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Legacies of historical land use on regional forest composition and structure in Wisconsin, USA (mid-1800s–1930s–2000s)

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Abstract. Historical land use can influence forest species composition and structure for centuries after direct use has ceased. In Wisconsin, USA, Euro-American settlement in the mid- to late 1800s was accompanied by widespread logging, agricultural conversion, and fire suppression. To determine the maximum magnitude of change in forest ecosystems at the height of the agricultural period and the degree of recovery since that time, we assessed changes in forest species composition and structure among the (1) mid-1800s, at the onset of Euro-American settlement; (2) 1930s, at the height of the agricultural period; and (3) 2000s, following forest regrowth. Data sources included the original U.S. Public Land Survey records (mid-1800s), the Wisconsin Land Economic Inventory (1930s), and U.S. Forest Service Forest Inventory and Analysis data (2000s). We derived maps of relative species dominance and tree diameters for the three dates and assessed change using spatial error models, nonmetric multidimensional scaling ordination, and Sørenson distance measures. Our results suggest that since the mid-1800s, hemlock and white pine have declined in absolute area from 22% to 1%, and the proportion of medium (25–<50 cm) and large-diameter (≥50 cm) trees of all species has decreased from 71% to 27% across the entire state. Early-successional aspen-birch is three times more common than in the mid-1800s (9% vs. 3%), and maple and other shade-tolerant species are increasing in southern areas formerly dominated by oak forests and savannas. Since the peak agricultural extent in the 1930s, species composition and tree size in northern forests have shown some recovery, while southern forests appear to be on a novel trajectory of change. There is evidence of regional homogenization, but the broad north–south environmental gradient in Wisconsin constrains overall species composition. Although the nature of the future forests will be determined in part by climate change and other exogenous variables, land use is likely to remain the driving factor.

Key words: forest inventory and analysis; forest landscape change; General Land Office; historical ecology; homogenization; land-use/land-cover change; land-use legacies; ordination; presettlement; species convergence; U.S. Public Land Survey; Wisconsin Land Economic Inventory.

INTRODUCTION

Land-use legacies can persist in forest ecosystems for tens to thousands of years. At the local scale, historical logging and agriculture can affect understory plant diversity (Dupouey et al. 2002, Gerhardt and Foster 2002), carbon and nitrogen cycling (Compton and Boone 2000, Fraterrigo et al. 2005), abundance of coarse woody debris (Currie and Nadelhoffer 2002), and, ultimately, ecosystem functioning (Foster et al. 2003, Rhemtulla et al. 2007). Across eastern North America, Euro-American settlement was accompanied by widespread logging and agricultural conversion. Although forests have regrown in many of these areas, a number of recent studies have shown that current forest composition and structure are quite different from those preceding Euro-American settlement (Foster et al. 1998, Hall et al. 2002, Friedman and Reich 2005, Schulte et al. 2007). Yet these studies only examine change between two dates and thus cannot determine the magnitude and trajectories of change following widespread forest clearing or the degree of recovery following subsequent regrowth. Understanding these trajectories of change is critical to evaluating whether current management plans are successfully restoring pre-settlement forest diversity and structure.

In Wisconsin, land-use and land-cover transitions accompanying Euro-American settlement are generally consistent with those observed elsewhere in the Western Hemisphere (DeFries et al. 2004). In northern Wisconsin, which was extensively forested prior to the arrival of Euro-American settlers, forests were almost entirely cut over in a very short period of time (1870–1920) and then burned, often repeatedly, in accompanying slash fires (Mitchell and LeMay 1952). Although some of this land was subsequently cleared for agriculture, most of it was simply left to reforest naturally. In southern Wisconsin,

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native savannas and deciduous forests were cleared and converted to agriculture. Total agricultural land peaked in the 1930s to 1940s and has declined only moderately since then (Rhemtulla et al. 2007). Several studies suggest that the combination of logging and slash fires followed by fire suppression in the 1930s has led to a loss of coniferous species and increase in deciduous species in northern Wisconsin (Mladenoff and Howell 1980, White and Mladenoff 1994, Radeloff et al. 1999, Steen-Adams et al. 2007). Few studies have attempted to assess changes in forest composition in southern Wisconsin, but it appears that a modest amount of agricultural land has reverted to forest cover since the 1930s (Bürgi and Turner 2002, Rhemtulla et al. 2007) and that fire suppression and other land-use policies are leading to a loss of oak in favor of maple and other shade-tolerant hardwoods (Peet and Loucks 1977, Nowacki et al. 1990, Lorimer 1993, Abrams 1998). Across the larger Great Lakes region, species diversity and structural complexity in forest ecosystems has declined since the pre-settlement era (Schulte et al. 2007). There has also been a trend toward forest homogenization, as shown by an increase in similarity in species composition and abundance among a group of communities through time (Olden and Poff 2003).

Most landscape change studies in this region and the United States more generally examine change between only two dates: prior to the onset of Euro-American settlement and currently (but see Mladenoff and Howell 1980, White and Mladenoff 1994). While such studies show that forest composition and structure have changed markedly over that time period, they cannot provide an assessment of forest characteristics at the period of greatest change, nor can they assess to what degree forest ecosystems have recovered since then. Barring land-use practices that are sufficiently intense to bring about catastrophic long-term shifts in ecosystem state (Scheffer et al. 2001), we might expect species composition in resilient ecosystems to recover over time. Using chronosequence data, Wassenaar and colleagues (2005) examined recovery in understory herbs and trees over a period of 22 years following vegetation removal for mining in South Africa and found that species assemblages converged through time, becoming more similar to undisturbed benchmark sites. Christensen and Peet (1984) found similar successional convergence in herb and tree composition over a period of >80 years following old-field abandonment in upland forest stands in North Carolina, although convergence was not always gradual and monotonic (Peet 1992). It may be, however, that the land-use history of Wisconsin is more similar to a large, infrequent disturbance, particularly in the north, where forests were cut and burned repeatedly over a short period of time. The intensity and size of such disturbances can affect the abundance and spatial distribution of biological residuals (surviving individuals, seed banks, microbial soil communities, etc.), thus leading to high variability in community composition and slower recovery times (Turner et al. 1998).

In this study, we analyze forest change across the entire state of Wisconsin among three dates: at the onset of Euro-American settlement (mid-1800s), at the height of the agricultural period (1930s), and currently (2000s). The study area encompasses two regions that were very different prior to settlement, the northern mixed forests and southern oak savannas, thus allowing us to examine trajectories of change due to land use across a broad vegetation gradient. We address three specific questions: (1) How have relative dominance and spatial distribution of overstory tree species and diameter size classes changed through time? (2) How did historical land use at the peak agricultural period (1930s) influence these changes? (3) Is there evidence of recovery in forest ecosystems since the 1930s, or are they following new trajectories of change?

METHODS

Study area

The study area is the state of Wisconsin (~145 000 km^2) in the U.S. upper Midwest (approximately 42°30′ N to 47°3′ N and 86°49′ W to 92°54′ W). Using a common U.S. Department of Agriculture (USDA) Forest Service hierarchical ecosystem classification system, we stratified Wisconsin into 39 ecoregion subsections as our basic sample unit, grouped into two floristic provinces: Province 212 (Laurentian Mixed Forest; $n = 24$) and Province 222 (Eastern Broadleaf Forest; $n = 15$; Fig. 1) (Keys et al. 1995). For simplicity, we refer in the text to Province 212 as the "Northern Province" (or "North") and to Province 222 as the "Southern Province" ("South").

The climate in Wisconsin is humid continental with cold, dry winters and warm, humid summers, moderated by the influence of the Great Lakes. Mean January temperature ranges from −13.3°C in the Northern Province to −6.7°C in the Southern Province; mean July temperature ranges from 18.9°C to 22.2°C. Two-thirds of annual precipitation (760–890 mm) falls during the growing season. Landforms and soils are mostly of glacial origin. Outwash and till plains, end moraines, and kettle lakes and wetlands are common in northern Wisconsin (Keys et al. 1995). The northwestern Pine Barrens and the central sand plain (on former glacial Lake Wisconsin) are dominated by sandy soils, while clay soils are common along Lakes Michigan and Superior. The unglaciated Driftless Area, in southwestern Wisconsin, is the most topographically diverse, with loess-capped ridges and deep river valleys.

