Biotic Impoverishment and Homogenization in Unfragmented Forest Understory Communities

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Abstract: *Ecological change is often hard to document because of a lack of reliable baseline data. Several recent then-versus-now surveys of temperate forest and grassland communities demonstrate losses of local plant species, but most are based on data from a single site. We resurveyed understory communities in 62 upland forest stands in northern Wisconsin (U.S.A.) for which quantitative baseline data exist from 50 years ago. These stands are within a largely unfragmented region but vary in species composition and successional stage. We collected data on changes in (1) total and native species richness, (2) the ratio of exotic to native species, (3) the relative abundance of habitat generalists, and (4) community similarity among sites. We also compared how these rates of change varied over time. Over the past 50 years, native species density declined an average of 18.5% at the 20-*m^2 *scale, whereas the ratio of exotic species to native species increased at 80% of all sites. Habitat generalists increased, and habitat specialists declined, accounting in part for an 8.7% rise in average similarity in species composition among sites. Most of these changes cannot be related to succession, habitat loss, or invasion by exotic species. Areas without deer hunting showed the greatest declines in native species density, with parks and research natural areas faring no better than unprotected stands. Animal-pollinated and animal-dispersed species also declined, particularly at unhunted sites. These results demonstrate the power of quantitative multistand data for assessing ecological change and identify overabundant deer as a key driver of community change. Because maintaining forest habitats alone fails to preserve plant diversity at local scales, local biotic simplification seems likely to continue in the region unless active efforts are taken to protect diversity.*

Key Words: exotic species, habitat specialist, protected area, species loss, succession, white-tailed deer

Empobrecimiento Biótico y Homogenización en Comunidades de Sotobosque en Bosques No Fragmentados

Resumen: *El cambio ecológico es difícil de documentar debido a la falta de datos básicos confiables. Varios muestreos recientes de comunidades de pastizales y bosques templados que comparan datos históricos con datos actuales demuestran la pérdida de especies locales de plantas, pero la mayoría se basan en datos de un solo sitio. Muestreamos comunidades de sotobosque en 62 bosques en Wisconsin (E. U. A.) para los que existen datos cuantitativos básicos desde hace 50 años. Estos bosques están en una región mayormente no fragmentada pero varían en la composición de especies y etapa sucesional. Recopilamos datos sobre cambios en (1) la riqueza de especies totales y nativas, (2) la proporción de especies exóticas - nativas; (3) la abundancia relativa de generalistas de hábitat y (4) la similitud de la comunidad entre sitios. También comparamos la variación de estas tasas de cambio en el tiempo. En los últimos 50 años, la densidad de especies nativas disminuyó 18.5% en promedio en la escala de 20* m^2*, mientras que la proporción de especies nativas-exóticas aumentó en 80% de los sitios. Los generalistas de hábitat incrementaron y los especialistas de hábitat decrecieron, lo que explica en parte el incremento de 8.7% en promedio de similitud en la composición de especies entre sitios. La mayoría de estos cambios no se pueden relacionar con la sucesión, la pérdida de hábitat o la invasión por especies exóticas. Las áreas sin cacería de venados mostraron las mayores declinaciones en la densidad de especies nativas, los parques y áreas naturales de investigación no estuvieron en mejores condiciones que los*

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bosques no protegidos. Las especies polinizadas por animales y las dispersadas por animales también declinaron, particularmente en sitios sin cacería. Estos resultados demuestran el poder de los datos cuantitativos multibosque para evaluar cambios ecológicos e implicar a la sobre abundancia de venados como el principal factor de cambio en la comunidad. Debido a que sólo el mantenimiento de los hábitats de bosque no preserva la diversidad de plantas a escala local, parece que la simplificación biótica local continuará en la región a menos que se realicen esfuerzos activos para proteger la diversidad.

Palabras Clave: áreas protegidas, especialistas de hábitat, especies exóticas, pérdida de especies, sucesión, venado de cola blanca

Introduction

The sixth mass extinction event is underway, driven in part by widespread habitat loss and degradation (Smith et al. 1993; Pimm et al. 1995). Current and future losses (the "extinction debt"; Tilman et al. 1994) are often inferred based on the species-area relationship. The species-area curve, however, is an incomplete predictor of species loss because it fails to account for the effects of invasive species, pollution, overexploitation, altered biotic interactions, and other kinds of ecological degradation (Wilcove et al. 1998; Sakai et al. 2001; Rosser & Mainka 2002). Population extinctions often result from degradation of habitats that otherwise appear intact. If unabated, this cryptic degradation will ultimately lead to the endangerment and, eventually, the extinction of many species (Hobbs & Mooney 1998). Within habitats, community impoverishment occurs as native species decline and invasive species become more abundant (McKinney & Lockwood 1999).

To accurately evaluate long-term shifts in community composition, one must match data on current conditions with reliable data on historical conditions or must conduct long-term monitoring programs. Although there are examples of multidecade programs (e.g., the Rothamsted Insect Survey, the North American Breeding Bird Survey, and the British Ornithological Trust Surveys), their rarity makes most current ecological change invisible (Magnuson 1990). In the cases where reliable baseline data exist, temperate native plant diversity appears to be declining locally with accompanying increases in exotic species (Kwiatkowska 1994; Robinson et al. 1994; Drayton & Primack 1996; Leach & Givnish 1996; Fischer & Stöcklin 1997; Rooney & Dress 1997; Duncan & Young 2000). Such local losses in plant species richness could imply systematic regional threats to plant diversity if similar patterns of decline occur across sites. However, most studies only compare lists of species present at one site during two sampling periods. Without site replication and species abundance data, our ability to infer systematic shifts in community structure and consequent regional threats to diversity is limited.

Comprehensive ecological surveys conducted by John Curtis and colleagues 50 years ago in Wisconsin (Curtis 1959) provide a unique opportunity to evaluate both local and regional shifts in plant species abundance and community structure. In a previous study, Leach and Givnish (1996) resurveyed 54 prairie remnants in southern Wisconsin. They found systematic species losses of 6–65%, with the highest losses occurring in sites lacking regular fires and that had been invaded by woody shrubs.

