

A consumer's guide to nestedness analysis

Werner Ulrich, Mário Almeida-Neto and Nicholas J. Gotelli

W. Ulrich (wulrich@uconn.edu), Department of Ecology and Evolutionary Biology, University of Connecticut, Storrs, CT 06269-3043, USA
M. Almeida-Neto, Instituto de Física de Caracás, Universidade Federal de Pernambuco, CEP 55080-900, Aracaju, Brazil
N. J. Gotelli, Department of Biology, University of Connecticut, Storrs, CT 06269-3043, USA

The distinction between geographical and bipartite

merely by establishing the statistical pattern of nestedness. Pinning down the different mechanisms usually will require additional data beyond the original presence–absence matrix, such as the sequence of extinctions that have led

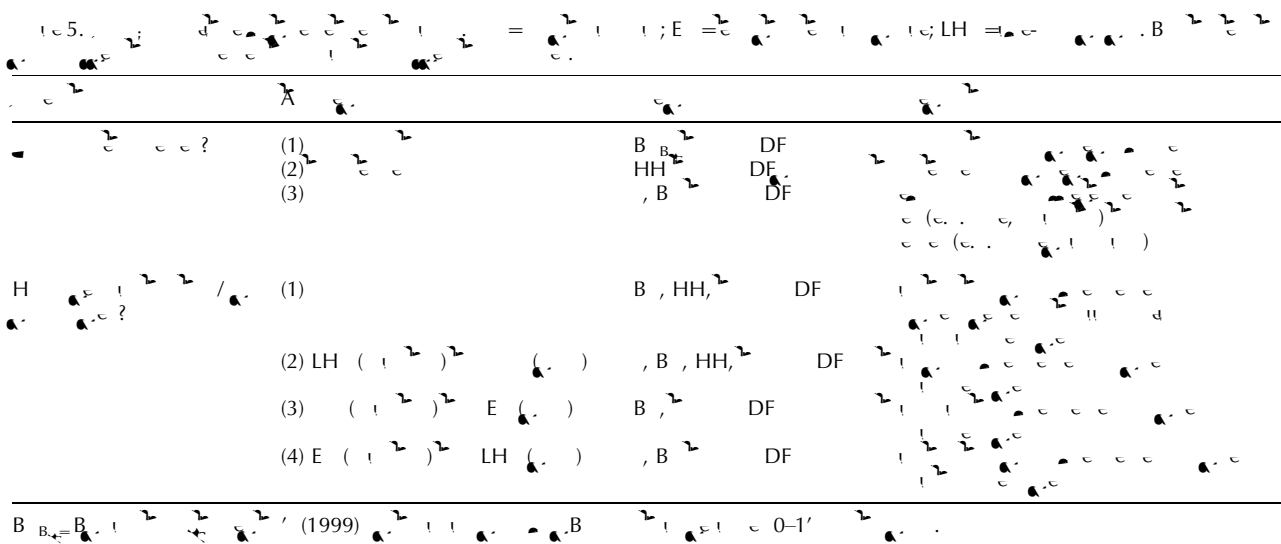
a pollination network preferentially interact with already well-connected (abundant) species. These patterns suggest that passive sampling explanation might account for nestedness patterns in pollinator networks: abundant pollinators and plant species simply have higher chances to visit and to be visited by their more abundant counterparts (Table 2). Furthermore, the aforementioned selective extinction and colonization models apply to interaction networks as well.

Jordano et al. (2003, 2006) drew attention to ‘forbidden interactions’ within interaction networks (Fig. 1B). These are interactions that are impossible due to physical or

1.3. A			
	A ()	A	D
0 (. . .)	A .1986		
1 (. . .)	C .1991		
(. . .)	C .1991		
(. . .)	C .1991		
(. . .)	C .1991		
(. . .)	. 1992		

McCabe 2002) is still needed to meaningfully compare the strength of the pattern for different matrices.

Wright et al. (1998) reported the 'percent metric' values of the gap-counting metrics N1, UA, UT and UC (abbreviations in Table 3) to be positively correlated with

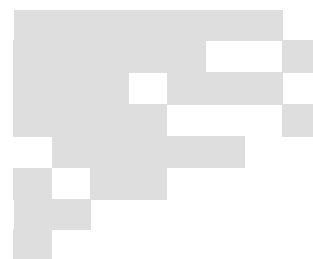
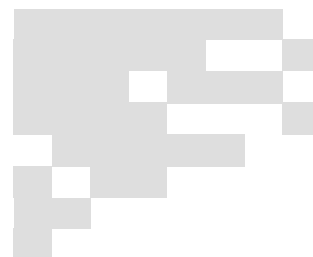


about the interpretation of nestedness patterns. The temperature metric was designed specifically for insular floras and faunas, in which ordered sequences of colonization and extinction can be reasonably associated with unexpected gaps in the incidence matrix. Thus, Atmar and Patterson's (1995) data compilation – on which many subsequent tests were based – contains nearly exclusively island matrices. However, it is unclear whether the temperature concept should be applied to interaction networks (Bascompte et al. 2003, Dupont et al. 2003, Ollerton et al. 2003). In networks of interacting species, there is no a priori reason to assume that certain species pairs are less probable than others and to weight the cells by their distance to the isocline. None of the three explanations for nestedness in such matrices (Table 2) explicitly refers to differential occurrence and absence probabilities. More appropriate metrics for interaction networks are NODF (Almeida-Neto et al. 2008), BR (Brualdi and Sanderson 1999), and HH (Hausdorf and Hennig 2003). Nevertheless, these points deserve further attention and a critical meta-analysis and re-analysis of published networks of interacting species is needed.

