

Post-settlement ecological changes in the forests of the Great Lakes National Parks

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Citation: Paulson, A. K., S. Sanders, J. Kirschbaum, and D. M. Waller. 2016. Post-settlement ecological changes in the forests of the Great Lakes National Parks. *Ecosphere* 7(10):e01490. 10.1002/ecs2.1490

Abstract. National parks of the United States seek to preserve the natural and cultural heritage of the United States, yet parks in the eastern and Midwestern United States were established after periods of human settlement and disturbance. In the Great Lakes region, fire and windfall originally dominated as disturbance agents, driving dynamics in prairies, savannas, and in many forested ecosystems. However, fire suppression over the last century has radically lengthened fire return intervals. Additionally, widespread logging, slash burning, mining, and agricultural settlement successively shifted the dominant forms of land use, greatly altering these forests. From 2008 to 2014, the National Park Service's Great Lakes Inventory and Monitoring Program surveyed vegetation in nine Great Lakes National Parks. We compared these surveys with data derived from the mid- to late-1800s Public Land Survey (PLS) to assess shifts in forest composition. Community composition has changed dramatically since the mid-19th century. Preferred timber species (e.g., *Pinus strobus* and *Tsuga canadensis*) and fire-adapted species (e.g., *Quercus macrocarpa* and *Pinus banksiana*) have declined across the region, while aspen (*Populus* spp.) and/or maple (*Acer* spp.) have consistently increased. Ordinations reveal both these general trends and substantial divergence in composition within particular parks since the PLS. Past logging practices and mesification following fire suppression account for most general trends across the region, while local differences in edaphic conditions, ungulate herbivory, and disturbance regimes account for many park-to-park differences. Understanding how these factors, alone and in combination, have affected forests in these parks provides both a picture of regional forest dynamics and tools that improve our ability to manage these parks. Continuing to monitor forest vegetation in these parks will allow us to test our understanding of forest dynamics and to use these parks as the "land laboratories" that Leopold envisioned.

Key words: fire history; Great Lakes National Parks; Indiana; logging history; long-term change; mesification; mesophication; Michigan; Minnesota; Public Land Survey; Special Feature: Science for Our National Parks' Second Century; Wisconsin.

Received 17 August 2016; accepted 22 August 2016. Corresponding Editor: Debra P. C. Peters.

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INTRODUCTION

There are currently 309,429 protected areas across the world, accounting for 14% of the earth's terrestrial surface (Deguignet et al. 2014). These protected areas vary in their levels of protection,

management goals, and functions (Naughton-Treves et al. 2005). Protected areas protect biodiversity from external threats (Margules and Pressey 2000, Bruner et al. 2001), preserve areas with extraordinary beauty and unique features (Leopold et al. 1963), reduce deforestation and

land-cover change (Andam et al. 2008, Nagendra 2008), and can play a role in poverty reduction (Andam et al. 2010). To maintain these functions and plan for future changes, natural resource managers must first establish their management goals. For example, to prepare for climate change, natural resource managers might set goals to sustain the natural resources found under current climate conditions ("persistence"), or they might adopt a strategy of "directed change" to favor the kinds and distributions of natural resources expected to match future climatic conditions (Fisichelli et al. 2016). Yet, in order to manage for "persistence" or "directed change," managers must understand the ranges of variability that have historically occurred within their protected areas (Keane et al. 2009). These include historically dominant disturbance regimes and the major land-use changes that have occurred within these areas (Foster et al. 2003). Understanding these legacies and current trajectories of change enhances our understanding of the ecological context of natural areas and thus our ability to manage them wisely.

In the United States, the National Park Service (NPS) is tasked with managing a system of 413 national park units (i.e., national monuments, national lakeshores, hereafter "national parks," <https://www.nps.gov/aboutus/faqs.htm>). These national parks protect a range of natural, cultural, and historic landmarks. The NPS Organic Act of 1916 tasked the agency with preserving these resources "unimpaired for future generations." Yet, as the NPS celebrates its 2016 centennial, there is growing recognition that national parks are part of dynamic ecosystems (e.g., Janzen 1983, Hansen and DeFries 2007) and that parks are "coupled natural-human systems" (Knowles et al. 2012). Further, extensive changes in land use and cover occurred across North America before the United States established its national parks, particularly in the east and Midwest. These disturbances greatly modified the trajectories of ecological change in what would become the national parks. While there are several region-wide assessments of change since presettlement times in the upper Midwest of the United States (e.g., Friedman and Reich 2005, Schulte et al. 2007), there are few park-level assessments of change (e.g., Janke et al. 1978 at Isle Royale NP), complicating our efforts to establish a baseline

with which to guide current management of the national parks.

To help us understand current ecological conditions and how they differ from those that historically dominated, ecologists use both paleoecology and historical records. For instance, fire scars, pollen cores, and charcoal records reveal the dynamic mosaic of prairies, savannas, wetlands, and forests that once covered the upper Midwest of the United States (Loope 1991, Anderson 1998, Davis et al. 2000, Hotchkiss et al. 2007). Here, dominant disturbance processes changed radically following European settlement, causing profound changes in land cover and vegetation dynamics. As European settlement spread westward, the upper Midwest experienced a logging boom in the late 19th and early 20th centuries (Fritz 1986, Alverson et al. 1994). The harvesting of selected species, accompanied by the need to clear land for agriculture, drastically altered Midwestern landscapes, including the lands that are now national parks (Beals and Cottam 1960, Fritz 1986, Judziewicz and Koch 1993). For a brief period following European settlement in the Great Lakes region, this extensive logging and the associated slash fires led to an increased fire frequency (White and Host 2008). Widespread fire suppression, however, began by the early 1900s and extended through most of the region during the 20th century. This fire suppression led to fire return intervals orders of magnitude longer than before European settlement (Frelich and Lorimer 1991, Cleland et al. 2004, Guyette et al. 2006). Fire suppression threatens the diversity and persistence of prairies, savannas, and fire-dependent forested ecosystems across the region (Heinselman 1973, Abrams 1992, Leach and Givnish 1999, Li and Waller 2015, Alstad et al. 2016). In addition to shifting primary disturbance regimes, European settlement brought great declines in the populations of predators and ungulates like American bison, moose, elk, and white-tailed deer. After going almost extinct in many parts of the region, deer then increased greatly through much of the 20th century (Alverson et al. 1988, Craven and Van Deelen 2008, Wydeven and Pils 2008) with cascading effects on many other species (Rooney and Waller 2003, Côté et al. 2004, Waller 2008, McShea 2012).

These widespread changes in disturbance regimes and animal populations precipitated broad shifts in the structure and composition

Table 1. Common and Latin species names and authorities used in this study.

