0 | 100 1 | 00 | 0 | 95 | 0 | 30 | |
| Aggregated | I Uniform aggregated | 0 | 97 | 51 | 9 | 100 | 0 | 16 | 28 | 26 1 | 7 6 | ,9 (| 4 32 | 18 | 88 | 0 | 97 | 0 | 0 | 98 | \sim | | 0 | 95 | 87 | 0 | 43 | 4 | 15 | |
| | Compartmented | 0 | 95 | 66 | 17 | 94 | 0 | 16 | 76 | 18 6 | 0 |) 8(| 9 20 | 58 | 71 | 8 | 94 | - | 0 | 92 | 19 | 33 | 0 | 84 | 87 | 1 | 7 29 | 28 | 14 | |
| | Nested | 0 | 100 | 100 | 0 | 100 | 0 | 26 | 72 | 5 6 | 2 (| 10 | 0 62 | 5 | 93 | 2 | 100 | 0 | 0 | 100 | 0 | 100 | 0 | 100 1 | 00 | 0 4 | 2 43 | 22 | 30 | |
| Fixed fill n | natrices | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Random | Uniform random | 4 | 9 | 2 | 4 | 4 | 3 | 2 | 0 | 5 | 2 | 9 | 4 | - | 0 | 5 | 2 | 4 | °. | 4 | | 2 | 4 | | 2 | | ŝ | | | |
| | Exponential-exponential random | 0 | 100 | 0 | 100 | 100 | 0 | 100 | 0 | 0 1. | 00 | 2 | 5 50 | 45 | 0 | 73 | 100 | 0 | 0 | 100 | 13 | 29 | 0 | 100 | 97 | 1 40 | 0 | 25 | 2 | |
| | Exponential-uniform random | 0 | 100 | 66 | 0 | 100 | 0 | 2 | 93 | 0 | 00 | .8 | 7 54 | 5 | 79 | ŝ | 100 | 0 | 0 | 100 | 0 | 96 | 0 | 100 | 66 | 0 10 | 0 | 37 | 11 | |
| Segregated | Uniform segregated | 98 | 0 | 14 | 11 | 0 | 78 | 12 | 11 | 71 (| 3 (| 3 2 | | 0 | 79 | 0 | 0 | 96 | 83 | 0 | 4 | 15 | 2 | 2 | 9 | 0 | 4 | 2 | ŝ | |
| | Exponential segregated | 0 | 94 | 30 | 4 | 91 | 0 | 0 | 85 | 3 0 | 38 (| 5; | 7 32 | ŝ | ĉ | 27 | 92 | 0 | 0 | 93 | 8 | 2 | 0 | 76 | 67 | 0 | 8 | 4 | ~ | |
| | Turnover | 0 | 94 | 0 | 74 | 100 | 0 | 87 | 0 | 81 1 | 8 | 10 | 0 64 | 17 | 100 | 0 | 87 | 0 | 0 | 93 | 0 | 66 | 0 | 100 | 00 | 0 | 92 | 0 | 29 | |
| Aggregated | I Uniform aggregated | 0 | 94 | 50 | 5 | 66 | 0 | 11 | 41 | 26 2 | 1 C |)9 ((| 7 (| 27 | 92 | 0 | 95 | 0 | 0 | 96 | 22 | \sim | 0 | 98 | 77 | 0 | 42 | 10 | \sim | |
| | Compartmented | 0 | 95 | 71 | 16 | 95 | 0 | 12 | 81 | 10 7 | 7 | .7. | 7 7 | 73 | 76 | 10 | 94 | 0 | 0 | 95 | 24 | 44 | - | 92 | 94 | 6 |) 23 | 30 | 23 | |
| | Nested | 0 | 100 | 66 | 0 | 100 | 0 | 32 | 60 | 0 1(| 00 | .8 | 5 40 | 0 | 97 | 0 | 100 | 0 | 0 | 100 | 0 | 66 | 0 | 100 | 00 | 0 10 | 0 | 6 | 41 | |

| igher (sco | | Antriv | attern | ixed size mat | andom L | | egregated L E | ggregated L | ixed fill matri | andom L | ш | egregated L E | ggregated L |
|--------------------|-----------------------|--------------------|---|---------------|---|---|--|---|-----------------|---|-------------------------------|--|-------------------------------------|
| re above the upper | | | Matrix type | rices | Jniform random :xponential-exponential | random Exponential-uniform random | Uniform segregated Exponential segregated Turnover | Uniform aggregated Compartmented Vested | ices | ∪niform random Exponential-exponential random | Exponential-uniform random | Uniform segregated Exponential segregated Turnover | Jniform aggregated Compartmented |
| 95% c | | C-sc | > UCL | | 4 σ | 22 | 75 38 100 | 93 100 | | ~ ~ ~ | 22 | 98 79 | 99 |
| onfid∈ | Metric ì | ore | < LCL | | 4 σ | 12 | 000 | 000 | | 3 5 | - | 000 | 0 - |
| ince li | indepen | Toget | > UCL | | ς Γ | 22 | 75 38 100 | 89 93 100 | | - 4 | 22 | 98 79 91 | 99 95 |
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| er (scc | rting | Chao | - NCL < | | 1 2 | 0 | 555 16 | 5 2 97 | | 7 - | 0 | 13 69 26 (| 6 4 |
| re bel | | | LCL >L | | 0.12 | *** | 1 1 1 1 1 1 1 1 1 1 | 7 34 0 5 8 6 | | . , | 37 | 1 0 12 9 4 | 6 9 78 9 |
| ow th | | C _{Tum} | 1> 10 | | 1 2 | en en | 2 0 00 | 202 | | 4 4 | 1 3 | 5 0 0 0 0 | 5 - |
| e low | | | -CL >L | | 2 4 | - | 0 ~ (0 + 0 | 9 21 | | | 5 | 0 ~ 0 | 0 |
| er 95°, | ō | C _{Segr} | iCL < L | | 1 2 | 5 20 | 0 m 0 | 3 5 0 27 5 36 | | 20 | 35 | 4 - 6 | 1 25 |
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| fidenc | _ | BR _{turn} | 01 < LC | | 5 2 | 18 | 1 1 2 | 7 36 35 | | 5 | 16 | 2 0 1 14 0 | 6 30 |
| se limi | | | JU > U(| | 1 5 | 0 | 54 1 100 | 92 76 98 | | 0 4 | 0 | 76 10 87 | 94 80 |
| t, LCL | | R^2 | CT <lc< td=""><td></td><td>- 4</td><td>99</td><td> 0</td><td>040</td><td></td><td>4 L</td><td>78</td><td>04 -</td><td>9</td></lc<> | | - 4 | 99 | 0 | 040 | | 4 L | 78 | 04 - | 9 |
|) than | Sort | Z |) 1 - UC | | 7 4 | 0 | 4 0 0 | 2 35 35 | | л ж | 0 | 8 64 0 | 4 0 |
| expec | ing acco colum | ODF | r <lci< td=""><td></td><td>- σ</td><td>51</td><td>4 1 99</td><td>11 92 13</td><td></td><td>4 10</td><td>53</td><td>1 0 84</td><td>10 93</td></lci<> | | - σ | 51 | 4 1 99 | 11 92 13 | | 4 10 | 53 | 1 0 84 | 10 93 |
| ted fro | ording tc n totals | E | - > UCI | | 0 1 | - | - 4 - | 4 8 0 | | | 2 | 3 13 2 | 4 7 |
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| distri. | | Blo | > UCL | | 7 7 | 1 | 0 1 3 | 4 1 0 | | | 23 | 3 4 | 11 |
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| ores o | depende | bs | < TCL > | | 3 7 | 0 | 9 3 3 100 | 62 42 97 | | о т | 0 | 15 7 83 | 76 43 |
| f the f | ent on r | JoinOc | • NCL < | | . 1 | 5 | 6 1 100 | 29 55 95 | | 7 7 | 2 | 8 82 | 37 73 |
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| Inull | ting | <i>a</i> | rcr > (| | 7 7 | ~ ~ ~ ~ | 95 2 35 | 8 E 8 | | ω 4 | ~ | 904 | 2 2 |
| model | | DNN | I> 12 | | ~ ~ ~ | | ω 4 O | 2 8 | | 4 - | 4 | 6 6 9 | 0 |
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Table 4. Numbers of matrices (100 matrices each of nine types and two size/fill options as described in the methods section) that were detected by 15 different metrics as having scores significantly higher (score above the upper 95% confidence limit. U(CI) or lower (score helow the lower ds?, confidence limit. U(CI) or lower (score helow the lower ds?, confidence limit. U(CI) or lower (score helow the lower ds?, confidence limit. U(CI) or lower (score helow the lower ds?, confidence limit. U(CI) or lower (score helow the lower ds?).

