Fifty years of change in southern Wisconsin forests: patterns of species loss and homogenization

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Abstract

We use quantitative surveys from the UW Plant Ecology Lab in the 1950's to infer long-term shifts in species composition of southern Wisconsin forests. Succession has shifted tree composition away from oaks (*Quercus*) and towards more mesic species (*Acer* spp.). More than 80% of sites lost native understory species richness with an average decline of 22.4% . Species losses are almost twice as high in late successional stands than early successional stands with relatively shade intolerant taxa showing the most conspicuous declines. Rates of native species loss, floristic quality and community homogenization are negatively correlated with measures of forest fragmentation and urbanization. Current land use patterns also influenced rates of species loss, with lack of deer management emerging as a key predictor of species loss. Invasion of both native and exotic species both respond more to surrounding landscape features than to local site factors, but in opposite ways. Declines in recruitment in more fragmented landscapes is more important than extirpation in explaining overall changes in native species richness. Exotic species invasions are strongly dictated by human dominance of the landscape regardless of local site conditions. Thus, both native species diversity and exotic species invasions reflect the surrounding species pool and their respective abundances and dispersal abilities.

Finally, we evaluate how gradients in local site conditions and surrounding landscape composition influence the composition of southern Wisconsin forests and how these relationships have changed over time. Overstory composition in both time periods strongly reflects underlying moisture and nutrient gradients despite significant successional changes. In contrast, proximal drivers of native herb species composition o shifted from local overstory and local edaphic factors to metrics of landscape fragmentation and urbanization. Species persistence and abundance patterns appear to reflect meta-population and meta-community dynamics in fragmented landscapes than local edaphic conditions. These results strongly support the idea that to sustain plant diversity in the face of landscape fragmentation and urbanization, we need to think and manage at landscape scales, protecting larger blocks of habitat from development and re-establishing landscape connectivity between isolated populations.

Long-term shifts in southern Wisconsin forest communities.

I. Are understory changes linked to shifts in overstory conditions?

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Abstract

We use extensive quantitative surveys of Wisconsin plant communities by John Curtis and colleagues during the 1950's as baseline data for inferring long-term shifts in the species composition and structure of these communities. Sixteen of 110 forested sites surveyed by Curtis in southern Wisconsin have been developed (14), farmed (1), or intensively grazed (1). We re-surveyed the remaining 94 forest stands in 2002-2004 to obtain data on forest under-and over-story species composition in order to infer shifts in overstory composition (succession), tree seedling densities, native and exotic species richness and abundance, and overall floristic quality. Succession has generally shifted tree composition away from oaks (*Quercus*) and towards more shade-tolerant species (*Acer* spp., *Carya cordiformis*, *Ulmus* spp, and *Prunus serotina*). Stands initially dominated more by shade intolerant trees like oaks and occurring on coarse textured nutrient poor soils have shifted the most in composition, generally gaining overstory richness and diverging in composition. In contrast, forests on richer sites have tended to lose species and converge in composition. Tree seedling densities have declined by over 50% with a 16% decline in species richness. *Quercus* spp. and *Ostrya virginiana* declined the most in seedling abundance. Although woody species have declined in absolute abundance, they have increased 15% in abundance relative to herbaceous species, reflecting more dominance by shrubs in the understory. Exotic species occurred in 13 stands in 1949-1950 representing 5.5% of the flora but now occur in 76 stands and account for 8.4% of the species present. Most sites (80%) lost understory native species with mean species density declining 25% at the 1 m^2 scale and 22.4% at the 20 m^2 scale. Gains in exotic species richness and abundance are not closely linked to declines in native species cover and richness but are correlated with declines in native floristic quality. Rates of native understory species loss are almost twice as high in late successional stands relative to early successional stands with grasses, sedges and similar narrow leaved taxa showing the most conspicuous declines. Although closing canopies have clearly driven some of these conspicuous shifts in forest understory composition and diversity, the surprising amount and kinds of change observed further imply that other forces are also at work.

Keywords: oak forest; species losses; biotic homogenization; floristic quality; succession

Introduction

Both community ecology and conservation biology seek to understand the forces driving changes in community structure and composition and how these forces may act in concert across landscapes so as to cause communities to converge or diverge in composition. Their efforts are stymied, however, by a scarcity of long-term data replicated at many sites across a region. This problem, termed "the invisible present " Magnuson (1990) or "the shifting baseline syndrome" (Pauly 1995), represents a major limitation in understanding long-term trends in ecological communities. Without reliable baseline data, it is impossible to infer whether and how communities are changing and whether these changes are consistent across sites. This, in turn, impedes our ability to infer how modifications in site conditions, local management, or surrounding landscape conditions might modify these patterns of change so as to better sustain biological diversity or other values.

Studies of longer-term shifts in forest communities are few. Those that do exist (e.g., Kwiatkowska 1994, Robinson et al. 1994, Fischer and Stöcklin 1997, Rooney and Dress 1997) consistently report sizable losses of understory plant diversity and invasions of exotic plants over intermediate time scales (Waller and Rooney 2004). These studies generally support the notion that major shifts in community composition are occurring even (and sometimes particularly) at seemingly undisturbed or protected sites (Leach and Givnish 1996, Rooney et al. 2004, Wiegmann and Waller 2006). These studies, however, are usually based on species lists from a single site, limiting our ability to infer how pervasive and consistent the observed changes are. Terborgh (1999) hypothesized that such changes might be pervasive, while pointing out that the lack of baseline data hinders our ability to demonstrate such trends.

Here, we report the results of re-surveying 94 forest stands distributed across southern Wisconsin 55 years after they were first surveyed by John Curtis and colleagues of the Univ. of Wisconsin Plant Ecology Laboratory (PEL). Their initial surveys of these sites and hundreds of other sites across the state were summarized in his seminal book, *The Vegetation of Wisconsin* (Curtis 1959). This work was aimed at providing a full and quantitative description of the state's plant communities and to test Gleason's (1926) idea that plant species respond individually to gradients in environmental conditions, resulting in a continuous variation in plant community composition. Because they carefully archived the original data, we were able to precisely re-locate and re-sample the same stands. These baseline data have also been used to study long-term changes in Wisconsin prairie remnants (Leach and Givnish 1996) and in northern Wisconsin forests (Rooney 2004, Wiegmann & Waller 2006).

Our proximal goal here is to is to characterize the nature and range of changes that have occurred in southern Wisconsin forests. Because succession is an obvious factor driving ecological change in these forests (Lorimer 1984, 2003) , we focus here on shifts in the overstory, how these depend on initial site and forest conditions, and how shifts in the understory reflect changes in overstory conditions. Because considerably more plant diversity occurs in forest understories than in the canopy, we pay particular attention to shifts in understory composition. We also explore the role of exotic plant invasion in driving some of these changes in composition and diversity. We expect understory species losses and community homogenization to be greater in the forests of southern Wisconsin than in the north as the southern forests used to experience recurrent fires and continue to shift in composition with succession to other canopy types and increased shrub cover. In addition, the southern forests are more fragmented and occur in a more sparsely populated and developed landscape with a higher prevalence of exotic species. In subsequent papers, we explore the role of landscape factors (forest fragmentation and development intensity - Rogers et al, forthcoming 2) and shifts in the links between over- and under-story composition and local edaphic conditions (Rogers et al. forthcoming 3).

Background

At the time of European settlement, southern Wisconsin was a patchy mosaic of woodland and prairie with a predominance of oak savanna south of the biogeographic / climatic gradient referred to as the “Tension Zone” (Curtis 1959). Open vegetation in southern Wisconsin was probably maintained by fires set by pre-Columbian Americans who used fire to manage the landscape (Dorney 1981). As European settlers cleared the original vegetation, they fragmented and disrupted both these ‘firesheds’ and the patches of forest that occurred where fires were less frequent and intense. These changes both drastically reduced the frequency and intensity of fires on the landscape, and also reduced forest patches to tiny islands lost in the sea of the modern agricultural and urban landscape. As fires declined in frequency, size, and intensity, oak savannas and prairies often gave rise to the oak forests sampled by Curtis and colleagues (Cottam 1949). This vegetation type was probably less common in previous centuries as evidenced by the open grown trees that persist in many of the sampled stands (Curtis 1959). We therefore expect succession to have had significant influences on the forests we sampled in 2002-04, reducing the prevalence and abundance of shade intolerant species (particularly black oaks types) while favoring shade tolerant species, as already reported (Peet and Loucks 1977, Lorimer 1984, McCune and Cottam 1985). Such shifts in canopy succession may have complex effects on understory diversity. Under the intermediate disturbance hypothesis (Connell 1978), for example, we expect early succession forests to gain species while later successional forests should lose species. Roads, development, and fragmentation have also likely contributed to the invasion of many weedy exotics while limiting the dispersal of native woodland plants among forest patches. Hunting and these landscape changes have also reduced or eliminated certain species that effectively disperse seeds including passenger pigeons, large mammals, and seed dispersing ant species.

METHODS

Study area

Study sites occurred throughout Southern Wisconsin (Fig. 1) and are all located within the Eastern Deciduous Forest Province (Albert 1995). Their elevation ranges from 177-488 m above sea level. The climate is continental, with precipitation ranging from 61-84 cm, increasing from west to east. Topography varies considerably across the study area, primarily between the glaciated region to the east with Silurian origins and the unglaciated ‘driftless’ area to the west. The glaciated region displays various landforms, including glacial till, moraines, drumlins, and outwash plains. In contrast, the driftless area is mostly highly dissected upland of Ordovician origin (Albert 1994) with agriculture limited to valley bottoms, leaving many forested slopes. Forests in this region are more common now than in the pre-settlement landscape and less dissected by development and roads.

Site selection and vegetation sampling

Curtis et al. chose an initial set of potential study sites by contacting regional foresters, land managers and educators throughout Wisconsin. Of these, they only sampled stands at least 6 ha in area, uniform in topography, with no evidence of domestic grazing, and no recent logging activity. Sites meeting these criteria were sampled by first randomly choosing an initial sampling point 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 method (Cottam and Curtis. 1949) at 40 points spaced evenly along a square U-shaped transect (mean distance ~ 15 - 20m). A 'walk-through' list of all vascular plants within the sampled boundary was also made for each site. They also recorded the presence/absence of all herb, shrub, and tree seedling species in each of twenty 1-m^2 quadrats placed at the first 20 points along the transect. Some deviations from these general methods occurred in some stands in response to local conditions (e.g., parallel lines vs. the u-shaped transect).

We relocated and resurveyed 117 of these stands in 2002-04 using similar but more intensive methods, taking effort to replicate the spatial scale of the original sample. Of the 237 stands we considered for the Southern Forest Project, 27 stands had unreliable data and 95 lacked quantitative information on understory composition. We rejected these stands outright. Of the remaining 114 sites, 14 were developed for residential or commercial use, 1 was actively grazed by cattle, one was converted to crop land, and four sites were inaccessible (usually because the landowner refused access), leaving 94 sites for this analysis (Fig. 1). We sampled any forest that retained its tree canopy except for yards, pine plantations, and stands used for pasture. We included forest patches even when they occurred in partly residential areas if they exceeded 6 undeveloped hectares.

At each site, we worked from the original hand-drawn map to identify the stand to be sampled to within a few hectares. To expand the sample size, capture uncertainty in the exact location of the original transect, and measure variation due to sampling location, we replicated the original survey transect four times, endeavoring to retain the same aerial extent as the original survey and locate each replicate within a homogenous portion of the stand (as judged by canopy composition, slope, and land-use history). We located replicate #1 in that portion of the stand we judged to be most similar to what was described in the original survey (as judged by slope, topography, canopy composition of largest trees, and the absence of recent disturbance). Each replicate transect began at a randomly chosen starting location and contained twenty 1m^2 quadrats spaced at roughly 20m intervals (approximating the average distance between quadrats in the original study). We sampled trees using the same random pairs method used in the original survey (Cottam 1949) but replicated 2x, resulting in 160 trees per site (compared to 80 trees per stand in 1950). Replicate one was again assigned to the sampling location most closely fitting the original selection criteria and therefore correspond spatially to replicates 1&2 of the understory sample. The random-pairs method assumes random tree placement and tends to over sample large trees, making it somewhat unreliable for estimating stem density (Cottam and Curtis. 1955). However, we chose to retain the original methods because 1) the method improves considerably at larger sample size (appendix), and 2) it is important to match the original methods to allow direct comparisons of the results, without additional bias introduced due to changes in sampling regime. Finally, plot-less methods are efficient and quickly provide a dispersed sample of canopy trees, a critical factor that allowed for a larger sample of stands in both time periods.

Within the twenty 1m² quadrats in each replicate, we recorded the identity of all herbs, shrubs and tree seedlings (<50 cm height, ignoring that years' class) present. Although we also made 'walk-through' lists of the species present at each site, we do not analyze these further as they vary in area sampled, time spent searching, and skill levels of the observers.

Soil characteristics

We collected soil samples from ten randomly dispersed points in the sample area at each site, sampling at least 300 cc from the top 10cm of soil in each. These were then pooled and refrigerated until taken for analysis at the UW Soil & Plant Analysis Laboratory. These were assayed for soil texture (% sand, silt, and clay) and constituents (% organic matter, pH, % total nitrogen, phosphorus, potassium, calcium, and magnesium). We subjected these data to principal components analysis to extract a set of independent synthetic variables representing variation in soil conditions across these sites.

STATISTICAL ANALYSES

Taxonomic Synchronization

In 2002-04, we identified all taxa to species in the field using keys from Gleason and Cronquist (1991) and Voss (1972, 1985, 1996) and the UW–Herbarium's species list. All questionable species were collected for later determination and verification by experts (vouchers on deposit at WIS). We entered all data from the original PEL summary sheets into a database which we then cross-checked against the original field data, correcting the few errors PEL staff made in transferring these data. From these, we compiled a full species list, translating the various names, abbreviations, and codes used in the original data to current nomenclature as compiled by the UW herbarium (http://botany.wisc.edu/herbarium/; see Appendix A). In most cases, taxonomic synchronization was a simple matter of updating names (e.g., *Hepatica acutiloba* to *Anemone acutiloba*). In other cases, however, the PEL data lumped species, split taxa that are now combined, or applied inconsistent taxonomic resolution between observers. In these cases, we combined taxa into the next highest taxonomic group (e.g. *Carex spp, Dryopteris carthusiana, Botrychium multifidum*). Great care must be taken when lumping taxa not to obscure ecological and regional differences in similar taxa as in the *Quercus rubra complex, Corylus americana/cornuta, Anemone acutiloba/americana, Ribes missouriensis /cynosbati,* and *Trillium cernuum/flexipes*. The species within such groups often have distinctive ecological requirements or separate ranges within the northern and southern forests of Wisconsin. Lumping such species could significantly affect analyses and interpretation of these data. As different levels of taxonomic resolution also may be appropriate for different types of analysis, we must make such decisions carefully and with an intimate knowledge of the species' habits and habitats of the region . To assess the effects of such decisions, we compared estimates of species loss and homogenization across different levels of taxonomic resolution (Appendix B). We found that although point estimates of species loss and homogenization shifted with variation in taxonomic resolution and sample size, relationships of dependent variables to the various predictor variables remained qualitatively and quantitatively similar. These results give us confidence that trends we report here are robust.

Assessing overstory change and effects of succession

Increased shade and competition from the forest overstory can fundamentally change the growing environment for understory species. Similarly, changes in shrub and sapling cover can radically alter the light and soil resources available for herbaceous species in the understory. We assessed shift in overstory composition by computing several variables. Our first approach involved assessing changes in tree stem density and stand basal area (expected to decline and increase, respectively). The tree sampling in 1950 and 2002-04 provided estimates of stem density by species and associated basal areas. We used these to estimate overall stem density and total basal area per ha for each stand in each time period and changes in these variables.

To assess rates and effects of succession, we first used a weighted average of Curtis's (1959) Climax Adaptation Values (CAV) to place each stand along a Continuum Index (CI). These CAV values reflect the judgment of Curtis's peers regarding the fidelity of individual canopy species to particular position along a gradient of soil nutrients. Peet and Loucks (1977) developed a parallel successional index for southern Wisconsin forests that complements these CAV values by breaking Curtis' uni-dimensional gradient into a bi-dimensional gradient representing both edaphic conditions and disturbance. Their Successional Index (SI) is based on these inferred Successional Adaptation Values (SAV). We computed both CI and SI values by averaging the CAV and SAV values for all trees present at each site, weighted by both relative basal area and relative density. We also calculated rates of change in these values for each stand using $N_{2000} = \lambda N_{1950,}$ where ln(λ) represents the rate of change and N is the variable of interest. We assessed the role of succession in driving changes in various dependent variables using these indexes of succession as predictor variables in correlation and multiple regression analyses.

Changes in Richness and Heterogeneity

Because the number of species sampled generally increases with the area sampled, we need a standardized sample area to directly compare species occurrences and richness between 1950 and 2003. This is simple in the case of quadrat richness (species/m^2) where we simply compare these average values. However, sample areas (and the number of trees sampled for trees) were several times higher in 2002-04 than in 1950 (and also varied somewhat among the original Curtis samples). We therefore standardized the sampling area for herbs, shrubs, and tree seedlings to 20 m^2 corresponding to the usual area sampled in 1950. We similarly standardized the tree samples to 80 individuals. We investigated several methods of estimating species richness at these scales, including using the first replicate, averaging the replicates from 2002-04, and passive sampling (Gotelli and Graves 1996). As all three methods yield similar results and trends (Appendix C), we only report the results from passive sampling here. Communities that are losing rarer native species and gaining common and exotic species often tend to converge in species composition in a process termed biotic homogenization (McKinney and Lockwood 1999b, Olden and N.L.Poff 2003). Measures of community similarity and therefore biotic homogenization generally depend on which similarity measure is used, data transformations and sample size. We therefore experimented with alternative methods of estimating changes in community similarity: varying sample size, measures of abundance (presence, frequency, and relative frequency) and similarity measures. As was the case with taxonomic resolution, results were generally similar among methods (Appendix C) and we only report data for the Sørenson distance measure based on replicate 1 and derived from both presence and relative abundance data from the 20 $1m^2$ samples in either time period.

To quantify dominance by habitat generalists, we use the coefficients of conservatism (C of C) developed by the WDNR (Bernthal 2003) and available on the UW Herbarium website. Swink & Willhelm (1994) first developed this approach which is based on tabulating expert opinions on the range of habitats for each native species in the regional flora. C of C values range from 0 – 10 with values of 0 representing extreme habitat generalists while values of 10 represent species with high fidelity to undisturbed, intact habitats. For each site, we calculated a floristic quality index (FQI) defined as the mean C of C weighted by abundance, (Rooney and Rogers 2002) in each sample period and then calculated the rate of change as above. We compare values between time periods using paired t-tests and as a function of canopy changes and native species richness. We then use correlation and multiple regression to test for effects on changes in FQI on changes in community similarity.

We test the significance of changes in species richness, average similarity among sites, species habitat breadth, and successional index using paired t-tests, with sites serving as replicates. To track 55 year changes in the frequency of individual species through time, we use non-parametric G-tests **(Sokal& Rholf)**, accumulating values across sites to test for regional shifts in abundance.

We estimate rates of change between the two sample periods using $N_{2000} = \lambda N_{1950,}$ where ln (λ) is the rate of change, and N is the variable of interest. We add 0.01 to both the numerator and denominator when calculating rates of change in exotic species and woody taxa to avoid dividing by zero. We use Pearson correlation and multiple regression to test the significance of relationships between these estimated rates of change and various predictor variables.

Ordination and species contributions to similarity

To look at changes in community composition and to gain insight into the types of species most sensitive to change, use non-metric multi-dimensional scaling (NMS) to reduce the species/site matrix to a set of orthogonal synthetic axes that represent sites in species space such that samples of similar composition are closer together in ordination space than sites with few species in common. To test for differences between time periods in ordination space, we then use ANOSIM **(Clark 1993)** as implemented in Primer 5, a nonparametric procedure for testing the hypothesis of no difference between groups in the similarity matrix. To get estimates of individual species contributions to group identity in ordination space, we use the SIMPER analysis as implemented in Primer 5. We then use these shifts in relative importance of individual species, coupled with changes in total frequency (sum of site frequencies for each taxa) to gain insight into potential mechanisms contributing to shifts in species abundance. If succession is indeed driving observed changes, we expect thin leaved, shade tolerant species to increase in importance at the expense of thick leaved, sun loving taxa (Givnish 1979, 1987)**.**

RESULTS

Forests in southern Wisconsin are losing oaks, gaining mesic species like maples, and experiencing increases in the cover of shrubs relative to herbs. These shifts in the overstory, in turn, appear linked to conspicuous declines in understory species richness, cover, and heterogeneity. We describe these trends in turn, starting with changes in the overstory.

Shifts in stand density and structure

These forests appear to be declining in tree density with concomitant increases in average tree size. Tree density appeared to decease about 10% (from 380 to 318 trees/ha, $p < 0.0001$). This apparent decline in density may also account for the unexpected decrease in stand basal area/ha (from 25.7 to 23.1 m^2/hectare, $p = 0.02$). In contrast, mean individual tree basal area increased slightly but not significantly over the last fifty years (from 716 to 751 cm^2, $p = 0.315$).

Shifts in tree species composition

The canopies of these forests are undergoing systematic shifts in composition and structure. All *Quercus* species significantly declined in importance while more shade-tolerant taxa including *Acer* spp., *Carya cordiformis, Ulmus spp.,* and *Prunus serotina* all increased (Figures 2a & 2b). The black oaks (*Q. rubra & Q. velutina*) have declined faster than oaks in the white oak group (55% vs. 29%). Note that across all oak species, these declines in importance are driven by dramatic declines in density rather than declines in average tree basal area, which has actually increased as the stem size distribution has shifted from an approximation of the reverse j shaped curve often seen in expanding population to the humpshaped distribution expected in mature populations (Fig. 3). This observed shift is entirely consistent with that expected for a population in decline.

Shifts in forest tree richness and heterogeneity

Based on the standardized samples of 80 trees, tree richness increased on average 11.5%, (from 9.0 in 1950 to 10.0 species/site in 2002, $p < 0.001$). As one might expect, this increased richness brought increases in canopy heterogeneity. Average canopy similarity decreased 8% (from 35.1 to 32.3, $p < 0.001$) calculated from species' frequencies and 13.8% (from 36.9 to 31.8, $p < 0.0001$) when calculated using dominance.

Tree seedlings declined conspicuously in density and diversity (table 1). Species richness for tree seedlings at the 20 m^2 scale also declined about 16% (from 5.38 to 4.51 species, $p < 0.001$). Overall seedling densities declined by more than 50%, with particularly conspicuous declines in *Quercus spp.* and *Ostrya virginiana.* Certain shade tolerant species including *Acer saccharum & Tilia americana* showed less dramatic declines in abundance and actually increased in terms of relative abundance. In contrast, weedier trees (*Acer platanoides, Celtis occidentalis, Acer negundo* and *Carya cordiformis*) all showed significant increases in frequency (G-test, $p < 0.01$). Overall declines in tree seedlings suggest that these stands may be shifting toward shrub dominance **(**Lorimer 1994**).**

Successional changes

The average SAV score rose 33.4% (from 4.62 to 6.17, $p < 0.0001$) when measured using stem frequency data and 28.5% (3.95 to 5.08, $p < 0.0001$) when measured using relative basal area. Both measures indicate that later successional species are increasing and starting to dominate southern Wisconsin forests. The amounts of successional change (as judged by shifts in SAV scores) also vary in response to the successional state of the stand in 1950 (Fig. 4). Oak-dominated stands with low initial SAV values showed greater increases in SAV (r^2= 59.3%, $P < 0.0001$), greater gains in tree richness ($r^2 = 30.3\%$, $P < 0.001$), and more declines in average similarity ($r^2 = 23.6\%$, $p < 0.001$). The increased relative dominance of shade tolerant seedlings mentioned above suggests that these successional trends will continue.

Effects of edaphic factors on canopy changes

Edaphic factors had small but significant effects on shifts in forest tree richness and patterns of canopy similarity (table 2). Stands on coarse textured, nutrient poor soils tended to gain canopy species and to increase in heterogeneity. In contrast, stands on fine textured, relatively nutrient rich soils tended to lose canopy species and to converge in canopy composition**.** Early successional forests also tended to increase in richness and heterogeneity while later successional forests tended to lose canopy species and converge in composition. These variables, however, are not independent in that coarse, nutrient poor soils tend to have a low initial successional index. In a step-wise multiple linear regression model, the initial SAV emerges as the most significant predictor of changes in canopy richness, though soil texture and successional stages improves the adjusted r^2 of model from 32.5% to 45.7% . Initial successional state is also the best predictor of changes in site similarity, though the model also improves with the addition of soil texture and successional changes to the models (increases adjusted r^2 of 25.1% to 31. 9%).

NMS Ordination Results and species contributions to similarity

The relative magnitude and consistency of these shifts in overstory composition are perhaps best understood with ordination (NMS, 3 dimensional solution with a final stress of 0.13). In species space, the resurvey data shows higher variability and dispersion than does the original data . A non parametric ANOVA of year vs. 3-dimensional ordination space (ANOSIM in Primer, MRRP in PCORD) show a significant difference between sample periods in tree ordination space. The separation of the two groups is difficult to see in two dimensions, no matter which pair of axis is used (Fig. 5). In three dimensions, the separation clarifies somewhat with the proper imagination (imagine the cloud of stands in 3 dimensional ordination space exploding with the resample stands radiating outward). The lack of clear definition along and one or two dimensions suggests multiple influences and alternate successional pathways, perhaps driven by regional or landscape variation.

Analysis of species contributions to the 3 – dimensional ordination solution provide a much clearer picture of species changes, however (table 3). In the original survey, the average similarity between plots was 34.6 with *Quercus rubra & Quercus alba* contributing the most to the group in ordination space (contributing 31.3% & 27.9% respectively and 59.2% collectively), with *Acer saccharum and Tilia americana* running a distant third and fourth (10.7% & 8.2% respectively and 18.9%). In the resurvey data, average similarity decreased to 32.5% and the species dominance of the top four species is reversed. Together, *A.saccharum & T. americana* contribute 37.6% to the overall solution while the combined influence of *Q. alba and Q. alba* was reduced to 26.3%. The resurvey data also had more species contributing to the ordination, six species accounted for > 90 % of the variation in the original survey whereas in the re-sample it took nine species to get > 90% of variance explained.

Changes in understory herbs and shrubs

Southern Wisconsin forests are losing significant amounts of their vascular plant diversity at all scales considered in this study. Across the understories of these 94 sites, Curtis and colleagues sampled 233 taxa (13 exotic) in 1950. Of these, 68 (29%) did not appear in replicate 1 of the resample while 46 (19.7%) did not appear anywhere in the resurvey at all, despite a 4x increase in sampling intensity. However, we detected an additional 55 taxa (22 exotic) in the sample from replicate and additional 90 species (37 exotic) for a total of 233 species (31 exotic) for the first replicate and 289 (45 exotic) taxa for the entire resample. Thus, we observe an 8.2% decrease in the regional native species pool when corrected for sample size. Conversely, the regional pool more than doubled (+ 238%) for exotic species increasing from 5.5% of the total species pool in 1950 to 13.3% today.

We also observe conspicuous declines in understory species richness within sites. Of the 94 sites resurveyed (figure 6), 70 (75%) showed declines in native species richness at the 20 m^2 scale while only 24 gained species or remained stable. Species density declined from 8.5/m^2 in 1950 to 6.4/m^2 in 2005, a 25% reduction **(**$t = 7.30$, $p < 0.0001$). In 1950, the average site had 38.1 native species/20m^2 but this declined 22.4% to 29.5/20m^2 by 2002-04 ($t = 8.25$, $p < 0.0001$). Native understory herbs declined 25.6% overall (28.7 vs. 21.3, $t = 7.27$, $p < 0.0001$). In contrast, woody shrubs persisted much better than either tree seedlings or herbaceous plants, declining only about 5% (9.5 vs. 9.0, $t = 3.39$, $p = .053$). This differential persistence led to a

14.7% increase in the relative abundance of woody species (18.5% to 21.7%, t = - 3.08, p = 0.003) in the understory, despite the fact that shrub species occurrences actually declined significantly. The shrub to tree seedling ratio (based on their frequencies in $20m^2$) has increased 11% (from 0.598 to 0.664, t = 4.5, p = 0.006). Thus, shrubs now dominate both herbs and tree seedlings in many of these understories.

Shifts in native understory floristic quality and heterogeneity

Changes in community heterogeneity in southern Wisconsin forest understories changed in interesting ways as shifts in homogeneity among sites depended on the similarity measure used. Similarities calculated from abundance data demonstrate some convergence in community composition (biotic homogenization) while similarities calculated from presence data only showed divergence. The mean Sørensen (Bray-Curtis) similarity based on native species (excluding tree seedlings) increased 5.1% (from 31.1 to 32.6, t = - 3.47, p = 0.004). Native shrub similarity, in particular, increased steeply (18% from 0.282 to 0.332, t = - 6.25, p < 0.0001). In contrast, native similarity showed only weakly significant changes, increasing 3.5% (t = -2.04, p = 0.045) . The estimate of changes in community similarity based on the presence or absence of native species (giving equal weight to rare species) gives a contrasting result. This measure declined 9.3% (from 27.8 to 25.2, t = 4.91, p < 0.0001), suggesting that these forest understories are diverging in composition, but converging in terms of species dominance. Simultaneously, habitat generalist increased as the floristic quality of the native forest understory taxa showed significant declines, dropping from 3.64 to 3.83 (8.7%, t =4.01, p < 0.001) between the two sample periods

Invasions of exotics

Exotic species have invaded many southern Wisconsin forests over the last fifty years. While exotic taxa were present in only 13 stands (14%) in 1950 they now occupy 76 sites (80.9%). Their relative abundance has also increased seven-fold, from an average 1.2% in 1950 to 8.4 % in 2002-04. Even at sites where exotic species were already present, their relative abundance has increased four-fold (from 2% to 8%). Including exotic species in the calculation of community similarity tends to increase heterogeneity, providing no support to the idea that exotic invasions are increasing biotic homogenization (see appendix for full results) .

Is succession related to changes in community composition?

Canopy composition and successional state appear closely linked to understory composition and dynamics in southern Wisconsin forests. As noted above, early successional stands changed more than late successional stands and because of this correlation stands undergoing more successional change in the canopy lost fewer understory species ($r = 0.275$, $p = 0.007$).

Nevertheless, late successional forests lost more understory species than early successional forests, particularly at the most local ($1m^2$) level (figure 7). Similarly, stands showing greater increases in canopy volume (BA/hectare) had greater rates of species loss ($r= -0.306$, $p = 0.001$). In a multiple regression, both initial SI and changes in volume remain significant ($r^2 = 23.1\%$, $p < 0.0001$), each contributing about equally to explaining overall variation.

Understory estimates of floristic quality also appear related to canopy conditions with late successional forests tending to have higher floristic quality. This link, however, appears to be weakening as reflected in a decline in the strength of the correlation between SAV and FQI ($r = 0.482$ in 1950 , vs. $r = 0.316$ in 2005).

Forests in the hillier unglaciated (‘driftless’) region of SW Wisconsin are undergoing less severe shifts in understory composition than the flatter and more fragmented forests that occur in SE Wisconsin. These regions differ conspicuously in rates of native species loss (-0.18 vs. -0.43 at $1m^2$, $p = 0.006$; -0.12 vs. -0.41 at $20m^2$, $p < .001$), the rates at which sites are gaining exotic species (0.86 vs. 1.45, $p = 0.001$), and the rates at which sites are converging in composition (homogenization: 1.89 vs. 2.12, $p = 0.002$). Such stark differences suggest that landscape features like forest patch size and the intensity of surrounding land use (agriculture, roads, and development) may have important effects on long-term forest plant dynamics (see Rogers et al. 2, in prep).

Effects of species loss and succession on changes in community heterogeneity

Not surprisingly, stands that are gaining (or at least not losing) species are gaining (or declining less) in floristic quality ($r = 0.381$, $p < 0.0002$). However, shifts in species richness had few direct effects on community heterogeneity. Although succession appears linked to the changes we observe in understory native richness, the relationship with changes in average similarity is less clear. In general, late successional stands on fine textured, nutrient rich sites have converged more in species composition than have early successional stands or those on coarse-textured, nutrient poor soils (table 4). However, stepwise linear regression drops all measures of SAV and only retains measures of soil texture (% Clay, % Silt) and soil calcium (adjusted $r^2 = 21.25$, $p < 0.0001$).

NMS Ordination and Species Contributions

NMS ordinations of native understory, native herbs and native shrubs each returned a 3 – dimensional solution with a final stress of 0.15, 0.15 and 0.17 respectively. All three ordinations show conspicuous native community composition when sites are plotted in species space (figure 8). ANOSIM analysis confirms this result, showing highly significant difference between 1950 and 2005 sample groups. In 999 permutations for each test, not once did the permuted statistic exceed the test statistic (Global R of 0.243, 0.262, 0.135 respectively, all p – values < 0.001). Analysis of within group species contributions also reveal dramatic changes in species composition and provide insight into possible mechanisms of change. As noted above, average similarity declined, a point emphasized by the number of species contributing to 90% of the similarity between stands. In the original survey 38, 27 and 11 species collected explained contributed 90% to the similarity matrices of the native understory, native herbs and native shrubs analyses respectively. In the resurvey, the number of species needed to achieve 90% is reduced to 25, 17, and 7 species respectively, further evidence of biotic homogenization of forest understories.

Shifts in the identity of species dominance are highly suggestive of successional as a critical mechanism of species loss and homogenization. For understory herbs, thin leaved, shade tolerant herbs such as *Circaea lutetiana and Arisaema triphyllum* increased in importance while thick leaved, sun loving taxa such as *Carex spp, Gallium spp, Amphicarpaea* *bracteata* showed conspicuous declines (table 5). Similar results are seen in changes in native understory shrub species. Shade intolerant taxa such as *Cornus racemosa and Corylus americana* decline in their contribution to community similarity while shade tolerant taxa such as *Parthenocissus spp, Ribes missouriense, and Prunus virginiana* increased in contribution (table 6). *Parthenocissus spp.*, in particular, showed the greatest increase in relative dominance, it's individual contribution to within group similarity increasing from 29.9 % in the original survey to 49.3% today, perhaps reflecting supplements from connected vines growing on trees.

Do exotic species invasions drive changes in community composition?

Across all southern Wisconsin forests, shifts in understory native species richness appeared unrelated to either the presence or local abundance of exotic taxa (relationships at all scales not significant, analyses not shown). However, if we restrict analyses to the glaciated SE region of the state, the rate of species gain / loss increases at sites that gained more exotic species ($r^2 = 9.5\%$, $p < 0.001$). This suggests that sites gaining exotic species are also likely to gain native species as well. However, shifts in floristic quality temper those gains as more conservative taxa are replaced by weedy generalists. As expected, floristic quality of native species in either time period is negatively correlated with exotic richness and abundance in 2005 ($r = 0.443$ for 1950 FQI and 0.429 for current FQI, $p < 0.0001$). It may be that poor quality sites are more susceptible to invasion by exotic taxa, causing further reductions in floristic quality.

Although presence of exotic species tends to increase heterogeneity when calculated including exotic taxa, stands with higher abundances of exotic species are generally more homogenized in native species composition than less invaded stands. This again reflects the fact that stands vulnerable to exotic species invasions are also more likely to be losing rare and local native species.

DISCUSSION

Many changes are happening on decades long time scales and large spatial scales that are not detectable via the typically short-term periods of most research projects and therefore are often over-looked. The result is a blind spot in long-term conservation planning, the so-called “invisible present” (Magnuson 1990) or “shifting baseline syndrome” (Pauly 1995). The invisible present hides local and regional changes in biological diversity, seriously undermining the ability of land managers to make informed management decisions and to convincingly argue that we face immediate threats to biodiversity. All too often, the lack of evidence is taken as evidence that no problem exists often resulting in the mistaken assumption that protected natural areas are safe from degradation.

Successional dynamics have clearly affected shifts in canopy species richness, composition and heterogeneity in southern Wisconsin forests over the last 50 years. Our results confirm the wide-spread decline of oaks and subsequent increase of mesic species in southern Wisconsin forests and provide empirical evidence for the consequences of these shifts on understory richness, composition and heterogeneity. Late successional forests have lost more species and undergone more community homogenization than early successional stands, as did stands with greater increases in basal area/hectare. Shifts in species composition in all layers also support the idea that succession is a major force of change in understory communities, with shade-tolerant species replacing shade-intolerant species at all levels of analysis. Exotic species invasion had little direct influence on native species loss or community homogenization, actually increasing community heterogeneity in most cases. This result appears to contradict McKinney and Lockwood's (1999a) suggestion that exotic invasions would increase biotic homogenization. Olden & Poff (2003) show that changes in similarity are related to both the number of sites invaded and by the identity of the invading species. Individual species invasions will decrease average similarity until they approach invading half the stands (less if locally abundant), after which point further invasion or increased local dominance serve to increase community similarity. Given that most exotic species in the data set are still rare, it makes sense that their overall effect is to decrease average similarity. For our data, only garlic mustard (*Alliaria petiolata*) and common dandelion (*Taraxacum officinale*) are common enough to contribute to overall community homogenization.

