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Fifty years of change in northern upland forest understories: Identity and traits of “winner” and “loser” plant species

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ABSTRACT

Resurveys of plant communities provide valuable information on changes in species composition over time and clues about how species respond to environmental change. We report results from resurveys of 62 upland forest stands in northern Wisconsin and the western Upper Peninsula of Michigan first surveyed around 1950. We identify plant species that have significantly increased or decreased in frequency in 1 m² quadrats (‘winners’ and ‘losers’) and evaluate the traits that distinguish these groups. Twenty-one winner species increased across sites (by 25–400%), while 21 loser species decreased (by 21–95%). Winners include both common, native species and five invading exotics. Many are grasses or sedges and most are abiotically pollinated or dispersed (e.g., *Carex*, which increased 286%). Losers are mostly rarer native forbs that rely on animals for pollination and/or dispersal. Losers appear sensitive to desiccation, anthropogenic disturbance, and/or herbivory by white-tailed deer (e.g., *Streptopus roseus*, which decreased 73%). Declines in loser species are heterogeneous and stochastic across sites whereas increases in winners are more uniform and deterministic. Increases in common widespread native species account for most of the community change we observe across sites. The fact that winners resist or tolerate deer herbivory while many losers are sensitive to deer suggests that deer may be a key driver of the shifts we observe in these forests.

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1. Introduction

As anthropogenic disturbances become more pervasive, a few species adapted to such disturbances tend to increase, becoming “winners,” while “loser” species sensitive to such disturbances tend to decline (McKinney and Lockwood, 1999). As common, disturbance-tolerant species increase in abundance and rarer disturbance-sensitive species decline, local diversity declines. If such anthropogenic disturbances are widespread, similar shifts in local diversity across sites will accumulate into a systematic trend across the region. Concomitantly, win-

ners tend to expand their geographic range while losers may contract (Baskin, 1998). These systematic shifts in local community composition result in “biotic homogenization”, a process driving losses in biodiversity across spatial scales (Brown, 1989; McKinney and Lockwood, 1999, 2001).

Most studies of biotic homogenization focus on gross regional scales to document declines in among-site diversity as species that are widely-tolerant and often exotic expand their range across countries or even continents, while local and restricted species decline or go extinct (Lockwood et al., 2000; Rahel, 2000; McKinney, 2004). Here, we instead investigate

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biotic homogenization on a smaller scale, examining 50-year changes in upland mesic forest understories across northern Wisconsin and the western Upper Peninsula of Michigan. Previous analyses of these data show that stands across the region are converging in composition (Rooney et al., 2004). Understory species richness has significantly declined while the mean similarity in species composition among sites has increased as specialist species decline and common habitat generalists increase.

What changes in species composition are driving this homogenization? Do 'winner' and 'loser' species display distinct sets of traits? We expect species with similar traits to respond similarly to systematic shifts in habitat conditions and disturbance regimes (Hobbs, 1997). Identifying traits associated with winner and loser species could therefore cast light on what mechanism(s) might be driving changes in these communities. Two recent historical studies of temperate plant communities found such associations. In their study of 54 prairie remnants in southern Wisconsin, Leach and Givnish (1996) documented large extinction rates (8–60%) over a 32–52-year period that were most pronounced at unburned sites and fell disproportionately on plants that were short, small-seeded, and nitrogen fixers. They interpreted these patterns as evidence that fire suppression is driving many of these losses. In the urbanized landscape around Auckland, New Zealand, Duncan and Young (2000) found that rare, short species (especially those in wetland, shrubland, or prairie vegetation) were more likely to decline than tall, common species. They concluded that habitat loss, shifts in disturbance, and the introduction of aggressive exotics all contributed to the declines they observed.

In this study, we first identify 50-year 'winner' and 'loser' species in the understories of upland forests in the Upper Great Lakes region. We then assess the degree to which these winners and losers differ with regard to several functional traits (e.g., height, modes of pollination and dispersal, growth form) and whether these differences match our a priori predictions. We then use multivariate statistics to summarize these differences and explore how independently these traits act to distinguish winners from losers. Finally, we assess what these associations suggest regarding the potential mechanisms driving ecological change in the region.

1.1. Background

Human activity over the last 150 years has dramatically altered the forests in the Upper Great Lakes region. Before European settlement, most of the landscape was a matrix of primary forest with mixed hardwoods dominating mesic sites and large tracts of white pine and red pine (*Pinus strobus* and *Pinus resinosa*) on sandier, more xeric sites (Brown and Curtis, 1952). Between 1880 and 1920, these forests were mostly cleared. Current forests in the region are younger and often even-aged, reflecting regular timber harvests (Frelich and Lorimer, 1991; Alverson et al., 1994; Whitney, 1994). This logging represents a significant departure from the primarily small-scale wind- or ice-driven disturbances that dominated the landscape previously. Herbaceous species typical of mature forests often recover or re-invade slowly following disturbance as they often have limited dispersal capability,

sensitive germination requirements, slow vegetative spread, and/or low rates of growth and reproduction (Beattie and Culver, 1981; Bierzychudek, 1982; Duffy and Meier, 1992; Matlock, 1994; Ruben et al., 1999). Logging typically brings soil compaction, soaring light intensities, and moisture stress. Such disturbances usually decimate sensitive native herbs or reduce populations of the mutualist mycorrhizae, pollinator, or disperser species they depend on. In contrast, such disturbances enhance the invasion and population growth of many weedier species with effective dispersal and broad physiological tolerance (Meier et al., 1995).

Upper Great Lakes forests have also experienced dramatic fluctuations in dominant herbivore and predator populations. Following European settlement, white-tailed deer (*Odocoileus virginianus*) populations declined greatly due to over-harvesting, but then rebounded sharply in the 20th century in response to favorable habitat conditions and restrictions on hunting (Leopold et al., 1947). Pre-settlement deer populations were probably 2–4 deer/km² (McCabe and McCabe, 1984), but densities now average 6–15 deer/km² across most of the region (Wisconsin DNR, 2005). The extirpation of elk (*Cervus elaphus*), woodland bison (*Bison bison athabasca*), moose (*Alces alces*), cougar (*Felis concolor*) and wolf (*Canis lupus*) populations by the early 20th century eliminated all natural predators and competitors for deer. Wolves re-colonized parts of northern Wisconsin beginning in the 1980s, but their populations (~354 individuals, Wisconsin DNR, 2003) remain far below historical levels. Nevertheless, wolf packs now appear to be re-asserting at least local effects on deer densities and sensitive plants (Anderson et al., in review).

Deer herbivory can strongly affect understory plant communities (Waller and Alverson, 1997; Côté et al., 2004). Up to 87% of the spring and summer diet of white-tailed deer in northern Wisconsin is composed of herbaceous species (McCaffery et al., 1974). Herbs may be particularly vulnerable to deer as they never outgrow browsing impacts. Among herbs, grasses and sedges (graminoids) tolerate grazing better than forbs (non-graminoid flowering herbs) because their low intercalary meristems remain protected even as blades are consumed. Severely depressed reproductive and growth rates in many understory forbs have been recorded in areas with high deer densities (Anderson, 1994; Augustine and Frelich, 1998). Populations of many understory herbs appear slow to recover from these impacts (Balgooyen and Waller, 1995; Webster et al., 2005; D. Flaspohler, pers. commun.).

