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Forest change in the Driftless Area of the Midwest: From a preferred to undesirable future



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ABSTRACT

In the midwestern and eastern U.S., oaks (Quercus spp.) have been a dominant component of forests for at least the last 10,000 years, providing vital habitat for numerous wildlife and plant species that have adapted to oak forest conditions. However, the current state of these oak systems, in which there has been a general lack of successful oak regeneration and recruitment and an increase in the relative dominance of mesophytic species, may be nearing critical thresholds. If reached, restoring oak systems through natural regeneration and other methods, such as prescribed fire, may become especially challenging if not impossible. An understanding of spatial variation in oak dominance over time can inform and potentially improve the efficacy of intervention strategies. Using Public Land Survey and Forest Inventory and Analysis (FIA) inventories, we evaluated changes in the composition of timberland across ecoregional subsections in the Driftless Area of the Midwest at three time periods (pre-settlement 1800s, 1990s, and 2000s). We identified an overall decrease in oak dominance, and particularly dominance of the white oak (Quercus alba L, Q. macrocarpa Michx., and Q. bicolor Willd.) species group since the presettlement era, and an increase in other eastern soft hardwoods. Within the last 20 years, both the red oak (Q. rubra L., Q. ellipsoidalis E.J. Hill and Q. velutina Lam.) and white oak species groups decreased in dominance, with an increase in hard maple-basswood (A. saccharum Marsh., A. nigra L., and Tilia americana L.) species group dominance, indicating further mesophication of forests in the region. However, we found a notable decrease in hard maple-basswood relative dominance within the small diameter class across most of the regions within the last 10-20 years, with an increase in dominance of other, non-oak, species. Our findings complement qualitative evidence from interviews with natural resource professionals from the region and offer further information on the potential for forest conversion to "undesirable" forest conditions, as identified as a source of concern by some professionals. There was spatial variation in these trends, however, with some pronounced differences across adjacent state boundaries. The variation in forest change across state boundaries suggests the role of state-level socioeconomic and policy factors in affecting forest conditions, and thus the potential for a targeted and timely approach to promoting preferred pathways of change.

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1. Introduction

Oak-dominated forests (*Quercus* spp.) of the midwestern and eastern United States are experiencing substantial changes, as the combination of natural succession and human-related factors have created conditions that typically favor more mesic, shade-tolerant, broad-leaved forest types (termed the "mesophication" of the forests; Nowacki and Abrams, 2008). The consequences of this conversion may have profound impacts on ecosystem services. For instance, oaks provide important resources for a variety of plants and animals (McShea and Healy, 2002; Rodewald and Abrams, 2002; Fralish, 2004) and are highly valued by society for economic and cultural reasons (Starrs, 2002). Yet, management to promote and retain oak as a dominant forest component is fraught with difficulties, including the need for adequate forest disturbance. For example, prior to Euro-American settlement, the disturbance of oak forests by periodic fire was common (Abrams, 1992), and



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early- to mid-successional, fire-adapted oak forests maintained a competitive advantage over later-successional forest types. Spatial variation in fire disturbance maintained landscape-level heterogeneity of ecosystem types (Nowacki and Abrams, 2008). Changing land ownership patterns and management decisions since settlement have contributed to altered fire regimes, particularly fire exclusion, and consequently early- to mid-successional communities have subsequently dwindled in extent (Williams, 1989; Askins, 2001; Hanberry et al., 2012). Presently, fire suppression and widespread selective harvesting (often high-grading) of oak forests have led to within-stand and landscape-level forest homogeneity, favoring later-successional forest types (Kittredge et al., 2003; Nowacki and Abrams, 2008; Rhemtulla et al., 2009).

Forest managers seeking to promote oak regeneration face combined ecological, economic, and social issues that inhibit the efficacy of typical oak management prescriptions, such as overstory removal and prescribed fire (Knoot et al., 2009), especially since the majority of forestland in the U.S. is privately owned (Butler and Leatherberry, 2004). Periodic disturbance is crucial to the persistence of oak (Johnson et al., 2009), but management aimed at maintaining or restoring early- to mid-successional types may appear counterintuitive to conservation-minded small private landowners (Askins, 2001). In addition, trends in forest parcelization and land tenure in the U.S. (Best and Wayburn, 2001; Zhang et al., 2009) reduce the likelihood that landowners will embrace the long-term land management perspectives that are required for perpetuating oak (Knoot et al., 2010).

The current state of oak forests in the midwestern and eastern U.S., in which there has been a general lack of successful oak regeneration and recruitment and an increase in the relative dominance of mesophytic species, may be nearing critical thresholds. If reached, restoration through natural regeneration and other methods, such as prescribed fire, may become especially challenging, if not impossible (Nowacki and Abrams, 2008). Yet, changes in forest composition can be highly variable across the landscape, likely due to complex and interacting driving factors (Fei et al., 2011). For example, social forces, including but not limited to forest parcelization and short land tenure, constrain landowner decision making regarding oak at multiple spatial scales (Knoot et al., 2010). Ecological drivers of forest change (e.g., availability of oak regeneration, soil moisture availability) also occur at multiple scales and vary over space and time (Iverson et al., 1997; Nowacki and Abrams, 2008; McEwan et al., 2011). There are a variety of policy mechanisms, including economic incentives, which could be used to encourage landowners to conserve oak (Fischer and Bliss, 2008). But spatially informed approachesthose which identify regions where forest change is most rapid and pronounced or where forest composition appears stablecould help increase the effectiveness of the limited funding devoted to landowners assistance.

The purpose of our research was to evaluate the magnitude and direction of forest change among three time periods-1832-1857, 1990-1996, and 2006-2010-across the Midwest Driftless Area, particularly focusing on change in the dominance of oaks. This region of the Midwest has experienced an overall decrease in the total spatial extent and dominance of oak-hickory forests over the last century and half (Rhemtulla et al., 2009). Yet, questions remain concerning how different species groups of oaks have changed over time relative to other dominant tree species and whether trends in oak forest composition follow similar trajectories in other regions (Abrams, 2003). We address three main questions in this study: (1) To what extent has the dominance of different oak species groups, relative to other tree species groups, changed over time? (2) Are changes in forest composition consistent across the region or, alternatively, do trajectories vary depending on location? (3) What is the likely future trajectory of change? We expect this quantitative assessment of the spatial variation in forest change across the region can promote dialogue on preferred alternative futures for the forest resources, how to attain them, and the development of targeted policies to achieve such visions.

2. Methods

2.1. Study area

The Driftless Area, also known as the Paleozoic Plateau or Blufflands, is roughly 50,000 km² in size, is dissected by the Mississippi River flood plain, and includes portions of Minnesota, Wisconsin, Iowa, and Illinois (Fig. 1). This geologically unique region was circumvented by ice during the most recent glaciation (Hobbs, 1999) and is characterized by a loess-capped plateau and steep ravines formed by several large rivers that flow through the region. Prairie soils can be found on the ridges, with thick silt loams (loess) covering cherty residuum, with an underlying dolomite bedrock, and silt loam over sandstone on valley walls found in some parts of the region (Albert, 1995). Soils are typically considered Udalfs, with Udolls on the valley floors (Albert, 1995). The Driftless Area is considered part of the humid, hot continental climate division (mean annual precipitation = 82 cm, mean January temperature = -9.7 °C, mean July temperature = 22.3 °C; Wendland et al., 1992), and is contained within the eastern deciduous forest province (Bailey, 1983).

