

Homogenization of northern U.S. Great Lakes forests due to land use

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Abstract Human land use of forested regions has intensified worldwide in recent decades, threatening long-term sustainability. Primary effects include conversion of land cover or reversion to an earlier stage of successional development. Both types of change can have cascading effects through ecosystems; however, the long-term effects where forests are allowed to regrow are poorly understood. We quantify the regional-scale consequences of a century of Euro-American land use in the northern U.S. Great Lakes region using a combination of historical Public

Land Survey records and current forest inventory and land cover data. Our analysis shows a distinct and rapid trajectory of vegetation change toward historically unprecedented and simplified conditions. In addition to overall loss of forestland, current forests are marked by lower species diversity, functional diversity, and structural complexity compared to pre-Euro-American forests. Today's forest is marked by dominance of broad-leaf deciduous species—all 55 ecoregions that comprise the region exhibit a lower relative dominance of conifers in comparison to the pre-Euro-American period. Aspen (*Populus grandidentata* and *P. tremuloides*) and maple (*Acer saccharum* and *A. rubrum*) species comprise the primary deciduous species that have replaced conifers. These changes reflect the cumulative effects of local forest alterations over the region and they affect future ecosystem conditions as well as the ecosystem services they provide.

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Introduction

Human land use of forested regions has intensified worldwide over the last two centuries, due to shifting cultural practices, increasing human

population, and global industrialization (Williams 2003). Primary effects include conversion of land cover or reversion to an earlier stage of successional development, which may or may not be the prime intent. Both types of change can have cascading effects through ecosystems, including impacts on water flows, nutrient cycles, vegetation and soil composition and structure, and terrestrial and aquatic species diversity (Foley et al. 2005). Recent research shows that land use change legacies can have profound influences on the nature of regeneration that occurs (Foster et al. 2003) and, under some environments, removal of forest cover and resulting alteration of the physical environment strongly inhibit forest regeneration (Mallik 1995).

In the northern portions of the U.S. Great Lakes states (Minnesota, Wisconsin, Michigan), widespread and destructive logging of the original forests occurred 100–150 years ago, from the mid-1800s to the early 1900s (Williams 1989). The mixed conifer-broadleaf deciduous forests of this region experienced logging that at the time was globally unprecedented in its speed and intensity, with over 20 million ha deforested in 60 years (Williams 1989). Logging was followed by repeated and often intense slash fires. Unlike the southern portions of these states, where oak savanna, prairie, and hardwood forests were converted to persistent agriculture, farming was promoted but failed in many areas of the north, with widespread farm abandonment (Gough 1997). Following successful fire suppression efforts in the 1930s, the region was reforested largely through natural regeneration (Graham et al. 1963).

Today, ecosystems of the northern Great Lakes region are often perceived as recovered from the land use changes associated with Euro-American settlement. Reforestation, the appearance of naturalness of the current forest, and the success of commercial forestry and natural amenity-based recreation in the region today are taken as evidence of recovery (Potts et al. 2004). The fact that Wisconsin has led the nation in paper manufacture from wood pulp for the last 50 years is an example of recovery of the forest industry (WIA 2003). Further evidence includes the re-establishment of the endangered eastern grey wolf (*Canis lupus*) over recent decades (Mladenoff et al. 1997).

Evaluating recent and emerging conservation issues associated with land use change in the Great Lakes region and elsewhere, however, requires a broad understanding of the spatial and temporal context of change. Examples can be drawn from ecological, social, and economic arenas and include conserving biodiversity (Mladenoff and Stearns 1993), deriving locations and targets for fuel-reduction thinning treatments (Allen et al. 2002), and maintaining ecological and economic resilience in the face of global climate change (Kling et al. 2003). Range of natural variability guidelines based on historic conditions have been used increasingly since the 1960s to evaluate change (Landres et al. 1999; Allen et al. 2002). While there is a great need for long-term and regional scale understanding, most existing information in the Great Lakes region and elsewhere is based on short-term, localized studies.

Within this context of perceived forest recovery and fine-scale knowledge, our goal is to quantitatively understand forest change across the northern Great Lakes region. We examine the following questions: To what extent have forests across the region been restored? To what extent do current conditions resemble prior extent, species diversity, structure, and function? Is the history of vegetation change uniform throughout the region or, alternatively, do multiple trajectories of change exist, depending on location and initial conditions? To answer these questions, we use three broad-scale data sets to compare land cover and forest conditions from the period just prior to intensive Euro-American settlement and land use in the region (mid-1800s) with those of the present (1990s). We summarize broad land cover classes, tree genera, and tree size metrics calculated from these datasets by 55 regional ecosystems, or ecoregions (land units measuring 1,500–15,000 km² in extent and similar in coarse climate, landform, and soil characteristics), that comprise the northern Great Lakes region (Fig. 1). In comparison to most studies that assess ecosystem change, our analysis is both extensive (100–150 years and 257,000 km²) and detailed. Most studies spanning pre-Euro-American settlement to present are conducted over local to landscape scales (ca. 100–32,000 km²), and