2. Methods

2.1. Field sites and sampling

To document historical changes in understory plant species abundances, we resurveyed 62 northern upland forest understories distributed across northern Wisconsin and the western Upper Peninsula of Michigan (Fig. 1). These stands were initially surveyed between 1948 and 1951 (Curtis, 1959; Rooney et al., 2004). These forests are dominated by *P. strobus* (white pine), *Tsuga canadensis* (hemlock), and/or *Acer saccharum* (sugar maple). *Acer rubrum* (red maple), *A. saccharum*, *P. strobus*, *Quercus rubra* (white oak), and/or *T. canadensis* comprise >67% of

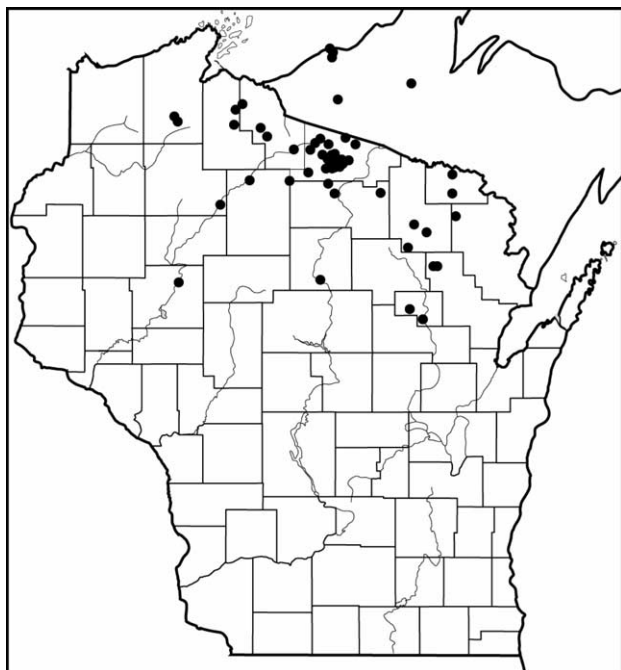


Fig. 1 – Map showing study site locations in Northern Wisconsin and the western Upper Peninsula of Michigan.

their basal area. To minimize stand heterogeneity due to different soils or geomorphology, we restricted sites to three sub-sections (3, 5, and 6) of one ecological section (Northern Highlands, IX) as classified under the regional Ecological Classification System (Albert, 1995). All sites included in the study were forested, not cut in the last five years (although some were partially-logged since 1950), and >3 ha. Five sites from the 1950 survey were disqualified by these criteria.

In May and June of 2000–2001, we relocated each study stand using information from the original study sheets including Section/Township/Range coordinates, detailed site maps, and descriptions of local landmarks, forest cover, and stand topography. These efforts usually put us within 200 m of the original sampled site. As the original surveys avoided plot-based methods and permanent quadrats, we were unable to match exact quadrat locations. Nevertheless, by sampling many more quadrats than in the original survey and by surveying 62 sites, we feel confident that the inferences drawn here regarding regional change are reliable.

To sample the understory vegetation of a stand, we placed three 20 × 20 m cells spaced 20 m apart at least 50 m from the road (to eliminate any edge effects; Euskirchen et al., 2001), avoiding wet depressions, logging roads, and trails that cut through the survey area. Initial transect placement and direction were random. We then recorded the presence of each understory species along six 20 m long strips of adjacent 1 m² quadrats located along two adjacent edges of each cell. This provided 6 × 20 = 120 quadrats per site. The original researchers recorded presence/absence data for only 20 of these 1 m² quadrats per site and these were spaced ~6 m apart along a large U-shaped transect. Our sampling method resembles the historic method in characterizing approximately 0.25 ha but is six times more intensive than the original survey to ensure

detection of rarer species in 2000. Sub-sampling every sixth quadrat from our more intensive sample mirrors the original intensity and dispersion of the herb quadrats sampled in the historic survey. All stands were revisited in August of the same year to check taxonomic identifications of late summer species. Spring ephemeral species (herbs with leaves that emerge in April/May but senesce before canopy closure) are not included in our analyses as neither survey sampled reliably for these. We follow authorities and nomenclature given in Wetter and Cochrane (2001). Rooney et al. (2004) provide fuller descriptions of local climate, the sites, and survey methods.

2.2. Identification of winners and losers

To identify the significant winners and losers in Upper Great Lakes understories over the 50-year period, we used replicated G-tests for goodness of fit (Sokal and Rohlf, 1981). These test the null hypothesis that the proportion of quadrats occupied by each species did not change over time. Using sites as replicates, we calculated G_{total} , G_{pooled} , and $G_{heterogeneity}$ test-statistics for each understory species to determine if shifts in quadrat frequency over time are significant across sites and consistent in direction and magnitude. We used G-tests because they are non-parametric and have an additive property, allowing one to sum the effects of species' changes in frequency across sites. We use the sum of individual G-statistics from all sites (G_{total}) to test for cumulative changes in quadrat frequency in either direction across sites. The G_{pooled} test-statistic, based on the sum of quadrats occupied by a species at each sampling period across all sites, tests for overall net increases or decreases in quadrat frequency. This statistic can detect regional shifts in frequency even if shifts within sites lack significance. Finally, the $G_{heterogeneity}$ test-statistic ($G_{total} - G_{pooled}$) determines whether species' shifts in frequency are consistent across sites.

To ensure biological as well as statistical significance, we limit our replicated G-tests to species present in at least two sites and 45 quadrats sampled in either sampling period. We also restrict our analyses to species that increased or decreased by at least 20% relative to their initial frequency in 1950. These criteria limited the G-test analyses to 73 of the original 175 understory species. Tree seedlings and saplings were excluded. We used Holm's (1979) correction at $p < 0.05$ to account for any spurious inflation of Type I errors due to repetitive G-test analyses. We classify species as "winners" or "losers" only if their changes in quadrat frequency were large and consistent enough to make both G_{total} and G_{pooled} significant. We further classify winners as "invaders" if they were absent from the original survey. Species that did not significantly change in quadrat frequency by our G-test criteria are "no change" species. Finally, to test whether species classified as winners and losers differ in how predictable their shifts are among sites, we calculated proportional heterogeneities ($G_{heterogeneity}/G_{total}$) for all significant winners and losers and applied a two sample t test to compare these two groups.

2.3. Community dynamics

Biotic homogenization, the increase in biological similarity among communities, is not synonymous with declines in

species richness (Olden and Rooney, 2006). Homogenization can arise from species invasion, species extinction, or both and can either increase or decrease species richness (Rahel, 2000; Olden and Poff, 2004). In these forest plant communities, stands that gained the most species over the last 50 years increased in similarity to other stands (Rooney et al., 2004). To test whether and how increases in winners and declines in losers are correlated with changes in local species density, we applied two simple regression analyses. Our response variable was change in species density at site k at the 20 m² scale:

$$\Delta S_k = S_{2000k} - S_{1950k},$$

where S_{2000k} is species density in the 2000 survey and S_{1950k} is species density in the historical survey. Because our sampling in 2000 was 6x more intensive than the historical survey, we standardized S_{2000k} to 20 m² using a passive sampling algorithm (Gotelli and Graves, 1996; Rooney et al., 2004). Our predictor variable was change in the relative frequency of losers or winners at site k across all 62 sites. We define change in relative frequency of losers at site k as $\Delta R_{k, \text{losers}} = R_{2000k, \text{losers}} - R_{1950k, \text{losers}}$, where

$$R_{1950k, \text{losers}} = \frac{\text{(the total \# of quadrats occupied by losing species at site } k \text{ in 1950)}}{\text{(the total \# of quadrats occupied by all species at site } k \text{ in 1950)}}$$

with similar definitions for $R_{1950k, \text{winners}}$, $R_{2000k, \text{losers}}$, and $R_{2000k, \text{winners}}$.

