

REGIONAL LEGACIES OF LOGGING: DEPARTURE FROM PRESETTLEMENT FOREST CONDITIONS IN NORTHERN MINNESOTA

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Abstract. Forests in the Great Lakes region of Canada and the United States have been important timber producing resources for more than 100 years. Logging and fire suppression have caused major, but unquantified change in those forests, which includes both the magnitude of compositional change and its spatial patterns. Hence, a spatially explicit regional-scale change analysis was conducted using General Land Office Survey records from the late 1800s and the 1990 U.S. Forest Service Inventory and Analysis Survey, for a 3.2 million hectare study area in northeastern Minnesota, USA. These data document altered species abundance, proportional basal area, and spatial distribution patterns. Regionally, the proportionally most abundant species shifted from the presettlement period (spruce, 21%; larch, 15%; and paper birch, 15%) to aspen (30%), spruce (16%), and balsam fir (16%) in 1990. In terms of proportional basal area dominance, white pine declined from 20% to 5%, birch from 16% to 13%, spruce from 14% to 9%, and larch from 12% to 2%, while aspen increased from 8% to 35%. Based on ordination of species abundance and proportional basal area, physiographic zones varying in geology and hydrology were characterized by different species composition in the 19th century and experienced largely parallel rather than convergent shifts in community composition since that time.

Maps were developed for the regional study area using a 10 × 10 km spatial resolution to document spatial patterns of species proportional basal area. White pine co-dominated (was ranked first or second in proportion of basal area) 45% of the 253 100-km² presettlement zones, but none of the 1990 zones. Forest zones co-dominated by red pine, jack pine, and larch also largely disappeared. These forests were largely supplanted by aspen co-dominated communities, which accounted for 82% of the 1990 forest zones and represent diminished regional landscape diversity. Although the same 11 species made up the 1990 as well as the 19th century forest, change in their relative abundance and dominance was profound such that 85% of the 253 zones now contain community types (i.e., dominant species pairs) that did not dominate anywhere in the presettlement era.

Key words: change; Forest Inventory and Analysis; General Land Office; logging; Minnesota; southern boreal forest.

INTRODUCTION

Land use–land cover change has been identified as one of the most important components of global change (Vitousek 1994). Large-scale changes to forest composition, spatial structure, and disturbance regimes have direct implications for terrestrial carbon sinks, water quality, and floral and faunal habitats. Land use dynamics such as these have profound implications for society, conservation of biodiversity, and myriad natural ecological services. The U.S. National Academy of Sciences identified these interrelationships among the eight most pressing environmental challenges (Committee on Grand Challenges in Environmental Sciences 2001). Directly linking long-term forest changes with anthropogenic disturbance regimes is difficult as the overstory and understory may have dif-

ferent responses to the same perturbation, and response patterns may be temporally asynchronous or occur below limits of our observational resolution.

World wide, change in southern boreal forests was profound in the 20th century and has been linked to the reduction of fires and the nearly simultaneous introduction of logging (Kuusela 1992, Carleton 2000, Reich et al. 2001). In northeastern Minnesota and adjacent Ontario, fiber production represents a significant component of the regional economy. Therefore, quantifying previous changes, monitoring current trends, and predicting future forest conditions, will be valuable in the development of regional and national long-term management and policy for sustainable forests. Timber harvesting elsewhere in the Lake States region of the United States had already reached its maximum extraction period by the 1880s, when much of northeastern Minnesota was just beginning to be harvested (Sedjo 1990). Prior to timber harvesting, forest fires were the primary disturbance agent in northeastern

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Minnesota (Heinselman 1973). Fire adapted species such as jack pine (*Pinus banksiana*), paper birch (*Betula papyrifera*), and aspen (*Populus tremuloides*) were abundant soon after fires and were replaced by later successional species such as spruce (*Picea* spp.), balsam fir (*Abies balsamea*), and northern white cedar (*Thuja occidentalis*) (Heinselman 1973, Grigal and Ohmann 1975, Ohmann and Grigal 1979, Frelich and Reich 1995). Fire suppression policies initiated in the late 19th and early 20th century following several large-scale conflagrations represented a major departure from the natural disturbance history in this region. Thus an important question regarding forest change is how has fire suppression and logging influenced the southern boreal forest?

The focus of this paper is on the influence of logging (and associated fire suppression) as a driver of regional forest change in the southern boreal forest. Recognition of the differences between forest harvesting and natural disturbance processes has increased, and many are advocating that management be conducted following natural disturbance dynamics (Hunter 1993, Neimelä 1999, Bengtsson et al. 2000). In many areas major human disturbance began long before the concepts of natural disturbance-based management (Seymour and Hunter 1999) were formalized. Hence we are only now beginning to consider the full implications of early forest management practices from a disturbance-oriented context. It is important to identify how those practices have altered forest systems, and determine whether these agents of change impact systems in ways similar to or different from natural processes. While changing disturbance regimes are recognized as one of the primary drivers of forest change, measuring and characterizing change remains difficult.

Understanding how forest change develops and where that change occurs are both important questions for management and conservation biology. For instance it is critical to address how variation in disturbance regimes affects the composition, abundance, and spatial organization of forest communities at all scales. Studies of landscape-scale changes in forests have often used a forest fragmentation perspective, and are often more concerned with vegetation patch isolation and faunal metapopulation dynamics, and migration corridors, than with direct changes to forest vegetation (Hanski 1982, Harris 1984, Flather and Sauer 1996).

Pre-20th century fire return intervals were on the order of 50–300 years in northeastern Minnesota (Heinselman 1973). Throughout the 20th century fire was not a major component of the landscape disturbance regime, with return intervals estimated to be as long as 1000–2000 years (Heinselman 1973, 1996). Previously, we found that the spatial structure of the presettlement forest (~1880s) in northeastern Minnesota was dependent on the mix of species adaptive strategies and their clustering tendencies in combination with regional physiography and disturbance his-

tory (Friedman et al. 2001). The combined influences of variable fire return intervals and the suite of regeneration strategies resulted in an all-age forest mosaic throughout the region (Heinselman 1973, Friedman et al. 2001). Logging practices however, with shorter than natural disturbance period rotation cycles can impact canopy species composition, dominance, and spatial distribution patterns, potentially limiting the development of mosaics with uneven aged systems (Bormann and Likens 1979, Phillips and Shure 1990). More generally, differences between natural and anthropogenic driven disturbance processes are widely considered large enough to have substantially altered forest composition, abundance, and spatial structure although evidence is relatively sketchy or limited by spatial scale or land coverage (Whitney 1986, Jackson et al. 2000).

Minnesota's forest resources have been the focus of several investigations (1936, 1953, 1962, 1977, and 1990) that used regional-scale USDA Forest Service data to provide estimates of timber supplies or supply changes on productive forestland (Jakes 1980, Kingsley 1991, Leatherberry et al. 1995). These studies were done well after the first major wave of logging and none used a spatially explicit framework. Hence, no investigation of forest change has been conducted at the regional scale spanning the presettlement period to any modern forest inventory survey in Minnesota. Currently, forest management is driven by ecological, social, and economic values with substantial attention given to the historical natural range of variability, disturbance, and species composition patterns. These patterns have served as benchmarks in forest restoration, forest biodiversity conservation, and long-term planning guidelines. To the extent that historical data represent hypothetical "natural" forest and presettlement forests are often used as surrogates for natural forest, it is critical that quantitative assessments of past and present forests be made to the extent possible with common metrics. We address that need herein with the development of a comprehensive regional-scale assessment of composition and structural changes in northeastern Minnesota forests.

Two recent studies have compared presettlement with modern forest vegetation in central North America (e.g., Radeloff et al. 1999, Jackson et al. 2000). Our study extends these in several ways. First, our study region, the southern boreal zone, differs physiographically, climatically, and in disturbance history from the Wisconsin jack pine barrens studied by Radeloff et al. (1999) and the mixed northern hardwood-boreal zone studied by Jackson et al. (2000) in southeastern Ontario. Our research also differs in being tree-based for both the presettlement and the modern data, in quantifying both abundance and basal area patterns, and in analyzing nested spatial scales from 10-km cells to physiographic provinces to the region.

Formal investigations of regional-scale vegetation change are needed to improve our understanding of the

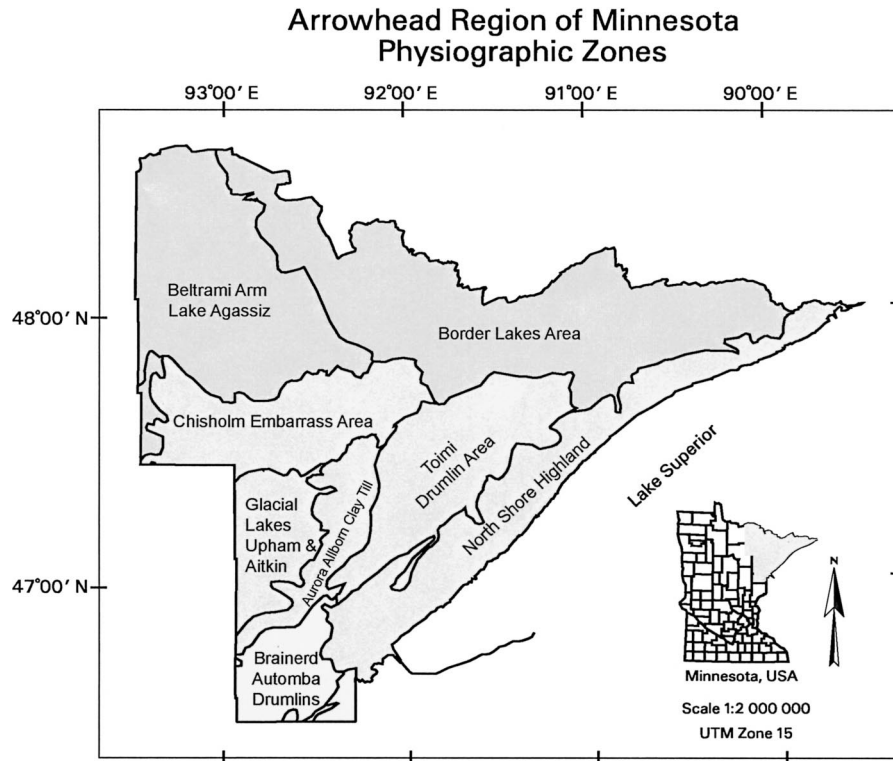


FIG. 1. Location of study area and physiographic zones in northeastern Minnesota, USA.

development processes that gave rise to the existing forest. This study addresses long-term forest change comparing the presettlement (~1880s) and 1990s forest conditions within a 3.2×10^6 hectare landscape in the U.S. Forest Service Aspen–Birch Unit, a five-county region in extreme northeastern Minnesota (Kingsley 1991; Fig. 1). Our overarching hypotheses guiding this work were that: (1) elimination of coniferous canopy seed trees by logging and the subsequent loss of the advanced regeneration saplings following slash fires promoted a shift in the regional composition patterns in favor of shade-intolerant deciduous species; and (2) given the profound differences between coniferous (fire dependent) and deciduous (wind dispersed seed and vegetative cloning) species regeneration strategies, and regionally consistent disturbance shifts from crown fire to logging, species composition would converge over time across physiographic zones and soils.