The vegetation of Wisconsin can be divided into two broad physiognomic units that correspond to the ecological provinces used to stratify the study area. Prior to Euro-American settlement, northern Wisconsin was dominated by closed forests, with a mosaic of shade-tolerant Eastern hemlock (*Tsuga canadensis*), yellow birch (*Betula alleghaniensis*), sugar maple (*Acer*

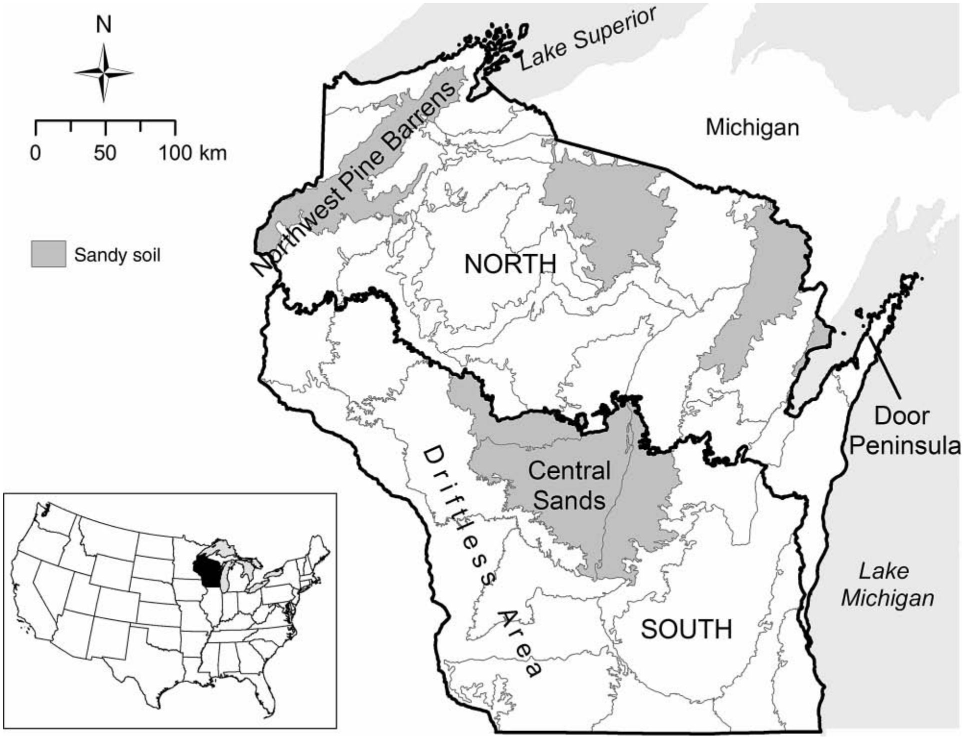


Fig. 1. Map of the Wisconsin, USA, study area showing location within North America. The main map shows the ecoregion subsections (sample units for the statistical analysis) that were grouped into two ecological provinces: North and South. Subsections with a high proportion of sandy outwash soils are shown (darker gray fill).

saccharum), basswood (*Tilia americana*), and elm (*Ulmus* spp.) in mesic upland areas; pine (*Pinus* spp.), aspen (*Populus tremuloides*), and paper birch (*Betula papyrifera*) on more xeric, fire-prone sites; and lowland conifers, including tamarack (*Larix laricina*) and northern white cedar (*Thuja occidentalis*) on wetter sites (Curtis 1959, Schulte et al. 2002). Wind events of intermediate severity were the major disturbance agent (Frelich and Lorimer 1991, Schulte and Mladenoff 2005). Oak (*Quercus* spp.) was common along the boundary with the Southern Province, and American beech (*Fagus grandifolia*) predominated along Lake Michigan. Southern Wisconsin was composed primarily of open oak savanna ecosystems interspersed with smaller amounts of treeless prairie (Bolliger et al. 2004). Open pine stands were common in the central sand plain, and closed deciduous forests occurred along Lake Michigan and on mesic sites in the Driftless Area. Low-intensity, frequent ground fires of both lightning and Native American origin likely maintained the savanna–prairie mosaic (Curtis 1959).

Widespread logging and clearing for agriculture changed the land cover of Wisconsin fundamentally by the 1930s (Fig. 2; Rhemtulla et al. 2007). In the Northern Province, the conifer–hardwood forests were almost completely logged and then burned, sometimes repeatedly, in associated slash fires (Mitchell and LeMay 1952). Much of the forest along the forest–savanna transition zone and along Lake Michigan was cleared for agriculture. In the Southern Province, most of the savanna and prairie ecosystems were also converted to agriculture, although some small patches of savanna were retained as woodlots and eventually succeeded to closed forest, especially in the Driftless Area (Curtis 1956, Rhemtulla et al. 2007). These general land-cover patterns were retained into the 1990s. In the Northern Province, forests have been recovering, although agriculture continues to dominate in the southern and southeastern portions of the region. Agriculture is still the main land-cover type in southern Wisconsin, though some cropland has been abandoned and succeeded to closed forest in the Driftless Area.

Data sources

Public Land Survey (PLS; mid-1800s).—The U.S. Public Land Survey was initiated in 1785 to divide western lands into civil survey sections (1 mile × 1 mile; 2.6 km^2) for settlement. At the corners and midway between the corners of each section, surveyors recorded the species, diameter, and distance to two to four "witness" trees (Stewart 1979). Many ecologists have subsequently used these tree data to reconstruct vegetation at the onset of Euro-American settlement (Bourdo 1956, Siccama 1971, Mladenoff and Howell 1980, Whitney 1987, Schulte et al. 2007). In Wisconsin,

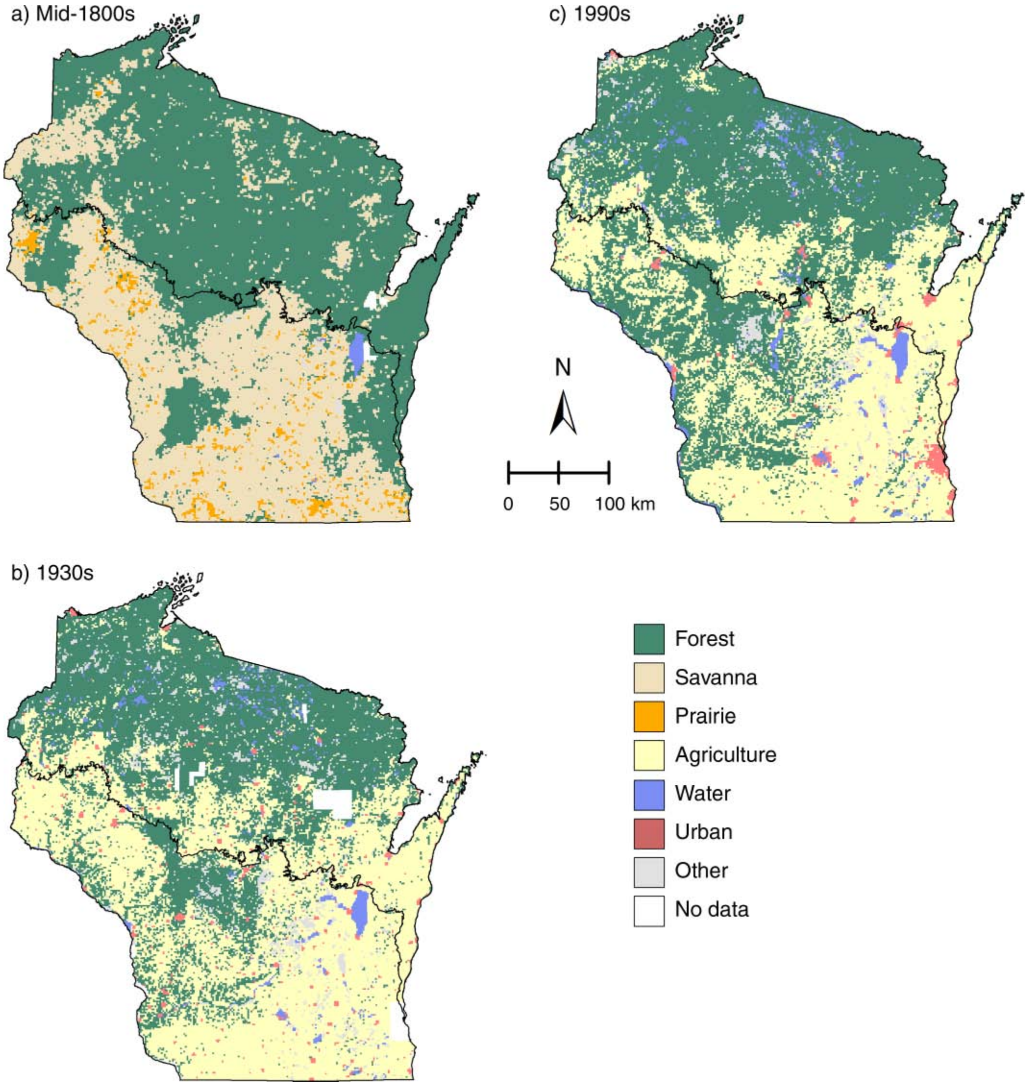


FIG. 2. Dominant land cover in Wisconsin in the (a) mid-1800s, (b) 1930s, and (c) 1990s (WISCLAND data set; Reese et al. 2002; adapted from Rhemtulla et al. [2007]). The savanna class includes a range of stand densities from open savanna to woodland.

the survey was conducted from south to north from 1832 to 1891 and contains ~57 000 survey sections and 445 500 witness tree records. To minimize bias in the data, we used relative measures of abundance calculated at coarse resolution over large areas (Manies and Mladenoff 2000).

Wisconsin Land Economic Inventory (WLEI; 1930s).—A complete land inventory was conducted in Wisconsin from 1928 to 1938, at the height of the agricultural period (Koch 2006). Surveyors walked transects at 0.4- to 0.8-km intervals and made field maps of land cover (minimum polygon size = 0.8 ha), including stand stocking (a measure of tree density) and diameter class for all forest types (Bordner et al. 1936, Koch 2006). They subsequently compiled tables summarizing the acreage of every land-cover type in each survey section (Wisconsin Historical Society, 1928–1938); we used these tables to calculate and map proportional land cover.

