Assessment of Anthropogenic Disturbances to Mesic Northern Forests and Summary of Restoration Strategies: A Multi-Scale Approach

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Cover images: 1998 digital orthoquad of old-growth hemlock/hardwood forest from the Sylvania Wilderness and photograph of canopy gap within beech/sugar maple forest (Photo by Gary Reese).

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EXECUTIVE SUMMARY

Mesic northern forest is a forest type of moist-to-dry mesic sites lying mostly north of the transition zone, characterized by the prevalence of sugar maple and beech. Hemlock and white pine are frequently important canopy components. Mesic northern forests are found chiefly in morainal landscapes and typically on loamy sand to sandy loam. The natural disturbance regime is characterized by frequent, small windthrow gaps, which allow for the regeneration of the shade-tolerant canopy dominants. Catastrophic windthrow occurred infrequently with several generations of trees passing between large-scale, severe disturbance events. As result, mesic northern forests historically dominated vast areas of mesic uplands of the Great Lakes and were multi-generational, with old-growth conditions lasting many centuries. Large contiguous tracts of old-growth and late-successional mesic northern forest provide important habitat for numerous plants, vertebrates, and invertebrates that are dependent on the diverse functional, structural, and composition attributes of mesic northern forest.

Intensive and pervasive anthropogenic disturbance during the past 150 years has altered the extent, landscape pattern, natural processes, structure, and species composition of mesic northern forest.

- Mesic northern forest, especially old-growth and late-successional forest, has been drastically reduced in acreage. Large tracts of primary old-growth forest, concentrated in the western Upper Peninsula, constitute less than 0.2% of Michigan.
- Mesic northern forest has become fragmented, with most old-growth and late-successional stands persisting as remnant patches enmeshed in a matrix of agricultural lands, early-successional forest, and young northern hardwoods.
- Short rotation timber management has replaced gap-phase dynamics as the dominant disturbance factor impacting structure and composition.
- Structural alterations include the reduction of large-diameter trees, snags, and coarse woody debris.

- Hemlock and white pine have declined in importance within these systems, and have been completely eliminated from many landscapes.
- Chronically high deer densities have limited tree recruitment and altered floral composition and structure.
- Genetic diversity has eroded as old-growth and late-successional forests have declined.

Anthropogenic disturbance has degraded mesic northern forest across spatial scales. Therefore, biodiversity management requires a multi-scale approach. Efforts to restore mesic northern forest will be most successful when managers emulate natural disturbance regimes and manage landscapes within the historical range of variability. Historical hindsight and ecological insight can help guide restoration. General recommendations for landscape-level restoration include:

- Leave large tracts of mesic northern forest (especially old-growth and late-successional forest) unharvested and allow natural processes such as windthrow and succession to operate unhindered.
- Increase the acreage of mesic northern forest by allowing early-successional forest to convert to late-successional forest.
- Reduce forest fragmentation by decreasing forest harvest levels, halting the creation of wildlife openings within mesic forest systems, closing redundant forest roads, limiting the creation of new roads, and allowing existing wildlife openings and old fields to revert to forest.
- Extend rotation periods of managed forest beyond 100 years to allow for the development of late-successional characteristics and species.
- Reduce high deer densities to levels where herbivory no longer limits tree recruitment and reduces floral diversity.
- Increase fire management across the landscape to increase the available seed source of fire-dependent species such as white pine.

It is imperative that landscape-level management efforts be accompanied by site-level restoration and biodiversity management. Stand-level recommendations include:

- Maximize forest continuity by retaining large-diameter (> 60 cm) snags, coarse woody debris, and old, living trees.
- Where snags and coarse woody debris are lacking, increase structural heterogeneity by creating snags through girdling, felling trees, and if necessary, skidding in large-diameter, long-lived, slowly decaying conifer species.
- Retain and promote white pine and hemlock where they persist
    - Maintain and create suitable sites for establishment through retention of nurse logs and exposure of mineral soil through prescribed surface fires or scarification.
    - Resources permitting, erect deer exclosure fences to protect hemlock and white pine recruitment.
- Where hemlock and white pine seed sources are absent, underplant saplings.
- Mimic gap-phase dynamics and promote dead-tree dynamics when harvesting mesic northern forests.
- Maintain the genetic legacy of managed forest by retaining old trees and promoting natural regeneration

Degradation of mesic northern forest occurred because of repeated and ubiquitous anthropogenic disturbance, the impact of which reverberates across spatial scale. Restoration of mesic northern forests will require a multi-scale approach and sustained and widespread effort by resource managers across the Great Lakes. Restoration and biodiversity management of mesic northern forests will benefit a wide array of flora and fauna including cavity nesters, canopy-dwelling species, epiphytic lichens, species of detritus-based food webs, understory saprophytic plants, and interior forest obligates, including numerous neotropical migrants.

INTRODUCTION

This paper provides an overview of the mesic northern forest community, discussing the range, physiographic context, vegetational composition, natural processes, and importance to biodiversity of this ecological system. The primary focus of this paper is how anthropogenic disturbance has altered the composition, structure, and landscape pattern of this community type and how conservationists and resource managers can use ecological insight to restore degraded mesic northern forests. Emphasis will be placed on how these systems have changed at different scales and how restoration efforts can address biodiversity issues at multiple scales.

Overview

Mesic northern forest is a forest type of moist-to-dry mesic sites lying mostly north of the transition zone, characterized by the presence of northern hardwoods, mainly *Acer saccharum* (sugar maple) and *Fagus grandifolia* (American beech). Conifers, *Tsuga canadensis* (Eastern hemlock) and *Pinus strobus* (white pine), are frequently important. This community type breaks into two broad classes: northern hardwood forest and hemlock/hardwood forest. Mesic northern forests are found chiefly on coarse-textured ground and end moraines and typically on loamy sand to sandy loam. The natural disturbance regime is characterized by gap-phase dynamics: frequent, small windthrow gaps allow for the regeneration of shade-tolerant canopy dominants. Catastrophic windthrow occurred infrequently with several generations of trees passing between large-scale, severe disturbance events. As a result, mesic northern forests historically dominated vast areas of mesic uplands of the Great Lakes and were multi-generational, with old-growth conditions lasting many centuries.

Range

The mesic northern forest has existed as a dominant assemblage in the Great Lakes for approximately 4,000 to 8,000 years, following the peak of the last interglacial warming trend (Davis 1976, Lindsey and Escobar 1976), extending eastward from northern Minnesota and southeastern Manitoba across the northern U.S. and southern Canada to Maine and Nova Scotia (Barnes 1991). Within Michigan, this forest type is predominantly found throughout the Upper Peninsula and in the northern half of the Lower Peninsula above the climatic transition (tension) zone. Mesic northern forest also sporadically occurs below the transition zone along the Great Lakes shores of the Lower Peninsula, where lake effect modifies the local climate.

Physiographic Context

Mesic northern forest occurs on a wide variety of soils, typically on loamy sand to sandy loam and occasionally on sand, loam, and clay. Soils range widely in pH from extremely acidic to moderately alkaline but are more commonly extremely acid to medium acid. According to the Köppen classification, the Northern Hardwood-Conifer region has a cool snow-forest climate with warm summers. The daily maximum temperature in July ranges from 24 to 29 °C (75 to 85 °F) and the daily minimum temperature in January ranges from –21 to –9 °C (–5 to 15 °F). The mean number of freeze-free days is between 90 and 160 days, and the average number of days per year with snow cover of 2.5 cm or more is between 80 and 140 days. The normal annual total precipitation ranges from 610 to 1,270 mm (Albert et al. 1986, Barnes 1991).

A forest type of moist-to-dry mesic sites lying predominantly north of the tension zone, mesic northern forest is found chiefly on coarse-textured ground and end moraines, but also occurs commonly on silty/clayey lake plains, thin glacial till over bedrock, and medium-textured moraines. It also occurs locally on kettle-kame topography, moderately well-drained to well-drained sandy lake plain, and sand dunes (Whitney 1986, Michigan Natural Features Inventory 2003, Frelich and Reich 1999, Woods 2000b, Frelich 2002, Cleland et al. 2004).

Vegetation Description

The mesic northern forest is a broadly defined community type with numerous regional, physiographic, and edaphic variations. The following shade-tolerant trees can dominate or co-dominate the canopy of this community: sugar maple, hemlock, and beech. Other important components of the canopy include: *Betula alleghaniensis* (yellow birch), *Fraxinus americana* (white ash), *Tilia americana* (American basswood), white pine, *Quercus rubra* (red oak), and *Thuja occidentalis* (white cedar).

In terms of their relative importance as arboreal components in the mesic northern forest, these trees differ greatly among themselves in different parts of the region and locally within the same region (Nichols 1935). Significant variation in composition of communities is proportional to marked differences in local topography, soil, disturbance factors, geographic context (Barnes 1991), and biotic factors, such as competitive interactions (Frelich et al. 1993) and browsing pressure (Alverson et al. 1988). The leading dominant of this community is sugar maple (Curtis 1959), which thrives on moderately well-drained to excessively drained deep soils (Pregitzer 1981). Sugar maple is typically found in association with beech, basswood, yellow birch, and red oak. Basswood, which is characteristic of nutrient-rich sites, is most prevalent in mixed-hardwood stands in the western Upper Peninsula and most closely associated with sugar maple (Woods 2000a). The proportion of conifers and hardwoods other than sugar maple often increases when groundwater or bedrock influence the rooting zone (Pregitzer 1981). In the northern Lower Peninsula and in the eastern Upper Peninsula, sugar maple and beech occur commonly as co-dominants, frequently thriving on heavy-textured soils such as silt loam and clay loam. The absence of beech in the western Upper Peninsula is probably due to the increased dryness, shorter growing seasons, and extreme minimum winter temperatures of this region (Barnes 1991).

Frequently present in these stands are large but widely spaced white pine, often relics of an earlier successional stage generated by windthrow and/or forest fire (Nichols 1935, Whitney 1986, Abrams and Orwig 1996, Abrams 2001). White pine can attain supercanopy status within mesic northern forest. White pine reached its greatest abundance on drier southeast-facing slopes of well-drained moraines and ice-contact features (Whitney 1990, Leahy and Pregitzer 2003). The primary canopy components of conifer-dominated mesic northern forests are usually hemlock and yellow birch. Hemlock-dominated stands are generally found on moist or poorly drained sites. Mixed stands of hemlock and yellow birch or pure stands of yellow birch occur primarily in depressions or sites adjacent to swamps (Barnes 1991, Woods 2000a, Woods 2000b). These poorly drained areas are typically characterized by high water tables and shallow rooting zones (Whitney 1990). White cedar can occur as a canopy associate within these hemlock/yellow birch forests.

Circa 1800, forests of eastern hemlock and yellow birch were frequent on moderately to poorly drained till plains and outwash plains, especially in the western Upper Peninsula. This assemblage was predominately found around lake and bog margins and in complex mosaics with sugar maple/hemlock forest on the surrounding better-drained soils. Beech/sugar maple/hemlock forests, which dominated nearly 17% of the state's surface in the 1800s, were mostly found on large expanses of rolling moraines in the northern Lower Peninsula and eastern Upper Peninsula (Comer et al. 1995, Leahy and Pregitzer 2003). This species mix was also found on the clay lake plain along Saginaw Bay. Eastern hemlock and white pine were the conifers most commonly occurring in mixed stands with hardwoods. Eastern hemlock and beech were occasionally co-dominant, most commonly on moderately drained sand plains. Assemblages dominated by hemlock and white pine were prevalent in the 1800s on moderately drained lake plain and outwash plain extending from Saginaw Bay through the Upper Peninsula. Large areas of hemlock–dominated forest grew on the clay plain of Huron and Sanilac counties. Extensive tracts of sugar maple and white cedar located in dunes or over calcareous bedrock were known from the surveyors' notes and are found today locally in dunes along the Great Lakes shoreline, on Great Lakes islands, and on the drumlin fields of Menominee County (Comer et al. 1995).

