THE MICHIGAN BIG WOODS RESEARCH PLOT AT THE EDWIN S. GEORGE RESERVE, PINCKNEY, MI, USA

by

David Allen, Christopher W. Dick, Robyn J. Burnham, Ivette Perfecto,
John Vandermeer

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**DAVID ALLEN, CHRISTOPHER W. DICK, ROBYN J. BURNHAM,
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Abstract

The Michigan Big Woods research plot is a 23-ha forest dynamics research area at the Edwin S. George Reserve in Pinckney, MI, USA and is part of the Smithsonian Institution's ForestGEO network of research stations. The plot's free-standing woody vegetation (trees and shrubs) were censused three times, in 2003, 2008–2010, and 2014; lianas were censused on 20 ha from 2017 to 2018. Stems equal to or larger than 1 cm DBH are included for both trees and lianas. During the most recent tree census the plot included 33,690 tree and shrub individuals, comprising 45,564 stems representing 42 woody species and 22 families. The 20 ha liana census included 679 individuals comprising seven species, six genera, and four families. Compared to other ForestGEO plots in temperate broadleaf forests the plot has comparable levels of diversity and stem density, but a lower free-standing basal area, 30.6 m^2 ha^{-1}. It is likely that the plot area has a history of managed burning by Native Americans, and after European colonization, fire suppression, use as a pastured woodlot, and finally agricultural abandonment in the early 1900s. The forest is undergoing rapid succession as the oak-hickory canopy is being replaced by individuals of more mesic species (e.g., black cherry and red maple). The data from this plot offer an excellent resource to study the process of forest mesophication in the absence of a regular burning regime.

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INTRODUCTION

Changes to climate, disturbance regimes, populations of pests, pathogens, and competitors have resulted in dramatic shifts in the composition of forests in the eastern United States (Nowacki and Abrams, 2015; Pederson et al., 2015; Lovett et al., 2006). The causes and consequences of these changes in composition affect the capability of forests to offer critical ecosystem services. Networks of research plots are powerful tools that allow comparison across sites and through time to understand ecological processes that would not be clear at a single site (Keller et al., 2008; Smith, 2002). The Smithsonian Institution's ForestGEO network of forest research plots (Anderson-Teixeira et al., 2015) is an international partnership including 67 plots across 27 countries each sampled with a standardized protocol (https://forestgeo.si.edu/). Here we describe the Michigan Big Woods research plot, a ForestGEO plot in the Edwin S. George Reserve (ESGR) near Pinckney, Michigan (Figure 1). This is an important addition to the ForestGEO network because it is only one of 17 plots in temperate forests, and is in a forest undergoing the rapid successional changes typical of many eastern North American forests.

This forest's dramatic successional change is likely the result of its complex history of human use. The canopy is dominated by oaks and hickories, presumed to be a remnant of Native American fire use practices. The oak-hickory canopy is being replaced by more mesic-adapted species, especially red maple and black cherry, with abundant patches of the understory shrub, witch-hazel (*Hamamelis virginiana*). This replacement of canopy oaks may be the result of fire suppression after European colonization (Nowacki and Abrams, 2008). Similar replacement of canopy oaks has been observed elsewhere in eastern deciduous forest (Abrams, 1996; Fei et al., 2011; McEwan et al., 2011; Nowacki and Abrams, 2008). In the last 50 years, several invasive shrubs have spread through the understory, including Japanese barberry (*Berberis thunbergii*), which has formed an impenetrable thicket in parts of the forest.

Establishment of the Michigan Big Woods research plot began in 2003 with the census of all free-standing trees and shrubs, ≥ 3.2 cm diameter at breast height (DBH) (10 cm circumference) in a 12-ha portion of the current plot (Figure 2). In 2008, the 12-ha plot was censused again. And from 2008–2010, an additional 11 ha were added to form the current 23-ha plot. In 2014, all trees and shrubs in the 23-ha plot were recensused using the ForestGEO protocol (Condit, 1998), which included all stems ≥ 1 cm DBH. Thus, the original 12-ha of ≥ 3.2-cm DBH trees and shrubs in the plot have been censused three times over an 11-year period, providing important data on basic forest dynamics. A liana census of 20 ha was conducted in 2017 and 2018 (the region outlined with a dashed line in Figure 2). Data from the tree and shrub censuses are available on Deep Blue Data (Allen et al., 2019). Liana data are available for 10 hectares of the 20-ha liana plot in the undergraduate thesis of John Bradtke at the University of Michigan (Bradtke, 2018).

The purpose of this article is to provide a physical and biotic characterization of the Michigan Big Woods research plot with a review of research to date as a resource for future researchers. We provide diversity measures, stem density, and basal density for the plot. These values are compared to those in other ForestGEO plots in temperate broadleaf or mixed forests. We anticipate that Michigan Big Woods plot will add to our understanding of forest dynamics, especially regarding the details of canopy oak replacement.

LOCATION

The Edwin S. George Reserve (ESGR) is a 525 ha ecological reserve in southeast Michigan (42°27'46.5" N, 84°00'21.9" W) maintained by the University of Michigan for research, education, and conservation since 1930 (Cantrall, 1943). The reserve is located in Livingston County, MI about 7.7 km west of Pinckney, MI and about 30 km northwest of the University of Michigan campus in Ann Arbor (Figure 1). Southeast Michigan is a highly fragmented landscape with a large fraction of the land either developed or under agriculture. However, the ESGR abuts the Pinckney and Waterloo State Recreation Areas, both of which are largely forested and together cover over 12,000 ha.

TOPOGRAPHY, SOILS, CLIMATE

The topography within the plot is hilly for southeast Michigan, resulting from extensive glacial scouring, with characteristically rugged moraine and basin topography of hills and knobs separated by kettle holes and basins. An esker runs through the plot (the main road on the southern portion of the plot — see Figures 1 and 2) and comprises approximately 4 ha of the plot area. Two ephemeral ponds in the plot are visible in the stem map as areas without trees (Figure 2). The elevation in the plot ranges from 270 m to 305 m above sea level.

Soils are generally thin and sandy. Above 275 m there are mineral soils which are largely Boyer–Oshtemo sandy loam or Miami loam. Below 275 m the soils are mainly histosols dominated by Carlisle and Rifle muck (Soil Survey Staff, National Resources Conservation Service, USDA 2018).

The climate is warm-summer humid continental (Dfb in the Köppen climate classification system). From 1981-2010 the average temperature was highest in July at 21.4° C and coldest in January at -5.3° C. Over that time, three months a year had average temperatures below 0° C and five months a year above 10° C. The average annual precipitation was 857 mm, of which 70% came in the months of May through November (NOAA, 2018). Annual snowfall and days with

