

PLANT SPECIES CHANGE IN NORTHERN WISCONSIN  
WET-MESIC FOREST COMMUNITIES FROM 1952 TO 2005

by

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## Abstract

The northern wet-mesic forest community type (cedar swamp) is a unique component of the northern Great Lakes states landscape comprising approximately 810,000 hectares. These communities are considered regionally significant for a variety of reasons including contributions to deer wintering habitat, wildlife browse, Native American medicinal and ceremonial uses, as well as habitat for rare species of plants. Recent research on prairies, southern upland, and northern upland forest communities of Wisconsin has shown significant losses in native plant species, increases in exotic species, and an increase in similarity among communities over approximately the past 50 years. These changes may also be taking place within northern wet-mesic forest communities. In this research, quantitative data were used from a 1952 data set of 34 northern wet-mesic forest communities to examine changes in plant species abundance and to assess species gains and losses. I also looked at possible mechanisms of these changes. Field work was conducted May-July 2005 to determine understory and overstory plant species abundance at the 34 sites. Northern wet-mesic communities have not experienced a significant decline in native species and have experienced an increase in a few important plant species that define the community such as *Coptis trifolia* (goldthread) (150%), *Trientalis borealis* (starflower) (182%), and *Carex* spp. (sedges) (230%). Exotic species have significantly increased at most of the sites over the past 53 years, from 4 sites and 12 quadrats in 1952 to 20 sites and 121 quadrats in 2005 ( $\chi^2 = 16.485$ ,  $p < 0.0001$  and  $\chi^2 = 99.014$ ,  $p < 0.0001$ ). This increase in exotic species is a common and growing trend found throughout Wisconsin's plant communities that contributes directly to the degradation of these communities. It is therefore of great

importance to seek management practices that minimize impact to these unique communities and to set aside blocks of land to protect these areas from degradation.

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## INTRODUCTION

The northern wet-mesic community type (cedar swamp) is a unique component of the northern Great Lakes states' landscape, comprising approximately 810,000 hectares (Johnston, 1977). Northern white cedar, *Thuja occidentalis*, is the main overstory component of the northern wet-mesic community. Cedar is a long-lived (up to 400 years), slow-growing, shade-tolerant conifer that typically forms dense swamps on organic and calcium-rich mineral soils in low, poorly drained topography, although it can occasionally occur on well-drained upland sites (Habeck, 1958; Heitzman et al., 1999). Northern wet-mesic forests are considered regionally significant due to their contributions to water quality, timber production, deer wintering habitat, wildlife browse, Native American medicinal and ceremonial uses, as well as providing habitat for rare species of plants (Curtis, 1959; Johnston, 1977; Johnston, 1990; Meeker et al, 1993; Epstein et al., 1999). However, the regeneration of cedar is being adversely affected by a variety of site-specific factors, which include yearly variations in seed production, absence of rotting logs for successful seed regeneration, and increased deer herbivory (Curtis, 1959; Johnston, 1977; Johnston, 1990). Human influence has also altered the landscape in which cedar grows through fragmentation of habitat (e.g. road building, agriculture, and urban development), creating a more spatially heterogeneous landscape than in pre-settlement times (Wilcove et al., 1998; Brososke et al., 1999). As the health of cedar is jeopardized, so too may be the health of understory plant species that depend upon the cedar swamp and the habitat they provide. It is likely that the same factors adversely affecting cedar also affect the diversity of understory plants of this community. As an integrated ecosystem, northern wet-mesic forest communities are being affected by



a variety of factors that may lead to the alteration of these unique plant communities.

The purpose of this study is to examine the overstory and understory floral changes over 50 years, and possible mechanisms driving these changes, in the northern wet-mesic forest community of Wisconsin.

### Description of Northern Wet-Mesic Forests

Northern white cedar is the main overstory species within northern wet-mesic communities, and comprehension of its life history is rudimentary to understanding the wet-mesic ecosystem. Cedar is a monoecious tree that forms its male and female cones on separate branchlets, disperses pollen in the spring, and forms female cones that disperse seeds in early autumn (Johnston, 1990). Seed production in an average-sized cedar is approximately 60,000 to 260,000 seeds per year and occurs in large quantities after the tree reaches 30 years of age, with larger seed crops occurring at two to five year intervals (Johnston, 1990). Cedar seedlings establish more readily on moist substrates, especially rotting logs and stumps under ample light conditions (Curtis, 1959; Johnston, 1990). However, seedling establishment is constrained by drought and browsing, so maintenance of seedbed moisture as well as protection from browse are two of the most important factors in seedling survival (Curtis, 1959; Johnston, 1990). Cedar not only produces a large amount of seed, but it also has prolific vegetative reproduction on sites where moisture conditions are adequate (Johnston, 1990). At maturity, cedar averages 12-15 m in height and 30-60 cm in diameter with maximum dimensions reaching 30 m in height and 180 cm in diameter (Curtis, 1959; Johnston, 1990).

Northern wet-mesic forests are found throughout the Great Lakes region, in the eastern half of southern Canada and into the northeastern United States (Johnston, 1990). At northern wet-mesic forest sites, cedar typically forms dense clusters with canopy coverage that may reach 100 percent (Curtis, 1959). This dense foliar canopy tends to exclude other tree species. However, black ash (*Fraxinus nigra*) and balsam fir (*Abies balsamea*), the other major dominants of the northern wet-mesic community, become established in canopy gaps. Cedar may also be found growing in northern wet-mesic communities with an overstory mixture of black spruce (*Picea mariana*), tamarack (*Larix laricina*), eastern hemlock (*Tsuga canadensis*), red maple (*Acer rubrum*), balsam poplar (*Populus balsamifera*), yellow birch (*Betula alleghaniensis*), paper birch (*Betula papyrifera*), and white spruce (*Picea glauca*) (Curtis, 1959; Johnston, 1990; Van Deelen, 1999).

The total understory vascular flora of wet-mesic communities was recorded as 193 species by Curtis (1959). This flora includes a wide variety of plant groups such as club mosses (e.g. *Huperzia lucidula*), graminoids (e.g. the sedges *Carex disperma* and *C. trisperma*), ferns (*Osmunda cinnamomea*), ericaceous shrubs (e.g. *Ledum groenlandicum*), Canada yew (*Taxus canadensis*), native honeysuckles (*Lonicera* spp.), and members of the lily (e.g. *Maianthemum canadense*), composite (e.g. *Aster* spp.), rose (e.g. *Rubus pubescens*), and orchid (e.g., *Platanthera obtusata* and *Listera cordata*) families (Curtis, 1959; Van Deelen, 1999). According to Curtis' 1959 study, the three most abundant families in northern wet-mesic forests were the composite family (9.2%), lily family (6.1%), and sedge family (5.7%).

### Baseline Data and Historical Studies

Long-term baseline data are necessary to track historic shifts in species composition within ecosystems. Such data, however, are rare, resulting in a lack of documentation of important temporal changes (Magnuson, 1990). This could be used to study the interrelationships between a variety of factors, such as invasive flora and fauna as well as human exploitation, and their corresponding ecological consequences. In Wisconsin, we are fortunate that, in the 1950's, J. T. Curtis and colleagues of the Plant Ecology Laboratory at the University of Wisconsin-Madison performed a statewide vegetation survey of the geographic ranges, community composition, and vegetation-environment relationships of plant communities which provides baseline data for future studies. Utilizing data from such long-term studies, researchers may be able to develop a better understanding of the changes that are occurring in temperate zone ecosystems (Rooney et al., 2004).

In cases where dependable baseline data exist, there is evidence that non-native species are increasing and native species are in decline (Robinson et al., 1994; Drayton & Primack, 1996; Leach & Givnish, 1996; Fisher & Stöcklin, 1997; Rooney & Dress, 1997; McKinney & Lockwood, 1999; Duncan & Young, 2000; Rooney et al., 2004). This scenario could eventually produce homogenous ecosystems that contain a few widespread generalist species and fewer specialist species (McKinney & Lockwood, 1999). These changes may be further accelerated by human exploitation, which often drives ecological alterations such as habitat fragmentation, influx of invasive species, pollution, hydrological changes, and disruption of biotic interactions (Wilson, 1992; Wilcove et al., 1998; Sakai et al., 2001).

Researchers have recently utilized Curtis prairie, northern upland forest, and southern upland forest data sets to document temporal population and community level changes. For example, Leach & Givnish (1996) surveyed 54 prairie remnants in southern Wisconsin and found that 8-60% of the original plant species were lost since Curtis' surveys. Their study demonstrated that prairie plants that are short in stature, small-seeded, or nitrogen-fixing, and those plants growing in highly productive, very wet areas experienced the most significant overall losses. They also postulated that these patterns of loss in diversity were related to fire suppression and landscape fragmentation.

Similarly, Rooney et al. (2004) resurveyed 62 upland forest sites in northern Wisconsin and found an average decline of 18.5% in the number of native species at the 20 m<sup>2</sup> scale, a decrease in habitat specialists, and an increase in habitat generalists, accounting for an 8.7% increase in homogeneity among sites. Wiegmann & Waller (2006) also studied plant changes in northern upland forests by identifying understory species that have significantly increased as well as decreased. They also identified attributes for each species such as exotic/native status, pollination and dispersal mode, and growth form to test whether these attributes predispose a species to increase or decrease in abundance. Their study showed that exotic species, abiotically-pollinated and abiotically-dispersed species, and graminoid growth-form species are increasing in abundance, while native species, biotically-pollinated and dispersed species, and forb growth-form species are decreasing in abundance in northern upland forests. The most recent study to utilize the Curtis data to track environmental change was conducted on the southern upland forest community type by Rogers et al. (in prep.), who found a 33.6%

decrease in native species as well as increases in exotic species and habitat generalists from 1950 to 2000.

The four studies that have utilized the Curtis data for comparison have identified significant change in the examined communities. Based upon the magnitude of change that is occurring in these separate Wisconsin plant communities, northern wet-mesic forests may also be expected to exhibit a degree of change. Northern wet-mesic forests need to be examined in order to test for plant species community changes. Results may be utilized by resource managers with the goal of improving ecosystem health and sustainability.

### Dynamic Nature of Plant Communities

Plant communities are not static entities; rather they are constantly changing over time and across the landscape (Watt, 1947). In the northern Wisconsin landscape many natural communities have developed following natural disturbances of differing magnitude and duration, with human influence adding a greater number of possibilities for community change. The major factors that may cause important changes in northern wet-mesic plant communities are: (1) climate change, (2) range expansion, (3) succession, (4) land use changes, (5) timber harvest, (6) windstorms, (7) fire, (8) hydrological changes, (9) insect and plant disease, (10) ice and snow damage, (11) exotic species, (12) loss of biotic pollinators and dispersers, and (13) mammalian herbivory. The first three factors are long-term factors that do not rapidly affect a community or communities across a region. The last ten factors listed are individually capable of

triggering rapid changes in the species composition of a community; these factors often interact with one another causing rapid and major changes in the vegetation of a community.

#### Climate Change and Range Expansion

Landscape level changes are those which occur across a broad geographic area, such as northern Wisconsin. Examples of natural disturbance on this scale are climate change and the migration or range expansion of plant species. Over the past 850,000 years the climate has naturally oscillated approximately every 100,000 years between periods of glacial advance and glacial retreat. Since the end of the Wisconsin glaciation, approximately 12,000 years ago, average global temperatures have risen, peaking approximately 7,000 years ago, and then steadily declined over the last 7,000 years (Gurevitch et al., 2002). At this rate, the growth of glaciers could be observed within the next few thousand years (Gurevitch et al., 2002). Shorter climatic fluctuations are typical of the time periods between glaciation. Most notable was a period known as the “Little Ice Age” between 1500-1850, in which cold temperatures, glacial advances, and low solar activity were observed (Gurevitch et al., 2002). These climatic changes affect the presence of plant species across a landscape over a fairly long time scale; however some plant species may be affected by brief periods of cold temperatures over a few hundred years. This type of climate change affects the rate of migration of species, allowing for new species to move into an area where they have the potential to alter the flora in a community or region.

Although natural patterns of climate change are progressing toward another ice age, anthropogenic sources of climate change currently overshadow those natural

changes, resulting in a mean increase in global temperature. Human activities such as energy use, urbanization and land use changes, are the primary sources of global climate change (Karl & Trenberth, 2003). The increase in the amount of carbon dioxide and other greenhouse gases such as methane and nitrous oxide in the earth's atmosphere, secondary to human activities, has led to current concerns about climatic change and global warming (Barnes et al., 1998). Carbon dioxide has increased 31% since pre-industrial times from 280 parts per million by volume (ppmv) to greater than 370 ppmv today, with half of that increase occurring from 1965 to the present (Karl & Trenberth, 2003). This increase in atmospheric carbon dioxide, along with other greenhouse gases, traps outgoing radiation from earth to space, increasing temperature on the magnitude of 0.5°C since 1800 with a 0.27° to 0.39°C increase since 1900 (Barnes et al., 1998; Karl & Trenberth, 2003). Arrhenius, a Swedish scientist, predicted that a doubling of the earth's atmospheric carbon dioxide level could warm the planet by 5°C (9°F) (Ramanathan, 1988).

Determining changes in atmospheric carbon levels is only part of climate change. Identifying the shifts in the sources and sinks of carbon is also important (Barnes et al., 1998). For example, temperate peatlands across the globe, which are characterized by *Sphagnum* spp. (bog mosses), cover 3.46 million hectares globally (Gorham, 1991), contain approximately 455 gigaton (Gt.) of carbon, and are a large sink for atmospheric carbon (Moore, 2002). According to Moore (2002), this amount of carbon is close to the amount of carbon stored in all living things on earth. Most of this carbon is stored in the living and dead tissue of *Sphagnum* species (Clymo & Hayward, 1982). Increased global temperature and carbon dioxide levels will enhance *Sphagnum* productivity, and result in

faster decomposition rates (Moore, 2002). When coupled with changing patterns of precipitation (i.e. warmer, drier summers and milder, wetter winters) resulting from global warming, which cause peat loss and bog contraction, bogs can turn from carbon sinks to atmospheric carbon sources, contributing to global warming (Moore, 2002). Northern wet-mesic forest communities contain various species of sphagnum mosses in the initial stages of development and then slowly give way to a variety of other mosses and liverworts that are considered to be the “hallmark of the conifer swamp” (Curtis, 1959). The increased volume of carbon dioxide released into the atmosphere is relevant to the well-being of the northern wet-mesic forest in a circular manner; because global warming increases carbon dioxide release from sphagnum within northern wet-mesic forests, further increases in atmospheric carbon dioxide will occur, which will, in turn, perpetuate global warming. Overall, little information is known about what the effects of long-term exposure to increased carbon dioxide levels will be on wild vegetation (Mooney et al., 1991). Additionally, the effects of increased carbon dioxide may play a role in altering the decomposition rate and nutrient balance of communities, thereby affecting plant species composition (Mooney et al., 1991).

The migration and expansion of plants affects the assemblages of plant species found across the landscape and corresponding regional ecosystems. The post-glacial migration and expansion of plant species ranges has occurred throughout time, with limits to expansion occurring when the species encountered unsuitable climate or large physical barriers. The range of a species is considered as the extent of mature, reproducing individuals (Woods & Davis, 1989). Range expansion occurs when propagules are dispersed hundreds or thousands of meters beyond existent vegetation



fronts, thereby establishing a new population (Woods & Davis, 1989). Beginning 10,000 years ago with the melting of the glaciers, plants began to migrate northward (Gurevitch et al., 2002). Pollen core data collected in eastern North American lakes and bogs suggests that each tree species was unique in its movements northward, with wind-dispersed trees moving the furthest each year, and bird-dispersed species moving more slowly (Davis et al., 1989; Gurevitch et al., 2002). Research by Woods & Davis (1989) on American beech (*Fagus grandifolia*) demonstrated that its migration was marked by periods of rapid expansion and relative stability. Woods & Davis (1989) attributed the variation in range expansion to physical barriers (i.e., Lake Michigan) and climatic variations.

As overall global temperatures increase, range expansion of species that were previously limited by colder temperature will occur. The species that occur at the southern limit of their range will be the first to experience the effects of rising temperatures and changing precipitation patterns that accompany global warming (Davis & Zabinski, 1992). Change in frequency of disturbances such as fire, windstorms, or insects in response to climate change may also play a role in shaping the vegetation of an area (Heinselman, 1996).

