NULL MODEL ANALYSIS OF SPECIES CO-OCCURRENCE PATTERNS

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Abstract. The analysis of presence–absence matrices with ''null model'' randomization tests has been a major source of controversy in community ecology for over two decades. In this paper, I systematically compare the performance of nine null model algorithms and four co-occurrence indices with respect to Type I and Type II errors. The nine algorithms differ in whether rows and columns are treated as fixed sums, equiprobable, or proportional. The three models that maintain fixed row sums are invulnerable to Type I errors (false positives). One of these three is a modified version of the original algorithm of E. F. Connor and D. Simberloff. Of the four co-occurrence indices, the number of checkerboard combinations and the number of species combinations may be prone to Type II errors (false negatives), and may not reveal significant patterns in noisy data sets. L. Stone and A. Robert's checkerboard score has good power for detecting species pairs that do not co-occur together frequently, whereas D. Schluter's *V* ratio reveals nonrandom patterns in the row and column totals of the matrix. Degenerate matrices (matrices with empty rows or

nonsignificant pattern (Type II error)? To answer these questions, I tested each of the nine simulation algorithms and four co-occurrence indices with matrices of known structure. For Type I errors, the algorithms and indices were tested against random matrices. For Type II errors, the algorithms and indices were tested against structured matrices that had increasing amounts of random ''noise'' added (Gotelli et al. 1997).

METHODS

Presence–absence matrices

The data are organized as a presence–absence matrix with $i = 1$ to R rows and $j = 1$ to C columns. Each row represents a species and each column represents a site or sample. Entry a_{ij} in the matrix represents the presence (1) or absence (0) of species i in sample j. Let S_i equal the row total for row i, that is, the total number of occurrences of species i across the sites. Let T_j equal the column total for column j, that is, the total number of species occurring in site j. Let

TABLE 1. Summary of four co-occurrence indices.

	Index			
	CHECKER	C score	V ratio	COMBO
Description	Number of species pairs forming perfect checkerboard distributions	Checkerboard score	Variance ratio	Number of unique species combinations
Calculation	Scan matrix rows for species pairs forming checkerboards	$\Sigma(S_i - Q)(S_k - Q)/((R)(R-1)/2)$	s^2(column sums)$/ \Sigma$ row s^2	Scan matrix columns for unique species combinations
Source	Diamond (1975)	Stone and Roberts (1990)	Robson (1972); Schluter (1984)	Pielou and Pielou (1968)
Theoretical range	0 to $R(R-1)/2$	0 to $\Sigma S_i S_k / ((R)(R-1)/2)$	0 to ∞	1 to 2^R
Pattern expected in a competitively structured community	Observed > simulated	Observed > simulated	Observed < simulated	Observed < simulated
Comments	Most readily testable prediction of Diamond's (1975) assembly rules	Measures species segregation, but does not require perfect checkerboard distributions	Measures pattern in marginal totals of matrix	May reflect "forbidden species combinations" (Diamond 1975)

Notes: S_i = total for row i; R = number of rows (=species) in the matrix; Q = number of sites in which both members of a species pair are present.

ing could be applied to the rows of the species occurrence matrix, which represent occurrence frequencies of each species. The null model could retain observed row totals, allow rows to be equiprobable, or set probabilities proportional to observed row totals.

Thus, a universe of $3^2 = 9$ simple null models (SIM1 to SIM9) could be constructed using only information contained in the row and column totals. These models differ in whether rows and columns are treated as fixed sums, equiprobable, or proportional. All of the algorithms are plausible candidates for a null model, and some have been used in other analyses in biogeography and ecology (Table 2). Table 3 gives a hypothetical data matrix, and Fig. 1 illustrates the simulation procedure for each algorithm with this matrix. I have systematically compared the behavior of all nine algorithms with the four different indices.

Kinds of data

Two types of data sets are used in co-occurrence analysis. The first type I call "island lists." These represent nearly complete lists of species from islands or well-defined habitat patches. The lists are often accumulated from many thorough censuses, and can be found in the literature for well-studied vertebrate taxa and "popular" invertebrate taxa such as butterflies. Island lists are typically nondegenerate matrices, because missing species and empty islands are often not recorded or reported.

The second type of data set I call "sample lists." These represent lists of species taken from standardized samples within areas of relatively homogeneous habitat. These lists are generated from short-term ecolog-

ical censuses, such as pitfall traps, cores, bait samples, sweep samples, line, belt, and quadrat samples, point counts, and timed censuses. Often these lists are incomplete, and may not include rare or undersampled species, so that total species richness must be estimated by extrapolation (Colwell and Coddington 1994). Sample lists often form degenerate matrices, because some samples may contain no species.