To address such issues, we used General Land Office (GLO; Almendinger 1997) and Forest Inventory and Analysis (FIA) survey data to: (1) compare species composition and basal area dominance patterns spanning a 100–120 year period between the presettlement era and the 1990 FIA survey, and identify the kind of change that has occurred; (2) evaluate whether these changes were parallel or convergent in different soil types and physiographic zones, and (3) characterize spatial patterns of the forest in both time periods, and the ways these changed over time.

METHODS

The long-term forest change analysis was conducted by comparing GLO records of an arbitrarily defined region in northeastern Minnesota with a subset of the 1990 Eastwide Forest Inventory and Analysis survey database developed and maintained by the U.S. Forest Service (Fig. 1). The region includes several physiographic zones that differ in geological substrate, soils, and hydrology. GLO land survey records were made available from the Minnesota Department of Natural Resources and were developed previously to describe compositional and landscape-scale spatial characteristics for this region (Friedman et al. 2001). Comparing these databases presents numerous challenges. In the following sections, we describe differences between the GLO and FIA surveys and how we reconciled those differences to the extent possible (see Friedman et al. 2001 for more detail). The two surveys characterized the same region, but the selection process differed, as did procedures followed in the collection of the data. Below we introduce each of the surveys, discuss survey-specific biases, and address problems associated with standardizing these differences. Species abundance (defined using proportions of all trees by population count) and relative dominance (defined by proportional basal area) patterns are then developed for the entire region, and by stratifying within physiographic zones, soil texture classes, and 10×10 km

cells. Finally, an approach to quantifying the landscape-scale forest community transition is developed.

Although the GLO and FIA methodologies differed in ways that are not completely reconcilable, we argue that it is valuable to assess vegetation change using these two data sets once certain standardization protocols have been put in place, and these data likely provide our best opportunity to make a quantitative assessment of century-scale change. We have however, limited our analysis to comparisons of species composition and proportional basal area, associations with physiographic zones, soil texture classes, and characteristics of the spatial distribution patterns of species composition and proportional basal area distribution patterns throughout northeastern Minnesota.

GLO and FIA records were imported to ARC/INFO (a geographic information system), to facilitate data processing, including the association with environmental data represented in digital maps. Plot locations recorded in Universal Transverse Mercator Zone 15 NAD83 coordinates, were associated with biophysical information for trees associated with each plot. GLO land survey data were derived from 28 779 systematically located sites referencing 74 792 nonsystematically selected bearing and witness tree records. The FIA tree data were derived from 3971 systematically sampled plots producing 113 487 systematically selected trees.

GLO land survey description

Although the GLO land survey was not designed as a vegetation survey, these data are among the best records of the presettlement forests in North America, and have been used in numerous investigations to characterize forest composition, species associations with site characteristics, disturbance, and long-term vegetation change (Almendinger 1985, Iverson and Risser 1987, Delcourt and Delcourt 1996). The GLO land survey was made in this region in the late 1800s as part of the development of the township-range grid used to systematically map land throughout the United States. In Minnesota, as elsewhere, this systematic grid was established to survey land for the public land survey; however trees were used as monuments marking the intersection of grid points and along lines between the intersecting points. In a highly systematic fashion a specific number of bearing and witness trees (from 1 to 4) were surveyed at section (~10 km) and quarter-quarter section (~0.6 km) intersection locations on this grid, in effect producing a systematic survey of the forest vegetation.

Sampling bias and errors in the GLO records are always a concern and thus there is always uncertainty in these data. However, the regional species pool is small and all species are easily identified. Almendinger (1997) addressed a number of limitations and potential problems with the use of the Minnesota GLO data in ecological analyses. He evaluated potential sources of

error due to bias in bearing tree selection, and relevant to the scope and contrasts of our study, he concluded that "species bias is not a serious concern over large areas and comparisons of relative tree abundances are useful." He found no evidence of potential bias in an analysis of differences among species in distance from survey corners; we independently reached a similar conclusion for the data in this study and found no other indicators of potential bias (see Friedman 2001, Friedman et al. 2001). Moreover, Almendinger (1997) used GLO data from the Chippewa National Forest region (~150 km west of our study region) as a test case for an alternative assessment of potential bias. He compared the relative frequency of tree types as bearing trees vs. their relative frequency as mentioned in line notes in the GLO survey data, reasoning that the line notes are free from bias associated with the task of blazing and scribing bearing trees. From this assessment, Almendinger (1997) concluded that there was not a strong case for species bias, but suggested that the relative frequency of aspen, birch, and spruce possibly may have been underestimated by as much as 1–3% in the GLO data due to potential species bias. The large differences in our paper for GLO survey vs. FIA survey for aspen (11% changing to 30%, see *Results*) is much larger than any potential bias could explain, and the directional change over time for aspen (aspen was much more common in 1990) and birch (less common in 1990 than in the GLO era) were opposite despite their being similarly potentially "avoided" as bearing trees. Therefore, despite the uncertainty that can not be removed, the GLO data seem to provide reasonable estimates of relative tree abundances.

In this study we treat GLO land survey locations as surrogates of forest inventory plots that include species identification and tree diameter at breast height, and do not differentiate between bearing and witness tree designations. To reconcile taxonomic ambiguities, we standardized the GLO records following Almendinger (1997, see Friedman et al. 2001) and identified 11 taxa (spruce, combining black and white spruce), paper birch, larch (*Larix laricina*), aspen, northern white cedar, jack pine, red pine (*Pinus resinosa*), white pine (*Pinus strobus*), balsam fir, ash (primarily *Fraxinus pennsylvanica*), and maple (primarily *Acer rubrum* but also *A. saccharum*) that each contributed at least 1% and collectively made up 98% of the total tree pool.

FIA survey description

The FIA survey is designed for long-term repeated measurements of the productive timberland in the United States. Permanent field plots representing approximately one acre (0.4 ha) were established using statistical double sampling techniques to achieve a stratified sample of forest types. Numerous land use conditions eliminated a fraction of the potential plots, such as those including forest reserves (land withdrawn from commercial timberland use), unproductive timber-

lands, marshes, and alternate land use activities emphasizing uses other than timber production. For those plots where data (species abundance, growth, mortality) were to be collected, a hierarchical plot design was used. Environmental data were collected at the plot level, while specific information for inventoried trees was compiled at a series of 10 nested subplots using a variable radius plot design (Birdsey and Schreuder 1992).

Trees <12.5 cm in diameter at breast height (dbh) were inventoried in 2.03 m radius plots at each of the 10 subplots, and hence were sampled with equal probability regardless of their size (Birdsey and Schreuder 1992). Trees ≥ 12.5 cm in dbh were sampled at each cluster point with a 37.5-BAF prism, which effectively resulted in a spatially more intensive inventory of the largest size class trees. Basal area expansion factors (BAF) were then used to adjust basal area estimates of all trees according to the field estimated size class. Species composition was calculated as relative frequency and basal area estimates $\Sigma BA = \pi \times (\text{dbh}/2)^2$ were derived from the tree tally list.

Influence of tree size class distributions

To address the concern that the GLO data were biased against either small or larger sized diameter trees, which would potentially lead to errors in a direct comparison with the FIA data, we examined tree size distribution differences, on a species basis, among the two data sets. These did not differ markedly (data not shown). Nonetheless, we next assessed whether such variation could impact proportional abundance and dominance using the FIA data as a test. First, we examined how expanding the FIA database influenced the relative rankings of the species. Since the unexpanded FIA data are biased toward larger size individuals, comparison of the unexpanded and the expanded versions provides an arbitrary view of the influence this can have on the proportional dominance of species. These two FIA data sets (adjusted and unadjusted for sampling bias) only differed minimally in terms of the species proportional abundances and contributions to total basal area (data not shown). Second, we calculated species proportional basal area within soil texture classes, and within physiographic zones, contrasting distributions of all trees (adjusted to eliminate sample bias) regardless of diameter vs. only trees at least 12.5 cm in dbh (thereby testing for the influence of a severe bias in favor of large rather than small trees). All of these permutations of the FIA data set found that intentional size-related sampling bias had modest impact on the relativized (proportional) metrics used in this study, and hence suggest that potential but unknown size related bias in the GLO data set would also likely have had minimal impacts on these same metrics.

Standardizing differences in numbers and locations of surveyed trees

Mismatches between both the numbers and locations of surveyed sites and trees of the GLO and FIA surveys

make it difficult to compare individual GLO and FIA survey sites. There were roughly an order of magnitude more GLO sites than FIA plots, but each of the latter had 10 times as many trees. Thus individual FIA plots are associated with very few nearby, but not spatially overlapping GLO sites (each with only four or fewer trees). Thus species abundance patterns at specific FIA plots are not representative of nearby GLO sites and neither individual FIA (1 per ~ 800 ha) nor GLO sites (1 per ~ 110 ha) are representative of local (100–1000 of ha) landscape patterns, due to a high degree of fine-scale environmental heterogeneity. To compensate for the sampling design differences we examined various vector-based sampling grid sizes (5×5 km, 10×10 km, and 20×20 km), evaluating each on the basis of the total number of FIA plots represented in each gridded zone, ultimately selecting the 10×10 km grid.

Initially, this 10×10 km vector map included 382 unique cells. However for certain cells, either GLO or FIA plots were scarce. To compensate for the differences between the GLO and FIA survey plot distribution patterns, a minimum of six FIA plots and 30 GLO sites per zone was defined as a cutoff, eliminating approximately one-third of the cells. In this process we eliminated GLO sites located on forest reserve areas (Appendix A), such as the Boundary Waters Canoe Area Wilderness, as these were excluded by the FIA survey. Eliminated cells were largely located along the North Shore Highland, (i.e., Lake Superior shoreline) or along the U.S. and Canadian border (Fig. 1). These cells were generally odd shaped and substantially smaller than 100 km^2 in area. After eliminating these, 253 cells with a mean of 15 FIA plots (and mean total of 429 trees) and 98 GLO sites (and mean total of 255 trees) per zone remained. Both GLO and FIA plots were generally widely dispersed within individual cells occurring on a wide variety of ecological sites typical of the cell, thus providing a relatively representative sampling of each 10×10 km cell in both surveys.

Species distribution patterns in the presettlement period were found in part to be related to physiographic zones and to coarse-scale soil texture classes (Friedman et al. 2001). In this study, we treat physiographic zones and soil texture classes as coarse level stratifying sampling schemes.