Climate change is expected to shift the range and importance of plant species (Iverson & Prasad, 2002). It is estimated that climate changes associated with the doubling of the earth's atmospheric carbon dioxide could change the composition of one-third of the forests on earth (Melillo, 1999; Shriner & Street, 1998) and that in northern temperate regions for every 1°C rise in average temperature, plant species ranges may expand 100 km north (Prentice, 1986; Davis, 1989). In addition to range expansion, an

increase in global temperature of 2°C would facilitate vegetation change through modifications in competition between plant species resulting in relative abundance changes (Davis, 1989) as older trees die and there is no recruitment of younger trees in the understory. However, a lag time is hypothesized between climate change and the replacement of species (Webb, 1987; Davis, 1986). This is because climate change will not kill a plant directly, but rather, in the case of dominant forest trees, will slowly lead to successional change (Davis, 1989). According to Davis (1989) a lag time in the adjustment of overstory species abundances will not be as profound in most communities because some logging practices remove the overstory species and thereby facilitate the expansion of species adapted to climatic changes (Davis, 1989). Davis (1989) also theorizes that species' lag times will be a major problem for areas such as unmanaged forests and reserves which protect unique habitat or rare plants and are therefore reservoirs of species diversity. Reserves and unmanaged forest only account for a small percentage of the total land area and were typically created to preserve rare or endangered plants, animals, and plant communities. These areas will be slowly altered in species abundance as new species invade that are better adapted to the climatic conditions and consequently change the competitive conditions, light conditions, microclimate, soil decomposition rates and nutrient availability of in these reserves (Pastor & Post, 1988; Davis, 1989). Further, the dispersal of rare species out of these reserve areas in response to climate change will often be difficult due to limited seed source, the absence of natural vectors because of the reserves' relatively small size and the surrounding disturbed landscape, and the possible absence of adequate abiotic conditions at surrounding sites

(Davis, 1989). Therefore, climate change has the potential to have a dramatic affect on species diversity across the landscape.

The effect of five different climate change scenarios on the habitat redistribution of the 76 tree species, including white cedar in the eastern United States was presented by Iverson and Prasad (2002). The study found that the species most significantly impacted in the model simulations included trembling aspen (*Populus tremuloides*), big-tooth aspen (*Populus grandidentata*), sugar maple (*Acer saccharum*), paper birch (*Betula papyrifera*), and white cedar (*Thuja occidentalis*). The study concluded that the first four of the above species could have their suitable habitat extirpated from the United States in three out of five model simulations over the next 50 years. For cedar the simulation predicted a bleak outcome. It was the only species where all five model simulations showed that suitable habitat would be eliminated from the United States leaving areas in Canada, to the north, as the only suitable habitat.

Climate change and the migration/range expansion of species are slow processes that can gradually shape the landscape and the plant communities that occur there. These processes are important disturbance factors in northern wet-mesic forests. The model created by Iverson and Prasad (2002) predicts the future outcome of climate change on cedar. However, the extirpation of cedar from northern wet-mesic forests may have been occurring in response to climate change over the past 53 years. The current abundance of cedar across sites was compared to the abundance of cedar in 1952 to test for possible decrease in the relative abundance of cedar across its range. This would serve as a non-specific measure of climate change on cedar in northern wet-mesic forests.

Succession

Succession is considered to be the changes that occur in an ecological community following a disturbance that reduces the overstory as well as the gradual natural changes in community structure and composition over time in the absence of disturbance (Connell & Slatyer, 1977; Heinselman, 1996). Odum (1971) defined succession as:

“an orderly process of community development that involves changes in species structure and community processes with time...it is...directional...predictable... [and] results from modification of the physical environment by the community...It culminates in a stabilized ecosystem in which maximum biomass...and [linkages] between organisms are maintained per unit of available energy flow.”

Succession is a subtle factor at work in plant communities that creates vegetation composition changes that can alter a community over the time period of a number of years. Change in the vegetation of natural forest communities occurs as the component species of a community pass through their life cycles of establishment, growth, and eventually death. Each species that occurs in a natural community affects all other plant and animals by modifying the environment. The structure and composition as well as light, temperature, soil acidity, nutrient cycle rates and pathways all change as a community matures (Heinselman, 1996).

Forest succession is often characterized as a change in species composition or the replacement of some tree species at a site by other tree species (Barnes et al., 1998). An example of forest succession is the transition of shade-tolerant to pioneer species following a windstorm or fire which reduces the overstory of a forest drastically over a short period of time (Barnes et al., 1998). However, succession can also take place in the

absence of a destructive disturbance. In forests, as a stand of trees ages and undergoes succession, a self-thinning process occurs in which trees grow larger, tree density declines, and basal area per unit area increases (Somers & Farrar, 1991; Zhang et al., 1993) as shade intolerant species give way to shade tolerant species (Curtis, 1959; Connell & Slayter, 1977). These effects play a role in modifying the environment for understory plants by increasing the amount of shade and competition from forest overstory plants (Rooney et al., 2004).

Mature cedar is classified as a shade-tolerant species, while its seedlings are considered even more shade-tolerant (Johnston, 1990). Cedar is classified as a climax species due to its longevity and shade tolerant nature; in the absence of disturbance, cedar will dominate a stand (Kurmis et al., 1986). Cedar will also establish itself as a pioneer in old fields, windthrow areas, fire openings, forest harvest areas, and in openings created by hydrological change, but is also likely to succeed less shade-tolerant, short-lived species such as balsam poplar (*Populus balsamifera*), tamarack (*Larix laricina*), and black spruce (*Picea mariana*) (Johnston, 1990). In pre-European settlement times, the majority of northern wet-mesic forests occurred as multi-aged stands (Frelich, 1999). Therefore, in the absence of disturbance, change in overstory or understory plant species likely occurred in northern wet-mesic forests over the past 53 years. Specifically, tree species should be increasing in diameter and shade tolerant species should be out competing shade intolerant species in the absence of disturbance.

#### Land Use Changes

Landscape fragmentation with corresponding habitat loss is identified as one of the five leading mechanisms of extinction in the United States, on par with invasive

species, direct exploitation, pollution, and disease (Wilcove et al., 1998). These disturbances tend to create a heterogeneous habitat across the landscape. Fragmentation of the landscape may result from natural processes or human activities. Natural sources of fragmentation are fires, windstorms, floods, or avalanches, dependent upon the region where the disturbance is occurring (Barnes et al., 1998). The fragmentation of the landscape which results from human activities such as corridor building and land development tends to create abrupt edges, and is more widespread and systematic than natural fragmentation (Barnes et al., 1998). Human-induced fragmentation leads to a decrease in the composition and diversity of the flora, including a reduction in forest cover, floral biotic simplification, increased number of ecosystem types, increased patch number, and decreased patch size and complexity due to intrusion by roads, agricultural land, and urban development (Harris, 1984; Saunders et al., 1991; Mladenoff et al., 1993; Barnes et al., 1998). Such fragmentation also leads to the creation of an extensive ring around the forest patch termed “edge effect”, which is a gradual boundary with contrasting surrounding land use differing from the interior of the forest (Barnes et al., 1998).

Patches of vegetation with abrupt edges are influenced by changes in the microclimate (i.e., radiation flux, wind movement, and water flux) of the remnant vegetation patch. They are also affected by isolation factors (i.e., time since isolation, distance from other patches, connectivity, and changes in the surrounding landscape) from other vegetation patches as well as individual vegetative and biotic conditions (e.g., presence of predators) when compared with interior patches of vegetation (Barnes et al., 1998; Saunders et al., 1991). These factors play an important role in the overstory and

understory plant species assemblages that are found in northern wet-mesic forests. By altering the abiotic and biotic conditions of a site, certain species that may have once been present may become locally extinct.

Human activity (e.g., greater movement across the landscape) and landscape fragmentation have created conditions that encourage an increase in the number of vertebrate herbivores and an increase in exotic species, both of which affect the northern wet-mesic community (Alverson et al., 1988; Rooney et al., 2004). Corridors, such as roads, increase the amount of edge in a landscape, which, according to Watkins et al. (2003), increases species richness within a localized area. However, this is secondary to a greater frequency and abundance of exotic species. An increase in edge habitat can also increase the number of herbivores such as the white-tailed deer (*Odocoileus virginianus*), which have an effect on sensitive understory plant species and overstory plant species such as cedar (Alverson et al., 1988; Rooney, 2001). Vertebrate herbivores such as white-tailed deer are considered to be edge species and thus thrive in fragmented environments. Even though the northern Wisconsin landscape is considered less fragmented than many other landscapes (Rooney et al., 2004), it is far more fragmented than it was previously. Historically, it existed as a relatively continuous stretch of forest, composed of mixed hardwoods, swamp conifers, and pine stands (Curtis, 1959).

No readily available data currently exists on the degree of landscape fragmentation from the 1950s, but an accurate measure of current land use in Wisconsin exists. Air photos from the 1950s are available, but these photos have not yet been interpreted and cannot be compared to current land use. Therefore, accurate comparisons

regarding current land use can not be made between the different northern wet-mesic communities in this study.

#### Timber Harvest

The forests of northern Wisconsin have been altered by a variety of human disturbances in the period between the last glaciation and present day. Within the last 150 years, European-American settlement has largely altered these forests from an extensive swath of primary forest to secondary growth forest (Curtis, 1959). This is primarily due to extensive logging from 1840 through the 1920's (Curtis, 1959). Following logging, much of the land in northern Wisconsin reverted back to forest. In eastern Wisconsin, much of the land was used for agriculture rather than reverting to forest (Curtis, 1959). Specifically, northern wet-mesic communities were also affected by the logging of the mid-to late 1800s' and some by the extensive fires that followed logging (Curtis, 1959). Some of these communities were also drained and ditched in an effort to create suitable agricultural land; however, this practice was more extensive in southern Wisconsin than in the north (Curtis, 1959).

Current management of cedar varies across the region by landowner. On the Ottawa National Forest in the upper peninsula of Michigan and on the Chequamegon-Nicolet National Forest in northern Wisconsin, cedar is not actively managed for timber (Schmidt, 2003). The Wisconsin Department of Natural Resources does not have a policy against cedar timber harvest; however, cedar logging rarely occurs (Schmidt, 2003). The forest management practices on tribal lands have included the harvest of cedar; however, recent management practices are thought to be more restrictive (Danielson, 2002). Cedar is not only harvested for timber purposes by tribal members,



but the bark is also stripped from the trees and utilized for traditional uses (Linda Parker, personal communication, 2006). There are no restrictions on the harvest of cedar by private landowners in either Michigan or Wisconsin and it is therefore left up to the philosophy of the landowner (Schmidt, 2003). Timber management of northern wet-mesic forests is currently rare on most public lands and some private lands throughout the study area. The impact of timber harvest on northern wet-mesic forests was not specifically studied.

#### Windstorms

Wind damage (windthrow) disturbances in forest ecosystems can affect their composition, structure, and function on local and regional scales (Barnes et al., 1998). The frequency and intensity of wind can affect areas as small as a single tree, or up to hundreds of hectares of forest (Barnes et al., 1998). Windthrow creates change by opening the forest canopy and exposing the forest floor and the seedlings and saplings to increased sunlight, thereby allowing for growth into the canopy (Curtis, 1959). In northern wet-mesic forests, windthrow plays a role in shaping the age-class and structure of a stand through the development of an uneven-aged forest type (Johnston, 1990), with a stand-leveling wind event estimated to occur approximately every 1000-2000 years (Frelich, 1999). Windthrow in northern wet-mesic forests most often occurs in trees with basal defects, in communities adjacent to rock ledges, and at sites opened by logging (Burns & Honkala, 1990). Wind damage (e.g. uprooting and breakage) in northern wet-mesic forests occurs mostly along stand edges and in older trees with stem defects (Johnston, 1977; Johnston, 1990). Cedar lends itself to windthrow because of shallow root systems that tend to be lateral in formation (Schmidt, 2003) Windthrow trees that

have lain on the forest floor can eventually become suitable seedbeds for the regeneration of cedar seedlings with 75 to 85 percent of seedlings developing on rotten logs and stumps (Nelson, 1951; Curtis, 1959). Cedars that are tipped by wind can initially experience reduced viability, but these trees usually exhibit rapid growth from branches that have been lowered to the forest floor from layered regeneration (Schmidt, 2003). Forest gaps created by windthrow also encourage the establishment and recruitment of cedar seedlings (Pregitzer, 1990). Historically, this resulted in a short time period for new species to invade the open area, thereby creating a forest dominated by cedar that excludes most other species (Curtis, 1959). However, present-day windthrow in northern wet-mesic forests may have a greater chance of releasing other trees such as spruce, fir, and hardwood species rather than cedar as a result of the impact that white-tailed deer are having on cedar regeneration (Pregitzer, 1990; Alverson et al., 1994). Thus, windthrow may play a significant role in overstory and understory floral composition in the northern wet-mesic forest. However, specific measurement of the impact that windstorms have as a disturbance in northern wet-mesic forests was not analyzed.

## Fire

Data concerning the impact of wildfire in cedar swamps are limited. However, a shallow root system, thin bark, and high oil content make cedar susceptible to fire (Johnston, 1990). A prescribed burn on the Superior National Forest conducted in an area with a cedar overstory resulted in one-third of the cedar perishing through either excessive heat to the canopy and root system or direct flame (Schmidt, 2003). Yet, use of fire in regenerating cedar has been found effective. A study conducted by Verme and Johnston (1986) compared fire, mechanical, and no treatment methods and their effects

on cedar regeneration. The study results found an increased density of cedar seedlings on burned areas possibly as a result of reduced competition from sphagnum moss which inhibits seedlings (Verme & Johnston, 1986). Although fire regimes in northern wet-mesic forest are not well documented, Frelich (1999) created a simulation model of the successional pathway of these communities which estimates a fire return interval of 150-300 years. Therefore, fire has the potential to alter northern wet-mesic forest structure and plant composition, but its specific impacts were not studied in this research.

#### Hydrological Change

Restricted soil aeration due to high water levels can be a threat to northern wet-mesic forests by reducing growth and/or causing mortality (Stoekeler, 1967). Drought conditions can also lead to cedar mortality especially in seedlings that are growing in moss that is susceptible to summer drying (Schmidt, 2003). Road and pipeline building as well as beaver (*Castor canadensis*) damming have a direct effect on northern wet-mesic communities by altering drainage patterns within these communities (Stoekeler, 1967; Johnston, 1977; Johnston, 1990). This alteration can result in abnormally high water levels, restricting soil aeration and decreasing the growth rate or killing stands of cedar (Johnston, 1990) and its understory component. Major hydrological change was noted in this study, but minor changes such as pH were not collected due to the lack of baseline data needed to make accurate comparisons.

#### Insect and Plant Disease

Insects and disease shape the structure and species composition of a community as different agents affect different species. Insects and disease can affect plant communities by weakening or killing overstory trees in patches or singly (Barnes et al.

1998). Cedar is relatively free from both of these types of agents (Curtis, 1946; Johnston, 1990), although black carpenter ants (*Camponotus pennsylvanicus*) and red carpenter ants (*C. ferrugineus*), which decrease timber value and increase susceptibility to wind breakage by attacking the decaying heartwood of live trees, are the chief insect pests of naturally grown cedar (Johnston, 1990). Young cedars are susceptible to foliar diseases and older trees are susceptible to heart rot fungi as well as root and stringy tree butt rot (*Poria subacida*) (Johnston, 1990).

American elm (*Ulmus americana*) was historically a moderately common component of wet forests, occurring in northern wet-mesic forests of northern and eastern Wisconsin (Curtis, 1959). In the 1930s, Dutch elm disease caused by a fungus (*Ophlostoma ulmi*) was introduced to Ohio from Europe (Barnes et al., 1998). Over a period of 50 years, Dutch elm disease killed virtually all mature elm of various plant communities in the Midwest and eastern United States (Barnes et al., 1998). After elm was removed from the forest community, other tree species migrated into the altered communities replacing the elm (Barnes et al., 1998). The initial survey of this study was completed prior to the invasion of *Ophlostoma ulmi* into the region and for this reason a decrease in the percentage of American elm was expected in the 2005 survey. Although cedars themselves are not very susceptible to insects and disease, they are affected by broader forest changes that result from the susceptibility of other tree species to insects and disease.

