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NULL MODEL ANALYSIS OF SPECIES NESTEDNESS PATTERNS

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Abstract.
nestedness when it is present. Among the eight indices, the popular matrix temperature metric did not have good statistical properties. Instead, the Brualdi and Sanderson discrepancy index and Cutler's index of unexpected presences performed best. When used with the fixed-fixed algorithm, these indices provide a conservative test for nestedness. Although previous studies have revealed a high frequency of nestedness, a reanalysis of 288 empirical matrices suggests that the true frequency of nested matrices is between 10% and 40%.

Key words: biogeography; matrix temperature; nestedness; nestedness temperature calculator; null model; passive sampling; presence–absence matrix; statistical test.

Introduction

A common biogeographic pattern is species nestedness: smaller communities form proper subsets of larger communities (Patterson and Atmar 1986, Atmar and Patterson 1993). In an ordered binary presence–absence matrix, nestedness leads to a maximally "packed" pattern of ones and zeroes. Unexpected presences or absences from a maximally packed matrix can be used to quantify the extent of nestedness, both for the matrix as a whole and for individual species (Atmar and Patterson 1993).

Although Darlington (1957) first described the pattern of nestedness and its possible causes, the study of nestedness was popularized by the pioneering work of munities were the primary causes of nested patterns. However, subsequent analyses have revealed potential problems with the NTC and the index of matrix temperature. Wright et al. (1998) found that the matrix temperature index is sensitive to matrix size. Fischer and Lindenmayer (2002) and Higgins et al. (2006) showed that the randomization procedure of NTC is prone to identify nestedness as an artifact of passive sampling.

and column totals (and thus retain more of the structure of the original matrix) may be less sensitive to matrix size, but may also have less power to detect nestedness (Cook and Quinn 1998).

The statistical significance of any nestedness index value has to be tested against some null hypothesis. The respective null distributions are obtained from null models that generate expected index values and the associated confidence limits. Before large meta-analyses are conducted with empirical data sets, it is therefore important to understand the statistical properties of the different indices and null model algorithms (Gotelli 2001). There are two goals of the current study: (1) to to the point in the center of the matrix that represents the percentage of matrix fill (Fig. 1). The curved isocline in the NTC approximates these linear isoclines, but crosses them twice.

Third, we excluded from the computation of matrix temperature those matrix cells that fell directly on the isocline. If presences or absences close to the isocline are more probable than those that are distant from the isocline, cells directly at the boundary between the filled and the empty parts of the matrix should simply reflect Poisson errors. Their presence might contribute to noise in the matrix, making it more difficult to detect nestedness when it is present. Exclusion of these points also seems appropriate because of small differences that might arise from using linear vs. nonlinear isoclines.

Null model algorithms

indicate approximate statistical significance at the 5% error level (two-tailed test). The SES is derived from meta-analysis (Gurevitch et al. 1992) and can be used to compare results among different matrices and algorithms (Gotelli and McCabe 2002).

Diagnostic tests

We used two additional tests to evaluate the statistical behavior of the FF algorithm. First, for the set of nested matrices, we used linear regressions of the SES of each index on matrix shape (the ratio m/

(probability of incorrectly accepting the null hypothesis $= 0.59$).

Empirical matrices

Table 3 gives the frequencies with which nestedness was detected for the 288 empirical matrices compiled by Atmar and Patterson (1995). The proportion of significant matrices varied from a low of 0–1% (all nestedness metrics with the LF algorithm) to a high of 80% (the EE algorithm with the BR nestedness index). The variation in the detection of nestedness mirrored the results of the benchmark tests with random and non-random matri-

matrices illustrate the classic trade-off between type I and type II statistical errors. The FF algorithm, in which row and column totals are preserved, has good type I error properties when tested against null matrices (Table 1), but has poor power for detecting nestedness in patterned matrices (Table 2). Because the FF algorithm preserves row and column totals, the observed matrix will more closely resemble matrices created by the FF algorithm than by algorithms that relax row or column totals. This similarity makes it more difficult for the FF algorithm to detect nestedness. Other algorithms, including PE and EF, which were introduced by Patterson and Atmar (1986), have good power to detect nested matrices (Table 2), but are prone to reject the null hypothesis for random matrices (Table 1). For standard statistical tests, guarding against Type I error has traditionally been a high priority (Gotelli and Ellison 2004), so the FF algorithm should be used on these grounds for a conservative test of nestedness. The FF algorithm used with the N_1 index had the best chance of detecting nested matrices (41%; Table 2).

For this test, 13% of the compiled empirical matrices were significantly nested. Because this is a conservative test, this result represents a lower bound on the true frequency of nestedness in nature. Alternatively, we could use a test that has more power, but at a cost of increased type I error. From the analyses in Table 1 and Table 2, the combination of the N_0 metric with the PE algorithm has a moderately high type I error frequency ($P = 0.19$), but comparably good power for detecting nestedness ($P = 0.76$). By this criterion, 42% of the empirical matrices were nested (Table 3). Thus, the true frequency of nestedness in the empirical matrices is probably between 13% and 42%. This is a substantial fraction, although it is probably lower than the frequencies of 20% (UA index with the EP algorithm) to 70% (NC index with the PE algorithm) reported by Wright et al. (1998) for matrices with $P < 0.01$.

An additional complication is that the N_0 and N_1 indices appear to be sensitive to matrix size, so that the probability of detecting nestedness will depend on how large or small the matrix is (Table 4). Wright et al. (1998) reported a similar result for the EE and PE algorithms. With N_1 and the FF algorithm, there is a greater chance of detecting nestedness with large matrices than with small. Based on regression of SES against matrix size (Table 4), a nested matrix of at least 340 elements (row number $\times$ column number) is needed for an SES of -2 (the traditional $P =$

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