Contributed Paper

Paying the Extinction Debt in Southern Wisconsin Forest Understories

DAVID A. ROGERS,*‡ THOMAS P. ROONEY,† TODD J. HAWBAKER,‡ VOLKER C. RADELOFF,‡ AND DONALD M. WALLER§

*Department of Biological Sciences, University of Wisconsin, Parkside, 900 Wood Road, P.O. Box 2000, Kenosha, WI 53141-2000, U.S.A., email rogersd@uwp.edu
†Department of Biological Sciences, Wright State University, 3640 Colonel Glenn Highway, Dayton, OH 45435, U.S.A.
‡Department Forest and Wildlife Ecology, University of Wisconsin, Madison, 1630 Linden Drive, Madison, WI 53706, U.S.A.
§Department of Botany, University of Wisconsin, Madison, 430 Lincoln Drive, Madison, WI 53706, U.S.A.

Abstract: *The lack of long-term baseline data restricts the ability to measure changes in biological diversity directly and to determine its cause. This hampers conservation efforts and limits testing of basic tenets of ecology and conservation biology. We used a historical baseline survey to track shifts in the abundance and distribution of 296 native understory species across 82 sites over 55 years in the fragmented forests of southern Wisconsin. We resurveyed stands first surveyed in the early 1950s to evaluate the influence of patch size and surrounding land cover on shifts in native plant richness and heterogeneity and to evaluate changes in the relative importance of local site conditions versus the surrounding landscape context as drivers of community composition and structure. Larger forests and those with more surrounding forest cover lost fewer species, were more likely to recruit new species, and had lower rates of homogenization than smaller forests in more fragmented landscapes. Nearby urbanization further reduced both alpha and beta understory diversity. Similarly, understory composition depended strongly on local site conditions in the original survey but only weakly reflected the surrounding landscape composition. By 2005, however, the relative importance of these factors had reversed such that the surrounding landscape structure is now a much better predictor of understory composition than are local site conditions. Collectively, these results strongly support the idea that larger intact habitat patches and landscapes better sustain native species diversity and demonstrate that humans play an increasingly important role in driving patterns of native species diversity and community composition.*

Keywords: extinction debt, fragmentation, homogenization, metacommunity dynamics, southern Wisconsin, species loss, urbanization

Pago de la Deuda de Extinción en Sotobosques de Bosques del Sur de Wisconsin

Resumen: *La falta de datos de largo plazo restringe la habilidad para medir cambios en la diversidad biológica directamente y determinar su causa, lo cual obstaculiza los esfuerzos de conservación y limita la prueba de principios básicos de ecología y biología de la conservación. Utilizamos un muestreo histórico para seguir cambios en la abundancia y la distribución de 296 especies de sotobosque nativas en 82 sitios a lo largo de 55 años en los bosques fragmentados del sur de Wisconsin. Volvimos a muestrear bosques muestreados por primera vez a inicios de la década de 1950 para evaluar la influencia del tamaño del parche y la cobertura de suelo circundante sobre cambios en la riqueza y heterogeneidad de plantas nativas y para evaluar cambios en la importancia relativa de las condiciones locales del sitio versus el contexto del paisaje circundantes como controladores de la composición y estructura de la comunidad. Los bosques más extensos y los que tenían mayor cobertura forestal alrededor perdieron menos especies, tuvieron mayor probabilidad de reclutar nuevas especies y tuvieron menos tasas de homogenización que los bosques menos extensos en paisajes más fragmentados. La urbanización cercana redujo aun más la diversidad alfa y beta del*

sotobosque. De manera similar, la composición del sotobosque dependió principalmente de las condiciones locales del sitio en el muestreo original pero solo reflejó débilmente la composición del paisaje circundante. Sin embargo, en 2005 la importancia relativa de estos factores se revirtió de tal modo que la estructura del paisaje ahora pronostica mucho mejor la composición del sotobosque que las condiciones locales del sitio. Colectivamente, estos resultados soportan la idea que los parches de hábitat intacto y los paisajes más extensos dan mejor sustento a la diversidad de especies nativas y demuestran que los humanos pueden jugar un papel cada vez más importante en el manejo de la diversidad y composición de especies nativas.

Introduction

The principles of island biogeography and metapopulation biology represent a firm theoretical foundation for the field of conservation biology, underpinning the claim that large, connected habitat patches better sustain biodiversity than small, unconnected ones (Meffe & Carroll 1997; Simberloff 1997). Although the effects of fragmentation and habitat loss have been demonstrated for birds (Brooks et al. 1999) and large mammals (Miller & Harris 1977), effects on vascular plants have rarely been shown (Zartman & Nascimento 2006). Moreover, because responses of plant communities often lag behind landscape fragmentation (Lindborg & Eriksson 2004; Helm et al. 2006; Zartman & Nascimento 2006), these changes may be overlooked. For example, two earlier studies from the same ecoregion as this study examined whether forest islands in fragmented habitats follow the patterns predicted by island biogeography theory (Levenson 1976; Middleton & Merriam 1983). Results of both studies showed little relationship between patch size and understory richness, perhaps reflecting a lag between when habitat loss fragmentation occurred and when the "extinction debt" (Tilman et al. 1994) is paid. This led to the potentially erroneous conclusions that island biogeography is not an appropriate theoretical framework for studying plant communities in fragmented landscapes.

Recent work in a variety of ecological contexts suggests that aspects of diversity other than richness are also influenced by habitat loss and fragmentation, specifically findings that show community composition tends to homogenize in response to landscape changes (Olden & Poff 2003; McKinney 2006). Although biotic homogenization is often assumed to reflect increases in weedy exotic invaders (McKinney & Lockwood 1999), increases in compositional similarity among stands can also reflect shifts in the abundances of native species in response to surrounding landscape conditions (Rooney et al. 2004; McKinney 2006).