Fig. 2 is an example of a matrix based on island lists: the 17 species of finches (Fringillidae) from 19 of the largest islands in the West Indies. The islands have been well censused for the past century, although extensive habitat change and species extinctions have been recorded. The matrix contains a range of species occurrence frequencies from single-island endemics (*Loxia leucoptera*) to widespread species (*Tiara bicolor*). Similarly, the total number of finch species on the islands ranges from 1 (Antigua) to 7 (Hispaniola). Total bird species richness on these islands ranges from 16 (St. Martin, Barbados) to 79 (Cuba, Hispaniola).

Fig. 3 is an example of a matrix based on sample lists: the species of ground-foraging ants collected in 25 pitfall trap samples in an open field in Prince Edward County, Virginia. These data are part of a regional census of ants at 33 sites in the eastern United States. At each site, 25 pitfall traps (50-mL plastic centrifuge tubes, 27 mm diameter) were established in a 5 × 5m grid. Traps were opened for 48 h, and the ants from each trap were identified to species when possible (details in Arnett 1998). Most of the species in the collection occurred in only a single sample, and 13 of the 25 traps contained no ants. The most common taxon (

TABLE 2. Summary of nine null model algorithms for species co-occurrence analysis.

Constraint	Constraint		
	Columns equiprobable	Columns proportional	Column sums fixed
Rows equiprobable	SIM1 $P(a_{ij})\ 5\ 1/RC$ All species and sites are equiprobable. Classic randomization test in which all matrix rearrangements are equally likely. Sokal and Rohlf (1995:803)	SIM6 $P(a_{ij})\ 5\ T_j/NR$ All species are equiprobable. Sites differ in suitability. Probabilities of occurrence in sites proportional to observed species richness/site. Inverse of SIM7.	SIM3 $P(a_{ij}$

COLUMNS EQUIPROBABLE

SIM1

	Site 1	Site 2	Site 3	Site 4	Site 5	Site 6
Species A	0.033	0.033	0.033	0.033	0.033	0.033
Species B	0.033	0.033	0.033	0.033	0.033	0.033
Species C	0.033	0.033	0.033	0.033	0.033	0.033
Species D	0.033	0.033	0.033	0.033	0.033	0.033
Species E	0.033	0.033	0.033	0.033	0.033	0.033

Rows Equiprobable

	Site 1	Site 2	Site 3	Site 4	Site 5	Site 6
Species A	0.050	0.050	0.050	0.050	0.050	0.050
Species B	0.017	0.017	0.017	0.017	0.017	0.017
Species C	0.033	0.033	0.033	0.033	0.033	0.033

Rows Proportional

FIG

COLUMN TOTALS FIXED

SIM3

	Site 1	Site 2	Site 3	Site 4	Site 5	Site 6
Species A	0.200	0.200	0.200	0.200	0.200	0.200
Species B	0.200	0.200	0.200	0.200	0.200	0.200

Rows

FIG. 1. Continued.

el tests. The general result was that degenerate matrices did increase the frequency with which the null hypothesis was rejected. However, for well-behaved algorithms, this increase was usually ‚ 10%. The effect of degenerate matrices was usually much less than the effect of the algorithm or index selected.

Estimating Type I errors

Estimating Type I errors means using each algorithm and index to statistically evaluate a "random" test matrix, which is presumably random with respect to species interactions. For each combination of index and algorithm, I created 100 such test matrices, and kept track of the 100 upper- and lower-tail probabilities for each test. If the test is robust to Type I error, ; 10 of the 100 test matrices should have been nonrandom at P ‚ 0.05 (in either tail). On the other hand, if the test is prone to Type I error, the number of times the null hypothesis is rejected will be much greater than 10. Algorithms or indices that are prone to Type I errors should not be used because there is a danger that we will incorrectly reject the null hypothesis for a data set that is random.

How, exactly, should a "random" matrix be constructed for such a test? I used four procedures to create different kinds of test matrices. Each matrix was created using the observed marginal totals from the West Indian finch matrix (Fig. 2). The four kinds of test matrices were:

Test 1—Complete randomization. The 55 species occurrences were completely randomized across the 19 3 17 5 323 cells of the matrix. This is equivalent to SIM1.

Test 2—Randomize each row, columns equiprobable. The species occurrences in each row were randomized among the 19 sites. This is equivalent to SIM2.

Test 3—Randomize each row, columns proportional. The species occurrences in each row were randomized among the 19 sites, with the probability of occurrence being proportional to the column total in the matrix. This is equivalent to SIM4.