#### Ice and Snow Damage

Ice and snow damage is fairly common and directly affects overstory cedar trees by breaking limbs and causing stem breaks that can force trees into permanently leaning

positions, thus causing canopy openings (Curtis, 1946). Ice and snow damage provides an entry for pathogens or weakens trees, thereby increasing their susceptibility to insect attack (Barnes et al. 1998). Also, damage and/or death can occur to cedars that grow along roadways due to excessive salt spray from the use of de-icing salts on roads in winter (Johnston, 1990). The effects of ice and snow damage over the past 53 years was not studied directly due to a lack of reliable data from 1952.

Northern wet-mesic forests are naturally dense, closed-canopy communities where canopy coverage may reach 100 percent (Curtis, 1959). Under these shaded conditions, the establishment of plants in the understory is limited to canopy gaps due to some form of disturbance such as; land use change, logging practices, windstorms, fire, hydrological change, insect/disease, and ice/snow damage (Curtis, 1946; Curtis, 1959; Stoeckeler, 1967; Johnston, 1990; Barnes et al., 1998; ). In these canopy gaps, regenerating overstory species as well as understory species occur more frequently and therefore compete for light. Under these circumstances, the taller species (height classes are based upon average shoot height (< 20cm, 20-40cm, and >40cm)) within these gaps often out-compete the shorter species for light. Therefore, if northern wet-mesic forests have experienced a greater amount of disturbance leading to openings in the canopy, then taller plants should have increased significantly over the last 53 years over short plants.

#### Exotic Species

Changes in plant species composition within a community are often the result of degradation of habitat, with community impoverishment occurring as native species decline and non-native species increase in abundance (McKinney & Lockwood, 1999; Rooney et al., 2004). Exotic species can play significant roles in the communities that

they invade by displacing native vegetation and altering productivity, function, and diversity (Barnes et al., 1998). Human movements facilitate the establishment of exotic species by physically transporting plants or seeds (Barnes et al., 1998). In a study of northern upland forests, Rooney et al. (2004) found that on 62 surveyed sites, only one exotic species occurred at one site in 1950, while the 2000 survey found exotic species at 43 sites. These communities, however, remain dominated by native species. Rooney et al. (2004) also found that habitat generalists, those species which are common to a site, increased, while habitat specialists, those species which are relatively rare, decreased. No specific data exist on the degree to which exotic species affect the northern wet-mesic community, or the number of habitat generalists compared to habitat specialists. Exotic species may find it difficult to become established in northern wet-mesic communities due to wet conditions, a dense forest canopy that allows very little light to penetrate to the forest floor, and the regeneration abilities of cedar (Curtis, 1959). However, when the forest canopy is opened through timber harvesting, windthrow or disease/insect invasion, an increased herbivore pressure may allow exotic species to become established.

Exotic species have the ability to take advantage of a wide variety of habitats, especially those disturbed by some form of human intervention. Research by Rooney et al. (2004) and Wiegmann and Waller (2006) have shown that exotic species have increased in northern upland forests over the past fifty years. Five of the 21 plant species that increased significantly (“winner” species identified by Wiegmann and Waller (2006)) were exotic species that had increased significantly since 1950. Rooney et al. (2004) reported that only one study site out of 62 had an exotic species in 1950 while 43 sites had exotic species in 2000. If exotic species have increased significantly over the

last 53 years in a similar manner to the results of Rooney et al. (2004) and Wiegmann and Waller (2006), then those species should be “winner” species, while the species that they have displaced would be “loser” species or those that have decreased significantly.

#### Loss of Biotic Pollinators and Dispersers

The pollination and dispersal modes of plants determine how well they will survive under different environmental conditions. Biotically pollinated and dispersed plants are those that are pollinated and dispersed by either insects or mammals while abiotically pollinated and dispersed plants rely upon the wind for recruitment. Research has shown that habitat fragmentation can decrease the number of biotic pollinators and dispersers that are available to pollinate and disperse plants (Buchmann & Nabhan, 1996). Under conditions with fewer available biotic pollinators and dispersers, plants that are abiotically-pollinated and dispersed should be favored over those that rely on biotic pollination and dispersal methods. Wiegmann and Waller (2006) found that the pollination and dispersal method between winner and loser species was significantly different; winner species had a significantly higher amount of abiotically pollinated and dispersed plants than loser species. Therefore, if biotic pollinators and dispersers have significantly decreased over the last 53 years, then biotically-pollinated and dispersed species should show this change through a similar decrease.

#### Mammalian Herbivory

Disturbance can also take the form of vertebrate browsing, resulting in population and foliage declines that severely affect a population’s viability. Animals that can contribute to decreased success in cedar regeneration include snowshoe hare (*Lepus americanus*), porcupine (*Erethizon dorsatum*), red squirrel (*Tamiasciurus hudsonicus*),

red-backed voles (*Clethrionomys grapperi*), moose (*Alces alces*), and white-tailed deer all of which have been noted to have a detrimental effect on cedar (Fowells, 1965; Johnston, 1990). Porcupines feed on foliage or girdle stems decreasing growth or killing the tree whereas red squirrels clip branchlets with flower buds or cone clusters reducing available seeds for reproduction (Curtis, 1946; Johnston, 1990). Red-backed voles browse on seedling terminal or lateral branches affecting cedar survival, while hare browsing on the foliage of seedling and sapling stage cedar also affects cedar survival and has been noted to have a greater impact than deer browse at some locations (Fowells, 1965). Moose browsing of cedar may also occur in areas where the species overlap, such as on Isle Royale; however, cedar is not a preferred food of moose (Miller, 1992).

Declines in the abundance of some plant species in northern wet-mesic communities may be related to the lack of recruitment of cedar, generally caused by white-tailed deer herbivory. In northern wet-mesic communities, white-tailed deer-browsing has a detrimental effect on the seedling and sapling stages of cedar development (Johnston, 1977; Johnston, 1990), as well as on the growth and health of understory plants. Estimated historic deer numbers in Wisconsin ranged from 2-4 deer per km<sup>2</sup> (Alverson et al., 1988), whereas current densities are much higher, a mean density of  $10.1 \pm 1.0$  per km<sup>2</sup> for 1989-1996 (Rooney et al., 2002). A larger deer population has a greater effect on browse-sensitive plant species. This effect is magnified in the winter when deer congregate in areas dominated by cedar (Curtis, 1959). The nutritional needs of white-tailed deer require that, on average, 2 kg of browse is consumed per day or the equivalent of all available browse below 2 m on a 7.5 cm diameter tree (Fowells, 1965). Cedar that is less than 2 m tall can withstand and continue



to thrive with deer browse that removes 15-20% of the foliage; however, browsing that is heavier than this retards growth and eventually kills the tree (Aldous, 1952). Mature cedar can withstand heavy browsing below the 2 m. line with without serious injury (Aldous, 1952).

In some areas a very high rate of cedar seedling and sapling mortality due to high browsing pressure has led some researchers to call the current stands of cedar in Wisconsin “the living dead,” indicating that the current generation of cedars may be the last (Alverson et al., 1994; Rooney et al., 2002). The establishment and recruitment of cedar seedlings in the Upper Great Lakes states at 77 sites of multiple ownerships, site conditions, and deer densities was studied by Rooney et al. (2002). The study reported that the initial establishment of cedar seedlings was improved in areas with a high input of seed and in areas of high light levels while recruitment of saplings (>30 cm tall) depends on the level of deer browse (Rooney et al., 2002).

Browsing pressure from deer varies throughout the state, and is dependent on the degree of landscape fragmentation in an area and the amount of pressure put on deer by hunting. Wisconsin allows an annual hunt for deer; however, some areas are not open to deer hunting. These areas include special parts of state parks, areas adjacent to residential areas, and private landowners who do not allow hunting on their property (Rooney et al., 2004). Other areas such as Menominee Tribal land have lower deer densities (Rooney et al., 2002) due to greater hunting pressures. Areas where deer hunting is not allowed may act as a refuge for deer, increasing their effect on the local plant species (Martin & Balzinger, 2002). In their study of northern upland forests, Rooney et al. (2004) found that, over a 50 year period, sites without deer hunting lost

60% of their vascular plant species while sites with deer hunting only lost 16% of their species. Northern wet-mesic forests may also be experiencing this magnitude of plant species loss due to intense browse pressure. This effect on the dominant overstory species can affect the understory composition as well, both in direct browse pressure and indirect changes due to decreases in cedar dominance.

Grazing livestock also play a role in shaping the plant species composition of some ecological communities (Barnes et al., 1998). Curtis (1959) found that in mesic upland forests used as pasture, the area was used by livestock for shade rather than browse. However, due to trampling, the livestock nearly destroyed the understory. Northern wet-mesic forests, especially in eastern Wisconsin, have been used as grazing areas for livestock in the past, as noted by many stand records collected by the UW-Madison Plant Ecology Laboratory study of the 1950's (Christensen, 1954); however, no data exist regarding the specific impact of livestock grazing upon northern wet-mesic forests.

The growth form of a plant can determine how well it can tolerate herbivory. Graminoid and fern species are less susceptible to deer browse and tend to persist in heavily browsed communities compared with other groups of plants such as forbs (Rooney, 2001). This is because graminoids can resprout quickly after being browsed (Wiegmann & Waller, 2006) and ferns are unpalatable and are typically avoided by deer (Rooney, 2001). Forb species are broad-leaved, non-graminoid, non-woody species that are, depending upon the species, particularly vulnerable to browsing due to the removal of photosynthetic tissue, which reduces a plant's growth and reproductive abilities (Rooney, 2001). Balgooyen & Waller (1995) found that blue-bead-lily (*Clintonia*

borealis), a common lily family herb that occurs in northern wet-mesic communities, declined significantly in areas with high deer browse pressure, while Augustine and Frelich (1998) reported that browse on trilliums (*Trillium* spp.) is detrimental to the plant because it typically defoliates the plant and removes the reproductive structures. Woody seedlings are also susceptible to deer browse, especially some of the common swamp conifer species such as Canada yew, eastern hemlock, and cedar, all of which are important food sources for deer in the winter months (Curtis, 1959; Rooney et al., 2000; Rooney et al., 2002). Therefore, if browsing mammals have had a significant impact on the vegetation of northern wet-mesic forests over the past 53 years, then forbs and woody plants should have significantly decreased while ferns and graminoids should have significantly increased.

### Summary

In summary, little is known about the current plant species diversity within northern wet-mesic forests of Wisconsin or how it has changed over the past 53 years. Research has shown that a variety of natural disturbances and conditions can affect the integrity of the community. Anthropogenic disturbances also affect northern wet-mesic forests and are becoming more pervasive, potentially leading to habitat degradation as well as an increase in common, disturbance-tolerant species and declines in rare, disturbance-sensitive species (McKinney & Lockwood, 1999). If anthropogenic disturbances are widespread, similar shifts in local diversity across northern wet-mesic communities could accumulate across the region, which can drive biodiversity losses across spatial scales (McKinney & Lockwood, 1999). This study used baseline data

collected by John Curtis and colleagues in 1952 (Curtis, 1959) to investigate local and regional shifts in plant species abundance and community structure of northern wet-mesic forest communities. Previous analysis of three other plant communities in this region show that within the community type there is less diction between sites, understory richness is declining, mean similarity in species composition among sites has increased, habitat specialist species have declined, common habitat generalist species have increased, exotic species have increased, graminoid species have increased, forbs have decreased, and biotically-pollinated and dispersed-species have decreased, while those that rely upon abiotic pollination and dispersal have increased.

In this study, shifts in understory species composition and species that significantly increased “winners” and decreased “losers” (Wiegmann & Waller, 2006), if any, were assessed over a 53 year period in northern wet-mesic forest of northern Wisconsin. The degree to which winner and loser plant species differ in regard to functional traits such as native/exotic status, modes of pollination and dispersal, growth form, and plant height was also assessed. I hypothesized that northern wet-mesic forest communities were experiencing: (1) declines in local native species richness, (2) increases in exotic species, (3) domination by a few habitat generalists, (4) declines in species that rely on biotic pollinators and dispersers, (5) increase in graminoid and ferns, (6) a decrease forb and woody growth forms, and (7) an increase in overall plant height. Finally, I assessed the potential mechanisms driving ecological change in the region.

## METHODS

### Study Area

To document changes in northern wet-mesic forests, 34 sites distributed across northern Wisconsin were resurveyed (Fig. 1). The landscape rises gently from the low elevation Silurian and Ordovician limestone/dolomite bedrock along the shores of Lake Michigan in the east to the thick glacial till soils of Precambrian shield rock in north-central Wisconsin followed by the deep loamy soils overlying Precambrian and Cambrian bedrock in the northwestern part of the state (Albert, 1995). Average elevation above sea level for the sites range from 177-500 m. Average annual precipitation for this area ranges from 550-780 mm with 120 growing days in the northwest to 175 growing days in the southeast portion of the study area (Albert, 1995).

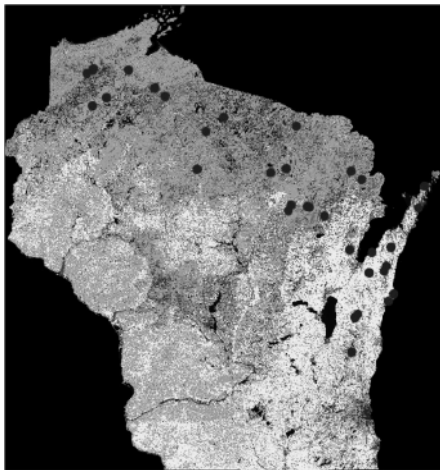


Figure 1. Map of 34 study sites located across northern Wisconsin.

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### Sampling Method

Between 1942 and 1956, J. T. Curtis and colleagues at the Plant Ecology Laboratory at the University of Wisconsin-Madison conducted a statewide vegetation survey to examine the relationship between vegetation and the environment as well as plant community composition (Curtis, 1959). The surveys covered 1420 sampling sites, including 1045 native terrestrial sites, as well as aquatic and weed communities (Curtis, 1959). Curtis (1959) used some basic criteria to choose his sampling sites. These

included a minimum size of 6.07 hectares to reduce the edge effect from wind movement, uniform topography, lack of domestic grazing, lack of recent logging, and a homogeneous stand.

A standard sampling protocol was used by Curtis and colleagues. They initially walked the site to record herb, shrub, and tree seedling presence/absence and to check its condition and homogeneity (Curtis, 1959). Each stand used in the study had to be free from serious disturbance within the lifespan of the then current generation of trees (Curtis, 1959). Serious disturbance to a stand was considered to be past grazing by domestic animals and/or selective logging that had decreased the canopy coverage by 10 percent or more (Curtis, 1959). Any stand that did not meet these criteria was not used in the study. After a stand was chosen for study, a portion was then selected for sampling that was at least 30 m from the edge of the stand (Curtis, 1959). The size of the area was then determined in order to calculate the distance between sampling points (Curtis, 1959). The researchers spaced 20 1-m<sup>2</sup> quadrats along a U-shaped transect (mean distance between quadrats was 6.5 m) and at each point recorded the presence of all herbs, shrubs, and tree seedlings within the 1-m<sup>2</sup> quadrat. This characterized the vegetation of approximately 0.25 ha. (Curtis, 1959; Rooney et al., 2004). At each quadrat, the composition, density, and basal area of the canopy trees was also recorded via the random pairs or point-quarter method (Cottam & Curtis, 1949; Cottam & Curtis, 1955; Cottam & Curtis, 1956; Curtis, 1959).

In May, June, and early July of 2005, I resurveyed 38 of the original Curtis northern wet-mesic communities. Four of the initial 38 sites selected for survey were no longer forested and were disqualified from the survey. The study sites were located using

the original survey sheets which contained the Section/Township/Range coordinates, site maps, stand topography, forest cover, and landmark descriptions. The sites furthest south were sampled first. This timing of survey allowed the detection of some of the unique plant species that define the community such as early-blooming orchids and graminoids and also made use of phenological differences from south to north. In order to ensure accurate data comparison, the same sampling technique used by Curtis was used in the 2005 survey.

In order to compare data accurately between the two sampling periods, species lists were matched. A number of alterations in plant species nomenclature since 1952 have occurred. Also, the Plant Ecology Lab misidentified, lumped, or split a number of plant taxa in their analyses. For example, sedges (*Carex* spp.) were split into *Carex* spp. and three-seeded sedge (*Carex trisperma*) by Curtis and colleagues. Rooney et al. (2004) corrected this problem by categorizing species to genus or eliminating species that may have been misidentified. I used the same technique in my analysis and relied upon recommendations by plant taxonomists Dr. Emmet Judziewicz and Dr. Robert Freckmann to lump species.

