Forest Ecology and Management 430 (2018) 413–420

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Structural and compositional shifts in forests undergoing mesophication in the Wayne National Forest, southeastern Ohio

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ARTICLE INFO

Keywords:
Oak regeneration
Mesophication
Central Hardwood Region
Oak–hickory forests
Forest succession
Maple

ABSTRACT

Mesophication refers to the positive feedback cycle that occurs when fire suppression causes compositional shifts from oak (*Quercus* spp.) to other, primarily mesophytic, species. Because mesophytic species tend to be associated with relatively high-moisture sites, we sought to understand the extent to which physiographic and edaphic factors influence this process by examining forest successional dynamics over a period of 22 years. In 2016, we resampled a network of permanent plots first sampled in 1994 that were stratified across different landscape positions (e.g., north-facing slopes vs. south-facing slopes) in the Athens Unit of the Wayne National Forest in southeastern Ohio. By studying the changes in forest structure and composition relative to ecological land type, our results suggest little, if any, resistance to mesophication on sites with low moisture availability. For example, the relative density of red maple (*Acer rubrum*) large saplings on dry ridges increased 25%, while zero oaks were recorded in the large sapling layer on dry ridges in 2016. However, we did observe that American beech (*Fagus grandifolia*) is becoming substantially more abundant in the understory and may be more influential than red maple in determining the future species composition of these forests. American beech is expected to respond differently than red maple to future scenarios under predicted climate change, and is subject to a suite of novel pathogens that have broad implications for forest management in the region.

1. Introduction

The term mesophication was coined to describe the positive feedback cycle whereby oak (*Quercus*)-dominated forests slowly transition to forests dominated by mesophytic species (Nowacki and Abrams, 2008). This is primarily a result of the fire suppression policies of the early 20th century. Reducing the occurrence and intensity of fire enabled fire-intolerant species to establish in the understory, inhibiting the ability of fire-tolerant species to compete. Thick bark, deep rooting, vigorous resprouting, and rot resistance after scarring—all characteristics of oak—are adaptations that offer a competitive advantage in ecosystems susceptible to fire (Abrams, 2006). Thus, in a landscape subjected to low- to mixed-severity surface fires, oak became an important part of the forests in the eastern United States (Lorimer, 2001). The suppression of most fires, however, has largely eliminated this competitive advantage.

The shift in species composition associated with mesophication affects the abiotic environment. Oak leaf litter contains high lignin and phenolic contents that slow decomposition rates and increase flammability of the fuel bed (Abrams, 1990). The rigid and irregular structure of oak leaves also leads to a low packing ratio, allowing them to dry more quickly and remain dry for longer periods of time (Nowacki and Abrams, 2008). In contrast, mesophytic species, including maple (*Acer* spp.), yellow-poplar (*Liriodendron tulipifera*), and American basswood (*Tilia americana*), have low lignin contents and thinner leaves that lie flat and adhere to the forest floor. This creates conditions where moisture is trapped, air pockets are minimized, and decomposition is accelerated—conditions that are not conducive to fire (Nowacki and Abrams, 2008). Further, red maple (*Acer rubrum*) has been shown to conduct more than twice as much stemflow as oak, but similar amounts of throughfall (Alexander and Arthur, 2010). This mechanism leads to a positive feedback during invasion by red maple, where individual trees are able to direct more water and nutrients to their own root systems, offering a competitive advantage in ecosystems with limited water

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https://doi.org/10.1016/j.foreco.2018.08.030
Received 25 June 2018; Received in revised form 13 August 2018; Accepted 15 August 2018

availability. Consequently, the increase of mesophytic species abundance simultaneously reduces fire intensity and probability of occurrence, and improves conditions for mesophytic species establishment.

This shift in species composition has implications for both ecosystem functioning and wildlife habitat. For example, maple-dominated forests are associated with lower C:N ratios and greater nitrate production and loss compared with forests dominated by northern red oak (*Quercus rubra*; Lovett et al., 2004). Similarly, red maple leaf litter has been shown to immobilize nitrogen, reducing resource availability (Alexander and Arthur, 2014). The increased water demand of mesophytic species also results in increased evapotranspiration, reducing water availability and increasing the susceptibility to drought (Caldwell et al., 2016). The differences in the physical and chemical characteristics of oak and maple leaf litter also results in differential breakdown rates in vernal pools, which can control the integrity of the trophic structure of these fragile communities (Mehring and Maret, 2011). Oak also provides critical hard mast, as their acorns are among the primary food source for many birds and mammals during the dormant season of temperate deciduous forests (McShea et al., 2007). In fact, the tendency for oak to produce irregular acorn crops influences population dynamics of many bird and mammal species that have annual fluctuations linked to oak masting (Rodewald, 2003). A large-scale shift to mesophytic species threatens to reduce forage quality and quantity for many wildlife species (Wood et al., 2012).