| lable 5. Spea | rman's rank | k order corr | elation of Z | -scores of T | o metrics appli | ed to all 180 | 00 M _{fixed-fill} a | nd M _{fixed size} | matrices. Co | rrelation coet | ticients > 0. | / are marke | ed in bold. | | |
|-------------------|-------------|--------------|--------------|--------------|-----------------|---------------|------------------------------|----------------------------|--------------|----------------|---------------|-------------|-------------|---------|----------|
| Metrics | Block | BR | BR_{tum} | Chao | Clumping | C-score | C_{Segr} | C_{Turn} | EmbAbs | JoinOcc | Morisita | NND | Nodf | R^{2} | Together |
| Block | | 0.72 | -0.47 | 0.20 | -0.57 | 0.66 | 0.63 | 0.43 | 0.88 | -0.85 | -0.15 | -0.14 | -0.64 | -0.76 | -0.31 |
| BR | 0.44 | | -0.12 | 0.36 | -0.95 | 0.98 | 0.80 | 0.69 | 0.86 | -0.90 | -0.32 | -0.24 | -0.89 | -0.47 | -0.42 |
| BR_{turn} | -0.10 | 0.31 | | -0.02 | -0.03 | -0.08 | -0.27 | -0.11 | -0.34 | 0.25 | -0.11 | 0.08 | -0.03 | 0.40 | -0.03 |
| Chao | -0.25 | -0.20 | -0.06 | | -0.42 | 0.38 | 0.28 | 0.30 | 0.29 | -0.34 | -0.03 | -0.34 | -0.32 | -0.14 | -0.73 |
| Clumping | -0.23 | -0.31 | 0.01 | -0.07 | | -0.96 | -0.77 | -0.60 | -0.77 | 0.84 | 0.33 | 0.24 | 0.86 | 0.36 | 0.49 |
| C-score | -0.54 | -0.63 | -0.14 | 0.10 | 0.55 | | 0.79 | 0.72 | 0.80 | -0.84 | -0.34 | -0.31 | -0.90 | -0.36 | -0.39 |
| C _{Segr} | -0.16 | -0.42 | -0.32 | 0.39 | -0.29 | 0.21 | | 0.32 | 0.83 | -0.81 | -0.10 | -0.34 | -0.58 | -0.56 | -0.22 |
| C _{Tum} | -0.54 | -0.44 | 0.10 | -0.14 | 0.67 | 0.62 | -0.29 | | 0.42 | -0.47 | -0.32 | -0.26 | -0.67 | 0.04 | -0.23 |
| EmbAbs | 0.88 | 0.44 | -0.12 | -0.10 | -0.40 | -0.57 | -0.02 | -0.70 | | -0.97 | -0.08 | -0.17 | -0.70 | -0.80 | -0.36 |
| JoinOcc | -0.88 | -0.62 | -0.04 | 0.23 | 0.36 | 0.69 | 0.26 | 0.61 | -0.90 | | 0.12 | 0.20 | 0.74 | 0.75 | 0.44 |
| Morisita | 0.31 | 0.47 | 0.30 | -0.36 | 0.17 | -0.30 | -0.63 | 0.10 | 0.20 | -0.43 | | -0.24 | 0.56 | -0.17 | 0.26 |
| DNN | 0.17 | 0.13 | -0.05 | -0.13 | 0.06 | 0.03 | -0.06 | -0.09 | 0.25 | -0.18 | 0.08 | | 0.09 | 0.07 | 0.04 |
| Nodf | 0.15 | 0.40 | 0.03 | 0.44 | -0.79 | -0.41 | 0.30 | -0.67 | 0.34 | -0.30 | -0.17 | -0.02 | | 0.30 | 0.47 |
| R^{2} | -0.87 | -0.62 | -0.04 | 0.22 | 0.39 | 0.73 | 0.19 | 0.72 | -0.89 | 0.94 | -0.34 | -0.14 | -0.32 | | 0.29 |
| Together | -0.53 | -0.61 | -0.17 | 0.12 | 0.47 | 0.80 | 0.20 | 0.59 | -0.57 | 0.67 | -0.29 | 0.00 | -0.38 | 0.71 | |
| | | | | | | | Fixed – fix | ed null mod | lel | | | | | | |

Equiprobable - equiprobable null model

idealized matrices (checkerboard, maximum turnover, compartmented turnover, compartmented segregation, turnover-independent segregation, and a mixed matrix, Table 6, Fig. 2). In all comparisons, there were usually more significant results with the fixed – fixed null model than with the equiprobable – equiprobable null model, except for the mixed matrix, which did not differ from random for any of the indices with either null model (Table 6). For all comparisons, whenever an index was statistically significant with both null models, it deviated from the null hypothesis in the same direction, regardless of the matrix pattern.

Empirical matrices

Of the 471 empirical matrices, 138 (29%) and 107 (23%), respectively, were detected by the *C*-score and the Clumping score as having a non-random structure when applied with FF (Table 7, 8). In 65 (14%) cases, both metrics jointly had scores above the upper two-sided 95% confidence limit, thus indicating simultaneous aggregation and segregation under a traditional interpretation of these scores (Table 8). Thirty-one percent of the matrices exhibited significant species turnover as measured by C_{Turn} or R^2 . Both of these metrics jointly classified 102 of 191 significant matrices as being spatially segregated (Table 8). The fact that only two matrices were classified differently (Table 8) shows that both metrics capture the same pattern. Of the 91 matrices that were jointly identified by the *C*-score and R^2 as being segregated and having turnover, 49 were also identified by Clumping and 30 by JoinCount as being aggregated. These are matrices in which species occurrences were aggregated along the matrix diagonal after ordination. These patterns did not differ for matrices of different taxa or for matrices sampled at different spatial scales (Table 7). C_{Seer} identified about 3% of the matrices as having turnover-independent segregation (Table 7). The NODF metric identified only seven matrices (1.5%) as being significantly nested (not shown). BR, in contrast, identified 98 matrices (21%) as being significantly nested (Table 7).

A scale-specific analysis (Table 7) revealed greater frequencies of nested, turnover and segregated/aggregated patterns for matrices assembled at the biogeographic scale versus the local scale. Compared to the standard presence–absence matrices (biogeographic, local), the interaction matrices had lower proportions of segregated and turnover patterns, but higher proportions of aggregated matrices. There were moderate differences among taxa in patterns of species co-occurrences (Table 7). Based on the C_{Turn} and R^2 scores, bird and plant matrices exhibited higher degrees of species turnover than herptile and invertebrate matrices. In contrast, fish, herptile, and mammal matrices appeared to have stronger patterns of checkerboard segregation than matrices for other taxa.

Discussion

The statistical performance of null models

Null models became popular in the late 1970s, when ecologists began to ask whether patterns of species co-occurrence