white spruce (*Picea glauca*), black spruce (*P. mariana*), tamarack (*Larix laricina*), northern white-cedar (*Thuja occidentalis*), sugar maple (*Acer saccharum*), yellow birch (*Betula alleghaniensis*), white birch (*B. papyrifera*), American beech (*Fagus grandifolia*), quaking aspen (*Populus tremuloides*), American basswood (*Tilia americana*), and American elm (*Ulmus americana*) (Albert 1995). Other common, though less dominant, tree species included balsam fir (*Abies balsamifera*), red maple (*Acer rubrum*), silver maple (*A. saccharinum*), bigtooth aspen (*P. grandidentata*), balsam poplar (*P. balsamifera*), white ash (*Fraxinus americana*), black ash (*F. nigra*), green ash (*F. pennsylvanica*), northern red oak (*Quercus rubra*), and northern pin oak (*Q. ellipsoidalis*). Hemlock, beech, and yellow birch had a marked presence in the eastern half of the study area in comparison to the Minnesota portion; with the exception of outliers, the range boundaries of hemlock and beech are in Wisconsin. Patches of more open vegetation existed within the forested matrix. Barrens communities were found on xeric glacial outwash plains and were dominated by herbaceous vegetation and low, but variable tree densities of jack pine, northern pin oak, red pine, white pine, red oak, and/or aspen (Albert 1995). Wetland communities, dominated by either grasses and sedges or sphagnum, formed large, open patches within the forests. Expansive grass and/or sedge wetlands were found along Lakes Michigan and Huron (Albert 1995). The peatlands of northern Minnesota covered areas as large as 180-km². Northern Michigan also contained sizeable peatlands. Windthrow and fire were dominant disturbances affecting meso-scale (10–100 km²) patterning prior to settlement.

Unit of analysis

Subsection-level ecosystems within the Laurentian Mixed Forest Province form the basic unit of analysis (Fig. 1 and supplementary material). Subsections are one level of ecoregional patterning in the USDA Forest Service Ecoregion Classification System (Cleland et al. 1997), which hierarchically divides the U.S. into units that are relatively homogenous in some ecological feature.

Subsections correspond to patterning in subregional climate, geomorphic process and surficial geology, soils, and potential natural communities (Cleland et al. 1997). Subsections vary between 1,425 km² and 15,493 km² in extent, providing a robust scale for analyzing both the historical public land survey (PLS) and current forest inventory and analysis (FIA) data employed in this paper. Studies recommend using the PLS at landscape or broader scales to eliminate fine-scale biases that might be associated with individual surveyors (Schulte and Mladenoff 2001). Similarly, FIA inventories were designed to “provide reliable estimates for large sampling areas,” such as counties or subsections (Miles 2001). In preliminary analysis, we assessed the potential of using land type association (LTA)-level ecoregions, one level below subsections in the hierarchical framework (Cleland et al. 1997), as units of analysis. We found too few FIA points represented at that level to provide a reliable estimate of forest conditions. Furthermore, subsection-level ecoregions are beneficial in that they comprise a meaningful unit for engaging the public in discussions of ecological change. Subsections are hereafter referred to as ‘ecoregions’ in this paper.

Data on pre-Euro-American conditions

We assessed historical ecosystem conditions from the U.S. General Land Office original Public Land Survey records (Stewart 1935), collected between 1836 and 1907 in the region. Prior work has given us a good understanding of the nature of bias and inaccuracy in PLS-derived data (Bourdo 1956; Manies et al. 2001). Based on this, we are confident in its ability to represent broad-scale vegetation patterns such as those investigated here (>2.6-km² resolution and >100 km² extent) (Schulte and Mladenoff 2001). We summarized tree genera and size data from the PLS by relative dominance, a common metric of biomass allocation among groups (Cottam and Curtis 1956). Data were summarized by ecoregion. The number of PLS corners per ecoregion varies between 789 and 16,484 depending on its extent, with a mean density of 1.1 corner/km². Trees are only considered by genera because many trees were not recorded at the species level

by PLS surveyors. Although statistical models differentiating ambiguously-recorded trees to species have been developed for Wisconsin (Mladenoff et al. 2002), this work has not been completed for the entire study area.

The proportional extent of land in open vegetation was also calculated by ecoregion. For presettlement, this assessment was based on tree density, as calculated from bearing tree distances (Cottam and Curtis 1956). PLS corners with a tree density falling between 0 and 46 trees/ha were considered to be in an open condition (Anderson and Anderson 1975). PLS corners falling within lakes and streams were eliminated from the datasets prior to this calculation.

As a conservative index of the extent of old forest, we calculated the percent and standard deviation of trees ≥ 51 cm in diameter by ecoregion. We did not consider the full diameter distribution because the PLS records are known to be biased toward mid-sized diameters, and surveyors rarely recorded trees < 20 cm in diameter (Bourdo 1956; Manies et al. 2001). All trees < 20 cm were eliminated from the analysis. Large trees would only have been recorded by the surveyors if no mid-sized trees were nearby the corner post (Manies et al. 2001) and, hence, can be used as an indicator of old forest.

Data on present conditions

Current ecosystem conditions were represented through federal forest inventory and analysis data (Miles et al. 2001) and National Land Cover Data (NLCD) (Vogelmann et al. 2001), both collected during the early to mid-1990s across the region. Tree genera and size data were summarized by ecoregion from fifth cycle FIA data. The number of forest inventory plots per ecoregion ranges between 73 and 2,773 depending on its extent, with a mean density of 0.2 plots/km². Relative dominance was calculated in the same manner as with the PLS data.

The extent of open land was based on the NLCD, as derived from 1992 Landsat thematic mapper satellite imagery (Vogelmann et al. 2001). We included all cultivated land, barren land, shrub land, and upland and lowland

herbaceous categories from the NLCD as open land, most of which is cultivated (87.8%). NLCD pixels falling within open water were eliminated from the datasets prior to this calculation.