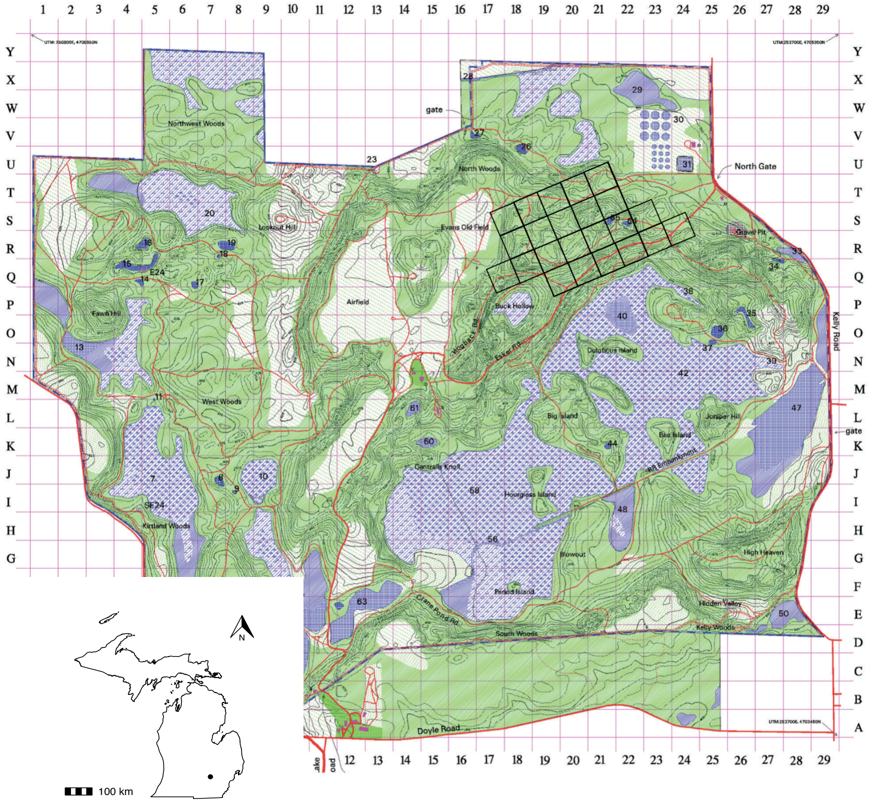

Figure 1: Location of the Michigan Big Woods plot in the E. S. George Reserve (ESGR). The plot is shown as a 23 ha grid in the northeast quadrat. The inset map shows the location of the ESGR in the state of Michigan, USA.

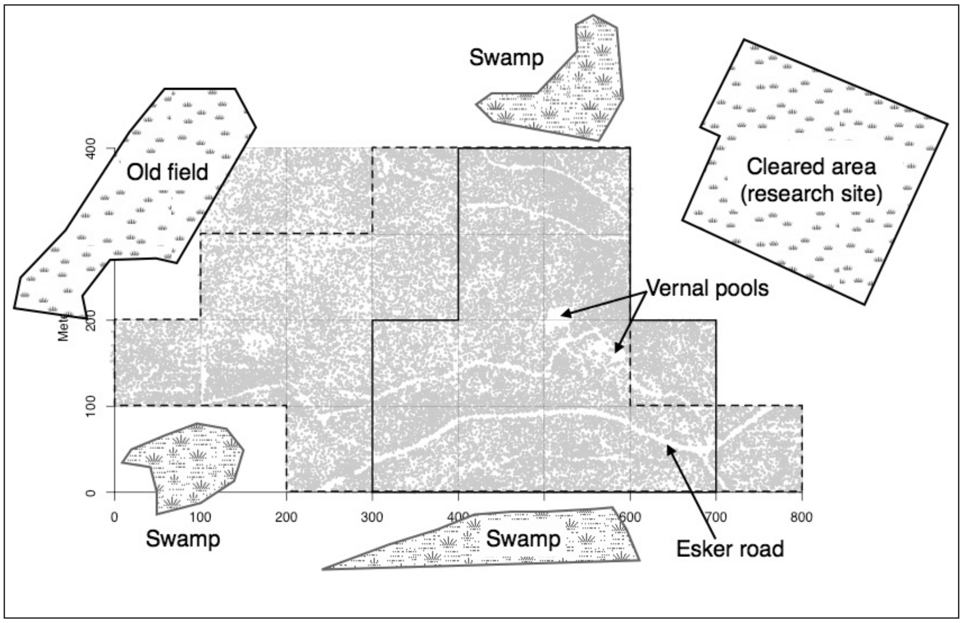

Figure 2: Stem map with all tree and shrub main stems alive in 2014 indicated. The region indicated by the thick black lines is the original 12 ha which were sampled in 2003. The entire plot was sampled for trees and shrubs in 2008–2010 and 2014. The 20 ha region indicated by the dashed black lines was sampled for lianas in 2017 and 2018. Roads, trails, and ponds can be seen as locations without stems. The irregular plot boundaries were necessary to avoid swamps, a field, and experimental ponds. All unlabeled areas surrounding the plot are forest.

snow cover vary substantially from year to year.

VEGETATION

The dominant vegetation at the ESGR is black oak-white oak-hickory forest (USNVC code CEBL002076) according to the US National Vegetation Classification system (USNVC, 2016). The canopy is dominated by oaks and hickories but relatively few individuals of these species are present in the sub- and mid-canopy. Instead, these strata are dominated by red maple, black cherry, and witch-hazel (see Figure 3 for a photograph of this). Nowacki and Abrams (2015) suggest that the decline of canopy oaks is largely due to European fire suppression and subsequent spread of fire-sensitive, shade-tolerant species which competitively exclude oaks. McEwan et al. (2011), on the other hand, suggest that oak decline has multiple causes including fire suppression, decreased drought severity since the mid-1800s, land-use changes, and changes in herbivore populations, especially white-tailed deer.

Figure 3: Photograph taken within the plot. The typical size structure of the forest can be seen here with large (> 20 cm DBH) white oak *(Quercus alba*) individuals and snag and a high density of smaller, pole-sized (<20 cm DBH) red maples (*Acer rubrum*). In other areas of the plot simi-lar structure is found, with large oaks (*Quercus* spp.) and dense smaller red maples, black cherries (*Prunus seroti-na*), and witch-hazels (*Hamamelis virginiana*).

The ESGR is home to six species of oaks (*Quercus alba, Q. bicolor, Q. ellipsoidalis, Q. macrocarpa, Q. rubra, and Q. velutina*). Oaks commonly hybridize and within the Great Lakes region there is evidence of hybridization among the three of the *Quercus* section Lobatae oaks in the ESGR (Owusu et al., 2015; Sullivan et al., 2016; Voss, 1985). Within the plot we find many individuals with intermediate morphological characteristics, and Warren H. Wagner considered it a hybrid zone (John Vandermeer, personal communication). The 48 tree, liana, and shrub species larger than 1 cm in diameter in the plot are listed in Tables 1 and 2.

Within the plot several species are represented by only one individual— native yellow birch (*Betula alleghaniensis*), and introduced crab apple (*Malus* sp.), black locust (*Robinia pseudoacacia*), and pear (*Pyrus* sp). The shrubs gray dogwood (*Cornus racemosa*), prickly gooseberry (*Ribes cynosbati*), and the exotic vine Asian bittersweet (*Celastrus orbiculatus*) also have only one or two mapped individuals in the plot, but are common at sizes < 1 cm diameter. Notable is a single large (>50 cm DBH), mast-fruiting American beech (*Fagus grandifolia*), with 62 saplings (<20 cm DBH), presumably offspring of this individual, but scattered throughout the plot as would be expected from bird and small mammal dispersal. Also notable are two adult American basswood individuals (*Tilia americana*), along with 101 basswood saplings, most of which are near the adults. On the other hand, the many American elm saplings are not clustered around the one adult individual. This pattern may be explained by the mortality of large elms from Dutch Elm Disease over recent decades. See Figure 4 for the distribution of individuals of these species.

There are many invasive shrub and vine species in the ESGR. The most common are Japanese barberry (*Berberis thunbergii*), autumn-olive (*Elaeagnus umbellata*), and multiflora rose (*Rosa multiflora*). These species often grow in dense stands in the forest understory possibly displacing the few native understory shrubs, other than witch-hazel. Because of this unique ecological role, these invasive shrubs and climbers may have a large effect on recruitment dynamics within the plot. Autumn-olive is especially invasive in the old fields of the ESGR (Li et al., 2017), and its penetration via road edges into the forest is extensive (Figure 5A). It is notable that much of the recruitment seems to be from old fields and other open areas surrounding the plot, however, significant clusters with apparent origins inside the plot could derive from the attractiveness of their fruits to birds. Japanese barberry is common and forms a dense layer in the understory in some parts of the plot (Figures 5B and 6). Because of its stature it does not reach 1 cm in diameter at breast height, so was not captured in the census. As such we conducted a separate survey to map barberry cover. Tree-of-heaven (*Ailanthus altissima*), honeysuckles (*Lonicera maackii* and *L. tatarica*) and Asian bittersweet (*Celastrus orbiculatus*) are not nearly as dense as barberry, autumn-olive, or multiflora rose.