Reconciling landscape types

In contrast to the GLO land survey, the FIA plot survey was not designed to survey the entire landscape. Accordingly, to address concern about this potential bias, we considered the various landscape components included or excluded from this survey. Land use classes associated with the potential FIA survey plots were reclassified, collapsing 24 terrestrial land use categories and two aquatic categories into four terrestrial categories: productive timberland, miscellaneous uplands, reserved forestland, and unproductive forestland (and water, hereafter ignored) to assess plot sampling inten-

TABLE 1. Species abundance, expressed as a percentage, of all species contributing at least 1% to the General Land Office Survey recorded in the late 1880s.

| Species | Composition (% of all trees) | | Basal area (% of total) | |
|---|---------------------------------|------|----------------------------|------|
| | GLO | FIA | GLO | FIA |
| Conifers | | | | |
| White pine | 6.2 | 1.1 | 20.4 | 5.2 |
| Spruce | 21.0 | 16.2 | 13.5 | 9.1 |
| Larch | 15.4 | 2.9 | 11.6 | 1.5 |
| Red pine | 2.8 | 1.9 | 7.1 | 4.3 |
| Northern white cedar | 6.5 | 6.3 | 6.2 | 10.9 |
| Balsam fir | 9.5 | 15.7 | 5.3 | 7.6 |
| Jack pine | 6.5 | 2.4 | 4.9 | 3.0 |
| <i>Pinus</i> spp. (undifferentiated to species) | 1.5 | | 3.8 | |
| Broad-leaved deciduous | | | | |
| Paper birch | 14.9 | 11.3 | 15.9 | 12.8 |
| Aspen | 10.7 | 29.9 | 7.6 | 34.8 |
| Maple | 1.4 | 6.3 | 1.2 | 5.7 |
| Ash | 1.4 | 5.0 | 0.7 | 3.6 |
| Miscellaneous species | 2.2 | 0.9 | 1.8 | 1.4 |

Notes: Composition is defined as percentage of all trees; basal area as percentage of total basal area. Forest Inventory and Analysis (FIA) species composition patterns are from the 1990 survey. Species abundance is reported as a single species when the General Land Office Survey (GLO) records identified trees to the species level; otherwise, combined totals for congeneric species are reported. Differences in sampling methodologies in the two surveys account for the differences in basal area estimates for miscellaneous species. Species are listed here and in all subsequent tables by group (conifers and broad-leaved deciduous); within groups they are ranked from high to low by basal area during the presettlement period.

sity across each of the physiographic zones (Appendix A). Plots associated with productive timberlands were the largest percentage (75.3%) of the potential terrestrial FIA survey plots and in keeping with the FIA mission were, in fact, the only plots inventoried. Smaller percentages of the plots, where trees were not inventoried, were associated with reserves (11.1%), miscellaneous uplands (9.5%), and unproductive forestland (4.0%). Miscellaneous uplands represent land use practices that include a variety of farm uses, including shelterbelts, idle farms without trees, Christmas tree farms, pasture and rangeland with and without trees, and several other land uses. These sites generally occur on relatively productive upland soils, and they most likely supported forest cover at the time of the presettlement public land survey. Unproductive forestland (Appendix A) includes some upland settings, such as rocky outcrops, but more frequently, low-lying land with high water tables. These forested wetlands often support expansive stands of larch and spruce, at densities too low to be considered productive forest.

The non-inventoried FIA plots all represent land types that were likely included in the systematic GLO land survey (i.e., today's miscellaneous uplands, reserved forestland, or unproductive forestlands). Of the un-surveyed FIA plots 16% were in the unproductive class (which we assume are largely lowlands). This rough proportionality of lowland to upland is similar to the overall percentage of plots (10–18%) classified as lowland (percentage of sites with organic soils or with low permeability soils) in the GLO land survey

(Friedman et al. 2001) suggesting that the non-inventoried FIA plots likely omitted a roughly representative fraction of different land types. Additionally, contrasts of FIA and GLO data are not noticeably different for physiographic zones with high or low numbers of non-sampled FIA plots, which should be more likely to occur if omission of plots created severe bias in the FIA survey.

Assessing spatial and temporal differences in physiographic zones

Nonmetric multidimensional scaling (PC-ORD Version 4.0 MjM Software McCune and Mefford 1999) was used to assess the species compositional and proportional basal area patterns and changes between the GLO and FIA survey periods. We used the autopilot (slow and thorough) mode to develop the best solution initializing the runs with 40 iterations with real data and 50 runs with randomized data.

Transition matrix and maps of species basal area change

Species proportional basal area within each of the 253 cells was calculated for the GLO and FIA survey periods. We developed a proportional basal area classification with five classes (Class 1 = 0–2.0%, Class 2 = 2.1–5.0%, Class 3 = 5.1–15.0%, Class 4 = 15.1–25.0%, and Class 5 = >25%) and made maps illustrating distribution patterns of species proportional basal area in each of the 253 cells. Difference maps were calculated by first subtracting the FIA survey species

TABLE 2. Percentages of species composition (percentage of all trees, first row) and basal area (BA; percentage of basal area, second row) for the General Land Office survey (late 1800s) and the Forest Inventory and Analysis Survey (1990) data sets for eight physiographic provinces in northeastern Minnesota, USA (see map in Fig. 1).

| Species | Data type | Border Lakes area | | North Shore Highland | | Toimi Drumlin area | | Aurora Alborn Clay-Till area | |
|--------------------------------------|-----------|-------------------|------|----------------------|------|--------------------|------|------------------------------|------|
| | | GLO | FIA | GLO | FIA | GLO | FIA | GLO | FIA |
| Conifers | | | | | | | | | |
| White pine | trees | 5.8 | 3.0 | 10.7 | 0.7 | 7.3 | 0.9 | 4.2 | 0.8 |
| | BA | 18.7 | 15.0 | 23.8 | 2.6 | 22.5 | 4.0 | 14.7 | 5.3 |
| Spruce | trees | 19.2 | 17.5 | 17.8 | 7.1 | 29.3 | 26.6 | 23.0 | 19.0 |
| | BA | 14.7 | 11.1 | 13.8 | 7.2 | 18.2 | 14.0 | 12.4 | 8.5 |
| Larch | trees | 8.4 | 1.0 | 9.1 | 0.4 | 16.2 | 3.1 | 24.1 | 5.1 |
| | BA | 6.8 | 0.5 | 7.4 | 0.3 | 14.6 | 2.0 | 16.9 | 2.3 |
| Red pine | trees | 3.9 | 2.4 | 0.4 | 0.7 | 1.0 | 2.7 | 3.4 | 1.2 |
| | BA | 6.9 | 5.1 | 0.6 | 1.3 | 3.5 | 4.5 | 7.5 | 2.7 |
| Northern white cedar | trees | 4.0 | 4.4 | 10.1 | 8.9 | 4.4 | 6.8 | 3.9 | 2.5 |
| | BA | 4.2 | 7.6 | 8.9 | 16.6 | 3.4 | 11.5 | 3.6 | 3.9 |
| Balsam fir | trees | 9.3 | 19.6 | 17.6 | 15.9 | 7.6 | 16.0 | 4.1 | 12.3 |
| | BA | 4.7 | 7.7 | 10.0 | 7.0 | 3.8 | 7.5 | 3.6 | 8.2 |
| Jack pine | trees | 16.4 | 5.0 | 0.1 | 0.2 | 9.3 | 3.9 | 3.3 | 1.7 |
| | BA | 12.3 | 5.4 | 0.1 | 0.3 | 6.9 | 4.4 | 6.5 | 3.7 |
| <i>Pinus</i> spp. (undifferentiated) | trees | 2.5 | | 0.6 | | 1.4 | | 1.4 | |
| | BA | 6.3 | | 1.3 | | 3.8 | | 5.0 | |
| Broad-leaved deciduous | | | | | | | | | |
| Paper birch | trees | 17.0 | 14.7 | 22.4 | 18.2 | 16.7 | 12.7 | 16.6 | 9.1 |
| | BA | 15.1 | 10.0 | 23.8 | 21.8 | 16.8 | 18.3 | 16.0 | 9.0 |
| Aspen | trees | 11.9 | 25.7 | 5.3 | 26.2 | 5.2 | 20.8 | 13.2 | 36.7 |
| | BA | 8.7 | 34.2 | 6.6 | 23.2 | 4.9 | 28.9 | 11.6 | 46.6 |
| Maple | trees | 0.4 | 5.0 | 3.4 | 14.4 | 0.5 | 3.2 | 1.0 | 6.4 |
| | BA | 0.2 | 2.2 | 2.6 | 14.3 | 0.4 | 2.2 | 0.3 | 3.6 |
| Ash | trees | 0.5 | 1.6 | 1.5 | 6.2 | 0.5 | 2.9 | 0.7 | 4.4 |
| | BA | 0.4 | 1.1 | 0.8 | 4.1 | 0.4 | 2.0 | 0.4 | 3.6 |
| Miscellaneous | trees | 0.5 | 0.2 | 0.9 | 1.0 | 0.3 | 0.3 | 1.1 | 0.9 |
| | BA | 0.3 | 0.0 | 0.8 | 1.2 | 0.4 | 0.5 | 1.0 | 2.6 |

basal area percentage from the GLO basal area percentage, then assigning the difference to a class range.

Each cell was assigned to a community type by ranking species proportional basal area, selecting the first and second highest ranking species. The GLO and FIA survey periods were compared by tallying the proportion of cells where each species was ranked first, and either first or second. We pooled all cells dominated by a common species in the GLO period, and calculated transition probabilities between the GLO and the FIA survey periods with the formula: $P_{ijt} = n_{ij} / \sum n_{ij}$; where P_{ijt} is the probability of a community type i in the GLO time period becoming type j in the FIA time period, n_{ij} is the frequency of types initially as type i that have become type j , and the summation is from $j = 1$ to n (Pastor and Johnston 1992, White and Mladenoff 1994).

RESULTS

Evidence developed in this analysis indicates that the forest has undergone substantial compositional and spatial change. Data are shown for both abundance (percentage of all trees) and proportional basal area (labeled as dominance), since differences among species in average tree size are reflected by different species rankings in the two metrics. Transition properties describing the reallocation of proportional basal area

contributions of individual species within 100-km² cells indicate that many species (e.g., white pine and larch) have experienced a region-wide, but patchy, reduction in importance while others have increased (e.g., aspen and maple). Moreover, community level change analyses indicate that the communities present in the presettlement forest are generally no longer present.