Here, we used the baseline data compiled by Curtis (1959) and colleagues to investigate understory changes in the upland forests of northern Wisconsin. This region maintains primarily unfragmented forest conditions (Barry et al. 2001; Fig. 1). We resurveyed 62 upland forest stands approximately 50 years after the initial Curtis surveys. Our primary objective was to assess shifts in understory community composition and, in particular, to determine if biotic impoverishment is occurring. We hypothesized declines in local native species richness and increases in exotic species. We also predicted that communities are becoming dominated by a few habitat generalists, resulting in fewer compositional differences among sites ("biotic homogenization"; McKinney & Lockwood 1999).

Our second goal was to identify possible mechanisms for the changes we observed. We therefore evaluated the degree to which successional changes and states or differences in stand protection or local deer management can account for the shifts in community composition observed. We also compared particular functional groups of species to see whether some were more likely to decline and whether these declines differed among sites that differ in management or successional changes. To this end, we identified pollination and dispersal guilds (sensu Root 1967) and asked how animal-pollinated and -dispersed species fared relative to abiotically pollinated species and species that rely on wind or gravity for dispersal.

Methods

Study Area

We conducted this research in the northern highlands plateau of northern Wisconsin and the extreme western portion of Michigan's Upper Peninsula (Fig. 1). This

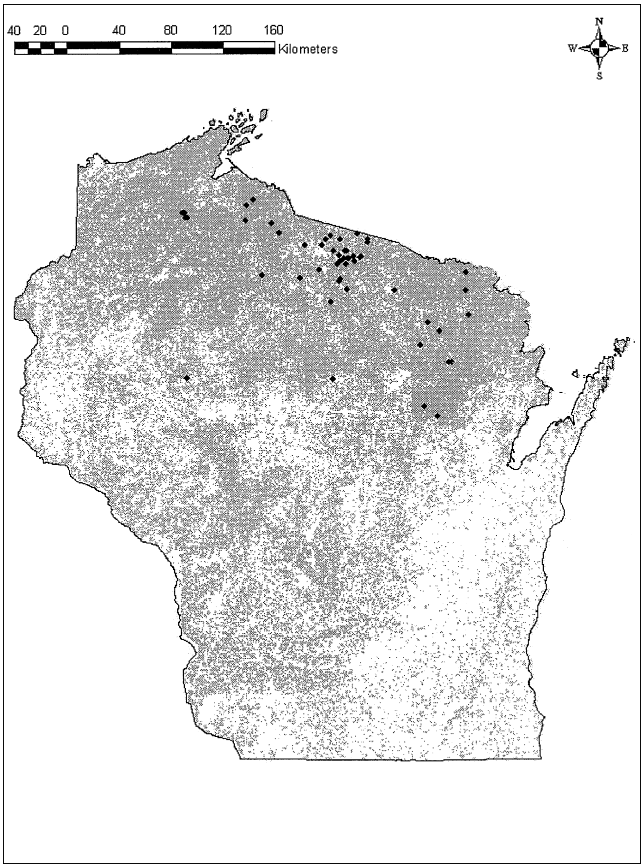

Figure 1. Location of study sites in Wisconsin. Shaded areas indicate forest and forested wetlands, have a 30-m resolution, and are derived from the WISCLAND data set. Six sites in adjacent upper Michigan are not shown.

plateau is 520–570 m above sea level. The climate is continental (average minimum temperature is −20° C in winter and average maximum is 32° C in summer). The region receives an average of 550–780 mm of precipitation annually (Albert 1995). The Precambrian bedrock is covered by glacial landforms, including ground moraines and outwash plains. The Spodosol soils vary from loams to loamy sands (Albert 1995).

Prior to European settlement, the northern highlands were extensively forested, mostly with mature stands (Curtis 1959). By the 1920s, more than 95% of the forest had been cleared for lumber (Whitney 1994). All large mammalian carnivores and most large ungulate species were extirpated from the region by the early twentieth century. Because of replanting, natural regeneration, and abandoned agricultural activities, forest is the dominant land cover in the region today, covering approximately 70% of the area (Fig. 1). Timber harvest is the dominant land use, and it replaces fire and windthrow as the major disturbance regime in the region (Alverson et al. 1994). Lakes (15%), wetlands (9%), and urban or agricultural land (6%) comprise the remaining landcover types (MacKenzie 1994).

Figure 2. Deer density in the northern Wisconsin deer management unit between 1962 and 1999. Annual population density is based on post-hunt sex-age-kill census statistics compiled by the Wisconsin Department of Natural Resources (1998 and unpublished data). Data were smoothed with a 5-year centered moving average. Arrows indicate the timing of understory surveys.

White-tailed deer (*Odocoileus virginianus*) strongly affect the structure and composition of forest plant and animal communities, making deer overabundance a major conservation issue (Waller & Alverson 1997). Deer were nearly hunted to extinction in the late nineteenth century but rebounded vigorously through the twentieth century (Alverson et al. 1988). The state of Wisconsin began using the age and sex of harvested animals to estimate deer density in the early 1960s (the "sex-age-kill" method; Creed et al. 1984). These data indicate that deer densities in the northern forest region have increased considerably over the last 40 years (Fig. 2).

Historic and Contemporary Field Methods

From 1942 to 1956, the Plant Ecology Laboratory at the University of Wisconsin conducted a statewide vegetation survey to determine the geographical ranges, community composition, and vegetation-environment relationships of plant species (Curtis 1959). Over 1000 terrestrial sites throughout the state were sampled during this period. The criteria for inclusion in Curtis's study were similar for all forest stands sampled. Stands needed to be >6 ha in area, to be uniform in topography, and to exhibit no evidence of domestic grazing. Over half the sites we resurveyed ($n = 38$) showed minimal human intervention in

1950, with only a few large decayed stumps present but no evidence of extensive logging. Other sites were either second-growth forest ($n = 18$), as evidenced by abundant decayed stumps and forked trees, or of fire origin ($n = 6$). We selected this biased set of stands to represent presettlement forest conditions.