We also provide evidence to support Connell's intermediate disturbance hypothesis, where early successional stands are more dynamic and gaining species (or at least losing them less rapidly) while late successional stands are losing overall species richness (this is investigated further in chapter 3 – which separates extinction and invasion). However, species loss was universal across most sites, differing mainly in magnitude.

Our results bring new urgency to the continuing problem of oak decline throughout eastern North America, especially as it applies to stands on fine textured, nutrient rich soils (Lorimer 2003, Abrams 2003) . Perhaps creating new habitats for oak regeneration is another way to increase oaks in the landscape and thereby create habitats for understory plants affiliated with oak canopies. Restocking pine plantations and old fields (especially when adjacent to existing oak forests) could provide habitat for oak regeneration, increasing patch size and forest cover and thus improving conservation value. To increase oak regeneration, we will either need to more actively manage current stands or establish new stands under pine plantations or via direct planting in old/abandoned fields (ideally adjacent to existing forests). This will also sustained limits on deer densities or local exclusion (via fencing) during the critical establishment phase and for decades afterwards. Oak regeneration, understory diversity and floristic quality can also be improved by the reducing the density of weedy tree saplings and shrubs such as *Acer negundo, Parthenocissus spp., and Prunus virginiana* as well as highly invasive exotic taxa such as *Lonicera x bella and Rhamnus cathartica* (Lorimer 1994).

Forest management ultimately involves choosing what we want the land to look like. In highly fragmented and isolated forest patches, this will require active management (i.e. importing desired species as canopy conditions change). Our analysis reveal widespread declines in most taxa, many of which are still reasonably abundant from a conservation perspective. Now is the time to protect these declining populations, before the forces of genetic drift and metapopulation dynamics drive these species to regionally rare levels that would require legal protection. A regional strategy of conservation of woodland/savanna elements, including specific decisions of how much on what kinds of forest we want would be a logical first step toward achieving this goal. Local, state and federal incentives like the wetland reserve program or forest crop law could also help reduce woodland exotics, restore remnants and promote dispersal of desired species.

Acknowledgements

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Figures

Figure 1: Map of 94 sites in southern Wisconsin

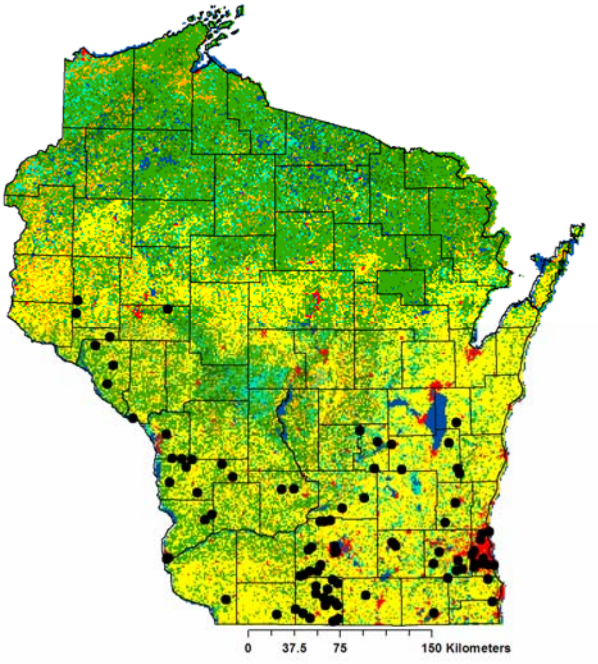


Figure 2a: Changes in Relative Density of Canopy Species

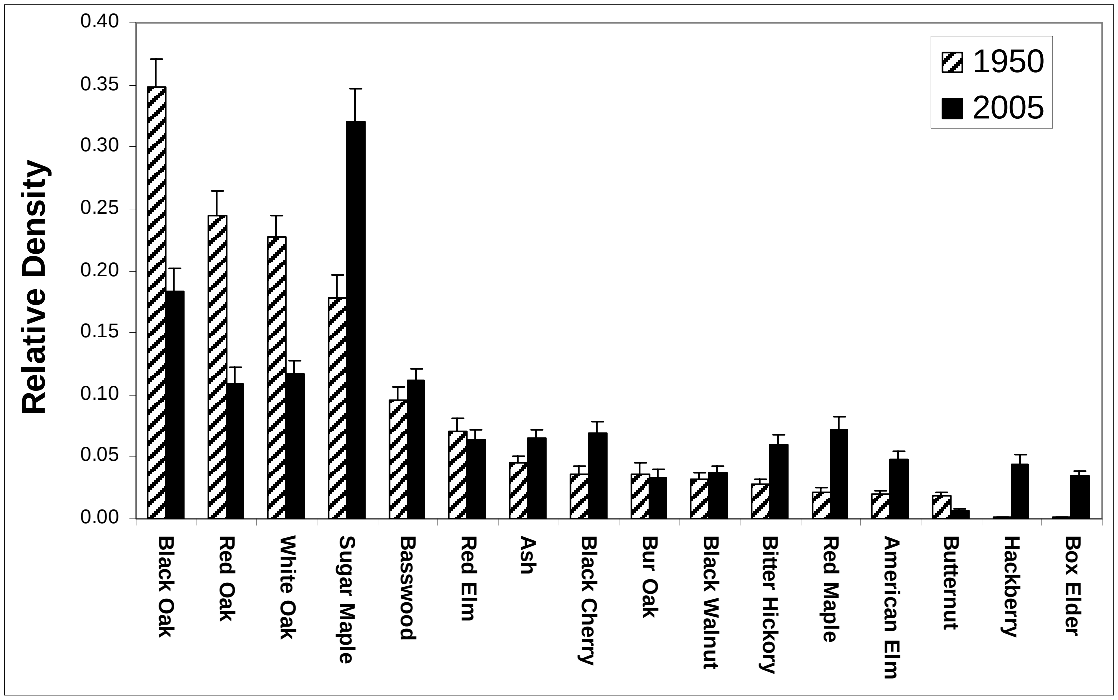


Figure 2b: Changes in Relative Basal Area of Major Canopy Species

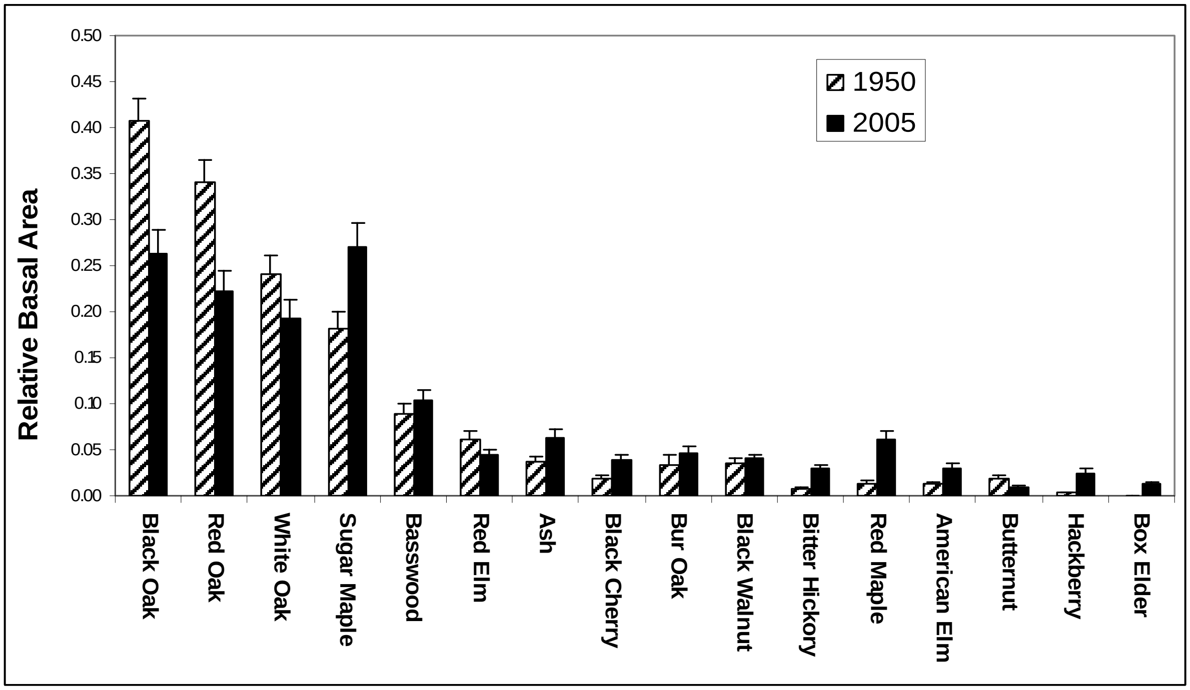


Figure 3: Changes in Size Class Distribution of Oak Stems

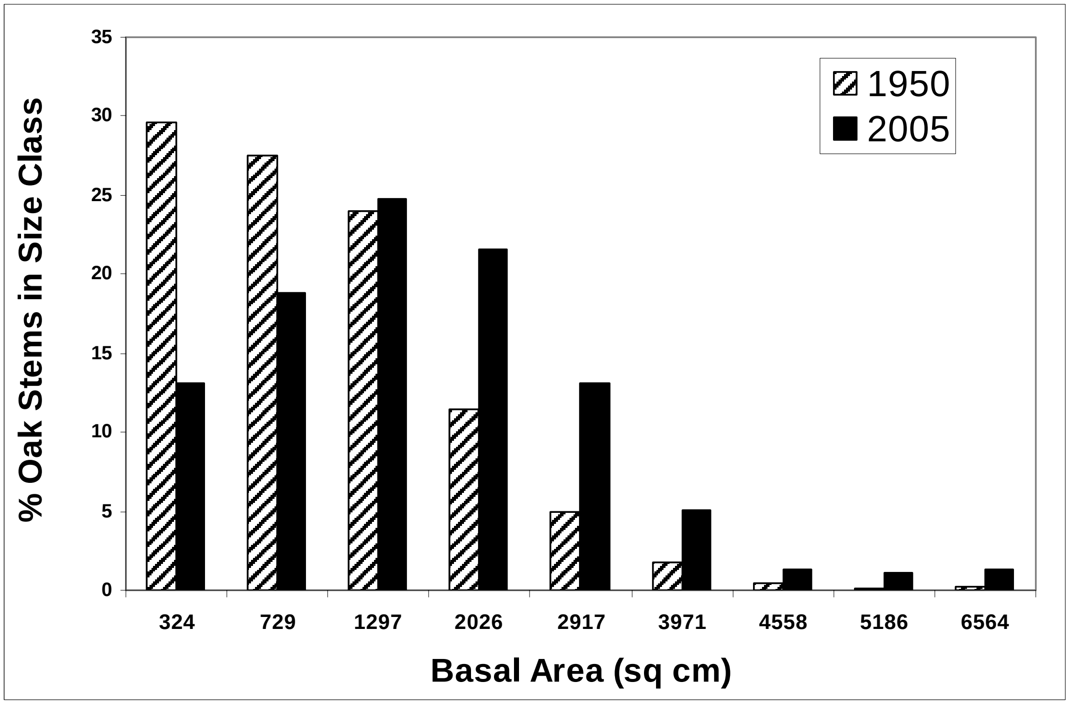


Figure 4: Simple linear regression of Original SAV score vs. Change in SAV score. Adjusted $R^2 = 58.9\%$, $p < 0.001$.

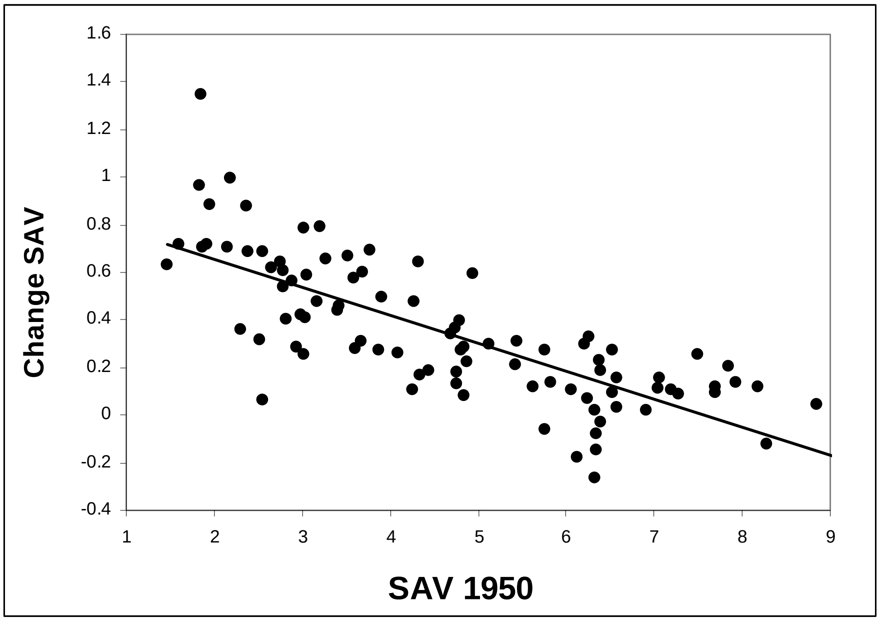


Figure 5: Combined Ordination of Canopy Data

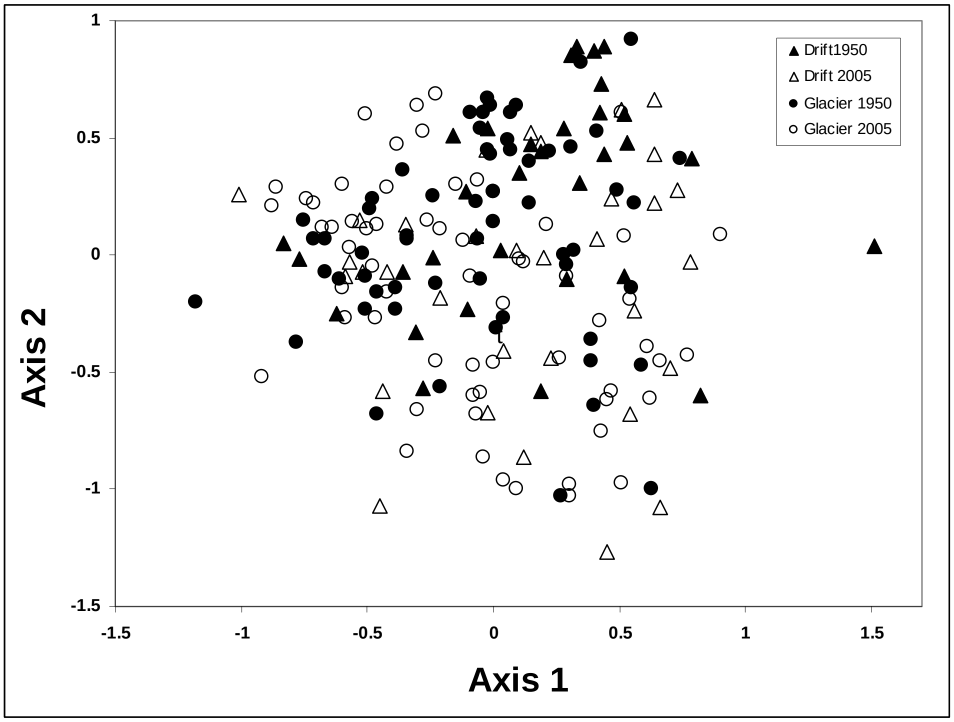


Figure 6: Changes in species Richness. All differences are significant at $p < 0.01$ using a paired t-test.

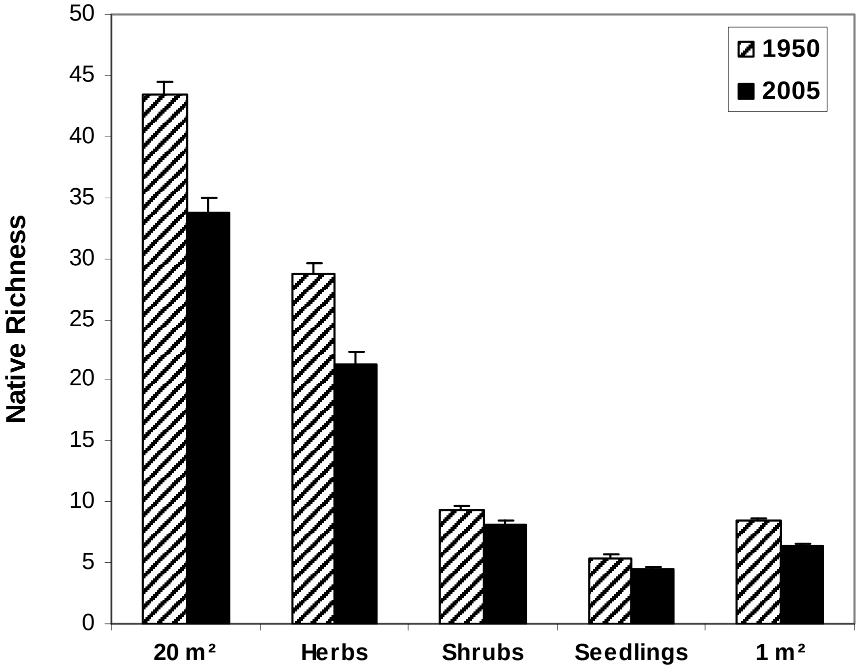


Figure 7: Simple Linear Regression of Succession Adaptation Value in 1950 vs. rates of species loss/m². Adjusted $R^2 = 20.8\%$, $p < 0.001$

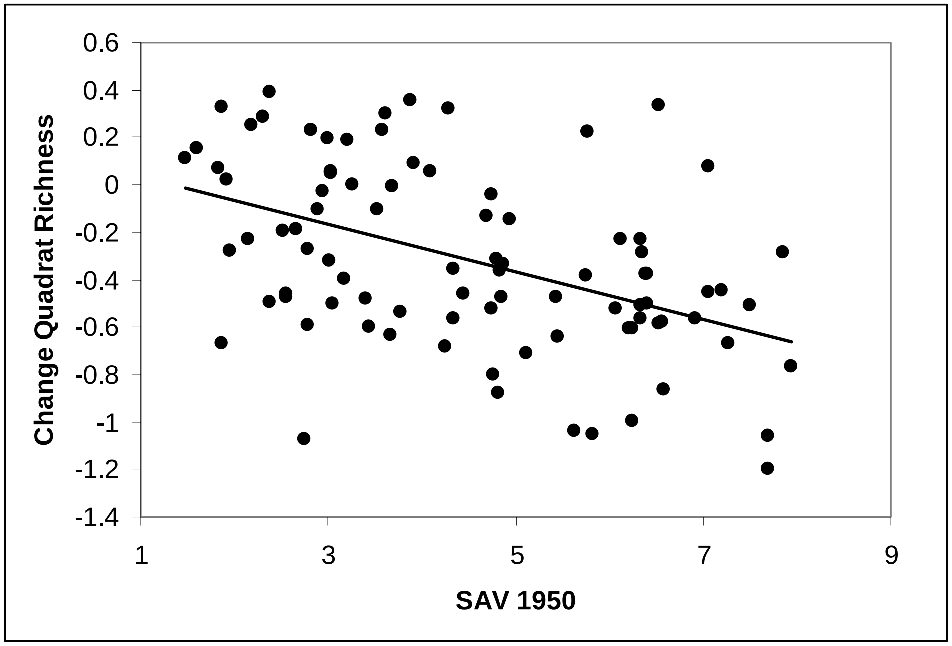
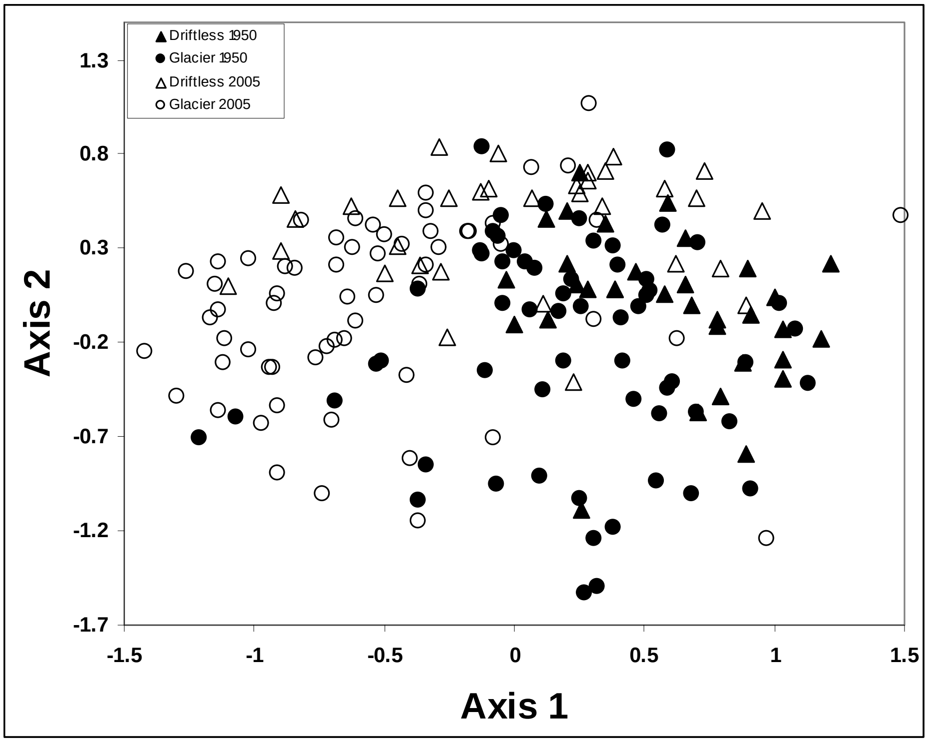
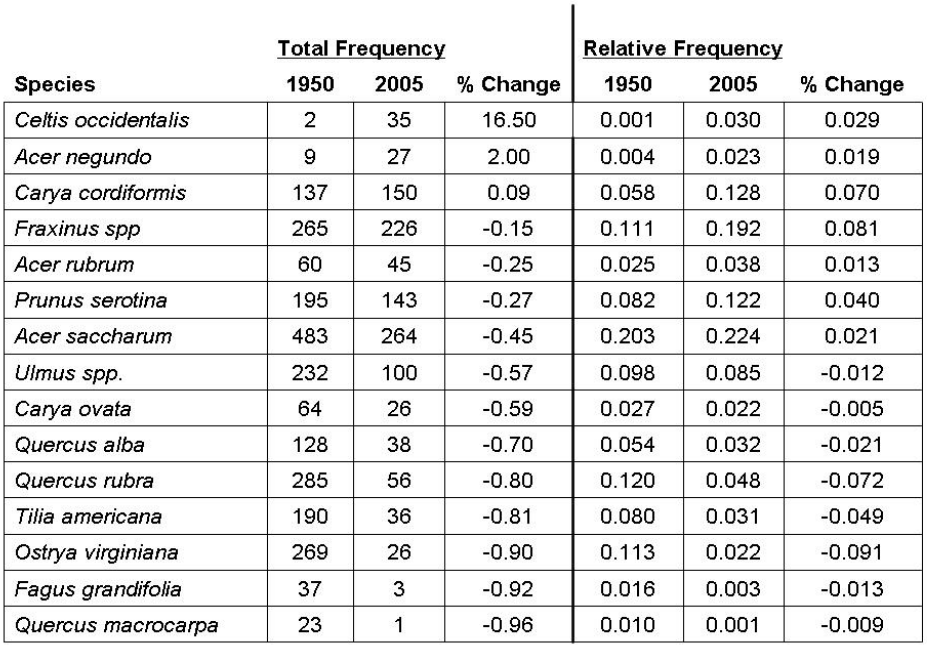


Figure 8: Combined Ordination of Native Herbs



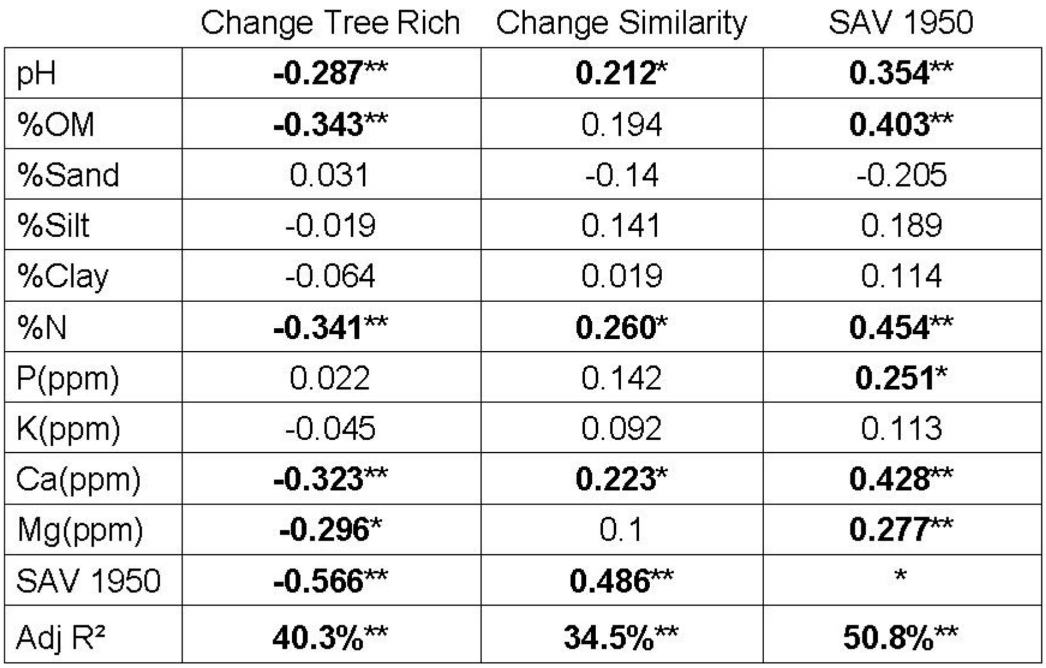
Tables

Table 1 : Changes in seedling total and relative frequency. The chi-squared approximations of the G statistic were conducted on the total frequency values for each species in each time period



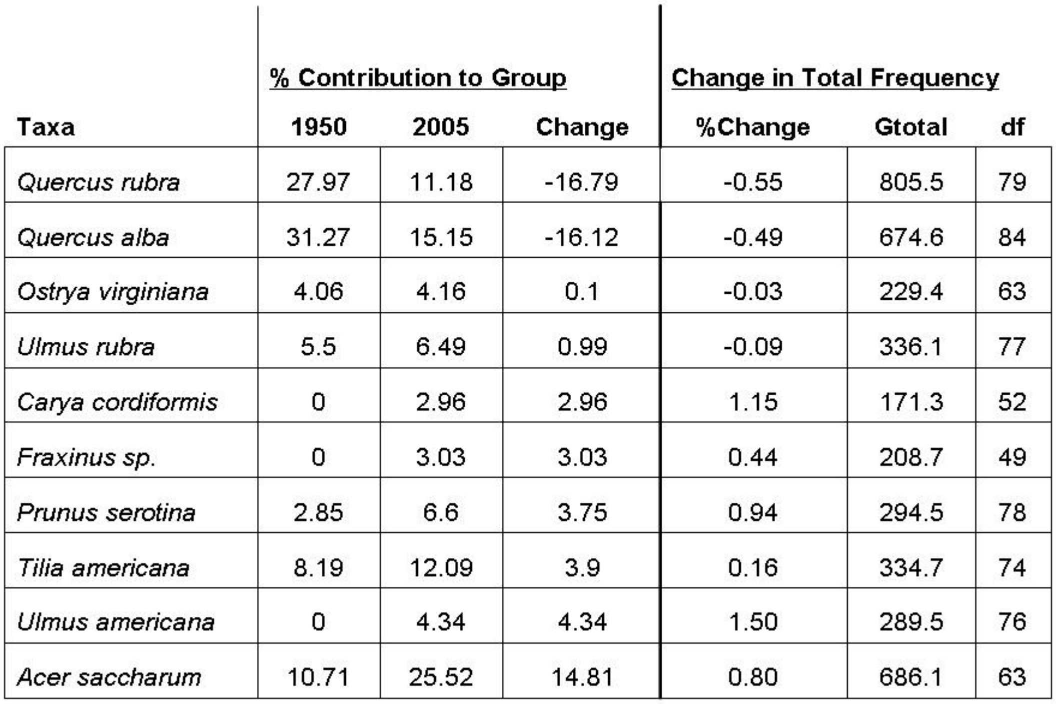
	Total Frequency			Relative Frequency		
Species	**1950**	**2005**	**% Change**	**1950**	**2005**	**% Change**
Celtis occidentalis	2	35	16.50	0.001	0.030	0.029
Acer negundo	9	27	2.00	0.004	0.023	0.019
Carya cordiformis	137	150	0.09	0.058	0.128	0.070
Fraxinus spp	265	226	-0.15	0.111	0.192	0.081
Acer rubrum	60	45	-0.25	0.025	0.038	0.013
Prunus serotina	195	143	-0.27	0.082	0.122	0.040
Acer saccharum	483	264	-0.45	0.203	0.224	0.021
Ulmus spp.	232	100	-0.57	0.098	0.085	-0.012
Carya ovata	64	26	-0.59	0.027	0.022	-0.005
Quercus alba	128	38	-0.70	0.054	0.032	-0.021
Quercus rubra	285	56	-0.80	0.120	0.048	-0.072
Tilia americana	190	36	-0.81	0.080	0.031	-0.049
Ostrya virginiana	269	26	-0.90	0.113	0.022	-0.091
Fagus grandifolia	37	3	-0.92	0.016	0.003	-0.013
Quercus macrocarpa	23	1	-0.96	0.010	0.001	-0.009

Table 2: Spearman rank correlations of edaphic factors and changes in Tree richness. * $p < 0.05$, ** $p < 0.01$



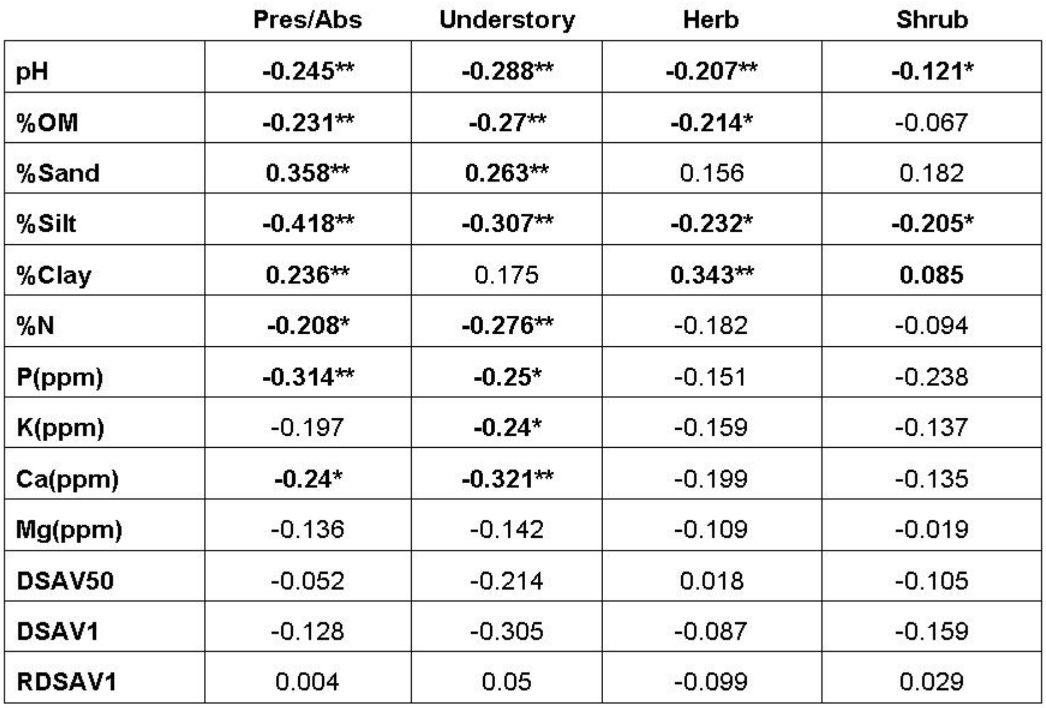
	Change Tree Rich	Change Similarity	SAV 1950
pH	-0.287**	0.212*	0.354**
%OM	-0.343**	0.194	0.403**
%Sand	0.031	-0.14	-0.205
%Silt	-0.019	0.141	0.189
%Clay	-0.064	0.019	0.114
%N	-0.341**	0.260*	0.454**
P(ppm)	0.022	0.142	0.251*
K(ppm)	-0.045	0.092	0.113
Ca(ppm)	-0.323**	0.223*	0.428**
Mg(ppm)	-0.296*	0.1	0.277**
SAV 1950	-0.566**	0.486**	*
Adj R^2	40.3%**	34.5%**	50.8%**

Table 3: Canopy compositional shifts



	% Contribution to Group			Change in Total Frequency		
Taxa	**1950**	**2005**	**Change**	**%Change**	**Gtotal**	**df**
Quercus rubra	27.97	11.18	-16.79	-0.55	805.5	79
Quercus alba	31.27	15.15	-16.12	-0.49	674.6	84
Ostrya virginiana	4.06	4.16	0.1	-0.03	229.4	63
Ulmus rubra	5.5	6.49	0.99	-0.09	336.1	77
Carya cordiformis	0	2.96	2.96	1.15	171.3	52
Fraxinus sp.	0	3.03	3.03	0.44	208.7	49
Prunus serotina	2.85	6.6	3.75	0.94	294.5	78
Tilia americana	8.19	12.09	3.9	0.16	334.7	74
Ulmus americana	0	4.34	4.34	1.50	289.5	76
Acer saccharum	10.71	25.52	14.81	0.80	686.1	63

Table 4 : Changes in average native similarity in relation to soil and SAV



	Pres/Abs	Understory	Herb	Shrub
pH	**-0.245****	**-0.288****	**-0.207****	**-0.121***
%OM	**-0.231****	**-0.27****	**-0.214***	-0.067
%Sand	**0.358****	**0.263****	0.156	0.182
%Silt	**-0.418****	**-0.307****	**-0.232***	**-0.205***
%Clay	**0.236****	0.175	**0.343****	**0.085**
%N	**-0.208***	**-0.276****	-0.182	-0.094
P(ppm)	**-0.314****	**-0.25***	-0.151	-0.238
K(ppm)	-0.197	**-0.24***	-0.159	-0.137
Ca(ppm)	**-0.24***	**-0.321****	-0.199	-0.135
Mg(ppm)	-0.136	-0.142	-0.109	-0.019
DSAV50	-0.052	-0.214	0.018	-0.105
DSAV1	-0.128	-0.305	-0.087	-0.159
RDSAV1	0.004	0.05	-0.099	0.029

Table 5: Changes in contribution to within group (1950 vs. 2005) native herb similarity for the top species in either time period (90% total variance explained within each group)

	% Contribution			Total Frequency		
Species	**1950**	**2005**	**Change**	**1950**	**2005**	**% Change**
Carex sp	10.4	4.3	-6.2	562	241	-0.57
Galium concinnum	4.6	0.0	-4.6	394	58	-0.85
Osmorhiza claytonii	6.8	2.9	-3.9	485	327	-0.33
Amphicarpaea bracteata	3.8	1.1	-2.7	337	174	-0.48
Sanicula marilandica	3.1	0.7	-2.4	296	159	-0.46
Smilacina racemosa	10.9	8.9	-2.0	573	416	-0.27
Phryma leptostachya	3.0	1.0	-1.9	293	158	-0.46
Desmodium glutinosum	3.2	1.3	-1.9	335	214	-0.36
Aralia nudicaulis	1.7	0.0	-1.7	186	59	-0.68
Uvularia grandiflora	2.3	1.1	-1.2	262	182	-0.31
Podophyllum peltatum	1.6	0.9	-0.7	176	92	-0.48
Viola pubescens	1.6	1.1	-0.5	240	145	-0.40
Athyrium filix-femina	0.8	0.9	0.0	98	117	0.19
Thalictrum dioicum	1.0	1.1	0.1	150	128	-0.15
Galium triflorum	1.8	2.4	0.6	304	240	-0.21
Geranium maculatum	13.3	13.9	0.6	694	600	-0.14
Geum canadense	0.9	7.6	6.7	121	384	2.17
Arisaema triphyllum	2.5	14.4	12.0	276	610	1.21
Circaea lutetiana	8.0	26.6	18.6	511	881	0.72

Table 6 : Changes in contribution within group (1950 vs. 2005) similarity for the top native shrub taxa in either time period (90% total variance explained within each group)

	% Contribution to group			% Change Total Frequency		
Species	Shrub50	Shrub05	% Change	% Change	Gtot	df
Parthenocissus spp	29.94	49.25	19.31	0.261364	609.5	93
Prunus virginiana	13.15	11.43	-1.72	0.111111	248.3	89
Cornus racemosa	10.93	4.04	-6.89	-0.91096	530.5	74
Corylus americana	7.93	0.85	-7.08	-2.7377	468.4	59
Rubus allegheniensis	5.82	5.11	-0.71	-0.075	375.4	68
Toxicodendron spp	5.15	2.35	-2.8	-0.53535	341.6	75
Vitis riparia	3.88	1.95	-1.93	-0.58904	215	77
Celastrus scandens	4.33	0.08	-4.25	-5.4	421.6	52
Ribes cynosbatii	3.89	14.06	10.17	0.688172	284.2	83
Rubus idaeus	2.44	0.89	-1.55	-1.23333	312.4	52
Smilax ecirrhata	3.42	1.95	-1.47	-0.24242	190.3	71

Long-term shifts in southern Wisconsin forest communities.