Private landowners, state and federal agencies, and other natural resource organizations have a vested interest in maintaining the oak resource in the eastern U.S. However, the costs associated with restoration can be too great for land managers to justify, leading to unmanaged forests as a result of limited resources (e.g., funding, equipment, personnel). Therefore, understanding how these forests have the ability to resist invasion by red maple and other mesophytic species—and what characteristics confer that resistance—may help land managers concentrate their limited resources on those forests easiest and most cost-effective to restore.

We sought to study forest stand dynamics over a period of 22 years across different landscape positions in southeastern Ohio. Specifically, we associated environmental variables with species composition, particularly that of the regeneration layers. By resampling a network of permanent plots used to develop an ecological classification system for the Athens Unit of the Wayne National Forest, we examine the influences of physiographic and edaphic factors on mesophication, specifically as they relate to changes in forest structure and composition.

2. Materials and methods

2.1. Study area

The Wayne National Forest (WNF) includes approximately 97,500 ha of the Unglaciated Allegheny Plateau Province in southeastern Ohio. This study focuses on the Athens Unit—one of three administrative units—located in Athens, Hocking, Morgan, Perry, and Vinton Counties, and covering approximately 29,300 ha (Fig. 1). The bedrock geology is characterized by inter-bedded sedimentary strata of the Pennsylvanian age (Pearcy et al., 1999). The soils have formed in parent material of sequences of loess, colluvium, and residuum from the common lithologic types of sandstone, shale, siltstone, and limestone. These soils are mostly well-drained or moderately well-drained fine-loamy texture (Pearcy et al., 1999). The average depth to bedrock is 50–100 cm (Pearcy et al., 1999). The unglaciated landscape of the Wayne National Forest may be characterized by its hilly terrain, steep narrow valleys, and outcroppings of bedrock. The climate is characterized as continental, with hot, humid summers and cool winters (Owenby and Ezell, 1992). The average frost-free period is 180 days, and precipitation is evenly distributed throughout the year. Annual precipitation ranges from 81 to 96 cm (mean = 87 cm), and annual temperatures range from 10.2 to 12.8 °C (mean = 11.4 °C; Daly et al., 2008). Located in the mixed-mesophytic forest region (Braun, 1950), the study area is predominantly second-growth forest, established after heavy cutting approximately 80–140 years ago. Early land survey records indicate oak, and to a lesser extent hickory, dominated the forests over much of this area (Hutchinson et al., 2003). American beech (*Fagus grandifolia*), sugar maple (*Acer saccharum*), and yellow-poplar were also frequent in narrow valleys and bottomlands, but not abundant overall (Gordon, 1969).

2.2. Field methods

In early 1993, work began on developing an ecological classification system for the Wayne National Forest (Hix and Chech, 1993). Forest stands were selected from the U.S. Department of Agriculture (USDA) Forest Service Vegetation Management Information System database, screening for stands at least 70 years old. Field surveys eliminated stands with evidence of recent anthropogenic disturbance, such as stumps, dominance of early-successional tree species, indications of fire, significant windthrow, or large canopy gaps. A stratified random sampling design was used to select stands for sampling in order to represent all physiographic features and landform types.

Transects were then established in each stand, consisting of two to four plots at least 20 m from transect endpoints and 40 m apart from one another, situated parallel to the contour of the hillslope. In the summer of 2016, 100 of the plots originally sampled in 1994 were relocated and resampled.

We sampled the vegetation of each plot using a nested sampling design, which included a 500-m^2 circular plot, a concentric 100-m^2 circular subplot, and eight rectangular 1-by-2 m quadrats, each arranged 2 m beyond the 500-m^2 and 100-m^2 plot centers at all cardinal directions (N, NE, E, SE, S, SW, W, NW). If a quadrat contained some obstruction (e.g., a tree trunk), it was relocated an additional 2 m beyond plot center. Within the 500-m^2 plot, all woody vegetation > 10 cm diameter at breast height (1.37 m; dbh) was recorded, including species and dbh. Within the 100-m^2 subplots, all saplings (*i.e.*, woody plants > 1.37 m tall) were identified and placed into one of two size classes: small (< 5 cm dbh) or large (5–10 cm dbh). Nomenclature follows Braun (1961). An importance value (IV) was calculated for the stems of each tree speciesgreater than 10 cm dbh by averaging relative density and relative dominance (*i.e.*, relative basal area) among plots of each transect. Species' sapling abundance values were compared using relative density.