Curtis and colleagues sampled stands following a standard protocol. They 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 with either the random-pairs or quarter method (Cottam & Curtis 1949, 1955) at 20 points spaced evenly along a square U-shaped transect (mean distance 6.5 m). At each point, they also recorded the presence or absence of all herbs, shrubs, and tree seedlings within a 1-m^2 quadrat. The 20 points and quadrats sampled per stand characterize the vegetation of approximately 0.25 ha.

In 2000–2001 we used similar but more intensive methods to relocate and resurvey forest understory communities in these stands. Using original stand maps, we relocated 67 stands in 2000–2001. Five were no longer forested or were recently logged. We sampled the remaining 62 stands (Fig. 1). Nine sites were in reserves (state parks or research natural areas). The remaining stands were in the matrix of managed forest lands (31 in county, state, or national forests, 3 on tribal lands, and 19 on private land).

In each stand, we laid out three 20 × 20 m plots spaced 20 m apart, with the first initiated at a random position and orientation starting 50 m from the edge. This starting point ensured that all our quadrats would match Curtis's in being at least 30 m from the edge (given the random orientation). Research in this region indicates that plant community composition is only affected at distances up to 30 m from the forest edge (Euskirchen et al. 2001). We measured diameters at breast height (dbh) of all woody species >2.5 cm dbh in the three 20 × 20 m plots. (Data are available from T.P.R. or online at http.//www.botany.wisc.edu/waller/homogenized/supplementary_docs.html.) We recorded the presence of all vascular plants <2.5 cm dbh in each of 120 1-m^2 quadrats distributed along six 1 × 20 m strip transects located along the first and second sides of each plot. We examined temporal shifts in understory composition, defined as all vascular plants (herbs and shrubs) but not tree seedlings. Our sampling resembled Curtis's (1959) in characterizing approximately 0.25 ha of forest. Because our sampling was more intensive, we adjusted our samples to provide unbiased comparisons.

To ensure accurate comparisons between the 1950 and 2000 data sets, we had to first match species lists. In addition to changes in systematic nomenclature since 1950, the Plant Ecology Laboratory misidentified or lumped some taxa and split other taxa into species that are no longer recognized. We categorized such species only to genus and eliminated problematic species that Curtis et al. may have misidentified. To do this, we relied on independent recommendations from two expert local taxonomists. The final combined species list contained 175 taxa, 156 identified to species and 19 to genus.

Using data from all 62 sites, we examined the similarity in species composition between the two time periods with Jaccard's index, a similarity index based on presence and absence data. We also examined how Jaccard's index changed when rare species were excluded. To do this, we ranked species in order of their abundance, based on the mean of their relative frequency in 1950 and 2000. (Relative frequency was the number of quadrats in which a species occurred divided by sum of the number of quadrats in which all species at that site occurred: $n_i/\Sigma n$). We then plotted the Jaccard's index as calculated, using species of progressively higher relative frequency.

Data Analysis

Changes in Understory Communities

We first compared changes between 1950 and 2000 in species density at each site at both quadrat (1 m^2) and site (20 m^2) scales. We also estimated the ratio of non-native to native species, the similarity among sites in species composition and relative frequency, and the average habitat breadth of species present. We tested the significance of changes in all five of these variables with paired t tests between survey periods (1950 vs. 2000), with sites serving as replicates. We also used sign tests to determine whether the changes between time periods were consistent across sites (null hypothesis: the dependent variable is as likely to increase as decrease). To reduce the likelihood of a Type I error, we corrected all p values reported in the results section by the Bonferroni procedure.

Comparing species density (number of species per unit area) is the appropriate way to compare species diversity on a standardized basis when counts of individuals are not available or appropriate (Gotelli & Graves 1996). We examined species density at 1-m^2 and 20-m^2 scales, representing the minimum and maximum extent of Curtis's sampling. Because we sampled sites more extensively than Curtis did, we subsampled the 2000–2001 data to obtain appropriate and unbiased estimates to compare with the Curtis data. We estimated species density in two ways. First, we sampled every sixth quadrat of the 120 quadrats at each site, providing six subsamples of 20 quadrats, each spaced similarly to the 20 quadrats sampled in 1950. Second, we calculated passive subsamples of the 2000–2001 data by computing the probability, R, that a species i that occurs n_i times in the 120 quadrats of the 2000 sample would occur in a random subsample of 20 quadrats: $R = 1 - (1 - a_j/A_T)^{n_i}$, where a_j is the area of the subsample (20 quadrats), A_T is the area of the total sample (120 quadrats), and n_i is number of quadrats in which species *i* occurs of the 120-quadrat sample. The sum of these probabilities over all species *i* gives the number of species expected in the subsample (Gotelli & Graves 1996). The two approaches gave highly correlated results for the number of species present and rates of species loss ($df = 60$; $r = 0.997$; $p < 0.001$, for both). Both approaches gave qualitatively identical results in all analyses. We also used the passive sampling model to determine how many species we would have detected regionally (i.e., at all 62 sites) if we only sampled 20 quadrats per site. Using the passive subsampling equation above, we also examine the ratio of non-native to native species in 1950 and 2000. We considered a species non-native if it is listed as "introduced" in the Wisconsin Vascular Plants and Lichens Flora (http://www.botany.wisc.edu/wisflora/composition.html).

To assess how distinct sites are floristically, we estimated the average degree of similarity for each site to the other 61 sites. To estimate community similarity, we calculated the complement of the Sørensen distance (also termed the Czekanowski coefficient or the Bray-Curtis measure):

$$S = 1 - [(\Sigma|x_{ij} - x_{ik}|)/\Sigma(x_{ij} + x_{ik})],$$

where x_{ij} and x_{ik} are the number of quadrats containing species *i* at site *j* or *k*. Values of *S* range from zero, for no similarity in species composition, to 1.0, for identical species composition and relative abundance. We computed the mean similarity of each site to all other sites for both time periods to judge whether understory communities are converging in species composition.