As community homogenization increases in response to fragmentation and urbanization, one might hypothesize that community composition increasingly reflects landscape conditions rather than local environmental factors. Such a decoupling of species–environment re-lationships has been inferred in New England forests (Foster 1998) but remains understudied. Vellend et al. (2007) compared patterns of community similarity and gradient analyses between old-field forests and natural forests of similar age and found higher average similarity and a weaker biotic–environmental relationship in forests with a history of agricultural use. Although space-for-time studies have limitations (Johnson & Miyanishi 2008), results of these studies suggest a temporal trend toward community homogenization and a weakening of biotic–environmental relationships in response to anthropogenic landscape modification.

The widespread absence of long-term baseline data (Magnuson 1990) makes it difficult to discern the cumulative impacts of these forces over time, which hampers conservation efforts (Soulé 1979; Terborgh 1999). Most studies of the effects of habitat loss and fragmentation on plant species rely on substituting space for time to infer long-term effects (Matlack 2005; Helm et al. 2006), employ simulation models (Matlack 2005), or reflect short-term experiments (Debinsky & Holt 2000). Results of long-term studies that do exist (e.g., Robinson et al. 1994; Drayton & Primack 1996; Rooney & Dress 1997) suggest that substantial changes are occurring, but many studies lack quantitative data (e.g., Ouborg 1993) or spatial replication (Waller & Rooney 2004).

The high-quality baseline data on plant communities collected and archived by the University of Wisconsin Plant Ecology Laboratory (PEL) provides a unique opportunity to overcome these limitations. These data were collected as a foundation for a quantitative description of the state's plant communities (Curtis 1959). These surveys are useful for analyzing long-term (40- to 55-year) shifts in plant community composition and have been used to describe changes in remnant prairies (Leach & Givnish 1996), upland forests of northern Wisconsin (Rooney et al. 2004), and cedar glades (Mills 2008).

In Rogers et al. (2008), we expanded on this work by describing changes at 94 upland forest sites across southern Wisconsin. There, we explored the relative influences of initial canopy composition, succession, exotic species invasions, and edaphic factors on changes in native understory richness, heterogeneity, and composition. We found widespread declines in native species

density (averaging a 25% decline across 20 m² quadrats), community homogenization (average 16% increase in average similarity), and consistent shifts in species composition toward more shade-tolerant species. Surprisingly, we found neither the richness nor abundance of exotic species are likely drivers of species loss or community homogenization in this system. Rather, shifts in richness and heterogeneity generally reflect increased rates of species loss, decreased colonization and community homogenization in mesic or late-successional stands, in stands with large increases in basal area per hectare, and in stands with high initial diversity.

Here we used the same data to explore how patch characteristics and surrounding landscape conditions affect these community changes. Specifically, we tested whether patch size, isolation, and urbanization predict shifts in native species richness, heterogeneity, and composition. We expected smaller forest patches in fragmented and more urbanized landscapes to have greater species losses and more community homogenization. Furthermore, we expected such dynamics would improve the relationship between native species richness and patch size to better fit the pattern predicted by the theory of island biogeography. Similarly, we expected the strength of relationships between local environmental factors and plant community composition to decline relative to patch characteristics and surrounding landscape condition.

Methods

Background

Before European settlement, southern Wisconsin landscapes were fire-sculpted into a mosaic of prairies, savannas, and forests (Curtis 1959). By the time Curtis sampled and described the vegetation of the region, Euro-American settlement had largely eliminated the original prairies and savannas and reduced forest patches to isolated islands within a matrix of crops, pasture, and urban development (Curtis 1956). This remains the case today, except that urbanization, industrial agriculture, and more intensive forms of development have replaced some of the former agricultural lands, further fragmenting habitats and reducing landscape permeability (Radeloff et al. 2005).

Community Diversity and Dynamics

To assess patterns of native species loss and community homogenization, we estimated rates of change in native species richness, average similarity, and community homogenization between 1948–1951 (henceforth 1950) and 2002–2005 (henceforth 2005) for 82 forested sites spread across southern Wisconsin (Fig. 1) originally described by Curtis and McIntosh (1951). During the orig-

inal sample period, they quantified understory composition at a series of 20 points evenly spaced around a large square of approximately 4 ha, which provided a sample of 20 1-m² quadrats. In each quadrat, they tallied all the vascular plant species present, which allowed them to estimate the frequency of each species at each site (out of the 20 quadrats).

In 2005 we used identical methods to resample the 82 stands (see Rogers 2006 and Rogers et al. (2008) for more detail on sampling methods and taxonomic synchronization between sample periods.) These data sets included totals of 241 native species in 1950 and 198 native species in 2005 (296 species when pooled). For each site in each time period, we calculated native species richness (total number of species encountered in the 20 1-m² samples) and the average similarity in native understory composition between each site and all other sites. Average similarities were calculated with the Sørenson similarity index based on species relative frequencies (McCune et al. 2002). We calculated 50-year rates of change for these variables based on the equation $N_{2000} = \lambda N_{1950}$, where $\ln\lambda$ is the rate of change and N is the variable of interest (adding 0.01 to the numerator and denominator to avoid dividing by zero).