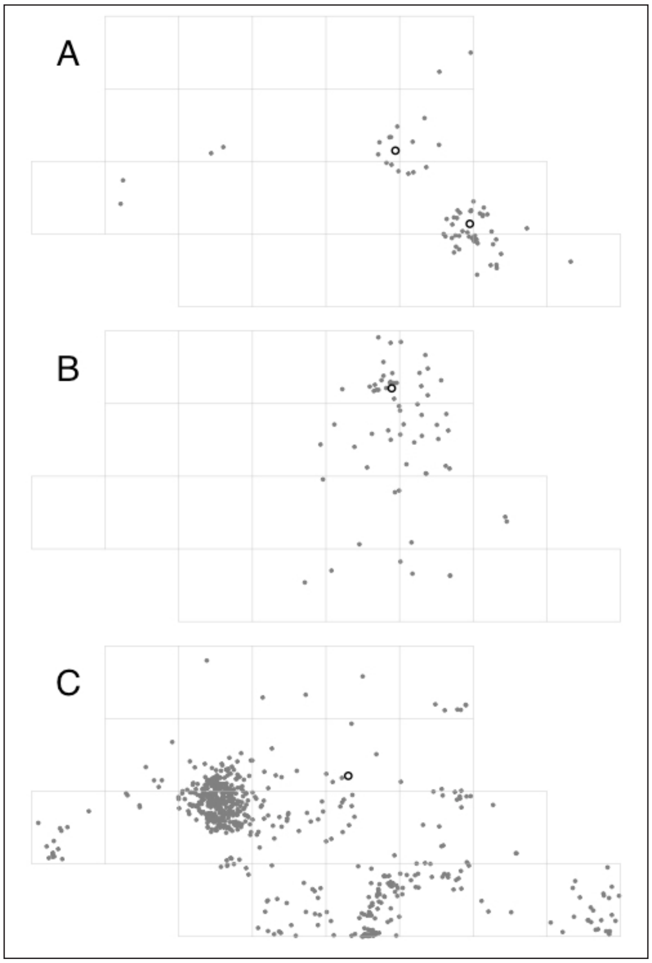

Figure 4: Stem map of three species characterized by a few large individuals and a substantial number of saplings. In each subfigure individuals with DBH >50 cm are indicated with a black circle and all other individuals with a gray dot. (A) American basswood (*Tilia americana*). (B) American beech (*Fagus grandifolia*). (C) American elm (*Ulmus americana*).

Tables 1 and 2 present all woody tree, shrub, and liana species with individuals ≥ 1 cm DBH found within the Big Woods plot. The documented vascular plant species found in the entire ESGR can be found at https://sites.lsa.umich.edu/esgr/data-resources/biodiversity-of-the-esgr/vascular-plants/.

HUMAN USE AND DISTURBANCE

Historical reconstructions of pre-colonization vegetation suggest that the ESGR contained black oak barren, mixed oak forest, mixed hardwood swamp, and wet prairie (Comer et al., 1995). The plot was most likely predominately a black oak barren with nearby mixed oak forest and wet prairie (Figure 7). Black oak barren is a fire-dependent community (Kost et al., 2007). Thus, the ESGR is likely to have had a history of pre-settlement fire, probably from Native American burning (Abrams and Nowacki, 2008).

After European colonization the ESGR consisted of cultivated fields, pastures, woodlots and wetlands. Based on 1938 interviews with farmers who had spent most of

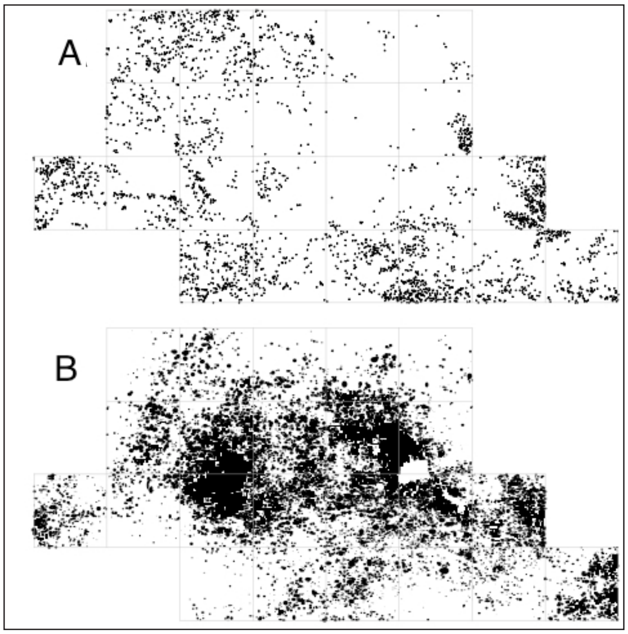

Figure 5: Map of two invasive shrubs in the plot. (A) Stem map of autumn olive *(Elaeagnus umbellata*) individuals in the plot. The species was introduced in public lands near the E.S. George Reserve by the Michigan Department of Natural Resources in the early 1990s. (B) Map of barberry shrubs (*Berberis thunbergii*) in the plot.

Figure 6: Photograph of the plot in an area of dense barberry (*Berberis thunbergii*) understory cover.

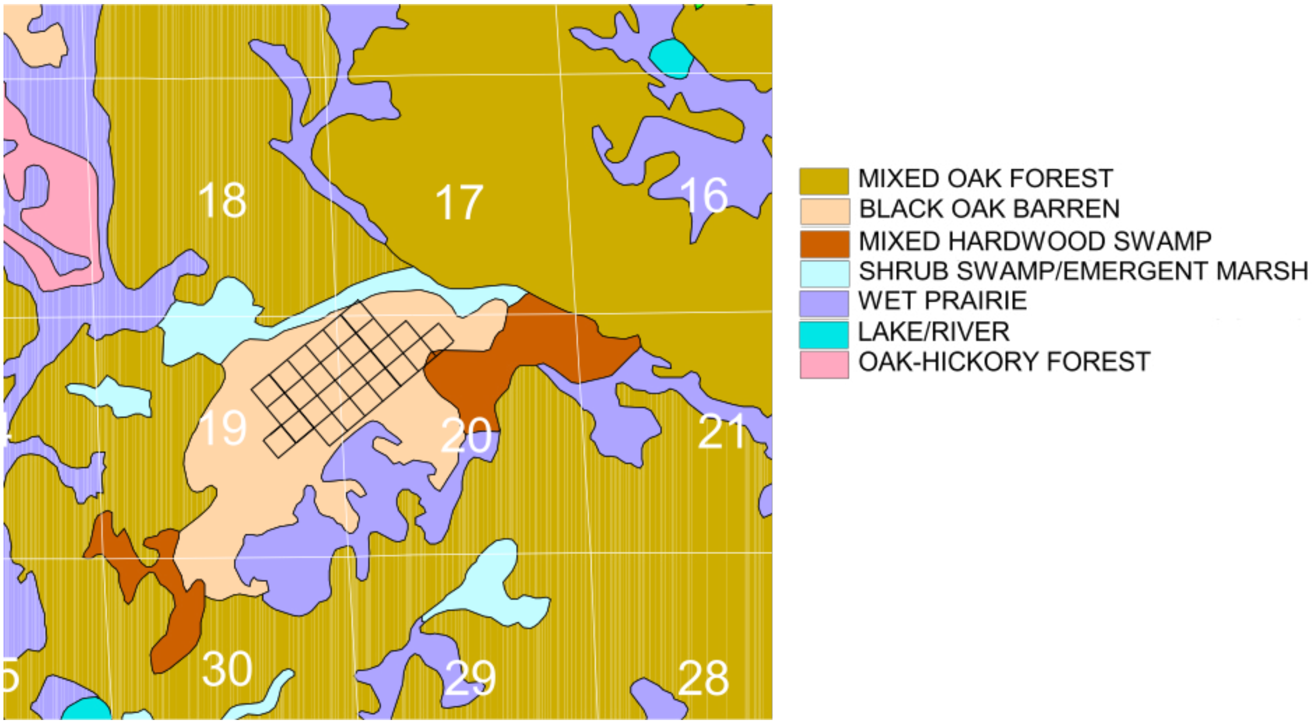

Figure 7: Approximate location of the Michigan Big Woods plot on a pre-settlement vegetation reconstruction map. The grid of black squares is the approximate location with each square 1 ha. The figure is modified from the Livingston county map in Comer et al. (1995).