| Matrix type Metric Observed value Lower 95% confidence limit Lower 95% confidence limit Lower 95% confidence limit Upper 95% confidence limit Checkerboard Clumping Cscore 0.037 0.189 0.208 0.003 0.044 Cscore 0.317 0.189 0.208 0.003 0.066 Cscore 0.350 0.060 0.150 0.006 0.0270 Maximum turnover Clumping 0.040 0.323 0.500 0.010 0.4235 Maximum turnover Clumping 0.004 0.000 0.002 0.001 0.007 Cscore 0.108 0.1100 0.105 0.044 0.099 Cscare 0.000 | | | | Fixed – fixe | d null model | Equiprobabl | e null model |
|---|------------------|------------|----------------|----------------------------|-------------------------------|----------------------------|-------------------------------|
| Checkerboard Clumping C-score 0.095 0.031 0.040 0.044 0.079 C-score 0.317 0.189 0.208 0.083 0.167 C-score 0.317 0.189 0.208 0.083 0.167 C-score 0.350 0.060 0.150 0.006 0.025 EmbAds 0.000 0.325 0.500 0.110 0.235 NDDF 0.000 0.000 0.002 0.001 0.007 Maximum turnover Clumping 0.004 0.000 0.002 0.001 0.007 C-score 0.108 0.100 0.105 0.044 0.099 0.035 0.044 0.099 C-score 0.108 0.100 0.600 0.000 0.305 0.148 0.355 Turnover Clumping 0.029 0.007 0.013 0.010 0.027 Compartmented Clumping 0.527 0.151 0.376 0.144 0.323 Compartmented <td< th=""><th>Matrix type</th><th>Metric</th><th>Observed value</th><th>Lower 95% confidence limit</th><th>Upper 95% confidence limit</th><th>Lower 95% confidence limit</th><th>Upper 95% confidence limit</th></td<> | Matrix type | Metric | Observed value | Lower 95% confidence limit | Upper 95% confidence limit | Lower 95% confidence limit | Upper 95% confidence limit |
| C-score 0.317 0.189 0.208 0.083 0.167 C _{swg} 0.050 0.060 0.150 0.006 0.096 C _{num} 0.480 0.170 0.270 0.101 0.235 Maximun turnover R ² 0.577 0.240 0.417 0.200 0.413 NODF 0.000 0.000 0.002 0.001 0.007 Cascore 0.108 0.100 0.002 0.001 0.007 C _{swg} 0.000 0.000 0.000 0.044 0.090 C _{swg} 0.000 0.010 0.600 0.005 0.315 Maximum turnover C _{swg} 0.090 0.044 0.090 0.348 0.455 0.335 C _{swg} 0.0907 0.590 0.883 0.405 0.315 0.357 Turnover Clamping 0.029 0.007 0.013 0.010 0.202 compatimented C-score 0.182 0.155 0.144 0.357 | Checkerboard | Clumping | 0.095 | 0.031 | 0.040 | 0.044 | 0.079 |
| C _{sup} EmbAbs 0.050 0.060 0.150 0.006 0.096 EmbAbs 0.000 0.325 0.500 0.100 0.425 R ² 0.577 0.240 0.417 0.200 0.413 Maximum turnover R ² 0.601 0.000 0.002 0.001 0.007 Csage 0.004 0.000 0.002 0.001 0.007 Csage 0.000 0.044 0.000 0.000 0.040 Csage 0.000 0.040 0.000 0.040 0.000 0.001 Csage 0.000 0.040 0.000 0.000 0.010 0.005 0.035 Csage 0.007 0.013 0.005 0.148 0.357 Turnover Clumping 0.027 0.013 0.014 0.323 Compartmented C-score 0.188 0.145 0.156 0.374 Csage 0.027 0.013 0.007 0.019 0.007 0.500 | | C-score | 0.317 | 0.189 | 0.208 | 0.083 | 0.167 |
| $ C_{nm} 0.480 0.170 0.270 0.101 0.235 Maximum turnover LmbAbs 0.000 0.325 0.500 0.100 0.425 Maximum turnover Lmping 0.004 0.000 0.002 0.001 0.007 C_{score} 0.108 0.100 0.002 0.001 0.007 C_{sigs} 0.000 0.044 0.090 0.044 0.090 C_{sigs} 0.000 0.048 0.450 0.065 0.305 C_{sigs} 0.907 0.590 0.883 0.405 0.819 Compartmented Cscore 0.188 0.145 0.156 0.307 Compartmented Cscore 0.188 0.145 0.157 0.146 Compartmented Cscore 0.189 0.007 0.079 0.079 Compartmented $ | | C_{Sogr} | 0.050 | 0.060 | 0.150 | 0.006 | 0.096 |
| EmbAds 0.000 0.325 0.500 0.100 0.425 NODF 0.000 0.000 0.000 0.000 0.001 0.007 Maximum turnover Clumping 0.004 0.000 0.002 0.001 0.007 Clumping 0.004 0.000 | | CTurn | 0.480 | 0.170 | 0.270 | 0.101 | 0.235 |
| R ² 0.577 0.240 0.417 0.200 0.413 NODF 0.000 0.000 0.000 0.382 0.623 Maximum turnover Clumping 0.004 0.000 0.002 0.001 0.007 Cscore 0.108 0.100 0.105 0.044 0.090 Clum 0.490 0.048 0.450 0.065 0.305 EmbAds 0.907 0.590 0.683 0.405 0.319 NODF 0.055 0.014 0.055 0.148 0.357 Compartmented Cscore 0.188 0.145 0.156 0.075 0.146 Compartmented Cscore 0.182 0.143 0.376 0.146 0.323 Compartmented Cscore 0.188 0.177 0.109 0.007 0.079 Clumping 0.527 0.132 0.101 0.323 0.502 0.522 0.025 0.035 0.015 0.303 Compartmented Cscore | | EmbAbs | 0.000 | 0.325 | 0.500 | 0.100 | 0.425 |
| NAximum turnover NODF 0.000 0.000 0.002 0.001 0.007 Clumping 0.004 0.000 0.002 0.001 0.007 Cscore 0.108 0.100 0.015 0.044 0.000 Cscore 0.490 0.048 0.450 0.065 0.305 EmbAbs 0.000 0.100 0.600 0.000 0.350 R ² 0.907 0.590 0.883 0.405 0.819 NODF 0.055 0.014 0.055 0.148 0.357 Turnover Clumping 0.029 0.007 0.013 0.010 0.028 compartmented Cscore 0.188 0.145 0.156 0.312 0.169 Clumping 0.527 0.151 0.376 0.104 0.323 compartmented Cscore 0.746 0.394 0.645 0.312 0.612 compartmented Cscore 0.200 0.73 0.098 0.075 0.033 </td <td></td> <td>R^2</td> <td>0.577</td> <td>0.240</td> <td>0.417</td> <td>0.200</td> <td>0.413</td> | | R^2 | 0.577 | 0.240 | 0.417 | 0.200 | 0.413 |
| Maximum turnover Clumping 0.004 0.000 0.002 0.001 0.007 C_{score} 0.108 0.100 0.105 0.044 0.090 C_{sorg} 0.000 0.000 0.040 0.000 0.005 0.035 C_{sorg} 0.907 0.590 0.683 0.405 0.819 R^2^2 0.907 0.590 0.683 0.405 0.819 rurnover (Imping 0.027 0.013 0.010 0.028 compartmented Cscore 0.188 0.145 0.156 0.148 0.357 Cturno 0.527 0.151 0.376 0.104 0.323 Cturno 0.527 0.151 0.376 0.104 0.323 Cturno 0.52 0.025 0.035 0.015 0.033 compartmented Clumping 0.52 0.025 0.035 0.015 0.033 compartmented Clumping 0.52 0.025 0.035 0.015 < | | NODF | 0.000 | 0.000 | 0.000 | 0.382 | 0.623 |
| C-score 0.108 0.100 0.105 0.044 0.090 C _{supp} 0.000 0.000 0.040 0.000 0.041 0.000 0.041 C _{supp} 0.490 0.488 0.450 0.065 0.305 EmbAbs 0.000 0.100 0.600 0.000 0.350 R ² 0.907 0.590 0.883 0.405 0.819 NODF 0.055 0.014 0.055 0.148 0.357 Cumping 0.029 0.007 0.013 0.010 0.028 compartmented C-score 0.188 0.145 0.156 0.075 0.146 C _{sup} 0.027 0.032 0.109 0.07 0.079 C _{sup} 0.746 0.394 0.645 0.312 0.612 C _{sup} 0.746 0.394 0.645 0.312 0.612 compartmented C-score 0.200 0.073 0.098 0.078 0.515 compartmented | Maximum turnover | Clumping | 0.004 | 0.000 | 0.002 | 0.001 | 0.007 |
| | | C-score | 0.108 | 0.100 | 0.105 | 0.044 | 0.090 |
| C_{lum}^{2} 0.4900.0480.4500.0650.305 $EmbAbs$ 0.0000.1000.6000.0000.350 R^2 0.9070.5900.8830.4050.819 $NODF$ 0.0550.0140.0550.1480.357compartmented G_{score} 0.290.0070.0130.0100.028 C_{min} 0.5270.1510.3760.1040.323 C_{lum} 0.5270.1510.3760.1040.323 R^2 0.7460.3940.6450.3120.612 R^2 0.7460.3940.6450.3120.612 C_{lum} 0.0270.0270.0330.0980.0780.151 C_{score} 0.2000.0730.0980.0780.151 C_{score} 0.2000.0730.0980.0780.151 C_{score} 0.2000.0730.0980.0780.151 C_{score} 0.2000.0730.0980.0780.557 R^2 0.5150.2420.4820.2780.557 $RODF$ 0.0000.2790.3740.2990.534 $Turnover$ C_{lum} 0.0900.0430.1790.0570.305 R^2 0.5150.2420.3560.0400.086 R^2 0.5150.2420.3560.3100.325 R^2 0.5150.2420.3560.3100.325 R^2 0.5150.2420.356 | | C_{Sogr} | 0.000 | 0.000 | 0.040 | 0.000 | 0.040 |
| $EmbAbs$ R^2 0.0000.1000.6000.0000.350Turnover compartmentedClumping0.0290.0070.0130.0100.028 C_score 0.1880.1450.1560.0750.146 C_score 0.1880.1450.1560.0750.146 C_{segr} 0.0270.0320.1090.0070.079 C_{tum} 0.5270.1510.3760.1040.323EmbAbs0.0000.3000.6000.0000.500 R^2 0.7460.3940.6450.3120.612NODF0.0480.0790.1090.2700.502compartmentedCscore0.2000.0730.0980.0780.151 C_score 0.2000.0730.0980.0780.151 C_score 0.2000.0730.0490.0000.469 C_tum 0.1340.0920.1530.0970.242 $EmbAbs$ 0.0000.1250.4690.0000.469 C_tum 0.0150.0010.0060.0000.066 C_tum 0.0900.0430.1790.5770.305 $EmbAbs$ 0.0000.0020.0350.0110.0000.0316 R^2 0.7180.4900.7700.3680.849 R^2 0.7180.4900.7700.3680.849 R^2 0.7180.4900.7700.3680.849 R^2 0.7180.4900 | | C_{Turp} | 0.490 | 0.048 | 0.450 | 0.065 | 0.305 |
| R^2 0.9070.5900.8830.4050.819NODF0.0550.0140.0550.1480.357compartmented C_{score} 0.1880.1450.1560.0100.028compartmented C_{score} 0.0270.0320.1090.0070.079 C_{turn} 0.5270.1510.3760.1040.323 $EmbAbs$ 0.0000.3000.6000.0000.500 R^2 0.7460.3940.6450.3120.612 $NODF$ 0.0480.0790.1090.2700.502compartmented C_{score} 0.2000.0730.0980.0780.151 $Cumping$ 0.5220.0250.0350.0150.033compartmented C_{score} 0.2000.0730.0980.0780.151 C_{turn} 0.1340.0920.1530.0000.662 C_{turn} 0.1340.0920.1530.0090.469 R^2 0.5150.2420.4820.2780.557Turnover(Clumping)0.0000.2790.3740.2990.534 R^2 0.5150.2420.4820.2780.557Turnover(Clumping)0.0000.0010.0060.0000.005 R^2 0.5150.2420.4820.2780.557 R^2 0.5150.2420.4820.2780.557 R^2 0.5150.2420.4820.2780.557 <td></td> <td>EmbAbs</td> <td>0.000</td> <td>0.100</td> <td>0.600</td> <td>0.000</td> <td>0.350</td> | | EmbAbs | 0.000 | 0.100 | 0.600 | 0.000 | 0.350 |