Historically, the Driftless Area was composed of diverse land cover types including tallgrass prairie, oak savanna, and sugar maple-basswood forest (Albert, 1995; Shea et al., 2014). The land-scape has experienced pronounced changes in land cover over the last century and half, as much of the savanna and prairie were replaced by agricultural lands (Rhemtulla et al., 2007) and the suppression of fire promoted a greater extent of closed-canopy forests (Curtis, 1959). Currently the landscape is composed primarily of agricultural lands and deciduous forest (Fry et al., 2011).

2.2. Description of data

We evaluated changes in tree species group relative dominance in the Driftless Area using Public Land Survey (PLS) and the USDA Forest Service Forest Inventory and Analysis (FIA) program data. Pre-settlement relative dominance was derived from Public Land Survey records collected in the Driftless Area from 1832 to 1857. The PLS was established by the U.S. General Land Office as a means of demarcating 1.6 km by 1.6 km (1 mi by 1 mi) section boundaries for sale and settlement. PLS surveyors marked the intersection points of each section (section corners) and halfway between the section corners (quarter corners), while also blazing and taking notes on two to four "witness" trees near corner points. In their notes, surveyors kept track of species, diameter, azimuth, and distance from corner for each witness tree. In the Driftless Area, surveys were completed before widespread Euro-American settlement. Because these records are extensive and provide spatially explicit information on vegetation and other landscape features, PLS records have been widely used by researchers to identify pre-settlement vegetation in various regions of the Midwest and elsewhere (Schulte and Mladenoff, 2001). We used data from a geographic information system (GIS) database containing PLS witness tree information (the species, diameter, azimuth, and distance from corner) for all section and quarter corners in the Driftless Area (Shea et al., 2014). While there is some degree of error in the PLS witness tree records, typically associated with surveyor bias, our use of the data to assess relative changes in species group dominance across broad spatial scales limits the impact of surveyor bias (Schulte and Mladenoff, 2001; Liu et al., 2011).



Fig. 1. Study area within North America and the subsection ecoregions that comprise the Driftless Area of the Midwestern U.S. and encompass portions of Wisconsin, Minnesota, Iowa, and Illinois. Our study focused on the subsections within the Wisconsin, Minnesota, and Iowa portions of the region.

We used FIA program data to assess changes in forest composition, as measured by tree species group relative dominance, from two time periods within the last 20-30 years. The FIA monitoring program was mandated by Congress in the McSweeney-McNary Forest Research Act of 1928 and amended by the Forest and Rangeland Renewable Resources Planning Act of 1974 with the goal of regularly assessing the state of the nation's public and private forestlands (Smith, 2002). For more than 80 years, each state's forestland has been surveyed on a cycle of about every 8-15 years; the dates for each survey varied by state (USDA Forest Service, 2013). In accordance with specifications set forth in the Farm Bill of 1999, the FIA program began an annual inventory of measuring plots in each state each year, completing a full survey of the plots over a five-year period within eastern states (over ten years in western states), providing timely information for managers and policy makers (O'Connell et al., 2014). We focused our analysis on the Wisconsin, Iowa, and Minnesota subsections of the study region, excluding subsections in Illinois from further analysis given the limited number of FIA inventory plots available for analysis in that part of the Driftless Area. FIA establishes plots on both forested and nonforested conditions, but in these states only plots in forested conditions are measured in the field; we constrained our analyses to forested FIA plots. We compared FIA data collected in the most recent periodic surveys for each state and year where digital data were available (Iowa, 1990; Minnesota, 1990; and Wisconsin, 1996; considered hereafter the "previous" inventories) to the data collected through "annual" inventories (completed from 2006– 2010), hereafter considered "current" inventories. All FIA data was extracted from the Forest Inventory and Analysis Database (FIADB), available online at http://apps.fs.fed.us/fiadb-downloads/ datamart.html. Publicly available FIA data involves the process of perturbing plot locations, where a portion of plots are "swapped" with other plot locations to protect data confidentiality and owner privacy (LaPoint, 2005). To limit the potential effects of swapping inventory plot data we used true plot locations and the data were summarized to the level for analysis that preserves data security.

2.3. Data analysis

We evaluated forest conditions within subsection-level ecosystems that comprise the Driftless Area (Fig. 1). Subsections are one of the ecological units within the U.S. Forest Service's hierarchical framework (Cleland et al., 1997; McNab et al., 2007). Similar patterns in climate, physiography, geologic substrate, and potential natural communities designate subsection boundaries (Cleland et al., 1997). There are six subsections that compose the study region, including the Western Paleozoic Plateau (Lf; Fig. 1), that covers portions of Minnesota and Iowa, and the Mississippi-Wisconsin River Ravines subsection (Lc; Fig. 1) that includes portions of all four states. Four additional subsections are located primarily in Wisconsin (La-Menominee Eroded Pre-Wisconsin Till, Lb-Melrolse Oak Forest and Savannah, Ld-Kickapoo-Wisconsin River Ravines, and Le-Mineral Pint Prairie-Savannah; Fig. 1). Subsections range between about 3000 and 21,000 km² in size. Because some subsections were represented in more than one state, and survey dates varied by state, our unit of analysis was the subsection by state. The number of witness trees recorded by PLS surveyors totaled 92,737; per unit of analysis this number ranged between 6969 and 22,880. The number of forested FIA inventory plots collected per unit of analysis ranged from 51 to 375 in the periodic inventories, which is similar to the range of inventory plots in the current, annual forest inventories (range of 45–456 plots) (Table 1).

To compare pre-settlement and post-settlement relative dominance, tree species were combined into broader groups, and adapted from USDA Forest Service FIA species groups, because some species were not well represented across the region. We developed three larger groupings of those species of interest: (1) white oak species group including white oak (Ouercus alba L.), bur oak (Q. macrocarpa Michx.), and swamp white oak (Q. bicolor Willd.); (2) red oak species group including northern red oak (Q. rubra L.), northern pin oak (Q. ellipsoidalis E.J. Hill), and black oak (Q. velutina Lam.); and, (3) hard maple-basswood group including sugar maple, black maple (A. nigra Michx.), and American basswood (Tilia americana L.). These consolidated tree species groups provided greater specificity than allowed by an analysis by forest type, while also resulting in greater sample sizes than allowed by individual species. The remaining FIA species groups that we assessed were considered to be well-represented across the region, and included: hickory (bitternut hickory [Carya cordiformis (Wangenh.) K. Koch] and shagbark hickory [Carya ovata (Mill.) K. Koch); ash (white ash [Fraxinus americana L.], green ash [F. pennsylvanica Marshall], and black ash [F. nigra Marshall]); cottonwood-aspen (eastern cottonwood [Populus deltoides W. Bartram ex Marshall], bigtooth aspen [P. grandidentata Michx.], quaking aspen [P. tremuloides Michx.]); other eastern soft hardwoods (black cherry [Prunus serotina Ehrh.], paper birch [Betula papyrifera Marshall], boxelder [A. negundo L.], butternut [Juglans cinerea L.], American elm [Ulmus americana L.], slippery elm [U. rubra Muhl.], river birch [Betula nigra L.], common hackberry [Celtis occidentalis L.l. and black willow [Salix nigra Marshall]): and eastern noncommercial hardwoods (apple spp. [Malus spp.], hophornbeam [Ostrya virginiana (Mill.) K. Koch]). We evaluated forest change by comparing the relative dominance of these species groups among time periods. Within each subsection, we calculated the relative dominance using basal area of all live trees within each species group on timberland using trees >2.54 cm (1 in.) in diameter at breast height (dbh) and the following equation:

$$RD_{i} = \left(\frac{\sum_{j=1}^{m} \text{basal area}_{ij}}{\sum_{i=1}^{n} \sum_{j=1}^{m} \text{basal area}_{ij}}\right) \times 100$$
(1)

where *RD* is relative dominance, *n* is the number of species groups, and *m* is the number of individuals of a given species group in the subsection and basal area_{*ij*} is the basal area of individual *j* of species group *i*.