their lives in the area, marshes and wooded areas were used for pastures and upland fields were cultivated (Cantrall, 1943). Pastures and cultivation were most intensive before 1900 (Cantrall, 1943). The area of the plot with its steeper topography was probably unfit for cultivation, and thus was probably used as a pastured woodlot. However, it was probably abandoned relatively early, and by 1940 there was already a closed canopy forest in area that is now the plot (Figure 8). Scars of land use exist within the plot, including an old, now buried, barbed wire fence, an old roll of barbed wire and, indicating more recent activities, a large number of shotgun cartridges. Unpublished student work indicates the headstamps of the shotgun shells were manufactured between 1898 and 1932 (Williams et al., 2008).

In 1927-1928 Detroit industrialist Edwin S. George purchased eleven contiguous farms and fenced (2.3 m height) them as a game preserve. In 1930 he donated the land to the University of Michigan Museum of Zoology with the provision that he could live there until his death. Following his death in 1940 the University established the Edwin S. George Reserve. Subsequently, it was administered by the Museum of Zoology and then the Department of Ecology and Evolutionary Biology as an area for research, education, and conservation.

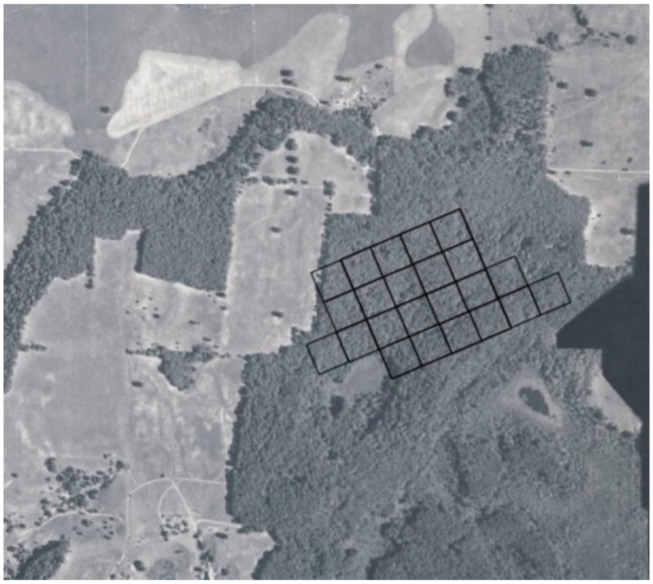

Figure 8: 1940 Aerial photograph of the part of the ES George Reserve where the Michigan Big Woods plot is located. The grid of black squares is the approximate location with each square 1 ha. This illustrates the closed canopy nature of the forest as of 1940.

FAUNA

The ESGR was the site of a long-running white-tailed deer (*Odocoileus virginianus*) demography study (McCullough, 1979). There is currently a 3.5 m fence around the reserve which maintains a resident deer herd. Once the original 2.3 m fence was completed in 1927, the reserve was stocked with six deer (McCullough, 1979). After the University of Michigan took over the ESGR, an annual deer census was started, which involved numerous volunteers. The first, in 1933, recorded 160 deer (Hickie, 1937), a surprisingly rapid rise in the population (McCullough, 1982). Based on this and the resulting effect on vegetation, ESGR managers decided that deer population control was necessary. The first deer cull was in 1937 and since then there have been periodic culls as deemed needed. The annual deer population size and number culled up to 1980 can be found in McCullough (1982) and McCullough (1979).

The deer drive censusing continued until at least 1980 (McCullough, 1982). Post-cull populations from 1933 to 1980 averaged 83 deer (16 km^{-2}). The dense autumn olive cover in the reserve now complicates the deer drive census, which has been discontinued, although the cull continues periodically. These culls take place in winter after the breeding season and target a set number of animals based on observations of deer browse and activity (Sorin, 2004). The number of animals targeted is generally between 20 and 30, but it can be as great as 100 in years when a dramatic population reduction is desired (Sorin, 2002, 2004). In 2008 the post-cull population was estimated at 82 deer using an aerial infrared sensor (Storm et al., 2011). Sorin (2002) speculated that the cull keeps the population at a rough equilibrium. We believe that this continues to present day with a high, though stable, deer population in the reserve.

Deer browse probably has a large effect on the vegetation on the ESGR. Personal observations from the 1970s to present (Vandermeer, pers. obs.) commonly report a very low understory biomass, usually attributed to the effect of deer browse. This deer browse likely affects tree recruitment dynamics, as seedlings differ in their palatability to deer. Further deer probably contribute to the spread of autumn olive on the reserve, since deer heavily browse autumn olive's potential competitors but rarely eat it.

In addition to the resident deer herd, the reserve supports a diverse faunal community. In Harmon's (2016) short camera survey white-tailed deer, fox squirrels, coyotes, and wild turkey were recorded at high densities (Table 3). Coyotes may help to limit the ESGR's deer population by predation on fawns. Through the 1970s there were no reported sightings of coyotes on the ESGR (Vandermeer pers. comm.), but they are now quite common, as evidenced by frequent sightings, vocalizations, and fecal samples. The fox squirrel is a major disperser of acorns and hickory nuts and likely an important component to dispersal in the current forest, but perhaps less important as succession favors red maple and black cherry over oaks. Similarly, wild turkeys may decline with this change. However, wild turkeys have been suggested as seed dispersers of Japanese barberry (Ehrenfeld, 1997) and nest success increases with the thorny, dense vegetation of autumn olive, Japanese barberry, and multiflora rose (Fuller et al., 2013). Species lists for selected animal taxa can be found at https://sites.lsa.umich.edu/esgr/data-resources/biodiversity-of-the-esgr/.

RESEARCH AT ESGR

The ESGR has been a continuously active research site of the University of Michigan since the 1930s. In addition to work at the Big Woods research plot and studies of deer herd (McCullough, 1979), there are decades-long studies of turtle demography (Congdon et al., 1994), amphibian communities (Werner et al., 2007), ant communities (Talbot, 2012; Yitbarek et al., 2011; Li et al., 2017), and old field succession (Evans, 1975). Recent published studies have emphasized the role of invasive plants at the reserve (Bonilla and Pringle, 2015; Brym et al., 2011; Brym et al., 2014; Li et al., 2017). Jedlicka et al. (2004) examined the effect of gypsy moth defoliation on oak, red maple, and black cherry trees in the plot area, but before the plot was established. A complete list of the greater than 500 Masters and PhD theses, published books, and journal articles based on work done at the ESGR is archived at https://sites.lsa.umich.edu/esgr/publications-2/.

METHODS

Plot establishment and sampling

Free-standing vegetation

In establishing the original 12 ha plot in 2003, we placed stakes at the corners of each 100 m x 100 m quadrat. We sampled each quadrat in ten 100 m x10 m belt transects that ran the length of the quadrat. We recorded distance along transect, side of transect, and distance from transect, and later transformed these into a global plot coordinate system. We measured free-standing woody vegetation (trees and shrubs) at 1.4 m above the ground, with a minimum tree diameter of 3.2 cm (10 cm circumference at breast height) and marked all stems with numbered aluminum tags. Secondary stems on individual trees were excluded from the sample.

We resampled these 12 ha using the above methodology in 2008. And from 2008-2010 we expanded the plot to include an additional 11 ha to form the current plot boundaries. In 2014, we resampled all 23 ha. In the 2014 census we included trees $\geq$ 1 cm DBH and all secondary stems, following the ForestGEO sampling methods (Condit, 1998). The irregular plot boundaries resulted from avoiding adjacent swamps, fields, and a system of experimental ponds

(Figure 2). Each 100 x 100 m quadrat (hectare) is identified by unique alphabetic character(s).