#### Data Analysis-Understory

Analytical methods for this project were similar to those used by Rooney et al. (2004) and Wiegmann & Waller (2006) who both conducted similar research on the northern upland forests of Wisconsin. In order to test how similar plant communities were between the two time periods, a binary similarity coefficient, the Jaccard coefficient, was used. Jaccard's coefficient is a measure of similarity between two

samples when only presence/absence data was available (Krebs, 1989). Jaccard's and other binary similarity coefficients weight all species evenly (Krebs, 1989).

Changes were compared between 1952 and 2005 in species richness at the quadrat (1m<sup>2</sup>) and site scale using t-tests (null hypothesis: there is no difference in species richness between 1952 and 2005). I also calculated the ratio of non-native vs. native species in 1952 and 2005, the average similarity between sites in species composition, as well as the mean habitat breadth of the species present. Replicated G-tests were used for goodness of fit to identify significant winners and losers over the past 53 years. For all analyses, an alpha level of 0.05 was utilized. Minitab 14 was used for all t-test and chi-squared statistical analyses.

Species richness is the count of the number of species in a certain area. I examined how changes in species richness differed among sites by calculating the percent change in species richness for each site over 53 years. Land use surrounding each site and the public or private status of each site may have an effect on site species richness as well as the Jaccard's similarity index. Each site was classified according to its public/private status as well as its location in the study area (i.e., eastern or northern Wisconsin). These groupings were then analyzed using t-tests to test for differences in plant species richness and similarity values on public compared to private land as well as differences in plant species richness and similarity values in northern versus eastern Wisconsin. ArcView 3.3, a Geographic Information System (GIS) program, was used to analyze the land use surrounding each site.

Non-native and native species were identified by consulting the UW-Stevens Point Freckmann Herbarium Vascular Plants website



(<http://wisplants.uwsp.edu/VascularPlants.html>). In order to compare the ratio of non-native to native plant species in 1952 and 2005 at the site and quadrat level, a  $\chi^2$  test was run on a 2 x 2 contingency table. A Yates continuity correction factor was calculated for each 2 x 2 contingency table. Contingency tables test for significant shifts in the relative frequency of native or non-native species (null hypothesis: the presence/absence of exotic species was the same in 1952 and 2005).

I evaluated the average degree of similarity of each site in comparison to the other 34 sites to provide a floristic measure of how sites are distinct in comparison to one another. In order to calculate the community similarity, a complement of the Bray-Curtis distance coefficient was calculated:  $S = 1 - [(\sum |x_{ij} - x_{ik}|) / \sum (x_{ij} + x_{ik})]$ . The values  $x_{ij}$  and  $x_{ik}$  are the number of quadrats that contain species  $i$  at either site  $j$  or  $k$  (Krebs, 1989). The values of  $S$  range from 1.0, indicating that there is identical species composition and relative abundance between sites, to zero, which indicates that there is no similarity in species composition between sites (Krebs, 1989). This measure ignores cases in the community samples where species are absent in both communities (Krebs 1989). The comparison of the mean similarity between each one site and all other sites gives an indication of whether or not sites are becoming more similar to one another over a 53 year period.

Most of the species found in the study have a number of habitat types in which they are found throughout the state of Wisconsin. A weighted habitat breadth index ( $H$ ) was used to calculate the mean habitat specialization of each species at each site and sampling period, where  $H$  is the mean number of habitats of all plant species in 1952 vs. 2005. A mean habitat specialization score was calculated for each stand by weighting

habitat specialization values for each species by the relative frequency of that species at each site. There are 17 separate habitats that have been identified by Curtis (1959) and can be found online at the Wisconsin State Herbarium (<http://www.botany.wisc.edu/wisflora/curtis.asp>). Plants that occur at all 17 habitats are considered to be extreme habitat generalists, while those that occur in only one habitat are considered extreme habitat specialists. Comparison of the mean habitat specialization between the two time periods indicates whether habitat generalists or specialists have been more successful.

In order to determine which understory species are increasing (“winners”) and which are decreasing (“losers”), I used replicated G-tests for goodness of fit. This allowed me to say with statistical certainty which species increased and decreased. G-tests are calculated in a similar manner to  $\chi^2$  and are considered to be a conservative test of low power. They are also non-parametric and can be used to determine the effect of species change in frequency across sites. In this analysis I tested the null hypothesis that over time, there is no change in the proportion of quadrats occupied by each species. Using sites as replicates,  $G_{\text{total}}$ ,  $G_{\text{pooled}}$ , and  $G_{\text{heterogeneity}}$  test statistics were calculated for each understory species. These test statistics allowed me to determine if shifts in quadrat frequency are significant across sites and consistent in magnitude and direction. The  $G_{\text{total}}$  test statistic can be defined as the sum of each individual understory species G-statistic from each site and can be used to test for changes in quadrat frequency across sites. The  $G_{\text{pooled}}$  test statistic is the sum of quadrats that are occupied by a species across all sites in each sampling period.  $G_{\text{pooled}}$  is used to determine shifts, net increases or decreases, in the frequency of quadrats and can also be used to detect significant regional

shifts in frequency that may otherwise not be detected at the site level. When  $G_{\text{pooled}}$  is greater than 4.0 with 1 degree of freedom, then  $p < 0.05$ . The  $G_{\text{heterogeneity}}$  test statistic ( $G_{\text{total}} - G_{\text{pooled}}$ ) is used to determine the consistency of the shifts in species frequency. Species with significant values are not consistent in their frequency changes across sites while species with a non-significant value shift consistently across sites.

Out of a total of 196 species, replicated G-tests were conducted on only 66 species. Species that occurred in less than 35 quadrats, which equates to less than 5% of all quadrats, in either time period were excluded from the analysis in order to ensure adequate statistical power to test for biological and statistical significance. Species were classified as “winners” if they increased significantly, “losers” if they decreased significantly, and “no-change” if species did not change significantly. Species had to achieve statistical significance with both the  $G_{\text{total}}$  and  $G_{\text{pooled}}$  test statistics in order to be classified as “winners” or “losers”. A significant  $G_{\text{heterogeneity}}$  score indicates that species are not increasing or decreasing evenly across sites while a non-significant  $G_{\text{heterogeneity}}$  score means that species are increasing or decreasing evenly across sites or that there is insufficient data to detect a change. In order to protect against increased Type I errors due to repetitive G-test analyses, Holm’s correction factor (1979) was utilized. Proportional heterogeneities ( $G_{\text{heterogeneity}} / G_{\text{total}}$ ) were also calculated for all the significant winners and losers. These heterogeneity values were then tested using a two sample t-test to compare the means of the winners and losers.

### Species attributes

Plants have a number of different traits that contribute to how successful a species will be in a certain community and under different conditions. I identified five categories

of species' traits based on morphological characteristics to test if these traits predicted whether a species would be a winner or loser. These categories were native/exotic status, pollination mode, dispersal mode, plant height, and growth form. I relied upon the recommendation of plant taxonomists Dr. Emmet Judziewicz and Dr. Robert Freckmann as well as plant floras (Gleason & Cronquist, 1991; Voss, 1996) to classify each species into the correct category. Winner, no-change, and loser species were statically analyzed in 2x2  $\chi^2$  contingency tables to test for significant changes.

I classified species as either native or exotic. Out of the 66 species that were used in the G-test analysis, two were classified as exotic while the rest were classified as native. It was predicted that exotic species would have increased significantly in northern wet-mesic communities over the past 53 years. Forty-four plant species were classified as biotically pollinated and twenty-four were classified as biotically dispersed. It was expected that abiotically pollinated and dispersed species would have significantly increased over the past 53 years if habitat alterations and loss of biotic pollinators and dispersers has occurred. If northern wet-mesic communities were experiencing a greater amount of disturbance since 1952, the results should indicate that winner species are significantly taller than loser species. Winner, no-change, and loser species were classified into three height classes based upon their average shoot height (< 20cm, 20-40cm, and >40cm) with 19 plants in the 20 cm height class, 20 plants in the 20-40 cm height class and 27 plants in the >40cm height class. Four plants were classified as graminoid, nine plants were labeled as ferns or fern allies, 21 plants were classified as woody vegetation and 32 plants were considered forbs. It is predicted that if deer browse has created a significant change in plant species over the past 53 years, graminoid and

fern species should be winner species, while forbs and swamp conifer seedlings should be losers.

### Data Analysis-Overstory

Northern wet-mesic forest communities are dominated by northern white cedar. Changes in the abundance of cedar could have a large impact on the plant species found within the community. In order to determine if cedar abundance had changed over time, replicated G-tests for goodness of fit were used in order to determine, with statistical certainty, which overstory species were increasing and decreasing. Quadrats were not used to sample the overstory of sites; instead, 40 random-pair plots were recorded at each site. These random-pairs served as replicates to test the null hypothesis that, over time, there was no change in the proportion of random-pair plots occupied by each overstory species. A total of 29 overstory species were recorded between the two time periods; however, only species that occurred in greater than 5% of all random-pair points were used, or 68 random-pair points.

In order to assess how sites are changing in respect to succession, mean basal area (BA) was calculated for each overstory species and averaged for each site (Curtis & McIntosh, 1951; Curtis, 1959). As time between disturbances increases, trees grow larger and the assemblage of species present in a community can change. Basal area is a measure of a cross sectional area (in square feet) of a tree trunk usually measured at 4.5 feet above the ground. In this analysis, basal area is expressed as square feet of basal area per acre, averaged for each site and compared between time periods. Analyses of basal area for all of the trees in both time periods, as well as just cedar basal area, were calculated and compared using a paired t-test.

## RESULTS

### Understory

In 2005, 38 northern wet-mesic sites were relocated, however only 34 of these sites were resurveyed. Extensive vegetation changes had occurred at four of the sites (10.5%), altering them from wet-mesic to open grass and sedge-dominated marsh or alder thicket. Vegetation change appeared to be attributed to flooding at the sites from damming by beavers or road-construction activities.

### Species richness

At the 34 sites that were surveyed, I found 196 species, while Curtis recorded 193 species in 1952 (Appendix 1). There was no significant change in average species richness at the site level between 1952 and 2005 (paired  $t = 0.25$ ,  $p = 0.797$ ) (Table 1). Fourteen sites gained species, 18 sites lost species, and two sites experienced no change in species richness over the last 53 years. When exotic species were excluded from analysis, no significant difference was found between the two time periods (paired  $t = 0.76$ ,  $p = 0.45$ ) (Table 1). Fifteen sites gained species while 19 sites lost species. Some sites increased in percent change in species richness whereas others decreased (Figure 2). Seventeen sites were located on public land and 17 sites were located on private land. No significant difference was found in species richness change between public and private lands (paired  $t = -0.43$ ,  $p = 0.67$ ) (Table 2). Twenty one sites were located in northern Wisconsin while 13 sites were in eastern Wisconsin. A significant difference was found in changes of species richness between northern and eastern Wisconsin sites ( $t = 2.11$ ,  $p = 0.047$ ) (Table 2). Northern Wisconsin sites experienced a mean increase of

approximately two species over 53 years while eastern Wisconsin sites showed a mean decrease of 4.6 species.

#### Jaccard's similarity coefficient

Species composition of the 34 northern wet mesic communities sampled changed over the past 53 years. Based on Jaccard's community similarity index, the similarity between 1952 northern wet mesic forests and 2005 northern wet mesic forests was 0.59. This indicates that approximately three out of five species present in 1952 were also present in 2005. When the Jaccard similarity index values were compared for public vs. private land and eastern Wisconsin vs. northern Wisconsin, no significant difference was found for private vs. public land ( $t = 0.06$ ,  $p = 0.947$ ) (Table 2) meaning that the species assemblages on private land are similar to those on public land. A significant difference was found between eastern and northern Wisconsin ( $t = 3.11$ ,  $p = 0.003$ ) (Table 2), which means that species assemblages in eastern Wisconsin sites are different than those of northern Wisconsin sites.

#### Bray-Curtis community similarity

The mean similarity of all sites decreased slightly over the past 53 years. In 1952 the mean similarity was 0.61 while it was 0.60 in 2005. No significant difference was found in the mean similarity of sites between time periods (paired  $t = 1.02$ ,  $p = 0.31$ ) (Table 1). The average similarity increased at 12 sites and decreased at 22 sites.

#### Exotic species

There was significant difference in abundance of exotic species in 1952 vs. 2005 ( $\chi^2 = 14.49$ ,  $df = 1$ ,  $p = 0.0001$ ) (Table 3). Therefore, I rejected the null hypothesis in favor of the alternate hypothesis: the presence/absence of exotic species at sites in 2005 is

different from 1952. Exotic species were found at only 4 out of 34 sites in 1952 while they were found at 20 sites in 2005. There was a significant difference in the percent of exotic to native species in 1952 vs. 2005 (paired  $t = -5.28$ ;  $p = <0.0001$ ) (Table 1).

Exotic species presence averaged 0.29% per site in 1952 and 3.43% in 2005 while the ratio of exotic to native species ranged from 0% to 2.94% in 1952 and 0% to 12% in 2005.

There is also significant evidence for difference between exotic species presence in quadrats at 1952 vs. 2005 ( $\chi^2 = 97.21$ ,  $df = 1$ ,  $p < 0.0001$ ) (Table 3). Out of a total of 680 quadrats, exotic species were found at 12 quadrats in 1952 and at 121 quadrats in 2005.

A significant difference was found in the number of exotic species that occurred at eastern Wisconsin sites compared to northern Wisconsin sites ( $\chi^2 = 6.55$ ,  $df = 1$ ,  $p = 0.01$ ) (Table 3). This indicates that eastern Wisconsin sites experienced a greater increase in exotic species over the last 53 years compared to northern Wisconsin sites.

#### Habitat breadth index

Comparison of weighted habitat specialization between the two time periods resulted in no significant difference (paired  $t = 1.87$ ,  $p = 0.070$ ) although the results were suggestive that specialists are becoming more abundant (Table 1). The average habitat breadth of sites in 1952 was 6.54 while it was 6.30 in 2005. The average habitat breadth of species increased at 15 of the sites and decreased at 19 of the sites. Overall, habitat generalists have slightly decreased in favor of habitat specialists over the past 53 years.

#### Replicated G-test for goodness of fit



The G-test analysis identified 12 winner species, 4 loser species, and 50 no-change species. Winner species increases ranged from 135% to 480% since 1952 (Fig. 3). Winner species were all native species and a diverse mix of graminoids, ferns, and forbs, which are the dominant growth form. Winners also had a variety of traits including varying heights, dispersal, and pollination mechanisms. The loser species group experienced losses that ranged from 29% to 57% compared to 1952. This group was made up of native species that include one seedling, one fern, and two forbs (Fig. 4). The other 50 species exhibited no significant changes in abundance.

Winner species were represented by a diverse mix of nine plant families, which include the Araceae, Balsaminaceae, Cyperaceae, Dryopteridaceae, Equisetaceae, Liliaceae, Poaceae, Primulaceae and Ranunculaceae (Table 4). No one family dominated, but the Araceae, Dryopteridaceae, and Ranunculaceae each had two winner species. *Carex* spp. were the most prevalent winner “species” in the study, occupying 205 quadrats in 1952 and 473 in 2005, thus exhibiting a 230% increase. Locally, *Carex* spp. was found at 43% of quadrats in 1952 and 68% of quadrats in 2005. Regionally, they were found at 68% of sites in 1952 and 100% of sites in 2005 (Table 2). Lady fern (*Athyrium filix-femina*) experienced the greatest regional change increasing from 32% of sites in 1952 to 79% of sites in 2005. Locally, this species increased from 10% of quadrats in 1952 to 20% in 2005. This species also exhibited the greatest increase (480%) of all winner species. Starflower (*Trientalis borealis*) was the winner species that showed the greatest increase in local abundance increasing from 12% of quadrats in 1952 to 39% of quadrats in 2005. This species

increased by 182%, but was the only winner species to experience a decline in regional presence, decreasing from 91% of sites in 1952 to 88% of sites in 2005. All other winner species fell in between these extreme examples of increases and decreases.

