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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 m^2 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, winners 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/km^2 (McCabe and McCabe, 1984), but densities now average 6–15 deer/km^2 across most of the region (Wisconsin DNR, 2005). The extirpation of elk (*Cervus elaphus*), woodland bison (*Bison bison athabascae*), 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

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