NATURAL PROCESSES

The natural disturbance regime in mesic northern forest is characterized by frequent small-scale wind disturbance or gap-phase dynamics and infrequent intermediate- and large-scale wind events. The Great Lakes region is one of the most active weather zones in the northern hemisphere, with polar jet streams positioned overhead much of the year. More cyclones pass over this area than any other area in the continental U.S. (Frelich and Lorimer 1991). Severe low-pressure storm systems frequently generate windthrow gaps, openings in the canopy created by the death of a large branch or one or more trees (Canham and Loucks 1984, Runkle 1984). In a study in the western Upper Peninsula, Frelich and Lorimer (1991) found that 60% of the canopy trees attained their canopy ascendance as the result of periodic small-gap formation. In addition to thunderstorms, glaze or ice storms are a significant source of disturbance in hardwood forests of North America (Abell 1934, Lemon 1961, Melancon and Lechowicz 1987). The buildup of ice can cause a hundredfold increase in canopy mass, and subsequently, glaze results in pruning of small branches, severe breakage of large branches, complete stem breakage, and the creation of canopy gaps (Lemon 1961, Melancon and Lechowicz 1987, Rhoades et al. 2002). Canopy trees affected but not killed by glaze are often subsequently infected by fungus and/or infested by insects and die standing or are eventually windthrown (Abell 1934).

Whether from windthrow or ice breakage, research suggests that approximately 1% of the total area of a given mesic forest is within recent gap (less than one year old), and estimates of average canopy residence time range between 50 and 301 years (Runkle 1982 and 1991: 50-200; Lorimer et al. 1988: 50-250, Frelich and Lorimer 1991: 145-175; Frelich and Graumlich 1994: 167-232; Woods 2000a: 128-186; Woods 2000b: 100-200; Lorimer et al. 2001: 193-301; Ziegler 2002: 184-211). Frelich and Lorimer (1991) documented rates of canopy mortality in old-growth hemlock/hardwoods ranging from 5.7 to 6.9%, while Lorimer et al. (2001) observed baseline mortality rates of 1.5 to 2.9% (both studies were conducted in the Upper Great Lakes region). Frequent windthrow events generate a forest mosaic of different aged patches of gaps of a wide range of sizes; the majority of gaps are between 100 and 400 m^2 (Runkle 1981, Runkle 1984). These small-scale disturbance events are the primary source of forest turnover. Gaps close by 1) adjacent canopy trees filling the space through lateral growth of their limbs or 2) saplings within the gap filling the gap from below (Runkle 1982, McClure et al. 2000). The creation of canopy gaps results in temporary increases in the availability of light, water, and nutrients and decreases in root competition, which allow canopy recruitment of saplings (Moore and Vankat 1986, Franklin et al. 1987, Beaudet and Messier 2002). Tree species exhibit gap partitioning, responding differently to variation in gap size, origin, orientation, and age (Runkle 1982, Poulson and Platt 1989, Barnes et al. 1998, Rankin and Tramer 2002). For example, sugar maple, beech, and hemlock thrive in the common small canopy gaps (20-100 m^2), while yellow birch, red oak, white ash, and white pine require larger canopy gaps (often > 400 m^2), which occur less frequently (Runkle 1984, Quinby 1991, Abrams and Orwig 1996, Barnes et al. 1998, Davis et al. 1998, Abrams 2001). As gap size increases, woody species diversity and the size and number of stems increase (Runkle 1982). Gaps formed by wind-uprooted trees are typically larger with more exposed bare soil than gaps formed by stem breakage. Stem-breakage gaps may favor root-sprouted saplings (e.g., beech and basswood) and existing advanced regeneration, while uprooted tree gaps can allow recruitment of mid-tolerant opportunists as well as the shade-tolerant dominants (Barnes et al. 1998). Runkle (1984) observed that as gap age increased, so too did the importance of beech saplings. As noted by Poulson and Platt (1989), in addition to size and age, the orientation of a gap influences light regimes and patterns of canopy replacement. For example, the long northern edge of east-west-oriented gaps receives high-intensity sunlight through the course of the day, while the eastern and western edges of north-south-oriented gaps receive low-intensity morning and afternoon sunlight (Poulson and Platt 1989). In a study of windthrow in an old-growth, beech/sugar maple forest in Michigan, Brewer and Merritt (1978) observed that the direction of windfall was primarily east and south, reflecting the prevailing wind directions. Spatial and temporal heterogeneity of treefall gaps allows for the maintenance of shade-tolerant canopy dominance and the persistence of mid-tolerant opportunists at low densities (Runkle 1981, Runkle 1982, Runkle 1984, Poulson and Platt 1989).

Recruitment of saplings within treefall gaps is typically by shade-tolerant species (primarily sugar maple and beech, but also hemlock) that can wait suppressed beneath the closed canopy (Runkle 1982). In a Michigan, old-growth, beech/sugar maple forest, Woods (1979) found that almost all small gaps were replaced by beech and sugar maple. Hemlock, beech, and sugar maple are small-gap specialists that can remain in a suppressed understory state for prolonged periods prior to release and canopy ascension, and these species often rely on a series of canopy gaps to reach the overstory (Stearns 1951, Canham 1985, Canham 1988, Canham 1990, Poulson and Platt 1996, Marks and Gardescu 1998, McClure et al. 2000). Typically, sugar maple dominates the small understory size classes and beech is most prevalent in the sapling class (Poulson and Platt 1996). Both species display architectural plasticity, exhibiting growth in small canopy gaps (15-75 m^2) an order of magnitude greater than rates of suppressed sapling growth (Canham 1988). The relative abundance of beech typically increases with low rates of treefall, while sugar maple and hemlock often increase following periods with higher rates of gap formation (Canham 1988, Poulson and Platt 1996, Woods 2000b). When rates of canopy disturbance are low, beech may take less time to be released because of its greater capacity for suppressed growth compared to maple and hemlock. Beech saplings have long lateral branches that grow horizontally to exploit the scattered and perpetually shifting light flecks under closed canopy conditions. As treefall disturbance increases, sugar maple may be favored because of its strong apical dominance and greater capacity for vertical growth in small gaps (Poulson and Platt 1996). In addition to different rates of treefall, variability of sapling recruitment is also influenced by landform and soil characteristics of specific sites (Barnes et al. 1998). For example, acidic sandy or clay lake plain sites with poor drainage are often characterized by dominance of beech recruitment, while nutrient-rich, well-drained, clayey morainal sites are frequently dominated in the overstory and understory by sugar maple (Barnes et al. 1998). Canopy dominance often shifts from hemlock to sugar maple as soil pH and calcium increase (Woods 2000a). As noted above, gap size also influences recruitment, with large gaps providing suitable regeneration niches for species of intermediate shade tolerance such as yellow birch, white pine, white ash, and basswood.

Intermediate disturbance events are thought to be responsible for the generation of large, multiple treefalls that create openings larger than gaps created by the baseline mortality of gap dynamics (i.e., >

400 m^2). Recent research indicates that periodic wind and ice storms can cause these intermediate disturbances (Peterson 2000, Canham et al. 2001, Lorimer et al. 2001, Rhoades et al. 2002, Lafon 2004, Woods 2004). Intermediate disturbance events can significantly reduce the canopy of mesic northern forest over tens or hundreds of acres and allow for the recruitment of mid-tolerant, often as even-aged cohorts. The community and population dynamics following intermediate storm events differ from smaller, more frequent gap-type disturbance. In a study comparing gap-phase dynamics and intermediate disturbance in late-successional hemlock/northerrn hardwood forest, Woods (2004) found that baseline mortality from gap dynamics was hyperdispersed and generated small openings, while storm mortality was strongly clustered and produced large multiple-tree gaps. In addition, yellow birch suffered high baseline mortality but little storm damage (no yellow birch greater than 55 cm was killed), while large diameter sugar maple and beech suffered from high storm mortality (with larger trees subject to greater risk of mortality) (Peterson 2000, Woods 2004). Yellow birch—with its wide-spreading roots—has low windthrow vulnerability (Tyrrell and Crow 1994a, Canham et al. 2001, Woods 2004). Resistance to windthrow allows this long-lived, small-seeded species of intermediate shade tolerance to exploit large openings created by severe disturbance (McClure et al. 2000, Peterson 2000, Lorimer et al. 2001). Severe ice storms have also been classified as intermediate disturbance since they occur less frequently than small-scale windthrow and can affect larger portions of the canopy (Lafon 2004). Estimated return interval for severe glaze storms ranges between 20 and 100 years (Melancon and Lechowicz 1987). Tree mortality and degree of damage from severe ice storms is related to tree size, age and health, crown position, slope, aspect, and interspecific differences in wood strength and canopy architecture (Rhoades et al. 2002, Lafon 2004). As with wind disturbance, canopy ice damage increases in probability as tree size increases (Peterson 2000, Rhoades et al. 2002, Lafon 2004). Duguay et al. (2001) found hemlock and yellow birch to be the least damaged canopy trees in old-growth forest affected by ice storm, while Rhoades et al. (2002) observed that in response to an intense ice storm, beech was most damaged, sugar maple was most resistant, and yellow birch was intermediate. Survivors of intermediate disturbances comprise a major component of the future forest canopy (Peterson 2000). Large gaps produced by

intermediate disturbance events allow newly established mid-tolerant seedlings (i.e., yellow birch, white pine, basswood, white ash, and red oak) to outgrow shade-tolerant advanced regeneration (McClure et al. 2000, Lorimer et al. 2001). Yellow birch recruitment is particularly prevalent following intermediate disturbance of hemlock-dominated forests. Hemlock canopy has a strong inhibitory effect on the advanced regeneration of other species. The sparse advanced regeneration beneath hemlock canopy reduces competition and favors yellow birch regeneration when canopy gaps are large (Abrams and Orwig 1996, Woods 2000a). Webster and Lorimer (2002) observed that as gap size increased above 400 m^2 within hemlock/yellow birch forest, yellow birch replaced hemlock as the primary canopy successor. Intermediate disturbance, by generating large gaps, allows for the infrequent episodic establishment of small, even-aged cohorts of mid-tolerant and occasionally shade-intolerant species within mesic northern forest (Canham et al. 2001, Woods 2000b, Woods 2004).

Prior to intensive anthropogenic disturbance, intermediate- and large-scale disturbance events were pivotal in maintaining mid-tolerant and shade-intolerant species on the landscape and increasing heterogeneity of forest structure and composition (Rhoades et al. 2002, Carleton 2003). Large-scale, stochastic events were extremely uncommon in mesic northern forests. Catastrophic stand-leveling blowdowns were infrequent disturbance factors in the northern portion of Michigan and Wisconsin, with estimated return intervals greater than 1,200 years (Canham and Loucks 1984, Whitney 1986, Frelich and Lorimer 1991). Canham and Loucks (1984) estimated the return time for large-scale windthrow (> 1.0 ha) to be 1,210 years in forests of northern Wisconsin. This return time is remarkably similar to Whitney’s (1986) estimated windthrow recurrence interval of 1,220 years in hemlock/white pine/northern hardwood forests of northern Lower Michigan. Investigating primary hemlock/hardwood forests of the Upper Peninsula, Frelich and Lorimer (1991) estimated that the rotation period of wind disturbance which leveled 60% or more of the canopy on a given site to be more than 1,500 years. The principal mechanisms for large-scale windthrow are tornadoes and downbursts from thunderstorms. Downbursts are parcels of air in down drafts that shoot out from the base of a thunderstorm and splatter in all directions upon impact with the earth (Canham and Loucks 1984, Frelich and Lorimer 1991, Frelich and Reich 1996). As noted by Tyrrell and Crow (1994b), catastrophic disturbances act infrequently on a large scale, and non-catastrophic disturbances act frequently at smaller spatial scales. Large-scale disturbances with long return intervals are superimposed on small-gap and intermediate disturbance regimes (Lorimer et al. 1988).

Catastrophic fires also occurred infrequently within mesic northern systems, typically following a catastrophic wind event. Using 19th-century land-survey evidence, Whitney (1986) estimated a fire rotation of 1,400 years in hemlock/hardwood forests of northern Lower Michigan. Cleland et al. (2004) found a very similar fire rotation (1,385 years) for mesic northern forests in northern Lower Michigan, and Frelich and Lorimer (1991) posited that canopy-killing fires occurred at an interval of 2,797-4,545 years in hemlock/hardwood forests of the upper Great Lakes region. Most fires within these systems followed catastrophic blowdowns (Lorimer and White 2003). Evidence of charcoal in the forest floor and fire scars on canopy dominants indicates that stands dominated by hemlock in the overstory were often the result of crown fires (Hix and Barnes 1984, Simpson et al. 1990). In addition, even-aged cohorts of white pine within mesic northern forests were typically the result of catastrophic windthrow and/or fire (Sharik et al. 1989, Abrams and Orwig 1996, Foster et al. 1996, Abrams 2001). However, the historic infrequency of fire in mesic northern forests is manifested by the paucity of early-successional, shade-intolerant species in land-survey evidence of the Upper Great Lakes region: less than 5% of the circa-1800 northern hardwood forest was composed of pioneer species (Frelich and Lorimer 1991). The closed-canopy conditions of mesic forests and the high humidity and moisture levels of the soil and leaf litter make these ecosystems highly resistant to the passage of fire (Curtis 1959, Grimm 1984, Barnes 1991, Lorimer and White 2003, Cleland et al. 2004).