Regional patterns: species composition and proportional basal area

The two surveys identified the same dominant 11 species. However significant changes occurred in species composition and spatial distribution patterns within and across physiographic zones. At the regional scale species with increased proportional abundance levels from the GLO to the FIA era include aspen (up from 10.7% to 29.9% of the trees), followed by balsam fir (9.5% to 15.7%), maple (1.4% to 6.3%), and ash (1.4% to 5.0%) (Table 1). Reduced proportional abundance was noted for spruce (down from 21.0% to 16.2%), larch (15.4% to 2.9%), paper birch (14.9% to 11.3%), jack pine (6.5% to 2.4%), white pine (6.2% to 1.1%), and red pine (2.8% to 1.9%) with little change in northern white cedar (6.5% to 6.3%) (Table 1). The trees identified as pine but not to species in the GLO land survey exacerbate the differences, with the total for all

TABLE 2. Extended.

| Glacial Lakes Upham and Aitkin | | Chisholm-Embarrass area | | Brainerd Automba Drumlins | | Beltrami Glacial Lake Agassiz | |
|--------------------------------|------|-------------------------|------|---------------------------|------|-------------------------------|------|
| GLO | FIA | GLO | FIA | GLO | FIA | GLO | FIA |
| 2.6 | 0.2 | 5.7 | 0.6 | 9.2 | 0.9 | 3.5 | 0.9 |
| 13.5 | 1.4 | 16.9 | 2.9 | 29.7 | 4.2 | 14.7 | 4.1 |
| 22.3 | 23.6 | 18.8 | 15.1 | 10.7 | 6.8 | 22.1 | 16.4 |
| 13.8 | 8.8 | 10.3 | 8.1 | 5.2 | 3.4 | 16.1 | 8.4 |
| 42.8 | 16.8 | 14.6 | 2.5 | 23.2 | 4.9 | 14.3 | 2.3 |
| 30.4 | 8.4 | 11.7 | 1.8 | 12.5 | 3.4 | 11.9 | 1.3 |
| 1.2 | 0.2 | 5.8 | 3.1 | 1.0 | 2.5 | 4.1 | 1.8 |
| 4.1 | 1.2 | 15.2 | 8.8 | 3.9 | 7.2 | 11.2 | 5.0 |
| 8.3 | 3.1 | 6.0 | 4.1 | 6.8 | 3.4 | 7.6 | 8.2 |
| 9.9 | 4.8 | 4.7 | 5.6 | 5.2 | 3.5 | 8.5 | 12.9 |
| 4.4 | 12.7 | 8.5 | 14.6 | 4.2 | 10.3 | 9.6 | 15.9 |
| 1.8 | 11.6 | 3.7 | 8.2 | 2.2 | 6.6 | 5.7 | 7.5 |
| 0.2 | 0.4 | 9.8 | 4.5 | 0.8 | 0.4 | 5.1 | 1.7 |
| 0.2 | 1.6 | 9.5 | 7.6 | 0.8 | 0.3 | 4.7 | 1.9 |
| 0.6 | | 2.2 | | 0.9 | | 1.4 | |
| 3.6 | | 6.2 | | 2.1 | | 3.3 | |
| 9.0 | 3.5 | 16.6 | 10.1 | 17.3 | 9.2 | 9.1 | 7.1 |
| 13.6 | 6.8 | 14.0 | 9.7 | 20.1 | 11.9 | 7.1 | 5.7 |
| 5.2 | 29.7 | 8.2 | 35.1 | 12.6 | 32.6 | 19.8 | 35.3 |
| 6.1 | 42.1 | 5.4 | 38.9 | 9.9 | 32.4 | 14.4 | 45.4 |
| 0.7 | 2.3 | 1.7 | 5.5 | 4.6 | 11.4 | 0.3 | 3.5 |
| 0.7 | 3.2 | 1.2 | 3.3 | 4.5 | 10.2 | 0.2 | 2.4 |
| 0.8 | 6.1 | 1.0 | 3.9 | 1.6 | 14.4 | 1.4 | 6.1 |
| 0.8 | 6.6 | 0.7 | 3.3 | 1.3 | 11.6 | 1.1 | 3.9 |
| 1.9 | 1.5 | 1.1 | 0.7 | 7.1 | 3.3 | 1.7 | 0.8 |
| 1.7 | 3.5 | 0.5 | 1.8 | 2.6 | 5.4 | 1.2 | 1.4 |

pinus changing from 17.0% in the GLO to 5.4% by 1990. Change was also noted in the proportional basal area allocation among species. Of the species with increased proportional basal area over time, aspen ranks first, increasing from 7.6% to 34.8% (Table 1). No other species increased its share of the proportional basal area by more than ~5%. The largest reduction in relative basal area was in white pine, which declined from 20.4% in the presettlement period to 5.2% in the FIA survey, with all pines combined going from 36.2% to 12.5% (Table 1). Spruce and larch declined over time in proportional basal area from 13.5% to 9.1% and from 11.6% to 1.5%, respectively.

Change within and among physiographic zones

Patterns of change over time were consistent across all physiographic zones (Table 2). Species that increased in one physiographic zone did so in all physiographic zones, and species that declined did so universally. Aspen markedly increased to at least 21% of composition and 23% of the basal area in every physiographic zone (Table 2). These changes were so large that by 1990 it was the dominant species in every physiographic zone, even in those zones where it had been relatively unimportant in the presettlement era (Fig. 1 and Table 2). Maple also increased markedly in abun-

dance and proportional basal area in all physiographic zones, despite a 15-fold difference in abundance in the GLO data among zones. Balsam fir had a marked increase in proportional abundance in 8 of the 9 physiographic zones, (Table 2), but balsam fir increased its fraction of total basal area in only four of the nine zones.

White pine declined dramatically in abundance everywhere except the Border Lakes Region and by 1990 its abundance was <1% in every other zone (Table 2). Historically (i.e., GLO era) due to its large average size (Friedman et al. 2001), white pine represented from 15–30% of the relative basal area in every zone, but by 1990 it was <6% in all zones except the Border Lakes Region (15%; Table 2). Substantial decreases in larch relative abundance and proportional basal area were observed in all physiographic zones. Jack pine and paper birch generally declined in abundance in most physiographic zones, whereas northern white cedar was variable in how it changed across the region (Table 2).

Soil associations

Species proportional abundance and proportional basal area distribution patterns changed within each of the five soil texture classes. Aspen proportional abun-

TABLE 3. Composition (percentage of all trees, first row) and proportional basal area (BA) (percentage of all basal area, second row) distribution patterns among soil texture classes.

| Species | Data type | Soil texture class | | | | | | | | | |
|--------------------------------------|-----------|--------------------|------|---------------|------|--------|------|-------------|------|----------|------|
| | | Coarse | | Coarse-medium | | Medium | | Medium-fine | | Organics | |
| | | GLO | FIA | GLO | FIA | GLO | FIA | GLO | FIA | GLO | FIA |
| Conifers | | | | | | | | | | | |
| White pine | trees | 6.8 | 3.3 | 6.3 | 3.59 | 9.1 | 1.2 | 4.3 | 1.9 | 2.7 | 1.5 |
| | BA | 23.5 | 6.3 | 19.1 | 7.3 | 21.0 | 1.4 | 16.6 | 2.9 | 12.7 | 3.5 |
| Spruce | trees | 20.4 | 15.8 | 18.8 | 15.4 | 21.5 | 11.9 | 20.9 | 12.5 | 28.0 | 16.7 |
| | BA | 12.0 | 9.8 | 13.9 | 8.7 | 13.6 | 8.3 | 14.9 | 8.3 | 17.1 | 11.9 |
| Larch | trees | 15.3 | 3.6 | 9.4 | 1.8 | 16.2 | 2.8 | 14.8 | 3.3 | 35.6 | 10.0 |
| | BA | 11.3 | 1.5 | 7.7 | 0.7 | 13.5 | 1.3 | 12.5 | 1.4 | 24.9 | 5.8 |
| Red pine | trees | 4.2 | 4.3 | 3.4 | 2.2 | 1.7 | 0.7 | 1.1 | 0.9 | 1.0 | 0.7 |
| | BA | 11.7 | 10.2 | 8.2 | 3.7 | 3.78 | 1.6 | 3.6 | 2.7 | 3.6 | 1.7 |
| Northern white cedar | trees | 5.0 | 3.9 | 6.5 | 4.4 | 6.5 | 4.6 | 9.2 | 4.96 | 5.2 | 4.9 |
| | BA | 4.0 | 9.1 | 6.5 | 12.7 | 6.4 | 8.6 | 10.4 | 12.0 | 6.3 | 9.6 |
| Balsam fir | trees | 8.3 | 16.6 | 11.9 | 15.3 | 7.2 | 16.4 | 10.1 | 15.2 | 3.9 | 14.5 |
| | BA | 3.9 | 7.7 | 6.7 | 6.5 | 4.9 | 8.2 | 6.5 | 9.4 | 2.5 | 8.7 |
| Jack pine | trees | 10.9 | 4.8 | 9.0 | 3.5 | 2.7 | 1.2 | 3.5 | 1.3 | 1.4 | 1.2 |
| | BA | 7.9 | 6.8 | 6.3 | 2.9 | 3.17 | 1.3 | 2.4 | 0.7 | 1.4 | 1.4 |
| <i>Pinus</i> spp. (undifferentiated) | trees | 1.4 | | 1.5 | | 1.1 | | 2.0 | | 1.0 | |
| | BA | 4.2 | | 3.7 | | 2.2 | | 4.6 | | 5.0 | |
| Broad-leaved deciduous | | | | | | | | | | | |
| Paper birch | trees | 15.2 | 15.4 | 18.1 | 17.2 | 20.5 | 17.9 | 8.8 | 13.9 | 10.6 | 13.4 |
| | BA | 13.0 | 12.7 | 17.0 | 13.5 | 21.2 | 17.8 | 9.6 | 6.8 | 14.5 | 10.4 |
| Aspen | trees | 9.3 | 20.8 | 11.1 | 22.2 | 6.1 | 23.7 | 21.1 | 28.1 | 7.6 | 21.4 |
| | BA | 5.9 | 29.7 | 8.1 | 33.7 | 6.7 | 34.9 | 15.7 | 45.0 | 9.06 | 35.1 |
| Maple | trees | 1.1 | 5.9 | 1.5 | 8.8 | 2.2 | 9.7 | 0.6 | 4.7 | 1.1 | 7.1 |
| | BA | 1.0 | 2.4 | 1.3 | 7.6 | 1.76 | 8.5 | 0.6 | 2.6 | 1.3 | 4.1 |
| Ash | trees | 0.7 | 4.0 | 1.0 | 4.2 | 1.2 | 7.3 | 1.7 | 8.9 | 0.7 | 6.4 |
| | BA | 0.5 | 2.8 | 0.7 | 2.1 | 0.79 | 5.8 | 1.2 | 5.7 | 0.7 | 4.9 |
| Miscellaneous spp. | trees | 1.4 | 1.4 | 1.5 | 1.3 | 1.3 | 2.5 | 1.9 | 4.3 | 1.1 | 2.2 |
| | BA | 0.9 | 0.9 | 0.6 | 0.5 | 0.9 | 2.3 | 1.4 | 2.5 | 0.8 | 2.9 |

Note: All trees ≥ 1.0 inch (~ 2.5 cm) in dbh are included.

dance and proportional basal area increased, such that it ranked first (FIA data) by far in both of these measures on all soil texture classes (Table 3), including the coarsest texture and organic classes where it was of modest importance in the presettlement era. White pine, larch, and spruce, which collectively made up 33.2–46.8% of the basal area on the coarse, coarse-medium, and medium texture classes in the presettlement period declined and made up from 11.0–17.6% of the basal area in the modern era on each of those soil classes (Table 3). Red pine and jack pine had greater basal area proportion on coarse texture soils than on medium-fine textured soils in both time periods and maintained a stable proportion of basal area over time only on the coarsest textured soil classes (Table 3).

