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Original article

Comparison of co-occurrence structure of temperate forest herb-layer communities in 1949 and 2000

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ARTICLE INFO

Article history:

Received 21 September 2007

Accepted 29 June 2008

Published online ■

Keywords:

Assembly rules

Null model

Checkerboard distribution

C-score

Co-occurrence

Species loss

Community structure

Temperate forest

Understory herbs

ABSTRACT

When species presence-absence data are analyzed across a range of sites, many communities show a “checkerboard distribution” in which two or more species do not co-occur despite sharing geographic ranges and habitat requirements. It is not clear how the loss of native species might shift the underlying checkerboard structure. I tracked changes in the incidence of 175 vascular plant species across 59 sites in northern Wisconsin that have declined in species density between 1950 and 2000. Based on C-scores and the number of perfect checkerboard distributions, there was significant co-occurrence structure in both time periods. The nature of that structure depended on the particular null model was constructed. When only row values are fixed, plant species showed greater degrees of co-occurrence than the null model predicted, while fixing both rows and columns yielded less co-occurrence than found in the null model. Changes in species density did not strongly influence co-occurrence patterns, reflecting relative stability of co-occurrence patterns over a 50-year interval. This suggests that minor losses of species will not necessarily lead to fundamental changes in co-occurrence structure.

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1. Introduction

When presence-absence data are analyzed across a range of sites or insular habitats, many communities show non-random patterns of species association, including both nestedness (Wright et al., 1998) and segregated species co-occurrence (Gotelli and McCabe, 2002). The absence of species co-occurrence has been used to infer interspecific competition (Diamond, 1975; Gotelli and Rohde, 2002; Gotelli and Ellison, 2002), and analyses of co-occurrence patterns are being used to study facilitative interactions (Dullinger et al., 2007; Maestre et al., 2008). A number of co-occurrence metrics with accompanying null model randomization tests have now been developed, allowing researchers to evaluate if patterns of

community structure differ from randomly-generated communities in both classic archipelago systems or replicated samples from the same habitat type (Gotelli, 2000). Because multiple deterministic (Schluter, 1984) and stochastic (Bell, 2001; Ulrich, 2004) processes can generate positive or negative associations among species and because associations between species can switch from positive to negative (or vice versa) at different spatial scales (Wiens et al., 1987), researchers cannot naively draw inferences about what processes produce observed co-occurrence structure. Nonetheless, investigating co-occurrence at explicit scales can provide insights into the recurring patterns seen in ecological communities (Gotelli and McCabe, 2002).

Increasingly, anthropogenic forces drive changes in community structure and composition in many regions (Báldi,

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doi:10.1016/j.actao.2008.06.011

2003; Waller and Rooney, 2004). Loss of native species (Balmford et al., 2003; Thomas et al., 2004) and invasion of non-native species (Saunders et al., 2003; Holdaway and Sparrow, 2006) can shift observed patterns of co-occurrence within communities, but it is not clear if the underlying structure of co-occurrence is changing in response to these invasions and extinctions.

In this study I compare measured co-occurrence patterns in temperate forest understory communities at two points in time. My goal is to determine whether these understory communities exhibit a co-occurrence structure, and if so, whether this structure is influenced by species loss. The study relies on data on 175 vascular plant species occurrences in the herbaceous layer (0–2 m), collected in 1949 and again in 2000 from 59 forest stands in northern Wisconsin. Analyzing these data, Rooney et al. (2004a) found that the mean number of species per 20 m² per site declined significantly from 24.9 to 21.5 species. Four invasive species appeared at sites after the 1949 survey, but without exception they were numerically uncommon in 2000 (Rooney et al., 2004b). Using null model analysis of community structure (Gotelli and Graves, 1996), I determine whether the co-occurrence structure of the vascular plants in the herbaceous layer exhibit segregation or aggregation (less or more co-occurrence than would be expected due to chance, respectively). I also test to see whether co-occurrence patterns have changed between sampling periods, and specifically assess whether changes in species density at a site through time affect shifts in co-occurrence patterns.

2. Materials and methods

2.1. Data sources

Between 1942 and 1956, Professor John Curtis and his students at the University of Wisconsin surveyed the state's vegetation. This culminated in a statewide description of plant community composition and vegetation-environment relationships (Curtis, 1959). In 2000–2001, 62 of these sites located in northern mesic forest communities were resampled (Rooney et al., 2004a). During both time periods, all vascular herbs and shrubs were sampled using 1-m² quadrats. Quadrats contained an average of five species in both time periods.