Because of the low probability of large-scale, stand-replacing disturbance in this community type, numerous generations of trees passed between catastrophes, and individual canopy trees are long-lived.

After release, sugar maple, beech, hemlock, and white pine can remain in the canopy for hundreds of years. Overstory sugar maple and beech can live 400 years, and 200-year-old trees are common. White pine can reach 500 years of age but are more typically over 200 years (Curtis 1959, Goodman et al. 1990, Tubbs and Houston 1990, Abrams and Orwig 1996, Abrams 2001, Lorimer et al. 2001, Tardif et al. 2001, Leahy and Pregitzer 2003). Hemlock is an extremely long-lived species with many canopy hemlock reaching 200-500 years and some living as long as 800 years (Whitney 1990, Tyrrell and Crow 1994b, Abrams and Orwig 1996, Abrams 2001, Lorimer et al. 2001, Tardif et al. 2001, Leahy and Pregitzer 2003). On average, four to five generations of late-successional trees historically occupied a site before successional processes were initiated again by catastrophic wind and/or fire (Canham and Loucks 1984). As a result, mesic northern forests tended to be multi-generational (uneven-aged), with continually changing old-growth conditions lasting several centuries and covering the majority of the mesic uplands of the northern Great Lakes (Frelich and Lorimer 1991, Seichab and Orwig 1991, Frelich 1995, Barnes et al. 1998, Zhang et al. 1999, Woods 2000a, Woods 2000b, Carelton 2003, Schulte and Mladenoff 2005). Old-growth forests contain high levels of genetic diversity, the key to adaptability and continued evolution, accumulated over many generations (Buchert et al. 1997).

Old-growth conditions include a high quantity of dead wood (snags, stumps, and fallen logs) in a diversity of ages, sizes, and stages of decomposition; high basal area; large-diameter canopy dominants (numerous trees > 100 cm in diameter at breast height and a diameter distribution described by a strong reverse J curve); soil macropores (from large decaying lateral roots); multilayered canopies (supercanopies existing where white pine is a canopy component); numerous canopy gaps of diverse age and size; and pit and mound topography from continual, frequent gap formation (Brewer and Merritt 1978, Parker 1989, Whitney 1989, Runkle 1991, Martin 1992, Lorimer and Frelich 1994, Tyrrell and Crow 1994b, Abrams and Orwig 1996, McCarthy and Bailey 1996, Martin and Bailey 1999, Abrams 2001, Lorimer et al. 2001, Carleton 2003). Many of these traits of old-growth and late-successional mesic northen forest begin developing after 100 years. Forests slowly accumulate attributes of late-successional forest and species over time (Hagan and Whitman 2004, Whitman and Hagan 2004). In addition to gradual development, many old-growth characteristics increase after a threshold age (e.g., after 275-300 years in hemlock/hardwood forest when significant hemlock mortality contributes to the necromass) (Tyrrell and Crow 1994b).

The high degree of compositional stability of this forest type (Curtis 1959) allows for ample opportunity for competitive interactions between dominant species to influence the patch structure of the landscape (Frelich et al. 1993, Woods 2000a). Studying old-growth hemlock/hardwood forest in the Sylvania Wilderness of the western Upper Peninsula, where hemlock and sugar maple show strong spatial segregation, Frelich et al. (1993) concluded that hemlock and sugar maple exhibit strong positive self-association and negative reciprocal association. Each species alters its local environment, creating conditions in its immediate vicinity that favor self-recruitment and discourage establishment of seedlings of the other dominant. Sugar maple is disadvantaged by the dense shade and low nutrient conditions in the podzolized understory of hemlock-dominated stands. In sugar maple–dominated stands, hemlock seedlings are unable to penetrate the thick, coarse duff and are often smothered by the ubiquitous leaf fall of sugar maple (Frelich et al. 1993).

IMPORTANCE TO BIODIVERSITY

Old-growth and late-successional mesic northern forests provide critical habitat for numerous vertebrates and invertebrates that are dependent on the diverse structural, compositional, and functional attributes. These systems are reservoirs of biodiversity and represent a continuous heritage of natural disturbance and regeneration (McCarthy et al. 2001, Frelich and Reich 2003). In addition, these forests function as genetic reserves and colonization sources for plant and animal species (Mladenoff et al. 1993, Rooney and Dress 1997, Mosseler et al. 2003). The high volumes of necromass in a diversity of ages, sizes, and stages of decomposition support a diverse array of plants, animals, protists, bacteria, and fungi (Carleton 2003, Rubino and McCarthy 2003). Large contiguous tracts of old-growth and mature mesic northern forest provide important habitat for epiphytic lichens, cavity nesters, species of detritus-based food webs, canopy-dwelling species, understory saprophytic plants, and interior forest obligates, including numerous neotropical migrants (Juday 1988, Mladenoff et al. 1993, Howe and Mossman 1996 in Rooney and Waller 2003, Carleton 2003, Frelich and Reich 2003, Mosseler et al. 2003). Forest warblers, flycatchers, thrushes, vireos, woodpeckers, and woodland raptors are area-sensitive groups dependent on these forests; their populations are larger and fare better within larger habitat patches (Vora 1994). This community provides summer nesting habitat for many neotropical migrants, especially interior forest obligates such as *Dendroica caerulescens* (black-throated blue warbler), *Dendroica virens* (black-throated green warbler), *Piranga olivacea* (scarlet tanager), and *Seiurus aurocappilus* (ovenbird). In a study in the Upper Peninsula of Michigan, Doepker et al. (1992) found that neotropical migrants exhibited a preference for stands with 80% canopy closure where overstory conifer coverage was three times greater than hardwood coverage. Hemlock and white pine canopy composition are especially important for Michigan's avifauna. Supercanopy white pine and hemlock emerging from the canopies of mesic northern forest are highly important for numerous species, functioning as cavity trees and roosting, nesting, perching, and foraging habitat. Extensive tracts of mesic northern forest are utilized by large mammals such as *Alces alces* (moose, state special concern), *Canis lupus* (gray wolf, state and federally threatened), and *Martes martes* (pine marten). Old mesic forests, especially stands with significant conifer canopy, are exploited by numerous animals for winter refuge (Mosseler et al. 2003). Hemlock stands provide critical snow intercept cover for moose during the winter (Minzey and Robinson 1991).

Numerous rare species are associated with mesic northern forest. Two listed raptor species frequently nest in mesic northern forests: *Buteo lineatus* (red-shouldered hawk, state threatened [ST]) and *Accipiter gentilis* (Northern goshawk, state special concern [SC]). Rapids clubtail (*Gomphus quadricolor*, SC) is a rare dragonfly that utilizes quiet water pools and cool rapid streams that flow through mesic northern forests. Rare plants associated with mesic northern forests include: *Adlumia fungosa* (climbing fumitory, SC), *Asplenium rhizophyllum* (walking fern, ST), *Asplenium scolopendrium* (hart's-tongue fern, state endangered), *Asplenium trichomanes-ramosum* (green spleenwort, ST), *Botrychium mormo* (goblin moonwort, ST), *Carex assiniboinensis* (Assiniboia sedge, ST), *Cystopteris laurentiana* (Laurentian fragile-fern, SC), *Dentaria maxima* (large toothwort, ST), *Disporoum hookeri* (fairy bells, ST), *Dryopteris filix-mas* (male fern, ST), *Galearis spectabilis* (showy orchis, ST), *Galium kamtschaticum* (boreal bedstraw, ST), *Panax quinquefolius* (ginseng, ST), *Tipularia discolor* (cranefly orchid, ST), *Triphora trianthophora* (three-birds orchid, ST), and *Viola novae-angliae* (New England violet, ST).

ANTHROPOGENIC DISTURBANCE

The extent, landscape pattern, species composition, natural processes, and structure of mesic northen forest of the Great Lakes have been altered by intensive and pervasive anthropogenic disturbance over the past 150 years, following European settlement. Human activity has replaced natural disturbance as the primary force driving mesic northern forest dynamics (Hannah 1999, Frelich and Lormer 1991) and has caused extensive loss of acreage and fragmentation, reduction of structural complexity, alteration of biogeochemical pathways, and homogenization of floral and faunal composition (Van Deelen et al. 1996, Crow and Perera 2004). This section discusses how anthropogenic disturbance has impacted mesic northern forests across spatial scales. At the landscape level, these systems have been reduced in acreage, with old-growth and late-successional mesic northern forest declining dramatically and forest fragmentation altering the landscape structure of remnant forest. The remaining mesic northern forest has experienced widespread simplification of species composition, structural heterogeneity, and genetic diversity. Impacts to within-stand properties will be examined with respect to modern silvicultural trends, introduced pathogens and insects, and high densities of deer.

Direct Native American influence on this forest type in Michigan was limited to localized disturbance near encampments. For example, clearing for agriculture using fire resulted in a prevalence of red oak and white pine in the canopy of the mesic northern forest of Colonial Point on the northern shores of Burt Lake (Albert and Minc 1987). Several Great Lakes islands (e.g., Harbor Island and Garden Island) support red-oak–dominated mesic forests that likely originated following similar disturbance (Penskar et al. 2000, Penskar et al. 2001). Indigenous peoples indirectly influenced mesic ecosystems across the Great Lakes by maintaining low levels of white-tailed deer, which at high densities can drastically alter the structure and composition of mesic northern forest (detailed discussion below). In addition, Native Americans helped maintain a frequent fire regime in adjacent fire-prone communities, and thereby contributed to preserving a landscape seed source for fire-dependent species such as white pine and red oak, important canopy components of mesic forests. Presently, the prevalent catalyst of fires is lightning strike, but historically, Native Americans played an integral role in the fire regime, accidentally and/or intentionally igniting fire-prone ecosystems (Day 1953, Chapman 1984, Loope and Anderton 1998).

Extensive logging came on the heels of European settlement of the northern Great Lakes in the mid-19th century. Widespread selective logging of first white pine and then hemlock and northern hardwoods at the end of the 19th century and the beginning of the 20th century was followed by extensive slash fires. The logging and subsequent wildfires greatly reduced the extent of late-successional mesic northern forest and diminished the role of conifers as a widespread component of the canopy (Whitney 1987, Benson 1989, Karamanski 1989, Jackson et al. 2000, Zhang et al. 2000, Stearns and Likens 2002, Leahy and Pregitzer 2003). Cutting followed by slash fires favored the conversion of mesic northern forest to early-successional stands of aspen, white birch (*Betula papyrifera*), and oak (Whitney 1984, Whitney 1986, Whitney 1987, Palik and Pregitzer 1995, Frelich and Reich 1999, Jackson et al. 2000, Zhang et al. 2000, Frelich 2002, He et al. 2002, Leahy and Pregitzer 2003, Cleland et al. 2004). A significant proportion of deforested land that failed to regenerate was planted by the Civilian Conservation Corp in the 1930s to pine plantation with pine stock from Michigan and southern Wisconsin (Leahy and Pregitzer 2003, Bresse et al. 2004, Cleland et al. 2004). Sustained and ubiquitous harvesting of remaining mesic northern forest has reduced the structural and compositional complexity of mesic northern forest. Old-growth forest has dwindled from close to 70% to less than 10% of the Great Lakes landscape (Frelich 1995). Remnants of northern hardwood-hemlock forests unscathed by logging are among the rarest vegetation types in the Lake States, with just 0.6% remaining (Frelich and Reich 1996). According to Noss et al. (1995), old-growth eastern deciduous forest is among the 21 most endangered ecosystems in the United States. In Michigan, 5.8% of the northern hardwood commercial forest is old growth (Frelich 1995). In the 1800s, approximately 32% (over 12 million acres) of Michigan was mesic northern forest (Comer et al. 1995). Just over 0.4% of mesic northern forest in pre-European settlement condition remains in Michigan. Large tracts of primary old-growth forest are limited to the Upper Peninsula in the Porcupine Mountains (31,000 acres), the Sylvania Wilderness (17,950 acres), and the Huron Mountains (4,000 acres).