Finally, we estimated apparent rates of colonization and extirpation for each stand to examine how these factors may drive changes in richness. We calculated the number of apparent extirpations as richness in 1950 minus the number of species present in both sample periods. We calculated apparent colonizations as richness in 2005 minus the number of species present during both sample periods. To standardize by richness, we also calculated percent extinct (no. extinct/richness $_{1950}$) and percent colonized (no. colonized/richness $_{2005}$). Because any finite sample misses some rare species, our estimates of extinction and colonization are potentially biased relative to their true values. Nevertheless, similar frequencies of false absences should occur in both samples (Lamb et al. 2009). Thus we expected any systematic bias to be small and are confident our estimates fairly represent the relative rates of extinction and colonization among stands (Rogers 2006). As previous analyses showed clear differences in response between the herbaceous and woody components of the understory community, we maintained this division and compared how species with different growth forms responded to landscape predictors.

Environmental Data

At each site we collected soil samples at 10-cm depth from 10 points evenly distributed through the sampled area, pooling subsamples into a single sample from each stand. The samples were analyzed at the laboratory for texture and nutrients, including percent sand, silt, clay, N, P, K, Ca, and Mg.
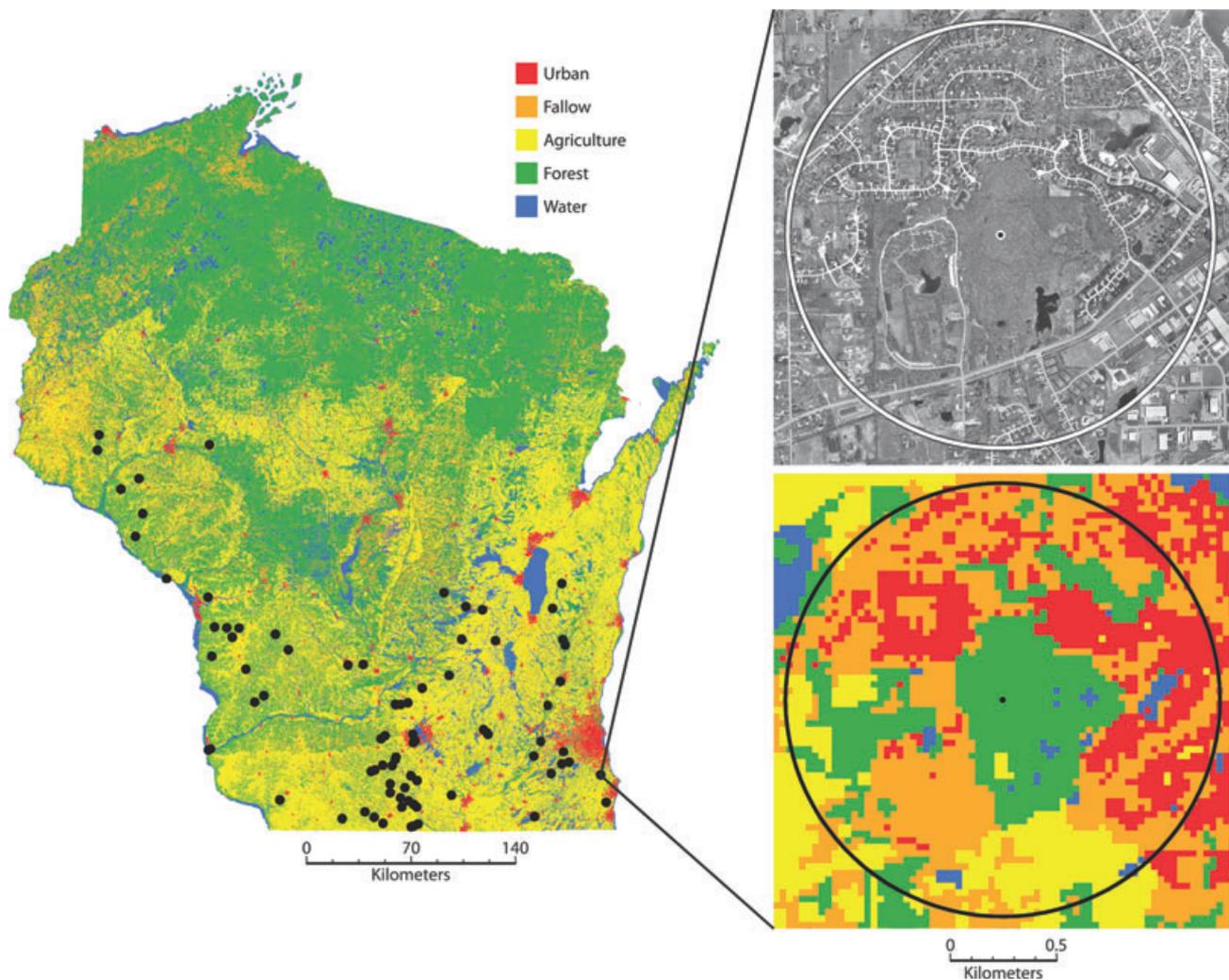
Figure 1. Locations of 82 sites and expanded views of a single site showing the 1-km buffers used to calculate road and housing density from 2000-era air photographs and land-cover classes from WISCLAND imagery.

Canopy composition represents an important environmental condition for understory species because it exerts direct influences on understory plants via shading; competition for soil, water, and nutrients; alleopathy, and other interactions. In the original survey, they used the random pairs method to quantify canopy composition in each stand (Cottam & Curtis 1956) at a series of 40 points arranged around the same transect used to survey the understory. In the resurvey, we followed the identical procedure, which provided a sample of 80 trees in each time period. We then calculated an importance value ([relative density + relative basal area]/2) for each species in each time period and used these values for the analyses described later.