Taxonomic group	Latin name with authority	Common name
Trees	<i>Abies balsamea</i> (L.) Mill	Balsam fir
	<i>Acer negundo</i> L.	Box elder
	<i>Acer pensylvanicum</i> L.	Striped maple
	<i>Acer rubrum</i> L.	Red maple
	<i>Acer saccharinum</i> L.	Silver maple
	<i>Acer saccharum</i> Marsh.	Sugar maple
	<i>Acer spicatum</i> Lam.	Mountain maple
	<i>Betula alleghaniensis</i> Britton	Yellow birch
	<i>Betula papyrifera</i> Marshall	Paper birch
	<i>Fagus grandifolia</i> Ehrh.	American beech
	<i>Larix laricina</i> (Du Roi) K. Koch	Tamarack
	<i>Pinus banksiana</i> Lamb.	Jack pine
	<i>Pinus resinosa</i> Aiton	Red pine
	<i>Pinus strobus</i> L.	White pine
	<i>Populus balsamifera</i> L.	Balsam poplar
	<i>Populus deltoides</i> W. Bartram ex Marshall	Cottonwood
	<i>Populus grandidentata</i> Michx.	Bigtooth aspen
	<i>Populus tremuloides</i> Michx.	Trembling aspen
	<i>Quercus alba</i> L.	White oak
	<i>Quercus macrocarpa</i> Michx.	Bur oak
	<i>Quercus rubra</i> L.	Red oak
	<i>Quercus velutina</i> Lam.	Black oak
	<i>Thuja canadensis</i> L.	White cedar
	<i>Tilia americana</i> L.	Basswood
	<i>Tsuga canadensis</i> (L.) Carrière	Hemlock
Mammals	<i>Ulmus</i> sp. L.	Elm
	<i>Alces alces</i> L.	Moose
	<i>Bison bison</i> L.	American bison
	<i>Cervus elaphus canadensis</i> Exleben	Elk
Insects and disease	<i>Odocoileus virginianus</i> Zimmermann	White-tailed deer
	<i>Agrilus planipennis</i> Fairmaire	Emerald ash borer
	<i>Ophiostoma</i> spp. Syd. and P. Syd.	Dutch elm
	<i>Pristiphora erichsonii</i> Hartig	Larch sawfly

of forests in the Great Lakes region (Frelich and Lorimer 1985, Friedman and Reich 2005, Schulte et al. 2007). Oak savannas became closed forests (Leach and Givnish 1999, Rogers et al. 2008). Areas once dominated by hemlock began to shift toward sugar maple dominance (Frelich and Lorimer 1985, White and Mladenoff 1994, Schulte et al. 2007; see Table 1 for Latin species names and authorities). Aspen and maple now dominate much of the region (Schulte et al. 2007). The former landscape mosaic of disturbance patches of varied sizes and ages has disappeared, leaving behind a simpler system dominated by smaller, but often more intensive, patches of disturbance (Frelich and Lorimer 1991, Frelich 1995, White and Host 2008). The region has also experienced widespread mesification (or “mesophication”: Nowacki and Abrams 2008, Hanberry et al.

2012), increasing the homogeneity of forest structure and composition (Amatangelo et al. 2011, Johnson et al. 2013, Li and Waller 2015).

To assess the nature and extent of ecological change in the national parks of the upper Midwest requires both historical baseline data and contemporary data to compare with that baseline. One such baseline is the Public Land Survey (PLS), which was conducted just before European settlement in the region. The PLS grid was laid out by surveyors who recorded tree sizes and species, along with lakes, rivers, and other natural features (Stewart 1935, Schulte and Mladenoff 2001). These data have already been used to assess changes in ecological conditions across the region (e.g., Friedman and Reich 2005, Schulte et al. 2007, Fahey 2014). Despite numerous limitations and biases (Bourdo 1956, Bouldin 2008), the PLS data



Fig. 1. National park units of the Great Lakes Inventory and Monitoring Network. Abbreviations as in Table 2.

provide a valuable and unique record of forest vegetation in the mid- to late-1800s that is useful for comparisons with contemporary survey data.

In this study, we compare historical data from the PLS with contemporary data collected by the NPS's Inventory and Monitoring (I&M) Program. This program provides vital information about the state of natural resources within national parks. In the Great Lakes region, the Great Lakes I&M Network (or GLKN) monitors forest composition and conditions via detailed vegetation surveys at nine national parks (Fig. 1, Table 2). Comparing these modern data with historical data from the PLS records provides a valuable picture of long-term change, helping us to understand how park vegetation is affected by varying forces occurring both inside and outside park boundaries.

Our primary goal was to characterize the nature and extent of ecological change within and

among the national parks in the Great Lakes region since the 19th century. To assess changes in forest composition, we compared data on the identity and size of overstory trees between the 1800s PLS and the 2000s era GLKN surveys. We sought answers to three particular questions:

1. How has the tree composition of forests in these national parks changed?
2. Do parks show similar patterns of change?
3. What factors might cause the general trends or differences that we observe among parks?

Our particular interests are to document how closely the changes in the national parks parallel regional changes and to understand the special role that disturbances play in sustaining the structure and diversity of forests in these parks.

Table 2. Details of PLS and GLKN sampling in the national park units of the Great Lakes Inventory and Monitoring Network.

Park	Year est.	Forested area (ha)	PLS survey year	PLS corner count (no. of trees)	GLKN survey year	GLKN plot count (no. of trees)
Apostle Islands NL	1970	16,912	1852–1857	353 (720)	2011	48 (1878)
Grand Portage NM	1958	259	1892–1893	53 (136)	2014	23 (671)
Indiana Dunes NL	1966	5542	1829–1834	64 (122)	2012	50 (1240)
Isle Royale NP	1940	49,468	1847–1848	1015 (1947)	2010	52 (2794)
Mississippi NRRRA	1988	4802	1847–1853	187 (408)	2011	33(726)
Pictured Rocks NL	1966	27,538	1841–1855	377 (744)	2009	59 (2404)
St. Croix NSR	1968	19,097	1847–1864	628 (1230)	2013	50 (1467)
Sleeping Bear Dunes NL	1970	27,242	1838–1853	317 (619)	2009	50 (1784)
Voyageurs NP	1975	50,171	1881–1892	615 (1563)	2008	38 (2058)

Notes: The tree number refers to the number of trees above the diameter at breast height cutoff used in this study; see *Treatment of the PLS and GLKN data* for details.

PLS, Public Land Survey; GLKN, Great Lakes I&M Network; NL, National Lakeshore; NM, National Monument; NP, National Park; NRRRA, National River and Recreation Area; NSR, National Scenic Riverway; est., established.

METHODS

Study areas

Our work focused on the nine national parks included within the GLKN in the upper Midwest of the United States (Fig. 1, Table 2). Forests in these parks generally reflect the dominant forest type of the region where they occur. Parks to the northwest are dominated by boreal forest (Grand Portage, Isle Royale, Voyageurs). Park forests in northern Wisconsin and the Upper Peninsula of Michigan reflect both northern hardwoods (Apostle Islands, Pictured Rocks) and, to the east, beech-maple forest (Sleeping Bear Dunes, Pictured Rocks). More southerly parks include upland oak forests and riparian lowlands (Mississippi, Saint Croix) or oak savanna (Indiana Dunes). Three parks include large islands (Apostle Islands, Isle Royale, and Sleeping Bear Dunes), while two include a sizable urban interface (Indiana Dunes and Mississippi). Five parks include designated or proposed wilderness areas (Apostle Islands, Isle Royale, Pictured Rocks, Sleeping Bear Dunes, and Voyageurs). All nine parks include significant aquatic resources in the form of large rivers (Mississippi and Saint Croix), large inland lakes (Voyageurs), and being situated directly on or in a Great Lake (the other six). Swamps, bogs, fens, ephemeral pools, and floodplains occur commonly throughout the network. Lakes Superior and Michigan moderate climate conditions at many of these parks (Apostle Islands, Grand Portage, Indiana Dunes, Isle

Royale, Pictured Rocks, and Sleeping Bear Dunes) by producing cooler summers and warmer winters than inland areas.