We collected physiographic data in the general vicinity of each plot, including landform (*i.e.*, uplands, hillslope, structural bench, and bottomland), slope percent, length of slope, distance to ridgetop, and slope aspect. The slope length and distance to ridgetop were used to calculate a percent distance to ridgetop (PDR) for each plot. Soil measurements were also collected during the original 1994 sampling. The soil was sampled to a depth of 60 cm using a probe at four points on the perimeter of each 100 m^2 subplot in order to describe the variation in each horizon. A 1-m deep soil pit was also excavated on the first plot of each transect in order to record a complete soil profile description. Soil measurements included thickness and texture of the A, B, and E horizons, and depth to mottling. Integrated soil moisture index (IMI) values for each plot were provided by the USDA Forest Service. IMI is a GIS-derived metric of soil moisture which incorporates slope aspect, cumulative flow of water downslope, curvature of the landscape, and water-holding capacity of the soil (Iverson et al., 1997).

2.3. Statistical analyses

The Ecological Classification System for the Wayne National Forest developed by Hix et al. (1997) defines ELTPs by landform, slope position, depth to mottled soil, and thickness of the A soil horizon. We used ELTPs modified from this ECS, including dry uplands, southwest-facing upper slopes, southwest-facing lower slopes, northeast-facing upper

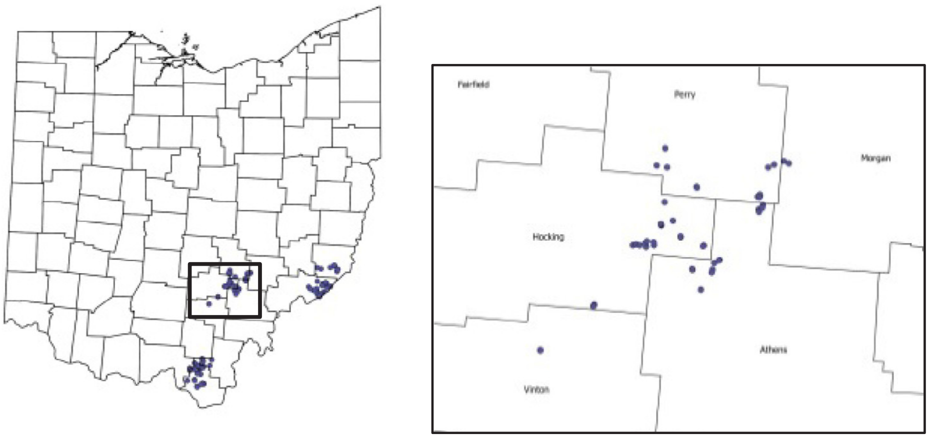

Fig. 1. Plots distributed across the Athens Unit of the Wayne National Forest in southeastern Ohio.

slopes, northeast-facing lower slopes, and bottomlands. Broader ELTs include dry uplands, southwest-facing slopes, northeast-facing slopes, and bottomlands. This categorization balanced sample size with spatial resolution in a way that retains meaningful vegetation patterns. Other studies mapping ELTs and ELTPs across the Wayne National Forest follow a similar approach (Iverson et al., 2018). We calculated descriptive statistics for the environmental and vegetation data sets by ecological land type (ELT). Principal components analysis (PCA) was used to examine separation of plots based on the environmental variables used in developing this ECS: soil texture (X), thickness of the solum (T), thickness of the A and B horizons (Ta and Tb, respectively), soil mottling (Dmot), transformed aspect (Tasp), landform (LF), percent distance to ridge (PDR), and IMI. For analysis, aspect was cosine transformed ($\cos(45^\circ - \text{aspect}) + 1$), where the maximum value of 2.0 is assigned to northeasterly aspects, and the minimum value of 0.0 is assigned to southwesterly aspects. Multiple response permutation procedures (MRPP) were computed using Euclidean distance, and pairwise comparisons were made between northerly and southerly slopes. For multivariate analyses, species that occurred on less than 5% of plots were removed in order to reduce noise and enhance detection of relationships between community composition and environmental factors (McCune and Grace, 2002). We also calculated various diversity metrics by ELT and vegetation strata (e.g., trees, large saplings, and small saplings), including the Shannon–Weiner Index of Diversity, Simpson's Similarity, Pielou's Evenness, and richness. These metrics were compared across ELTs and between sampling periods. Two groups were created for making general comparisons: "mesophytes" and "oaks". Mesophytes, here, includes red maple, sugar maple, American beech, American basswood, and yellow-poplar. Oaks include white oak (*Quercus alba*), black oak (*Q. velutina*), scarlet oak (*Q. coccinea*), chestnut oak (*Q. prinus*), and northern red oak.