Forest Inventory and Analysis (FIA; 2000s).—The USDA FIA program has established survey plots for every ~2500 ha of forest land (Perry 2003). At each plot, the species, diameter, and condition of every tree in four subplots (0.0168 ha each) is recorded (USDA Forest Service 2006). These plot estimates can then be extrapolated across larger areas using FIA "tree expansion factors." Twenty percent of plots are sampled each year over a five-year cycle; we used sixth-cycle data collected from 2000 to 2004 (6478 plots) for most of our analysis and used supplemental data from 1996, 1983, 1968, 1956, and 1938 to analyze trajectories of change in species composition (see *Trajectories of change in species composition*). Data for the three earliest surveys are only available in summarized format (e.g., USDA Forest

Service 1938). To maintain the privacy of landowners, the FIA publishes only approximate plot locations (to within 1.6 km) and swaps data between ≤20% of privately owned plots. To minimize bias due to uncertain plot location, we summarized data at coarse resolution over Forest Service ecoregion subsections (Sabor et al. 2007, Schulte et al. 2007).

Change analysis

To compare the three data sets, we grouped individual tree species in the PLS and FIA to match the forest types recorded by the WLEI: ash–elm (*Fraxinus* spp. and *Ulmus* spp.); early-successional aspen–birch (*Populus tremuloides*, *P. grandidentata*, and *Betula papyrifera*); cedar–tamarack (*Thuja occidentalis* and *Larix laricina*); eastern hemlock (*Tsuga canadensis*); jack pine (*Pinus banksiana*); northern hardwoods (*Acer* spp., *Tilia americana*, *Betula alleghaniensis*, *Fagus grandifolia*); oak–hickory (*Quercus* spp., *Carya* spp.); red pine (*Pinus resinosa*); spruce–fir (*Picea* spp. and *Abies balsamea*); and white pine (*P. strobus*) (Appendices A and B).

The PLS does not provide very accurate estimates of absolute extent (total area; Manies and Mladenoff 2000), so we conducted most of the analyses using relative measures of abundance. At each of the three dates, we calculated relative dominance (relative basal area, a common measure of biomass distribution; Cottam and Curtis 1956) of each forest type and the proportion of trees in three diameter classes: small (12.5–<25 cm), medium (25–<50 cm), and large (≥50 cm). For the PLS, we grouped individual witness trees by forest type at the section level and then calculated relative dominance of each type in each section. For the WLEI, we estimated tree density using stand stocking class and mean diameter (Larsen 2002) and then calculated relative dominance at the section level. In both cases, we then averaged the section-level data across the ecoregion subsections to match the coarser resolution of the FIA data. For Fig. 3 only, we estimated absolute extent of forest types in the PLS by assigning each section to the dominant type and then summing total area by each type.

Previous research has suggested that public land surveyors were biased against choosing very small or large trees (Manies et al. 2001); the Wisconsin PLS data set, for example, has few trees ≤12.5 cm or ≥55 cm. Small trees are therefore commonly eliminated from all data sets when using the PLS in change analysis (e.g., Schulte et al. 2007). For the relative dominance calculations, however, we chose not to remove small trees (<12.5 cm) from any of the data sets, as doing so would have eliminated much of the data from the WLEI. Over 30% of the WLEI data consists of small-diameter even-aged stands (the result of recent widespread logging), and removing these trees from the analysis would have led to significant changes in the apparent species composition, including a 26% decrease in mean aspen dominance and 15% increase in northern hardwoods. The analysis of relative species dominance in the PLS and FIA did not change significantly with and without small trees, likely because recently disturbed stands were much less common in those landscapes. For the analysis of proportion of trees by diameter class, however, we conservatively chose to eliminate small trees (<12.5 cm) from all data sets. We felt comfortable with this small inconsistency in our methods because small trees have a smaller influence on relative dominance measures (which are based on basal area) but a much larger influence on calculations of proportion of trees by diameter class. Nonetheless, we ran all analyses both with and without small trees and found the results to be robust.

We tested for changes in relative dominance and tree diameter using spatial linear regression (to account for spatial autocorrelation) and the difference between time periods as the response variable (to account for temporal autocorrelation). We normalized the data using a square-root transformation (Sokal and Rohlf 1981). We experimented with several different spatial neighborhood weights (common boundary, distance, and nearest neighbors) in the preliminary analysis, and as the results were similar, we selected common boundary neighborhood weights for simplicity in the final spatial model. We fitted separate models for each pair of dates, forest type, and diameter class and controlled for experiment-wise error with an unmodified Bonferroni correction (Legendre and Legendre 1998). We ensured that the residuals were not spatially correlated using Moran's *I* (Cliff and Ord 1981).

Overall changes in composition and structure

We analyzed overall changes in forest composition and structure using nonmetric multidimensional scaling (NMS) ordination, an iterative optimization method that is well suited to nonnormal data sets (McCune and Grace 2002). We used ecoregion subsections as sample units, Sørensen (Bray-Curtis) distance measures, and ran the NMS using the autopilot slow mode in PC-ORD (500 iterations, instability criterion of 0.0000001, stepping down from six- to one-dimensional solution, 250 real runs tested against 250 randomized runs; McCune and Mefford 1999). To test whether differences among the three dates and between the two provinces were significant, we used the multi-response permutation procedure (MRPP), a nonparametric randomization procedure that tests for multivariate differences between preexisting groups (Mielke and Berry 2001, McCune and Grace 2002). We first tested for differences among all six groups, then split the analysis by province to test for differences among time periods. We conducted a protected test by first comparing all three dates and proceeding with pairwise tests only if the former was significant and used an unmodified Bonferroni correction to control for experiment-wise error (Legendre and Legendre 1998). We used Sørensen distance measures to match those used in the ordination.

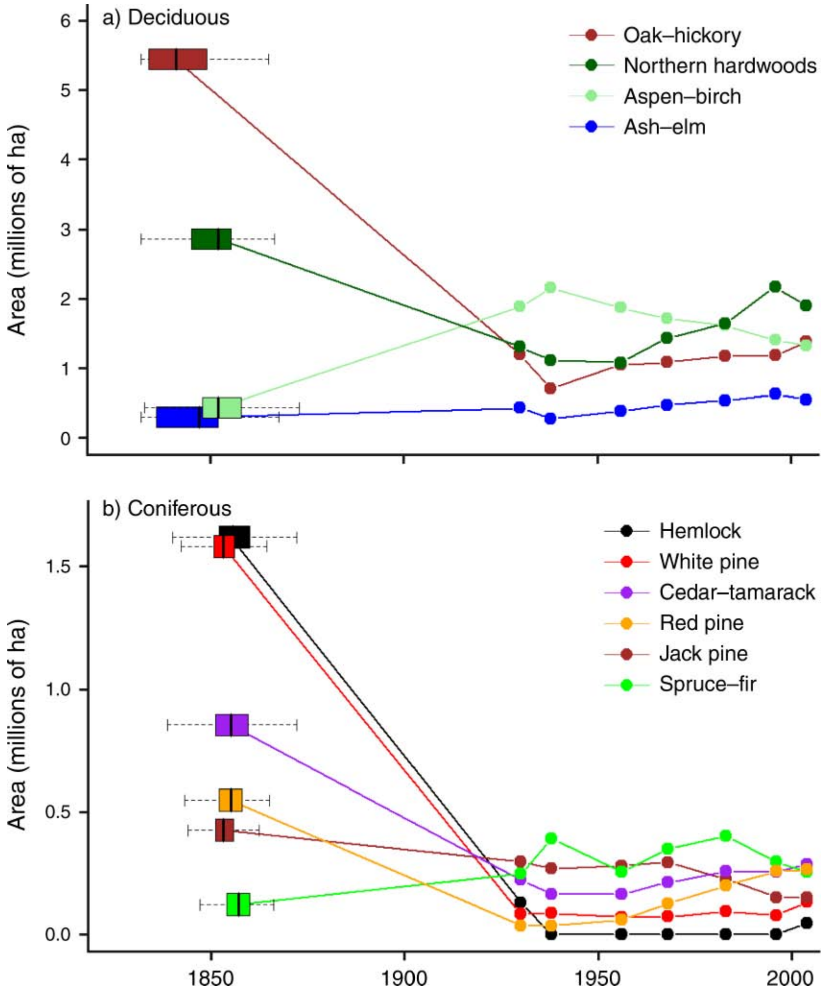


FIG. 3. Change in total area occupied by (a) deciduous and (b) coniferous forest types in Wisconsin from the mid-1800s to the present. Note that the *y*-axes differ between the two graphs. Because the mid-1800s data were collected over a 60-year period, we have represented that time period as a boxplot showing the range of dates over which the survey sections dominated by a particular species were surveyed. Boxplots show the median and first and third quantiles; whiskers extend to ±1.5 interquartile ranges. Since the survey proceeded from south to north, species that were more abundant in the south, notably oak–hickory and ash–elm, have an earlier range of dates. Data include both forest and savanna ecosystems. Definitions of forest types are provided in Appendix A. Data were taken from: U.S. Public Land Survey (boxplots), Wisconsin Land Economic Inventory (ca. 1935), and U.S. Forest Service Forest Inventory and Analysis (1938, 1956, 1968, 1983, 1996, 2004).