Public Land Survey data

The PLS was conducted throughout the 19th century to delineate U.S. territories for sale and settlement purposes (Stewart 1935, Schulte and Mladenoff 2001). The areas that now compose the GLKN national parks were surveyed between 1838 and 1892 (Table 2). PLS surveyors demarcated the land using a system of 36-mi² townships (93.2 km², 9.7 km per side) divided into 36 sections (1 mile or 1.6 km per side, 2.6 km²). Surveyors walking along section lines marked one to four witness trees at each section corner, quarter corner (mid-way between section corners), and meander corner (where survey lines intersected features such as lakes, rivers, or ecosystem boundaries). For each witness tree, surveyors recorded the species, diameter at breast height (dbh), and distance and bearing from the corner (Stewart 1935, Schulte and Mladenoff 2001). Despite the biases inherent in the PLS (Bourdo 1956, Manies et al. 2001, Bouldin 2008), the PLS data provide the best available spatially explicit record of tree cover at the time of widespread European settlement in the region (Liu et al. 2011).

We obtained digitized PLS data for Voyageurs, Mississippi, and portions of Saint Croix from the Minnesota Geospatial Commons (<https://gisdata.mn.gov/dataset/biota-original-pls-bear>

ing-trees, Almendinger 1996, U.S. Surveyor General 1847–1908). We obtained similar data for Apostle Islands and portions of Saint Croix from the Wisconsin Department of Natural Resources. Data for Sleeping Bear Dunes, Pictured Rocks, and Isle Royale came from the US Forest Service, while Notre Dame University provided data for Indiana Dunes. We extracted PLS points within the boundary of each park from these data sets. Because PLS data for Grand Portage National Monument were not previously digitized, we used ArcGIS Desktop 10.1 (Environmental Systems Research Institute, Redlands, California, USA) to digitize the section and quarter corner records from scanned images of the original PLS notebooks for this park (Bureau of Land Management, <http://www.glore.cords.blm.gov/default.aspx>).

Great Lakes Inventory and Monitoring Program data

GLKN staff sampled 403 vegetation monitoring plots (23–59 per park) between 2008 and 2014. All plots were located in areas with $\geq 10\%$ forest cover, and plot locations were selected using a generalized random-tessellation stratified design to ensure that sites were both randomly located and spatially balanced within each park (Stevens and Olsen 2004). The GLKN used the hybrid plot design (Johnson et al. 2008) to record all trees greater than or equal to 2.5 cm dbh present in each of three parallel 50×6 m belt transects ($900 \text{ m}^2/\text{plot}$). Surveyors recorded the dbh, species, and live/dead status for each tree. For the details of GLKN sampling methods, see Sanders and Grochowski (2014a, b). Taxonomic identification of the GLKN data followed the Integrated Taxonomic Information System (ITIS 2015).

Treatment of the PLS and GLKN data

The PLS and GLKN data sets differ in their purpose, sampling design, taxonomic resolution, and level of detail. As PLS surveyors walked section lines, they noted trees at regular intervals with little interest in collecting accurate ecological data. They identified just one to four trees at each survey point and only recorded common names for these trees. Thus, we are often uncertain about the exact species identity of these trees. For example, within the Apostle Islands, surveyor's records of "maple" could reflect either *Acer saccharum* or *A. rubrum*. To make the PLS and GLKN data comparable, we pooled several

species to either the genus or subgenus level (e.g., "red oak group") in both the PLS (Appendix S1: Table S1) and GLKN (Appendix S1: Table S2) data sets.

The PLS data may also be biased in that surveyors avoided marking small corner trees (Bourdo 1956). To account for this undersampling, we examined the size distribution of PLS trees for each park to determine the size threshold below which few trees were measured. This method produced cutoffs of 10.2 cm dbh for Isle Royale and Voyageurs national parks and 15.2 cm dbh for other parks. We removed all trees smaller than these cutoffs from both the PLS and GLKN data sets prior to further analysis. The PLS surveyors may have also avoided senescent trees, causing them to undersample large trees. We did not attempt to compensate for this, as modern forests in the region are mostly second growth with trees that are smaller than any very large trees the PLS surveyors may have avoided. The contemporary GLKN data reflect fewer survey points but higher sampling intensity at each site (mean = 37 trees per plot above our dbh cutoff), equivalent to the number of trees identified at 10–20 section corners.

Analyses of forest change

To assess changes in the overstory of forests within these parks, we calculated the changes in relative basal area (RBA) for each taxon between the PLS and GLKN surveys. Relative basal area (also referred to as relative dominance) estimates a species' proportional dominance within a stand (Cottam and Curtis 1956). It is calculated as the basal area (BA) of a single species divided by the total basal area of all species. We used relative rather than absolute basal area, because absolute basal area responds to local edaphic conditions and/or the time since last disturbance. Additionally, RBA allows us to compare data from surveys completed using different sampling schemes. For each survey period, we calculated the RBA of each taxon at two spatial scales: the park and plot levels. Park-level RBA calculations included all trees surveyed within the park boundary during a given survey period. However, no PLS corners fell within Grand Portage's narrow boundary. We therefore included all PLS corners within 1.6 km of this park's boundary for park-level analyses. Several

taxa represented less than 2% of the total basal area during both survey periods. We pooled these taxa into a single category ("Other spp."), which we analyzed as a single group. The species composition and pooled basal area of this "other" category varied among parks.

To assess the spatial variation in forest composition within parks, we also conducted plot-level analyses. For these, we identified all PLS witness trees within 1.6 km of GLKN plots and excluded any GLKN points with fewer than four PLS witness trees within this buffer. The number of PLS trees within this buffer ranged from 4 to 39, with an average of 19 PLS trees per 1.6-km buffer. We calculated the RBA for this subset of PLS trees and compared this with the RBA of the GLKN trees surveyed at that sample plot. To visually assess changes in forest composition at this plot level, we performed multivariate ordinations and developed maps that indicate the species with the highest RBA at each plot.

We used nonmetric multidimensional scaling (NMDS, McCune and Grace 2002) to visualize the differences in forest composition (via RBA) at both the plot and park level. To minimize possible artifacts or distortion introduced by including rare species, we removed species with a summed RBA of less than 5% across all plots and time periods prior to analysis. We then used the square-root and Wisconsin transformations (Oksanen et al. 2015) to standardize the plot-level RBA within all sites. We calculated the Bray–Curtis distances among all pairs of sites, creating the distance matrix used in the NMDS analyses. A scree plot of the stress versus the number of ordination dimensions within each park revealed that three dimensions captured most of the variation. We used multiple random starting configurations for each park to ensure that we had a stable solution. To examine changes through time, we drew vectors connecting the PLS and GLKN points for each plot or park. At the plot level, we drew ellipses to reflect the standard deviation of plot scores within each time period. We then calculated the correlations between the RBA for each common species and the ordination axes, and plot these as vectors on the ordination graphs. At Pictured Rocks, all plots clustered together in the initial ordination, due to a plot that consisted of 100% jack pine

basal area. To better visualize the differences among the remaining plots in Pictured Rocks, we removed this outlier.

We conducted all analyses in R version 3.2.2 (R Core Team 2015). To conduct the spatial analyses, we used the packages *rgdal* (Bivand et al. 2015), *sp* (Bivand et al. 2013), and *rgeos* (Bivand and Rundel 2015). We used the package *vegan* (Oksanen et al. 2015) for NMDS analyses. We used *ggplot2* (Wickham 2009), *maptools* (Bivand and Lewin-Koh 2016), and *gridExtra* (Auguie 2015) to produce the maps and figures.

RESULTS

Changes in overall community composition

Our first question focused on how national park forests have changed over time. We observed shifts in the relative tree basal area that reveal both the broad patterns of forest change common to most of these nine parks, and local changes within particular parks (Fig. 2 and Appendix S2: Figs. S1–S3). Aspen and maple increased at six parks each, reflecting the broad shifts that were also observed across the region during the same time period (e.g., Friedman and Reich 2005, Schulte et al. 2007). In contrast, fire-dependent species like jack pine, red pine, and bur oak have declined, as have species favored by the timber industry during the logging boom (such as white pine and eastern hemlock).