We also tested whether the homogenization process followed Hubbell's (2001) zero sum model assumption where local increases in the abundance of some species are accompanied by corresponding decreases in the abundance of others. Under this assumption, sites with greater increases in winners should also have greater decreases in losers. We tested this prediction by regressing change in the relative frequency of winners ($\Delta R_{k, \text{winners}}$) against change in the relative frequency of losers ($\Delta R_{k, \text{losers}}$) across sites, k .

2.4. Do species attributes affect population changes?

Before identifying significant winners and losers, we categorized species as to species traits primarily using morphological information from floras (Fernald, 1970; Gleason and Cronquist, 1991; Voss, 1996). We test whether particular attributes predispose species to decline or increase according to the following a priori predictions:

- (1) *Native/exotic status.* Successful exotics tolerate a wide range of conditions and disperse widely, often with human assistance. Such traits allow them to invade and establish in new areas, especially disturbed habitats (Hobbs and Mooney, 1998). We therefore classified all 73 species as either native or exotic to the Upper Great Lakes ecoregion. On average, we expect native species to have declined and exotics to have increased over the past 50 years.
- (2) *Pollination and dispersal mode.* We predicted that winners would be abiotically pollinated and dispersed, primarily by wind, as such traits allow reproductive success even

in disturbed environments or those lacking adequate populations of pollinating and dispersing animals (Bond, 1994; Buchmann and Nabhan, 1996). Alternatively, showy flowers or fruits could serve as 'flags' to make biotically pollinated and dispersed species more conspicuous to browsing deer (Anderson, 1994; Augustine and Frelich, 1998). We therefore classified understory species as to whether they were abiotically or biotically pollinated and dispersed based on the structure of their reproductive organs.

- (3) *Vagility.* Metapopulation theory suggests that species with restricted seed dispersal will be more vulnerable to extinction than vagile plants with efficient wide dispersal (Hanski and Gilpin, 1991). We expect plants with efficient dispersal to easily colonize new habitat and "rescue" isolated subpopulations from extinction (Brown and Kodric-Brown, 1977). We classified species as either long or short distance dispersers based on the structure of their fruits. Long distance dispersers are conspicuously adapted for wind or animal dispersal, while short distance dispersers are adapted for ant or gravity dispersal. We predict win-

ners to be more adapted for long distance dispersal than losers.

- (4) *Vegetative height.* Leach and Givnish (1996) and Duncan and Young (2000) both found taller plants to have lower probabilities of extinction than shorter plants in open environments. We therefore predicted that tall species would be favored over short species for their superior competitive abilities in disturbed landscapes. We grouped species into three height classes based on their average shoot height (<20 cm; 20–40 cm; >40 cm).
- (5) *Growth form.* Herbaceous plants tolerate herbivory differently depending on their growth form. As a group, graminoids resist ungulate browsing well as they have the capacity to re-sprout vigorously from basal meristems. In contrast, many forbs are vulnerable to a single browsing event that can remove all reproductive and/or photosynthetic capacity for that year (Augustine, 1997). Although ferns do not necessarily tolerate herbivory well, deer usually avoid browsing on ferns (Gill, 1992; Rooney, 2001). We therefore classified understory species into three forage classes: forbs, graminoids, and ferns/fern allies. If deer herbivory drives understory change, we expect winners to be graminoids and ferns more often and losers to be forbs (Waller and Alverson, 1997; Rooney, 2001).
- (6) *Successional position.* Because many exotics and graminoids thrive in high light environments, increased light associated with disturbance from logging and/or roads might also favor these species over other plants. To test the hypothesis that winners are associated with high light environments and losers with low light conditions, we assigned all understory species a position on a synthetic axis of succession associated with early to late succes-

sional forest canopies. We constructed this synthetic axis using principal components analysis (PCA) of four canopy measurements taken from each stand in 2000: tree density, total basal area of trees, average basal area of the three largest trees, and average climax adaptation value (Curtis and McIntosh, 1951; Rooney et al., 2004). The values of this first PCA successional axis range from -2 to $+2$, with -2 representing early successional stands and $+2$ representing late successional stands. We computed a weighted average succession score for each understory species based on the forests within which it occurred:

$$SS_i = (\sum_k p_{ik}^* PCA_k) / p_i$$

where p_{ik} equals the total number of quadrats species i occupied in 2000 at site k , PCA_k is the PCA succession score for site k , and p_i equals the total number of quadrats occupied by species i across all sites in 2000 ($= \sum p_{ik}$). If frequent disturbances drive understory change, we predict winners should be associated with early successional forests and losers should be associated with late successional forest types.

2.5. Tests of species attribute predictions

To test whether winner, loser, and no change species differed in each of the four categorical traits, we applied two-way χ^2 tables to test for significant differences in the frequency of that attribute between winner, loser, and no change species. To test whether winner, loser, and no change species differed in their weighted average stage of succession, we used ANOVA to compare the PCA scores between the three groups.

Many species traits in our analysis are confounded. For example, all graminoids in this study are abiotically pollinated. Abiotic pollination could be associated with winner/loser status because of its indirect correlation with growth form. To account for such associations among traits, we performed multivariate tests using S-Plus (<http://www.insightful.com>). We used logistic regression with a step-wise, backwards elimination approach to evaluate which set of traits best distinguished between winner and loser groups. We entered all species traits that were initially significant by the above χ^2 or ANOVA tests into the initial analysis. In subsequent steps, we assessed the independent significance of each predictor variable by doing a χ^2 test on the change in deviance when it was added last to the combined model. We then eliminated the predictor with the least significance when it was added last to the model until all variables in the model were independently significant at $p < 0.05$. We also tested the significance of each variable when it was alone in the model, comparing these results to the χ^2 and ANOVA analyses.

3. Results

3.1. Significant winners and losers

We analyzed population changes in 73 species, accounting for 97.5% of the occurrences of all species present in 1950 and

97.1% of species occurrences in 2000. The replicated G-tests reveal 21 species to be significant “loser” species with declines ranging from 21% to 95% since 1950 (Fig. 2(a) and (b); see Appendix A for additional data). Except for two shrubs, one fern, and one lycopod, all losers are forbs (non-graminoid flowering herbs) with a diversity of habits and species traits. We similarly identified 21 “winner” species with increases that ranged from 25% to 400% (Fig. 3(a)–(c); see Appendix A for additional data). We consider eight of these 21 species to be “invaders” as they were not present in appreciable densities in 1950. The 31 remaining species showed no significant consistent changes in abundance (“no change” species).

Most losers (20 of 21) did not decline uniformly across sites. Rather, they declined precipitously at most sites while declining only slightly or not at all at others (as judged by $G_{\text{heterogeneity}}$). In contrast, eight of the 21 winners increased consistently across sites, including seven of the eight “invaders”. Thus, losers had higher average heterogeneity across sites (79%) than winners (47%) ($t = 3.72$, $df = 41$, $p < 0.001$). The 21 losers represent 14 plant families including the Caprifoliaceae, Liliaceae, Pyrolaceae, Rosaceae, and Rubiaceae (Table 1). Although these declining forbs are a heterogeneous group, all are native and most characterize pre-European settlement forests: *Aralia nudicaulis*, *Clintonia borealis*, *Circaea alpina*, *Cornus canadensis*, *Huperzia lucidula*, *Linnaea borealis*, *Mitchella repens*, *Mitella diphylla*, *Orthilia secunda*, *Osmorhiza claytonii*, *Pyrola rotundifolia*, *Streptopus roseus*, and *Uvularia sessilifolia* (Curtis, 1959). *S. roseus*, a native lily once common in mesic sites, declined 73% since 1950 and disappeared at 42% (22/53) of sites where it was initially present despite samples in 2000 that were 6× more intensive. It only appeared in two new sites at very low abundance. *Aster macrophyllus*, a dominant aster in pine sites, was the second most conspicuous loser, declining 51% across sites. Despite these heavy declines within and among sites, all losers remained present somewhere in the 2000 survey.