Although Friedman and Reich (2005) show that the biased size distribution data associated with PLS likely has little effect on the relative vegetation metrics we calculate, we eliminated all trees < 20 cm in diameter from the FIA data before calculating the proportion of trees > 51 cm in diameter, as with the PLS dataset.

Analysis methods

We used a combination of map-based and tabular analyses and nonmetric multidimensional scaling (NMS) to reveal the extent and pathway of change between the pre-European and current periods. We included genus-level tree dominance data as a compositional measure, the percent of trees ≥ 51 cm in diameter and the standard deviation in size of trees ≥ 51 cm in diameter as a surrogate measures for an old forest structure, and the landscape-characteristic of percent open lands in the NMS analysis. The NMS was performed in PC-ORD (McCune and Mefford 1999) using the Bray-Curtis distance measure, a robust measure for ecological community data (McCune and Grace 2002). Preliminary NMS analyses were run with as many as six ordination axes, but substantial contributions to stress reduction were consistently made by only the first three axes. The specifications for the final NMS run included three axes, a random starting configuration, and 40 iterations with real data; this solution had a final stress of 10.26 and a final instability of 0.00001, based on 183 iterations. The amount of variation explained is high ($r^2 = 0.92$) and the amount of stress, or the departure from monotonicity, in our final solution is low for ecological community data (McCune and Grace 2002). The Mantel test was used to test for dissimilarity between the two time periods; correlation was used to compute the dissimilarity matrices and the test was run using a Monte Carlo randomization to evaluate the test statistic.

Table 1 Summary statistics from non-metric multidimensional scaling (NMS) ordination between pre-Euro-American and present periods

Compositional and structural variables	Axis 1 <i>r</i>	Axis 2 <i>r</i>	Axis 3 <i>r</i>
Ash (<i>Fraxinus</i> spp.)	-0.23	-0.38	0.59
Aspen (<i>Populus</i> spp.)	0.13	0.06	0.81
Basswood (<i>Tilia americana</i>)	-0.36	-0.47	0.33
Beech (<i>Fagus americana</i>)	-0.18	-0.41	-0.44
Birch (<i>Betula</i> spp.)	-0.20	0.56	-0.29
Cedar (<i>Thuja occidentalis</i>)	-0.17	0.31	0.14
Elm (<i>Ulmus</i> spp.)	-0.06	-0.42	-0.15
Fir (<i>Abies balsamifera</i>)	-0.15	0.58	0.47
Hemlock (<i>Tsuga canadensis</i>)	-0.45	0.02	-0.77
Hickory (<i>Carya</i> spp.)	0.04	-0.41	0.05
Maple (<i>Acer</i> spp.)	-0.77	-0.35	0.17
Oak (<i>Quercus</i> spp.)	0.23	-0.63	0.30
Pine (<i>Pinus</i> spp.)	0.80	0.05	-0.42
Spruce (<i>Picea</i> spp.)	0.21	0.76	0.24
Tamarack (<i>Larix laricina</i>)	0.40	0.57	-0.14
Extent open vegetation	0.08	-0.33	0.86
Percent tree diameters ≥ 51 cm	0.09	-0.22	-0.51
Standard deviation in trees ≥ 51 cm in diameter	-0.02	0.18	-0.51

Data for tree genera are based on relative dominance values

Methodological limitations

Shortcomings of this research include our inability to fully assess species and structural changes associated with forest age, due to field methods associated with the PLS (Bourdo 1956; Manies et al. 2001; Mladenoff et al. 2002). To overcome these limitations, we refer to landscape-level historical studies (e.g., Whitney 1987; Mladenoff et al. 1993; Friedman and Reich 2005) and contemporary field studies (e.g., Heinselman 1973; Frelich and Lorimer 1991a; Woods 2000) from the region for assistance with understanding of species-level site preferences and disturbance response. Our assessment of changes in size structure only considers trees with large diameters, which is reasonable given the constraints of the PLS data, but provides only a superficial assessment of regional variation and change in the abundance of old forest. Our analysis is further limited to the period prior to Euro-American settlement and 100–150 year later; the settlement period is only indirectly considered. More spatially-explicit knowledge of the types, timing, and severity of disturbances that occurred during settlement and the biotic legacies

remaining thereafter would enhance our understanding of the change mechanisms involved and lend to improved predictions of ecosystem response to future disturbances and forest threats (Foster et al. 2003). Several state and federal reports from the era are helpful in providing more detailed information on forest conditions just after settlement (e.g., Cunningham and Moser 1938), but they lack the spatial detail required by analyses such as ours.

Results

The three ordination axes from the NMS together explain most of the variation ($r^2 = 0.92$) in the data and reveal the general extent and direction of change among ecoregions (Table 1 and Fig. 2). Within the NMS results, most of the variance is explained by axis 1 and axis 3 (axis 1 $r^2 = 0.20$; axis 2 $r^2 = 0.14$; axis 3 $r^2 = 0.57$). Salient trends revealed by this analysis include conversion of forests to open ecosystems, shift from conifer-dominated to broadleaf deciduous-dominated forests, and homogenization of the overall composition and structure of the regional forest (Fig. 2B).