The ordinations also reveal large and sometimes contrasting changes in community composition between the PLS and GLKN surveys within and across parks (Figs. 3–5). Within parks, these shifts in community composition are so strong that modern forests show little overlap with historical forest composition (Figs. 3–5). These within-park ordinations also show that seven of nine parks have diverged in community composition since the 19th century. That is, with the exceptions of Grand Portage and Voyageurs, points reflecting the modern surveys cluster less tightly than those representing historical forest composition at these parks (Figs. 3–5). In the combined analysis across all parks, we see that most parks are shifting in a similar direction, with forest communities in six of the nine parks converging toward greater similarity (Fig. 5; exceptions: Grand Portage, Indiana Dunes, and Mississippi).

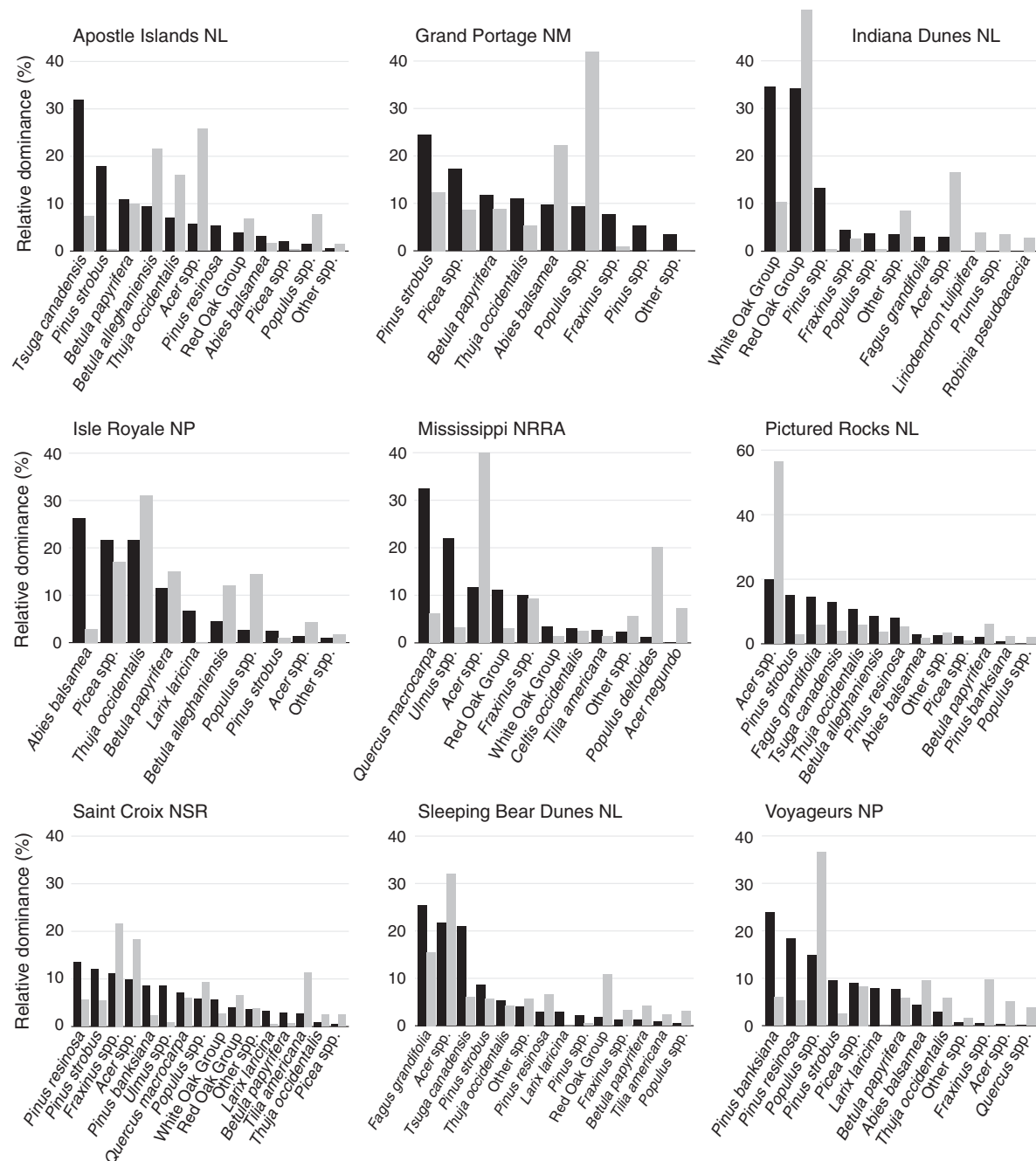


Fig. 2. Park-level relative basal area of key overstory taxa during the Public Land Survey (black bars) and Great Lakes I&M Network survey (gray bars). The y-axis is on the same scale for all parks except Pictured Rocks. Abbreviations as in Table 2.