Test 4—Randomize each row, columns proportional to the logarithm of island areas. The species occurrences in each row were randomized among the 19 sites, with the probability of occurrence proportional to the logarithm of island area.

Thus, in the first three kinds of test matrices, there is an identical simulation procedure that is used to evaluate the matrix. Test 4 incorporates independent data on island areas in order to construct test matrices. Only nondegenerate test matrices were used in these analyses. Once each test matrix was created, it was evaluated statistically with 1000 randomizations of each of the 36 combinations of algorithms (9) and indices (4). I repeated this process for 100 test matrices of each combination. The computer program kept track of the number of times the null hypothesis was rejected (either

Species	Cuba	Hispaniola	Jamaica	Puerto Rico	Guadeloupe	Martinique	Dominica	St. Lucia	Barbados	St. Vincent	Grenada	Antigua	St. Croix	Grand Cayman	St. Kitts	Barbuda	MonSt.errat	St. Martin	St. Thomas	Row Sum
Carduelis dominicensis	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Loxia leucoptera	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Volatinia jacarina	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1
Sprophila nigricollis	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1
Melopyrrha nigra	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	2
Loxigilla portoricensis	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Loxigilla violacea	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
Loxigilla noxis	0	0	0	0	1	1	1	1	1	1	1	1	0	0	1	1	1	1	0	12
Melanospiza richardsoni	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1
Tiara olivacea	1	1	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	5
Tiara bicolor	0	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	17
Tiara canora	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Loxipasser anoxanthus	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1

FIG. 2. An example of an ''islands list'' matrix of West Indian finches (Fringillidae). Data from Gotelli and Abele (1982).

tail) and the average, or expected value of the index for each simulation. Because there is no a priori way to decide which of the four kinds of random matrices (Test 1 through Test 4) are most valid, I averaged the results across all four in order to compare the different simulation algorithms (SIM1 through SIM9) and different co-occurrence indices (CHECKER through COMBO).

Estimating Type II errors

Estimating Type II errors means using each algorithm and index to statistically evaluate a nonrandom test matrix. Such a nonrandom matrix should reflect the effects of species interactions. A test that was vulnerable to Type II error would fail to detect nonrandom patterns in such a structured matrix. How should such a nonrandom matrix be constructed? One strategy would be to build a specific model of species inter-

actions and use this model to create the test matrix. Examples of this strategy include Case and Sidell (1983), Colwell and Winkler (1984), Hastings (1987), and Kelt et al. (1995).

However, a weakness of this approach is that the results are always contingent on the particular model chosen for comparison. In addition, it may not represent a fair test of the null model. As some critics have point-

Pitfall Trap Number

Species	(1,1)	(1,2)	(1,3)	(1,4)	(1,5)	(2,1)	(2,2)	(2,3)	(2,4)	(2,5)	(3,1)	(3,2)	(3,3)	(3,4)	(3,5)	(4,1)	(4,2)	(4,3)	(4,4)	(4,5)	(5,1)	(5,2)	(5,3)	(5,4)	(5,5)	Row sum
Aphaenogaster rudis complex	1	0	0	0	1	0	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	5
Aphaenogaster treatae	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	1	0	3
Camponotus castaneus	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Crematogaster lineolata	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Formica inserta	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Formica subserecia	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
Myrmecina americana	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Pheidole morrisi	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Pheidole vinelandica	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1
Smithistruma sp	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1

FIG. 3. An example of a ''sample list'' matrix of Virginia ants. Source: unpublished data from A. E. Arnett and N. J.