II. Are understory changes linked to fragmentation?

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Abstract

We resurveyed 94 forested sites in southern Wisconsin 50+ years after initial survey to determine how well landscape metrics of fragmentation, urbanization, and land use could account for patterns of ecological change in forest understory plant communities. In the original survey, estimates of richness and heterogeneity were only weakly related to landscape measures. However, in the resample, much stronger patterns emerged with rates of species loss and community homogenization positively correlated with measures of habitat loss and urbanization. These differential losses resulted improved the ability of island biogeography theory to predict diversity patterns in these forest “islands”. Current land use patterns also influenced rates of species loss. Unhunted stands lost native herbaceous species at twice the rate of stands where hunting was allowed. Stands with high trail density experienced higher rates of native community homogenization and greater losses of floristic quality than did stand with few trails, especially for native herbaceous species. These results support fundamental tenets of conservation biology in that native species richness, heterogeneity and quality are more effectively maintained in large intact habitat patches with minimal human infrastructure.

Introduction

Habitat loss and fragmentation have been implicated in declines in the genetic diversity, fecundity, gene flow, species richness and community heterogeneity of indigenous species (Young 1996, Curtis 1956, Janzen 1983, Euskirchen 2001)**.** Documenting and understanding the effects of habitat loss and fragmentation is thus a central goal of conservation biology. Unfortunately, because of the general lack of long-term baseline data, conservation is often blind to accumulated changes in community composition over time (Terborgh 1999, Magnuson 1990, Soule 1979). Empirical data on long–term changes in biodiversity would allow us to examine some of the basic underlying theoretical assumptions of conservation biology and ecology, including the application of insular island biogeography (MacArthur & Wilson 1967) to isolated habitat patches. Most studies on the effects of fragmentation by necessity rely on substituting space for time to infer long-term effects or are limited to simulation. The long term empirical studies that do exist (Robinson 1994, Drayton 1996, Rooney 1997) suggest dramatic effects but typically lack spatial resolution and/or replication.

We seek to add to this body of knowledge by using quantitative data from 94 upland forest sites originally surveyed by the UW Plant Ecology Lab (PEL) in the late 1940’s and early 50’s to link patterns of species loss and community homogenization (Rogers 1) to measures of landscape fragmentation and human land use. Curtis wrote at length of the effects of the habitat fragmentation and changes in fire regime had on plant communities both in the short and long term (Curtis 1956). In a remarkably prescient essay in *Man’s Role in Changing the face of The Earth*, Curtis made clear predictions regarding how landscape changes would effect the future of forest understory plants.

The potential effects of fragmentation outlined by Curtis are familiar to any student of conservation biology. Dispersal opportunities are limited, and the species pool available for immigration changes dramatically in composition, shifting species composition to habitat generalists or those that favor the particular context now imposed on the plant community. Furthermore, more homogenous land-use practices across broad geographic areas that formerly encompassed different historical disturbance patterns, physical environments, landscape contexts, and biotic communities, contribute to an overall homogenization of plant communities in space, further altering the species pool and immigration patterns. Since the large scale fragmentation and disruption that happened in the mid 1800's and described by Curtis, the landscape has continued to change. Urbanization, industrial agriculture, and other forms of intensive development, for example, have further reduced landscape permeability while facilitating the introduction of novel taxa to the species pool. This intensification further exacerbate the fragmentation effects of initial settlement and virtually eliminate immigration between forest patches, allowing the patch by patch extirpations of individual populations on the landscape without rescue (Brown 1977) from surrounding patches.

MacArthur and Wilson (1967) codified these ideas with the publication of the theory of island biogeography (IBG). In the early 1970's, their work inspired a series studies of southeastern Wisconsin forests in the to test whether these forest "islands", essentially completely cut off from one another, would follow the patterns predicted by IBG (Levenson 1976). Surprisingly, this work found very little evidence for the relationship between patch size and richness in a standardized sample. Perhaps the effects of habitat loss and fragmentation requires a lag period (as species disappear and aren't replaced) before the species richness levels “relax” to predicted levels, a process that could require many decades and were not yet manifest by the 1970’s.

Regardless, IBG has become a bedrock principle in Conservation Biology (Meffe 1997) and most scientist agree that large patches are better at retaining diversity than are small ones, SLOSS debate not withstanding. Following this principle, we predict that small forest patches in fragmented landscapes will have higher rates of species loss and greater rates of community homogenization than patches in fragmented or urbanized landscapes. Obviously, humans also have direct impacts on plant communities and the land-use history of any particular stand can have dramatic impacts on species richness and composition. This problem (in so far it would obscure regional changes) is somewhat ameliorated by the large sample size and by the fact that all forest were carefully chosen by the PEL such that they had never been plowed, heavily grazed or heavily logged and so represent the better examples of native forests in 1950. We applied similar criteria to the stands in our re-survey, losing about 15% of the original stands to development or shifting land use practice (Pasture – converted to pine or other species). In an attempt to shed some light in the effects of local land use, the remaining 94 stands were systematically evaluated for current land uses such as logging history, deer management and trail density. We then compare species loss and community homogenization in light of these factors.

Methods

Estimates of species loss and community homogenization

We estimated rates of native species loss and community homogenization by resurveying 94 forested sites, originally surveyed in the late 1940’s and early 1950’s and archived in the Botany Department at UW Madison. Working from archived and published materials, we reconstructed the sampling methods and locations of the original survey and so derived a sample of 20, 1m^2 quadrats spaced at approximately 20m intervals for each time period. For each site in each time period, we estimated native species richness at 1 & 20m^2 as well as the average among site similarity for understory composition. We then calculated the rate of change in each variable between the two sample periods. To test for differences of growth form in response to landscape predictors, we further divided understory composition into herbaceous and woody species (excluding tree seedlings). We thoroughly vetted the data in terms of taxonomic resolution, sample size, data transformation and variation in similarity measures used (appendix) and found that our estimates of change are robust in terms of the narrative they tell. For these analyses, we use the same data and transformation as used in our investigation of successional changes (Rogers 1). Specifically, we use 1) estimates of native richness at 1m^2, & 20m^2, 2) rates of change in native richness at 1& 20m^2, 3) average similarities of the understory including separate analysis of the herb and shrub layers, and 4) rates of change in average similarities for the understory layers.

Quantifying the landscape

Using current digital orthophotos and WISCLAND, we digitized houses, roads and land cover using ArcGIS. Houses were digitized and stored as point coverages, roads as line coverages, and land cover as polygon coverages. Roads were considered as any linear feature that is visibly connected to other roads. Driveways less than 50-m in length were not digitized. Land cover polygons were classified into major land cover; the class catalog followed the National Land Cover classification system, with a minimum mapping unit size of 1 ha.

Housing, land cover, and roads are available in different units of analysis and we used "buffer analysis" to integrate them at 1, 2 and 5 km scales. In a GIS, we identified the area that was within specified distance from the center of each study site. Within this buffer, we summarized the number of houses, density of roads, land cover abundance and computed landscape indices. Based on the land cover data, we computed land cover class abundance and selected landscape indices that quantify fragmentation for inclusion as additional independent variables in the statistical analysis. We used % Forest, % Grassland (includes fallow land), % Agriculture (includes active hay meadows & plowed fields), and % Urban (such that all values add up to 100). Measures of land cover were highly correlated at all three spatial scales and showed similar responses with dependent variables (see appendix). However measures at 5km was the most informative and are therefore those reported here (although a thorough analysis of the effect of scale is warranted - e.g. 1 km scale might be more informative in the driftless area, logged stands etc.). Habitat patches also vary in their size, shape, type, heterogeneity and boundary characteristics which can have important effects on ecological processes. We measured the patch size in stands containing study sites, and quantified fragmentation using the proximity index, a gravity-based measure of patch separation.

Land use

To examine direct human impact, we also classified stands according to current land use practices as observed in the field. We evaluated the effects hunting, logging, and land ownership and access through a combination of informal land owner interviews and systematic observation of specific stand attributes. To test the effects of hunting we divided our sites into two classes: areas open to hunting vs. those that were closed to hunting. To test the effects of logging, we compared stands with no evidence of logging vs. those that had been logged to some degree. Logged stands were further divided into sub-categories: early vs. recent logging (threshold 15 years) and heavy vs. light intensity (> 40% removal). To test the effect of the density of logging and/or hiking trails, stands were classified by the density of these features (high vs. low density, threshold being 1 trail/hectare). As a way to compare the magnitude of land use effects to landscape effects, we also divide the stands by patch size with the threshold being 80 hectares between small and large classes (median of patch size). Similarly, because of the profound influence of the region's glacial history on landscape features, we also categorize each stand as to whether they had been covered by the most recent glacial maximum.

Data Analysis

We first tested the ability of these categorical and continuous variables as univariate predictors of species loss and community homogenization using one-way analysis of variance and Spearman rank correlation. We then combined these variable into predictive models of change, using MANOVAs and step-wise linear regressions respectively. Response variables included rates of native species loss and various estimates of homogenization. Predictor variables include all land use categories and landscape metrics outlined above. For the step-wise regressions, we also included an index of the initial successional state (Peet & Loucks 1977) and initial richness as predictor variables (Rogers 1).

Results

Measures of landscape fragmentation were significant predictors of species and community homogenization. Landscape predictors of understory richness and average similarity also shifted in importance with the resample data conforming more closely to the distribution predicted by insular island biogeography. Current land use also influenced rate of species loss and community homogenization, but had less overall impact then the effects of landscape fragmentation. We report these trends in turn, starting with native species loss.

Changes in native species richness

Both estimates of native species richness as well as the rates of change are significantly negatively correlated with measure of landscape fragmentation and positively correlated with measures of human dominance (table 1). In 1950, species richness/m^2 had no significant correlation with any single measure of landscape fragmentation or human dominance. At $20m^2$, there was some influence on species richness, showing a negative correlation with road density and positive correlation with mean patch size. Overall, however, these variables had little predictive power. In a stepwise multiple regression with alpha at 0.15, adj r^2 was 9.14% to predict species/m^2 and 15.32 % to predict species/$20m^2$ (in the stepwise model, only road density was retained).

In 2005, we saw these trends fully manifest. In the re-sample data, most measures of landscape fragmentation and human dominance were highly significantly correlated with native species richness (table 1). Most measures of landscape fragmentation that showed no significant trend in predicting species richness in 1950 became strong predictors today, forest cover being one such example (figure 1). As with the original survey data, mean patch size was the single strongest predictor, though the strength of the relationship more than doubled (figure 2). As in 1950, measures of urbanization were negatively correlated native understory richness, though the strength of the correlation again strengthened (table 1). Stepwise linear regression reflects these changes in the strength of the univariate predictors outlined above, returning a model that retains forest cover, patch size and road density with an adjusted r^2 of 25.5% ($p < 0.001$) for predicting richness/m^2 and 42.8% for predicting richness/$20m^2$ ($p < 0.001$). Not surprisingly, forest fragmentation and human dominance were also significantly correlated with rates of species loss (table 1). Stands that were surrounded by relatively more forests were less likely to lose native species than were sites in more fragmented landscapes, with the strongest effect on richness/m^2 (figure 3). Patch size was also significantly correlated with rates of species loss with larger patches losing species at a slower rate than small patches ($r = 0.379$, $p< 0.001$). Since richness in both time periods is related in similar ways to the predictor variables, initial species richness is also strongly correlated with richness in the resurvey data (figure 4). Stepwise multiple regressions including this variable in the model predicting species loss does not change the overall importance of landscape factor in predicting species richness in 2005, but does significantly improve the predictive power of the model, increasing r^2 from 22.8% to 35.9%.

Changes in average similarity

Measures of landscape fragmentation and urbanization also showed significant correlations with our estimates of average among stand similarity and rates of homogenization (table 2). In 1950, agricultural land cover was the only statistically significant correlate with average community similarity. In 2005, the index of agricultural cover remained significant, but was joined by measures of forest fragmentation, improving the predictive power of all variables (r^2 increased from 6.8% to 13.6%). Results for herb and shrub communities showed differential effects of fragmentation on herbaceous and woody communities. Landscape factors exerted a disproportionate influence on herb community similarity while the predictive power of the variables to predict shrub average similarity actually declined (table 3).

Likewise, measures forest fragmentation and human dominance had strong influences on rates of community homogenization. Large stands with greater amounts of % forest in the landscape were less likely to homogenize than smaller stands in urban/agricultural matrix. As above, the strongest individual relationship between rates of change in species/m^2 and forest cover (figure 5, $r^2 = 15.6$, $p < 0.0001$). A stepwise linear regression of all predictor variables retained only forest cover and road density, together explaining 28.9% of variation in herb community homogenization.

Effects of land- use

Land use factors also played a significant role in explaining species loss and community homogenization. Stands with evidence of logging since the original survey, showed no statistically significant effect on rates of species loss or homogenization, although they did trend towards lower species loss in logged stands.

In terms of species loss, unhunted stands showed twice the rate of species loss at both 1 & 20m^2 (-0.4439 vs. -0.2342, $F = 12.7$, $p = 0.013$ for changes at 1m^2), perhaps contributing to the significantly higher rates of species loss at protected sites. This effect is stronger still if we single out native herbs, which were lost at almost 2.5x faster rate in unhunted stands compared to hunted ones (-0.5655 vs. -0.295, $p = 0.012$ for changes at 20m^2). As seen above with the continuous data, small patches loss species at a much higher rate than large patches as did stands in the unglaciated portion of the study area, showing much stronger influence and rates of change than any single category of land use. To avoid conflating patch size with effects of glacial history (patches tend to be larger in unglaciated region), we looked at the effect of patch size within the glaciated portion of our study region. Within unglaciated regions, small isolated patches still lost species at a faster rate than did large connected patches (stepwise regression with all predictor variables yielded a combined $r^2 = 47.9\%$, $p < .000001$). In the glaciated region the same pattern emerges, although the effect is much weaker (combine $r^2 = 19.7\%$, $P < 0.0001$).

In terms of community homogenization, trails and patch size were the only categorical variables that yielded significant differences in rates of homogenization (table 6). Small stands and those with high trail densities were associated with higher rates of homogenization in herbaceous species ($F = 14.03$, $p < 0.001$ and $F = 5.24$, $p = 0.024$). Unhunted stands do trend toward higher rates of homogenization than did hunted stands, however differences were only marginally significant ($F = 3.86$, $p = 0.051$).

Discussion

These findings strongly support current conservation theory and suggest that current conservation strategies are underpinned by robust assumptions that are well supported by empirical data. Forest patches in largely intact habitats lost fewer species and had slower rates of biotic homogenization. Conversely, small isolated patches had greater rates of change. These differential rates of change have led to changes in the species/area relationship of southern Wisconsin understories. Unlike the same forest patches fifty years ago, these isolated forest patches strongly conform to the theory of island biogeography and the principles of conservation biology. These results suggest that the forests sampled by the PEL in the 1950's had still not fully felt the dramatic influences of European settlement and that such lag effects can take decades or centuries to be fully manifest on the landscape, the so called extinction debt (Tilman).

Our findings also suggest that local management of forests can also have dramatic direct and indirect effect of floristic richness and variability. The effect of hunting is particularly dramatic, strongly suggesting that deer continue to have dramatic impacts on forest understories in Midwestern forests, a result widely reported elsewhere (Rooney 2001, Alverson 1988). The impact of high trail densities also has conservation implications and points toward the “benign neglect” effect (Soule 1983), where the high human use of nominally protected areas can lead to catastrophic, if unintended, consequences in understory diversity. The short term and long term effects are also suggestive. The relatively benign or even positive, impacts of logging is encouraging, given that the vast majority of forests in southern Wisconsin are in private hands and subject to economic exploitation. It is quite likely that silvicultural techniques that minimize trail densities and other impacts can play an important role in the regional maintenance of native understory communities and we encourage continued efforts towards the establishment of harvesting methods that mimic natural processes (e.g. Mladenoff 1994).

For protected areas, our results are less reassuring. As southern Wisconsin forests continue to mature and shift towards increased dominance by more mesic species (Lorimer 1993, Adams 2003), forest understories become much shadier and radically shift the growing conditions for resident herbs (Rogers 1). Many species are disappearing in the face of changing canopy conditions and the constraints imposed by forest fragmentation and human dominance effectively eliminate many shade tolerant species from invading those new habitats. In some cases, appropriates species may have to be brought by savvy managers. As was the case above, best management practices would actively discourage visitation of high quality natural areas and to make the reduction of human “improvements” a high priority.

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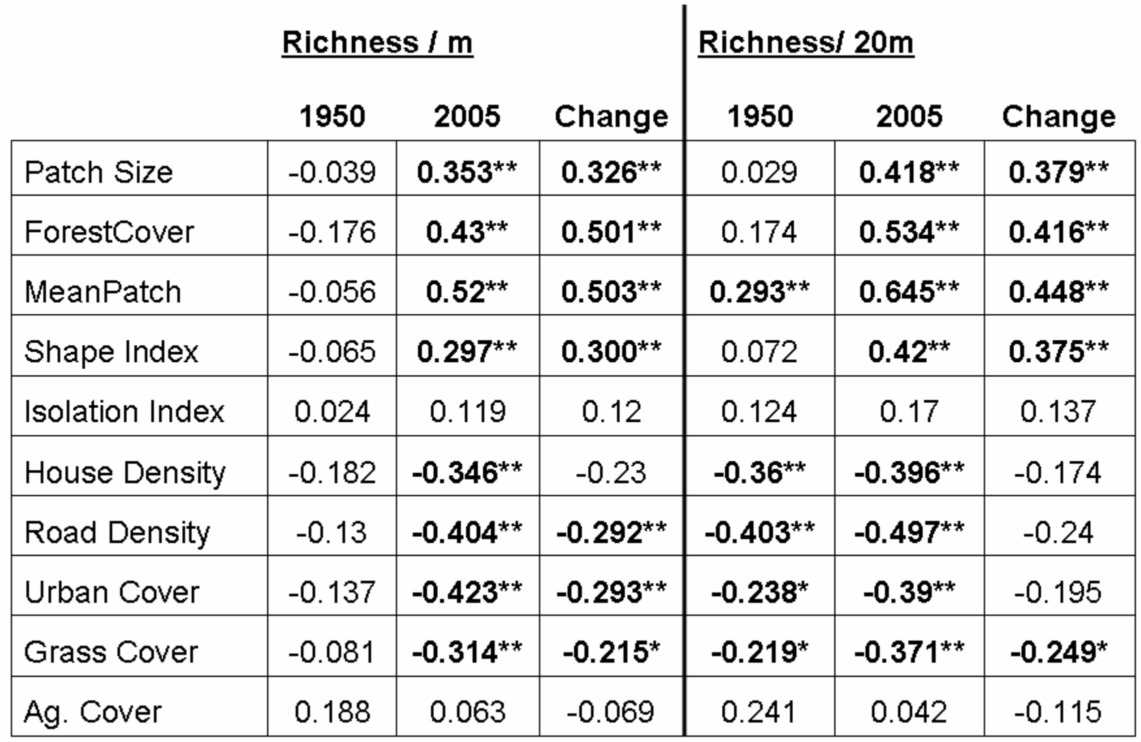
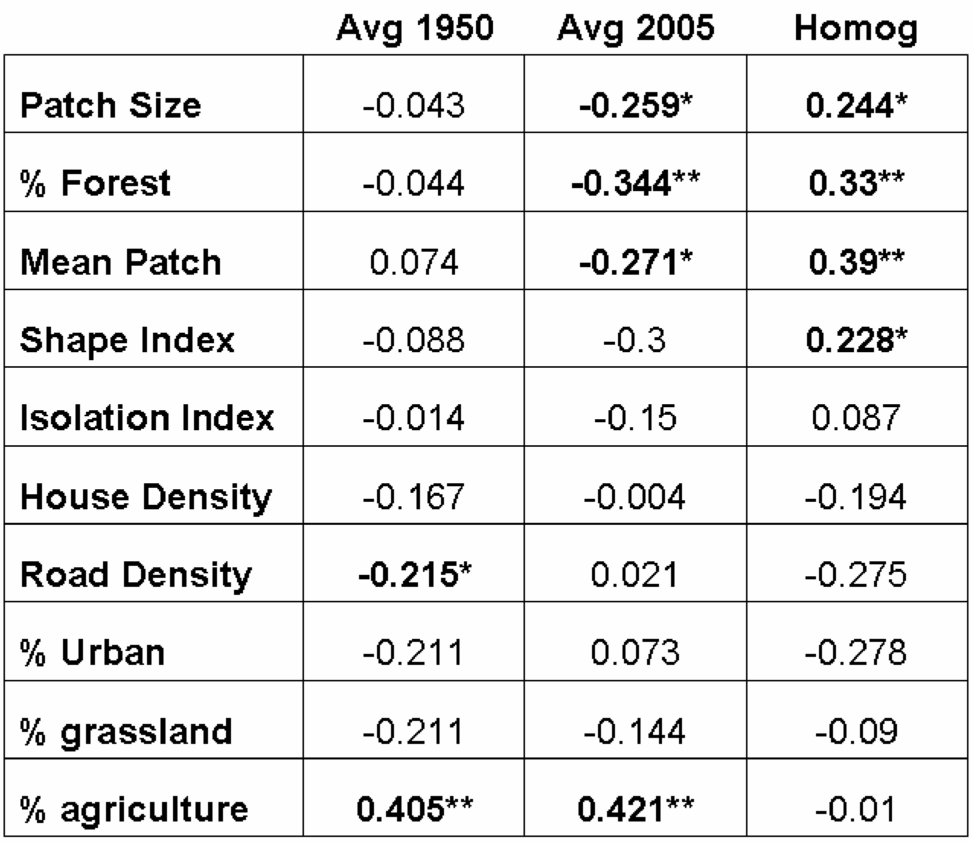
Table 1: Landscape predictors of species richness and rates of species loss



	Richness / m			Richness/ 20m		
	1950	2005	Change	1950	2005	Change
Patch Size	-0.039	0.353**	0.326**	0.029	0.418**	0.379**
ForestCover	-0.176	0.43**	0.501**	0.174	0.534**	0.416**
MeanPatch	-0.056	0.52**	0.503**	0.293**	0.645**	0.448**
Shape Index	-0.065	0.297**	0.300**	0.072	0.42**	0.375**
Isolation Index	0.024	0.119	0.12	0.124	0.17	0.137
House Density	-0.182	-0.346**	-0.23	-0.36**	-0.396**	-0.174
Road Density	-0.13	-0.404**	-0.292**	-0.403**	-0.497**	-0.24
Urban Cover	-0.137	-0.423**	-0.293**	-0.238*	-0.39**	-0.195
Grass Cover	-0.081	-0.314**	-0.215*	-0.219*	-0.371**	-0.249*
Ag. Cover	0.188	0.063	-0.069	0.241	0.042	-0.115

Table 2: Correlation of similarity and rates of homogenization in the understory



	Avg 1950	Avg 2005	Homog
Patch Size	-0.043	-0.259*	0.244*
% Forest	-0.044	-0.344**	0.33**
Mean Patch	0.074	-0.271*	0.39**
Shape Index	-0.088	-0.3	0.228*
Isolation Index	-0.014	-0.15	0.087
House Density	-0.167	-0.004	-0.194
Road Density	-0.215*	0.021	-0.275
% Urban	-0.211	0.073	-0.278
% grassland	-0.211	-0.144	-0.09
% agriculture	0.405**	0.421**	-0.01

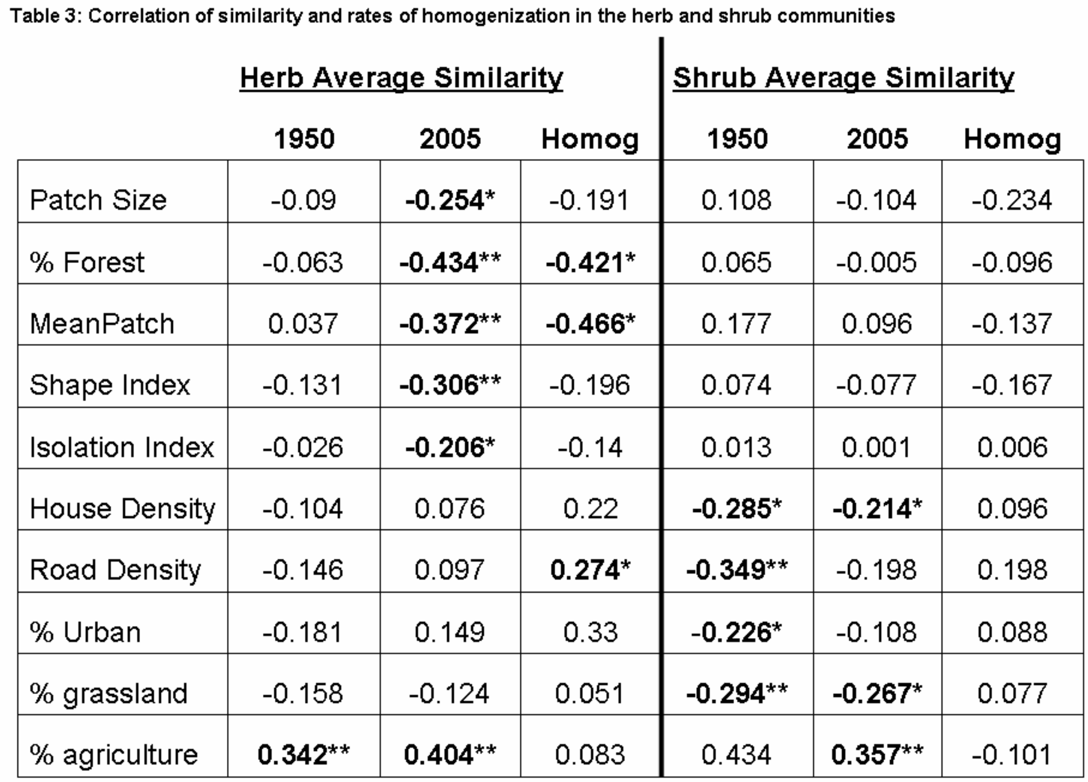


Table 3: Correlation of similarity and rates of homogenization in the herb and shrub communities

	Herb Average Similarity			Shrub Average Similarity		
	1950	2005	Homog	1950	2005	Homog
Patch Size	-0.09	**-0.254***	-0.191	0.108	-0.104	-0.234
% Forest	-0.063	**-0.434****	**-0.421***	0.065	-0.005	-0.096
MeanPatch	0.037	**-0.372****	**-0.466***	0.177	0.096	-0.137
Shape Index	-0.131	**-0.306****	-0.196	0.074	-0.077	-0.167
Isolation Index	-0.026	**-0.206***	-0.14	0.013	0.001	0.006
House Density	-0.104	0.076	0.22	**-0.285***	**-0.214***	0.096
Road Density	-0.146	0.097	**0.274***	**-0.349****	-0.198	0.198
% Urban	-0.181	0.149	0.33	**-0.226***	-0.108	0.088
% grassland	-0.158	-0.124	0.051	**-0.294****	**-0.267***	0.077
% agriculture	**0.342****	**0.404****	0.083	0.434	**0.357****	-0.101

Figure 1: The relationship between forest cover and native understory richness in 1950 compared to that in 2005

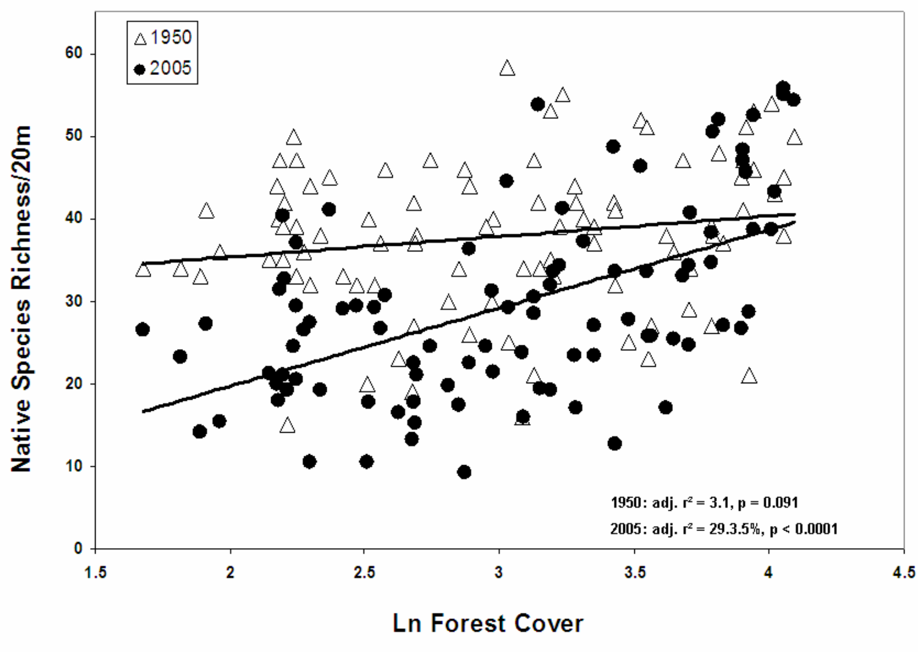


Figure 2: The relationship between mean patch size and native understory richness in 1950 compared to that in 2005

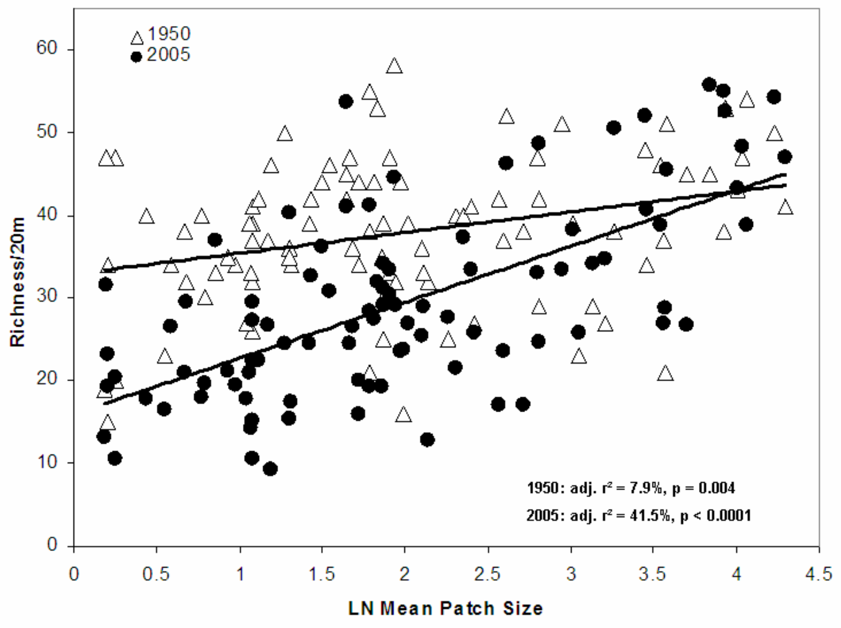


Figure 3: Rates of species loss as a function of % forest cover at km radius from plot center

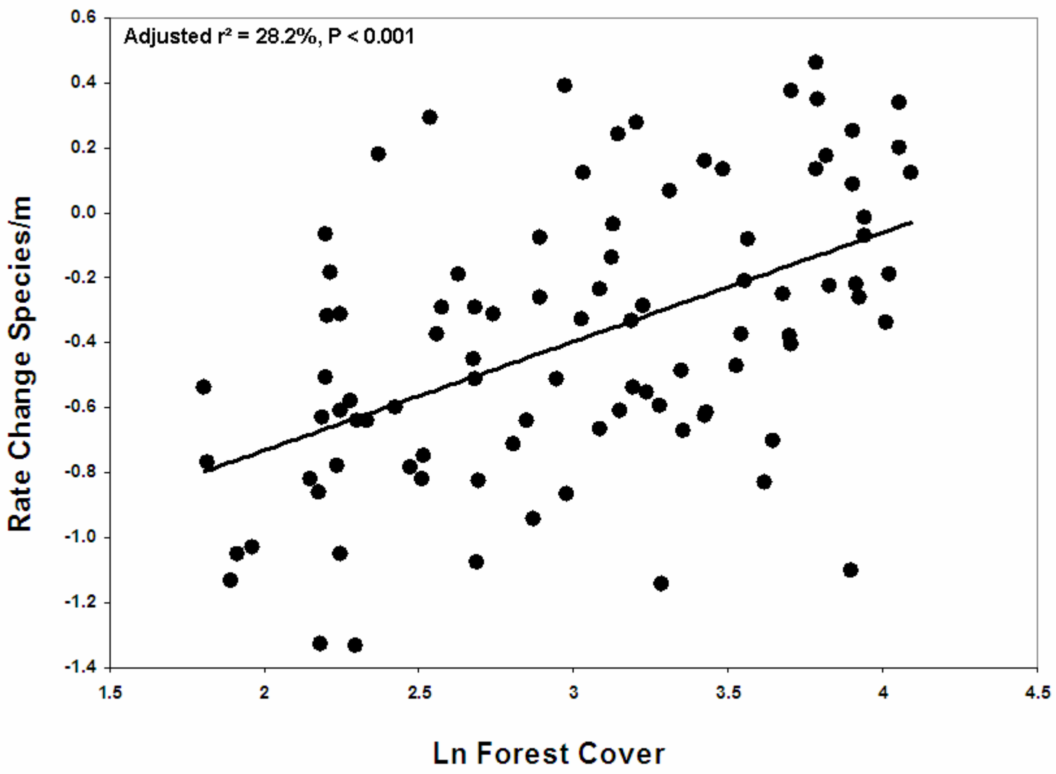


Figure 4: Correlation between native understory richness in 1950 and 2005

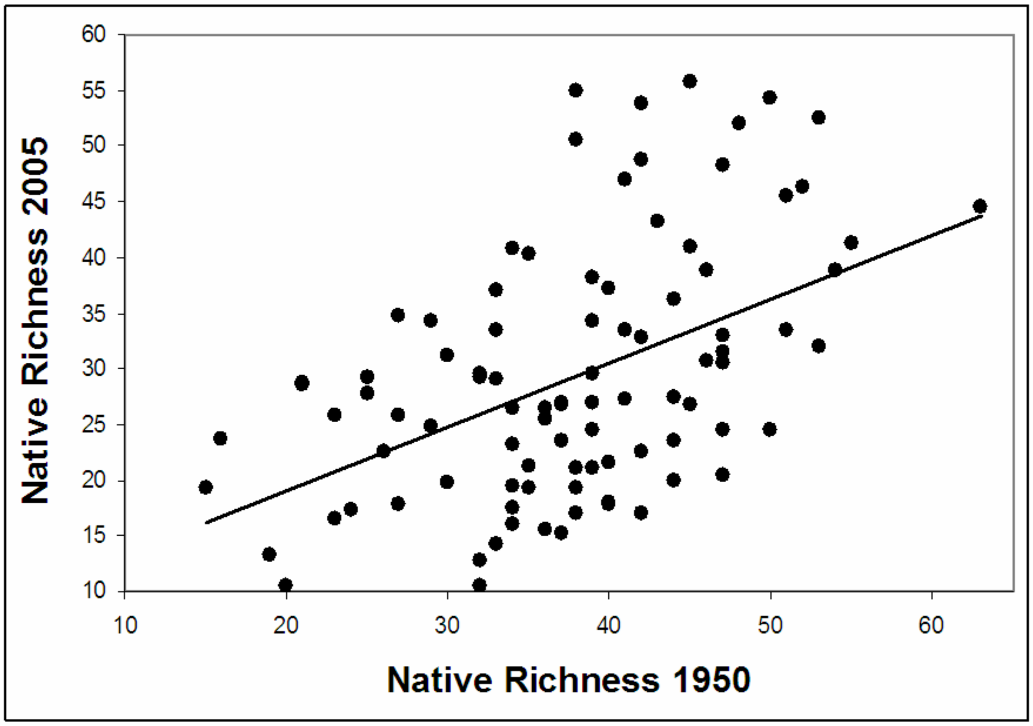


Figure 6: Effects of forest cover on rates of change in average herb similarity.