The 21 winners represent 13 plant families, including Cyperaceae, Dryopteridaceae, Liliaceae, and Poaceae (Table 1). Poaceae (a grass family) was the most common plant family, representing 33% of all winners. *Oryzopsis asperifolia* and *Schizachne purpurascens* were the two most abundant Poaceae in our study area. These species increased by 54% and 217%, respectively. The genus *Carex* (Cyperaceae), however, increased even more dramatically (286%). Regionally, *Carex* was present in 98% of our survey sites in 2000 versus 63% in 1950. *Carex* expanded locally as well, occurring in 48% of quadrats in 2000 vs. 20% in 1950. Among the 21 winners, there were eight new invaders, none of which were abundant enough to be detected in 1950. This group includes three exotic forbs (*Galeopsis tetrahit*, *Hieracium aurantiacum*, *Veronica officinalis*), two exotic grasses (*Poa nemoralis*, *Poa pratensis*), and three native grasses (*Cinna latifolia*, *Bromus kalmii*, *Poa saltuensis*) (Fig. 3(b)). As noted above, all of these except *G. tetrahit* increased uniformly across the sites where they were found. Among exotic invaders, *H. aurantiacum*, *V. officinalis*, and *G. tetrahit* were the most regionally ubiquitous, occurring in 47%, 31%, and 23% of the sites, respectively. *G. tetrahit* was also the most abundant exotic locally, occurring in an average of 17% of the quadrats sampled in sites where it was present. *P. pratensis* and *P. nemoralis*, grasses frequently used to seed

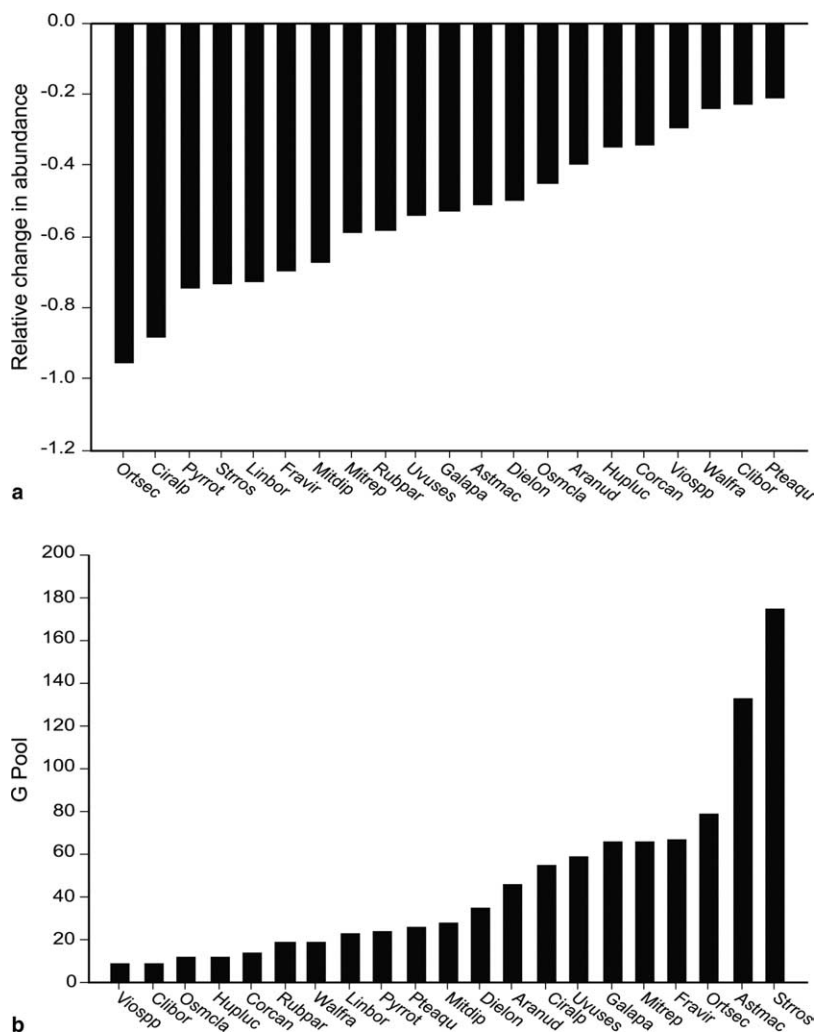


Fig. 2 – Population dynamics over 50 years for species identified as ‘losers’. (a) Change in quadrat frequency (1 m²) across all sites relative to 1950 for loser species. (b) Levels of significance (G_{pool} values) for losers. All losers are significant for heterogeneity across sites ($p < 0.05$), except *Orthilia secunda*. For full species names, see Table 1.

logging roads, also increased, occurring in 8% and 10% of the quadrats when present. Although the frequency of exotics at each site remains low, the number of sites where they are found has increased dramatically from one to 49 sites over the 50-year period.

3.2. Community dynamics

Local species density (per 20 m²) declined at sites with increases in winners and declines in losers. Although species density declined on average 18% across sites, changes within sites ranged from –71% to +151%. More sites lost species (65%) than gained species (35%). Winners appear to be displacing other species as declines in species density correspond more to increases in winners ($r^2 = 0.174$, $p = 0.001$) than declines in losers ($r^2 = 0.086$, $p = 0.020$). Increases in winners are also closely related to declines in losers across sites (Fig. 4), supporting Hubbell’s zero-sum assumption. The overall increase in the frequency of winners, however, exceeds the decline in losers (78% vs. 50%, respectively). Invaders account

for only about 12% of the increase in winners vs. 88% from native species present in the initial survey.

3.3. Do species attributes predict shifts in abundance?

Winner, loser, and no change species differ significantly in growth form, native/exotic status, and modes of pollination and dispersal (Fig. 5(a)–(d)). As predicted, winners are more likely to be graminoids, exotic, and abiotically pollinated and dispersed. In contrast, losers are more likely to be forbs, native, and biotically pollinated and dispersed. Most notably, no graminoids or exotics are losers yet many are winners (42% and 24%, respectively – Fig. 5(a) and (b)). Although ferns/fern allies did not significantly increase over the 50-year period, there were substantial increases in two common ferns: *Athyrium filix-femina* (400%) and *Dryopteris intermedia* (100%).