Many oaks in the plot have morphology intermediate between northern pin (*Q. ellipsoidalis*), northern red (*Q. rubra*), and black (*Q. velutina*). Therefore, during the 2003 and 2008–2010 censuses oaks in the red oak section (*Q.* section Labatae) were recorded as black oak, with the understanding that there could be misidentifications or hybrids. During the 2014 census we made an attempt to classify the oaks within the red oak section. We classified individuals based on diagnostic characters (Barnes and Wagner, 2004; Voss, 1985; Voss and Reznicek, 2012) including bark texture, inner bark color and taste, glossiness of the leaf blade, and, if available, fraction of acorn covered by the cup. Individuals with intermediate characteristics between red oak species were classified as hybrids. Based on those characteristics we find the two hybrids *Q.* x *hawkinsiae* (*Q. rubra* x *Q. velutina*) and *Q.* x *palaeolithicola* (*Q. ellipsoidalis* x *Q. velutina*).

Lianas

From May to August of 2017 and 2018, 20 hectares of the previously established 23 hectare Michigan Big Woods plot were subgridded into 20 x 20 m cells using 50 cm lengths of rebar and labeled 1.25 cm diameter pvc pipe. All woody climbing stems (lianas) ≥1.0 cm diameter were measured at 1.3 m above the last rooting point (DBH), following the protocols established by Gerwing et al. (2006) and Schnitzer et al. (2008). All individuals were spray-painted at the point of measurement and numerically tagged with a circular metal tag, attached to the primary stem with plastic-coated metal wire. Stems were mapped using 5 x 5 m sub-cells to exact positions within their respective 20 x 20 m cell, and within each hectare. These geographic stem data were transformed to global plot data coordinates. Multiple-stemmed individuals were denoted by the primary stem number, followed by sequential letters, with only the primary stem tagged. Non-cylindrical (irregular) stems were measured using the largest and smallest stem diameters.

In addition to lianas ≥1 cm, climbing species richness of each 20 x 20 m cell was recorded as a complete species list, regardless of stem diameter, allowing calculation of frequencies of all climbing species across the 500 cells censused. The full species list includes both small-stemmed species and species represented by stems ≥1cm in DBH.

Species were identified in the field using morphological characteristics and taxonomic nomenclature provided by the Michigan Flora (Voss & Reznicek 2012). Ten individuals of *Vitis* ≥1.0 cm DBH were not identified to species in the field and were not collected. For analysis, these individuals were assumed to be *V. aestivalis*, due to its overwhelming presence in the plot. Two instances of *Vitis* individuals <1.0 cm were assigned similarly to *V. aestivalis*. Five individuals <1.0 cm of *Lathyrus* lacked floral characteristics, which are needed for species identification. These were assumed to be *L. venosus*, the most common species of *Lathyrus* at the ESGR.

Barberry

Japanese barberry (*Berberis thunbergii*) forms dense thickets in parts of the plot, so it could play an important role in forest dynamics. It was not included in the above surveys because it does not reach 1 cm at breast height. We designed a separate survey to map barberry cover. We surveyed barberry using the 100 m x10 m belt transects described in the "Free-standing vegetation" survey section above from June to August 2015. For each barberry individual, we recorded the distance along the transect, side of the transect, and distance from the transect. These were transformed into the global plot coordinate system. We measured the size of each individual by treating it as an ellipse and measured its largest radius and the radius orthogonal to that. For areas where the entire belt transect was full of barberry we recorded the distance along the transect where barberry cover started and ended.

Analysis and comparison to other ForestGEO plots

Here we provide some basic metrics on the diversity, stem, and basal density, changing canopy composition, and spatial patterning of the Big Woods plot. We make some comparisons to other ForestGEO plots in temperate broadleaf or mixed forests (Table 4). All analyses were conducted in R (R Core Team, 2017). Unless otherwise mentioned, analyses below are based on the 23 ha tree and shrub census not the 20 ha liana census. We provide some limited description of the liana census, but for a more complete treatment of the first 10 hectares of the liana census, see Bradtke (2018).

Stem-size distribution

We compared the stem-size distribution of trees and shrubs within the plot to the expectations under metabolic and demographic theory (Muller-Landau et al., 2006). Metabolic theory predicts a power law distribution of stem sizes, while equilibrium demographic theory predicts Weibull distribution of stem sizes if growth is a power function of diameter and mortality is constant (Muller-Landau et al., 2006). We used maximum likelihood inference to fit power and Weibull distributions to our observed stem size distribution (White et al., 2008; Lai et al., 2013). We compared these two fits with the Akaike information criterion (AIC). To visually compare these fits we binned stems in 1 cm DBH bins and plotted the observed and predicted stem size distributions. These analyses were conducted using R code from the supplementary material of Lai et al. (2013).

Diversity metrics

We calculate the Fisher's alpha for tree and shrubs in each hectare and report the mean and standard error (Table 5). We also report the number of species, genera, and families. This analysis we repeated for minimum tree size classes of 1 cm, 5 cm, 10 cm, 20 cm, 30 cm, and 60 cm DBH. This analysis follows Losos and Leigh (2004) for comparison to their results for other ForestGEO plots. We also calculate the plot-wide Shannon diversity to compare with those reported in the Supplementary Material of LaManna et al. (2017). These analyses were conducted in R using the vegan package (Oksansen et al., 2015).

Change in species composition of canopy over time

For the original 12 ha we calculated the number and fraction of individuals with a DBH ≥ 20 cm in each species. This DBH limit was used as an approximate lower limit of canopy trees. We calculated these values for each of the three censuses to ask how the species composition of the canopy changed over the 11 years between first and last tree censuses. For this analysis all oaks were grouped into one category and all hickories into another.

Spatial pattern

For the nine species with the most individuals in the 2014 census we calculated the pair correlation function (PCF) between a range of 0 and 40 m. The PCF, $g(r)$, is the density of individuals in a ring of radius r around a focal individual divided by the average density of those individuals (Velázquez et al., 2016). The PCF measures whether these individuals are clustered, $g(r) > 1$, or regularly spaced, $g(r) < 1$. We conducted this analysis separately on each of the nine most common species using main stems for the most recent census. We compared the PCF for each species to the expectation under spatial randomness. To calculate this expectation for each species we randomly placed the individuals within the plot boundaries 1000 times and then calculated the PCFs for these random placements. We then compared the actual PCF to the 95% confidence interval of the random placement PCFs. This analysis was conducted using the spatstat package in R (Baddeley et al., 2015).

The PCF is preferable to the more commonly used Ripley's K because it is non-cumulative (Perry et al., 2006; Velázquez at al., 2016). The value of a cumulative spatial harder to interpret the scale of spatial patterning compared to a non-cumulative statistic.

RESULTS

The most recent tree and shrub census included a total of 33,690 woody self-supporting individuals and 45,564 stems (Table 1) in the plot. The trees and shrubs represented 42 species, 32 genera, and 22 families. Collectively, the three most common species accounted for over 62% of individuals and over 64% of stems. The three species of oaks, their hybrids, *Carya glabra*, *Prunus serotina*, and *Acer rubrum* accounted for over 92% of the basal area in the plot. Other temperate broadleaf forests show a similar stem and basal dominance by a small number of species (Bourg et al., 2013; Butt et al., 2009; Johnson et al., 2018; Orwig et al., 2015; Wang et al., 2011). In the Michigan Big Woods plot, three invasive tree and shrub species accounted for 9% of individuals and 13% of stems, but only 0.3% of the basal area.