To evaluate long-term as well as recent changes in tree species composition of the Driftless Area, we examined the relative dominance of tree species groups in each time period through a combination of tabular, graphical and map-based representations. We analyzed changes in species group dominance over time using nonmetric multidimensional scaling (NMS) and multi-response permutation procedure (MRPP). Both NMS and MRPP were performed using PC-ORD (McCune and Mefford, 1999) with the Bray-Curtis (Sørensen) distance measure. Both of these non-parametric techniques are appropriate for ecological community data (McCune and Grace, 2002), such as ours. NMS was used to evaluate pathways of change in dominance among species groups over the three time periods at the subsection level. We used an automated search with a random starting configuration, 250 iterations with the real data, and at least 250 runs to evaluate stability. Preliminary analyses were run with up to six dimensions, but a substantial amount of stress reduction was achieved with the first two axes. Our final configuration had a final stress of 8.94 and instability of <0.00001 based on 43 iterations, and explained a substantial amount of the variation in the data (cumulative $r^2 = 0.96$). The level of stress in this configuration is considered low and indicates that there is little risk of drawing false inferences (McCune and Grace, 2002). Pearson correlations for each species group were calculated with the resulting ordination axis scores, from which the axes were interpreted. We used MRPP to evaluate differences in community composition between time periods. Each time period (pre-settlement, previous, and current) was defined as a group; the groups were composed of the data from each subsection in the corresponding time period. We used pairwise comparisons to determine whether composition varied significantly between each of the time periods.

As relative dominance predominantly reflects changes in the basal area of larger trees, we further evaluated modern trajectories of change between previous and current FIA inventories (roughly 20 years) by describing relative dominance according to three stand-size classes for stocked stands, with at least 10% full stocking, to develop a more comprehensive understanding of changes in forest structure. Each FIA plot was assigned a stand-size class–large, medium, or small–classified according to the

Table 1

Project subsections, described by state (IA, WI, and MN), within the Driftless Area of the Midwestern U.S., subsection area (km²), number of original Public Land Survey witness trees, the number of US Forest Service Forest Inventory and Analysis (FIA) plots for the previous and current inventories that contained timberland and percentage of the area considered forested.

Subsection	Subsection Name	km ²	Total non-zero plots			
			PLS witness trees	Previous ^a	Current ^b	% of area forested ^c
LcIA	Mississippi-Wisconsin River Ravines	3600	7241	77	54	38
LfIA	Western Paleozoic Plateau	4416	7570	51	45	23
LaWI	Menominee Eroded Pre-Wisconsin Till	3741	6969	88	123	45
LbWI	Melrose Oak Forest and Savanna	6947	12,635	247	289	13
LcWI	Mississippi-Wisconsin River Ravines	11,059	22,880	375	456	35
LdWI	Kickapoo-Wisconsin River Ravines	3235	7524	112	134	49
LeWI	Mineral Point Prairie-Savanna	5051	8245	60	74	43
LcMN	Mississippi-Wisconsin River Ravines	5034	12,071	348	179	47
LfMN	Western Paleozoic Plateau	5681	7602	83	65	11

^a Previous periodic FIA inventories by state and year: Iowa, 1990; Minnesota, 1990; and Wisconsin, 1996.

^b Current annual FIA inventories conducted from 2006 to 2010.

^c LANDFIRE (2010).



Fig. 2. Mean relative dominance over three time periods and across subsections for tree species groups that were considered to be represented across the Driftless Area of the Midwestern U.S.; species groups are organized according to dominance at presettlement. Presettlement relative dominance was derived from Public Land Survey records collected in the Driftless Area from 1832 to 1857. "Previous" periodic FIA inventories, by the state and year in which they were conducted, refer to: lowa, 1990; Minnesota, 1990; and Wisconsin, 1996. "Current" annual FIA inventories were conducted from 2006 to 2010.

predominant size of live trees present, based on stocking. As specified by the USDA Forest Service FIA inventory handbook, standsize classes were defined differently for hardwoods and softwoods: "large" stand-size class, trees >27.9 cm diameter at breast height (dbh) for hardwoods and >22.9 cm dbh for softwoods; "medium" stand-size class, trees 12.7–27.7 cm dbh for hardwoods and 12.7–22.6 cm dbh softwoods; and "small" stand-size class, trees <12.4 cm dbh (O'Connell et al., 2014). For each subsection we calculated relative dominance of tree species groups within each stand-size class. We specifically assess trajectories of change in the smaller stand-size classes.

3. Results

3.1. Composition over three time periods

Prior to European settlement, forestland in the region was largely dominated by the white oak species group (59%), followed to a lesser degree by the red oak species group (18%), hard maple-basswood (9%) and other eastern soft hardwoods (5%) (Fig. 2, Appendix A). Since pre-settlement times, the region has seen an overall loss of white oak dominance, with an initial decrease in mean dominance by over 40% between pre-settlement and early FIA records (1990s), and a continued decrease between the previous (1990s) and more current FIA surveys (2010) of 3.5% (Fig. 3). In contrast, we found the red oak species group to experience a slight increase between pre-settlement time periods and the previous FIA survey (1.4%), but then decrease in dominance by 4.3% in the last 10–20 years (Fig. 3). All other tree species groups that were evaluated experienced an increase between pre-settlement and previous FIA records (Figs. 2 and 3); most pronounced is the increase of nearly 16% in dominance of the "other eastern soft hardwoods" tree species group (Fig. 3). Between the previous and current FIA surveys (10-20 years), hard maple-basswood had the greatest increase (+2.6%) compared to other species groups. some of which experienced a slight increase of 1% (i.e., other eastern soft hardwoods, ash, hickory), a slight decrease (i.e., cottonwood), or have stayed the same, such as noncommercial tree species (Fig. 3).

We noted considerable variation in the relative dominance and change in dominance across subsections. For the three most dominant groups during the pre-settlement period (i.e., white and red oak, and hard maple-basswood), white oak dominance varied widely from 28% in the northern subsection of Wisconsin (Menominee Eroded Pre-Wisconsin Till, LaWI), to 82% in the southern subsection of Wisconsin (Mineral Point Prairie-Savanna, LeWI) (Fig. 4, Appendix A). The lower dominance of white oak in the northern subsection of Wisconsin parallels findings from a recent study by Shea et al. (2014), in which the this portion of the Driftless Area consisted of more diverse tree species cover classes, some of which were associated with areas of sandy glacial outwash.