Abiotic pollination and dispersal are disproportionately common among winners. Half (52%) of winners are abiotically pollinated compared to 10% of losers (Fig. 5(c)). Similarly, 70%

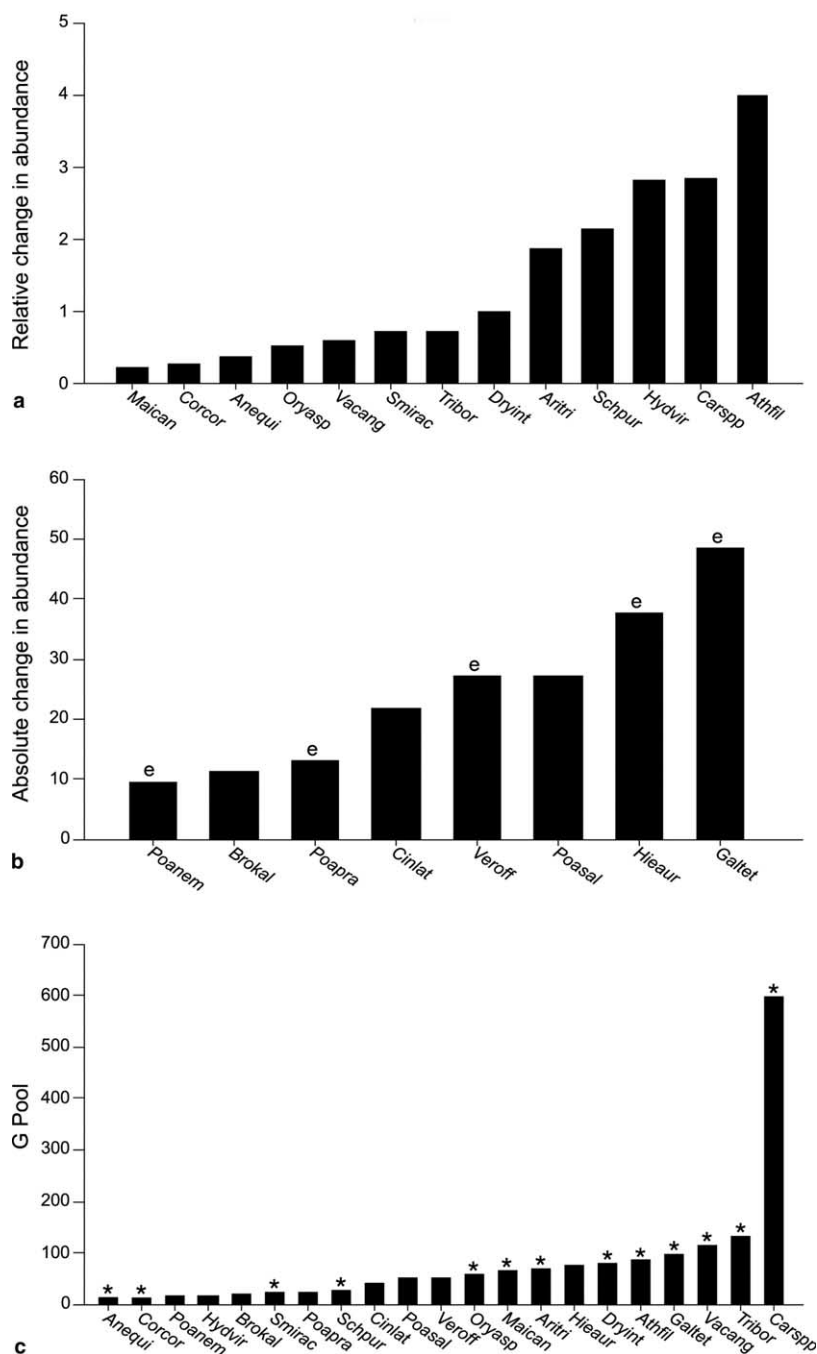


Fig. 3 – Population dynamics over 50 years for species identified as ‘winners’ or ‘invaders’. (a) Change in quadrat frequency (1 m²) across all sites relative to 1950 for winner species. (b) Absolute change in quadrat frequency for invader species (i.e., those not present in the initial survey). *e* denotes exotic species. (c) Levels of significance (*G*_{pool} values) for all winner and invader species. * Indicates significant heterogeneity across sites (*p* < 0.05). For full species names, see Table 1.

of winners are abiotically dispersed, compared to only 33% of losers (Fig. 5(d)). However, no significant differences exist between winner, loser, and no change species in vagility ($\chi^2 = 0.467$, *df* = 2, *p* = 0.792), vegetative height ($\chi^2 = 8.892$, *df* = 4, *p* = 0.299), or successional position (*SS* = 0.033, *df* = 2, *p* = 0.956). Thus, long and short distance dispersers, short and tall species, and early and late successional species have fared similarly over the last 50 years at these sites.

The multivariate logistic regression provides a test of the relative and combined importance of the four individually significant predictor variables: growth form, native/exotic status, pollination mode and dispersal mode. Growth form and native/exotic status emerge as the best predictors of understory change (Table 2), accounting together for 34% of the deviance in winner/loser status ($\chi^2 = 19.86$, *df* = 3, *p* < 0.001). Although all four variables are significantly associated with

Table 1 – Significant ‘winners’ and ‘losers’ in Upper Great Lakes understory communities as determined by replicated G-tests

Species name	Species code	Plant family	Native/exotic	Growth form	Pollination mode	Dispersal mode
Winners/Invaders						
<i>Anemone quinquefolia</i>	Anequi	Ranunculaceae	N	Forb	B	B
<i>Arisaema triphyllum</i>	Aritri	Araceae	N	Forb	B	B
<i>Athyrium filix-femina</i>	Athfil	Dryopteridaceae	N	Fern	A	A
<i>Bromus kalmii</i>	Brokal	Poaceae	N	Graminoid	A	A
<i>Carex</i> spp.*	Carspp	Cyperaceae	N	Graminoid	A	–
<i>Cinna latifolia</i>	Cinlat	Poaceae	N	Graminoid	A	A
<i>Corylus cornuta</i>	Corcor	Betulaceae	N	Shrub	A	B
<i>Dryopteris intermedia</i>	Dryint	Dryopteridaceae	N	Fern	A	A
<i>Galeopsis tetrahit</i>	Galtet	Lamiaceae	E	Forb	B	A
<i>Hieracium aurantiacum</i>	Hieaur	Asteraceae	E	Forb	B	A
<i>Hydrophyllum virginianum</i>	Hydvir	Hydrophyllaceae	N	Forb	B	A
<i>Maianthemum canadense</i>	Maican	Liliaceae	N	Forb	B	B
<i>Oryzopsis asperifolia</i>	Oryasp	Poaceae	N	Graminoid	A	A
<i>Poa nemoralis</i>	Poanem	Poaceae	E	Graminoid	A	A
<i>Poa pratensis</i>	Poapra	Poaceae	E	Graminoid	A	A
<i>Poa saltuensis</i>	Poasal	Poaceae	N	Graminoid	A	A
<i>Schizachne purpurascens</i>	Schpur	Poaceae	N	Graminoid	A	A
<i>Smilacina racemosa</i>	Smirac	Liliaceae	N	Forb	B	B
<i>Trientalis borealis</i>	Tribor	Primulaceae	N	Forb	B	A
<i>Vaccinium angustifolium</i>	Vacang	Ericaceae	N	Shrub	B	B
<i>Veronica officinalis</i>	Veroff	Scrophulariaceae	E	Forb	B	A
Losers						
<i>Aralia nudicaulis</i>	Aranud	Araliaceae	N	Forb	B	B
<i>Aster macrophyllum</i>	Asmac	Asteraceae	N	Forb	B	A
<i>Circaea alpina</i>	Ciralp	Onagraceae	N	Forb	B	B
<i>Clintonia borealis</i>	Clibor	Liliaceae	N	Forb	B	B
<i>Cornus canadensis</i>	Corcan	Cornaceae	N	Forb	B	B
<i>Diervilla lonicera</i>	Dielon	Caprifoliaceae	N	Shrub	B	A
<i>Fragaria virginiana</i>	Fravir	Rosaceae	N	Forb	B	B
<i>Galium aparine</i>	Galapa	Rubiaceae	N	Forb	B	B
<i>Huperzia lucidula</i>	Hupluc	Lycopodiaceae	N	Lycopod	A	A
<i>Linnaea borealis</i>	Linbor	Caprifoliaceae	N	Forb	B	B
<i>Mitchella repens</i>	Mitrep	Rubiaceae	N	Forb	B	B
<i>Mitella diphylla</i>	Mitdip	Saxifragaceae	N	Forb	B	A
<i>Orthilia secunda</i>	Ortsec	Pyrolaceae	N	Forb	B	A
<i>Osmorhiza claytonii</i>	Osmcla	Apiaceae	N	Forb	B	B
<i>Pteridium aquilinum</i>	Pteaqu	Dennstaedtiaceae	N	Fern	A	A
<i>Pyrola rotundifolia</i>	Pyrrot	Pyrolaceae	N	Forb	B	A
<i>Rubus parviflorus</i>	Rubpar	Rosaceae	N	Shrub	B	B
<i>Streptopus roseus</i>	Stros	Liliaceae	N	Forb	B	B
<i>Uvularia sessilifolia</i>	Uvuses	Liliaceae	N	Forb	B	B
<i>Viola</i> spp.*	Viospp	Violaceae	N	Forb	B	B
<i>Waldsteinia fragarioides</i>	Walfra	Rosaceae	N	Forb	B	B