Loser species were represented by 4 separate families: Liliaceae, Dryopteridaceae, Oleaceae, and Violaceae (Table 1). Violets (*Viola* spp.) experienced the greatest loss, decreasing 57% relative to 1952. Violets were found at 100% of the sites in 1952, but were only found at 74% of the sites in 2005 (Table 5). Blue-bead-lily exhibited the greatest regional loss, decreasing from 82% to 50% of the sites between 1952 and 2005. However, it increased locally at the quadrat level, by increasing from 29% of quadrats in 1952 to 32% of quadrats in 2005. Black ash (*Fraxinus nigra*) showed the largest local change, decreasing from 29% to 15% at the quadrat level between the two time periods.

Most winners (11 out of 12) and all loser species increased and declined, respectively, unevenly across sites (determined by the  $G_{\text{heterogeneity}}$  value). Lady fern was the lone winner species that increased evenly across all sites. No significant difference was found when the average heterogeneity, across sites, of losers (96%) was compared to the average heterogeneity of winners (84%) (paired  $t = -1.97$ ;  $df = 14$ ;  $p = 0.068$ ).

No significant change was found between winner, loser, and no-change groups in native/exotic status, pollination mode, dispersal mode, growth form, or plant height (Figs. 5-9). Neither the winner nor loser categories contained any exotic species, but two exotics were present in the no-change category. No significant difference was found in the native/exotic status between all groups ( $\chi^2 = 0.660$ ,  $df = 2$ ,  $p = 0.710$ ) (Fig. 5). Abiotic and biotic pollination modes were evenly split for loser species and somewhat evenly split for the winner species; 42% of winner species were abiotically pollinated

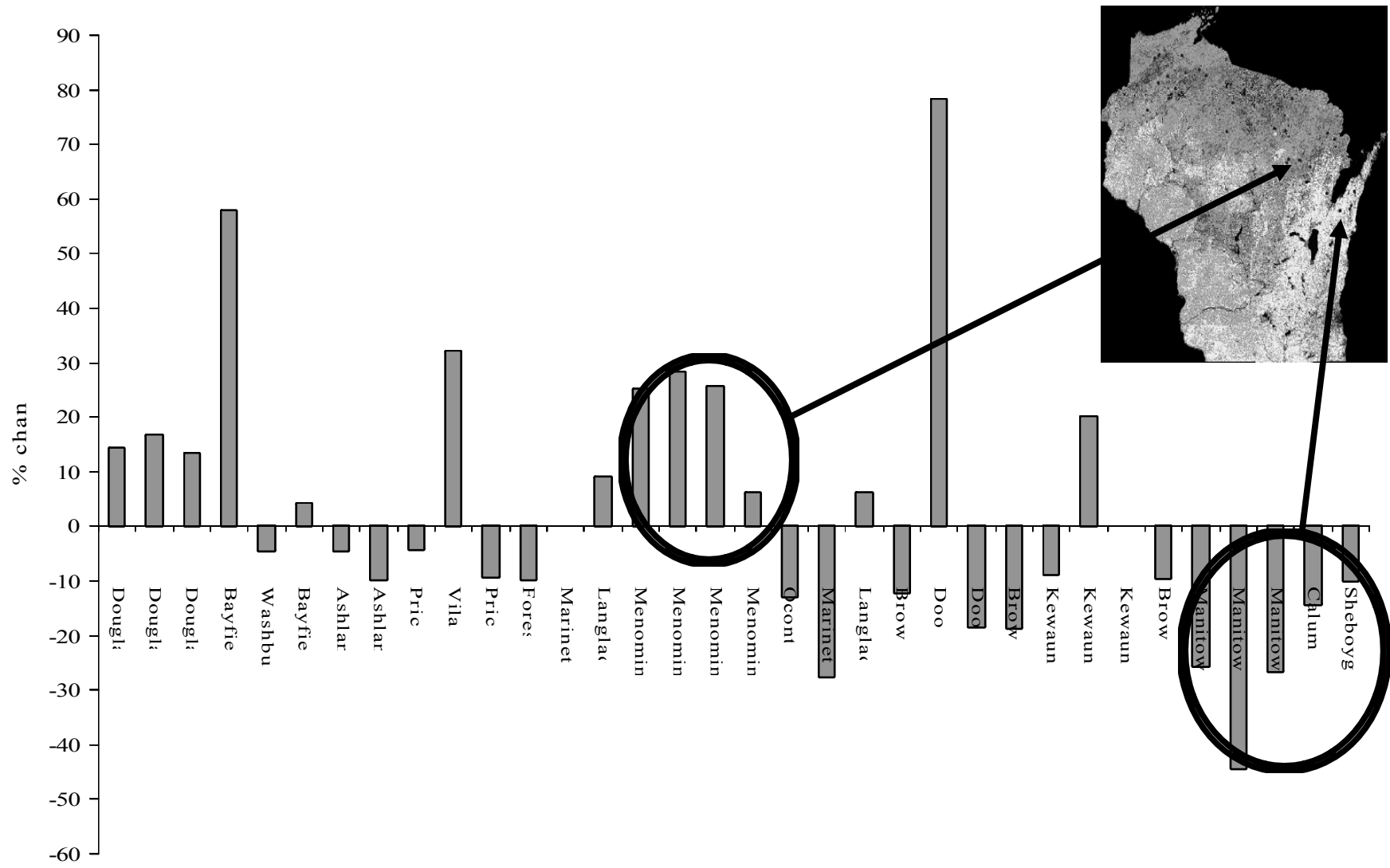


Figure 2. Percent change in species richness for each site between 1952 and 2005 geographically located from northwest Wisconsin to southeastern Wisconsin. The break between northern and eastern Wisconsin sites occurs between Langlade and Brown counties.

Table 1. Paired t-tests examining the differences among overall species richness, native species richness, site similarity, percent exotic species per site, and the mean habitat specialization value of sites between 1952 and 2005.

	1952		2005		p value
	Mean	Std. Dev.	Mean	Std. Dev.	
Overall species richness	42.62	9.68	42.21	9.04	0.79
Native species richness	42.50	9.71	41.24	9.49	0.45
Site similarity	0.61	0.05	0.60	0.06	0.31
Percent exotic species per site	0.02	0.008	0.03	0.04	0.0001
Habitat specialization value	7.72	0.46	7.56	0.54	0.07

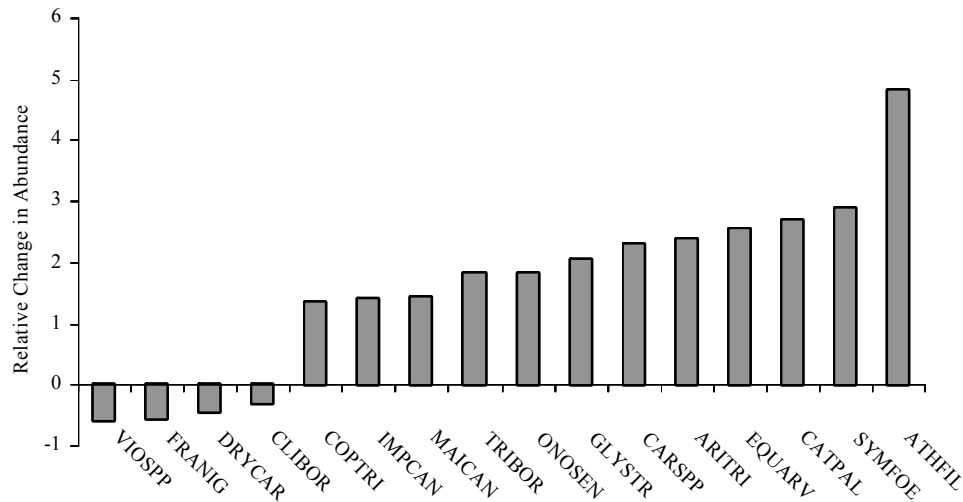
Table 2. T-tests examining the change in species richness and Jaccard's similarity index between private and public site ownership as well as northern vs. eastern Wisconsin site location between 1952 and 2005.

	Private or North		Public or East		p value
	Mean	Std. Dev.	Mean	Std. Dev.	
Private/Public site ownership (richness)	-1.06	8.29	0.24	10.44	0.67
North/East Wisconsin site location (richness)	2.19	8.25	-4.62	9.67	0.05
Private/Public site ownership (Jaccard's)	0.59	0.03	0.59	0.02	0.94
North/East Wisconsin site location (Jaccard's)	0.59	0.02	0.57	0.01	0.007

Table 3. Chi-squared analyses examining the differences among the number of exotic species at sites, the number of exotic species present at quadrats, and the number of exotic species by region in 1952 vs. 2005.

	1952 or East	2005 or North	$\chi^2$	df	p value
	# of occurrences	# of occurrences			
Exotic species change by site	4	20	99.01	1	0.0001
Exotic species change by quadr	12	121	16.49	1	0.0001
Exotic species by region	33	11	6.55	1	0.01

while 58% were biotically pollinated (Fig. 6). No-change species had 30% abiotic pollination and 70% biotic pollination. No significant differences were detected in the pollination mode between all groups ( $\chi^2 = 1.125$ ,  $df = 2$ ,  $p = 0.570$ ) nor between winners and losers ( $\chi^2 = 0.085$ ,  $df = 1$ ,  $p = 0.771$ ). For winner species, 75% were abiotically dispersed and 25% were biotically dispersed, while 62% of no-change species had abiotic dispersal and 38% had biotic dispersal (Fig. 7). No significant difference were found in the dispersal mode between all groups ( $\chi^2 = 1.049$ ,  $df = 2$ ,  $p = 0.592$ ) and between winner and loser species ( $\chi^2 = 0.873$ ,  $df = 1$ ,  $p = 0.350$ ). Forbs were the dominant growth form for winner (58%), no-change (46%), and loser (50%) groups (Fig. 8). No significant change was found



**Figure 3.** Change in the average quadrat frequency (1 m<sup>2</sup>), from 1952 to 2005, for each winner and loser species across all sites. Refer to table four for species names.

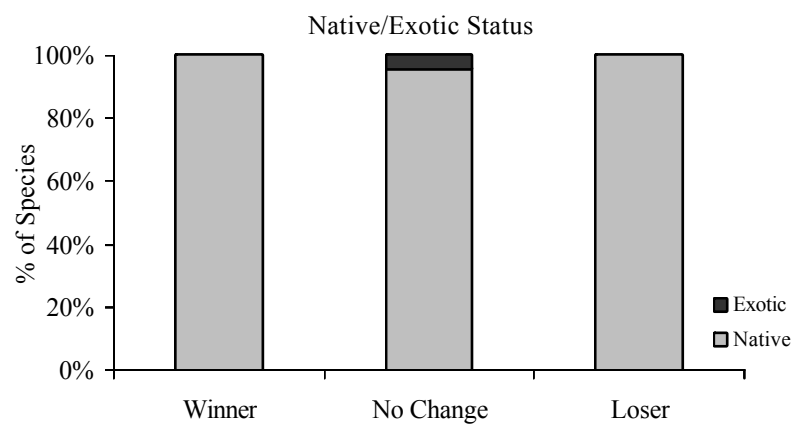
**Table 4.** Significant winner and loser understory species determined by replicated G-tests.

Species name	Species code	Plant family	Native/exotic	Growth form	Pollination mode	Dispersal mode
<b>Winners</b>						
Arisaema triphyllum	ARITRI	Araceae	N	Forb	B	B
Athyrium filix-femina	ATHFIL	Dryopteridaceae	N	Fern	A	A
Caltha palustris	CATPAL	Ranunculaceae	N	Forb	B	A
Carex spp.	CARSPP	Cyperaceae	N	Graminoid	A	-
Coptis trifolia	COPTRI	Ranunculaceae	N	Forb	B	A
Equisetum arvense	EQUARV	Equisetaceae	N	Fern Ally	A	A
Glyceria striata	GLYSTR	Poaceae	N	Graminoid	A	A
Impatiens capensis	IMPCAN	Balsaminaceae	N	Forb	B	A
Maianthemum canadense	MAICAN	Liliaceae	N	Forb	B	B
Onoclea sensibilis	ONOSEN	Dryopteridaceae	N	Fern	A	A
Symplocarpus foetidus	SYMFOE	Araceae	N	Forb	B	B
Trientalis borealis	TRIBOR	Primulaceae	N	Forb	B	A
<b>Losers</b>						
Clintonia borealis	CLIBOR	Liliaceae	N	Forb	B	B
Dryopteris carthusiana or D. intermedia	DRYCAR	Dryopteridaceae	N	Fern	A	A
Fraxinus nigra	FRANIG	Oleaceae	N	Seedling/Woody	A	A
Viola spp.	VIOSPP	Violaceae	N	Forb	B	B
Native/Exotic: N=native, E=exotic; Pollination and Dispersal mode: A=abiotic, B=biotic						

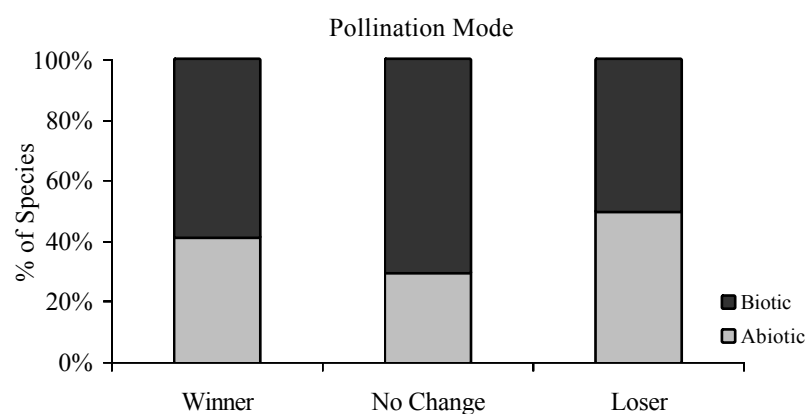
Table 5. Shifts in local and regional abundance of winner and loser understory species. Regional abundance is the proportion of sites occupied out of 34 sites and is represented in the “% of sites occupied” column for each time period. Local abundance is the average percentage of 1 m<sup>2</sup> quadrats that a species occupies at the sites it is present at. This figure is represented in the “Mean frequency” column for each time period. The percent of 1 m<sup>2</sup> quadrats occupied by a species across the landscape is represented in the “Total frequency” column.

Species name	% of sites occupied (1952)	% of sites occupied (2005)	Mean frequency (1952) (%)	Mean frequency (2005) (%)	Total frequency (1952) (%)	Total frequency (2005) (%)
Winners						
<i>Arisaema triphyllum</i>	47	59	10	20	5	12
<i>Athyrium filix-femina</i>	32	79	10	20	3	15
<i>Caltha palustris</i>	26	59	14	18	4	10
<i>Carex</i> spp.	68	100	43	68	31	68
<i>Coptis trifolia</i>	68	71	37	46	26	34
<i>Equisetum arvense</i>	29	68	17	18	5	12
<i>Glyceria striata</i>	56	71	16	27	9	18
<i>Impatiens capensis</i>	71	82	24	29	17	24
<i>Maianthemum canadense</i>	94	97	28	38	27	38
<i>Onoclea sensibilis</i>	47	68	13	17	6	11
<i>Symplocarpus foetidus</i>	12	21	11	21	3	4
<i>Trientalis borealis</i>	91	88	12	39	2	35
Losers						
<i>Clintonia borealis</i>	82	50	29	32	25	17
<i>Dryopteris carthusiana</i> or <i>D. intermedia</i>	94	74	29	21	28	16
<i>Fraxinus nigra</i>	76	65	29	15	22	10
<i>Viola</i> spp.	100	74	33	19	33	14

in the growth form between all the groups ( $\chi^2 = 10.054$ ,  $df = 6$ ,  $p = 0.122$ ) and between winner and loser groups ( $\chi^2 = 3.704$ ,  $df = 3$ ,  $p = 0.295$ ). Finally, winners and no-change groups both have 42% of species classified as having plant heights greater than 40 cm while loser species are mostly classified (50%) in the 20 to 40 cm category (Fig. 9). No significant change was found in plant height between all groups ( $\chi^2 = 1.005$ ,  $df = 4$ ,  $p = 0.909$ ) and between winner and loser species ( $\chi^2 = 0.444$ ,  $df = 2$ ,  $p = 0.801$ ).