Current dominance of the white oak group ranges between 9% in the Mississippi-Wisconsin River Ravines (LcIA) and Kickapoo-Wisconsin River Ravines (LdWI) subsections to 26% in the southern most subsection in Wisconsin (Mineral Point Prairie-Savanna, LeWI) (Fig. 4). Overall total declines in dominance between presettlement and the previous FIA inventories in the 1990s ranged between a loss of 12% dominance in the Menominnee Eroded Pre-Wisconsin Till subsection (LaWI) to a loss of 56% dominance in the Mineral Point Prairie-Savanna subsection (LeWI) (Fig. 4, Table 2). Nearly all subsections have experienced a continued decline in white oak dominance within the last 20 years (ranging



Fig. 3. Change in the relative dominance between three time periods of tree species groups that were considered to be represented across the Driftless Area of the Midwestern U.S. Pre-settlement relative dominance was derived from Public Land Survey records collected in the Driftless Area from 1832 to 1857. "Previous" periodic FIA inventories, by the state and year in which they were conducted, refer to: Iowa, 1990; Minnesota, 1990; and Wisconsin, 1996. "Current" annual FIA inventories were conducted from 2006 to 2010.

between -1% and -10%), with the Melrose Oak Forest and Savanna subsection (LbWI) in Wisconsin experiencing a slight (1%) increase (Fig. 4, Table 2).

The red oak group was considerably less dominant than the white oak group during the pre-settlement time period, ranging between 10% in the Menominee Eroded Pre-Wisconsin Till subsection (LaWI) to 29% in the Melrose Oak Forest and Savanna subsection (LbWI) in relative dominance (Fig. 4, Appendix A). As we noted, red oak experienced a mean increase overall between presettlement and previous inventories (Fig. 3). However, four of the nine subsections experienced a decline in red oak dominance (decreasing by roughly 1-4%; Table 2), including both subsections in Iowa (Mississippi-Wisconsin River Ravines, LcIA; Western Paleozoic Plateau, LfIA) and the most southern (Mineral Point Prairie-Savanna, LeWI) and western subsections (Mississippi-Wisconsin River Ravines, LcWI) in Wisconsin. The remaining five subsections experienced an increase in dominance, ranging from an increase of approximately 3% to 8%, largely experienced by those most northern subsections in Minnesota and Wisconsin (Table 2). Our analysis highlights the decrease across all subsections in red oak dominance in the last 20 years (Table 2). The subsections in Minnesota (Mississippi-Wisconsin River Ravines, LcMN; Western Paleozoic Plateau, LfMN) experienced the greatest decrease in red oak dominance (-9% and -10%, respectively), which is notable given that the same subsections in Iowa (LcIA and LfIA) experienced less substantial declines in red oak dominance (-1% and -5%, respectively; Table 2).

The hard maple-basswood group was less dominant than oaks overall across the region historically (Fig. 2), and across most of the subsections, ranging between 1% and 8% in relative dominance across seven of the nine subsections (Fig. 4, Appendix A). Hard maple-basswood dominance has consistently increased between each time period across these seven subsections, with current relative dominance between 4% and 23% (Fig. 4, Appendix A). The most substantial increases between pre-settlement and the 1990s occurred in the Mississippi-Wisconsin River Ravines subsections in Ninnesota and Iowa (LfMN, 7.7%; LfIA, 7.5%), and the Mineral Point Prairie-Savanna subsection in Wisconsin (LeWI, 6.2%). Between the 1990s and 2000s, major increases in hard maple-basswood dominance continued in LcIA (6.9%), LfMN (5.6%), and LeWI (6.2%).



Fig. 4. Relative dominance of three main tree species groups over three time periods in the Driftless Area of the Midwestern U.S. Relative dominance values were derived using Public Land Survey (mid-1800's) and the USDA Forest Service Forest Inventory and Analysis program data (1990's and 2000's).

Table 2

Change in the relative dominance over three time periods (mid-1800's to 1990's and 1990's to 2010) of three focal tree species groupings (white oak, red oak, and hard maplebasswood) by subsection.

Subsection	Change over time (%) Presettlement to 1990's ^a			Change over time (%) 1990's ^a to 2010 ^b			
	White Oak	Red Oak	Maple-Basswood	White Oak	Red Oak	Maple-Basswood	
LcIA	-47.3	-3.6	9.3	-6.0	-1.4	6.9	
LfIA	-51.0	-3.2	7.5	-1.4	-5.4	1.3	
LcMN	-33.1	2.6	3.3	-10.4	-9.4	3.1	
LfMN	-55.1	4.6	7.7	-3.0	-10.3	5.6	
LaWI	-11.6	8.3	-8.6	-6.3	-1.8	0.3	
LbWI	-38.9	4.4	0.8	1.2	-3.6	1.3	
LcWI	-42.6	-1.5	1.7	-1.2	-0.7	0.4	
LdWI	-32.5	2.8	-3.4	-3.7	-3.6	-1.8	
LeWI	-55.8	-1.3	6.2	-0.8	-2.3	6.2	

^a Previous periodic FIA inventories, by state and year: Iowa, 1990; Minnesota, 1990; and Wisconsin, 1996.

^b Current annual FIA inventories conducted from 2006 to 2010.

The opposite pattern was found for the two subsections in Wisconsin in which hard maple-basswood was most dominant in presettlement times (Menominee Eroded Pre-Wisconsin Till, LaWI, 20%; Kickapoo-Wisconsin River Ravines, LdWI, 25%) and has since decreased between pre-settlement times and previous FIA surveys (-9% and -3%, respectively), with the Kickapoo-Wisconsin River Ravines subsection (LdWI) in Wisconsin experiencing a continued decline of nearly 2% in hard maple-basswood dominance in the last 20 years (Fig. 4, Table 2).

NMS results further illuminated similarities as well as variation among subsections in pathways of change in dominance among species groups over the three time periods (Fig. 5, Table 3). Despite differences in pre-settlement conditions among each of the subsections, we found a consistent shift away from white oak dominance and toward other tree species over time (Axis 1) that persisted in more recent time periods for most subsections. Some subsections showed a directional shift toward more red oak dominance in the time period following pre-settlement, with more recent shifts toward hard maple-basswood dominance (Axis 2) and dominance of other tree species groups (Axis 1) in the 10-20 years between previous and current inventories. MRPP indicated a significant difference in community composition between pre-settlement and previous FIA inventories (A = 0.37, t = -9.48, p < 0.001), but no significant differences between previous and current FIA inventories (A = -0.02, t = 0.74, p = 0.76).

3.2. Change in the last 20 years according to stand-size class

We evaluated relative dominance of oak species groups and hard maple-basswood across the different stand-size classes by examining current values as well as changes between previous and current surveys. For all species groups the relative dominance within the large stand-size class was very similar to the overall rel-

Table 3

Pearson correlations (*r*-values) with ordination axes from the nonmetric multidimensional (NMS) analysis.

