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# A decades-long case study: Understanding the effects of mesophication on the forest community with emphasis on *Carya* spp. dynamics[1]

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**Abstract.** Lack of fire and increasingly wet conditions in eastern North America are thought to interact in a way that depresses the recruitment of fire-adapted species like *Quercus* and *Carya* while promoting the growth and recruitment of mesophytic species like *Acer*. This process, referred to as forest mesophication, has tended to focus on the consequences for *Quercus* with more limited attention on *Carya*. Additionally, forest mesophication has the potential to alter traditional forest community and topographic relationships as environmental conditions continue to shift. This study questioned if *Carya* populations have responded to forest mesophication over the last 38 yr. Also, this study questioned if long-term changes in forest composition maintained traditional aspect-species relationships in response to forest mesophication. In Athens County, Ohio, forest surveys of *Carya* and associated overstory, midstory, sapling, and seedling vegetation were conducted in 1983 and 2021. Survey results from 1983 and 2021 were analyzed to determine shifts in *Carya* population structure and shifts in forest community composition and diversity. *Carya* populations decreased by approximately 50% since the original 1983 survey across all species, topographic positions, and aspects. Current populations are composed of mostly large individuals with little evidence of recruitment over the last several decades. The midstory and sapling forest layers have experienced decreases in species diversity, mostly through increases in *Acer* and *Fagus grandifolia* Ehrh., and decreases in *Quercus* and *Carya*. Species compositions from the sapling and seeding layers retained aspect differences and reflected overstory species compositions. The midstory and overstory layers have experienced shifts in species composition over time with the midstory layer no longer retaining topographic and aspect relationships with species composition. Changes in forest composition may be trending towards a loss in topographic distinction in species composition for forest communities in the region. *Carya* populations appear unlikely to remain a significant portion of the forest community given the observed lack of recruitment into larger size classes past the sapling stage. Long-term changes in forest composition, due in large part to mesophication, are becoming evident and have the potential to drastically alter forest composition in the very near future without direct intervention.

Key words: climate change, fire ecology, forest structure, long-term analyses

In eastern North America, poor recruitment of *Quercus* and *Carya* in many forest types has been recognized for several decades (Larsen 1953, Lorimer 1984, Abrams 1992). Maintaining *Quercus* and *Carya* in various forest types is important to land managers, conservationists, and forest researchers due to the utilization of both groups for wood products and their critical role as a food and habitat resource for wildlife (Burns and Honkala 1990, Dhungel *et al.* 2023). Maintaining mature *Carya ovata* Mill. K.Koch and *Quercus alba* L. individuals is particularly important for conserving wildlife habitat; for example, with the endangered Indiana bat (*Myotis sodalis*) (Schroder *et al.* 2017). Understanding how and why forest types may be shifting is inherently difficult due to tree longevities. Therefore, long-term studies documenting species composition changes are crucial to determine the extent and severity of *Quercus* and *Carya* recruitment failure.

Forest mesophication is an observed phenomenon throughout much of eastern North America in which dominant xerophytes like *Quercus* and *Carya* are being replaced by mesophyte species in the forest understory. This process has largely contributed to a decline in *Quercus* and *Carya* recruitment. The leading hypotheses contributing to this phenomenon are described as an intensifying combination of forest fire suppression and increasingly wet conditions that creates a more favorable environment for shade-tolerant mesophytes (Nowacki

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and Abrams 2008). Forest survey reports from the early 1900s describe species like *Acer rubrum* L. and *Acer saccharum* Marsh. as occupying canopy status in cool, moist habitat conditions, and while seedlings from these species were present in all forest types, individuals reaching canopy status were rare in *Quercus*-dominated forest types due to reduced competitive ability under drier conditions (Green and Secrest 1909, Griggs 1914, Hawley and Hawes 1918). It was not until the mid-20th century that reports of traditionally *Quercus*-dominated landscapes being overtaken by *Acer* began to appear (Curtis and McIntosh 1951, Larsen 1953, Dix 1957, Monk 1961). These early studies attribute this change to forest succession and the development of a climax community, a prevailing idea of the time.

Research on the mesophication phenomenon in recent decades has attempted to uncover the ecological mechanisms contributing to the decline in *Quercus* and *Carya* regeneration. One possible theory proposes that *Quercus*-dominated communities resulted from past fire regimes and frequent disturbance (Lorimer 1984, Abrams 1992). For example, it was proposed that *Quercus rubra* L. recruitment was controlled by a myriad of factors alongside fire, including climate, other nonfire disturbances, and controlling competition among vigorous stump-sprouting species (Crow 1988). The consensus in recent decades is that forest fire suppression following frequent ignitions from humans in the postsettlement era was the primary driver behind the mesophication process, and reintroducing fire will increase *Quercus* recruitment (Iverson *et al.* 2017, Alexander *et al.* 2021, Radcliffe *et al.* 2021). In short, Nowacki and Abrams (2008) and Alexander *et al.* (2021) explain that without fire, species like *A. rubrum* and *A. saccharum* regenerate and recruit to the canopy aggressively, leading to a buildup of leaf litter that retains moisture and burns cooler if and when fire occurs. This process leads to a positive feedback loop that can shift forest conditions away from those that provide a competitive advantage: fire-adapted, xerophytic species (Nowacki and Abrams 2008, Alexander *et al.* 2021). In addition, parts of eastern North America have become wetter over the last century in part due to climate change influencing precipitation and drought patterns (Ficklin *et al.* 2015). Increased precipitation and less frequent, less intense droughts likely contribute to those shifts in abiotic and biotic factors that create and sustain wetter forest understory conditions, to the detriment of *Quercus* and *Carya*. Thus, it is multiple factors that are contributing to the mesophication phenomenon (McEwan *et al.* 2011).