In addition to the reduction of vast acreages of primary old-growth forest, late-successional mesic northern forest (120- to 200-year–old forest) is rapidly disappearing from managed forests. In many areas, forest cover has remained stable or even slowly increased following the logging era, but older age classes of forests have dwindled. Technological advances in harvesting and processing lumber and burgeoning markets for nearly all species and younger age classes have rendered older trees much less important for wood manufacturing. Landowners have less incentive to grow large trees because large dimensional solid lumber is being replaced by stronger-engineered laminates. Late-successional trees are often past financial and silvicultural maturity: the economic prime of northern hardwoods in today's markets is between 60 and 100 years. The myopic focus of the ecological and environmental community on pristine old-growth forest has resulted in an underappreciation of, and subsequently less conservation effort in, second-growth late-successional forests that have harvest history but also posses old-growth characteristics. Late-successional forests and species that depend on this forest stage are slipping through the coarse filter of conservation. The loss of this age class from the forested landscape represents a major threat to biodiversity. Numerous species are dependent on forest continuity, the persistence of large living trees, dead trees, and fallen logs, features common in late-successional forest but absent in young forests.

Once these old forest elements are lost from a managed landscape it can take centuries to regain them (Hagan and Whitman 2004, Whitman and Hagan 2004).

Prior to the logging era, old-growth and late-successional mesic northern forest was the prevailing forest type in mesic upland systems. Early-successional forest, generated by infrequent catastrophic windthrow and/or fire, occurred as scattered patches within the matrix of long-lived, shade-tolerant forest, which was maintained by small-scale gap-phase dynamics (Frelich and Reich 1999). Numerous scientists estimate that pioneer species made up less than 5% of the circa-1800 mesic northern forests of the upper Great Lakes region (Whitney 1987, Frelich and Lorimer 1991, Albert 1995, Corner and Albert 1999a-1999f, Cleland et al. 2004). Lorimer and White (2003) found pioneer species to occupy 1-3% of the landscape dominated by northern hardwoods in the northeastern U.S. Currently, most old-growth and late-successional mesic northern forests persist as remnant patches enmeshed in an anthropogenically disturbed landscape where the forested matrix is dominated by early-successional forest and young northern hardwoods (Mladenoff et al. 1993, White and Mladenoff 1994, Tyrrell and Crow 1994b, Van Deelen et al. 1996, Rooney and Dress 1997, Foster et al. 1996, Mourelle et al. 2001, Ziegler 2002).

Conservation scientists have argued that in addition to habitat loss, habitat fragmentation poses a severe threat to biodiversity (Noss and Cooperrider 1994). Not only have vast acreages of mesic northern forest been lost or converted to other forest types, much of the remaining mesic northern forest is fragmented. The landscape patterning of forested systems has been drastically altered by continued forest harvesting, road building, and intensive land-use (especially agriculture and development). In a comparison of an unaltered old-growth forest landscape and a disturbed forest landscape of the upper Great Lakes, Mladenoff et al. (1993) determined that an actively managed landscape is more fragmented with smaller and simpler patches of forest, decreased connectivity, and less interior habitat. They also determined that important landscape-scale spatial relationships were missing from the intensively managed landscape. For example, the old-growth forest landscape was characterized by an important ecosystem juxtaposition of hemlock forest next to lowland conifer, a spatial relationship which was lacking in the disturbed landscape. Lowland conifer forests provide a seed source for hemlock establishment in adjacent uplands, a hospitable medium for the movement of animals and plants between conifer stands, and a refuge for hemlock during climatically dry periods (Mladenoff et al. 1993). Forests of the Great Lakes have become more and more fragmented with decreases in connectivity, mean patch size, maximum patch size, large landscape-integrating patches, and interior forest habitat, and increases in edge density and edge length (Mladenoff et al. 1993, Heilman et al. 2002, Bresse et al. 2004). The compartmentalization of lands into jurisdictional units that ignore ecological boundaries has contributed to this fragmentation. Forestry and wildlife management practices that focus on species- and stand-based management have directly and indirectly promoted landscape fragmentation and exacerbated edge effects through prescriptions that generate and maintain small discrete patches of habitats or stand types (Bresse et al. 2004).

As native forests become increasingly fragmented ecosystems, their dynamics shift from being primarily internally driven to being externally and anthropogenically driven. The affects of forest fragmentation on native plants and animals and ecosystem processes are profound and alarming (Heilman et al. 2002). Fire regimes in fragmented landscapes are reduced because roads, agriculture, and development enhance modern forest fire suppression (Leahy and Pregitzer 2003). Bresse et al. (2004) note that most forestry harvests occur along road corridors, leading to an increase in younger and non-forested stands along roads. The small and insularized nature of forest fragments may make them too small to support the full array of species formerly found in the landscape (Rooney and Dress 1997). Local population extinctions within fragments are accelerated by reduced habitat and population size. Because of fragment isolation, inter-patch colonization may fail to compensate for local extinctions (Hewitt and Kellman 2004). Within fragmented forest, avian diversity is reduced by nest predation and nest parasitism. Numerous neotropical migrant songbirds are dependent on interior forest habitat and are highly susceptible to nest parasitism and predation (Robinson et al. 1995, Heske et al. 2001, Heilman et al. 2002). Forest succession within fragmented landscapes can be delayed or drastically modified since seed exchange is greater for early-successional trees than for mid- or late-successional species (McEuen and Curran 2004). Native plant diversity within forested fragments is threatened by low seedling survivorship, infrequent seed dispersal, high levels of herbivory, and growing prevalence of invasive exotic species and native weeds, which thrive along the increasing edges and disperse throughout fragmented landscapes along roads (Brosofske et al. 2001, Heilman et al. 2002, Hewitt and Kellman 2004).

In addition to reduction of total area of mesic northern forest, the shift from old-growth and late-successional forest to early-successional and second-growth forest, and forest fragmentation, the species composition and structural character of these forests has been altered by the logging era and slash fires and the subsequent forestry and land-use. Forest harvesting tends to simplify forest composition and structure on the landscape and stand levels (He et al. 2002, Crow and Perera 2004). In the Great Lakes region more than 99% of the mature hemlock/hardwood forest has been eliminated (Noss et al. 1995), and hemlock has been reduced from its former position as a regional dominant, now occupying only 0.5% of the landscape and persisting in only a few regions (Mladenoff and Stearns 1993, White and Mladenoff 1994, Borgmann et al. 1999). White pine was so thoroughly decimated from some areas that its prior existence was doubted (Whitney 1986). Loss of conifer seed sources occurred not only within mesic northern forests but throughout the landscape as adult white pine and hemlock were harvested ubiquitously during the logging era. In addition, the slash fires that followed the logging killed seedlings and saplings and incinerated seeds residing in the litter and in the seed bank (Whitney 1987, Sharik et al. 1989, Abrams and Orwig 1996, Jackson et al. 2000, Abrams 2001, Cleland et al. 2004). Hemlock and white pine regeneration have diminished with the drastic reduction in seed source, and also due to the rise of winter browse pressure from the increasing deer population (Alverson et al. 1988) and the paucity of suitable establishment substrate such as decaying logs (nurse logs), moss beds, and tip-up mounds

(Rooney et al. 2000), features associated with old-growth and late-successional stands and also necessary for yellow birch establishment (Graham 1941, Curtis 1959). In addition to the dramatic loss of mesic conifers, the composition of deciduous hardwoods has also been affected by modern forestry practices. Yellow birch has declined in importance due to the above-mentioned decline in establishment sites for its small seeds and heavy deer browse pressure, and also because of the lack of sufficient light in gaps created by selective logging and thinning (Hannah 1999, Woods 2000a, Zhang et al. 2000). Many mesic northern forests are dominated solely by sugar maple, which is favored in gaps created by selective logging and was often left to produce maple syrup (Beaman 1970, Dodge and Harman 1985a, Host et al. 1987). In addition, beech was often culled because of its poor timber value (Ward 1956, Beach and Stevens 1990, Barnes 1991). Conversely, many stands that were high-graded of valuable timber (i.e., sugar maple and red oak) are now beech-dominated. Frequent and repeated harvests of mesic northern forests have favored the increase in canopy importance of mid-tolerant trees such as red maple, white ash, and black cherry and shade-intolerant, early-successional species, especially bigtooth aspen, trembling aspen, and occasionally white birch (Rooney and Dress 1997, Hannah 1999, Zhang et al. 2000, Leahy and Pregitzer 2003).

Mesic northern forests have undergone dramatic changes in structure and natural processes over the last 150 years. Structural complexity and importance of gap-phase dynamics have decreased. These changes are most vividly illustrated by studies that contrast circa-1800 forests as described by the original land surveyors with current forests in the same location and also by comparisons of primary or old-growth forest to managed forest. In their assessment of the historical changes in the forests of the eastern Upper Peninsula, Zhang et al. (2000) found that the diameter distribution of long-lived species was truncated; circa 1800, there were fewer but larger trees, especially hemlock and white pine. The shift in the diameter distribution to smaller size classes was accompanied by a decrease in mean diameter and also in variance of diameters. These forests have increased in density but decreased in basal area due to the current prevalence of short-lived, early-successional species such as aspens and white birch. Leahy and Pregitzer (2003) examined circa-1800 and present-day forests in northeastern Lower Michigan and found similar results. The current forest in northeastern Lower Michigan is characterized by smaller trees that are more densely aggregated compared to circa-1800 forests.

Old-growth mesic forests are uneven-aged, vertically complex systems characterized by numerous overstory trees older than 200 years, multiple canopy layers (including supercanopies where white pine is present), large canopy gaps, numerous tip-up mounds, approximately 250 trees/ha, basal area greater than 25 m^2/ha, 16-36mg/ha of fallen dead wood covering approximately 2% of the forest floor, greater than 15 snags/ha, diameters ranging between 70 and 210 cm, and high plant-species richness (Thompson 1980, Parker 1989, Martin 1992, Tyrrell and Crow 1994b, Rooney and Dress 1997, Forrester and Runkle 1999, Runkle 2000, Lorimer et al. 2001, Carleton 2003, Webster and Lorimer 2003). Old-growth systems typically have greater mean aboveground biomass than managed systems (Goodale and Aber 2001). The most notable differences between late-successional mesic forest and managed mesic forest is the lack of large-diameter trees, trees older than 200 years, and significant volume of snags and coarse woody debris (Tyrrell and Crow 1994b, Lorimer et al. 2001, Hagan and Whitman 2004). Structural heterogeneity has declined in managed forests with the elimination of older age classes and supercanopy white pine and hemlock. In addition, mean canopy residence time has decreased. Northern hardwoods reach their economic and silvicultural prime between 60 and 100 years of age, and the optimal financial return is realized in these systems with 60- to 80-year harvest rotations (Hagan and Whitman 2004, Whitman and Hagan 2004). As a result, a high proportion of managed mesic forests are less than 100 years old and many are even-aged (Rooney and Dress 1997, Hannah 1999). Many of the late-successional and old-growth characteristics that develop within mesic northern forests begin accruing at 100 years (Hagan and Whitman 2004). As noted by Tyrrell and Crow (1994b), in addition to gradual development, many old-growth traits in hemlock/northern hardwoods increase beyond the threshold age of 275 to 300 years when canopy hemlock begin dying and contributing to standing snag density and coarse wood loads. Younger managed forests never develop large, old trees that can create large tip-up mounds or contribute large canopy gaps, large diameter snags, and coarse woody debris. The absence of long-lived conifers such as hemlock and white pine within these systems results in the decrease of slowly decaying snags and dead and downed logs (Tyrrell and Crow 1994b, Campbell and Gower 2000). Harvests of mesic northern forest typically remove most of the bolewood, further inhibiting the development of necromass (Frelich and Reich 2003). O'Hanlon-Manners and Kotanen (2004) suspect that the lack of coarse woody debris in young, managed stands may increase the susceptibility of hemlock populations to fungal pathogens that reside in the soil and that are insignificant in more structurally diverse settings in which hemlock seedlings can take refuge on downed logs. Even within forests that have been designated as old-growth, land managers often salvage blowdown following windthrow (Stearns and Likens 2002, Frelich and Reich 2003).

