Comparison of Structural and Compositional Attributes of Northern Hardwood Forests in Michigan and Minnesota

Marcella A. Windmuller-Campione[1]

Abstract.—Northern hardwood forests are structurally and compositionally diverse resulting in multiple "types" of northern hardwood forest communities. Within the northern Great Lakes Region of the United States (Michigan, Minnesota, and Wisconsin), Minnesota represents a transition zone for multiple tree species with some tree species reaching their western, northern, or southern edge of their range including sugar maple (*Acer saccharum*). To explore the potential influence of range limits on the structure and composition of northern hardwood forest communities, I utilized the Forest Inventory and Analysis database on a subset of counties in eastern Minnesota and the western Upper Peninsula of Michigan. One hundred and eleven plots across 10 counties in the two states were coded as the maple/basswood/beech forest type. Between the two states, there were many similarities in site conditions and overall metrics of forest communities (average diameter, age, regeneration density). However, Minnesota and Michigan northern hardwood forests are compositionally different; Michigan northern hardwood forests were more commonly dominated by sugar maple and red maple (*Acer rubrum*), while American basswood (*Tilia americana)* and northern red oak (*Quercus rubra*) were more common in Minnesota. A nonmetric multidimensional scaling ordination showed clear separation between plots from Michigan and Minnesota in ordination space. As interactions among climate change, invasive species, ownership patterns, and disturbance regimes continue to influence species composition in forest communities, understanding the range of potential northern hardwood community composition and structure can provide opportunities to explore alternative silvicultural approaches.

INTRODUCTION

The northern hardwood forest cover type encompasses an extensive area of the northern Great Lakes Region (defined as Michigan, Minnesota, Wisconsin, USA, and Ontario, Canada; hereafter referred to as GRL), extending across the northeastern United States and southern Canadian providences (Braun 1950). This cover type represents a diverse mix of overstory species, soil conditions, moisture regimes, and disturbance dynamics. "The Manager's Handbook for Northern Hardwoods in the North Central States" (Tubbs 1977) documents seven different forest types; only two of the forest types are dominated by sugar maple (*Acer saccharum* Marshall). The other five forest types have lesser amounts of sugar maple and a broader mix of hardwood and conifer species including northern red oak (*Quercus rubra* L.), paper birch (*Betula papyrifera* Marshall), and eastern hemlock (*Tsuga canadensis* (L.) Carrière). However, sugar maple dominated forest types are often the "poster child" for northern hardwood management (Crow et al. 2002, Hupperts et al. 2018, Neuendorff et al. 2007, Scheller and Mladenoff 2002).

The prevalence of research on sugar maple dominated forest types is likely due to in part to its historic and current economic value (Dey et al. 2017, Godman and Mendel 1978). After the

[1] Associate Professor of Silviculture, Department of Forest Resources, University of Minnesota, 1530 Cleveland Ave. N., St. Paul, MN 55108. To contact, call 612-624-3400) or email mwind@umn.edu.

extensive cut-over of eastern white pine (*Pinus strobus* L.) and other conifer species in the GRL during Euro-American colonization, lumber companies that did not move westward had to switch to harvesting hardwood forests (Whitney 1987). There was a push to move from exploitive high-grading to exploring concepts of sustained yield. One research forest to explore this concept was the Dukes Experimental Forest (EF), located outside of Marquette, MI, which was established in 1926 (Kern et al. 2014). The Dukes EF had limited selective harvesting of American elm (*Ulmus americana* L.) and American basswood (*Tilia americana* L.) and was a mostly unharvested with northern hardwood forest dominated by sugar maple (>80 percent of merchantable sized trees) where researchers explored both even- and uneven-aged management. However, one of the most well known products from the Dukes EF was the Arbogast marking guide; it was cited as being applied to millions of hectares in the Lake States (Arbogast 1957). The Arbogast marking guide focuses on the development of a well regulated and balanced diameter distribution through the use of ratios, commonly called the q factor, which creates a reverse-J diameter distribution and is implemented with a relatively frequent cutting cycle (10 to 15 years) using single-tree selection system. This silvicultural system has been documented through multiple long-term experiments in the GLR, e.g., Dukes EF, Argonne Experimental Forest, and Ford Forestry Center (Bassil et al. 2019, Campione et al. 2012, Kenefic and Kern 2015, Metzger and Tubbs 1971, Neuendorff et al. 2007) to maintain high quality sugar maple dominant forests (see Webster et al. 2018 for noted shortcomings).

