Sugar maple (*Acer saccharum*) forest community dynamics across an environmental gradient from the prairie-forest border to interior forest biome

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Abstract

Forest ecosystems are dynamic entities that are subject to a variety of biotic and abiotic environmental changes. Invariably, climate is one of the principal factors controlling the distribution of ecosystems and past fluctuations in climate are known to have shaped the Midwestern United States forests. The Upper Great Lakes region of North America includes Minnesota, Wisconsin, and Michigan, and is characterized by a gradual south to north climatic gradient that defines the eastern deciduous forests (oak-hickory) to the south, the northern mixed hardwood forests (maple, hemlock, and beech) in northern Michigan and Wisconsin, and the sub-boreal forest (spruce-fir) in the far northern parts of the region. Additionally, the Upper Great Lakes region lies at the intersection of three major contrasting air masses: the cold, dry, polar continental air mass descending from the north; the dry, continental westerlies; and the warm, moist, tropical maritime air mass coming from the Gulf of Mexico. Interactions among these three air masses have created a southwest to northeast climatic gradient across the region resulting in a drier and warmer environment in southwest Minnesota as opposed to wetter and cooler conditions in Upper Michigan. It is in this context that the Upper Great Lakes region ecosystems were formed. They include the prairie-forest border (Zone 1), a transition zone between the tall grass prairies and the northern forests in Minnesota; the forest interior (Zone 2), which extends beyond the prairie-forest border into northern Wisconsin; and the deep forest (Zone 3), which lies in Michigan's Upper Peninsula. In recent years, numerous concerns about global environmental changes and their impact on the Upper Great Lakes northern hardwood forests have emerged. Increases of

temperature caused by ongoing climate change, along with the proliferation of white-tailed deer (*Odocoileus virginianus*) populations and invasive European earthworms are predicted to drastically change the overstory and understory of northern hardwood forests. Sugar maple (*Acer saccharum*) is a common late successional species in the Great Lakes region and is widespread in dry mesic to mesic northern temperate forests. Sugar maple forests provide habitat for many wildlife species while trees are valued for their products (e.g. timber and syrup). This PhD dissertation aims to advance the understanding of the Upper Great Lakes northern hardwood forests by studying sugar maple forest community dynamics across an environmental gradient from prairie-forest border to interior forest biome and discuss their future in a context of global environmental changes. Rather than adopting a field-based approach, 3515 plots including tree and seedling data from the Forest Inventory and Analysis (FIA) program were studied, with 378 plots in Zone 1, 1823 plots in Zone 2, and 1314 plots in Zone 3. Analyses incorporated a combination of ordinations (Bray-Curtis and successional vector overlay), Ordinary Least Squares (OLS) regression models, and Aikaike's Information Criteria (AIC) provided a means for model selection.

Chapter 1 investigated the contemporary overstory and understory forest composition of sugar maple communities and successional dynamics across the Upper Great Lakes region, and considered three hypotheses: (1) hardwood forests form a series of distinct communities via association of sugar maple with other tree species in the overstory across the Upper Great Lakes region; (2) sugar maple dominates the understory and succession to sugar maple is occurring in all of the communities—therefore the

overstory communities identified are not stable; and (3) mesophication (which was used as a broad concept to include increasing maple proportion within mixed maple-oak forests) in sugar maple-red oak communities is progressing towards greater dominance of sugar maple. Sugar maple dominated forests were identified in association with red oak, bur oak-aspen, and basswood at the prairie-forest border, red oak-red maple, quaking aspen, and basswood in the forest interior, and quaking aspen, red maple-balsam fir, and hemlock-yellow birch-white cedar in the deep forest of Upper Michigan. Mesophication is occurring in most sugar maple-red oak communities of the prairie-forest border and sugar maple regeneration dominates in combination with white ash, ironwood, and bitternut hickory (Zone 1), red maple, balsam fir, and ironwood (Zone 2), and balsam fir (Zone 3), indicating that the distinct overstory communities may not be stable and that sites are trending towards relative homogeneity. However, despite the regeneration success of sugar maple, some stands had no sugar maple regeneration and we predict a decline in future sugar maple abundance resulting from the long term effects of deer browsing, earthworm invasion, and increased drought effects due to global environmental change.

In Chapter 2, tree and seedling richness-site productivity relationships were examined in sugar maple forests of the Upper Great Lakes region. First, the form of the species richness-site productivity relationship of the overstory and understory of sugar maple forests was investigated on three data sets (i.e. whole data set, upper 90^{th} quantile subset, and random sample subset) by testing the null hypothesis that the species richness-site productivity is flat. The alternative hypotheses were that the richness-site

productivity relationship is 1) hump-shaped, 2) positive monotonic, 3) negative monotonic, and 4) U-shaped. Second, after noticing that sugar maple abundance approached 100% on some plots, the existence of threshold effects of sugar maple abundance on species richness was investigated by testing the null hypothesis that no threshold effect exists (i.e. species richness decreases linearly with increase sugar maple abundance) against that alternative that there is a threshold effect of sugar maple abundance (i.e. species richness display threshold responses to increase basal area). Results varied across zones and data sets, indicating that sample size might be influencing the results. Overall, there was a significant positive relationship between tree richness and site productivity but a flat seedling richness-site productivity relationship. The addition of sugar maple basal area to the models greatly improved the results. There was no apparent threshold effect but sugar maple abundance had very strong negative effect on species richness, which appeared to increase from the prairie-forest border towards Upper Michigan.

Chapter 3 focused on the ecological niche of sugar maple seedlings from the prairie-forest border to the interior of the forest biome. Sugar maple seedling sensitivity to current forest structure and composition (sugar maple basal area and stand age), as well as site level environmental conditions (sand proportion, soil depth, slope, and TRASP - an index related to aspect) was assessed under the hypothesis that sugar maple seedlings respond differently to environment variables across the region and have a broader environmental niche in the Upper Peninsula of Michigan than at the prairie-forest border. As expected, basal area of sugar maple was generally positively related to sugar

maple seedling density, while the effects of % sand and soil depth varied across the three zones. TRASP, an index related to aspect, had a strong negative influence on seedling abundance at the prairie-forest border and interior zones (Zones 1 and 2, respectively), but had no influence in the deep interior zone (Zone 3). The overall interpretation of the models and patterns across the climate gradient indicated that sugar maple seedling abundance is currently insensitive to environmental variables (i.e. has a very broad environmental niche) in Upper Michigan, with many stands currently growing on sites with relatively high percent sand content, shallow soils, and southerly slopes. The expected shift in future climate would make the climate of Upper Michigan like that of the prairie-forest border by late 21st century, thereby reducing the probability of seedling establishment on many sites currently with high dominance of sugar maple. Additionally, high deer populations and earthworm invasion will narrow the niche of sugar maple in Upper Michigan even more so than changing climate alone.

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Chapter 1

Sugar maple (*Acer saccharum*) communities and successional dynamics across the Upper Great lakes region

with Lee E. Frelich

Successional patterns and community dynamics of mesic hardwood forests in the Upper Great Lakes Region are responding to a variety of changes including fire exclusion near the prairie-forest border and logging followed by fire during the late 1800s to early 1900s, as well as high levels of deer browsing, invasive species, and early phases of climate change. Predictions made during the mid-1900s were that sugar maple would increase in abundance in a variety of mesic hardwood forest communities, from relatively warm oak-maple at the edge of the prairie to cool and moist hemlock and mixed boreal-hardwood communities deep in the interior of the forest biome. However, no large-scale analysis has been done to assess the status of community structure and successional patterns across this climate gradient. In order to asses forest compositional changes in hardwood forests across the Upper Great Lakes region, we used Forest Inventory and Analysis (FIA) data and a combination of Bray-Curtis ordination and successional vector overlay methods to test the hypotheses that (1) hardwood forests form a series of distinct communities via association of sugar maple with other tree species in the overstory across the Upper Great Lakes region; (2) sugar maple dominates the understory and succession to sugar maple is occurring in all of the communities—therefore the overstory communities identified are not stable; and (3) mesophication (which was used as a broad concept to include increasing maple proportion within mixed maple-oak forests) in sugar maple-red oak communities is progressing towards greater dominance of sugar maple. Our results supported all three hypotheses. Sugar maple dominated forests were identified in association with red oak, bur oak-aspen, and basswood at the prairie-forest border, red oak-red maple, quaking aspen, and basswood in the forest interior, and quaking aspen,

red maple-balsam fir, and hemlock-yellow birch-white cedar in the deep forest of Upper Michigan. Mesophication is occurring in most sugar maple-red oak communities of the prairie-forest border and sugar maple regeneration dominates in combination with white ash, ironwood, and bitternut hickory (Zone 1), red maple, balsam fir, and ironwood (Zone 2), and balsam fir (Zone 3), indicating that the distinct overstory communities may not be stable and that sites are trending towards relative homogeneity. However, despite the regeneration success of sugar maple, some stands had no sugar maple regeneration and we predict a decline in future sugar maple abundance resulting from the long term effects of deer browsing, earthworm invasion, and increased drought effects due to global environmental change.

Introduction

Succession has long been a focus of ecological research. It refers to the directional change in species composition of a plant community over time and leads to different species assemblages (Glenn-Lewin et al. 1992; Connell and Slayter 1977). On mesic sites in the Upper Great Lakes region (Minnesota, Wisconsin, and Upper Peninsula of Michigan), succession progresses from short-lived, shade-intolerant early-successional species such as quaking aspen (*Populus tremuloides*), bigtooth aspen (*Populus grandidentata*), and paper birch (*Betula papyrifera*) to long-lived, shade-tolerant late-successional species such as sugar maple (*Acer saccharum*) or basswood (*Tilia americana*) (Heinselman 1954).

Modern species assemblages of the Upper Great Lakes region result from glacial and interglacial phases of the Quaternary period (Davis 1983). Over the past 21,000 years, plant associations appeared and disappeared and plant abundance fluctuated in response to environmental changes (Williams et al. 2004). Species' ranges and abundances responded individualistically to late-Quaternary environmental changes rather than as ecological communities (Webb et al. 1983; Davis 1981; Davis 1976) thus, creating some unique plant associations that no longer exist today (Williams et al. 2001; Overpeck et al. 1992). The current northern mesic forest of the Upper Great Lakes region has subsisted as a dominant assemblage for 5,000-8,000 years and, except near the prairie-forest border, was relatively stable until European settlement (Davis 1981; Davis 1976). It is dominated by sugar maple and includes yellow birch (*Betula alleghaniensis*), basswood, American elm (*Ulmus americana*), northern red oak (*Quercus rubra*), red maple (*Acer rubrum*), white ash (*Fraxinus americana*), hemlock (*Tsuga canadensis*), and American beech (*Fagus grandifolia*); although Minnesota is mostly missing the latter three species and has lesser amounts of yellow birch (Curtis 1959). Pollen records show that drastic changes in the Great Lakes forests started in the mid-19th century with the disruption of historic disturbance regimes following European settlement, and that the magnitude of change during the last 150 years is 2.4 times greater than changes over the past 1,000 years (Cole et al. 1998).

Oak forests with frequent fires close to the prairie-forest border had been slowly invaded by maple over the past several hundred years, in response to a slowly cooling climate, but the locations and timing of maple invasion were determined by climate

variation and firebreaks, establishing patchy co-dominance of maple and oaks across the landscape (Umbanhowar 2004; Grimm 1984; Grimm 1983). This process of maple advance into oak forests has accelerated during the last several decades due to fire exclusion, cessation of understory burning by Native Americans, and a period of relatively wet climate, including even those areas to the south and west of fire breaks where oaks had maintained dominance up until European settlement (McEwan et al. 2011; Rogers et al. 2008; Ozier et al. 2006; Spyreas and Matthews 2006; Shotola et al. 1992; Peet and Loucks 1977; Curtis and McIntosh 1951). The process of invasion by maple and other late-successional fire sensitive species into oak forests has been termed "Mesophication" (Nowacki and Abrams 2008; Schulte et al. 2007; Rooney et al. 2004b), and is also a type of succession, but in forests where succession had been held in check at early stages for centuries. Although this concept was originally applied to changes in pure oak forests in recent times, here we are broadening the concept to include increasing maple proportion within mixed maple-oak forests as well as ongoing (over centuries) and possibly accelerated (in recent decades), invasion of oak forests by maple. Mesophication has mostly occurred near the prairie-forest border, but also to a small extent in the interior of the forest biome in the Great Lakes Region (Hanberry et al. 2012; Nowacki and Abrams 2008). In contrast, succession within the interior of the forest biome throughout northern Wisconsin and Upper Michigan has mostly occurred as a result of recovery from land clearing, farming, logging and fires that resulted from European settlement.

In the 1940s and 1950s, J. T. Curtis and colleagues surveyed > 2000 sites in Wisconsin to assess plant community composition along different environmental

gradients (Waller et al. 2012). He predicted that human-caused environmental changes such as fire suppression would cause shade-tolerant species to replace fire-dependent oak savanna and woodland ecosystems after only one generation (Curtis 1959). Additionally, Heinselman (1954) used quantitative data to show that shade-tolerant sugar maple and balsam fir (*Abies balsamea*) species occupied the understory of many aspen-birch stands in the Upper Great Lakes region, most of which originated from land clearing and slash burning by European settlers during the late 19th and early 20th centuries, and suggested that many of these stands may be converting to different forest types by 1990.

Since the 1990s, several researchers have revisited many of Curtis' sites in order to document compositional changes over the past 50 years (Waller et al. 2012). Results from these studies reinforce predictions from Curtis (1959) and Heinselman (1954); they are unanimously revealing shifts in both the overstory and understory species composition (Mudrak et al. 2009; Kraszewski and Waller 2008; Rogers et al. 2008; Bushman 2005). It is clear that forests are converting to sugar maple or other shade-tolerant species across mesic sites dominated by hardwoods, stands dominated by hemlock, and dry-mesic sites dominated by pines (Amatangelo et al. 2011).

In this paper, we estimated contemporary forest composition of sugar maple communities across the Upper Great Lakes region, which extends from Minnesota to Upper Michigan and is characterized by a southwest to northeast climatic gradient from the prairie-forest border in Minnesota to deep within the forest biome in Michigan's Upper Peninsula (McNab et al. 2007; Changnon et al. 2002; Cleland et al. 1997; McNab and Avers 1994). Rather than adopting an intensive site-based approach, we used existing

forest inventory data from the U.S. Department of Agriculture Forest Service, Forest Inventory and Analysis Program (U.S.D.A. 2008) to assess broadscale successional trends in these communities.

Our first step was to estimate the average abundance of the overstory species composition of sugar maple dominated forests in the Upper Great Lakes region and examine how sugar maple tree communities change from the prairie-forest border—characterized by a combination of frequent droughts, dry seasons, frequent historical fires, and high evapotranspiration to the wetter and cooler climate of the deep forest of the Upper Peninsula of Michigan (Changnon et al. 2002). Our second step was to investigate the successional pathways of forest communities with a significant component of sugar maple. In our last step, we investigated the understory of sugar maple-oak dominated sites for the presence of shade-tolerant recruitment species as suggested by the literature.

We hypothesize that (1) hardwood forests form a series of distinct communities via association of sugar maple with other tree species in the overstory across the Upper Great Lakes region; (2) sugar maple dominates the understory and succession to sugar maple is occurring in all of the communities—therefore the overstory communities identified are not stable; and (3) mesophication in sugar maple-red oak communities is progressing towards greater dominance of sugar maple.

Methods

Study area

The Upper Great Lakes region includes three main ecological provinces defined by dominant climatic regimes, potential native vegetation, and biomes: the prairie parkland, the eastern broadleaf forest, and the Laurentian mixed forest provinces (McNab et al. 2007; Cleland et al. 1997; McNab and Avers 1994) (Figure 1.1).

The prairie parkland occupies the western part of Minnesota and extends to the southern parts of Wisconsin and Michigan. Mean annual temperatures (1971-2000) vary from 2ºC in the north to 9ºC to the south. This province has a continental climate with cold winters, hot summers, and mean annual precipitation of 46 cm in the north to 84 cm in the south. Precipitation mainly occurs in the form of snow in the north but is almost entirely rain in the south. Mean evapotranspiration exceeds mean precipitation during the growing season (May through September), with water deficits of 3.8 cm along the western edge of the prairie parkland to 2.0 cm in southern Minnesota. Semi-arid loamy soils are well-to-moderately well-drained. Pre-settlement vegetation was dominated by tall grass prairie but today agriculture is the dominant land use.

The eastern broadleaf forest extends from northwestern Minnesota to southeastern Michigan. Mean annual temperatures vary from 4ºC in the northwest of the province to 10ºC in Michigan. The overall climate is continental with warm to hot summers. Precipitation averages 65 to 93 cm and approximately equals evapotranspiration. Two-thirds of it falls during the growing season which lasts about 125 days inland and up to 180 days along Lake Michigan. Local reliefs (20 to 180 m) are apparent in Wisconsin as a result of past glaciation. Winter precipitation is mostly snow and averages 100 cm. Soil moisture regime is dominantly mesic with frequent growing season water deficits ranging

from 2.0 cm in Minnesota up to 1.2 cm in Wisconsin. Pre-settlement vegetation was dominated by maple-basswood forests or oak savannas at the prairie-forest border as a result of fire frequency variations (Grimm 1984) whereas oak-hickory forests dominate sandy sites and beech-maple forests grow on loamy soils in Michigan. Today, agriculture, urban and industrial development constitute the major land uses. The transition (ecotone) from eastern broadleaf forest to prairie parkland is sharp (Danz 2009; Grimm 1983) whereas the transition between eastern broadleaf forest and Laurentian mixed forest is gradual (Fisichelli et al. 2013a; Goldblum and Rigg 2002; Braun 1950).

The Laurentian mixed forest lies in the northern part of the Upper Great Lakes region and extends into Canada. Average annual temperatures range from 3ºC to 6ºC. Average annual precipitation varies between 61 and 115 cm, with fifty percent of precipitation falling during the growing season (May through September). Average annual snowfall varies from 100 to 165 cm, but can be up to 833 cm due to the Lake-effect snow. The climate is classified as continental with lake effects influence along the Great Lakes. Winters (i.e. days below or at freezing temperature) are longer with considerable snow coverage and summers are short and warm compared to the prairie parkland and the eastern broadleaf provinces. To the contrary of the prairie parkland and the eastern broadleaf provinces, there is a moisture surplus rather than a deficit, and the mean growing season potential evapotranspiration minus precipitation reaches -11 cm in the northern part of the Laurentian mixed forest. Hilly landscapes with shallow soils occur along Lake Superior and result from past glaciations. A mosaic of conifer stands, northern hardwood stands, and mixed stands occupies the region, and vegetation consists

of forests that are a transition between boreal and broadleaf deciduous (Goldblum and Rigg 2002; Davis 1983; Braun 1950). Early successional species such as paper birch, bigtooth aspen, trembling aspen (*Populus tremuloides*), and red maple have increased in abundance compared to pre-European settlement times, while hemlock and white pine (*Pinus strobus*) abundance has reduced due to a combination of logging, post-logging fire, and white-tailed deer (*Odocoileus virginianus*) browsing (Rooney et al. 2000).The dominant land use is forestry and outdoor recreation.

FIA data

The Forest Inventory and Analysis (FIA) Program of the U.S. Department of Agriculture Forest Service is a nationwide program that collects and publishes data from all ownership of forest land in the US since 1929 although annual inventories started in 1999 (U.S.D.A. 2009). The FIA Program features a complete and systematic national sample design for all forest lands (i.e. at least 0.4 ha and 36.3 m wide with a minimum of 10% stocked by forest trees) in the US (Bechtold and Patterson 2005). It is conducted in three phases, although data from the first two phases only were used in this study. In Phase 1, land area is stratified using remotely sensed imagery in the form of aerial photography and/or satellite imagery to reduce variance in the estimates. In Phase 2, the landscape is divided into contiguous 2428 ha hexagons containing one randomly located permanent ground plot each, for a total of ~125,000 forested plots nationwide. Sampling intensity varies between states, but because the FIA plot design is a combination of systematic arrangement and random sampling, varying sample intensities only affects the

precision of the estimates. Field crews sample approximately 20% of FIA plots annually in the eastern US where they collect variables (e.g. forest type, tree species, soil attributes) on each permanent ground plot with 100% measurement of a systematic panel of plots completed every five years in the eastern US (U.S.D.A. 2008). Each plot is designed to cover a 0.4 ha sample area. A plot consists of one central subplot and an equilateral triangle arrangement of three peripheral subplots spaced 36.6 m apart from the central subplot, at azimuths of 120, 240, and 360 degrees. Each subplot also includes a 2.1 m fixed-radius microplot which is offset from the center of the subplot (3.7 m at an azimuth of 90 degrees). All trees with a diameter at breast height (dbh) of at least 12.7 cm are recorded on subplots. Seedlings (≤ 2.54 cm dbh and at least 30.5 cm in height for hardwood species) are inventoried in microplots.

We downloaded FIA raw data files for Minnesota, Wisconsin, and Michigan from the FIA database website (FIADB, http://apps.fs.fed.us/fiadb-downloads/datamart.html). This study is mostly based upon data collected between 2008 and 2012, which corresponds to a full cycle at the time of data upload (November 2013), although we also used data from the earliest available FIA cycle, 2000-2004, to compare changes in seedling abundance with the 2008-2012 data. To protect the confidentiality of the exact location of FIA plots, plot coordinates are spatially perturbed before being released to the public. The perturbed plot coordinates were adjusted to be within ± 1 mile of the true plot location which is of little consequence on our study given the regional scale presented in this work. We selected plots including at least one live sugar maple tree or at least one sugar maple seedling and aggregated them into three contiguous zones: Zone 1 (466

plots) is near the prairie biome and covers Minnesota and Wisconsin, although we excluded Northern Minnesota from our analyses because of small sample size; Zone 2 (1978 plots) is in the forest biome and includes northern Wisconsin; Zone 3 (1419 plots) is deep into the forest biome, with the best climate for trees, and includes the Upper Peninsula of Michigan (Figure 1.1).

Data analysis

Species selection and data sets

Tree species were selected based on tree and seedling abundance in each zone. In the preliminary data analysis phase, we explored both absolute and relative density and opted for tree relative basal area and seedling relative density for further analyses. We choose tree species with an average relative basal area of 1% or more, and seedling species with an average relative density of at least 1% among plots in each zone (Table 1.1).

We used three data sets for our analyses. The maple data set (2008-2012) was used to test the first and second hypotheses (i.e. identification of sugar maple tree communities and successional pathways, respectively). It includes plots with at least one sugar maple tree or one sugar maple seedling (3866 plots). We identified 218 red oak forest type plots (hereafter red oak only data set) from FIA (2008-2012), 110 of which were already included in the maple dataset. After adding the red oak forest type plots to the maple dataset, we obtained 3974 plots, which we defined as the maple-red oak data set. We used the maple-red oak and red oak only data sets to test the third hypothesis (i.e.

mesophication) and investigated changes in sugar maple seedling abundance by comparing the 2008-2012 data to the 2000-2004 data.

Ordination

Sugar maple communities in each zone were identified in PC-ORD v. 5.10 (McCune and Mefford 2006). Ordinations were based on relative basal area of trees and we used Bray-Curtis ordination with Sorensen distance measures and variance-regression endpoint selection method in order to minimize the influence of outliers. Bray-Curtis ordination not only remains a robust method compared to newer methods of ordination such as Nonmetric Multidimentional Scaling (NMS) but it is also an effective strategy for large data sets and data that disregards the assumption of linear relationships among species (McCune and Grace 2002; Beals 1984). We used the overlay method with a cutoff r2 value of 0.100 for our biplots to visually identify the other tree species that mix with sugar maple to form gradients in community composition. Sugar maple communities subsets were formed by selecting plots with large basal area for the species used for the overlay (i.e. > 75th percentile basal area in the main matrix; large symbols on biplots); for instance, in Zone 1, the sugar maple-basswood community includes plots above the 75th percentile of basswood relative basal area; the sugar maple-bur oak-aspen community includes plots above the 75th percentile of the sum of bur oak and aspen relative basal area (JeriLynn E. Peck, personal communication). In order to investigate and depict successional trends of sugar maple tree communities, we generated successional vectors overlay (Philippi et al. 1998; McCune 1992) on each sugar maple

community subset by creating two sample units: 1) overstory sample unit including relative basal area of trees, and 2) understory sample unit including relative density of seedlings. Each sample unit consisted of the same plots classified in the same order, so that the overstory and understory locations for each plot were projected into the same ordination space. By connecting the data points from the overstory sample unit to the understory sample unit (McCune and Grace 2002), we were able to infer trajectories of sugar maple overstory communities (i.e.,visualize potential overstory compositional changes based on the assumption that the understory is the future of the overstory) (Sanders and Grochowski 2013; Woodall et al. 2013; Dey et al. 2012; Salk et al. 2011). Finally differences between overstory and understory communities were tested with multi-response permutation procedure (MRPP), a nonparametric method that tests for multivariate differences between groups (Peck 2010; McCune and Grace 2002). A Sorensen distance measure was used for the MRPP in order to be consistent with the distance measure used in the Bray-Curtis ordination.

Results

The Bray-Curtis analysis revealed a continuum of sugar maple communities across the Upper Great Lakes region (Figure 1.2 and Table 1.2). In Zone 1, axis 1 captured 15.57% of the total variation in the data set, while axes 2 and 3 captured 15.62% and 12% of the total variation, respectively. In Zone 2, axis 1 explained 24.97% of the total variation; axis 2 and 3 explained 17.10% and 13.75% of the total variation, respectively. In Zone 3, axis 1 accounted for 28.61% of the total variation, while axis 2

and 3 explained 17.89% and 17.73% to the total variation, respectively. In all three zones, high abundances of sugar maple appeared in the negative portion of axis 1 while other species abundances were in the positive portion of axis 1. Four sugar maple communities exist in Zone 1: sugar maple, sugar maple-red maple, sugar maple-bur oak-aspen, and sugar maple-basswood. Three sugar maple communities were identified in Zone 2: sugar maple-basswood, sugar maple-red oak-red maple, and sugar maple-quaking aspen. Four sugar maple communities occurred in Zone 3: sugar maple, sugar maple-quaking aspen, sugar maple-red maple-balsam fir, and sugar maple-hemlock-yellow birch-white cedar (Figure 1.2 and Table 1.2).

Successional vectors overlay indicated that the overstory composition was different from the understory composition and results were supported by significant MRPP tests (p-value < 0.0001). In all of the sugar maple communities, axes 1, 2, and 3 combined accounted for 38.48% to 61.94% of the total variation, with axis 1 and 2 explaining 18.78%-32.92% and 10.88%-20.7% of the total variation, respectively. In Zone 1, the successional vectors overlay showed that sugar maple transitioned towards sugar maple and white ash; sugar maple, ironwood, bitternut hickory, and white ash were found in the understory of sugar maple-red oak tree community in Zone 1; the understory of sugar maple-bur oak-aspen in Zone 1 included sugar maple, white ash, and ironwood, whereas sugar maple and white ash seedling dominated under the sugar maple-basswood community in Zone 1 (Fig. 1.3, Table 1.3). In Zone 2, regeneration of sugar maple, white ash, and ironwood was apparent under the sugar maple-basswood tree community. The successional vector overlay in the sugar maple-red oak-red maple tree community in

Zone 2 indicated a trajectory to sugar maple and red maple. Sugar maple and balsam fir seedlings occurred in the sugar maple-quaking aspen tree community in Zone 2 (Figure 1.4, Table 1.3). Finally, sugar maple, red maple, and ironwood are regenerating in the sugar maple tree community in Zone 3 while sugar maple and balsam fir seedlings pathways were observed in all other sugar maple tree communities in Zone 3 (i.e. sugar maple-quaking aspen, sugar maple-red maple-balsam fir, sugar maple-hemlock-yellow birch-white cedar, Figure 1.5, Table 1.3).