| NODF 0.055 0.014 0.055 0.148 0.357 Turnover compartmentedClumping 0.029 0.007 0.013 0.010 0.028 CompartmentedCscore 0.188 0.145 0.156 0.075 0.146 Cscore 0.027 0.032 0.109 0.007 0.079 Cturnover Cturn 0.527 0.151 0.376 0.104 0.323 EmbAbs 0.000 0.300 0.600 0.000 0.500 R ² 0.746 0.394 0.645 0.312 0.612 CompartmentedCscore 0.200 0.073 0.098 0.078 0.073 CompartmentedCscore 0.200 0.073 0.098 0.073 0.097 Clumping 0.527 0.052 0.025 0.035 0.015 0.033 CompartmentedCscore 0.200 0.073 0.098 0.078 0.073 Clumping 0.000 0.075 0.015 0.469 0.000 0.662 CturnoverR ² 0.515 0.242 0.482 0.278 0.557 TurnoverClumping 0.000 0.012 0.374 0.299 0.534 independentCscore 0.070 0.044 0.058 0.040 0.086 segregationCscore 0.077 0.007 0.368 0.849 Mixed matrixNODF 0.213 0.121 0.134 0.077 0.037 R ² | | R^2 | 0.907 | 0.590 | 0.883 | 0.405 | 0.819 |
| Turnover compartmentedClumping G_{score} 0.0290.0070.0130.0100.028compartmented G_{score} 0.1880.1450.1560.0750.146 G_{segr} 0.0270.0320.1090.0070.079 G_{turn} 0.5270.1510.3760.1040.323EmbAbs0.0000.3000.6000.0000.500 R^2 0.7460.3940.6450.3120.612NODF0.0480.0790.1090.2700.502compartmented G_{score} 0.2000.0730.0980.0780.151 G_{segr} 0.11340.0920.1530.0970.242EmbAbs0.0000.1250.4690.0000.469 R^2 0.5150.2420.4820.2780.557TurnoverClumping0.0050.0010.0060.0000.066independent G_{segr} 0.0370.0040.0580.0400.086segregation G_{segr} 0.0370.0000.0430.1790.0570.305findependent G_{cegr} 0.0370.0000.0490.0000.306segregation G_{segr} 0.0370.0000.2710.0360.312Mixed matrixClumping0.0090.0430.1790.0570.305 R^2 0.7180.4900.7700.3680.4840.491Mixed matrixClumping0.0090.0 | | NODF | 0.055 | 0.014 | 0.055 | 0.148 | 0.357 |
| compartmentedC-score0.1880.1450.1560.0750.146 C_{segr} 0.0270.0320.1090.0070.079 C_{rum} 0.5270.1510.3760.1040.323 $mbAbs$ 0.0000.3000.6000.0000.500 R^2 0.7460.3940.6450.3120.612NODF0.0480.0790.1090.2700.502compartmentedC-score0.2000.0730.0980.0780.151 C_{segr} 0.1690.0000.0680.0000.062 C_{run} 0.1340.9920.1530.0970.242 $EmbAbs$ 0.0000.1250.4690.0000.469 R^2 0.5150.2420.4820.2780.557NODF0.0000.2790.3740.2990.534TurnoverClumping0.0050.0010.0060.0000.086segregationC-score0.0370.0000.0490.0000.086segregationC-score0.0370.0000.0490.0000.316 R^2 0.7180.4900.7700.3680.849Mixed matrixClumping0.0090.0060.0130.0070.021 R^2 0.7180.4900.7700.3680.4390.325Mixed matrixClumping0.0090.0060.0130.0070.021 R^2 0.7180.4900.7770.007< | Turnover | Clumping | 0.029 | 0.007 | 0.013 | 0.010 | 0.028 |
| C_{segr} 0.027 0.032 0.109 0.007 0.079 C_{tum} 0.527 0.151 0.376 0.104 0.323 $EmbAbs$ 0.000 0.300 0.600 0.000 0.500 R^2 0.746 0.394 0.645 0.312 0.612 $NODF$ 0.048 0.079 0.109 0.270 0.502 $compartmented$ C_{score} 0.200 0.073 0.098 0.0078 0.151 C_{score} 0.200 0.073 0.098 0.000 0.062 C_{tum} 0.134 0.092 0.153 0.097 0.242 $EmbAbs$ 0.000 0.279 0.374 0.299 0.534 Turnover $Clumping$ 0.055 0.001 0.006 0.000 0.006 R^2 0.515 0.242 0.482 0.278 0.557 $NODF$ 0.000 0.279 0.374 0.299 0.534 Turnover $Clumping$ 0.005 0.001 0.006 0.000 0.006 $segregation$ C_{score} 0.073 0.000 0.044 0.058 0.404 0.086 R^2 0.718 0.490 0.770 0.368 0.849 $rembAbs$ 0.000 0.000 0.211 0.000 0.316 R^2 0.718 0.490 0.770 0.368 0.849 $rembAbs$ 0.009 0.026 0.133 0.007 0.021 R^2 0.718 | compartmented | C-score | 0.188 | 0.145 | 0.156 | 0.075 | 0.146 |
| C_{turn}^{0} 0.5270.1510.3760.1040.323EmbAbs0.0000.3000.6000.0000.500 R^2 0.7460.3940.6450.3120.612NODF0.0480.0790.1090.2700.502compartmentedC-score0.2000.0730.0980.0780.151 C_{segr} 0.1690.0000.06680.0000.062 C_{turn} 0.1340.0920.1530.0970.242 $EmbAbs$ 0.0000.1250.4690.0000.469 R^2 0.5150.2420.4820.2780.557NODF0.0000.2790.3740.2990.534TurnoverClumping0.050.0010.0060.000independentC-score0.0700.0440.0580.0400.086segregationC_score0.0710.0000.2110.0000.312 R^2 0.7180.4990.7700.3680.849NODF0.2190.2670.3560.1300.325Mixed matrixClumping0.0090.0060.0130.0070.021 R^2 0.5130.1210.1340.0710.137 R^2 0.2190.2650.1430.3580.1040.319 R^2 0.2550.0120.0770.0070.021 R^2 0.2550.0120.0770.0210.374 R^2 0.2550.143 <td>·</td> <td>Csogr</td> <td>0.027</td> <td>0.032</td> <td>0.109</td> <td>0.007</td> <td>0.079</td> | · | Csogr | 0.027 | 0.032 | 0.109 | 0.007 | 0.079 |
| ImbAbs R^2 0.0000.3000.6000.0000.500 R^2 0.7460.3940.6450.3120.612NODF0.0480.0790.1090.2700.502compartmented G_{score} 0.2000.0730.0980.0780.151 G_{score} 0.2000.0730.0980.07780.151 G_{score} 0.1690.0000.0680.0000.062 G_{turn} 0.1340.0920.1530.0970.242InbAbs0.0000.2790.3740.2990.534TurnoverClumping0.0050.0010.0060.0000.066 R^2 0.5150.2420.4820.2780.557NODF0.0000.2790.3740.2990.534TurnoverClumping0.0050.0010.0060.0000.006segregation G_{score} 0.0700.0440.0580.0400.086segregation G_{score} 0.0000.0000.2710.0000.316 R^2 0.7180.4900.7700.3680.849NODF0.2190.2670.3560.1300.325Mixed matrixClumping0.0090.0060.0130.0070.021 R^2 0.7180.1210.1340.0710.137 R^2 0.2550.0120.7770.3680.849NODF0.2150.1210.1340.0710.317 <td< td=""><td></td><td>CTurn</td><td>0.527</td><td>0.151</td><td>0.376</td><td>0.104</td><td>0.323</td></td<> | | CTurn | 0.527 | 0.151 | 0.376 | 0.104 | 0.323 |
| R^2 0.7460.3940.6450.3120.612NODF0.0480.0790.1090.2700.502compartmentedClumping0.0520.0250.0350.0150.033C-score0.2000.0730.0980.0780.151C-score0.1690.0000.06680.0000.062C-score0.1340.0920.1530.0970.242EmbAbs0.0000.1250.4690.0000.469 R^2 0.5150.2420.4820.2780.557NODF0.0000.02790.3740.2990.534TurnoverClumping0.0050.0010.0060.0000.006segregationC-score0.0700.0440.0580.0400.086segregationC-score0.0700.0430.1790.0570.305R ² 0.7180.4900.7700.3680.849Mixed matrixClumping0.0090.0060.0130.0070.021R ² 0.2190.2670.3560.1300.3250.0120.7700.3680.849Mixed matrixClumping0.0090.0060.0130.0070.0210.74C-score0.1230.1210.1340.0710.1370.325C-score0.1230.1210.1340.0070.021C-score0.1230.1210.1340.0070.021C-score0.1230 | | EmbAbs | 0.000 | 0.300 | 0.600 | 0.000 | 0.500 |
| Segregative compartmentedNODF0.0480.0790.1090.2700.502Segregative compartmented $Clumping$ 0.0520.0250.0350.0150.033 C_{score} 0.2000.0730.0980.0780.151 C_{segr} 0.1690.0000.0680.0000.062 C_{tum} 0.1340.0920.1530.0970.242 $EmbAbs$ 0.0000.1250.4690.0000.469 R^2 0.5150.2420.4820.2780.557NODF0.0000.2790.3740.2990.534Turnover independent segregation C_{score} 0.0700.0440.0580.0400.086 C_{segr} 0.0370.0000.0490.0000.0320.0370.0000.032 C_{tum} 0.0900.0000.2110.0000.3160.325Mixed matrix R^2 0.7180.4900.7700.3680.849NODF0.2190.2670.3560.1300.325Mixed matrix C_{sogr} 0.0250.0120.0770.0070.074 R^2 0.1230.1210.1340.0710.137 C_{sogr} 0.2550.1430.3580.1040.319 R^2 0.5030.3920.6790.3260.639 R^2 0.5030.3920.6790.3260.639 | | R^2 | 0.746 | 0.394 | 0.645 | 0.312 | 0.612 |
| Segregative compartmented $Clumping$ $C-score$ 0.052 0.025 0.035 0.015 0.033 $C-score$ 0.200 0.073 0.098 0.078 0.151 C_{segr} $Turmover$ 0.169 0.000 0.068 0.000 0.062 $NODF$ 0.000 0.125 0.469 0.000 0.469 R^2 0.515 0.242 0.482 0.278 0.557 $NODF$ 0.000 0.279 0.374 0.299 0.534 Turnover independent segregation $C-score$ 0.070 0.044 0.058 0.040 0.086 R^2 0.037 0.000 0.043 0.179 0.557 0.305 R^{2} 0.001 0.006 0.000 0.032 R^2 0.718 0.000 0.043 0.179 0.557 R^2 0.718 0.490 0.770 0.368 0.849 $NODF$ 0.219 0.267 0.356 0.130 0.325 R^2 0.718 0.490 0.770 0.368 0.849 $NODF$ 0.219 0.267 0.356 0.130 0.325 R^2 0.718 0.121 0.134 0.071 0.137 R^2 0.255 0.143 0.358 0.104 0.319 R^2 0.503 0.392 0.679 0.326 0.639 R^2 0.503 0.392 0.679 0.326 0.639 R^2 0.503 0.39 | | NODF | 0.048 | 0.079 | 0.109 | 0.270 | 0.502 |