However, not all northern hardwood forests are dominated by sugar maple. Sugar maple reaches its western range in Minnesota which roughly corresponds with the border of the Prairie Parkland province (Godman et al. 1990). The northern range of sugar maple extends slightly north of Minnesota into the Canadian providence of Quebec. Minnesota is also the western and/or northern range limit(s) for other common northern hardwood associates including eastern hemlock, yellow birch (*Betula alleghaniensis* Britton), and northern red oak (Burns and Honkala 1990). Thus, the composition of northern hardwood forests in Minnesota are likely different than northern hardwood forests of northern Wisconsin and the Upper Peninsula of Michigan and thus may require different silvicultural strategies. There has been limited work to explore if structural and composition differences exist among northern hardwood forests in the GLR region (but see Burton et al. 2009).

The overarching goal of this paper is to explore and quantify structural and compositional differences within forest classified as northern hardwood in two regions, northern Minnesota and the Upper Peninsula of Michigan, using the Forest Inventory and Analysis (FIA) database. By assessing current species composition and structure within the northern hardwood forest type in the GLR, we can increase our understanding of the range of variability within this forest type and thus explore potential alternative management practices.

METHODS

Sites

The GLR of Minnesota, Wisconsin, and Michigan covers four of Bailey's (1983) ecosystem provinces: Prairie Parkland, Tall-grass Prairie, Laurentian Mixed Forest, and the Eastern Deciduous Forest. Topography and soil conditions have been influenced by past glacial activity, creating a landscape with low topographic relief and a wide variety of soil types ranging from sandy outwash plains to rich peat bogs (Stearns 1997). Nutrient availability and water holding capacity greatly influence forest composition and cover; northern hardwoods are commonly observed on mesic, nutrient rich sites in both Michigan and Minnesota (Aaseng et al. 2011, Burger and Kotar 2003).

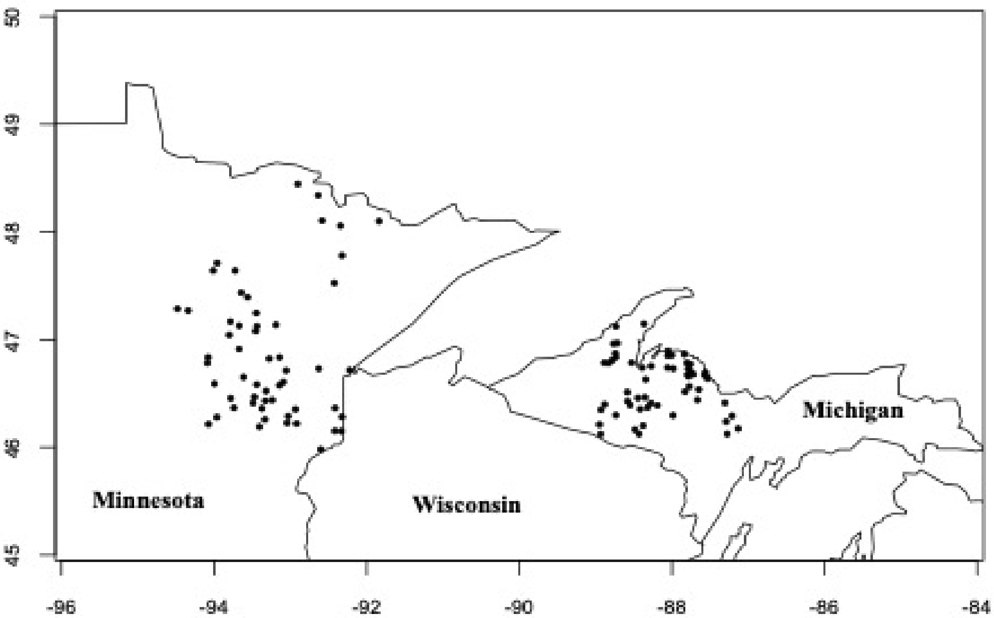

Figure 1.—Locations of FIA plots in Minnesota and Michigan used in analysis. Publically available plot data were used in mapping so plot locations represent "fuzzed" data.

Ten counties were selected for the study in Minnesota and Michigan which cover a range of environmental conditions, especially distance from a Great Lake (Fig. 1). Minnesota counties included in the sampling were: Aitkin, Carlton, Cass, Crow Wing, Itasca, Pine, and St. Louis. Michigan counties included in the sampling were: Baraga, Houghton, Iron, and Marquette. This does not represent a full list of counties in which northern hardwoods are present in Michigan and Minnesota but does represent the northern hardwood forest type for the region. More eastern counties of the Upper Peninsula of Michigan were not selected for this study due to the increased presence of American beech (*Fagus grandifolia* Ehrh.), which reaches its western range in the central Upper Peninsula of Michigan. Current impacts of beech bark disease (*Cryptococcus fagisuga/Neonectria spp.* complex) are influencing the forest dynamics of eastern northern hardwood forests (see Nyland et al. 2006 for the discussions). Thus, northern hardwood forests were selected in the western and central Upper Peninsula of Michigan.