Field survey methodology between the two time periods differed but provided comparable data. In the 1940s and 1950s, Curtis and his students chose an initial sampling point randomly but at least 30 m from a forest edge. From this point, they sampled the composition, density, and basal area of canopy trees using the random pairs at 20 points spaced evenly along a square U-shaped transect (mean distance 6.5 m). At each point, they also recorded the presence/absence of all herbs, shrubs, and tree seedlings within a 1-m² quadrat. The 20 points and quadrats sampled per stand characterize the vegetation of approximately 0.25 ha. In 2000–2001, researchers relocated and resurveyed forest understory communities in these stands using similar but more intensive methods. In each stand, three 20 × 20-m plots were established at a random position and orientation

starting 50 m from the edge. The presence of all vascular plants <2.5 cm DBH in each of 120 one m² quadrats distributed along six 1 × 20 m strip transects located along the first and second sides of each plot. This resembled the original 1950 survey in characterizing approximately 0.25 ha of forest. For more information on sampling procedures, see Rooney et al. (2004a).

I evaluated species co-occurrence in quadrats within each of 59 sites during both time periods. (Three of the original 62 sites were excluded because they were unusually species poor, with the majority of quadrats examined being empty.) To standardize sampling efforts between time periods, a subset of 20 quadrats spaced at 6 m intervals from the 2000 to 2001 dataset were selected. This matches the extent of the 1950 sample while minimizing the any spatial autocorrelation of plant species occurrence. For each site in each time period, data were represented in a presence-absence matrix, with rows containing species, and columns representing quadrats.

2.2. Quantifying co-occurrence

Co-occurrence was quantified using a three-step process. First there is a computation of quantitative indices of the data matrix that describe the observed co-occurrence patterns at a given site. This is followed by a randomization test to shuffle the observed data matrix 1000 times, with the index recalculated each time. At each site, the observed index was compared to the distribution of simulated indices. Co-occurrence patterns were considered statistically significant if the observed index was significantly larger or smaller than 95% of the simulated indices. In the final step, meta-analysis synthesized patterns across all sites. A standardized effect size was calculated for each site, thus permitting direct comparisons among sites and between years.

I computed two indices of species co-occurrence patterns that quantified checkerboard distributions in different ways. The checkerboard score, or C-score (Stone and Roberts, 1990) measures the average number of checkerboard “units” for each species pair. A checkerboard unit is a 2 × 2 submatrix for two species and two quadrats, in which presence-absence patterns are either 10/01 or 01/10. For each species pair, the C-score was calculated as $(C_i - M_{ij})(C_j - M_{ij})$ where C_i and C_j were the number of occurrences, or row totals, of species i and j , respectively, and M_{ij} is the number of quadrats that contained both species. The observed C-score for a site was calculated as the sum of all C-scores divided by $(S)(S - 1)/2$, where S was the number of species present at the site.

I also calculated the number of species pairs showing a perfect checkerboard distribution at each site (Diamond, 1975). When two species are never present in the same sample unit at a given site, they form a perfect checkerboard distribution. The perfect checkerboard distribution is the sum of all such species pairs at a site, and ranges in value from zero to a maximum value of $(S)(S - 1)/2$. Both metrics are related. For a given species pair, the C-score measures the tendency of species to form checkerboards, whereas the perfect checkerboard distribution measures in absolute terms if species pairs form a perfect checkerboard distribution at the site (Gotelli, 2000).

2.3. Generating random communities

I computed observed and simulated values for the C-score and perfect checkerboard distribution using ECOSIM v. 7.0 software (Gotelli and Entsminger, 2004). For each observed co-occurrence statistic, two procedures were used to generate the null model. In the first procedure, the randomization algorithm allowed the number of species present per quadrat to vary, but the number of quadrats occupied by species i remained constant. In model terms, marginal sums for rows were fixed, while columns were equiprobable (the “fixed-equiprobable” algorithm). Gotelli (2000) recommends this algorithm when analyzing samples collected in areas of homogenous habitat. This null model generates random communities in which all quadrats are equally suitable for all species. Sometimes the fixed-equiprobable algorithm produced empty columns, reflecting quadrats with no species. As this is biologically-realistic, such degenerate matrices were retained when computing simulated C-scores and perfect checkerboard distributions indices for each site.