Trajectories of change in species composition

Following the approach of Wassenaar et al. (2005), we compared relative forest composition between each individual date and the mid-1800s to assess the degree of recovery following land-use change. We first calculated a "reference vector" for the mid-1800s by calculating the mean relative dominance of each forest type across all ecoregion subsections. For each data set in turn (including the mid-1800s), we then calculated the Sørensen distance (formula from McCune and Grace 2002) between each individual ecoregion subsection and the reference vector and then calculated the mean and SE of all of these distance measures. We thus had an estimate of the range of variability among ecoregion subsections in the mid-1800s, as well as estimates of the distance between relative dominance at each individual date and relative dominance in the mid-1800s reference vector. For a more detailed explanation of the method, including diagrams, see Wassenaar et al. (2005).

RESULTS

Change in absolute forest extent

Across the state, the extent of forest and savanna declined from 96% of the total area in the mid-1800s to 39% in the 1930s, then increased slowly to 44% by the early 2000s (Fig. 2). Our estimates of total forest and savanna extent in the mid-1800s are slightly higher than those of Finley (88%; Bolliger et al. 2004) and Curtis (~90%; 1959), likely because we employed an objective density-based classification system to separate prairies

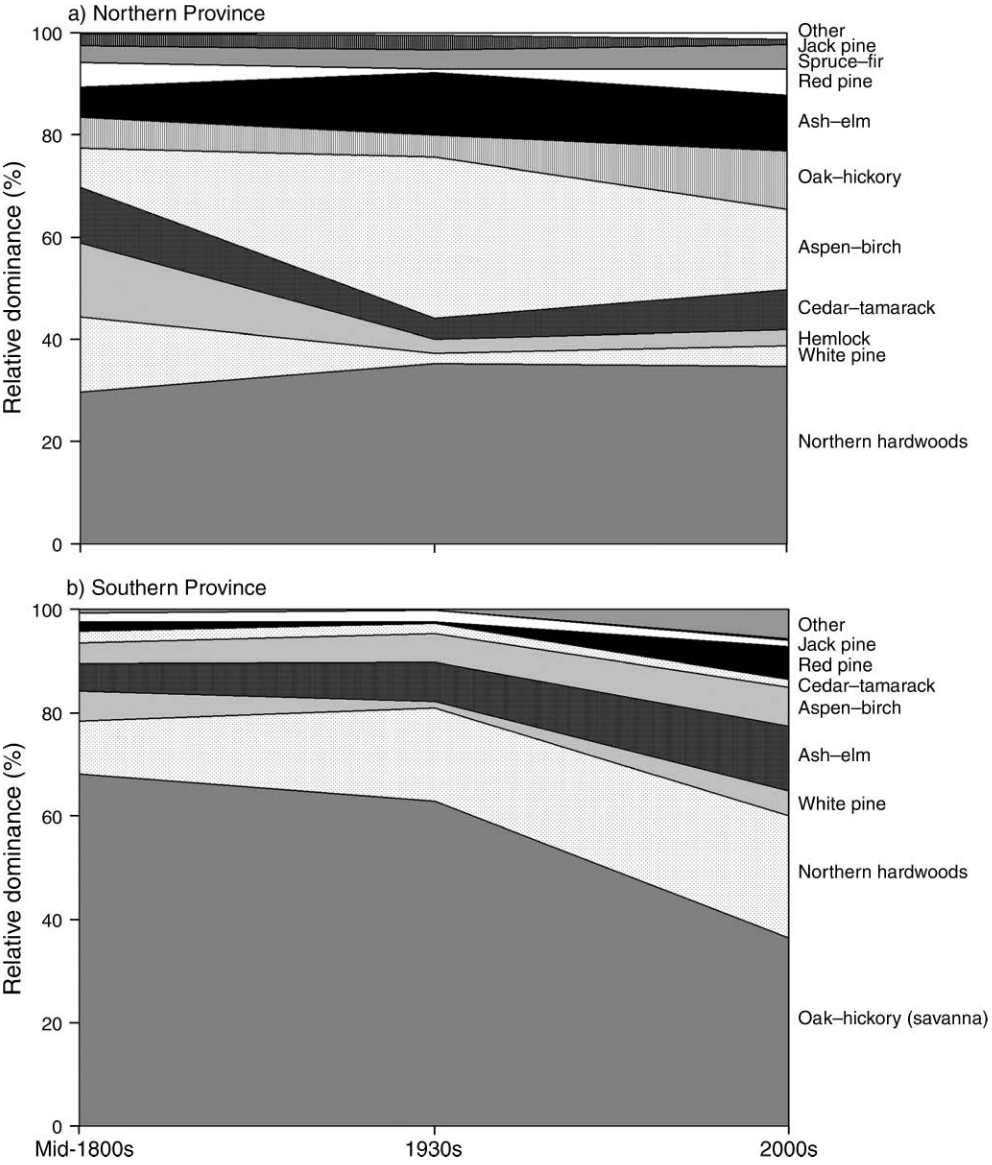


FIG. 4. Change in relative dominance (percentage of basal area) by forest type from the mid-1800s to the present in the (a) Northern Province and (b) Southern Province. Species are graphed in order of increasing dominance at the mid-1800s period. Hemlock and spruce–fir are included with the "other" category in the Southern Province since they occur in such small amounts. We purposely kept the dates approximate to reflect the duration of time over which each data set was collected. Fig. 3 provides a general sense of the temporal variability in the mid-1800s data set. Definitions of forest types are provided in Appendix A. Results of the statistical analysis showing which changes are significant are in Appendix D.

from savannas and forest (Bolliger et al. 2004, Rhemtulla et al. 2007). In the Northern Province, there was no change in the total area of forest between the 1930s and the 2000s (56% at both dates); agricultural land use remained dominant in the southern portion of the province. In the Southern Province, forest extent increased from 24% in the 1930s to 30% in the 2000s; much of the forest regrowth occurred in the Driftless Area in southwestern Wisconsin.

Of the deciduous types, oak–hickory (which occurs largely in the south) experienced the greatest decline across the state, from 38% of the total extent in the mid-1800s to 8% in the 1930s and then increasing to 10% in the 2000s (Fig. 3). The northern hardwoods underwent a similar trajectory of decline and increase (from 20% to 9% to 12%), although this trend has been reversed over the past decade as these hardwoods have started to decline again. Aspen–birch was the only forest type to increase greatly, from 3% in the mid-1800s to 13% in the 1930s, before decreasing slowly to 9% currently. Ash–elm changed only slightly over the last 150 years (2% to 4%).