Community composition responses among physiographic zones

Community composition generally changed in parallel among physiographic zones. This analysis, based upon NMDS ordination, compares species proportional abundance and basal area patterns among physiographic zones for the two periods (Fig. 2). The dominant patterns indicate that each of the physiographic zones has moved from positions on the right side of the abundance ordination to positions further to the left and

higher on Axis 2 (Fig. 2A) or to positions in the lower left when considering proportional basal area (Fig. 2B). Large initial differences existed among physiographic zones and roughly parallel changes occurred in all zones, such that each is quite different than in the 1880s. The hypothesized convergence across physiographic zones was not supported however.

Examination of the species correlations (data not shown) with each NMDS Axis clarifies the nature of the observed change. Aspen, ash, and maple each have negative Pearson *R* values on Axis 1 of the ordination of species proportional abundance patterns (Fig. 2A) whereas larch, birch, and white pine were positively associated with this Axis. Larch and spruce had negative Pearson *R* values on Axis 2 while balsam fir, ash, and maple had large positive Pearson *R*. Correlations with NMDS proportional basal area ordination axes tell a similar story. Species with positive correlations with Axis 1 include white pine and larch while species with negative correlations include aspen, maple, and others (Fig. 2B). Species positively correlated with Axis 2 include white pine and paper birch, while aspen is very strongly negatively correlated with this Axis. Thus, change during the 20th century was generally associated with co-occurring increases in aspen, maple, ash, and fir, and decreases in larch, spruce, pine, and birch.

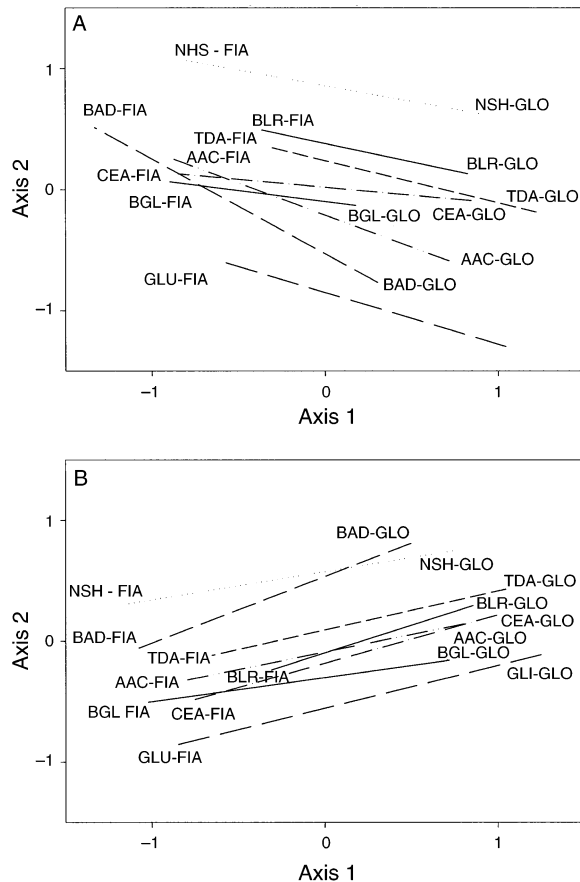


FIG. 2. Nonmetric multidimensional scaling ordination of (A) species proportional composition and (B) species proportional basal area within physiographic zones during the presettlement and modern era. The ends of each line represent the ordination points for each zone during the GLO and the FIA eras. Symbols represent physiographic zones: NSH, North Shore Highland; BLA, Border Lakes Area; BAD, Brainerd Automba Drumlins; CEA, Chisholm-Embarrass area; GLU, Glacial Lakes Upham and Aitkin; AAC, Aurora Alborn Clay Till; TDA, Toimi Drumlin area; BGL, Beltrami Arm Lake Agassiz. "FIA" indicates Forest Inventory and Analysis Data; "GLO" indicates General Land Office Survey Data.

Transitions: landscape-scale spatial patterns

Mapped data from the 10-km grids illustrate spatial distribution patterns at the landscape scale (Figs. 3–5). Each set of maps depicts the proportional basal area within each 100-km² cell. All of the species exhibit heterogeneous spatial distribution (Figs. 3–5) and state transition tables (Table 4, Appendix B) demonstrate marked changes in basal area class membership in the majority of 100-km² zones.

Ascending species.—The enormous and ubiquitous 20th century increase in aspen is evident in the regional map (Fig. 3) and the transition matrix (Appendix B, panel A). In the presettlement period, aspen dominated few cells and these were located in the northwestern part of the region (Fig. 3). In comparison, in 1990 the number of cells where aspen accounted for at least 25%

of the proportional basal area greatly increased and these were found in all physiographic regions (Fig. 3). The change map shows that aspen has increased by >20% in ~40% of the cells (Fig. 3).

Northern white cedar and balsam fir both increased modestly region-wide in proportional basal area in a patchy pattern (Fig. 3). Maple was not an important species in the presettlement period but by 1990 had become a co-dominant in the Lake Superior uplands (see Fig. 1) and to a lesser extent in the northwestern portion of the study area (Fig. 3). Ash was also unimportant in the GLO era, and increased in importance in many cells throughout much of the region (data not shown).

Declining species.—Paper birch was most abundant within 50 km of the shore of Lake Superior in both the GLO and FIA eras (Fig. 4). Birch's modest overall net decline in proportional dominance (from 16% to 13% for the region) gives an illusion of stability; however, many individual 100-km² cells within 50 km of Lake Superior increased or decreased substantially in birch dominance (Fig. 4, Appendix B). This indicates the dynamic nature of forest change at intermediate grain (100 km²) landscape scales (and would likely be even greater at finer scales than measured here) even for a species that retains similar overall dominance at the coarser grain (32 000 km²) regional scale.

Red pine and jack pine had similar and marked heterogeneity in spatial patterns of basal area dominance, being concentrated in the north central and northwest portions of the region presettlement and in 1990, but sharply declining in dominance over time (Fig. 4). Spruce also had marked heterogeneity in spatial distribution that remained stable from the late 19th to the late 20th century, being most abundant in the central and far northwest parts of the region (Fig. 5), and the species remains important, despite declining overall. Larch was the most abundant in the western portion of the study area in the GLO era and retained that spatial pattern while declining markedly by 1990 (Fig. 5). The widespread nature of white pine dominance in the presettlement period is evident in the GLO era map (Fig. 5). Cells with highest proportional basal area ($\geq 25\%$) were primarily concentrated in the southern portions of the region, but cells with high proportional basal area (>15%) were located throughout the region. The FIA-era map and the transition matrix (Appendix B) show that there was a profound and across-the-board decline in white pine.

Transitions: community type dynamics

Marked changes among community types are evident when types are defined by the dominant or co-dominant species (first or second highest proportion of basal area; Table 5). In the GLO-era white pine was the dominant species in 30% (co-dominant in 45%) of the 253 100-km² cells followed by paper birch (18%), spruce (13%), larch (12%), red pine (8%), jack pine (8%), aspen (6%),

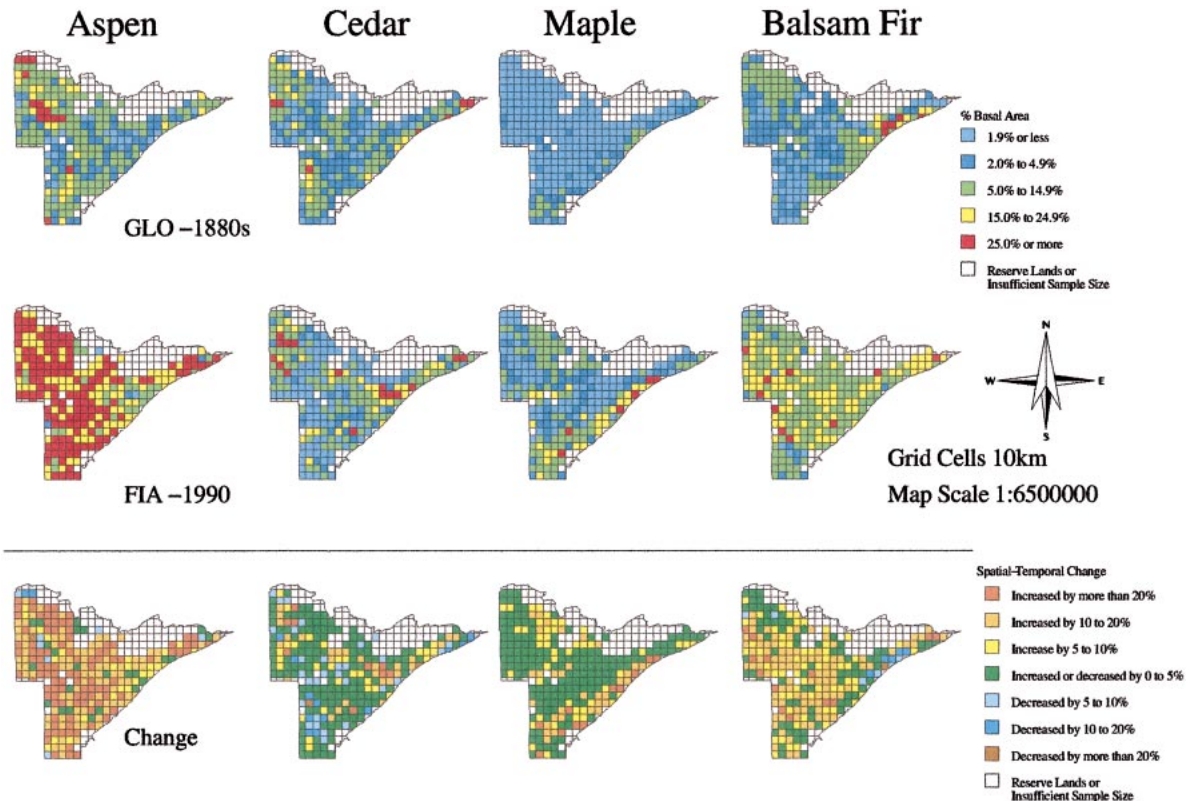


FIG. 3. Spatial distribution patterns of aspen, northern white cedar, maple, and balsam fir, four species with increased proportional basal area in northeastern Minnesota during the past century. Species proportional basal area (percentage of total basal area) is shown for each of 253 100-km² zones, in both the presettlement (approximately 1880–1900) and modern (1990) era, based on GLO and FIA databases (see *Methods*). Also shown is the change over time, calculated by first subtracting the FIA survey species basal area percentage from the GLO basal area percentage, and then assigning the difference to a class range.

cedar (4%), and balsam fir (2%). In 1990, these patterns were distinctly different (Table 5). White pine has been completely eliminated as a dominant or co-dominant from any 100-km² zone in the forest. The second most radical decline was seen in larch which decreased as either a dominant or co-dominant from 30% to 3% of all cells (Table 5). Thus, there has been a near virtual disappearance of pine, larch, and several other stand types, and a replacement by aspen, which increased from 11% to 82% in terms of the percentage of cells where it was either dominant or co-dominant.