Across the 10 counties included in the study, the climate is characterized by cold winters and warm, humid summers. Temperatures can range from 32 °C with high humidity (80 percent) during the growing season and –35 °C during the winter months (Neary et al. 2012). Average annual precipitation ranges from 50 to 60 cm in northern Minnesota (Neary et al. 2012); average annual precipitation in Houghton County, Michigan is 85.4 cm. The majority of precipitation falls within the growing season. However, areas close to the Great Lakes are influenced by "lake effect" with smaller seasonal differences in temperatures (i.e., warmer winters and cooler summers) and greater "lake effect" snow (Norton and Bolsenga 1993).

Current forest cover has been greatly influenced by recent management decisions during European colonization including agricultural conversion and exploitive logging practices during the early 20th century (Stearns 1997). Agricultural conversion and subsequent increases in urban communities have decreased forest cover by 40 percent in the GLR (Schulte et al. 2007). Destructive logging practices in the early 20th century shifted forest composition to more early successional broadleaf species (i.e., aspen (*Populus* spp.)) and reduced the abundance of long-lived conifers (i.e., eastern white pine). Additionally, destructive high-grading practices in northern hardwood forests were common in the region (Erickson et al. 1990). While both states include a diverse mix of federal, tribal, state, county, nonprofit, private industrial, and private nonindustrial family forests (Windmuller-Campione et al. 2020), there are some differences within the ownership patterns. Within Michigan, 61 percent of the 8.1 million hectares of forest land is owned by private individuals and organizations; state and local and federal management contributes 23 percent and 15.5 percent, respectively (USDA Forest Service 2020a). Within private ownership in Michigan, there are 1.2 million hectares managed by private industrial forest corporations. Private landowners are still the biggest portion of land owners in Minnesota; they own 45 percent of the approximately 7.1 million hectares of forest land (USDA Forest Service 2020b). State and local organization and federal organization manage 38.7 percent and 16.5 percent of forested lands, respectively. Within private ownership in Minnesota, less than 500,000 hectares are owned and managed by private industrial forest corporations.

Data

The United States Department of Agriculture (USDA) Forest Service's Forest Inventory and Analysis (FIA) program is responsible for the collection of a national-scale forest inventory across all ownerships in the nation (Oswalt et al. 2014). Currently, data are collected using a nationally consistent three-phase sampling design (Bechtold and Patterson 2005). Phase 1 of the sampling design uses satellite imagery to stratify forested and nonforested conditions. Forests are defined as lands that have a minimum of 10 percent coverage of tree species canopies, are at least 0.4 ha in size, and are at least 36.6 m wide. Phase 2 of the FIA program utilizes Phase 1 land cover classification to establish forest plots approximately one every 2,428 ha of forested land. The Phase 2 plots consist of four, 7.2-m fixed-radius circular subplots arranged in a triangle with one subplot in the center. Within each subplot, overstory trees (diameter at breast height [d.b.h.] >12.7 cm) are assessed. Within each of the four subplots there is a series of microplots where saplings (d.b.h. 2.54 to 12.6 cm), seedlings (d.b.h. <2.54 cm), and other vegetative variables are measured. The sapling and overstory layer were combined for analysis. Phase 3 plots include additional measures for forest health, soils, and other environmental variables and are completed on a subset of Phase 2 plots. For this study, Phase 2 plots were used. Data are freely available and open to the public (https://apps.fs.usda.gov/fia/datamart/datamart.html).

The FIA database was queried for all single-condition plots sampled in 2014 and 2015 classified as maple/beech/birch (forest type code 800) located in six counties in Minnesota and four counties in Michigan. Forest condition classes are defined as portions of plots with distinct differences in vegetation cover or land management (Woudenberg et al. 2010). This resulted in a total of 111 plots with 56 in Michigan and 55 in Minnesota. The dataset does not represent a full inventory cycle or capture all plots classified as the northern hardwood type in either Minnesota or Michigan during the sampling years. However, due to the updated FIA grid systems, the years and counties selected represent an unbiased estimate of northern hardwood forests in of the selected regions.