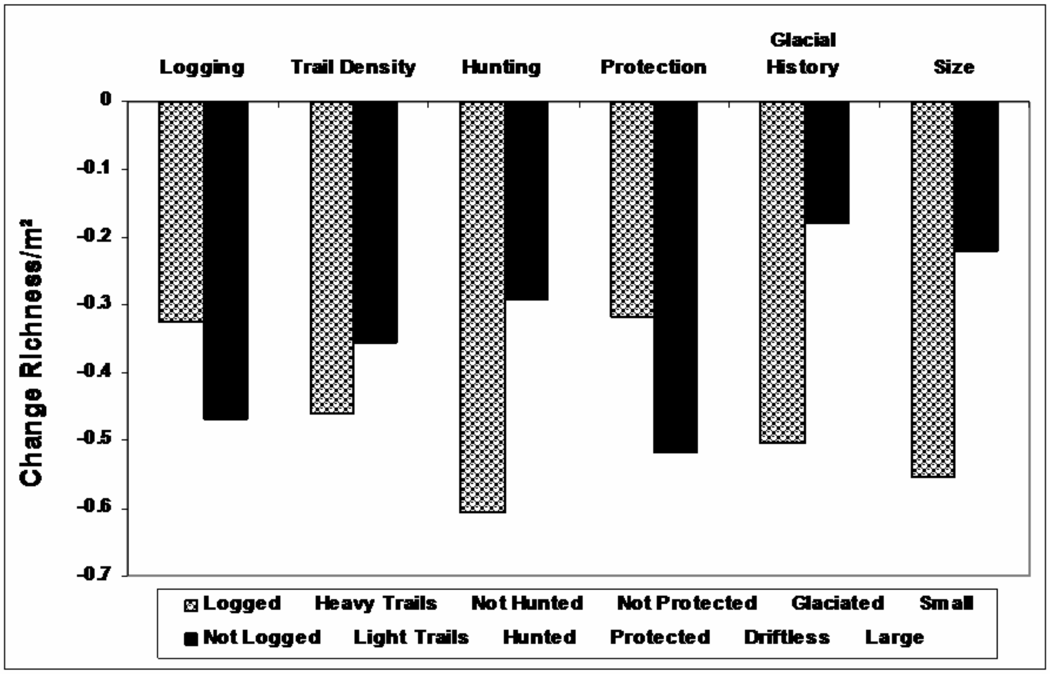
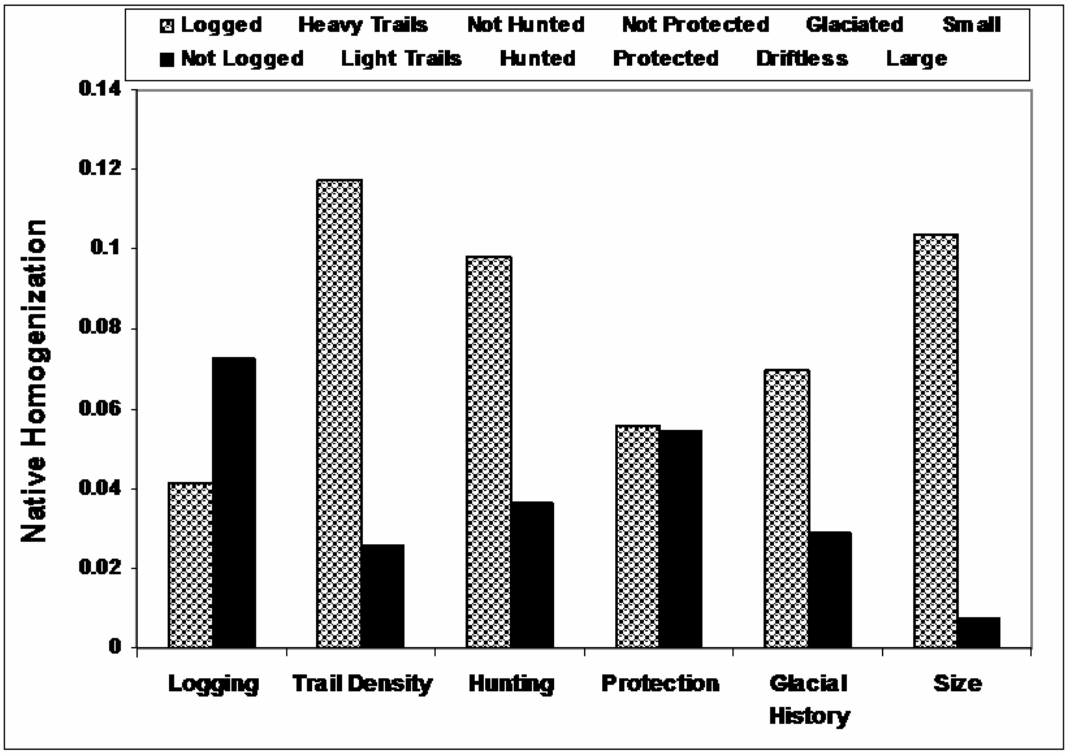


Figure 7: Effects of rates of homogenization in forest understorys



The relative roles of site and landscape factors in plant invasions: A historical approach

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Abstract

To determine whether local site or surrounding landscape variables most affect patterns of weedy plant invasion, we resurveyed 94 upland forest sites in southern Wisconsin (U.S.A.) half a century after they were surveyed by J. Curtis and colleagues. These initial surveys provided baseline data on species richness, heterogeneity in composition among quadrats and sites, and canopy successional state. We supplemented these data with contemporary measures of under-and over-story composition, soil texture, soil nutrients, and surrounding landscape cover. Both native and introduced vascular plant species responded more to landscape factors (particularly forest cover and road density) than to local site factors, but in opposite ways. Native species were more likely to invade larger patches of early successional forest in landscapes dominated by forest cover with few human modifications. In contrast, exotic species typically invade small, fragmented stands subject to considerable human influence. Soil factors and successional status appear unrelated to exotic invasions, undermining the idea that resource availability drives invasions. Rather, nearby seed sources and human disturbance appear to facilitate exotic species invasion. Stands of higher initial diversity also experienced fewer exotic species invasions, supporting the diversity resistance hypothesis. Subsequent losses of native species from these sites, however, appear unrelated to exotic species invasions. Instead, changes in native species richness reflect dramatic declines in recruitment coupled with higher rates of extirpation in fragmented landscapes. These results underscore the importance of landscape cover and processes both to limit exotic species invasions and to facilitate native plant dispersal and persistence.

Introduction

Exotic species invasions represent a major threat to biodiversity and ecosystem services throughout the world. In the U.S., economic damage alone has been estimated to be as high as $137 billion per year (Pimentel 2001). The ecological damage to ecosystems can be equally devastating, Wilcove et al. (1998) estimate that exotic invading species are second only to habitat loss and fragmentation as threats to threatened and endangered species in the U.S. Exotic species have also appear to reduce plant diversity (Woods 1993, Meekins 1999, Schmidt 1999), inhibit tree regeneration (Woods 1993, Lorimer 1994, Beckage 2000) and increase nest predation (Schmidt 1999). Alarmingly, traditional conservation measures such as reserves and natural areas are not immune to this threat (Drayton and Primack 1996). What factors affect a site's susceptibility or resistance to invasion by exotic species? Are there intrinsic or extrinsic factors that allow sites to resist or accommodate invasion? Do some invasions reflect ecosystem degradation rather causing it? Answering these questions could help direct control and remediation efforts and allow managers to better direct resources towards effective solutions.

Communities with higher initial species richness may better resist invasions by non-native species. This "diversity-resistance" hypothesis assumes that high diversity sites better resist invasion because all available niches are filled, leaving few resources for additional species. It has attracted interest from several researchers who often find negative correlations between native and exotic richness at small (1-10 m^2) scales (Tilman 1997, Kennedy et al 2002, Lindig-Cisneros 2002, Fargione 2005). However, other field studies have found the opposite pattern, generally at larger scales (stand level and larger), where richer regional floras tend to have greater rates of invasion than regions with poor regional richness. (Stohlgren 1999, Levine 2004, Knight & Reich 2005).

Resource availability may also affect rates and patterns of invasion (Davis et al. 2005). This hypothesis assumes that some communities may be sub-optimal in terms of exploiting the locally available resources. Excess resources may also become temporarily available in many ways after physical disturbances such as logging or wind-throw when light and nutrients become more readily available (Davis et al. 2000). Many abiotic factors (e.g., soil texture, pH and nutrient availability, slope and aspect) are known to influence rates of invasions (Von Holle 2005). Although we expect excess resources or open niches to favor invading species, site conditions that promote invasion should favor both native and non-native invaders alike. Thus, under the resource availability hypothesis, we expect sites with higher local levels of resources (e.g., light or soil nutrients) to experience more invasions, with invasions by exotic species paralleling invasions by natives. This approach integrates with established theory that widely recognizes invasion and colonization as fundamental processes that regulate biodiversity at local and regional scales (Elton 1958, MacArthur & Wilson 1967, Hubbell 2001).

We often lack empirical evidence on patterns of invasion in natural systems to test these hypotheses. We particularly lack long-term monitoring data from natural plant communities which might allow us to directly assess the nature and effects of species invasions. Many studies (e.g., Gibson 1988, Brothers & Spingarn 1992, Gilbert &Lechowicz 2005) instead seek to substitute space for time by comparing invaded to un-invaded sites and presuming that these differences in invasion correspond to correlated differences in current site conditions. Such studies are useful but could be misleading if the correlations with current conditions are due to other unmeasured or unsuspected factors. It would be better to measure pre-invasion conditions in the community rather than infer from current conditions the factors that may have conferred resistance or susceptibility to invasion. An alternative approach is to experimentally plant exotics while varying initial conditions (soil nutrients, native diversity). While useful, such studies are necessarily small in scale and report patterns at only a few locations, making it difficult to generalize to natural systems.

A third approach we pursue here is to exploit historic baseline data from a range of sites that were subsequently invaded (or not). Unfortunately, such historic data are rare and often cover only a few stands making it difficult to infer just which factors contribute the most to species invasions.

For this study, however, we have access to the unique historic data provided by John Curtis and colleagues in preparation for the book, <u>The Vegetation of Wisconsin</u> (Curtis 1959). Curtis and colleagues collected quantitative data for hundreds of species at hundreds of sites, providing a large sample size that covers a broad geographic region. This allows us to overcome the limited spatial and temporal extent of previous studies. In particular, by directly measuring both local biotic, abiotic site factors and surrounding landscape features, we are in a position to assess their relative contribution to susceptibility or resistance to species invasions at local and regional scales.

We use this historical approach to first describe patterns of species invasion and to weigh the relative importance of biotic, abiotic and landscape factors in conveying resistance or susceptibility to such invasions. Here, we follow Davis (et al, 2002, 2005) and define invasion as a new species appearing at a stand where it was not observed in the original sample, including both native and exotic species. If the stand invasibility is independent of exotic/native status, we should expect native and exotic invaders to be positively related (Davis et al. 2005). Alternatively, the abundance and dominance of exotic species may depend most on the degree of human dominance of the landscape. Conversely, we expect patterns of invasion by native species to be positively related to patch size and negatively to measures of forest fragmentation, where large patches in forest landscapes are better able to recruit native species, replacing extirpations and thereby maintaining native diversity. We also expect that invaders of both types will share attributes known to favor invaders such as high dispersal rates, high reproductive output, etc.

Methods

Sampling Methods & Site Selection

To investigate how sites differ in their susceptibility to exotic species invasion, we use historic baseline dataset originally collected by J.T. Curtis and colleagues in the late 1940's and early 50's and summarized in his classic text, *The Vegetation of Wisconsin* (1959). These data were archived in Birge Hall, Department of Botany, University of Wisconsin Madison. To be included in Curtis' original study, stands needed to be > 6 ha in area, uniform in topography, with no evidence of recent domestic grazing or logging activity. To sample the vegetation, they first randomly chose an initial sampling point 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 method

(Cottam 1949) at 40 points spaced evenly along a square U-shaped transect (mean distance 20 m). This technique sampled a total area of approximately 2-4 hectares, varying with the size of the stand. In an effort to quantify the abundance of herbs, shrubs and tree seedlings present, they also recorded the presence/absence of all herbs, shrubs, and tree seedlings within 1 m^2 quadrats placed at the center of each of the first 20 points along the transect. See chapter 1 of this thesis for detailed information on sampling methods.

Working from the original hand-drawn map, we relocated and resurveyed a sub-set of these stands in 2002-04 using similar but more intensive methods, making a special effort to replicate the spatial scale of the original sample. We sampled any forest that maintained a tree canopy excluding residential yards, pine plantations and pasture. We included partially fragmented forest patches (e.g. partial residential) if there was minimum of 6 hectares of undeveloped land – including the 30 m buffer.

From a randomly chosen starting location, we sampled herbs, shrubs and tree seedlings as present or absent in 80, 1m^2 quadrats spaced at 15 m intervals (equal to the average distance between quadrats in the original study) along a U-shaped transect. Trees were sampled with the same random pairs method used in the original survey (Cottam 1949), but again with increased sampling effort, Curtis sampled 80 trees per stand versus an average of 160 for the current effort. We divided our total sample of 80 quadrats into 4 replicates of 20 quadrats each. In cases where the stand had different stand histories (e.g. logging in half of stand), the sampling was stratified such that replicate 1 was in the portion of the stand that most closely matched the original site condition (low disturbance, homogenous canopy). We collected soil samples from each stand, sampling points distributed through the sampled areas from the top 4” of soil below the litter layer and pooling these for analysis. We analyzed soils for both soil nutrients (pH, % Organic Matter, Ca, Mg, P, K, and total N) and particle size (% sand, silt, clay) at the UW soil and plant analysis laboratory.

Houses, roads and land cover within five kilometers were digitized on screen from current digital orthophotos using ArcGIS. Roads were considered as any linear feature that is visibly connected to other roads., driveways less than 50-m in length were not digitized. Land cover polygons were classified into major land cover; the class catalog will follow the National Land Cover classification system, with a minimum mapping unit size of 1 ha. We used ArcGIS to identify the area within 5 km distance of each study site. Within this buffer, we summarized the number of houses, density of roads, land cover abundance and computed landscape indices. Based on these land cover data, we computed landscape indices to quantify forest cover and fragmentation including patch size, % forest cover, mean patch size, a shape index (edge vs. area), and an isolation index (a gravity-based measure of patch separation).

Analysis

We estimated species invasions by first identifying species that had invaded the sample space of each site over the last fifty years, based on equal samples of twenty, 1m^2 quadrats. For each stand, we the calculated both the frequency and relative frequency of both native and exotic invading species. We use these data to generate the total frequency (total abundance) and total relative frequency of both native and exotic invaders at each stand. We repeat this for each of the four replicates in the resample, the average of the 4 replicates and all 80 quadrats combined. For each time period, we also calculated the native richness at both 1 and 20 m² scales. Finally, we calculated the average Jaccard similarity between all pairs of quadrats as a measure of within-site heterogeneity.

We also calculated the rate of native species turnover by first calculating the number of native species shared between both time periods and using that to generate the number of native species lost (Richness 1950 - Richness Shared) as well as native species gained (Richness 2005 – Richness Shared) for each stand. Native extirpation rates were estimated as native species lost/ native richness 1950. Native immigration rates were estimated as native richness gained/ native richness 2005. As with estimates of heterogeneity (Rogers Ch. 1), we use only replicate 1 for this analysis to retain species identity information while controlling for variation in sample size. To directly measure turnover, we also measured self-similarity between time periods using both presence/absence (Jaccard's Index) and relative abundance data (Sørensen's Index).

Our estimates of extirpation and invasion are based solely on the sample data, and do not represent the "true" extirpation or invasion but rather extirpation from and invasion into the sample space. While this accurately represents turnover for common species, it is less reliable for changes in rare species which may be missed in any limited sample. Undoubtedly, some "extirpated" species were indeed present in 2003 while some "invading" species were already present in 1950 (to say nothing of the species that were extirpated and then re - invaded!). We have not yet found a satisfactory way to correct our estimates of extirpation or invasion for error due to sampling that does not rely on questionable assumptions (e.g. stability of co-occurrence patterns through time). We therefore divide our sample into suitable replicates and use these to test the consistency of identified trends.

As expected, estimates of species richness, total frequency and relative frequency of invading exotic and native species were all highly correlated across the four replicates (Pearson correlation coefficients were 0.857, 0.969, and 0.959 respectively for exotics , 0.938, 0.968, 0.865 respectively for natives, all P's < .001). All measures of invasibility also produced very similar results in response to predictor variables, with the average values usually giving the best fit. We therefore use the average richness, average total frequency, and average relative frequency in all analyses of both exotics and natives. Fortunately, the large sample size ameliorates the sampling problem, allowing us to generalize population trends across the region despite not being able to reliably infer local changes at any given site.

To test the effects of canopy succession and composition, we calculated a modified version of the original PEL continuum index (CI) – based on the Climax Adaptation Values (CAV) values published by Curtis (1959). In addition, we created a successional index (SI) based on published Successional Adaptation Values (SAV) developed by Peet & Loucks (1977) for southern Wisconsin forests. We calculated the CI and SI scores for each sample by taking an average of CAV or SAV values weighted by the abundance of each tree species present in the sample. CI and SI values in each time period were then used to calculate the amount of change in each stand according to the formula: $N_{2000} = \lambda N_{1950}$, where λ = discrete magnitude of change for any variable N of interest. Finally, we multiplied our estimates of density and average basal area per tree to estimate total basal area/hectare for each stand in each time period and their rates of change over the 50 year interval.

To test how biotic and abiotic factors affect a site's susceptibility to invasion, we compared the rates of change in exotic species richness, abundance and relative abundance against the initial site richness at both 1 and 20 m^2 scales. We also tested how change in within-site homogeneity (the average Jaccard similarity among quadrats within a site) depends on housing and road density, forest cover, urbanization and soil nutrients using regression analysis.

Results

Exotic Invasions

Over the last fifty-five years, 45 exotic species invaded the sample space of the 94 southern Wisconsin forests included in this study (Table 1). Exotic taxa only existed in 19 of the 94 stands (19%) in 1950 but occupy an average of 77.6 stands (83 %) in 2003. The average frequency of exotics, when present, more than doubled from 2.9 quadrats (14.5%) in 1950 to 6.5 quadrats (32.3%) in 2005 as did the relative frequency of exotic taxa (from 2.5% in 1950 to 5.3 % in 2005). The average stand was invaded by 2.01 exotic species (S.D. = 1.45) over all stands and 2.15 species/stand (S.D. = 1.4) when considering only stands where exotics occurred. Garlic mustard (*Alliaria petiolata*) was the most successful invader, followed by European buckthorn (*Rhamnus cathartica*), common dandelion (*Taraxacum officinale*) and Bell's honeysuckle (*Lonicera x bella*) (Table 1).

Exotic species invasions declined moderately in stands with greater initial species richness at $20m^2$ (Fig. 1), supporting the diversity resistance hypothesis. Exotic invasions were also associated with greater within-site homogeneity as reflected by average between quadrat similarity. Exotic invasions, however, were not correlated with either initial CI or SI or with changes in CI or SI (Table 2). Surprisingly, current native and exotic species richness appear unrelated ($r = -0.181$, $p = .081$) in contrast to previous studies (Gilbert & Lechowitz 2005). Soil nutrients showed only weak relationships with exotic invasions, although exotics appear slightly less likely to invade sandy sites (Table 2).

Landscape variables show the best predictors of exotic species invasions (table 2). Housing and road density within the 5km buffer are both strongly and positively related to exotic invasions as is forest fragmentation (Figure 2).

In a stepwise linear regression that initially included all predictor variables and an alpha = 0.15, only road density and initial native richness remained in the model, collectively explaining 28.2 % of the total variance (24.18% & 3.37 % respectively) in exotic species richness. These results strongly suggest that landscape context is much more important than native species richness in determining rates of exotic invasion.

Native Invasions

All 94 stands gained at least one new native species, with an average of 14.1 new native species/stand (sd = 6.69). The average total frequency of invading native taxa was 35.1 observations/stand (sd = 22.1). Invading native species contributed on average 28.5% (sd = 13.9) of the total observations at a site in 2005.

In contrast to exotic invasions, initial species richness at both 1 and 20m^2 scales showed no relationship to native species invasions. Initial canopy composition and successional indices and their rates of change were strong influences on rates of native species invasion (Table 2, Fig. 3). Mesic late successional stands were less likely to be invaded by new native species than early successional stands. However, early successional stands generally experienced greater changes in SI, leading to greater rates of invasion in stands that had undergone the greatest successional change (Table 2). In a multiple regression both predictors remain significant and return a better fit ($r^2 = 32.5\%$, $p < .001$) than either measure alone. Native species were also slightly more likely to invade stands with sandy soil, suggesting that drier, more open conditions facilitate native species turnover (Table 2).

As with exotic species invasions, landscape measures of land cover showed the strongest correlations with native species invasions. However, the directions of these relationships are usually opposite of the patterns seen with exotic invasions (Table 2). Native species, for example, were more likely to invade stands with higher forest cover at a 5km radius (Fig. 4). Conversely, native invasion declined with increased with urbanization and road density (Table 2, Fig. 5).

A stepwise linear regression of apparent native species invasions intially based on all predictor variables retained only mean patch size, starting successional index and road density, contributing 39.1%, 7.7% & 2.8% respectively for a combined adjusted r^2 of 48.6 %, $P < 0.0001$).

Discussion

Although our data lend some support to the diversity resistance hypothesis, the rates at which both native exotic species invade southern Wisconsin forests clearly depend most on the surrounding landscape context. However, native and exotic species respond in opposing ways to landscape and site variables. Patterns of invasion generally reflect basic principles of community ecology and conservation biology. Stands subjected to heavy human influence in highly fragmented landscapes were more likely to be invaded by exotics and less likely to be invaded by native species. Conversely, large intact forest patches were more likely to recruit new native species and better able to resist exotic species invasions. These results strongly support the idea that anthropogenic disturbances explain the vast majority in the variation in exotic species invasions, regardless of local site conditions. They also underscore the important role played by dispersal and the surrounding species pool in local patterns of species diversity and community composition. Habitat specialists are generally rare in modern fragmented landscapes, yet exotic species are often widely planted in these landscapes (residential, commercial, along highways, etc.) and are pre-adapted to life in human dominated landscapes. These changes in propagule pressure surrounding fragments inevitably leads to invasion of these patches by those exotics, invasions being simply a function of the surrounding species pool (Eriksson 1993). The actual species that invades is simply a function of its dispersal ability and its regional abundance.

Life history traits of the members of the species pool are also important in considering which species invade an particular stand and the differences observed here between patterns of exotic and native species invasion could also simply reflect differences in life history traits between native and exotic species. In future work we intend to examine how variation among life history traits covaries with patterns of invasion.

There is a strong longitudinal gradient in the data as well, as stands in southeastern Wisconsin are generally smaller and more isolated and higher road & housing densities than in southewest Wisconsin. This gradient also reflects differences between the unglaciated (western) and glaciated regions(eastern) of southern Wisconsin. These parallel patterns in variation among the predictor variables creates statistical problems that are not fully dissected here. Thus, we cannot say with statistical certainty that the correlations presented here represent the ecological reality on the ground. Nonetheless, the patterns we report certainly dovetail with expectations from classical ecology and conservation biology theory.

One way to address this problem is to perform separate analysis on the glaciated and unglaciated regions and see if these patterns remain. Within the glaciated set of stands (63 stands) the patterns were essentially the same; exotic species invaded highly fragmented landscapes with high road and housing density while natives invaded large intact patches with low measures of human influence. We did, however, detect an increased influence of soil properties on native invasions. Stands on nutrient poor, well drained soils showed a greater tendency to have been invaded by new native species, although these factors are still much weaker than are measures of patch size and forest fragmentation.

When we restricted our analyses to the 31 stands in the unglaciated portion of the study area, patterns were again similar to those reported above. However, there was increased importance of surrounding agriculture and initial within-site similarity in predicting exotic species invasion and a decreased importance of soil nutrients and texture in relation to all measures of both native and exotic species invasions.

The consistency of these results across heterogeneous landscapes of southeastern and southwestern Wisconsin suggests that the correlations we report here for native and exotic species invasions are generalizeable for southern Wisconsin forests. If indeed these patterns reflect actual ecological causation, they impart key management implications. For forests in southern Wisconsin, managing for large, unfragmented stands with low road and trail density is likely to promote native species invasions while promoting resistance to exotic species invasions. These patterns bring to light a distinct paradox. The same underlying ecological process can be both a blessing and a curse. Disturbance is a necessary to maintain diversity, yet opens the door for potential invaders. The key is to maintain regional populations/ecosystems so that species are recruited from a larger native pool and to maintain corridors for dispersal.

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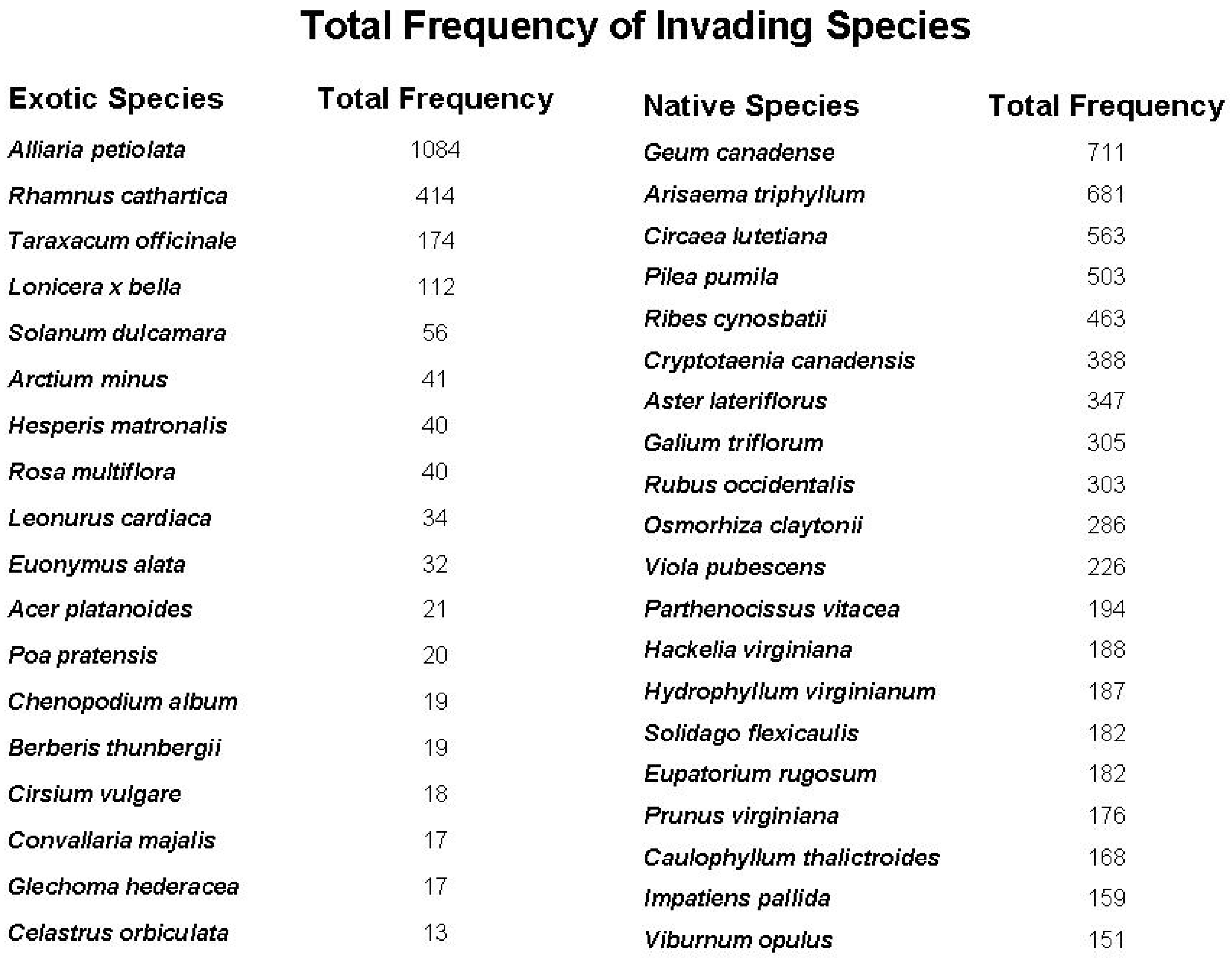
Table 1: Comparison of total frequency for select native and exotic species as invader.



Total Frequency of Invading Species

Exotic Species	Total Frequency	Native Species	Total Frequency
Alliaria petiolata	1084	*Geum canadense*	711
Rhamnus cathartica	414	*Arisaema triphyllum*	681
Taraxacum officinale	174	*Circaea lutetiana*	563
Lonicera x bella	112	*Pilea pumila*	503
Solanum dulcamara	56	*Ribes cynosbatii*	463
Arctium minus	41	*Cryptotaenia canadensis*	388
Hesperis matronalis	40	*Aster lateriflorus*	347
Rosa multiflora	40	*Galium triflorum*	305
Leonurus cardiaca	34	*Rubus occidentalis*	303
Euonymus alata	32	*Osmorhiza claytonii*	286
Acer platanoides	21	*Viola pubescens*	226
Poa pratensis	20	*Parthenocissus vitacea*	194
Chenopodium album	19	*Hackelia virginiana*	188
Berberis thunbergii	19	*Hydrophyllum virginianum*	187
Cirsium vulgare	18	*Solidago flexicaulis*	182
Convallaria majalis	17	*Eupatorium rugosum*	182
Glechoma hederacea	17	*Prunus virginiana*	176
Celastrus orbiculata	13	*Caulophyllum thalictroides*	168
		Impatiens pallida	159
		Viburnum opulus	151

Table 2: Correlations between measures of exotic and species invasions and important predictor variables.

* p < .05 ; ** p < .001	**Exotic Rich**	**Exotic Freq**	**Exotic Rel Freq**	**New Native**	**New Native Freq**	**New Native RelFreq**
Richness 1950	**-0.332****	**-0.203***	**-0.313****	0.154	0.109	-0.170
Avg Quad Similarity	**0.259***	**0.307****	**0.301****	-0.175	-0.162	-0.177
Ln(house density)	**0.438****	**0.294***	**0.418****	**-0.341****	**-0.305***	-0.218
Ln(road density)	**0.492****	**0.297***	**0.446****	**-0.437****	**-0.395****	-0.227
% Urban	**0.385****	0.183	**0.321***	**-0.363****	**-0.330****	**-0.200**
% Grassland						
% Forest	**-0.231***	**-0.208***	**-0.282***	**0.407****	**0.307***	**0.287***
Stand Size	-0.171	-0.129	-0.167	**0.409****	**0.388****	**0.220***
Soil pH	0.098	0.164	0.186	-0.178	-0.201	-0.254
Soil % N	0.044	0.076	0.118	-0.148	-0.144	-0.138
Soil % Sand	**-0.262***	0.104	0.092	**0.199***	0.191	**0.215***
Soil Ca (ppm)	0.070	0.107	0.140	-0.124	-0.138	-0.164
CI 1950	-0.160	-0.096	-0.015	**-0.278***	**-0.386****	**-0.258***
SI 50	-0.034	-0.074	0.046	**-0.459****	**-0.512****	**-0.308***
Change CI	0.044	-0.014	-0.027	0.084	0.162	0.184
Change SI	-0.003	-0.045	-0.126	**0.460****	**0.512****	**0.295***

Figures

Figure 1: Correlation between exotic invasions and initial site richness

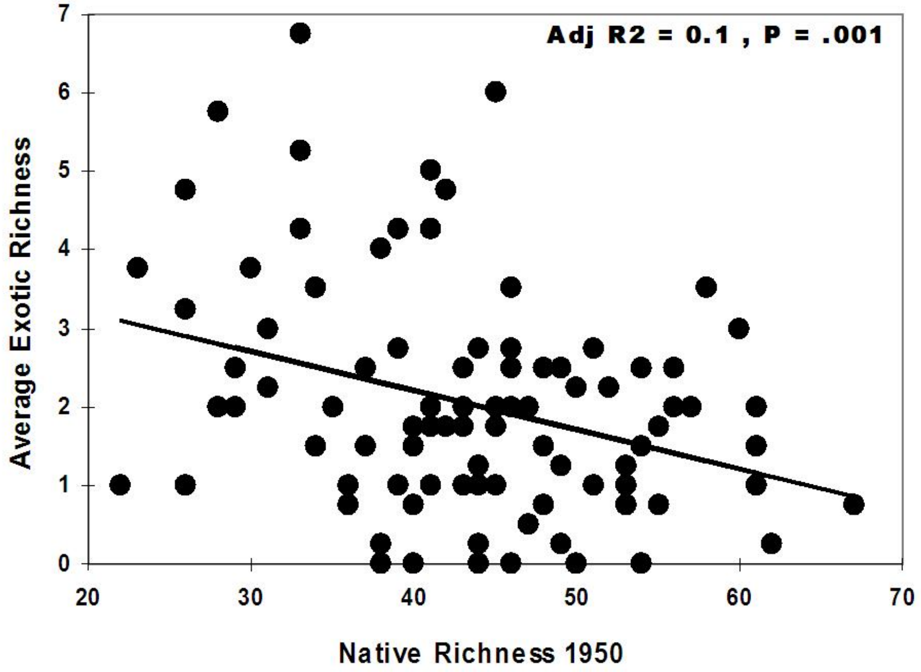


Figure 2: Correlation between road density and exotic species invasions

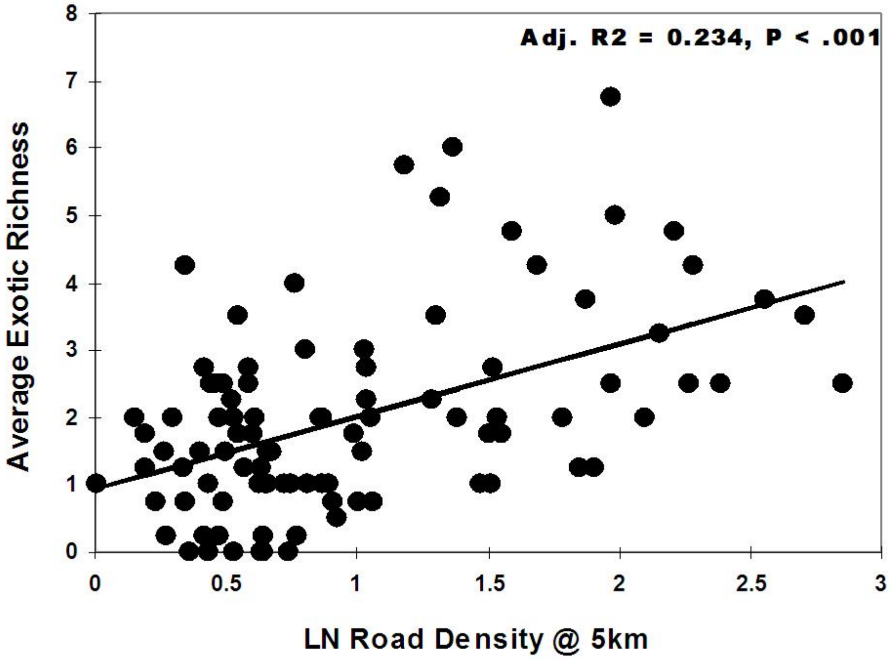


Figure 3: Correlation between native species invasions and initial successional index

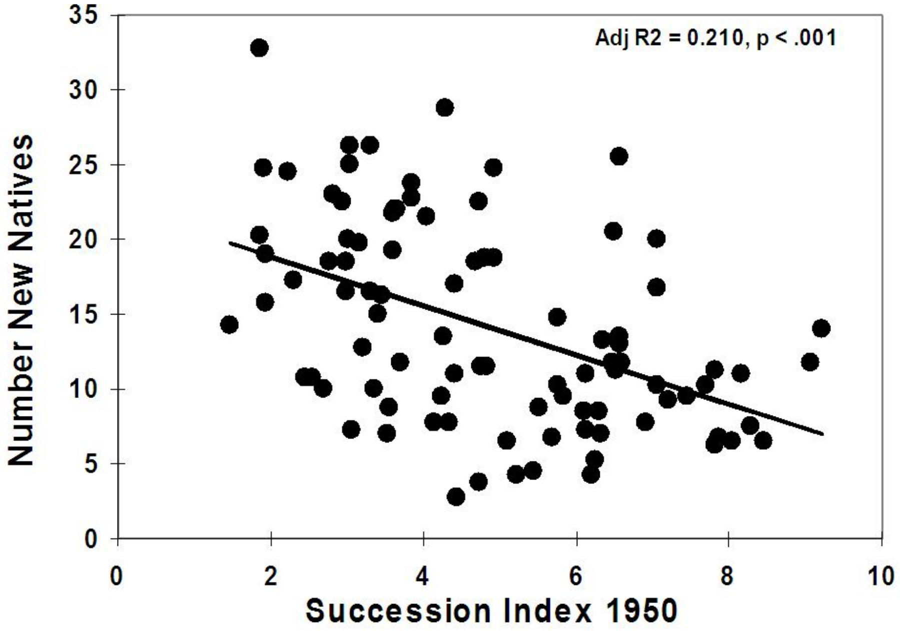


Figure 4: Correlation between native species invasion and surrounding forest cover

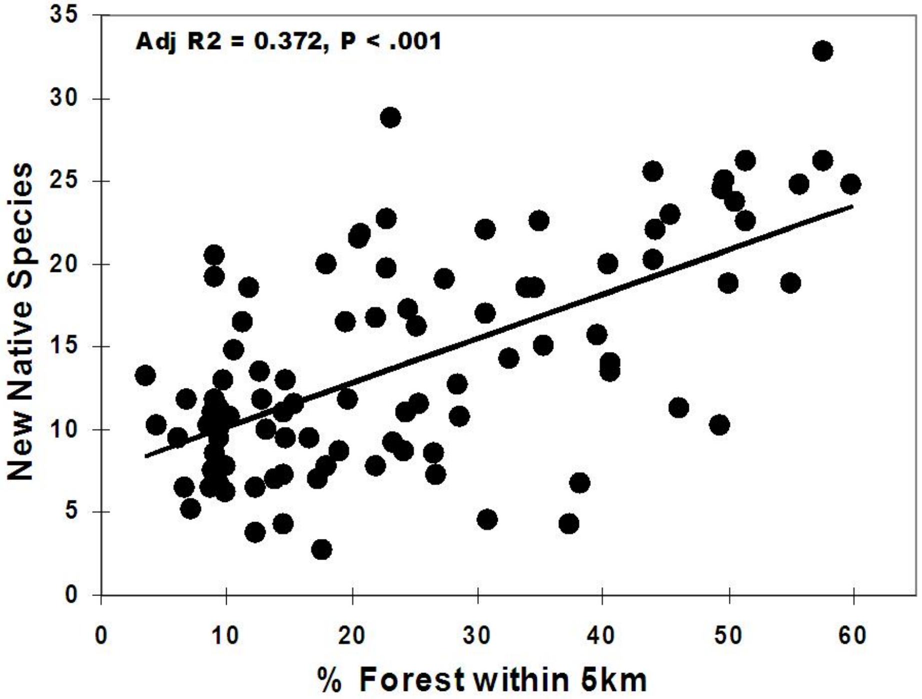


Figure 5: Correlation between native species invasion and road density

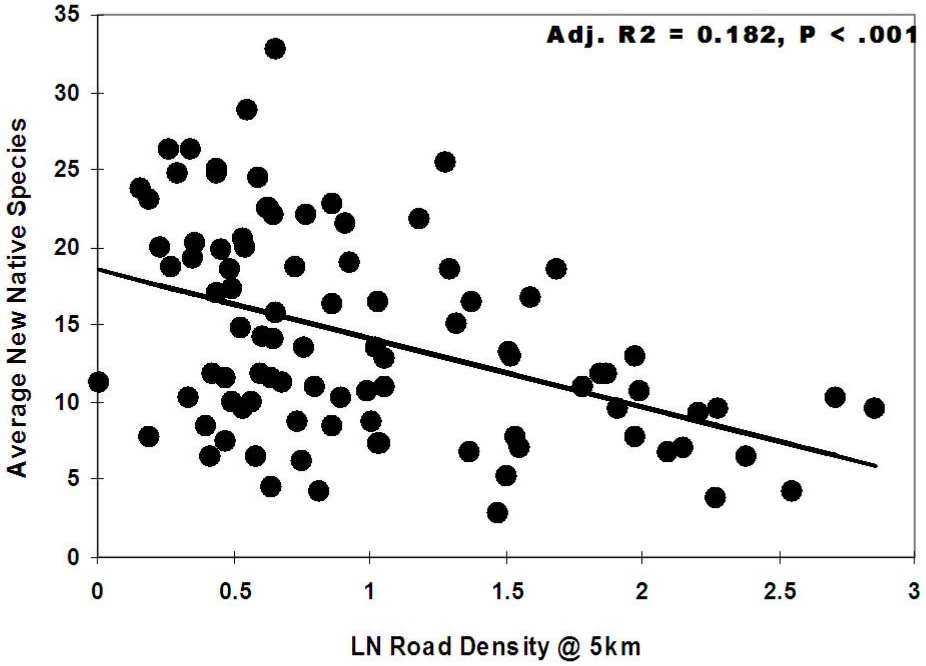
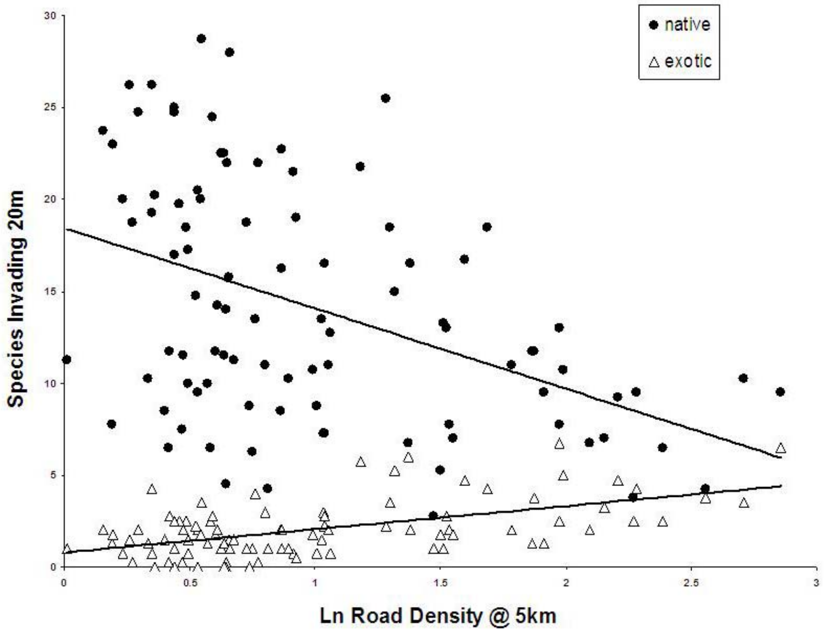


Figure 6: Contrasting relationship between and road density and exotic vs. native invasions.