| Compartmented compartmentedC-score0.2000.0730.0980.0780.151 C_{Segr} 0.1690.0000.0680.0000.062 C_{Turn} 0.1340.0920.1530.0970.242EmbAbs0.0000.1250.4690.0000.469 R^2 0.5150.2420.4820.2780.553NODF0.0000.2790.3740.2990.534Turnover independent segregationC-score0.0700.0440.0580.0400.086 C_{Segr} 0.0370.0000.0430.1790.0570.305 $EmbAbs$ 0.0000.0000.2110.0000.316 R^2 0.7180.4900.7700.3680.849Mixed matrix $Clumping$ 0.0250.0120.0770.0070.021 C_{Segr} 0.0250.0120.0770.0070.021 R^2 0.7180.4900.7700.3680.849Mixed matrix $Clumping$ 0.0250.0120.0770.0070.074 C_{Segr} 0.0250.0120.0770.0070.074 C_{Segr} 0.2650.1430.3580.1040.319EmbAbs0.3210.1430.4640.0000.500 R^2 0.5030.3920.6790.3260.632 | Segregative | Clumping | 0.052 | 0.025 | 0.035 | 0.015 | 0.033 |
| C_{segr} 0.1690.0000.0680.0000.062 C_{turn} 0.1340.0920.1530.0970.242 $EmbAbs$ 0.0000.1250.4690.0000.469 R^2 0.5150.2420.4820.2780.557NODF0.0000.2790.3740.2990.534TurnoverClumping0.0050.0010.0060.0000.006independentC-score0.0700.0440.0580.0400.086segregationC_segr0.0370.0000.0430.1790.0570.305 R^2 0.7180.4900.7700.3680.849NODF0.2190.2670.3560.1300.325Mixed matrixClumping0.0090.0060.0130.00710.137 C_{segr} 0.0250.0120.0770.0070.074 C_{segr} 0.0250.0120.0770.0070.074 R^2 0.5330.3210.1430.3580.1040.319 $EmbAbs$ 0.3210.1430.3580.1040.319 R^2 0.5030.3920.6790.3260.639 | compartmented | C-score | 0.200 | 0.073 | 0.098 | 0.078 | 0.151 |
| C_{Ium}^{2} 0.1340.0920.1530.0970.242EmbAbs0.0000.1250.4690.0000.469 R^2 0.5150.2420.4820.2780.557NODF0.0000.2790.3740.2990.534TurnoverClumping0.0050.0010.0060.0000.006independentC-score0.0700.0440.0580.0400.086segregationC_segr0.0370.0000.0490.0000.032 C_{Ium} 0.0900.0430.1790.0570.305EmbAbs0.0000.0000.2110.0000.316 R^2 0.7180.4900.7700.3680.849Mixed matrixClumping0.0090.0060.0130.0070.021 C_{score} 0.1230.1210.1340.0710.137 C_{score} 0.1230.1210.1340.0710.137 C_{score} 0.0250.0120.0770.0070.074 C_{Tun} 0.2650.1430.3580.1040.319 $EmbAbs$ 0.3210.1430.4640.0000.500 R^2 0.5030.3920.6790.3260.639 | · | Csogr | 0.169 | 0.000 | 0.068 | 0.000 | 0.062 |
| I_{aut} I_{aut} 0.000 0.125 0.469 0.000 0.469 R^2 0.515 0.242 0.482 0.278 0.557 $NODF$ 0.000 0.279 0.374 0.299 0.534 Turnover $Clumping$ 0.005 0.001 0.006 0.000 0.006 independent C -score 0.070 0.044 0.058 0.040 0.086 segregation C_{segr} 0.037 0.000 0.043 0.179 0.057 0.305 C_{Turn} 0.090 0.043 0.179 0.057 0.305 $EmbAbs$ 0.000 0.000 0.211 0.000 0.316 R^2 0.718 0.490 0.770 0.368 0.849 $NODF$ 0.219 0.267 0.356 0.130 0.325 Mixed matrix $Clumping$ 0.009 0.006 0.013 0.007 0.021 C_{segr} 0.025 0.012 0.077 0.007 0.074 C_{segr} 0.265 0.143 0.358 0.104 0.319 $EmbAbs$ 0.321 0.143 0.464 0.000 0.500 R^2 0.503 0.392 0.679 0.326 0.639 | | C_{Turp} | 0.134 | 0.092 | 0.153 | 0.097 | 0.242 |
| R^2 0.5150.2420.4820.2780.557NODF0.0000.2790.3740.2990.534TurnoverClumping0.0050.0010.0060.0000.006independentC-score0.0700.0440.0580.0400.086C-score0.0370.0000.0490.0000.032C-rum0.0900.0430.1790.0570.305EmbAbs0.0000.0000.2110.0000.316 R^2 0.7180.4900.7700.3680.849NODF0.2190.2670.3560.1300.325Mixed matrixClumping0.0090.0060.0130.0070.021C-score0.1230.1210.1340.0710.137C-score0.2650.0120.0770.0070.074C-score0.3210.1430.3580.1040.319EmbAbs0.3210.1430.4640.0000.500R^20.5030.3920.6790.3260.639 | | EmbAbs | 0.000 | 0.125 | 0.469 | 0.000 | 0.469 |
| NODF0.0000.2790.3740.2990.534Turnover independent segregationClumping0.0050.0010.0060.0000.006C-score0.0700.0440.0580.0400.086C-score0.0370.0000.0490.0000.032C-rum0.0900.0430.1790.0570.305EmbAbs0.0000.0000.2110.0000.316 R^2 0.7180.4900.7700.3680.849NODF0.2190.2670.3560.1300.325Mixed matrixClumping0.0090.0060.0130.0070.021C-score0.1230.1210.1340.0710.137C-score0.2550.0120.0770.0070.074C-score0.2650.1430.3580.1040.319EmbAbs0.3210.1430.4640.0000.500 R^2 0.5030.3920.6790.3260.639 | | R^2 | 0.515 | 0.242 | 0.482 | 0.278 | 0.557 |
| Turnover independent segregation $Clumping$ $C-score$ 0.005 0.001 0.006 0.000 0.006 $C-score$ 0.070 0.044 0.058 0.040 0.086 C_{segr} 0.037 0.000 0.049 0.000 0.032 C_{Turn} 0.090 0.043 0.179 0.057 0.305 $EmbAbs$ 0.000 0.000 0.211 0.000 0.316 R^2 0.718 0.490 0.770 0.368 0.849 NODF 0.219 0.267 0.356 0.130 0.325 Mixed matrix $Clumping$ 0.009 0.006 0.013 0.007 0.021 C_{score} 0.123 0.121 0.134 0.071 0.137 C_{segr} 0.025 0.012 0.077 0.007 0.074 C_{segr} 0.265 0.143 0.358 0.104 0.319 $EmbAbs$ 0.321 0.143 0.464 0.000 0.500 R^2 0.503 0.3922 0.679 0.326 0.639 | | NODF | 0.000 | 0.279 | 0.374 | 0.299 | 0.534 |
| independent segregationC-score0.0700.0440.0580.0400.086 C_{segr} 0.0370.0000.0490.0000.032 C_{Tum} 0.0900.0430.1790.0570.305EmbAbs0.0000.0000.2110.0000.316 R^2 0.7180.4900.7700.3680.849NODF0.2190.2670.3560.1300.325Mixed matrixClumping0.0090.0060.0130.0070.021 C_{score} 0.1230.1210.1340.0710.137 C_{segr} 0.0250.0120.0770.0070.074 C_{Tum} 0.2650.1430.3580.1040.319EmbAbs0.3210.1430.4640.0000.500 R^2 0.5030.3920.6790.3260.639NODF0.2310.3730.23740.2140.143 | Turnover | Clumping | 0.005 | 0.001 | 0.006 | 0.000 | 0.006 |
| segregation C_{Segr} 0.037 0.000 0.049 0.000 0.032 C_{Turn} 0.090 0.043 0.179 0.057 0.305 $EmbAbs$ 0.000 0.000 0.211 0.000 0.316 R^2 0.718 0.490 0.770 0.368 0.849 NODF 0.219 0.267 0.356 0.130 0.325 Mixed matrix $Clumping$ 0.009 0.006 0.013 0.007 0.021 $C-score$ 0.123 0.121 0.134 0.071 0.137 C_{Segr} 0.025 0.012 0.077 0.007 0.074 C_{Segr} 0.265 0.143 0.358 0.104 0.319 $EmbAbs$ 0.321 0.143 0.464 0.000 0.500 R^2 0.503 0.3922 0.679 0.326 0.639 $NODF$ 0.231 0.3772 0.2347 0.1427 0.1427 | independent | C-score | 0.070 | 0.044 | 0.058 | 0.040 | 0.086 |
| C_{Turn} 0.0900.0430.1790.0570.305 $EmbAbs$ 0.0000.0000.2110.0000.316 R^2 0.7180.4900.7700.3680.849NODF0.219 0.267 0.3560.1300.325Mixed matrixClumping0.0090.0060.0130.0070.021 $C-score$ 0.1230.1210.1340.0710.137 C_{Segr} 0.0250.0120.0770.0070.074 C_{Turn} 0.2650.1430.3580.1040.319 $EmbAbs$ 0.3210.1430.4640.0000.500 R^2 0.5030.3920.6790.3260.639 | segregation | Csogr | 0.037 | 0.000 | 0.049 | 0.000 | 0.032 |
| $EmbAbs$ 0.0000.0000.2110.0000.316 R^2 0.7180.4900.7700.3680.849NODF0.219 0.267 0.3560.1300.325Mixed matrixClumping0.0090.0060.0130.0070.021 C -score0.1230.1210.1340.0710.137 C_{segr} 0.0250.0120.0770.0070.074 C_{sum} 0.2650.1430.3580.1040.319 $EmbAbs$ 0.3210.1430.4640.0000.500 R^2 0.5030.3920.6790.3260.639NODE0.0310.3730.2370.2340.217 | | C_{Turp} | 0.090 | 0.043 | 0.179 | 0.057 | 0.305 |
| R^2 0.7180.4900.7700.3680.849NODF0.219 0.267 0.3560.1300.325Mixed matrixClumping0.0090.0060.0130.0070.021C-score0.1230.1210.1340.0710.137C-score0.0250.0120.0770.0070.074C-score0.2650.1430.3580.1040.319EmbAbs0.3210.1430.4640.0000.500 R^2 0.5030.3920.6790.3260.639 | | EmbAbs | 0.000 | 0.000 | 0.211 | 0.000 | 0.316 |
| NODF 0.219 0.267 0.356 0.130 0.325 Mixed matrixClumping 0.009 0.006 0.013 0.007 0.021 C-score 0.123 0.121 0.134 0.071 0.137 C-score 0.025 0.012 0.077 0.007 0.074 C-score 0.265 0.143 0.358 0.104 0.319 EmbAbs 0.321 0.143 0.464 0.000 0.500 R^2 0.503 0.392 0.679 0.326 0.639 | | R^2 | 0.718 | 0.490 | 0.770 | 0.368 | 0.849 |
| Mixed matrix Clumping 0.009 0.006 0.013 0.007 0.021 C -score 0.123 0.121 0.134 0.071 0.137 C_{Segr} 0.025 0.012 0.077 0.007 0.074 C_{Turn} 0.265 0.143 0.358 0.104 0.319 $EmbAbs$ 0.321 0.143 0.464 0.000 0.500 R^2 0.503 0.392 0.679 0.326 0.639 NODE 0.321 0.372 0.234 0.247 0.402 | | NODF | 0.219 | 0.267 | 0.356 | 0.130 | 0.325 |
| C-score 0.123 0.121 0.134 0.071 0.137 C_segr 0.025 0.012 0.077 0.007 0.074 C_Turn 0.265 0.143 0.358 0.104 0.319 EmbAbs 0.321 0.143 0.464 0.000 0.500 R^2 0.503 0.392 0.679 0.326 0.639 NODE 0.231 0.272 0.234 0.247 0.142 | Mixed matrix | Clumping | 0.009 | 0.006 | 0.013 | 0.007 | 0.021 |
| C_{Segr} 0.0250.0120.0770.0070.074 C_{Turn} 0.2650.1430.3580.1040.319EmbAbs0.3210.1430.4640.0000.500 R^2 0.5030.3920.6790.3260.639NODE0.3210.3720.2340.2470.102 | | C-score | 0.123 | 0.121 | 0.134 | 0.071 | 0.137 |
| C_{Turn} 0.2650.1430.3580.1040.319 $EmbAbs$ 0.3210.1430.4640.0000.500 R^2 0.5030.3920.6790.3260.639NODE0.3210.2720.2340.2470.102 | | Ccorr | 0.025 | 0.012 | 0.077 | 0.007 | 0.074 |
| EmbAbs 0.321 0.143 0.464 0.000 0.500 R^2 0.503 0.392 0.679 0.326 0.639 NODE 0.321 0.272 0.234 0.247 0.462 | | CTurn | 0.265 | 0.143 | 0.358 | 0.104 | 0.319 |
| R^2 0.503 0.392 0.679 0.326 0.639 | | EmbAbs | 0.321 | 0.143 | 0.464 | 0.000 | 0.500 |
| | | R^2 | 0.503 | 0.392 | 0.679 | 0.326 | 0.639 |
| INODE 0.331 0.273 0.334 0.247 0.482 | | NODF | 0.331 | 0.273 | 0.334 | 0.247 | 0.482 |