Species information and trait assignments. Native/exotic: N= native, E=exotic; Pollination and Dispersal Mode: A = abiotic, B = biotic. *Carex and small violet species were lumped to genus as the original survey failed to distinguish different species reliably.

winner/loser status in separate models, pollination and dispersal mode fail to independently predict winner/loser status once growth form and native/exotic status are included in the model.

4. Discussion

Over the last 50 years, upland forest understories have shifted substantially in composition with marked increases in 21 ‘winner’ species and marked declines in 21 ‘loser’ species. However, the composition and dynamics of these two groups

are strikingly different. Several of the winners are native species that were already common and widespread in 1950 (e.g., *Arisaema triphyllum*, *A. filix-femina*, *Carex* spp. and *S. purpurascens*; Fig. 3(a) and (c)). Others are exotic invader species that were not present 50 years ago (e.g., *H. aurantiacum*, *V. officinalis* and some grasses; Fig. 3(b)). Although 38% of the winner species are invaders, invaders only represent 12% of the total increase in winner species. Grasses and sedges together represent a high proportion of the winners and invaders (38% and 63%, respectively). Loser species, in contrast, represent a heterogeneous group of 17 native forbs, two shrubs,

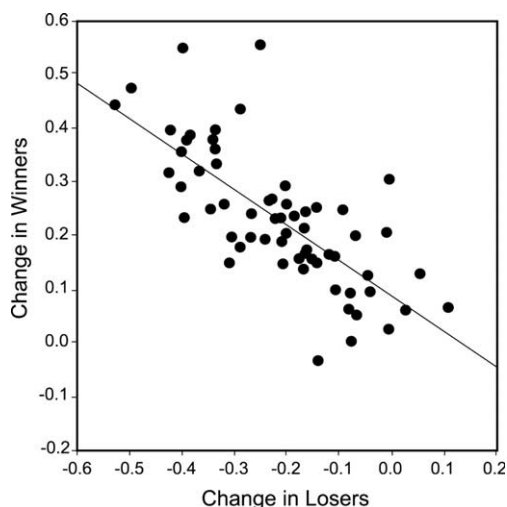


Fig. 4 – Test of Hubbell’s (2001) zero sum assumption. Changes in the relative frequency of winners at each site k ($\Delta R_{k, \text{winners}}$) are plotted against changes in the relative frequency of losers at the same site ($\Delta R_{k, \text{losers}}$). Regression: $y = -0.659x - 0.089$; $r^2 = 0.537$, $p = 0.000$, $N = 62$ sites.

one fern, and one *Lycopodium* distributed among 14 plant families (Table 1). Although heterogeneous, these declining species are all native and characteristic of pre-settlement forest understories (Curtis, 1959). Declines in species density (at 20 m²) reflect increases in winners more than declines in losers.

Thus, locally expanding populations of a few broadly-tolerant native species are associated with species losses and increased homogenization. In contrast, several previous studies emphasize invasions by weedy exotics as the mechanism driving homogenization (Lockwood et al., 2000; Rahel, 2000, 2002; Olden and Poff, 2003; McKinney, 2004). Exotics do not appear common enough in the interior forest plant communities we studied to drive species losses and homogenization. However, their influence seems likely to increase, particularly as lag periods often separate initial colonization from subsequent rapid population growth (Sakai et al., 2001). Continued monitoring of exotic population densities and impacts in these forests is important.

Despite these broad trends, we found considerable variability among sites. Several stands suffered no declines in species diversity (at 20 m²). Interestingly, increases appear more consistent than decreases. Eight of 21 winner species increased uniformly across sites, versus only one of 21 loser species. Such heterogeneity suggests that local environmental factors particularly influence local declines. Unfortunately, such patterns of species change would be invisible to managers monitoring composite indicators at other scales. Species richness, for example, remained stable at both the very local (1 m²) and regional (62 site) scales (Rooney et al., 2004).

Declines in losers mirror increases in winners (Fig. 4), supporting Hubbell’s (2001) zero-sum assumption that gains by some species come at the expense of other species. The persistence of rare species in the landscape even as they decline in abundance also fits predictions from Hubbell’s model

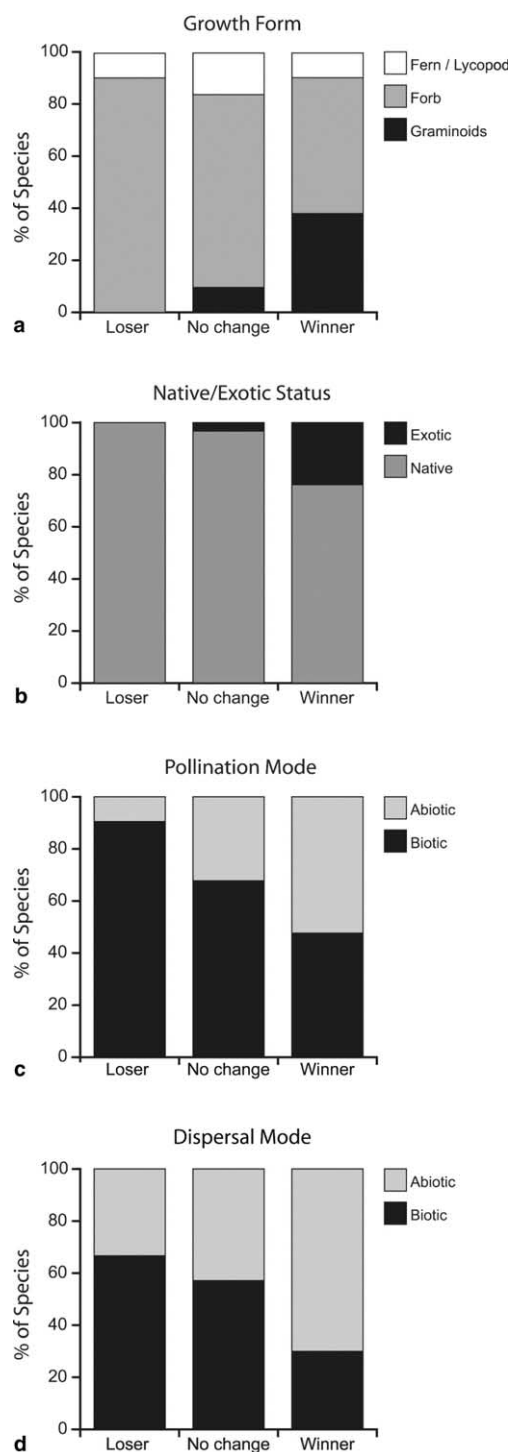


Fig. 5 – Proportion of ‘winner’, ‘loser’, and ‘no change’ species with various traits. (a) Differences in growth form between all groups ($\chi^2 = 13.90$, $df = 4$, $p = 0.008$) and between winners and losers only ($\chi^2 = 13.25$, $df = 2$, $p = 0.001$). (b) Differences in native/exotic status between all groups ($\chi^2 = 9.67$, $df = 2$, $p = 0.008$) and between winners and losers only ($\chi^2 = 7.61$, $df = 1$, $p = 0.006$). (c) Differences in pollination mode between all groups ($\chi^2 = 8.95$, $df = 2$, $p = 0.011$) and between winners and losers only ($\chi^2 = 9.70$, $df = 1$, $p = 0.002$). (d) Differences in dispersal mode between all groups ($\chi^2 = 5.99$, $df = 2$, $p = 0.05$) and between winners and losers only ($\chi^2 = 5.65$, $df = 1$, $p = 0.018$).