We estimated the mean habitat specialization for species present at each site and sampling time using a habitat breadth index (*h*). This index reflects the number of habitat types a species is known to occupy in Wisconsin according to Curtis (1959) and identified by the Wisconsin State Herbarium (http://www.botany.wisc.edu/wisflora/curtis.html). The mean number of habitats occupied by all the plant species present at a site in either 1950 or 2000 is *H*. Values of *H* range from 1, for narrow habitat breadth and high habitat specialization, to 17, for wide habitat breadth and no habitat specialization. Changes in mean habitat specialization reveal whether habitat generalists or specialists fared better over the past 50 years.

Rates of change between 1950 and 2000 were calculated using the difference equation $N_{2000} = \lambda\ N_{1950}$, where $\ln(\lambda)$ is the rate of change, and *N* is the variable of interest in 1950 and 2000. We computed rates of change in species density at the 20-m^2 scale, the ratio of exotic to native species, mean similarity in species composition, and mean habitat specialization. We added 0.01 to the numerator and denominator of the ratio of non-native to native species to avoid dividing by zero. We used Pearson correlation coefficients to test for significant relationships among these rates.

Plant species adapted to animal pollination or dispersal may be more likely to decline than species adapted to abiotic pollination and dispersal (Bond 1995). Most temperate-forest understory herbs are pollinated by insects, making them vulnerable to reproductive failure due to pollinator declines. In addition, plants with showy flowers or fruits are conspicuous, which might make them more attractive to deer. We categorized species according to their known modes of pollination and dispersal (either abiotic or biotic; data available from T.P.R. or online at http.//www.botany.wisc.edu/waller/homogenized/supplementary_docs.html). We constructed 2 × 2 contingency tables to test for significant shifts in the relative frequency of species with abiotic pollination or dispersal since 1950. We use *G* tests to test for significant changes at individual sites and across the pooled data set. We use the *G* test for heterogeneity to evaluate the consistency of shifts among sites.

The Role of Site Protection, Deer, and Succession

We expect plant communities on lands formally protected as parks or natural areas to fare better than communities on lands lacking such protection. We therefore identified sites that corresponded to World Conservation Union Protected Area categories I through V and classified these stands as protected. Two of these nine sites were research natural areas (category I) and seven were state parks (category II). In all cases, protection was established prior to sampling in the 1950s. The remaining 53 sites consisted of private and government-owned forest lands classified as unprotected.

We also tested how deer hunting affected changes in forest understory communities by dividing our sites into two categories: those open to deer hunting and those where hunting is prohibited. Most sites (52) are open to deer hunting. Hunting is prohibited in 3 study sites located in state parks and at 5 sites adjacent to residential communities. One private landowner also prohibits hunting. These lands act as refugia for deer, where deer densities are higher and their impacts on vegetation greater than in the surrounding landscape (Leopold 1943; Martin & Baltzinger 2002).

Increased shade and competition from forest overstory plants naturally change the environment for understory plants. Can succession explain the changes we observed in forest understory communities? To answer this question, we tested whether indices of succession are related to understory change. As stands undergo succession, trees undergo a self-thinning process. During this process, trees grow larger, tree density declines, and basal area per unit area increases (Somers & Farrar 1991; Zhang et al. 1993; Frelich 2002) as shade-intolerant species decline and give way to shade-tolerant species (Curtis 1959; Connell & Slayter 1977). We assessed four variables likely to reflect successional status: density of trees >2.5 cm dbh, total basal area of trees >2.5 cm dbh/ha, average basal area of the three largest trees, and a mean "climax adaptation value" (CAV; Curtis & McIntosh 1951; Curtis 1959) for the stand. Curtis (1959) assigned each tree species a CAV score between 1 and 10, such that species with higher CAV scores persist the most in late-successional forests. We estimated a mean CAV for each stand by weighting CAV values for each species by the relative basal area for that species within the stand, resulting in a site CAV index between 1 for early successional and 10 for late successional). We regressed all indicators of community change—shifts in species density and rates of change in mean similarity, exotic species, and mean habitat breadth—against these four successional predictor variables. We also integrated these variables into a composite index of succession using principal components analysis (PCA). A PCA constructs synthetic axes from linear combinations of variables in a manner that captures the most variance within the data set with each succeeding axis. We performed PCA on a matrix consisting of the four stand measurements by 124 rows (62 sites $\times 2$ time periods). We used position of a stand along the first axis in either 1950 or 2000 ($PC1_{1950}$ or $PC1_{2000}$) to estimate its successional state in either sampling period, and we estimated successional change by measuring change along this axis ($PC1_{2000} - PC1_{1950}$). To determine whether statistical distribution of successional states differed between 1950 and 2000, we compared $PC1_{2000}$ with $PC1_{1950}$ by using a Kolmogorov-Smirnov two-sample test.

To assess how each site's protected status, deer-hunting pressure, successional state, and successional change affected understory changes, we tested the ability of these categorical and continuous predictor variables to affect our indicators of community change with two-way analyses of covariance). These dependent variables included the rates of species loss, homogenization, non-native species invasion, and increases in generalist species, and the rates of change in the frequency of biotically pollinated and dispersed species.

Results

Changes in Diversity

Across all sites, we observed little change in regional species diversity. Curtis recorded 138 species in 1950, and we found 135.4 species in 2000 (adjusted to match the 1950 sampling effort). Species density did not change at the quadrat (1-m^2) level, with 4.89 ± 0.30 (SE) species per quadrat in 1950 versus 5.29 ± 0.30 in 2000 ($n = 62$; paired $t = 1.42$; $p = 0.08$). Average species density increased at the 1-m^2 scale at about half (34 of 62) the sites.