The maple-red oak data set indicated that 70% of plots included sugar maple seedlings in 2000-2004 (Zone 1 = 54%, Zone 2 = 68%, Zone 3 = 84%) compared to 73% plots in 2008-2012 (Zone 1 = 61%, Zone 2 = 71%, Zone 3 = 84%). Among the plots that contained sugar maple seedlings, the sugar maple seedling relative density in 2000-2004 was on average 45% (Zone 1 = 45%, Zone 2 = 42%, Zone 3 = 49%). This proportion was 40% in 2008-2012 (Zone 1 = 39%, Zone 2 = 38%, Zone 3 = 43%) (Table 1.4. (a)). The proportion of plots with sugar maple seedlings present in 2000-2004 but not in 2008-2012 was 13% (Zone 1 = 22%, Zone 2 = 14%, Zone 3 = 9%), while the proportion of plots with sugar maple seedlings present in 2008-2012 but not in 2000-2004 was 16% (Zone 1 = 28%, Zone 2 = 18%, Zone 3 = 9%).

The red oak only data set indicated that 39% of plots included sugar maple seedlings in 2000-2004 (Zone 1 = 22%, Zone 2 = 44%, Zone 3 = 69%) compared to 35% plots in 2008-2012 (Zone 1 = 22%, Zone 2 = 40%, Zone 3 = 46%). Among the plots that contained sugar maple seedlings, the sugar maple seedling relative density in 2000-2004 was on average 34% (Zone 1 = 34%, Zone 2 = 35%, Zone 3 = 31%). This proportion was

36% in 2008-2012 (Zone 1 = 41%, Zone 2 = 35%, Zone 3 = 32%) (Table 1.4. (b)). The proportion of plots with sugar maple seedlings present in 2000-2004 but not in 2008-2012 was 22% (Zone 1 = 29%, Zone 2 = 19%, Zone 3 = 33%), while the proportion of plots with sugar maple seedlings present in 2008-2012 but not in 2000-2004 was 14% (Zone 1 = 29%, Zone 2 = 12%, Zone 3 = 0%).

Discussion

Our results support all three hypotheses given in the Introduction. First, sugar maple dominated forests form a continuum of sugar maple tree communities within and across zones of the Upper Great Lakes region (hypothesis 1), by associating with different tree species across the gradient from the prairie-forest border to the deep forest of Upper Michigan. Second, across the Upper Great Lakes region, sugar maple regeneration dominates in combination with white ash and ironwood (Zones 1 and 2), as well as red maple and balsam fir (Zones 2 and 3), indicating that the distinct overstory communities may not be stable and that sites are trending towards relative homogeneity (hypothesis 2).Third, results based on the red oak only data sets suggest a progression towards greater abundance of sugar maple seedlings (i.e. increase in average sugar maple seedling relative density) in 2008-2012 compared to 2000-2004, especially near the prairie forest border. While this increase is evident for the red oak only data set, the average sugar maple relative density for the sugar maple-red oak data set decreased in 2008-2012 compared to 2000-2004, although the proportion of plots with sugar maple seedlings is greater in 2008-2012 than in 2000-2004. This may suggest that sugar maple-

red oak communities are progressing towards greater dominance of sugar maple, which may be partly explained by mesophication (hypothesis 3).

Hypothesis 1: Distinct sugar maple tree communities across the Upper Great Lakes region

Sugar maple is known to be a major component in many forest types of North America (Burns and Honkala 1990; Eyre 1980) and grows on a wide range of mesic soils (Horsley et al. 2002; Cogbill 2000). In the Upper Great Lakes region, the distribution of beech, hemlock and yellow birch becomes more and more limited from east to west while sugar maple encompasses most of the region, therefore adapting by forming communities with species that are present (Tirmenstein 1991). Co-dominant species across the area include red oak, bur oak, aspen and basswood in southern Minnesota and Wisconsin (Zone 1), basswood, red oak, red maple, and quaking aspen in northern Wisconsin and central Minnesota (Zone 2), and quaking aspen, red maple, balsam fir, hemlock, yellow birch, and white cedar in the Upper Peninsula of Michigan (Zone 3) (Table 1.2). We assert that the difference in species composition across the Great Lakes region is mainly associated with changes in environmental conditions where a drier climate with frequent droughts and historical fire events prevails at the prairie-forest border compared to a cooler and wetter environment in the deep forest of Michigan (Changnon et al. 2002). In the Upper Peninsula of Michigan, sugar maple dominates mesic northern forests with hemlock, yellow birch, and red maple as co-dominant species (Frelich 2002; Barnes 1991; Curtis 1959; Braun 1950). Because this area is subject to heavy lake-effect snow

from Lake Superior, snowfall plays an important role in the abundance of sugar maple, hemlock, and beech by influencing soil moisture, nutrient availability, and fire history; for instance, at low annual snowfall, sugar maple and beech importance value are less than hemlock; at moderate snowfall, sugar maple increases while hemlock decreases; and at high annual snowfall, sugar maple is significantly more important (Henne et al. 2007). Although beech is also a common co-dominant species of sugar maple in the Upper Peninsula of Michigan our ordinations did not show a distinct beech-maple forest community. This might be caused by the absence of beech in the western Upper Peninsula where temperatures are colder and droughts are more frequent (Barnes 1991; Woods and Davis 1989).

Hypothesis 2: Understory sugar maple dominance and overstory instability

Several factors contribute to the conversion of the sugar maple overstory communities identified in hypothesis 1 to distinct understory communities, where sugar maple seedlings co-dominate with white ash, ironwood, red maple, balsam fir, and some bitternut hickory. Our results are consistent with the successional trends identified by Kotar's forest habitat classification system. He identified that additionally to sugar maple seedlings, bitternut hickory, white ash, basswood, red maple, and shagbark seedlings were increasing in abundance in stands dominated by sugar maple in Zone 1, but that red and white oak, which were important in presettlement, are not regenerating today (Kotar and Burger 1996). In Zone 2, sugar maple and ironwood species were common in the understory (Kotar et al. 1988), and in Zone 3, additionally to sugar maple seedlings, red

maple, balsam fir, and some ironwood seedlings are commonly present (Burger and Kotar 2003). These successional trends may have resulted from a combination of succession and anthropogenic changes. Early successional species such as aspen are likely to be replaced by late successional and shade tolerant sugar maple (Tirmenstein 1991) and balsam fir species (Uchytil 1991). Sugar maple and balsam fir have high tolerance for shade and also the potential to successfully outcompete yellow birch seedlings (Sullivan 1994), which also suffer from heavy deer browsing (White 2012). The disappearance of hemlock as a co-dominant species in the understory also may be explained by intense deer browsing. There is now strong evidence in the literature that high levels of deer browsing on hemlock populations have contributed to the success of sugar maple in the understory (Jenkins 1997; Doepker et al. 1995; Frelich and Lorimer 1985; Marquis and Brenneman 1981; Stoeckeler et al. 1957). With lesser amounts of hemlock, sugar maple has a stronger potential to replace its most shade-tolerant competitor, hemlock (Brown and Curtis 1952). On the other hand, red maple, a generalist species, has become increasingly common in northern forests, mainly due to its low requirements for resources, reduced fire frequency, and human caused disturbances such as logging (Fei and Steiner 2007; Abrams 1998; Abrams and Nowacki 1992; Lorimer and Frelich 1984). Together, red maple and sugar maple have become the most abundant species in modern forest understories compared to the pre-settlement forest (Zhang et al. 2000). As for the presence of ash and ironwood in the sugar maple-red oak understory community, we suspect that earthworms are favoring ash species and deer population increase is allowing ironwood to invade (Matonis et al. 2011). The distinct understory

communities resulting from a combination of successional processes and anthropogenic changes in sugar maple dominated forests indicate that overstory communities of the Great Lakes region are not stable and may undergo compositional changes.

Hypothesis 3: Mesophication in sugar maple-red oak communities

The increase of the average sugar maple seedling relative density in the understory of red oak communities (based on the red oak only data set) may be explained by mesophication in Zone 1 while succession is most likely occurring in Zone 2. In Zone 1, we suspect that mesophication is progressing towards greater dominance of sugar maple due to fire exclusion (Hanberry et al. 2012). Oak decline in abundance is now apparent in southeast and west-central region of Minnesota (Hanberry et al. 2012; Danz 2009), as well as in southeast Wisconsin (Rhemtulla et al. 2009; Rogers et al. 2008). Previous studies have shown that fire is an important component to red oak regeneration as it regulates the proportion of red oak in sugar maple-red oak forests (Grimm 1983) and contributes to red oak establishment in Zones 1 and 2 (Bragg et al. 2004; Frelich 2002). Except for transitional dry mesic sites, red oak was an unimportant species in pre-settlement forests, yet post-settlement logging, slash fire practices, and suppression of frequent grass fires in the Central Plains region and areas previously dominated by tall grass prairies created perfect conditions for its establishment (Nowacki et al. 1990). Once established, canopy closure combined with a decrease in fire frequency and intensity jeopardized oak species recruitment, and favored shade tolerant species (e.g. sugar maple, red maple) establishment in the understory (Hanberry et al. 2012; Nowacki and Abrams

2008; Lorimer 2003). In Zone 2 however, red oak was initially established after major wind catastrophes followed by fire (Curtis 1959) and increased in abundance as a consequence of logging and slash fires practices later followed by fire suppression and the absence of deer that prefer to browse on red oak seedlings (McEwan et al. 2011; Rhemtulla et al. 2009; Radeloff et al. 1999; White and Mladenoff 1994). While the land was cleared for agriculture, most sites were left to reforest naturally and they are now undergoing successsion to shade tolerant species like maple (Rhemtulla et al. 2009).

Factors contributing to the success of sugar maple in the past few decades

In order to better understand the future of sugar maple dominated forests, it is important to address the factors explaining the success of sugar maple in the past several decades based on previous studies. They include single-tree selection management practices, the prevalence of disease and heavy deer browsing of competing tree species, mesophication of oak forests, and wetter climatic conditions. Single-tree selection has been used since the 1920s in managing northern hardwood forest of the Upper Great Lakes region to improve stand growth and stocking of tree species (Nyland 1998; Crow et al. 1981). By creating small gaps, single-tree selection in maple forests has proven to increase sugar maple abundance in the understory and disfavor the establishment and recruitment of other species that may require larger canopy gaps (e.g. yellow birch), therefore leading towards greater homogeneity in composition and reducing species diversity (Gronewold et al. 2010; Webster and Lorimer 2005). In southern Minnesota and Wisconsin, the oak and maple group has been observed with important amounts of

basswood (Curtis 1959). The maple-basswood association was recognized as the regional climax in the Big-Woods (Daubenmire 1936), and elm was reported to be one of the dominant tree species in the area, accounting for 27% of the bearing trees (Grimm 1984). In the late 1920s, Dutch elm disease reached the eastern United States (Gibbs 1978), irrupted in central Illinois in the mid-1950s (Neely et al. 1960), and in the late 1970s, it rapidly spread through Minnesota (Shrum and French 1977). The removal of elms by Dutch elm disease may have created favorable conditions for sugar maple population increase and establishment (Lin and Augspurger 2006), and might also partly explain the widespread occurrence of sugar maple-dominated stands.

In the late 1950s, Curtis (1959) observed that deer browsing was responsible for low densities of hemlock seedlings and saplings in hemlock stands and suggested that hemlock forests will eventually succeed to sugar maple forests. Several studies later reinforced Curtis' research by showing that hemlock, the preferred deer browse tree species, has decreased in density allowing un-preferred browsed tree species such as sugar maple, red maple and ironwood to successfully regenerate (White 2012; Salk et al. 2011; Rooney and Waller 2003; Rooney et al. 2000; Auclair et al. 1996; Kittredge and Ashton 1995; Frelich and Lorimer 1985). In oak-dominated forests, deer browsing has also been shown to partly favor sugar maple and contribute to oak regeneration failure (Marquis et al. 1976), as acorns provide an important source of food for deer while the stems of young oaks constitute their winter provisions (Dickman and Lantagne 1997).

Mesophication of oak forests has also contributed to the successful establishment of sugar maple in oak forests and is attributed to the decrease of fire frequency in

Minnesota (Hanberry et al. 2012). We suspect that mesophication is widespread in Zone 1 and occurring in a few parts of Zone 2. Before European settlement, fire was widespread and had an important impact on vegetation patterns and species assemblages (Abrams and Nowacki 1992). Frequent fires were critical in maintaining the open nature of oak savannas and open understories of oak forests by controlling light availability, creating microsites, and cleaning out the understory, thus preventing succession to fire-sensitive, shade-tolerant species (Rebertus and Burns 1997; Tester 1989; Grimm 1984; Grimm 1983; Curtis 1959). After European settlement, fire suppression and land-use changes profoundly affected vegetation in ways that mesophytic species like sugar maple increased and replaced fire dependent xerophytic like oak, pine, and chestnut (Hanberry et al. 2012; Nowacki and Abrams 2008). Finally, climate records over the past 500 years indicate reduced drought frequency and severity as well as increase moisture availability across eastern North America in the last century that could have favored maple over oaks (McEwan et al. 2011).

Implications for the future of sugar maple

While it is obvious that sugar maple is a successful species across the Great Lakes regions, we predict that the successional momentum towards sugar maple could slow or even reverse in the future due to the long term effects of deer browsing, earthworm invasion, and increased drought effects with a warming climate (Joyce et al. 2013; White 2012; Mattison 2011). In the prairie-forest order region (zone 1) forests may enter a post-mesophication phase. Given the scarcity of preferred browse species (hemlock and

yellow birch in Zones 2 and 3, red oak in Zones 1 and 2) after several decades of heavy deer browsing, species further down on the preference list, such as sugar maple, may become a source of food for deer and experience recruitment failure. Such a case has already been documented by monitoring of permanent mapped plots in Upper Michigan (Salk et al. 2011; Matonis et al. 2011). Earthworms, which are not native to the northern Great Lakes Region (James 1995), have become widespread due to use as recreational fishing baits (Gates 1982). A suite of invading earthworm species, including the nightcrawler (*Lumbricus terrestris*), leaf worm (*Lumbricus rubellus*), and angleworms (*Aporrectodea* spp), cause multiple changes to soil structure and ecosystem function (Frelich et al 2006). Reduction in duff thickness, compaction of the A horizon, and lower N and P availability when the worms invade all contribute to decline in growth and seed-producing ability of mature sugar maple trees (Larson et al. 2010; Hale et al. 2006; Frelich et al. 2006). Exposed bare mineral soils created by earthworms and increasing total earthworm biomass in northern hardwood forests have caused sugar maple seedling density and total cover to decrease and have resulted in rapid loss of the understory plants and tree seedlings, in particular sugar maple seedlings (Fisichelli et al. 2013b; Holdsworth et al. 2007; Frelich et al. 2006; Hale et al. 2005b; Hale et al. 2005a). In the future, we expect regeneration failure of sugar maple to continue on earthworm invaded sites while red maple may prosper, since it germinates well on bare mineral soil and is not as negatively affected by nutrient loss and drier soils as sugar maple is (Mattison 2011).

Forest ecosystems are also facing new challenges with the rapid increases in the global mean annual temperature and changes in disturbance regime (Joyce et al. 2013). Sugar maple is known for its sensitivity to drought (Horsley and Long 1999). In the Great Lakes region, climate scenarios predict a 3°C to 7°C increase in temperature in winter by the end of the century and 3°C to 11°C rise in summer (Kling et al. 2005). Precipitation is projected to rise in the winter and decrease in the summer, and the region may become drier overall because of future increased evaporation and transpiration that exceed surpluses of precipitation (Kling et al. 2005; Kling et al. 2003). Past drought episodes have contributed to sugar maple dieback, and with future drought scenarios, sugar maple dieback is expected to happen again by 2045-2085 (Auclair et al. 1996).

We propose that many stands will enter a post-mesophication phase where sugar maple might not be able to survive the combination of warmer climate, drought, deer browsing, and earthworm invasion (Frelich and Reich 2010). Even though our results showed that sugar maple regeneration is successful in the understory of sugar maple communities across the Upper Great Lakes region, the question arises: is there already evidence for a post-mesophication phase caused by changes in climate over the last century in addition to browsing and earthworm invasion in some stands? Recent field-based studies have demonstrated that combinations of these factors impede the growth of temperate mesic forest species, including sugar maple (Fisichelli et al. 2013b; Salk et al. 2011). Sugar maple seedling relative abundance has declined in 2008-2012 compared to 2000-2004 (Table 1.4 (a)). Morevover, approximately 39%, 29%, and 16% of our plots in Zone 1, Zone 2, and Zone 3, respectively showed no sugar maple seedling regeneration

for the maple-red oak data set. There were 33%, 27%, and 16% of plots in Zones 1, 2, and 3, respectively, without sugar maple seedling regeneration for the maple data set. This result is consistent with the field studies cited above, although at a much larger spatial extent, and with less detail as to cause of absence of sugar maple seedlings. The spatial pattern with a higher percentage of plots without sugar maple regeneration in Zones 1 and 2, than Zone 3, is also consistent with expectations for ongoing changes working against sugar maple, which should have lesser magnitude of negative impacts in the deep interior forest zone, where the climate is extremely favorable for sugar maple and potentially able to mitigate negative effects of environmental changes as described above. Therefore, we hypothesize that some sugar maple dominated sites are entering a post-mesophication phase and propose that future studies should investigate this hypothesis in more detail.

Table 1.1. Summary data for selected species. Tree relative basal area (a) and seedling relative density (b) are calculated from plots including at least one sugar maple tree or one sugar maple seedling from the 2008-2012 FIA data.

(a) Tree species

	Zone 1			Zone 2			Zone 3		
Species	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max
Balsam fir (*Abies balsamea*)	0.1	0.0	15.2	3.1	0.0	74.6	5.1	0.0	87.2
American beech (*Fagus grandifolia*)	0.3	0.0	56.7	0.3	0.0	60.6	2.1	0.0	71.9
American elm (*Ulmus americana*)	6.9	0.0	81.5	1.0	0.0	70.3	0.3	0.0	45.0
American hornbeam (*Carpinus caroliniana*)	0.0	0.0	2.3	0.0	0.0	6.7	0.0	0.0	3.4
Basswood (*Tilia americana*)	11.3	0.0	92.0	9.2	0.0	80.0	3.3	0.0	67.4
Bigtooth aspen (*Populus grandidentata*)	4.0	0.0	91.2	2.6	0.0	91.2	1.7	0.0	100.0
Bitternut hickory (*Carya cordiformis*)	2.7	0.0	54.1	0.3	0.0	65.7	0.0	0.0	0.0
Black ash (*Fraxinus nigra*)	1.3	0.0	56.9	2.9	0.0	98.1	1.7	0.0	87.6
Black cherry (*Prunus serotina*)	1.9	0.0	35.6	0.8	0.0	68.5	1.5	0.0	61.3
Black walnut (*Juglans nigra*)	1.2	0.0	60.3	0.0	0.0	13.7	0.0	0.0	0.0
Boxelder (*Acer negundo*)	1.4	0.0	66.6	0.0	0.0	25.0	0.0	0.0	2.3
Bur oak (*Quercus macrocarpa*)	5.2	0.0	70.7	1.8	0.0	94.7	0.1	0.0	27.5
Chockecherry (*Prunus virginiana*)	0.1	0.0	21.8	0.0	0.0	2.4	0.0	0.0	4.3

Green ash (*Fraxinus pennsylvanica*)	2.4	0.0	68.5	1.0	0.0	65.7	0.3	0.0	23.3
Hackberry (*Celtis occidentalis*)	0.2	0.0	11.7	0.0	0.0	5.2	0.0	0.0	0.0
Hemlock (*Tsuga canadensis*)	0.0	0.0	13.7	2.7	0.0	86.8	5.9	0.0	100.0
Ironwood (*Ostrya virginiana*)	2.1	0.0	88.2	0.7	0.0	83.6	0.5	0.0	37.1
Mountain maple (*Acer spicatum*)	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0	0.5
Paper birch (*Betula papyrifera*)	2.2	0.0	68.3	4.0	0.0	74.5	2.6	0.0	65.9
Quaking aspen (*Populus tremuloides*)	4.0	0.0	73.9	11.8	0.0	100.0	8.8	0.0	100.0
Red maple (*Acer rubrum*)	3.0	0.0	53.5	12.8	0.0	99.6	16.3	0.0	95.8
Red oak (*Quercus rubra*)	11.5	0.0	89.6	8.1	0.0	100.0	1.9	0.0	92.7
Red pine (*Pinus resinosa*)	0.3	0.0	83.2	1.3	0.0	100.0	1.7	0.0	100.0
Serviceberry spp. (*Amelanchier* spp.)	0.0	0.0	2.8	0.0	0.0	1.6	0.0	0.0	4.3
Shagbark hickory (*Carya ovata*)	2.8	0.0	90.3	0.0	0.0	0.0	0.0	0.0	0.0
Slippery elm (*Ulmus rubra*)	2.2	0.0	46.7	0.0	0.0	21.2	0.0	0.0	0.0
Sugar maple (*Acer saccharum*)	17.9	0.0	100.0	24.0	0.0	100.0	31.2	0.0	100.0
White ash (*Fraxinus americanan*)	3.3	0.0	71.2	2.0	0.0	68.9	0.9	0.0	66.7
White cedar (*Thuja occidentalis*)	0.1	0.0	28.7	1.4	0.0	91.9	3.6	0.0	83.8
White oak (*Quercus alba*)	6.1	0.0	78.5	0.7	0.0	58.8	0.0	0.0	0.0
White pine (*Pinus strobus*)	1.3	0.0	70.3	1.9	0.0	86.6	1.5	0.0	89.3
White spruce (*Picea glauca*)	0.0	0.0	9.6	1.2	0.0	98.8	2.3	0.0	79.2
Yellow birch (*Betula alleghaniensis*)	0.3	0.0	33.5	2.5	0.0	73.7	5.1	0.0	64.5

(b) Seedling species

	Zone 1			Zone 2			Zone 3		
Species	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max
Balsam fir (*Abies balsamea*)	0.2	0.0	50.0	8.2	0.0	100.0	12.4	0.0	100.0
American beech (*Fagus grandifolia*)	0.2	0.0	72.7	0.5	0.0	100.0	4.1	0.0	100.0
American elm (*Ulmus americana*)	4.0	0.0	100.0	1.1	0.0	100.0	0.4	0.0	65.7
American hornbeam (*Carpinus caroliniana*)	2.6	0.0	94.4	4.3	0.0	100.0	0.4	0.0	56.6
Basswood (*Tilia americana*)	2.6	0.0	58.3	1.3	0.0	100.0	0.4	0.0	24.1
Bigtooth aspen (*Populus grandidentata*)	0.5	0.0	40.0	1.1	0.0	84.5	0.5	0.0	61.9
Bitternut hickory (*Carya cordiformis*)	4.8	0.0	100.0	0.4	0.0	53.3	0.0	0.0	0.0
Black ash (*Fraxinus nigra*)	2.7	0.0	86.7	5.7	0.0	100.0	3.0	0.0	85.5
Black cherry (*Prunus serotina*)	5.7	0.0	100.0	2.7	0.0	100.0	3.3	0.0	100.0
Black walnut (*Juglans nigra*)	0.5	0.0	44.4	0.0	0.0	3.2	0.0	0.0	0.0
Boxelder (*Acer negundo*)	2.5	0.0	92.9	0.1	0.0	50.0	0.0	0.0	11.1
Bur oak (*Quercus macrocarpa*)	0.2	0.0	18.8	0.2	0.0	25.0	0.1	0.0	80.0
Chockecherry (*Prunus virginiana*)	7.1	0.0	100.0	2.9	0.0	100.0	1.1	0.0	85.1
Green ash (*Fraxinus pennsylvanica*)	5.1	0.0	100.0	3.1	0.0	100.0	0.6	0.0	64.7
Hackberry (*Celtis occidentalis*)	2.3	0.0	100.0	0.0	0.0	0.0	0.0	0.0	0.0
Hemlock (*Tsuga canadensis*)	0.2	0.0	100.0	0.6	0.0	100.0	1.8	0.0	91.7
Ironwood (*Ostrya virginiana*)	9.6	0.0	100.0	7.1	0.0	100.0	5.2	0.0	89.6

Mountain maple (*Acer spicatum*)	0.0	0.0	4.9	2.1	0.0	100.0	1.7	0.0	81.9
Paper birch (*Betula papyrifera*)	0.1	0.0	25.0	0.6	0.0	71.4	0.3	0.0	33.3
Quaking aspen (*Populus tremuloides*)	2.4	0.0	100.0	6.9	0.0	100.0	4.2	0.0	100.0
Red maple (*Acer rubrum*)	1.0	0.0	66.7	4.5	0.0	100.0	10.4	0.0	89.8
Red oak (*Quercus rubra*)	0.7	0.0	50.0	2.3	0.0	80.4	1.6	0.0	66.7
Red pine (*Pinus resinosa*)	0.0	0.0	12.5	0.0	0.0	33.3	0.1	0.0	66.7
Serviceberry spp. (*Amelanchier* spp.)	0.4	0.0	35.0	1.7	0.0	63.6	2.1	0.0	52.4
Shagbark hickory (*Carya ovata*)	0.9	0.0	50.0	0.0	0.0	0.0	0.0	0.0	0.0
Slippery elm (*Ulmus rubra*)	1.8	0.0	55.6	0.0	0.0	13.0	0.0	0.0	0.0
Sugar maple (*Acer saccharum*)	26.0	0.0	100.0	27.7	0.0	100.0	36.5	0.0	100.0
White ash (*Fraxinus americanan*)	9.1	0.0	100.0	9.6	0.0	100.0	2.7	0.0	100.0
White cedar (*Thuja occidentalis*)	0.0	0.0	0.0	0.1	0.0	50.0	0.7	0.0	64.3
White oak (*Quercus alba*)	0.4	0.0	52.3	0.1	0.0	47.1	0.0	0.0	0.0
White pine (*Pinus strobus*)	0.5	0.0	100.0	0.8	0.0	100.0	0.5	0.0	63.2
White spruce (*Picea glauca*)	0.0	0.0	2.4	0.8	0.0	100.0	1.6	0.0	100.0
Yellow birch (*Betula alleghaniensis*)	0.0	0.0	4.2	0.5	0.0	100.0	1.6	0.0	100.0

Table 1.2. Sugar maple tree communities across the Upper Great Lakes region. Tree communities were formed by selecting plots with large basal area for the species we used for the overlay (i.e. > 75th percentile basal area in the main matrix; large symbols on biplots); for instance, in Zone 1, the sugar maple-basswood community includes plots above the 75th percentile of basswood basal area.

Tree communities	Zone 1	Zone 2	Zone 3
Sugar maple	✓		✓
Sugar maple-Red oak	✓		
Sugar maple-Bur oak-Aspen	✓		
Sugar maple-Basswood	✓	✓	
Sugar maple-Red oak-Red maple		✓	
Sugar maple-Quaking aspen		✓	✓
Sugar maple-Red maple-Balsam fir			✓
Sugar maple-Hemlock-Yellow birch-White cedar			✓

Table 1.3. Successional patterns of sugar maple tree communities across the Upper Great Lakes region. Table is based on successional vector overlay results (see Figures 1.3 to 1.5).

	Understory		
Tree community	Zone 1	Zone 2	Zone 3
Sugar maple	Sugar maple White ash		Sugar maple Red maple Ironwood
Sugar maple-Red oak	Sugar maple Ironwood Bitternut hickory White ash		
Sugar maple-Bur oak-Aspen	Sugar maple White ash Ironwood		
Sugar maple-Basswood	Sugar maple White ash	Sugar maple White ash Ironwood	
Sugar maple-Red oak-Red maple		Sugar maple Red maple	
Sugar maple-Quaking aspen		Sugar maple Balsam fir	Sugar maple Balsam fir
Sugar maple-Red maple-Balsam fir			Sugar maple Balsam fir
Sugar maple-Hemlock-Yellow birch-White cedar			Sugar maple Balsam fir

Table 1.4. Proportion of plots with sugar maple seedlings in 2000-2004 and 2008-2012. The maple-red oak data set (3974 plots) includes plots with at least one sugar maple tree or one sugar maple seedling or red oak forest type FIA plots (a). The red oak only data set (218 plots) refers to plots classified as red oak forest type by FIA (b). Numbers in parentheses indicate the average relative density of sugar maple seedling among the plots that contained sugar maple seedlings.