The "vegan" package of the R statistical software was used for most analyses (R Development Core Team, 2013). Diameter distributions were created for all trees greater than 10 cm dbh across all plots sampled. The "fitdistrplus" package was used to calculate parameters for Weibull functions fit to these diameter distributions (Delignette-Muller and Dutang, 2015). These were interpreted following Thoman et al. (1969). Weibull shape and scale parameters were calculated with maximum likelihood estimation, and confidence intervals were generated through bootstrap resampling. The shape parameter (c) for each distribution was then used to infer the age structure of the forest stands we sampled (Bailey and Dell, 1973).

3. Results

3.1. Environmental conditions

PCA confirmed the presence of an underlying gradient of environmental conditions within the sampled plots. The first two axes of the PCA explained 59.4% of the variation in the environmental variables; the first three explain 76.8%. The first axis is correlated with transformed aspect, percent distance to ridgetop, IMI, thickness of the solum, and landform ($r = 0.35$, 0.49, 0.55, 0.32, and 0.46, respectively; $p < 0.05$). The second axis is correlated with percent distance to ridgetop, slope percent, thickness of the solum, soil mottling, and texture of the B horizon ($r = -0.25$, -0.36, 0.45, -0.54, and 0.53, respectively, $p < 0.05$).

3.2. Changes in structure

In the 22 years since these plots were first sampled, the average basal area (m^2/ha) of these forests increased 3.7 m^2/ha. The average density decreased by 24 trees/ha. Though the density of trees decreased, the density of saplings increased substantially. Large saplings (*i.e.*, 5.1–10.0 cm dbh) increased by 171 stems/ha, and small saplings (*i.e.*, < 5.1 cm dbh) increased 195 stems/ha. The richness of large and small sapling species was virtually unchanged.

The distribution of these changes among ELTs, however, is not homogenous (Table 1). The basal area of canopy trees increased more among drier sites (*i.e.*, uplands, southerly upper & lower slopes, and northerly upper slopes) than it did on more mesic sites (*i.e.*, northerly lower slopes and bottomlands; Palus, 2017). The density and species richness of canopy trees decreased across all classes, except for bottomlands. The density of small and large saplings also changed inconsistently across the landscape. The density of small saplings increased significantly on northerly lower slopes, and large saplings increased significantly on southerly lower slopes. Both small and large saplings decreased on all other sites.

Overall, diameter distributions shifted to the right (*i.e.*, trees got bigger), and while peaks in these distributions tend to diminish over time, they became more pronounced among mesophytic species (Fig. 2). From the Weibull shape parameters, it can be inferred that all species except yellow-poplar have positively skewed, unimodal curves (Thoman et al., 1969). The distribution of yellow-poplar approximates a normal curve. The shape parameter for white oak shifted from 2.60 in 1994 to 2.91 in 2016.

3.3. Change in species composition

MRPP analyses suggest there are discernible patterns in plant

Table 1
Changes in structural characteristics, including basal area (m^2/ha), density (stems/ha), and richness (# species), in plots distributed across the Athens Unit of the Wayne National Forest from 1994 to 2016 (mean ± SE). ELTPs include uplands, southwest-facing upper slopes (SUS), southwest-facing lower slopes (SLS), northeast-facing upper slopes (NUS), northeast-facing lower slopes (NLS), and bottomlands.