Given that large areas of forest with significant *Quercus* and *Carya* components have likely been subjected to the mesophication process for nearly 80 yr, the relationship between the forest community and topography may be shifting from classical assumptions. *Quercus* and *Carya* in the Midwest and Appalachian regions have traditionally been associated with ridgetop or southwest-facing aspects (topographic positions with increased radiation and lower soil moisture) and/or acidic, infertile soils (Muller 1982, Burns and Honkala 1990, Nowacki *et al.* 1990, McEwan *et al.* 2005, Radcliffe *et al.* 2020). It is under these conditions that *Quercus* and *Carya* recruitment would be expected to be robust. However, numerous studies over the last 40 yr have reported low numbers of *Quercus* and *Carya* recruitment under these conditions (Johnson 1979, Abrams 1992, McEwan *et al.* 2011, Goins *et al.* 2013). If fire exclusion and mesophication exert a stronger limitation on recruitment, then topographic positions traditionally advantageous to this group may not provide the competitive advantage they once did.

Given that mesophytic species have been well documented to be increasing in abundance throughout eastern deciduous forests, topographic position may now be less important to influencing community composition compared to earlier in the 20th century. Two long-term studies from the mid-20th century reported large increases in *Acer* seedlings throughout the forest understory (Weaver and Ashby 1971, Lorimer 1984). Contemporary long-term studies continue to identify shifts in the subcanopy tree abundances away from traditional topographic patterns. For example, xeric ridgetop communities in southeast Ohio have experienced increases in *A. rubrum* and *Fagus grandifolia* Ehrh. despite the drier habitat conditions (Palus *et al.* 2018, Radcliffe *et al.* 2020). Long-term research plots in the Missouri Ozarks also reported increases in understory *A. saccharum* densities, but this was specifically on the wetter, eastern-facing aspects (Olson *et al.* 2014). The increase in *A. saccharum* densities in the Missouri Ozarks may signal that ecological conditions are shifting in a way that gives a competitive edge to the species, despite not being a traditionally abundant species in the area (Nigh *et al.* 1985). Overall, forest mesophication may have the potential not only to alter tree recruitment patterns but also alter the relationship between topography and forest community composition.

While mesophication research has largely focused on the dynamic between *Quercus* and *Acer*, the *Carya* component of many forest types has largely been ignored. *Carya* in eastern North America often make up significant portions of the forest overstory in dry, upland forests, but can also have a presence in various other forest types (Burns and Honkala 1990). When describing forest compositional changes, *Carya* is often combined with *Quercus*. Treating *Quercus* and *Carya* as a single functional group may not be appropriate, as recent studies have demonstrated some key differences between *Quercus* and *Carya*. Subcanopy *Carya* individuals may have greater shade tolerance, a greater ability to persist in understories, and a more steady influx of young individuals compared to *Quercus* (Lefland *et al.* 2018; Pile Knapp *et al.* 2021). However, *Carya* is also experiencing reductions in understory presence throughout its range. Palus *et al.* (2018) found reductions in *Carya* canopy presence in upland habitats and generally, extremely low numbers of subcanopy individuals in southeast Ohio. As with general forest compositional changes, changes in *Carya* population structure can be determined using long-term data sets to better understand this important taxa. By grouping *Quercus* and *Carya* together to describe forest compositional changes, shifts in *Carya* population structures and patterns may be obscured by *Quercus*.

In 1983, two opposing *Quercus-Carya* forest stands, located on north- and south-facing aspects, were surveyed as part of a larger study on *Carya* demography (McCarthy and Wistendahl 1988). Part of this study included tagging adult *Carya* individuals and recording nearby trees within the overstory, midstory, sapling, and seedling layers (McCarthy and Wistendahl 1988). The 1983 study found that subcanopy forest layers were primarily composed of *A. saccharum*, *A. rubrum*, and *F. grandifolia*, which seemed most likely to eventually replace the overstory *Carya* individuals. Many of the tagged *Carya* individuals from the original study are still identifiable, and by revisiting these locations, long-term changes in forest structure and the impacts on *Carya*, in particular, can be quantified.

By revisiting the original study area, this research aimed to answer two main questions: (a) Do long-term changes in forest composition coincide with the projected outcomes of mesophication, and are traditional slope position-aspect species relationships still relevant? (b) How have the population structures of *Carya glabra* Mill., *C. ovata*, and *Carya tomentosa* Sarg. changed over the past 40 yr? We predicted that changes to forest composition would reflect the outcomes of long-term mesophication in the subcanopy layers, while overstory compositions would remain stable. Also, traditional slope position aspect-species relationships would remain identifiable in the canopy and subcanopy forest layers. *Carya* populations were predicted to reflect maturing populations with most individuals present as large canopy individuals, and fewer individuals in the subcanopy layers, given the small amount of subcanopy *Carya* in the original 1983 survey.

**Methods.** The study used the original pair of opposing southwest- and northeast-facing aspects from McCarthy and Wistendahl (1988) located within the approximately 1,110-ha Waterloo Wildlife Area (39.351°, −82.266°) in Athens County, Ohio. Together the total sampled area was approximately 12 ha. The southwest-facing aspect experienced prescribed burns in 2019 and 2021, while the northeast-facing aspect experienced a single low-level burn in 2016 (Ohio Department of Natural Resources [ODNR], K. Ritchie, personal communication). In all cases, the fires were reported to burn poorly with limited efficacy (ODNR, personal communication). These are the only prescribed burns at the sites dating back to the mid-1950s, although prior burns may have occurred in the 1930s and 1940s (ODNR, personal communication). Waterloo Wildlife Area is owned by the State of Ohio and has been managed by the ODNR for recreation and hunting since the 1940s, with previous land uses including agriculture, livestock grazing, and selective timber harvesting (ODNR 2022). The forested area is currently composed of interconnected *Quercus-Carya* and *Acer-Fagus* forest communities (ODNR 2022). Waterloo Wildlife Area occurs in the Unglaciated Allegheny Plateau Region. Elevation at the site ranges from 220 m to 310 m above sea level with soils typed as Typic Hapludalfs and silty loam Dystrudepts (Deforest and Snell 2020). The mean annual temperature in the immediate area is 11.4°C, and the mean annual precipitation is 114 mm.