Unexpected presences and absences

A perfectly nested matrix contains no absences (holes or unexpected absences) within its filled part and no presences (outliers or unexpected presences) within its empty part. The gap and temperature metrics use the numbers of holes and outliers to quantify the degree of nestedness. However, neither holes nor outliers have been defined consistently in the literature (Wright et al. 1998, Bird and Boecklen 1998). For example, in Fig. 2, numbers of holes and outliers defined by N0 and N1 differ from those defined by T. This inconsistency in definition has consequences for the use of holes and outliers in subsequent analyses, for instance in the identification of idiosyncratic species and sites in biogeographic analysis (below). Gap metrics define holes and outliers based on rows and columns only. However, in our view, the position of holes and outliers in the matrix intimately depends on the number and distribution of absences and presences within the whole matrix (Arita et al.

	1	2	3	4	5	6	7	8	Σ
A	1	1	1	1	1	1	1	0	7
B	1	1	1	1	1	0	0	1	6
C	1	1	1	0	1	1	1	0	6
D	1	1	1	1	0	0	0	1	5
E	0	1	1	1	1	1	0	0	5
F	1	0	1	1	0	0	0	0	3
G	1	1	0	0	0	0	0	0	2
H	1	0	0	0	0	0	0	0	1
Σ	0								



2008). To date, only the temperature concept uses a clear matrix-wide definition of holes and outliers, although there is some vagueness in the original definition of the isocline that separates filled and empty parts of the matrix (Rodríguez-Gironés and Santamaría 2006, Ulrich and

be large enough for the fixed – fixed model to be applicable. The effect of matrix size on the power of a statistical test has been largely ignored in nestedness analysis (Fischer and Lindenmayer 2005).

The performance of different nestedness metrics is also influenced by the choice of the null model. For the Patterson and Atmar dataset, Fig. 3 illustrates regressions of Z-scores versus matrix size for the best-performing gap metrics (UT, BR.), and the temperature and NODF metrics under the equiprobable (A, B) and the fixed – fixed (C, D) models. Irrespective of metric, the equiprobable null model gave for most matrices extraordinarily large Z-scores and identified them as being highly nested. The fixed – fixed appeared to be much more conservative and identified only a small fraction of the matrices as being nested. Under the equiprobable null model, Z-scores of all four metrics were highly positively correlated, and thus exhibited similar statistical power. Under the fixed – fixed model, these correlations vanished and different metrics identified different matrices as being nested (Fig. 3C–D): of the 286 empirical matrices, 113 were identified by at least one of the metrics as being nested. However, only 10 matrices were jointly identified as being not random by all four metrics. Most similar in performance were NODF and T, with 29 joint significances. Moreover, the ranking of matrices according to the degree of nestedness depended on the null model used, and the ranks of Z-scores obtained from the equiprobable and the fixed – fixed nulls were only weakly correlated. The metrics that behaved most similarly with the different null models were UT (Spearman's rank $r=0.33$, $p<0.01$) and BR ($r=0.29$, $p<0.01$), whereas the respective ranks of T and NODF were not significantly correlated.

The equiprobable–equiprobable null model assumes that both columns and rows are equivalent, so that the probability of a species occurrence is the same for any cell in the null matrix. However, species differ in abundance and therefore in colonization ability (the mass effect) and sites differ in carrying capacities. There is growing acceptance that null models that do not consider species-specific

differences and variability among sites should not be used in biogeographic studies (Jonsson 2001, Ulrich and Gotelli

The sampling problem has also a theoretical perspective. Do rare and endemic species strengthen the nested pattern and therefore conform to models of selective colonization and extinction (Patterson 1990, Patterson and Atmar 2000) or are their occurrences random, so that when they are properly censused, they contribute to a reduction in nestedness? Additional exploration of the effects of species rarity and sampling errors in nestedness analysis would be worthwhile.

Idiosyncratic species

Atmar and Patterson (1993) termed species that decrease the matrix wide nestedness 'idiosyncratic' (Fig. 1A). One goal of nestedness analysis was always to identify such 'deviating' species and to infer the causes of idiosyncrasy. Atmar and Patterson (1993) explained the existence of idiosyncratic species by post-isolation immigration, geographic barriers, and competitive exclusion. Idiosyncratic species can be described as running counter to ecological and geographic gradients of species occurrence. For diatom communities Soininen (2008) showed that idiosyncratic species had wider geographic range sizes than 'normal' species, a pattern that surely deserves attention. Moreover, assemblages dominated by idiosyncratic species appeared to have rather high local species turnover (Soininen 2008). This finding is consistent with the selective extinction hypothesis for nestedness (Patterson 1990).