Despite this stasis in very local and regional plant diversity, understory plant communities in northern Wisconsin underwent significant local biotic impoverishment. Species density at the 20-m^2 scale declined by an average of 15% per site (Fig. 3a; paired $t = 4.05$, $p = 0.005$), with 40 of the 62 sites losing species (sign test; $p = 0.15$). The density of native plant species declined even more (18.5% at the 20-m^2 scale).

The mean Jaccard's similarity index between sampling periods was 0.66, indicating that only 2 of every 3 species was present in both time periods (data are available from T.P.R. or online at http.//www.botany.wisc.edu/waller/homogenized/supplementary_docs.html). Because Jaccard's index ignores abundance, rare species strongly influenced this result. When we only included species with an average relative frequency of 0.1% or greater, 9 of every 10 species were present in both time periods. Including only species with an average relative frequency of 0.4% or greater resulted in all species being present during both time periods (Fig. 4).

Changes in Species Composition and Community Structure

Only one of 62 sites contained an exotic species in 1950 compared with 43 sites in 2000 (Fig. 3b; sign test; $p < 0.001$). The ratio of exotic to native species in 2000 ranged from 0 to 0.20, indicating that these communities remain dominated by natives. Habitat generalists fared better than habitat specialists (Fig. 3c): the average habitat breadth of species present increased at 58 of the 62 sites (sign test; $p < 0.001$). The increase in generalists may account in part for the 31% rise in average similarity among the sites or the degree of biotic homogenization (Fig. 3d). Average similarity increased at 42 of the 62 sites (sign test; $p = 0.035$).

Changes in species density at the 20-m^2 scale were positively correlated with changes in similarity among sites (Fig. 5a). Thus, sites gaining species became more similar in species composition to other sites, whereas sites losing species became more distinct from other sites. Community similarity also increased with increases in habitat generalists (Fig. 5b). There was a weak positive correlation between rates of increase in the ratio between exotic and native species and rates of change in species density at the 20-m^2 scale (Fig. 5c), indicating that sites gaining species are more likely to have gained exotic species.

The G tests revealed highly significant local declines in the proportion of animal-pollinated and animal-dispersed species (Table 1). Animal-pollinated and animal-dispersed species significantly increased at 2 and 4 sites, respectively, but significantly declined at 38 and 22 sites. Magnitudes of decline also varied among sites, as demonstrated by the significant heterogeneity values.

Effects of Succession

None of the univariate correlations between our four indices of succession (changes in the density of trees >2.5 cm dbh/ha, total basal area of trees >2.5 cm dbh/ha,

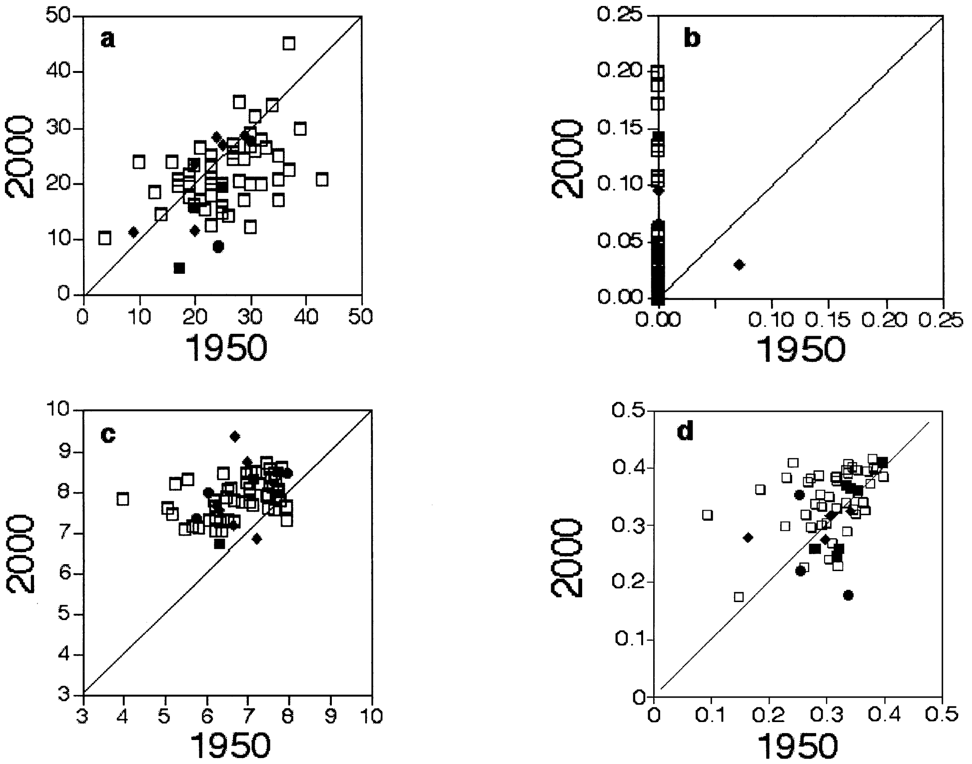

*Figure 3. Changes over 50 years at 62 sites in northern Wisconsin in (a) species density/20 m^2 (*t = 4.05; p = 0.005*); (b) ratio of non-native to native species (*t = 6.24; p < 0.0001*); (c) average habitat breadth index, or* H, *of species in the community (*t = 10.23; p < 0.0001*); and (d) Bray-Curtis similarity of each site to all other sites (*t = 2.93; p = 0.024*). All statistical tests were paired* t *tests, and* p *indicates a Bonferroni adjusted* p *value for five tests (*p = 5p*). Symbol key: • protected area without deer hunting, ◆ protected area with deer hunting, ■ unprotected area without deer hunting, □ unprotected area with deer hunting. For all sites df = 60, and in all figures line slope = 1.*

average basal area of the three largest trees, or mean CAV) and our four indicators of ecological change (rates of change in species density, mean community similarity, non-native species, and mean habitat breadth) were significant (range of Pearson $r = -0.18$ to 0.16; df = 62). Similarly, none of these indicators of ecological change showed dependence on our composite index of successional change ($PC1_{2000} - PC1_{1950}$) in the two-way analysis of covariance (Table 2). Thus, successional change since 1950 was not associated with rates of species loss, exotic species invasion, biotic homogenization, or loss of habitat specialists. As expected, basal area per hectare, average basal area of the three largest trees measured, and stand CAV all had positive loadings on PC1 (0.68, 0.94, and 0.63, respectively), whereas the density of trees per hectare had a negative loading (−0.63). Thus, this axis (which explains 52.7% of the total variance) accurately represented a successional axis. Comparing the distributions of successional stages present in 1950 to those present in 2000 revealed no net change in average successional state (Kolmogorov-Smirnov two-sample test; $p = 0.13$). Despite these negative results, the successional-state stands reached in 2000 did not influence the changes we observed. Later-successional forests lost fewer species and were more likely to gain habitat generalists than early successional forests (Table 2).