FIELD METHODS. In summer 2021, all adult *Carya* individuals with a diameter at breast height (DBH) $\geq$ 10 cm were located and identified to species. Slope position, aspect, DBH, and, if possible, any remaining identification tags from the original 1983 survey were recorded for each individual. The recorded *Carya* individuals were then used as the plot centers for sampling nearby overstory, midstory, sapling, and seedling individuals. Ten randomly placed plots were also established on each slope, with representation along the slope gradient, to determine forest composition at points not directly adjacent to mature *Carya* trees. This was done to ensure that forest compositions around *Carya* trees were representative of the larger sampling unit. Each experimental and control plot was divided into quarters and oriented in the same method as McCarthy and Wistendahl (1988), with the two plot axes being parallel and perpendicular to the slope gradient. Within each quarter, the nearest overstory and midstory trees were identified to species, DBH measured, and distance to plot center recorded. Per the original survey, overstory trees were defined as those with a DBH $\geq$ 10 cm, and midstory trees were defined as those with a DBH $\geq$ 2.5 cm and $<$ 10 cm (McCarthy and Wistendahl 1988).

Nested circular plots for all experimental and control plots were established 3 m from the plot center in one randomly selected quarter of each plot to record sapling and seedling compositions (circular plot sizes of 25 $m^2$ and 1 $m^2$, respectively). Overall, 52 *Carya* were identified with plots established on the south-facing aspect, 32 on the north-facing aspect, and 10 control plots on each aspect for a total of 104 plots. Saplings were classified as any individual with a DBH $\leq$ 2.5 cm and height $\geq$ 30 cm, and seedlings were classified as any individual with a height $<$ 30 cm. Within each nested subplot, saplings and seedlings were identified by species and tallied. For seedlings only, *Quercus* was grouped into its respective subgenera, the white oaks (*Quercus* subg. *Quercus*) and the red oaks (*Quercus* subg. *Erythrobalanus*) due to leaf and bud immaturity (Gleason and Cronquist 1991).

Microenvironmental characteristics were recorded within each 1-$m^2$ seedling plot. The measured variables were those with the potential to influence seedling establishment and included slope percent, aspect, canopy cover, soil moisture, soil pH, and soil cover class. Canopy cover was determined using a convex spherical densiometer (Forestry Suppliers, Jackson, MS), and soil moisture was measured with a HydroSense$^{TM}$ water content reflectometer (Campbell Scientific, Logan, UT). To determine soil pH, field-fresh A-horizon soil samples were sieved through a 2.0-mm sieve to homogenize each sample. Sieved soils were then used to make a 1:1 soil and water mixture from which pH was measured using an Oakton EcoTestr pH meter (Environmental Express, Charleston, SC). Soil cover classes were determined by the percentage of leaf litter, bare mineral soil, herbaceous vegetation, and coarse woody debris located in the plot.

DATA ANALYSIS. All statistical analyses were completed using the statistical software R v. 4.4.4 (R Core Team 2021). To address how species diversity has changed and how the impact of mesophication has affected species diversity, we calculated Shannon's diversity index (H′) and species richness (S) from the R package vegan (Oksanen *et al.* 2020). In the overstory and midstory layers, species diversity was calculated for both the 1983 and 2021 surveys and by both aspects. In the sapling and seedling layers, only 2021 data were used, as seedling and sapling data from 1983 are not available. Seedling and sapling diversity was calculated separately for each aspect as well as for those plots located under *Carya* and the randomly placed control plots. Differences in Shannon's diversity index and species richness were tested via the Kruskal-Wallis test. When statistical differences were detected, Dunn's post-hoc test was used for pair-wise comparisons. Each recorded environmental variable in the seedling and sapling forest layers was compared by aspect for significant differences via a two-sample *t* test if all required assumptions were satisfied (incline); otherwise the alternative Welch two-sample *t* test (canopy cover, pH) or Wilcoxon signed-rank test (soil moisture, soil cover class) were utilized.

To visualize differences in species composition within each forest layer, nonmetric multidimensional scaling (NMDS) was used. For the overstory and understory layers, species compositions were compared by aspect and sampling year. Sapling and seedling species compositions for 2021 were compared by aspect and control plots. First, dissimilarity hemi-matrices were created for each forest layer and plot type, respectively, to visualize potential differences in species composition. Each dissimilarity hemi-matrix was created using chord distance from the "metaMDS" function from the R package vegan (Oksanen *et al.* 2020). Chord distance was selected as it can analyze species abundances for which zeroes in the data are common and meaningful, as absence of species in a

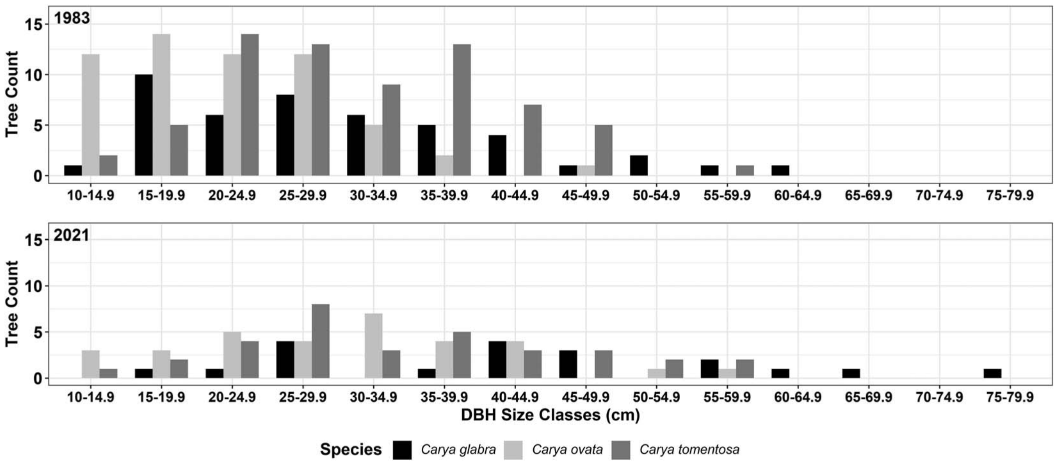

FIG. 1. Overstory *Carya* population survey by species and survey year broken down in 5-cm DBH size classes. DBH = diameter at breast height.

plot may have a potential ecological implication. Nonmetric multidimensional scaling was then used to visualize species compositions at each forest layer using three dimensions and 75 iterations with a random initial starting point. To detect significant differences ($P < 0.05$) in species composition by plot type, pairwise permutation multivariate ANOVA (MANOVA) was applied from the R package RVaideMemoire (Hervé 2021).