From a statistical perspective, idiosyncratic species should be more common among species of intermediate occupancy simply because these species have more potential combinations of unexpected absences and presences. At intermediate occurrence frequencies, statistical tests for idiosyncratic distributions will have maximum power, whereas at very high or low occurrence frequencies, the tests will be very weak. For example, a species that occurs only at one island (an endemic) has only one possibility for a gap. The same holds for a widespread species, which is absent from only one island. In contrast, a species that occurs at four of ten islands has six possibilities for gaps. Existing null model protocols cannot easily control for such factors because they are inherent in the occurrence frequencies of each species.

In conservation ecology, the identification of idiosyncratic sites has been discussed with regard to the single-large-or-several-small (SLOSS) debate (Atmar and Patterson 1993, Boecklen 1997, Patterson and Atmar 2000, Fischer and Lindenmayer 2005, Fleishman et al. 2007). Atmar and Patterson (1993) argued that the widespread occurrence of nested subsets speaks for the value of single larger areas to protect because they necessarily contain more species than any number of smaller sites. However, Boecklen (1997) and Fischer and Lindenmayer (2005) convincingly showed that this argument is only valid for perfectly nested subsets, which are very rare in nature. Even for highly significantly (but not perfectly) nested subsets, the total species numbers from subsets of many smaller sites are often higher than the respective number of species from a single larger site of the equivalent total area.

Nestedness and species co-occurrence

Nestedness is a pattern of species co-occurrence intrinsically related to the degree of species aggregation. A perfectly nested matrix is also a matrix with a maximum number of perfect pair wise species aggregations, but the opposite does not necessarily hold. Fig. 4 relates the Z-scores for BR and NODF of 286 Atmar and Patterson data matrices to the respective Z-transforms of the widely used C-score (Stone and Roberts 1990), which measures matrix-wide species' segregation. With the equiprobable–equiprobable null model, both metrics are highly correlated ($r=0.97$; $p < 0.0001$) indicating that they capture essentially the same pattern. In other words in these matrices a nested pattern corresponds to species aggregation and vice versa. Indeed the C-score is a normalized matrix wide count of the number of joint occurrences (Stone and Roberts 1990) and measures therefore essentially the same as NC (Wright and Reeves 1992). This result together with the strong correlations shown in Fig. 3 call for a reassessment of what has actually been measured in previous analyses of nested subsets that have used the equiprobable–equiprobable null model. We are afraid that many previous studies have quantified a pattern of matrix-wide species aggregation instead of nestedness. Further analysis is needed to determine whether nestedness is measuring something above and beyond a simple pattern of species aggregation.

As with the nestedness metrics in Fig. 3, the relationships of C-scores with BR and NODF vanished under the fixed-fixed model (Fig. 4C–D). In fact, both nestedness metrics showed a weak negative correlation with the C-score (BR: $r=-0.62$; $p < 0.001$; NODF: $r=-0.48$; $p < 0.01$). When co-occurrence and nestedness patterns are both analyzed with the fixed-fixed model, the majority of matrices remained significantly segregated (Fig. 4; Gotelli and McCabe 2002, Gotelli and Ulrich unpubl.) whereas only a small minority appeared to be significantly nested (Ulrich and Gotelli 2007a). The contrasting results in Fig. 3 and 4 again emphasize that patterns of nestedness and species segregation depend on the particular combination of metric and null model that are used. These combinations must be carefully benchmarked against artificial random data sets before they can be used to understand patterns in empirical data matrices.

The correlation between nestedness and co-occurrence metrics might be used to identify non-random species associations. An idiosyncratic species is by definition more segregated than expected in a nested pattern, and this pattern could be useful in co-occurrence analysis. The detection of non-random species segregation is central to the ecological assembly rule discussion (Diamond 1975, Weiher and Keddy 1999), and has motivated much of the work on matrix-wide measures of species segregation. However, detecting individual species pairs that are non-random has proven to be a statistical challenge (Sfenthourakis et al. 2006, Gotelli and Ulrich unpubl.). The reason is simple. Even a moderate number of species gives hundreds or even thousands of unique species pairs, of which tens or even hundreds will be significantly non-random just by chance at the 5% or 1% error benchmarks. Recent attempts to solve the problem of identifying true non-random species pairs used sequential Bonferroni corrections and Bayesian

approaches (Ulrich and Gotelli unpubl, but see Moran 2003). It would be useful to know whether the species identified by these analyses are also idiosyncratic in a nestedness analysis. Table 6 shows how such an approach might work: 13 species pairs formed by 41 Amazon

idiosyncratic, so perhaps these pairs are not significantly non-random, even after being selected by a sequential Bonferroni test.

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