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SPECIES CO-OCCURRENCE: A META-ANALYSIS OF J. M. DIAMOND'S ASSEMBLY RULES MODEL

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Abstract. J. M. Diamond's assembly rules model predicts that competitive interactions between species lead to nonrandom co-occurrence patterns. We conducted a meta-analysis of 96 published presence–absence matrices and used a realistic ''null model'' to generate patterns expected in the absence of species interactions. Published matrices were highly nonrandom and matched the predictions of Diamond's model: there were fewer species combinations, more checkerboard species pairs, and less co-occurrence in real matrices than expected by chance. Moreover, nonrandom structure was greater in homeotherm vs. poikilotherm matrices. Although these analyses do not confirm the mechanisms of Diamond's controversial assembly rules model, they do establish that observed co-occurrence in most natural communities is usually less than expected by chance. These results contrast with previous analyses of species co-occurrence patterns and bridge the apparent gap between experimental and correlative studies in community ecology.

Key words: community assembly rules; meta-analysis; null models; presence–absence matrix; species co-occurrence.

INTRODUCTION

A fundamental question in ecology is whether general assembly rules determine the structure of natural communities (Weiher and Keddy 1999). Many types of assembly rules have been described, including constant body-size ratios (Dayan and Simberloff 1994), favored states (Fox and Brown 1993), guild proportionality (Wilson 1989), species nestedness (Patterson and Atmar 1986), and trait–environment associations (Keddy and Weiher 1999). However, the most influential model remains Diamond's (1975) original treatment of community assembly rules (Gotelli 1999).

distributions, and incidence functions. Connor and Simberloff (1979) used a Monte Carlo null model analysis to demonstrate that many of the patterns attributed by Diamond (1975) to interspecific competition could also arise in communities that were assembled by random colonization and were competition-free. These exchanges touched off a debate in community ecology that has continued over the past 25 yr (reviews in Strong et al. 1984, Wiens 1989, Gotelli and Graves 1996, Weiher and Keddy 1999).

The initial debates focused on the statistical issues surrounding null models and potential flaws in the analysis of Connor and Simberloff (Diamond and Gilpin 1982, Gilpin and Diamond 1982, Connor and Simberloff 1983, 1984). More recent studies (Stone and Roberts 1990, Manly 1995, Sanderson et al. 1998) and the availability of software for null model analysis (Gotelli and Entsminger 1999, Patterson 1999, Colwell 1999) have clarified these issues. The statistical properties of many null model algorithms have been studied by evaluating their performance with random matrices and with structured matrices that include stochastic noise (e.g., Kelt et al. 1995, Gotelli et al. 1997, Shenk et al. 1998, Gotelli 2000).

Even with the availability of these improved statistical methods, the generality of Diamond's (1975) assembly rules model remains unknown. Many authors have made broad assertions about the generality (or lack thereof) of assembly rules based on the analysis of a single presence–absence matrix. Much of the debate over assembly rules has rested on the reanalysis of a handful of presence–absence matrices for the birds of island archipelagoes (Gotelli and Graves 1996), such as the Vanuatu (formerly New Hebrides) Islands. In this paper, we use a null model analysis of 96 published presence–absence matrices to test the predictions of Diamond's (1975) assembly rules model. A meta-analysis demonstrates the generality of these patterns and reveals taxon-specific differences in community organization.

METHODS

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fields (0.25 m^2) to large islands in oceanic archipelagoes (2.3 × 10^{10} m^2). The data from each study were organized as a presence–absence matrix in which each row represents a species or taxon and each column represents a site. The entries in the matrix indicate the presence (1) or absence (0) of a particular species in a particular site (Simberloff and Connor 1979).

We used a subset of modified data matrices from those provided by Patterson (1999). Data sets were assembled from original literature citations, according to the following criteria: only taxa described in the original citation that were extant at the time of the collection or census were included; nonnative species were included only when the data were included by the original authors; data sets that included both aquatic and terrestrial taxa were partitioned into two matrices; species occurrences labeled as questionable by the original authors were excluded; the most inclusive data set from overlapping studies was selected; data sets from artificial substrates were excluded; data sets that were partitioned on the basis of habitat types rather than sites were excluded; subspecies were lumped and treated as a single taxon. The original investigators in these studies were usually not addressing whether competition was an important force in structuring communities. Rather, they were seeking to construct species lists for a prescribed taxonomic group. Thus, the data probably do not suffer from a preselection bias towards communities that are structured by competition.

For each matrix, we measured from survey maps, gazetteers, navigational charts, and atlases the following variables: the latitude and longitude of the geographical center of the set of sites, the average area of the censused sites, and the minimum north-south and east-west spans that included all of the sites. Studies were classified according to the biogeographical regions designated by Pielou (1979). Average site area was calculated from data provided in the original papers or from encyclopedias and atlases. Presence–absence matrices and raw data are available from Patterson (1999).