(a) Maple-red oak dataset

	2000-2004	2008-2012
Zone 1	54 (45)	61 (39)
Zone 2	68 (42)	71 (38)
Zone 3	84 (49)	84 (43)
All three zones	70 (45)	73 (40)

(b) Red oak only dataset

	2000-2004	2008-2012
Zone 1	22 (34)	22 (41)
Zone 2	44 (35)	40 (35)
Zone 3	69 (31)	46 (32)
All three zones	39 (34)	35 (36)

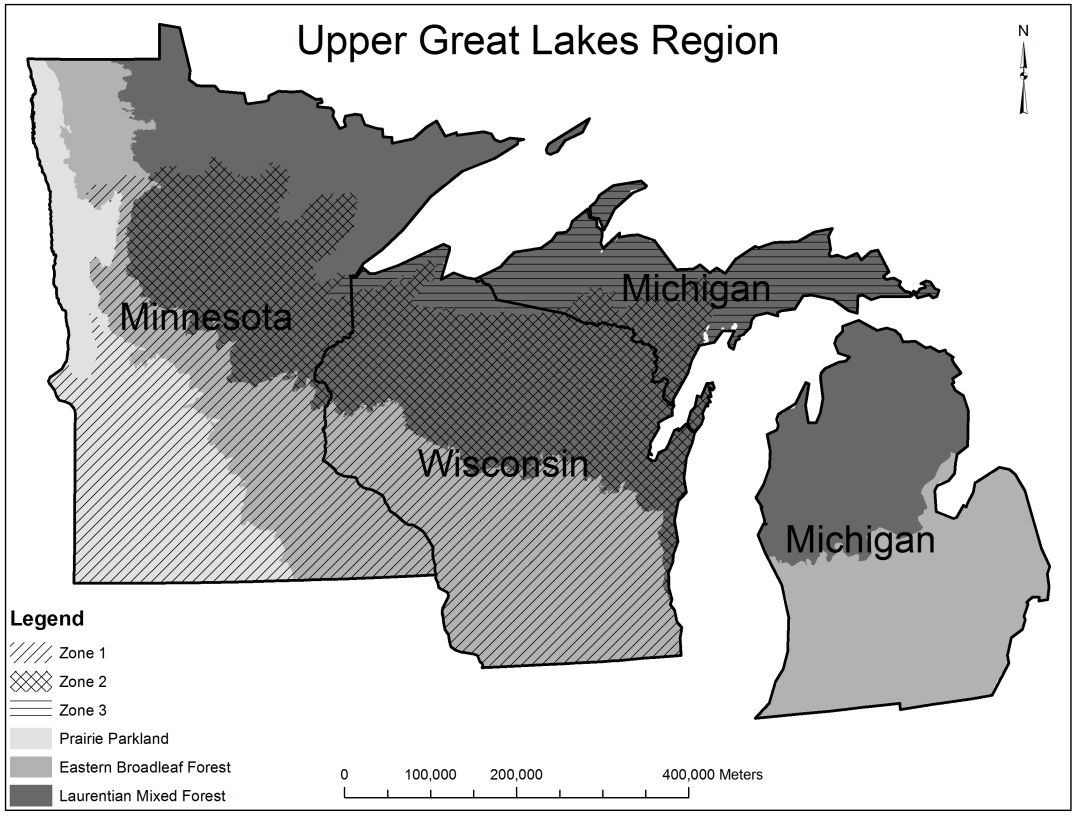

Figure 1.1. Map of the study area. Zones of interest are overlapping with ecological provinces (i.e. Prairie Parkland, Midwest Broadleaf Forest, and Laurentian Mixed Forest) (McNab et al. 2007). The Prairie-Forest Border (PFB) forms the transition zone between the tall grass prairies and the northern forests (Zone 1, 466 FIA plots), the forest interior extends beyond the PFB into northern Wisconsin (Zone 2, 1978 FIA plots), and the deep forest lies in Michigan's Upper Peninsula (Zone 3, 1419 FIA plots).

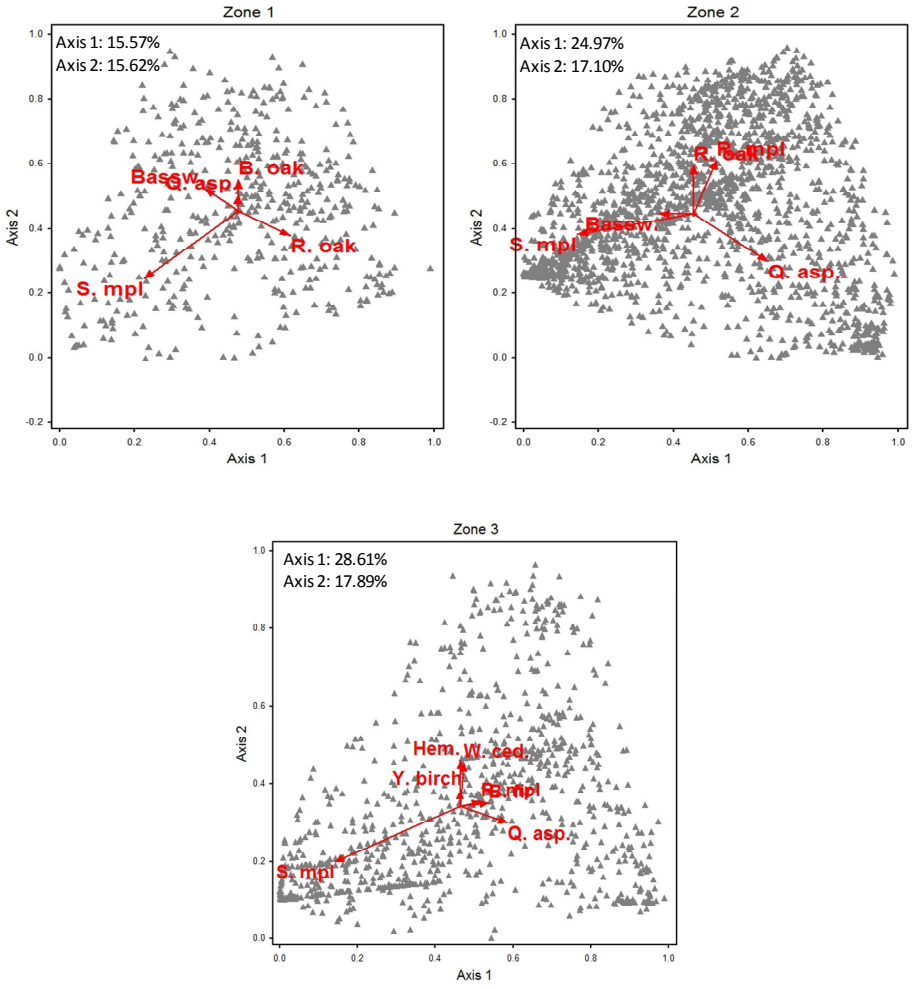

Figure 1.2. Ordination plots of sugar maple communities across the Upper Great Lakes region. The joint plots show the relationship of multiple responses to Axis 1 and 2. Upper left graph represents Zone 1, upper right graph represents Zone 2, and bottom graph represents Zone 3. Vectors are radiating from the centroid. The direction of each vector indicates its relative association with the two axes while the length of each vector is proportional to the magnitude of the association.

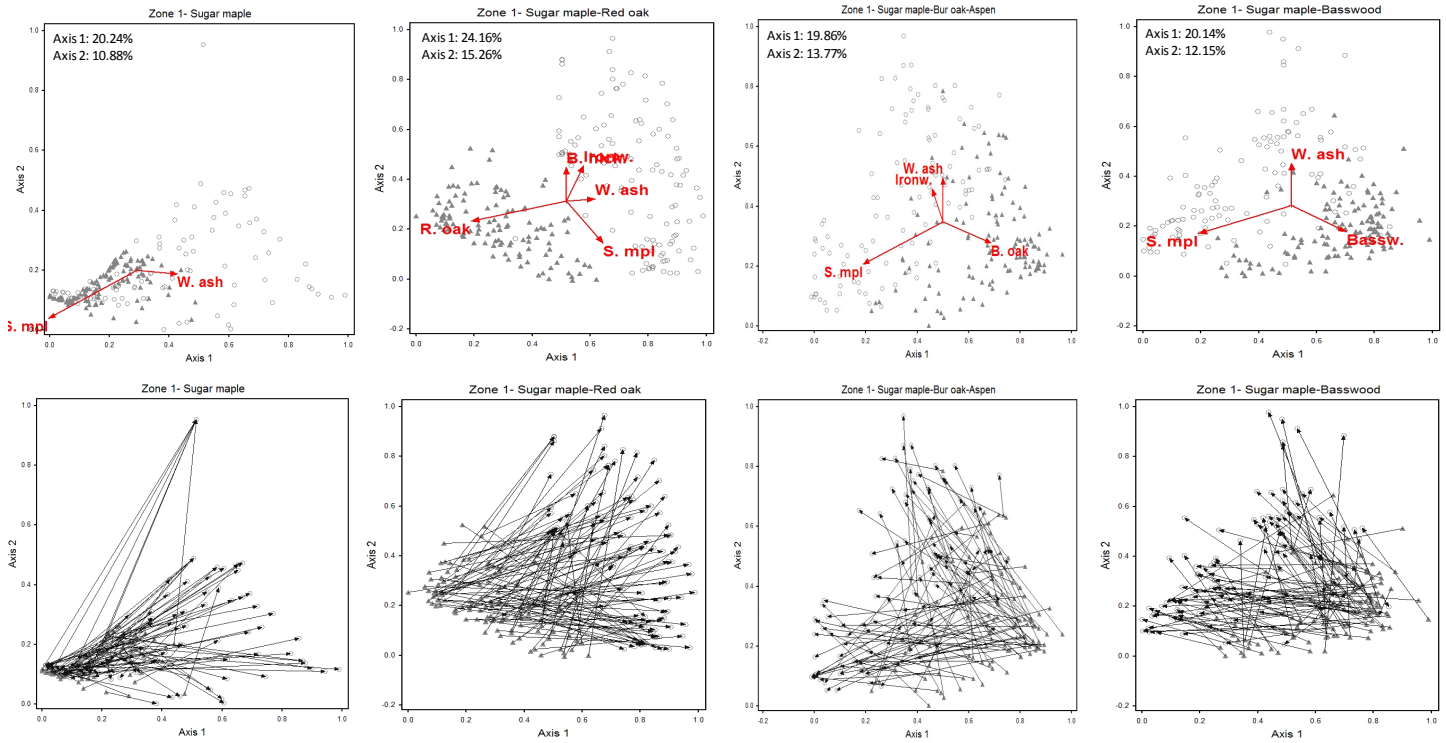

Figure 1.3. Successional vector overlay plots of sugar maple communities in Zone 1. For clarity, the top graphs show the joint plot without the successional vectors and the bottom graphs show the joint plot with the successional vectors. Triangles (▲) indicate overstory and open circles (○) indicate understory.

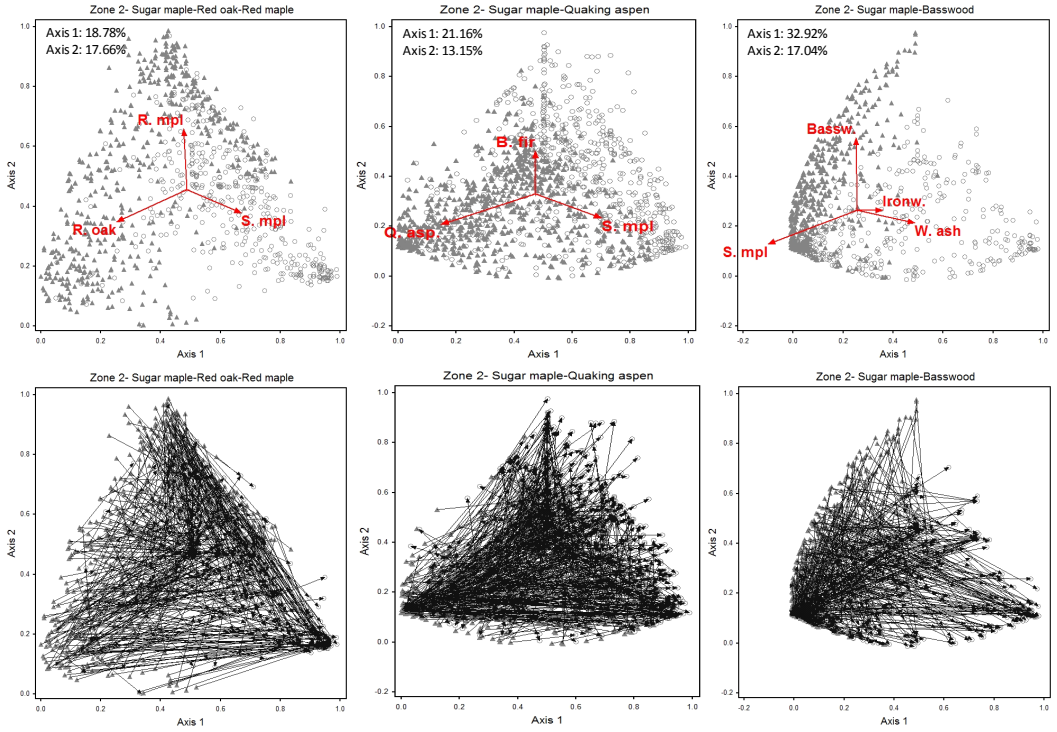

Figure 1.4. Successional vector overlay plots of sugar maple communities in Zone 2. For clarity, the top graphs show the joint plot without the successional vectors and the bottom graphs show the joint plot with the successional vectors. Triangles (▲) indicate overstory and open circles (○) indicate understory.

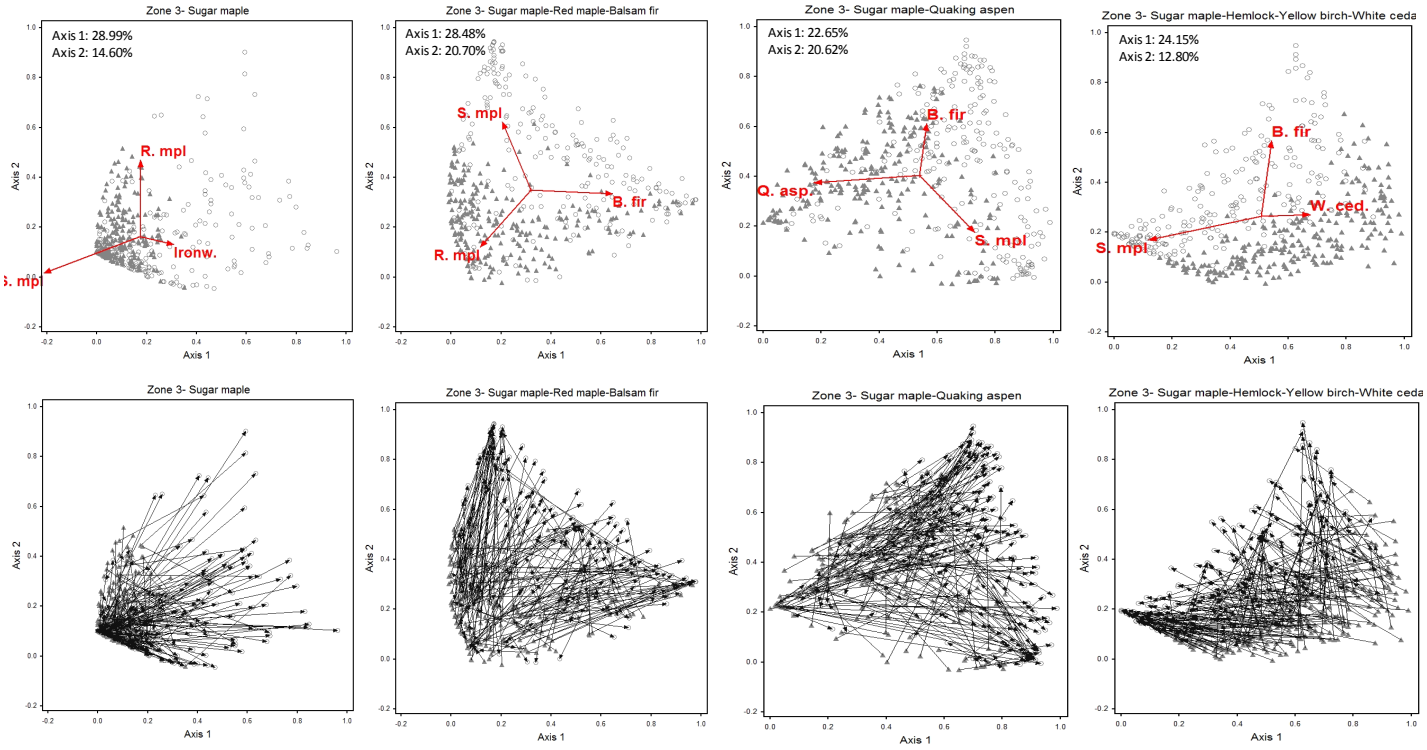

Figure 1.5. Successional vector overlay plots of sugar maple communities in Zone 3. For clarity, the top graphs show the joint plot without the successional vectors and the bottom graphs show the joint plot with the successional vectors. Triangles (▲) indicate overstory and open circles (○) indicate understory.

Chapter 2

Tree and seedling richness-productivity relationships in sugar maple (*Acer saccharum*) forest of the Upper Great Lakes region

with Lee E. Frelich

Hundreds of hypotheses have been proposed to explain the variation in species richness in ecology and site productivity has been recognized as being the most important processes regulating species richness. The species richness-productivity relationship has been studied for decades, yet, the form of this relationship and the possible mechanisms responsible for this pattern remain controversial. Five main distributions are proposed as an attempt to explain the species richness-productivity relationship: hump-shaped, positive monotonic, negative monotonic, U-shaped, or flat. The hump-shaped distribution is the most common pattern and refers to an increase in species richness at low levels of site productivity followed by a decrease at high levels of site productivity. Most species richness-productivity relationships studies have been conducted in ecosystems other than forests, although few studies have focused on this relationship in temperate deciduous forests. In an attempt to gain a better understanding of the overstory and understory species richness in relation to site productivity in temperate deciduous forests of the Upper Great Lakes region (Minnesota, Wisconsin, and Upper Peninsula of Michigan), we used data from Forest Inventory and Analysis plots (FIA) plots and a set of ordinary least squares (OLS) models on three data sets: a whole data set, an upper 90th quantile of species richness subset, and a random sample subset. First, we investigated the form of the tree and seedling richness-site productivity relationship in sugar maple dominated forests of the Upper Great Lakes region. Second, we added sugar maple relative basal area to our richness-site productivity analyses after noticing that sugar maple abundance approaches 100% on some plots in all zones and therefore dominates the tree layer. We tested if there was a threshold effect in sugar maple abundance that leads to a decrease of

other species. Results varied across zones and data sets, indicating that sample size might be influencing our results. Overall, a significant positive relationship between tree richness and site productivity was apparent as opposed to a flat seedling richness-site productivity relationship. The addition of sugar maple basal area to our models greatly improved our results. No threshold effect was apparent but we observed that sugar maple abundance had very strong negative neighborhood effect on species richness, which seemed to increase from the prairie-forest border towards Upper Michigan.

Introduction

According to the species-area theory, larger areas tend to contain a larger number of species (Wilson and MacArthur 1967). Based upon this assumption, the species-energy theory suggests a positive relationship between available energy - a general measure of site productivity due to factors such as climate, topography, or soil chemistry - and species richness (Wright 1983; Brown 1981). As an explanation for the species-energy theory, the More Individuals Hypothesis states that "more productive sites can support higher total abundances and, since species richness is an increasing function of total abundance, so will it be of productivity" (Srivastava and Lawton 1998). Amongst the hundreds of hypotheses that have been proposed to explain the variation in species richness (Palmer 1994), productivity (i.e. the rate at which energy flows through an ecosystem; Rosenzweig and Abramsky 1993) is recognized as being one of the most important processes regulating species richness and a key factor influencing biodiversity and ecosystem functions (Field et al. 2009; Tilman et al. 1997; Grime 1979). The

relationship between species richness and site productivity has been studied since the mid-1960s (Waide et al. 1999; Pianka 1966; Leigh 1965) and research clearly shows that site productivity is a strong and consistent predictor of species richness (Currie et al. 2004; Francis and Currie 2003; Hawkins et al. 2003).

Despite an increasing research effort investigating the species richness-site productivity relationship, the form of this relationship and the possible mechanisms responsible for this pattern remain controversial to the point that no general consensus on the topic has been reached (Adler et al. 2011; Waide et al. 1999; Abrams 1995). As a result, five main distributions are proposed as an attempt to explain the species richness-site productivity relationship: hump-shaped, positive monotonic, negative monotonic, U-shaped, or flat relationships (Mittelbach et al. 2001; Gross et al. 2000; Waide et al. 1999; Grace 1999). According to several studies, the hump-shaped distribution is the most common pattern attributed to the species richness-productivity relationship (see review by Mittelbach et al. 2001). This relationship has often been explained as a result of environmental stress and competitive exclusion, resulting in a unimodal distribution or "hump-shaped" relationship (Grime 1979). Adopted by many (Dodson et al. 2000; Tilman and Pacala 1993; Rosenzweig and Abramsky 1993), the humped model suggests that species richness decreases at low and high productivity levels and peaks at intermediate productivity level. At low productivity level, species richness is dependent upon limited resources and therefore responds to environmental stress; at intermediate productivity level, moderate levels of stress and competition allow species that could not survive towards low and high productivity levels to coexist; and at high productivity

level, species richness decreases with increased interspecific competition. While some authors characterized the hump-shaped model as being "ubiquitous" (Huston and Deangelis 1994) or "true" (Rosenzweig 1992), Abrams (1995) challenged the validity of the humped pattern by suggesting that other forms than the hump-shaped model exist. He argued that little is known about the mechanisms of competition in different communities and that at high productivity level, factors other than competition and exclusion explain reduced species richness. Other authors suggest that the form of the species richness-productivity relationship is highly scale dependent (Gross et al. 2000; Waide et al. 1999; Rosenzweig and Abramsky 1993). Mittlebach et al. (2001) examined the species richness-productivity relationship in 171 published studies, and observed that, at geographical scales smaller than the continental to global, such as the regional and local scales (<4000 km), the dominant model was the humped model (41-45% of all cases), followed by the positive relationship model. Examples of other factors explaining the form of species richness-productivity relationship include how data are aggregated and patterns examined (Gross et al. 2000), or the role of species pool and evolutionary history (Partel et al. 2007; Zobel 1997).

A review of the scientific literature shows that although species richness-site productivity relationship studies have been conducted in wetlands (Gough et al. 1994; Moore and Keddy 1989), grassland ecosystems (Gross et al. 2000; Grace 1999; Zobel and Liira 1997), aquatic ecosystems (Dodson et al. 2000), and even animal populations (Waide et al. 1999), few studies have focused on the species richness-site productivity relationship in temperate deciduous forests (Axmanova et al. 2012; Schuster and

Diekmann 2005), in particular in North America (Oberle et al. 2009). Given the debate around the hump-shaped model (Mittelbach et al. 2001; Waide et al. 1999), our first objective was to describe the form of the species richness-site productivity relationship in the overstory (tree) and understory (seedling) of temperate deciduous forests of the Upper Great Lakes region (Minnesota, Wisconsin, and Upper Peninsula of Michigan), specifically, in sugar maple dominated forests. As part of our second objective, we included sugar maple abundance to our models after noticing that the tree layer approached 100% sugar maple basal area on some plots across the entire study region. Given that sugar maple has a strong positive neighborhood effects that promotes self replacement (Frelich 2002; Frelich et al. 1993), we were interested in testing whether species richness decreased with increases of sugar maple abundance and investigating whether there was a threshold effect in sugar maple abundance that leads to the decrease of other species.

We studied the form of the species richness-site productivity relationship of the overstory and understory of sugar maple dominated forests (objective 1), by proposing the null hypothesis that the species richness-site productivity relationship of the Upper Great Lakes region is flat. Our alternative hypotheses were that the richness-site productivity relationship is 1) hump-shaped, 2) positive monotonic, 3) negative monotonic, and 4) U-shaped. We investigated the existence of threshold effects of sugar maple abundance on species richness (objective 2), by testing the null hypothesis that no threshold effect exists (i.e. species richness decreases linearly with increase sugar maple

abundance) against that alternative that there is a threshold effect of sugar maple abundance (i.e. species richness display threshold responses to increase basal area).

Methods

Study area

The Upper Great Lakes region includes three main ecological provinces defined by dominant climatic regimes, potential native vegetation, and biomes: the prairie parkland, the eastern broadleaf forest, and the Laurentian mixed forest provinces (McNab et al. 2007; Cleland et al. 1997; McNab and Avers 1994) (Figure 2.1).

The prairie parkland occupies the western part of Minnesota and extends to the southern parts of Wisconsin and Michigan. Mean annual temperatures vary from 2ºC in the north to 9ºC to the south. This province has a continental climate with cold winters, hot summers, and mean annual precipitation of 46 cm in the north to 84 cm in the south. Precipitation mainly occurs in the form of snow in the north but falls mostly as rain in the south. Mean evapotranspiration exceeds mean precipitation during the growing season (May through September), with water deficits of 3.8 cm along the western edge of the prairie parkland to 2.0 cm in southern Minnesota. Semi-arid loamy soils are well-to-moderately well-drained. Pre-settlement vegetation was dominated by tall grass prairie but today agriculture is the dominant land use.

The eastern broadleaf forest extends from northwestern Minnesota to southeastern Michigan. Mean annual temperatures vary from 4ºC in the northwest of the province to 10ºC in Michigan. The overall climate is continental with warm to hot summers.

Precipitation averages 65 to 93 cm and approximately equals evapotranspiration. Two-thirds of it falls during the growing season which lasts about 125 days up to 180 days along Lake Michigan. Local reliefs (20 to 180 m) are apparent in Wisconsin as a result of past glaciation. Winter precipitation is mostly snow and averages 100 cm. Soil moisture regime is dominantly mesic with frequent growing season water deficits ranging from 2.0 cm in Minnesota up to 1.2 cm in Wisconsin. Pre-settlement vegetation was dominated by maple-basswood forests or oak savannas at the prairie-forest border as a result of fire frequency variations (Grimm 1984) whereas oak-hickory forests dominate sandy sites and beech-maple forests grow on loamy soils in Michigan. Today, agriculture, urban and industrial development constitute the major land uses. The transition (ecotone) from eastern broadleaf forest to prairie parkland is sharp (Danz 2009; Grimm 1983) whereas the transition between eastern broadleaf forest and Laurentian mixed forest is gradual (Fisichelli et al. 2013a; Goldblum and Rigg 2002; Braun 1950).

The Laurentian mixed forest lies in the northern part of the Upper Great Lakes region and extends into Canada. Average annual temperatures range from 3ºC to 6ºC. Average annual precipitation varies between 61 cm and 115 cm, with fifty percent of precipitation falling during the growing season (May through September). Annual snowfall varies from 100 cm to 165 cm, but can be up to 833 cm due to the Lake-effect snow. The climate is classified as continental with lake effects influence along the Great Lakes. Winters (i.e. days below or at freezing temperature) are longer with considerable snow coverage and summers are short and warm compared to the prairie parkland and the eastern broadleaf provinces. To the contrary of the prairie parkland and the eastern

broadleaf provinces, there is a moisture surplus rather than a deficit, and the mean growing season potential evapotranspiration minus precipitation reaches -11 cm in the northern part of the Laurentian mixed forest. Hilly landscapes with shallow soils occur along Lake Superior and result from past glaciations. A mosaic of conifer stands, northern hardwood stands, and mixed stands occupies the region, and vegetation consists of forests that are a transition between boreal and broadleaf deciduous (Goldblum and Rigg 2002; Davis 1983; Braun 1950). The current land cover is forest and the dominant land use is forestry and outdoor recreation.