Community types were further delineated by identifying the specific combination of the two species contributing the first and second highest ranked proportional basal area within each of the 253 cells. Using this approach we identified 52 community types for the GLO era and 42 types in 1990 (Table 6). We identified two primary forms of change: (1) less than half (22 of 52) of all community types were observed in any cell in both survey periods, and the vast majority of these became much rarer in the modern era, and (2) 20 new community types, not present in the presettlement pe-

riod, were identified and dominant in the FIA era (Table 6).

Community types present in the GLO data but not in 1990 accounted for 78% of the cells of the presettlement forest (Table 6). White pine–paper birch (12%) was the most abundant community type in this group, with other important presettlement types including white pine–red pine (6%), paper birch–spruce (6%), paper birch–white pine (5%), and white pine–larch (4%).

Community types unique to the 1990 forest survey, plus one accounting for <1% of the GLO era cells, account for ~67% of the forest composition. Aspen–paper birch (17%) and aspen–balsam fir (16%) were the most abundant among this suite of community types. Only two other types, aspen–spruce (9%) and aspen–maple (6%) contributed at least 5% to the 1990 forest composition. Although the identical mixture of 11 species still dominated this forest region in the FIA as in the GLO era, the nature of the compositional dominance had changed dramatically (Fig. 6).

Transitions over time among communities were substantial. Very few cells retained the same community

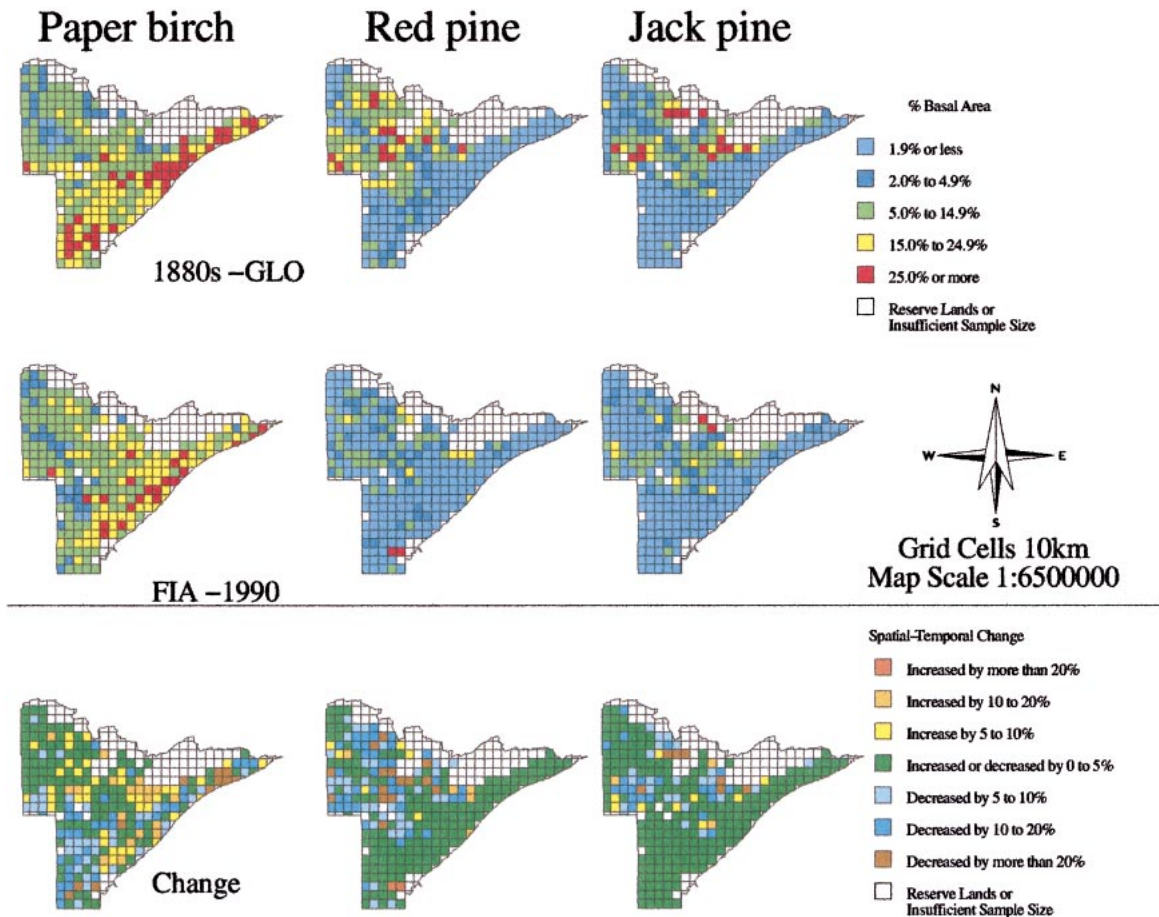


FIG. 4. Spatial basal area distribution patterns of paper birch, red pine, and jack pine, species that have moderately declined in northeastern Minnesota. For additional details, see Fig. 3 legend.

type dominance in the 1990 as in the GLO era. Cells dominated by aspen presettlement (Fig. 6) were retained with greater frequency (75%) than any other community type, and in the other 25% aspen remained co-dominant. Spruce communities remained spruce dominated in 15% (and co-dominant in another 27%) of the cells. Paper birch dominated cells remained birch dominated in 4% and co-dominant in 39% of the cases (Fig. 6). Paper birch communities, the second most abundant in the GLO era, were converted to 15 different FIA-era community types. No other community types maintained their dominant position between time periods in even a single cell.

Cells dominated by white pine in the GLO era transitioned to 18 different FIA-era community types. Aspen–paper birch (28%) and aspen–maple (12%) community types formed in 40% of the cells, and mixes of aspen–other (primarily spruce, cedar, ash, or fir) dominated an additional 46% of these cells (Appendix B). By 1990, aspen was the dominant member in 64% of the former birch-dominated cells. Cells formerly dominated by spruce were dominated in 1990 by three other community types (aspen–spruce [27%], aspen–balsam

fir [24%], and northern white cedar–aspen [12%]). Larch, red pine, and jack pine (Appendix B) dominated communities largely changed into those dominated by aspen, plus spruce, fir, and birch.

DISCUSSION

The substitution of logging for fire as the dominant disturbance regime in northeastern Minnesota led to major alteration of composition and dominance in this region, regardless of whether measured across physiographic zones, associations with soils, by species, or by community type. Attrition has been defined (Forman 1995) as the process by which landscape elements such as patches and corridors disappear. In our study, attrition of 100-km² community types was assessed as a regional scale process. Community type conversions, as we observed them, represent a replacement of the presettlement forest matrix with a new and substantially more homogeneous matrix (i.e., the dominance of aspen is much greater than the dominance of any species in the presettlement time).

Although the species pool remained essentially the same, structural characteristics (relative abundance,

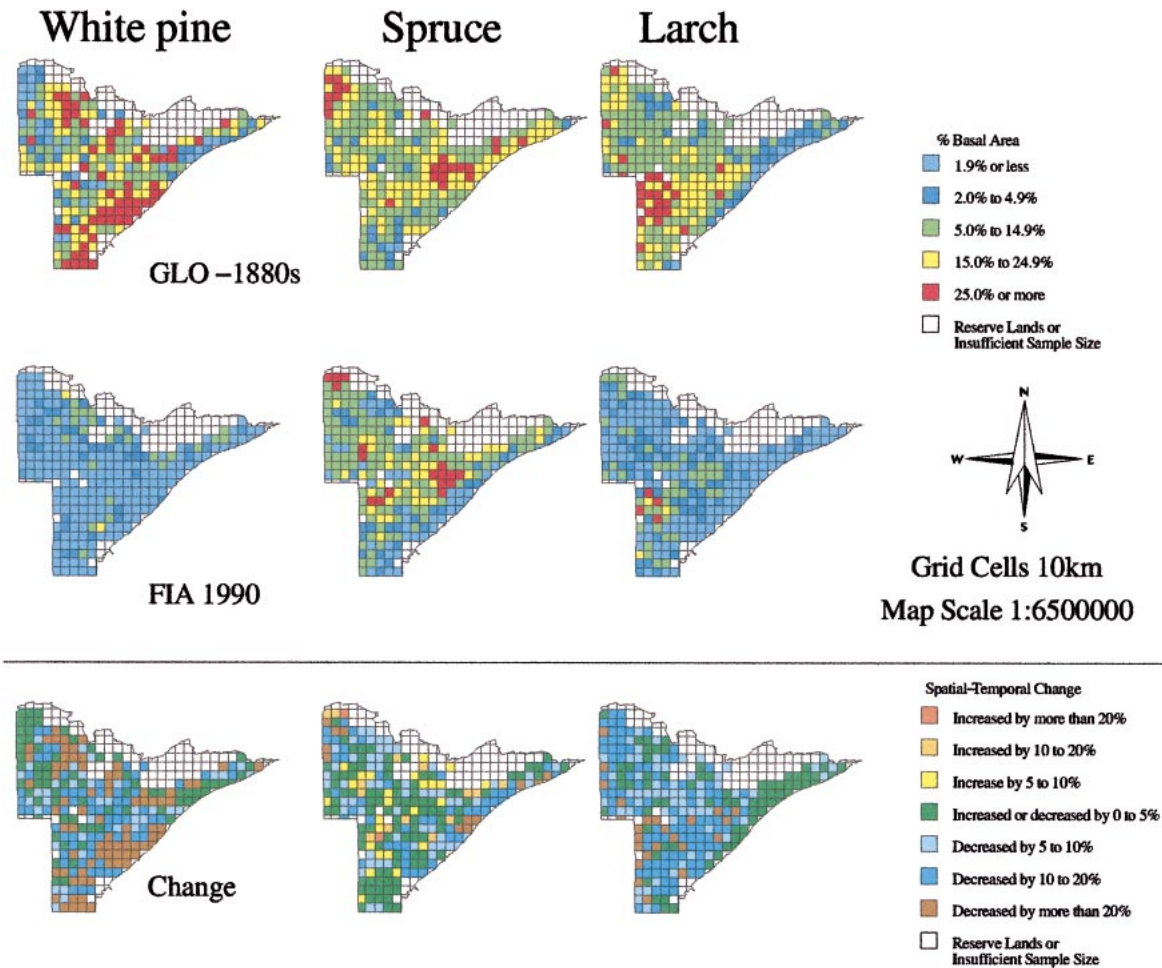


FIG. 5. Spatial distribution patterns of white pine, spruce, and larch, species with very large reduced proportional basal area in northeastern Minnesota. For additional details, see Fig. 3 legend.