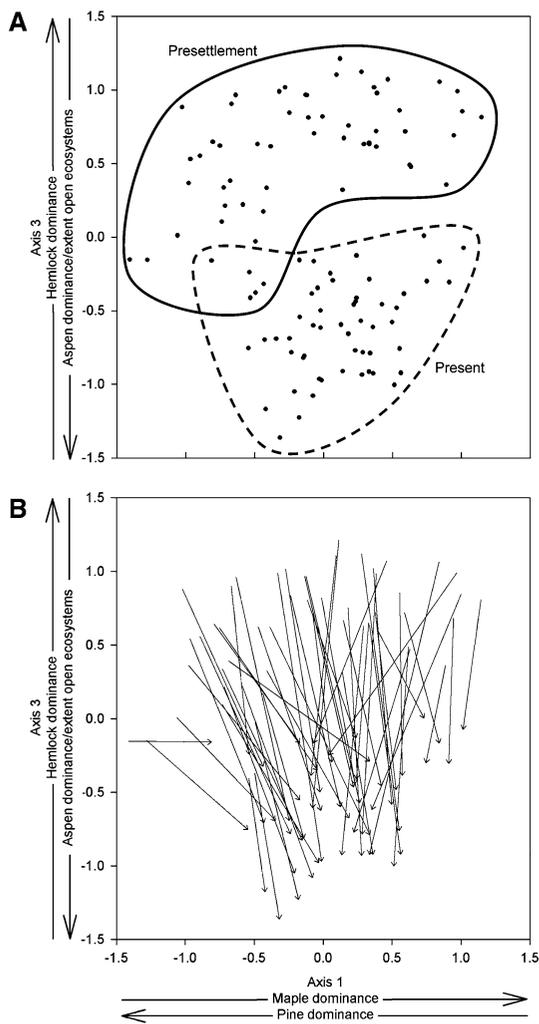


Fig. 2 Nonmetric multidimensional scaling (NMS) analysis showing: **(A)** variation among 55 ecoregions for the pre-Euro-American and present periods (each dot represents one ecoregion at one time period) and **(B)** change in ecoregions between periods (each vector represents one ecoregion)

Forests to openlands

The conversion of forest to open vegetation, largely row crop agriculture or grassland (Vogelmann et al. 2001), is a major change for the region (Figs. 2B, 3a; supplementary material). On average, $41.3 \pm 18.7\%$ of each ecoregion is in an open condition today compared to $12.3 \pm 9.3\%$ prior to Euro-American settlement. The trend toward row crop and grassland is more pronounced in some locations than others—ecoregions along the

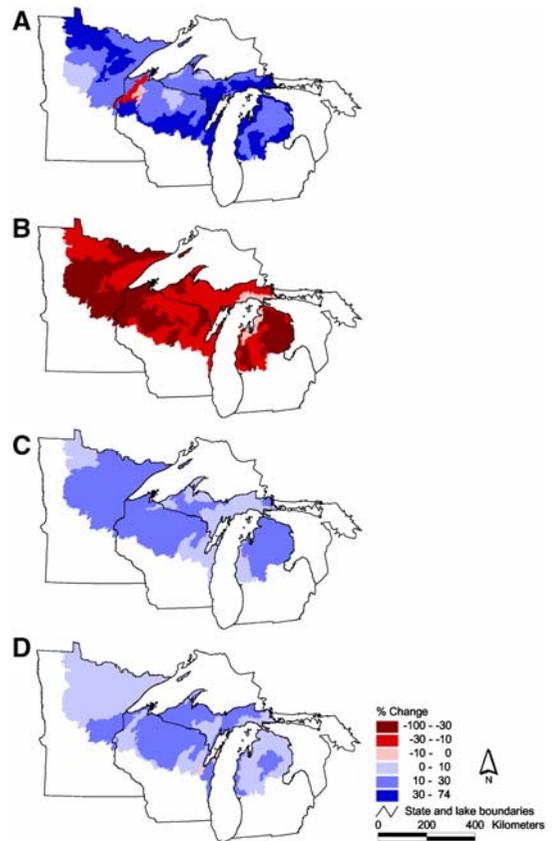


Fig. 3 Change in ecoregion characteristics in the northern U.S. Great Lakes region between pre-Euro-American land use and present, including **(A)** the extent of open vegetation, **(B)** dominance of conifers, **(C)** dominance of aspen (combined *Populus tremuloides* and *P. grandidentata*), and **(D)** dominance of maple (combined *Acer saccharum* and *A. rubrum*)

southern boundary of the study area experienced far greater than average conversion (Fig. 3A). Most of the ecoregions with the highest level of conversion occur in Wisconsin; these include the Manitowoc Till Plain (Zc; +73.7%), West Green Bay Till Plain (Za; +65.1%), East Lincoln Till Plain (Qc; +62.7%), and the Door Peninsula (Tf; +54.7%), which are now largely in rowcrops or grasslands. The Agassiz Lowland (Mb; +65.1%), which is a glacial lake bed in northern Minnesota, is an exception. Historically the area was dominated by tamarack peatlands. Today, the area is still largely in peatlands of a generally more open character, and aspen is now the dominant tree. Although attempts at agriculture were made in

Table 2 Relative dominance (RD) by tree genera for the pre-Euro-American settlement period (ca. 1850), the present (ca. 1990), and change between these two periods