Long-term shifts in southern Wisconsin forest communities

IV. Where have all the gradients gone?

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Abstract

Traditional ecological theory has interpreted shifts in the composition and structure of forest plant communities in terms of underlying gradients in abiotic (soil) conditions and successional processes following disturbance. Forest plant populations, however, are increasingly affected by the landscapes that surround them. We compare how local soil and successional gradients affect forest under- and over-story communities across 93 forest patches in southern Wisconsin relative to surrounding landscape conditions and how these relationships have changed between the early 1950's and 2005. The overstory composition of these forests in both time periods strongly reflect underlying moisture and nutrient gradients despite successional changes. Local site variables (canopy conditions and soil nutrients) were also strongly related to community composition and richness in the 1950's. By 2005, however, local site factors became less useful predictors of forest understories whereas surrounding landscape conditions became more accurate predictors. Fragment size and the intensity of surrounding development now strongly predict forest understory composition, matching predictions from Curtis (1956). This difference in responses probably reflects the faster dynamics of forest understories relative to the overstory. As plant communities become less coupled to local site conditions, classical ecological predictions based on local edaphic gradients become less useful. Species persistence and abundance patterns instead appear to be reflecting meta-population and meta-community dynamics. Managers wishing to sustain plant diversity in the face of landscape fragmentation and urbanization should therefore seek to protect larger blocks of habitat and community connectivity.

Keywords: meta-population dynamics; plant species persistence; extinction; temperate herbs; plant community structure.

"Man's action in this community almost entirely result in a decrease in its organization and complexity and an increase in the local entropy of the system. His activity in reducing the number of major communities, climax or otherwise, and in blurring the lines of demarcation between them by increasing the range of many of its components likewise reduces the non-randomness of his surroundings. Man, as judged by his record to date, seems bent on asserting the universal validity of the second law of thermodynamics, on abetting the running down of his portion of the universe"

J.T. Curtis 1959

Introduction

Analyses of forest community composition have historically focused on explaining which of several underlying environmental gradients best explain tree species distributions and abundance (e.g., Gleason 1926, Curtis 1959). Some recent work argues, however, that the same patterns of species distribution and abundance observed in nature could be explained by neutral processes (Bell 2001, Hubell 2001). Regardless, both approaches regard extinction and immigration as critical processes in diversity maintenance.

The ability for new populations to invade habitats as they respond to changing conditions (disturbance, succession) or to chance fluctuation is essential to the metapopulation viability of individual species on the landscape (Hanski 1996). Landscapes, however, are being increasingly disrupted by human activity, shifting historically dominant patterns of disturbance and altering these underlying links between local site conditions and plant communities. With increased human dominance of the surrounding landscape, permeability is reduced and dispersal in restricted for most species, while favoring vagile generalist species.

European settlement brought many such disruptions to the forests of North America (Curtis 1956, 1959, Mladenoff 1993, Foster 1993). Most historical studies of change have focused on overstory composition, reflecting the relative abundance of historical data on trees and the fact that most temperate tree species are well represented in the pollen record. For example, Foster (1998) uses land survey records to reconstruct vegetative cover across pre-settlement landscapes and to demonstrate that shifting patterns of human land use have altered the distribution and abundance of tree species. These, in turn, reflect shifting environmental gradients since European settlement. Paleoecologists routinely use pollen in sediments to date settlement by observing peaks in *Ambrosia* pollen, associated with the burst of weedy species associated with freshly plowed ground. However, our ability to detect other changes in herbaceous community composition is quite limited as most herbaceous are not wind pollinated. Such changes can sometimes be inferred by substituting space for time (Foster 1992). Little work has been done, however, to directly document how proximal drivers of understory plant distributions and community structure have shifted over time. This reflects the scarcity of both historical and palynological data for these communities.

Here, we use a unique set of historic baseline data to directly test whether forest understory plant communities in southern Wisconsin have shifted in their relationships to local and surrounding environmental conditions over the last half century. If landscape-level effects are becoming more important, we expect the composition and structure of forest communities to have become less related to local (e.g., soil) conditions than those same forests were 50 years ago. We might also expect measures of landscape fragmentation and human dominance of the landscape to be better predictors of community composition and structure. Remarkably, John Curtis (1956) predicted this – that the composition and structure of forest understories would shift from being strongly correlated with environmental measures and canopy composition historically to being more highly correlated with landscape fragmentation and measures of human occupancy in contemporary surveys.

The work reported here builds on our previous broad-scale analyses of overall shifts in under-and over-story plant communities at these sites (Ch. 1) and how these shifts relate to both successional change and changes in surrounding landscape conditions across these increasingly fragmented forests (Chs. 1, 2, & 3).

Background

In the late 1940's and early 1950's, the plant ecology lab (PEL) at the University of Wisconsin, under the direction of J.T. Curtis, embarked on an ambitious program of surveying the state's plant communities. These investigators sought to reconstruct a full picture of the pre-settlement vegetation of the state by sampling the more intact plant communities they could find to sample. They also sought to explore relationships between the composition and structure of these communities and the conspicuous environmental gradients that appeared to underlie these distributions. In particular, Curtis used quantitative data to derive a synthetic gradient that was relatively independent of pre-conceived ideas of stand classification dominant at the time (Nicolson 2000). Fortunately, these investigators also carefully archived their data in the Plant Ecology Lab at UW – Madison, including detailed maps and description that allowed us to rather precisely relocate the study sites (see Ch. 1). These efforts were highly successful, producing a series of classic papers and ultimately a book, *The Vegetation of Wisconsin* (Curtis 1959).

In analyzing the distribution of plant communities across southern Wisconsin forests, Curtis and colleagues derived a synthetic gradient (the Continuum Index) related to moisture and nutrient availably that provided fairly accurate predictions of canopy and understory composition. This xeric to mesic gradient managed to explain much variation in the richness and composition of forest understories in terms of soil conditions, time since disturbance, and the regional species pool. As such, it represents a classic ecological model linking community composition to underlying local site conditions. Under this view, environments deterministically "filter" species along light and nutrient gradients with each species' particular functional traits determining its position on these gradients. Thus, plants with similar functional traits tend to co-occur and we define these collections as the plant community.

These models have been quite influential in plant ecology, especially among land managers. Regionally, Curtis's book is widely used as a text, providing both conceptual models for land managers and extensive and precise lists of target species used in reconstructing and restoring native plant communities. These lists are commonly used to represent a "reference community" to restore communities that are presumed to exist at some particular point along the continuum. However, if these underlying gradients are not stable, we might be managing under a false assumption or miss regional processes that have direct effects on local diversity. Such approaches could also obscure the effects of regional processes, limiting our ability to retain species whose dynamics depend on these other processes.

Indigenous people already thriving in southern Wisconsin at the time of European settlement had an intimate relation with the biota and largely influenced the landscape through management, a fact not lost on Curtis (1956). However, fundamental relationships between environmental gradients and the biota that had evolved over millennia was likely still largely intact and the dynamics maintaining plant populations on the landscape well established. Under indigenous management, the landscape of southern Wisconsin was a dynamic mosaic of forest intermingled with prairie with a large portion of the landscape at any given time in some intermediate stage of development, the famed oak savanna of yore (Curtis 1959). As Europeans invaded the forest-prairie border region of southern Wisconsin, they radically altered the previous land-use regimes. Historic landscape processes that shaped the vegetation of the time were interrupted and novel habitats and opportunities were created, changing the ecological, evolutionary and landscape context of many species (Curtis 1956).

To establish his gradient, Curtis struggled to find forests that had escaped conspicuous degradation, allowing them to represent the underlying environmental gradients. In truth, notes from the original surveys often note some evidence of some logging or other forms of past land use. Sites were chosen to minimize these as much as possible, however. Perhaps based on his experience with rejected stands, Curtis also wrote at length about how habitat fragmentation and changes in fire regime affected plant communities in both the short and long term (Curtis 1956). In his essay in *Man's Role in Changing the face of The Earth*, Curtis made clear predictions as to the continued effect of these landscape changes on the future of forest understory plants (see quote in intro).

The effects outlined by Curtis are familiar to any student of conservation biology. Disturbances created by human land-use practices alter the type, intensity, frequency and spatial and temporal heterogeneity of disturbance. The increasing isolation of habitats restricts dispersal opportunities, shifting the species pool available for immigration toward habitat generalists or those pre-adapted to the new conditions. Furthermore, current land-use practices are more homogenous across broad geographic areas than previous disturbance regimes. These shifts further alter the regional species pool and immigration patterns, contributing to the overall homogenization of plant communities.

Since the large scale fragmentation and disruption that happened in the mid-1800's and described by Curtis, the landscape has continued to change. Although there has been considerable recovery of forests, expanding urbanization and intensified agriculture continue to in fundamentally alter the ecological landscape from the point of view of forest understory plants by further reducing landscape permeability for many native species while favoring a few generalist natives and introducing novel species to the species pool available for immigration. These newer changes further amplify the effects of initial settlement, setting the stage for further disruption of the biotic/environmental relationships. As such effects become pervasive, individual populations of once regionally common taxa gradually “wink out”, causing species to become rare or regionally extirpated. We therefore specifically predict that relationships between species distributions and local environmental gradients will decrease in importance over time. Conversely, landscape measures of human impact will increase in importance. Furthermore, we expect for these changes to be strongly felt in the understory species than in the overstory, owing to the higher rates of turnover in understory communities.

Data Collection

Vegetation Data

To quantify the abundance of herbs, shrubs and tree seedlings present, the original survey recorded the presence/absence of all herbs, shrubs, and tree seedlings within twenty $1m^2$ quadrats placed at regular intervals along the sample grid such that points were 15-20 meters apart. Trees were sampled using the random pairs method (Cottam 1956). Although this method gives somewhat biased estimates of stem density and Basal Area, it allowed for the rapid inventory of forest composition over large areas, as was required to derive underlying gradients from such a highly fragmented landscapes (Nicolson 2000).

Working from the original hand drawn maps, we relocated and resurveyed 135 of these stands in 2002-04 using methods that were similar to but more intensive than the original work.

We made special efforts to replicate the spatial scale of the original sample and to place samples in canopies of similar composition and heterogeneity with similar slope and aspects. We sampled any with an intact canopy, omitting yards, pine plantations and pastures. We also applied the original stand criteria to the re-sampled stands and sampled areas with homogenous canopy composition and minimal human disturbance. We included partially fragmented forest patches (e.g. partial residential) if there was minimum of 6 hectares of undeveloped land. After applying these restrictions, we retained 93 stands for this analysis (figure 1). We replicated the original sampling method as closely as possible, but sampled 4x for herbs and 2x for trees in an effort to more fully characterize each site and to provide estimates of variation among sub-samples. As plot locations were not permanently marked, this over-sampling also ensured that we were more likely the specific area first surveyed. See chapter 1 for more detail in the sampling methods and data transformations used.

Environmental Data:

At each site, we collected soil samples at 10 cm depth from 10 points evenly distributed throughout the sampled area. Sub-samples were pooled into single sample from each stand, homogenized and sent to the UW Soil and Plant Analysis Lab for analysis of texture & nutrients (we saved half of each sampled in have stored in cooler). We obtained data on % Sand, % Silt, and % Clay as well as % N, P, K, Ca, and Mg.

To assess landscape factors, we used a GIS to integrate WISCLAND (WDNR) with digital ortho-photos. These layers allowed us to characterize road density, housing density, patch size and patch shape index (edge/area ratio). We also calculate land cover, mean forest patch size and forest patch isolation within a 5 km buffer surrounding each stand. Land cover was divided into four classes: forest, agriculture (active cropping), grassland (include fallow fields, road edges, as well as prairies) & urban.

Canopy composition also represents an environmental condition from the point of view of understory species. Canopy composition integrates soil and landscape factors while also providing a measure of the direct influences the growing environment for understory plants through shading. We measure canopy composition in two ways, using a modified version of the continuum index as conceived by Curtis (1959), calculated here as the weighted average of original CAV values based on relative density of trees > 4” dbh. Our second measure employs the successional index (SI) developed by Peet & Loucks (1977) for southern Wisconsin tree species. We again using the weighted average of SAV scores based on the relative densities of canopy trees.

Analysis

We first removed exotic taxa from the data set. This reflects our focus on understanding on how native species respond to shifting environmental conditions and our desire to avoid the obvious effects of the known correlations between exotic abundance and urbanization (Rogers chapter 3). To reduce the dimensionality of the data while extracting most of the information from species x site matrix, we used ordination. into a set of orthogonal axes that represent independent patterns of covariation in species abundances. Each site is thereby rendered in 2 or 3 dimensional species space such that, when plotted, sites closer together are more similar in composition than sites further apart. We used non-metric multidimensional scaling (NMS) ordination as implemented in PCORD (McCune), using a Bray Curtis ordination as the starting configuration. We then apply correlation analysis between axis scores (ordered such that Axis 1 explains the greatest variation in the original data matrix, axis 2 the second greatest and so on) and measured environmental variables. We did this for both the canopy and understory layers. We tried this using several approaches that varied in the exclusion of rare taxa or using various measures of similarity. These approaches, however, had little influence on the results presented (see appendix 2 for details). Finally, to directly measure the correlation between the canopy and understory in both time periods, we performed Mantel tests between the canopy similarity matrix (Bray-Curtis similarity, using relative density measurements) and the herb similarity matrix (measured using Sorenson Distance measure based on the frequency of herb species in twenty 1m² quadrats).

Results

Canopy Analysis

The ordination analyses of canopy tree composition reveal close correlation with both local soil conditions and with successional condition (Table 1). These associations are strikingly similar across the two time periods, both conforming to the pattern originally described by Curtis. The 1950 ordination returns a two-dimensional solution (stress = 0.13) that explains 76% of the variance in the original community data (axes 1 & 2 explaining 58% and 18% respectively). The 2005 ordination was similar, also providing a two dimensional solution that explained 75% of the original variance, but with more equal loadings on both axes (45% & 30% respectively). Soil nutrients were the best predictors of canopy composition and closely follow the continuum and successional indices along both axis of the ordination. The strength of the relationships have changed little over time, although succession may be increasing in importance. Landscape variable most lacked significance except for effects of fragmentation which appears to be diminishing. Weedy native species that used to characterize small, isolated patches (*Acer negundo, Fraxinus pensylvanica, etc.)* now appear to be more widespread across the landscape, having successfully invading the larger patches and occurring in both early and late successional stands. This might account for the decline of significance of forest cover in the surrounding landscape since 1950.

Understory Analysis

In strong contrast to our analysis of canopy composition, ordination analyses of the understory show striking differences between the two time periods (Table 2). The initial ordination of herb community composition in 1950 data resembles the analysis of canopy composition, showing a strong dependence on soil nutrient conditions and the successional state of the forest canopy (Table 2). This 2 - dimensional solution explains 75% of the variance in the original community matrix, with most information (50%). the second axis 2 explained 25% of total variation and was also correlated with soil nutrients and canopy metrics. However, patch size and forest cover at 5km was also significantly correlated (Table 3) with this axis, suggesting that fragmentation and landscape effects were having some influence on community composition even in 1950.

In contrast, understory composition in 2005 strongly reflects landscape conditions rather than local environmental gradients (Table 2). NMS ordination returned a 3 dimensional solution explaining 87% of the total variance of the original community matrix with axes 1 and 2 explaining 45% and 34% of the variance respectively. Measures of land use, forest fragmentation and urbanization are the best predictors of understory composition, showing the strongest correlations with the most informative axis of the ordination (Table 2). Although soil Ca was marginally significantly correlated with axis 1, the influence of local site conditions were weak with the main axis of the ordination. Nonetheless, soil nutrients are still important predictors, showing significant correlations with the secondary axis. Although soil nutrients were important, their ability to explain axis 2 was limited, explaining only 29.5% of the variance compared to 48.4% for axis 1 in the 1950 ordination (Table 2).

Discussion

As predicted by Curtis (1956), these results strongly support the idea that the once strong link between local environmental gradients and community composition as been interrupted for forest understories in southern Wisconsin. Instead, community composition has shifted to reflect surrounding landscape conditions. The implications are enormous and complex. For one, ecologist are trained in classic models while the rules and underlying assumptions may no longer be valid. More to the point, human and their land use decisions play an ever more critical role in influencing the richness and composition of understory plant communities. We must recognize and embrace this reality if we have any hope to maintain many common species on the landscape in the face of the inevitable consequences of landscape fragmentation (Soule 1979). This may mean actively aiding dispersal, and establishing regional networks of natural areas that identify and share reservoirs of plant populations that are available for the critical immigration process. These results also underscore the importance of Curtis’ original survey as a proxy reference system for restoration projects. Without the original work, individual species responses to specific environmental gradients would be obscured, thereby making conservation and management more difficult.

Because of the clear effects of forest fragmentation, we need to think about finding novel ways of restoring connections between fragments. Swapping plants and seeds between patches, keeping inventories and doing long term studies of population dynamics and introducing appropriate species as the canopy matures or changes, taking advantage of canopy gaps & blow-downs to introduce fugitive species. Such measures could slow or reverse the general decline of many species in southern Wisconsin forest understories. To this end, we need better data on life histories and functional traits and the role of gap dynamics in maintaining species viability within isolated patches We heartily endorse the efforts of Lorimer (1993) and others to regenerate oaks on mesic soils, however new oak patches in old fields and adjacent to exiting patches of maturing forest would also be helpful – perhaps the pine to oak model could be exploited, to create new oak patches as habitat for invading natives as well as increase patch size, another important variable.

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Figure 1: Map of study locations in southern Wisconsin

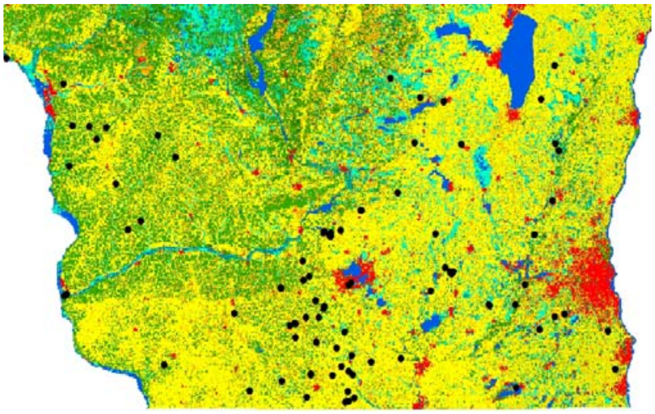
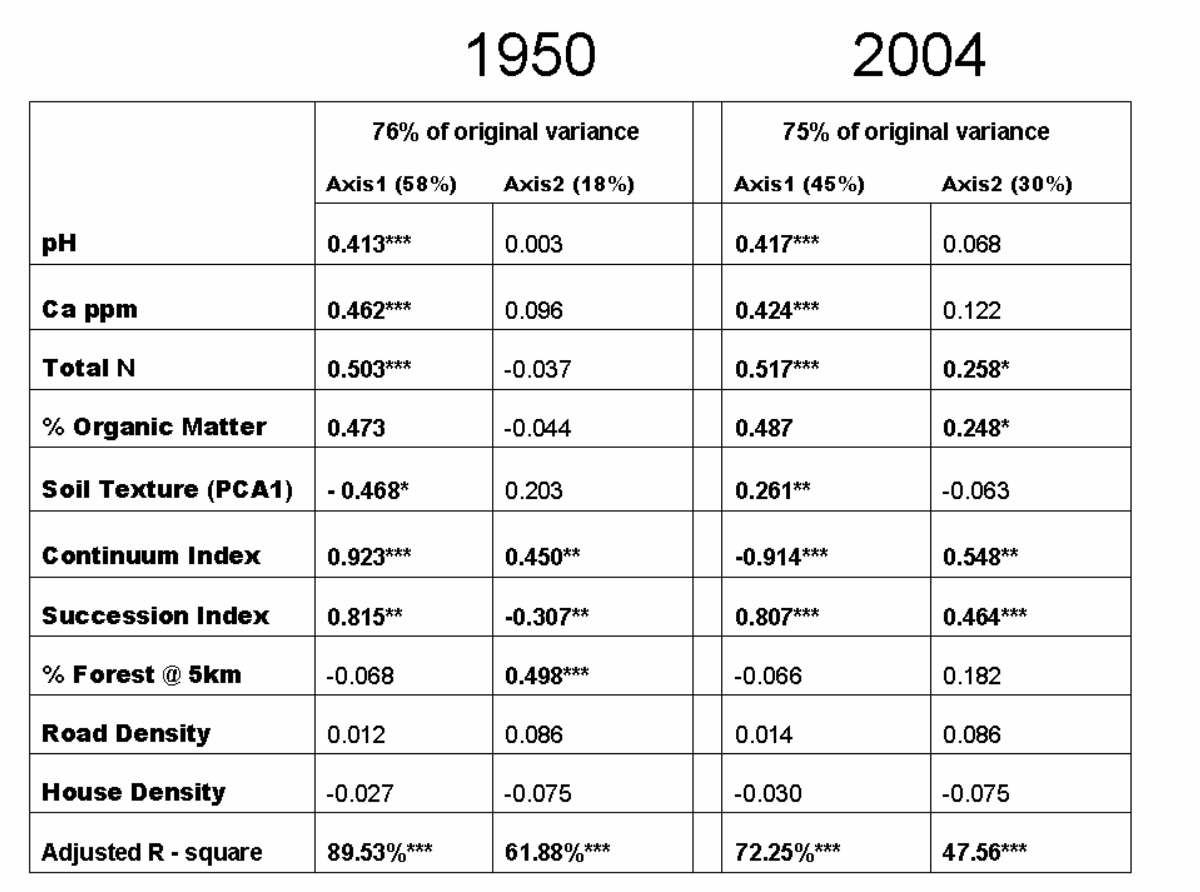
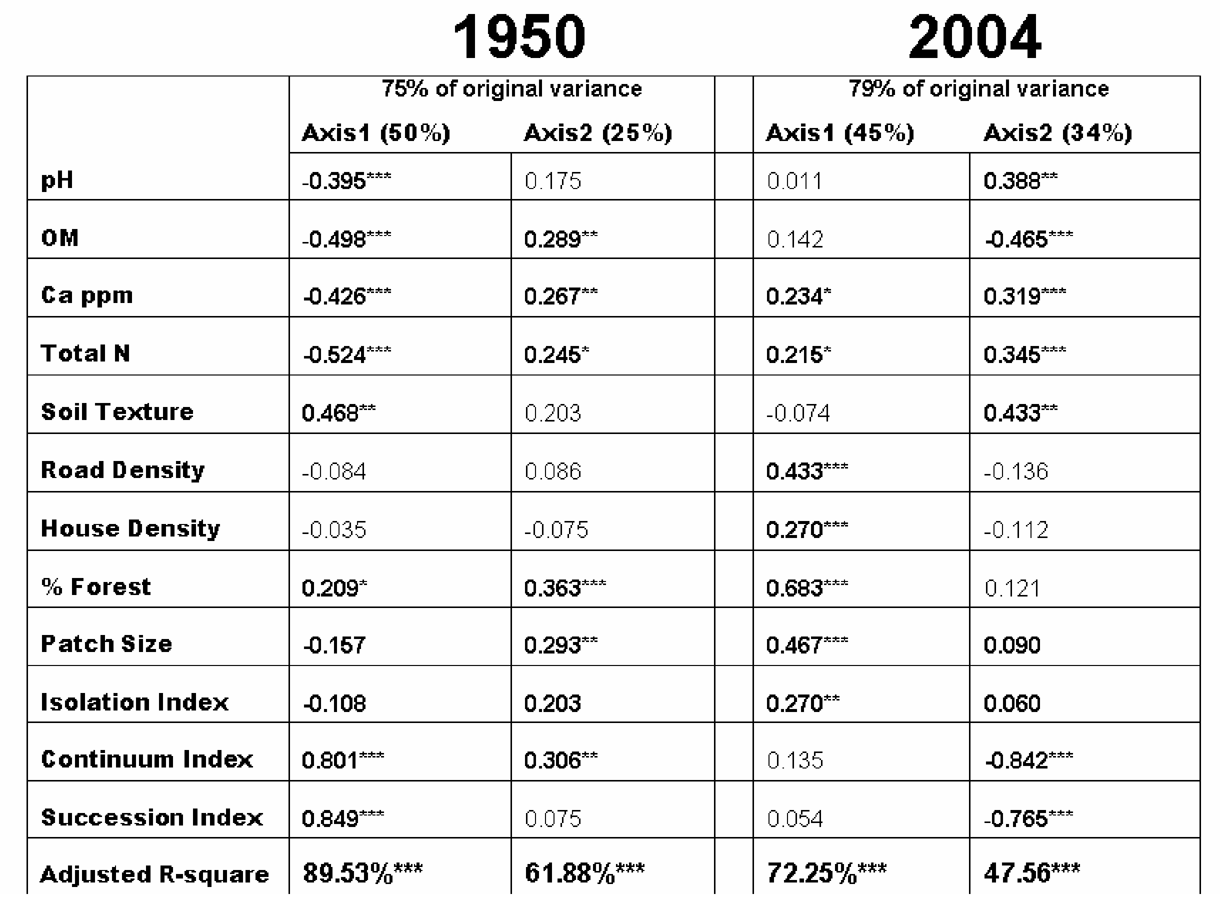


Table 1: Comparison of correlations between the ordination axes and environmental variables for the canopy based on measures of relative density



	1950		2004	
	76% of original variance		75% of original variance	
	Axis1 (58%)	Axis2 (18%)	Axis1 (45%)	Axis2 (30%)
pH	0.413***	0.003	0.417***	0.068
Ca ppm	0.462***	0.096	0.424***	0.122
Total N	0.503***	-0.037	0.517***	0.258*
% Organic Matter	0.473	-0.044	0.487	0.248*
Soil Texture (PCA1)	- 0.468*	0.203	0.261**	-0.063
Continuum Index	0.923***	0.450**	-0.914***	0.548**
Succession Index	0.815**	-0.307**	0.807***	0.464***
% Forest @ 5km	-0.068	0.498***	-0.066	0.182
Road Density	0.012	0.086	0.014	0.086
House Density	-0.027	-0.075	-0.030	-0.075
Adjusted R - square	89.53%***	61.88%***	72.25%***	47.56***

Table 2: Comparison of correlations between the ordination axes and environmental variables for the understory based on measures of relative frequency in 20 1m² quadrats at 94 sites in each time period



	1950			2004	
	75% of original variance			79% of original variance	
	Axis1 (50%)	Axis2 (25%)		Axis1 (45%)	Axis2 (34%)
pH	-0.395***	0.175		0.011	0.388**
OM	-0.498***	0.289**		0.142	-0.465***
Ca ppm	-0.426***	0.267**		0.234*	0.319***
Total N	-0.524***	0.245*		0.215*	0.345***
Soil Texture	0.468**	0.203		-0.074	0.433**
Road Density	-0.084	0.086		0.433***	-0.136
House Density	-0.035	-0.075		0.270***	-0.112
% Forest	0.209*	0.363***		0.683***	0.121
Patch Size	-0.157	0.293**		0.467***	0.090
Isolation Index	-0.108	0.203		0.270**	0.060
Continuum Index	0.801***	0.306**		0.135	-0.842***
Succession Index	0.849***	0.075		0.054	-0.765***
Adjusted R-square	89.53%***	61.88%***		72.25%***	47.56***

Introduction to Appendices

Sampling a population to estimate the composition and structure is a fundamental concept in ecology and necessary to reduce an infinitely complex universe into a manageable set of data. Sample size, sample spacing, and taxonomic resolution can all have profound influences on the eventual description of community composition and structure. We have been re-sampling forest plant communities throughout Wisconsin forest sampled in the late 40's and 50's by JT Curtis and colleagues in preparation of the book "Vegetation of Wisconsin". Because we know that sampling method can have statistically significant effects on results and conclusions, we need to consider how our choices of methodology for re-sampling effort influence our interpretation of our results. To be clear, we don't want our analysis to simply reflect the fact that the stands were sampled by different people and methods, but rather reflect actual changes in composition and structure.

We tried many different ways of addressing these changes and then did meta-analyses to assess their effect on overall pattern observed and the attached appendices is a summary of those efforts. We divide the problem into two sections. Appendix 1 is a comparison between sampling methods and their effect on estimated changes. Appendix 2 evaluates the influences of taxonomic resolution, sample size, data reduction and measures of similarity on observed patterns.

We also add a third appendix which provides g-tests for individual species of both the canopy and understory. these data are meant to support conclusions in Chapter 1 and to provide and outline for my next manuscript to be derived from these data.

Appendix 1: A comparison of alternate methods of resampling PEL sites and its influence on pattern observed

Introduction

As our lab turned its attention to the southern forests and was preparing for initial sampling, we were engaged in an internal debate regarding sampling methods. One camp argued that it was best to replicate the original sampling as closely as possible. The other countered that we could improve upon the method by increasing the sample size of 1m² quadrats and switching methods for estimating tree composition from plot-less methods to permanently marked quadrats, a method used in the northern forest resample (Rooney 2004, Wiegmann 2005). The advantages of the permanent quadrats are two fold: 1) it gives a more accurate representation than plotless methods of stem density and average basal area with plotless methods tending to favor slightly large trees, show greater deviation from the “true” mean, and under represent species that are clumped, such as *Tilia americana* (Cottam 1953, Cottam & Curtis 1949, 1955, Mueller-Dumbois 1974). 2) Permanent quadrats are better for long-term studies of change, virtually eliminating variance due to sampling in then vs. now comparisons. The counter- counter arguments were: 1) plotless methods are more efficient in terms of trees sampled/unit time both allowing for greater dispersion of sample units within the stands and allowing data collectors to cover more stands during the sampling season. 2) Bias due changes in sampling regime could influence results, like seeing increases in *Tilia americana* when there was none. To resolve this issue, we decided our initial sampling would consist of both approaches in order directly compare differences and ultimately to see if it mattered in terms of the narrative we would derive regarding changes in canopy and understory richness and composition.

Curtis' original method consisted of a square transect covering approximately 2-3 hectares in total area, with 40 sampling points space evenly along the transect. For all 40 sample points, trees were measure using one of two plotless methods, random pairs (Cottam 1948) or point – quarter, with the random pairs method used most frequently and exclusively for the SUF data set. In practice, data collectors often deviated from the square transect and would often shape it in order to accommodate topography, or stand shape. The distance between points is something of a mystery as well. We know that the spacing was not always consistent in sampled stands; at smaller stands points were sometimes closer together. However, since we never saw any evidence of repeated trees in the original data and the total sample was consistently 80 trees, we can reasonably assume that the minimum distance between trees was large enough to avoid this problem. I'd estimate this minimum distance at around 15m – in our experience with the method. Beals (1956) spaced his sample points around 25m apart using similar methods. So we know its somewhere in this range.

For this first season, we replicated the sampling methods as best as possible, but increasing the sample 3x for the trees and 6x for the herbs. Spacing between each sample point in each replicate was 20 m. From the same starting point, we also installed permanent transects identical to those used in our previous work (Rooney 2004). In short, the method consists of three square transects (a "cell"), each 20m on a side. For each cell, we recorded the diameter of all plants greater than 2.54 cm DBH. We laid out 20 contiguous 1m² quadrats along the first two sides of the cell, for a total of 40 m² for each cell and total of 120m² for each stand. In this case, cells were placed in a stratified random matter, such that no cells overlapped and that all areas of the stands had equal chance of being sampled.

When considering simple taxonomic richness, it's a fairly straightforward exercise. As long as consistent rules are applied, there is almost no effect on estimates of changes since we can safely call an unknown or something identified at the genus level a taxon and counts it as a unique species.

Analysis

We start by comparing the two methods directly in terms of species richness and heterogeneity using simple paired t-tests in both the canopy and understory layers. We then use NMS ordination to test whether samples from the respective methods can be classified as different groups in species space (is there a consistent bias, or an effect due to differences in species richness). We also compare methods at the individual species level (are there differences in site occupancy, average frequency when present, total frequency)

We then ask whether any differences detected due to sampling method makes a difference in the ultimate narrative we want to tell. Are the mechanisms of change we are documenting robust in the face of differences due to sampling? We use correlation analysis to test for correlation between various measures of change and to test for relationships between those measures and predictor variables.