TABLE 4. Data are ratios of the frequency of 10×10 km zones by basal area class in the 1990 FIA survey to the GLO land survey.

| Species | Basal area membership class | | | | | χ^2 | <i>P</i> |
|-------------------------------|-----------------------------|--------------------|---------------------|----------------------|-------------------|----------|----------|
| | Class 1 (0–2%) | Class 2 (+2–5%) | Class 3 (+5–15%) | Class 4 (+15–25%) | Class 5 (+25%) | | |
| Conifers | | | | | | | |
| White pine | 5.87 | 1.30 | 0.38 | 0.02 | 60‡ | 251.8 | 0 |
| Spruce | 23.5 | 1.54 | 0.94 | 0.47 | 0.82 | 61.3 | 0 |
| Larch | 10.84 | 1.64 | 0.38 | 0.04 | 0.16 | 213.8 | 0 |
| Red pine | 1.51 | 1.10 | 0.56 | 0.25 | 0.16 | 41.1 | 0 |
| Northern white cedar | 1.86 | 0.34 | 0.89 | 1.81 | 0.94 | 48.1 | 0 |
| Balsam fir | 0.08 | 0.14 | 1.65 | 10.5 | 2.0 | 187.2 | 0 |
| Jack pine | 1.25 | 0.80 | 0.81 | 0.57 | 0.14 | 16.4 | 0.003 |
| Broad-leaved deciduous | | | | | | | |
| Paper birch | 1.00 | 1.11 | 1.09 | 1.05 | 0.53 | 6.19 | 0.18 |
| Aspen | 0.09 | 0.04 | 0.21 | 3.45 | 9.78 | 269.8 | 0 |
| Maple | 0.40 | 1.73 | 5.78 | 25† | 6† | 137.7 | 0 |
| Ash | 0.40 | 3.55 | 77 | 13† | 5† | 177.6 | 0 |
| Other | 0.24 | 3.45 | 12.11 | 8† | 0‡ | | |

Notes: The χ^2 test statistics are based on the frequency values. Daggers (†) indicate that the actual number of zones in that basal area class in the 1990 survey and that there were no zones in this basal area class at the time of the GLO land survey. Double daggers (‡) indicate that there were no zones in that basal area class in the 1990 FIA survey and the actual number zones present at the time of the GLO land survey.

TABLE 5. Percentage occurrence of species as a singular dominant and as a co-dominant (one of top two) species for both the GLO and FIA survey periods.

| Species | GLO (%) | | FIA (%) | |
|------------------------|----------|------------------------|----------|------------------------|
| | Dominant | Dominant + co-dominant | Dominant | Dominant + co-dominant |
| Conifers | | | | |
| White pine | 29.6 | 45.4 | 0 | 0 |
| Spruce | 13.0 | 33.9 | 9.88 | 20.18 |
| Larch | 11.5 | 30.1 | 1.58 | 2.77 |
| Red pine | 8.3 | 16.6 | 0.79 | 3.56 |
| Northern white cedar | 3.56 | 7.51 | 6.72 | 13.44 |
| Balsam fir | 1.9 | 4.35 | 4.74 | 25.34 |
| Jack pine | 7.91 | 13.0 | 0.79 | 3.95 |
| Broad-leaved deciduous | | | | |
| Paper birch | 17.8 | 38.0 | 7.91 | 28.81 |
| Aspen | 6.32 | 11.1 | 63.2 | 81.8 |
| Maple | ... | ... | 1.98 | 10.28 |
| Ash | ... | ... | 1.98 | 6.33 |
| Miscellaneous | ... | ... | 0.39 | 2.76 |

Note: Dominance status was determined by ranking percentage basal area contribution within each of the 253 zones and identifying species that ranked first or second.

proportional basal area, and spatial distribution patterns) of the modern forest were very different from conditions in the presettlement era. The exceptionally high rate of GLO-era community type transitions (at a 10-km spatial resolution) to aspen dominated or co-dominated communities in 1990 is so complete that close to two-thirds of community types present in the forest today have almost no presettlement analogs. Moreover, most of the original community types including the seven most common (white pine–birch, white pine–red pine, birch–spruce, birch–white pine, spruce–larch, birch–larch, and white pine–larch) are not represented in the modern forest at the 100-km² scale (Table 6).

Our results are consistent with the results reported by several investigations of change in related forest types in eastern Ontario (Carleton and MacLellan 1994, Jackson et al. 2000) despite some important differences in methodology. Substituting logging for fire as the predominant form of disturbance in the southern boreal forest will shift competitive advantage to broad-leaved, shade-intolerant deciduous species from shade-tolerant coniferous species (Radeloff et al. 1999). Across the region, coniferous species composition has declined and deciduous species, especially aspen, have increased.

Resolution of species changes

By using the GLO and FIA records, we developed accounts of individual species composition and change. Alternatively, ecologists often rely on satellite technology to provide regional synoptic models of forest composition and use imagery from many dates to conduct change assessments. While the advantages of the technology are undisputed, limitations remain, which makes differentiating individual species difficult or nearly impossible. For example, the spectral signatures

of aspen and paper birch are sufficiently similar that these species are generally considered together rather than independently. Because of this, estimates of aspen and paper birch, as a classified type, suggest that both species have high regional abundance in this Minnesota forest (Bauer et al. 1994, Wolter et al. 1995). Our data though show that while aspen has increased dramatically, paper birch has actually declined, especially in abundance. Furthermore, our previous work in this region indicates that these species were negatively autocorrelated indicating that these species were spatially isolated (Friedman et al. 2001).

Uncertainties remain with respect to our estimates of presettlement forest composition and its change. Although bias in species selection in the GLO survey is unlikely to alter the general conclusions made in this study (see *Methods*), we must recognize that we can never be certain as to the error in those estimates. Moreover, reconciling the kinds of vegetation and landscapes sampled by the FIA survey with the systematic GLO survey also can not be done with certainty. Although as a result one must be circumspect in interpreting the changes in percentage values of abundance and basal area for each species, these estimates seem both to be reasonable and a significant advance, given the paucity of such estimates in general.

Local environmental influences on transitions

Composition patterns defined both by proportional abundance and basal area have shifted dramatically over the roughly 100-year period of this study within all physiographic zones. All of the physiographic zones “shifted” in the same direction, and generally with the same relative magnitude. Why have these changes occurred in such a parallel manner, rather than each of the physiographic zones diverging in disparate directions and magnitude or converging as aspen dominance

TABLE 6. Percentage community type composition for the GLO and FIA era survey periods.

| Community type | GLO (%) | FIA (%) |
|-------------------------------|---------|---------|
| Conifers | | |
| White pine | 29.6 | 0 |
| White pine–paper birch | 11.46 | ... |
| White pine–red pine | 6.32 | ... |
| White pine–black spruce | 3.56 | ... |
| White pine–larch | 4.35 | ... |
| White pine–other | 3.95 | ... |
| Black spruce | 13.0 | 9.9 |
| Black spruce–aspen | ... | 4.74 |
| Black spruce–paper birch | 2.37 | ... |
| Black spruce–larch | 4.74 | ... |
| Black spruce–white pine | 2.76 | 5.16 |
| Black spruce–other | 1.58 | ... |
| Larch | 11.43 | 1.58 |
| Larch–black spruce | 3.55 | ... |
| Larch–paper birch | 3.55 | 1.57 |
| Larch–other | 4.33 | ... |
| Red pine | 8.27 | 0.79 |
| Red pine–white pine | 3.16 | ... |
| Red pine–other | 5.11 | 0.79 |
| Northern white cedar | 3.5 | 6.73 |
| Northern white cedar–aspen | ... | 3.56 |
| Northern white cedar–other | 3.55 | 3.17 |
| Balsam fir | 2.64 | 4.74 |
| Balsam fir–aspen | ... | 2.76 |
| Balsam fir–black spruce–other | 2.64 | 1.97 |
| Jack pine | 7.88 | 0.78 |
| Jack pine–black spruce | 2.76 | ... |
| Jack pine–other | 5.12 | 0.78 |
| Broad-leaved deciduous | | |
| Paper birch | 17.0 | 7.88 |
| Paper birch–aspen | ... | 3.55 |
| Paper birch–black spruce | 5.53 | ... |
| Paper birch–white pine | 4.74 | ... |
| Paper birch–larch | 4.3 | 4.33 |
| Paper birch–other | 3.15 | ... |
| Aspen | 6.3 | 63.29 |
| Aspen–paper birch | ... | 17.0 |
| Aspen–balsam fir | ... | 16.2 |
| Aspen–black spruce | 2.37 | 9.09 |
| Aspen–maple | ... | 5.53 |
| Aspen–northern white cedar | ... | 4.7 |
| Aspen–ash | ... | 4.0 |
| Aspen–other | 3.94 | 6.76 |
| Maple | ... | 1.9 |
| Maple–other | ... | 1.97 |
| Ash | ... | 1.97 |
| Ash–other | ... | 1.97 |

Note: Community names were defined by the most dominant species in the species pairing. Hence the aspen–paper birch community type is considered to be different from a paper birch–aspen community type.

grows large? Regionally, physiographic zones are characterized by differences in climate, soil texture and permeability conditions, and propensity for natural fires. The presettlement species and community type composition patterns within each physiographic zone reflected species differences in adaptations to such conditions. Nonetheless, each physiographic zone contains

a different mix of the same landscape elements and supports the same general forest types. It should not be surprising to see that the zones have shifted largely in parallel, since each landscape element would tend to shift similarly across all zones of our study region. If aspen dominance were even larger (and other species driven to negligible abundance), compositional convergence across heterogeneous physiographic zones might occur.

Stand to regional diversity

The response of understory species to the substitution of fire with logging was investigated in a companion field based stand-scale assessment in which we controlled for stand age, origin, and replacement stand types (Reich et al. 2001). We reported that for stands currently of the same type, logging origin had no effect or enriched stand-scale biodiversity compared to wild-fire origin, perhaps because logging was a less severe form of disturbance compared to fire. Moreover, initial differences in composition due to fire vs. logging origin (Nguyen-Xuan et al. 2000) often become negligible within 30 years of stand origin (Reich et al. 2001). However, the present study and others in the larger region (Whitney 1986, 1987, Carleton and MacLellan 1994, Radeloff et al. 1999, Jackson et al. 2000) clearly show major differences in canopy tree composition following logging vs. fire. Hence, an important question, with respect to the effects of replacing fire by logging, is how to interpret data showing major changes in canopy type composition due to logging, along with minimal impacts on understory composition due to logging for stands of comparable post-disturbance type.