To address how *Carya* population structure has changed over 38 yr, survey counts from 1983 and 2021 were broken down by species, slope position, and aspect to identify potential patterns of change in population structure. The DBH distributions for each *Carya* species were compared with the Kolmogorov-Smirnov two-sample test to determine potential statistical differences in population size distributions. A Bonferroni correction was applied with determining significance when comparing all possible combinations of species-specific DBH distributions from the 2021 *Carya* survey ($\alpha = 0.017$). A Kolmogorov-Smirnov two-sample test was also used to compare the difference in total *Carya* DBH distributions between the 1983 and 2021 surveys.

**Results.** Overstory *Carya* individuals were represented by three species at the site, *C. ovata*, *C. glabra*, and *C. tomentosa*. A total of 84 overstory individuals were recorded across both aspects, compared to a total of 172 in the 1983 survey. This is a 51% reduction in overstory *Carya* (Fig. 1; Table 1), which also resulted in a 23% decrease in *Carya* basal area. There was not a discernible trend in mortality when analyzed by aspect, slope position, or species (Table 1). A pairwise comparison of the 2021 survey DBH distributions among the three species using the Kolmogorov-Smirnov test found a significant difference between *C. ovata* and *C. glabra* ($P = 0.01$). This differs from the 1983 survey results in which DBH distributions for *C. ovata* were significantly different from *C. glabra* ($P = 0.01$) and *C.*

Table 1. Census totals and change in *Carya* population size broken down by species, slope position, and aspect.

| Year | Species | Count | Change | Slope Position | Count | Change | Aspect | Count | Change |
|---|---|---|---|---|---|---|---|---|---|
| 1983 | *Carya glabra* | 45 | | Upper | 97 | | North | 62 | |
| | *Carya ovata* | 58 | | Middle | 61 | | South | 110 | |
| | *Carya tomentosa* | 69 | | Lower | 14 | | | | |
| | Total | 172 | | | | | | | |
| 2021 | *Carya glabra* | 19 | −58% | Upper | 41 | −58% | North | 32 | −48% |
| | *Carya ovata* | 32 | −45% | Middle | 36 | −41% | South | 52 | −53% |
| | *Carya tomentosa* | 33 | −52% | Lower | 7 | −50% | | | |
| Total | | 84 | −51% | | | | | | |

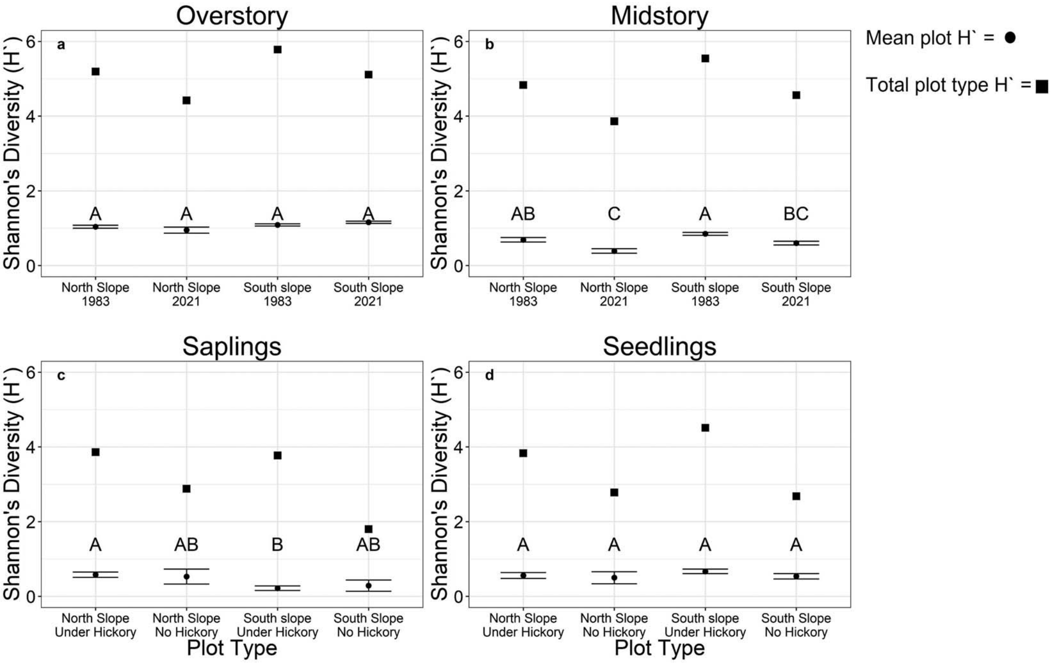

FIG. 2. Comparison of Shannon's diversity index (H′) by plot type for the overstory (a), midstory (b), sapling (c), and seedling (d) forest layers. Statistical differences via the Dunn's test in mean H′ (circle symbol) do not share a letter. Square symbols represent the overall H′ for that plot type.

*tomentosa* ($P < 0.001$). The *Carya* DBH distributions including all species between 1983 and 2021 were also significantly different ($P < 0.01$). The overall pattern in *Carya* population structure is dominated by mortality in most size classes, and there is little evidence of *Carya* saplings recruiting into smaller overstory size classes.