Tree species groups	Axis 1	Axis 2
White oak	-0.979	-0.133
Red oak	-0.190	0.895
Maple-Basswood	0.590	-0.549
Hickory	0.729	0.008
Ash	0.694	-0.172
Cottonwood	0.623	0.363
Other Eastern Soft Hardwoods	0.765	-0.127
Noncommercial Hardwoods	0.796	-0.212

ative dominance for the current FIA surveys (Fig. 6, Appendix E). Patterns of relative dominance differed from overall values in the medium and small stand-size classes, with generally lower relative dominance values for the oak and hard-maple species groups and an increase in dominance by the other species groups combined (Fig. 6, Appendix E). Relative dominance of white oak in the small stand-size class ranged from 0% to 8% in eight subsections; the remaining subsection had 20% (Mineral Point Prairie-Savanna, LeWI) relative dominance of white oak.

Relative dominance of red oak in the small stand-size class was similarly low, ranging from 0% to 5% in seven subsections with 13% relative dominance in two subsections (Western Paleozoic Plateau, LfMN; Melrose Oak Forest and Savanna, LbWI). Hard maplebasswood was absent within the small stand-size class in four subsections and reached a maximum relative dominance of 8% in the Mississippi-Wisconsin River Ravines subsection (LcWI) in Wisconsin. The combined group of all other species had greater than 77% relative dominance within the small stand-size class in every subsection, reaching 100% relative dominance in one subsection (Mississippi-Wisconsin River Ravines subsection, LcIA) in Iowa.



Fig. 5. Two dimensional nonmetric multidimensional scaling (NMS) ordination of tree composition in Driftless Area subsections. Successional vectors connect presettlement, previous, and current surveys within each subsection; vectors begin at pre-settlement surveys and end with the arrow symbol at current surveys. "Previous" periodic FIA inventories, by the state and year in which they were conducted, refer to: Iowa, 1990; Minnesota, 1990; and Wisconsin, 1996. "Current" annual FIA inventories were conducted from 2006–2010.



Fig. 6. Change in relative dominance of species groups within the various stand-size classes between previous and current annual FIA inventories. Previous periodic FIA inventories were carried out in lowa (1990), Minnesota (1990) and Wisconsin (1996). Current annual FIA inventories were conducted from 2006–2010. Stand-size classes are represented by three main classifications, including "large" diameter trees >27.9 cm (11 in.) diameter at breast height (dbh) for hardwoods and >22.9 cm (9 in.) dbh for softwoods; "medium" diameter trees 12.7–27.7 cm (5–10.9 in.) dbh for hardwoods and 12.7–22.6 cm (5–8.9 in.) dbh softwoods; and "small" diameter trees <12.4 cm (4.9 in.) dbh (USDA Forest Service, 2013).

Comparing changes in relative dominance values in the different stand-size classes between previous and current FIA surveys, we generally found a decrease in dominance of both white and red oak species groups within all the stand-size classes; an increase in dominance of hard maple-basswood in the large and medium stand-size classes; and a decrease in hard maple-basswood in the small stand-size class across most subsections (Fig. 6). Other species experienced an increase in dominance across nearly all subsections in each of the stand-size classes (Fig. 6). Some subsections displayed deviations from these general trends, including the western most subsection in Iowa (Western Paleozoic Plateau, LfIA) with a decrease in hard maple-basswood dominance in the medium stand-size class and an increase in white oak, red oak, and hard maple-basswood species groups dominance in the small stand-size class; this was the only subsection where relative dominance of other species declined within the small stand-size class. The adjoining subsection in Minnesota (Western Paleozoic Plateau, LfMN) also experienced an increase in red oak dominance in the small standsize class. The southern-most subsection in Wisconsin (Mineral Point Prairie Savanna, LeWI) experienced an increase of white oak relative dominance in the small stand-size class (Fig. 7).

We also noted differences in the magnitude and direction of change within the same subsections but across state boundaries. Hard maple-basswood went against the general trend in the Mississippi-Wisconsin River Ravines subsection in Wisconsin (LcWI), where it displayed an increase in maple-basswood relative dominance in the small stand-size class; the adjoining Mississippi-Wisconsin River Ravines subsection in Iowa (LcIA), however, had the greatest decline of hard maple-basswood relative dominance within the small stand-size class (-15.0%). Similarly, while the Western Paleozoic Plateau subsection in Iowa (LfIA) experienced a decline in white oak relative dominance in the small stand-size class, it differed from its counterpart in Minnesota (LfIMN) which had the most precipitous decline of white oak relative dominance (-12.3%). Further examples include the decrease in red oak

dominance in the large stand-size class within both subsections in Minnesota (LcMN, -8.7% and LfMN, -13.6%); declines that exceed what are found in the same subsections in Iowa (LcIA and LfIA; -.1% and -5.3%, respectively).

4. Discussion

Our evaluation of forest change in the Driftless Area of the Midwest documents a substantial shift toward less dominance by the white oak species group across all subsections. While red oak dominance initially increased between pre-settlement and 10-20 years ago, it has subsequently decreased along with white oak more recently, with variation in this general pattern across subsections. We also found a general increase in the dominance of hard maplebasswood in the last 10-20 years, but our further assessment of relative dominance by species group according to stand-size class suggests that many of the subsections may experience a decrease in dominance of hard maple-basswood in the future. Thus, we highlight three key areas for discussion: (1) the shift in relative dominance away from white oak dominance since pre-settlement, and more recent shift to hard maple-basswood and other species, (2) the suggested decrease in hard maple-basswood dominance over time and shift toward other, potentially "less desirable", species, and (3) the potential influence of social drivers on the trajectory of forest change across state boundaries.

4.1. Decrease in white oak dominance

Our findings point to a significant shift in the relative dominance of tree species groups across the region since pre-settlement, with a notable, widespread decline in white oak relative dominance. Conversely, relative dominance of the other eastern soft hardwoods species group, has exceeded that of white oak, red oak, and hard-maple basswood—the three historically



Fig. 7. Change in relative dominance of four main tree species groups within the small size class (<4.9 in. dbh) between previous and current annual FIA inventories. Previous periodic FIA inventories were carried out in Iowa (1990), Minnesota (1990) and Wisconsin (1996). Current annual FIA inventories were conducted from 2006 to 2010.

dominant groups. The other eastern soft hardwoods species group consists of less valued species from a timber perspective, such as boxelder [*A. negundo* L.], butternut [*Juglans cinerea* L.], and elm [*Ulmus americana* L. and *U. rubra* Muhl.], and some commercially desirable species such as black cherry [*Prunus serotina* Ehrh.].