In the second procedure, the randomization algorithm fixed the number of quadrats occupied by species i and the number of species present in quadrat j , based on the structure of the observed data matrix. This null model generates random communities in which quadrats differ in the number of species they can support, based on the observed number of species per quadrat. The distribution of values generated by this null model is different than the distribution generated by the fixed-equiprobable algorithm, because the underlying question being addressed is slightly different. The fixed-equiprobable algorithm allows us to examine co-occurrence patterns in space, whereas this more constrained model allows for the examination of co-occurrence patterns based on the known differences in species density among quadrats. Connor and Simberloff (1979) proposed these constraints for analyzing co-occurrence patterns in archipelago systems, and Gotelli and McCabe (2002) used this procedure in their meta-analysis of co-occurrence patterns. This is denoted as the rows and columns fixed, or “fixed-fixed” algorithm in this paper. Following Gotelli and McCabe (2002), I reshuffled these random matrices using the sequential swap procedure (Gotelli, 2000; Gotelli and Entsminger, 2002). This method of randomization has been criticized for being too conservative (Miklós and Podani, 2004), although further research revealed that the bias is small (Lehsten and Harmand, 2006).

For each site ($n = 59$), each time period ($n = 2$), each algorithm ($n = 2$), and each co-occurrence index ($n = 2$), I generated 1000 random matrices by reshuffling the matrix elements, recording the co-occurrence index value for each. Observed C-scores and perfect checkerboard distributions were compared to the scores of the 1000 randomized matrices. Statistical significance was determined using a randomization test, in which observed index was considered significant when it was greater than (segregation) or less than (aggregation) 95% of the randomly-generated indices.

I assessed the overall deviation from expected C-scores and perfect checkerboard distributions values by computing a standard effect size (SES) for each matrix (Gurevitch et al., 1992; Sanders et al., 2003). The SES measures the number of

standard deviations between the observed and expected value. It takes the form:

$$SES = (X_{\text{obs}} - X_{\text{exp}}) / SD_{\text{exp}}$$

where X_{obs} is the observed value of the C-score or perfect checkerboard distribution, X_{exp} is the mean value of the C-score or perfect checkerboard distribution of the 1000 randomized matrices, and SD_{exp} is the standard deviation of the distribution generated by the randomization procedure. A SES is computed for all 59 sites for each co-occurrence index in each time period for both algorithms. Under the null hypothesis, the sum of the SES for C-scores and perfect checkerboard distributions would equal zero, as SES can take both positive and negative values. If a 95% confidence interval of the sum of observed SES values overlaps 0, there is no statistically significant difference between observed and simulated values (Gurevitch et al., 1992).

2.4. Stability of co-occurrence through time

To determine if co-occurrence patterns remained stable through time, I compared the distribution of SES values of C-scores and perfect checkerboard distributions observed in 1950 and 2000 using Kolmogorov-Smirnov two sample tests (KS test). This non-parametric test is used to determine if the observed distribution of C-score and perfect checkerboard distribution SES values in 1950 and 2000 are drawn from the same underlying distribution. Since the fixed-equiprobable and fixed-fixed algorithms produce different SES values, one KS test was calculated for each, totaling four tests.

To examine how species density might influence co-occurrence patterns, I computed Spearman rank correlations relating species density (i.e. the number of species encountered in 20 quadrats) to the SES of the C-score and perfect checkerboard distribution values within sites for each time period. I also examined the Spearman rank correlation across sites between the change in the SES of the C-score (or perfect checkerboard distribution value) and the change in species density over time.

3. Results

Within individual sites (n species \times 20 quadrats), co-occurrence patterns are statistically significant at only a fraction of the sites in both time periods and for both co-occurrence metrics and null model algorithms (Fig. 1). Different null models yielded quite different patterns. When only the number of species occurrences was fixed (the fixed-equiprobable algorithm), both C-scores and the number of perfect checkerboard distributions revealed species aggregations at 20–36% of the sites in both time periods (Fig. 1A,B). When both the number of species occurrences and the number of species per quadrat were fixed (the fixed-fixed algorithm), less structure was evident, with 0–14% of the sites showing aggregation and 3–20% showing segregation (Fig. 1C,D). At a fraction of sites, there were fewer species pairs forming a perfect checkerboard distribution than would be expected due to chance, indicating aggregation. This was