Landscape Variables

Using ArcGIS and recent digital orthophotos, we digitized houses and roads within a 2-km buffer centered on each

of the 82 sites (Fig. 1). Houses were digitized and stored as point coverages and roads as line coverages. Houses were counted as single-family residences; homesteads with multiple outbuilding were counted as single units. Any linear feature visibly connected to an existing road (ignoring driveways < 50 m) was considered an additional road. The amount and type of surrounding land cover was estimated from WISCLAND (www.dnr.state.wi.us/maps) land-cover data (Fig. 1), which was derived from 30-m resolution Landsat TM images from 1992 and 1993 (Wisconsin DNR 1998). Within buffers with radii of 1, 2, and 5 km, we then calculated the proportion of land occupied by four cover classes (excluding open water): urban cover (impermeable surface), agriculture (actively cropped fields), grasslands (including fallow fields and road edges), and forest (all forest types combined). The overall accuracy of the WISCLAND classification is 94% at Anderson level 1 (Anderson et al. 1976). Single-class user's accuracies for land-cover classifications were 100%

for urban, 90% for agriculture, 73% for grassland, and 96% for forests (Wisconsin DNR 1998).

Forest patches vary in size, shape, and continuity, and this can affect ecological processes. We therefore measured the patch size for the forest stand within which each study site was located and quantified fragmentation with the mean proximity index, a gravity-based measure of patch separation (McGarigal & Marks 1995). Measures of land cover, fragmentation, and patch characteristics were made within buffers at 1, 2, and 5 km. All measures were highly correlated at all scales. Because measures at 5 km generally had the highest predictive power, we report those here.

Limited resources restricted our ability to obtain, digitize, orthorectify, interpret, and measure historical aerial images from 1950. Thus, we could not directly estimate habitat loss or changes in urbanization between 1950 and 2005. Nevertheless, regional land-use patterns (particularly forest and nonforest) were largely fixed by the 1950s and appear highly correlated with current land-use patterns (Curtis 1956; Rhemtulla et al. 2007; Olson 2008). Nevertheless, direct measures of changes in land cover would be preferable in future studies.

Analyses

After first checking for nonlinear responses, we used Spearman's rank correlations to test for relationships between the various landscape metrics and species richness and average similarity in each time period, the rates of change in these measures between time periods, and the apparent immigration and extinction rates. To reduce the risk of incorrectly rejecting null hypotheses, we present both uncorrected p values and corrected values after controlling for the false discovery rate (Benjamin & Hochberg 1995).

To test for changes in how community composition covaries with particular environmental variables, we applied partial Mantel tests (Goslee & Urban 2007). These compare the correlation structures present within similarity matrices (for canopy composition, shrub composition, and herbaceous composition) with themselves over time and with similarity matrices based on environmental, landscape, and geographic distances. We performed these analyses for both time periods and considered the importance of a variable to have changed if both means fell outside reciprocal 95% confidence intervals.

We calculated vegetation similarity for herbaceous and shrub communities from relative frequency values with the Sørenson similarity index after we removed species that occurred in fewer than four sites. We also used the Sørenson similarity index to calculate canopy similarity in each time period but used the importance values described earlier. We calculated environmental similarity from the normalized soil texture and nutrient data with the Euclidean distance measure. We normalized land-
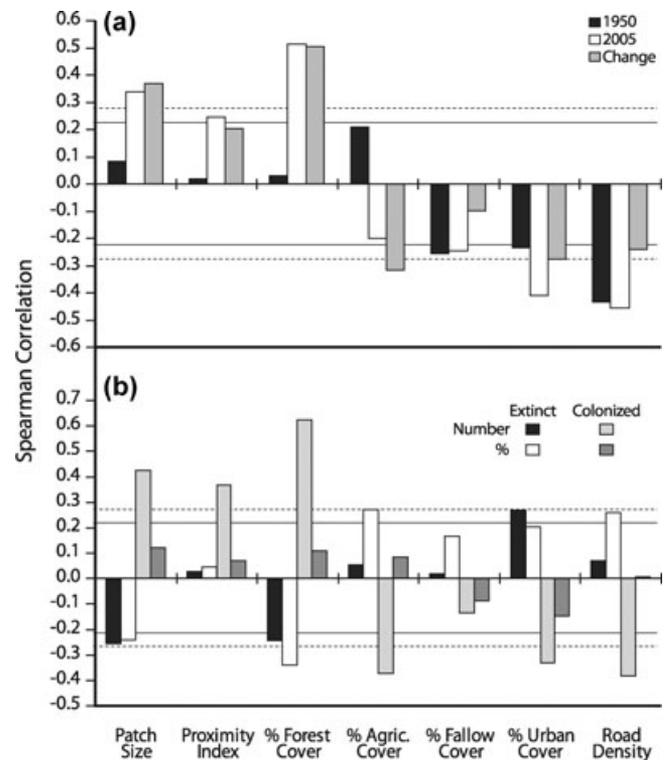

Figure 2. Comparison of Spearman's correlation values (a) between native herbaceous richness (no. species/20 m²) and landscape predictors for 1950 and 2005 and rate of change (log[2005/1950]) and (b) between landscape variables and number of extinct species, percentage of extinct species (no. extinct/richness 1950), number of colonizing species, and percentage of current species that were colonizers (no. colonized/richness 2005) for herbaceous understory species. Lines indicate critical threshold r values of statistical significance at p = 0.05 before (solid line, r = 0.210) and after (dotted line, r = 0.270) controlling for the false discovery rate (Benjamin & Hochberg 1995). Data tables used to create the figure are available from D.A.R.

scape variables (land cover, house and road densities, patch size, proximity index, and shape index) by rank and calculated landscape similarity with Euclidean distances. Finally, we calculated geographic proximity using Euclidean distances based on Wisconsin Transverse Mercator coordinates.