Effects of Site Protection and Hunting Status

Ironically, two of the three sites that lost more than 60% of their species density at the 20-m^2 scale were in state parks protected from direct human disturbance Protected areas also had high rates of decline in the proportion of animal-pollinated and -dispersed species: 40% and 36% declines, respectively, versus 17% and 14% declines outside protected areas. These results may reflect differences in deer abundance. Rates of decline paralleled those observed when sites were categorized by deer hunting. On average, sites without deer hunting lost more than 60% of their species, compared with 16% at hunted sites. Protected sites without deer hunting were particularly likely to lose animal-pollinated and -dispersed species (Fig. 6).

Two-way analysis of covariance indicated that protected status ($p < 0.001$) and deer hunting ($p < 0.001$) significantly affected declines in animal-pollinated and -dispersed species ($p = 0.02$ for protected status and $p = 0.01$ for deer hunting). There was also a significant interaction between protected status and deer hunting for both animal-pollinated ($p < 0.001$) and animal-dispersed species ($p = 0.001$). Protected sites without deer hunting exhibit higher rates of decline of both animal-pollinated and animal-dispersed species than unprotected sites or protected sites with hunting; different letters indicate

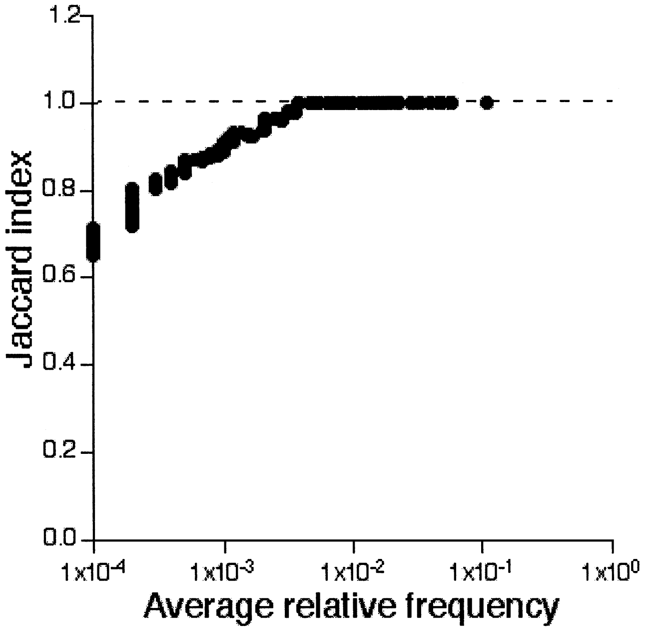

Figure 4. Similarity between species lists in 1950 and 2000, based on Jaccard's similarity index for presence-absence data. Each data point represents a species, based on its relative frequency averaged across both time periods.

significant differences for animal-pollinated ($p < 0.001$) and animal-dispersed ($p < 0.02$) species according to Scheffé's procedure. Successional state and the degree of successional change had no significant effect on the rates of decline of animal-pollinated or -dispersed species.

Discussion

Most understory plant communities in northern Wisconsin mesic forests have experienced substantial local biotic impoverishment over the past 50 years. The average site lost 18.5% of its original native flora, with native species density declining at 45 of the 62 sites. These losses occurred despite the absence of any change in overall regional or quadrat-level diversity. They also appear unrelated to succession. Patterns of impoverishment depended on the scale of measurement. At the scale of