OVERSTORY DIVERSITY AND COMPOSITION. Overstory results from the Kruskal-Wallis test of Shannon's diversity index values (H′) for aspect and year indicated no statistical difference in mean overstory diversity per sampling plot, even though total diversity decreased slightly in 2021 (Fig. 2a). A similar pattern was recorded for species richness (S) (Fig. 3a). Both *A. saccharum* and *F. grandifolia* have increased in proportion (15% to 26%, and 6% to 14% of the overstory, respectively), while *Carya* have decreased in proportion (19% to 13% of the overstory) (Fig. 3a). *Quercus* populations appear mostly stable, with a slight increase in proportion on the northern aspect compared to 1983 (26% to 27% of the overstory) (Fig. 3a). The loss of several species from the overstory layer, including *Fraxinus americana* L., *Cornus florida* L., *Sassafras albidum* Nutt. Nees, *Ulmus americana* L., and *U. rubra* Muhl., likely contributed to small shifts in species diversity, as this group made up only a small portion of the overstory community. Results from the NMDS and accompanying pairwise permutation MANOVA indicated significant differences ($P < 0.05$) in species composition by both aspect and survey year (Fig. 4a).

MIDSTORY DIVERSITY AND COMPOSITION. Decreases in H′ were the most prominent in the midstory forest layer. Mean H′ and S were not statistically different between aspects in 1983 and 2021, respectively. However, mean H′ and S for 2021 were also significantly lower than the 1983 values (Figs. 2b, 3b). The decrease in H′ is due to a large combined proportional increase in *A. saccharum* and *F. grandifolia* (41% to 86%), making up the vast majority of the midstory layer (Fig. 3b). The small *Carya* components on each aspect from 1983 have been nearly lost. The midstory *Quercus* component on the southern aspect has remained relatively stable but is made up almost entirely by *Quercus montana* Willd. (Fig. 3b). The NMDS also indicated that midstory species compositions have shifted since 1983 (Fig. 4b). The 1983 species compositions were also significantly different

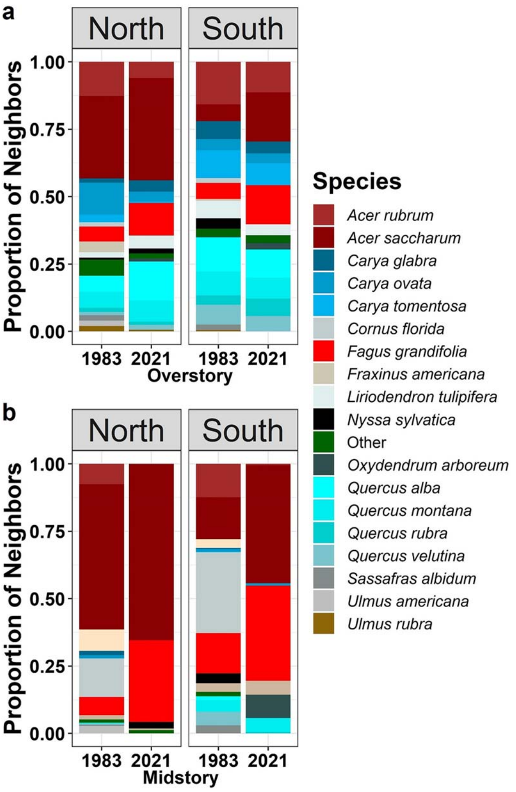

FIG. 3. Change in overstory (a) and midstory (b) species compositions from 1983 to 2021 shown as the proportion of species recorded from surveys. "Others" includes species with a survey count less than five at all survey periods and aspects (*Acer saccharinum*, *Aesculus flava* Sol., *Carpinus caroliniana* Walter, *Carya cordiformis* Wangenh. K. Koch, *Fraxinus pennsylvanica* Marsh., *Juglans nigra* L., *Pinus rigida* Mill., *Populus grandidentata* Michaux, *Prunus serotina* Ehrh., *Quercus acutissima* Carruth., *Robinia pseudoacacia* L.).

by aspect ($P < 0.001$). While no statistical differences were found between aspects in the 2021 survey ($P = 0.06$), this likely indicates that ecological differences in species composition may continue to exist in this forest layer.

SAPLING DIVERSITY AND COMPOSITION (2021 ONLY). Sapling H′ showed a similar trend to the midstory layer with a significant difference in both H′ and S between the north and south aspects for plots located under a *Carya* individual (Figs. 2c, 5). No significant differences in H′ or S were found between plots located under and away from a canopy *Carya* on their respective aspects or between plots located away from a canopy *Carya*. Sapling species richness largely reflected the current overstory composition, with the exception of *F. americana*, which is no longer present in the overstory (2% of overstory in 1983 *vs.* 0% in 2021) due to *Agrilus planipennis* (Fig. 5a). The NMDS indicated a significant difference in sapling species composition by aspect in plots located under canopy *Carya* individuals ($P = 0.01$; Fig. 6a). However, species compositions were not significantly different for plots under and away from canopy *Carya* on the same slope aspect. Species composition in plots located away from canopy *Carya* also did not differ significantly by aspect (Fig. 6a). The only environmental variables to show a significant difference by aspect were canopy cover ($t = 3.16$, d.f. $= 81.58$, $P = .002$, south $= 84 \pm 1\%$, north $= 89 \pm 1\%$), and soil moisture ($W = 394$, $P < 0.001$, south $= 10 \pm 0.3\%$, north $= 12 \pm 0.6\%$). Other environmental variables like pH (south pH $= 5.2$, north pH $= 5.3$) were not found to differ by aspect. The NMDS plot showed the northern aspect plots generally had higher canopy cover, greater soil moisture, and a thicker O-horizon. The southern aspect generally had a greater amount of bare mineral soil (Fig. 6a).

SEEDLING DIVERSITY AND COMPOSITION (2021 ONLY). Despite overall H′ and S for the seedling plot types being slightly lower in plots located away from a canopy *Carya*, there were no statistical differences in H′ or S among plot types (Figs. 2d, 5b). However, seedling species composition appeared to have distinct differences by aspect. Southern-facing aspects were dominated by *Liriodendron tulipifera* L. (likely due to a recent burn), while north-facing aspects were dominated by *A. saccharum*, *A. rubrum*, and *F. grandifolia* seedlings (Fig. 5b). There were significant differences in species composition by aspect for the plots both underneath and away from adult *Carya* individuals (Fig. 6b). There was also a significant difference in species compositions between the south-facing aspects ($P = 0.049$) but not for north-facing aspects ($P = 0.57$).