A

```
0 0 0 0 0 0 0 0 0 0 1 1 1 1 1 1 1 1 1 1

0 0 0 0 0 0 0 0 0 0 1 1 1 1 1 1 1 1 1 1

0 0 0 0 0 0 0 0 0 0 1 1 1 1 1 1 1 1 1 1

0 0 0 0 0 0 0 0 0 0 1 1 1 1 1 1 1 1 1 1

0 0 0 0 0 0 0 0 0 0 1 1 1 1 1 1 1 1 1 1

0 0 0 0 0 0 0 0 0 0 1 1 1 1 1 1 1 1 1 1
```
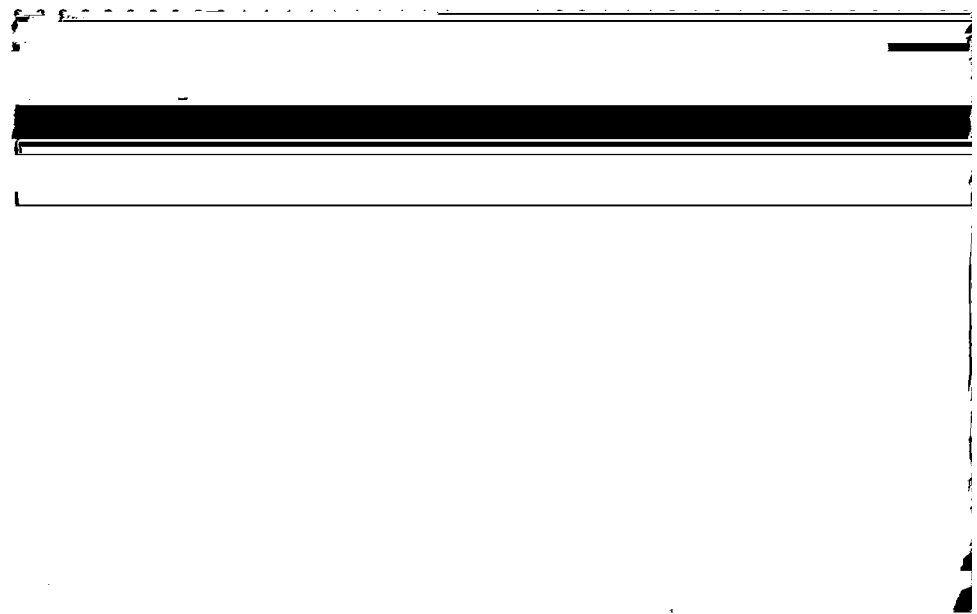
B

```
0 0 1 0 1 0 1 1 1 1 0 1 0 0 0 0 1 1 1 0

1 1 0 1 0 1 0 0 0 0 1 0 1 1 1 1 0 0 0 1

0 0 1 0 1 1 1 1 0 0 1 0 0 1 0 0 1 1 1 0

1 1 0 1 0 0 0 0 1 1 0 1 1 0 1 1 0 0 0 1

1 0 1 1 0 0 0 0 0 0 0 0 0 1 1 1 1 1 0 1 1

0 1 0 0 1 1 1 1 1 1 1 1 0 0 0 0 0 1 0 0
```

FIG. 4.   Two highly structured presence–absence matrices. Diamond and Gilpin (1982) presented these matrices as examples

TABLE 4. Summary of Type I error tests for null models.

Simulation algorithm	Co-occurrence index				
	CHECKER	*C* score	*V* ratio	COMBO	Average
SIM1	0.72				
SIM2	**0.07**				
SIM3					
SIM4					
SIM5					
SIM6					
SIM7					
SIM8					
SIM9					
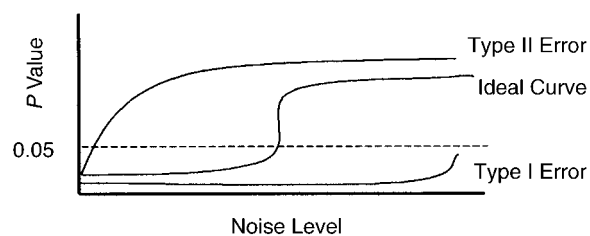
FIG. 5. Hypothetical error curves for a Type II noise test. As more and more site occurrences of species are randomized in the matrix, the *P* value will rise from significant to nonsignificant levels. A test is susceptible to Type I error if it never rises above the 0.05 mark, even when the matrix is entirely randomized. A test is susceptible to Type II error if it rises too quickly above the 0.05 mark, even when very little of the original pattern has been degraded by random transpositions. A test has a good balance of Type I and Type II errors if it stays below the 0.05 mark until approximately half of the matrix has been randomized, then quickly rises well above the 0.05 mark as more noise is added.

West Indian finch matrix was rearranged using SIM9, and the most extreme of 10 000 matrices was retained. For example, using the number of checkerboards as the index, the computer generated one matrix out of 10 000 that had 98 species pairs in perfect checkerboards. The average number of checkerboards for all the simulated matrices was only 89.73. However, when this extreme matrix was then tested with the *C* score and COMBO, the patterns for these indices were nonsignificant. The

TABLE 5. Extreme matrix analysis.