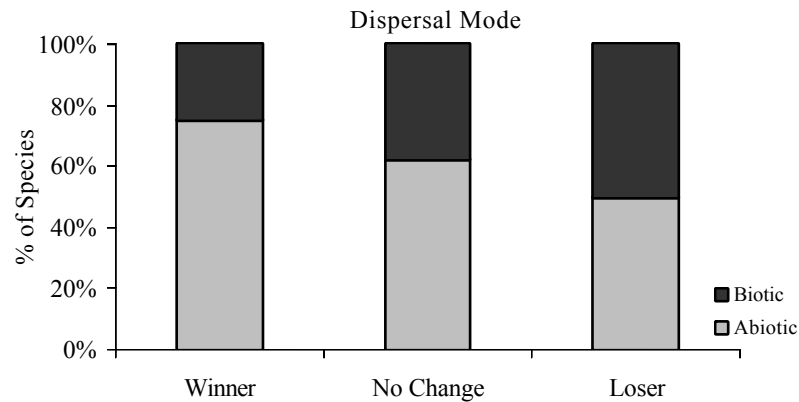


**Figure 4.** The proportion of native and exotic plants represented in winner, no-change, and loser species groups.

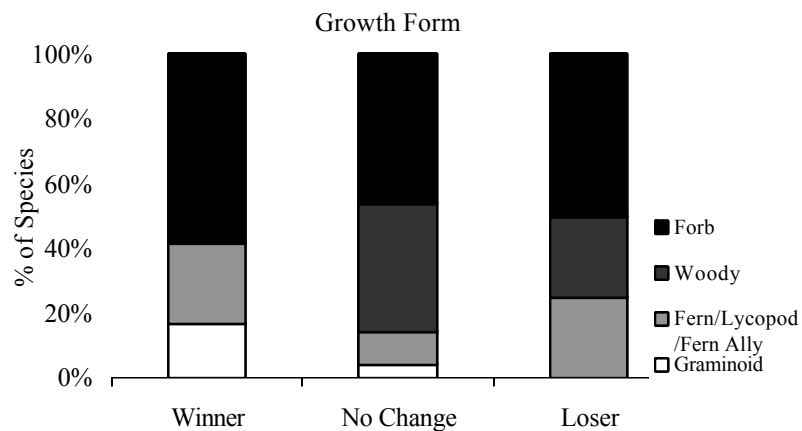


**Figure 5.** The proportion of abiotic and biotic pollination modes represented in winner, no-change, and loser species groups.

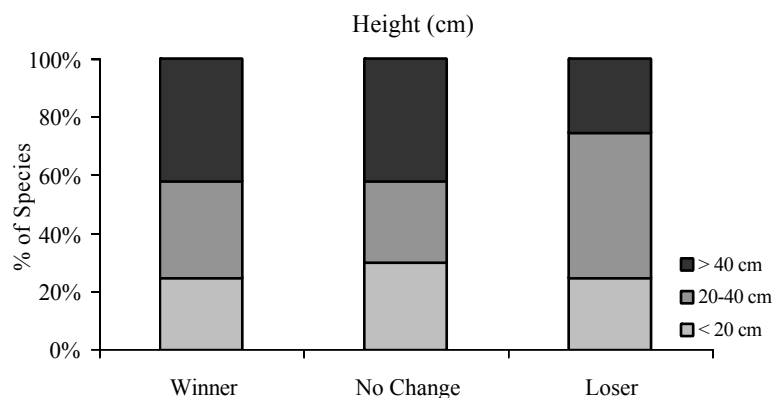




**Figure 6.** The proportion of abiotic and biotic dispersal modes represented in winner, no-change, and loser species groups.



**Figure 7.** The proportion of graminoid, fern, woody, and forb growth forms represented in winner, no-change, and loser species groups.



**Figure 8.** The proportion of differing plant heights represented in winner, no-change, and loser species groups.

## Overstory

The G-test analysis for the overstory species revealed two winner species, five loser species, and five no-change species. Winner species increases, since 1952, ranged from 115% to 256% (Fig. 10), while loser species decreased from 32% to 83% (Fig. 11). One out of two winner species and all loser species increased or declined, respectively, unevenly across sites according to the  $G_{\text{heterogeneity}}$  value.

For overstory species, cedar was by far the most common winner species, occurring at 100% of the sites in both 1952 and 2005. Cedar increased at 23 sites, decreased at 10 sites and stayed the same at one site. Cedar also increased locally from 41% of quadrats in 1952 to 48% in 2005 (Table 7). Black spruce (*Picea mariana*) was the winner species with the greatest increase (256%) both regionally (6% to 18%) and on a par with cedar locally (3% to 10%).

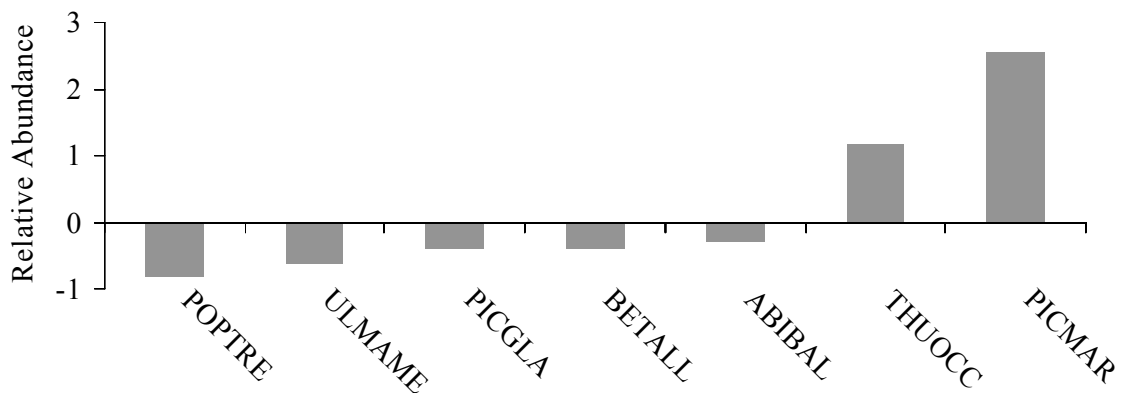
For loser species, trembling aspen (*Populus tremuloides*) was the largest loser species, decreasing 83% since 1952 (Fig. 11). It also experienced the largest decrease locally, declining from 7% to 3% of quadrats since 1952 (Table 7). Trembling aspen and American elm both showed similar declines regionally from 29% to 15% for aspen and 47% to 32% for elm. The other loser species: yellow birch, black spruce, and balsam fir all showed regional increases of 62% to 68%, 74% to 76%, and 29% to 41%, respectively. However, these species decreased locally from 12% to 7%, 11% to 8%, and 9% to 5% respectively.

The average basal area (BA) of all overstory species increased significantly across sites over the past 53 years (paired  $t = -4.34$ ;  $p = 0.0001$ ). Six sites lost BA while 28 sites gained BA relative to 1952. The dominant species, cedar, also experienced a significant

increase in average BA across sites (paired  $t = -6.08$ ;  $p = <0.0001$ ), increasing in BA at 31 sites.

**Table 6.** Paired t-tests examining the differences among overall basal area, cedar basal area, and CAV scores between 1952 and 2005.

	1952		2005		p value
	Mean	Std. Dev.	Mean	Std. Dev.	
Overall basal area	54.44	25.82	73.44	25.97	0.0001
Cedar basal area	53.45	35.54	85.44	36.86	0.0001



**Figure 9.** Change in the random-pairs frequency, from 1952 to 2005, for each winner and loser species across all sites. Refer to table seven for species names.

Table 7. Shifts in local and regional abundance of winner and loser understory species. Regional abundance is the proportion of sites occupied out of 34 sites and is represented in the “% of sites occupied” column for each time period. Local abundance is the average percentage of random-pair plots that a species occupies at the sites it is present at. This figure is represented in the “Mean frequency” column for each time period. The percent of random-pair plots occupied by a species across the landscape is represented in the “Total frequency” column.

Species name	Species code	Plant Family	% of sites occupied (1952)	% of sites occupied (2005)	Mean frequency (1952) (%)	Mean frequency (2005) (%)	Total frequency (1952) (%)	Total frequency (2005) (%)
Winners								
<i>Thuja occidentalis</i>	THUOCC	Cupressaceae	100	100	41	48	41	47
<i>Picea mariana</i>	PICMAR	Pinaceae	6	18	3	10	1	1
Losers								
<i>Betula alleghaniensis</i>	BETALL	Betulaceae	62	68	12	7	9	5
<i>Abies balsamea</i>	ABIBAL	Pinaceae	74	76	11	8	9	6
<i>Picea glauca</i>	PICGLA	Pinaceae	29	41	9	5	4	2
<i>Ulmus americana</i>	ULMAM E	Ulmaceae	47	32	6	4	3	1
<i>Populus tremuloides</i>	POPTRE	Salicaceae	29	15	7	3	2	0.4

## DISCUSSION

Northern wet-mesic communities have experienced changes in species richness over the past 53 years. Eastern Wisconsin sites have experienced a decrease in species richness while northern Wisconsin sites did not. Also, exotic species have increased across all sites. The Jaccard’s community similarity index between the 1952 and the 2005 northern wet-mesic communities scattered throughout northern Wisconsin was only

0.59, and of the 66 species tested for significant change in frequency, 6.25% have changed in frequency since 1952. Exploring the specific nature of the changes that are occurring in northern wet-mesic forests has the potential to provide insight into the future of these unique plant communities.

#### Major vegetation change at survey sites

Some northern wet-mesic sites have exhibited minor vegetation changes, such as an increase in the number of exotic species over the past 53 years, while others have exhibited major alterations such as complete vegetation shifts from one type of community to another. Northern wet-mesic forests are sensitive to hydrology changes (Stoeckeler, 1967). At 10.5% of the sites surveyed (4 of 38 sites), drastic vegetation change had occurred due to the alteration of drainage patterns. Specifically, evidence from the field indicates that the building of roads near and over the drainage outlets of northern wet-mesic forests, coupled with the damming of culverts by beavers led to flooded conditions. This in turn altered the vegetation at the sites. Altering the drainage patterns of northern wet-mesic forests can lead to the loss of these unique communities. Therefore, land management agencies and individuals interested in managing these areas should be aware of how management activities may change the water level and thus affect northern wet-mesic forests.

#### Absence of species richness change at local and regional spatial scales

On average, northern wet-mesic forest communities have not experienced a significant shift in local or regional species richness over the past 53 years. Although no significant change was found in this study, this does not definitely indicate an absence of change. There is often a lag time associated with a change in species diversity. Lindborg

and Erikson (2004) demonstrated that present-day species diversity is related to historic land use (i.e. 50-100 years before present) surrounding a given area. They found that the greater the connectivity between an area and its surroundings (e.g. the lower the fragmentation), the greater the species diversity. Therefore, sites that demonstrate high diversity and are subsequently cut-off from their historic surroundings, due to habitat loss and fragmentation, may respond immediately through a loss of species or there may be a lag before species loss occurs, a phenomenon referred to as “extinction debt” by Tilman et al. (1994). To fully understand if the lack of change in species richness found in this study is real and that these communities are truly not experiencing a change in species diversity, the historic land use surrounding each community under question would need to be analyzed in detail.

#### Species richness differences between land use

Historic land use data such as the amount and type of each land use practice surrounding the study sites are not readily available. Only current land use data are available for the sites and indicate a strong land use difference in eastern compared to northern Wisconsin. Species richness did not change evenly across sites. Some increased while others decreased. Certain groupings of communities within the study area changed more than others (e.g., an increase in species richness at Menominee Indian reservation sites and a decrease in species richness at sites in eastern Wisconsin). When sites are broken down based upon their geographic location (i.e. northern Wisconsin vs. eastern Wisconsin) and species richness is compared between these groupings, some interesting trends emerge.

Mladenoff et al. (1993) found that human-altered environments fragmentation increases, patchiness of the landscape increases, and patches become smaller and simpler in size and shape. This can then lead to a landscape of decreased connectivity which in turn will lead to increased habitat isolation and an increase in habitat edge to interior ratio (Mladenoff et al., 1993). In eastern Wisconsin compared to northern Wisconsin, there is more open land due to a higher percent of agriculture which leads to a more patchy landscape (increased isolation), greater amount of edge with more sharp edges (simpler patches). Throughout the entire study area, forest is the dominant land cover (47%), followed by agricultural land (27%), then wetlands (forested and non-forested) (20%) and lakes (4%) and finally urban area (0.1%). However, this can be broken down into regional differences between northern and eastern Wisconsin. For example, in the northern portion of the study area, 67% of the land is covered by upland forest, 21% is covered by wetlands, 3% is covered by lakes, 8% of the land is used for agricultural purposes, and 0.1% is urban. This is different from the eastern Wisconsin portion of the study area where 59% of the land is used for agriculture, 15% is forested, 18% is wetland, 6% is open water, and 1% is urban. Thus, eastern Wisconsin landscape is more fragmented with much more agricultural land compared to the relatively continuous swath of forest cover that constitutes the landscape of northern Wisconsin.

The greater landscape patchiness in eastern Wisconsin suggests why species diversity is decreasing in eastern Wisconsin. Maina and Howe (2000) found that most members of species abundances in fragmented area are at risk of extinction and replaced by vagile taxa such as weed species and through the release of common dominant species in the community. This in turn leads to a decline in species diversity

(Maina & Howe 2000). This is supported by study evidence which indicates that sites in eastern Wisconsin experienced a greater increase in the number of exotics species compared to northern Wisconsin (Table 3).

#### Exotic species increases

Exotic species have shown a significant increase at both the quadrat and site levels of scale over the past 53 years. Exotics occupied only 12 quadrats and four sites in 1952, but were present at 121 quadrats and 20 sites in 2005. The ratio of exotic to native species has also increased from an average of 0.3% to 3.4% over 53 years. Although sites are still dominated by native species, exotic species are becoming more common; this phenomenon has been identified in a number of studies to have the potential to drive biotic homogenization of a community (Lockwood et al., 2000; McKinney, 2004). Also, the sampled exotic species were absent from almost all sites 53 years ago. Although exotic species as a group have increased, no single exotic species became common enough to demonstrate significant increase over the past 53 years. On average, exotic species have not reduced native species richness, but this may change quickly within the coming years. In a similar time lag to that seen in species richness loss, the invasion of exotic species also has a time lag. In their 1998 study on the New Zealand mountain beech forests (*Nothofagus solandri* var. *cliffortioides*) that tracked an invasion of the herb *Hieracium lepidulum*, Wiser et al. (1998) found that the herb experienced a lag time between colonization time and population growth or an increase in abundance at sites. Wiser et al. (1998) attributed this to a dispersal limitation that only allowed the herb to occupy a small number of suitable sites at the beginning of the invasion before increasing



greatly in number. Therefore, it may be projected that exotic species will continue to increase across sites.

Of the six exotic species found in the 2005 study, only three were present in 1952; bittersweet nightshade (*Solanum dulcamara*), common dandelion (*Taraxacum officinale*), and narrow-leaved cattail (*Typha angustifolia*), while European swamp thistle (*Cirsium palustre*), orange hawkweed (*Hieracium aurantiacum*), and reed canary grass (*Phalaris arundinacea*) are new to the sites. All herbarium records and species information noted can be found at (<http://wisplants.uwsp.edu/VascularPlants.html>). Bittersweet nightshade is an introduced, potentially invasive, trailing perennial vine that was, according to herbarium records introduced into the southeastern portion of the state in the 1880s and has been moving steadily west and north. Common dandelion is an introduced and naturalized herb that can be found throughout Wisconsin. According to herbarium records it has been present in Wisconsin since at least the 1870s. Narrow-leaved cattail first appeared in southeastern Wisconsin in the 1930s and has been slowly expanding throughout Wisconsin. This plant is an introduced, potentially invasive, semi-aquatic herb that readily hybridizes with the native cattail, broad-leaved cattail (*Typha latifolia*). European swamp thistle is a recent invader of the Wisconsin landscape. This plant is considered an introduced and naturalized forb that was first recorded in north central Wisconsin in the early 1960s. It is currently locally common in eastern Wisconsin. Orange hawkweed is an introduced, invasive herb; there is a 1880s herbarium record from central Wisconsin, with later records showing its expansion throughout the state. Finally, reed canary grass, an ecologically invasive grass that occurs throughout Wisconsin, is typically able to form dense, monoculture stands that exclude all native

species in an area due to its rapid growth (Apfelbaum & Sams, 1987). Due to range expansion of these exotic species, as well as trends found by other researchers (Leach & Givnish, 1996; Rooney et al., 2004; Wiegmann & Waller, 2006; Rogers et al., in prep.) who have worked on related plant communities in the region, exotic species will likely persist and continue to increase unless action is taken to eradicate or control them.