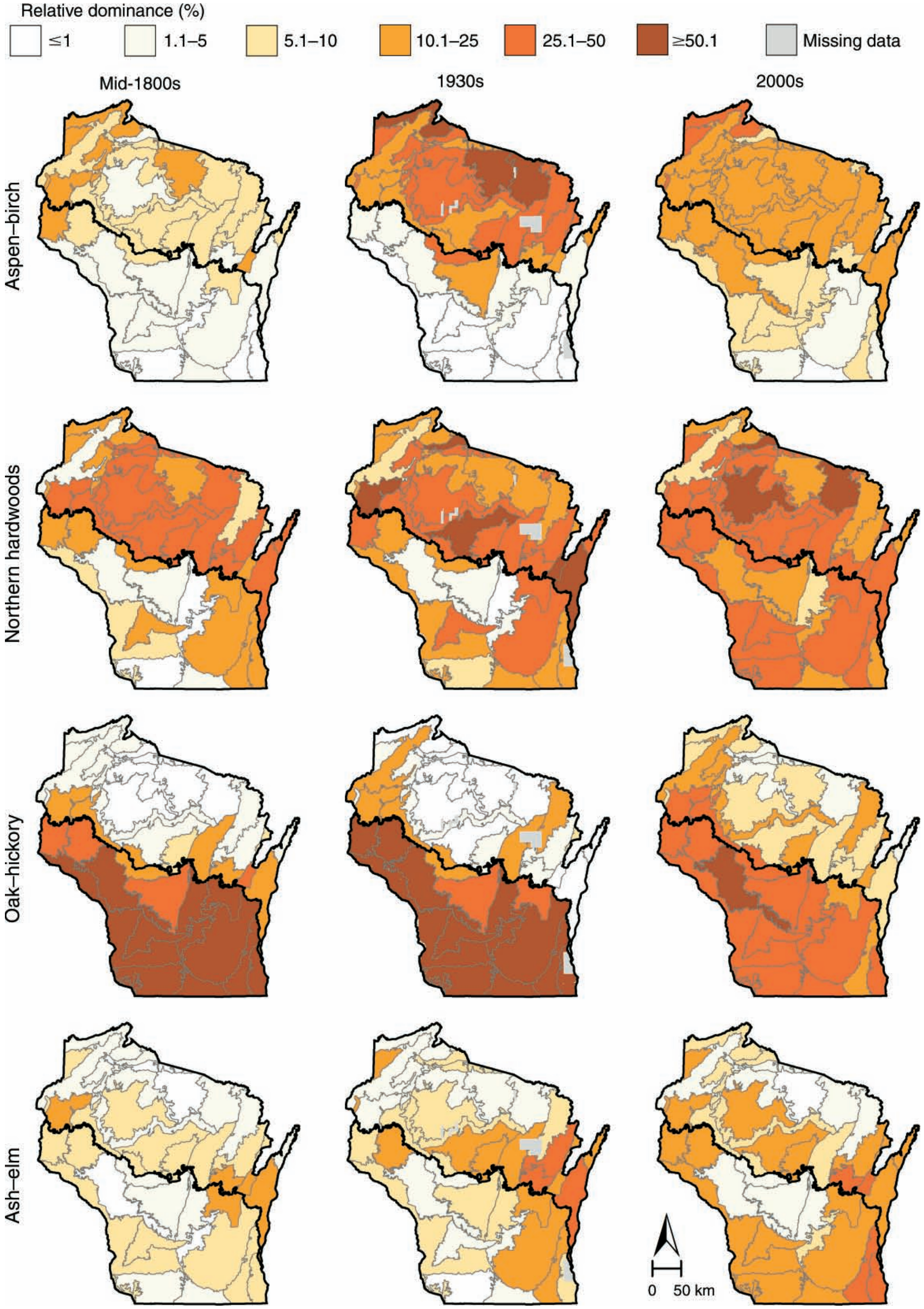
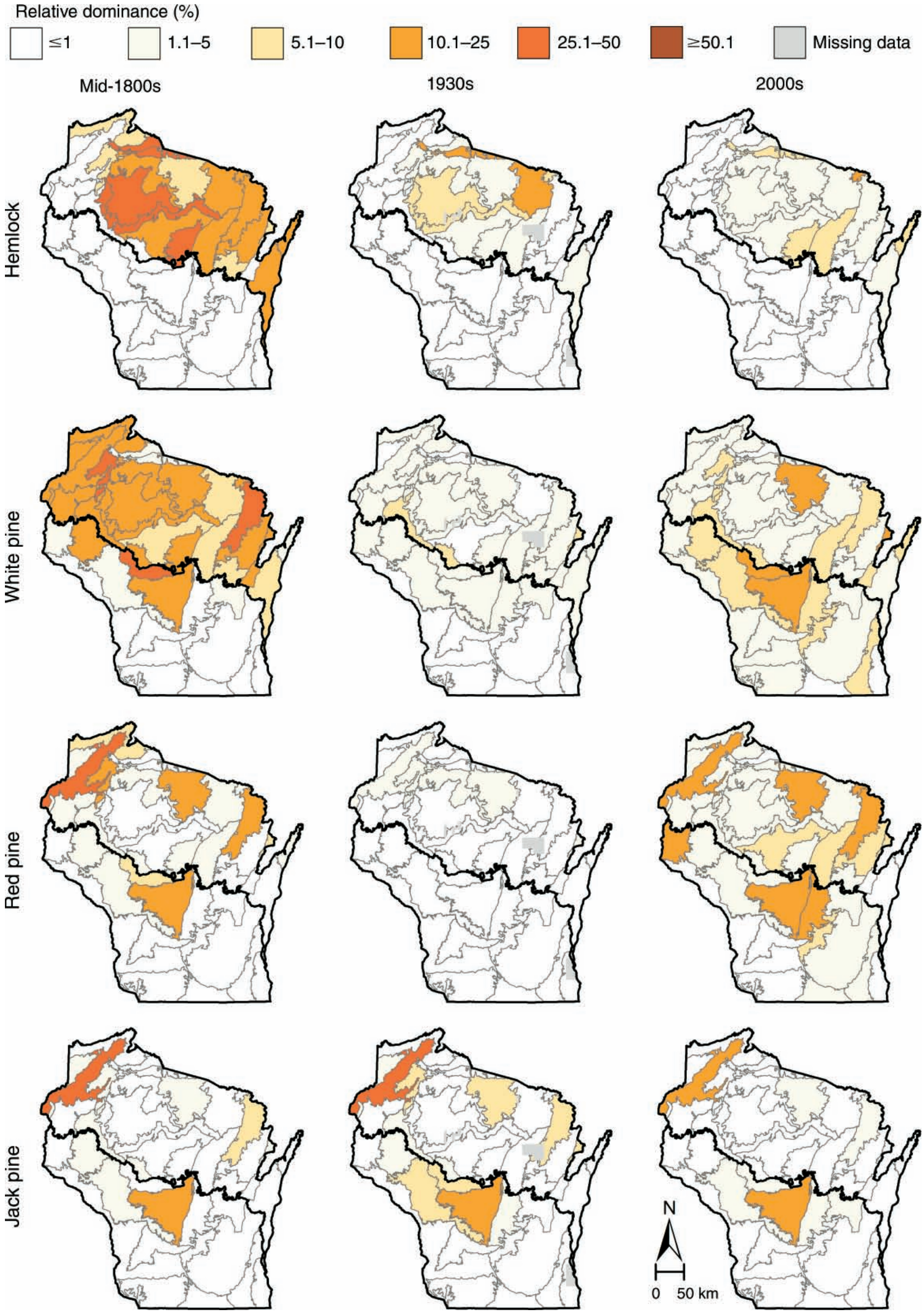


FIG. 5. Spatial variability in relative dominance (percentage of basal area) of each forest type by time periods. See Fig. 4 for further details.



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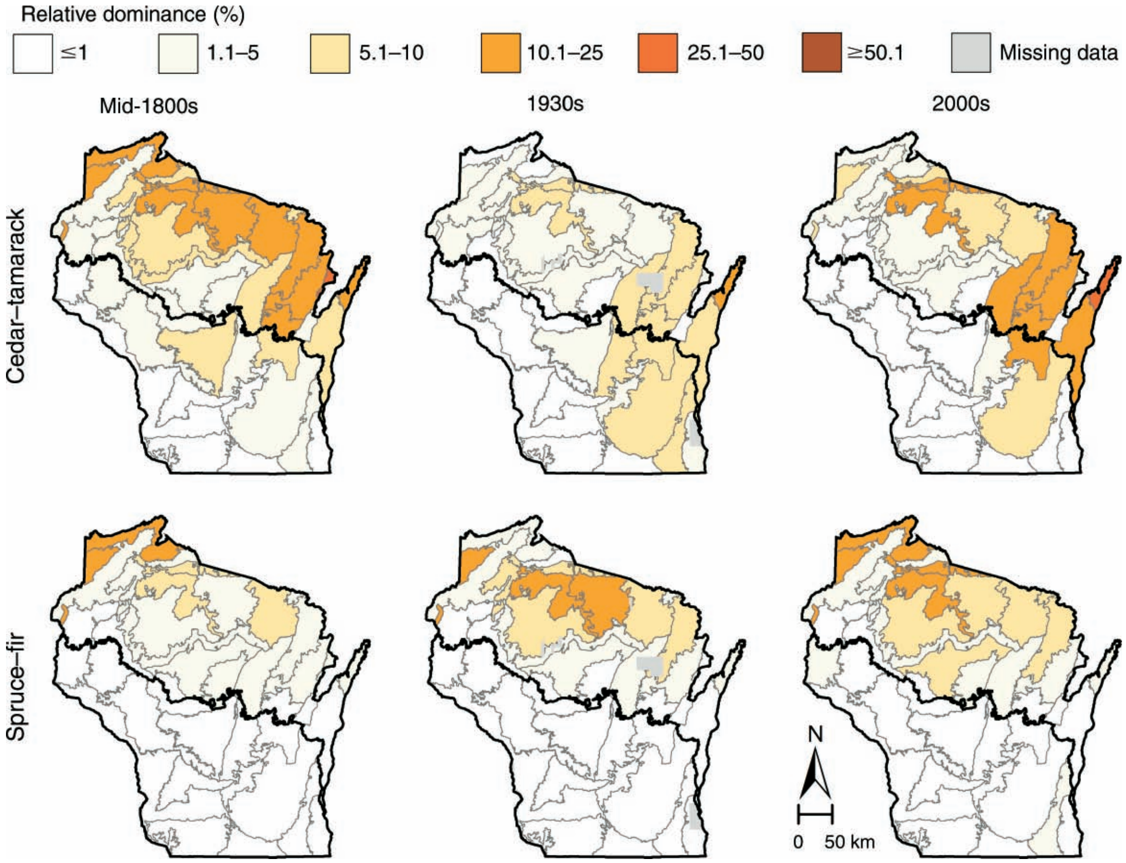

FIG. 5. Continued.

The extent of almost all coniferous types has declined considerably since the mid-1800s. White pine and hemlock decreased greatly from ~11% each to almost nothing (0.6% and 0.8%, respectively) in the 1930s and have increased only slightly since then. Red pine also declined from the mid-1800s to the 1930s (from 4% to 0.2%), but has since increased to 2%, while jack pine declined over the entire time period (from 3% to 1%). Cedar/tamarack decreased considerably from 6% to 1% and has increased only moderately (to 2%) since. Spruce–fir was the only coniferous type that increased (from 0.8% in the mid-1800s to 1.7% currently).

Change in relative species dominance

Northern Province.—Relative dominance (percentage of basal area) of deciduous tree species generally increased from the mid-1800s to the present (Fig. 4a), although changes were quite variable spatially (Fig. 5, Appendix C). The greatest increase in mean dominance occurred in the aspen–birch type, which increased from 8% in the mid-1800s to 32% in the 1930s ($P < 0.0001$) and declined to 16% ($P = 0.001$) after that (Appendix D). Change in aspen–birch was greatest in subsections that were further north, where less agricultural conversion occurred, and the type was much more heterogeneously distributed in the mid-1800s and the 1930s than presently. Dominance of northern hardwoods increased from 30% in the mid-1800s to 35% in the 1930s ($P = 0.034$). Change from the 1930s to 2000s was spatially variable and not significant ($P = 0.9$); dominance increased in subsections that were further north and decreased in areas still dominated by agricultural land use. Mean oak dominance increased from 6% to 12% ($P = 0.015$) over the entire time period, with most of the increase occurring from the 1930s to 2000s; originally predominant on sandy outwash soils in the Northern Province, oak is currently distributed across the entire province.