Gap-phase dynamics, the generation of small canopy gaps by small-scale disturbance events, have been replaced by short-rotation timber management as the dominant disturbance factor structuring mesic northern forests (Frelich and Lorimer 1991, Hannah 1999, Seymour et al. 2002). The extensive conversion of mesic forests to early-successional forests has reduced the frequency of treefall gaps since younger forests are less susceptible to windthrow (Canham and Loucks 1984). Recently disturbed areas exhibit a low susceptibility to disturbance for several decades (Frelich and Lorimer 1991). Windthrow not only generates coarse woody debris but also creates tip-up mounds. Tip-up mounds are proportional in size to the windthrown tree (Peterson 2000). The formation of treefalls is an important forest process that affects the fine-scale heterogeneity of forest soil by disrupting and redistributing soil horizons and altering soil development. The spatial distribution and diversity of common herbs and woody seedlings are related to this micro-relief or fine-scale patterning of forests (Beatty 1984). The exposed mineral soil of tip-up mounds allows for seed-to-soil contact and increases successful seedling establishment, especially of small-seeded species, (i.e., hemlock and yellow birch), whose hypocotyl cannot penetrate the thick leaf layer. Windthrow's influence on soil development is very different from the impact of tree harvesting, which causes compaction and rutting and does not generate tip-up mounds. The widespread replacement of natural disturbance regimes by short-rotation timber management has reduced pit and mound topography and the abundance of rotting logs, which are important establishment sites for hemlock, yellow birch, and white pine (Ducey and Gove 2000, Rooney et al. 2000).

The gaps created by natural treefalls are very different from the felling gaps of commercial harvests. Selective logging and thinning tend to produce single treefall gaps that are much smaller than the gaps generated within old-growth and late-successional forests, whose bigger trees open larger gaps. In addition, natural gaps are more likely to experience domino effects, while commercial loggers are typically careful not to damage residual stocking when felling trees. Natural gaps also tend to expand as new treefalls occur along the edges of previous large gaps (Poulson and Platt 1996, Beaudet and Messier 2002, Webster and Lorimer 2002). Gaps generated by selective logging tend to be filled by sugar maple (Curtis 1959), the seedlings of which often saturate the shaded understory of mesic northern forests (Barnes 1991, Jackson et al. 2000). Long-lived species like yellow birch and red oak, which are intermediate in shade tolerance and depend on multiple canopy gaps and intermediate disturbance events, often fail to regenerate within selectively harvested mesic northern forests. Yellow birch populations have declined as a result of insufficient light within harvested gaps, high levels of deer herbivory, and the lack of recruitment, due to the aforementioned decrease in suitable microsites for establishment (i.e., nurse logs and exposed mineral soil associated with tip-up mounds) (Hannah 1999, Woods 2000a).

In addition to selective harvesting and thinning, many mesic northern forests are intensively managed using small-patch clear-cuts. Repeated even-aged management of mesic northern forest is an anthropogenic disturbance that is even more dissimilar to the natural disturbance regime of frequent small-scale gaps and infrequent large-scale catastrophic windthrow (Seymour et al. 2002). Large catastrophic windthrows occurred very infrequently; multiple generations of trees often grew on a site for at least a millennium between major disturbances. Following the wind disturbance, blowdown remained on the site as necromass legacy or was partially consumed by fire. Clear-cutting of mesic northern forests leaves little coarse woody debris and typically occurs ten times more frequently than catastrophic windthrow. Harvesting often removes more carbon than does fire (Crow and Perera 2004). As noted by Seymour et al. (2002), widespread application of single-cohort silviculture on rotations under 100 years creates a landscape that has no natural precedent. Clear-cutting favors sprouting (coppicing), light-seeded, and wind-dispersed species (i.e., aspens, white birch, sugar maple, and red maple) (Davis et al. 1998, Leahy and Pregitzer 2003, Cleland et al. 2004). Historically, the natural disturbance regime of mesic northern forest created a shifting mosaic pattern of vegetation across the landscape with frequent small disturbances resulting in a diverse stand age structure within large blocks of uneven-aged forest, and infrequent catastrophic windthrow and fire creating patches of early-successional forest that move across the landscape over time (Zhang et al. 1999). Modern forestry tends to impose a stagnant pattern on landscapes with silvicultural practices maintaining cover types. For example, aspen stands that are succeeding to later-successional forest types such as pine are often harvested to maintain the aspen cover type.

Although fire was historically a very infrequent disturbance within mesic northern forests, fire disturbance was prevalent throughout the landscape and influenced the species composition and structure of these forests. Beginning in the 1920s, effective fire control by the U.S. Forest Service and state agencies reduced the acreage of forest fires ignited by humans or lightning in the Great Lakes region (Swain 1973). Institutional fire suppression has diminished the frequency, severity, and extent of fires (Swain 1973, Leahy and Pregitzer 2003, Cleland et al. 2004). As noted earlier, fire suppression is facilitated in today’s landscape by forest fragmentation and increased road density. Modern fire rotations are an order of magnitude longer than historical rotations (Cleland et al. 2004). Extended burning rotations have encouraged the development of denser forests (Leahy and Pregitzer 2003). Fire suppression has affected species composition at the landscape scale, increasing the proportion of fire-intolerant deciduous species (i.e., red maple) and decreasing fire-dependent species such as white pine and red oak (Foster et al. 1996, Abrams 1998, Cleland et al. 2004). The reduction of fire-dependent species in systems that historically burned frequently influences the seed rain that falls within adjacent mesic northern forests.

The shift from natural disturbance to anthropogenic disturbance as the primary force driving mesic northern forests has resulted in alteration of the biogeochemical processes of these forest ecosystems. In particular, logging has long-term impacts on forest carbon and nitrogen cycling. Logging removes large amounts of carbon and nitrogen and can result in the decrease in forest floor organic matter. Nutrients are removed through biomass export and hydrologic losses due to surface runoff. The slash fires that followed the early logging caused drastic losses in nutrients and carbon with the combustion of woody material and soil organic matter. Shifts in the tree species composition of mesic northern forest have affected the soil properties and nutrient dynamics. Compared to managed systems, old-growth forests have higher carbon and nitrogen capital and exhibit higher rates of nitrification (Goodale and Aber 2001, Latty et al. 2004).

Anthropogenic disturbances within mesic northern forest include the introduction of non-native pathogens and insects that have decimated populations of trees and altered the remaining forest composition and structure (Foster et al. 1996). Prior to the Dutch elm disease epidemic in the 1960s, *Ulmus americana* (American elm) and to a lesser extent *Ulmus rubra* (slippery elm) were common canopy associates in mesic northern forest. However, the disease has relegated elms to understory and subcanopy status: in many stands no elms greater than 15 cm (6 in) in diameter remain (Beaman 1970, Frye 1976). Beech bark disease is a disease complex that was introduced to North America around 1900 (Seymour et al. 2002). The disease results when the bark of beech trees is attacked by the beech scale

(*Cryptococcus fagisuga*) and subsequently invaded and killed by fungi, primarily *Nectria coccinea* var. *faginata*, and sometimes *N. galligena* (Houston and O'Brien 1998). Beech bark disease is just starting to spread through parts of Michigan (the eastern Upper Peninsula and the northwestern Lower Peninsula) and has the capacity to drastically alter gap dynamics, species composition, and vegetative structure (Forrester et al. 2003). Beech bark disease can cause widespread mortality of overstory beech and threatens to reduce the importance of beech as a canopy dominant of mesic northern forests. The impact to biodiversity of such a decline would be severe since beech is a critical species for numerous animal species (e.g., nesting tree for raptors, cavity tree for woodpeckers, fall food source for bear, etc.). In addition to causing high levels of canopy mortality, beech bark disease causes high levels of beech root sprouting which can suppress the regeneration of other species (Bohn and Nyland 2003). In 2002, a new exotic pest, the emerald ash borer (*Agrilus planipennis*), was identified in southeastern Michigan. This Asiatic beetle has already killed millions of ash trees and could potentially alter the species composition and structure of mesic northern forests (USDA Forest Service 2002, Roberts 2003). Hemlock woolly adelgid (*Adelges tsugae*), which has caused major changes in the structure, composition, and ecosystem function of hemlock forests in the eastern U.S., also represents a future threat to mesic northern forests of Michigan (Foster 2000).

The primary non-anthropogenic factor currently influencing the species composition and structure of mesic northern forests is deer herbivory. At high densities, deer can act as keystone herbivores, drastically altering vegetative structure and composition, which can lead to cascading trophic effects (Alverson et al. 1988, Strole and Anderson 1992, Rooney and Dress 1997, Waller and Alverson 1997, Augustine and Frelich 1998, Van Deelen 1999, Rooney 2001, Rooney and Waller 2003). Chronically high deer densities over the last half-century (or more) have limited tree recruitment of mesic northern forests and drastically altered their floral composition and structure (Whitney 1984, Abrams and Orwig 1996, Rooney and Dress 1997, Waller and Alverson 1997, Woods 2000a, Zhang et al. 2000, Abrams 2001). Deer populations of the Great Lakes have been favored by short-rotation, even-aged management geared toward pulp production and wildlife management and a decrease in or elimination of populations of natural predators (i.e., wolf, mountain lion, and wolverine) (Alverson et al. 1988, Van Deelen et al. 1996, Terborgh et al. 1999, Ripple and Beschta 2005). Woody plant species unpalatable to deer or tolerant of browsing (i.e., aspens, balsam fir, and red maple) have increased, while species intolerant of deer browsing have decreased (i.e., hemlock, cedar, yellow birch, and white pine) (Van Deelen et al. 1996).

Numerous studies have shown that winter deer herbivory can lead to the failure of hemlock, white pine, and cedar regeneration (Whitney 1984, Frelich and Lorimer 1985, Ziegler 1995, Abrams and Orwig 1996, Alverson and Waller 1997, Rooney and Waller 1998, Rooney et al. 2000). The intensity of browsing has prevented the establishment in many locations of seedling or sapling banks of palatable species, especially hemlock (Peterson and Pickett 1995, Peterson 2000). Deer-preferred winter browse is hemlock, which is heavily used when other food is scarce. High densities of deer are capable of eliminating hemlock regeneration within the 0.3-3.0 meter class (above snow fall and within reach of an outstretched neck) (Whitney 1984, Rooney and Waller 1998). Abundance of hemlock seedlings in smaller size classes is limited by suitable substrates or habitats for establishment. Microsites suitable for hemlock establishment include bare mineral soil, nurse logs, and moss beds (Graham 1941, Goder 1955 in Curtis 1959, Mladenoff and Stearns 1993, Rooney et al. 2000). Hemlock seedling establishment is limited by the abundance of microsites, since hemlock seeds are small and often incapable of penetrating the deep, smothering litter of hardwoods (Kavanagh and Kellman 1986). The landscape replacement of hemlock by hardwoods has reduced the habitat suitability for hemlock seedling establishment (Davis et al. 1998, Rooney et al. 2000). Once browsed, hemlock saplings, which grow very slowly, have extremely low recovery potential (Curtis 1959, Whitney 1984). White pine is intermediate in browse preference, and saplings less than two meters tall are particularly susceptible to herbivory during harsh winters when deer populations are high (Ziegler 1995, Tester et al. 1997). Insect and disease damage from white pine weevil (*Pissodes strobi*), white pine blister rust (*Cronartium ribicola*), and Armillaria root disease, and low fire disturbance throughout the landscape have also contributed to regeneration failure of white pine (Abrams and Orwig 1996, Tester et al. 1997, Smidt and Puettmann 1998, Abrams 2001, Burgess and Wetzel 2002, Stearns and Likens 2002). The reduction of dense understory vegetation (especially the evergreen component) by deer herbivory has increased the amount of light reaching the forest floor in some locations; in many mesic northern forests this increased light exposure has promoted the germination of mid-tolerant species, such as red maple, which grow rapidly and can outcompete white pine seedlings (Whitney 1984, Abrams and Orwig 1996, Abrams 2001). In contrast, at other sites, the reduced light transmission caused by shade-tolerant hardwoods and their advanced regeneration reduce the growth of white pine seedlings, which have difficulty establishing on fine-textured soils (Smidt and Puettmann 1998). In many locations white pine and hemlock are outcompeted by northern hardwood species, which have less rigorous seedling requirements and deeper rooting systems, benefit from fire exclusion, grow fast, often have sprouting capacity, and are less palatable to deer (Abrams and Orwig 1996).