The 20 ha liana census included a total of 679 woody climbing individuals and 761 stems greater than 1 cm DBH (Table 2). Collectively, the 679 individuals represented seven species, six genera, and four families. The most common species, the summer grape (*Vitis aestivalis*), accounted for 83% of climber individuals, 80% of climber stems, and 90% of climber basal area. The largest liana in the plot was a 9.4 cm diameter individual of summer grape.

Stem and basal density

The trees and shrubs in the Michigan Big Woods plot represent an average basal area of 30.6 $m^2\ ha^{-1}$. This is lower than most other ForestGEO plots in temperate broadleaf forests (Table 4). Only Lilly Dickey Woods (Indiana, USA) has a slightly lower basal area, 30.3 $m^2\ ha^{-1}$, while some plots have a basal area over 40 $m^2\ ha^{-1}$. In 14 tropical ForestGEO plots, the average basal area is 35.2 $m^2\ ha^{-1}$ with a standard deviation of 5.3 $m^2\ ha^{-1}$ (Losos and Leigh, 2004), while the basal area in three temperate or Mediterranean climate evergreen, needleleaf ForestGEO plots ranges from 47.3 to 64.3 $m^2\ ha^{-1}$ (Gilbert et al. 2010; Lutz et al. 2012; Lutz et al., 2013).

The Michigan Big Woods plot has an average of 1981 tree and shrub stems and 1465 individuals per ha. These values both fall within the middle of the range of other comparable ForestGEO plots (Table 4). This stem density represents almost one-third the stem densities of tropical ForestGEO plots (Losos and Leigh, 2004). In 14 tropical forest plots the average stem density is 5824 ha^{-1} with a standard deviation of 2808 ha^{-1} (Losos and Leigh, 2004).

The stem and basal density for the Michigan Big Woods plot are very similar to those found in the Lilly Dickey Woods (Indiana, USA). That plot is also within a forest composed of an oak-hickory canopy, but with a sub-canopy dominated by non-oak shade-tolerant species (Johnson et al., 2018).

Barberry is unevenly distributed throughout the plot (Figure 5B). A total of 35% of the forest floor is covered by barberry, but varies dramatically from 3% on one hectare to 78% on another. There are two large, dense barberry stands, centered at approximately (-50,200) and (200,225). Both of these stands are in relatively wet portions of the plot.

Stem-size distribution

The Weibull distribution fits the stem-size distribution better than the power law distribution (ΔAIC = 9521, Figure 9). The Weibull distribution often does better than the power law distribution at fitting stem-size frequencies in both tropical and temperate forests (Muller-Landau et al., 2006; Wang et al., 2009). Even so, there were clear differences between the observed distribution and Weibull fit. The

Weibull fit predicted too many >70 cm DBH stems and too few 30-60 cm DBH stems. This is not surprising as the Weibull distribution is the expectation under demographic equilibrium (Muller-Landau et al., 2006) and this forest is not at that stage. The pronounced abundance of stems in the 30-60 cm DBH range suggests a better fit would be a polynomial or rotated sigmoidal distribution. This also has been observed in Asian temperate forests (Want et al., 2009; Lai et al., 2013).

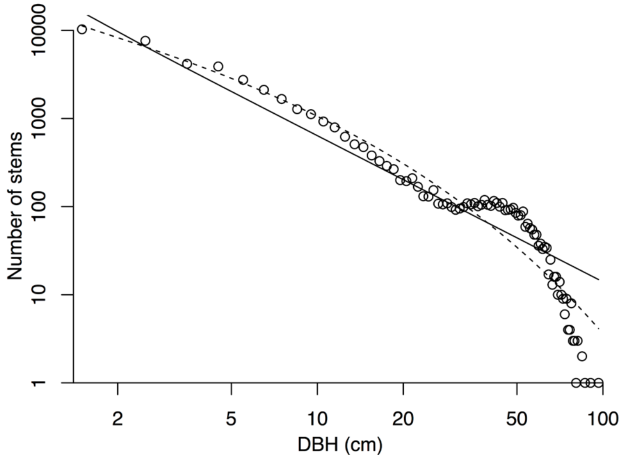

Figure 9: Stem-size distribution of all tree and shrub stems in the Michigan Big Woods plot. The data are binned by 1 cm diameter increments and bins with at least one individual are shown. Data from the plot are shown with circles. These data were fit to power and to Weibull distributions. Predicted values are shown in the solid line for the power distribution and dotted line for the Weibull distribution.

Diversity metrics

In the Michigan Big Woods plot, species diversity generally decreases with increasing minimum stem size (Table 5), a pattern also seen in other forest plots (Losos and Leigh, 2004; Gilbert et al., 2010). Plot-wide Shannon diversity was 2.1. This is comparable to values seen in other North American temperate broadleaf plots (Table 4). Species richness is much lower than in tropical forests and also lower than in Asian temperate forests (Table 4; LaManna et al. 2017; Losos and Leigh, 2004). Species richness is generally higher than that in European temperate forests and western North American evergreen, needleleaf forests (Table 4; LaManna et al., 2017).

Change in species composition of the tree canopy over time

The number of canopy (≥20 cm DBH) oaks decreased between the first and second, and again between the second and third censuses (Table 6). At the same time, the number of canopy black cherries, red maples, and hickories each increased in both periods. This resulted in a dramatic decrease in the fraction of oaks among canopy trees, although even in 2014 oaks still formed the majority of the canopy (Table 6). Thus, the plot is experiencing the same decline in canopy oaks seen in other oak-dominated forests in eastern North America (Fei et al., 2011; McEwan et al., 2011; Nowacki and Abrams, 2008). Within the plot, Allen et al. (2018) found that oak recruitment is negatively associated with proximity to canopy black cherries and red maples while black cherry and red maple recruitment is positively associated with proximity to a canopy oaks. Thus, as the red maples and black cherries continue to capture the canopy, oak recruitment will be further diminished.

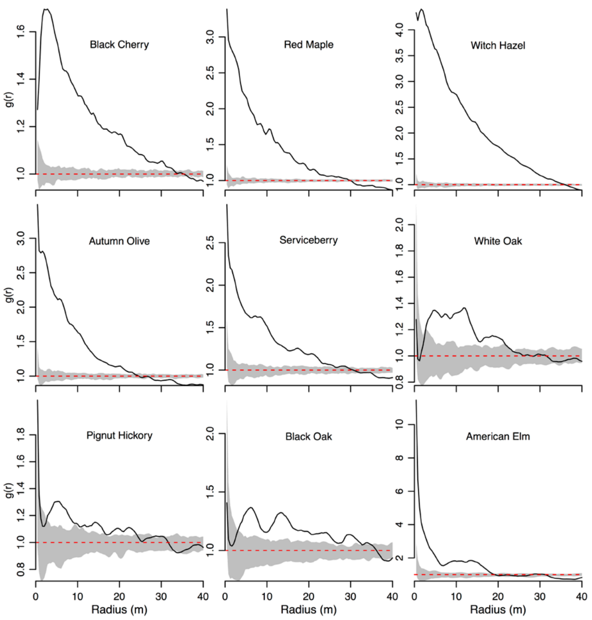

Figure 10: Pair correlation function (PCF) for each of the nine most common tree and shrub species. This includes only main stems alive during the 2014 census. The PCF, *g(r),* gives the density of conspecifics around the average focal individual in a ring of radius *r* divided by the average density of that species. Values greater than one indicate individuals are more aggregated at that scale and less than one more regularly spaced. In each graph the black line is the observed PCF and the gray interval is the 95% confidence intervals under spatial randomness.

Spatial pattern

Most species show strong spatial clustering at scales between 0 and 30 m (Figure 10). The three dominant understory species, black cherry, red maple, and witch-hazel, are particularly clustered with conspecifics and together form a clear mosaic (Figure 11). Oaks and hickories, on the other hand, are not nearly as aggregated. For these species, individuals are randomly distributed between 0 and 5 m, and then aggregated between 5 to 25 m. This is possibly because oaks and hickories within the plot are generally larger, and large trees have been observed to be less aggregated than small trees at smaller spatial scales (Lutz et al., 2013). However, it may represent the pattern of oak spatial distribution from the days in which the area was an oak barren.