Almost all coniferous types declined in dominance, generally with a strong decrease from the mid-1800s to 1930s, followed by a smaller increase from the 1930s to the present. Hemlock and white pine experienced the largest declines (from 14% to 3% and 15% to 2%, respectively), but while white pine dominance doubled from the 1930s to the present (from 2% to 4%, $P < 0.001$), hemlock dominance did not change significantly ($P = 1.5$). White pine recovery appeared to be strongest on sandy outwash plains. Red pine was lost almost completely from the Northern Province by the 1930s (from 5% to 1%, $P < 0.0001$), but this decline was matched by an increase (from 1% to 5%, $P = 0.001$)

from the 1930s to the 2000s (primarily in plantations) such that change over the entire period was not significant. The spatial pattern of red pine also changed, expanding so that it is now found across the entire Northern Province. Mean jack pine dominance did not change significantly from the mid-1800s to the 1930s (from 2% to 3%, $P = 0.2$), but decreased significantly from the 1930s to the 2000s (from 3% to 1%, $P = 0.02$). Jack pine was found predominantly on sandy outwash at all three dates. Cedar–tamarack followed the general trajectory of decrease (from 11% to 4%, $P < 0.0001$) followed by increase (from 4% to 8%, $P = 0.005$), and these changes were remarkably consistent across the Northern Province.

Southern Province.—All deciduous types other than oak–hickory increased from the mid-1800s to 2000s in the Southern Province, and unlike in the Northern Province, the direction of change during the two time intervals was the same (Fig. 4b). Oak–hickory, the most dominant type in the 1800s, declined greatly over the entire time period (from 68% to 36%, $P = 0.04$), with the greatest decrease occurring from the 1930s to the present (from 63% to 36%, $P < 0.0001$; Fig. 5, Appendix C). Northern hardwoods increased in dominance during both time intervals (from 10% to 18% and from 18% to 24%, respectively); by the 2000s, they appeared to be almost equal in dominance to oak–hickory. Changes in oak–hickory and hardwoods occurred earlier (mid-1800s to 1930s) in the southeastern part of the province, where agricultural conversion was more extensive, and later in the Driftless Area (1930s–2000s) during the period of agricultural abandonment. Aspen–birch and ash–elm increased moderately in dominance during both time periods. The range of aspen–birch contracted from the mid-1800s to the 1930s and then expanded by the 2000s, while the increase in ash–elm dominance was most pronounced in areas dominated by agriculture.

Coniferous species were generally much less abundant in the Southern Province. Red pine was the only type that changed significantly from the mid-1800s to the present (2% to 6%, $P = 0.005$), increasing in both dominance and spatial extent, likely because of its extensive use in plantations. White pine dominance did not change significantly (from 6% to 5%, $P = 2.5$), but expanded in range considerably; occurring primarily on sandy outwash in the 1800s, it expanded across most of the Southern Province by the 2000s, also likely in plantations. Jack pine remained relatively constant in both mean dominance and spatial extent. Cedar–tamarack dominance declined slightly from the 1930s to the 2000s (from 2.1% to 1.7%, $P = 0.008$), and its spatial distribution over the entire time period contracted toward the southeast. Hemlock and spruce–fir were rare at all three dates.

Change in diameter distribution

There was a great increase in the proportion of small (12.5–<25 cm) trees (from 30% to 75% in the North and from 28% to 70% in the South) accompanied by a large decrease in the proportion of medium (25–<50 cm) (from 60% to 24% in the North and from 61% to 28% in the South) and large (≥50 cm) trees (from 10% to 1% in the North and from 11% to 3% in the South; Fig. 6). The greatest changes occurred from the mid-1800s to the 1930s, with some recovery from the 1930s to the present (Appendix E). Public Land Surveyors (mid-1800s) most frequently recorded medium-sized trees, which were evenly distributed across the state; large trees, which were also common, appeared to be less frequent on sandy outwash plains (Fig. 7). By the 1930s, small trees were very abundant (~87%) and distributed evenly across the state; large and medium trees were found most frequently in the far north (where there were still a few remnant unlogged forests) and southeast (which was the first to be converted to agriculture, so regenerating woodlots were likely older). Between the 1930s and 2000s, large trees were mostly eliminated in the Northern Province (from 2% to 1%), but had increased in frequency in the Southern Province (from 0.3% to 3%), although neither of these changes was statistically significant. Similarly, the largest increase in medium trees occurred in the Southern Province (from 12% to

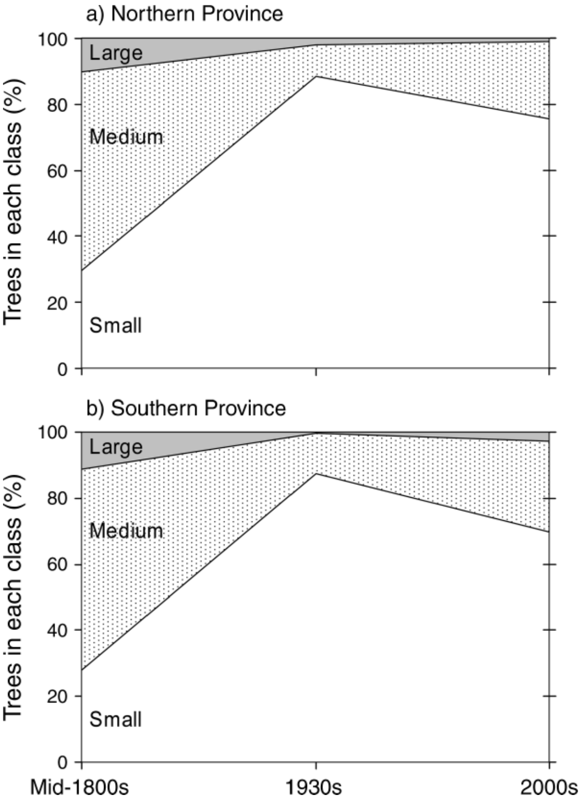

FIG. 6. Change in percentage of trees in each diameter class from the mid-1800s to the present in the (a) Northern Province and (b) Southern Province. Diameter classes are: small (12.5–<25 cm), medium (25–<50 cm), and large (≥50 cm). Results of the statistical analysis may be found in Appendix E.

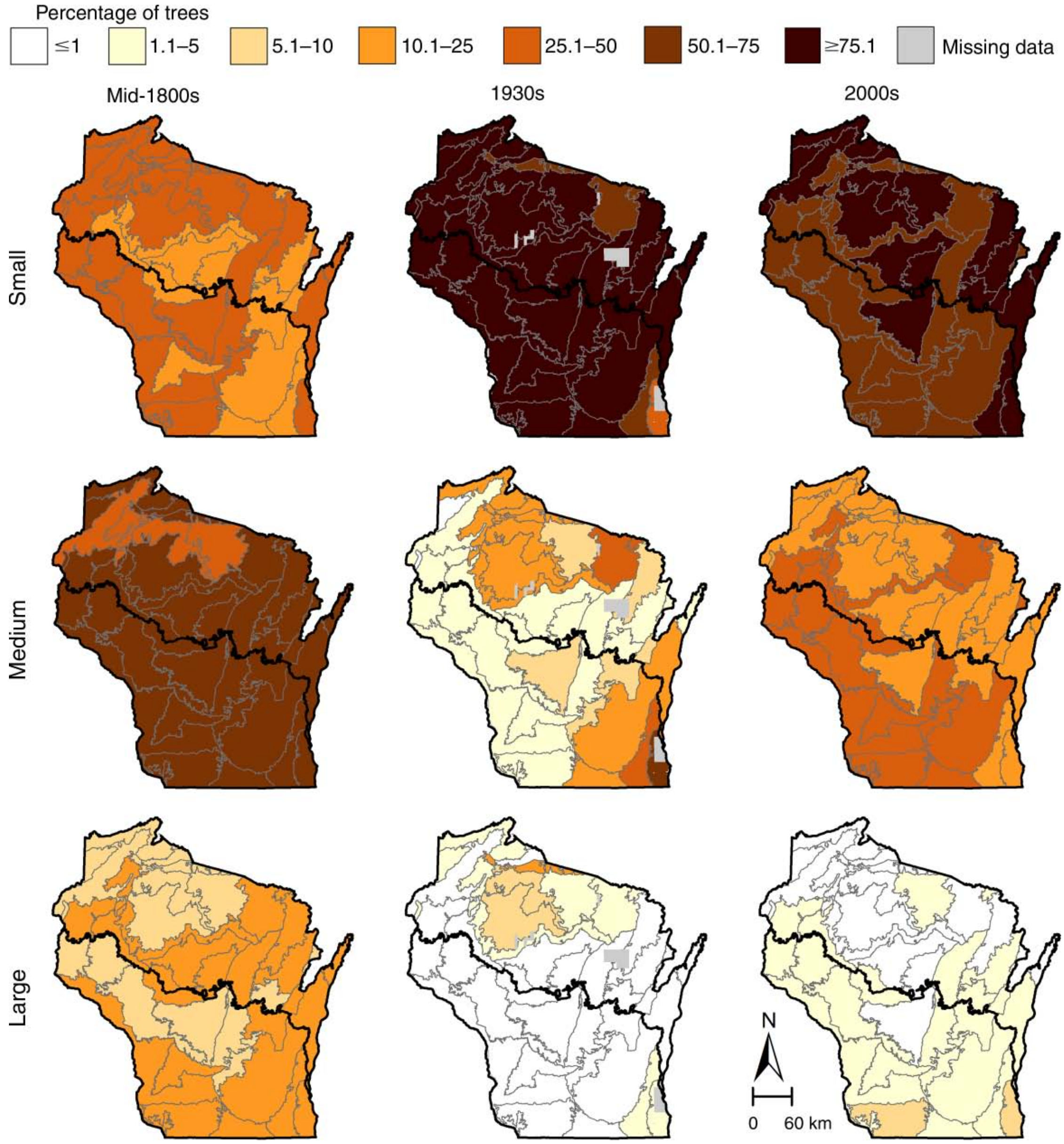

FIG. 7. Spatial variability in percentage of trees in each diameter class by time period. Diameter classes are: small (12.5–<25 cm), medium (25–<50 cm), and large (≥50 cm).