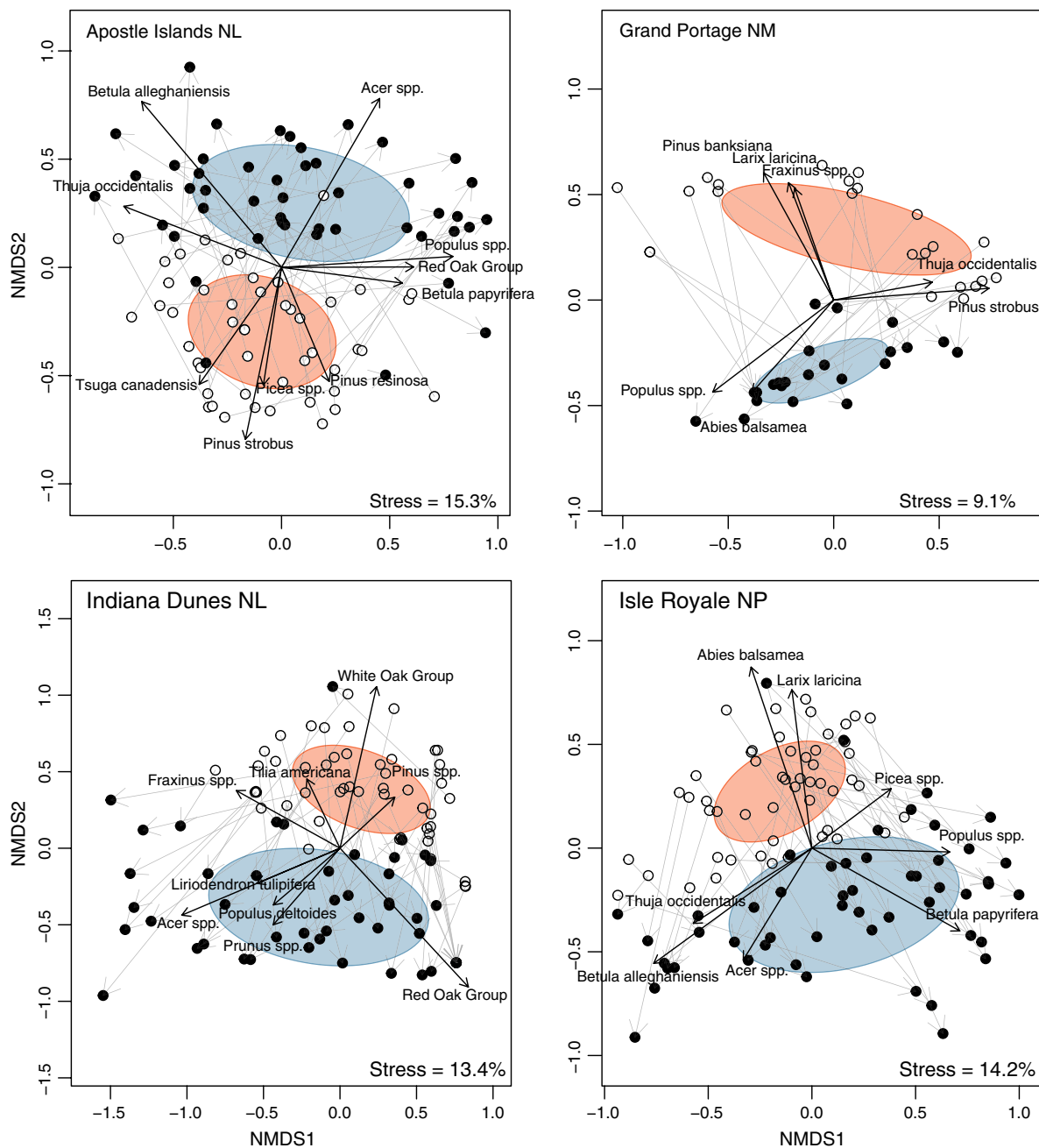


Fig. 3. Plot-level nonmetric multidimensional scaling (NMDS) results: Open circles represent Public Land Survey (PLS) plots; closed circles represent Great Lakes I&M Network (GLKN) plots; gray arrows indicate the change at each individual plot between the PLS and GLKN surveys; ellipses indicate the standard deviation of plot scores at each time period (red = PLS, blue = GLKN); black arrows indicate the direction and strength of correlation between species relative basal area and NMDS ordination axes. Abbreviations as in Table 2.

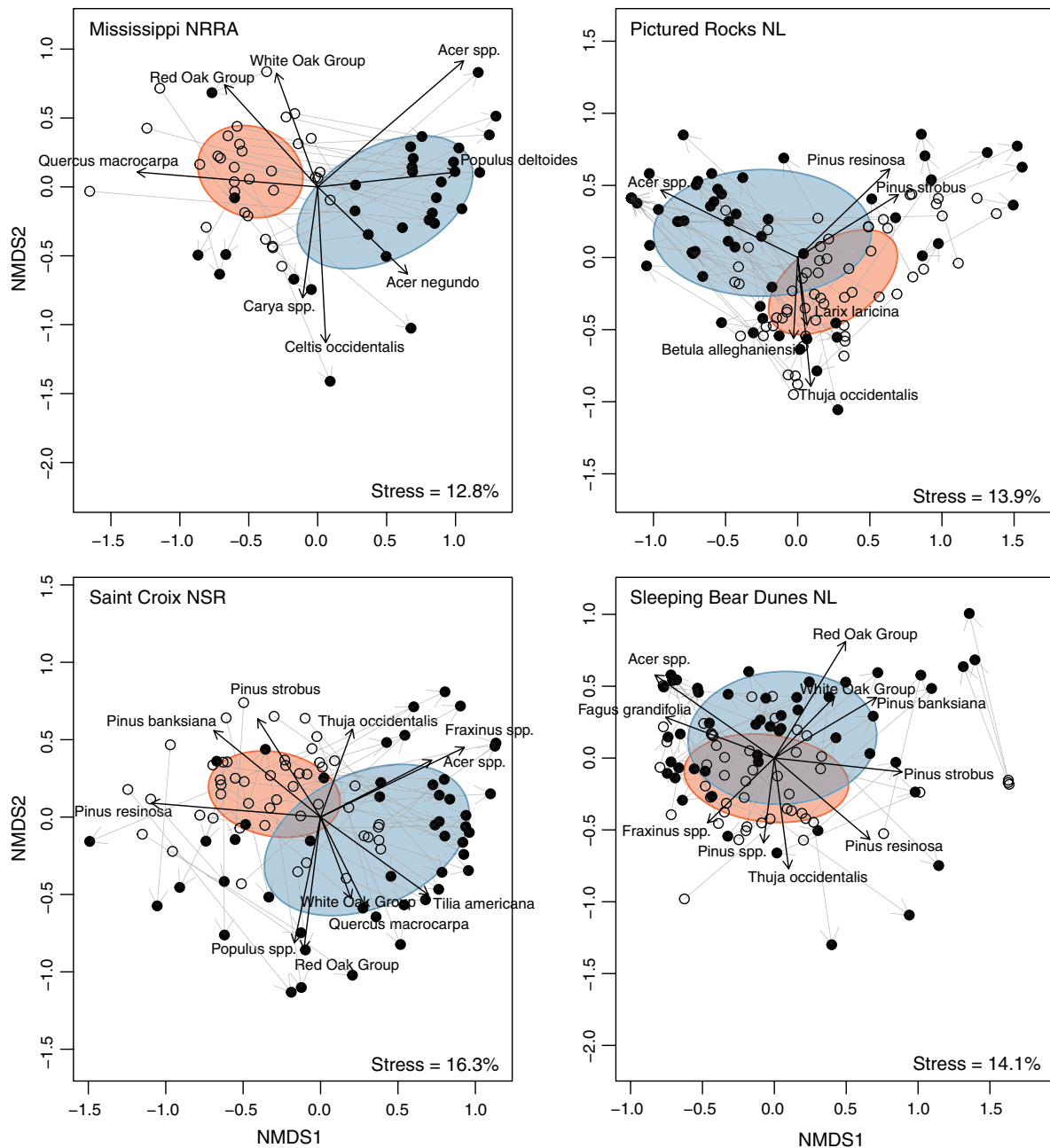


Fig. 4. Plot-level nonmetric multidimensional scaling (NMDS) results: Open circles represent Public Land Survey (PLS) plots; closed circles represent Great Lakes I&M Network (or GLKN) plots; gray arrows indicate the change at each individual plot between the PLS and GLKN surveys; ellipses indicate the standard deviation of plot scores at each time period (red = PLS, blue = GLKN); black arrows indicate the direction and strength of correlation between species relative basal area and NMDS ordination axes. Abbreviations as in Table 2.