Results

Herb Summary

Continuous quadrats tend to record fewer species per sample than spaced quads across the full pool of 120 quads (table 1). This simply reflects the fact that they taken from a larger sample area, even if total sample sampled is the same. If we reduce the sample to 20 quads, the difference between the two sampling methods is reduced, although still significant depending on the methods used to estimate richness of 20 quads. From this data set, using the average richness of each replicate is the most resistant method to differences in sampling design while the passive sampling approach (Rooney 2004), still retains a bias toward lower diversity for the continuous quadrat sample. This may account in part for the differences between my analysis of the Northwoods data & that published in the Con Bio paper (11.5% loss vs. 18% published). Continuous quads also have higher within site similarity than spaced quads, as expected given that it represents a smaller area sampled (albeit more intensively). Among site similarities are lower, perhaps reflecting the lower species richness of the continuous quadrat samples. As with estimates of richness, all measures of heterogeneity were highly correlated (consistently > 0.95 for Spearman rank correlation) and show similar response patterns to predictor variables.

Essentially the three cell method used for Rooney (2004) and Wiegmann (2006) has higher between site variability than the random pairs method. This is reflected in that the number of sites occupied by the average species was significantly higher for the random pairs method, while average frequency when present was higher for the Waller Method (table 2).

Fortunately for Wiegmann (2005), these differences cancel each other out when considering overall changes in species frequency. Consequently, the G-tests used for testing changes in the frequency of individual species are valid for Gtotal (the determinant for winner/loser status). However, it is likely that G – heterogeneity is unreliable or misrepresents local vs. regional changes. Future work looking at changes in individual species composition should keep this in mind.

In ordination analysis (NMS), there was no immediate visual separation between groups between sampling methods (figure 1). We used a permutation test (MRPP , McCune & Grace) to test for differences between groups and detected no differences between sampling methods in ordination space for understory species frequency. These results support little or no effect of method selection on detecting changes in species composition.

Tree Summary

Differences in sampling methods for trees were similar to those seen for the understory. The random pairs method tended to sample more individual trees than did three 400m² quadrats (table 3). Consequently, it's not surprising that estimates of tree richness are higher for the random pairs sample. We haven't looked at richness estimates based on a standard sample size of individuals, but it's somewhat of a moot point. I'm sure the differences between methods would be reduced, but there would still higher estimates of richness and heterogeneity with the random pairs simply because of the larger area sampled. Somewhat unexpectedly, there were no statistical differences in estimates of density, average basal area, or ba/hectare.

Between-site heterogeneity was also statistically different between sample methods with the large quads tending to have lower between site heterogeneity (35.6 vs. 31.1). However, as with the understory data, there was no detectable difference between sampling methods in ordination space (figure 2), though there was considerably greater distance between samples at the same site than we saw in the understory data. This is likely due to the very large differences in sample sizes (trees sampled) between the two methods

Conclusions

The two methods compared here show statistically different estimates of richness and heterogeneity with the original method consistently showing higher estimates of richness and similarity. Therefore, previously published results average species loss and homogenization may be biased. The real question is then, are these differences reflected in the data in terms of species composition or the story they tell? Considering that estimates of species loss and homogenization are highly correlated between the two methods and both estimates show very similar results compositionally, the overall effect on these results is likely minimal. The main problem is that the higher heterogeneity between stands –makes interpretation a little fuzzier across scales, increasing “noise” and decreasing signal. Aside from inflated frustration levels, the overall narrative is likely to change very little

However, the differences observed do suggest that sampling methods matter. Consequently, we chose to sample the remaining stands using the random pairs methods and 80 points dispersed through the stands, and $1m^2$ from the center of each point. Our final sample had 160 trees/site and 80, 1m² quadrats for a 2x and 4x oversample as compared to the original method. We divided the oversample into replicates each equal to the original sample. Replicate 1 of the trees corresponds to replicates 1 & 2 of the quadrat samples and were placed in our best guess as to the original location and condition of the stand.

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Table1: Comparing Richness Estimates by Method for Understory

Herb Layer	**Random Pairs**	**Cells**	**p-value**
Richness/m²	6.273	6.28	0.956
Richness/120m²	60.5	51.7	<0.0009
Richness/40m²	40.04	30.9	<0.0009
Average Richness/20m²	30.48	31.8	0.142
Passive Richness	34.79	30.6	<0.0009
Within Site Similarity	54.73	66.6	<0.0009
Between Site Similarity	40.03	38.6	0.003

Table 2: Average values for all understory species shared between the samples

	RPairs	Cells	P-value
Avg Sites/Species	5.71	5.04	< 0.001
AvgTotalFreq/Species	70.7	71.2	0.683
AvgFreq/Species	8	9.19	0.001

Table 3: Comparing Estimates of Richness & Similarity for Canopy

Canopy	**Random Pairs**	**Cells**	**p-value**
Tree Richness	13	8.11	<0.0009
Trees Sampled	221.61	52.7	<0.0009
Tree Density	407.5	433	0.152
Average Basal Area	107.22	103	0.452
Basal Area/Hectare	2690	2618	0.517
Average Tree Similarity	33.31	29.3	<0.0009

Figure 1: NMS Ordination of Understory Comparing 120 Quads

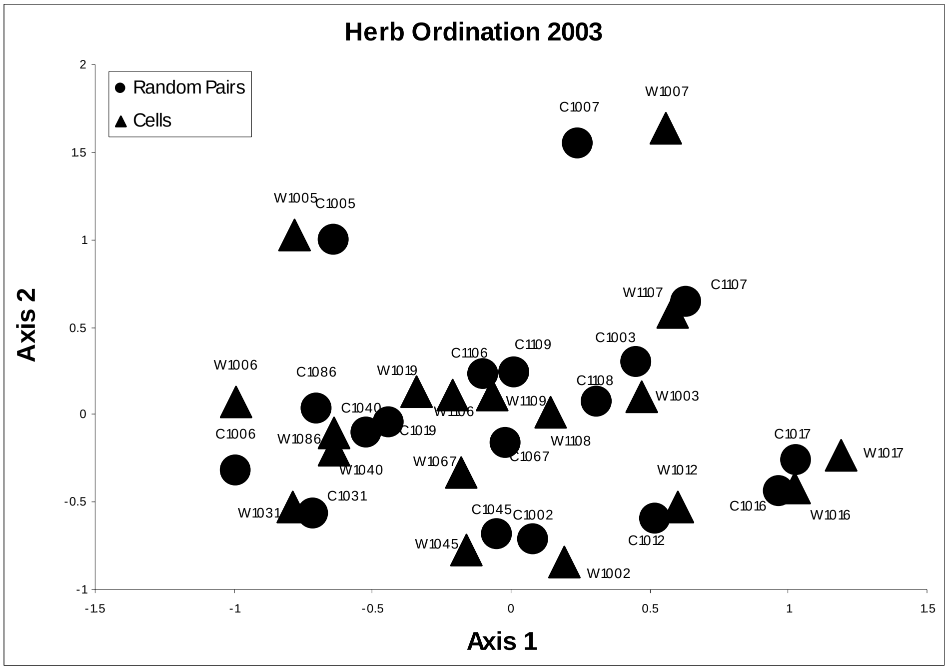
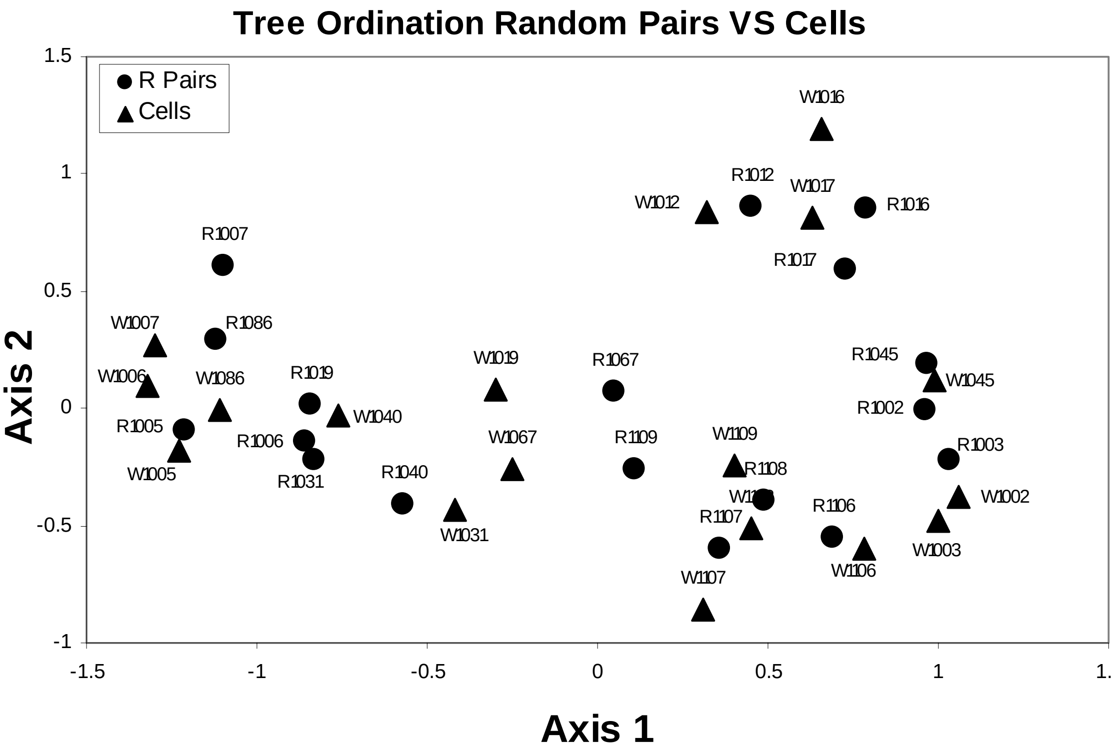


Figure 2: Ordination Of Trees



Appendix 2: Influence of taxonomic resolution, data transformation and similarity measures on estimates of rates of homogenization.

We sampled 4x as many quadrats per sites than the original survey. Obviously, a direct comparison of the data has the potential to bias our results towards higher species richness and average similarity. Therefore we need to reduce the resample data based on a fair comparison of the original sample size (frequency by species for 20, 1m² quadrats). Yet, we also want to keep all the information we have in hand. To make fair comparison of species richness is fairly straight forward. We can treat the over-sample like N replicates of 20 each and then take the average them to get an estimate of richness. For the purposes of this thesis, the data were divided into 4 replicates of 20 quadrats each. In stands where we stratified our sample (to avoid differing land-uses); we assigned replicates 1 & 2 from the portion of the stand most similar to the original in term of canopy composition, no disturbance, etc. Replicates 3 & 4 are then taken from the rest of the stand, such that points in each replicate are evenly spaced between quads (every other point). The average spacing between quads in each replicate was 20m.

For comparison, we also use the same passive sampling technique employed in Rooney 2004 for the entire pool of 80 quadrats. We also tried simply setting the minimum threshold of 5% for the re-sample data (equal to the minimum detection threshold for a sample of 20 quadrats). We expect this to be biased towards lower richness in 2003, because the more precise estimate favors the elimination species < 5%. We then compare the four replicates, the average of the replicates, the passive sample and the truncation estimate to test for robustness in our estimates of changes in species richness.

To make accurate comparisons of species composition, however, the situation is not so clear. Between two sample periods, it is critical to match taxonomic nomenclature. In most cases this was a simple matter of switching from one name to another (e.g., *Hepatica acutiloba* to *Anenome acutiloba*). However, in some cases, the PEL data combine some species, split taxa that are now combined, or applied inconsistent taxonomic resolution. In these cases, we simple lumped taxa into the next highest taxonomic group (e.g. *Carex sp, Dryopteris carthusiana, Botrychium multifidum*). Our general approach was to identify all taxa to the species level (ignoring sub-species, etc.) using Gleason (1992) and Voss (1996) for keys and the UW – Herbarium's list of species for current nomenclature. When considering simple taxonomic richness, as long as consistent rules are applied, there is almost no effect on estimates of changes since we can safely call an unknown or something identified at the genus level a taxon and counts it as a unique species.

A more difficult problem is posed however, when we want to include species identity in our analysis of similarity, ordination analysis, estimates of extirpation & invasion, etc. As we lump taxa we can obscure real ecological differences (for example, if we lump black and red oak, it obscures the CI). Being too restrictive isn't ideal either; we don't want to throw away useful information. In the end it really boils down to professional judgment, made from a thorough knowledge of the species and system in question and, of course, the questions being addressed. For example, *Corylus americana and Corylus cornuta*. *C.cornuta* clearly separates northern from southern forest types, yet both have similar niches in their respective ranges. Combining the species into a single taxa would obscure that difference. The optimal actual synchronized list used can vary depend on the scale of the analysis. Measures of community similarity can also be sensitive to differences in sample size and taxonomic resolution. We investigated several methods to reduce the data to a sample of 20 quads each. We then compare them using one-way ANOVAs. We also simultaneously compare different measures of similarity to evaluate their sensitivity to taxonomic resolution and sample size. Self Similarity using both presence/absence and relative frequency data. We evaluate average between site similarity using jaccard's, sorenson, Morisita and Horn indices. To tackle these uncertainties, we tried several levels of data reduction.

1) R**eplicates 1 -4** : Calculations are based on data derived from each of the four replicates analyses separately.
2) **80 Quads:** This sample represents the full sample of 80 quadrats in the 2005 resurvey.
3) **Passive:** We used the passive sample estimate of richness to set a richness threshold for each site in each time period. The composition of the sample was then determined by including taxa in decreasing rank order of abundance until the richness threshold was reached. Species with ties in sampled abundance were randomized in terms of rank order – essentially randomizing the identity of rare species included in the sample (from the pool of rare taxa present). We then estimated the frequency for each species based on a 20 quadrats sample (percent quadrats occupied in original sample * 20, rounded to 0 decimal places), rare species (estimated frequency < 1 quadrat) were assigned values of one.
4) **BF1:** Best Fit 1 - Similar to RAND above, but instead of selecting ties randomly, preference was given to species that had been present in the 1950 sample.

5) **BF2 :** Best Fit 2 - Similar to BF1, except that presence in 1950 was given priority over abundance in 1950, species not present in 1950 were included in decreasing order of abundance until species threshold was reached.

Results

Richness

The various measures of richness we experimented with provide very similar results, with the exception of the truncated list, which had a significantly lower estimate of species richness (Figure 1). Likewise, all estimates but the truncated list give similar estimates of species loss, thus giving highly correlated estimates of species loss (table 1). In turn, estimates of species loss were highly correlated with important predictor variables, regardless of method used to reduce richness based on 20 m^2 in either time period (table 2). We use the average richness of the four replicates for most of our analysis.

Similarity

We estimated the average between site similarity based on 107 sites in southern Wisconsin. Estimates of average similarity were sensitive to effects of sample size and taxonomic reduction for both frequency (figure 2) and relative frequency data. It’s worth noting that the Morisita and Horn measures gave higher estimates of average similarity than did the Bray Curtis (figures 3 & 4) and was somewhat less influenced by sample size, though it still retained bias towards higher similarity with the large sample.

Regardless of methods used, the larger sample size in the re-survey and would tend to bias average similarities in 2005 and thereby inflate estimates of homogenization when measured with the Bray Curtis similarity measure (figure 5). When measure with Morisita similarity, the effect of sample size still toward greater rates, but much less so (figure 6). Interestingly, the other three data reduction techniques maintain the large bias with this index. None of the methods we used to reduce species to an equal sample of 20, 1m² sample were completely effective at eliminating this bias. Fortunately however, all estimates of homogenization are highly correlated, regardless of method of data reduction (table 4). Not surprisingly, all measures of homogenization show similar responses to predictor variables (table 5).

Discussion

We choose to use the average of the four replicates for most of our analysis, using the Sorenson measure of community similarity and the realtive abundance trasformation of frequency data. This measure also has the vritue of being readily available in most ecological stats packages like PCORD & Primer. Interstingly, dissimilarity among sites increases over time when we used presence/absence data and Jaccard measure of dissimilarity (figure 2), but decreases when using frequency or relative frequency data and the Sorensen (figure 3) or Morisita measures of similarity. In other words, sites are more heterogeneous at the p/a level, but more homogenized when considering abundance.

Table 1: Correlations between estimates of richness/20m^2

	Rep1	Rep2	Rep3	Rep4
Rep2	0.921			
Rep3	0.863	0.884		
Rep4	0.873	0.887	0.928	
RepAvg	0.954	0.962	0.958	0.96

Table 2 : Correlations between estimates of species loss/20m^2 and various predictors of species loss. All p –values < 0.05

	Rep 1	Rep 2	Rep 3	Rep 4	Rep Average
Forest Cover	0.439	0.45	0.39	0.406	0.45
Mean Patch Size	0.394	0.427	0.385	0.378	0.423
Patch Size	0.337	0.339	0.362	0.366	0.379
Road Density	-0.205	-0.233	-0.243	-0.197	-0.233
Intial SI	-0.243	-0.282	-0.221	-0.22	-0.257

Table 3 : Correlations of estimates of average BC similarity

	rep1	rep2	rep3	rep4	80q	Random	BF1
rep2	0.926						
rep3	0.882	0.868					
rep4	0.891	0.893	0.909				
80q	0.951	0.961	0.941	0.953			
Random	0.946	0.944	0.935	0.947	0.987		
BF1	0.946	0.946	0.935	0.947	0.987	0.999	
BF2	0.939	0.929	0.925	0.936	0.975	0.983	0.983

Table 4: Correlations of estimates of homogenization (BC similarity)

	rep1	rep2	rep3	rep4	80q	Random	BF1
rep2	0.864						
rep3	0.826	0.793					
rep4	0.826	0.818	0.864				
80q	0.908	0.927	0.906	0.919			
Random	0.893	0.896	0.895	0.906	0.975		
BF1	0.908	0.923	0.905	0.918	0.999	0.974	
BF2	0.896	0.894	0.894	0.906	0.975	0.999	0.976

Table 5: Correlations of estimates of homogenization and important predictor variables. Similarity based on quadrat frequency. Data presented are spearman correlations above and p-values below.

Bray Curtis

	%Exotic	UrbanCover	ForestCover	WoodyDom	SpecieLoss
Rep1	-0.285	-0.147	0.277	-0.365	0.117
	0.003	0.134	0.004	0	0.232
Rep 2	-0.156	0.027	0.184	-0.422	0.126
	0.111	0.782	0.059	0	0.197
Rep 3	-0.259	-0.085	0.254	-0.331	0.179
	0.007	0.387	0.009	0.001	0.066
Rep 4	-0.176	-0.069	0.294	-0.314	0.144
	0.072	0.484	0.002	0.001	0.141
All 80 Quads	-0.221	-0.035	0.234	-0.411	0.157
	0.023	0.718	0.016	0	0.108
Passive Estimate	-0.236	-0.047	0.259	-0.403	0.163
	0.015	0.634	0.007	0	0.095

Morisita

Rep1	-0.311	-0.132	0.265	-0.454	0.212
	0.001	0.178	0.006	0	0.029
Rep 2	-0.147	0.041	0.126	-0.466	0.209
	0.133	0.675	0.199	0	0.032
Rep 3	-0.247	-0.057	0.187	-0.365	0.22
	0.011	0.563	0.055	0	0.023
Rep 4	-0.186	-0.029	0.247	-0.358	0.208
	0.056	0.771	0.011	0	0.032
All 80 Quads	-0.236	-0.052	0.216	-0.441	0.208
	0.015	0.593	0.026	0	0.033
Passive Estimate	-0.241	-0.02	0.2	-0.441	0.209
	0.013	0.842	0.04	0	0.031

Table 6: Correlations of estimates of homogenization and important predictor variables. Similarity based on relative frequency. Data presented are spearman correlations above and p-values below.

Bray Curtis

	%Exotic	UrbanCover	ForestCove	WoodyDom	SpeciesLoss
Rep1	-0.348	-0.157	0.316	-0.419	0.137
	0	0.109	0.001	0	0.161
Rep 2	-0.204	0.023	0.212	-0.444	0.143
	0.036	0.817	0.029	0	0.143
Rep 3	-0.306	-0.093	0.251	-0.342	0.163
	0.001	0.345	0.009	0	0.096
Rep 4	-0.224	-0.07	0.314	-0.318	0.132
	0.021	0.479	0.001	0.001	0.177
All 80 Quads	-0.273	-0.024	0.246	-0.448	0.163
	0.005	0.805	0.011	0	0.095
Passive Estimate	-0.29	-0.048	0.277	-0.433	0.174
	0.003	0.624	0.004	0	0.075

Morisita Horn

	%Exotic	UrbanCover	ForestCove	WoodyDom	SpeciesLoss
Rep1	-0.294	-0.12	0.259	-0.443	0.212
	0.002	0.219	0.007	0	0.029
Rep 2	-0.144	0.051	0.135	-0.453	0.217
	0.141	0.607	0.167	0	0.026
Rep 3	-0.253	-0.05	0.195	-0.367	0.238
	0.009	0.611	0.045	0	0.014
Rep 4	-0.175	-0.022	0.249	-0.343	0.216
	0.072	0.823	0.01	0	0.026
All 80 Quads	-0.22	-0.003	0.21	-0.446	0.234
	0.024	0.976	0.031	0	0.016
Passive Estimate	-0.238	-0.019	0.214	-0.434	0.228
	0.014	0.848	0.028	0	0.019
BF1 Homo	-0.236	-0.019	0.215	-0.434	0.231
	0.015	0.848	0.027	0	0.017
BF2 Homo	-0.211	0.002	0.214	-0.447	0.202
	0.03	0.981	0.028	0	0.037

Figure 1: One-way ANOVA comparing different methods of estimating richness/20m²

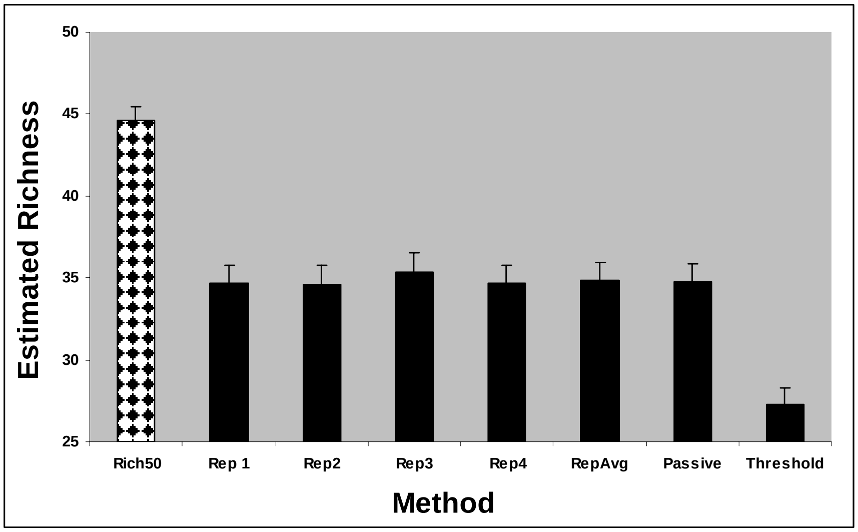
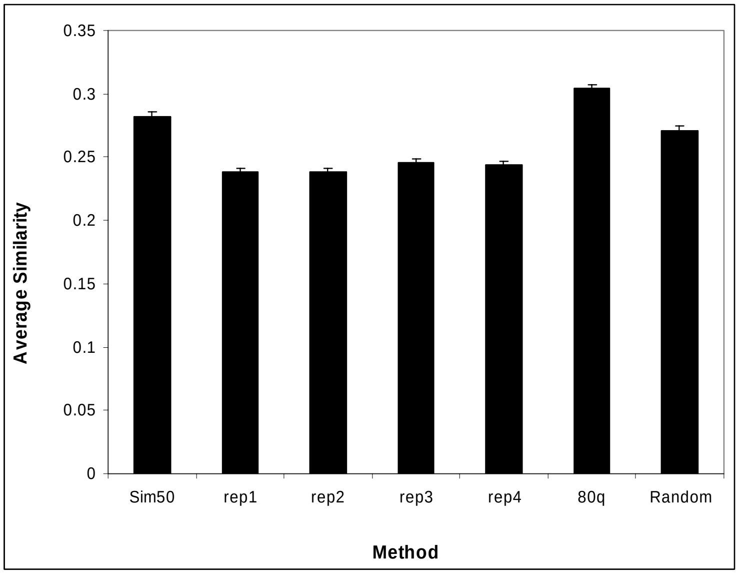
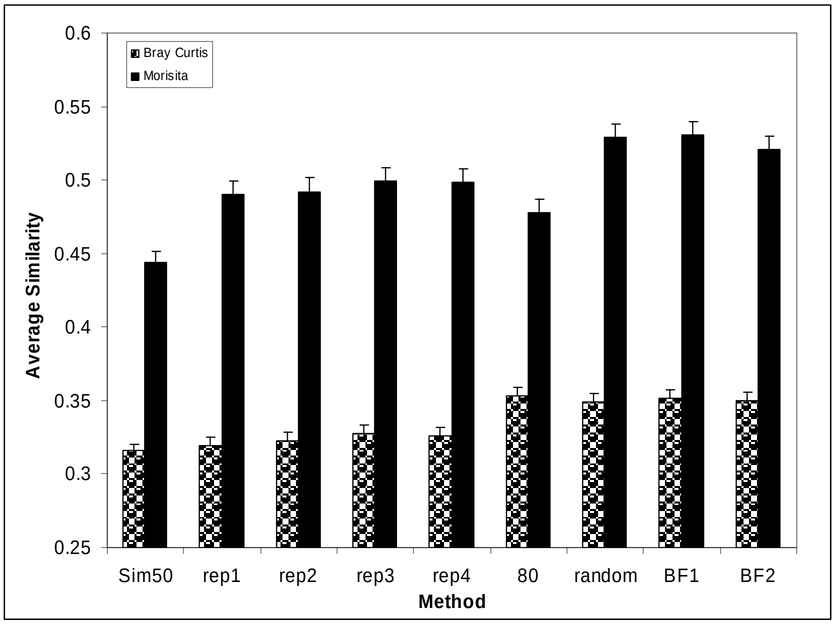


Figure 2 : Comparison of average Jaccard similarity (presence/absence)



```
Analysis of Variance
Source     DF        SS        MS        F        P
Factor      6   0.42872   0.07145    68.26    0.000
Error     742   0.77675   0.00105
Total     748   1.20546

Level       N      Mean     StDev  -----+---------+---------+---------+-
Sim50     107   0.71838   0.03908            (-*--)
rep1      107   0.76215   0.02890                             (--*-)
rep2      107   0.76194   0.03068                             (--*-)
rep3      107   0.75445   0.02989                          (--*-)
rep4      107   0.75634   0.02964                           (--*-)
80q       107   0.69568   0.03321   (-*--)
Random    107   0.72868   0.03391                (-*--)
                                   -----+---------+---------+---------+-
Pooled StDev =  0.03235               0.700     0.725     0.750     0.775
```

Figure 3: Comparison of among site similarity estimates (Frequency Data) varied by data reduction method and by similarity measure used



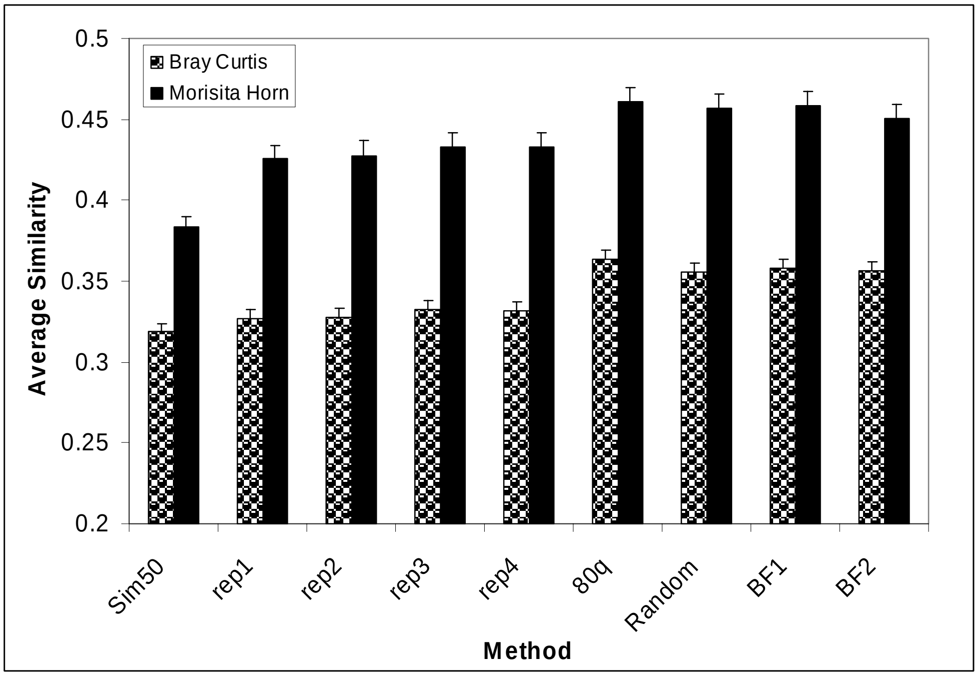
Sorenson Dissimilarity

```
Analysis of Variance : F = 7.87    P = 0.000

Level       N      Mean     StDev  ---+---------+---------+---------+---
Sim50     107   0.68395   0.04613                      (----*----)
rep1      107   0.68053   0.05536                    (----*-----)
rep2      107   0.67757   0.05891                  (-----*----)
rep3      107   0.67227   0.05861                (----*-----)
rep4      107   0.67426   0.05793                 (----*-----)
80        107   0.64648   0.05752   (----*-----)
random    107   0.65074   0.05996     (----*-----)
BF1       107   0.64821   0.06011    (----*-----)
BF2       107   0.65036   0.06084     (----*-----)
                                   ---+---------+---------+---------+---
Pooled StDev =  0.05742             0.640     0.660     0.680     0.700
```

Morisita Dissimilarity

```
Analysis of Variance : F = 8.55    P = 0.000

Level       N      Mean     StDev  --+---------+---------+---------+----
Sim50     107   0.55637   0.07658                            (----*----)
rep1      107   0.50982   0.09752              (-----*----)
rep2      107   0.50842   0.10559              (----*-----)
rep3      107   0.50111   0.10040            (----*----)
rep4      107   0.50142   0.09694            (----*----)
80q       107   0.52224   0.09244                  (----*----)
Random    107   0.47130   0.09897   (-----*----)
BF1       107   0.46966   0.09867   (----*----)
BF2       107   0.47941   0.09977      (----*----)
                                   --+---------+---------+---------+----
Pooled StDev =  0.09663            0.455     0.490     0.525     0.560
```

Figure 4: Comparison of among site similarity estimates (relative frequency data) varied by data reduction method and by similarity measure.



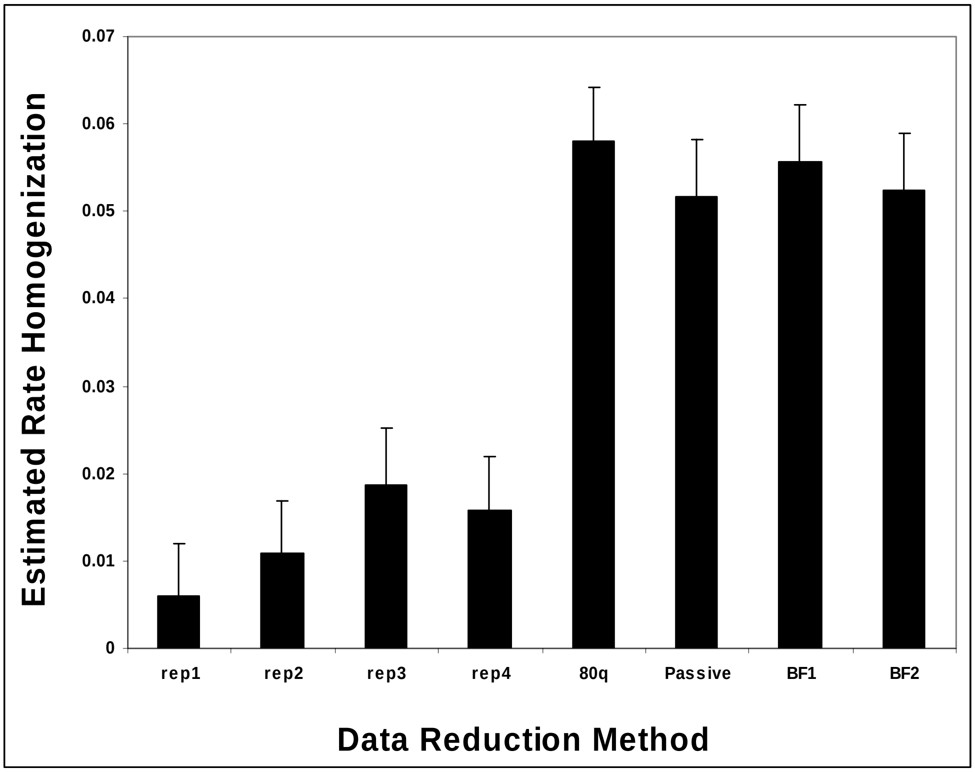
Sorenson Dissimilarity

```
Analysis of Variance : F = 9.48    P = 0.000

                                   Individual 95% CIs For Mean
                                   Based on Pooled StDev
Level       N     Mean     StDev  --------+---------+---------+--------
Sim50     107   0.68113   0.04690                         (-----*----)
rep1      107   0.67292   0.05613                     (----*-----)
rep2      107   0.67247   0.05850                     (----*-----)
rep3      107   0.66724   0.05737                  (-----*----)
rep4      107   0.66845   0.05663                   (----*-----)
80q       107   0.63637   0.05679   (----*-----)
Random    107   0.64436   0.05902       (----*-----)
BF1       107   0.64178   0.05915      (----*----)
BF2       107   0.64356   0.05934      (-----*----)
                                   --------+---------+---------+--------
Pooled StDev =  0.05676                  0.640     0.660     0.680
```

Horn Dissimilarity

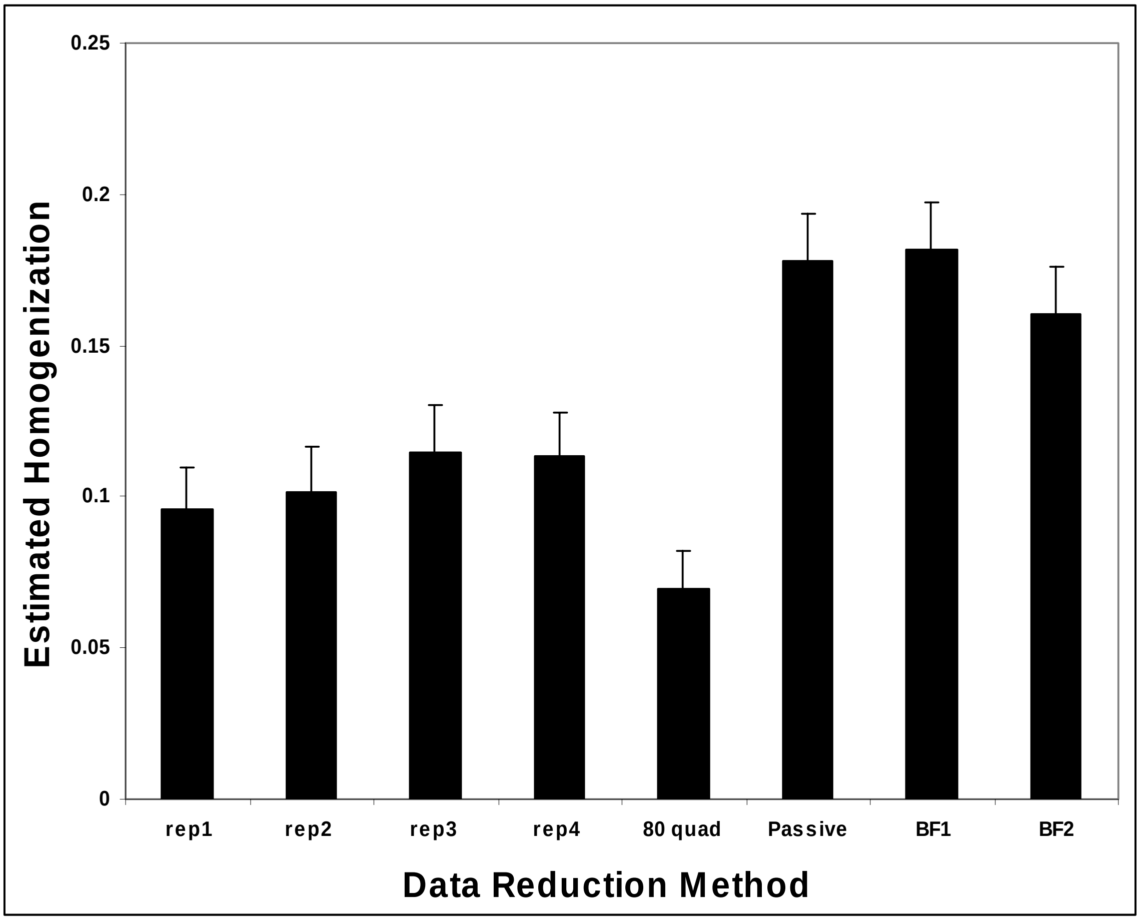
```
Analysis of Variance : F = 8.15    P = 0.000

                                   Individual 95% CIs For Mean
                                   Based on Pooled StDev
Level       N     Mean     StDev  -+---------+---------+---------+-----
Sim50     107   0.61675   0.06543                        (----*----)
rep1      107   0.57448   0.08793            (----*----)
rep2      107   0.57230   0.09469            (----*---)
rep3      107   0.56669   0.09086          (----*----)
rep4      107   0.56670   0.08872          (----*----)
80q       107   0.53895   0.09028  (----*----)
Random    107   0.54312   0.09043   (----*----)
BF1       107   0.54171   0.09018   (----*----)
BF2       107   0.54981   0.09127     (----*----)
                                   -+---------+---------+---------+-----
Pooled StDev =  0.08812           0.525     0.560     0.595     0.630
```

Figure 5: Comparisons of estimates of Homogenization between data reduction methods and the Bray Curtis similarity measure.



```
Analysis of Variance
Source     DF        SS        MS        F        P
Factor      7   0.38380   0.05483    12.88    0.000
Error     848   3.60848   0.00426
Total     855   3.99227
                                   Individual 95% CIs For Mean
                                   Based on Pooled StDev
Level       N      Mean     StDev  ---------+---------+---------+-------
rep1 Hom  107  -0.00601   0.06249                       (----*----)
rep2 Hom  107  -0.01084   0.06213                     (----*----)
rep3 Hom  107  -0.01870   0.06723                  (----*---)
rep4 Hom  107  -0.01569   0.06457                   (----*----)
80q Homo  107  -0.05801   0.06378   (----*----)
Passive   107  -0.05171   0.06696     (----*----)
BF1 Homo  107  -0.05566   0.06719    (----*----)
BF2 Homo  107  -0.05242   0.06726     (----*----)
                                   ---------+---------+---------+-------
Pooled StDev =  0.06523                  -0.050    -0.025    -0.000
```

Figure 6: Comparisons of estimates of Homogenization between data reduction methods and the Morisita Index.



```
Analysis of Variance
Source     DF        SS        MS        F        P
Factor      7    1.2899    0.1843     7.73    0.000
Error     848   20.2062    0.0238
Total     855   21.4961
                                   Individual 95% CIs For Mean
                                   Based on Pooled StDev
Level       N      Mean     StDev  ---+---------+---------+---------+---
rep1 Hom  107   -0.0956    0.1463                      (-----*-----)
rep2 Hom  107   -0.1017    0.1567                     (-----*-----)
rep3 Hom  107   -0.1146    0.1624                  (-----*-----)
rep4 Hom  107   -0.1131    0.1514                   (----*-----)
80 quads  107   -0.0693    0.1353                           (-----*-----)
Passive   107   -0.1782    0.1606    (----*-----)
BF1 Homo  107   -0.1817    0.1609   (-----*-----)
BF2 Homo  107   -0.1607    0.1594       (-----*-----)
                                   ---+---------+---------+---------+---
Pooled StDev =   0.1544            -0.200    -0.150    -0.100    -0.050
```

Appendix 2A: Notes on rational for taxonomic resolution

Sanicula marilandica/gregaria: PEL found dominance by SANMAR with a few SANGRE. We found mostly SANGRE with quite a bit of SANMAR – however it was impossible to distinguish one from the other in vegetative condition. We also saw quite a bit of Sanicula canadensis, which is easily distinguishable in vegetative condition. Unfortunately, it appears nowhere in the PEL study. For these reasons, all these taxa were lumped into a single category – “Sanicula sp.”