**Discussion.** Over the last 38 yr, changes in tree species composition are evident in the overstory and midstory layers at this study site, with the midstory layer also experiencing a decline (36% decrease) in species diversity. These results are consistent with the long-term projections of mesophication as outlined by both Nowacki and Abrams (2008) and Alexander *et al.* (2021) in

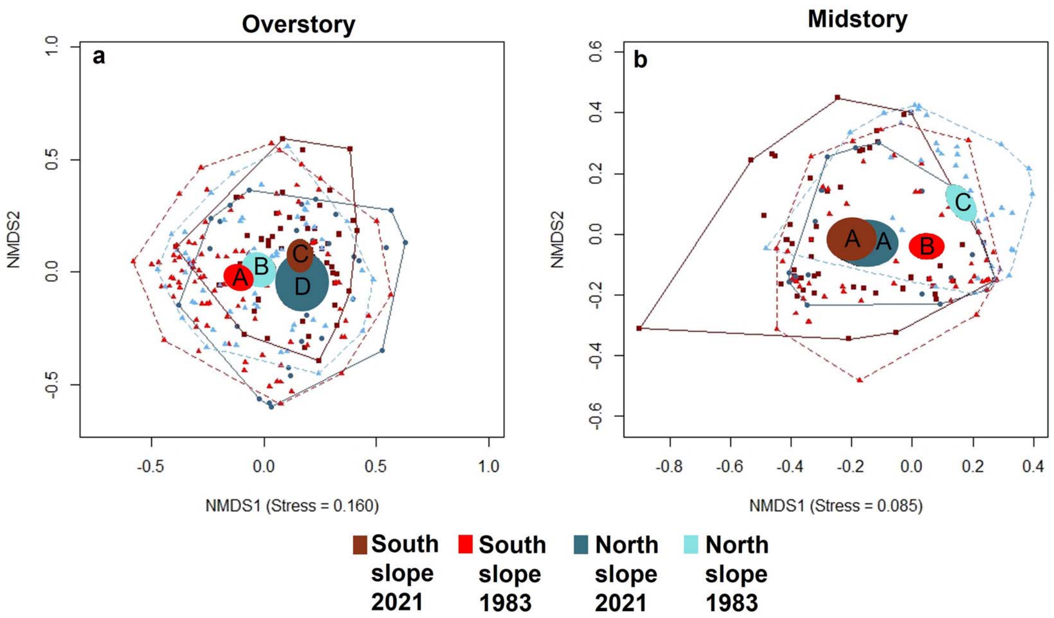

FIG. 4. Nonmetric multidimensional scaling results for overstory (a) and midstory (b) species compositions representing differences in community composition both by aspect and sampling period. Colored ovals are the 95% confidence interval of the true center representing the average composition. Ovals that do not share a letter are significantly different ($\alpha = 0.05$).

which community and landscape patterns appear to be changing. Furthermore, decades of fire suppression at this site are the likely culprit that initiated shifts in species composition. Such a change in the disturbance patterns resulting in less light reaching the forest canopy, combined with retaining more moisture-holding leaf litter (Brose *et al.* 2001, Nowacki and Abrams 2008, McEwan *et al.* 2011, Hanberry *et al.* 2020, Alexander *et al.* 2021) at the site, would have quickly shifted the competitive balance of understory individuals to genera like *Acer* and *Fagus*. These species likely built up in the understory regeneration layer in the roughly 40 yr between state ownership and the initial surveys in 1983 (McCarthy and Wistendahl 1988), and this has only accelerated given the overwhelming presence of *Acer* and *Fagus* in this most recent survey. The buildup of these species has been so overwhelming at this site that even burn attempts just prior to the most recent survey largely failed to show any signs of reversing current trends and it agrees with outcomes of other single-fire applications in other locations (Alexander *et al.* 2008, Brose *et al.* 2013).

Similarly, the lack of fire at these sites since ownership of Waterloo Wildlife Area transferred to Ohio in the mid-1940s (ODNR, personal communication) has likely resulted in most overstory *Carya* mortality occurring as single-tree mortality events. The gaps created by these single tree deaths have been largely overtaken by midstory *A. saccharum* and *F. grandifolia* individuals that already made up a large proportion of the forest midstory in 1983. This response of *A. saccharum* and *F. grandifolia* to single tree gap openings is consistent with what we know about these shade-tolerant species, in their ability to build up a regeneration layer, subsist for long periods of time in the understory, and respond quickly to canopy openings (Holzmueller *et al.* 2012, Allen *et al.* 2018, Moreau *et al.* 2019). This process has resulted in the opposing aspect community compositions becoming more similar over time as other species experience mortality and are replaced by the *A. saccharum* and *F. grandifolia* individuals that dominate the midstory layer.

The continuing presence of overstory *Quercus* and *Carya* on the south-facing aspect continues to indicate topographic-related community compositions. However, according to the midstory composition, these patterns appear unlikely to persist in the long term. Topographic distinctions are diminishing in the midstory layer of these stands with the dominance of *A. saccharum* and *F. grandifolia*. The inability for topographic position to hinder the