Table 6. Scores of important metrics of co-occurrence and lower and upper 95% confidence limits of the fixed – fixed and the equiprobable – equiprobable null models for the six idealized matrices of Figure 2. Statistically significant scores in bold face.

might be explained by chance, rather than by species interactions (Connor and Simberloff 1979). During the 1980s and the 1990s, ecologists began using null model methodology to test for other empirical community patterns, including body size ratios (Simberloff and Boecklen 1981), species nestedness (Patterson and Atmar 1986), favored states (Fox and Brown 1993), and, most recently, community phylogenetics (Webb et al. 2002). During the 2000s, some of these earlier analyses were re-assessed as ecologists began comparing the statistical performance of null models and metrics to artificial data sets with specified amounts of randomness and structure (Gotelli 2000, Ulrich and Gotelli 2007a, b, Ladau 2008). These tests used randomly constructed matrices to screen for algorithms with low type I errors and good power for detecting non-randomness (Gotelli 2001). This paper addresses an additional statistical issue that has only recently been considered: can null model tests uniquely discriminate among different kinds of non-random patterns (Presley et al. 2010, Gotelli and Ulrich 2011)? Our results (Table 3, 4) are relevant to earlier analyses of species cooccurrence (Gotelli and McCabe 2002, Lehsten and Harmand 2006) and more recently proposed theoretical frameworks for analyzing patterns of coherence, species turnover, and boundary clumping (Leibold and Mikkelson 2002, Presley et al. 2010).