Our findings on oak loss parallel insights gained from stand and landscape-level forest surveys in the midwestern and eastern U.S. In these studies, understory competition (Lorimer et al., 1994), often facilitated by widespread and dispersed high-grading (Kittredge et al., 2003) and a decrease in fire disturbance (Abrams, 1992), in combination with white-tailed deer (Odocoileus virginianus) herbivory (Rooney and Waller, 2003, have been suggested as contributing to a decline in oak regeneration and general "mesophication" of forests (Nowacki and Abrams, 2008) and homogenization of functional classes, or groupings of plants with similar responses to environmental conditions, has occurred (Hanberry et al., 2012). As found elsewhere in some areas of the midwestern and eastern U.S. (Whitney and Davis, 1986; Fralish et al., 1991; Nowacki et al., 1990), the red oak species group was historically not as dominant as white oak in the Driftless Area and was found to increase in dominance following European settlement. We found that more recently, the red oak species group has seen a similar trend as white oak in decreasing dominance, likely due, in part, to continued fire suppression and selective logging that favors later-successional species and species sensitive to fire (Abrams, 2003). The continued increase in hard maple-basswood and other eastern soft hardwood dominance from pre-settlement to the 1990s and through the 2000s suggests persistent mesophication, which can create conditions that are less prone to fire disturbance (Nowacki and Abrams, 2008) and that favor tree species-such as black cherry-which can outcompete slower-growing oak (Taylor and Lorimer, 2003). As Abrams (2003) points out, the initial question of "where has all the white oak gone?" may be replaced by the question in the future, "Where have all the oak species gone?"

Although we did not experimentally evaluate the causal factors of forest change, data collected through interviews with natural resource professionals from the Driftless Area are consistent with our findings from the quantitative evaluation of forest change and suggest the importance of interacting drivers of forest change more recently (Knoot et al., 2010). Findings from the interviews point to local land management decisions (e.g., high-grading) that were thought to benefit shade-tolerant species and hasten the loss of oak, while broad-scale factors, such as timber market prices and land parcelization, support such decisions (Knoot et al., 2010). Thus, in this region that is predominately privately owned, concern exists that these social and economic driving factors will persist and white and red oak species groups will continue to decrease throughout the region, with detrimental impacts on associated species diversity (Rodewald and Abrams, 2002; Rogers et al., 2008) and other ecosystem services provided by oaks.

4.2. Continued shift to "other" species

A shift toward hard maple-basswood and away from oak-dominated timberland could have ecological ramifications, such as a decrease in songbird diversity (Rodewald and Abrams, 2002; Wood et al., 2012). However, further findings from interviews with natural resource professionals suggest that an increase in the extent of the hard maple-basswood forest type can be viewed by some as advantageous due to a generally strong timber market for sugar maple; yet a shift toward other species, such as elm and ash was considered undesirable (Knoot et al., 2010). Through our analysis, we found an increase across most sections in the overall dominance of hard maple-basswood (Table 2), but a decline in the proportion of hard maple-basswood in the small stand-size class through much of the region more recently (Fig. 6) suggesting that this species group may contract in the future. Moreover, recent climate change models point to a decline in suitable conditions for sugar maple, as well as northern red oak (Q. rubra, L.), in the region (Prasad et al., 2007). Instead, under these climate scenarios, other tree species, such as elm and ash may have a stronger future in the Driftless Area. However, the likely spread of the emerald ash borer (Agrilus planipennis) (Poland and McCullough, 2006) and continued impact of Dutch elm disease on mature American elm (Ulmus americana L.) trees (Parker and Leopold, 1983) could restrict the continued expansion of these species and may lead to increased prevalence of exotic species and novel species compositions (Rogers et al., 2008; Schulte et al., 2011). Climate change models also suggest an expansion in the habitat appropriate for some oak species within the white oak group (Prasad et al., 2007). Findings from a recent study by Nowacki and Abrams (2014), in which the authors evaluated the relative influence of climate and disturbance on forest composition in the eastern U.S, suggest the dominant role of a reduced disturbance regime. A continued decline in the dominance of white oak would decrease the potential for natural regeneration of future oak forests, thus questioning whether some oak species could indeed maintain or increase dominance despite favorable climate conditions, especially in the absence of adequate disturbance.

4.3. Variation across state boundaries

The subsection-level boundaries we used in our study reflect regions with similar environmental conditions (Cleland et al.,

1997). Regional variation in forest composition is often attributed to spatial variation in environmental factors, such as soil moisture, topography, disturbance and climate (Iverson et al., 1997; Fuller et al., 1998; Hessburg et al., 2005; Hanberry et al., 2012), as well as land use history (Foster et al., 2003; Schulte et al., 2007; Thompson et al., 2013). For example, in our study region, the environmental factors, soil texture, topographic roughness, and distance from waterways, have been found to be associated with pre-settlement tree species cover and vegetation structure (Shea et al., 2014). Fire frequency also likely served an important role in shaping the composition and configuration of these historic cover types found (Hanberry et al., 2012; Shea et al., 2014). Thus, variation in forest composition between subsections may be expected given differences in environmental factors and disturbance regimes across the region: however, we hypothesized that the direction and magnitude of forest change would be similar for subsections that are intersected by state boundaries. We found that the magnitude of change in dominance of some species groups varies across state boundaries, a finding which underscores the likely influence of socioeconomic and policy forces on forest change. For example, the decline in red oak dominance within the western most subsections in Minnesota (LcMN and LfMN) is notably greater than in the same subsections in Iowa (LcIA and LfIA). Fei et al. (2011), in their study of the change in oak abundance in the eastern U.S. between 1980 and 2008, also identified unexpected differences in the trajectory of change across state boundaries, which they suggest may be related to past or current socioeconomic factors that are driving such differences. In our study region, given that most of the forestland in the region is privately owned, variability in forest change experienced more recently across state boundaries may be associated with the availability of different forest management programs that encourage active forest management by private woodland owners (Kilgore et al., 2007). Further research is needed to better understand potential socioeconomic factors that may help explain differences in the magnitude and trajectories of change found across state boundaries.

Given the notable changes found to occur within the last 10-20 years, our data suggest that if we are to retain oak then timely development, implementation, and assessment of forest policies that encourage oak regeneration are needed. An example of such a targeted approach includes a recent USDA Natural Resources Conservation Service's Driftless Area Landscape Conservation Initiative, in which landowners are provided funding support for actions that reduce erosion, enhance woodland biodiversity, restore prairies and oak savannas, and restore cold water streams (USDA NRCS, 2013). Landowner management of existing woodlands considered to be of high potential for oak regeneration (i.e., at least 25% oak canopy, significant advance regeneration, on south- or southwest slopes) is prioritized in this initiative through a ranking process. This example program targets management where landowners may be most successful at regenerating oak. However, an evaluation of the immediate and long-term impact of such programs at encouraging more widespread oak management on private lands and shifting current trajectories of forest change is essential. Moreover, our findings suggest that some subsections within the region are experiencing greater declines in oak dominance and shifts toward other species, while other areas appear more stable, highlighting an opportunity to use this information to explore different policy approaches and potential impacts of these decisions.

5. Conclusion

Since Euro-American settlement, oak species in the Driftless Area of the Midwest have experienced a decline in dominance, which appears to have persisted over time. In addition, the trajectory of forest change reveals that tree species group dominance has shifted toward more shade-tolerant tree species groups and potentially less desirable timber species, such as ash (Fraxinus spp.) and elm (Ulmus spp.). Spatial variation in the pattern of change was notable, likely due in part to environmental factors. Such findings parallel similar results from studies assessing forest change in the midwestern and eastern U.S. Yet, we also identified differences in the direction and extent of change in the last 10-20 years across state boundaries. This pattern suggests that socioeconomic and policy factors may have played a role in driving forest change during this relatively short time period of analysis. Through previous interviews with natural resource professionals from the region, it has been found that while oak is still a highly valued tree species group, the social and economic challenges associated with managing for oak have led some professionals to accept a shift toward shade-tolerant species such as sugar maple (Knoot et al., 2010). However, our assessment of changes in forest composition since Euro-American settlement, combined with recent climate change projections, suggests that shifts toward potentially less desirable species may be more likely in some portions of the region. Therefore, dialog among key forest stakeholders is needed to develop and evaluate appropriate, targeted, and timely mechanisms that can halt and potentially reverse shifts toward "undesirable" forest system conditions.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2014.12. 013.