Results of the stand-scale study (Reich et al. 2001) suggest that understory composition and diversity are largely a consequence of the dominant canopy species. Thus canopy species appear to be quite sensitive directly to the mode of disturbance (Whitney 1987, Carleton and MacLellan 1994, Radeloff et al. 1999, Jackson et al. 2000; see *Results*), and the understory and total plant community appear to be more sensitive directly to the canopy dominant species than to the mode of disturbance (Reich et al. 2001). Hence, given that the transition to logging caused major changes in overstory forest type in Minnesota (see *Results*), it likely indirectly caused major changes in understory composition and diversity. Since the major change in forest type was to aspen, a type with high biodiversity (Reich et al. 2001), logging disturbance has perhaps enhanced stand-scale diversity.

Regional scale diversity, however, declined after logging was introduced in this region based on data for regional diversity of 10 × 10 km-scale forest types (Fig. 7). In the presettlement era 71% of the 10-km cells were dominated in terms of basal area by one of the four most dominant species (white pine, birch, spruce, and larch), while in 1990 aspen alone dominated 63% of all such cells. Consider moreover, as an

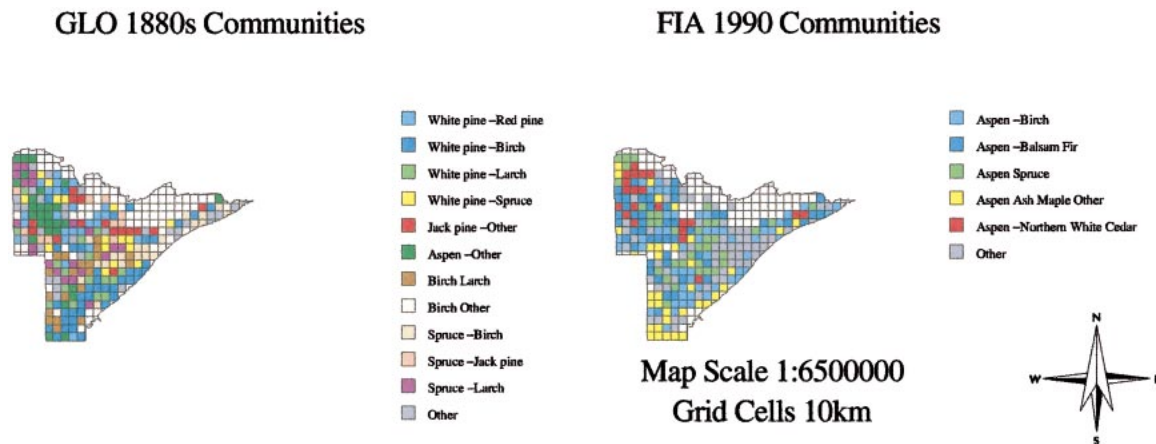


FIG. 6. Spatial distribution of forest community types in the presettlement (approximately 1880–1900) and modern (1990) era in northeastern Minnesota. Community types are defined by the species ranked first and second in proportional basal area within each of the 253 100-km² cells.

example, the dominance (Table 6) of white pine and aspen, respectively, in the two eras, and their respective spatial patterns: white pine (Fig. 7) in the GLO era and aspen in the FIA era (Fig. 3). These two species rep-

resent the most successful species in the respective time periods. Clearly the likelihood that a second, third, or fourth species would dominate or co-dominate a neighboring zone was greater in the presettlement era than in 1990. Before settlement, fires burned the region repeatedly, but patchily (Heinselman 1973) in both space and time, and thus enhanced the formation of the regional mosaic (Frelich and Reich 1995). Stand replacement initiated following logging reduces or perhaps maintains lower regional diversity, by altering the heterogeneity of natural regeneration processes that enhanced diversity of the forest canopy.

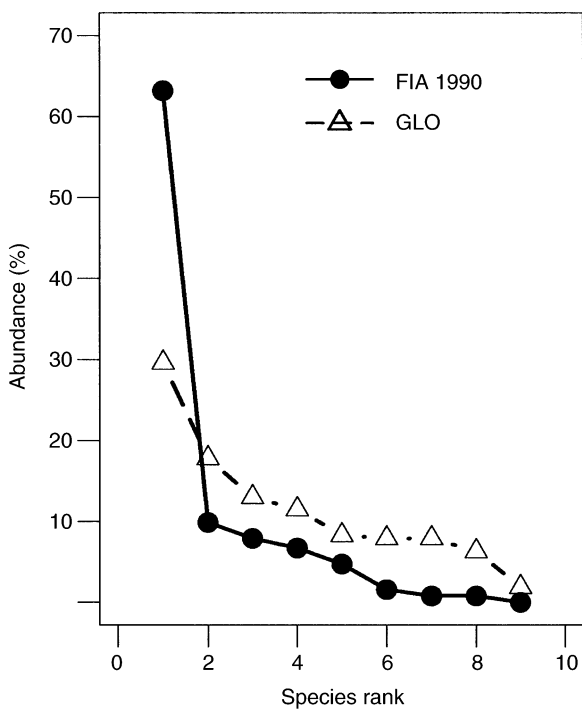


FIG. 7. Dominance–diversity curve (based on percentage of the 100-km² zones dominated by each species in each era) for the nine important species in northeastern Minnesota forests in the presettlement era and 1990. Species are plotted in decreasing order of dominance for each time period. Regional diversity, measured by species dominance patterns in the 253 10-km cells, has declined between the presettlement era and 1990, as dominance patterns have shifted from a relatively even distribution pattern to a substantially more homogeneous landscape dominated by aspen.

Causes of stand conversion from the GLO to the FIA era

Presettlement era fires in this region tended to be large catastrophic stand replacing events (Heinselman 1973, 1996); however they likely did not consume all mature seed producing individuals within the borders of the fire (Carlson 2001). In the presettlement period, those species with postfire adaptations such as serotinous cones (e.g., jack pine) or good germination in burned mineral seed beds (pines and birch) were often the first to occupy burned areas when they were within dispersal distances. Otherwise widely seed-dispersed or sprouting deciduous trees were the first to become established on burned areas, or they all co-occurred. These were replaced by later successional species (such as spruce, fir, and cedar) as the canopy filled and light levels in the understory were reduced (Grigal and Ohmann 1975, Frelich and Reich 1995).

Early intensive harvesting of conifers throughout northeastern Minnesota likely reduced the coverage of the seed producing coniferous overstory, thereby significantly restricting the broadscale spatial potential for regeneration. Intense slash fires also killed much advanced regeneration. The combined effect of the canopy removal, slash fires, and subsequent fire suppres-

sion substantially reduced the potential for pines to retain or regain dominance. Shade-intolerant deciduous species replace the conifers in logged southern boreal systems because species regeneration characteristics provide means for both vegetative and seed-based regeneration (Carleton et al. 1996). In general mechanical harvesting tends to improve sites for faster growing wind dispersed seed species that also have the ability to vegetatively regenerate. Once established, litter from deciduous hardwood species can increase soil nutrient supplies (Reich et al. 2001) and alter soil acidity (P. B. Reich, *unpublished data*) further enhancing a site for subsequent deciduous species cohorts.

Declines in major species

Abundance and spatial distribution patterns of white pine and larch are of particular importance. The decline of white pine has been known for some time and the reasons for it are reasonably well documented (Minnesota Department of Natural Resources 1996), but quantification of the change, especially with a spatial context, has been largely lacking. In this study we show that white pine relative abundance sharply declined from 6% and represented ~1% of the trees inventoried in the 1990 FIA survey. A direct consequence of this decline is the comprehensive loss of the white pine dominated community type in this region. As the primary tree species sought during the logging era in the region it was overharvested. White pine dominance has been lost in this region and the species will likely never regain its former role unless substantial efforts are undertaken. Recent efforts associated with the White Pine Restoration program initiated by the Minnesota Department of Natural Resources and by the U.S. Forest Service may represent the best chance for white pine in the region (Minnesota Department of Natural Resources 1996).

The demise seen in larch is a largely unrecognized consequence of fire suppression, introduction of logging, and other factors including insect stress. Larch was the second most abundant presettlement era species but by 1990 its relative abundance ranked seventh. Why has larch declined so substantially? The explanation is not as clear as for white pine. Larch is naturally decay resistant and was used throughout northeastern Minnesota for mining timbers, railroads, barns, and possibly telegraph poles by the early loggers and settlers in this region. However, speculation suggests that although larch was also a highly sought timber species, numerous, indirect pressures have also contributed to its reduced abundance. The larch sawfly (*Pristiphora erichsonii* Hgt) has been linked regionally to the decimation of larch. Population eruptions were noted from the 1920s onward, which may have resulted in the loss of nearly 1 billion board feet of larch (Minnesota Department of Natural Resources, *unpublished report*). Lack of fire may have also contributed to the loss of larch. Germination occurs on moss, moist mineral or

organic soils, and seed mortality does result from inundation (Fowells 1965). Seed is also prone to fungal attack and mortality due to damping-off. If fire is eliminated from larch dominated sites, thick litter layers of herbaceous understory sedges may restrict regeneration. Airflow over the seed would be restricted resulting in high moisture condition favorable to molds and fungus. Natural fires in these settings may have reduced the thatch layers sufficiently possibly increasing the potential for larch seed to successfully germinate.

Conclusions

This paper documents significant forest community change within and across physiographic regions of the Arrowhead region of Minnesota that is consistent with reports from eastern Ontario (e.g., Carleton and MacLellan 1994). That change occurred in northern Minnesota is not surprising given differing species responses to fire and logging. Substituting logging for fire as the predominant form of disturbance shifts competitive advantage to broad-leaved, shade-intolerant deciduous species. Characterizing the magnitude of change and its spatial dimensions does provide a needed perspective on the extent of the alteration of this forest landscape. The mix of forest types remains the same as in the presettlement era, such that at a stand scale, every modern stand likely has a presettlement analog. However, at the 100-km² scale, there has been a nearly complete replacement in 100 years of the original regional forest communities with new community types having no presettlement analog. Moreover, physiographic zones (~2000–8000 km²) differed compositionally in the presettlement era and experienced parallel changes over time, such that each is different than in the 1880s, but retains differences from other zones, and hypothesized convergence across physiographic zones was not supported. Forest ecologists, conservation biologists, and policy makers, should be aware of and concerned with the implications that these changes represent.

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APPENDIX A

A table showing the General Land Office (GLO) sampling intensity across physiographic zones in the Arrowhead region of Minnesota is available in ESA's Electronic Data Archive: *Ecological Archives* A015-018-A1.

APPENDIX B

Transition matrices for species proportional basal area between the General Land Office (GLO) and Forest Inventory and Analysis (FIA) surveys are available in ESA's Electronic Data Archive: *Ecological Archives* A015-018-A2.