28%), particularly in the Driftless Area, where forest regrowth was highest.

Overall change in community composition and structure

Results of the NMS ordination and MRPP tests show that community composition and structure were significantly different among all three dates and two provinces (Fig. 8, Table 1). Subsections in the mid-1800s were characterized by a higher proportion of medium/large trees and by coniferous species such as hemlock and white pine ($r^2 = 0.33$; see Plate 1). By the 1930s, species composition changed fundamentally. Most subsections had a much higher proportion of smaller trees. Oak–hickory dominance decreased in the Southern Province, while dominance of aspen–birch and northern hardwoods increased in the Northern Province. Moreover, the variability among ecosections within each province (in terms of distance along the y-axis) was much higher than in the mid-1800s.

Moderate recovery in tree size distributions and composition was evident in the 2000s. But there was also evidence of biotic homogenization between the subsections of the Northern and Southern Provinces, represented by decreasing distance between subsections in ordination space. Oak–hickory dominance decreased in the subsections of the Southern Province, thus moving the subsections on a trajectory away from mid-1800 conditions and towards the subsections of the Northern Province (Fig. 8b). Aspen dominance decreased in the Northern Province, and many of these subsections moved on a trajectory back toward mid-1800 conditions (Fig. 8b).

These diverging trajectories of change, subsections of the Northern Province shifting partly towards and subsections of the Southern Province shifting away from mid-1800 conditions, were even more apparent when the effects of changes in tree size were removed from the analysis (Fig. 9). In the Northern Province, forest composition was most different from mid-1800 conditions during the 1930s, but has partly recovered since that period. Variability among northern ecoregions was low at all dates. In the Southern Province, species composition was most different from mid-1800 conditions during the 1990s, and difference increased from the 1930s to the present. Difference declined from the 1990s to the 2000s. Variability among ecoregions was higher in the Southern Province and appears to have decreased through time.

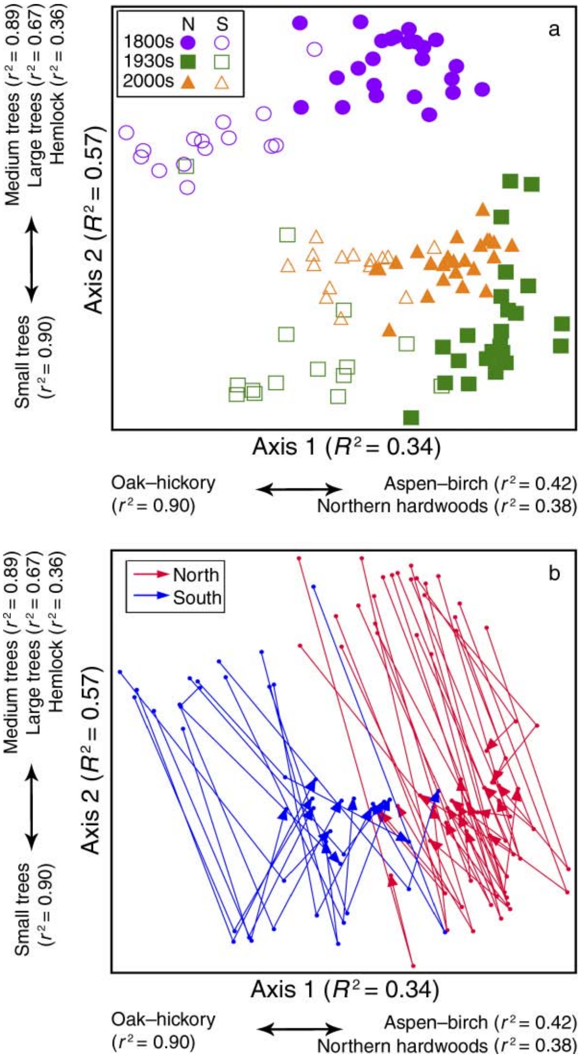

FIG. 8. Nonmetric multidimensional scaling (NMS) ordination showing (a) ecological subsections in the Northern Province (solid symbols) and Southern Province (open symbols) in the mid-1800s, 1930s, and 2000s; and (b) trajectories of change within each subsection over the entire period. Final ordination included two axes; stress = 12.967. Each axis shows Pearson correlation coefficients for those variables for which $r^2 > 0.35$. Each point in the ordination represents one subsection at one date; data for each subsection include relative dominance of each forest type and the proportion of trees in each of three diameter classes (calculated at the subsection level for the USDA Forest Service Forest Inventory and Analysis data and averaged from the section-level data for the U.S. Public Land Survey and Wisconsin Land Economic Inventory).

DISCUSSION

Drivers of change

The observed changes in species composition, stand structure, and spatial pattern over the past 150 years were driven by changes in land use and disturbance regimes. In the north, forests that were historically shaped by intermediate wind disturbance and occasional catastrophic fire events (Frelich and Lorimer 1991, Schulte and Mladenoff 2005) were almost completely cleared in <40 years and then left to reforest naturally (Rhemtulla et al. 2007). The scale and intensity of these changes favored the regeneration of hardwood species over conifers. The widespread and often intense slash fires that accompanied logging eliminated seed trees critical to the regeneration of white pine and hemlock. Hemlock regeneration was subsequently hindered by the high levels of deer herbivory, which increased due to the loss of predators and increase in favorable early-successional habitat. While white pine has begun to increase in mixed stands on dry to dry–mesic sites in northern Wisconsin, the prospects for hemlock are less promising. The higher quality leaf litter from the deciduous species, which have replaced hemlock, alter nutrient cycling, thereby contributing to a positive feedback with deer and climate, favoring continued dominance by deciduous species (Mladenoff 1987). Hemlock was established in northern forests approximately 3200 years ago during a particularly cool and wet climatic period and may have maintained its dominance through similar positive feedbacks (Davis et al. 1994). On sandy outwash soils in the north, jack pine, the most fire-adapted of the pines, was formerly maintained by frequent fire events and was likely more resilient to the logging slash fires. But fire suppression implemented since the 1930s, jack pine budworm (*Choristoneura pinus*) outbreaks, and more recent logging have slowly led to the loss of jack pine and increase in hardwoods, particularly oak and aspen (Radeloff et al. 1999).

Deciduous species generally increased in dominance in the North in response to intensifying land-use practices, although the rates and spatial pattern of change in individual species varied with land-use history. Aspen and paper birch, which have abundant wind-dispersed

TABLE 1. Tests of differences among groups in the ordination (see Fig. 8).

Comparison	Observed δ	Expected δ	Variance	T	P
All groups	0.223	0.413	0.000016	−47.54	0.00
Northern Province					
All three dates	0.229	0.336	0.000015	−35.66	0.00
Mid-1800s to 1930s	0.246	0.404	0.000029	−29.37	0.00
1930s to 2000s	0.221	0.256	0.000004	−17.17	0.00
Mid-1800s to 2000s	0.219	0.338	0.000016	−29.14	0.00
Southern Province					
All three dates	0.214	0.347	0.000039	−21.33	0.00
Mid-1800s to 1930s	0.234	0.356	0.000063	−15.41	0.00
1930s to 2000s	0.194	0.315	0.000048	−12.97	0.00
Mid-1800s to 2000s	0.213	0.272	0.000021	−17.54	0.00

Notes: The observed δ is the average within-group difference and is compared to the expected δ, which is calculated through a randomization process. All P values were Bonferroni corrected. Changes in forest species composition and structure were assessed in the Northern and Southern Provinces of Wisconsin, USA.

seeds that germinate best on mineral soils, were extremely well adapted to the conditions that prevailed following logging and slash fires. The increase in aspen–birch in the 1930s was highest in the far north and less pronounced in the agricultural region in the Northern Province, perhaps because fires were less extensive on lands converted to agriculture. Between the 1930s and the present, as forests were largely left to recover in the absence of disturbance, aspen declined across the Northern Province while hardwoods, largely maple, increased due to successional processes. Because of the classification system used by the WLEI, we were unable to discern changes in the individual species included in the northern hardwoods category. Other studies, however, have shown that yellow birch and beech have decreased dramatically in dominance since the mid-1800s, while sugar maple has increased significantly and is likely to become more dominant as forests continue to age (Schulte et al. 2007).