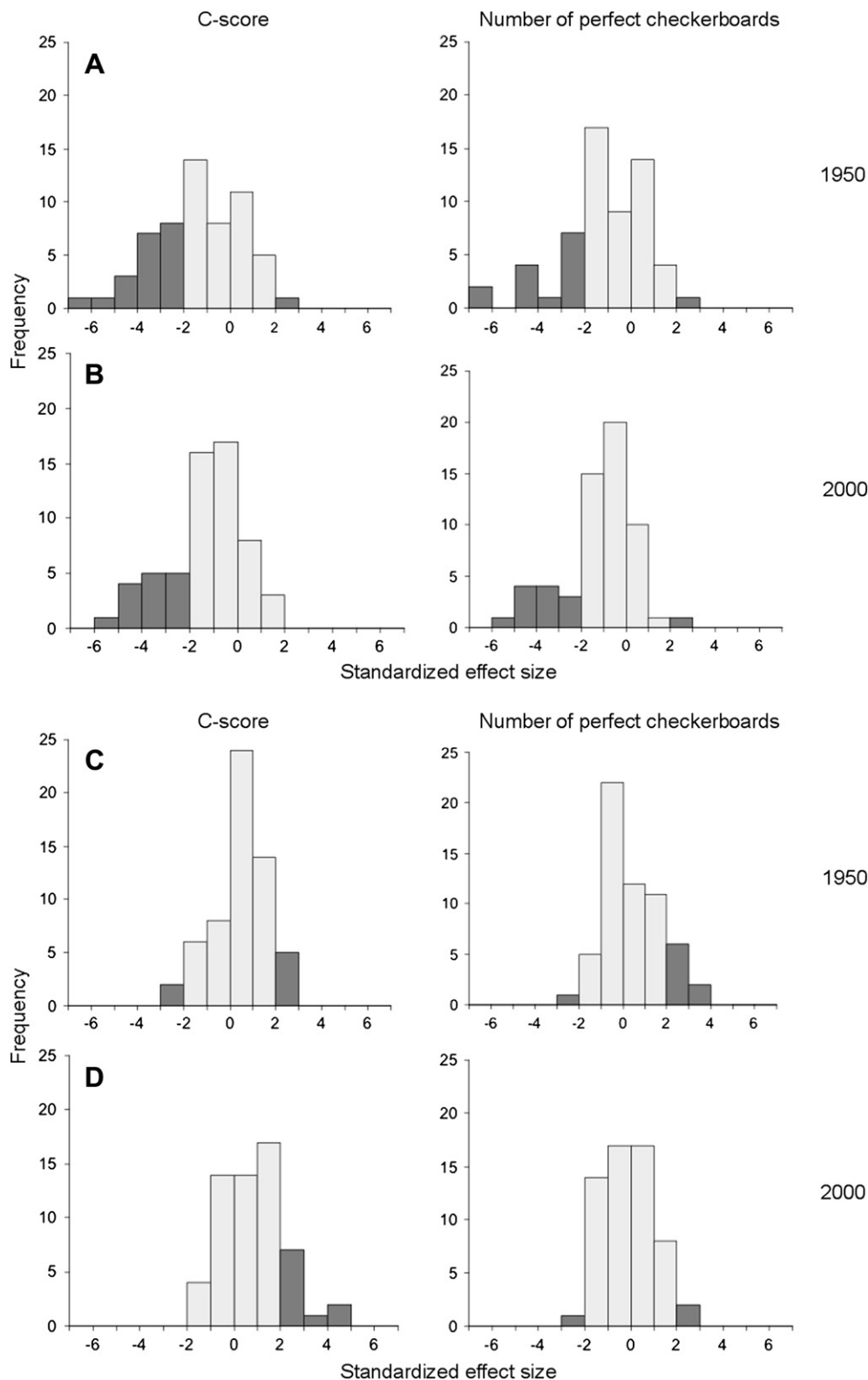


Fig. 1 – Modality of standard effect size (SES) across sites of C-scores and perfect checkerboard distributions based on the fixed-equiprobable null model in (A) 1950 and (B) 2000, and the fixed-fixed null model in (C) 1950 and (D) 2000. Light bars are within ± 2 standard deviations, the boundaries for statistically-significant patterns. Dark bars represent communities with statistically significant structure.

true under both null models, although the fixed-equiprobable algorithm produced aggregation at more sites than the fixed-fixed algorithm did (Fig. 1) as expected, given the lack of constraints on species number per quadrat.