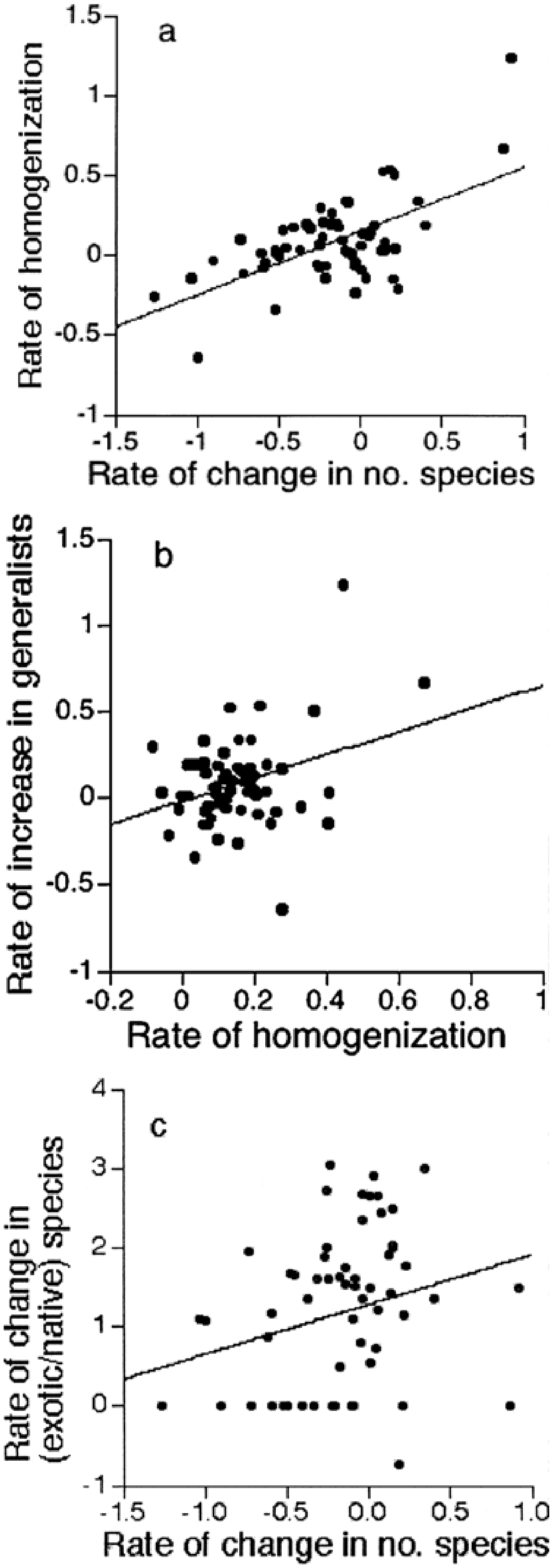

Figure 5. Pearson correlations between (a) rates of change in the number of species and rates of biotic homogenization ($r = 0.59$*;* $p = 0.0001$*); (b) rates of increase in generalists and rates of biotic homogenization (*$r = 0.42$*;* $p = 0.0006$*), and (c) rates of change in the number of species and rates of colonization by non-native species (*$r = 0.25$*;* $p = 0.047$ *(*$n = 62$ *for all correlations).*

Table 1. Replicated goodness-of-fit tests (*G* tests for heterogeneity) revealing changes in the relative frequency of animal-pollinated and animal-dispersed plants between 1950 and 2000.*

	Relative frequency (%)				
	1950	*2000*		*df*	*G*
Animal-pollinated plants	76.6	64.8	pooled	1	349.0
			heterogeneity	61	341.1
			total	62	690.1
Animal-dispersed plants	64.0	57.2	pooled	1	97.4
			heterogeneity	61	423.2
			total	62	520.6

**Probability* (p) *< 0.0001 for all.*

entire states, McKinney (2002) found that plant species richness increases as the influx of non-native species outpaces native species extinctions. As shown here, however, native population extinctions outpace non-native colonizations within local communities. Eventually, such cumulative losses could threaten regional diversity as well, in a manner analogous to the extinction debt associated with habitat loss (Tillman et al. 1994).

Most sites lost native species and habitat specialists while gaining exotic and already common species. Although the ratio of exotic to native species at our sites remained low (never exceeding 0.20), these invaders were absent 50 years ago. The increase in exotic species was not lower in protected areas and appeared unrelated to deer-hunting pressure and succession (Table 2). Although exotic species have not reduced native species richness at our sites thus far, that may change. Because there is often a lag between colonization and rapid population growth (Sakai et al. 2001), exotic populations seem likely to continue increasing across the region.

The loss of uncommon native species and the gain of exotic species are driving biotic homogenization in northern Wisconsin. Only one-third of the 62 sites became less homogenous over time. Because our measure of biotic homogenization incorporates both species composition and relative abundance (Bray & Curtis 1957), this homogenization reflects systematic declines of regionally uncommon species and increases in regionally abundant common species (Curtis 1956). The idea that generalist species are replacing specialists is supported by the positive correlation between increases in biotic homogenization and increases in habitat generalists (Fig. 5b). Sites that gained species also appeared to be increasing in biotic homogenization, however (Fig. 5a). This somewhat enigmatic result suggests that extinction is not the primary driver of biotic homogenization, but rather that common species in 1950 became even more abundant by 2000. In fact, sites that lost the most species showed little change in the degree of homogenization. The more species a site lost, the more distinct it became from the "average" site (eventually bearing zero similarity once it lost all species). Likewise, a species-poor site with little resemblance to the average site will become more similar to other sites as it gains species that are also present at other sites. Thus, extreme gains or losses in species richness at an average site will tend to make it less similar to comparable sites.

Other retrospective studies of change in forest understory communities have also documented a pronounced loss of local species (Kwiatkowska 1994; Drayton & Primack 1996; Rooney & Dress 1997) and increases in exotic species (Robinson et al. 1994; Drayton & Primack 1996). The generality and significance of these findings, however, are often limited by the tendency to study only one or two sites. This regional study of 62 sites, combined with the consistent finding of losses across studies, suggests that such losses may be pervasive and thus of great significance for conservation. Population extinctions imply progressive losses of potentially important ecosystem functions and services (Hughes et al. 1997). Species undergoing range contractions tend to lose genetic diversity (Hobbs & Mooney 1998). In addition, population declines and losses often presage endangerment or regional extinctions. The loss of even rare species from a community can also facilitate the invasion of exotic species (Lyons & Schwartz 2001), perhaps spurring more species losses.

Given the presence of such biotic impoverishment and homogenization, it behooves us to examine the detailed patterns of ecological change for clues they may provide to the mechanisms responsible. This was our motivation for examining variation among sites in species losses and variation among species in rates of decline. Rates of species loss were highest at sites without deer hunting (Table 2), reinforcing the view that deer overabundance is a key driver of ecological change in this region (Waller & Alverson 1997). Altered biotic interactions have cascading effects on community structure and ecosystem function (Terborgh et al. 2001), suggesting that biotic interactions need more attention from researchers and managers.

Declines in the relative abundance of animal-pollinated and animal-dispersed species, particularly in protected areas and areas without deer hunting, suggest that a systematic shift in guild structure is underway. Without comparable data for pollinator and disperser species, we cannot know what effect these shifts in plant species have on pollinator and disperser guilds. Declines in animal-pollinated plants could trigger a decline in pollinator abundance or species richness (Kearns & Inouye 1997). Alternatively, animal-pollinated plants may have declined in abundance because pollinators declined first or because showy flowers make species more conspicuous to deer. The much greater declines in animal-pollinated and -dispersed species in areas without deer hunting (Fig. 6) support this conspicuousness hypothesis.