Results

Herbaceous Community Richness and Heterogeneity

The correlations between measured landscape variables and herb community diversity increased greatly between 1950 and 2005 (Fig. 2a). Patch characteristics of size,
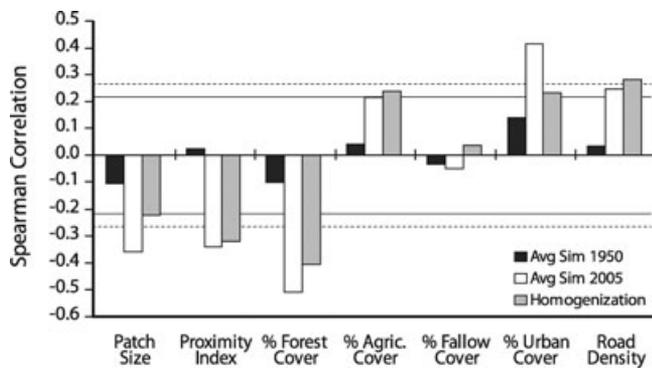
Figure 3. Comparison of Spearman's correlation values between average native-herbaceous community similarity (sim) (average of Sørenson similarity for all sites) and landscape predictors in 1950 and 2005 and for rate of homogenization between time periods (log[2005/1950]). Lines indicate critical threshold r *values of statistical significance at* p = 0.05 *before (solid line,* r = 0.210) *and after (dotted line,* r = 0.270) *controlling for the false discovery rate (Benjamin & Hochberg 1995). Data tables used to create the figure are available from D.A.R.*

proximity, and percent forest cover within 5 km that were uncorrelated with native species richness in 1950 were all correlated by 2005. Thus, the greatest rates of species loss over time were in small patches with small amounts of available habitat in the surrounding landscape. In contrast, the negative effects of surrounding urban cover and road density on species richness were already manifest in 1950; site diversity was lower in stands surrounded by higher densities of roads and urban cover. The magnitude of these effects increased since 1950 and contributed to higher rates of species losses in more urbanized landscapes.

Surrounding landscape factors influenced native species losses by affecting rates of apparent extirpation and colonization (Fig. 2b). In general, larger patches and those in more forested landscapes lost fewer native species and gained more new ones. Patches surrounded by high road densities and urban cover had much lower colonization rates and slightly higher rates of extirpation than patches surrounded by other forests and with low road density. Native species colonization richness was consistently more strongly correlated with patch characteristics and surrounding landscape context than were our measures of extirpation. This suggests that effects of habitat loss and fragmentation on species diversity were mediated by differences in recruitment.

Among-community similarity (homogenization) also responded strongly to landscape fragmentation and urbanization (Fig. 3). Large stands with more forest in

the surrounding landscape showed less convergence in herbaceous community composition than did smaller stands in a more urban-agricultural matrix. As with changes in native species richness, patch size and percent forest cover in the surrounding landscape were the most important variables linked to rates of homogenization ($r = -0.359$ and -0.509, respectively, $p < 0.001$).

Shrub Community Richness and Heterogeneity

In both time periods, shrub community richness and similarity and shrub estimated extirpation and colonization rates were only weakly related to landscape measures (data tables are available from D.A.R). In 1950 shrub richness increased with percent forest cover, average patch size, and proximity to other forest sites ($r = 0.302, 0.316$, and 0.284, respectively, $p < 0.05$). Similarity in shrub composition among stands was not significantly correlated with any landscape variable. In 2005 no landscape variables were significantly correlated with shrub richness or rates of extirpation or colonization but average similarity in shrub composition among stands tended to respond to nearby urban cover ($r = 0.246, p < 0.05$) and fallow land ($r = -0.274, p < 0.05$).

Partial Mantel Tests

Overall, correlations among composition of the three forest layers all declined since 1950 (Fig. 4a). When we examined correlations between the composition of the overstory and local edaphic, landscape, and geographic distances, we found edaphic factors predominated ($r = 0.219$ and 0.209, respectively), with no significant change in the strength of these correlations between time periods. In the shrub layer, local edaphic and geographic distances were equally important in controlling variation in 1950 community composition, but the correlation with edaphic distance declined in strength over time ($r = 0.159$ vs. 0.069, $p < 0.01$ on difference), whereas the influence of geographic distance was relatively stable ($r = 0.179$ vs. 0.182, respectively, no significant difference) and landscape similarity was unimportant in both time periods. In strong contrast, the drivers of community composition changed dramatically over the last 55 years (Fig. 4b). Variation in the herbaceous communities was also most strongly correlated with local edaphic and geographic distances in the original survey. In the resurvey data, the strength of the correlation with environmental factors showed a significant decline, whereas correlations with landscape and geographic distances increased sharply over time.