While the majority of the observed communities did not exhibit significant co-occurrence structure, data combined across all sites revealed strong patterns. As before, analyses based on more highly constrained fixed-fixed model demonstrated segregation, whereas analyses based on the fixed-equiprobable algorithm suggested overall aggregation (Fig. 2).

While individual site SES values varied through time, the overall distributions of SES's for C-scores and perfect checkerboard distributions did not shift significantly between 1950 and 2000 ($P > 0.25$ for both models and time periods, according to Kolmogorov-Smirnov two sample tests). In 1950, the SES of C-scores computed under the fixed-fixed model declined with increasing species density, reflecting reduced species segregation when species densities were high. This trend was not present in 2000, nor was there any clear relationship between the SES of C-scores and species density under the fixed-equiprobable algorithm (Table 1). Analysis of the SES of perfect checkerboard distributions computed under the fixed-equiprobable model increased with increasing species density, indicating less aggregation at higher species densities. Strangely, this completely reversed in 2000, as there was more aggregation at higher species densities. In both cases, the result was not particularly strong ($P = 0.04$). Likewise, no relationships between the SES of perfect checkerboard distributions computed under the fixed-fixed were evident in either time period (Table 1).

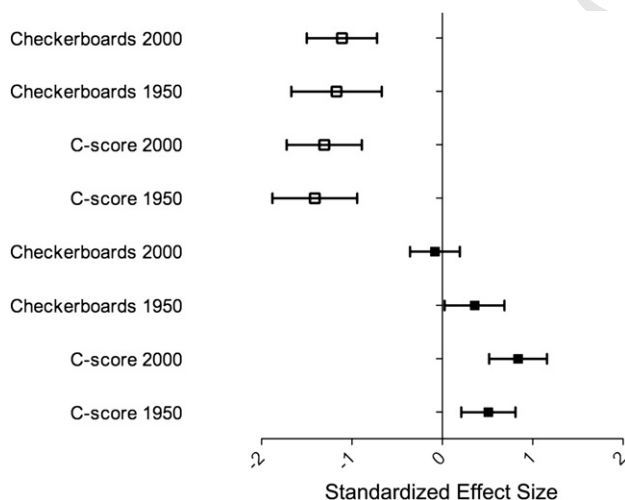


Fig. 2 – Meta-analysis of C-scores and the number of perfect checkerboard distributions (“checkerboards”) across 59 sites and two time periods generated by the fixed-equiprobable (open squares) and the fixed-fixed algorithms (solid squares), represented using the standardized effect size (SES). Vertical lines represent 95% confidence intervals. Values above zero indicate segregation, and values below indicate aggregation. With the exception of the number of perfect checkerboards in 2000 generated by the fixed-fixed algorithm, SES values do not overlap zero, indicating statistically-significant patterns.

Fifty-year shifts in the SES of C-scores within sites did not vary with changes in species density at these sites (Table 1). In contrast, the SES of the number of perfect checkerboard distributions under the fixed-fixed model decreased somewhat with decreasing species density, suggesting a trend towards aggregation (Table 1).

4. Discussion

This study characterized vascular plant co-occurrence patterns in forest understory communities, and asked whether species loss over 50 years influences these species-co-occurrence patterns. Several types of community structure, including rank-abundance patterns (Rooney and Dress, 1997; Rooney and Waller, 2003), nested subset structures (Báldi, 2003; Feely, 2003), and species-area relationships (Gonzalez, 2000; Collins et al., 2002; Ulrich and Buszko, 2003) can be affected by species loss. This study has provided insight into how temperate forest understory communities are structured, how stable this structure is through time, and whether continued species loss will likely further influence this structure.

One striking feature of this study was a change in the null model constraints resulted in the pattern of co-occurrence changing from aggregation to segregation. This could be interpreted as a non-robust biological pattern. This is possible, but unlikely for two reasons. The first is the general congruence of each measure of co-occurrence for a given model constraint. It seems unlikely that both measures would give similar sets of results if there was in fact no underlying pattern.

The second reason relates to the assumptions underlying each null model. Any change in the rules for constructing null communities effectively changes the null hypothesis. The fixed-equiprobable randomization procedure allocated species equiprobably among quadrats within sites. As a result, the mean and variance of species per quadrat was solely a stochastic function of the abundance of each species in the source pool. All quadrats were considered equal in their ability to support each species. In real communities, small-scale variation in environmental conditions (e.g. shade, soil organic matter, patchy distributions of below-ground mutualists or pathogens) could cause some quadrats to support more or fewer species than another, creating the patchiness actually observed in forest herb and shrub layers. Such variation in environmental factors most likely accounted for the apparent aggregation observed under the constraints of the fixed-equiprobable model. When applied to plant communities, the fixed-equiprobable randomization procedure tests whether species are aggregated or segregated within sampling units, and this does not necessarily provide insight into underlying species interactions.