In addition to the drastic changes to tree recruitment, deer browsing has had perhaps even greater impact to forb and shrub diversity and composition of mesic northern forests. Most herbaceous species and shrubs never outgrow the “molar zone” or zone of susceptibility to deer browse (Waller and Alverson 1997). With a single bite, deer can remove the leaf area and reproductive structures of long-lived understory forbs, many of which lack the capacity for regrowth after grazing. Many spring herbs require decades to fully recover from deer browsing. Herbaceous plants constitute 87% of deer’s summer diet. Concentrated herbivory can lead to reduction of forb reproductive capacity and plant size, and even to the local extirpation of sensitive plants (Alverson et al. 1988, Rooney and Dress 1997, Augustine and Frelich 1998, Rooney and Waller 2003). Indirect impacts of deer herbivory can include the reduction of pollinators and seed dispersers of sensitive herbs (Waller and Alverson 1997, Ruhren and Handel 2003). Canada yew, once a dominant understory component of many mesic northern forest of the Great Lakes, has been extirpated locally (Van Deelen et al. 1996). Close to a hundred threatened and endangered plants are jeopardized by deer herbivory (Miller et al. 1992). As a result of high deer densities across the Great Lakes, forb species that are less palatable and more tolerant of grazing have increased in frequency in mesic northern forests (i.e., ferns, graminoids, and club mosses): deer browse has contributed to the region-wide homogenization of forest flora and reduction of floral genetic diversity (Van Deelen et al. 1996, Rooney and Dress 1997, Augustine and Frelich 1998, Rooney 2001, Rooney and Waller 2003, Kraft et al. 2004).

Often overlooked and understudied is the influence of anthropogenic disturbance on genetic diversity of forests. Genetic diversity is the key to adaptability and continued evolution of species (Buchert et al. 1997). Reduction in the genetic diversity of species results in the reduction of fitness and capacity to respond to changing environments. Old-growth forests are genetic reserves, containing genetic diversity accumulated over many generations (Mladenoff et al. 1993, Buchert et al. 1997, Frelich and Reich 2003). Old forests contain locally adapted gene pools selected for by the local climate and natural disturbance regime (Buchert et al. 1997). As tree populations age, they increase in genetic diversity and reproductive fitness (Mosseler et al. 2003). Harvesting, especially high-grading of old forests, can lead to genetic erosion, inbreeding, genetic drift, and decrease in tree species fitness. Tree populations that have sustained genetic losses are susceptible to decline in productivity and loss of environmental fitness due to the reduction of locally adapted gene pools (Buchert et al. 1997). In younger stands, individual trees with inferior growth and survival may still exist and can be artificially selected by human harvest (Frelich and Reich 2003). In a study of genetic composition of harvested old-growth white pine, Buchert et al. (1997) found that as the population size of white pine decreased through harvesting, genetic diversity decreased substantially; the total and mean number of alleles was reduced by 25%. Of the alleles lost, a high proportion of low-frequency and rare alleles were lost, 40% and 80% respectively. This represent a significant reduction in long-term evolutionary potential because low frequency and rare alleles represent the genetic potential for future population adaptation to environmental changes, while current alleles of higher frequency are selected for by current or recent past environments (Buchert et al. 1997). The logging era undoubtedly had an erosive effect on the genetic diversity of tree populations of the Great Lakes, especially white pine and hemlock.

RESTORATION AND BIODIVERSITY MANAGEMENT

Anthropogenic disturbance has degraded mesic northern forests across spatial scales, from the erosion of the genetic diversity of its component species to the reduction of mesic northern forest acreage across the Great Lakes. The biodiversity management of mesic northern forests therefore requires a multi-scale approach with conservation and restoration efforts focused on both the landscape and stand levels. Success of restoration efforts at all spatial scales should be closely monitored to allow for adaptive management (Herman et al. 2004). The following section contains general recommendations of how resource managers, by employing techniques guided by historical hindsight and honed by ecological insight, can enhance the biodiversity of mesic northern forests at the landscape and stand level. The discussion will conclude with a synthesis of specific, site-level methods for restoring hemlock and white pine to mesic forests that have been depleted of these species.

Conservation and restoration efforts will be most successful when resource practitioners emulate natural disturbance regimes and manage landscapes within the historical range of variability (Mladenoff et al. 1993, Lorimer and White 2003, Cleland et al. 2004, Crow and Perera 2004). Maintaining the patterning, composition, and structure of forests within the spatial and temporal characteristics of prevailing natural disturbance regimes promotes ecosystem resilience by preserving landscape characteristics to which regional plants and animals have become adapted (Friedman et al. 2001, Lorimer and White 2003, Crow and Perera 2004). Prior to launching conservation and restoration efforts, resource managers must first evaluate the historical landscape to provide baseline information for restoration and ecosystem management (Bolliger et al. 2004). Because of the dynamic nature of ecological systems and the potentially confounding effect of climate, these retrospective insights should be considered as guidelines and a framework rather than absolute criteria on which to base decisions (Foster et al. 1996, Miller and Woolfenden 1999).

Comer et al. (1995) developed a digital map of the circa-1800 vegetation of Michigan based on the interpretation of the original land surveyors' notes. This map, available for the whole state and also by county (Web site: http://web4.msue.msu.edu/mnfi/data/veg1800.cfm) can be used as a coarse scale reference. Albert (1995) and Corner and Albert (1999a-1999f) have summarized changes from circa-1800 vegetation to current land cover by ecoregion, subsection, and sub-subsection across the state (Albert 1995), and by landtype associations for the Northern Lower Peninsula (Corner and Albert 1999a-1999f). These resources provide the historical context of current management within a hierarchical ecological classification, allowing for restoration efforts at several broad spatial scales. For finer scale information, researchers can analyze tree rings and pollen data in peat cores, refer to historical descriptions by settlers, and/or examine the notes of the original land surveyors. These notes, archived in Michigan's Historical Museum System, contain information the surveyors compiled at the section corners (witness tree species and diameter) and along the section lines (tree species and diameter, natural disturbances such as windthrow, wildfire, and beaver flooding, and cultural features such as Native American encampments and agriculture). These historical references, along with ecological insight, can provide managers with guidance about where to focus restoration efforts and what species compositions to manage for.

Information about historical vegetative associations with landforms and landscape contexts will help direct restoration efforts. The following is a summary of some of the more prevalent landscape-level associations of the canopy dominants of mesic northern forest. Poorly drained till plains and outwash plains, especially in the western Upper Peninsula, supported hemlock/yellow birch forest. This assemblage typically occurred adjacent to swamps and bogs, around lakes, and in complex mosaics with sugar maple/hemlock forest, which occurred on the better drained soils (Barnes 1991, Comer et al. 1995, Woods 2000a, Woods 2000b). Large expanses of rolling moraines in the northern Lower Peninsula and eastern Upper Peninsula and the clay lake plain along Saginaw Bay supported beech/sugar maple/hemlock forests. Moderately drained sand plains supported hemlock/beech and hemlock/white pine forests, while hemlock/white pine forest occurred on moderately drained lake plain extending from

Saginaw Bay through the Upper Peninsula. Calcareous bedrock, dunes, and drumlin fields supported extensive tracts of sugar maple and white cedar (Comer et al. 1995). Patches of early-successional forest occurred within the mesic uplands on sites recently disturbed by windthrow and fire. Fire disturbance was most frequent in mesic northern forests that occurred adjacent to or in close proximity to fire-dependent systems such as dry-mesic northern forest, dry northern forest, and pine barrens. Lorimer and White (2003) found that ridgetops and upper slopes have higher than average disturbance rates and are more dependable sources of suitable habitat for early-successional species.

In addition to historical references, some general observations about landscape trends of white pine and hemlock occurrence can help guide restoration efforts. Both of these mesic conifers occur in mesic northern forest systems that are associated with lakeshores, valley bottoms, ravines, and north- and east-facing slopes (white pine reaches its greatest abundance on drier southeast-facing slopes within the dry-mesic northern forest community) (Curtis 1959, Whitney 1990, Davis et al. 1998, Carleton 2003). In addition, white pine was historically prevalent along river corridors (Lorimer and White 2003), and hemlock stands were frequently associated with lowland conifer swamp and bog (Davis et al. 1998). In landscapes lacking current hemlock canopy, Mladenoff et al. (1993) suggest that successional conifer types, such as balsam fir, may be indicators of sites suitable for hemlock restoration. The presence of persisting hemlock and white pine seed trees and old conifer stumps can facilitate site selection for hemlock and white pine restoration. In addition, resource managers can utilize current soil and topographic maps and habitat classification guides (i.e., Burger and Kotar 2003) to determine where to allocate restoration efforts for appropriate species (Herman et al 2004).

The companion question "where to restore?" is "how much should be restored?" In terms of maximizing benefit to native biodiversity, the answer is "as much as possible." Mesic northern forest historically occurred as large blocks of old-growth and late-successional forest maintained by small-scale gap-phase dynamics.

Catastrophic windthrow and/or fire infrequently generated scattered patches of early-successional forest within the matrix of long-lived, shade-tolerant forest. As noted earlier, these early-successional forests typically constituted less than 5% of the landscape, and currently most old-growth and late-successional mesic northern forests occur as islands surrounded by a forested matrix dominated by early-successional forest and young northern hardwoods. Where old-growth and late-successional forests remain, the best management is to leave large tracts unharvested and allow natural processes (gap-phase dynamics: growth, senescence, and windthrow) to operate unhindered. Lorimer and Frelich (1991) estimated the maximum size of an individual downburst in the Great Lakes region to be 3,785 ha (9,353 acres). Given the large scale of the catastrophic disturbance to the landscape, recovery from perturbation requires protection of substantial area of forest. Johnson and Van Wagner (1985) suggest that a landscape should be at least twice the size of the largest disturbance event, while Shugart (1984 in Frelich and Lorimer 1991) posits that landscapes should be at least fifty times the size of the average disturbance patch. Protecting a series of unmanaged forest reserves throughout the range of mesic northern forest allows the species that depend on this system to make adjustments for global warming (Frelich and Reich 2003). Maximizing the size of blocks of old-growth and late-successional forest and increasing the connectivity of forest enhance the dispersal of organisms and processes among patches (Foster et al. 1996). Whitman and Hagan (2004) have developed an index to help identify forests that have potential to function as future old growth. Their index utilizes the density of large-diameter trees (> 40 cm in diameter) and the presence of three easily recognized lichen to identify late-successional forest in the landscape. Mossler et al. (2003) suggest developing and using an index of "old-growthness" to help identify potential forest blocks that are good candidates for restoration.

Increasing the total acreage of mesic northern forest throughout the landscape can be accomplished by allowing early-successional stands of aspen and white birch to revert back to late-successional forest employing the underutilized management tool of patience. Early-successional forest, especially aspen stands, can function as nurse crops for the rehabilitation of late-successional forests (Mosseler et al.

2003). Palik and Pregitzer (1995) found white pine to be the most dominant species of advanced regeneration under big-toothed aspen, and Peterson and Squiers (1995) observed a positive relationship between white pine growth rate and local aspen abundance as aspen stands age. White pine, with its prolific seed production, is capable of invading abandoned agricultural fields and unmanaged wildlife openings (Abrams 2001). White pine stumps and logs provide an excellent source for germination of hemlock seedlings (Goder 1955 in Curtis 1959). By allowing aspen stands, old fields, and wildlife openings to succeed to white pine, managers can re-establish the prevalence of the white pine seed source throughout the landscape and develop sites for eventual hemlock re-establishment. Conversion of wildlife openings and old agricultural fields to forest also contributes to increase of forest connectivity and decrease in forest fragmentation.

Dampening the effects of forest fragmentation can also be realized by reduction of forest harvest, halting the creation of new wildlife openings within forested landscapes, closing forest roads, and disallowing the construction of new roads for future forest harvests. Within fragmented landscapes, forest species may decline or become locally extinct because of cessation of plant colonization. In such instances seedling transplantation may be required to maintain the tree species composition of these fragmented forests (Hewitt and Kellman 2004). Along the edges of forest fragments, microclimatic and floristic edge effects can be reduced by encouraging shade-tolerant species such as sugar maple and beech through selective thinning or girdling of mid-tolerant and intolerant competition. Both sugar maple and beech have well-developed lateral canopies that promote effective closure, occlude high portions of sunlight, and insulate forest interiors from atmospheric edge effects (Mourelle et al. 2001). As noted above, forest fragmentation has been exacerbated by management practices that focus on species- and stand-based prescriptions that generate and maintain small, discrete patches of habitat (Bresse et al. 2004). Seymour et al. (2002) call for a fundamental shift in philosophy, challenging resource managers to match stand boundaries with large scale physiographic and edaphic features and to think of forests as large stands with substantial within-stand diversity and not as many small, uniform, single-cohort stands.