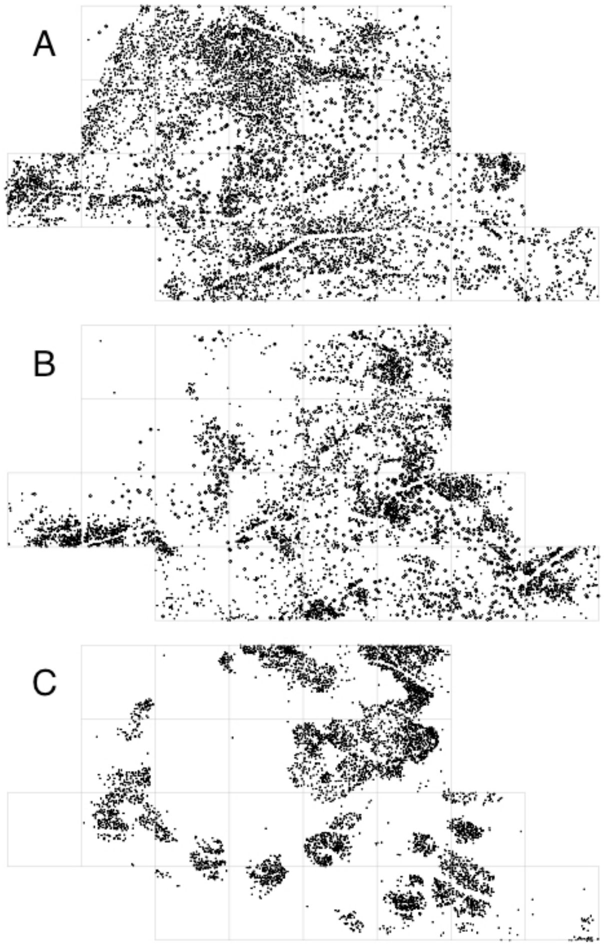

Figure 11: Stem map of the three most common tree and shrub species in the plot. For each subfigure, stems alive in the most recent census are shown. The gray squares are each 100 m x 100 m. The subfigures show the clustered strongly clustered pattern of these threes species and how they form a loose mosaic across the plot. (A) Black cherry. (B) Red maple. (C) Witch-hazel.

CONCLUSION

The Big Woods plot is an important addition to the ForestGEO global network of forest plots. It is one of only a few ForestGEO plots in North American broadleaf temperate forests and one of a few with a complete liana census. The plot has a long sampling history for trees and shrubs — three censuses over 11 years — compared to other temperate ForestGEO plots. Compared to other temperate ForestGEO plots it has similar stem density and species richness, but lower basal area. It is undergoing rapid succession as the oak canopy is replaced by more mesic species.

The general dynamics of this forest follow the qualitative pattern referred to by Abrams (1998) as the red maple paradox. In oak dominated forests across eastern North America a common pattern is for most of the very large trees to be oaks, while the advanced regeneration tend to be red maples, a situation that seems paradoxical since the overstory of a forest would seem eventually to emerge from the understory recruits. The most likely explanation for this situation is that Native American hunting and/or agriculture used fire as a management tool, effectively relegating the red maple individuals to swampy areas where they might escape the periodic fires. The ESGR plot reflects this interpretation well, with the addition of black cherry which we suppose was also in refuges near standing water prior to European settlement. Post fire dispersal modes correspond well with the current distribution of red maple and black cherry, in which the former has limited dispersal by samaras and is associated with wet areas of the plot; the latter bears bird dispersed fruits, more widely dispersed throughout the plot (Figure 11).

The future of the forest, at least in the near term (one century or less) is a dramatic reduction in oaks and hickories with rising codominance of, separated in space, red maple and black cherry. The long-term future may include further expansion of the currently small populations of American beech and sugar maple, as mesification takes hold.

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TABLE 1 - Number of individuals of each species in each size class in the 2014 tree and shrub census (23 ha) of Michigan Big Woods. Secondary stems are included in the stem number and basal area columns. Species not native to North America are indicated with an asterisk (*). Size classes follow Losos and Leigh (2004) and Gilbert et al. (2010) for comparison to other ForestGEO plots.

		Minimum stem diameter									
Species	Family	1 cm	2 cm	5 cm	10 cm	20 cm	30 cm	60 cm	Ind.	Stem	BA (m^2 ha^{-1})
Acer rubrum L. Red maple	Sapindaceae	337	2175	2452	1390	274	147	13	6788	6904	3.040
Acer saccharum Marshall Sugar maple	Sapindaceae	0	2	4	2	2	2	0	12	12	0.017
*Ailanthus altissima** (Mill.) Swingle Tree-of-heaven	Simaroubaceae	4	0	1	1	0	0	0	6	6	0.001
Amelanchier arborea (F. Michx) Fernald Serviceberry	Rosaceae	314	1172	809	51	1	0	0	2347	2839	0.217
Betula alleghaniensis Britton Yellow birch	Betulaceae	0	0	1	0	0	0	0	1	1	0.000
Carpinus caroliniana Walter Musclewood	Betulaceae	0	1	3	0	0	0	0	4	6	0.000
Carya cordiformis (Wang.) K. Koch Bitternut hickory	Juglandaceae	1	16	5	7	11	20	0	60	62	0.156
Carya glabra (Mill.) Sweet Pignut hickory	Juglandaceae	7	64	143	322	200	375	18	1129	1176	3.530
Carya ovata (Mill.) K. Koch Shagbark hickory	Juglandaceae	7	35	30	64	16	29	0	181	184	0.266
Cornus alternifolia L. f. Alternate-leaved dogwood	Cornaceae	7	0	0	0	0	0	0	7	11	0.000
Cornus amomum Mill. Silky dogwood	Cornaceae	5	2	0	0	0	0	0	7	8	0.000
Cornus florida L. Flowering dogwood	Cornaceae	12	134	206	9	0	0	0	361	384	0.046
Cornus racemosa Lam. Gray dogwood	Cornaceae	2	0	0	0	0	0	0	2	2	0.000
Corylus americana Walter American hazelnut	Betulaceae	16	5	0	0	0	0	0	21	38	0.000
*Elaeagnus umbellata** Thunb.	Elaeagnaceae	1865	1222	88	1	0	0	0	3176	5801	0.096

TABLE 1 CONTINUED

Autumn-olive											
Fagus grandifolia Ehrh. American beech	Fagaceae	5	19	21	17	5	3	0	70	70	0.047
Fraxinus americana L. White ash	Oleaceae	11	5	6	3	0	0	0	25	27	0.003
Hamamelis virginiana L. Witch-hazel	Hamamelidaceae	1143	3773	865	2	0	0	0	5783	13904	0.414
Ilex verticillata (L.) A. Gray Winterberry	Aquifoliaceae	1	3	0	0	0	0	0	4	26	0.000
Juglans nigra L. Black walnut	Juglandaceae	1	1	1	0	0	1	0	4	4	0.006
Juniperus communis L. Common juniper	Cupressaceae	1	2	3	0	0	0	0	6	7	0.001
Juniperus virginiana L. Eastern redcedar	Cupressaceae	0	1	2	6	1	0	0	10	10	0.009
Lindera benzoin (L.) Blume Spicebush	Lauraceae	68	24	0	0	0	0	0	92	141	0.001
*Lonicera sp** Honeysuckle	Caprifoliaceae	9	6	0	0	0	0	0	15	22	0.000
Malus sp Apple	Rosaceae	0	0	0	0	1	0	0	1	1	0.002
Ostrya virginiana (Mill.) K. Koch Hop hornbeam	Betulaceae	25	58	108	86	2	0	0	279	291	0.075
Populus grandidentata Michx. Big-tooth aspen	Salicaceae	2	2	4	6	5	16	0	35	35	0.116
Prunus serotina Ehrh. Black cherry	Rosaceae	561	1626	3453	2124	393	202	21	8380	8548	4.431
Prunus virginiana L. Chokecherry	Rosaceae	18	26	19	2	0	0	0	65	77	0.006
Pyrus sp.* Pear	Rosaceae	0	1	0	0	0	0	0	1	1	0.000
Quercus alba L. White oak	Fagaceae	14	68	63	133	194	579	92	1143	1167	5.961
Quercus rubra L. Red oak	Fagaceae	5	4	12	24	21	75	16	157	159	0.841
Quercus velutina Lam. Black oak	Fagaceae	4	25	25	22	77	698	103	954	962	6.580
Quercus x hawkinsiae Sudw.	Fagaceae	0	14	21	28	42	394	49	548	557	3.537