In the Southern Province, the decline in oak–hickory was linked to both settlement and the loss of the low-intensity ground fire regime, which previously maintained these savannas. The decline in oak–hickory occurred earlier in the southeast, the first area to be converted to agriculture, and later in the Driftless Area. Although much of the savanna and prairies was converted to agriculture (Rhemtulla et al. 2007), scattered forest remnants survived in settlers' woodlots (Curtis 1956). But fire suppression since the 1930s has gradually led to increased stand density in these remnants along with a shift to later successional hardwood species, especially red and sugar maple (Abrams 1998).

Regional recovery and homogenization

Successional pathways in terrestrial ecosystems are influenced by a number of factors operating at different scales, including history, disturbance intensity, and biophysical characteristics. At the local scale, if disturbance intensity is not high, species composition may converge through time in sites recovering from past land-use disturbance (Christensen and Peet 1984, Wassenaar et al. 2005). In ecosystems subject to large, infrequent disturbances, however, the abundance and spatial heterogeneity of biological legacies (such as seed trees, soil seed bank, rhizomes, or advanced regeneration) can drive initial composition and subsequent successional pathways (Turner et al. 1998). Although regional vegetation patterns are typically driven by biophysical factors, if historical land use is sufficiently intense (as it arguably is in Wisconsin), it may play a modifying role, leading to increasing regional homogenization (see, e.g., Foster et al. 1998, Bürgi et al. 2000).

In our study, change from the mid-1800s to the 1930s in both provinces was driven by changes in tree sizes and relative species dominance. From the 1930s to the present, species composition in many Northern subsections became more similar to their former historical condition, while southern subsections diverged significantly in species composition (Fig. 9). It is not surprising that change differed in the Northern and Southern Provinces when one considers the natural disturbance processes that formerly structured these ecosystems. Successional processes in northern forests were driven by intermediate-severity wind disturbances, with fire being a major force only in pine forests on sandy outwash plains (Schulte and Mladenoff 2005). Succession is therefore moving these forests back towards larger trees and later successional species composition. Although the trend is promising, recovery is likely to stall unless key species that were formerly dominant, hemlock, yellow birch, and white pine, begin to increase on the landscape. In southern Wisconsin, savanna ecosystems were maintained through a frequent low-intensity fire regime. Even on sites where agricultural land is being abandoned, contemporary land-use practices include the suppression of such fires. Forests are therefore succeeding toward species that are less fire resistant and more shade tolerant. Unless proactive management steps are taken to reverse this trend, further divergence is likely.

The ordination also reveals a decline in difference between northern and southern subsections, which suggests a trend toward statewide homogenization. This trend was driven largely by the replacement of oak–hickory by maples in the Southern Province and the gradual loss of aspen over the last few decades in the Northern Province. Although the reduction in north–south diversity across the state is pronounced, there is very little overlap between northern and southern subsections, thus suggesting that environmental gradients continue to be the dominant force structuring these communities. In a parallel study examining changes in broad land-cover types over the same time period, we found that current conditions in subsections in southern and central (more southerly subsections in the Northern Province) Wisconsin overlap substantially in ordination space, but are quite different from the northernmost subsections (Rhemtulla et al. 2007). So although the broad land-cover type (deciduous forest) might be similar in these two zones (southern and central), relative species composition is not. These "central" subsections are thus interesting because biophysically they are more similar to the northern subsections, but in terms of historical and current land use, they are more similar to the agriculturally dominated southern subsections. Land-use history thus appears to influence the overall land cover on a site, but species recovery appears to be more strongly aligned with biophysical factors. Over very broad regions with large environmental gradients, it appears that biophysical factors are a more important driver of species composition than human disturbance. Scale thus appears to be a critical variable when assessing the influence of land-use history (Bürgi et al. 2000).

Implications for management

Homogenization, loss of biodiversity, and decreased structural complexity can ultimately lead to a loss of resilience in forest ecosystems (Drever et al. 2006). Loss of foundation tree species such as hemlock, for example, can fundamentally alter local conditions, thus disrupting basic ecosystem processes such as decomposition and reducing biodiversity of associated forest taxa (Ellison et al. 2005). Moreover, compound disturbances of the sort that occurred at the height of the agricultural period in the 1930s can potentially trigger a shift in ecosystem composition to an alternative stable state (Scheffer et al. 2001). Such a shift has likely already occurred in southern Wisconsin, where the disruption of the historical low-intensity ground fire regime has led to the replacement of oak savannas by closed forests and may also have occurred in northern hardwood/hemlock forests where repeated slash fires triggered a shift to aspen/birch dominance (Frelich and Reich 1999). Restoring forest resilience is a high priority given the impending future challenges posed by climate change (Scheller and Mladenoff 2005), nonnative forest pests (such as the emerald ash borer, *Agrilus planipennis*), and continuing land-use pressures (Radeloff et al. 2005). Management techniques that mimic the historical disturbance regimes in effect prior to Euro-American settlement could help to restore forest resilience (Drever et al. 2006). In northern forests, this might include extended rotation forest management plans that foster old-growth characteristics, such as large trees, more snags, higher volumes of coarse woody debris, more

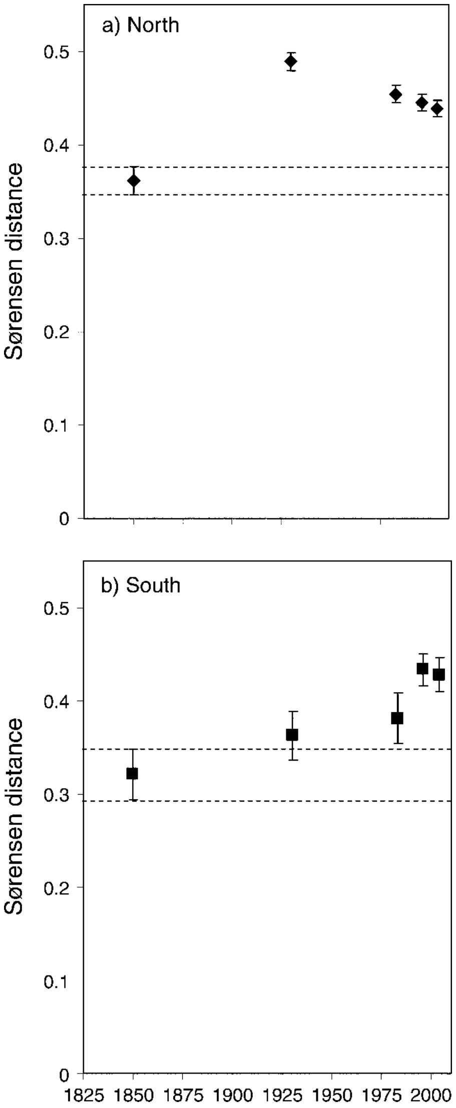

FIG. 9. Difference (Sørensen distance; mean ± SE) between species composition in the mid-1800s (prior to widespread Euro-American settlement) and following land-use change in the (a) Northern Province and (b) Southern Province. Dotted lines show the range of variability in species composition among ecoregion subsections in the mid-1800s. Data were taken from the U.S. Public Land Survey (mid-1800s), the Wisconsin Land Economic Inventory (ca. 1935), and the USDA Forest Service Forest Inventory and Analysis (1938, 1956, 1968, 1983, 1996, 2004).

PLATE 1. Remnant old-growth hemlock–hardwood stand in the Porcupine Mountains Wilderness State Park, Michigan, USA. Old-growth forests like these dominated northern Wisconsin prior to Euro-American settlement. Today, less than 0.3% of forests in Wisconsin are remnant old-growth, and the secondary forests which have replaced them are significantly different in terms of both stand structure and species composition. Photo credit: D. J. Mladenoff.

coniferous species, and old-growth species assemblages (e.g., Coates and Burton 1997, Goodburn and Lorimer 1998, Scheller and Mladenoff 2002, Latty et al. 2006). In southern Wisconsin, techniques such as prescribed burning, herbicide applications, and the creation of sizable gaps on suitable soils could help to promote oak regeneration (Lorimer 1993, Kruger and Reich 1997). Although the nature of the future forests will be constrained in part by climate change and other exogenous variables, the driving factor is likely to remain the types of land-use practices that we choose to implement.

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APPENDIX A

Forest types used to compare the U.S. Public Land Survey (mid-1800s), Wisconsin Land Economic Inventory (1930s), and U.S. Forest Service Forest Inventory and Analysis Database (2000s) (*Ecological Archives* A019-042-A1).

APPENDIX B

List of Latin names of species in Appendix A (*Ecological Archives* A019-042-A2).

APPENDIX C

Spatial variability of change in relative dominance (percentage of basal area) by forest type from the mid-1800s to 1930s, 1930s to 2000s, and mid-1800s to 2000s (*Ecological Archives* A019-042-A3).

APPENDIX D

Results of the statistical analysis of change in relative dominance (percentage of basal area) by forest type among all three time periods (*Ecological Archives* A019-042-A4).

APPENDIX E

Results of the statistical analysis of change in percentage of trees by size class among all three time periods (*Ecological Archives* A019-042-A5).