Discussion

In his seminal and often cited work on forest fragmentation in Cadiz township Wisconsin, John Curtis (the principal investigator of the original study) wrote, "The small
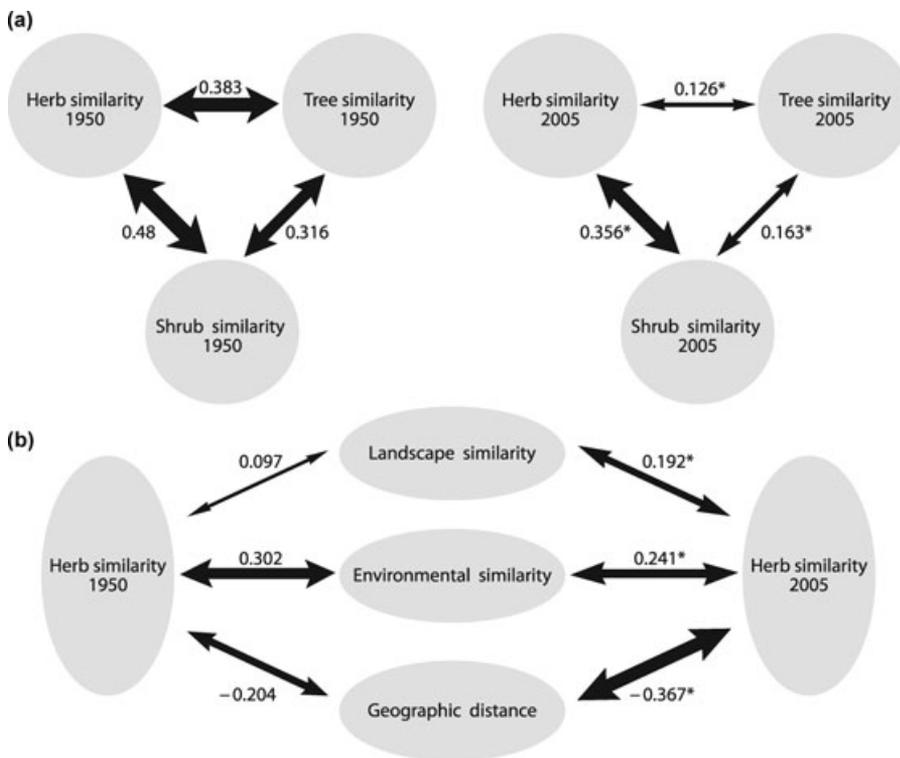
Figure 4. *Changes in partial Mantel correlation values (a) among tree, shrub, and herbaceous communities in each time period and (b) between herbaceous community composition and landscape similarity, environmental similarity, and geographic distance. Partial correlation values in the 2005 analyses marked with an asterisk (*) significantly changed in value (95% CIs do not overlap). Data tables used to create the figure are available from D.A.R.*

size and increased isolation of the stands tend to prevent the easy exchange of members from one stand to another.... As a result, the stands gradually lose some of their species and those remaining achieve unusual positions of relative abundance" (Curtis 1956: 729). Today, the long-term impacts of habitat loss and fragmentation that Curtis predicted for these forests have been realized and the extinction debt has been paid. The size and structure of habitat patches and their surrounding landscape context have emerged as increasingly important predictors of understory richness, heterogeneity, and composition in these forests. Large forest patches in largely intact landscapes lost fewer native species, were more likely to recruit new species, and experienced slower rates of biotic homogenization than did smaller and more isolated patches. As a result, the nonsignificant relationship between native species richness and patch size in 1950 became significant by 2005. Surrounding forest cover was even more strongly correlated with native species losses than was patch size alone and is now the single best predictor of native species richness (Fig. 2). This result suggests that interactions between nearby forest patches within this landscape are more important than patch size alone in the maintenance of local biodiversity. Regardless, upland forest patches in southern Wisconsin now conform to patterns expected from island biogeography theory, and the temporal changes observed resemble those seen in tropical animal communities (Faaborg 1979) and many other systems. These trends are so far largely confined to the herbaceous community, perhaps reflecting

their greater diversity, faster dynamics, or greater reliance on specialized pollinators and seed dispersers.

Although apparent rates of colonization and extirpation were clearly related to landscape variables and influenced changes in forest understory composition, landscape effects were more strongly correlated with patterns of colonization than extirpation, which suggests the differential ability to recruit new species to accommodate stochastic extirpations and changing canopy conditions are critical processes in this system. This result underscores the importance of the ability of new populations to invade habitats in response to shifts in changing conditions (e.g., succession) as an essential process for maintaining metapopulation and metacommunity viability (Moilanen & Hanski 1998; Leibold et al. 2004). Increased habitat isolation and anthropogenic influences on the landscape can reduce biotic connections among habitat patches and matrix permeability, particularly for species with restricted means of dispersal (Mitchell et al. 2002), and tends to favor abundant habitat generalists (Rooney et al. 2004).

As southern Wisconsin forests continue to mature and shift toward increased dominance by more mesic species (Rogers et al. 2008), forest understories are becoming shadier, radically shifting growing conditions for resident herbs. Many species are disappearing in the face of these changes (Rogers et al. 2008). Shade-tolerant species, however, may not be able to colonize these sites if they lack adaptations for plentiful seed production and long-distance dispersal. The two native species that increased

the most over time, *Geum canadense* and *Circaea lute-tiana* (Rogers et al. 2008), produce abundant small, stick-tight seeds that adhere to mammals, which allows them to partially overcome the dispersal limitation that landscape fragmentation may impose. Dispersal ecology may also explain why landscape variables apparently have little influence on these shrub communities. With the exception of the declining *Corylus cornuta* (Rogers et al. 2008), the shrubs in this study all produce berry fruits that are largely dispersed by birds, which may allow them to better overcome the effects of fragmentation compared with their herbaceous counterparts.

Between 1950 and 2005, relationships between edaphic variables and herbaceous community composition decreased, whereas landscape factors and geographic distance became more important. The growing importance of forest extent and the composition of the surrounding matrix here parallels patterns described for tree distributions in New England (Foster 1998) and primary versus secondary forest understories (Vellend et al. 2007). Our work extends the scope of these studies by focusing on primary forests that represented the best available habitats at the time of the original survey. This suggests that the erosion of species–environmental relationships reflects not only direct human disturbances but also the indirect effects of restricted dispersal and changes in the available species pool. In addition, the legacy of the PEL data permits repeated measures rather than substituting space for time, which reduces uncertainty regarding these patterns and more clearly reveals important historical processes.