Table 2 – Analyses of how biotic variables influence the likelihood that a species increased or decreased significantly in abundance between 1950 and 2000

Variable	df	Alone	Full model	Step	Final model
Growth Form	2	11.84**	4.47	4.89	12.26**
Native/exotic	1	7.91**	5.49*	7.07**	6.61**
Pollination mode	1	8.64**	2.53	2.53	–
Dispersal mode	1	5.65*	0.01	–	–

Variables that were not significant were excluded one at a time from the analysis via backwards elimination. Values show the change in model deviance from adding each predictor variable to the logistic regression model one at a time (Alone), last into a model that included all other variables (Full model), or combined with variables significant ($p < 0.05$) by backwards elimination (Final Model). The significance of these changes was tested using χ^2 tests.

*** $p < 0.001$.
 ** $p \leq 0.01$.
 * $p < 0.05$.

where rare species decline but persist in the larger metacommunity while local dominants increase. Regional richness can eventually decline, of course, as more sites lose local populations of rare species.

Other studies of long-term changes in plant communities found changes similar to those we describe. Local species diversity is declining (Robinson et al., 1994; Drayton and Primack, 1996; Leach and Givnish, 1996; Rooney and Dress, 1997; Kwiatkowska, 1994; Fischer and Stöcklin, 1997; Duncan and Young, 2000). Exotics are increasing (Robinson et al., 1994; Drayton and Primack, 1996; Hobbs and Mooney, 1998). Increasing species are generally adapted to disturbances associated with human activity, including many graminoids and species with abiotic pollination or dispersal (Curtis, 1956; Daehler, 1998; McKinney and Lockwood, 1999). Species sensitive to such disturbances are declining (McKinney and Lockwood, 1999). Thus, the patterns we describe here resemble those found in other temperate zone areas.

4.1. Species traits and functional homogenization

In biological communities around the world, functionally similar and related species are replacing diverse groups of natives (McKinney and Lockwood, 1999). In understory plant communities in northern Wisconsin, graminoids with abiotic pollination and dispersal increasingly dominate sites once occupied by various forbs. These changes reflect functional as well as taxonomic homogenization. Functional homogenization has received little recognition (Olden et al., 2004) but has strong implications for ecosystem function, stability, and resilience (Diaz and Cabido, 2001; Sankaran and McNaughton, 1999; Stachowicz et al., 2002). Although this study did not specifically test for functional homogenization, the observed shifts in abundance toward species with similar traits suggest that it may be occurring.

In the combined logistic regression analysis (Table 2), growth form and native/exotic status most effectively distinguish winner from loser species. Modes of pollination and dispersal are alone significant but fail to retain significance once growth form and native/exotic status are included in the model. This suggests that these traits are confounded. Graminoids, for example, are abiotically pollinated and often

abiotically dispersed. Nevertheless, abiotic pollination and dispersal may still contribute to the overall success or vulnerability of species by improving colonization and persistence in disturbed habitats (Daehler, 1998). Conversely, biotic pollination and dispersal may limit some native plants (Bond, 1994; Buchmann and Nabhan, 1996). Regardless of whether pollination and dispersal modes are directly involved in plant declines, marked declines in species with conspicuous animal-visited flowers and fruits may alter biotic interactions in the region. Such declines could contribute to declines in animal mutualists dependent on flower and fruit resources (Kearns and Inouye, 1997), further restricting opportunities for pollination and dispersal and ultimately affecting ecosystem processes. Strategies used by many temperate plant species to compensate for pollinator/disperser limitation (e.g., generalist strategies, self-compatibility, and vegetative spread) may fail to compensate for long-term declines in mutualist visits, threatening the continued existence of these species (Spira, 2001).

Graminoid species were far more likely to increase over the past 50 years in northern Wisconsin than forbs, ferns, or lycophytes. Graminoids typify the characteristics found in many winners. They are abiotically pollinated, most are abiotically dispersed, and many are clonal or exotic. These traits may contribute to the success of graminoids seen in habitats around the globe (Heywood, 1989; Weber, 1997; Daehler, 1998; Pysek, 1998; McKinney and Lockwood, 1999). Their pendulant, wind pollinated flowers ensure reproductive success in recently disturbed and/or pollinator-poor environments. Their fruits are usually small enough to be easily dispersed by wind or on the wheels of vehicles. Once established in an area, they are competitive because many have vigorous clonal growth and tolerance for a range of environmental conditions.

4.2. Mechanisms of homogenization

What mechanisms are driving the changes we observe in Upper Great Lakes understories? Although logging and succession can affect both understory structure and composition, most of our stands have not been logged recently, and the ANOVA results give no indication that succession is driving these

changes. Early and late successional species are evenly represented among winners and losers, and the average successional state of the canopies at these sites has not changed over the past 50 years (Rooney et al., 2004). Let us therefore consider other potential mechanisms of understory change.

Fire suppression could have contributed to the community changes we observed. Fire was a dominant disturbance in pine forests of the region until 1900 (Whitney, 1994), and dry-forest loser species like *A. macrophyllum*, *Fragaria virginiana*, *Pteridium aquilinum*, and *Waldsteinia fragarioides* may have been more abundant in the 1950s due to this legacy of slash fires. Declines in these species could, therefore, reflect ecosystem recovery. Detailed analyses of stand histories might reveal further insights as to how fire affects these understories.

As noted above, declining populations of animal mutualists could threaten the persistence of biotically pollinated and/or dispersed species. Habitat alterations, introduced exotic species, and/or pesticide use all threaten populations of animal mutualists (Bond, 1994; Buchmann and Nabhan, 1996). Studies of how pollinator and disperser populations co-vary with pollen and dispersal limitation in understory species could test this hypothesis. However, the fact that pollination and dispersal mode lose significance once growth form and native/exotic status are included in multivariate models casts doubt on this hypothesis.

The recent invasion of European earthworms poses another threat to understory species (Hendrix and Bohlen, 2002; Callahan et al., 2003; Hale et al., 2005). Large exotic earthworms (lumbricids), in particular, appear to reduce the leaf litter layer, disrupt the rooting zone and modify the soil environment so as to reduce densities of tree seedlings and rarer herbs while favoring some invasive plants (Kourtev et al., 1999; Gundale, 2002). By shifting decomposer communities from fungal- to bacterial-based, earthworms could also displace species with strong mycorrhizal associations (Bohlen et al., 2004). Small, litter-dwelling losers like *A. nudicaulis*, *M. repens*, *O. secunda*, *S. roseus*, and *U. sessilifolia* may be vulnerable to these effects. In contrast, species adapted to disturbed environments lacking fungal communities may thrive. We observed marked increases in *A. triphyl- lum*, *Carex* spp., *O. asperifolia*, and many exotics, all of which characterize areas invaded by exotic earthworms (Kourtev et al., 1999; Hale, 2004). Further work on site-to-site variation in earthworm densities might reveal whether exotic earthworms are associated with declines or increases in particular species.