	Pre-Euro-American settlement			Present			Change		
	Mean RD (%)	Max RD (%)	Ecoregion with max RD	Mean RD (%)	Max RD (%)	Ecoregion with max RD	Mean RD (%)	Max RD (%)	Ecoregion with max RD
Ash (<i>Fraxinus</i> spp.)	1.7	9.2	Zc	5.2	19.8	Zc	3.5	14.3	Tf
Aspen (<i>Populus</i> spp.)	3.3	13.4	Ma	16.1	32.2	Nc	12.8	24.6	Ja
Basswood (<i>Tilia americana</i>)	1.6	7.1	Za	3.1	9.6	Hi	1.5	8.1	Hi
Beech (<i>Fagus americana</i>)	5.4	36.5	Ha	0.8	7.6	Ri	-4.5	-32.0	Ha
Birch (<i>Betula</i> spp.)	10.9	30.6	Qc	7.4	20.9	Lb	-3.5	-25.3	Qc
Cedar (<i>Thuja occidentalis</i>)	6.4	22.2	Te	8.0	25.1	Tb	1.6	11.9	Mb
Elm (<i>Ulmus</i> spp.)	2.0	8.1	Za	1.0	6.1	Zb	-1.1	-5.2	Qb
Fir (<i>Abies balsamifera</i>)	2.2	9.2	Rk	5.8	14.3	Ma	3.6	9.9	Ld
Hemlock (<i>Tsuga canadensis</i>)	13.5	44.3	Jd	2.2	9.9	Jd	-11.3	-34.3	Jd
Hickory (<i>Carya</i> spp.)	<0.1	0.2	Zc	<0.1	0.3	Zb	< 0.1	0.2	Ha
Maple (<i>Acer</i> spp.)	12.1	36.4	Sb	22.3	48.7	Sn	10.1	28.4	Xd
Oak (<i>Quercus</i> spp.)	3.2	33.2	Zb	7.2	38.3	Hb	4.0	29.0	Hb
Pine (<i>Pinus</i> spp.)	27.2	80.5	Ka	9.7	32.3	Ka	-17.5	-53.7	Nc
Spruce (<i>Picea</i> spp.)	3.9	19.9	Le	4.9	26.3	Le	0.9	6.4	Le
Tamarack (<i>Larix laricina</i>)	5.9	43.9	Mb	1.6	10.8	Mb	-4.3	-33.1	Mb
All conifers	59.1	85.5	Ka	32.1	63.4	Le	-27.0	-55.1	Nc
All broadleaf deciduous	40.3	73.7	Zb	63.1	90.1	Qa	22.8	52.9	Nc

A brief description of each ecoregion is provided in supplementary material

the early 20th Century, they largely failed (Albert 1995).

The trend toward open lands is reversed, however, for the Bayfield Sand Plain (Ka; -22.8%) and Bayfield Till Plain (Xf; -6.3%) (Fig. 3A), areas that contained a high percentage of pine barrens and savanna prior to settlement; prevalent tree species on the Bayfield Sand Plain included red pine and especially jack pine, while white pine was more prevalent on the Bayfield Till Plain (Schulte et al. 2002). The magnitude of the conversion to agriculture also conceals the predominance of oak and pine savanna systems along the southern boundary of the region in Minnesota and Wisconsin. At least 20% of the land cover in several of these ecoregions was in openlands prior to settlement (supplementary material), including the Chippewa Plains (Na), Pine Moraines and Outwash Plains (Nc), Mille Lacs Uplands (Kb), and West and East Lincoln Till Plains (Qb and Qc). The Green Bay Clayey and Silty Lake Plain (Zb; 46.2%), Bayfield Sand Plain (Ka; 42.7%), and Pine Moraines and Outwash Plains (Nc; 38.1%) had highest percentage of presettlement barrens and savanna habitat overall.

Shifts in forest composition

A second predominant trend revealed in the NMS is a shift from conifer and mixed conifer-hardwoods forests to forest dominated by hardwoods alone (Table 1 and Fig. 2). The loss of conifer is substantial and consistent across all ecoregions (Table 2, Fig. 3B). Prior to settlement, conifers comprised nearly two-thirds of the tree dominance on average (Table 2). Thirty-seven of the 55 ecoregions have experienced over a 20% decline in conifer dominance, and average conifer dominance is presently one-third of its presettlement value. The greatest losses are witnessed with hemlock, pine, and tamarack genera (Table 2). Although the relative dominance of fir, spruce, and cedar is greater at present than in the past, these changes are small in magnitude (Table 2). The maximum changes in conifer dominance are greatest in the Minnesota and Wisconsin portions of the study area (Table 2). The Pine Moraines and Outwash Plains (Nc; -55.1%), Lake Superior Clay Plain (Ja; -48.3%), Tawas Lake Plain (Hh; -46.3%), and Mio Outwash Plain (Hg; -44.7%) have ecoregions experienced the greatest change

(supplementary material). With the exception of the Lake Superior Clay Plain, these areas have a prevalence of coarse-textured soils (Fig. 1), and declines have largely occurred in the pine genus.

Concomitant with the loss of conifer has been an increase in the overall dominance of hardwoods across the region (Table 1 and Fig. 2). Whereas changes by tree genera are in most cases variable by ecoregion, the increase in aspen has been both pervasive and of great magnitude: all 55 ecoregions have experienced increases aspen relative dominance (Fig. 3C). These increases are usually between 10 and 25% (38 of 55 ecoregions), and average aspen dominance for the current period is nearly five times the presettlement value (Table 2).

Increases in maple have been nearly as pervasive as those for aspen, though more variable in character (Fig. 3D). Maple was highly dominant within some ecoregions prior to settlement (Schulte et al. 2002), though overall dominance values were not on par with today (supplementary material); on average, maple relative dominance has nearly doubled between the two periods (Table 2). Maple dominance tends to be highest today within ecoregions where eastern hemlock was historically dominant (supplementary material). For example, a decline in hemlock dominance of -34.2% within the Lake Superior Lake Plain (Jd) is concomitant with a 22.3% increase in maple. Ecoregions exhibiting a similar pattern include the Winegar Moraines (Jc), Rib Mountain Rolling Ridges (Qd), Baraga-Keweenaw Coarse Rocky Till (Sn), and Northwest Wisconsin Loess Plain (Xd).