Table 2. Two-way analyses of covariance assessing the effects of four predictor variables(protected status, deer hunting, estimated successional state in 2000, and degree of successional change since 1950) on four metrics of ecological change: rates of species change, increases in mean similarity, ratio of non-native to native species, and mean habitat breadth index.[a]

		Species change		*Similarity*		*Non-native species*		*Habitat breadth*	
Source	*df*	*SS*	*F*	*SS*	*F*	*SS*	*F*	*SS*	*F*
Protected status	1	0.38	2.81	0.08	1.15	0.16	0.15	0.000	0.00
Deer hunting	1	1.16	8.67[b]	0.23	3.48	0.25	0.24	0.000	0.01
Protected × deer	1	0.07	0.53	0.00	0.03	0.04	0.03	0.010	0.65
Successional change	1	0.42	3.11	0.02	0.27	1.25	1.21	0.030	1.90
Successional state	1	0.58	4.30[c]	0.08	1.16	0.23	0.23	0.100	6.18[c]
Error	56	7.52		3.69		57.73		0.89	

[a] *Abbreviations: SS, sum of squares; F, F ratio.*

[b] *Probability* (p) < 0.01.

[c] *Probability* (p) < 0.05*, slope positive.*

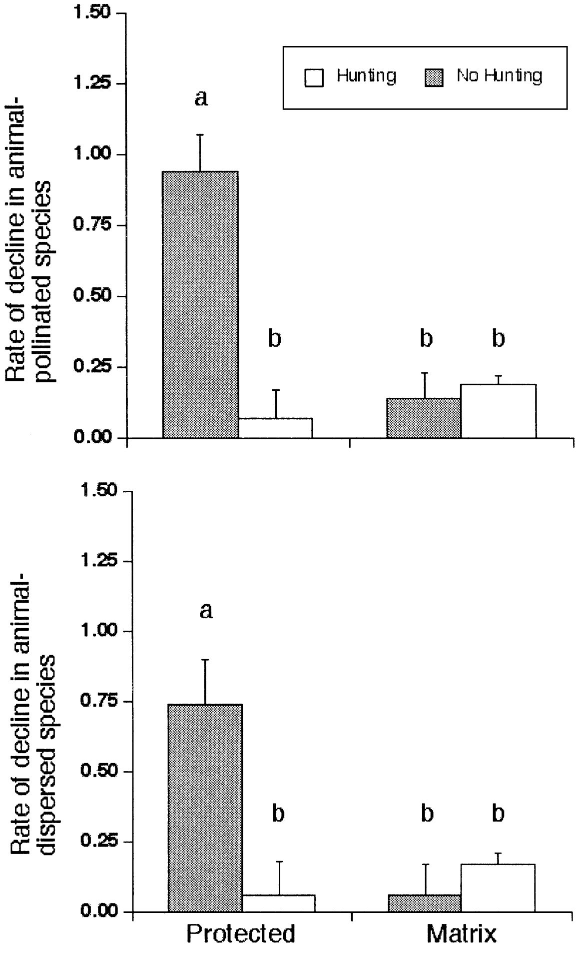

Figure 6. Rates of decline in the proportion of animal-pollinated (AP) and animal-dispersed (AD) species in communities in northern Wisconsin. Different letters indicate significant differences for AP (p < 0.001) *and AD* (p < 0.02) *with Sheffe's procedure.*

Some retrospective studies attribute losses of local plant species to habitat destruction or fragmentation (Robinson et al. 1994; Leach & Givnish 1996). Wilcove et al. (1998) identified five leading mechanisms of extinction in the United States: habitat loss and fragmentation, invasive species, direct exploitation, pollution, and disease. However, the local species losses we documented cannot be attributed to any of these mechanisms. The stands we surveyed remained extant, have experienced little habitat loss, and occupy a mostly unfragmented forest landscape. The abundance of non-native species remained low, and, contrary to expectation, sites with more exotic species were slightly more likely to gain in species richness (Fig. 5c). The plant species we surveyed are only rarely subject to exploitation. Atmospheric inputs of nitrogen or acid might account for species declines, but species losses were unrelated to variation among sites in soil pH (df $= 60$; $r = 0.09$; $p = 0.47$) and soil nitrogen (df $= 60$; $r = 0.14$; $p = 0.24$). We found no evidence that disease caused these losses; for example, we observed systematic declines across many unrelated taxa. Thus, the factors associated with local population declines and extirpations did not mirror mechanisms thought to directly threaten species with extinction. This implies that communities can still be seriously threatened and in need of active conservation even when the most obvious threats are not present.

These systematic declines in species richness signal that existing conservation efforts in the region are insufficient or ineffective. The widespread population declines and extirpations spanned many taxa and echo those found in other long-term studies. Together, these results suggest that a major and largely unacknowledged wave of biotic impoverishment is sweeping temperate forests throughout North America. Because biotic impoverishment has been a relatively slow process in northern Wisconsin, it would have gone entirely undetected except for the existence of Curtis's replicated quantitative baseline data. Thus, similar declines might well be occurring in many other regions and community types.

Given the significance of these trends and their implications, we need to expand monitoring efforts. None of these stands are currently part of any ongoing monitoring program (although all our plots are permanently marked). Had there been such a program, the detection of net species losses might have triggered corrective management actions on the part of land managers. Instead, the absence of information has been assumed to indicate an absence of impacts (Alverson et al. 1994). Inadequate monitoring may give us the particular false sense that ostensibly protected parks and preserves are secure when, in fact, they may be vulnerable (Janzen 1983; Terborgh 1999). Certainly, our current laissez faire strategy of maintaining habitats in most parks, research natural areas, and unprotected forest lands is failing to preserve their ecological integrity and diversity. Although protected lands provide an important function as no-management control areas, benign neglect does not automatically translate into biodiversity conservation (Soulé et al. 1979). We forecast continued local biotic simplification in this region if proactive measures are not taken to monitor changes in diversity, identify particular threats, and take measures to reduce those threats.

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