Our results further imply that the composition of surrounding nonforested habitats affect forest understories. Because our measures of the various land-cover classes were intercorrelated, we cannot definitively say which nonforest elements most affected patterns of species loss and homogenization. Nevertheless, in general, urban cover and road density were more strongly correlated with rates of species loss and homogenization than the amount of fallow land or agricultural cover. These patterns suggest that different types of land cover contribute to biological processes in habitat remnants (Kupfler et al. 2006). More detailed analyses of surrounding nonforest matrix elements may help identify these mechanisms.

These results have important implications for conserving temperate forest diversity. First, our findings match predictions based on island biogeography and metapopulation theory and provide strong support for the idea that these principles provide a firm foundation for designing conservation strategies (Meffe & Carroll 1997; Simberloff 1997). Second, our results provide strong evidence that a lag exists between when landscape conditions change and when those effects manifest themselves. Species richness in the forests sampled in the 1950s had apparently not yet reached an equilibrium despite the dramatic di-rect impacts of European settlement. Decades later, there was a relaxation toward a new equilibrium. This "extinction debt" (Diamond 1976; Tilman et al. 1994) poses challenges for conserving species in isolated fragments and suggests that active management may be necessary to sustain species diversity into the future. Changes in the forest understory may also threaten regional diversity through cascading effects on forest birds (Olson 2008) and other species.

A third implication is that ecologists, managers, and conservation planners can no longer assume classical ecological models emphasizing local site characteristics and succession suffice to predict future composition and dynamics of plant communities. Plant ecologists have traditionally sought to explain variation in community composition in terms of local site conditions, including climate, soils, and (for the understory) forest overstory composition and the resulting light conditions. Nevertheless, the assumptions underlying these paradigms have eroded. Our results point to a reduction in local site influences such as canopy composition and soil conditions on the composition and structure of herbaceous forest understory communities. In contrast, the influences of land cover and surrounding landscape factors on plant communities of the forest understory have grown considerably. The decoupling of individual species responses from local environmental gradients makes predicting plant community composition and response to management more problematic. Therefore, conservation biologists and managers of natural areas should pay more attention to landscape context and conditions. Because surrounding landscape conditions are rarely under the control of managers, the need to plan at landscape scales and work with surrounding landowners to achieve conservation goals is paramount. Maintaining even common species on the landscape in the face of habitat loss and landscape fragmentation may require either establishing regional networks of natural areas capable of sustaining historical metapopulation dynamics or actively assisting the dispersal and local recolonization of species particularly susceptible to impacts from surrounding habitat loss and landscape modification.

Acknowledgments

Literature Cited

Anderson, J. R., E. E. Hardy, J. T. Roach, and R. E. Witmer. 1976. A land use and land cover classification system for use with remote sensor data. Geological Survey professional paper 964. U.S. Geological Survey, Washington, D.C.

Benjamin, Y., and Y. Hochberg. 1995. Controlling the false discovery rate: a practical and powerful approach to multiple testing. Journal of the Royal Statistical Society (Series B) **57:**289-300.

Brooks, T. M., S. L. Pimm, and J. O. Oyugi. 1999. Time lag between deforestation and bird extinction in tropical forest fragments. Conservation Biology **13:**1140-1150.

Cottam, G., and J. T. Curtis. 1956. The use of distance measures in phytoscoiological sampling. Ecology **37:**451-460.

Curtis, J. T. 1956. Modification of mid-latitude grasslands and forests. Pages 721-736 in Man's role in changing the face of the earth. The University of Chicago Press, Chicago.

Curtis, J. T. 1959. The vegetation of Wisconsin. The University of Wisconsin Press, Madison, Wisconsin.

Curtis, J. T., and R. P. McIntosh. 1951. An upland forest continuum in the prairie forest border region of Wisconsin. Ecology **32:**476-496.

Debinsky, D. M., and R. D. Holt. 2000. A survey and overview of habitat fragmentation experiments. Conservation Biology **14:**342-355.

Diamond, J. 1976. Island biogeography and conservation: strategy and limitations. Science **193:**1027-1032.

Drayton, B., and R. B. Primack. 1996. Plant species lost in an isolated conservation area in metropolitan Boston from 1894 to 1993. Conservation Biology **10:**30-39.

Faaborg, J. 1979. Qualitative patterns of avian extinction on Neotropical land-bridge islands: lessons for conservation. The Journal of Applied Ecology **16:**99-107.

Foster, D. R., G. Motzkin, and B. Slater. 1998. Land-use history as long-term broad-scale disturbance: regional forest dynamics in central New England. Ecosystems **1:**96-119.

Goslee, S., and D. Urban. 2007. The ecodist package for dissimilarity-based analysis of ecological data. Journal of Statistical Software **22**(7):http://www.jstatsoft.org/v22/i07

Helm, A., I. Hanski, and M. Partel. 2006. Slow response of plant species richness to habitat loss and fragmentation. Ecology Letters **9:**72-77.

Johnson, E. A., and K. Miyanishi. 2008. Testing the assumptions of chronosequences in succession. Ecology Letters **11:**419-431.

Kupfler, J. A., G. P. Malanson, and S. B. Franklin. 2006. Not seeing the ocean for the islands: the mediating influence of matrix-based processes on forest fragmentation effects. Global Ecology and Biogeography **15:**8-20.

Lamb, E. G., E. Bayne, G. Holloway, J. Schieck, S. Boutin, J. Herbers, and D. L. Haughland. 2009. Indices for monitoring biodiversity change: are some more effective than others? Ecological Indicators **9:**432-444.

Leach, M. K., and T. J. Givnish. 1996. Ecological determinants of species loss in remnant prairies. Science **273:**1555-1558.