Much of Michigan’s mesic northern forest is immature (less than 100 years old) and has not yet attained the structural, compositional, and functional features of old-growth and late-successional mesic forest. Mimicking gap-dominated disturbances and promoting dead-tree dynamics can hasten late-successional and old-growth, uneven-aged conditions in immature and mature stands (Runkle 1991, Lorimer and Frelich 1994). In addition to retaining all naturally occurring snags and fallen logs, dead-tree dynamics can be enhanced by girdling overstory trees of variable diameters and species (especially species that have increased in importance due to sustained and frequent logging such as red maple, white ash, and black cherry). Manipulative treatments can create openings of natural sizes and at disturbance rates approximating old-growth conditions. Runkle (1991) suggests creating 0.005 to .01 ha (50 to 100 m^2) patches and maintaining 1% of a given area in new gap per year. Single-tree selection systems with return intervals of 100 to 150 years with opening sizes 0.001 to 0.01 ha (10 to 100 m^2) are comparable to natural treefall gaps (Seymour et al. 2002). Felling early- and mid-successional species to create these gaps can promote shade-tolerant species dominance. To maintain mid-tolerant species such as yellow birch and red oak as canopy components, managers will need to also incorporate the effects of rare, intermediate disturbance that maintain these long-lived shade intolerants (Carleton 2003, Woods 2004). Group-selection silviculture, which generates openings that are 0.04 to 0.1 ha (400 to 1000 m^2) in area, typically admits enough light for these gap-size-limited species (Seymour et al. 2002, Webster and Lorimer 2002).

As noted earlier, many characteristics of old-growth and late-successional forest accrue over time, with some traits developing after a threshold age (Tyrrell and Crow 1994b, Hagan and Whitman 2004). Development of uneven-aged, late-successional mesic northern forest takes between 200 and 400 years

(Canham and Loucks 1984, Tyrrell and Crow 1994b). Restoring structural, compositional, and functional characteristics of old-growth and late-successional forest requires patience. For managed forests, numerous ecologists recommend extending the timber rotation in mesic northern forest to lengthen the average canopy residence time beyond 100 years, the age at which late-successional and old-growth characteristics begin to develop (Seymour et al. 2002, Frelich and Reich 2003, Hagan and Whitman 2004). In addition, managers should strive to maximize forest continuity, which is key to the survival of many forest species, by retaining large-diameter dead and living trees (especially those over 200 years of age) as biological legacies (Seymour et al. 2002, Carleton 2003, Hagan and Whitman 2004, Whitman and Hagan 2004). Species that have declined in importance because of anthropogenic disturbance (i.e., hemlock, white pine, and yellow birch) should be retained where they persist. Late-successional and old-growth forest that have been disturbed by windthrow should not be salvaged (Frelich and Reich 2003). It is crucial to allow dead and dying wood to remain within these systems to become snags, stumps, and fallen logs because they provide critical wildlife habitat and substrate for seedling establishment.

Discussion of biological legacy typically focuses on snags, coarse woody debris, and old trees. Floristic and genetic diversity are aspects of forest continuity that conservationists should also consider. As mentioned earlier, maintenance of genetic diversity allows for long-term evolution. In order to maintain the genetic legacy of remaining intact old-growth and late-successional forest, stands must be carefully regenerated before any significant genetic erosion due to human activity occurs (Buchert et al. 1997). Retaining old trees and their alleles within these systems is critical because long-lived canopy residents have the genetic composition necessary to survive climatic extremes and competition over hundreds of years (Frelich and Reich 2003). Forest seed banks are important for maintaining genetic and species diversity (Leckie et al. 2000). Limiting soil disturbance within mesic northern forests helps reduce disruption of seed banks. Harvesting during winter months when snow cover or frozen soils limit soil disturbance is a means of reducing impacts to soils and seed banks. Animal species associated with vernal pools and the groundlayer plant community also benefit from winter harvests. The primary threat to floristic diversity of mesic northern forest is from deer herbivory: as mentioned above, deer herbivory can alter species composition and structure. Changes in herbaceous plant size and reproductive rates can be dramatically reversed when deer herbivory is eliminated for only two years (Augustine and Frelich 1998). Recovery of seedling and sapling banks (advanced regeneration) requires a more prolonged period of low deer densities (8 to 10 years with < 4 deer/km) (Whitney 1984, Alverson et al. 1988, Tester et al. 1997, Rooney et al. 2000). Conservation and restoration of mesic forest communities require active long-term management of deer at low densities, which may be realized through increased hunting pressure (Alverson et al. 1988, Augustine and Frelich 1998). Restoration of large mammalian predators (i.e., wolf, mountain lion, and wolverine) in the Great Lakes will also help bring down regional deer populations (Terborgh et al. 1999, Ripple and Beschta 2005). In addition, eliminating managed wildlife openings within forested landscapes and allowing early-successional forest to succeed to more long-lived forest will diminish suitable habitat for deer and reduce deer populations across the landscape. Where resources are available, deer exclosure fences may be erected around concentrations of sensitive herbs and susceptible saplings.

Hemlock Restoration

Restoration of hemlock is a high-priority regional conservation goal for the Great Lakes (Borgmann et al. 1999). Hemlock restoration will be most successful when coordinated with regional efforts to reduce deer densities, restore old-growth and late-successional structure to mesic northern forest, and promote hemlock seed sources throughout the landscape. Where overstory hemlock persists, the primary factors limiting hemlock populations are the paucity of suitable sites for seedling establishment and the dirth of sapling recruitment because of deer browsing. Restoring hemlock requires appropriate microsites for seedling establishment and sanctuary from excessive deer browse for successful recruitment (Rooney et al. 2000). Managers can enhance both aspects of hemlock demography with a variety of management techniques. Prior to allocating resources to site-specific management, a restoration strategy should be developed based on ground surveys for hemlock seedling and sapling abundance. Rooney and Waller (1998) suggest that survey quadrats need to be of sufficient scale (i.e., 100 m^2) in order to accurately detect hemlock seedling and sapling presence or absence since hemlock seedlings are frequently aggregated on suitable microsites. If large saplings are abundant, then active management for seedling establishment and sapling recruitment are not necessary. If seedlings and small saplings are abundant, the site has potential for recruitment of large saplings if browsing is controlled. Where seedlings and saplings are sparse, restoration should focus first on enhancing initial establishment (Rooney et al. 2000).

Hemlock seedlings, which are small and susceptible to desiccation and smothering by hardwood leaf litter, require suitable substrates for establishment (Rooney and Waller 1998, Rooney et al. 2000). Microsites include nurse logs, bare mineral soil, and moss beds (Goder 1955 in Curtis 1959, Mladenoff and Stearns 1993, Rooney et al. 2000). Bare mineral soil provides a good seedbed since hemlock seedlings are able to penetrate deeply enough to insure an adequate supply of moisture. Fires, by exposing large areas of mineral soil, can create conditions that promote the establishment of thick stands of hemlock seedlings (Davis et al. 1998). Prescribed surface fires have been employed successfully by foresters on the Menominee Indian Reservation in Wisconsin to promote hemlock seedling establishment (Pubanz personal communication). Hemlock seedlings were abundant following light surface fire, with some areas having in excess of 100,000 seedlings per hectare (Pubanz 1996 in Rooney and Waller 1998). Exposure of mineral soil and improved seedbed conditions for hemlock can also be accomplished by scarification (Rooney et al. 2000) but likely also requires reduction of understory hardwood competition through cutting, girdling, or herbicide (Goerlich and Nyland 2000, Webster and Lorimer 2002). Decaying wood provides a critical substrate for hemlock seedlings, and retention of coarse woody debris, especially of long-lived, large-diameter, slowly decaying conifer species will promote seedling establishment (Rooney and Waller 1998, Rooney et al. 2000). Compared to the soil surface, nurse logs are characterized by increased moisture and decreased moisture fluctuations (Ducey and Gove 2000). Nurse logs act like sponges, holding moisture throughout late summer droughts. They also provide seeds with an escape from smothering leaf litter and pathogenic soil fungi (O'Hanlon and Kotanen 2004). In stands that are lacking coarse woody debris, managers can intentionally fell or skid in long-lived, slowly decaying trees (especially conifers) to create future nurse logs. Added logs should be oriented east-west in order to maximize the moisture along the north-facing side of the log, which can provide a small moist microclimate (Rooney and Waller 1998). Hemlock canopy trees can produce prolific amounts of seeds (millions per hectare) every two to three years (Rooney and Waller 1998, Rooney et al. 2000). Management efforts designed to promote seedling establishment should be coordinated to correspond with years of high hemlock fecundity.

Successful efforts to promote hemlock seedling establishment do not necessarily translate into regeneration of hemlock saplings (Rooney and Waller 1998). Where deer densities are high, proximal management strategies designed to enhance seedling establishment may do little to ensure hemlock restoration at the stand level (Rooney et al. 2000). At sites where hemlock seedling and small saplings are abundant, recruitment of hemlock saplings will likely occur if deer densities are maintained at low levels (< 4 deer/km) for approximately a decade (Whitney 1984, Alverson et al. 1988, Rooney et al. 2000). Hemlock regeneration is abundant in all size classes on the Menominee Indian Reservation where deer densities have been historically low (Webster and Lorimer 2002). Strategies for reducing deer densities across the Great Lakes region were discussed above and include increased hunting pressure, increasing/restoring populations of deer predators, reduction of managed wildlife openings within forested landscapes, and allowing succession of deer habitat to more long-lived forest. Landscape-level reduction of deer densities will also help restore hemlock within lowland conifer systems, which historically functioned as refuges for hemlock during climatic transitions and seed sources for hemlock invasion into upland mesic systems (Mladenoff et al. 1993, Davis et al. 1998). Hemlock and cedar populations have been especially decimated in wintering deer yards (Van Deelen et al. 1996).

Where deer densities are high, managers need to also pursue cost-efficient restoration strategies that promote hemlock recruitment despite high deer populations. Erecting deer exclosure fences around hemlock recruitment can be employed on a site-specific basis but is not a feasible solution at the landscape level. Peterson and Pickett (1995) noted that hemlock seedlings and saplings that establish on or near concentrations of logs are taller and less browsed. Deer herbivory can be reduced by retaining high levels of coarse woody debris, which functions as a physical barrier to deer (Peterson and Pickett 1995). Likewise, the retention of dense patches of *Abies balsamea* (balsam fir) can create physical and visual barriers to deer and protect hemlock saplings. Borgmann et al. (1999) found that balsam fir facilitates hemlock growth and recruitment: hemlock saplings growing within balsam fir patches were denser and taller than hemlock found outside of the patches. Because balsam fir provides a refuge from deer browsing for hemlock saplings, the retention of fir in managed stands could provide a non-invasive and cost-effective way to preserve and locally restore hemlock (Borgmann et al. 1999).

Hemlock seedlings and saplings, when not subject to deer browse, can remain in the understory for prolonged periods of time (Curtis 1959, Whitney 1990). Once large saplings are present, active management for seedling establishment and sapling recruitment are not necessary. Suppressed hemlock can live over 100 years beneath the canopy (Curtis 1959, Davis et al. 1998). Hemlock is characterized by an extreme ability to withstand suppression (Kavanagh and Kellman 1986, Whitney 1990). Because of hemlock’s capacity to endure low light conditions, active management to promote canopy recruitment is not necessary; resource managers can rely on the natural development of treefall gaps to release hemlock saplings. Single-tree selection and group-selection harvest can also be employed to release hemlock seedlings and saplings. Forest management designed to promote hemlock recruitment must take the spatial distribution of hemlock regeneration into account; gap creation should take advantage of existing clumps of seedlings and saplings, and care should be taken to avoid damaging the advanced regeneration.