Analysis

For each plot, measures of overstory and understory density were expanded to calculate trees per hectare (TPH) and basal area per hectare. Additional variables including average diameter (cm), average height (m), site index (m), overstory species richness, overstory evenness, and overstory Shannon's diversity were summarized at the plot level. Student t-tests with an unequal variance in R (R Core Team 2019) were used to test for differences in structure and composition between the two states, Michigan and Minnesota. To further explore differences in composition and structure, diameter distributions using 5-cm diameter classes and average basal area per hectare by species was constructed for each state. Species whose average composition was less the 1.5 m^2 ha^{-1} of basal area were grouped into other conifers or other broadleafs. Each of these pooled categories represented on average less than 3 m^2 ha^{-1}.

Table 1.—Average structural attributes for the overstory and seedling layers and site characteristics with associated standard errors in parenthesis by state. Student t-test in R with unequal variances were used to test for statistical differences between the two states for each individual variable.

	Michigan		Minnesota		T-value & significance	Degrees of freedom
Overstory averages						
TPH	1391	(108)	1862	(173)	2.31*	DF = 90.8
Basal area/ha (m^2 ha^{-1})	29.19	(1.20)	26.55	(1.40)	1.43	DF = 106.3
Diameter (cm)	21.49	(0.50)	20.58	(0.70)	1.06	DF = 98.0
Height (m)	18.15	(0.36)	16.77	(0.57)	2.06	DF = 90.6
Species richness	4.91	(0.24)	5.76	(0.31)	2.19 *	DF = 102.5
Shannon's Diversity Index	1.07	(0.06)	1.35	(0.06)	3.39 ***	DF = 108.7
Evenness	0.67	(0.03)	0.55	(0.02)	3.98 ***	DF = 99.3
Seedling averages						
TPH	13153	(1621)	9649	(1058)	1.81	DF = 94.4
Site averages						
Slope (%)	10.75	(1.41)	6.55	(1.41)	2.11*	DF = 109.0
Site index	17.91	(0.39)	18.78	(0.47)	1.42	DF = 105.6
Stand age	73.21	(2.27)	69.18	(3.80)	0.91	DF = 88.5
Elevation (m)	412.17	(14.68)	401.20	(4.40)	0.72	DF = 61.3

Significance levels: *p<0.05; ** p<0.01; ***p<0.001

Nonmetric multidimensional scaling (NMS) ordination using PC-ORD version 6 (McCune and Mefford 2011) was used to compare the composition of northern hardwood forest communities between the counties in Michigan and Minnesota. NMS has relaxed normality assumptions and does not assume a linear response to environmental gradients which is common in ecological data (McCune et al. 2002). Overstory basal area per hectare by species and status (live or dead) was summarized at the plot level and used in the species or main matrix. Uncommon species were not removed. Additionally, both live and dead species were included in the ordination since they represent important structural components of the stand. Thirty-two environmental variables were used in the environmental or second matrix (appendix 2). Autopilot mode (slow and thorough) was selected using Sørensen (Bray-Curtis) distance measurement and a random starting point for both datasets. Two hundred and fifty runs were completed for both the real data and randomized data to determine dimensionality for both data sets. Chi-square analysis using Sørensen (Bray-Curtis) distance measurement was also run to explore associations between species.

RESULTS

Structural and Compositional Comparison

There were many site and structural similarities between northern hardwood forests of Minnesota and Michigan (Table 1). Northern hardwood sites in Minnesota and Michigan have on average a site index of 18 m at 50 years, a stand age of 70 years old, and an elevation of approximately 400 m. Additionally, stands have approximately 28 m^2 ha^{-1} of basal area per hectare with an average diameter of 21 cm, an average height of 17 m, and thousands of seedlings (d.b.h. <2.54 cm) regenerating. One of the main differences between the states was that northern hardwood forests in Minnesota had on average significantly greater overstory density than Michigan, 1862 TPH (±173) and 1391 TPH (±108), respectively. However, there was no significant difference in the overstory basal area between the two states (Table 1). Minnesota northern hardwood stands also