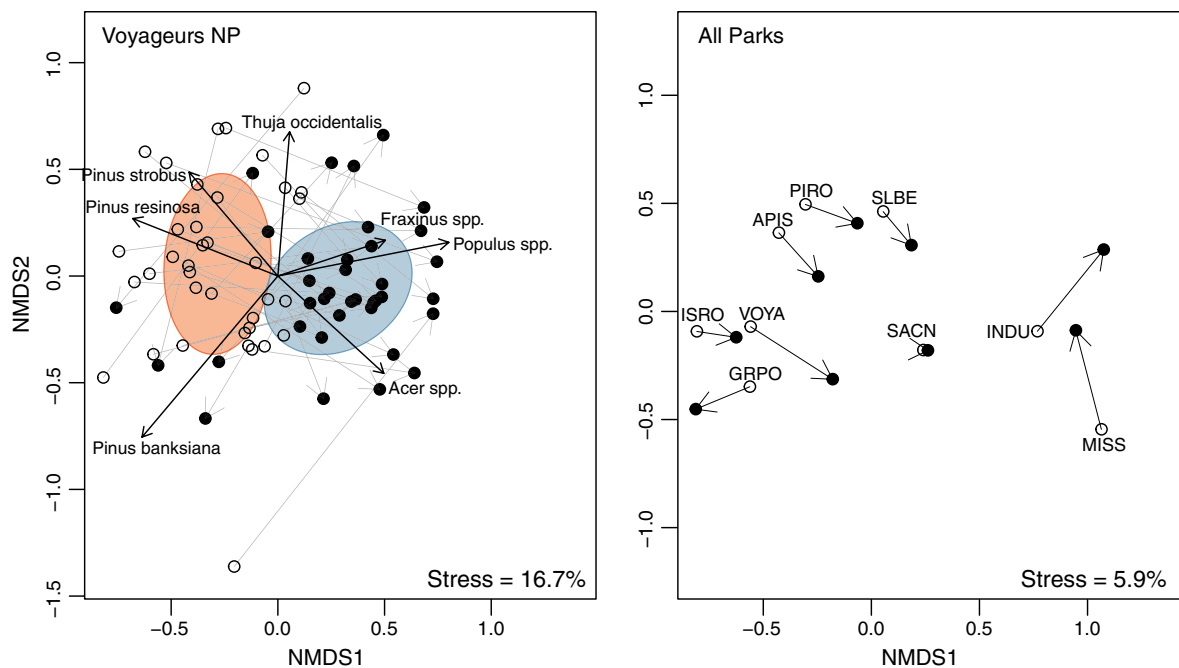


Fig. 5. Plot-level (Voyageurs NP) and park-level (all parks) nonmetric multidimensional scaling (NMDS) results: Open circles represent Public Land Survey (PLS) plots; closed circles represent Great Lakes I&M Network (GLKN) plots. For Voyageurs NP, gray arrows indicate the change at each individual plot between the PLS and GLKN surveys; ellipses indicate the standard deviation of plot scores at each time period (red = PLS, blue = GLKN); black arrows indicate the direction and strength of correlation between species relative basal area and NMDS ordination axes. For All Parks, black arrows indicate the change at each individual plot between the PLS and GLKN surveys. Abbreviations as in Table 2.

Increasing species

Species of the *Acer* genus increased across all parks where they were present, especially in areas with large components of northern hardwood and eastern deciduous forest types. Maples now represent more than 25% of the RBA at four parks: Apostle Islands (26%; Fig. 2), Mississippi (40%; Fig. 2), Pictured Rocks (56%; Fig. 2), and Sleeping Bear Dunes (32%; Fig. 2). Maples also increased in relative dominance at Indiana Dunes (by 14%; Fig. 2), Saint Croix (by 8%; Fig. 2), Voyageurs (by 5%; Fig. 2), and Isle Royale (by 3%; Fig. 2).

Although we were limited to evaluating the changes across all *Acer* taxa due to the coarse-scale taxonomy of the PLS, we can compare the modern abundance of different *Acer* taxa using the GLKN surveys. We identified six *Acer* taxa in the GLKN surveys: sugar maple, red maple, box elder, mountain maple, silver maple, and striped maple (Appendix S2: Fig. S4). At both Pictured Rocks and Sleeping Bear Dunes, sugar

maple composed the majority of maple RBA (43% and 25%, respectively), with smaller components of red maple at each park (12% and 6%, respectively). Many of the plots that transitioned to maple dominance during the GLKN surveys were formerly dominated by white pine, yellow birch, white cedar, or beech (Appendix S2: Fig. S2—Pictured Rocks NL; and Fig. S3—Sleeping Bear Dunes NL), demonstrating that edaphic conditions already favored these mesic species. At Apostle Islands, both red maple (15%) and sugar maple (11%) are important components of the modern forests. Here, plots now dominated by maples transitioned from hemlock, northern white cedar, and other types. Silver maple, a floodplain species, accounts for 40% of the maple RBA at Mississippi, and box elder accounts for an additional 7% RBA. Many of the sites where silver maple is now common were formerly dominated by elm (Appendix S2: Fig. S2). At Saint Croix, silver maple represents 10% of the maple

RBA (Appendix S2: Fig. S4), and sites shifting to maple were formerly aspen, ash, white oak, red oak, and white pine (Appendix S2: Fig. S3). At Indiana Dunes, maple became dominant at several inland plots that were formerly dominated by white oak (Appendix S2: Fig. S1). Red maple and sugar maple now account for most of the maple RBA at Indiana Dunes (11% and 4%, respectively; Appendix S2: Fig. S4).

Aspen increased in RBA across several parks and is now the most dominant species at Grand Portage and Voyageurs. Increases in aspen were especially apparent in areas formerly dominated by pines and in the three parks with high proportions of boreal forest (Voyageurs, Grand Portage, and Isle Royale). Aspen was already among the most dominant species at Voyageurs during the PLS, representing 15% of the RBA. Since then, it increased by 22% to become by far the most dominant species at the park (Fig. 2). At Grand Portage, PLS surveyors' notes indicate that many section lines were dominated by dense aspen and birch of 10–15 yr in age and that several areas showed evidence of past fires and wind-fall. Aspen now dominates the forests at Grand Portage (42%; Fig. 2). Aspen was present in low levels at both Apostle Islands and Isle Royale during the PLS (1.6% and 2.8%, respectively; Fig. 2) and has increased there, too, but not to the point of dominance (now 8% and 15%, respectively). Aspen RBA often increased in areas where fires occurred during the 1930s and 1940s. For instance, aspen is now the most dominant species at several plots on Oak Island where severe fires in the 1940s burned 80% of the island (Appendix S2: Fig. S1; Judziewicz and Koch 1993). A similar stand-replacing fire burned much of Isle Royale during 1936 (Hansen et al. 1973), again favoring aspen dominance in those formerly burned areas (Appendix S2: Fig. S2; Janke et al. 1978).

No other taxa increased as pervasively across all parks as maple and aspen, but several taxa increased at individual parks. At Mississippi, cottonwood increased by 19% between the two survey periods (Fig. 2). The GLKN surveys found little recent regeneration of cottonwood, with most individuals greater than 35 cm dbh, and none below 15 cm dbh, yet cottonwood now accounts for 20% of the basal area in the park. At Saint Croix, basswood increased by 9% (Fig. 2). At Indiana Dunes, species of the red oak group

(primarily black oak) are most dominant and have increased 17% above presettlement levels to now reflect 51% of the basal area (Fig. 2). The red oak group also increased in RBA at Sleeping Bear Dunes (by 9%; Fig. 2), but decreased at Mississippi (by 8%; Fig. 2). Ash RBA increased at both Saint Croix (11%; Fig. 2) and Voyageurs (9%; Fig. 2), but declined by 7% at Grand Portage (Fig. 2).

Decreasing species

Pines were among the most dominant species at six of the nine GLKN parks during the PLS, but have declined by 13–38% in RBA across these parks (Fig. 2). Pines declined the most at Voyageurs (38%), then the Apostle Islands (23%), Saint Croix (22%), Grand Portage (19%), Pictured Rocks (14%), and Indiana Dunes (13%). Declines in white pine drove these trends at most parks, although losses of red and jack pine were also high at Saint Croix and Voyageurs.

Hemlocks have also declined greatly, both regionally (Kurtz et al. 2015) and in these parks. In the 19th century, hemlock was a codominant tree at the three parks dominated by northern hardwood forests. Modern GLKN surveys demonstrate that hemlock declined at each of these parks, by 24% at Apostle Islands, 15% at Sleeping Bear Dunes, and 9% at Pictured Rocks (Fig. 2). Maple, cedar, or aspen have assumed dominance at many of the sites formerly dominated by hemlock (Appendix S2: Figs. S1–S3). We also found declines in species of the white oak group at Indiana Dunes and Mississippi (by 24% and 28%, respectively; Fig. 2). White oak species were not differentiated at Indiana Dunes by PLS surveyors, but the decline in the white oak group at Mississippi primarily reflects the loss of bur oak. Elms also declined at both Mississippi (by 19%; Fig. 2) and Saint Croix (by 8%; Fig. 2) as they have in riparian areas across much of Wisconsin (Johnson and Waller 2013).