Extreme matrix tested with:	Extreme matrix generated for:		
	CHECKER	*C* score	COMBO
CHECKER	**98**	86	91
	[89.73]	[89.68]	[89.18]
	(0.0001)	(0.986)	(0.258)
C score	2.65	**3.98**	3.79
	[2.73]	**[2.77]**	[2.77]
	(0.670)	**(0.0001)**	(0.001)
COMBO	17	14	**12**
	[15.50]	[15.28]	**[15.23]**
	(0.987)	(0.219)	**(0.0001)**

Notes: Each column represents a different co-occurrence index that was used to generate an extreme matrix with SIM9. Each row represents a co-occurrence index that was used to test the matrix generated for each column. The first entry is the observed co-occurrence index. The entry in square brackets is the expected value of the index from 1000 simulations (SIM9). The entry in parentheses is the tail probability for this pattern. Diagonal entries (in boldface) represent the original extreme matrix that was generated by 10 000 random transpositions using SIM9.

TABLE 6. Results of null model analyses of the West Indian finches co-occurrence matrix (Fig. 2).

	CHECKER	*C* score	*V* ratio	COMBO
Observed	91	3.79	1.23	10
SIM1	**71.23**	7.21	0.69	**18.56**
	(0.001)	(1.000)	(0.957)	(, **0.001**)
SIM2	94.86	**2.93**	0.76	**17.43**
	(0.873)	(, **0.001**)	(0.932)	(, **0.001**)
SIM3	**71.66**	7.30	0.76	**18.75**
	(, **0.001**)	(1.000)	(1.000)	(, **0.001**)
SIM4	90.10	**2.52**	1.14	**15.91**
	(0.552)	(, **0.001**)	(0.622)	(, **0.001**)
SIM5	**53.09**	5.76	1.08	**17.48**
	(0.008)	(0.983)	(0.914)	(, **0.001**)
SIM6	**61.85**	6.57	1.28	**17.94**
	(, **0.001**)	(1.000)	(0.520)	(, **0.001**)
SIM7	**53.71**	5.74	0.78	**17.39**
	(0.007)	(0.974)	(0.915)	(, **0.001**)
SIM8	**51.67**	5.11	1.25	**17.16**
	(0.004)	(0.920)	(0.585)	**(0.002)**
SIM9	89.30	**2.75**	n.a.	**15.12**
	(0.239)	(, **0.001**)		**(0.001)**

Notes: Each column is a different co-occurrence index and each row is a different simulation algorithm (see Tables 1 and 2 for details). The first row is the observed co-occurrence index for the matrix in Fig. 2. The other rows give the expected index, averaged over 1000 simulations of the algorithm. The *P* value for a one-tailed test is given in parentheses. Tail probabilities , 0.05 are indicated in boldface. The *V* ratio cannot be used with SIM9 (n.a.) because it maintains row and column sums (see the discussion in *The variance ratio as an index of nonrandomness* for details).

TABLE 7. Results of null model analyses of Virginia ants co-occurrence matrix (Fig. 3). Entries are as in Table 6.

	CHECKER	C score	V ratio	COMBO
Observed	48	2.07	0.98	10
SIM1	**32.35**	3.31	0.70	11.24
	(0.050)	(0.993)	(0.865)	(0.230)
SIM2	49.58	2.15	0.70	11.39
	(0.860)	(0.682)	(0.878)	(0.195)
SIM3	**30.04**	3.04	0.98	10.81
	(0.014)	(0.994)	(0.569)	(0.353)
SIM4	**41.89**	**1.67**	**1.71**	9.40
	(0.014)	**(0.007)**	**(0.034)**	(0.861)
SIM5	**23.52**	3.35	1.03	10.19
	(0.003)	(0.988)	(0.148)	(0.608)
SIM6	**26.05**	2.39	**1.73**	9.45
	(0.001)	(0.704)	**(0.029)**	(0.859)
SIM7	**24.92**	3.83	0.71	10.37
	(0.012)	(0.993)	(0.852)	(0.559)
SIM8	**20.37**	2.56	**1.72**	9.23
	(, 0.001)	(0.767)	**(0.033)**	(0.888)
SIM9	47.18	2.00	n.a.	10.71
	(0.175)	(0.199)		(0.406)

Table 7 illustrates the results of testing the Virginia ant matrix against all nine algorithms and four co-occurrence indices. In contrast to the results of the West Indian finch analysis, few of these tests are statistically significant for well-behaved algorithms. Ten species combinations were observed in this matrix, which was not statistically significant for any of the algorithms. There were more checkerboard species pairs (48) than expected compared with SIM1, and SIM3 to SIM8. However, these algorithms are prone to Type I error for this index (Table 1). The C score was significantly greater than expected only when compared to SIM4, which is also prone to Type I error for this index (Table 1). The only evidence for nonrandomness was in the V ratio, which was significantly less than expected for SIM4, SIM6, and SIM8. However, all of these models assume that there is variation in site quality, so that probabilities of occurrence are proportional to species richness totals for each site. Thus, "empty sites" in the original matrix will not be filled in these simulations. A more appropriate null model for the ant data would be SIM2, in which species occurrences are fixed and all sites are equiprobable. None of the co-occurrence indices showed a significant pattern with SIM2. Overall, there is little evidence that the small-scale co-occurrence of ant foragers in pitfall traps was nonrandom.