FIA data

The Forest Inventory and Analysis (FIA) Program of the U.S. Department of Agriculture Forest Service is a nationwide program that collects and publishes data from all ownership of forest land in the US since 1929 although annual inventories started in 1999 (U.S.D.A. 2009). The FIA Program features a complete and systematic national sample design for all lands in the US (Bechtold and Patterson 2005). It monitors only forest lands (i.e. at least 0.4 ha and 36.3 m wide with a minimum of 10% stocked by forest trees) and is conducted in three phases, although we used data from the first two phases only. In Phase 1, land area is stratified using remotely sensed imagery in the form of aerial photography and/or satellite imagery to reduce variance in the estimates. In Phase 2, the landscape is divided into contiguous 2428 ha hexagons containing one randomly located permanent ground plot each, for a total of ~125,000 forested plots nationwide. Sampling intensity varies between states, but because the FIA plot design is a

combination of systematic arrangement and random sampling, varying sample intensities only affects the precision of the estimates. Field crews sample approximately 20% of FIA plots annually in the eastern US where they collect variables (e.g. forest type, tree species, soil attributes) on each permanent ground plot with 100% measurement of a systematic panel of plots completed every five years in the eastern US (U.S.D.A. 2008). Each plot is designed to cover a 0.4 ha sample area. A plot consists of one central subplot and an equilateral triangle arrangement of three peripheral subplots spaced 36.6 m apart from the central subplot, at azimuths of 120, 240, and 360 degrees. Each subplot also includes a 2.1 m fixed-radius microplot which is offset from the center of the subplot (3.7 m at an azimuth of 90 degrees). All trees with a diameter at breast height (dbh) of at least 12.7 cm are recorded on subplots. Saplings (2.54 to 12.45 cm dbh) and seedlings (≤ 2.54 cm dbh and at least 30.5 cm in height for hardwood species) are inventoried in microplots.

We downloaded FIA raw data files for Minnesota, Wisconsin, and Michigan from the FIA database website (FIADB, http://apps.fs.fed.us/fiadb-downloads/datamart.html). Our study is based upon data collected between 2003 and 2007, which corresponds to a full cycle at the time of data upload (May 2009). To protect the confidentiality of the exact location of FIA plots, plot coordinates are spatially perturbed before being released to the public. The perturbed plot coordinates were adjusted to be within ± 1 mile of the true plot location which is of little consequence on our study given the regional scale presented in this work. We selected plots including at least one live sugar maple tree and aggregated them into contiguous zones: Zone 1 (378 plots) is near the prairie biome and

covers Minnesota and Wisconsin, although we excluded Northern Minnesota from our analyses because of small sample size; Zone 2 (1823 plots) is in the forest biome and includes northern Wisconsin; Zone 3 (1314 plots) is deep into the forest biome, with the best climate for trees, and includes the Upper Peninsula of Michigan (Figure 2.1).

Species richness was defined as the total number of species (i.e. tree or seedling) on each plot in each zone. Sugar maple basal area is expressed as the total basal area of sugar maple trees in square meter per hectare. We used SITECLCD from the FIA "Condition" table (COND) as our measure of site productivity. SITECLCD identifies the potential growth of a site by classifying forest land in terms of inherent capacity to grow crops of industrial wood. It is calculated in cubic feet per acre per year and is based on the culmination of mean annual increment of fully stocked natural stands (U.S.D.A. 2008). SITECLCD is based on the site trees available for the plot, i.e. the height that dominant or co-dominant trees are expected to attain at a base reference age. Classes range from 1 (225+ cubic feet/acre/year) to 7 (0-19 cubic feet/acre/year). We took the midpoint of each class and re-organized the original classes in order of increasing site productivity. We then converted our final classes to cubic meters per hectare. They were: 0.66; 2.10; 4.69; 7.14; 9.94; 13.61.

Data analysis

1. Exploratory data analyses

We started with basic exploratory data analyses to assess the means of tree and seedling richness in each zone and tested for significant differences. We used site

productivity as our independent variable and species richness (tree or seedling) as our dependent variable. ANOVAs were used to test for significant differences amongst zones (p-value ≤ 0.05) and followed up with a Tukey's HSD to test all possible two-way comparisons and find out which zones, if any, were significantly different (Cook and Weisberg 1999).

2. Species richness as a function of site productivity

Whole data set

The form of the relationship between species richness and site productivity was examined by using ordinary least squares (OLS) regression models in our three zones in two steps: first, we fit a linear model to distinguish between positive monotonic, negative monotonic, or flat relationships; second, a quadratic term was added to the linear term only if the quadratic term was significant (i.e. p-value < 0.05) (Cook and Weisberg 1999).

Upper quantile subset

The purpose of conducting multiple OLS regression models as explained above was to estimate the mean value of the distribution of the seedling and tree richness based on site productivity and sugar maple abundance. Since OLS only estimates the mean value of the response variable (here seedling or tree richness), it does not tell us about this relationship in the high species richness categories, in other words, in the high quantiles of seedling and tree richness. One way to account for this effect is to perform quantile regression analysis (Cade and Noon 2003). This technique was developed in the

late 1970s and consists of conducting regressions on various quantiles of the distribution (Koenker and Bassett 1978). The advantage of using quantile regression is that it ignores any assumptions about the distribution of the regression residuals and it is insensitive to outliers (Koenker 2005). Because it is a common phenomenon for most species to be absent from most plots in any sampling of the landscape (i.e. zero inflation problem), we reasoned that the upper quantile plots (i.e. those plots with the highest number of species) in each site productivity class may show species richness-site productivity relationships not apparent for all plots. Therefore, rather than applying a 90th quantile regression to the whole data set, we created a subset of the whole data set (i.e. "upper quantile subset") for each zone that contained plots above the 90th percentile of species richness at each site productivity level and examined the richness-site productivity relationship as explained in the previous paragraph.

Random sample subset

The species richness-site productivity analyses were further extended to another subset of data to investigate the effects of small sample size in the low and high productivity categories. In each site productivity class, we drew 100 random samples (with replacement) of plots and recorded the highest species richness each time. Because of differences in total number of plots in each zone (Zone 1 = 378 plots; Zone 2 = 1823 plots; Zone 3 = 1314 plots), the size of the random sample for each zone varied. In order to determine the size of the random sample in each zone, we selected the minimum number of plots (n) among all site productivity classes (for each zone) as a point of

reference for our random sample size; *n* was 81, 45, and 141 plots in Zone 1, Zone 2, and Zone 3, respectively. For instance, in Zone 1, we drew 100 random samples of 81 plots in each site productivity class and recorded the highest species richness at each drawing. We also used OLS regression analyses on this new data set of random sample (hereafter "random sample subset") and compared regression slopes among data sets (i.e. whole, upper quantile subset, and random sample subset) by means of an ANCOVA.

3. Species richness as a function of site productivity and sugar maple abundance

The relationship between species richness, site productivity, and sugar maple abundance was examined by means of multiple OLS regression to the whole data set only. Tree or seedling richness were the response variables; site productivity and its quadratic term, sugar maple abundance, and a two way interaction between site productivity and sugar maple abundance were the predictors. We evaluated a set of candidate models from a simple model including site productivity and basal area to a full model including all predictors and two-way interaction. A null model (intercept-only) was incorporated to each set of candidate models to determine the importance of the independent variables. Models were compared using Akaike's Information Criteria (AIC), which rewards the goodness of fit and penalizes models with too many predictors (i.e. avoids overfitting) while offering a balance between fit improvement (i.e. increased likelihood) and parsimony (Burnham and Anderson 2002). The model with the lowest AIC value is considered as the best model.

In all of our models, we transformed our data when appropriate and assessed the goodness of fit using the F-test lack of fit (i.e. p-value > 0.05 indicates that the model is adequate) along with a careful inspection of residual plots. Analyses were conducted in Arc (Cook and Weisberg 2004) and R (R Core Team 2013).

Results

1. Exploratory data analyses

Tree species richness in the Upper Great Lakes region was on average greater than seedling species richness (Table 2.1). Average tree richness decreased from the prairie-forest border to Upper Michigan (Zone 1 = 7.83; Zone 2 = 6.65; Zone 3 = 6.07) while average seedling richness was similar across the three zones (Zone 1 = 5.08; Zone 2 = 5.47; Zone 3 = 5.25; Table 2.1). ANOVA and Tukey's HSD tests indicated significant tree richness differences among all zones ($F = 92.83$, p-value < 0.001) and significant differences in seedling richness between Zone 1 and Zone 2 ($F = 4.545$, p-value = 0.011). On average, site productivity levels decreased from Zone 1 to Zone 3 while average sugar maple basal area increased from Zone 1 to Zone 3 (Table 2.1).

2. Species richness as a function of site productivity

The linear, quadratic, or multiple regression models highlighted below fit the data well after data transformation and inspection of the residuals and F-test for lack of fit, however, low R^2 indicated poor fits overall despite improving the explained variation in the significant quadratic models (Tables 2.2 to 2.4). Tree richness-site productivity linear

relationships from the whole data set were significant and slightly increasing in all zones (Table 2.2). When we added the quadratic term to each linear model, this relationship remained significant in Zones 2 and 3 with a slightly U-shaped pattern but was non-significant in Zone 1 (Table 2.2, Figure 2.2). The relationship between seedling richness and site productivity was non-significant and flat across zones and also the quadratic term was not significant (Table 2.2).

In the upper quantile subset, the linear relationship between tree richness and site productivity was significant and increasing in Zone 1 but non-significant in the other two zones where it was flat (Table 2.3). The quadratic term was significant in Zone 2 only and showed a U-shaped pattern (Table 2.3, Figure 2.3). The seedling richness-site productivity relationships were non-significant and flat in the linear models across zones (Table 2.3), however, the quadratic model in Zone 1 was significant and hump-shaped (Figure 2.3). The quadratic terms were not significant in Zones 2 and 3 (Table 2.3). The explained variation for the models in the upper quantile subset were low.

The linear models from the random sample subset showed a significant and increasing tree richness-site productivity relationship in Zones 2 and 3, but a non-significant and flat relationship in Zone 1 (Table 2.4). The quadratic term was significant in Zone 2 only, and the model showed a slight hump-shaped pattern (Figure 2.4). The seedling richness-site productivity linear models were all significant, although increasing in Zones 1 and 3 but decreasing in Zone 2. We found a significant U-shaped seedling richness-site productivity relationship in Zone 1 with the highest R^2 among all models

and data sets (R^2 = 0.388), and a slight hump in Zone 1 when we added the quadratic term (Table 2.4, Figure 2.4).

In summary, there was a flat tree richness-site productivity relationship in Zone 3 in the upper quantile and the random sample subsets, and in Zone 1 in the random sample subset (Table 2.5). Results indicated a significant increasing tree richness-site productivity relationship in Zone 1 for the whole data set and the upper quantile subset, a significant U-shaped pattern in Zones 2 and 3 for the whole data set and in Zone 2 from the upper quantile subset (Table 2.5). Additionally, there was a slight hump in Zone 2 for the random sample subset. For the seedling richness, the richness-site productivity relationship was flat and non-significant across zones for the whole data set, and in Zones 2 and 3 for the upper quantile subset (Table 2.5). Significant hump patterns were visible in Zone 1 (upper quantile subset) and Zone 2 (random sample subset). Finally, we noticed a significant U-shaped relationship in Zone 1 and a significant increasing trend in Zone 3, both from the random sample subset (Table 2.5).

3. Species richness as a function of site productivity and sugar maple abundance

AIC results indicated that the top models for tree richness (Table 2.6) and seedling richness (Table 2.7) in each zone included site productivity and basal area. One intercept-only model qualified as a candidate model (i.e. $\Delta_i < 2$) in Zone 1 (AIC = 1059.53, Table 2.7). With the exception of the set of best seedling richness models in Zone 1 (Table 2.11), all other seedling and tree richness models (Tables 2.8-2.10 and Tables 2.12-2.13, respectively) were significant, although the significance of all

parameters was achieved only in the top tree richness model in Zone 1 (AIC = 1623.33, Table 2.8). Overall, sugar maple basal area was significant and negative in most tree and seedling richness models and site productivity, its quadratic term, and the interaction between site productivity and basal area were not significant (Tables 2.8-2.15).

Results from the top model for each zone (i.e. lowest AIC value) indicate that most tree and seedling richness models were significant (Tables 2.14 and 2.15, respectively), expect for the top seedling richness model in Zone 1, although the significance of this model was marginal (p-value = 0.07, Table 2.15). R^2 for the tree richness models (0.14, 0.25, and 0.34 for Zone 1, Zone, and Zone 3, respectively; Table 2.14) were improved by adding sugar maple abundance into the equation as opposed to using site productivity alone, while R^2 remained low for seedling richness (0.009, 0.04, and 0.07 for Zone 1, Zone, and Zone 3, respectively; Table 2.15). Comparison of standardized parameters coefficients (SPE) indicated that sugar maple basal area was a more important predictor than site productivity in all zones (SPE, Tables 2.14 and 2.15). SPE also showed that sugar maple basal area had a significant negative impact on tree and seedling richness across zones, which increased from Zone 1 to Zone 3 (SPE, Tables 2.14 and 2.15). The significance of site productivity was apparent only for tree richness in Zone 1, for which it had a positive effect (Table 2.14). We further observed significant and strong negative correlations between richness and sugar maple abundance (Figure 2.5). More precisely, on sites with high sugar maple basal area (100%), tree richness was reduced to one species but seedling richness varied between 0 to 7 species, with a mean of 2 to 3 species (Table 2.16).

Discussion

Shape of species richness-site productivity relationships

Our null hypothesis of a flat richness-site productivity relationship was fully supported for seedling richness in the whole data set, indicating that site productivity has no effect on seedling richness across the Upper Great Lakes region, most likely because seedlings respond differently to productive environments than adults do (Grman 2013; Stevens et al. 2004; Tilman and Pacala 1993). However, for the whole data set, there was support for significant slightly increasing species richness with site productivity for trees, either linear (Zone 1) or with a curved increase (significant quadratic term, but mostly upward leg of the quadratic relationship represented, Figures 2.2b and 2.2c).

Best fit regression curves for the upper 90th percentile data set were generally in agreement with the whole data set except for tree richness in Zone 3 and seedling richness in Zone 1. Only seedling richness in Zone 1 had the expected flat pattern for the whole data set and hump-shaped relationship for the 90th percentile (Table 2.5), based on inspection of the scatter plots in Figure 2.2. Furthermore, we anticipated similar results for shape of the relationship between the upper quantile and random subsets, but found agreement only for tree richness in Zone 3. Such disparities suggest that differences in sample sizes among site productivity classes might be influencing the results (Cade and Noon 2003; Mittelbach et al. 2001). The lowest and highest site productivity classes had far fewer plots than the middle classes, so that fewer plots were in the upper quantile for low and high classes, giving a misleading visual impression of the shape of the upper

quantile. Inconsistent results between the upper quantile and random sample subsets indicate little support for using any model other than the whole data set.

Choice of independent variable as a surrogate for site productivity (FIA uses the potential growth of industrial wood, in cubic feet/acre/year) can lead to variations in the shape of the species richness-site productivity relationship. According to Abrams (1988), the relationship between productivity and diversity may depend upon the meaning of productivity and the type of resources that influence growth. Waide et al. (1999) pointed out that, while theoretical studies use net primary productivity as the independent variable, empirical studies use components or surrogates of net primary productivity as theirs. Under different circumstances, productivity has been measured in different ways, and studies have used climatic variables (Oberle et al. 2009), biomass (Axmanova et al. 2013), tree dbh and volume (Larpkern et al. 2011), or light availability (Reich et al. 2012) as proxy measures of site productivity. This difference in measure not only makes it challenging to depict consistency in the relationship between species richness and productivity, but it also makes it difficult to compare findings from several studies, thereby the importance of using direct measures of site productivity (e.g. soil nutrients and moisture) in an attempt to portray site productivity gradients (Adler et al. 2011).

In the significant models, the percentage of the variation explained by regression equations was low. The need for a high R^2, in our case, was of less concern because we were interested in investigating the shape of relationships between variables rather than making predictions of species richness for individual plots. Although R^2 statistics are used as a measure of goodness of fit, low or high R^2 have been shown to over- or under-

represent the data when interpreted alone (for instance, it is possible to have a low R^2 for a model that fits the data, or a high R^2 for a model that does not), thus the importance of examining the regression diagnostic plots carefully in addition to inspecting statistical tests (Cook and Weisberg 1999; Rawlings et al. 1998). In this study, low R^2 indicated that other factors than site productivity influence species richness, which is consistent with findings from previous studies of species richness-site productivity relationships (Adler et al. 2011). The addition of sugar maple abundance in our models for instance improved the percentage of the variation explained by the model and provided valuable information.

Since we found that tree richness increases slightly in all three zones using the whole data set, we were interested in further evaluating whether changes in tree richness were biologically significant (Johnson and Omland 2004). Based on the regression models in Table 2.2, we calculated how mean species richness changes across the range of site productivity levels for each zone and found that in Zone 1, species richness increased by two species from low to high productivity sites (i.e. from 7 to 9 species). In Zone 2, tree richness across site productivity levels was constant (i.e. 7 species), and in Zone 3, tree richness increased from 6 species on low productivity sites to 7 species on high productivity sites. Given such little variation in the results, we conclude that this increase in tree richness across site productivity levels has only modest biological significance.

Influence of site productivity and sugar maple basal area

By adding sugar maple abundance to our models, we gained a better explanation of the variation in tree and seedling richness. The significance of sugar maple basal area when added to our models provided valuable information on the importance of overstory abundance to species richness. In general, previous authors have pointed out that site productivity is only one factor influencing species richness and that other mechanisms contributing to richness-site productivity relationship include disturbance (Dyer and Baird 1997; Oliver 1981; White 1979; Connell 1978), latitudinal gradients and habitat diversity (Rohde 1992), species tolerance for different sets of climatic conditions (i.e. the physiological tolerance hypothesis) (Currie et al. 2004), or evolutionary mechanisms (Evans et al. 2005). Specifically, in our study area, variation in species richness among our plots may result from other local processes that regulate species richness, such as soils (Gough et al. 1994; Goldberg 1985; Daubenmire 1936), predation (Rooney et al. 2000; Doepker et al. 1995; Stoeckeler et al. 1957), invasive species (Holdsworth et al. 2007; Rooney et al. 2004a). These findings, including ours, highlight the importance of considering other factors than site productivity when attempting to understand species richness patterns (Simova et al. 2013; Adler et al. 2011).

We did not find evidence for a threshold effect in our data—species richness showed a steady linear decline with increasing basal area (Figure 2.5). Overstory abundance has been shown to influence species richness in several forest ecosystems including European deciduous forests (Axmanova et al. 2012) or boreal forests (Reich et al. 2012). The success of understory species in particular depends upon several factors including neighborhood effects, a major component to the spatial and temporal dynamic

of forests (Frelich and Reich 1999). Sugar maple exerts strong neighborhood effects in the form of dense shade and heavy litterfall of moderately large leaves that can smother seedlings of some species like hemlock and/or prevent access to mineral soils required by some species such as hemlock, yellow birch and red maple (Ferrari 1999; Frelich et al. 1993; Koroleff 1954). We found that, on sites with high sugar maple abundance (i.e. 100% basal area), several seedling species occurred in the understory (Table 2.16), which is an indication that sugar maple cannot eliminate all microsites that would support other species of seedlings. Therefore, all of the basal area models predict about four species of seedlings even at 100% sugar maple basal area.

In conclusion, we found that the seedling richness-site productivity relationship was flat and that tree richness increased slightly with site productivity, marginally significant biologically. Surrogates for site productivity should be used with care and direct measures of site productivity are recommended. Sugar maple abundance had a strong negative effect on species richness and explains a greater proportion of the variation of species richness that site productivity, which highlights the importance of exploring other factors that may influence species richness. No threshold effect of sugar maple abundance on species richness was apparent. On 100% sugar maple basal area sites, tree richness was reduced to one while seedling richness varied between 0-7, indicating that sugar maple can never exclude all other species of seedling even on sites with 100% sugar maple basal area.

Table 2.1. Descriptive statistics for the variables used in this study. All variables originate from the Forest Inventory and Analysis (FIA) National Program.

Variable	Zone	Mean	Minimum	Maximum
Tree richness	1	7.83	1.00	14.00
(count)	2	6.65	1.00	15.00
	3	6.07	1.00	14.00
Seedling richness	1	5.08	0.00	14.00
(count)	2	5.47	0.00	17.00
	3	5.25	0.00	15.00
Site productivity	1	4.50	0.66	13.61
(cubic meter per hectare)	2	4.42	0.66	13.61
	3	3.66	0.66	9.94
Sugar maple abundance	1	20.77	0.49	100.00
(% basal area)	2	30.10	0.47	100.00
	3	36.85	1.00	100.00

Table 2.2. Ordinary Least Square (OLS) regression parameters for the linear and quadratic models of the species richness-site productivity relationships (whole data set). R^2 refers to the coefficient of determination. The quadratic model was considered appropriate only if the quadratic term was significant. "n.s." denotes a non-significant relationship. Corresponding plots are shown in Figure 2.2.

(a) Tree richness

	Linear model			
	Form of the relationship	Linear term	Sig. of model	R^2
Zone 1	Increasing	0.132	0.011	0.017
Zone 2	Increasing	0.106	0.000	0.008
Zone 3	Increasing	0.111	0.001	0.008

	Quadratic model				
	Form of the relationship	Linear term	Quadratic term	Sig. of quadratic term	R^2
Zone 1	Flat	0.415	-0.026	n.s.	n.s.
Zone 2	Slight U-shaped	-0.144	0.025	0.008	0.012
Zone 3	Slight U-shaped	-0.281	0.044	0.003	0.014

(b) Seedling richness

	Linear model			
	Form of the relationship	Linear term	Sig. of model	R^2
Zone 1	Flat	-0.033	n.s.	n.s.
Zone 2	Flat	0.010	n.s.	n.s.
Zone 3	Flat	0.010	n.s.	n.s.

	Quadratic model				
	Form of the relationship	Linear term	Quadratic term	Sig. of quadratic term	R^2
Zone 1	Flat	0.233	-0.024	n.s.	n.s.
Zone 2	Flat	-0.068	0.008	n.s.	n.s.
Zone 3	Flat	-0.287	0.033	n.s.	n.s.

Table 2.3. Ordinary Least Square (OLS) regression parameters for the linear and quadratic models of the species richness-site productivity relationships (upper quantile subset). R^2 refers to the coefficient of determination. The quadratic model was considered appropriate only if the quadratic term was significant. "n.s." denotes a non-significant relationship. Corresponding plots are shown in Figure 2.3.

(a) Tree richness

	Linear model			
	Form of the relationship	Linear term	Sig. of model	R^2
Zone 1	Increasing	0.131	0.014	0.141
Zone 2	Flat	0.064	n.s.	n.s.
Zone 3	Flat	0.000	n.s.	n.s.

	Quadratic model				
	Form of the relationship	Linear term	Quadratic term	Sig. of quadratic term	R^2
Zone 1	Flat	0.339	-0.017	n.s.	n.s.
Zone 2	U-shaped	-0.395	0.043	0.000	0.063
Zone 3	Flat	-0.007	0.001	n.s.	n.s.

(b) Seedling richness

	Linear model			
	Form of the relationship	Linear term	Sig. of model	R^2
Zone 1	Flat	-0.022	n.s.	n.s.
Zone 2	Flat	-0.001	n.s.	n.s.
Zone 3	Flat	-0.041	n.s.	n.s.

	Quadratic model				
	Form of the relationship	Linear term	Quadratic term	Sig. of quadratic term	R^2
Zone 1	Hump-shaped	0.863	-0.077	0.003	0.166
Zone 2	Flat	-0.112	0.011	n.s.	n.s.
Zone 3	Flat	0.066	-0.011	n.s.	n.s.

Table 2.4. Ordinary Least Square (OLS) regression parameters for the linear and quadratic models of the species richness-site productivity relationships (random sample subset). R^2 refers to the coefficient of determination. The quadratic model was considered appropriate only if the quadratic term was significant. "n.s." denotes a non-significant relationship. Corresponding plots are shown in Figure 2.4.

(a) Tree richness

	Linear model			
	Form of the relationship	Linear term	Sig. of model	R^2
Zone 1	Flat	-0.030	n.s.	n.s.
Zone 2	Increasing	0.116	0.000	0.081
Zone 3	Increasing	0.130	0.001	0.040

	Quadratic model				
	Form of the relationship	Linear term	Quadratic term	Sig. of quadratic term	R^2
Zone 1	Flat	0.053	-0.009	n.s.	n.s.
Zone 2	Slight hump	0.505	-0.032	0.000	0.117
Zone 3	Flat	-0.101	0.025	n.s.	n.s.

(b) Seedling richness

	Linear model			
	Form of the relationship	Linear term	Sig. of model	R^2
Zone 1	Increasing	0.194	0.000	0.081
Zone 2	Decreasing	-0.152	0.000	0.079
Zone 3	Increasing	0.152	0.000	0.062

	Quadratic model				
	Form of the relationship	Linear term	Quadratic term	Sig. of quadratic term	R^2
Zone 1	U-shaped	-2.201	0.260	0.000	0.388
Zone 2	Slight hump	0.246	-0.033	0.002	0.101
Zone 3	Flat	-0.016	0.018	n.s.	n.s.

Table 2.5. Summary of the form of species richness-site productivity relationships across zones and among data sets. Full results are presented in Tables 2.2 to 2.4. The form of the species richness-site productivity relationship recorded in the table refers to best of the linear or the quadratic model.

(a) Tree richness

	Whole dataset	Upper quantile subset	Random sample subset
Zone 1	Increasing	Increasing	Flat
Zone 2	Slight U-shaped	U-shaped	Slight hump
Zone 3	Slight U-shaped	Flat	Increasing

(b) Seedling richness

	Whole dataset	Upper quantile subset	Random sample subset
Zone 1	Flat	Hump-shaped	U-shaped
Zone 2	Flat	Flat	Slight hump
Zone 3	Flat	Flat	Increasing

Table 2.6. AIC models of tree richness as a function of site productivity and sugar maple basal area in each zone. Models are ranked from the lowest to the highest AIC value in each zone. $\Delta i < 2$ provide substantial support for the best model (Burnham and Anderson 2002). K is the number of parameters included in the model, AIC is the Akaike's Information Criterion value, Δi is the difference between the AIC of the best fitting model and that of model *i*, and w*i* is the probability that a model *i* is the best among all candidate models. Model parameters: SP = Site productivity, SP^2 = Site productivity quadratic term, BA = Basal area. The symbol "x" between two parameters indicates a two way interaction.

(a) Zone 1

Model	K	AIC	Δi	wi
SP + BA	4	1623.33	0.00	0.39
SP + SP^2 + BA	5	1624.20	0.87	0.25
SP + BA + SPxBA	5	1624.45	1.12	0.22
SP + SP^2 + BA + SPxBA	6	1625.37	2.04	0.14
Intercept-only	2	1678.76	55.43	0.00

(b) Zone 2

Model	K	AIC	Δi	wi
SP + BA	4	3839.73	0.00	0.38
SP + BA + SPxBA	5	3840.33	0.60	0.28
SP + SP^2 + BA	5	3841.29	1.56	0.18
SP + SP^2 + BA + SPxBA	6	3841.51	1.79	0.16
Intercept-only	2	4364.81	525.08	0.00

(c) Zone 3

Model	K	AIC	Δi	wi
SP + BA	4	2584.21	0.00	0.47
SP + BA + SPxBA	5	2585.36	1.15	0.26
SP + SP^2 + BA	5	2586.17	1.97	0.17
SP + SP^2 + BA + SPxBA	6	2587.34	3.13	0.10
Intercept-only	2	3124.43	540.22	0.00

Table 2.7. AIC models of seedling richness as a function of site productivity and sugar maple basal area in each zone. Models are ranked from the lowest to the highest AIC value in each zone. $\Delta i < 2$ provide substantial support for the best model (Burnham and Anderson 2002). K is the number of parameters included in the model, AIC is the Akaike's Information Criterion value, Δi is the difference between the AIC of the best fitting model and that of model *i*, and w*i* is the probability that a model *i* is the best among all candidate models. Model parameters: SP = Site productivity, SP^2 = Site productivity quadratic term, BA = Basal area. The symbol "x" between two parameters indicates a two way interaction.