Local shifts in abundance

Balsam fir, yellow birch, and northern white cedar showed divergent patterns of change on island versus mainland parks. Balsam fir dominated forests at Isle Royale in the PLS (at 26% RBA), but has since declined to just 3% RBA (Fig. 2). The recent GLKN surveys show that dense, small-diameter balsam fir are prevalent

on the northeast side of the island, but most individuals are below the 10.2-cm dbh cutoff used in this study. In contrast, balsam fir increased at Grand Portage (by 13%; Fig. 2) and at Voyageurs (by 5%; Fig. 2). Yellow birch increased at our two island parks: Apostle Islands and Isle Royale (by 12% and 7%, respectively), but declined by 5% at Pictured Rocks. Similarly, cedar increased by 9% at both Apostle Islands and Isle Royale, but declined at Pictured Rocks (by 5%) and Grand Portage (by 6%).

DISCUSSION

General trends and probable causes

Forests in these nine Great Lakes National Parks changed greatly since the mid-19th century in response to major shifts in the dominant modes, frequencies, and intensities of disturbance. These changes occurred faster than any others observed over the past 2500 years (Cole 1995). We observed marked declines in fire-dependent oak and pine species, as well as the white pines and eastern hemlocks favored by early loggers. Following logging and slash fires, aspen quickly regenerated, coming to dominate many landscapes. Ensuing succession, combined with efforts to suppress fires, favored mid- to late-successional species, especially maples, as most forests became shadier and more mesic. Aspen and maple are now the most dominant species at six of the nine GLKN national parks and are among the most dominant species at the three remaining parks. These changes generally mirror those that occurred in the broader Great Lakes region over the same time interval (e.g., Friedman and Reich 2005, Schulte et al. 2007, Rhemtulla et al. 2009, Fahey 2014). Even studies extending across the northeastern United States tell similar stories (e.g., Thompson et al. 2013).

We expect early-successional species to thrive after major disturbances, and no recent disturbances in our region were as extensive or extreme as the great cutover that preceded the creation of these parks (Alverson et al. 1994). The most emblematic early-successional species in our region is trembling aspen (Cleland et al. 2001), which was the primary component of the aspen group defined in this study. Trembling aspen is now pervasive across the upper Midwest, especially in areas formerly dominated by pines

(Friedman and Reich 2005). We found that aspen RBA increased across six parks, especially in areas where extensive slash burning or intense natural fires took place. For instance, most of Grand Portage burned during the late 19th century, due to large fires set by humans and fueled by logging slash and drought conditions (White and Host 2003). The early-successional aspen that established following these fires at Grand Portage now exist as mature individual trees surrounded by numerous standing dead and fallen individuals (Sanders and Kirschbaum 2015b).

Ongoing succession and fire suppression led to a dramatic increase in maples at six of the nine parks. Sugar maple and red maple now dominate many forests at Apostle Islands, Indiana Dunes, Pictured Rocks, and Sleeping Bear Dunes (Fig. 2; Appendix S2: Figs. S1–S4). The patterns we observed in the GLKN parks indicate that the edaphic conditions that supported fire-dependent species can also support mesic maples. In fact, maples are associated with widespread patterns of mesification (Nowacki and Abrams 2008, Hanberry et al. 2012). For example, red maple often establishes under dry-mesic conditions with moderate light, but then casts shade, increasing humidity and soil moisture (Kreye et al. 2013). Its leaves also decompose quicker than fire-tolerant oaks and pines, accelerating nitrogen cycling (Alexander and Arthur 2010). These changes, in turn, favor more shade-tolerant and nutrient-demanding species.

Silver maple has increased appreciably at low-land sites in the riparian national parks (Mississippi and Saint Croix). Silver maple is notably flood tolerant, allowing it to tolerate increases in flooding frequency or duration, as well as the wetter conditions in many floodplain areas above dams (Johnson and Waller 2013). Its increases could also reflect the fact that many of the sites it now occupies along the Mississippi were formerly dominated by elm populations that were largely wiped out by Dutch elm disease in the 1960s and 1970s. However, at Saint Croix, silver maple now dominates at sites formerly occupied by aspen, ash, white oak, red oak, or white pine, suggesting that succession and mesification also contributed to its increases there. We also found a 7% increase in box elder RBA at Mississippi, similar to that found throughout the Driftless Area of the Midwest (Knott et al. 2015).

The tree taxa that declined broadly across these parks also reflect shifts in dominant disturbance regimes. For example, fire-obligate species such as jack pine and red pine, as well as many oaks at the southerly parks, all declined. Similarly, declines in the basal area of eastern hemlock and white pine surely reflect the logging that targeted those species in our area. The subsequent regeneration failure of hemlock at most sites across the region may be related to increases in the abundance of white-tailed deer in the mid- and late 20th century (Leopold et al. 1947, Swift 1948). Northern white cedar has also declined and failed to regenerate in apparent response to heavy browsing by white-tailed deer (Rooney et al. 2002, Forester et al. 2008, Zenner and Almendinger 2012, Bradshaw and Waller 2016). Despite these regionwide declines in cedar, we observed a 9% increase in cedar RBA at both Apostle Islands and Isle Royale. In the Apostles, deer are effectively absent on 11 of the park's 21 islands, but dense in the mainland unit and four of the other 10 islands (Apostle Islands National Lakeshore 2014). Only one of the seven sites now dominated by cedar occurs in an area of high deer density (the mainland unit). Sites transitioning to cedar were formerly dominated by hemlock, white pine, and balsam fir. Their transition to cedar, rather than sugar maple, may reflect edaphic factors such as wet or acidic soils.

While deer are absent on Isle Royale, moose colonized the island around 1908 (after the PLS) and became the dominant ungulate herbivore. Moose frequently browse balsam fir, and high moose densities can prevent the recruitment of balsam fir seedlings to the canopy (Snyder and Janke 1976, McInnes et al. 1992, McLaren and Peterson 1994, McLaren and Janke 1996). In fact, no fir trees have germinated and grown to tree size on the western half of Isle Royale since 1915 (R. O. Peterson, *personal communication*). This preference of moose for balsam fir helps to explain the 23% decline in balsam fir and 9% increase in cedar since the PLS. Most sites transitioning to cedar were dominated by balsam fir during the PLS (Appendix S2: Fig. S2). A second reason for the severe decline in balsam fir RBA is a 1936 stand-replacing fire that burned 20% of the island. In a prior comparison of the vegetation in the boreal zone of Isle Royale with PLS records, Janke et al. (1978) found declines in balsam fir

and increases in aspen and paper birch in areas within the fire boundary.

Outbreaks of insects and diseases also contributed to the shifts in tree dominance we document here. A larch sawfly outbreak largely eliminated tamarack at Isle Royale (Hansen et al. 1973). Dutch elm disease likely led to the large declines in elm at both Mississippi (by 19%) and Saint Croix (by 8%). The impending arrival of emerald ash borer to GLKN parks may soon eliminate most ash trees from the six parks where it is present. The impacts of emerald ash borer could be especially severe at Saint Croix, Voyageurs, and Mississippi, where ash represents 22%, 10%, and 9% of the RBA, respectively. Loss of ash in the riparian ecosystems at Saint Croix and Mississippi, in turn, could trigger further changes, including higher river flows, sedimentation, and reductions in habitat quality (Sanders and Kirschbaum 2015a).