Other regional trends include increases in the relative dominance of ash, basswood, and oak, though these changes are fairly small in magnitude with the exception of a few ecoregions (Table 2 and supplementary material). The pattern of change for oak is particularly heterogeneous. The dominance of oak has increased substantially with the Newaygo Outwash and Ice Contact (Hb; $+20.0\%$), Bayfield Sand Plain (Ka; $+18.3\%$), and Mio Outwash Plain (Hg; $+17.2\%$), ecoregions with a prevalence of coarse-textured sandy soils (Fig. 1). Oak dominance is also currently high within the St. Croix Moraine (Qa;

30.9%), West Lincoln Till Plain (Qb; 26.4%), and Manistee Outwash and Lake Sands (Ha; 20.0%), along the southern boundary of the region, but was also relatively high in these areas prior to Euro-American settlement (relative dominance of 16.6% , 15.7% , and 8.9% , respectively). Also located along the southern boundary, the Green Bay Clayey and Silty Lake Plain (Zb) exhibited exceptionally high oak dominance prior to Euro-American settlement (33.2%). Oak dominance has actually declined in this ecoregion to the current level of 19.4% relative dominance. Tree species that have made up this difference include quaking aspen, paper birch, and black cherry (*Prunus serotina*), which today have relative dominance values of 9.2% , 8.2% , and 6.3% , respectively.

The general trend from conifer to hardwood forests conceals some losses in some hardwood genera—beech and birch have also witness substantial declines between the two periods (Table 2). Though beech is restricted to the eastern half of the study area, all of the 25 ecoregions within its range have experienced a decrease its relative dominance; this decrease is $>10\%$ in 11 cases (supplementary material). Birch, especially yellow birch, was highly dominant within a substantial proportion of the region prior to settlement (Schulte et al. 2002). Its relative dominance has decreased in 36 ecoregions; these decreases are $>10\%$ in nine cases (supplementary material).

Shifts in tree size

The percentage of trees in a large size class (≥ 51 cm dbh) is consistently greater for the presettlement period. This pattern is true for 45 of 55 ecoregions (supplementary material), although the proportion of trees in this size class is not large in either case (presettlement mean = 7.3% ; present mean = 5.6%). The standard deviation in the size of large trees is also tends higher for the presettlement period (supplementary material), indicating a greater homogeneity at present in large tree sizes. The mean standard deviation across ecoregions at presettlement is 7.01 cm, compared to 3.67 cm at present.

The Vanderbilt Moraines (Hi) historically had an exceptionally high percentage of large trees (15.7%), and the Green Bay Clayey and Silty Lake Plain (Zb; 30.0%) does at present.

Regional homogenization

The NMS analysis also documents a homogenization in vegetation attributes over the entire northern U.S. Great Lakes region (Fig. 2). The mean distance among all ecoregions in multidimensional space across both time periods is 0.47 ± 0.05 , with a maximum distance between any two points of 0.86. When only the multidimensional distances for the pre-Euro-American period are considered, summary statistics remain relatively unchanged (mean = 0.44 ± 0.06 ; maximum = 0.86); thus, most of the heterogeneity in the data is contained within the presettlement period. The multidimensional distances are comparatively reduced for the present period (mean 0.35 ± 0.05 ; maximum = 0.69), documenting a loss in the overall heterogeneity of composition and structure across all 55 ecoregions that comprise the study area. Results of the Mantel test show that a significant relationship between the current and pre-Euro-American vegetation remains despite the substantial change ($r = 0.63$, $p < 0.01$).

Discussion

Regional ecosystem change

Our analysis reveals a pattern of regional vegetation change and homogenization between pre-Euro-American and present eras that differs from prevailing perceptions of recovery in the northern U.S. Great Lakes region (Fig. 2), but is supported by finer scale work, both stand (e.g., Frelich 1995; Stearns and Likens 2002) and landscape in character (e.g., Whitney 1987; Radeloff et al. 1999; Friedman and Reich 2005). The rate of change has furthermore been rapid—2.4 times the rate of vegetation change experienced within the preceding 1,000 years, as documented through regional pollen analysis (Cole et al. 1998).

One predominant change contrary to the perception of broad forest recovery is the permanent conversion of historically forested areas and their retention in open vegetation, largely row crop agriculture or pasture (Table 1 and Fig. 2). On average, $41.3 \pm 18.7\%$ of each ecoregion remains in an open condition today compared to $12.3 \pm 9.3\%$ prior to Euro-American settlement. This pattern is most pronounced along the southern boundary of the study area where open lands now comprise up to 85.0% of some ecoregions (Fig. 3A). In contrast, the trend is reversed for areas that were historically in barrens and savannas—now critically endangered communities—prior to Euro-American land use (Fig. 3A). For example, the percent cover of open ecosystems on the sand plain of northwest Wisconsin declined from 42.7% to 19.9% during this period, due to the elimination of American Indian burning and the suppression of natural fire in these systems (Radeloff et al. 2000).