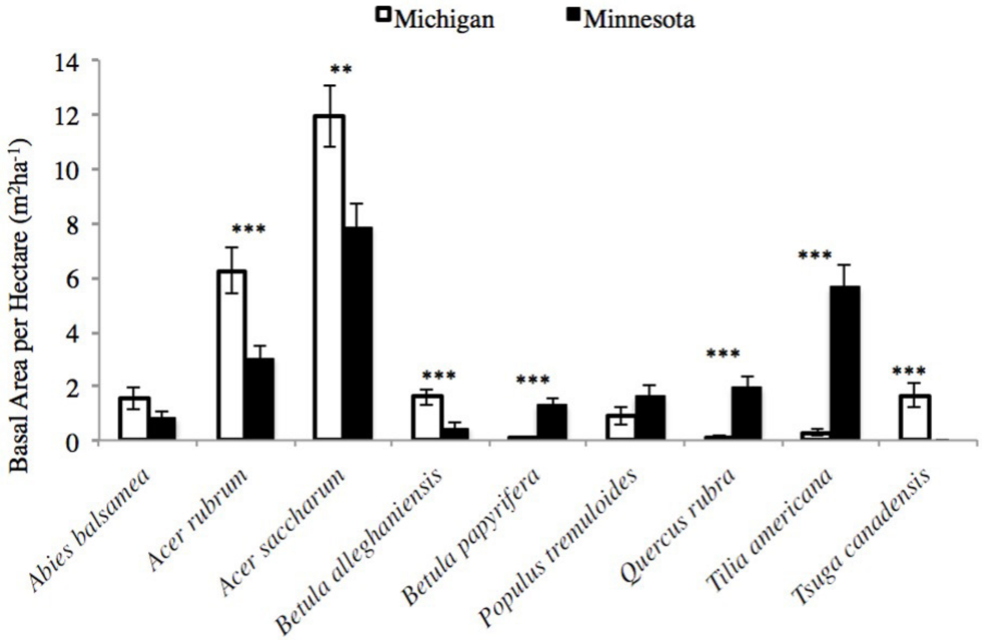

Figure 2.—Average basal area per hectare and associated standard error of the most dominant species present in Michigan and Minnesota northern hardwood forests. Student t-test with unequal variances were used to test for differences between states for each species. Levels of significance are * <0.05; ** <0.01; ***<0.001.

had significantly greater diversity than Michigan stands; all three measures of diversity (overstory species richness, overstory Shannon's diversity index, and overstory evenness) were significantly greater in Minnesota than Michigan (Table 1).

There were greater differences observed in the composition than the structure of northern hardwood stands in Minnesota and Michigan (Fig. 2). A total of 32 unique overstory species were observed in the 111 plots across the two states (appendix 1). Nineteen of the overstory species were common between the two states; five unique overstory tree species were observed in Michigan and eight unique overstory tree species were observed in Minnesota. Within the broader sampling area, many of the tree species had, on average, very low densities both in terms of trees per hectare and basal area per hectare. Nine species were common in Michigan and/or Minnesota: balsam fir (*Abies balsamea (L.) Mill*), red maple, sugar maple, yellow birch, trembling aspen (*Populus tremuloides* D.A. Perala*)*, northern red oak, American basswood, and eastern hemlock. Of the nine dominant species, only two species, balsam fir and trembling aspen, were not significantly different between the two states. Red maple, sugar maple, yellow birch, and eastern hemlock all had significantly greater density in Michigan compared to Minnesota. Greater density of paper birch, northern red oak, and American basswood were observed in Minnesota compared to Michigan (Fig. 2).

Diameter Distribution

The allocation of basal area by diameter class and by species was different between the two states (Fig. 3 A, B). There was greater basal area of red maple and sugar maple across diameter classes in Michigan compared to Minnesota (Fig. 3). There was less basal area in smaller diameter classes (<17.5 cm d.b.h.) in Michigan compared to Minnesota. The Minnesota diameter distribution had a relatively flat shape with a more even distribution of basal area across diameter classes up to 42.4 cm (Fig. 3B). This is in contrast to higher basal area in larger diameter classes in Michigan; the larger diameter classes, starting at 22.5 cm, display a strong reverse-J or negative exponential distribution.