DISCUSSION

Choosing the right algorithm

Although all nine algorithms are logically plausible, the analyses reveal that many of the algorithms would be unacceptable choices because they are very prone to Type I error, and would be expected to produce false positives with data sets that have little or no real structure. However, three algorithms consistently had low probabilities of Type I errors when compared with a variety of random data matrices: SIM2, SIM4, and SIM9 (Table 4). These algorithms share in common the property that they all maintain the observed row totals, that is the species occurrence frequencies. The algorithms differ in how the columns (5 sites) are treated. In SIM2, the sites are equiprobable, whereas in SIM4, the probability that a species occurs in a site is proportional to the column total for that site. Finally, SIM9 maintains the observed number of species in a site. Conceptually, these algorithms are satisfying, because they correspond to a colonization model in which species colonize an archipelago randomly with respect to one another. Note that the colonization of each species is not "random" with respect to the sites: occurrence frequencies are maintained for each species, and, in SIM4 and SIM9, differences among islands are maintained. But the species occurrences are random with respect to one another, which is an appropriate null model for detecting patterns caused by species interactions.

Critics have pointed out that extinctions are an important outcome of species interactions, so that incorporating species occurrence frequencies may "smuggle in" species interactions in the null model. Although this may be true, my analysis of Type I errors suggests that allowing species occurrence frequencies to vary may generate false positives in a null model test. This conclusion is reinforced by other debates in the null model literature. For example, Gilpin and Diamond's (1982) null model operates on the same principle as SIM8, which allows species occurrence frequencies to vary. Wilson (1987) showed that this model rejects the null hypothesis for random data sets constructed by the recipe for TEST1, although Gilpin and Diamond (1987) contend that Wilson (1987) did not correctly implement their model.

In an analysis of species co-occurrence as measured by "favored states" analysis, Fox and Brown (1993) used a null model that implicitly assumed species occurrence frequencies were equiprobable. Stone et al. (1996) and Wilson (1995) reanalyzed the data and adjusted species occurrences on the basis of observed frequencies and species geographic ranges. In these reanalyses, the co-occurrence patterns were no longer statistically significant.

Because the co-occurrence tests are very sensitive to variation in species occurrence frequencies, row totals should be preserved as a constraint in the null model. On the other hand, the results were surprisingly insensitive to variation in column totals (5 number of species per site), so this constraint should be modified to reflect sampling methods or variation in site quality. Specifically, SIM9 seems most appropriate for analyzing "island lists," especially for classic archipelago data in which there are strong species–area effects. On the other hand, SIM2 seems most appropriate for analyzing "sample lists," particularly when comparing standardized samples that have been collected in areas