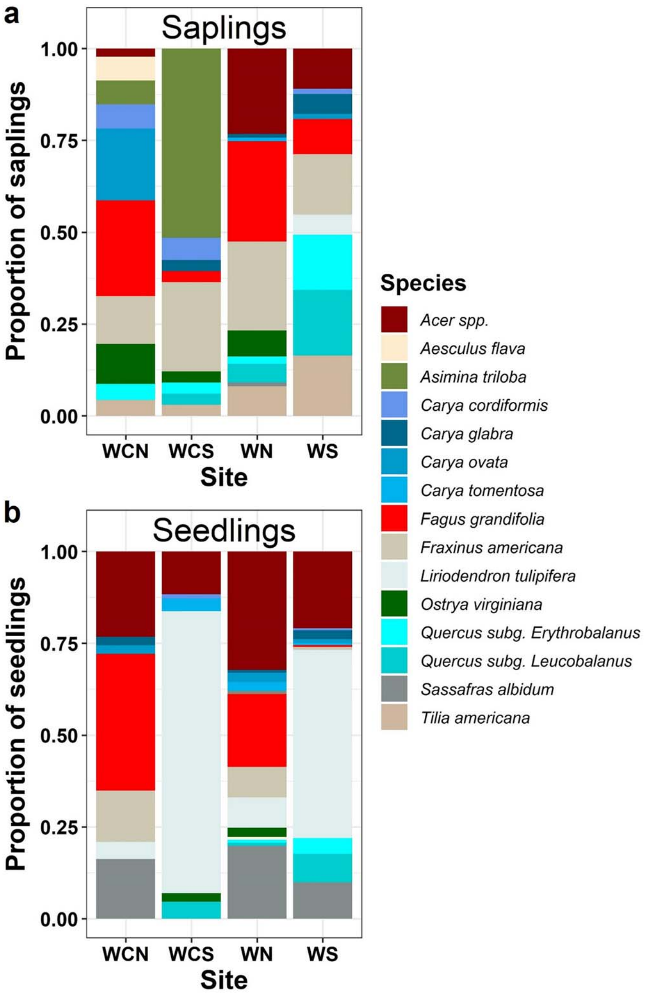

FIG. 5. Sapling (a) and seedling (b) species compositions from the 2021 survey as a proportion of the total number of saplings recorded. “WN” and WS” represent the north and south aspect sampling points located next to canopy *Carya* individuals, while “WCN” and “WCS” represent randomly placed control points along the respective aspect.

mesophication process has been documented elsewhere in southeast Ohio, most notably on dry sites that are converting to *A. rubrum* (Palus *et al.* 2018). Sites experiencing this major difference in overstory *vs.* midstory composition may be on the precipice of attaining a new stable state (*sensu* Nowacki and Abrams 2008), which leads to an overall change in forest type. Long-lived *Quercus* and *Carya* individuals in the overstory may obscure or draw out the effects of mesophication given their longevity, yet the possibility exists that within a generation, traditional landscape community patterns may be lost.

In the sapling layer, species compositions were more diverse than in the midstory, largely due to ongoing reproductive events by the overstory. Additionally, species composition and species diversity differences by aspect continue to exist in the saplings. The highest number of *Quercus* saplings were found under mature *Carya* individuals, which may be due to a combination of factors. Given the low-level surface burns on the south-facing aspect in recent years, this likely contributes to the disparities by aspect in *Quercus*, *Carya*, *Acer*, and *Fagus* saplings. Additionally, drier conditions associated with south-facing aspects and mycorrhizal associations shared among trees utilizing ectomycorrhizal fungi (Liang *et al.* 2021) may also contribute to this pattern. This combination of

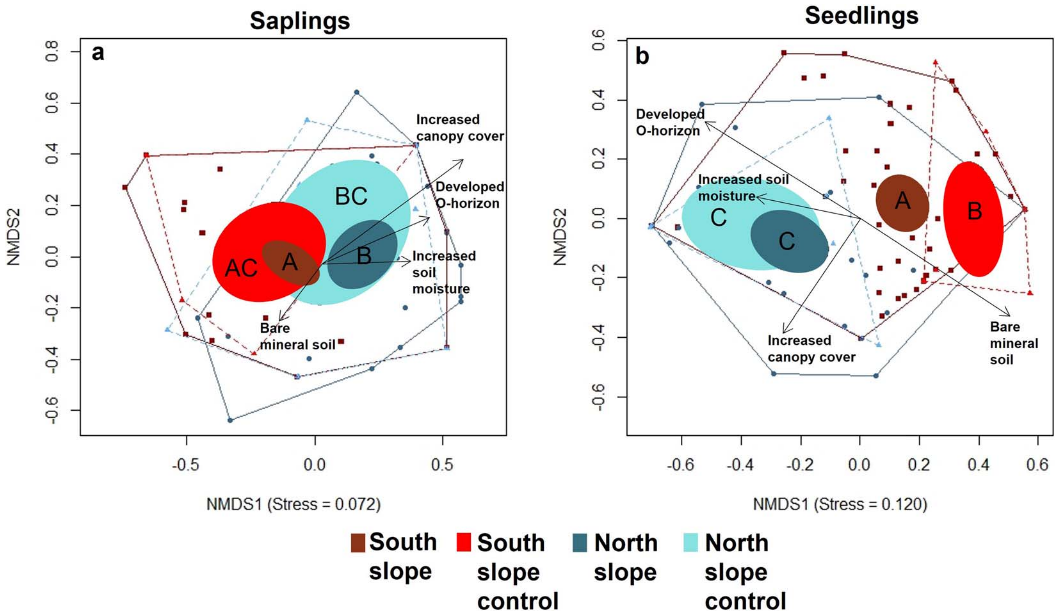

FIG. 6 Nonmetric multidimensional scaling results for sapling (a) and seedling (b) species composition differences by plots located under canopy *Carya* individuals and randomly placed controls plots by aspect. Colored ovals are the 95% confidence interval of the true center representing the average composition. Ovals that do not share a letter are significantly different ($\alpha = 0.05$). Labeled arrows represent environmental variables most influential to species composition.

environmental conditions and higher burn temperatures associated with leaf litter from xerophytic species may have resulted in conditions underneath large *Carya* individuals that are beneficial to *Quercus* recruitment (Kreye *et al.* 2018). It is unclear why *Carya* saplings did not show the same patterns as *Quercus* saplings, but this may be due to species-specific differences in reproduction or the balance between associated mycorrhizal fungi and proximity to large conspecifics (Liang *et al.* 2021). Despite the sapling layer not being as overwhelmed by *Acer* and *Fagus*, and continuing to show topographic differences compared to the midstory layer, a potential bottleneck seems to be present in which only the most shade-tolerant species appear capable of growing out of the sapling stage and into the midstory layer.