(a) Zone 1

Model	K	AIC	Δi	wi
SP + BA	4	1058.12	0.00	0.33
SP + SP^2 + BA	5	1058.47	0.35	0.28
Intercept-only	2	1059.53	1.42	0.16
SP + BA + SPxBA	5	1060.10	1.99	0.12
SP + SP^2 + BA + SPxBA	6	1060.44	2.33	0.10

(b) Zone 2

Model	K	AIC	Δi	wi
SP + BA	4	3126.97	0.00	0.30
SP + BA + SPxBA	5	3127.29	0.32	0.26
SP + SP^2 + BA + SPxBA	6	3127.45	0.48	0.24
SP + SP^2 + BA	5	3127.79	0.82	0.20
Intercept-only	2	3200.61	73.64	0.00

(c) Zone 3

Model	K	AIC	Δi	wi
SP + BA	4	1875.64	0.00	0.53
SP + SP^2 + BA	5	1877.58	1.93	0.20
SP + BA + SPxBA	5	1877.61	1.97	0.20
SP + SP^2 + BA + SPxBA	6	1879.54	3.90	0.08
Intercept-only	2	1975.62	99.97	0.00

Table 2.8. Ordinary Least Squares (OLS) regression for the best models (i.e. $\Delta i < 2$) of tree richness as a function of site productivity and sugar maple basal area in Zone 1. Best models are ranked from the lowest to the highest AIC value (see Table 2.6). #1 indicate the top best model and #3 the last model.

#1

Adj. $R^2 = 0.14$, F =31.93; p-value < 0.001

Coefficients	Estimate	Std. Error	t-value	p-value
Intercept	11.469	1.192	9.623	0.000
Site productivity	1.218	0.593	2.053	0.041
Basal area	-3.586	0.486	-7.383	0.000

#2

Adj. $R^2 = 0.14$; F = 21.67; p-value < 0.0001)

Coefficients	Estimate	Std. Error	t-value	p-value
Intercept	5.550	5.713	0.971	0.332
Site productivity	9.725	8.051	1.208	0.228
Site productivity^2	-2.997	2.828	-1.060	0.290
Basal area	-3.599	0.486	-7.408	0.000

#3

Adj. $R^2 = 0.14$; F = 21.57; p-value < 0.0001)

Coefficients	Estimate	Std. Error	t-value	p-value
Intercept	16.726	5.762	2.903	0.004
Site productivity	-2.475	4.005	-0.618	0.537
Basal area	-7.087	3.786	-1.872	0.062
Basal area x Site productivity	2.466	2.644	0.933	0.352

Table 2.9. Ordinary Least Squares (OLS) regression for the best models (i.e. $\Delta i < 2$) of tree richness as a function of site productivity and sugar maple basal area in Zone 2. Best models are ranked from the lowest to the highest AIC value (see Table 2.6). #1 indicate the top best model and #4 the model.

#1

Adj. $R^2 = 0.25$, $F = 306.4$; p-value < 0.001

Coefficients	Estimate	Std. Error	t-value	p-value
Intercept	4.527	0.121	37.550	0.000
Site productivity	0.089	0.065	1.380	0.168
Basal area	-0.432	0.018	-24.440	0.000

#2

Adj. $R^2 = 0.25$; $F = 204.8$; p-value < 0.0001)

Coefficients	Estimate	Std. Error	t-value	p-value
Intercept	4.896	0.335	14.613	0.000
Site productivity	-0.141	0.206	-0.687	0.492
Basal area	-0.568	0.116	-4.879	0.000
Basal area x Site productivity	0.085	0.072	1.181	0.238

#3

Adj. $R^2 = 0.25$; $F = 204.4$; p-value < 0.0001)

Coefficients	Estimate	Std. Error	t-value	p-value
Intercept	4.933	0.625	7.891	0.000
Site productivity	-0.440	0.803	-0.548	0.584
Site productivity^2	0.166	0.251	0.661	0.508
Basal area	-0.431	0.018	-24.100	0.000

#4

Adj. $R^2 = 0.25$; $F = 153.8$; p-value < 0.0001)

Coefficients	Estimate	Std. Error	t-value	p-value
Intercept	5.514	0.763	7.231	0.000
Site productivity	-0.911	0.877	-1.038	0.299
Site productivity^2	0.231	0.256	0.903	0.367
Basal area	-0.586	0.118	-4.961	0.000
Basal area x Site productivity	0.098	0.074	1.331	0.183

Table 2.10. Ordinary Least Squares (OLS) regression for the best models (i.e. $\Delta i < 2$) of tree richness as a function of site productivity and sugar maple basal area in Zone 3. Best models are ranked from the lowest to the highest AIC value (see Table 2.6). #1 indicate the top best model and #3 the last model.

#1

Adj. $R^2 = 0.34$, $F = 336.3$; p-value < 0.001

Coefficients	Estimate	Std. Error	t-value	p-value
Intercept	4.198	0.150	27.983	0.000
Site productivity	0.178	0.199	0.895	0.371
Basal area	-0.193	0.008	-25.767	0.000

#2

Adj. $R^2 = 0.34$; $F = 224.5$; p-value < 0.0001)

Coefficients	Estimate	Std. Error	t-value	p-value
Intercept	3.909	0.349	11.205	0.000
Site productivity	0.568	0.469	1.211	0.226
Basal area	-0.137	0.061	-2.237	0.026
Basal area x Site productivity	-0.075	0.082	-0.919	0.358

#3

Adj. $R^2 = 0.34$; $F = 224.1$; p-value < 0.0001)

Coefficients	Estimate	Std. Error	t-value	p-value
Intercept	4.387	1.040	4.217	0.000
Site productivity	-0.336	2.810	-0.120	0.905
Site productivity^2	0.342	1.867	0.183	0.855
Basal area	-0.193	0.008	-25.387	0.000

Table 2.11. Ordinary Least Squares (OLS) regression for the best models (i.e. $\Delta i < 2$) of seedling richness as a function of site productivity and sugar maple basal area in Zone 1. Best models are ranked from the lowest to the highest AIC value (see Table 2.7). #1 indicate the top best model and #4 the last model.

#1

Adj. $R^2 = 0.009$, F = 2.71; p-value = 0.07

Coefficients	Estimate	Std. Error	t-value	p-value
Intercept	4.244	0.5632	7.536	0.000
Site productivity	-0.167	0.2804	-0.594	0.553
Basal area	-0.530	0.2295	-2.308	0.022

#2

Adj. $R^2 = 0.01$; F = 1.80; p-value = 0.15)

Coefficients	Estimate	Std. Error	t-value	p-value
Intercept	3.919	2.726	1.438	0.151
Site productivity	0.062	1.895	0.033	0.974
Basal area	-0.313	1.791	-0.175	0.861
Basal area x Site productivity	-0.153	1.251	-0.122	0.903

#3

p-value < 0.001

Coefficients	Estimate	Std. Error	t-value	p-value
Intercept	3.211	0.051	63.460	0.000

#4

Adj. $R^2 = 0.11$; F = 2.35; p-value = 0.072)

Coefficients	Estimate	Std. Error	t-value	p-value
Intercept	0.872	2.698	0.323	0.747
Site productivity	4.680	3.802	1.231	0.219
Site productivity^2	-1.707	1.336	-1.278	0.202
Basal area	-0.537	0.229	-2.341	0.020

Table 2.12. Ordinary Least Squares (OLS) regression for the best models (i.e. $\Delta i < 2$) of seedling richness as a function of site productivity and sugar maple basal area in Zone 2. Best models are ranked from the lowest to the highest AIC value (see Table 2.7). #1 indicate the top best model and #4 the last model.

#1

Adj. $R^2 = 0.04$, $F = 39.67$; p-value < 0.001

Coefficients	Estimate	Std. Error	t-value	p-value
Intercept	2.890	0.099	29.155	0.000
Site productivity	-0.030	0.053	-0.566	0.572
Basal area	-0.129	0.015	-8.891	0.000

#2

Adj. $R^2 = 0.04$; $F = 26.97$; p-value < 0.0001)

Coefficients	Estimate	Std. Error	t-value	p-value
Intercept	2.557	0.276	9.281	0.000
Site productivity	0.178	0.169	1.052	0.293
Basal area	-0.007	0.096	-0.069	0.945
Basal area x Site productivity	-0.077	0.059	-1.296	0.195

#3

Adj. $R^2 = 0.04$; $F = 20.69$; p-value < 0.0001)

Coefficients	Estimate	Std. Error	t-value	p-value
Intercept	1.794	0.627	2.861	0.004
Site productivity	1.128	0.721	1.564	0.118
Site productivity^2	-0.285	0.210	-1.355	0.175
Basal area	0.015	0.097	0.158	0.874
Basal area x Site productivity	-0.093	0.061	-1.530	0.126

#4

Adj. $R^2 = 0.04$; $F = 26.79$; p-value < 0.0001)

Coefficients	Estimate	Std. Error	t-value	p-value
Intercept	2.344	0.514	4.560	0.000
Site productivity	0.683	0.660	1.035	0.301
Site productivity^2	-0.224	0.207	-1.084	0.279
Basal area	-0.132	0.015	-8.956	0.000

Table 2.13. Ordinary Least Squares (OLS) regression for the best models (i.e. $\Delta i < 2$) of seedling richness as a function of site productivity and sugar maple basal area in Zone 3. Best models are ranked from the lowest to the highest AIC value (see Table 2.7). #1 indicate the top best model and #3 the last model.

#1

Adj. $R^2 = 0.07$, $F = 53.98$; p-value < 0.001

Coefficients	Estimate	Std. Error	t-value	p-value
Intercept	2.582	0.115	22.537	0.000
Site productivity	0.268	0.152	1.766	0.078
Basal area	-0.060	0.006	-10.387	0.000

#2

Adj. $R^2 = 0.07$; $F = 35.98$; p-value < 0.0001)

Coefficients	Estimate	Std. Error	t-value	p-value
Intercept	2.381	0.794	2.997	0.003
Site productivity	0.817	2.146	0.381	0.703
Site productivity^2	-0.366	1.426	-0.256	0.798
Basal area	-0.060	0.006	-10.288	0.000

#3

Adj. $R^2 = 0.07$; $F = 35.97$; p-value < 0.0001)

Coefficients	Estimate	Std. Error	t-value	p-value
Intercept	2.541	0.266	9.534	0.000
Site productivity	0.324	0.358	0.904	0.366
Basal area	-0.051	0.047	-1.097	0.273
Basal area x Site productivity	-0.011	0.062	-0.173	0.863

Table 2.14. Ordinary Least Squares (OLS) regression for the top models (i.e. lowest AIC value) of tree richness as a function of site productivity and sugar maple basal area in each zone. "SPE" refers to the standardized parameter estimates for the independent variables.

(a) Zone 1

Adj. R^2 = 0.14, F =31.93; p-value < 0.001

Coefficients	Estimate	SPE	Std. Error	t-value	p-value
Intercept	11.469	--	1.192	9.623	0.000
Site productivity	1.218	0.099	0.593	2.053	0.041
Basal area	-3.586	-0.356	0.486	-7.383	0.000

(b) Zone 2

Adj. R^2 = 0.25, F = 306.4; p-value < 0.001

Coefficients	Estimate	SPE	Std. Error	t-value	p-value
Intercept	4.527	--	0.121	37.550	0.000
Site productivity	0.089	0.028	0.065	1.380	0.168
Basal area	-0.432	-0.498	0.018	-24.440	0.000

(c) Zone 3

Adj. R^2 = 0.34, F = 336.3; p-value < 0.001

Coefficients	Estimate	SPE	Std. Error	t-value	p-value
Intercept	4.198	--	0.150	27.983	0.000
Site productivity	0.178	0.020	0.199	0.895	0.371
Basal area	-0.193	-0.585	0.008	-25.767	0.000

Table 2.15. Ordinary Least Squares (OLS) regression for the top models (i.e. lowest AIC value) of seedling richness as a function of site productivity and sugar maple basal area in each zone. "SPE" refers to the standardized parameter estimates for the independent variables.

(a) Zone 1

Adj. R^2 = 0.009, F = 2.71; p-value = 0.07

Coefficients	Estimate	SPE	Std. Error	t-value	p-value
Intercept	4.244	--	0.5632	7.536	0.000
Site productivity	-0.167	-0.031	0.2804	-0.594	0.553
Basal area	-0.530	-0.120	0.2295	-2.308	0.022

(b) Zone 2

Adj. R^2 = 0.04, F = 39.67; p-value < 0.001

Coefficients	Estimate	SPE	Std. Error	t-value	p-value
Intercept	2.890	--	0.099	29.155	0.000
Site productivity	-0.030	-0.013	0.053	-0.566	0.572
Basal area	-0.129	-0.205	0.015	-8.891	0.000

(c) Zone 3

Adj. R^2 = 0.07, F = 53.98; p-value < 0.001

Coefficients	Estimate	SPE	Std. Error	t-value	p-value
Intercept	2.582	--	0.115	22.537	0.000
Site productivity	0.268	0.047	0.152	1.766	0.078
Basal area	-0.060	-0.279	0.006	-10.387	0.000

Table 2.16. Number of tree and seedling species occurring on low (≤1%) and high (100%) sugar maple abundance sites.

(a) Tree richness

	Basal area abundance	
	Low (≤1%)	High (100%)
Zone 1	9 to 13	1
Zone 2	4 to 14	1
Zone 3	5 to 10	1

(b) Seedling richness

	Basal area abundance	
	Low (≤1%)	High (100%)
Zone 1	2 to 10	0 to 3
Zone 2	1 to 11	1 to 6
Zone 3	1 to 12	1 to 7

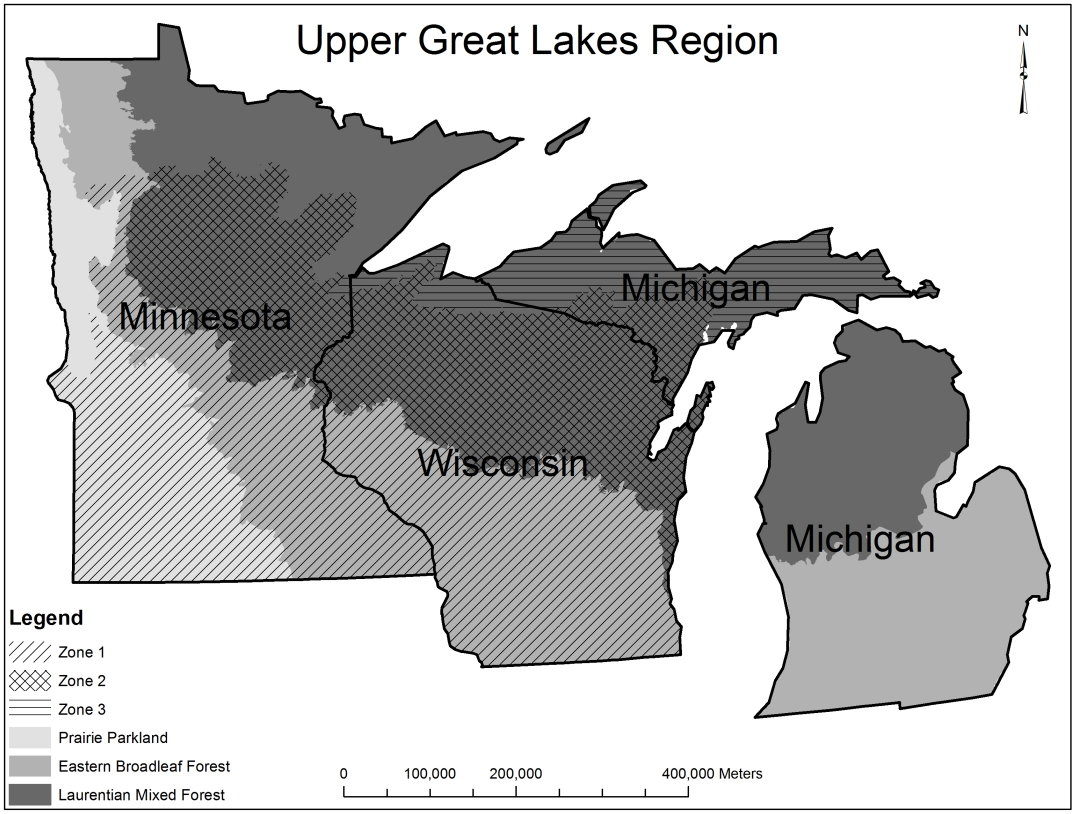

Figure 2.1. Map of the study area. Zones of interest are overlapping with ecological provinces (i.e. Prairie Parkland, Midwest Broadleaf Forest, and Laurentian Mixed Forest) (McNab et al. 2007). The Prairie-Forest Border (PFB) forms the transition zone between the tall grass prairies and the northern forests (Zone 1, 378 FIA plots), the forest interior extends beyond the PFB into northern Wisconsin (Zone 2, 1823 FIA plots), and the deep forest lies in Michigan's Upper Peninsula (Zone 3, 1314 FIA plots).

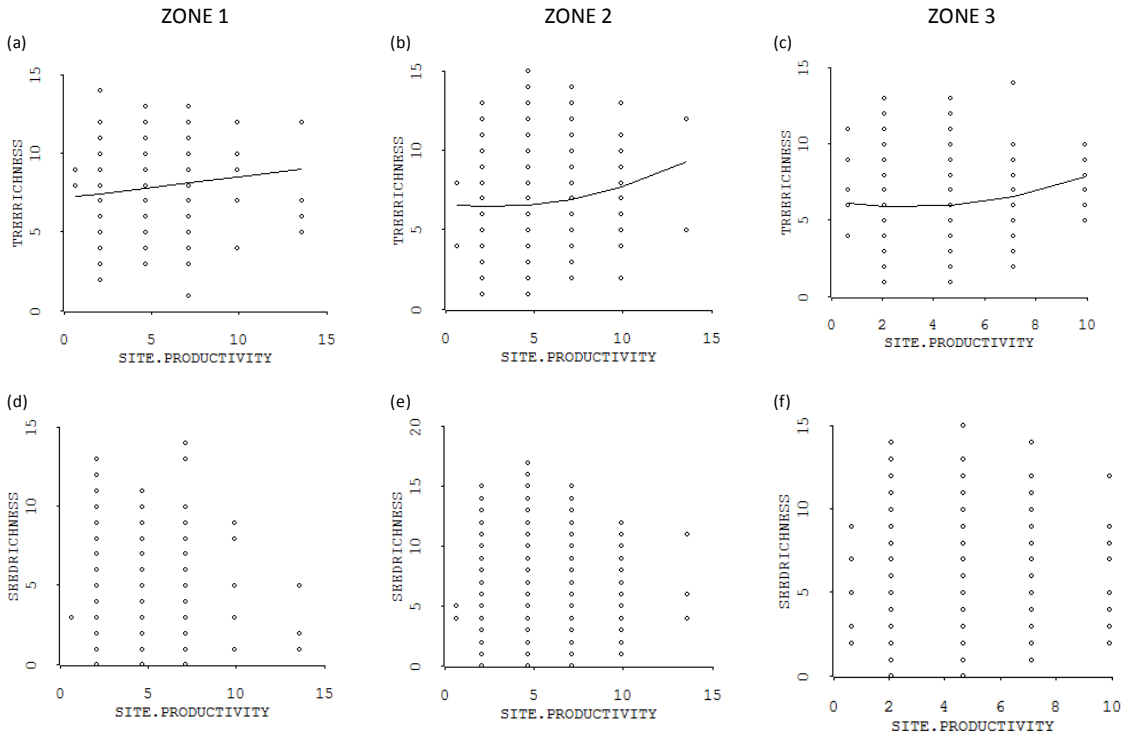

Figure 2.2. Scatter plots of the species richness-site productivity relationships for the whole data set. Tree richness in the upper plots ((a) through (c)) and seedling richness in the lower plots ((d) through (f)) are presented for Zone 1 (left), Zone 2 (middle), and Zone 3 (right). Species (tree or seedling) richness is the total number of species and site productivity is expressed in cubic meters per hectare per year. Significant trends are added when appropriate.

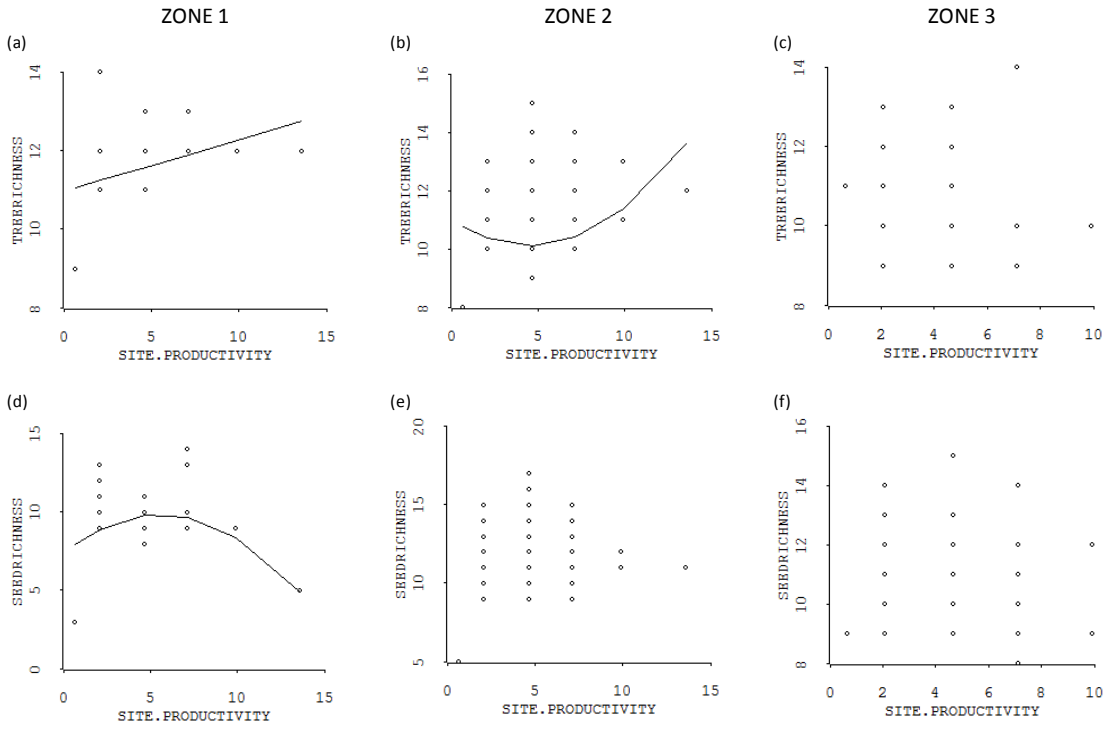

Figure 2.3. Scatter plots of the species richness-site productivity relationships for the upper quantile subset. Tree richness in the upper plots ((a) through (c)) and seedling richness in the lower plots ((d) through (f)) are presented for Zone 1 (left), Zone 2 (middle), and Zone 3 (right). Species (tree or seedling) richness is the total number of species and site productivity is expressed in cubic meters per hectare per year. Significant trends are added when appropriate.

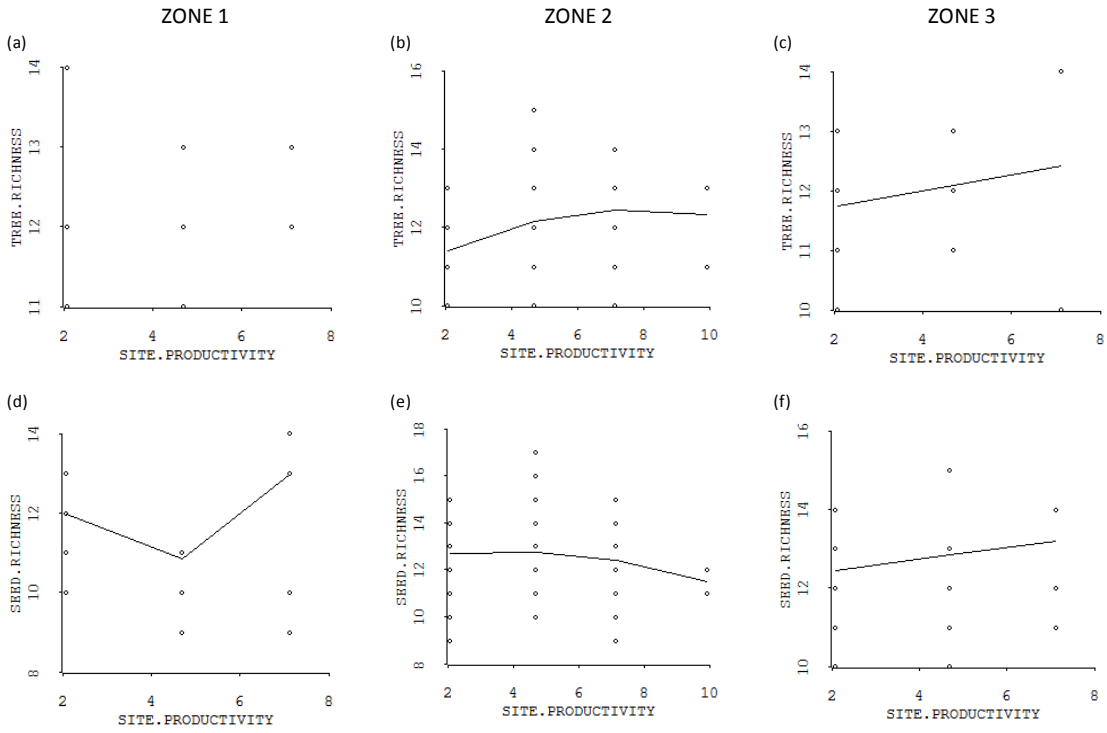

Figure 2.4. Scatter plots of the species richness-site productivity relationships for the random sample subset. Tree richness in the upper plots ((a) through (c)) and seedling richness in the lower plots ((d) through (f)) are presented for Zone 1 (left), Zone 2 (middle), and Zone 3 (right). Species (tree or seedling) richness is the total number of species and site productivity is expressed in cubic meters per hectare per year. Significant trends are added when appropriate.

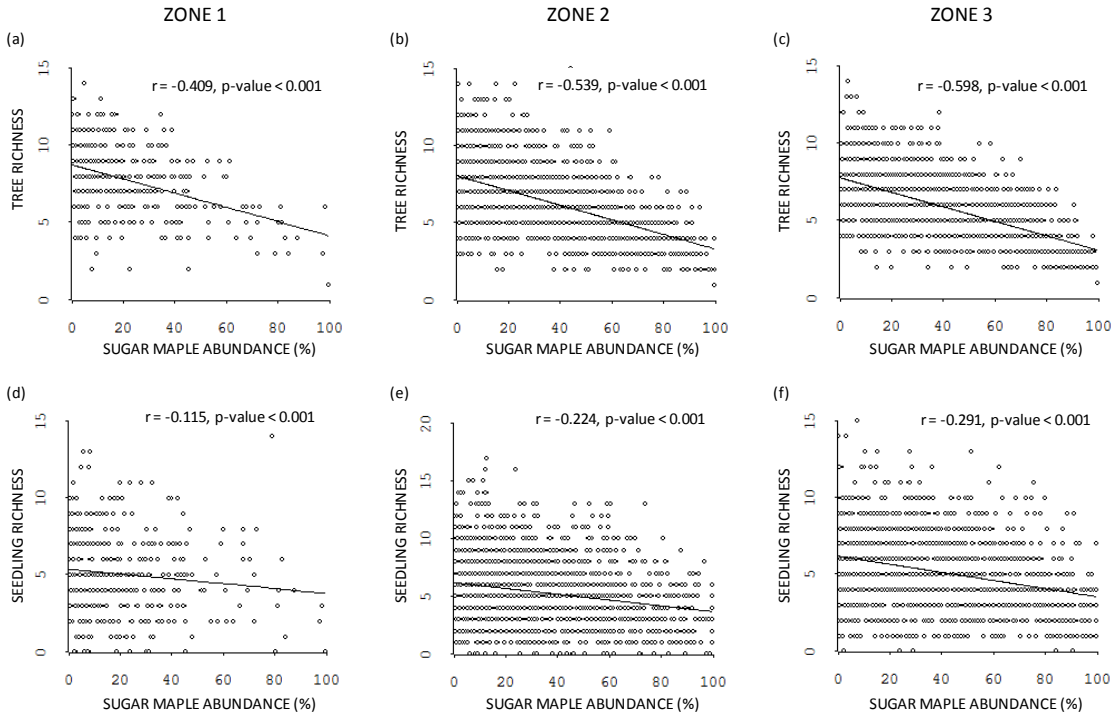

Figure 2.5. Scatter plots and correlations between sugar maple basal area and species richness in each zone for the whole data set. Tree richness in the upper plots ((a) through (c)) and seedling richness in the lower plots ((d) through (f)) are presented for Zone 1 (left), Zone 2 (middle), and Zone 3 (right). r = correlation coefficient.