Patterns of convergence and divergence

Within seven parks, ordinations revealed that forests diverged in composition since the 19th century (Figs. 3–5). Forest composition in PLS plots often clustered toward the conifer or oak species that dominated presettlement forests, while forests in GLKN plots diverged toward varying species composition. For instance, at Apostle Islands, forest composition in PLS plots clustered toward the dominant conifers. In contrast, points representing GLKN plots show little overlap with those representing the PLS, as forest composition has shifted and diverged either toward maple, toward yellow birch/cedar, or toward aspen/paper birch/the red oak group (Fig. 3). At Isle Royale, forests during the PLS clustered toward balsam fir and tamarack dominance, while modern GLKN plots clustered toward either paper birch/aspen or toward cedar/maple/yellow birch (Fig. 3). In contrast, the boreal forests in both Grand Portage (Fig. 3) and Voyageurs (Fig. 5) converged in composition, reflecting declines in white pine and the fire-dependent jack and red pines.

Despite the tendency for forest communities to have diverged in composition at the plot level within most parks, we see convergence in forest composition across parks in the region when examined at the park level (Fig. 5; All Parks—exceptions are Grand Portage and Indiana

Dunes). This convergence across parks suggests an overall trend of biotic homogenization, generally considered to reflect declines in less common species (often tied to specific habitats) and increases in already common widespread species (Olden and Poff 2003). Such homogenization resembles the patterns found in several forest types in the region using data from both overstory trees (Schulte et al. 2007, Hanberry et al. 2012) and the more diverse understory communities (Wiegmann and Waller 2006, Rogers et al. 2008, Johnson et al. 2013, Li and Waller 2015).

The value of long-term data, monitoring, and this study

The results presented here are only possible because of the inadvertent ecological baseline provided by the PLS. The NPS, in launching its I&M Program, is committed to monitoring forest composition as one of several key indicators of the health of natural resources in the national parks (Route and Elias 2007). Such monitoring supports valuable analyses of long-term ecological change like this study, illuminating unseen trends and providing special insights into the nature, extent, and causes of ecological change (cf. Waller and Rooney 2008). Monitoring is also necessary if agencies like the NPS are to adaptively manage the resources they oversee (Holling 1978, Lindenmayer and Likens 2009).

All efforts to monitor ecological conditions fall short in one respect or another. Here, we were limited by the crude taxonomy of the PLS surveyors, by the contrasting spatial layout and intensity of sampling between the two periods, and to comparisons of larger-diameter trees. To address these shortcomings, we used RBA to compare the modern and historical data. We did not address the current patterns of regeneration or tree density below our diameter cutoff (10.2 cm dbh for Isle Royale and Voyageurs, 15.2 cm dbh for all other parks). Even so, the regeneration of fire-dependent species is minimal at most parks (Sanders and Grochowski 2009, 2010, Sanders and Kirschbaum 2015a), and divergence away from presettlement conditions is continuing (Kirschbaum et al. 2016). Despite these limitations, this study succeeded in determining how forest composition has changed in these national parks, and the similarities and differences among parks in those changes. Our analyses differ from

other regional analyses of PLS data because they provide a comprehensive analysis of historical change within the national parks. While forests in the parks changed in ways similar to those in the broader region, many of the changes are unique to these parks and can be attributed to their location on islands and riverine ecosystems, varying patterns of ungulate herbivory, and fire history patterns. While regional-scale analyses are informative for understanding broad patterns, they can sometimes mask the changes occurring at finer scales. Our plot-level analyses using 1-mile buffers provide a new method to assess the change in locations that are more likely to share similar topographic and edaphic conditions. Still, care must be taken in the interpretation of PLS data at these small scales, as the PLS data cannot be used to reconstruct stands at particular locations (Schulte and Mladenoff 2001).

Implications for managing these parks

Forested NPS lands are generally “unmanaged” and, as such, differ from the surrounding lands by having more late-successional trees (Miller et al. 2016). They also have greater structural complexity (Crow et al. 2002), higher availability of coarse woody habitat (Goodburn and Lorimer 1998), and higher species richness (Paillet et al. 2010) than forests managed for timber. As national parks continue to diverge from lands in the surrounding matrix, they will provide important refuges from many anthropogenic disturbances, as well as an opportunity to protect and recover populations of species sensitive to these disturbances. Continued monitoring will help us understand these processes and to track recovery inside and outside park boundaries. Further, analyses such as those conducted here can be combined with paleoecological work (e.g., Davis et al. 2000), remotely sensed data (e.g., Kirschbaum et al. 2016), and ongoing monitoring data from the GLKN to piece together the historical range of variability within these parks.

The NPS is clearly committed to protecting these parks from disturbances like logging and invasive species. Nevertheless, fire suppression is practiced broadly within the NPS, particularly in parks within the Midwest, northeast, and east central United States. Fire management plans for these parks limit the use of natural ignitions and either prohibit or severely limit prescribed fires.

This ongoing fire suppression could further threaten the persistence and abundance of fire-adapted species, given that fire suppression both allows invasion by more mesic, fire-sensitive species and contributes to biotic homogenization. Although passive succession may suffice to restore mature forests and species to our region, we cannot expect to sustain and restore fire-dependent species unless we are ready to let fires burn more often and/or employ prescribed fires. Parks must also adapt to climate change if they are to sustain dependencies of species on one another for food, growth, reproduction, and ecosystem integrity (Hansen et al. 2014, Sanders and Grochowski 2014a). This will require fostering ecological conditions that allow species to persist and adapt locally in the short run and enough habitat connections to allow species to disperse to and colonize new locations in longer run.

CONCLUSIONS

While only a snapshot of the past forest, the PLS records provide a valuable baseline of forest composition at the time of widespread European settlement across the Great Lakes region. By comparing this baseline with the intensive GLKN surveys, we demonstrated the sizeable shifts in forest composition since the mid-19th century across all parks. Many of the changes we observed were due to past logging and land-use history, as well as ongoing fire suppression, ungulate herbivory, insect and disease outbreaks, and the successional processes related to each of these disturbances. National parks are undergoing dynamic cultural and biological change (Knowles et al. 2012), and just how parks will respond to future stressors is unclear. Long-term monitoring programs like the GLKN will allow us to assess the fine-scale changes at short temporal scales within parks. These monitoring efforts provide the scientific basis for management decisions and are thus critical for protecting these parks into the future and achieving the goals that they are committed to.

ACKNOWLEDGMENTS

We thank Rebecca Key, Al Kirschbaum, and Ulf Gafvert of the Great Lakes Inventory and Monitoring

Network in Ashland Wisconsin for GIS assistance and our NPS field technicians for assistance in data collection. John Paul Schmit, Bill Monahan, and an anonymous reviewer provided helpful comments to improve the manuscript. We also thank many for their efforts to digitize the Public Land Survey data in our region: D. Mladenoff's Forest Ecosystem and Landscape Ecology Group; J. Almendinger at the Natural Heritage Information System in the Minnesota DNR; D. Cleland at the USFS; colleagues at the Michigan DNR; and colleagues at the Morton Arboretum and Notre Dame University who digitized PLS data for Indiana Dunes (J. McLachlan, J. Peters, S. Halsey, J. McBride, A. Buerger, Q. Hamlin, C. Broderick, K. Bauer, and W. Chronister). Scout Kirby digitized PLS data from Grand Portage National Monument. The National Park Service, University of Wisconsin-Madison Department of Botany Flora Aeterna Fellowship, and the Lakes States Fire Science Consortium provided generous funding for this project.

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