Where deer numbers are high, uneven-aged management for hemlock typically fails because unbrowsed hardwoods capture gaps intended for hemlock. In areas where deer populations are low, silvicultural techniques can be employed to perpetuate hemlock. Protracted sequences of suppression and release that often occur with gap-phase dynamics and single-tree selection can cause hemlock wood-quality problems (i.e., ring shake, broken tops, and heart rot) (Webster and Lorimer 2002). Group selection may increase the quality of hemlock lumber by promoting faster growth and quicker canopy ascension. Although hemlock often successfully establishes beneath a hemlock canopy, hemlocks growing under hardwoods typically have better-developed crowns, due to increased light availability, and respond to release more rapidly (Kavanagh and Kellman 1986, Whitney 1990). Within larger gaps created by group selection, hemlock must often compete with yellow birch, which establishes by seed and can catch and overtop hemlock advanced regeneration. Webster and Lorimer (2002) found that within gaps greater than 400 m^2, yellow birch replaced hemlock as the prevalent canopy successors. Varying the sizes of group selection gaps is a management strategy that can be utilized to ensure the establishment of both of these underrepresented species.

In certain regions of the Great Lakes, not only are hemlock seedlings and saplings missing, but canopy hemlock seed sources are absent (e.g., Saginaw lake plain). In these locations, hemlock restoration will require experimentation in broadcasting hemlock seed and underplanting of hemlock saplings (Herman et al. 2004). When hemlocks first invaded uplands of the Great Lakes region, they invaded white pine forest. As noted above, white pine stumps and logs provide an excellent substrate for germination of hemlock seedlings (Goder 1955 in Curtis 1959). Once established in the landscape, hemlock exhibited a positive feedback, reproducing more frequently under hemlock than under hardwoods (Davis et al. 1998). As noted above, where hemlock was able to establish under hardwoods, hemlock regeneration responded favorably. Mangers may be able to re-establish hemlock in white pine forests without disturbing the canopy by underplanting saplings and broadcasting seed onto suitable microsites (i.e., white pine nurse logs and exposed mineral soil of tip-up mounds or burned areas). Given the favorable growth of established hemlock in hardwood stands, managers can attempt to underplant hemlock saplings in both conifer and hardwoods stands. Whenever possible, managers should use nearby genetic stock for seeding and underplanting because local gene pools have adapted to local environments.

Prospects for hemlock may seem dire given the high densities of deer and paucity of hemlock seedlings and saplings across the Great Lakes. However, time and history are on the side of hemlock and restoration ecologists. Hemlock is a very long-lived species, living as long as 800 years, with many canopy hemlock reaching 200-500 years (Whitney 1990, Tyrrell and Crow 1994b, Abrams and Orwig 1996, Tardif et al. 2001, Leahy and Pregitzer 2003), providing resource managers with ample time to reduce high deer densities and improve conditions for seedling establishment and sapling recruitment. Hemlock also experienced a severe decline in the mid-Holocene when climatic changes, insect outbreaks, and/or pathogen epidemics decimated populations of hemlock (Filion and Quinty 1993, Fuller 1998, Calcote 2003). The recuperation of hemlock from this drastic decline provides hope that it can once again recover, especially with dedicated assistance from resource managers.

White Pine Restoration

Many of the management strategies suggested for hemlock restoration can be applied to restoration of white pine. Both species suffer from a depleted seed source across the Great Lakes region, limited seedling establishment because of a scarcity of suitable microsites, and failure of sapling recruitment due to deer herbivory. White pine restoration will be most successful when coordinated with regional efforts to reduce deer densities, restore old-growth and late-successional structure to mesic northern forest, and promote the increase of white pine seed sources across the landscape. White pine differs from hemlock in that hemlock is extremely shade tolerant while white pine is intermediate in shade tolerance (Curtis 1959). White pine growing on mesic sites is at a competitive disadvantage (Dovciak et al. 2003) and in the absence of fire or large-scale wind disturbance is outcompeted by shade-tolerant hardwoods and hemlock. As a result, establishment and maintenance of white pine within mesic northern forests can be challenging, especially in fire-suppressed landscapes with high deer densities (Tester et al. 1997, Smidt and Puettmann 1998, Burgess and Wetzel 2002). Restoration management of white pine should involve increasing the seed source of white pine across the landscape, promoting appropriate microsites for seedling establishment, and providing favorable conditions for sapling recruitment and growth by limiting excessive deer browse and understory competition.

One of the primary means for re-establishing white pine as a prevalent seed source throughout the Great Lakes landscape is simply allowing early-successional forests and abandoned fields to convert to white pine. As noted above, aspen stands can function as nurse crops for the rehabilitation of white pine forests (Graham 1941, Curtis 1959, Palik and Pregitzer 1995, Peterson and Squiers 1995, Stearns and Likens 2002, Mosseler et al. 2003). White pine also often thrives under oak canopies, taking advantage of the favorable growth conditions in non-summer months when the hardwoods are leafless (Abrams 2001). Increasing the use of prescribed fire throughout the landscape, especially within dry-mesic northern forest and dry northern forest, will also promote landscape-wide increases in white pine seed sources.

Once it reaches 20 to 30 years (30 to 50 under forested conditions), white pine develops a prolific capacity to produce seeds with good seed crops occurring every 3 to 5 years (Curtis 1959, Sharik et al. 1989, Ziegler 1995, Abrams 2001). The landscape increase in white pine will likely increase seedling establishment of white pine within mesic northern forests since seedling establishment is partially limited by seed rain. Dovciak et al. (2003) found that white pine populations are initially spatially structured by seed rain and safe sites (microsites suitable for seedling establishment such as decaying wood and moss cover). Rotting logs and moss cover are common attributes of old-growth and late-successional forest. Increasing these older age-class characteristics of mesic northern forests will benefit both white pine and hemlock. White pine seedling establishment will be promoted by the retention of coarse woody debris, especially of large-diameter, long-lived, slowly decaying conifer species. Managers can intentionally fell or skid in long-lived, slowly decaying trees to create future nurse logs in stands that are lacking coarse woody debris.

Bare mineral soil also provides a suitable substrate for white pine seedling establishment. Managers can expose mineral soil by employing prescribed surface fires or by scarifying the soil. Mechanical scarification should be followed by cutting, girdling, or herbicide treatment to reduce hardwood and shrub competition, major limiting factors for white pine seedling growth (Chown et al. 1986, Burgess and Wetzel 2002). Low-intensity surface fires (under-burns) favor pine seedling establishment and growth by preparing a suitable seedbed, releasing nutrients, and controlling vegetative competition (Buchert et al. 1997). Under-burned stands often exhibit a mosaic of open, partial, and full canopy. Ground-fire scorching of overstory and subcanopy trees can result in patchy removal of portions of the canopy, which increases light and encourages seedling growth. Partial overstory harvest (shelterwood cuts) can also reduce canopy coverage and promote white pine seedling and sapling growth (Burgess and Wetzel 2002). Burning to control vegetative competition often requires multiple burns in consecutive years or even within the same year. Typically, one fire is sufficient to girdle understory balsam fir, a thin-barked species. However, multiple fires are required to control hardwood competition. Optimum stand age for understory prescribed burning to promote pine regeneration is between 50 and 150 years. When white pine trees reach 80 years, their bark becomes thick enough to provide protection from mortality caused by surface fires. To promote natural seeding, prescribed burning and mechanical scarification should be employed during years of high seed production and in the spring when seed production peaks (McRae et al. 1994). During poor seed years or in areas lacking seed sources, managers can underplant white pine seedlings or saplings to supplement or provide natural regeneration (Herman et al. 2004). Underplanted saplings also can offer white pine a competitive advantage over understory rivals (Burgess and Wetzel 2002). The northward transfer of seedlings or saplings from a distance of 2 to 2.5 degrees latitude can promote growth potential of white pine while incurring no risks of cold damage (Lu et al. 2003). Once again, whenever possible, managers should use nearby genetic stock for underplanting because local gene pools have adapted to local environments.

Once established, pine seedlings and saplings face numerous perils, including herbivory and insect and fungal infestation. White pine seedlings can benefit from growing in under-burned stands and under a shelter crop, which exhibits a wide range of canopy cover. Growing white pine under a canopy can be advantageous in preventing serious attack by white pine weevil, since shaded conditions and cool micro-environments retard white pine weevil development. Seedlings growing in areas of partial canopy are protected from blister rust (Vora 1994, Burgess and Wetzel 2002). Dense understory regeneration of white pine also provides protection from white pine tip weevil and blister rust (Smidt and Puettmann 1998). If blister rust does become established, pine restoration can be enhanced by the removal of infected branches and pruning of branches within two meters of the ground (Vora 1994). Protection from deer herbivory can be guaranteed by the use of fences or seedling protection tubes (Vora 1994). However, long-term protection of white pine saplings from deer herbivory at the landscape scale can only be realized by reducing deer densities across the Great Lakes region. Once again, increasing hunting pressure, reducing managed wildlife openings within forested landscapes, allowing succession of deer habitat to more long-lived forest, and increasing/restoring populations of natural deer predators will contribute to the reduction of deer densities.

Recruitment of white pine saplings into the canopy of mesic northern forest is disturbance dependent. Historically, windthrow events and infrequent fire allowed for even-aged cohorts of white pine to establish within mesic uplands. In addition, the generation of large canopy gaps allowed for white pine ascension to the canopy (Davis et al. 1998). Canopy recruitment of white pine can be realized by both uneven-aged and even-aged silvicultural systems. Canopy gaps favorable to white pine regeneration can be created by selective logging (Quinby 1991, Abrams 2001). When coordinated with site preparation (i.e., seedbed preparation and reduction of vegetative competition), shelterwood cuts can be a successful means of promoting white pine dominance (Smidt and Puettmann 1998, Burgess and Wetzel 2002, Dovciak et al. 2003). Smidt and Puettmann (1998) observed shelterwood treatments to be most effective for white pine recruitment in stands where the understory is suppressed by a midstory canopy dominated by shade-tolerant softwood species such as balsam fir.

In portions of the landscape where white pine persists as a seed tree, white pine seedlings and saplings establish across a broad range of environmental conditions. White pine is characterized by a high degree of ecological plasticity: it can be found across all successional stages over a wide range of topographic positions and moisture conditions and in communities as divergent as bogs and pine barrens (Curtis 1959, Abrams 2001). Prospects for restoring white pine to mesic northern forests are promising given its opportunistic capacity. Resource managers must act opportunistically as well, promoting white pine establishment and recruitment on portions of the landscape that retain significant components of white pine seed source. These enclaves of white pine can be treated as nuclei from which to gradually expand restoration effort.

CONCLUSION

Widespread and sustained anthropogenic disturbance for the past 150 years has drastically altered mesic northern forest of the Great Lakes region. Human activity, primarily forest harvesting, has replaced small-scale windthrow as the primary force driving forest dynamics and landscape patterning. Mesic northern forests historically dominated vast areas of mesic uplands and were multi-generational, with old-growth conditions lasting many centuries. The overall extent of mesic northern forest, especially old-growth and late-successional forest, has severely declined with remnant patches becoming increasingly fragmented and even-aged. Remaining mesic forest has been subject to simplification of species composition and structural complexity. Hemlock and white pine, once common canopy associates, have become rare and localized, as have structural characteristics of old-growth forest, such as large diameter trees, coarse woody debris, and snags. High deer densities have contributed to the reduction of both floristic diversity and structural heterogeneity of these systems as deer browsing reduces herbaceous species richness and limits recruitment of seedlings and saplings, especially hemlock and white pine. Anthropogenic impacts to mesic northern forests have occurred at multiple scales, ranging from landscape fragmentation to genetic erosion. Restoration efforts to enhance the biodiversity values of mesic northern forest therefore require a multi-scale approach. Historical hindsight and ecological insight can help guide restoration. Knowledge of vegetative correlations to environmental parameters and historical context will assist resource managers in deciding where to focus their efforts. Total acreage of mesic northern forest can be increased by allowing early-successional stands to succeed to later-successional forest, while the effects of forest fragmentation can be dampened by reducing harvest and forest roads. Restoring structural, compositional, and functional characteristics of old-growth and late-successional mesic forest will require patience. Extending rotations in managed forests to over 100 years will allow for the development of late-successional characteristics. Where these traits persist, managers can maximize forest continuity by retaining large dead and living trees, especially mesic conifers. Hemlock and white pine restoration will be most successful when coordinated with regional efforts to reduce deer densities, promote the increase of conifer seed sources across the landscape, and restore old-growth and late-successional structure to mesic northern forest. Degradation of mesic northern forests has resulted from repeated and ubiquitous anthropogenic disturbance. Restoration of mesic northern forest will require sustained and widespread effort by resource managers across the Great Lakes region.

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