A second principal trend is a loss in regional compositional diversity and structural complexity through a shift from dominance by needle-leaved conifers (largely evergreen) to forests dominated by broadleaf deciduous species (Table 2 and Fig. 2). Forests that were historically disturbed relatively infrequently by catastrophic fire or wind have shifted from largely mature and old-growth forests with many large trees and variable tree size-class distributions to young, even-aged forests (Frelich and Lorimer 1991a; Frelich 1995). The loss of conifers is substantial and consistent across the region and, thus, across a range of biophysical conditions. Prior to Euro-American land use, conifers comprised nearly two-thirds of the regional tree dominance; all 55 ecoregions have lower relative dominance of conifers today than historically (Fig. 3B). The greatest losses have occurred among eastern hemlock, pine, and tamarack (Table 1; Fig. 2). Declines in overall conifer abundance and/or basal area have also been recorded at landscape scales across the region (Whitney 1987; White and Mladenoff 1994; Radeloff et al. 1999; Friedman and Reich 2005). Loss of hemlock (supplementary material) and white pine (Whitney 1987; Radeloff 1999; Friedman and Reich 2005) appear to be consistent, and the dominance of balsam fir has

generally increased (supplementary material); other species level changes are variable given local conditions. For example, Whitney (1987), Radeloff et al. (1999), and Zhang et al. (2000) record increases in jack pine and red pine in some size classes and on some landscape positions. The loss of conifers within former mixed conifer-broadleaf forests also represents a loss of structural complexity at the stand scale, given differences in canopy architecture between conifer and broadleaf species and given that most conifers in the region are evergreen, whereas the broadleaf species are deciduous. Loss of conifers and/or shifts in conifer species at a stand-level also has been documented at several locations in the region (e.g., Frelich 1995; Stearns and Likens 2002).

Declines have also been substantial among some broadleaf species—beech and birch witnessed substantial decreases in dominance between the two periods. Palik and Pregitzer (1992) document loss of beech in a landscape within the Lower Peninsula of Michigan; a hemlock-beech-white pine forest was converted to predominantly big-toothed aspen between pre-settlement and the present. Yellow birch, a species that exhibits intermediate shade tolerance, was dominant within some ecoregions with mesic soils prior to Euro-American land use (Schulte et al. 2002). Yet, our results on the decline of yellow birch are conservative; full quantification of its historical importance is obfuscated by ambiguous designation among the two birch species present within the pre-Euro-American data. Landscape studies show that mesic hemlock-hardwood forests in the eastern portion of the study area have experienced declines in yellow birch (White and Mladenoff 1994; Woods 2000; Zhang et al. 2000), with concomitant increases in white birch (Whitney 1987; Zhang et al. 2000). White birch is a shade intolerant species requiring severe disturbances for regeneration and was a locally common component of the pre-Euro-American landscape (Schulte et al. 2002), but flourished in response to disturbances associated with settlement (Graham et al. 1963). Friedman and Reich (2005), however, document a decline in white birch between pre-settlement and the present, likely due to the

replacement of natural fire disturbance with logging. Our analysis bears this out for some ecoregions (Kb, Lb, Lc, Ld, and Ma), but not others (La and Le; supplementary material).

Concomitant with the loss of conifers, beech, and birch have been increases in young aspen and maple forests, which are both widespread and dominant at present (Fig. 3C, D). All ecoregions have experienced increases in aspen relative dominance, with average dominance at present five times its pre-Euro-American value. Like white birch, the aspens (quaking and big-tooth) are early successional species that became regionally dominant after the slash fires of the post-settlement era and have since been maintained by clear-cut logging practices (Graham et al. 1963). Increases in aspen at landscape scales have also been recorded in Minnesota (Friedman and Reich 2005), Wisconsin (White and Mladenoff 1994; Radeloff et al. 1999), and Michigan (Whitney 1987; Zhang et al. 2000), though its dominance is lower today than during the post-settlement period (Graham et al. 1963). Increases in shade tolerant maple species have been nearly as pervasive as those for aspen (Fig. 3C, D), with a near doubling between the two periods. Local studies show that maple-dominated forests both increased directly following the initial logging of the primary forests and, in the last half century, through succession of aspen and other forest types (e.g., Stearns and Likens 2002). Although sugar maple was an important species within some ecoregions prior to Euro-American land use (Schulte et al. 2002), current maple dominance is disproportionate to those witnessed historically, replacing hemlock, beech, birch, and pine (Fig. 2). Red maple is not expected to have been a canopy dominant across much of the pre-settlement landscape (Abrams 1998), but dramatic increases have been recorded at both stand- and landscape-scales in the region (Whitney 1987; Palik and Pregitzer 1992) and most of the maple increase in northeastern Minnesota can be attributed to this species (Friedman and Reich 2005). Reasons for maple's rapid expansion in the second half of the 20th century include the elimination of fire disturbance, its tolerance of current selective logging practices, and its tolerance of high rates of herbivory by white-tailed

deer (*Odocoileus virginianus*) (Palik and Pregitzer 1992; Abrams 1998). Other compositional trends include increases in the relative dominance of ash, basswood, and oak, although these changes are comparatively small in magnitude or extent (Table 2). The increases in oak are likely short-lived, however, as oaks were also established following the severe disturbances of the Euro-American settlement era. With the elimination of fire and regional prevalence of deer herbivory, oaks are now in decline (Lorimer 2003).