References

- Abrams, M.D., 1992. Fire and the development of oak forests. Bioscience 42 (5), 346–353.
- Abrams, M.D., 2003. Where has all the white oak gone? Bioscience 53 (10), 927-939.
- Albert, D. A., 1995. Regional landscape ecosystems of Michigan, Minnesota, and Wisconsin: A working map and classification. USDA For. Ser. Gen. Tech. Rep. NC-178, 250 p.
- Askins, R.A., 2001. Sustaining biological diversity in early successional communities: the challenge of managing unpopular habitats. Wildl. Soc. Bull. 29, 407–412.
- Bailey, R.G., 1983. Delineation of ecosystem regions. Environ. Manage. 7, 365–373. Best, C., Wayburn, L.A., 2001. America's Private Forests: Status and Stewardship.
- Island Press, Washington, D.C., 268 p. Butler, B.J., Leatherberry, E.C., 2004. America's family forest owners. J. For. 102 (7), 4–9.
- Cleland, D.T., Avers, P.E., McNab, W.H., Jensen, M.E., Bailey, R.G., King, T., Russell, W.E., 1997. National hierarchical framework of ecological units. In: Boyce, M.S.,

Haney (Eds.), Ecosystem Management Applications for Sustainable Forest and Wildlife Resources. Yale University Press, New Haven, CT, pp. 181–200.

- Curtis, J.T., 1959. The Vegetation of Wisconsin: An Ordination of Plant Communities. University of Wisconsin Press, Madison, WI, 657 p.
- Fei, S., Kong, N., Steiner, K.C., Moser, W.K., Steiner, E.B., 2011. Change in oak abundance in the eastern United States from 1980 to 2008. For. Ecol. Manage. 262, 1370–1377.
- Fischer, A.P., Bliss, J.C., 2008. Behavioral assumptions of conservation policy: conserving oak habitat on family-forest land in the Willamette Valley, Oregon. Conserv. Biol. 22, 275–283.
- Foster, D., Swanson, F., Aber, J., Burke, I., Brokaw, N., Tilman, D., Knapp, A., 2003. The importance of land-use legacies to ecology and conservation. Bioscience 53 (1), 77–88.
- Fralish, J.S., 2004. The keystone role of oak and hickory in the central hardwood forest. In: Spetich, M.A. (Ed.). Upland oak ecology symposium: history, current conditions, and sustainability, pp. 78–87. USDA For. Serv. Gen. Tech. Rep. SRS-73. 311 p.
- Fralish, J.S., Crooks, F.B., Chambers, J.L., Harty, F.M., 1991. Comparison of presettlement, second-growth and old-growth forest on six site types in the Illinois Shawnee Hills. Am. Midl. Nat. 125 (2), 294–309.
- Fry, J., Xian, G., Jin, S., Dewitz, J., Homer, C., Yang, L., Barnes, C., Herold, N., Wickham, J., 2011. Completion of the 2006 national land cover database for the conterminous United States. Photogramm. Eng. Remote Sens. 77 (9), 858–864.
- Fuller, J.L., Foster, D.R., McLachlan, J.S., Drake, N., 1998. Impact of human activity on regional forest composition and dynamics in Central New England. Ecosystems 1, 76–95.
- Hanberry, B.B., Palik, B.J., He, H.S., 2012. Comparison of historical and current forest surveys for detection of homogenization and mesophication of Minnesota forests. Landscape Ecol. 27, 1495–1512.
- Hessburg, P.F., Agee, J.K., Franklin, J.F., 2005. Dry forests and wildland fires of the inland Northwest USA: contrasting the landscape ecology of the pre-settlement and modern eras. For. Ecol. Manage. 211, 117–139.
- Hobbs, H., 1999. Origin of the Driftless Area by subglacial drainage—a new hypothesis. In: Mickelson, D.M., Attig, J.W. (Eds.), Glacial Processes Past and Present, pp. 93–102. Geological Society of America Special Paper 337.
- Iverson, L.R., Dale, M.E., Scott, C.T., Prasad, A., 1997. A GIS-derived integrated moisture index to predict forest composition and productivity of Ohio forests (U.S.A.). Landsc. Ecol. 12, 331–348.
- Johnson, P.S., Shifley, S.R., Rogers, R., 2009. The ecology and silviculture of oaks, 2nd ed. CABI Publishing, New York, NY, 503 p.
- Kilgore, M.A., Greene, J.L., Jacobson, M.G., Straka, T.J., Daniels, S.E., 2007. The influence of financial incentive programs in promoting sustainable forestry on the nation's family forests. J. For. 105, 184–191.
- Kittredge Jr., D.B., Finley, A.O., Foster, D.R., 2003. Timber harvesting as ongoing disturbance in a landscape of diverse ownership. For. Ecol. Manage. 180, 425– 442.
- Knoot, T.G., Schulte, L.A., Grudens-Schuck, N., Rickenbach, M., 2009. The changing social landscape in the Midwest: a boon for forestry and bust for oak? J. For. 107 (5), 260–266.
- Knoot, T.G., Schulte, L.A., Tyndall, J.C., Palik, B.J., 2010. The state, resilience, and potential future of disturbance-dependent oak forests as perceived by regional change agents. Ecol. Soc. 15 (4), 5, <<u>http://www.ecologyandsociety.org/vol15/</u> iss4/art5/>.
- LANDFIRE, 2010. LANDFIRE Forest Canopy Cover layer. U.S. Department of Interior, Geological Survey. Available online at <<u>http://landfire.cr.usgs.gov/viewer></u>; last accessed May 1, 2014.
- LaPoint, E., 2005. Access and use of FIA data through FIA Spatial Data Services. In: Proceedings of the Fifth Annual Forest Inventory and Analysis Symposium, 2003 November 18–20; New Orleans, LA. USDA For. Ser. Gen. Tech. Rep. WO-69, 222p.
- Liu, F., Mladenoff, D.J., Keuler, N.S., Schulte Moore, L., 2011. Broadscale variability in tree data of the historical Public Land Survey and its consequences for ecological studies. Ecol. Mono. 81, 259–275.
- Lorimer, Č.G., Chapman, J.W., Lambert, W.D., 1994. Tall understorey vegetation as a factor in the poor development of oak seedlings beneath mature stands. J. Ecol. 82 (2), 227–237.
- McCune, B., Grace, J., 2002. Analysis of Ecological Communities. MjM Software Design, Gleneden Beach, OR, 300 p.
 McCune, B., Mefford, M.J., 1999. PC-ORD: multivariate analysis of ecological data,
- McCune, B., Mefford, M.J., 1999. PC-ORD: multivariate analysis of ecological data, vol. 4.25. MjM Software Design, Gleneden Beach, OR.
- McEwan, R.W., Dyer, J.M., Pederson, N., 2011. Multiple interacting ecosystem drivers: toward an encompassing hypothesis of oak forest dynamics across eastern North America. Ecography 34, 244–256.
- McNab, W.H., Cleland, D.T., Freeouf, J.A., Keys, J.E., Nowacki, G.J., Carpenter, C.A., 2007. Description of ecological subregions: sections of the conterminous United States (CD-ROM), USDA For. Serv. Gen. Tech. Report WO-76B, 80 p.
- McShea, W.J., Healy, W.M., 2002. Oaks and acorns as a foundation for ecosystem management. In: McShea, W.J., Healy, W.M. (Eds.), Oak Forest Ecosystems Ecology and Management for Wildlife. The Johns Hopkins University Press, Baltimore, Maryland.