Co-occurrence indices

A major stumbling block to testing Diamond's (1975) model has been the difficulty in quantifying patterns in a presence–absence matrix and relating these patterns to assembly rules. Although Connor and Simberloff (1979) noted that some of Diamond's (1975) rules are tautologies, others can be made operational by using an appropriate co-occurrence index, specifying a priori the pattern expected with Diamond's (1975) model, and comparing the pattern to that generated by a well-tempered null model.

Pielou and Pielou (1968) first introduced the number of species combinations as an index of community structure. This index is directly related to Diamond's (1975:344) first and second assembly rules: ''1. If one considers all the combinations that can be formed from a group of related species, only certain ones of these combinations exist in nature. 2. These permissible combinations resist invaders that would transform them into a forbidden combination.'' If assembly rules 1 and 2 are met, a set of islands or sites should harbor significantly fewer species combinations than expected by chance.

A second useful index is the number of species pairs that never co-occur, forming ''checkerboard'' distributions. This index describes Diamond's (1975:344)

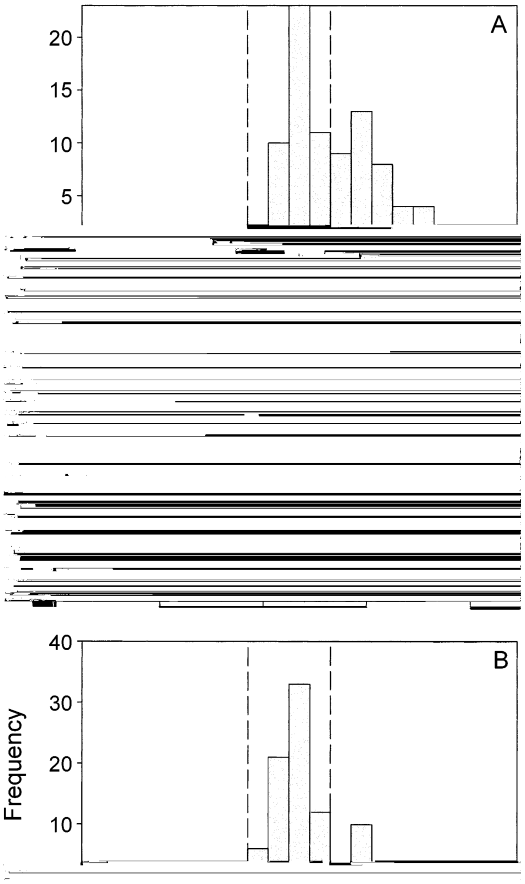

FIG. 1. Frequency histograms for standardized effect sizes measured in presence–absence matrices: (A) *C*

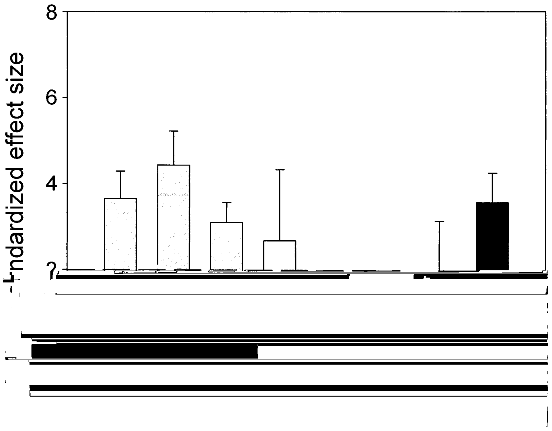

FIG. 2. Effect sizes for the *C* score of different taxonomic groups (means 6 1 SE; $F_{7,87}$ 5 2.20, *P* 5 0.041). The dashed line indicates a standardized effect size of 2.0, which is the approximate 5% significance level. Matrices for homeotherms (gray bars) were significantly more structured than matrices for poikilotherms (open bars; linear contrast $F_{1,87}$ 5 7.70, *P* 5 0.009). Sample sizes were: birds, *N* 5 25; bats, *N* 5 3; mammals, *N* 5 16; ants, *N* 5 3; invertebrates, *N* 5 18; fish, *N* 5 3; herps (reptiles and amphibians), *N* 5 15; plants, *N* 5 13.

deleting outliers and influential points to ensure the stability of the patterns. Finally, we used nonparametric tests to ensure that the patterns were robust to the nonnormality of the data in Fig. 1. Matrix size was a significant predictor of effect size (*P* 5 0.048), because large matrices enhanced the statistical power of the analysis. However, when matrix size was used as a covariate, differences among taxonomic groups were still statistically significant (*P* 5 0.035).

RESULTS

For all three co-occurrence indices, the standardized effect size differed significantly from zero: across the 96 studies, there were fewer species combinations, more species pairs exhibiting perfect checkerboard distributions, and larger *C* scores than expected by chance (Fig. 1). All of these patterns are in the direction predicted by Diamond's (1975) assembly rules model.

We next analyzed in detail the variation in the *C* score. Standardized effect size was not correlated with the latitude (*P* 5 0.544) or longitude (*P* 5 0.904) of species interactions (the ‘‘ghost of competition past’’; Connell 1980, Ricklefs and Schluter 1993).

Gotelli, N. J. 1999. How do communities come together? Science **286**:1684–1685.
Gotelli, N. J. 2000. Null model analysis of species co-oc-