Species co-occurrence

The combination of Stone and Robert's (1990) *C-score* with the fixed-fixed randomization algorithm (Gotelli 2000) has become a standard method for testing for patterns of species co-occurrence. Several studies have shown that this combination rejects the null hypotheses infrequently when tested against random matrices with heterogeneous row

| 0 | D | | | . / . | | | | | | | - | - | - | | |
|-----------------------|-------------------|----------------|-----------------|----------------|------------|-------------|------------|------------------------|------------|-------------------------|----------|---------------|--------------|--------|----------------------|
| | Pattern Metric | Co-occ C-sc | urrence sore | Co-occ Clum | urrence | Co-occ C | urrence | Turn C ₇ | over | Turnc R ² | jver | Cohei Emb. | rence Abs | Neste | edness 3 <i>R</i> |
| | z | aggregated | segregated | segregated | aggregated | aggregated | segregated | aggregated | segregated | negative | positive | aggregated | segregated | nested | antinestec |
| Scale | | | | | | | | | | | | | | | |
| Biogeographic | 195 | 0.51 | 42.05 | 1.54 | 27.69 | 3.59 | 5.13 | 3.08 | 38.97 | 0.51 | 39.49 | 28.21 | 1.54 | 27.18 | 0.51 |
| Local | 240 | 0.83 | 20.42 | 2.08 | 17.50 | 4.17 | 1.25 | 1.25 | 23.75 | 2.08 | 26.25 | 17.08 | 1.25 | 15.00 | 1.25 |
| Interaction | 36 | 0.00 | 19.44 | 0.00 | 30.56 | 11.11 | 5.56 | 2.78 | 33.33 | 0.00 | 25.00 | 11.11 | 0.00 | 11.11 | 2.78 |
| Total | 471 | 0.64 | 29.30 | 1.70 | 22.72 | 4.46 | 3.18 | 2.12 | 30.79 | 1.27 | 31.63 | 21.23 | 1.27 | 19.75 | 1.06 |
| Taxon | | | | | | | | | | | | | | | |
| Fish | 12 | 0.00 | 25.00 | 0.00 | 25.00 | 8.33 | 8.33 | 0.00 | 33.33 | 0.00 | 33.33 | 33.33 | 0.00 | 33.33 | 0.00 |
| Amphiba/Reptiles | 25 | 4.00 | 32.00 | 0.00 | 24.00 | 4.00 | 8.00 | 8.00 | 24.00 | 0.00 | 16.00 | 20.00 | 0.00 | 32.00 | 0.00 |
| Birds | 52 | 0.00 | 51.92 | 0.00 | 36.54 | 3.85 | 1.92 | 0.00 | 46.15 | 0.00 | 40.38 | 26.92 | 3.85 | 34.62 | 0.00 |
| Mammals | 65 | 0.00 | 43.08 | 1.54 | 24.62 | 7.69 | 7.69 | 1.54 | 20.00 | 0.00 | 38.46 | 30.77 | 0.00 | 29.23 | 0.00 |
| Insects | 214 | 0.47 | 18.69 | 2.34 | 15.42 | 2.34 | 0.93 | 2.34 | 25.70 | 2.34 | 28.50 | 13.08 | 1.40 | 14.02 | 0.93 |
| Other invertebrates | 26 | 0.00 | 26.92 | 7.69 | 23.08 | 11.54 | 3.85 | 3.85 | 30.77 | 0.00 | 34.62 | 34.62 | 0.00 | 11.54 | 3.85 |
| Plants | 30 | 3.33 | 63.33 | 0.00 | 36.67 | 0.00 | 3.33 | 0.00 | 66.67 | 0.00 | 46.67 | 50.00 | 00.0 | 13.33 | 3.33 |
| Unicellular organisms | 8 | 0.00 | 12.50 | 0.00 | 12.50 | 0.00 | 0.00 | 0.00 | 12.50 | 0.00 | 25.00 | 12.50 | 0.00 | 12.50 | 0.00 |
| Total | 432 | 0.69 | 30.79 | 1.85 | 21.99 | 3.94 | 3.01 | 2.08 | 30.32 | 1.16 | 32.41 | 22.22 | 1.16 | 20.14 | 0.93 |
| | | | | | | | | | | | | | | | |

and column totals, and has good power to detect checkerboard pairs embedded in noisy data matrices (Gotelli 2000, Ulrich and Gotelli 2007a). By this criterion, many empirical matrices exhibit significantly more species segregation than expected by chance (Gotelli and McCabe 2002).

However, Stone and Roberts (1990) warned that matrices with segregated species pairs must necessarily contain some species pairs that are aggregated. Indeed, in any presence–absence matrix positive and negative species associations are intimately linked. Consider three 4×4 submatrices of the form

| | A | (1 | 0 | 1 | 0 | ١ | |
|------------|----------------|----|---|---|----|----|----|
| 17 | В | 0 | 1 | 0 | 1 | | 1 |
| <i>M</i> = | ⁼ C | 1 | 0 | 1 | 0 | ar | ıd |
| | D | (1 | 0 | 1 | 0 |) | |
| | A | (1 | 0 | 1 | 0) | | |
| 3.7 | В | 0 | 1 | 0 | 1 | | 1 |
| N = | C | 0 | 1 | 1 | 0 | an | d |
| | D | (1 | 0 | 1 | 0 | | |
| | Α | (1 | 0 | 1 | 0 | 0 | 0) |
| 0 | B | 0 | 1 | 0 | 1 | 0 | 0 |
| 0= | С | 0 | 0 | 0 | 0 | 1 | 0 |
| | D | 0 | 0 | 0 | 0 | 0 | 1 |

where two species A and B form a checkerboard pair. In matrix M, any new species C that avoids either A or B will form a positive association with the complementary species of the form $\{\{1,1\},\{1,1\}\}\$ as does any new species D that is either linked with C or occurs everywhere. In matrix N, segregation of A, B, and C is not perfect. Nevertheless, any new species D, which is at least as abundant as A, B, or C will add at least one new positive association. Only new species with fewer occurrences than A and B might not add new positive associations as shown by matrix O. Hence, in equiprobably-filled matrices with a fill of less than 0.5, raw scores of the C-score and Clumping will always be positively correlated (Fig. 4A). Because the C-score has is theoretical maximum at 50% matrix fill matrices with higher fill will inevitably add more positive than negative associations and positive and negative associations will be negatively correlated (Fig. 4A). This correlation will be less apparent in matrices where species highly differ in the total numbers of occurrences (Fig. 4B). Nevertheless the C-score has always a tendency to be also a metric for positive species association (aggregation).

Specifically, any sufficiently filled perfect checkerboard matrix can be reordered by reciprocal averaging to reveal a perfectly aggregated pattern (Stone and Roberts 1990). Such a matrix has also a high degree of species turnover (Table 8). Irrespective of null model, the *C-score* identifies such a matrix as having far more checkerboard pairs than expected by chance while the *Clumping* score, C_{Segr} , and *EmbAbs* identify the same matrix as being aggregated. The significant R^2 value points to turnover (Table 8, Fig. 2). Hence

Table 8. Pair wise comparisons of seven co-occurrence and nestedness scores to identify patterns in 471 empirical presence–absence matrices. Note that for the *EmbAbs* score values above the upper two-sided 95% confidence limit indicate scatter of range. For R^2 and C_{turn} values above upper 95% confidence limits indicate species turnover.

| Metric pair | No. of sign | ificant scores | | No. of sigr | nificant scores | | |
|-------------------------|-------------|-------------------|--|-------------|-------------------|--|------------------------|
| | C-score | Clumping | joint indication of segregation/ aggregation | C-score | Clumping | joint indication of aggregation/ segregation | Contrasting results |
| C-score - Clumping | 138 | 107 | 65 | 3 | 8 | 0 | 5 |
| | R^2 | C _{Turn} | joint indication of turnover | R^2 | C _{Turn} | joint indication of no turnover | Contrasting results |
| R^2 - C_{Turn} | 149 | 145 | 102 | 6 | 10 | 2 | 2 |
| | R^2 | C-score | joint indication | R^2 | C-score | joint indication of | Contrasting |
| R^2 - C-score | 149 | 138 | of turnover 91 | 6 | 3 | no turnover 0 | results 1 |
| | EmbAbs | Clumping | joint indication of aggregation | EmbAbs | Clumping | joint indication of segregation | Contrasting results |
| EmbAbs - Clumping | 100 | 107 | 58 | 6 | 8 | 0 | 3 |
| | EmbAbs | C-score | joint indication of coherence/ segregation | EmbAbs | C-score | joint indication of scatter/ aggregation | Contrasting results |
| EmbAbs - C-score | 100 | 138 | 64 | 6 | 3 | 0 | 2 |
| | EmbAbs | R^2 | joint indication of coherence/ turnover | EmbAbs | R^2 | joint indication of scatter | Contrasting results |
| EmbAbs - R ² | 100 | 149 | 75 | 6 | 6 | 1 | 0 |
| | NODF | BR | joint indication of nestedness | NODF | BR | joint indication of antinestedness | Contrasting results |
| NODF - BR | 7 | 93 | 1 | 98 | 5 | 1 | 40 |

such a matrix can be viewed as combining three seemingly exclusive patterns (segregation, aggregation, turnover).