Leibold, M. A., et al. 2004. The metacommunity concept: a framework for multi-scale community ecology. Ecology Letters **7:**601-613.

Levenson, J. 1976. Forested woodlots as biogeographic islands. PhD dissertation. University of Wisconsin–Milwaukee. Milwaukee, Wisconsin.

Lindborg, R., and O. Eriksson. 2004. Historical landscape connectivity affects present plant species diversity. Ecology **85:**1840-1845.

McCune, B., J. B. Grace, and D. L. Urban. 2002. Analysis of ecological communities. MjM Software, Gleneden Beach, Oregon.

McGarigal, K., and B. J. Marks. 1995. FRAGSTATS: spatial pattern analysis program for quantifying landscape structure. General technical report PNW-351. U.S. Forest Service, Portland, Oregon.

McKinney, M. L. 2006. Urbanization as a major cause of biotic homogenization. Biological Conservation **127:**247-260.

McKinney, M. L., and J. L. Lockwood. 1999. Biotic homogenization: a few winners replacing many losers in the next mass extinction. Trends in Ecology & Evolution **14:**450-453.

Magnuson, J. 1990. Long term research and the invisible present. BioScience **40:**495-501.

Matlack, G. R. 2005. Slow plants in a fast forest: local dispersal as a predictor of species frequencies in a dynamic landscape. Journal of Ecology **93:**50-59.

Meffe, G. K., and C. R. Carroll. 1997. Principles of conservation biology. Sinauer Associates, Sunderland, Massachusetts.

Middleton, J., and G. Merriam. 1983. Distribution of woodland species in farmland woods. Journal of Applied Ecology **20:**625-644.

Miller, R. I., and L. D. Harris. 1977. Isolations and extirpations in wildlife reserves. Biological Conservation **12:**311-315.

Mills, J. E. 2008. Fifty years of change in Wisconsin cedar glades. The American Midland Naturalist **159:**214-224.

Mitchell, C. E., M. G. Turner, and S. M. Pearson. 2002. Effects of historical land use and forest patch size on myrmecochores and ant communities. Ecological Applications **12:**1364-1377.

Moilanen, A., and I. Hanski. 1998. Metapopulation dynamics: effects of habitat quality and landscape. structure. Ecology **79:**2503-2515.

Olden, J. D., and N. L. Poff. 2003. Toward a mechanistic understanding and prediction of biotic homogenization. The American Naturalist **162:**442-460.

Olson, A. 2008. Fifty years of change in southern Wisconsin forest bird communities. MS thesis. University of Wisconsin, Madison, Wisconsin.

Ouborg, N. J. 1993. Isolation, population size and extinction: the classical and metapopulation approaches applied to vascular plants along the Dutch Rhine-System. Oikos **66:**298-308.

Radeloff, V. C., R. B. Hammer, and S. I. Stewart. 2005. Sprawl and forest fragmentation in the U.S. Midwest from 1940 to 2000. Conservation Biology **19:**793-805.

Rhemtulla, J. M., D. J. Mladenoff, and M. K. Clayton. 2007. Regional land-cover conversion in the U.S. upper Midwest: magnitude of change and limited recovery (1850-1935-1993). Landscape Ecology **22:**57-75.

Robinson, G. R., M. E. Yurlina, and S. N. Handel. 1994. A century of change in the Staten Island flora: ecological correlates of species losses and invasions. Bulletin of the Torrey Botanical Club **124:**119-129.

Rogers, D. A. 2006. Fifty years of change in southern Wisconsin forests: patterns of species loss and homogenization. PhD dissertation. University of Wisconsin, Madison, Wisconsin.

Rogers, D. A., T. P. Rooney, D. Olsen, and D. M. Waller. 2008. Shifts in southern Wisconsin forest canopy and understory richness, composition and heterogeneity. Ecology **89:**2482-2492.

Rooney, T. P., and W. J. Dress. 1997. Species loss over sixty-six years in the ground-layer vegetation of Heart's Content, an old-growth forest in Pennsylvania, USA. Natural Areas Journal **17:**297-305.

Rooney, T. P., S. M. Wiegmann, D. A. Rogers, and D. M. Waller. 2004. Biotic impoverishment and homogenization in unfragmented forest understory communities. Conservation Biology **18:**787-798.

Simberloff, D. 1997. Biogeographic approaches and the new conservation biology. Pages 274-284 in S. T. A. Pickett, R. S. Ostfeld, M. Shachak, and G. E. Likens, editors. The ecological basis of conservation: heterogeneity, ecosystems, and biodiversity. Chapman & Hall, New York.

Soulé, M. E., B. A. Wilcox, and C. Holtby. 1979. Benign neglect—model of faunal collapse in the game reserves of East-Africa. Biological Conservation **15:**259–272.

Terborgh, J. 1999. Requiem for nature. Island Press, Washington, D.C.

Tilman, D., R. M. May, C. L. Lehman, and M. A. Nowak. 1994. Habitat destruction and the extinction debt. Nature **371:**65–66.

Vellend, M. K., et al. 2007. Homogenization of forest plant communities and weakening of species-environment relationships via agricultural land use. Journal of Ecology **95:**565–573.

Waller, D. M., and T. P. Rooney. 2004. Nature is changing in more ways than one. Trends in Ecology & Evolution **19:**6–7.

Wisconsin DNR (Department of Natural Resources). 1998. WISCLAND land cover (WLCGW930). Wisconsin DNR, Madison.

Zartman, C. E., and H. M. Nascimento. 2006. Are habitat-tracking metacommunities dispersal limited? Inferences from abundance-occupancy patterns of epiphylls in Amazonian forest fragments. Biological Conservation **127:**46–54.