In addition to a change in forest composition and structure to historically unique conditions, our analysis documents vegetation homogenization over the entire northern U.S. Great Lakes region (Fig. 2). Although current vegetation is still related to that of the pre-Euro-American era, substantial elements of past diversity and complexity have been lost, such as the shared forest dominance among multiple genera and the presence of large, old trees. The multidimensional distances within the datasets are reduced for the present period in comparison to the presettlement one; thus, documenting a loss in the overall regional heterogeneity. Concomitant with our forest overstory results, Rooney et al. (2004) have documented homogenization of forest understory communities in the region, based on more localized and shorter-term data. Although our characterization of changes in forest age is superficial, we do know from other historical data sources—including early explorer accounts, settler accounts, and timber mill receipts, forest reserves in the region—that mature and old-growth forests were prominent across the region (Williams 1989). Extensive empirical work (Frelich and Lorimer 1991a; Frelich 1995), as well as modeling studies (Frelich and Lorimer 1991b), further support this conclusion.

Current implications and future prospects

These results show that, despite nearly a century of regrowth and a few local or single species examples of successful restoration (Mladenoff et al. 1997; Radeloff et al. 2000; WIA 2003), forest systems across the northern U.S. Great Lakes region still bear the profound signature of

land conversion associated with the initial Euro-American land use era. Unlike much of the eastern U.S. which had undergone several centuries of human management prior to reforestation (Fuller et al. 1998), this cycle has played out in just over a century in the northern Lake States. Although forests have largely been re-established across northern portions of the region, these forests are on a new trajectory of change rather than recovery toward pre-Euro-American conditions (Fig. 4). We attribute lack of recovery to legacies associated with the initial, severe land use conversion, the persistent over-abundance of a keystone herbivore (white-tailed deer), and related management practices that are inattentive to processes that historically promoted vegetation diversity within the region. Legacies of the historical land use include the elimination of seed sources of former forest dominants, especially hemlock, white pine, and red pine (Mladenoff and Stearns 1993; Stearns and Likens 2002), and the broad establishment of aspen- and white birch-dominated forests as a result of widespread logging and intensive slash fires (Graham et al. 1963). The excessive deer abundance at present is a feedback of regional forest management; white-tailed deer at high densities are now regarded as a major threat to forest biodiversity and regeneration in the region and elsewhere (Rooney et al. 2004). The commercial logging that is now the

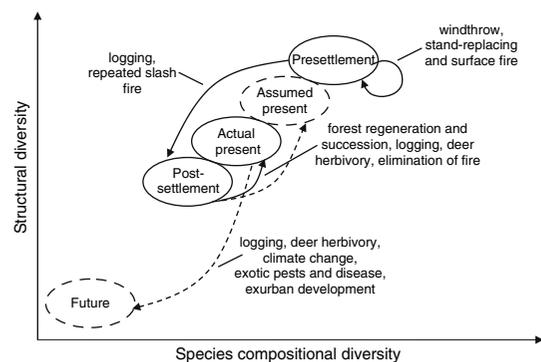


Fig. 4 Historic, present, and potential future states of the regional forest in the northern U.S. Great Lakes region, along with dominant processes that historically maintained regional forest diversity and drove change between periods. Solid lines represent conditions and process for which data are available (either in this study or in supporting literature). Dashed lines represent common assumptions and possible future conditions

most frequent and widespread forest disturbance across the region largely fails to mimic either the local or landscape effects of the historically prevalent disturbances of windthrow and fire (Mladenoff et al. 1993; Scheller and Mladenoff 2002). Rather, current practices of aspen clear-cutting and single-tree selection in maple stands continues to foster this divergence and simplification of the forests by largely favoring their regeneration over a greater diversity of tree species (Crow et al. 2002).

Our analysis also shows a loss of historical forest extent, species diversity, and structural complexity, and an increase in homogeneity, both within and across ecoregions (Fig. 2). These changes can be linked with (a) loss of economically important tree species such as white pine, yellow birch, and red oak, (b) loss of habitat diversity including conifer forests, mixed conifer-broadleaf forests, old forests with large trees, barrens, and savannas (Czederpiltz et al. 1999; Schulte et al. 2005; Latty et al. 2006), (c) loss of structural complexity over landscapes (Mladenoff et al. 1993), which served to regulate outbreaks of natural tree pests in the region (Knops et al. 1999), and (d) alteration of nutrient and carbon cycles, which lower the capacity of these forests to sequester carbon (Finzi et al. 1998). Loss in the diversity of canopy tree species is significant as it has been shown to homogenize functional diversity in terms of ecosystem processes and trophic interactions in the region and elsewhere (Campbell and Gower 2000; Bockheim and Crowley 2002; Whitehouse 2001; Ellison et al. 2005). Understory plant species diversity, abundance, and spatial pattern show simplification that parallels canopy homogenization in these forests (Miller et al. 2002; Scheller and Mladenoff 2005).

This lack of recovery and shift toward more homogeneous conditions has implications for future system resilience and sustainability, including the provision of clean water, wood and fiber, and other essential ecosystem services as diverse as carbon sequestration and recreation (Foley et al. 2005), and present a challenge to policymakers and natural resource managers. Management of the regional natural resource base in the northern Great Lakes region is further challenged by the emerging threats of exotic pests and

disease (MacFarlane and Meyer 2005), ownership fragmentation and exurban development (Radeloff et al. 2005), and global climate change (Scheller and Mladenoff 2005) (Fig. 4). While several state and national agencies are addressing these issues through planning processes (e.g. Minnesota Department of Natural Resources, Wisconsin's Brule State Forest, Chequamegon-Nicolet National Forest), the local practices that cumulatively caused rapid and widespread ecosystem change in the northern Great Lakes region continue globally today, in Canada, Russia, and many tropical regions (Williams 2003).

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