#### Habitat specialization and similarity indices

Sites in this study have not lost habitat specialists or gained habitat generalist species over the past 53 years. The loss of uncommon natives and the gain of common species have been cited as the primary mechanism of biotic homogenization (McKinney & Lockwood, 1999; Rooney et al., 2004). The similarity index used in this study failed to identify a significant difference in similarity between the 1952 and 2005 time periods, indicating that species composition among sites is similar. Had this study found losses in specialist species with corresponding increases in generalist species, as well as similarity differences between communities in the different time periods, this might imply the loss of potentially important ecosystem functions and services (Hughes et al., 1997). A species that declines across its range of habitat is in danger of losing genetic diversity (Hobbs & Mooney, 1998). Also, population declines and losses are a precursor to endangerment or extinction of species, which in turn can lead to a niche opening in a community, potentially facilitating the invasion of an exotic species (Lyons & Schwartz, 2001). This type of exotic species invasion can lead to further invasions (Rooney et al., 2004). The absence of specialist species loss, generalist species increases, similarity differences, losses of habitats across a species range, and population decline absence

suggest the continued maintenance of the integrity of northern wet-mesic forest communities sampled in this study at least at this present time.

#### G-test winners and losers

Over the course of the last 53 years, 12 northern wet-mesic forest species have increased significantly (“winner group”) while four species have decreased significantly (“loser group”) (Figure 3). The life history characteristics of winner and loser species are not substantially different from one another. Neither group is dominated by either natives or exotic species (Figure 5). It was predicted that exotic species would significantly increase in abundance if northern wet-mesic forests have experienced a large amount of human disturbance over the past 53 years. However, this analysis demonstrates that there has been no significant change in the abundance of exotic species over the past 53 years, indicating that those species which are significantly increasing in abundance are not dominated by exotic species. Neither group differs in its pollination or dispersal method (Figure 6 & 7). It was also predicted that abiotically pollinated and dispersed plants would significantly increase in abundance if sites had lost biotic pollinators and dispersers. However, this study failed to find a decrease in the abundance of biotically pollinated or dispersed plants due to decreases in biotic pollinators and dispersers, meaning that sites are not experiencing the amount of disturbance that was predicted. Neither group differs in height; it was predicted that taller plants would benefit in northern wet-mesic forests if these communities became more open over the last 53 years (Figure 9). However, the analysis failed to demonstrate a significant change in the abundance of tall plants. This means that the study sites, on average, have not experienced openings in the canopy due to some form of disturbance, but are similar to

conditions 53 years ago. Neither group is dominated by one growth form (Figure 8). It was predicted that woody species and forbs would decrease while ferns and graminoids would increase under pressure from browsing. However, the analysis showed that there has not been a significant change in the abundance of any of the four growth forms examined. Therefore, on average, the abundance of woody species and forbs has not been significantly affected over the last 53 years by browsing. A number of studies have shown that deer browse has had a significant effect on certain plants important to northern wet-mesic communities (Rooney, 2001; Rooney et al., 2002; Rooney & Waller, 2003). This apparent contradiction may be due to presence of significant deer browse effects by 1952. None of the null hypotheses were refuted through research findings. Potential abiotic and biotic factors that may be responsible for the unanticipated results related to winner and loser species are theorized in the following section.

Mechanisms contributing to plant species changes observed in northern wet-mesic communities

A number of mechanisms were hypothesized to contribute to predicted plant species abundance changes in Wisconsin's northern wet-mesic forests. These mechanisms were hypothesized to be either anthropogenic or natural in origin and occurring at different spatial scales. Specifically, these mechanisms were (1) climate change, (2) range expansion, (3) succession, (4) land use changes, (5) timber harvest, (6) windstorms, (7) fire, (8) hydrological changes, (9) insect and plant disease, (10) ice and snow damage, (11) exotic species, (12) loss of biotic pollinators and dispersers, and (13) mammalian herbivory.

Fluctuation in regional climate is a naturally occurring phenomenon that changes slowly, over the course of a few hundred to a few thousand years (Gurevitch et al., 2002). Because of the generally slow nature of naturally-occurring climate change, the effects of this change have probably not been detected due to the relatively short time frame of this study. Anthropogenic actions such as fossil fuel energy use, urbanization, and land use changes are contributing to global climate change by increasing the amount of carbon dioxide and other greenhouse gases in the earth's atmosphere, which traps outgoing radiation from earth to space, increasing earth's temperature and leading to global warming (Barnes et al., 1998; Karl & Trenberth, 2003). This increase in temperature can lead to the range expansion of some species by providing suitable climatic conditions for their growth that may have not been present before current human-induced climatic trends (Davis, 1989). Certain exotic species, as well as some native species, may respond favorably to changes in climate by undergoing range expansion into areas not previously occupied (Davis, 1989). These species may then compete with the species in the area, leading to the decrease and possibly extirpation of these native species.

Climate change can also play a role in shaping overstory species presence and abundance in northern wet-mesic forests. Iverson and Prasad (2002) predict that cedar will eventually be extirpated from its current range in the United States due to global climate change. The anticipated effect of climate change over the past 53 years was the possible decrease in cedar abundance and possible extirpation of cedar in some northern wet-mesic forests. Data do not support this. Cedar abundance was found to have increased since 1952 sampling suggesting that global climate change has not produced measurable impacts on cedar at this point.

Landscape fragmentation and habitat loss has been identified by Wilcove et al. (1998) as one of the leading mechanisms of species extinction in the United States. Fragmentation can lead to a decrease in the plant richness, a reduction in forest cover, flora simplification, and a decrease in patch size due to parameters induced by roads, agricultural land, and urban development (Barnes et al., 1998; Harris, 1984; Saunders et al., 1991). Landscape fragmentation can lead to decreased species diversity and can also lead to increased deer numbers because these animals thrive in a fragmented environment. This in turn can have a detrimental affect on certain plant species. Deer herbivory has been highlighted as an important mechanism leading to the simplification of forest understory in the Upper Great Lakes due to increased deer densities over the past 50+ years (Waller & Alverson, 1997). Deer herbivory could be responsible for an increase in the abundance of sedges and decrease in blue-bead-lily found in this study. A number of recent studies have shown that forb species decrease and graminoid species increase with high deer density (Gill, 1992; Miller et al., 1992; Rooney & Dress, 1997; Rooney, 2001) and that deer may selectively browse plants that are larger and have a more conspicuous flower rather than abiotically pollinated or dispersed plants (Anderson, 1994; Balgooyen & Waller, 1995; Augustine & Frelich, 1998). Research by Rooney et al. (2004) supports this by showing that the greatest declines in biotically-pollinated and dispersed species occurred in areas that lacked hunting. Blue-bead-lily is quite palatable to herbivore species and was identified as an important spring food of deer in northern Wisconsin (McCaffery et al., 1974). Balgooyen & Waller (1995) found that blue-bead-lily experienced significant declines in abundance in areas of high deer densities in their study of the impacts of varying deer densities on herbaceous and woody plant species.

They also demonstrated a negative correlation between deer densities and the number of blue-bead-lily leaves and scape height. Szabo (2002) found that blue-bead-lilies grown in deer exclosures were significantly taller and had a greater number of leaves compared to those plants grown outside of the exclosures. These studies indicate that blue-bead-lily is significantly affected by deer browse and may be experiencing significant declines in northern wet-mesic forests because of browse pressure.

Sedges are a diverse group of plants; 29 separate species were identified during the 2005 survey, but these species were combined to match the 1952 Curtis sampling effort. As a result, detection of change by species was not possible. Sedges have a number of characteristics that have helped them to become winner species. These characteristics are their ability to abiotically pollinate, abiotically disperse, their clonal nature and their un-palatability to deer (Rooney, 2001; Wiegmann & Waller, 2006). In a disturbed environment, these characteristics can help sedges to increase, such as in the northern upland forest community (Wiegmann & Waller, 2006). However, northern wet-mesic communities appear to be fairly intact and relatively undisturbed. Therefore, the significant increase in the number of sedges may be due to a better 2005 sampling effort compared with 1952.

Succession affects overstory and understory structure and composition of a community. Succession is one of the mechanisms at work in this study and can be observed in the significant increases and decreases of some of the important overstory and understory species. Some of the changes in plant species that have occurred over the past 53 years are likely related to the significant increase in white cedar and overall basal area, as well as the significant increase in cedar abundance. Two “loser” species, violets

and black ash, both respond negatively to increases in shade. Violets are plants that rely upon periodic minor disturbances in order to maintain their abundance (Dr. Harvey Ballard, personal communication, 2006). If northern wet-mesic communities are becoming more shaded due to a greater amount of cedar in the overstory, then the decline in violets may reflect succession. Although this seems a likely scenario to explain the change in violets, Wiegmann & Waller (2006) also found that violets are decreasing in northern upland forests. Therefore, a different mechanism could be responsible for the hindrance of violet growth and reproduction. Black ash seedlings also appear to be decreasing potentially because of an increase in cedar shading. Black ash is a shade-intolerant tree (Harlow et al., 1979) that does not regenerate under a heavy canopy of cedar and therefore must take advantage of canopy gaps created by windthrow in the cedar overstory (Curtis, 1959). An increase in cedar basal area and abundance in northern wet-mesic communities could be leading to the decrease in black ash.

Successional change may also be leading to a significant increase in the abundance of starflower (*Trientalis borealis*) and goldthread (*Coptis trifolia*). The increase in abundance and basal area of canopy cedar may not only be shading these communities, but may also be acting as an insulating layer, buffering the forest floor from wind and extreme temperature variation (Dr. Robert Freckmann, personal communication, 2006). Starflower is a common northern wet-mesic community species which relies heavily upon vegetative reproduction from below-ground tubers (Anderson, 1970). In a greenhouse experiment, Anderson and Louckes (1973) demonstrated that starflower produced more and heavier tubers when day length was shortened and nighttime temperature was cool rather than during long days and warm nights. These



shorter day and cooler night conditions may be created by the increased abundance and basal area of cedar. Goldthread, a small plant (<12 cm) characteristic of northern wet-mesic communities (Voss, 1998), has similar habitat requirements to that of starflower and therefore may respond to changing conditions in a similar manner (Dr. Robert Freckmann, personal communication, 2006). Sensitive fern (*Onoclea sensibilis*) is a common fern of swamps, open woods, and open meadows that is known for its sensitivity to frost (Gleason & Cronquist, 1991). This plant may also be increasing because of the insulating effect of an increased cedar overstory protecting it from cold air that collects in low areas of the landscape known as frost pockets (Dr. Robert Freckmann, personal communication 2006). Because of this insulating effect, sensitive fern may be protected from early season frosts and may be able to photosynthesize longer into the fall. Further research is needed to examine specific micro site differences of northern wet-mesic communities under open and closed canopy conditions.

Some of the winner species such as jack-in-the-pulpit (*Arisaema triphyllum*), water-arum (*Caltha palustris*), common horsetail (*Equisetum arvense*), fowl manna grass (*Glyceria striata*), orange jewelweed (*Impatiens capensis*), Canada mayflower (*Maianthemum canadense*), and skunk-cabbage (*Symplocarpus foetidus*) are typically found under conditions where a greater amount of light is present than those which are found under a thick canopy of cedar. Therefore, these winner species may be increasing at sites where cedar has become less abundant over the past 53 years. Even though on average, cedar basal area has increased at most of the sites (31) and cedar abundance has increased significantly at most sites (23) over the past 53 years, cedar abundance has not increased evenly across sites as judged by the  $G_{\text{heterogeneity}}$  value. Although most sites are

experiencing an increase of cedar in the canopy, a number of sites are not, which could explain why some of the winner species, better suited for open environments, are increasing. In most cases, shade intolerant species are increasing at the sites where cedar has not increased.

The overstory of northern wet-mesic communities has increased in overall basal area, cedar basal area, cedar abundance, and black spruce abundance. Results also indicate that these communities are decreasing in balsam fir, yellow birch, American elm, white spruce, and trembling aspen. The G-test and basal area evidence indicates that the amounts of mature cedar in northern wet-mesic communities are increasing in abundance, while common deciduous and coniferous tree species are decreasing in abundance. The increase in overall tree basal area indicates that the trees within sites are, on average, increasing in size. This is supported by anecdotal evidence that timber harvesting within the studied northern wet-mesic communities was rare over the last 53 years. The increase in abundance of cedar may be leading to significant decreases in the abundance of yellow birch and trembling aspen. Tree data from 1952 and 2005 indicate that many of the yellow birch and trembling aspen were larger diameter than the other recorded trees, indicating that these were older trees. These older trees may have died over the past 53 years, resulting in the significant decline of these two species. Yellow birch is considered to have intermediate shade tolerance, but requires a canopy opening for successful regeneration, while trembling aspen is a pioneer species requiring open conditions for regeneration (Curtis, 1959). Therefore, regeneration of these species may have then been hampered by the increase in cedar abundance leading to increased shade. Most northern wet-mesic communities have experienced successional change over the last 53 years in

the form of increased cedar basal area, which has led to understory plant species changes.

Mechanisms of community change such as windstorms, ice and snow damage, insects/disease, fire, and decrease in biotic pollinators and dispersers can play a role in shaping vegetation communities. However, these five disturbances did not appear to have played a large role in altering the composition, structure, or function of my sampled northern Wisconsin wet-mesic forest communities over the last 53 years.

The effects of major windstorms, ice and snow damage, and fire were not observed in any of the 34 northern wet-mesic forests surveyed in this study. A few trees at each site may have succumbed to minor windstorms and/or ice and snow damage evidenced by missing limbs and leaning positions of some trees (personal observation). Evidence of fire was not observed in any of the communities visited. Also, statistical analyses conducted on the winner and loser species to determine if taller species outcompeted shorter species over the last 53 years, due to openings in the canopy, failed to produce significant results suggesting that the canopy trees of the sampled communities remained intact.

Non-native insects such as *Ophlostoma ulmi* have contributed to the decline of American elm by acting as a vector for Dutch elm disease. American elm was a minor component of northern wet-mesic forests 53 years ago (Curtis, 1959), and as predicted, has significantly decreased in abundance over the past 53 years, most likely due to Dutch elm disease.

Declines in the relative abundance of biotically-pollinated and dispersed species were not observed in this study; however, a comparable study that examined northern

upland forests of Wisconsin found significant declines in the relative abundance of both biotically-pollinated and dispersed species especially in areas where deer hunting was prohibited (Rooney et al; 2004; Wiegmann & Waller, 2006). These declines of biotically pollinated and dispersed species may be the result of deer preferring large, showy flowers and may trigger a decline in pollinator abundance as well as plant species richness (Kearns & Inouye, 1997). Declines in biotically pollinated and dispersed species may also be the result of declines of the animal mutualists that pollinate and disperse these species due to habitat alterations, exotic species, and/or pesticide use (Buchmann & Nabhan, 1996; Wiegmann & Waller, 2006). Even though the abundance of biotically pollinated and dispersed as well as abiotically pollinated and dispersed plant species has not been altered over the past 53 years, the potential for similar declines in biotically pollinated and dispersed species is possible due to northern wet-mesic communities' proximity to northern upland forests in the same landscape, and similar mechanisms affecting both communities.

There are a number of mechanisms that have the potential to interact in multiple ways. For example, habitat fragmentation contributes to increased deer numbers, which can increase browsing pressure on sensitive plant species. This increase in browse pressure can lead to deer consuming more showy flowers and fruits thereby contributing to a decline in biotic pollinators and dispersers (Kearns & Inouye, 1997). Thus, the results of this study cannot be used to determine which mechanisms are leading to the changes observed in this study. However, the results of the study do show patterns over a number of sites and over a broad area of land. The results also suggest windthrow, and lack of biotic pollinators and dispersers may not be important factors in the observed

changes while supporting other hypotheses such as the impact of succession and deer herbivory.

### Study Shortcomings

As with any study, a greater number of sites and a higher sampling frequency would give researchers a more accurate picture of the current state of northern wet-mesic forest communities. A greater number of sample sites in northern wet-mesic communities would better represent these communities across the landscape. A greater sampling frequency of the study sites would allow researchers to track when changes occur in these communities, such as when an exotic species first enters a site and its subsequent spread throughout the site and to other sites. An increase in sampling frequency would also lessen the chances of sampling in an abnormal year caused by annual temperature and precipitation fluctuations. Both sample years (1952 and 2005) of this study could have been abnormal years (e.g. one year could have been in a drought while the other could have been very wet). Some plant species may not be present in either very wet or very dry years leading to misleading findings of plant changes in abundance or presence. More years of sampling would average out these fluctuations.