In contrast, the fixed-fixed procedure tests whether species are aggregated or segregated relative to the observed distribution of species among quadrats. In other words, the mean and variance of species per quadrat was not determined by a stochastic function, but from the data themselves. By relaxing the assumption of all quadrats being equally suitable for each species, the fixed-fixed algorithm generated a different null hypothesis than that generated by

Table 1 – Spearman rank correlations between co-occurrence indices and species density per 20-m² in 1950, 2000, and the change in species density (Δ density) per 20-m², $\ln(S_{1950}/S_{2000})$

Test	Algorithm	Species density per 20-m ²		Δ density
		1950	2000	
C-score	Fixed–equiprobable	0.06	–0.17	–0.16
Checkerboard Pairs	Fixed–equiprobable	0.27*	–0.27*	–0.04
C-score	Fixed–fixed	–0.26*	0.14	0.01
Checkerboard Pairs	Fixed–fixed	0.03	0.19	0.34**

* $P \leq 0.05$; ** $P \leq 0.01$.

fixed–equiprobable. I concur with Gotelli's (2000) recommendation that the fixed–equiprobable algorithm is useful for comparing standardized samples collected in a homogenous habitat, but only insofar as that "standardized sample" is equally suitable for all species. While samples from a plankton net drag can provide such standardization, vegetation quadrats probably cannot under most circumstances. The fixed–fixed algorithm appears more appropriate for analyzing co-occurrence patterns among forest herbs.

When analyses from individual sites across all sites were combined via the analysis of standard effect sizes, spatially aggregated co-occurrence patterns under the fixed–equiprobable model and significant segregation under the fixed–fixed model were observed (except for perfect checkerboard distribution in 2000). These findings mirror the recent meta-analysis by Gotelli and McCabe (2002), who used C-scores and the fixed–fixed constraint. They also found fewer species co-occurring than expected by chance despite the fact that individual data sets often lacked statistical significance. Because the C-score measures the degree of checkerboardness rather than the presence perfect checkerboard distributions, it is less sensitive to noise in the data (Gotelli, 2000) and may more reliably detect co-occurrence patterns than the perfect checkerboard distribution under these conditions.

The Kolmogorov–Smirnov tests indicated no significant shift in the SES distributions of C-scores or perfect checkerboard distributions through time, despite net species losses at most sites. However, species losses at most sites were relatively minor, on the order of 15% (Rooney et al., 2004a), so it is not clear if this pattern would persist at higher levels of species loss or following the invasion of a competitively-superior species (see Sanders et al., 2003). Relationships between co-occurrence patterns and species density were weak and variable in both time periods (Table 1). Likewise, species losses tended not to influence co-occurrence patterns.

Significant community structuring exists in the temperate forest herbaceous layer of Wisconsin's mixed coniferous–deciduous forests. The most important finding of this study is the relative stability of co-occurrence patterns over a 50-year interval, even though sites lost species. This suggests that minor losses of species will not necessarily lead to fundamental changes in co-occurrence structure. However, biodiversity loss is an ongoing process in plant communities (Waller and Rooney, 2004). Using this and other baselines, future researchers should test to see whether larger species losses than observed here do lead to changes in community structure. If so, then mounting species losses could trigger community disassembly.

Acknowledgements

I thank many landowners for letting us sample their lands, including the U.S. Forest Service, Wisconsin Department of Natural Resources, Menominee Nation, Lac du Flambeau Band of Lake Superior Ojibwe, Dairymen's Inc., and many private landowners. S. Wiegmann, D. Rogers, J. Crants, M. Leahy, S. Poulos, A. Kennedy, B. Holtzman, and M. Suidan provided assistance in the field, and many of John Curtis' students and colleagues, especially Ed Beals, Grant Cottam, Orié Loucks, and Jim Habeck for details about the 1950 surveys. Trout Lake Station provided housing during portions of this study. D. Waller, F. Maestre and an anonymous reviewer critiqued earlier versions of this study. Financial support comes from NSF DEB 9974041 and 0236333, and NRI-CSREES-USDA 2003-35320-13584.

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