Quercus velutina/rubra: These two taxa are notoriously difficult to distinguish from each other, with the species co-occurring in nature and with a lot of introgression between the two types – leading to all kinds of problems as different observers key in on different traits . We are tempted to treat them as a single taxa, but hesitate given they clear ecological differentiation observed in the field (Q. velutina is more prevalent on poor soils). Our approach here is to constrain each site to contain only one of the two species. The identity chosen for the site was chosen based on which species was dominant in the 1950’s data.

Fraxinus pensylvanica/americana: PEL has tons of FRAAME all over the place, whereas we only observed it at a few locations (SE & extreme SW counties). These taxa are readily distinguished from one another as saplings and we are confident that FRAPEN is much more common than FRAAME. It really seems like PEL screwed this one up. So, unless we want to assume that FRAPEN has actually replaced FRAAME in southern Wisconsin forests

Aster cordifolius/saggitifolius/drummondi: These taxa are very similar in vegetative condition and their status as independent species is still in doubt (Gleason 1992). Although treated by Curtis as separate taxa, we treat them here as a single species.

Table 1: Taxonomic Synonomy between original sample & resample

Curtis Name	Rogers Name
Acalypha rhomboidea	Acalypha rhomboidea
Acalypha sp	Acalypha sp
Acer negundo	Acer negundo
Acer rubrum	Acer rubrum
Acer saccharum	Acer saccharum
Acer spicatum	Acer spicatum
Achillea millefolium	Achillea millefolium
Actaea alba	Actaea pachypoda
Actaea rubra	Actaea rubra
Actaea sp	Actaea sp
Adiantum pedatum	Adiantum pedatum
Agastache scrophulariaefolia	Agastache scrophulariaefolia
Agrimonia gryposepala	Agrimonia gryposepala
Agropyron repens	Elytrigia repens
Agropyron subsecunda	Elymus trachycaulus
Allium canadense	Allium canadense
Allium tricoccum	Allium tricoccum
Ambrosia artemesifolia	Ambrosia artemesifolia
Ambrosia psilostachya	Ambrosia psilostachya
Ambrosia trifida	Ambrosia trifida
Amelanchier laevis	Amelanchier laevis
Amelanchier sp	Amelanchier sp
Amorpha canescens	Amorpha canescens
Amphicarpaea bracteata	Amphicarpaea bracteata
Andropogon furcatus	Andropogon gerardii
Andropogon scoparius	Schizachyrium scoparium
Anemone canadensis	Anemone canadensis
Anemone cylindrica	Anemone cylindrica
Anemone patens	Anemone patens
Anemone quinquefolia	Anemone quinquefolia
Anemone sp	Anemone sp
Anemone virginiana	Anemone virginiana
Anemonella thalictroides	Thalictrum thalictroides
Angelica atropuporea	Angelica atropuporea
Antennaria parlinii	Antennaria parlinii
Antennaria sp	Antennaria sp
Aplectrum hyemale	Aplectrum hyemale
Apocynum androsaemifolium	Apocynum androsaemifolium
Apocynum cannabinum	Apocynum cannabinum
Aquilegia canadensis	Aquilegia canadensis
Arabis canadensis	Arabis canadensis
Arabis laevigata	Arabis laevigata
Arabis lyrata	Arabis lyrata
Arabis sp.	Arabis sp.
Aralia hispida	Aralia hispida
Aralia nudicaulis	Aralia nudicaulis
Aralia racemosa	Aralia racemosa

Curtis Name	**Rogers Name**
Arctium minus	Arctium minus
Arctium sp	Arctium minus
Arenaria lateriflora	Arenaria lateriflora
Arisaema atrorubens	Arisaema triphyllum
Arisaema dracontium	Arisaema dracontium
Asarum canadense	Asarum canadense
Asclepias ovalifolia	Asclepias ovalifolia
Asclepias phytolaccoides	Asclepias exaltata
Asclepias sp	Asclepias sp
Asclepias syriaca	Asclepias syriaca
Asclepias tuberosa	Asclepias tuberosa
Asclepias verticillata	Asclepias verticillata
Aster azureus	Aster oolentangiensis
Aster cordifolius	Aster cordifolius
Aster laevis	Aster laevis
Aster lateriflorus	Aster lateriflorus
Aster linariifolius	Aster linariifolius
Aster macrophyllus	Aster macrophyllus
Aster paniculatus	Aster lanceolatus
Aster ptarmicoides	Solidago ptarmicoides
Aster shortii	Aster shortii
Aster simplex	Aster simplex
Aster sp	Aster sp
Aster sagittifolius	Aster sagittifolius
Aster urophyllus	Aster sagittifolius
Athyrium angustum	Athyrium filix-femina
Athyrium thelypteris	Deparia acrostichoides
Aureolaria flava	Aureolaria grandiflora
Baptisia leucantha	Baptisia alba
Baptisia leucophaea	Baptisia bracteata
Baptisia sp	Baptisia sp
Betula lutea	Betula alleghaniensis
Betula papyrifera	Betula papyrifera
Bidens sp	Bidens sp
Blephilia hirsuta	Blephilia hirsuta
Boehmeria cylindrica	Boehmeria cylindrica
Botrychium multifidum	Botrychium multifidum
Botrychium sp	Botrychium sp
Botrychium virginianum	Botrychium virginianum
Bouteloua hirsuta	Bouteloua hirsuta
Brachyelytrum erectum	Brachyelytrum erectum
Brachyelytrum sp	Brachyelytrum sp
Bromus latiglumis	Bromus altissimus
Bromus purgans	Bromus kalmii
Cacalia tuberosa	Arnoglossum plantagineum
Calamagrostis canadensis	Calamagrostis canadensis
Campanula americana	Campanula americana
Campanula rotundifolia	Campanula rotundifolia
Camptosorus rhizophyllus	Asplenium rhizophyllum

Curtis Name	Rogers Name
Cardamine bulbosa	Cardamine bulbosa
Cardamine douglasii	Cardamine douglasii
Carex albursina	Carex albursina
Carex amphibola	Carex grisea
Carex blanda	Carex blanda
Carex cephalophora	Carex cephalophora
Carex convoluta	Carex rosea
Carex deweyana	Carex deweyana
Carex digitalis	Carex digitalis
Carex hirtifolia	Carex hirtifolia
Carex laxiflora	Carex blanda
Carex pedunculata	Carex pedunculata
Carex pensylvanica	Carex pensylvanica
Carex plantaginea	Carex plantaginea
Carex radiata	Carex radiata
Carex rosea	Carex rosea
Carex sp	Carex sp
Carex sprengelii	Carex sprengelii
Carex woodii	Carex woodii
Carpinus caroliniana	Carpinus caroliniana
Carya cordiformis	Carya cordiformis
Carya ovata	Carya ovata
Carya sp	Carya sp
Cassia fasiculata	Chamaecrista fasciculata
Caulophyllum thalictroides	Caulophyllum thalictroides
Ceanothus sp	Ceanothus americanus
Ceanothus americanus	Ceanothus americanus
Celastrus scandens	Celastrus scandens
Celtis occidentalis	Celtis occidentalis
Cephalanthus occidentalis	Cephalanthus occidentalis
Cerastium vulgare	Cerastium fontanum
Chenopodium album	Chenopodium album
Chenopodium sp	Chenopodium sp
Chimaphila umbellata	Chimaphila umbellata
Circaea alpina	Circaea alpina
Circaea latifolia	Circaea lutetiana
Circaea quadrisulcata	Circaea lutetiana
Cirsium altissimum	Cirsium altissimum
Cirsium discolor	Cirsium discolor
Cirsium sp	Cirsium sp
Claytonia virginica	Claytonia virginica
Clematis virginiana	Clematis virginiana
Clintonia borealis	Clintonia borealis
Comandra richardsiana	Comandra umbellata
Conopholis americana	Conopholis americana
Convallaria majalis	Convallaria majalis
Convallaria sp	Convallaria majalis
Convolvulus sp	Calystegia spithamaea
Convolvulus spithamaeus	Calystegia spithamaea

Curtis Name	Rogers Name
Coptis trifolia	Coptis trifolia
Corallorhiza maculata	Corallorhiza maculata
Coreopsis palmata	Coreopsis palmata
Coreopsis sp	Coreopsis sp
Cornus alternifolia	Cornus alternifolia
Cornus femina	Cornus racemosa
Cornus foemina	Cornus racemosa
Cornus rugosa	Cornus rugosa
Corydalis sempervirens	Corydalis sempervirens
Corylus americana	Corylus americana
Corylus cornuta	Corylus cornuta
Crataegus sp	Crataegus sp
Cryptotaenia canadensis	Cryptotaenia canadensis
Cypripedium pubescens	Cypripedium parviflorum
Cystopteris bulbifera	Cystopteris bulbifera
Cystopteris fragilis	Cystopteris fragilis
Danthonia spicata	Danthonia spicata
Daucus carota	Daucus carota
Dentaria laciniata	Cardamine concatenata
Desmodium acuminatum	Desmodium glutinosum
Desmodium bracteosum	Desmodium cuspidatum
Desmodium cuspidatum	Desmodium cuspidatum
Desmodium illinoense	Desmodium illinoense
Desmodium nudiflorum	Desmodium nudiflorum
Dicentra canadensis	Dicentra canadensis
Dicentra cucullaria	Dicentra cucullaria
Diervilla lonicera	Diervilla lonicera
Dioscorea sp	Dioscorea villosa
Dioscorea villosa	Dioscorea villosa
Dirca palustris	Dirca palustris
Dodecatheon meadia	Dodecatheon meadia
Dryopteris goldiana	Dryopteris goldiana
Dryopteris linneana	Gymnocarpium dryopteris
Dryopteris marginalis	Dryopteris marginalis
Dryopteris spinulosa	Dryopteris carthusiana
Dryopteris thalyteroides	Thelypteris palustris
Ellisia nyctelea	Ellisia nyctelea
Elymus canadensis	Elymus canadensis
Elymus villosus	Elymus villosus
Elymus virginicus	Elymus virginicus
Epifagus virginiana	Epifagus virginiana
Epilobium angustifolium	Epilobium angustifolium
Epipactis pubescens	Goodyera repens
Equisetum arvense	Equisetum arvense
Equisetum laevigatum	Equisetum laevigatum
Erechtites hyeracifolia	Erechtites hieracifolia
Erigeron philadelphicus	Erigeron philadelphicus
Erigeron pulchellus	Erigeron pulchellus
Erigeron ramosus	Erigeron strigosus

Curtis Name	Rogers Name
Eryngium yuccifolium	Eryngium yuccifolium
Erythronium albidum	Erythronium albidum
Erythronium americanum	Erythronium americanum
Eupatorium maculatum	Eupatorium maculatum
Eupatorium perfoliatum	Eupatorium perfoliatum
Eupatorium purpureum	Eupatorium purpureum
Eupatorium rugosum	Eupatorium rugosum
Euphorbia corollata	Euphorbia corollata
Evonymus atropurpurea	Euonymus atropurpurea
Fagus grandifolia	Fagus grandifolia
Fern sp	Unknown
Festuca obtusa	Festuca subverticillata
Floerkea proserpinacoides	Floerkea proserpinacoides
Fragaria vesca	Fragaria vesca
Fragaria virginiana	Fragaria virginiana
Fraxinus americana	Fraxinus americana
Fraxinus nigra	Fraxinus nigra
Fraxinus pennsylvanica	Fraxinus pennsylvanica
Fraxinus quadrangulata	Fraxinus quadrangulata
Fraxinus sp	Fraxinus sp
Galium aparine	Galium aparine
Galium boreale	Galium boreale
Galium circaezans	Galium circaezans
Galium concinnum	Galium concinnum
Galium lanceolatum	Galium lanceolatum
Galium triflorum	Galium triflorum
Gaylussacia baccata	Gaylussacia baccata
Geranium maculatum	Geranium maculatum
Geranium robertianum	Geranium robertianum
Gerardia flava	Aureolaria grandiflora
Geum canadense	Geum canadense
Geum virginianum	Geum virginianum
Gnaphalium obtusifolium	Gnaphalium obtusifolium
Goodyera pubescens	Goodyera pubescens
Habenaria hookeri	Platanthera hookeri
Habenaria hyperborea	Platanthera hyperborea
Hackelia virginiana	Hackelia virginiana
Hamamelis virginiana	Hamamelis virginiana
Helianthemum candense	Helianthemum canadense
Helianthemum sp.	Helianthemum canadense
Helianthus grosseratus	Helianthus grosseratus
Helianthus occidentalis	Helianthus occidentalis
Helianthus sp	Helianthus sp
Helianthus strumosus	Helianthus strumosus
Heliopsis helianthoides	Heliopsis helianthoides
Hepatica acutiloba	Anenome acutiloba
Hepatica americana	Anenome americana
Heracleum maximum	Heracleum lanatum
Heracleum sp	Heracleum lanatum

Curtis Name	**Rogers Name**
Hesperis matronalis	Hesperis matronalis
Heuchera richardsonii	Heuchera richardsonii
Hieracium aurantiacum	Hieracium aurantiacum
Hieracium canadense	Hieracium kalmii
Hieracium scabrum	Hieracium scabrum
Hieracium sp	Hieracium sp
Houstonia longifolia	Houstonia longifolia
Humulus lupulus	Humulus lupulus
Hydrastis canadensis	Hydrastis canadensis
Hydrophyllum appendiculatum	Hydrophyllum appendiculatum
Hydrophyllum virginianum	Hydrophyllum virginianum
Hypoxis hirsuta	Hypoxis hirsuta
Hystrix patula	Elymus hystrix
Ilex verticillata	Ilex verticillata
Impatiens biflora	Impatiens capensis
Impatiens pallida	Impatiens pallida
Isopyrum biternatum	Enemion biternatum
Jeffersonia diphylla	Jeffersonia diphylla
Juglans cinerea	Juglans cinerea
Juglans nigra	Juglans nigra
Juglans sp	Juglans sp
Juniperus communis	Juniperus communis
Juniperus virginiana	Juniperus virginiana
Koeleria cristata	Koeleria macrantha
Krigia biflora	Krigia biflora
Lactuca canadensis	Lactuca canadensis
Lactuca sp	Lactuca sp
Lactuca spicata	Lactuca biennis
Laportea canadensis	Laportea canadensis
Lappula virginiana	Hackelia virginiana
Lathyrus ochroleucus	Lathyrus ochroleucus
Lathyrus palustris	Lathyrus palustris
Lathyrus venosus	Lathyrus venosus
Lechea tenuifolia	Lechea tenuifolia
LEGUME	Unknown
Lespedeza capitata	Lespedeza capitata
Lespedeza virginica	Lespedeza virginica
Liatris aspera	Liatris aspera
Lilium philadelphicum	Lilium philadelphicum
Liparis lilifolia	Liparis lilifolia
Lithospermum canescens	Lithospermum canescens
Lithospermum incisum	Lithospermum incisum
Lithospermum latifolium	Lithospermum latifolium
Lobelia spicata	Lobelia spicata
Lonicera canadensis	Lonicera canadensis
Lonicera dioica	Lonicera dioica
Lonicera oblongifolia	Lonicera oblongifolia
Lonicera prolifera	Lonicera reticulata
Lonicera tatarica	Lonicera tatarica

Curtis Name	**Rogers Name**
Lupinus perennis	Lupinus perennis
Luzula campestris	Luzula acuminata
Lycopodium annotinum	Lycopodium annotinum
Lycopodium lucidulum	Huperzia lucidula
Lycopodium obscurum	Lycopodium obscurum
Lycopus americanus	Lycopus americanus
Lysimachia ciliata	Lysimachia ciliata
Lysimachia lanceolata	Lysimachia lanceolata
Lysimachia quadrifolia	Lysimachia quadrifolia
Maianthemum canadense	Maianthemum canadense
Menispermum canadense	Menispermum canadense
Milium effusum	Milium effusum
Mitchella repens	Mitchella repens
Mitella diphylla	Mitella diphylla
Mitella nuda	Mitella nuda
Monarda fistulosa	Monarda fistulosa
Monotropa uniflora	Monotropa uniflora
Muhlenbergia cuspidata	Muhlenbergia cuspidata
Muhlenbergia frondosa	Muhlenbergia frondosa
Muhlenbergia schreberi	Muhlenbergia schreberi
Myrica asplenifolia	Comptonia peregrina
Nepeta cataria	Nepeta cataria
Nepeta hederacea	Glechoma hederacea
No species	No species
Onoclea sensibilis	Onoclea sensibilis
Orchis spectabilis	Galearis spectabilis
Oryzopsis asperifolia	Oryzopsis asperifolia
Oryzopsis racemosa	Oryzopsis racemosa
Osmorhiza claytonii	Osmorhiza claytonii
Osmorhiza longistylis	Osmorhiza longistylis
Osmunda cinnamomea	Osmunda cinnamomea
Osmunda claytoniana	Osmunda claytoniana
Ostrya virginiana	Ostrya virginiana
Oxalis acetosella	Oxalis acetosella
Oxalis sp	Oxalis sp
Oxalis stricta	Oxalis stricta
Oxalis violacea	Oxalis violacea
Oxypolis rigidior	Oxypolis rigidior
Panax quinquefolius	Panax quinquefolius
Panax trifolius	Panax trifolius
Panicum crepiensis	Unknown
Panicum dichotomiflorum	Panicum dichotomiflorum
Panicum implicatum	Panicum acuminatum
Panicum latifolium	Panicum latifolium
Panicum sp	Panicum sp
Panicum sp	Panicum sp
Parietaria pensylvanica	Parietaria pensylvanica
Parthenocissus inserta	Parthenocissus vitacea
Pedicularis canadensis	Pedicularis canadensis

Curtis Name	Rogers Name
Pedicularis lanceolata	Pedicularis lanceolata
Petalostemon candidum	Dalea candida
Petalostemon purpureum	Dalea purpurea
Phleum pratense	Phleum pratense
Phlox divaricata	Phlox divaricata
Phlox pilosa	Phlox pilosa
Phryma leptostachya	Phryma leptostachya
Physalis heterophylla	Physalis heterophylla
Physalis virginiana	Physalis virginiana
Physocarpus opulifolius	Physocarpus opulifolius
Phytolacca decandra	Phytolacca americana
Picea glauca	Picea glauca
Pilea pumila	Pilea pumila
Pinus strobus	Pinus strobus
Pinus sylvestris	Pinus sylvestris
Plantago major	Plantago major
Poa compressa	Poa compressa
Poa pratensis	Poa pratensis
Poa sp	Poa sp
Podophyllum peltatum	Podophyllum peltatum
Polemonium reptans	Polemonium reptans
Polygala polygama	Polygala polygama
Polygala sanguinea	Polygala sanguinea
Polygala sp.	Polygala sp.
Polygonatum commutatum	Polygonatum biflorum
Polygonatum pubescens	Polygonatum pubescens
Polygonum convolvulus	Polygonum convolvulus
Polygonum sp	Polygonum sp
Polygonum virginianum	Polygonum virginianum
Polymnia canadensis	Polymnia canadensis
Polypodium vulgare	Polypodium virginianum
Populus deltoides	Populus deltoides
Populus grandidentata	Populus grandidentata
Populus tremuloides	Populus tremuloides
Potentilla argentea	Potentilla argentea
Potentilla arguta	Potentilla arguta
Potentilla norvegica	Potentilla norvegica
Potentilla simplex	Potentilla simplex
Potentilla sp	Potentilla sp
Prenanthes alba	Prenanthes alba
Prenanthes racemosa	Prenanthes racemosa
Prunella vulgaris	Prunella vulgaris
Prunus americana	Prunus americana
Prunus nigra	Prunus nigra
Prunus pumila	Prunus pumila
Prunus serotina	Prunus serotina
Prunus virginiana	Prunus virginiana
Pteretis nodulosa	Matteuccia struthiopteris
Pteridium latiusculum	Pteridium aquilinum

Curtis Name	**Rogers Name**
Pycnanthemum virginianum	Pycnanthemum virginianum
Pyrola elliptica	Pyrola elliptica
Pyrola rotundifolia	Pyrola rotundifolia
Pyrola secunda	Orthilia secunda
Pyrus americana	Sorbus americana
Pyrus ioensis	Malus ioensis
Pyrus sp	Unknown
Quercus alba	Quercus alba
Quercus bicolor	Quercus bicolor
Quercus borealis	Quercus rubra
Quercus ellipsoidalis	Quercus ellipsoidalis
Quercus macrocarpa	Quercus macrocarpa
Quercus velutina	Quercus velutina
Ranunculus abortivus	Ranunculus abortivus
Ranunculus fascicularis	Ranunculus fascicularis
Ranunculus recurvatus	Ranunculus recurvatus
Ranunculus septentrionalis	Ranunculus hispidus
Ratibida pinnata	Ratibida pinnata
Ratibida sp	Ratibida sp
Rhamnus cathartica	Rhamnus cathartica
Rhus glabra	Rhus glabra
Rhus radicans	Toxicodendron radicans
Rhus typhina	Rhus typhina
Ribes americanum	Ribes americanum
Ribes cynosbati	Ribes cynosbati
Ribes glandulosum	Ribes glandulosum
Ribes missouriense	Ribes missouriense
Ribes nigrum	Ribes nigrum
Ribes sp	Ribes sp
Robinia pseudoacacia	Robinia pseudoacacia
Rosa sp	Rosa sp
Rubus allegheniensis	Rubus allegheniensis
Rubus hispidus	Rubus hispidus
Rubus strigosous	Rubus idaeus
Rubus occidentalis	Rubus occidentalis
Rubus parviflorus	Rubus parviflorus
Rubus sp	Rubus sp
Rudbeckia hirta	Rudbeckia hirta
Rudbeckia laciniata	Rudbeckia laciniata
Salix sp	Salix sp
Sambucus canadensis	Sambucus canadensis
Sambucus pubens	Sambucus racemosa
Sanguinaria canadensis	Sanguinaria canadensis
Sanicula gregaria	Sanicula gregaria
Sanicula marilandica	Sanicula marilandica
Sanicula sp	Sanicula sp
Saxifraga pensylvanica	Saxifraga pensylvanica
Scrophularia lanceolata	Scrophularia lanceolata
Scrophularia marilandica	Scrophularia marilandica

Curtis Name	Rogers Name
Scutellaria parvula	Scutellaria parvula
Sedum purpureum	Sedum telephium
Selaginella sp	Selaginella rupestris
Shepherdia canadensis	Shepherdia canadensis
Silene antirrhina	Silene antirrhina
Silene stellata	Silene stellata
Silphium integrifolium	Silphium integrifolium
Silphium perfoliatum	Silphium perfoliatum
Silphium terebinthinaceum	Silphium terebinthinaceum
Smilacina racemosa	Smilacina racemosa
Smilacina stellata	Smilacina stellata
Smilax ecirrhata	Smilax ecirrhata
Smilax herbacea	Smilax herbacea
Smilax hispida	Smilax hispida
Smilax tamnoides	Smilax hispida
Solanum nigrum	Solanum ptycanthum
Solanum sp	Solanum sp
Solidago altissima	Solidago canadensis
Solidago canadensis	Solidago canadensis
Solidago flexicaulis	Solidago flexicaulis
Solidago gigantea	Solidago gigantea
Solidago hispida	Solidago hispida
Solidago latifolia	Solidago flexicaulis
Solidago nemoralis	Solidago nemoralis
Solidago rigida	Solidago rigida
Solidago sp	Solidago sp
Solidago speciosa	Solidago speciosa
Solidago ulmifolia	Solidago ulmifolia
Sorbus aucuparia	Sorbus aucuparia
Spartina pectinata	Spartina pectinata
Sphenopholis intermedia	Sphenopholis intermedia
Sporobolus vaginiflorus	Sporobolus vaginiflorus
Staphlea sp	Staphylea trifolia
Staphylea trifolia	Staphylea trifolia
Steironema ciliata	Lysimachia ciliata
Stipa spartea	Stipa spartea
Streptopus roseus	Streptopus roseus
Symphoricarpos albus	Symphoricarpos albus
Symphoricarpos sp	Symphoricarpos albus
Symplocarpus foetidus	Symplocarpus foetidus
Taenidia integerrima	Taenidia integerrima
Taraxacum officinale	Taraxacum officinale
Taraxacum sp	Taraxacum officinale
Taraxacum sp	Taraxacum officinale
Taxus canadensis	Taxus canadensis
Tephrosia virginiana	Tephrosia virginiana
Thalictrum dasycarpum	Thalictrum dasycarpum
Thalictrum dioicum	Thalictrum dioicum
Thaspium aureum	Thaspium trifoliatum

Curtis Name	**Rogers Name**
Thuja occidentalis	Thuja occidentalis
Tilia americana	Tilia americana
Tilia sp	Tilia americana
Tovara virginiana	Polygonum virginianum
Tradescantia ohiensis	Tradescantia ohiensis
Tradescantia virginiana	Tradescantia virginiana
Trientalis americana	Trientalis borealis
Trientalis borealis	Trientalis borealis
Trillium cernuum	Trillium cernuum
Trillium gleasoni	Trillium flexipes
Trillium grandiflorum	Trillium grandiflorum
Trillium recurvatum	Trillium recurvatum
Trillium sessile	Trillium recurvatum
Trillium sp	Trillium sp
Triosteum perfoliatum	Triosteum perfoliatum
Tsuga canadensis	Tsuga canadensis
Ulmus americana	Ulmus americana
Ulmus fulva	Ulmus rubra
Ulmus sp	Ulmus sp
Ulmus thomasii	Ulmus thomasii
Unknown	Unknown
Unknown grass	Unknown grass
Unknown2	Unknown2
Urtica dioica	Urtica dioica
Uvularia grandiflora	Uvularia grandiflora
Uvularia sessilifolia	Uvularia sessilifolia
Vaccinium canadense	Vaccinium myrtilloides
Vaccinium pensilvanicum	Vaccinium angustifolium
Vaccinium pensilvanicum	Vaccinium angustifolium
Vaccinium sp	Vaccinium sp
Verbascum thapsus	Verbascum thapsus
Verbena urticifolia	Verbena urticifolia
Veronica longifolia	Veronica longifolia
Veronica serpyllifolia	Veronica serpyllifolia
Veronicastrum virginicum	Veronicastrum virginicum
Viburnum acerifolium	Viburnum acerifolium
Viburnum affine	Viburnum rafinesquianum
Viburnum lantana	Viburnum lantana
Viburnum lentago	Viburnum lentago
Viburnum opulus	Viburnum opulus
Viburnum trilobum	Viburnum opulus
Vicia americana	Vicia americana
Vicia caroliniana	Vicia caroliniana
Viola canadensis	Viola canadensis
Viola conspersa	Viola labradorica
Viola cucullata	Viola cucullata
Viola eriocarpa	Viola pubescens
Viola incognita	Viola blanda
Viola pallens	Viola macloskeyi

Curtis Name	Rogers Name
Viola pedata	Viola pedata
Viola pedatifida	Viola pedatifida
Viola pubescens	Viola pubescens
Viola sagittata	Viola sagittata
Viola sp	Viola sp
Viola sp	Viola sp
Vitis aestivalis	Vitis aestivalis
Vitis bicolor	Vitis aestivalis
Vitis riparia	Vitis riparia
Woodsia ilvensis	Woodsia ilvensis
Xanthium strumarium	Xanthium strumarium
Xanthium strumarium	Xanthium strumarium
Xanthoxylum americanum	Zanthoxylum americanum
Zanthoxylum americanum	Zanthoxylum americanum
Zizia aurea	Zizia aurea

Table 2: List of synchronization used

ExpandedSpecies	**SyncSpecies**
Acalypha rhomboidea	*Acalypha rhomboidea*
Acer negundo	*Acer negundo*
Acer platanoides	*Acer platanoides*
Acer rubrum	*Acer rubrum*
Acer saccharum	*Acer saccharum*
Acer spicatum	*Acer spicatum*
Achillea millefolium	*Achillea millefolium*
Actaea pachypoda	*Actaea pachypoda*
Actaea rubra	*Actaea rubra*
Actaea sp	*Actaea pachypoda*
Adiantum pedatum	*Adiantum pedatum*
Aesculus glabra	*Aesculus glabra*
Aethusa cynapium	*Aethusa cynapium*
Agastache scrophulariaefolia	*Agastache scrophulariaefolia*
Agrimonia gryposepala	*Agrimonia gryposepala*
Ajuga reptans	*Ajuga reptans*
Alliaria petiolata	*Alliaria petiolata*
Allium canadense	*Allium canadense*
Allium tricoccum	*Allium tricoccum*
Ambrosia trifida	*Ambrosia trifida*
Amelanchier sp	*Amelanchier sp*
Amorpha canescens	*Amorpha canescens*
Amphicarpaea bracteata	*Amphicarpaea bracteata*
Andropogon gerardii	*Andropogon gerardii*
Anemone acutiloba	*Anemone acutiloba*
Anemone americana	*Anemone americana*
Anemone cylindrica	*Anemone cylindrica*
Anemone quinquefolia	*Anemone quinquefolia*
Anemone sp	*Anemone sp*
Anemone virginiana	*Anemone virginiana*
Angelica atropurpurea	*Angelica atropurpurea*
Antennaria sp	*Antennaria sp*
Aplectrum hyemale	*Aplectrum hyemale*
Apocynum androsaemifolium	*Apocynum androsaemifolium*
Apocynum cannabinum	*Apocynum cannabinum*
Aquilegia canadensis	*Aquilegia canadensis*
Arabis canadensis	*Arabis canadensis*
Arabis laevigata	*Arabis laevigata*
Aralia nudicaulis	*Aralia nudicaulis*
Aralia racemosa	*Aralia racemosa*
Arctium minus	*Arctium minus*
Arenaria lateriflora	*Arenaria lateriflora*
Arisaema dracontium	*Arisaema dracontium*
Arisaema triphyllum	*Arisaema triphyllum*

ExpandedSpecies	**SyncSpecies**
Aronia melanocarpa	*Aronia melanocarpa*
Asarum canadense	*Asarum canadense*
Asclepias exaltata	*Asclepias exaltata*
Asplenium rhizophyllum	*Asplenium rhizophyllum*
Aster cordifolius	*Aster sagittifolius*
Aster drummondii	*Aster sagittifolius*
Aster lanceolatus	*Aster lanceolatus*
Aster lateriflorus	*Aster lateriflorus*
Aster macrophyllus	*Aster macrophyllus*
Aster oolentangiensis	*Aster oolentangiensis*
Aster sagittifolius	*Aster sagittifolius*
Aster shortii	*Aster shortii*
Aster sp	*Aster sp*
Athyrium filix-femina	*Athyrium filix-femina*
Aureolaria grandiflora	*Aureolaria grandiflora*
Berberis thunbergii	*Berberis thunbergii*
Betula alleghaniensis	*Betula alleghaniensis*
Betula papyrifera	*Betula papyrifera*
Bidens frondosus	*Bidens frondosus*
Bidens sp	*Bidens frondosus*
Blephilia hirsuta	*Blephilia hirsuta*
Boehmeria cylindrica	*Boehmeria cylindrica*
Botrychium dissectum	*Botrychium multifidum*
Botrychium multifidum	*Botrychium multifidum*
Botrychium virginianum	*Botrychium virginianum*
Brachyelytrum erectum	*Brachyelytrum erectum*
Bromus kalmii	*Bromus kalmii*
Bromus pubescens	*Bromus pubescens*
Calystegia spithamaea	*Calystegia spithamaea*
Campanula americana	*Campanula americana*
Campanula rotundifolia	*Campanula rotundifolia*
Cardamine concatenata	*Cardamine concatenata*
Cardamine douglassii	*Cardamine douglassii*
Carex albursina	*Carex albursina*
Carex arctata	*Carex sp*
Carex blanda	*Carex sp*
Carex cephaloidea	*Carex sp*
Carex cephalophora	*Carex sp*
Carex deweyana	*Carex sp*
Carex formosa	*Carex sp*
Carex gracillima	*Carex sp*
Carex grisea	*Carex sp*
Carex hirtifolia	*Carex sp*
Carex intumescens	*Carex sp*
Carex normalis	*Carex sp*

ExpandedSpecies	**SyncSpecies**
Carex oligocarpa	*Carex sp*
Carex pedunculata	*Carex sp*
Carex pensylvanica	*Carex sp*
Carex plantaginea	*Carex plantaginea*
Carex radiata	*Carex sp*
Carex rosea	*Carex sp*
Carex sp	*Carex sp*
Carex sparganioides	*Carex sp*
Carex sprengelii	*Carex sp*
Carpinus caroliniana	*Carpinus caroliniana*
Carya cordiformis	*Carya cordiformis*
Carya ovata	*Carya ovata*
Caulophyllum thalictroides	*Caulophyllum thalictroides*
Ceanothus americanus	*Ceanothus americanus*
Celastrus orbiculata	*Celastrus orbiculata*
Celastrus scandens	*Celastrus scandens*
Celtis occidentalis	*Celtis occidentalis*
Cerastium fontanum	*Cerastium fontanum*
Chelidonium majus	*Chelidonium majus*
Chenopodium album	*Chenopodium album*
Chenopodium simplex	*Chenopodium simplex*
Chimaphila umbellata	*Chimaphila umbellata*
Cinna arundinacea	*Cinna arundinacea*
Cinna latifolia	*Cinna latifolia*
Circaea alpina	*Circaea alpina*
Circaea lutetiana	*Circaea lutetiana*
Cirsium altissimum	*Cirsium altissimum*
Cirsium arvense	*Cirsium arvense*
Cirsium sp	*Cirsium sp*
Cirsium vulgare	*Cirsium vulgare*
Claytonia virginica	*Claytonia virginica*
Clematis virginiana	*Clematis virginiana*
Coeloglossum viride	*Coeloglossum viride*
Comandra umbellata	*Comandra umbellata*
Conopholis americana	*Conopholis americana*
Convallaria majalis	*Convallaria majalis*
Conyza canadensis	*Conyza canadensis*
Corallorhiza maculata	*Corallorhiza maculata*
Coreopsis palmata	*Coreopsis palmata*
Cornus alternifolia	*Cornus alternifolia*
Cornus racemosa	*Cornus racemosa*
Cornus rugosa	*Cornus rugosa*
Corylus americana	*Corylus americana*
Crataegus sp	*Crataegus sp*
Cryptotaenia canadensis	*Cryptotaenia canadensis*