This study could also be improved by increasing the number of quadrats sampled at each site. This more intensive sampling would increase detection of rare species. For example, we do not know whether rare, browse-sensitive species such as certain orchids (e.g. showy lady's-slipper (*Cypripedium reginae*)) have declined since 1952 because they are too uncommon to be detected using the Curtis survey protocol of only 20 quadrats per site. Increasing the number of quadrats sampled to a number greater than 20 could improve the chance of detecting rare plant species.

Curtis's plant ecology laboratory misidentified or lumped taxa, or split taxa into no-longer- recognized groups. Plant species lists of 1952 had to be matched to contemporary species lists to accurately match data. This was accomplished by lumping some species together such as members of the genus *Carex*, where two species were identified in 1952 and 29 species were identified in 2005. All species in both time periods falling under the genus *Carex* were lumped together in one group labeled *Carex* sp. to allow comparison. The implication of this lumping was that detecting changes in abundance of specific plant species has been reduced for some species.

There is evidence that misidentification of several species in the field lead to apparent, significant changes in plant species abundances; Spinulose wood fern (*Dryopteris carthusiana*) and fancy wood fern (*Dryopteris intermedia*) have significantly declined over the past 53 years while lady fern has increased. Fern species are not particularly susceptible to deer browse (Rooney, 2001) and fancy wood fern was found to be significantly increasing in northern upland forests (Wiegmann & Waller, 2006). Spinulose wood fern and fancy wood fern may be "decreasing" in this study due to misidentification and confusion with lady fern by field technicians during the original 1952 survey. Similarly, black spruce may be increasing and white spruce may be decreasing because of the misidentification of white spruce as black spruce by field technicians in the 1952 survey. These two species are closely related in form and size and can be easily misidentified in the field. Balsam fir may also have been misidentified in 1952 and therefore recorded at a greater abundance than was actually present. This is possible because balsam fir exhibits a similar growth form and can grow in habitats similar to black spruce.

The regeneration of tree species, especially cedar, is an important function in northern wet-mesic forests because tree seedlings and saplings provide the future canopy of these communities. Comparing the amount of seedlings and saplings in 1952 to the amount in 2005 could provide researchers with information on what species will constitute the future forest canopy of northern wet-mesic forests. Significant decreases in cedar regeneration could indicate an impending canopy alteration in northern wet-mesic forests because young cedar are not replacing older cedar while significant increases in cedar regeneration may indicate healthy northern wet-mesic forests that will thrive into the future. However, the 1952 Curtis study provides inconsistent data regarding cedar regeneration. This prevents viable comparison to 2005 data. The 2005 data were complete in this aspect future studies may be able to utilize the 2005 data.

Hydrological changes within northern wet-mesic forests have a significant effect on the plant species that occur in these unique communities (Stoekeler, 1967); however, this important component was not measured in this study. The effect that hydrological change has on northern wet-mesic forests is evidenced by the vegetation change (e.g., overstory die-off and subsequent understory vegetation shift) that occurred at sites as a result of flooding from road building and beaver activity. Other hydrological change that may be important to the plant species that occur in northern wet-mesic communities may include pH level, the amount of runoff absorbed by the community, and groundwater flow; however, these potentially important hydrology-related measures were not assessed in this study.

Some of the understory species (violets and black ash) have experienced significant decreases in abundance that may be attributed to successional changes caused

by shading from cedar overstory leading to decreased light availability in the understory. Also, decreases in light levels may also be contributing to the increase in goldthread and starflower. In order to determine if light availability is a mechanism of change, accurate light level data needed. This would allow researchers to positively determine whether or not species theorized to be affected by changes in light levels are actually changing because of the availability of light.

Although the study sites are well-distributed across Wisconsin, they may not reflect many of the changes that are occurring in all 810,000 hectares of northern wet-mesic forests throughout the Great Lakes states. In fact, the northern wet-mesic forests used in this study only represent a total of approximately 300 hectares. Researchers should expand upon the methods of J.T. Curtis and colleagues to include soil, hydrological, and light data as well as more intense sampling of sites to pick up fine scale plant changes such as rare orchids. Although additional data sets would answer pertinent questions, Curtis's data has been invaluable to plant ecology researchers in Wisconsin tracking plant changes.

### Conclusion

In their 2004 study of northern Wisconsin upland forests, Rooney et al. (2004) called for more research to examine whether the biotic impoverishment they found in their study was also occurring in other regions and plant communities. Without the use of long-term monitoring plots, changes such as the expansion of tolerant natives and the decline of sensitive native species may go unnoticed in the phenomenon known as the "invisible present" (Magnuson, 1990). Evidence from this study demonstrates that the



changes I hypothesized to be occurring in northern wet-mesic communities are not occurring at the magnitude forecasted. Essentially, northern wet-mesic communities are fairly similar, in botanical composition, to what they were 53 years ago, except for a so-far small increase in exotic species. These results are in contrast to those of Rooney et al. (2004) and Wiegmann & Waller (2006), who found significant changes in northern upland forest plant communities; Leach & Givnish (1996), who recorded significant changes in Wisconsin prairies; and Rogers et al. (in prep.), who demonstrated significant plant changes in southern upland forests. Significant plant changes are occurring in a number of Wisconsin plant communities, yet northern wet-mesic communities remain as yet relatively unaltered, at least at the scale of this study.

Northern wet-mesic communities may have been protected to this point by their lack of accessibility. These areas did not appear to have been significantly utilized over the past 53 years. Although northern wet-mesic communities appear to be more stable than some other Wisconsin plant communities (northern upland forest, southern upland forest, and prairies), there seem to be a few early warning signs that northern wet-mesic communities may be moving in the direction of these other communities. One such example is the significant increase in the number of exotic species found across quadrats and sites. Given the nature of exotic species, they will probably continue to increase in northern wet-mesic communities, and displace native species, unless management action is taken. An increase in exotic species will lead to an increase in similarity between sites, making these communities less unique.

Northern wet-mesic forests are a unique vegetation community in the Great Lakes region and are considered important for their contribution to water quality, plant and

animal habitats, and cultural and economic uses. This study has found some significant changes in exotic species presence, overstory abundance and basal area, understory abundance, and geographic site location as well as no change in average species richness, native species richness, mean similarity, mean habitat specialization, public/private land status, native/exotic status, pollination and dispersal modes, plant height, and plant growth form.

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APPENDIX ONE. Species list of 144 plants found at sites in 1952 and 2005.

<i>Abies balsamea</i>	<i>Dryopteris cristata</i>	<i>Osmorhiza claytonii</i>	<i>Picea glauca</i>
<i>Acer rubrum</i>	<i>Epilobium ciliatum</i> or <i>E. coloratum</i>	<i>Osmunda cinnamomea</i>	<i>Thuja occidentalis</i>
<i>Acer saccharum</i>	<i>Equisetum arvense</i>	<i>Pilea pumila</i>	<i>Tilia americana</i>
<i>Acer spicatum</i>	<i>Eupatorium maculatum</i>	<i>Fagus grandifolia</i>	<i>Toxicodendron rydbergii</i>
<i>Adiantum pedatum</i>	<i>Fragaria virginiana</i>	<i>Platanthera huronensis</i>	<i>Trientalis borealis</i>
<i>Agrostis perennans</i>	<i>Fraxinus nigra</i>	<i>Poa</i> spp.	<i>Trillium cernuum</i>
<i>Alnus incana</i>	<i>Fraxinus pennsylvanica</i>	<i>Polygala paucifolia</i>	<i>Trillium grandiflorum</i>
<i>Amelanchier</i> spp.	<i>Galium trifidum</i>	<i>Polygonatum pubescens</i>	<i>Tsuga canadensis</i>
<i>Amphicarpaea bracteata</i>	<i>Galium triflorum</i>	<i>Polygonum sagittatum</i>	<i>Ulmus americana</i>
<i>Anemone quinquefolia</i>	<i>Gaultheria hispida</i>	<i>Populus balsamifera</i>	<i>Urtica dioica</i>
<i>Aralia nudicaulis</i>	<i>Gaultheria procumbens</i>	<i>Populus tremuloides</i>	<i>Viola</i> spp.
<i>Aralia racemosa</i>	<i>Geum</i> spp.	<i>Prunella vulgaris</i>	<i>Vitis riparia</i>
<i>Arisaema triphyllum</i>	<i>Glyceria canadensis</i>	<i>Prunus serotina</i>	
<i>Asarum canadense</i>	<i>Glyceria striata</i>	<i>Pteridium aquilinum</i>	
<i>Aster lanceolatus</i>	<i>Gymnocarpium dryopteris</i>	<i>Pyrola elliptica</i>	
<i>Aster lateriflorus</i>	<i>Huperzia lucidula</i>	<i>Quercus rubra</i>	
<i>Aster macrophyllum</i>	<i>Hydrophyllum virginianum</i>	<i>Ranunculus recurvatus</i>	
<i>Aster puniceus</i>	<i>Ilex mucronata</i>	<i>Rhamnus alnifolia</i>	
<i>Aster umbellatus</i>	<i>Ilex verticillata</i>	<i>Ribes americanum</i>	
<i>Athyrium filix-femina</i>	<i>Impatiens capensis</i>	<i>Ribes lacustre</i>	
	<i>Iris virginica</i> or <i>I. versicolor</i>	<i>Ribes</i> spp.	
<i>Betula alleghaniensis</i>	<i>Lactuca canadensis</i>	<i>Ribes triste</i>	
<i>Bidens</i> spp.	<i>Laportea canadensis</i>	<i>Rubus idaeus</i>	
<i>Botrychium virginianum</i>	<i>Ledum groenlandicum</i>	<i>Rubus pubescens</i>	
<i>Brachyelytrum erectum</i>	<i>Linnaea borealis</i>	<i>Rumex</i> spp.	
<i>Bromus</i> spp.	<i>Lonicera canadensis</i>	<i>Saxifraga pensylvanica</i>	
<i>Calamagrostis canadensis</i>	<i>Lonicera oblongifolia</i>	<i>Scutellaria galericulata</i>	
<i>Calla palustris</i>	<i>Lonicera villosa</i>	<i>Scutellaria lateriflora</i>	
<i>Caltha palustris</i>	<i>Lycopodium annotinum</i>	<i>Solanum</i> spp.	
<i>Campanula aparinoides</i>	<i>Lycopodium clavatum</i>	<i>Solidago</i> spp.	
<i>Carex</i> spp.	<i>Lycopodium dendroideum</i> or <i>L. obscurum</i>	<i>Sorbus</i> spp.	
<i>Chelone glabra</i>	<i>Lycopus</i> spp.	<i>Spiraea alba</i>	
<i>Cicuta maculata</i>	<i>Lysimachia thyrsoiflora</i>	<i>Stachys palustris</i>	
<i>Cinna</i> spp.	<i>Maianthemum canadense</i>	<i>Stellaria</i> spp.	
<i>Circaea alpina</i>	<i>Maianthemum stellatum</i>	<i>Streptopus roseus</i>	
<i>Cirsium muticum</i>	<i>Maianthemum trifolium</i>	<i>Symplocarpus foetidus</i>	
<i>Clintonia borealis</i>	<i>Matteuccia struthiopteris</i>	<i>Taraxacum officinale</i>	
<i>Comarum palustre</i>	<i>Mitchella repens</i>	<i>Taxus canadensis</i>	
<i>Coptis trifolia</i>	<i>Mitella diphylla</i>	<i>Thalictrum dioicum</i>	
<i>Cornus alternifolia</i>	<i>Mitella nuda</i>	<i>Osmunda regalis</i>	
<i>Cornus canadensis</i>	<i>Moneses uniflora</i>	<i>Oxalis montana</i>	
<i>Cornus stolonifera</i>	<i>Onoclea sensibilis</i>	<i>Packera aurea</i>	
<i>Corylus cornuta</i>	<i>Orthilia secunda</i>	<i>Parthenocissus vitacea</i>	
<i>Diervilla lonicera</i>			
<i>Dryopteris carthusiana</i> or <i>D. intermedia</i>	<i>Oryzopsis asperifolia</i>	<i>Phegopteris connectilis</i>	

Appendix one continued.

Species list of 48 plants found at sites in 1952, but not 2005

<i>Achillea millefolium</i>	<i>Epilobium leptophyllum</i>	<i>Potentilla simplex</i>
<i>Actaea</i> spp.	<i>Erigeron</i> spp.	<i>Prenanthes alba</i>
<i>Anaphalis margaritacea</i>	<i>Galium aparine</i>	<i>Prunus pensylvanica</i>
<i>Anemone acutiloba</i>	<i>Geranium maculatum</i>	<i>Prunus virginiana</i>
<i>Antennaria</i> sp.	<i>Hamamelis virginiana</i>	<i>Pyrola rotundifolia</i>
<i>Betula papyrifera</i>	<i>Juncus</i> spp.	<i>Ranunculus abortivus</i>
<i>Betula pumila</i>	<i>Lactuca biennis</i>	<i>Ribes hudsonianum</i>
<i>Chamaedaphne calyculata</i>	<i>Lysimachia ciliata</i>	<i>Salix</i> spp.
<i>Circaea lutetiana</i>	<i>Mentha arvensis</i>	<i>Sambucus canadensis</i>
<i>Clematis virginiana</i>	<i>Monarda fistulosa</i>	<i>Sanguinaria canadensis</i>
<i>Cornus rugosa</i>	<i>Monotropa uniflora</i>	<i>Sanicula</i> spp.
<i>Cryptotaenia canadensis</i>	<i>Osmunda claytoniana</i>	<i>Schizachne purpurascens</i>
<i>Cypripedium reginae</i>	<i>Physocarpus opulifolius</i>	<i>Sium suave</i>
<i>Cystopteris</i> spp.	<i>Picea mariana</i>	<i>Vaccinium macrocarpon</i>
<i>Drosera</i> sp.	<i>Poa palustris</i>	<i>Viburnum acerifolium</i>
<i>Epilobium angustifolium</i>	<i>Polygonum cilinode</i>	<i>Waldsteinia fragarioides</i>

Species list of 52 plants found at sites in 2005, but not 1952

<i>Agrimonia gryposepala</i>	<i>Fraxinus americana</i>	<i>Pinus strobus</i>
<i>Asclepias incarnata</i>	<i>Galium asprellum</i>	<i>Platanthera obtusata</i>
<i>Aster ciliolatus</i>	<i>Galium boreale</i>	<i>Platanthera psycodes</i>
<i>Cardamine bulbosa</i>	<i>Goodyera repens</i>	<i>Polygonum arifolium</i>
<i>Cardamine diphylla</i>	<i>Goodyera tessellata</i>	<i>Populus grandidentata</i>
<i>Cardamine pratensis</i>	<i>Halenia deflexa</i>	<i>Pyrola asarifolia</i>
<i>Chrysosplenium americanum</i>	<i>Heracleum lanatum</i>	<i>Ranunculus hispidus</i>
<i>Cicuta bulbifera</i>	<i>Hieracium aurantiacum</i>	<i>Ribes glandulosum</i>
<i>Cirsium palustre</i>	<i>Larix laricina</i>	<i>Ribes hirtellum</i>
<i>Cirsium</i> spp.	<i>Lemna minor</i>	<i>Rubus hispidus</i>
<i>Corallorhiza trifida</i>	<i>Listera cordata</i>	<i>Thalictrum dasycarpum</i>
<i>Cypripedium parviflorum</i> var. <i>pubescens</i>	<i>Lonicera hirsuta</i>	<i>Thelypteris palustris</i>
<i>Elymus virginicus</i>	<i>Luzula acuminata</i>	<i>Typha</i> spp.
<i>Epilobium</i> sp.	<i>Maianthemum racemosum</i>	<i>Vaccinium angustifolium</i>
<i>Equisetum fluviatile</i>	<i>Menyanthes trifoliata</i>	<i>Vaccinium myrtilloides</i>
<i>Equisetum scirpoides</i>	<i>Petasites frigidus</i>	<i>Vaccinium oxycoccus</i>
<i>Eriophorum</i> spp.	<i>Phalaris arundinacea</i>	<i>Viburnum lentago</i>
		<i>Viburnum trilobum</i>