TABLE 1 CONTINUED

Autumn-olive										
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Malus sp Apple	Rosaceae	0	0	0	0	1	0	0	1	1	0.002
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Quercus x hawkinsiae Sudw.	Fagaceae	0	14	21	28	42	394	49	548	557	3.537

TABLE 2 - Number of individuals of each species in each size class in the 20 ha liana census in the Michigan Big Woods plot. Secondary stems are included in the total number of stems and basal area columns. Species non-native in North America are indicated with an asterisk (*).

		Minimum diameter							
Species	Family	1 cm	2 cm	3 cm	4 cm	5 cm	Ind.	Stem	BA (m^2 ha^{-1})
Celastrus orbiculatus * Thunb. Asian bittersweet	Celastraceae	2	0	0	0	0	2	2	0.00001
Parthenocissus quinquefolia (L.) Planch. Virginia creeper	Vitaceae	3	4	2	0	1	10	10	0.00036
*Rosa multiflora** Thunb. Multiflora rose	Rosaceae	65	1	0	0	0	66	101	0.00057
Rubus allegheniensis (Porter) Porter's Common blackberry	Rosaceae	3	0	0	0	0	3	3	0.00002
Toxicodendron radicans (L.) Kuntze Poison ivy	Anacardiaceae	3	5	2	1	7	18	20	0.00146
Vitis aestivalis Michx. Summer grape	Vitaceae	186	163	112	47	57	565	610	0.02568
Vitis riparia Michx. Riverbank grape	Vitaceae	9	4	2	0	0	15	15	0.00023
Total		271	177	118	48	65	679	761	0.02832

TABLE 3 - Number of captures of the most common large vertebrates over the E.S. George Reserve during a short camera trap study in October of 2016. These data are from an unpublished student project (Harmon, 2016). Fourteen cameras were deployed for between 4 and 6 days, for a total of 74 camera days.

Common name	Species	Number of captures	Captures per camera day
White-tailed deer	*Odocoileus virginiana*	1579	21.34
Fox squirrel	*Sciurus niger*	285	3.85
Coyote	*Canis latrans*	268	3.62
Wild turkey	*Meleagris gallopavo*	246	3.32
Raccoon	*Procyon lotor*	92	1.24
Opossum	*Didelphis virginiana*	35	0.47
Eastern cottontail	*Sylvilagus floridanus*	13	0.18
Red fox	*Vulpes vulpes*	3	0.04

TABLE 4 - Comparison of Michigan Big Woods plot to other temperate broadleaf or mixed ForestGEO plots. Values shown for free-standing vegetation. For the Michigan Big Woods plot these values represent only the 23-hectare tree and shrub census. If no reference is given plot information is from https://forestgeo.si.edu/sites-all.

Name	Latitude	Longitude	Stem (ha^{-1})	Ind (ha^{-1})	B.A. (m^2 ha^{-1})	Num. spp.	Shannon	<10 cm DBH ind. (ha^{-1})	≥50cm DBH ind. (ha^{-1})	References
Changbaishan	42.38 N	128.08 E	2365	1556	43.2	52		1135	67	Wang et al. (2011) Hao (2017)
Donlingshan	39.96 N	115.43 E	5164	2607		58				Liu et al. (2011)
Baotianman	33.49 N	111.94 E				118				Lai et al. (2013)
Zofin	48.66 N	14.71 E	2404	2343		11	0.1			LaManna et al. (2017)
Traunstein	47.94 N	12.67 E				29				
Speulderbos	52.25 N	5.70 E				15				
Wytham Woods	51.77 N	1.34 W	1128	906	33.3	23	1.4			Butt et al. (2009)
Harvard Forest	42.54 N	72.18 W	3103	2222	42.2	54	2.7	1566	21	Orwig et al. (2015)
SERC	38.89 N	76.56 W		1504	40.8	70	2.2			Driscoll et al. (2016) LaManna et al. (2017)
UMBC	39.25 N	76.71 W								
SCBI	38.89 N	78.15 W	1508	1166	34.1	64	2.6	841	57	Bourg et al. (2013)
Haliburton	45.29 N	78.64 W				30				
Big Woods	**42.46 N**	**84.00 W**	**1981**	**1465**	**30.6**	**42**	**2.1**	**1071**	**40**	
Lilly Dickey	39.24 N	86.22 W		1113	30.3	33	1.9			Johnson et al. (2018) LaManna et al. (2017)
Wabikon Lake	45.55 N	88.80 W		1484	32	36	2.1			Wang et al. (2011) LaManna et al. (2017)
Tyson Research	38.52 N	90.56 W		1500		42	2.4			LaManne et al. (2017)

TABLE 5 - Diversity and abundance metrics for the tree and shrub census of the Michigan Big Woods plot for individuals larger than six minimum diameter sizes. The values are number of stems (N), number of families (F), number of genera (G), number of species (S), and Fisher's alpha (〈). The mean and standard error of these values for each hectare are reported. The whole plot values are also reported. All data are for the most recent census and include secondary stems. Size classes and diversity metrics follow Losos and Leigh (2004) and Gilbert et al. (2010) for comparison to other ForestGEO plots.

DBH (cm)	Mean per hectare					Whole plot				
	N	F	G	S	α	N	F	G	S	α
≥ 1	1981.0 ±107.3	12.0 ± 0.4	14.3 ± 0.5	19.1 ± 0.6	2.9 ± 0.1	45564	22	32	42	4.6
≥ 5	786.5 ± 27.8	10.1 ± 0.4	11.7 ± 0.4	15.7 ± 0.4	2.8 ± 0.1	18089	16	23	30	3.5
≥ 10	398.5 ± 14.1	7.4 ± 0.3	8.6 ± 0.4	12 ± 0.3	2.3 ± 0.1	9166	15	20	26	3.3
≥ 20	190.3 ± 5.2	5.4 ± 0.2	5.8± 0.2	8.7 ± 0.3	1.9 ± 0.1	4377	10	14	19	2.6
≥ 30	129.0 ± 5.2	4.4 ± 0.2	4.5 ± 0.2	7.2 ± 0.3	1.7 ± 0.1	2967	8	10	15	2.1
≥ 60	13.7 ± 1.2	2.3 ± 0.2	2.3 ± 0.2	4 ± 0.2	2.2 ± 0.2	316	5	5	7	1.3

TABLE 6 - Number and proportion, in parentheses, of individuals > 20 cm DBH of four taxonomic groups over the three censuses. Here we analyzed only the original 12 ha of the plot, to compare the same area over the three censuses. Oak includes white oak, northern red oak, black oak, and red oak section hybrids. Hickory includes bitternut, shagbark, and pignut hickories. No other species accounted for more than 3% of individuals over 20cm DBH in any of the three censuses.

		2003	2008	2014
Oak	*Quercus* spp.	1368 (0.635)	1307 (0.595)	1229 (0.538)
Black cherry	*Prunus serotina*	276 (0.128)	321 (0.146)	370 (0.162)
Red maple	*Acer rubrum*	215 (0.100)	251 (0.114)	330 (0.144)
Hickory	*Carya* spp.	209 (0.097)	223 (0.102)	243 (0.106)
Total		2155 (1.000)	2195 (1.000)	2285 (1.000)

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