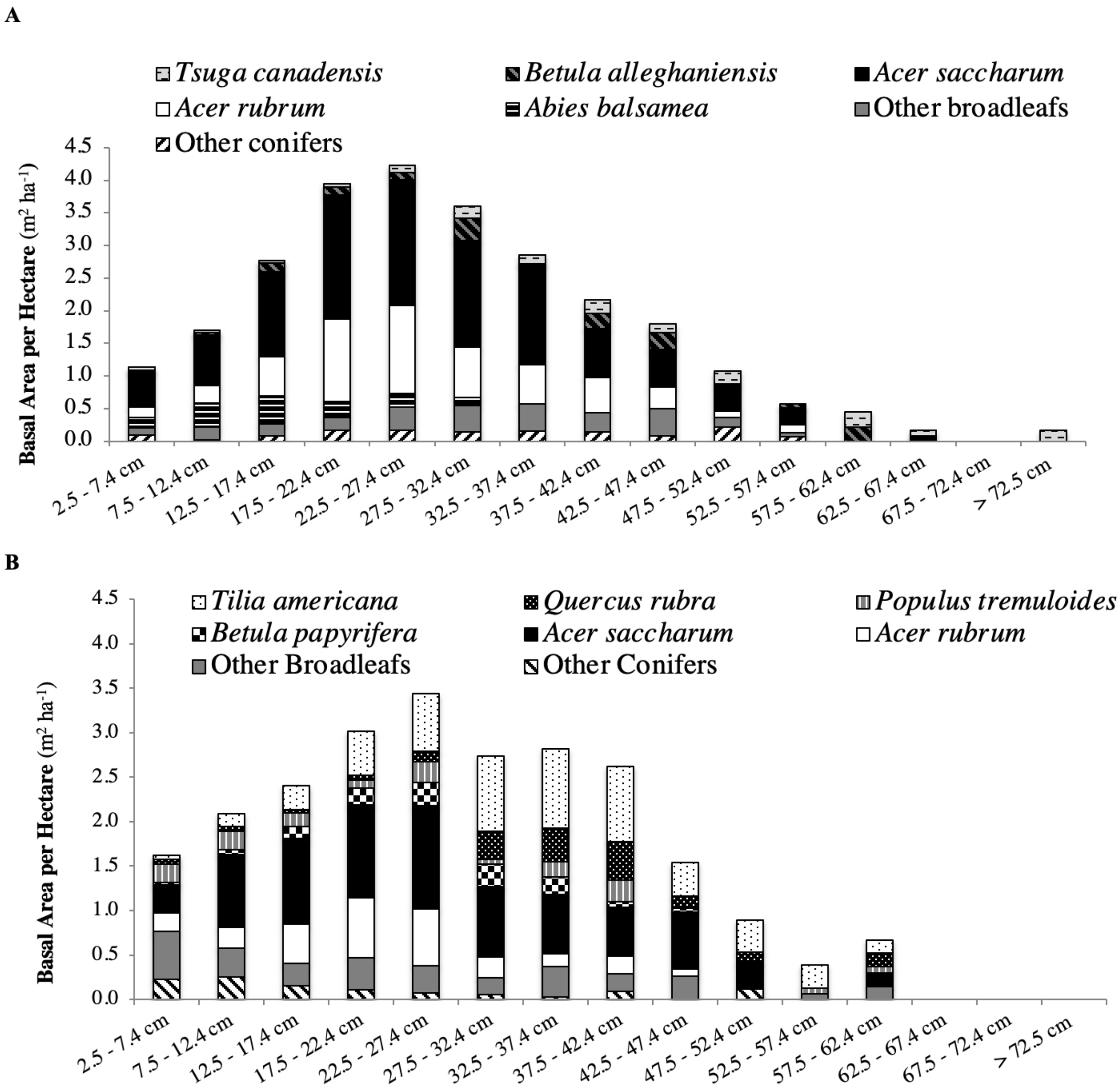

Figure 3.—Average distribution of basal area per hectare (m^2ha^{-1}) by species and diameter class for northern hardwood forests in Michigan (A) and Minnesota (B) counties. Five centimeter diameter classes were used for analysis. Species with less than 1.5 m^2 ha^{-1} basal area on average were grouped into one of two categories: other broadleafs or other conifers.

Nonmetric Multidimensional Scaling (NMS) Ordination

The NMS ordination resulted in a three-dimensional solution, explaining 84.7 percent of the variance in overstory community composition between Minnesota and Michigan, and had a final stress of 14.72 and final instability of 0.00 (Fig. 4). Axis 1 and axis 2 were most informative, explaining 44 percent and 25 percent of the variation, respectively. Strong separation between plots in Minnesota and Michigan was displayed in the ordination. Three environmental variables were considered important to understanding the underlying ecological gradient (r^2 >0.2) on either axis 1 or axis 2. Axis 1 was associated with the plot average specific gravity of tree species present and the plot average height of overstory tree species. More negative values on axis 1 were associated with plots with higher average specific gravity and greater average height. Axis 2 was strongly associated with the longitude of overstory plots with more negative values associated with more eastern sites and more positive values associated with more western sites.