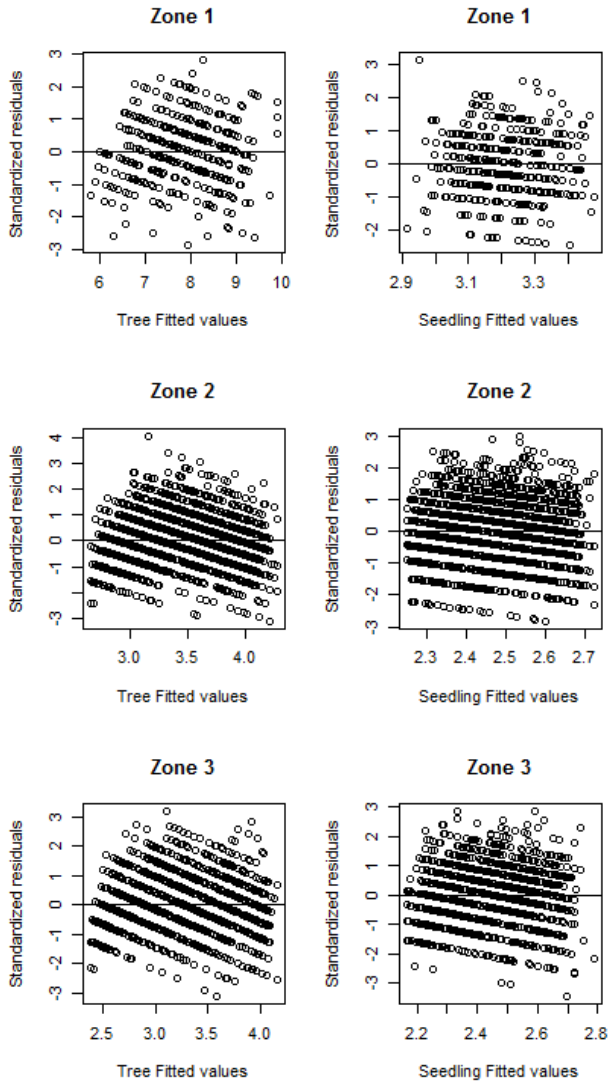

Figure 2.6. Standardized residual plots of species richness as a function of site productivity and sugar maple abundance in each zone. Tree richness (left) and seedling richness (right) are presented for Zone 1 (top), Zone 2 (middle), and Zone 3 (bottom). Plots are based on the top ordinary Least Square (OLS) regression models (i.e. lowest AIC; see Tables 2.14 and 2.15).

Chapter 3

Ecological niche of sugar maple (*Acer saccharum*) seedlings from prairie-forest border to interior of forest biome

with Lee E. Frelich

The relationship between vegetation and environmental factors has been long been recognized as a major determinant of plant species distribution and abundances. Paleoecological records indicate that the spatial composition and distribution of species have shifted in response to past environmental changes although past changes were driven by natural forces. Recent anthropogenic changes such as the increase in temperature have the potential to negatively affect the ecological niche of many species across the landscape in particular the seedlings of tree species, which are known to be a good indicator of future overstory composition. Sugar maple (*Acer saccharum*), a common late successional species in the Great Lakes region, increases in abundance from the prairie-forest border to the Upper Peninsula of Michigan. The climatic gradient of the Upper Great Lakes region (Minnesota, Wisconsin, and Upper Michigan) provides an ideal framework to study sugar maple seedling-environment relationships and to better understand future implications of global environmental change on hardwood forests. In this paper, we investigated sugar maple seedling sensitivity to current forest structure and composition (sugar maple basal area and stand age), as well as site level environmental conditions (sand proportion, soil depth, slope, and TRASP - an index related to aspect). We did this for three zones (prairie-forest border, interior of the forest biome, and deep interior of the forest biome), using data from Forest Inventory and Analysis plots (FIA) plots and multiple regression with multi-model inference for set of top models determined by AIC. We hypothesized that sugar maple seedlings respond differently to environment variables across the region and have a broader environmental niche in the Upper Peninsula of Michigan than at the prairie-forest border. Results show that as

expected, basal area of sugar maple was generally positively related to sugar maple seedlings density, while the effects of % sand and soil depth varied across the three zones. TRASP, an index related to aspect had a strong negative influence on seedling abundance at the prairie-forest border and interior zones, but had no influence in the deep interior zone. The overall interpretation of the models and patterns across the climate gradient indicate that sugar maple seedling abundance is currently insensitive to environmental variables (i.e., has a very broad environmental niche) in Upper Michigan, with many stands currently growing on sites with relatively high percent sand content, shallow soils, and south slopes. The expected shift in future climate would make the climate of Upper Michigan like that of the prairie-forest border by late in the 21st Century, thereby reducing the probability of seedling establishment on many sites currently with high dominance of sugar maple uninhabitable.

Introduction

One of the main concerns of ecology is to understand the processes responsible for species distribution and diversity. Countless studies have focused on the relationship between vegetation and environmental factors and they unanimously agree that environmental gradients are a major factor that structures plant communities and patterns of abundance across the landscape within species (Danz et al. 2011; Salemaa et al. 2008; Messaoud et al. 2007; Dovčiak et al. 2003; Janssens et al. 1998; Brooker and Callaghan 1998; Grimm 1984). In the Great Lakes region, the distribution of major tree species (e.g. *Acer saccharum*, *Acer rubrum*, *Quercus rubra*, *Tsuga canadensis*) occur along a

southwest to northeast gradient portraying distinct environmental conditions (Goldblum and Rigg 2002; Walker et al. 2002; Zhang et al. 2000; Curtis 1959). Paleoecological records clearly show that the spatial composition and distribution of species has shifted many times in response to past environmental changes (Umbanhowar et al. 2006; Baker et al. 2002; Woods and Davis 1989). While these changes were driven by natural forces and occurred over periods of thousands of years (Davis 1989; Davis 1983), today's environmental changes have been accelerated at an unprecedented pace by anthropogenic factors since the Industrial Revolution (Cole et al. 1998; Stearns 1997).

Worldwide, the year of 2012 was among the 10 warmest years in the record since 1850, with global atmospheric CO2 concentrations nearing 400 ppm, about 1.4 times greater than in the late 1700s (Blunden and Arnt 2013). Over the Great Lakes region, climate models predict a 2.2°C to 2.8°C 30-year average temperature increase from 1971-2000 to 2041-2070, with an increase of 2.2°C to 3.3°C in the winter and 1.7°C to 2.5°C in spring (NOAA 2013). Northwestern Minnesota is predicted to experience the greatest temperature increase in the winter, while greatest increases in temperature in spring are simulated for Michigan and eastern Wisconsin in the 2041-2070 period. Thirty-year average precipitation changes are also expected to occur from 1971-2000 to 2041-2070, with largest simulated precipitation increases of 10-12% in northern Wisconsin and the Upper Peninsula of Michigan (NOAA 2013). In general, average precipitation is expected to rise in the winter but decrease in the summer, and the Upper Great Lakes region may become drier overall because of future increased evaporation and transpiration that exceed surpluses of precipitation (NOAA 2013; Kling et al. 2005; Kling

et al. 2003). Consequently, species habitats are predicted to shift to the north or northeast up to 480 km, while ecotonal zones such as the prairie-forest border may move to the northeast (Walker et al. 2002; Iverson et al. 1998; Iverson and Prasad 1998; Overpeck et al. 1991). In addition to climate change, several authors suggest that other environmental stress such as increasing white-tailed deer (*Odocoileus virginianus*) populations (Fisichelli et al. 2012; White 2012; Salk et al. 2011) and invasive European earthworms (Frelich et al. 2006; Hale et al. 2005b) will negatively affect ecological communities. The question arises then, how will forests respond and adapt to such rapid environmental changes? One way to investigate this response is to gain a better understanding of the relationship between species and their environment (Messaoud and Houle 2006).

Tree recruitment is critical for the regeneration and establishment of plant populations (Clark et al. 1999) and forest understory composition provides a good indication of potential future overstory composition (Sanders and Grochowski 2013; Dey et al. 2012; Salk et al. 2011; Kobe et al. 2002; Oliver and Larson 1996). Seedling growth and survival differ from one species to another in their environmental requirements (Wright and Westoby 1999; Ashton et al. 1998; Cornett et al. 1998; Ashton and Larson 1996) and the successful establishment of seedlings depends partly on dispersion, germination and growth of seeds (Schupp 1995; Harper et al. 1970) while environmental variables have been recognized for decades as playing an important role in seedling establishment and range limits of species (MacArthur 1984).

Sugar maple (*Acer saccharum*) is a common late successional species in the Great Lakes region (Burns and Honkala 1990) and is widespread in dry mesic to mesic northern

temperate forests (Curtis 1959). Sugar maple forests provide habitat for many wildlife species while trees are valued for their products (e.g. timber and syrup) (Whitney and Upmeyer 2004). Sugar maple forms a gradient of communities within and across zones of the Upper Great Lakes region (Minnesota, Wisconsin, and Upper Michigan; see Chapter 1) and increases in abundance from the prairie-forest border to the Upper Peninsula of Michigan where it reaches its greatest abundance on the richer loamy soils of the hemlock-northern hardwood forests (Albert 1995; Barrett et al. 1995). In an effort to understand future implications of global environmental change on sugar maple forests, we investigated sugar maple seedling-environment relationships across the Upper Great Lakes region. Previous studies have shown that attributes such as proportion of sand, soil depth, slope and aspect regulate the balance between mesic and dry forest species (Hanberry et al. 2013; Goldblum et al. 2010; Wyckoff and Bowers 2010; Umbanhowar 2004; Barton and Gleeson 1996). For example, xerophytic tree species like pine or oak are more likely to occur on deep sandy or shallow soils, and warmer sites (i.e. south facing slopes) than mesic forest species, which include maple, ash, and beech (McNab 2011). This sensitivity should change along a climate gradient and seedlings of a mesic forest species like sugar maple should be more sensitive to sand and aspect near the prairie-forest border than deep in the interior of the forest biome. Therefore, our goal was to determine sugar maple seedling sensitivity to current forest structure and composition (sugar maple basal area and stand age), as well as site level environmental conditions (sand proportion, soil depth, slope, and TRASP - an index related to aspect), including interaction effects. We proposed the null hypothesis that the environmental niche of sugar

maple seedlings is the same across the Upper Great Lakes region compared to the alternative that it is broader in the Upper Peninsula of Michigan; that is, sugar maple seedlings respond differently to environment variables across the Upper Great Lakes region and are less sensitive to environmental variables in the Upper Peninsula of Michigan where climatic conditions are more favorable to its establishment and growth, than in the prairie-forest border.

Methods

Study area

The Upper Great Lakes region includes three main ecological provinces defined by dominant climatic regimes, potential native vegetation, and biomes: the prairie parkland, the eastern broadleaf forest, and the Laurentian mixed forest provinces (McNab et al. 2007; Cleland et al. 1997; McNab and Avers 1994) (Figure 3.1).

The prairie parkland occupies the western part of Minnesota and extends to the southern parts of Wisconsin and Michigan. Mean annual temperatures vary from 2ºC in the north to 9ºC to the south. This province has a continental climate with cold winters, hot summers, and mean annual precipitation of 46 cm in the north to 84 cm in the south. Precipitation mainly occurs in the form of snow in the north but falls is almost entirely rain in the south. Mean evapotranspiration exceeds mean precipitation during the growing season (May through September), with water deficits of 2.0-3.8 cm along the western edge of the prairie parkland. Semi-arid loamy soils are well-to-moderately well-drained.

Pre-settlement vegetation was dominated by tall grass prairie but today agriculture is the dominant land use.

The eastern broadleaf forest extends from northwestern Minnesota to southeastern Michigan. Mean annual temperatures vary from 4ºC in the northwest of the province to 10ºC in Michigan. The overall climate is continental with warm to hot summers. Precipitation averages 65 to 93 cm and approximately equals evapotranspiration. Two-thirds of it falls during the growing season which lasts about 125 days up to 180 days along Lake Michigan. Local reliefs (20 to 180 m) are apparent in Wisconsin as a result of past glaciation. Winter precipitation is mostly snow and averages 100 cm. Soil moisture regime is dominantly mesic with lower growing season water deficits (1.2-2.0 cm) than the prairie parkland. Pre-settlement vegetation was dominated by maple-basswood forests or oak savannas at the prairie-forest border as a result of fire frequency variations (Grimm 1984) whereas oak-hickory forests dominate sandy sites and beech-maple forests grow on loamy soils in Michigan. Today, agriculture, urban and industrial development constitute the major land uses. The transition (ecotone) from eastern broadleaf forest to prairie parkland is sharp (Danz 2009; Grimm 1983) whereas the transition between eastern broadleaf forest and Laurentian mixed forest is gradual (Fisichelli et al. 2013a; Goldblum and Rigg 2002; Braun 1950).

The Laurentian mixed forest lies in the northern part of the Upper Great Lakes region and extends into Canada. Average annual temperatures range from 3ºC to 6ºC while mean annual precipitation varies between 61 and 115 cm. Fifty percent of precipitation falls during the growing season (May through September). Annual snowfall

varies from 100 to 165 cm, but can be up to 833 cm due to the Lake-effect snow. The climate is classified as continental with lake effects influence along the Great Lakes. Winters (i.e. days below or at freezing temperature) are longer with considerable snow coverage and summers are short and cool compared to the prairie parkland and the eastern broadleaf provinces. To the contrary of the prairie parkland and the eastern broadleaf provinces, there is a moisture surplus rather than a deficit, and the mean growing season potential evapotranspiration minus precipitation reaches -11 cm in the northern part of the Laurentian mixed forest. Hilly landscapes with shallow soils occur along Lake Superior and result from past glaciations. A mosaic of conifer stands, northern hardwood stands, and mixed stands occupies the region, and vegetation consists of forests that are a transition between boreal and broadleaf deciduous (Goldblum and Rigg 2002; Davis 1983; Braun 1950). The current land cover is forest and the dominant land use is forestry and outdoor recreation.

FIA data

The Forest Inventory and Analysis (FIA) Program of the U.S. Department of Agriculture Forest Service is a nationwide program that collects and publishes data from all ownership of forest land in the US since 1929 although annual inventories started in 1999 (U.S.D.A. 2009). The FIA Program features a complete and systematic national sample design for all lands in the US (Bechtold and Patterson 2005). It monitors only forest lands (i.e. at least 0.4 ha and 36.3 m wide with a minimum of 10% stocked by forest trees) and is conducted in three phases, although we used data from the first two

phases only. In Phase 1, land area is stratified using remotely sensed imagery in the form of aerial photography and/or satellite imagery to reduce variance in the estimates. In Phase 2, the landscape is divided into contiguous 2428 ha hexagons containing one randomly located permanent ground plot each, for a total of ~125,000 forested plots nationwide. Sampling intensity varies between states, but because the FIA plot design is a combination of systematic arrangement and random sampling, varying sample intensities only affects the precision of the estimates. Field crews sample approximately 20% of FIA plots annually in the eastern US where they collect variables (e.g. forest type, tree species, soil attributes) on each permanent ground plot with 100% measurement of a systematic panel of plots completed every five years in the eastern US (U.S.D.A. 2008). Each plot is designed to cover a 0.4 ha sample area. A plot consists of one central subplot and an equilateral triangle arrangement of three peripheral subplots spaced 36.6 m apart from the central subplot, at azimuths of 120, 240, and 360 degrees. Each subplot also includes a 2.1 m fixed-radius microplot which is offset from the center of the subplot (3.7 m at an azimuth of 90 degrees). All trees with a diameter at breast height (dbh) of at least 12.7 cm are recorded on subplots. Saplings (2.54 to 12.45 cm dbh) and seedlings (≤ 2.54 cm dbh and at least 30.5 cm in height for hardwood species) are inventoried in microplots.

We downloaded FIA raw data files for Minnesota, Wisconsin, and Michigan from the FIA database website (FIADB, http://apps.fs.fed.us/fiadb-downloads/datamart.html). Our study is based upon data collected between 2003 and 2007, which corresponds to a full cycle at the time of data upload (May 2009). To protect the confidentiality of the

exact location of FIA plots, plot coordinates are spatially perturbed before being released to the public. The perturbed plot coordinates were adjusted to be within ± 1 mile of the true plot location which is of little consequence on our study given the regional scale presented in this work. We selected plots including at least one live sugar maple tree and aggregated them into contiguous zones: Zone 1 (378 plots) is near the prairie biome and covers Minnesota and Wisconsin, although we excluded Northern Minnesota from our analyses because of small sample size; Zone 2 (1823 plots) is in the forest biome and includes northern Wisconsin; Zone 3 (1314 plots) is deep into the forest biome, with the best climate for trees, and includes the Upper Peninsula of Michigan (Figure 3.1).

We selected our response variable (sugar maple seedling density) and four of our six predictors (sugar maple basal area, stand age, slope, and aspect) from the FIA database (U.S.D.A. 2008). Sugar maple seedling density is expressed as the number of seedlings per hectare and sugar maple basal area as the total basal area of sugar maple trees in square meters per hectare. FIA records stand age in the field, and this variable is assigned to the nearest year. Slope refers to the angle of slope, in percent, of the plot. Aspect is defined as the direction of the slope to the nearest degree, with North being recorded as 360. Since aspect is a circular variable, it was difficult to distinguish values near zero from 360 values since they essentially represent to same direction, therefore, we converted aspect into the following index:

$$\text{TRASP} = \frac{1-(cosine((\frac{\pi}{180})(aspect-30))}{2}$$

TRASP varies between 0 and 1 and assigns 0 to NNE aspects (typically the coolest and wettest orientation) and 1 to SSW aspects (typically the hotter and driest slopes) (Roberts and Cooper 1989).

SSURGO data

We extracted our soil depth and percent sand variables (predictors) from the Soil Survey Geographic (SSURGO) database. SSURGO is a geographic database representing soil maps and is based on field methods that compile county soil surveys (U.S.D.A. 1995). Surveyors observe soil attributes along delineation boundaries before determining map unit composition by field traverses and transects. Each county uses slightly different criteria for their soil surveys and spatial discontinuities cause differences across state and county lines, nonetheless, SSURGO provides the most detailed level of soil physical and chemical data in digital form (U.S.D.A. 1995). SSURGO data is mapped as separate polygons (i.e. map units) that gather soil information at a scale ranging from 1:12,000 to 1:63,360, with most details collected at the former scale. SSURGO data sets consist of a combination of map and tabular data, although few areas in central and northern Minnesota were either missing the tabular data or tabular and spatial information at the time of download (September 2009). We used the Soil Data Viewer (U.S.D.A. 2007) to obtain soil polygons for Minnesota, Wisconsin, and Michigan. We then performed a shapefile join between SSURGO and exact FIA plot locations in ArcGIS 9.3 (ESRI 2008) to extract SSURGO soil attributes for each FIA plot. Sand is defined as particles between

0.05 mm and 2 mm in diameter and is expressed as a percentage. Depth is recorded in centimeters up to 200 cm deep. Beyond 200 cm, the value of Depth is set to 201 cm.

Data analysis

Sugar maple seedlings per hectare was our response variable. A set of six environmental variables (sugar maple basal area, sand proportion, stand age, slope, depth of soil, and TRASP) and nine two-way interactions (basal area by sand, basal area by stand age, basal area by depth, basal area by TRASP, sand by depth, sand by TRASP, depth by TRASP, slope by TRASP, and slope by depth) were the predictors. Correlation coefficients (r) among predictors were weak and varied between -0.15 and 0.29. ANOVAs were used to test for significant differences of variables amongst zones (p-value $\leq$ 0.05) and followed up with a Tukey's HSD to test all possible two-way comparisons and find out which zones, if any, were significantly different (Cook and Weisberg 1999).

We used the Akaike's Information Criterion (AIC) method to determine the best subset of models in each zone (Burnham and Anderson 2002). We are presenting a multi-model approach to model selection to determine which parameters are important to sugar maple seedlings in the Upper Great Lakes region rather than identifying a single best model. In traditional model selection methods such as forward selection, hypothesis testing (i.e. significant or not significant) is used to determine the next variable that is added. Once the significance level (i.e. p-value) for adding a variable is greater than the one specified by the researcher, the selection process stops. Hence, results may vary

according to the order in which models are computed (e.g. forward vs backward). AIC rewards the goodness of fit and penalizes models with too many predictors (i.e. avoids overfitting) while offering a balance between fit improvement (i.e. increased likelihood) and parsimony (Burnham and Anderson 2002). Prior to calculating AIC values, we corrected non linearity and non-homogenous variance in each zone by transformation of the response and the predictors using a combination of Box-Cox and Box-Tidwell transformation (Ryan 1997). Analyses included series of regressions models from a simple model including one variable to more complex models including the six predictors and nine two-way interactions. A null model (i.e. intercept-only) was incorporated to each set of candidate models to determine the importance of the independent variables. We computed AIC values according to the following:

$$\text{AIC} = -2*\ln(\text{likelihood}) + 2*K$$

where ln is the natural logarithm, ln(likelihood) is the numerical value of the log-likelihood at its maximum point, and K is the number of parameters in the model. Regression models were compared by calculating AIC differences (Δi):

$$\Delta_i = AIC_i - \text{min AIC}$$

where Δi is the difference between the AIC of the best fitting model and that of model i, AIC_i is the AIC for the model i, and min AIC is the minimum AIC value of all models. As a rule of thumb, $\Delta i < 2$ provides substantial support for model i (Burnham and Anderson 2002). Finally, we calculated Akaike weights of evidence for each model to help us select the best set of models (i.e. $\Delta_i < 2$) as follows:

$$w_i = \frac{exp(-0.5*\Delta_i)}{\sum_{r=1}^{R} exp(-0.5*\Delta_r)}$$

where w_i are the Akaike weights and the denominator is the sum of the relative likelihood for all candidate models. w_i varies between 0 and 1 and indicate the probability that a model *i* is the best among all candidate models. All models with $\Delta_i < 2$ were fitted for significance and assessed for goodness of fit using the F-test lack of fit (i.e. p-value > 0.05 indicates that the model is adequate) and careful visual inspection of the residual plots.

We conducted all of our analyses in R (R Core Team 2013) and Arc (Cook and Weisberg 2004).

Results

On average, sugar maple seedling density increased from Zone 1 to Zone 3 (i.e. from the prairie-forest border to the Upper Peninsula of Michigan), with seedling density being 2.4 times greater in Zone 3 than it is in Zone 1 (Table 3.1). Similarly, in Zone 3, sugar maple basal area was about 1.5 times greater in Zone 3 than in Zone 1. Percent of sand was on average higher in Zones 2 and 3 (48.78% and 59.24%, respectively) than in Zone 1 (38.35%). Average stand age varied little across the region with averages of 70 years in Zones 1 and 2 and 68 years in Zone 3. Despite this small variation in average stand age, Zone 3 hosts some older stands (204 years old maximum) than Zone 1 and 2 do (124 and 189 years old maximum, respectively). The mean value of depth indicates that soils are deeper in Zone 2 (167 cm) while averaging 150 cm in Zone 1 and 129 cm in Zone 3. Since SSURGO assigns a systematic value of 201 cm for soils beyond 200 cm deep, calculating soil depth averages might be biased. Thus, it is worth noticing that the

minimum value for depth decreases from Zone 1 (38 cm) to Zone 3 (19 cm). Percent of slope was almost three times greater in Zone 1 than it was in Zones 2 and 3 with average slope values of 20.45% in Zone 1 and about 7% in Zones 2 and 3. Average TRASP index was 0.32, 0.27, and 0.24 for Zone 1, Zone 2, and Zone 3, respectively. ANOVA and Tukey's HSD tests indicated that all variables, except for stand age, were statistically different amongst zones (p-value ≤ 0.001).

All models in the best sets (i.e. $\Delta_i < 2$, Tables 3.2 to 3.4) were statistically significant (p-value ≤ 0.05) across zones and F-test lack of fit indicated that these models fit the data well. In Zone 1 (Table 3.2), TRASP was included in all five best models and sand occurred in the top four models. Sand and TRASP interactions were important parameters in two out of the five best models and the last three best models included basal area. Depth and the interaction of basal area by depth appeared in the last best model only. In Zone 2 (Table 3.3), basal area, stand age, and TRASP were included in all seven best models. Sand was included in five of the best models and so was the interaction between sand and TRASP. Interactions between basal area and TRASP and basal area and stand age were included in three and two out of seven models while the basal area and sand interaction occurred only in one model. In Zone 3 (Table 3.4), all eight best models included basal area and sand; depth was included in seven of the eight models. Stand age only occurred in the eighth best model, as did the basal area by stand age interaction. The most common interactions were basal area by sand (six out of eight models), basal area by depth (five out of eight models), and sand by depth (three out of

eight models). Slope was not included in any of our best models, neither was the intercept-only model.

F-test statistic for the OLS regression for the best models in each zone were all significant (Tables 3.5 through 3.7) and plots of residuals for the top model ($\Delta_i = 0$) in each zone indicated that the models fit the data well (Figure 3.2). However, the significance of all parameters was achieved in only one model in each zone: in Zone 1, this model included sand (t = 2.045, p-value = 0.042) and TRASP (t = -2.491, p-value = 0.014) (model #2, Table 5); in Zone 2, it included basal area (t = 8.173, p-value < 0.001), stand age (t = 4.672, p-value < 0.001), and TRASP (t = -2.240, p-value = 0.025) (model #3, Table 6); and in Zone 3, it included basal area (t = 7.471, p-value < 0.001), sand (t = 2.493, p-value = 0.013), and their interaction (t = -2.371, p-value = 0.018) (model #3, Table 3.7).

The effects of environmental variables and two way interactions on sugar maple seedling abundance varied across zones (Table 3.8). Basal area had a positive effect on sugar maple seedling abundance in all models where it was included except for model #5 in Zone 1 (Table 3.5). Sand had a slight positive effect in the models where it was included in Zones 1 and all but one model in Zone 3 (Tables 3.4 and 3.7); sand was negative in models in Zone 2 (Table 3.6). Stand age has very little effect but was positive in all models in Zone 2 with the exception of #7 (Table 3.6); it was also slightly positive in Zone 3 where it appeared in the last model only (Table 3.7). Soil depth was negative in all models in which it was included (#5 in Zone 1, Table 5; all models except #3 in Zone 3, Table 3.7). TRASP appeared in all models in Zones 1 and 2 and had mostly a negative

effect except in #4 of Zone 1 and #6 of Zone 2 (Tables 3.5 and 3.6, respectively). TRASP was absent from all top models in Zone 3 (Table 3.7). The interaction between sand and TRASP was negative in Zone 1 but positive in Zone 2 and the interaction between basal area and TRASP in Zone 2 was negative. Interactions of basal area with stand age and sand were positive in Zone 2 but negative in Zone 3. The basal area and depth interaction was positive in Zone 1 and 3; so was the sand and depth interaction in Zone 3.

Discussion

Current conditions

Our results confirm that sugar maple tree basal area and seedling density are lower at the prairie-forest border and increase towards the Upper Peninsula of Michigan. This is consistent with previous studies showing that sugar maple abundance increases from the prairie-forest border to the Upper Peninsula of Michigan (Albert 1995; Barrett et al. 1995). The strong and positive effect of sugar maple basal area on sugar maple seedling abundance may be attributed to strong self-positive neighborhood effects of sugar maple, where local overstory abundance at the plot scale creates ideal conditions for its own reproduction, by creating summer shade and deep leaf litter (Frelich 2002; Frelich et al. 1993). This effect seems weaker at the prairie-forests border as indicated by the occurrence of sugar maple basal area in all of our best models in Zones 2 and 3 but only in the last three models in Zone 1. Basal area positive effect is reinforced with stand age and sand in Zone 2, but those effects counteract sugar maple seedling abundance in Zone 3, indicating that other important environmental factors - possibly soil nutrients,

temperature, precipitation, or herbivory - may be influencing the understory of sugar maple forest (St Clair et al. 2008).