Differences in seedling composition likely reflected year-to-year variations in tree reproduction and the short-term effects of the single low-intensity 2019 prescribed fire on the south-facing aspect. At the sampling time of summer 2021, leaf litter on this slope face was scant and closely associated with the large numbers of *L. tulipifera* seedlings present on the south-facing aspect, while *Acer* and *F. grandifolia* seedlings had greater proportions on the north-facing aspect with a thicker O-horizon. The larger proportions of *Acer* and *F. grandifolia* on the north-facing aspect are consistent with other nearby sites undergoing mesophication (Palus *et al.* 2018). However, the proportions of seedlings vary from the transition matrices and predictions made for the site by McCarthy and Wistendahl (1988). The dominance of *A. saccharum* over *A. rubrum*, and the dominance of *A. saccharum* in general for the seedling layer, were not predicted in the original study and may reflect the site becoming increasingly more mesic. Similarly, *F. grandifolia* was not predicted to make up as much of the seedling layer as it now does, and again may suggest the area is undergoing mesophication faster than originally predicted. Given the stochasticity of the seedling layer and the longevity of the mature canopy species, the long-term effects of mesophication may be difficult to detect in the seedling layer compared to sapling and/or midstory layers.

Mortality had the greatest impact on the overall *Carya* population structure, as more than half of the originally identified canopy individuals are no longer present. Species, slope position, and aspect appeared unimportant in influencing mortality. Additionally, other environmental factors like pH did not differ among aspects and were unimportant to mortality and species compositions. The similar rates of mortality at every aspect and slope position are concerning given that *Carya* should have the greatest competitive advantage on drier ridgetop and upper slope locations compared to other topographic positions (Burns and Honkala 1990). Additionally, the lack of species-specific mortality rates for the three observed species may suggest that *Carya* in the region is uniformly responding to the new succession trajectory caused by fire suppression. Despite the small sample size and spatial limitations of this study, the −52% (−1.35% per year) mortality over 38 yr is greater than in similar studies that included overstory *Carya* mortality in some form, which indicated a mortality rate of 1% per year or less (Clinton *et al.* 2003; Radcliffe *et al.* 2021). *Carya* mortality rates also appear to differ from those of *Quercus*. In Appalachia, *Carya* appears to have a lower mortality than individuals from *Quercus* subg. *Erythrobalanus* (∼52% over 25 yr), but higher than *Quercus* subg. *Quercus* (∼25% over 25 yr) (Greenberg *et al.* 2011, Pile Knapp *et al.* 2021). However, these differences may be highly contingent on site quality and local environmental conditions. More research focused on *Carya* may help determine if the mortality rate of this study is unique to the site, or more typical of long-term *Carya* population dynamics.

In its current state, there are no signs of recruitment among all three *Carya* species. Hence, it appears unlikely that a meaningful *Carya* component will be sustained in this forest community without significant intervention. No midstory individuals were observed in sample plots, and anecdotally, only two midstory *Carya* individuals were observed throughout the entirety of the sample area. Given the lack of data on *Carya* regeneration in regard to mesophication, similar scenarios may be present in other locations. Despite mortality obscuring most of the population structure changes in individuals greater than 10 cm DBH, several trends can still be observed. As with the midstory layer, the two smallest overstory size classes show large reductions since the original survey, which agrees with the long-term outcomes of recruitment failure and population decline. Current differences in population structure by species may be explained by their representation in certain size classes compared to the size classes in which most individuals were grouped in the original survey. Overall, while mortality dominates the changes in population structures at this site, a trend toward minimal recruitment supports the impacts of forest mesophication on *Carya*.

**Conclusions.** Primarily this research aimed to determine if long-term changes in forest composition and diversity resembled the long-term outlooks of forest mesophication and if traditional slope-position-aspect-species relationships continued to exist. A trend of community composition being dominated by mesophytic species was most prominent in the midstory forest layer, where two species (*A. saccharum* and *F. grandifolia*) made up an overwhelming majority of the individuals. Once-prominent community differences based on slope position and aspect no longer exist. This trend was beginning to be observed in the overstory layer through increases in these two mesophytic species and decreases in *Carya*. Sapling and seedling layers still maintain some semblance of overstory species compositions and general topographic patterns due to ongoing reproductive events, but appear unable to recruit. This research also aimed to determine how *Carya* population structures have changed over a 38-yr period. While the 51% overall mortality of overstory *Carya* obscured possible trends in population, a noticeable drop-off in individuals associated with the smallest overstory size classes reflects a failure in *Carya* to recruit from the midstory to the overstory.

The long-term nature of the study and the ability to observe compositional and species diversity shifts over long periods of time is valuable to understanding how mesophication is directly impacting forest structure and species-specific topographic relationships. The drastic increase of *A. saccharum* and *F. grandifolia* in the forest midstory is a cause for concern. Sampling plots 38 yr ago contained a diverse array of species in the midstory. The midstory now is almost entirely composed of two species. Even though the sapling and seedling layers of the forest largely resembled the species composition of the overstory, a bottleneck is currently present that is preventing *Carya* and *Quercus* from leaving the sapling stage. At this point, only *A. saccharum* and *F. grandifolia* appear capable of ascending to eventual canopy status, both due to their dominance in the midstory and their being the only two species to increase in abundance in the overstory over the last 38 yr. Without intervention, these stands appear unable to maintain significant *Quercus* and *Carya* components on their own.

Given the length of time in which mesophication has likely been acting on the various subregions of eastern North American forests, long-term studies identifying how forests are changing will be critical to tailoring management strategies for the future. Identifying forests that have been reliably surveyed in the past that can be resurveyed will provide much-needed spatial replication for these types of long-term studies. The various ways in which future climate change will impact eastern North America adds another layer of complexity to long-term management of forests undergoing mesophication. Some regions that historically were drier and had frequent drought may return and bring back conditions in which *Quercus* and *Carya* regeneration thrived on their own (Iverson *et al.* 2019), yet regions becoming wetter in recent decades (Ficklin *et al.* 2015) will continue to experience mesophication. As seen in this study, mesophication may be impacting forest structure to the point where traditional landscape patterns for forest communities may disappear.

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