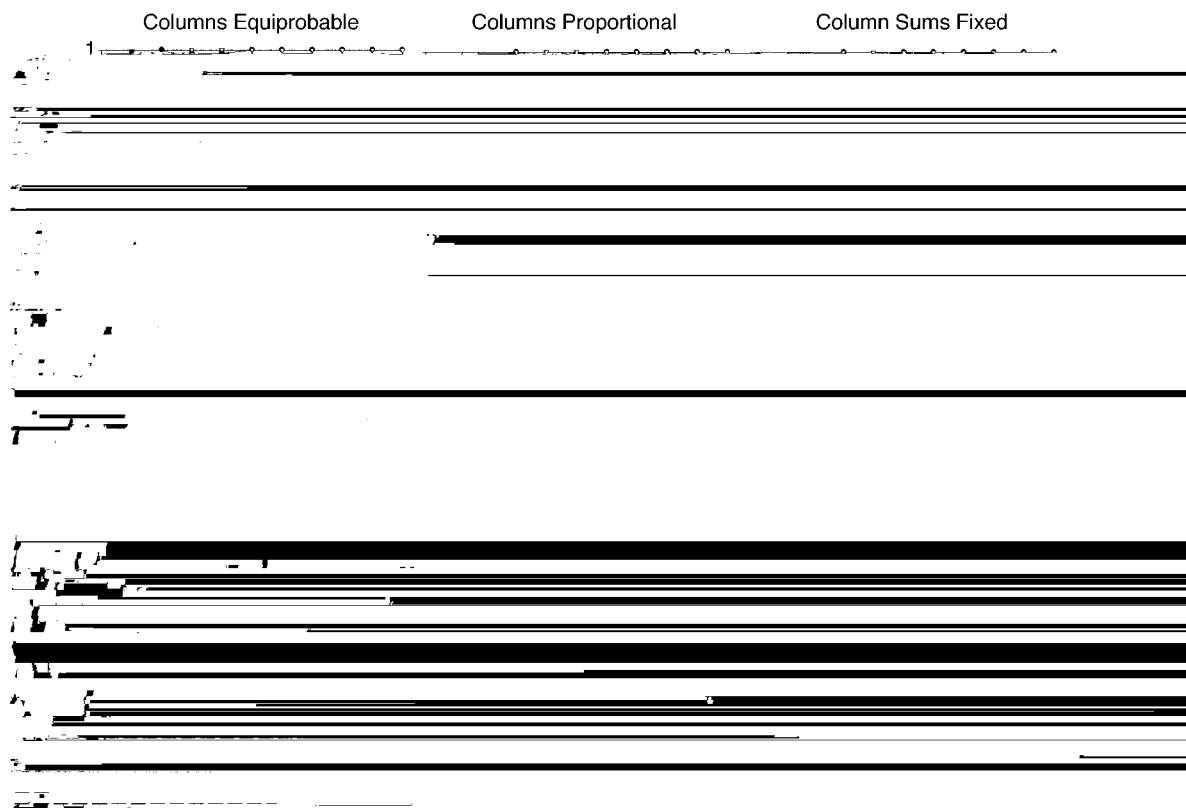Columns Equiprobable   Columns Proportional   Column Sums Fixed

FIG. 6. Type II error tests for SIM1–SIM9. Each panel depicts the four co-occurrence metrics tested against a different simulation algorithm. The x-axis is the noise level, that is, the number of site occurrences that have been randomly transposed within each row of the perfect checkerboard matrix (Fig. 4A). The y-axis is the P value, shown on a log scale, with the 0.05 level indicated by a dashed line. Each point represents the average P value for five independent trials. Key to symbols: open circle 5 C score; solid diamond 5 V ratio; open triangle 5 number of species combinations (COMBO); solid circle 5 number of species pairs forming perfect checkerboards (CHECKER). Compare these curves to the idealized curves in Fig. 5.

of homogenous habitat. SIM4 is somewhat of a hybrid between these two, because it allows column totals to vary, but in proportion to observed totals. However, it may cause the null hypothesis to be incorrectly rejected, especially if used with the C score or CHECKER.

Choosing the right index

The choice of index is not as clear-cut as the choice of which algorithm to use, in part because each index seems to measure a slightly different aspect of species co-occurrence (Table 5). The number of checkerboards (CHECKER) and the number of species combinations (COMBO) are most relevant to the historical development of ideas on community assembly (Diamond 1975). However, both of these indices may cause the null hypothesis to be incorrectly accepted (Fig. 6), because they are sensitive to rearrangements of species occurrence patterns. A change in a single species occurrence can create or destroy a perfect checkerboard, or add or delete a species combination. Consequently, these measures will also be sensitive to measurement error, which may be common in presence–absence matrices.

In contrast, the C score and the V ratio are based on the average co-occurrence and covariance, respectively, of all species pairs. Therefore, minor changes in the data do not affect these indices as much. The C score, in particular, seems relatively insensitive to noise in the data, and can still detect pattern even when ¡ 50% of the species occurrences in a perfect checkerboard matrix have been randomized (Fig. 6). When used with SIM2 or SIM9, the C score has good statistical properties and is not prone to false positives (Table 4). Finally, this index measures the checkerboard pattern of species mutual exclusion that reflects competitive interactions, but is not as restrictive as a count of perfect checkerboard pairs (CHECKER).

The variance ratio as an index of nonrandomness

The behavior of the V ratio is somewhat unusual, and deserves special comment. Of all the co-occurrence indices, it is the one index that is uniquely determined by the row and column totals, and not by the actual co-occurrence pattern itself. For this reason, it cannot be tested with SIM9, which retains row and column totals, and therefore generates no variation in the V ratio. For the V ratio, ''The null hypothesis of no as-

sociation (H_0) states that the sum of the [species'] co-variances is zero'' (Schluter 1984: 999). However, this turns out to be a somewhat different measure of co-occurrence than the C score and CHECKER.