Aspect is known to indirectly control vegetation through soil moisture and solar insolation (McAndrews 1966). For instance, given similar soils, north-facing sites have the capacity of storing more water during dry spells than south-facing sites, which in turn are much drier because they receive greater insolation, and therefore, are more susceptible to higher levels of evapotranspiration than north-facing slopes (Geroy et al. 2011). TRASP, an index related to aspect, followed the expected pattern across the three zones, with strong negative parameter estimates near the prairie-forest border in Zone 1, and the forest interior of Zone 2, but was excluded from the set of best models in the deep interior forests of Zone 3. Thus, aspect became insignificant in its influence on seedling density as the summer climate became cooler with lower water deficits.

At first glance, percent sand appeared to have ambiguous effects on sugar maple seedling density, with positive parameters in the best models for Zones 1 and 3 and negative for Zone 2. Average percent sand was about 11% lower in Zone 1 (38.35%) than in Zone 2 (49.78%) and about 21% lower than in Zone 3 (59.24%). Thus, sugar maple stands selected to be included in the study grow on progressively sandier soils as the summer climate becomes cooler across the climate gradient from edge of prairie to the deep interior of the forest biome. Although sand had a positive effect on sugar maple seedling abundance in Zone 1, in addition to the low percent sand there, it negatively interacted with TRASP, indicating that sugar maple seedlings may not be supported on warmer sites with sandy soils at the prairie-forest border where a drier climate prevails

compared to the Upper Peninsula of Michigan (Fisichelli et al. 2013a; Danz 2009; Umbanhowar 2004; Pastor and Post 1988). The negative effect of sand on sugar maple seedling abundance in Zone 2 may be attributed to a higher average proportion of sand in this zone compared to Zone 1, which could amplify sugar maple sensitivity to drought (Horsley and Long 1999) due to the low water holding capacity properties of sand (Petersen et al. 1968). The positive sand by TRASP interaction in Zone 2 might reflect cooler and wetter conditions in Zone 2 compared to Zone 1 that favors sugar maple seedlings. In other words, even though the proportion of sand is higher in Zone 2 than in Zone 1, the difference in climate may favor sugar maple seedling abundance and partially mitigate the negative effects of TRASP. In Zone 3, we found that sand had a positive effect on sugar maple seedling abundance but found no effect of TRASP. This was an expected result for the deep interior of the forest biome, where relatively cool and moist climate allow sugar maple seedlings to do well on south facing slopes and sandy soils compared to warmer regions to the south and west. Therefore, if the climate in Upper Michigan becomes similar to Zones 1 and 2 as projected for global warming scenarios (NOAA 2013; Kling et al. 2005; Sousounis and Grover 2002), negative impacts are likely to occur rapidly in Upper Michigan where the proportion of sand is the highest.

Only one of the top five models for Zone 1 included soil depth. This was unexpected given the relatively droughty climate at the prairie-forest border, and the hypothesized need for the greater water holding capacity of deep soils (Geroy et al. 2011; Changnon et al. 2002). Instead, a deeper minimum soil depth occurred among maple stands in Zone 1 and the previously mentioned negative influence of TRASP on seedling

abundance likely overrode the impact of soil depth in the other 4 top models. Soil depth was not a significant factor in any top model for Zone 2—an expected result given the lack of bedrock near the surface in that zone. In Zone 3, it is difficult to explain why soil depth came out as a negative factor in seven of eight top models. This negative effect may be attributed to widespread occurrence of maple stands on shallow soils due to hardpans throughout the area and rocky areas near Lakes Superior and Michigan. Also, deep soils may favor a mixture of pines, oaks, hemlock and other species that compete with sugar maple. Despite the ambiguous result for soil depth, over all, it is clear that in Zone 3, the climate is so favorable to sugar maple, that soil depth, sandiness, and high TRASP do not limit the species like they can in Zones 1 and 2 (Whitney 1987; Curtis 1959). Also, the zone is not quite far enough north for TRASP to have a positive effect, in which case sugar maple seedlings would be more abundant on south-facing aspects.

Implications for a warmer climate

It was clear from our results that the niche of sugar maple seedlings varies across the Upper Great Lakes region. Current environmental conditions are more favorable to sugar maple seedlings growing in the Upper Peninsula of Michigan than at the prairie-forest border, where seedlings are more sensitive to TRASP, and where sugar maple stands have a higher minimum soil depth and lower mean percent sand on sites where they occur. According to future projections for a warmer climate (Blunden and Arnt 2013), climatic envelopes for species ranges and biomes are expected to shift northward (Prasad et al. 2007; Iverson et al. 2004) with a migration rate between 100 and 500 km

per century (Woodall et al. 2009; Carmel and Flather 2006; Neilson et al. 2005; Walker et al. 2002). Woodall et al (2009) proposed that southern species will fill northern species niches as they migrate north. This may imply regeneration failure of sugar maple at the prairie-forest border, prairie replacing forests and thus, "savannification" of the forest (Frelich and Reich 2010). At the Upper Peninsula of Michigan, where regeneration is currently very successful, future climatic conditions might become similar to what we know at the prairie-forest border today (Kling et al. 2005). Under such conditions, we predict that seedling sensitivity to environmental conditions in Upper Michigan will increase, resulting in a decline in seedling regeneration and a change in its ecological niche. By 2100, importance values of sugar maple abundance in Upper Michigan are projected to decrease from 20 today to 4-10 depending on the climate scenario (Prasad et al. 2007). The results of this study are consistent with that projection. Our data indicates that at the Upper Peninsula of Michigan, 8% of plots currently occur on shallow soils (< 50 cm) with 4% of plots on soils less than 38 cm (i.e. the minimum soil depth among the 378 plots for Zone 1), 9% of plots occur on south-southwest facing slopes, i.e. 158-247 degrees of aspect (Whitney 1991), and 31% of plots on sandy soils (> 75%). Such sites may not support abundant sugar maple in the future if the environmental niche for successful regeneration narrows as the climate of Zone 3 becomes similar to that of Zone 1. In addition to the predicted increase in average temperature (Blunden and Arnt 2013), other factors such as European earthworm invasions and increasing deer populations will inhibit sugar maple seedling regeneration in the future (Frelich and Reich 2010). Deer populations are patchy across the landscape due to differences in fragmentation and wolf

pack territories, and earthworm invasion effects are also patchy because of slow spread of nightcrawlers from many introductions points. Therefore, a patchy mosaic of these effects will occur on top of patchy effects due to environmental factors such as percent sand, soil depth and aspect, leading to substantial heterogeneity in reduction of the regeneration niche for sugar maple across the landscape (Callan et al. 2013; Mattison 2011; Hale et al. 2006; Rooney and Waller 2003). The complex nature of this heterogeneity in regeneration success is likely to obscure any coherent signal related to climate change.

Table 3.1. Variable characteristics of the study area. Depth and sand variables were extracted from the FIA database; all others variables originated from the SSURGO database. TRASP is an index related to aspect and varies between 0 (NNE aspect, cooler sites) and 1 (SSW aspect, warmer sites). ANOVA and Tukey's HSD tests indicated that all variables, except for stand age, were statistically different amongst zones (p-value $\leq$ 0.001).

Type	Variable	Zone	Mean	Minimum	Maximum
Response	Seedling	1	4835.00	185.00	77617.00
	(number per hectare)	2	8441.00	185.00	114665.00
		3	11617.00	185.00	90028.00
Predictor	Basal area	1	6.51	0.54	27.54
	(square meter per hectare)	2	9.01	0.38	43.31
		3	10.87	0.20	49.49
	Sand	1	38.35	0.00	96.50
	(percent)	2	49.78	0.00	96.80
		3	59.24	0.00	98.90
	Stand Age	1	70.38	5.00	124.00
	(years)	2	70.39	2.00	189.00
		3	68.04	1.00	204.00
	Depth	1	150.13	38.00	201.00
	(centimeters)	2	167.09	30.00	201.00
		3	129.03	19.00	201.00
	Slope	1	20.45	0.00	78.00
	(percent)	2	7.38	0.00	52.00
		3	7.17	0.00	67.00
	TRASP	1	0.32	0.00	1.00
	(index)	2	0.27	0.00	1.00
		3	0.24	0.00	1.00

Table 3.2. Best AIC (i.e. $\Delta i < 2$) models of sugar maple seedling density in Zone 1. K is the number of parameters included in the model, AIC is the Akaike's Information Criterion value, Δi is the difference between the AIC of the best fitting model and that of model *i*, and w*i* is the probability that a model *i* is the best among all candidate models. Model parameters: B = Basal area, A = Stand age, S = Sand proportion, D = Depth of soil, T = TRASP (index related to aspect). The symbol "x" between two parameters indicates two way interactions.

Model	K	AIC	Δi	wi
S + T + SxT	5	667.36	0.00	0.08
S + T	4	667.55	0.19	0.08
B + S + T + SxT	6	668.18	0.83	0.06
B + S + T	5	668.73	1.37	0.04
B + D + T + BxD	6	668.93	1.57	0.04

Table 3.3. Best AIC (i.e. $\Delta i < 2$) models of sugar maple seedling density in Zone 2. K is the number of parameters included in the model, AIC is the Akaike's Information Criterion value, Δi is the difference between the AIC of the best fitting model and that of model *i*, and w*i* is the probability that a model *i* is the best among all candidate models. Model parameters: B = Basal area, A = Stand age, S = Sand proportion, D = Depth of soil, T = TRASP (index related to aspect). The symbol "x" between two parameters indicates two way interactions.

Model	K	AIC	Δi	wi
B + S + A + T + SxT	7	3985.35	0.00	0.09
B + S + A + T + BxA + SxT	8	3986.08	0.73	0.07
B + A + T	5	3986.42	1.07	0.06
B + S + A + T + BxT + SxT	8	3986.43	1.08	0.06
B + S + A + T + BxS + SxT	8	3986.91	1.56	0.04
B + A + T + BxT	6	3986.93	1.58	0.04
B + S + A + T + BxA + BxT + SxT	9	3986.99	1.64	0.04

Table 3.4. Best AIC (i.e. $\Delta i < 2$) models of sugar maple seedling density in Zone 3. K is the number of parameters included in the model, AIC is the Akaike's Information Criterion value, Δi is the difference between the AIC of the best fitting model and that of model *i*, and w*i* is the probability that a model *i* is the best among all candidate models. Model parameters: B = Basal area, A = Stand age, S = Sand proportion, D = Depth of soil, T = TRASP (index related to aspect). The symbol "x" between two parameters indicates two way interactions.

Model	K	AIC	Δi	wi
B + S + D + BxS + BxD + SxD	8	2253.55	0.00	0.08
B + S + D + BxS + BxD	7	2253.69	0.14	0.07
B + S + BxS	5	2254.61	1.06	0.05
B + S + D + BxS	6	2254.80	1.25	0.04
B + S + D + BxS + SxD	7	2255.01	1.45	0.04
B + D + BxD	5	2255.05	1.49	0.04
B + S + D + BxD + SxD	7	2255.24	1.69	0.03
B + S + A + D + BxS + BxA + BxD	9	2255.51	1.96	0.03

Table 3.5. Ordinary Least Squares (OLS) regression for the best models (i.e. $\Delta i < 2$) of sugar maple seedling-environmental relationships in Zone 1. Environmental variables include current forest structure and composition (sugar maple basal area and stand age), and site level environmental conditions (sand proportion, soil depth, slope, and aspect index). #1 indicate the top best model and #5 the last of the best models (see also Table 3.2).

#1

Zone 1 (Adj. $R^2 = 0.07$, $F = 4.49$; p-value = 0.005)

Coefficients	Estimate	Std. Error	t-value	p-value
Intercept	7.212	0.275	26.191	0.000
Sand	0.015	0.006	2.509	0.013
TRASP	-0.022	0.567	-0.038	0.970
Sand x TRASP	-0.019	0.013	-1.469	0.144

#2

Zone 1 (Adj. $R^2 = 0.05$, $F = 5.62$; p-value = 0.004)

Coefficients	Estimate	Std. Error	t-value	p-value
Intercept	7.442	0.227	32.727	0.000
Sand	0.009	0.004	2.045	0.042
TRASP	-0.734	0.295	-2.491	0.014

#3

Zone 1 (Adj. $R^2 = 0.09;7$ $F = 3.66$; p-value = 0.007)

Coefficients	Estimate	Std. Error	t-value	p-value
Intercept	6.254	0.936	6.679	0.000
Basal area	0.733	0.685	1.071	0.286
Sand	0.016	0.006	2.594	0.010
TRASP	0.034	0.569	0.059	0.953
Sand x TRASP	-0.021	0.013	-1.579	0.116

#4

Zone 1 (Adj. R^2 = 0.06, F = 4.01; p-value = 0.009)

Coefficients	Estimate	Std. Error	t-value	p-value
Intercept	6.656	0.905	7.356	0.000
Basal area	0.614	0.683	0.898	0.370
Sand	0.009	0.005	2.061	0.041
TRASP	-0.736	0.295	-2.497	0.013

#5

Zone 1 (Adj. R^2 = 0.05;7 F = 3.46; p-value = 0.01)

Coefficients	Estimate	Std. Error	t-value	p-value
Intercept	12.067	2.664	4.529	0.000
Basal area	-3.547	2.058	-1.723	0.087
Depth	-0.031	0.016	-1.951	0.053
TRASP	-0.920	0.305	-3.017	0.003
Basal area x Depth	0.026	0.012	2.098	0.037

Table 3.6. Ordinary Least Squares (OLS) regression for the best models (i.e. $\Delta i < 2$) of sugar maple seedling-environmental relationships in Zone 2. Environmental variables include current forest structure and composition (sugar maple basal area and stand age), and site level environmental conditions (sand proportion, soil depth, slope, and aspect index). #1 indicate the top best model and #7 the last of the best models (see also Table 3.3).

#1

Zone 2 (Adj. $R^2 = 0.09$; $F = 23.57$; p-value < 0.0001)

Coefficients	Estimate	Std. Error	t-value	p-value
Intercept	5.681	0.285	19.945	0.000
Basal area	1.122	0.135	8.317	0.000
Sand	-0.002	0.003	-0.706	0.481
Stand age	0.010	0.002	4.646	0.000
TRASP	-1.054	0.376	-2.802	0.005
Sand x TRASP	0.014	0.007	2.078	0.038

#2

Zone 2 (Adj. $R^2 = 0.09$; $F = 19.86$; p-value < 0.0001)

Coefficients	Estimate	Std. Error	t-value	p-value
Intercept	6.432	0.726	8.854	0.000
Basal area	0.630	0.458	1.375	0.169
Sand	-0.002	0.003	-0.711	0.477
Stand age	0.000	0.010	-0.035	0.972
TRASP	-1.069	0.376	-2.840	0.005
Basal area x Stand age	0.007	0.006	1.124	0.262
Sand x TRASP	0.014	0.007	2.119	0.034

#3

Zone 2 (Adj. R^2 = 0.09; F = 37.49; p-value < 0.0001)

Coefficients	Estimate	Std. Error	t-value	p-value
Intercept	5.610	0.249	22.549	0.000
Basal area	1.101	0.135	8.173	0.000
Stand age	0.011	0.002	4.672	0.000
TRASP	-0.319	0.142	-2.240	0.025

#4

Zone 2 (Adj. R^2 = 0.09; F = 19.79; p-value < 0.0001)

Coefficients	Estimate	Std. Error	t-value	p-value
Intercept	5.505	0.340	16.200	0.000
Basal area	1.229	0.175	7.015	0.000
Sand	-0.002	0.003	-0.676	0.499
Stand age	0.010	0.002	4.642	0.000
TRASP	-0.340	0.838	-0.406	0.685
Basal area x TRASP	-0.413	0.433	-0.954	0.340
Sand x TRASP	0.013	0.007	1.961	0.050

#5

Zone 2 (Adj. R^2 = 0.09; F = 19.70; p-value < 0.0001)

Coefficients	Estimate	Std. Error	t-value	p-value
Intercept	6.007	0.570	10.535	0.000
Basal area	0.913	0.344	2.650	0.008
Sand	-0.009	0.010	-0.828	0.408
Stand age	0.010	0.002	4.663	0.000
TRASP	-1.032	0.378	-2.730	0.006
Basal area x Sand	0.004	0.006	0.660	0.509
Sand x TRASP	0.014	0.007	2.016	0.044

#6

Zone 2 (Adj. R^2 = 0.09; F = 28.50; p-value < 0.0001)

Coefficients	Estimate	Std. Error	t-value	p-value
Intercept	5.389	0.308	17.508	0.000
Basal area	1.238	0.175	7.063	0.000
Stand age	0.011	0.002	4.665	0.000
TRASP	0.541	0.719	0.752	0.452
Basal area x TRASP	-0.524	0.430	-1.219	0.223

#7

Zone 2 (Adj. R^2 = 0.09; F = 17.18; p-value < 0.0001)

Coefficients	Estimate	Std. Error	t-value	p-value
Intercept	6.291	0.739	8.513	0.000
Basal area	0.712	0.465	1.532	0.126
Sand	-0.002	0.003	-0.679	0.497
Stand age	-0.001	0.010	-0.112	0.911
TRASP	-0.288	0.839	-0.343	0.732
Basal area x Stand age	0.007	0.006	1.199	0.231
Basal area x TRASP	-0.452	0.434	-1.042	0.298
Sand x TRASP	0.013	0.007	1.995	0.046

Table 3.7. Ordinary Least Squares (OLS) regression for the best models (i.e. $\Delta i < 2$) of sugar maple seedling-environmental relationships in Zone 3. Environmental variables include current forest structure and composition (sugar maple basal area and stand age), and site level environmental conditions (sand proportion, soil depth, slope, and aspect index). #1 indicate the top best model and #8 the last of the best models (see also Table 3.4).

#1

Zone 3 (Adj. $R^2 = 0.13$; $F = 27.97$; p-value < 0.0001)

Coefficients	Estimate	Std. Error	t-value	p-value
Intercept	3.634	0.717	5.071	0.000
Basal area	0.394	0.336	1.173	0.241
Sand	0.000	0.007	0.042	0.966
Depth	-0.314	0.128	-2.455	0.014
Basal area x Sand	-0.004	0.002	-1.917	0.056
Basal area x Depth	0.116	0.063	1.854	0.064
Sand x Depth	0.001	0.001	1.458	0.145

#2

Zone 3 (Adj. $R^2 = 0.13$; $F = 33.10$; p-value < 0.0001)

Coefficients	Estimate	Std. Error	t-value	p-value
Intercept	3.055	0.597	5.120	0.000
Basal area	0.474	0.332	1.428	0.154
Sand	0.009	0.004	2.307	0.021
Depth	-0.219	0.110	-1.989	0.047
Basal area x Sand	-0.005	0.002	-2.223	0.026
Basal area x Depth	0.110	0.063	1.761	0.078

#3

Zone 3 (Adj. R^2 = 0.13; F = 53.39; p-value < 0.0001)

Coefficients	Estimate	Std. Error	t-value	p-value
Intercept	1.922	0.233	8.235	0.000
Basal area	1.043	0.140	7.471	0.000
Sand	0.009	0.004	2.493	0.013
Basal area x Sand	-0.005	0.002	-2.371	0.018

#4

Zone 3 (Adj. R^2 = 0.13; F = 40.52; p-value < 0.0001)

Coefficients	Estimate	Std. Error	t-value	p-value
Intercept	2.124	0.278	7.654	0.000
Basal area	1.002	0.143	7.017	0.000
Sand	0.008	0.004	2.283	0.023
Depth	-0.029	0.021	-1.342	0.180
Basal area x Sand	-0.005	0.002	-2.140	0.033

#5

Zone 3 (Adj. R^2 = 0.13; F = 32.80; p-value < 0.0001)

Coefficients	Estimate	Std. Error	t-value	p-value
Intercept	2.609	0.456	5.716	0.000
Basal area	0.955	0.147	6.500	0.000
Sand	0.001	0.007	0.132	0.895
Depth	-0.106	0.062	-1.720	0.086
Basal area x Sand	-0.004	0.002	-1.853	0.064
Sand x Depth	0.001	0.001	1.338	0.181

#6

Zone 3 (Adj. R^2 = 0.13; F = 53.22; p-value < 0.0001)

Coefficients	Estimate	Std. Error	t-value	p-value
Intercept	3.573	0.550	6.491	0.000
Basal area	0.191	0.309	0.620	0.536
Depth	-0.225	0.109	-2.062	0.039
Basal area x Depth	0.110	0.062	1.777	0.076

#7

Zone 3 (Adj. R^2 = 0.13; F = 32.74; p-value < 0.0001)

Coefficients	Estimate	Std. Error	t-value	p-value
Intercept	4.149	0.665	6.238	0.000
Basal area	0.159	0.314	0.508	0.612
Sand	-0.009	0.005	-1.716	0.087
Depth	-0.334	0.128	-2.613	0.009
Basal area x Depth	0.112	0.063	1.787	0.074
Sand x Depth	0.002	0.001	1.841	0.066

#8

Zone 3 (Adj. R^2 = 0.13; F = 23.96; p-value < 0.0001)

Coefficients	Estimate	Std. Error	t-value	p-value
Intercept	2.598	0.675	3.848	0.000
Basal area	0.744	0.380	1.961	0.050
Sand	0.009	0.004	2.371	0.018
Stand age	0.006	0.004	1.415	0.157
Depth	-0.216	0.110	-1.960	0.050
Basal area x Sand	-0.005	0.002	-2.294	0.022
Basal area x Stand age	-0.004	0.003	-1.470	0.142
Basal area x Depth	0.109	0.063	1.737	0.083

Table 3.8. Summary of the effects of environmental variables on sugar maple seedling abundance across the Upper Great Lakes region. "+" indicates a positive effect, "–" a negative effect in the main effect (a) or two-way interaction (b). The symbol "x" between two environmental variables is a two way interaction. Only one model in each zone included parameters that were all significant (p-value ≤ 0.05), and "*" indicates these significant parameters. For instance, the model for which all parameters were significant in Zone 1 included sand and TRASP. A light grey shaded box means that the corresponding variable had one opposite effect among the set of best models, for instance, basal area in Zone 1 had a positive effect in all best models but one, where it had a negative effect. An open box means that the effect occurs only in one of the best models and thus may be considered as a neutral effect in the context of multi-model inference, for example, depth in Zone 1 was included in only one of five models.

(a) Main effect

	Effect		
Variable	Zone 1	Zone 2	Zone 3
Basal area	+	+*	+*
Sand	+*	–	+*
Stand age		+*	+
Depth	–		–
TRASP	–*	–*	

(b) Two-way interaction

	Effect		
Variable	Zone 1	Zone 2	Zone 3
Sand x TRASP	−	+	
Basal area x TRASP		−	
Basal area x Stand age		+	−
Basal area x Sand		+	−
Basal area x Depth	+		+
Sand x Depth			+

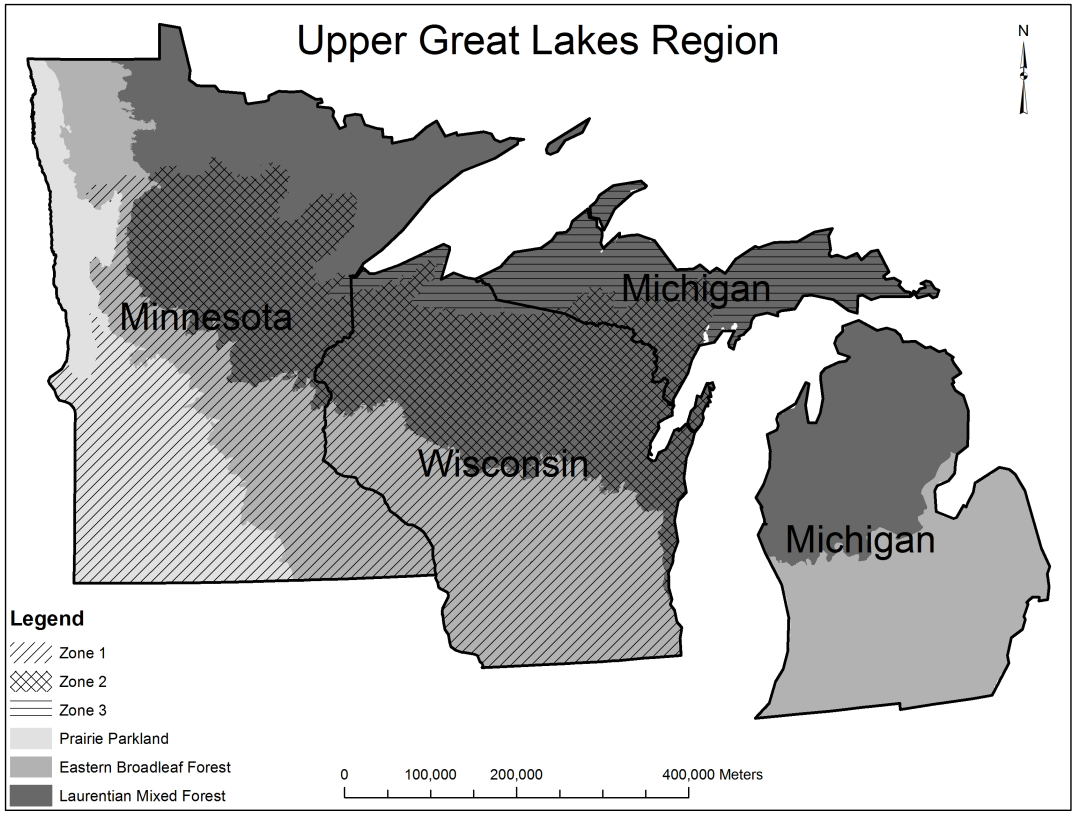

Figure 3.1. Map of the study area. Zones of interest are overlapping with ecological provinces (i.e. Prairie Parkland, Midwest Broadleaf Forest, and Laurentian Mixed Forest) (McNab et al. 2007). The Prairie-Forest Border (PFB) forms the transition zone between the tall grass prairies and the northern forests (Zone 1, 378 FIA plots), the forest interior extends beyond the PFB into northern Wisconsin (Zone 2, 1823 FIA plots), and the deep forest lies in Michigan's Upper Peninsula (Zone 3, 1314 FIA plots).

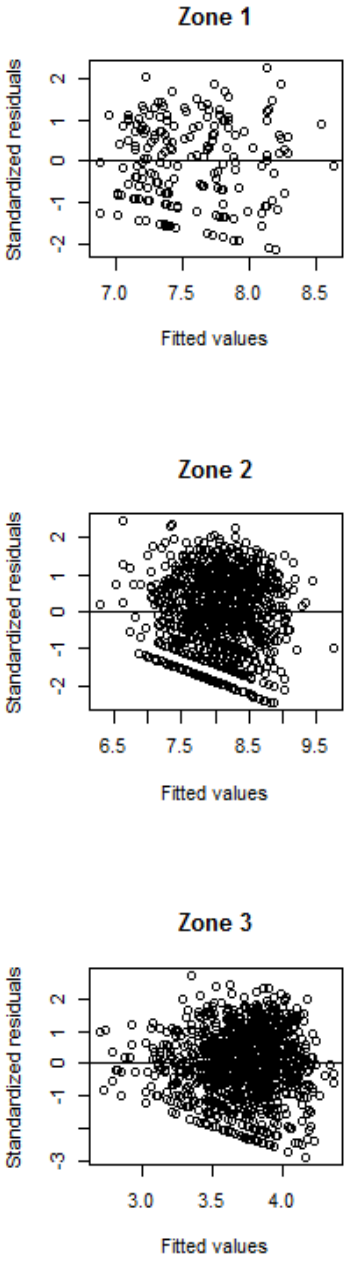

Figure 3.2. Standardized residual plots of sugar maple seedling-environmental relationships in each zone. Plots are based on the top ordinary Least Square (OLS) regression models (i.e. lowest AIC; see Tables 3.2 to 3.4).