While this link is apparent for raw scores it holds also when comparing scores with those obtained from a null distribution that constraints row and column totals. The fixed – fixed null model does not eliminate the intimate link between the numbers of aggregated and checkerboard 2×2 submatrices. As a result, the significance levels of the *C*-score and *Clumping* will still be positively correlated (Fig. 5). With the exception of the nested and proportionally segregated matrices (with their limited null spaces) high Z-scores of *Clumping* were in all cases combined with respective high *C*-scores irrespective of matrix size and fill.



Figure 4. (A) In uniform – uniform matrices raw scores of the *C-score* (open dots) and the clumping score (black dots) are positively linked up to a matrix fill of 50%. Above 50% fill the clumping score increases with fill while the *C-score* decreases. (B) In proportional – proportional matrices the region of fill where both scores are positively linked is shifted towards low fill. Results from 100 $M_{fixed size}$ matrices.

The same holds for the relationship between the *C-score* and *Togetherness*. The latter was designed to measure joint occurrences and therefore niche similarity (Stone and Roberts 1992), and the raw scores of both metrics do behave properly. Dormann et al. (2009) showed that these metrics capture the antagonistic patterns of negative and positive association in ecological interaction matrices. However, when applied in combination with the fixed – fixed null model (Table 4) both metrics give identical results that do not allow for an unequivocal matrix classification.

Perhaps the most useful step forward is to recognize that the C-score represents an average calculated over all possible species pairs. Analysis of which individual species pairs show aggregation or segregation provides insight into the performance of the index. Although the interpretation of the *C*-score is complicated when it is applied to all the species pairs in a matrix, it is straightforward when applied to a single pair of species. In a meta-analysis of the Patterson and Atmar empirical matrices, Gotelli and Ulrich (2010) found that consistent non-randomness (as measured by the C-score) was caused by a preponderance of negatively associated species pairs. Even using the most conservative criterion (based on an empirical Bayes approach) for classifying species pairs as statistically significant, there were approximately four times as many species pairs exhibiting segregation as aggregation. At least for these empirical matrices, the frequencies of aggregation and segregation measured among species pairs were consistent with the overall C-score. However, future analyses should dissect the C-score pattern of non-randomness to identify particular pairs of species with positive and negative associations.



Figure 5. Relationship between Z-scores (fixed – fixed null model) of the Clumping score and the C-score ($M_{fixed size}$ and $M_{fixed fill}$ combined). Open squares: Turnover matrices, Stars: nested matrices, plus signs: proportionally segregated matrices, black dots: all other matrices. Quadratic regression for black dots: $R^2 = 0.79$.

Coherence, species turnover and boundary clumping

Our analysis in general demonstrated that metrics that use marginal totals for calculation such as *NODF*, *Chao* or *Morisita* perform poorly when used with null models that constrain these totals (Table 4). Recently, these metrics (Almeida-Neto et al. 2008, Chao et al. 2008, Leibold and Mikkelson 2002, Presley et al. 2010) and multispecies extensions of the Soerensen and Jaccard indices of species overlap (Baselga et al. 2007, Baselga 2010) have been proposed to quantify patterns of nestedness or species cooccurrence. These authors showed that the metrics behave well as raw scores and with null models that assume equiprobable occurrence probabilities. However, these metrics have not been tested rigorously with more constrained null models and should be used with caution (Almeida-Neto et al. 2012) in combination with the fixed – fixed null model.

We also showed that metrics based on nearest neighbor distances (*NND*) and local variances differences (*JoinCount*, *Block*) appeared also to be of little value. In matrices of higher fill (> 50%) most occurrences have at least one direct neighbor. As a consequence, metrics of the NND family (Clark and Evans 1954) achieve their minimum value and therefore lose any statistical power. These nearest-neighbor metrics appear to be of value only in very large matrices of relatively low fill. At least in presence–absence matrices, metrics of the *JoinCount* and *Block* family suffer from the same restrictions.

Our analysis did not point to any simple classification schemes of ecological presence–absence matrices. In comparison to the fixed – fixed null models, *NODF* detected 241 of the 1800 $M_{fixed fill}$ and $M_{fixed size}$ matrices as being significantly nested. Of these matrices, 133 were also detected by R^2 as having significant species turnover and 208 by the *C-score* as being segregated. Only 14 of these 241 significantly nested matrices were detected by *Clumping* as being aggregated. In turn, 205 of these 241 nested matrices were identified as being significantly not aggregated. Further, C_{Segr} detected 238 matrices as having turnover independent (checkerboard) segregation and R^2 identified 877 has having significant turnover. As many as 194 of these matrices were jointly detected by C_{Segr} and R^2 as having significant turnover and turnover independent segregation. These were mainly matrices of a high degree of nestedness (not shown). This mix of classifications in combination with the apparent differences in the power of certain metrics makes any clear-cut classification scheme for ecological matrices challenging.

Previous attempts to classify ecological presence-absence matrices and to link this classification with ecological processes (Leibold and Mikkelson 2002, Presley et al. 2010, Podani and Schmera 2011, but see Gotelli and Ulrich 2011, 2012) were largely based on idealized artificial matrices. These approaches particularly focused on the gradient between nestedness and species turnover and aggregation and segregation. Our results highlight the intimate link between an aggregated and a segregated pattern. A matrix might be highly aggregated and segregated (Fig. 2) as had been demonstrated previously for a perfect checkerboard matrix (Stone and Roberts 1990). Because a nested subset pattern is a special form of species aggregation, nestedness may not be really distinct from species segregation. Almeida-Neto et al. (2007) and Podani and Schmera (2011) focused on the gradient from nestedness to antinestedness and equated antinestedness with species segregation. We showed that species segregation can be divided in true species turnover and turnover independent (diffuse) segregation. Thus classification schemes that focus on the aggregation-segregation dichotomy might miss important aspects of matrix structure.

Species turnover is intimately linked to β -diversity (Tuomisto 2010) and refers to the replacement in species composition across sites. Temporal turnover is an explicit component of the theory of island biography (MacArthur and Wilson 1963, Simberloff 1976) but spatial turnover (among sites) is more often linked to environmental gradients, and to vicariant speciation triggered by environmental barriers. For these reasons, spatial turnover is a common pattern in biogeography (Tuomisto 2010). The second, turnover-independent, part of species segregation has gained much less attention, although it is the classical pattern on which most discussions on the assembly rule concept focused (Diamond 1975, Weiher and Keddy 1999). Within the competition framework, we might speculatively think of C_{Segr} as capturing the effect of actual competition as a force towards species segregation and of C_{Turn} as quantifying 'the ghost of competition past' (Connell 1980). Our analysis of empirical presence–absence matrices clearly points to turnover as the dominant pattern of species segregation (Table 6).

Irrespective of spatial scale (local or regional) and type of matrix (biogeographic – interaction) less than 6% of matrices were significantly diffusely segregated but more than 20% showed significant turnover. In accordance with expectation the degree of turnover was highest for matrices at regional to continental scales.

Our results point to a gradient from a nested subset pattern to a turnover pattern (Table 5) as has been previously hypothesized (Gaston and Blackburn 2000, Baselga 2010). Nestedness was originally interpreted as an ordered sequence of species extinction (Atmar and Patterson 1993, Ulrich et al. 2009) whereas turnover has been interpreted as an ordered sequence of species replacement across an environmental gradient (Tuomisto 2010). In combination with the fixed – fixed null model C_{Segr} identified at least 58% of the nested matrices as being also checkerboarded (Table 5). C_{Segr} is not strongly correlated to *BR* and *NODF* (Table 6). Thus, a nestedness metric in combination with the *C-score* that does not differentiate between the two types of segregation might give an incorrect classification.

Summary

Our analysis showed that metrics designed to quantify different and sometimes exclusive matrix properties are often correlated (Table 5). Undesired correlations, even if statistically not significant, might strongly influence the interpretation of pattern. Such undesired correlations are particularly obvious using the fixed – fixed null model. For instance *Clumping* correlated positively with the *C-score*, *Tog*, R^2 and negatively with *NODF*, while *EmbAbs* was negatively correlated with the *C-score* and *Clumping*. This seemingly contradictory behavior casts further doubts on the utility of simple classification schemes (Leibold and Mikkelson 2002, Presley et al. 2010). The use of multiple metrics – perhaps dissected for pairs of individual species or sites – may be necessary for valid pattern identification.

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Supplementary material (available online as Appendix O20325 at < www.oikosoffice.lu.se/appendix >). Appendix A1 (Figure A1.docx: Typical presence–absence matrices used for testing the performance of metric – null model combination. Figure A2.docx: Relationships between the R^2 metric and nine metrics of matrix structure (raw scores and Z-transforms of two null models) for the fixed size matrices. Figure A3.docx: Relationships between the R^2 metric and nine metrics of matrix structure (raw scores and Z-transforms of two null models) for the fixed fill matrices. Figure A4.docx: Relationships between the R^2 metric and nine metrics of matrix structure (raw scores and Z-transforms of two null models) for the fixed fill matrices. Figure A4.docx: Relationships between the R^2 metric and nine metrics of matrix structure (raw scores and Z-transforms of two null models) for all 900 artificial fixed fill and 900 fixed size matrices.

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