What, precisely, does the V ratio measure? It measures the variability in the number of species per site. In a null community, we would expect the number of species per site to vary because of chance colonization. However, if species richness is regulated because of biological interactions, communities should converge on a relatively constant number of species per site. This is the niche limitation hypothesis of Wilson et al. (1987), which states that the variance in species richness per site should be unusually small if the number of species within a guild is limited by competition (Colwell 1979).

If all the sites have exactly the same number of species, there is no variance among sites, and the observed V ratio is zero. The reason the V ratio detects a highly significant pattern for the matrix in Fig. 4A is not because of the large number of checkerboard arrangements of species, but because each site in the matrix contains exactly 20 species. Thus, the V ratio, used with SIM2 or SIM4, is a useful probe for determining whether species interactions are constraining the number of coexisting species. There is no evidence of this for either the West Indian bird matrix (Table 6) or the Virginia ant matrix (Table 7), because in both of these examples, there is considerable heterogeneity in species richness per site. Variation among sites probably also explains Schluter's (1984) finding that most published co-occurrence matrices exhibit V ratios greater than 1.0.

The importance of row and column totals

All of the algorithms presented in this paper make use of information in the row and column totals to constrain the randomizations. Critics of null models have claimed that this procedure is circular because the marginals themselves reflect competitive interactions (Grant and Abbott 1980, Colwell and Winkler 1984). However, my analyses demonstrate that row and column constraints do not prevent the null model from detecting patterns in nonrandom matrices, even when the pattern has been considerably degraded by adding noise (Fig. 6). Moreover, the use of marginal constraints forms the basis for contingency table analysis (Fienberg 1980), which has been widely used in the analysis of species co-occurrence patterns (Whittam and Siegel-Causey 1981). If one wishes to test the hypothesis that marginal constraints are affected by species interactions, the V ratio, perhaps used with SIM2 or SIM4, would be an appropriate model.

Practical advice for the empiricist

Some ecologists may despair at the results of these analyses. After all, the same data matrix may yield random or highly significant patterns, depending on which algorithm or index is used for analysis (Tables 6 and 7). However, the same troubling result can be obtained from conventional parametric analyses. Data transformations, interaction terms, model structure, and designation of fixed and random factors can generate an equally bewildering diversity of outcomes in a ''standard'' analysis of variance (Scheiner and Gurevitch 1993). Ecologists need to move beyond the idea that there is a single ''one-size-fits-all'' null model that is appropriate. Rather, the null model and index should be chosen based on the kind of data (island lists vs. sample lists) collected and the question being asked. For a preliminary analysis of co-occurrence patterns of island list data, I suggest using the C score with SIM9. This combination is not vulnerable to false positives, has good power in the face of noisy data, and measures a pattern of co-occurrence that would be consistent with competitive exclusion.

But I would also recommend examining the outcome of other models and other indices, as in Tables 6 and 7. There is great value in exploring the results of several null models that incorporate different degrees of randomness. Statistical purists will not approve of this approach because it undercuts the rigorous interpretation of calculated probability values, and because it may tempt ecologists to go on ''fishing expeditions'' and search for an analysis that supports their preconceptions. The advantage of this approach is that it pinpoints how changing the assumptions of the model alters the results, which is an essential comparison for any confrontation of a model with real data (Hilborn and Mangel 1997). Certainly the interpretation of the West Indian finch matrix and the Virginia ant matrix was enhanced by consideration of a variety of null models.

The models presented here are by no means exhaustive, and it is easy to imagine other algorithms that could have been used. Ecologists will continue to develop new kinds of null models that incorporate spatial and temporal variability in populations and communities (Thomson et al. 1996, Roxburgh and Chesson 1998). However, the most important progress in null model analysis will probably come from the analysis of new data sets. Much of the older null model literature is dominated by analysis and reanalysis of published islands lists, such as the West Indian finch matrix (Fig. 2). These second- and third-hand data sets have a number of limitations, including species taxonomy, sample standardization, source pool limits, and geographic variation (Gotelli and Graves 1996). Home-grown data sets, such as the Virginia ant matrix (Fig. 3), may offer the best chance for examining species co-occurrence patterns, because the methods of collection and analysis can be tailored to the questions being asked. Of course, such data sets are more time consuming and costly to obtain than using published island lists, but ultimately, they should be more rewarding for understanding co-occurrence patterns in nature.

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SUPPLEMENTARY MATERIALS

The software utilized in the analysis presented here (EcoSim) is available in ESA's Electronic Data Archive: *Ecological Archives* E081-022. The software may be downloaded at no cost. All of the algorithms described in the paper are included.