Conclusions

This PhD dissertation showed that sugar maple communities with significant admixtures of other tree species in the Upper Great Lakes region are currently not stable, and that mesophication and succession are occurring across the region. Site productivity had a significant and positive effect on tree richness in the region but the relationship between seedling richness and productivity was flat. Sugar maple basal area had a very strong negative neighborhood effect on species richness but no apparent threshold effect was observed. The abundance of sugar maple seedlings is currently insensitive to environmental variables (i.e. has a very broad environmental niche) in Upper Michigan as opposed to the prairie-forest border, suggesting that, the expected shift in future climate would make the climate of Upper Michigan like that of the prairie-forest border by late 21st century, thereby reducing the probability of seedling establishment on many sites currently with high dominance of sugar maple. This would alter the current successional trends towards future sugar maple dominance found for the communities identified on many sites in the interior forests and deep interior forest zones. Moreover, heavy deer browsing and invasion of European earthworms are predicted to narrow the niche of sugar maple and drastically change the composition of sugar maple forests in the future. However, the forest is likely to be resilient in that other species will be able to replace sugar maple if its abundance declines because (1) sugar maple forms communities with a number of other tree species across the climate gradient of the Upper Great Lakes region, (2) species richness analyses showed that several other tree species are usually present, and (3) several species of seedlings are present even when sugar maple constitutes 100%

of the mature tree basal area. The ecological and economical importance of sugar maple across the region is such that future research should continue to follow sugar maple seedling success in varied environments to improve predictions for dynamics of northern hardwood forests in the context of global environmental change.

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Appendix A: Supplementary information for Chapter 3

Table S3.1. List of complete AIC models of sugar maple seedling density in Zone 1. First model is the best model (i.e. $\Delta i = 0$). K is the number of parameters included in the model, AIC is the Akaike's Information Criterion value, Δi is the difference between the AIC of the best fitting model and that of model *i*, and w*i* is the probability that a model *i* is the best among all candidate models. Model parameters: B = Basal area, A = Stand age, S = Sand proportion, D = Depth of soil, T = TRASP (index related to aspect), O = Slope. The symbol "x" between two parameters indicates two way interactions.

Model	K	AIC	Δi	wi
S + T + SxT	5	667.36	0.00	0.08
S + T	4	667.55	0.19	0.08
B + S + T + SxT	6	668.18	0.83	0.06
B + S + T	5	668.73	1.37	0.04
B + D + T + BxD	6	668.93	1.57	0.04
S + A + T + SxT	6	669.36	2.00	0.03
S + A + T	5	669.55	2.19	0.03
B + S + T + BxS + SxT	7	669.62	2.26	0.03
T	3	669.75	2.39	0.03
D + T	4	669.98	2.63	0.02
B + S + A + T + SxT	7	670.10	2.75	0.02
B + S + T + BxT + SxT	7	670.15	2.79	0.02
B + S + T + BxS	6	670.19	2.84	0.02
S + A + D + T + SxT	7	670.25	2.90	0.02
S + A + D + T	6	670.37	3.01	0.02
S + A + D + T	6	670.37	3.01	0.02
B + D + T + BxD + DxT	7	670.40	3.04	0.02
T + O	4	670.50	3.14	0.02
B + S + T + BxT	6	670.67	3.31	0.02
B + S + A + T	6	670.69	3.33	0.02
B + S + A + T	6	670.69	3.33	0.02
B + D + T + BxD + BxT	7	670.82	3.46	0.02

B + T	4	671.02	3.66	0.01
B + S + A + T + BxA + SxT	8	671.15	3.79	0.01
D + T + DxT	5	671.32	3.97	0.01
B + D + T	5	671.39	4.04	0.01
B + S + A + T + BxS + SxT	8	671.55	4.19	0.01
B + S + T + BxS + BxT + SxT	8	671.57	4.21	0.01
A + T	4	671.74	4.39	0.01
S	3	671.75	4.40	0.01
S + A + D + T + SxD + SxT	8	671.77	4.41	0.01
S + A + D + T + DxT	7	671.82	4.46	0.01
A + D + T	5	671.98	4.63	0.01
S + A + D + T + SxD	7	672.03	4.67	0.01
B + S + A + T + BxT + SxT	8	672.07	4.71	0.01
B + D + T + BxD + BxT + DxT	8	672.08	4.72	0.01
B + S + T + BxS + BxT	7	672.11	4.75	0.01
B + S + A + T + BxA	7	672.13	4.78	0.01
B + S + A + T + BxS	7	672.16	4.80	0.01
S + D	4	672.22	4.87	0.01
B + D + T + DxT	6	672.31	4.95	0.01
T + O + TxO	5	672.50	5.14	0.01
B + S + A + T + BxS + BxA + SxT	9	672.57	5.21	0.01
B + S + A + T + BxT	7	672.62	5.27	0.01
B + T + BxT	5	672.82	5.46	0.01
B + S	4	672.99	5.63	0.01
B + A + T	5	673.00	5.65	0.01
B + S + A + T + BxA + BxT + SxT	9	673.12	5.77	0.00
S + A + D + T + SxD + SxT + DxT	9	673.31	5.96	0.00
A + D + T + DxT	6	673.32	5.97	0.00
B + D + T + BxT	6	673.36	6.01	0.00
A + D + T + O	6	673.44	6.09	0.00
S + A + D + T + SxD + DxT	8	673.45	6.09	0.00
S + A + D + T + SxD + DxT	8	673.45	6.09	0.00
B + S + A + T + BxS + BxT + SxT	9	673.49	6.14	0.00
B + S + A + T + BxS + BxA	8	673.59	6.23	0.00
B + S + D	5	673.60	6.25	0.00
B + S + D + BxD	6	673.61	6.26	0.00
S + A	4	673.73	6.37	0.00
B + S + O	5	673.76	6.40	0.00
S + D + SxD	5	673.81	6.45	0.00
B + D + T + BxT + DxT	7	674.06	6.70	0.00

B + S + A + T + BxS + BxT	8	674.07	6.72	0.00
B + S + A + T + BxA + BxT	8	674.08	6.73	0.00
S + A + D	5	674.16	6.80	0.00
D	3	674.35	7.00	0.00
A + D + T + O + DxO	7	674.37	7.02	0.00
B + A + T + BxA	6	674.38	7.03	0.00
S + A + O	5	674.40	7.04	0.00
Intercept only	3	674.63	7.28	0.00
B + S + BxS	5	674.80	7.44	0.00
B + A + T + BxT	6	674.80	7.44	0.00
B + S + A	5	674.86	7.50	0.00
O	3	674.88	7.53	0.00
A + D + T + O + DxT	7	674.92	7.56	0.00
B + S + D + SxD	6	675.15	7.79	0.00
B + S + D + BxD + SxD	7	675.16	7.80	0.00
B + S + D + BxS	6	675.38	8.03	0.00
B + S + A + D + BxD	7	675.39	8.03	0.00
B + S + A + D	6	675.40	8.04	0.00
B + S + A + D	6	675.40	8.04	0.00
A + D + T + O + TxO	7	675.44	8.09	0.00
B + S + O + BxS	6	675.49	8.13	0.00
B + S + A + T + BxS + BxA + BxT	9	675.51	8.16	0.00
S + A + D + O	6	675.52	8.17	0.00
B + S + D + BxS + BxD	7	675.53	8.17	0.00
D + O	4	675.57	8.22	0.00
B + S + A + O	6	675.65	8.29	0.00
S + A + D + SxD	6	675.74	8.39	0.00
B + D	4	675.84	8.48	0.00
A + D + T + O + DxT + DxO	8	675.87	8.51	0.00
B	3	675.96	8.61	0.00
B + D + BxD	5	676.05	8.69	0.00
B + A + T + BxA + BxT	7	676.20	8.84	0.00
A + D	4	676.31	8.95	0.00
B + S + A + BxA	6	676.51	9.16	0.00
A	3	676.62	9.27	0.00
B + S + A + BxS	6	676.66	9.31	0.00
S + A + D + O + DxO	7	676.74	9.39	0.00
A + D + T + O + DxT + TxO	8	676.87	9.51	0.00
B + S + A + D + BxD + SxD	8	676.93	9.57	0.00
B + S + A + D + SxD	7	676.94	9.58	0.00

B + S + D + BxS + SxD	7	677.01	9.65	0.00
B + S + A + D + BxA	7	677.10	9.74	0.00
D + O + DxO	5	677.11	9.76	0.00
B + S + D + BxS + BxD + SxD	8	677.12	9.76	0.00
S + A + D + O + SxD	6	677.16	9.80	0.00
B + S + A + D + BxS	6	677.19	9.83	0.00
B + S + A + O + BxA	6	677.26	9.91	0.00
B + S + A + D + BxA + BxD	8	677.28	9.92	0.00
B + S + A + D + BxS + BxD	8	677.31	9.95	0.00
B + S + A + O + BxS	7	677.39	10.03	0.00
A + D + O	5	677.54	10.19	0.00
A + D + O + D + O	7	677.54	10.19	0.00
B + A + D	5	677.68	10.33	0.00
A + D + T + O + DxT + DxO + TxO	9	677.75	10.40	0.00
B + A + D + BxD	6	677.88	10.53	0.00
B + A	4	677.88	10.53	0.00
B + A + O	5	678.27	10.91	0.00
B + S + A + BxS + BxA	7	678.32	10.96	0.00
S + A + D + O + SxD + DxO	8	678.34	10.98	0.00
B + S + A + D + BxA + BxD + SxD	9	678.79	11.44	0.00
B + S + A + D + BxS + SxD	8	678.80	11.45	0.00
B + S + A + D + BxS + SxD	8	678.80	11.45	0.00
B + S + A + D + BxS + BxA	8	678.88	11.53	0.00
B + S + A + D + BxS + BxD + SxD	9	678.89	11.53	0.00
B + S + A + O + BxS + BxA	8	679.00	11.64	0.00
B + S + A + D + BxS + BxA + BxD	9	679.19	11.83	0.00
B + A + D + BxA	6	679.35	11.99	0.00
B + A + BxA	5	679.50	12.14	0.00
B + A + D + BxA + BxD	7	679.74	12.38	0.00
B + A + O + BxA	6	679.83	12.47	0.00
B + S + A + D + BxS + BxA + SxD	9	680.47	13.11	0.00

Table S3.2. List of complete AIC models of sugar maple seedling density in Zone 2. First model is the best model (i.e. $\Delta i = 0$). K is the number of parameters included in the model, AIC is the Akaike's Information Criterion value, Δi is the difference between the AIC of the best fitting model and that of model *i*, and w*i* is the probability that a model *i* is the best among all candidate models. Model parameters: B = Basal area, A = Stand age, S = Sand proportion, D = Depth of soil, T = TRASP (index related to aspect), O = Slope. The symbol "x" between two parameters indicates two way interactions.

Model	K	AIC	Δi	wi
B + S + A + T + SxT	7	3985.35	0.00	0.09
B + S + A + T + BxA + SxT	8	3986.08	0.73	0.07
B + A + T	5	3986.42	1.07	0.06
B + S + A + T + BxT + SxT	8	3986.43	1.08	0.06
B + S + A + T + BxS + SxT	8	3986.91	1.56	0.04
B + A + T + BxT	6	3986.93	1.58	0.04
B + S + A + T + BxA + BxT + SxT	9	3986.99	1.64	0.04
B + A + T + BxA	6	3987.38	2.03	0.03
B + S + A + D + SxD	7	3987.49	2.14	0.03
B + S + A + T + BxS + BxA + SxT	9	3987.55	2.20	0.03
B + A + T + BxA + BxT	7	3987.67	2.32	0.03
B + S + A + T	6	3987.68	2.33	0.03
B + S + A + T	6	3987.68	2.33	0.03
B + S + A + T + BxS + BxT + SxT	9	3987.81	2.46	0.03
B + S + A + D + BxS + BxD + SxD	9	3987.87	2.52	0.03
B + S + A + D + BxD + SxD	8	3987.98	2.63	0.03
B + S + A + D + BxS + SxD	8	3988.30	2.95	0.02
B + S + A + D + BxS + SxD	8	3988.30	2.95	0.02
B + S + A + T + BxT	7	3988.30	2.95	0.02
B + S + A + T + BxA	7	3988.59	3.24	0.02
B + A + O	5	3988.60	3.25	0.02
B + S + A + D + BxA + BxD + SxD	9	3988.66	3.31	0.02
B + S + A + D + BxS + BxA + SxD	9	3988.94	3.59	0.02
B + S + A + T + BxS	7	3988.99	3.64	0.02
B + S + A + T + BxA + BxT	8	3988.99	3.64	0.02
B + S + A + T + BxS + BxT	8	3989.35	3.99	0.01

B + A	4	3989.44	4.09	0.01
B + A + O + BxA	6	3989.47	4.12	0.01
B + S + A + O	6	3989.71	4.36	0.01
B + S + A + T + BxS + BxA	8	3989.79	4.44	0.01
B + S + A + T + BxS + BxA + BxT	9	3989.88	4.53	0.01
B + A + D	5	3990.03	4.68	0.01
B + A + BxA	5	3990.39	5.04	0.01
B + A + D + BxD	6	3990.46	5.11	0.01
B + S + A + O + BxA	7	3990.52	5.17	0.01
B + S + A + O + BxS	7	3990.82	5.47	0.01
B + A + D + BxA	6	3990.90	5.55	0.01
B + S + A	5	3991.06	5.70	0.01
B + S + A + D	6	3991.19	5.84	0.01
B + S + A + D	6	3991.19	5.84	0.01
B + A + D + BxA + BxD	7	3991.22	5.87	0.01
B + S + A + O + BxS + BxA	8	3991.50	6.15	0.00
B + S + A + D + BxD	7	3991.73	6.38	0.00
B + S + A + BxA	6	3991.96	6.61	0.00
B + S + A + D + BxA	7	3991.99	6.64	0.00
B + S + A + D + BxS + BxD	8	3992.14	6.79	0.00
B + S + A + BxS	6	3992.22	6.87	0.00
B + S + A + D + BxS	7	3992.36	7.01	0.00
B + S + A + D + BxA + BxD	8	3992.42	7.07	0.00
B + S + A + D + BxS + BxA + BxD	9	3992.61	7.26	0.00
B + S + A + BxS + BxA	7	3993.01	7.66	0.00
B + S + A + D + BxS + BxA	8	3993.03	7.68	0.00
B + S + T + SxT	6	4004.85	19.49	0.00
B + S + T + BxT + SxT	7	4005.91	20.56	0.00
B + T	4	4006.11	20.76	0.00
B + T + BxT	5	4006.58	21.23	0.00
B + S + T + BxS + SxT	7	4006.58	21.23	0.00
B + S + T	5	4007.44	22.09	0.00
B + D + T	5	4007.46	22.11	0.00
B + S + T + BxS + BxT + SxT	8	4007.49	22.14	0.00
B + S + D + SxD	6	4007.82	22.47	0.00
B + D + T + BxT	6	4007.86	22.51	0.00
B + D + T + BxD	6	4007.89	22.54	0.00
B + S + T + BxT	6	4008.01	22.66	0.00
B + S + D + BxD + SxD	8	4008.48	23.13	0.00
B + D + T + DxT	6	4008.48	23.13	0.00

B + D + T + BxD + BxT	7	4008.51	23.16	0.00
B	3	4008.60	23.25	0.00
B + D + T + BxT + DxT	7	4008.70	23.35	0.00
B + S + D + BxS + BxD + SxD	8	4008.86	23.51	0.00
B + S + D + BxS + SxD	7	4008.95	23.60	0.00
B + S + T + BxS	6	4008.97	23.62	0.00
B + D + T + BxD + DxT	7	4009.07	23.72	0.00
B + S + T + BxS + BxT	7	4009.32	23.97	0.00
B + D + T + BxD + BxT + DxT	8	4009.53	24.18	0.00
B + D	4	4009.81	24.46	0.00
B + S + O	5	4009.86	24.51	0.00
B + S	4	4010.25	24.90	0.00
B + D + BxD	5	4010.42	25.07	0.00
B + S + D	5	4011.15	25.80	0.00
B + S + O + BxS	6	4011.24	25.89	0.00
B + S + BxS	5	4011.66	26.31	0.00
B + S + D + BxD	6	4011.85	26.50	0.00
B + S + D + BxS	6	4012.56	27.21	0.00
B + S + D + BxS + BxD	7	4012.66	27.31	0.00
S + A + D + T + SxD + SxT + DxT	9	4046.13	60.78	0.00
S + A + D + T + SxD + DxT	8	4047.65	62.30	0.00
S + A + D + T + SxD + DxT	8	4047.65	62.30	0.00
S + A + D + T + SxD + SxT	8	4048.31	62.96	0.00
S + A + D + T + SxD	7	4048.39	63.04	0.00
A + D + T + O + TxO	7	4048.76	63.41	0.00
A + D + T + O + DxT + TxO	8	4049.08	63.73	0.00
A + D + T + DxT	6	4049.16	63.81	0.00
A + D + T	5	4049.36	64.01	0.00
A + T	4	4049.49	64.14	0.00
S + A + D + T + SxT	7	4050.21	64.86	0.00
S + A + D + SxD	6	4050.23	64.88	0.00
S + A + D + O + SxD	7	4050.23	64.88	0.00
S + A + D + T + DxT	7	4050.48	65.13	0.00
A + D + T + O + DxT + DxO + TxO	9	4050.51	65.16	0.00
S + A + D + T	6	4050.70	65.35	0.00
S + A + D + T	6	4050.70	65.35	0.00
S + A + T + SxT	6	4050.78	65.43	0.00
A + D + T + O + DxT	7	4050.80	65.45	0.00
A + D	4	4050.93	65.58	0.00
A + D + T + O	6	4051.05	65.70	0.00

A	3	4051.27	65.92	0.00
S + A + T	5	4051.27	65.92	0.00
A + D + O	5	4051.45	66.10	0.00
A + D + O + D + O	7	4051.45	66.10	0.00
A + D + T + O + DxT + DxO	8	4051.84	66.49	0.00
S + A + D + O + SxD + DxO	8	4052.22	66.87	0.00
S + A + D	5	4052.53	67.18	0.00
S + A + D + O	6	4052.75	67.40	0.00
A + D + T + O + DxO	7	4052.98	67.63	0.00
S + A + O	5	4053.14	67.79	0.00
S + A	4	4053.20	67.85	0.00
S + A + D + O + DxO	7	4054.66	69.31	0.00
T	3	4086.86	101.51	0.00
D + T	4	4087.63	102.28	0.00
T + O + TxO	5	4087.70	102.35	0.00
Intercept only	3	4087.88	102.53	0.00
D + T + DxT	5	4088.04	102.69	0.00
S + T + SxT	5	4088.21	102.86	0.00
D	3	4088.49	103.14	0.00
S + D + SxD	5	4088.62	103.27	0.00
S + T	4	4088.74	103.39	0.00
T + O	4	4088.76	103.41	0.00
O	3	4088.98	103.63	0.00
D + O	4	4089.81	104.46	0.00
S	3	4089.85	104.50	0.00
S + D	4	4090.29	104.94	0.00
D + O + DxO	5	4091.70	106.35	0.00

Table S3.3. List of complete AIC models of sugar maple seedling density in Zone 3. First model is the best model (i.e. $\Delta i = 0$). K is the number of parameters included in the model, AIC is the Akaike's Information Criterion value, Δi is the difference between the AIC of the best fitting model and that of model *i*, and w*i* is the probability that a model *i* is the best among all candidate models. Model parameters: B = Basal area, A = Stand age, S = Sand proportion, D = Depth of soil, T = TRASP (index related to aspect), O = Slope. The symbol "x" between two parameters indicates two way interactions.

Model	K	AIC	Δi	wi
B + S + D + BxS + BxD + SxD	8	2253.55	0.00	0.08
B + S + D + BxS + BxD	7	2253.69	0.14	0.07
B + S + BxS	5	2254.61	1.06	0.05
B + S + D + BxS	6	2254.80	1.25	0.04
B + S + D + BxS + SxD	7	2255.01	1.45	0.04
B + D + BxD	5	2255.05	1.49	0.04
B + S + D + BxD + SxD	7	2255.24	1.69	0.03
B + S + A + D + BxS + BxA + BxD	9	2255.51	1.96	0.03
B + S + A + D + BxS + BxD + SxD	9	2255.55	2.00	0.03
B + S + A + D + BxS + BxD	8	2255.69	2.14	0.03
B + D	4	2256.21	2.66	0.02
B + S + A + BxS + BxA	7	2256.29	2.73	0.02
B + S + T + BxS	6	2256.31	2.76	0.02
B + S + O + BxS	6	2256.38	2.83	0.02
B + D + T + BxD + DxT	7	2256.39	2.84	0.02
B + S + D + SxD	6	2256.45	2.90	0.02
B + S + A + D + BxS + BxA	8	2256.55	3.00	0.02
B + S + A + BxS	6	2256.61	3.06	0.02
B + S + D + BxD	6	2256.65	3.10	0.02
B + S + A + D + BxS + BxA + SxD	9	2256.65	3.10	0.02
B + S + T + BxS + BxT	7	2256.77	3.22	0.02
B + S + A + D + BxS	7	2256.80	3.25	0.02
B + D + T + BxD	6	2256.85	3.30	0.01
B	3	2256.92	3.37	0.01
B + D + T + BxD + BxT + DxT	8	2257.00	3.45	0.01
B + S + A + D + BxS + SxD	8	2257.01	3.45	0.01

B + S + A + D + BxS + SxD	8	2257.01	3.45	0.01
B + A + D + BxD	6	2257.04	3.49	0.01
B + D + T + BxD + BxT	7	2257.05	3.50	0.01
B + A + D + BxA + BxD	7	2257.17	3.62	0.01
B + S + A + D + BxA + BxD + SxD	9	2257.22	3.67	0.01
B + S + A + D + BxD + SxD	8	2257.24	3.69	0.01
B + S + D	5	2257.40	3.85	0.01
B + D + T + DxT	6	2257.49	3.94	0.01
B + S + T + BxS + SxT	7	2257.82	4.27	0.01
B + S + A + T + BxS + BxA	8	2257.98	4.43	0.01
B + D + T	5	2257.98	4.43	0.01
B + S + A + O + BxS + BxA	8	2258.04	4.49	0.01
B + A + D	5	2258.20	4.65	0.01
B + A + D + BxA	6	2258.23	4.68	0.01
B + S	4	2258.24	4.69	0.01
B + D + T + BxT + DxT	7	2258.29	4.74	0.01
B + S + A + T + BxS	7	2258.31	4.76	0.01
B + S + A + O + BxS	7	2258.38	4.83	0.01
B + D + T + BxT	6	2258.40	4.85	0.01
B + S + T + BxS + BxT + SxT	8	2258.44	4.89	0.01
B + S + A + D + SxD	7	2258.45	4.90	0.01
B + S + A + T + BxS + BxA + BxT	9	2258.62	5.07	0.01
B + S + A + D + BxD	7	2258.65	5.10	0.01
B + T	4	2258.69	5.14	0.01
B + S + A + T + BxS + BxT	8	2258.77	5.21	0.01
B + S + A + D + BxA + BxD	8	2258.80	5.25	0.01
B + A + BxA	5	2258.90	5.35	0.01
B + A	4	2258.92	5.37	0.01
B + T + BxT	5	2259.19	5.64	0.00
B + S + A + D	6	2259.40	5.84	0.00
B + S + A + D	6	2259.40	5.84	0.00
B + S + A + D + BxA	7	2259.47	5.92	0.00
B + S + A + T + BxS + BxA + SxT	9	2259.50	5.95	0.00
B + S + A + T + BxS + SxT	8	2259.82	6.27	0.00
B + S + O	5	2259.95	6.39	0.00
B + S + T	5	2259.99	6.44	0.00
B + S + A	5	2260.24	6.69	0.00
B + S + A + BxA	6	2260.26	6.71	0.00
B + S + A + T + BxS + BxT + SxT	9	2260.44	6.89	0.00
B + S + T + BxT	6	2260.54	6.98	0.00

B + A + O + BxA	6	2260.56	7.01	0.00
B + A + O	5	2260.59	7.04	0.00
B + A + T + BxA	6	2260.67	7.12	0.00
B + A + T	5	2260.69	7.14	0.00
B + A + T + BxT	6	2261.19	7.64	0.00
B + A + T + BxA + BxT	7	2261.34	7.78	0.00
B + S + T + SxT	6	2261.57	8.02	0.00
B + S + A + O	6	2261.95	8.39	0.00
B + S + A + O + BxA	7	2261.96	8.41	0.00
B + S + A + T	6	2261.99	8.44	0.00
B + S + A + T	6	2261.99	8.44	0.00
B + S + A + T + BxA	7	2262.01	8.46	0.00
B + S + T + BxT + SxT	7	2262.26	8.71	0.00
B + S + A + T + BxT	7	2262.53	8.98	0.00
B + S + A + T + BxA + BxT	8	2262.72	9.17	0.00
B + S + A + T + SxT	7	2263.57	10.02	0.00
B + S + A + T + BxA + SxT	8	2263.61	10.06	0.00
B + S + A + T + BxT + SxT	8	2264.26	10.71	0.00
B + S + A + T + BxA + BxT + SxT	9	2264.45	10.90	0.00
S + A + D + SxD	6	2375.12	121.57	0.00
S + A + D + T + SxD	7	2377.06	123.51	0.00
S + A + D + O + SxD	7	2377.08	123.53	0.00
S + D + SxD	5	2377.68	124.13	0.00
S + A + D + T + SxD + DxT	8	2377.94	124.39	0.00
S + A + D + T + SxD + DxT	6	2377.94	124.39	0.00
S + A + D + O + SxD + DxO	8	2377.97	124.42	0.00
S + A + D + T + SxD + SxT	8	2377.99	124.44	0.00
S + A + D + T + SxD + SxT + DxT	9	2378.65	125.10	0.00
A + D + T + O + TxO	7	2383.36	129.81	0.00
A + D + T + O + DxT + TxO	8	2384.07	130.52	0.00
S + A + D	5	2384.77	131.22	0.00
A + D + T + O + DxT + DxO + TxO	9	2385.31	131.76	0.00
A + D	4	2385.34	131.79	0.00
S + A + D + T	6	2386.54	132.99	0.00
S + A + D + T	6	2386.54	132.99	0.00
S + A + D + T + DxT	7	2386.65	133.10	0.00
S + A + D + O	6	2386.77	133.22	0.00
S + A + D + O + DxO	7	2386.91	133.36	0.00
A + D + T	5	2387.15	133.60	0.00
S + A + D + T + SxT	7	2387.31	133.76	0.00

A + D + O	5	2387.34	133.79	0.00
A + D + O + D + O	7	2387.34	133.79	0.00
A + D + T + DxT	6	2387.47	133.92	0.00
S + D	4	2387.48	133.93	0.00
D	3	2387.77	134.22	0.00
A + D + T + O	6	2389.03	135.48	0.00
A + D + T + O + DxO	7	2389.28	135.73	0.00
A + D + T + O + DxT	7	2389.40	135.85	0.00
D + T	4	2389.63	136.08	0.00
D + O	4	2389.76	136.21	0.00
D + T + DxT	5	2389.95	136.40	0.00
D + O + DxO	5	2390.09	136.54	0.00
A + D + T + O + DxT + DxO	7	2390.81	137.26	0.00
S + A	4	2394.97	141.42	0.00
T + O + TxO	5	2395.07	141.52	0.00
A	3	2395.17	141.62	0.00
S + A + T	5	2396.72	143.17	0.00
A + T	4	2396.96	143.41	0.00
S + A + O	5	2396.96	143.41	0.00
S + A + T + SxT	6	2397.84	144.29	0.00
Intercept only	3	2398.45	144.90	0.00
S	3	2398.55	145.00	0.00
T	3	2400.31	146.76	0.00
S + T	4	2400.38	146.83	0.00
O	3	2400.44	146.89	0.00
S + T + SxT	5	2401.48	147.93	0.00
T + O	4	2402.19	148.64	0.00