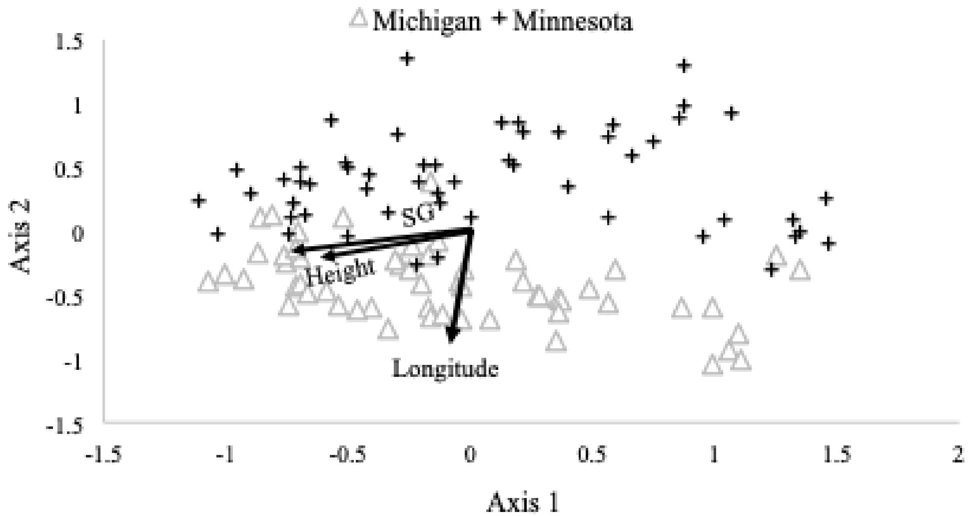

Figure 4.—Nonmetric multidimensional scaling (NMS) ordination displaying compositional differences in northern hardwood plots in Michigan and Minnesota. Axis 1 explained 44 percent of the variation, while axis 2 explained 25 percent of the variation. Plot locations and environmental variables with a $r^2>0.2$ are displayed in ordination space. Definitions: SG–plot average of specific gravity; Height–plot average height in meter; Longitude–"fuzzed" longitudinal values of FIA plots.

DISCUSSION

The FIA plots within northern Minnesota and the Upper Peninsula (UP) of Michigan highlight the diversity in species and structural composition that is within the northern hardwood forest type. Across the two states, 32 unique overstory species were observed including long-lived, shade-tolerant conifers, short-lived, shade-intolerant hardwoods, and the full range of silvics for other species (Burns and Honkala 1990) (appendix 1).

While this full range of species were present across the two states, there were some notable differences in terms of species composition, structure, and diversity. The NMS ordination which utilized species composition within the main matrix, resulted in pretty district separation in ordination space for plots from Michigan and Minnesota (Fig. 4). One of the factors contributing to differences between the two states may relate to individual species ranges and the boundaries (Burns and Honkala 1990). Minnesota represents the edge of many species ranges and may contribute to different path of stand development (Gill et al. 2016). For example, while eastern hemlock does have some very limited populations in Minnesota, this species is almost exclusively absent from Minnesota northern hardwood forests compared to the UP of Michigan where there is active research exploring management techniques related to regeneration (Webster and Lorimer 2002).

Another factor may be related to the types of silvicultural systems utilized within the northern hardwood forest types in Minnesota and Michigan. The selection system (single, group, or a combination) with natural regeneration is one of the most common and prevalent types of silvicultural systems utilized within northern hardwood forests (Nyland 1998), especially in Michigan (Pond et al. 2014). Multiple studies across the region document the ability of single tree selection with natural regeneration to generate high economics returns and the sustained recruitment of shade tolerant species (e.g., sugar maple) (Horsley et al. 2003, Neuendorff et al. 2007). There was no significant difference among ownerships within Michigan, in the implementation of single tree selection; there was a range among the ownership classes in how single tree selection utilizing the Arbogast method was implemented (Pond et al. 2014). When natural regeneration is successful, the single tree selection system results in the increased dominance of sugar maple, an aesthetically appealing stand, and the potential for high quality products (veneer quality trees) (Kiernan et al. 2008).

However, there are some notable limitations of single tree selection with natural regeneration (Walters et al. 2020). One limitation first relates to the assumption that natural regeneration will happen (Henry et al. 2021, Millington et al. 2013). Deer browse, drought, exotic earthworms, and many other factors may result in regeneration failures which may not be accounted for in single tree selection systems (Holdsworth et al. 2007, Powers and Nagel 2009). A second limitation that is increasingly being explored is the loss of overstory species diversity. For multiple decades, managers and researchers have been exploring silvicultural techniques which can increase species diversity, especially of mid- and shade-intolerant species, in maple dominated northern hardwood stands (e.g., Hupperts et al. 2020, Poznanovic et al. 2013, Shields et al. 2007).