ExpandedSpecies	**SyncSpecies**
Cuscuta gronovii	*Cuscuta gronovii*
Cypripedium parviflorum	*Cypripedium parviflorum*
Cystopteris bulbifera	*Cystopteris bulbifera*
Cystopteris fragilis	*Cystopteris fragilis*
Dactylis glomerata	*Dactylis glomerata*
Danthonia spicata	*Danthonia spicata*
Daucus carota	*Daucus carota*
Deparia acrostichoides	*Deparia acrostichoides*
Desmodium cuspidatum	*Desmodium cuspidatum*
Desmodium glutinosum	*Desmodium glutinosum*
Desmodium illinoense	*Desmodium illinoense*
Desmodium nudiflorum	*Desmodium nudiflorum*
Dicentra cucullaria	*Dicentra cucullaria*
Diervilla lonicera	*Diervilla lonicera*
Dioscorea villosa	*Dioscorea villosa*
Diplazium pycnocarpon	*Diplazium pycnocarpon*
Dirca palustris	*Dirca palustris*
Dodecatheon meadia	*Dodecatheon meadia*
Dryopteris carthusiana	*Dryopteris carthusiana*
Dryopteris cristata	*Dryopteris cristata*
Dryopteris goldiana	*Dryopteris goldiana*
Dryopteris marginalis	*Dryopteris marginalis*
Duchesnea indica	*Duchesnea indica*
Echinocystis lobata	*Echinocystis lobata*
Ellisia nyctelea	*Ellisia nyctelea*
Elymus hystrix	*Elymus hystrix*
Elymus villosus	*Elymus villosus*
Elymus virginicus	*Elymus virginicus*
Enemion biternatum	*Enemion biternatum*
Epifagus virginiana	*Epifagus virginiana*
Epilobium coloratum	*Epilobium ciliatum*
Epipactis helleborine	*Epipactis helleborine*
Equisetum arvense	*Equisetum arvense*
Equisetum laevigatum	*Equisetum laevigatum*
Equisetum pratense	*Equisetum arvense*
Erechtites hieracifolia	*Erechtites hieracifolia*
Erigeron annuus	*Erigeron annuus*
Erigeron philadelphicus	*Erigeron philadelphicus*
Erigeron pulchellus	*Erigeron pulchellus*
Erythronium albidum	*Erythronium albidum*
Erythronium americanum	*Erythronium americanum*
Euonymus alata	*Euonymus alata*
Euonymus atropurpurea	*Euonymus atropurpurea*
Euonymus europaea	*Euonymus europaea*
Eupatorium purpureum	*Eupatorium purpureum*

ExpandedSpecies	**SyncSpecies**
Eupatorium rugosum	*Eupatorium rugosum*
Euphorbia corollata	*Euphorbia corollata*
Fagus grandifolia	*Fagus grandifolia*
Festuca subverticillata	*Festuca subverticillata*
Floerkea proserpinacoides	*Floerkea proserpinacoides*
Fragaria vesca	*Fragaria virginiana*
Fragaria virginiana	*Fragaria virginiana*
Fraxinus americana	*Fraxinus pennsylvanica*
Fraxinus nigra	*Fraxinus nigra*
Fraxinus pennsylvanica	*Fraxinus pennsylvanica*
Fraxinus quadrangulata	*Fraxinus quadrangulata*
Galearis spectabilis	*Galearis spectabilis*
Galium aparine	*Galium aparine*
Galium boreale	*Galium boreale*
Galium circaezans	*Galium circaezans*
Galium concinnum	*Galium concinnum*
Galium lanceolatum	*Galium lanceolatum*
Galium triflorum	*Galium triflorum*
Gaylussacia baccata	*Gaylussacia baccata*
Geranium maculatum	*Geranium maculatum*
Geum canadense	*Geum canadense*
Glechoma hederacea	*Glechoma hederacea*
Glyceria striata	*Glyceria striata*
Goodyera pubescens	*Goodyera pubescens*
Hackelia virginiana	*Hackelia virginiana*
Hamamelis virginiana	*Hamamelis virginiana*
Helianthemum canadense	*Helianthemum canadense*
Helianthus grosseserratus	*Helianthus grosseserratus*
Helianthus sp	*Helianthus sp*
Helianthus strumosus	*Helianthus strumosus*
Heliopsis helianthoides	*Helianthus strumosus*
Heracleum lanatum	*Heracleum lanatum*
Hesperis matronalis	*Hesperis matronalis*
Heuchera richardsonii	*Heuchera richardsonii*
Hieracium kalmii	*Hieracium kalmii*
Hieracium scabrum	*Hieracium scabrum*
Hieracium sp	*Hieracium sp*
Humulus lupulus	*Humulus lupulus*
Huperzia lucidula	*Huperzia lucidula*
Hydrastis canadensis	*Hydrastis canadensis*
Hydrophyllum appendiculatum	*Hydrophyllum appendiculatum*
Hydrophyllum virginianum	*Hydrophyllum virginianum*
Hypericum perforatum	*Hypericum perforatum*
Ilex verticillata	*Ilex verticillata*
Impatiens capensis	*Impatiens pallida*

ExpandedSpecies	**SyncSpecies**
Impatiens pallida	*Impatiens pallida*
Jeffersonia diphylla	*Jeffersonia diphylla*
Juglans cinerea	*Juglans cinerea*
Juglans nigra	*Juglans nigra*
Juncus tenuis	*Juncus tenuis*
Juniperus virginiana	*Juniperus virginiana*
Krigia biflora	*Krigia biflora*
Lactuca biennis	*Lactuca biennis*
Lactuca serriola	*Lactuca serriola*
Laportea canadensis	*Laportea canadensis*
Lathyrus ochroleucus	*Lathyrus ochroleucus*
Lathyrus venosus	*Lathyrus venosus*
Leersia virginica	*Leersia virginica*
Leonurus cardiaca	*Leonurus cardiaca*
Lespedeza capitata	*Lespedeza capitata*
Liatris aspera	*Liatris aspera*
Ligustrum vulgare	*Ligustrum vulgare*
Lilium michiganense	*Lilium philadelphicum*
Lilium philadelphicum	*Lilium philadelphicum*
Lithospermum canescens	*Lithospermum canescens*
Lithospermum latifolium	*Lithospermum latifolium*
Lobelia inflata	*Lobelia inflata*
Lobelia spicata	*Lobelia spicata*
Lonicera canadensis	*Lonicera canadensis*
Lonicera reticulata	*Lonicera reticulata*
Lonicera x bella	*Lonicera x bella*
Lupinus perennis	*Lupinus perennis*
Lycopodium obscurum	*Lycopodium obscurum*
Lysimachia ciliata	*Lysimachia ciliata*
Lysimachia quadrifolia	*Lysimachia quadrifolia*
Maianthemum canadense	*Maianthemum canadense*
Malus ioensis	*Malus ioensis*
Malus pumila	*Malus pumila*
Matteuccia struthiopteris	*Matteuccia struthiopteris*
Menispermum canadense	*Menispermum canadense*
Milium effusum	*Milium effusum*
Mitchella repens	*Mitchella repens*
Mitella diphylla	*Mitella diphylla*
Monarda fistulosa	*Monarda fistulosa*
Monotropa uniflora	*Monotropa uniflora*
Morus alba	*Morus alba*
Muhlenbergia frondosa	*Muhlenbergia frondosa*
Muhlenbergia schreberi	*Muhlenbergia schreberi*
No species	*No species*
Oenothera biennis	*Oenothera biennis*

ExpandedSpecies	**SyncSpecies**
Onoclea sensibilis	*Onoclea sensibilis*
Orthilia secunda	*Orthilia secunda*
Oryzopsis asperifolia	*Oryzopsis asperifolia*
Oryzopsis pungens	*Oryzopsis pungens*
Oryzopsis racemosa	*Oryzopsis racemosa*
Osmorhiza claytonii	*Osmorhiza claytonii*
Osmorhiza longistylis	*Osmorhiza longistylis*
Osmunda cinnamomea	*Osmunda cinnamomea*
Osmunda claytoniana	*Osmunda claytoniana*
Ostrya virginiana	*Ostrya virginiana*
Oxalis sp	*Oxalis sp*
Oxalis stricta	*Oxalis stricta*
Oxalis violacea	*Oxalis violacea*
Panax quinquefolius	*Panax quinquefolius*
Panax trifolius	*Panax trifolius*
Panicum acuminatum	*Panicum xanthophysum*
Panicum latifolium	*Panicum latifolium*
Panicum sp	*Panicum sp*
Parietaria pensylvanica	*Parietaria pensylvanica*
Parthenocissus vitacea	*Parthenocissus vitacea*
Pedicularis canadensis	*Pedicularis canadensis*
Phalaris arundinacea	*Phalaris arundinacea*
Phlox divaricata	*Phlox divaricata*
Phryma leptostachya	*Phryma leptostachya*
Physalis virginiana	*Physalis virginiana*
Physocarpus opulifolius	*Physocarpus opulifolius*
Phytolacca americana	*Phytolacca americana*
Pilea pumila	*Pilea pumila*
Pinus strobus	*Pinus strobus*
Plantago major	*Plantago major*
Poa alsodes	*Poa alsodes*
Poa compressa	*Poa compressa*
Poa pratensis	*Poa pratensis*
Poa sp	*Poa sp*
Podophyllum peltatum	*Podophyllum peltatum*
Polemonium reptans	*Polemonium reptans*
Polygala polygama	*Polygala polygama*
Polygonatum biflorum	*Polygonatum biflorum*
Polygonatum pubescens	*Polygonatum pubescens*
Polygonum cespitosum	*Polygonum persicaria*
Polygonum cilinode	*Polygonum scandens*
Polygonum convolvulus	*Polygonum scandens*
Polygonum persicaria	*Polygonum persicaria*
Polygonum scandens	*Polygonum scandens*
Polygonum sp	*Polygonum sp*

ExpandedSpecies	**SyncSpecies**
Polygonum virginianum	*Polygonum virginianum*
Polymnia canadensis	*Polymnia canadensis*
Polypodium virginianum	*Polypodium virginianum*
Populus grandidentata	*Populus grandidentata*
Populus tremuloides	*Populus tremuloides*
Potentilla argentea	*Potentilla argentea*
Potentilla norvegica	*Potentilla norvegica*
Potentilla simplex	*Potentilla simplex*
Potentilla sp	*Potentilla sp*
Prenanthes alba	*Prenanthes alba*
Prunella vulgaris	*Prunella vulgaris*
Prunus americana	*Prunus nigra*
Prunus nigra	*Prunus nigra*
Prunus pumila	*Prunus pumila*
Prunus serotina	*Prunus serotina*
Prunus virginiana	*Prunus virginiana*
Pteridium aquilinum	*Pteridium aquilinum*
Pyrola elliptica	*Pyrola elliptica*
Quercus alba	*Quercus alba*
Quercus macrocarpa	*Quercus macrocarpa*
Quercus rubra	*Quercus rubra*
Quercus velutina	*Quercus rubra*
Ranunculus abortivus	*Ranunculus abortivus*
Ranunculus fascicularis	*Ranunculus fascicularis*
Ranunculus hispidus	*Ranunculus hispidus*
Ranunculus recurvatus	*Ranunculus recurvatus*
Ratibida pinnata	*Ratibida pinnata*
Rhamnus cathartica	*Rhamnus cathartica*
Rhamnus frangula	*Rhamnus frangula*
Rhus glabra	*Rhus glabra*
Rhus hirta	*Rhus hirta*
Ribes americanum	*Ribes americanum*
Ribes cynosbati	*Ribes missouriense*
Ribes missouriense	*Ribes missouriense*
Ribes sp	*Ribes sp*
Robinia pseudoacacia	*Robinia pseudoacacia*
Rosa multiflora	*Rosa multiflora*
Rosa sp	*Rosa sp*
Rubus allegheniensis	*Rubus allegheniensis*
Rubus hispidus	*Rubus pubescens*
Rubus idaeus	*Rubus idaeus*
Rubus occidentalis	*Rubus occidentalis*
Rubus pubescens	*Rubus pubescens*
Rubus sp	*Rubus sp*
Rudbeckia hirta	*Rudbeckia hirta*

ExpandedSpecies	**SyncSpecies**
Rudbeckia laciniata	*Rudbeckia laciniata*
Rudbeckia triloba	*Rudbeckia hirta*
Rumex crispus	*Rumex crispus*
Rumex obtusifolius	*Rumex obtusifolius*
Salix sp	*Salix sp*
Sambucus canadensis	*Sambucus canadensis*
Sambucus racemosa	*Sambucus racemosa*
Sanguinaria canadensis	*Sanguinaria canadensis*
Sanicula gregaria	*Sanicula gregaria*
Sanicula marilandica	*Sanicula marilandica*
Sanicula sp	*Sanicula sp*
Schizachyrium scoparium	*Schizachyrium scoparium*
Scilla sibirica	*Scilla sibirica*
Scrophularia lanceolata	*Scrophularia marilandica*
Scrophularia marilandica	*Scrophularia marilandica*
Scutellaria lateriflora	*Scutellaria lateriflora*
Setaria viridis	*Setaria viridis*
Silene stellata	*Silene stellata*
Smilacina racemosa	*Smilacina racemosa*
Smilacina stellata	*Smilacina stellata*
Smilax ecirrhata	*Smilax ecirrhata*
Smilax herbacea	*Smilax herbacea*
Smilax hispida	*Smilax hispida*
Solanum dulcamara	*Solanum dulcamara*
Solanum ptycanthum	*Solanum ptycanthum*
Solanum sp	*Solanum sp*
Solidago canadensis	*Solidago canadensis*
Solidago flexicaulis	*Solidago flexicaulis*
Solidago gigantea	*Solidago gigantea*
Solidago hispida	*Solidago hispida*
Solidago nemoralis	*Solidago nemoralis*
Solidago sp	*Solidago sp*
Solidago ulmifolia	*Solidago ulmifolia*
Sorbus sp	*Sorbus sp*
Staphylea trifolia	*Staphylea trifolia*
Stellaria aquatica	*Stellaria aquatica*
Stellaria media	*Stellaria media*
Symphoricarpos albus	*Symphoricarpos albus*
Symplocarpus foetidus	*Symplocarpus foetidus*
Taenidia integerrima	*Taenidia integerrima*
Taraxacum officinale	*Taraxacum officinale*
Tephrosia virginiana	*Tephrosia virginiana*
Thalictrum dasycarpum	*Thalictrum dasycarpum*
Thalictrum dioicum	*Thalictrum dioicum*
Thalictrum thalictroides	*Thalictrum thalictroides*

ExpandedSpecies	**SyncSpecies**
Thuja occidentalis	*Thuja occidentalis*
Tilia americana	*Tilia americana*
Toxicodendron radicans	*Toxicodendron radicans*
Tradescantia ohiensis	*Tradescantia ohiensis*
Trientalis borealis	*Trientalis borealis*
Trillium cernuum	*Trillium cernuum*
Trillium flexipes	*Trillium flexipes*
Trillium grandiflorum	*Trillium grandiflorum*
Trillium recurvatum	*Trillium recurvatum*
Triosteum aurantiacum	*Triosteum perfoliatum*
Triosteum perfoliatum	*Triosteum perfoliatum*
Tsuga canadensis	*Tsuga canadensis*
Ulmus americana	*Ulmus americana*
Ulmus pumila	*Ulmus americana*
Ulmus rubra	*Ulmus americana*
Urtica dioica	*Urtica dioica*
Uvularia grandiflora	*Uvularia grandiflora*
Uvularia sessilifolia	*Uvularia sessilifolia*
Vaccinium angustifolium	*Vaccinium angustifolium*
Verbascum thapsus	*Verbascum thapsus*
Verbena urticifolia	*Verbena urticifolia*
Veronica serpyllifolia	*Veronica serpyllifolia*
Veronicastrum virginicum	*Veronicastrum virginicum*
Viburnum acerifolium	*Viburnum acerifolium*
Viburnum dentatum	*Viburnum dentatum*
Viburnum lantana	*Viburnum lantana*
Viburnum lentago	*Viburnum lentago*
Viburnum opulus	*Viburnum opulus*
Viburnum rafinesquianum	*Viburnum rafinesquianum*
Viburnum trilobum	*Viburnum trilobum*
Vicia americana	*Vicia americana*
Viola blanda	*Viola blanda*
Viola canadensis	*Viola canadensis*
Viola cucullata	*Viola sororia*
Viola labradorica	*Viola labradorica*
Viola macloskeyi	*Viola macloskeyi*
Viola pedata	*Viola pedata*
Viola pubescens	*Viola pubescens*
Viola sororia	*Viola sororia*
Viola sp	*Viola sp*
Vitis aestivalis	*Vitis aestivalis*
Vitis riparia	*Vitis riparia*
Zanthoxylum americanum	*Zanthoxylum americanum*
Zizia aurea	*Zizia aurea*

Table 3: Final species list used for analysis of composition (unknowns) were used to calculate richness

Acalypha rhomboidea
Acer negundo
Acer platanoides
Acer rubrum
Acer saccharum
Acer spicatum
Achillea millefolium
Actaea pachypoda
Actaea rubra
Adiantum pedatum
Aesculus glabra
Aethusa cynapium
Agastache scrophulariaefolia
Agrimonia gryposepala
Ajuga reptans
Alliaria petiolata
Allium canadense
Allium tricoccum
Ambrosia artemisiifolia
Ambrosia trifida
Amelanchier sp
Amorpha canescens
Amphicarpaea bracteata
Andropogon gerardii
Anemone acutiloba
Anemone americana
Anemone cylindrica
Anemone quinquefolia
Anemone virginiana
Angelica atropurpurea
Antennaria sp
Aplectrum hyemale
Apocynum androsaemifolium
Apocynum cannabinum
Aquilegia canadensis
Arabis canadensis
Arabis laevigata
Aralia nudicaulis
Aralia racemosa
Arctium minus
Arenaria lateriflora
Arisaema dracontium
Arisaema triphyllum
Aronia melanocarpa
Asarum canadense
Asclepias exaltata
Asplenium rhizophyllum
Aster lanceolatus
Aster lateriflorus
Aster macrophyllus
Aster oolentangiensis
Aster sagittifolius
Aster shortii
Athyrium filix-femina
Aureolaria grandiflora
Berberis thunbergii
Betula alleghaniensis
Betula papyrifera
Bidens frondosus
Blephilia hirsuta
Boehmeria cylindrica
Botrychium multifidum
Botrychium virginianum
Brachyelytrum erectum
Bromus kalmii
Bromus pubescens
Calystegia spithamaea
Campanula americana
Campanula rotundifolia
Cardamine concatenata
Cardamine douglassii
Carex albursina
Carex plantaginea
Carex sp
Carpinus caroliniana
Carya cordiformis
Carya ovata
Caulophyllum thalictroides
Ceanothus americanus
Celastrus orbiculata
Celastrus scandens
Celtis occidentalis
Cerastium fontanum
Chelidonium majus
Chenopodium album
Chenopodium simplex
Chimaphila umbellata
Cinna arundinacea
Cinna latifolia
Circaea alpina
Circaea lutetiana
Cirsium altissimum
Cirsium arvense
Cirsium vulgare
Claytonia virginica
Clematis virginiana
Coeloglossum viride
Comandra umbellata
Conopholis americana
Convallaria majalis
Conyza canadensis
Corallorhiza maculata
Coreopsis palmata
Cornus alternifolia
Cornus racemosa
Cornus rugosa
Corylus americana
Crataegus sp
Cryptotaenia canadensis
Cuscuta gronovii
Cypripedium parviflorum
Cystopteris bulbifera
Cystopteris fragilis
Dactylis glomerata
Danthonia spicata
Daucus carota
Deparia acrostichoides
Desmodium cuspidatum
Desmodium glutinosum
Desmodium illinoense
Desmodium nudiflorum
Dicentra cucullaria
Diervilla lonicera
Dioscorea villosa
Diplazium pycnocarpon
Dirca palustris
Dodecatheon meadia
Dryopteris carthusiana
Dryopteris cristata
Dryopteris goldiana
Dryopteris marginalis
Duchesnea indica
Echinocystis lobata
Ellisia nyctelea
Elymus hystrix
Elymus villosus
Elymus virginicus
Enemion biternatum

Epifagus virginiana
Epilobium ciliatum
Epipactis helleborine
Equisetum arvense
Equisetum laevigatum
Erechtites hieracifolia
Erigeron annuus
Erigeron philadelphicus
Erigeron pulchellus
Erythronium albidum
Erythronium americanum
Euonymus alata
Euonymus atropurpurea
Euonymus europaea
Eupatorium purpureum
Eupatorium rugosum
Euphorbia corollata
Fagus grandifolia
Festuca subverticillata
Floerkea proserpinacoides
Fragaria virginiana
Fraxinus nigra
Fraxinus pennsylvanica
Fraxinus quadrangulata
Galearis spectabilis
Galium aparine
Galium boreale
Galium circaezans
Galium concinnum
Galium lanceolatum
Galium triflorum
Gaylussacia baccata
Geranium maculatum
Geum canadense
Glechoma hederacea
Glyceria striata
Goodyera pubescens
Hackelia virginiana
Hamamelis virginiana
Helianthemum canadense
Helianthus grosseserratus
Helianthus strumosus
Heracleum lanatum
Hesperis matronalis
Heuchera richardsonii
Hieracium kalmii
Hieracium scabrum
Hieracium sp
Humulus lupulus
Huperzia lucidula
Hydrastis canadensis
Hydrophyllum appendiculatum
Hydrophyllum virginianum
Hypericum perforatum
Ilex verticillata
Impatiens pallida
Jeffersonia diphylla
Juglans cinerea
Juglans nigra
Juncus tenuis
Juniperus virginiana
Krigia biflora
Lactuca biennis
Lactuca serriola
Laportea canadensis
Lathyrus ochroleucus
Lathyrus venosus
Leersia virginica
Leonurus cardiaca
Lespedeza capitata
Liatris aspera
Ligustrum vulgare
Lilium philadelphicum
Lithospermum canescens
Lithospermum latifolium
Lobelia inflata
Lobelia spicata
Lonicera canadensis
Lonicera reticulata
Lonicera x bella
Lupinus perennis
Lycopodium obscurum
Lysimachia ciliata
Lysimachia quadrifolia
Maianthemum canadense
Malus ioensis
Malus pumila
Matteuccia struthiopteris
Menispermum canadense
Milium effusum
Mitchella repens
Mitella diphylla
Monarda fistulosa
Monotropa uniflora
Morus alba
Muhlenbergia frondosa
Muhlenbergia schreberi
Oenothera biennis
Onoclea sensibilis
Orthilia secunda
Oryzopsis asperifolia
Oryzopsis pungens
Oryzopsis racemosa
Osmorhiza claytonii
Osmorhiza longistylis
Osmunda cinnamomea
Osmunda claytoniana
Ostrya virginiana
Oxalis stricta
Oxalis violacea
Panax quinquefolius
Panax trifolius
Panicum latifolium
Panicum xanthophysum
Parietaria pensylvanica
Parthenocissus vitacea
Pedicularis canadensis
Phalaris arundinacea
Phlox divaricata
Phryma leptostachya
Physalis virginiana
Physocarpus opulifolius
Phytolacca americana
Pilea pumila
Pinus strobus
Plantago major
Poa alsodes
Poa compressa
Poa pratensis
Podophyllum peltatum
Polemonium reptans
Polygala polygama
Polygonatum biflorum
Polygonatum pubescens
Polygonum persicaria
Polygonum scandens
Polygonum virginianum
Polymnia canadensis
Polypodium virginianum
Populus grandidentata
Populus tremuloides
Potentilla argentea
Potentilla norvegica
Potentilla simplex
Prenanthes alba
Prunella vulgaris
Prunus nigra
Prunus pumila
Prunus serotina
Prunus virginiana

Pteridium aquilinum
Pyrola elliptica
Quercus alba
Quercus macrocarpa
Quercus velutina
Quercus rubra
Ranunculus abortivus
Ranunculus fascicularis
Ranunculus hispidus
Ranunculus recurvatus
Ratibida pinnata
Rhamnus cathartica
Rhamnus frangula
Rhus glabra
Rhus hirta
Ribes americanum
Ribes missouriense
Robinia pseudoacacia
Rosa multiflora
Rosa sp
Rubus allegheniensis
Rubus idaeus
Rubus occidentalis
Rubus pubescens
Rubus sp
Rudbeckia hirta
Rudbeckia laciniata
Rumex crispus
Rumex obtusifolius
Salix sp
Sambucus canadensis
Sambucus racemosa
Sanguinaria canadensis
Sanicula gregaria
Sanicula marilandica
Schizachyrium scoparium
Scilla sibirica
Scrophularia marilandica
Scutellaria lateriflora
Setaria viridis
Silene stellata
Smilacina racemosa
Smilacina stellata
Smilax ecirrhata
Smilax herbacea
Smilax hispida
Solanum dulcamara
Solanum ptycanthum
Solidago canadensis
Solidago flexicaulis
Solidago gigantea
Solidago hispida
Solidago nemoralis
Solidago ulmifolia
Sorbus sp
Staphylea trifolia
Stellaria aquatica
Stellaria media
Symphoricarpos albus
Symplocarpus foetidus
Taenidia integerrima
Taraxacum officinale
Tephrosia virginiana
Thalictrum dasycarpum
Thalictrum dioicum
Thalictrum thalictroides
Thuja occidentalis
Tilia americana
Toxicodendron radicans
Tradescantia ohiensis
Trientalis borealis
Trillium cernuum
Trillium flexipes
Trillium grandiflorum
Trillium recurvatum
Triosteum perfoliatum
Tsuga canadensis
Ulmus americana
Urtica dioica
Uvularia grandiflora
Uvularia sessilifolia
Vaccinium angustifolium
Verbascum thapsus
Verbena urticifolia
Veronica serpyllifolia
Veronicastrum virginicum
Viburnum acerifolium
Viburnum dentatum
Viburnum lantana
Viburnum lentago
Viburnum opulus
Viburnum rafinesquianum
Vicia americana
Viola blanda
Viola canadensis
Viola labradorica
Viola macloskeyi
Viola pedata
Viola pubescens
Viola sororia
Vitis aestivalis
Vitis riparia
Zanthoxylum americanum
Zizia aurea

Appendix 3: Winners and Losers in 94 southern Wisconsin forests

We used the chi-squared approximation of the g-test for homogeneity to estimate changes in the frequency of individual species in the data set. We first calculated the global total frequency (sum of all frequencies in both time periods) and elimated all species with a global total < 25 observations. We also eliminated all taxa not present at at least 6 sites in either time period. Finally, we only report species that changed at least 105 in either direction. After applying these filters, all species examined showed statistically significant changes. This coarse filter approach is only meant to illustrate major trends. Further analysis is warranted in determining changes in abundance of individual species.

We have data in hand on % leaf N, digestabilty, specific leaf mass, maximum leaf height, dispersal mode, clonality, etc.). These data have not been fully analysed in the context of community structure in either time period or how such functional traits influence changes in total or relative abundance. Unfortunately, we haven’t had time to devote to these analyses and only present the raw data here. This alone gives strong insight into the functional traits driving reported changes. We expect winners to be shade tolerant, browse resistant or unpalatable, and good dispersers.

Trees

Changes in tree species is well outlined in chapter 1 (table 1). All oaks showed significant declines in abundance while shade tolerant and fire sensitive species showed conspicuous increases. Oak decline is well underway across the region and easily captured by our work.

Shrubs

There were 16 species that showed significant declines in abundance while only 11 species showed gains, including 3 exotics (table 2). Loser shrubs tend to be associated with oak savanna , oak opening and early successional forests vegetation and thus tend to be fairly shade intolerant. Winners are exotics (inevitably) and native shrub that are shade tolerant and exhibit strong clonal growth forms (*Ribes spp, Prunus virginiana, Parthenocissus spp.*).

Herbs

For herbaceous species, there were 60 specis with significant declines in species abundance while 19 withh significant increases (figure 3). Some of the biggest losers in terms of percent change are left over savanna elements like *Aster shortii, Apocynum androsaemifolium and Helianthus strumosus.* The role of succession is also evident in these forests with strong declines in narrow leaved (*Carex spp. and Gallium)* and thick leaved taxa (*Aster macrophyllus, Sanguinaria canadensis, Desmodium glutinosa)*. Of species that have gained the advantage, *Arisaema triphyllum* more than tripled in abundance, joining *Parthenocissus spp, Prunus virginiana, Circea luteiana, Geum canadense, Ribes missouriensis* and the new-comer *Allilaria petiolata* to become the main dominants in these forests.

Table 1: Data are total frequency out of 80 trees/samplesummed over 94 sites (> 5 df)

Tree Species	**1950**	**2005**	**%change**	**Gtotal**	**df**
Losers					
Juglans cinerea	54	19	-0.65	61.8522	30
Quercus rubra	1581	709	-0.55	805.461	79
Quercus alba	1596	821	-0.49	674.623	84
Quercus velutina	418	220	-0.47	164.562	14
Fagus grandifolia	88	57	-0.35	26.543	7
Populus grandidentata	83	73	-0.12	129.37	40
Ulmus rubra	475	432	-0.09	336.107	77
Quercus macrocarpa	122	115	-0.06	83.7235	35
Ostrya virginiana	310	301	-0.03	229.413	63
Winners	**1950**	**2005**	**%change**	**Gtotal**	**df**
Celtis occidentalis	3	94	30.33	105.093	22
Acer platanoides	0	29	29	31.4667	6
Acer negundo	4	109	26.25	118.429	32
Acer rubrum	82	274	2.34	243.495	39
Ulmus americana	125	312	1.50	289.503	76
Carya cordiformis	137	294	1.15	171.268	52
Prunus serotina	235	456	0.94	294.536	78
Acer saccharum	940	1689	0.80	686.122	63
Fraxinus pennsylvanica	199	286	0.44	208.707	49
Carya ovata	243	295	0.21	134.097	53
Tilia americana	598	693	0.16	334.684	74
Juglans nigra	104	120	0.15	98.9178	37

Table 2: Data are total frequency out of 20 quadrats/ site summed over 94 sites (> 5 df & more than 25 observations), change > 10%

Shrub Losers	**1950**	**2005**	**%Change**	**Gtot**	**df**
Rosa sp	43	2	-0.95349	148.4	31
Crataegus sp	89	10	-0.88764	301.2	35
Celastrus scandens	128	20	-0.84375	421.6	52
Carpinus caroliniana	49	8	-0.83673	141.5	17
Cornus rugosa	36	9	-0.75	123	25
Corylus americana	228	61	-0.73246	468.4	59
Viburnum acerifolium	47	16	-0.65957	142.4	21
Viburnum rafinesquianum	34	13	-0.61765	101.5	24
Gaylussacia baccata	23	9	-0.6087	57.27	2
Lonicera reticulata	53	21	-0.60377	114.8	43
Rubus idaeus	134	60	-0.55224	312.4	52
Cornus racemosa	279	146	-0.4767	530.5	74
Vitis riparia	116	73	-0.37069	215	77
Toxicodendron radicans	152	99	-0.34868	341.6	75
Zanthoxylum americanum	91	60	-0.34066	299.4	48
Smilax ecirrhata	82	66	-0.19512	190.3	71

Shrub Winners	**1950**	**2005**	**%Change**	**Gtot**	**df**
Rhamnus cathartica*	0	103	103	145.02	43
Viburnum opulus*	1	41	40	46.269	25
Lonicera x bella*	7	37	4.285714	34.626	34
Viburnum lentago	11	39	2.545455	72.888	50
Ribes cynosbatii	87	279	2.206897	284.24	83
Rubus occidentalis	59	150	1.542373	184.88	74
Ribes americanum	14	34	1.428571	58.679	31
Smilax hispida	10	19	0.9	46.052	24
Parthenocissus vitacea	520	704	0.353846	609.46	93
Sambucus racemosa	12	16	0.333333	44.782	41
Prunus virginiana	224	252	0.125	248.34	89

Table 3: Herb Winners & Losers based on total observations in either time period (94 sites, 20 quads at each. Data are pruned such that total global observations > 25, df > 5 and % change > 15%.

Herb Winners	1950	2005	%Change	Gtot	df
Alliaria petiolata	0	272	272	730	42
Aster lateriflorus	3	87	28	125	42
Taraxacum officinale	6	43	6.166667	57	48
Pilea pumila	18	124	5.888889	259	48
Polygonum virginianum	7	44	5.285714	43	27
Festuca subverticillata	8	34	3.25	49.6	31
Hackelia virginiana	14	51	2.642857	98.6	45
Ranunculus recurvatus	11	40	2.636364	57.4	42
Geum canadense	121	384	2.173554	451	88
Asarum canadense	11	34	2.090909	16.6	11
Arisaema triphyllum	276	610	1.210145	772	85
Laportea canadensis	41	87	1.121951	128	30
Dryopteris carthusiana	11	21	0.909091	52.2	21
Eupatorium rugosum	37	68	0.837838	168	36
Circaea lutetiana	511	881	0.72407	654	93
Cryptotaenia canadensis	81	133	0.641975	447	49
Caulophyllum thalictroides	54	71	0.314815	123	55
Solidago flexicaulis	69	89	0.289855	146	40
Athyrium filix-femina	98	117	0.193878	154	65

Herb Losers	1950	2005	%Change	Gtot	df
Aster shortii	91	3	-0.967	345.53	32
Galium boreale	55	3	-0.945	190.17	14
Fragaria virginiana	99	7	-0.929	355.20	49
Apocynum androsaemifolium	42	3	-0.929	135.69	27
Helianthus strumosus	96	11	-0.885	314.34	36
Potentilla simplex	57	7	-0.877	192.08	34
Aster macrophyllus	109	14	-0.872	344.02	25
Galium concinnum	394	58	-0.853	1272.34	71
Parietaria pensylvanica	66	10	-0.848	235.46	29
Lysimachia quadrifolia	25	4	-0.840	93.89	12
Solidago canadensis	30	5	-0.833	116.99	19
Solidago ulmifolia	135	24	-0.822	513.97	43
Prenanthes alba	64	12	-0.813	201.98	40
Pyrola elliptica	53	10	-0.811	167.87	30
Lactuca canadensis	30	7	-0.767	121.54	27
Sanguinaria canadensis	240	57	-0.763	600.55	59
Pteridium aquilinum	110	27	-0.755	265.56	30
Botrychium virginianum	120	30	-0.750	445.41	63
Agrimonia gryposepala	22	6	-0.727	84.27	30
Polygonatum pubescens	108	31	-0.713	375.58	36

Herb Losers	1950	2005	%Change	Gtot	df
Anemone quinquefolia	125	38	-0.696	405.13	56
Aster sagittifolius	85	26	-0.694	312.98	50
Aralia nudicaulis	186	59	-0.683	545.77	52
Carex albursina	59	19	-0.678	181.45	22
Desmodium nudiflorum	69	24	-0.652	158.97	21
Phlox divaricata	28	10	-0.643	83.98	10
Brachyelytrum erectum	73	29	-0.603	162.68	39
Thalictrum thalictroides	47	20	-0.574	118.69	14
Viola sororia	202	86	-0.574	526.29	78
Carex sp	562	241	-0.571	908.72	93
Smilacina stellata	39	17	-0.564	115.93	23
Trillium flexipes	69	31	-0.551	219.74	28
Anemone americana	168	82	-0.512	576.39	33
Maianthemum canadense	59	29	-0.508	140.89	28
Aralia racemosa	24	12	-0.500	61.43	22
Amphicarpaea bracteata	337	174	-0.484	792.36	73
Podophyllum peltatum	176	92	-0.477	339.98	70
Trillium grandiflorum	62	33	-0.468	117.27	21
Sanicula marilandica	296	159	-0.463	1153.85	74
Phryma leptostachya	293	158	-0.461	1048.07	70
Cystopteris fragilis	37	21	-0.432	82.34	13
Viola pubescens	240	145	-0.396	764.03	67
Polygonatum biflorum	59	37	-0.373	140.21	51
Desmodium glutinosum	335	214	-0.361	819.87	66
Ranunculus hispidus	40	26	-0.350	74.86	35
Dioscorea villosa	55	36	-0.345	89.36	47
Osmorhiza claytonii	485	327	-0.326	1714.36	84
Adiantum pedatum	106	72	-0.321	213.96	48
Mitella diphylla	50	34	-0.320	158.01	18
Uvularia grandiflora	262	182	-0.305	421.49	66
Smilacina racemosa	573	416	-0.274	685.24	93
Galium triflorum	304	240	-0.211	848.77	75
Elymus hystrix	31	26	-0.161	103.95	38
Trillium recurvatum	44	37	-0.159	17.83	7
Osmunda claytoniana	32	27	-0.156	75.13	29
Thalictrum dioicum	150	128	-0.147	135.09	54
Actaea rubra	42	36	-0.143	80.44	53
Geranium maculatum	694	600	-0.135	496.84	90