- Nowacki, G.J., Abrams, M.D., 2008. The demise of fire and "mesophication" of forests in the eastern United States. Bioscience 58, 123–138.
- Nowacki, G.J., Abrams, M.D., 2014. Is climate an important driver of post-European vegetation change in the Eastern United States? Glob. Change Biol. doi: http:// dx.doi.org/10.1111/gcb.12663.
- Nowacki, G.J., Abrams, M.D., Lorimer, C.G., 1990. Composition, structure, and historical development of northern red oak stands along an edaphic gradient in north-central Wisconsin. For. Sci. 36, 276–292.
- O'Connell, B.M., LaPoint, E.B., Turner, J.A., Ridley, T., Pugh, S.A., Wilson, A.M., Waddell, K.L., Conkling, B., 2014. The Forest Inventory and Analysis Database: Database Description and User Guide Version 6.0 for Phase 2. USDA For. Serv. http://www.fia.fs.fed.us/library/database-documentation/current/ver6.0/ FIADB_user%20guide_6-0_p2_5-6-2014.pdf (last accessed 31.07.14).
- Parker, G.R., Leopold, D.J., 1983. Replacement of Ulmus Americana L. in a mature east-central Indiana woods. Bull. Torrey Bot. Club 110, 482–488.
- Poland, T.M., McCullough, D.G., 2006. Emerald ash borer: invasion of the urban forests and the threat to North America's ash resource. J. For. 104, 118–124.
- Prasad, A.M., Iverson, L.R., Matthews, S., Peters, M., 2007-ongoing. A Climate Change Atlas for 134 Forest Tree Species of the Eastern United States (database). Northern Research Station, USDA Forest Service, Delaware, OH. <<u>http://www.nrs.fs.fed.us/atlas/tree</u>> (last accessed 05.10.14).
- Rhemtulla, J.M., Mladenoff, D.J., Clayton, M.K., 2007. Regional land-cover conversion in the U.S. upper Midwest: magnitude of change and limited recover (1850– 1935–1993). Landscape Ecol. 22, 57–75.
- Rhemtulla, J.M., Mladenoff, D.J., Clayton, M.K., 2009. Legacies of historical land use on regional forest composition and structure in Wisconsin, USA (mid-1800s-1930s-2000). Ecol. Appl. 19, 1061–1078.
- Rodewald, A.D., Abrams, M.D., 2002. Floristics and avian community structure: implications for regional changes in eastern forest composition. For. Sci. 48 (2), 267–272.
- Rogers, D.A., Ronney, T.P., Olson, D., Waller, D.M., 2008. Shifts in southern Wisconsin forest canopy and understory richness, composition, and heterogeneity. Ecology 89, 2482–2492.
- Rooney, T.P., Waller, D.M., 2003. Direct and indirect effects of white-tailed deer in forest ecosystems. For. Ecol. Manage. 181, 165–176.
- Schulte, L.A., Mladenoff, D.J., 2001. The original US Public Land Survey records: their use and limitations in reconstructing presettlement vegetation. J. For. 99, 5– 10.
- Schulte, L.A., Mladenoff, D.J., Crow, T.R., Merrick, L.C., Cleland, D.T., 2007. Homogenization of northern U.S. Great Lakes forests due to land use. Landsc. Ecol. 22, 1089–1103.
- Schulte, L.A., Mottl, E.C., Palik, B.J., 2011. The association of two invasive shrubs, common buckthorn (*Rhamnus cathartica*) and Tartarian honeysuckle (*Lonicera tatarica*), with oak communities in the Midwestern United States. Can. J. For. Res. 41, 1981–1992.
- Shea, M.E., Schulte, L.A., Palik, B.J., 2014. Reconstructing vegetation past: Pre-Euro-American vegetation for the Midwest Driftless Area, USA. Ecol. Rest. 32, 417– 433.
- Smith, W.B., 2002. Forest inventory and analysis: a national inventory and monitoring program. Environ. Pollut. 116, S233–S242.
- Starrs, P.F., 2002. Perspectives on cultural values of California oaks. In: Standiford, R.B., McCreary, D., Purcell, K.L. (Eds.). Proc. of the Fifth Symposium on Oak Woodlands: Oaks in California's Changing Landscape, pp. 21–30. USDA Forest Service Gen. Tech. Rep. Gen. PSW-GTR-184. 10 p.
- Taylor, S.O., Lorimer, C.G., 2003. Loss of oak dominance in dry-mesic deciduous forests predicted by gap capture methods. Plant Ecol. 167, 71–88.
- Thompson, J.R., Carpenter, D.N., Cogbill, C.V., Foster, D.R., 2013. Four centuries of change in northeastern United States forests. PLoS ONE 8, 9. http://dx.doi.org/ 10.1371/journal.pone.0072540.
- USDA Forest Service, 2013. Forest Inventory and Analysis: Fiscal Year 2012 Business Report. FS-1020. USDA For. Serv. http://www.fia.fs.fed.us/library/bus-org-documents/docs/FIA_Annual_Report_2012-opt.pdf> (last accessed 31.07.14).
- USDA Natural Resources Conservation Service. 2013. Driftless Area Landscape Conservation Initiative, Fact Sheet. http://www.nrcs.usda.gov/Internet/FSE_DOCUMENTS/stelprdb1143000.pdf> (last accessed 03.06.14).
- Wendland, W.M., Kunkel, K.E., Conner, G., Decker, W.L., Hillaker, H., Naber-Knox, P., Nurnberger, F.V., Rogers, J., Scheeringa, K., Zandlo, J., 1992. Mean 1961–1990 temperature and precipitation over the Upper Midwest. Research Report 92–01. Midwestern Climate Center, Champagne, Illinois.
- Whitney, G.G., Davis, W.C., 1986. Thoreau and the forest history of Concord, Massachusetts. J. For. History 30, 70–81.
- Williams, M., 1989. Americans and Their Forests: a Historical Geography. Cambridge University, Cambridge, Massachusetts, 599 p.
- Wood, E.M., Pidgeon, A.M., Liu, F., Mladenoff, D.J., 2012. Birds see the trees inside the forest: the potential impacts of changes in forest composition on songbirds during spring migration. For. Ecol. Manage. 280, 176–186.
- Zhang, Y., Liao, X., Butler, B.J., Schelhas, J., 2009. The increasing importance of smallscale forestry: evidence from family forest ownership patters in the United States. Small-scale For. 8 (1), 1–14.