While sugar and red maple are components of Minnesota's northern hardwood forests, they are not necessarily always the dominant species (Fig. 2). Minnesota's northern hardwood forests have greater species richness, Shannon's diversity, and evenness compared to Michigan (Table 1). Basswood, northern red oak, and paper birch all have greater overstory density in Minnesota compared to Michigan. Basswood, northern red oak, and paper birch are considered mid-tolerant or shade-intolerant species (Burns and Honkala 1990). While these species are more common in Minnesota's northern hardwood forests, there are limited examples of research studies exploring silvicultural methods to maintain or promote mixed species northern hardwood stands in Minnesota. However, there are examples in the University of Minnesota's Great Lakes Silviculture Library (GLSL) of silvicultural systems that managers are using that detail the use of larger gaps/opening through seed tree, shelterwoods systems (with or without residuals), or group selection system to regenerate mid- and shade-intolerant species (https://silvlib.cfans.umn.edu/). The utilization of these other regeneration harvests may in part be driven by the higher prevalence of northern red oak which is a mid-tolerant species compared to the extremely shade tolerant sugar maple (Burns and Honkala 1990)

There are numerous factors (environmental and anthropogenic) which have influenced the current species composition and structure of northern hardwood forest communities within Minnesota and Michigan. However, as climate change, invasive species, and shifting disturbance regimes influence northern hardwood forests, natural resource managers will require adaptation (D'Amato and Palik 2021). While single tree selection was considered the "gold standard" for northern hardwood management, this standard is changing and alternative methods are being explored (Huppert et al. 2020, Walters et al. 2020).

Natural resource managers will critically need to evaluate each individual northern hardwood stand and not assume natural regeneration will happen (Walters et al. 2020); natural resource managers will need to address and evaluate each of three legs of the regeneration triangle (seed source, seed bed, and environment) for each of the multiple species within a northern hardwood stand (Nyland 2006). While there is limited potential to "control" the environment, there may be opportunities to explore how residual trees, down dead wood, and different layers of vegetation may influence the local environmental conditions for regenerating seedlings. Multiple methods and techniques (salmon blading, variable radius gaps, shelterwoods with residuals, and enrichment plantings) have and are being implemented successfully to regenerate individual species, increase tree level diversity, and are documented in the GLSL. These treatments can potentially expand the "silvicultural norms" in northern hardwood management and also expand the norms for how data and results are shared through living case studies on the GLSL and within peer-reviewed literature.

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APPENDIX 1

Table 2.—Overstory tree species and presence in respective states used in the ordination from the FIA from the selected country

Species	Observed in Minnesota	Observed in Michigan
Abies balsamea	X	X
Acer pensylvanicum		X
Acer rubrum	X	X
Acer saccharinum	X	
Acer saccharum	X	X
Acer spicatum	X	X
Amelanchier spp.		X
Betula alleghaniensis	X	X
Betula papyrifera	X	X
Carpinus caroliniana	X	
Carya cordiformis	X	
Fagus grandifolia		X
Fraxinus americana		X
Fraxinus nigra	X	X
Fraxinus pennsylvanica	X	X
Juglans cinerea	X	
Ostrya virginiana	X	X
Picea glauca	X	X
Picea mariana	X	X
Pinus banksiana	X	
Pinus strobus	X	X
Populus balsamifera	X	
Populus grandidentata	X	X
Populus tremuloides	X	X
Prunus serotina	X	X
Prunus virginiana	X	
Quercus macrocarpa	X	
Quercus rubra	X	X
Thuja occidentalis	X	X
Tilia americana	X	X
Tsuga canadensis		X
Ulmus americana	X	X

APPENDIX 2

Table 3.—Environmental variables used in the ordination and the correlation with axis 1 and 2

Environmental Variable	FIA Variable Code	R^2 Value Axis 1		R^2 Value Axis 2	
Overstory tree species richness	calculated$^+$	0.047		0.028	
Overstory Shannon's Diversity	calculated$^+$	0.127		0.047	
Overstory evenness	calculated$^+$	0.079		0.116	
Seedling TPH	calculated$^+$	0.045		0.003	
Average height (m)	calculated$^+$	0.312	*	0.042	
Average crown ratio	calculated$^+$	0.015		0.007	
Average diameter (cm)	calculated$^+$	0.120		0.001	
TPH	calculated$^+$	0.033		0.000	
Basal area/hectare (m^2 ha^{-1})	calculated$^+$	0.104		0.137	
Specific gravity	SG	0.470	*	0.032	
Latitude	LAT	0.051		0.020	
Longitude	LON	0.004		0.628	*
Stand Age	STAGE	0.176		0.038	
Site index for the condition	SICOND	0.045		0.032	
Slope	SLOPE	0.011		0.001	
Aspect	ASPECT	0.014		0.000	

* Strongly correlated r^2>0.2

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