Several lines of evidence suggest that herbivory by deer is a major factor simplifying forest understories in the Upper Great Lakes. Deer densities and corresponding rates of herbivory have increased markedly in most of the region since the 1950s (Waller and Alverson, 1997). In addition, previous studies in temperate forests find that graminoids increase in areas with high deer herbivory while many forbs decline (Trumbull et al., 1989; Gill, 1992; Miller et al., 1992; Rooney and Dress, 1997; Rooney, 2001). Overabundant deer may also favor species with abiotic pollination and dispersal as large plants with conspicuous flowers or fruits are often grazed selectively (Allison, 1990; Anderson, 1994; Balgooyen and Waller, 1995;

Augustine and Frelich, 1998). Interestingly, we found the most conspicuous declines in biotically pollinated and dispersed species in areas that lack hunting (e.g., state parks – Rooney et al., 2004).

We face a number of potential mechanisms that could interact in complex ways. Browsing deer, for example, could be attracted to conspicuous flowers and fruits which they eat, contributing to declines in animal mutualists (Kearns and Inouye, 1997; Lamont et al., 1993). Thus, we cannot use the results of this observational study to determine exactly which forces are driving the changes we observe. Nevertheless, our results show clear and consistent patterns over many sites across a broad region. They also cast doubt on some of the more obvious mechanisms (like succession) while supporting other hypotheses (like deer herbivory). The associated syndromes of traits also link to the parallel literature that exists on traits associated with rarity (Rabinowitz et al., 1986; Fiedler and Ahouse, 1992; Gaston, 1994) and exotic invasives (Hobbs and Humphries, 1995; Hobbs and Mooney, 1998; Pysek, 1998).

5. Conclusions

Forest understories in the Upper Great Lakes region are undergoing substantial ecological change. Although we do not yet know just how various mechanisms interact to drive these changes, human activities appear directly or indirectly linked to many of these changes. These effects probably extend beyond community composition and diversity to include biotic interactions and ecosystem function. Although regional (γ) diversity in the Upper Great Lakes has remained stable over the last fifty years, sustained overbrowsing and other disturbances associated with human management of these forests may ultimately threaten regional diversity. As human activities spread and intensify, their cumulative effects could cause local extirpations to accumulate to the point where region-wide extinctions occur (Gilpin and Soule, 1986; Ehrlich and Daily, 1993; Hobbs and Mooney, 1998). Such disturbance-related effects appear to be accelerating in the region (Rooney et al., 2004). Rates of deer herbivory, in particular, have increased markedly since the 1950s. If these impacts continue to expand in the future, we predict that exotic invasions, species losses, and homogenization will accelerate.

The results of this study also demonstrate that quantitative, long-term, retrospective studies are essential if we are to detect and respond to ecological change. Most studies of homogenization are limited by the use of presence/absence data from individual sites to document colonization and extinction and to identify winner and loser species (Lockwood et al., 2000; Rahel, 2000; McKinney, 2002, 2004). Quantitative data from dispersed sites provide a fuller picture of ecological change by allowing us to identify more precisely winner and loser species and assess their local and regional shifts in abundance, (Collins et al., 2002; Olden and Poff, 2003; Waller and Rooney, 2004). Expansions of broadly tolerant natives and declines and local extirpations of species like *S. roseus* would go unnoticed without reliable baseline data and careful resurveys. To lift the veil on the 'invisible present' (Magnuson, 1990) and to generate the data needed to test alternative

drivers of change, ecologists will need to monitor in a more detailed, consistent, and sustained manner.

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Appendix A

Shifts in the local and regional abundance of ‘winner’ and ‘loser’ species over a 50-year period in Upper Great Lakes forest understory communities. Regional abundance is represented by ‘% of Sites Occupied’ and refers to the proportion of 62 sites at which that species occurred. Local abundance is reflected in the ‘Mean frequency’ values. These refer to the average percentage of 1 m² quadrats occupied by that species at sites where the species was present. ‘Total frequency’ refers to the % of quadrats occupied across the whole landscape. ‘–’ indicates that the species was not abundant enough to be detected in the 1950 survey. ⁺Carex and small violet species were lumped to genus as the original survey failed to distinguish different species reliably.

Species name	% of sites occupied (1950)	% of sites occupied (2000)	Mean frequency (1950) (%)	Mean frequency (2000) (%)	Total frequency (1950) (%)	Total frequency (2000) (%)
Winners/Invaders						
<i>Anemone quinquefolia</i>	42	75	17	15	9	12
<i>Arisaema triphyllum</i>	24	41	15	24	3	10
<i>Athyrium filix-femina</i>	15	68	11	11	2	8
<i>Bromus kalmii</i>	–	7	–	14	–	1
<i>Carex</i> spp. ⁺	63	98	20	48	12	47
<i>Cinna latifolia</i>	–	32	–	6	–	2
<i>Corylus cornuta</i>	61	58	20	48	15	19
<i>Dryopteris intermedia</i>	49	76	20	26	10	20
<i>Galeopsis tetrahit</i>	–	23	–	17	–	4
<i>Hieracium aurantiacum</i>	–	47	–	7	–	3
<i>Hydrophyllum virginianum</i>	2	2	15	50	<1	1
<i>Maianthemum canadense</i>	100	100	49	61	50	62
<i>Oryzopsis asperifolia</i>	61	85	32	36	20	30
<i>Poa nemoralis</i>	–	8	–	10	–	1
<i>Poa pratensis</i>	–	13	–	8	–	1
<i>Poa saltuensis</i>	–	44	–	5	–	2
<i>Schizachne purpurascens</i>	9	39	15	11	1	4
<i>Smilacina racemosa</i>	42	68	13	13	5	9
<i>Trientalis borealis</i>	78	92	28	42	22	38
<i>Vaccinium angustifolium</i>	22	32	27	31	6	10
<i>Veronica officinalis</i>	–	31	–	7	–	2
Losers						
<i>Aralia nudicaulis</i>	83	63	21	17	18	11
<i>Aster macrophyllum</i>	70	58	38	22	27	13
<i>Circaea alpina</i>	20	12	13	3	2	<1
<i>Clintonia borealis</i>	64	53	21	19	13	10
<i>Cornus canadensis</i>	41	25	21	22	8	5
<i>Diervilla lonicera</i>	37	41	20	9	8	4
<i>Fragaria virginiana</i>	31	27	19	8	7	2
<i>Galium aparine</i>	76	64	18	9	13	6
<i>Huperzia lucidula</i>	36	32	20	15	7	5
<i>Linnaea borealis</i>	20	15	10	4	2	1
<i>Mitchella repens</i>	53	32	14	10	9	4
<i>Mitella diphylla</i>	14	5	18	8	2	1
<i>Orthilia secunda</i>	5	8	7	2	3	<1
<i>Osmorhiza claytonii</i>	32	30	18	10	5	3
<i>Pteridium aquilinum</i>	54	51	47	42	26	21
<i>Pyrola rotundifolia</i>	24	14	7	3	2	1
<i>Rubus parviflorus</i>	9	7	32	17	3	1
<i>Streptopus roseus</i>	80	51	19	7	15	4
<i>Uvularia sessilifolia</i>	59	59	21	10	12	6
<i>Viola</i> spp. ⁺	83	63	9	12	10	7
<i>Waldsteinia fragarioides</i>	40	34	52	46	19	15

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