	Uplands		SUS		SLS		NUS		NLS		Bottomlands	
	1994	2016	1994	2016	1994	2016	1994	2016	1994	2016	1994	2016
All trees												
Basal area	26.9	33.9	24.8	31.4	25.5	29.4	24.2	27.8	29.9	28.4	24.6	25.8
Density	345.0	336.7	330.4	340.7	350.0	308.6	273.6	238.2	322.1	247.4	236.0	248.0
Richness	6.3	6.1	5.7	6.1	5.7	5.5	5.9	5.2	6.3	5.4	5.4	6.0
Large saplings												
Density	263.6	408.3	322.2	425.9	250.0	592.9	272.7	454.5	205.3	421.1	370.0	410.0
Richness	1.6	1.5	1.9	1.5	1.4	1.6	1.6	1.9	1.6	1.2	2.3	1.9
Small saplings												
Density	2027.3	1463.6	2259.3	1844.4	1928.6	1632.7	2177.3	2495.0	1310.5	3888.9	2740.0	1520.0
Richness	5.1	4.3	5.8	5.5	5.4	4.6	4.9	5.9	3.7	5.8	6.6	4.5
n	5		14		7		11		8		5	

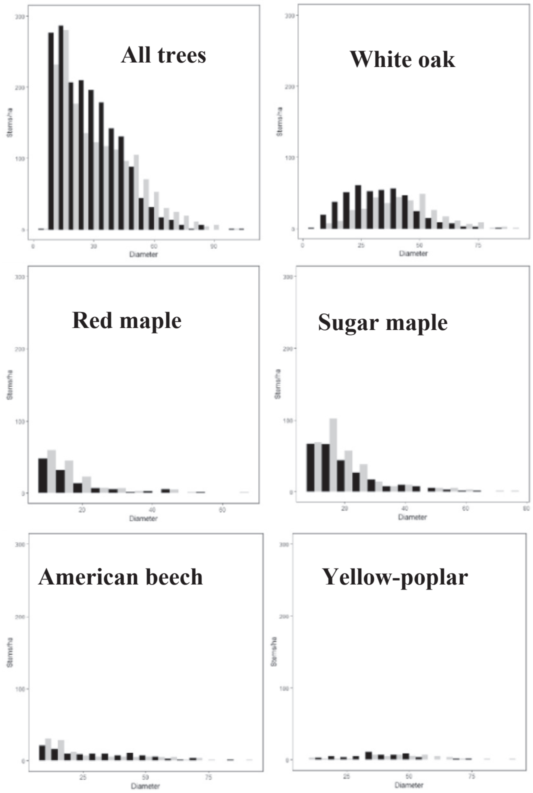

Fig. 2. Diameter distributions across the plots sampled across the Athens Unit of the Wayne National Forest. Black bars represent 1994 data; gray bars represent 2016 data.

Table 2
MRPP results, testing the hypothesis of no difference between two or more groups. Grouping variables include ELT (top table), ELTP (middle table), and year (bottom table). The chance-corrected within-group agreement—the effect size—is indicated by *A*. This statistic describes within-group homogeneity compared to that expected by chance alone.

	Observed	Expected	p	A
Trees (1994)	57.32	61.63	0.001	0.07
Trees (2016)	58.94	59.97	0.098	0.017
Large saplings (1994)	88.15	88.89	0.21	0.0083
Large saplings (2016)	83.52	86.34	0.047	0.033
Small saplings (1994)	73.34	77.10	0.003	0.049
Small saplings (2016)	78.78	81.33	0.003	0.031
Trees (1994)	57.37	61.63	0.001	0.069
Trees (2016)	56.64	59.97	0.002	0.055
Large saplings (1994)	87.98	88.89	0.25	0.01
Large saplings (2016)	84.76	86.34	0.20	0.018
Small saplings (1994)	73.17	77.10	0.002	0.051
Small saplings (2016)	77.74	81.33	0.001	0.044
Trees	60.81	60.51	0.996	-0.0049
Large saplings	87.64	88.44	0.034	0.009
Small saplings	79.18	80.66	0.001	0.018

community composition when comparing among ELTs, ELTPs, and year (Table 2). MRPP reveals no clear differences in the species composition of large saplings in 1994 ($p = 0.212$, $A = 0.008$) or trees in 2016 ($p = 0.098$, $A = 0.017$) when compared among ELTs (*i.e.*, uplands, southerly slopes, northerly slopes, and bottomlands; Table 2). There is some underlying pattern, though, in all other strata. When slopes are divided into upper- and lower-slope positions, the large saplings of both sampling events are the only strata that do not show any clear patterns in species composition by ELTP (1994: $p = 0.252$, $A = 0.010$; 2016: $p = 0.204$, $A = 0.018$). The community composition of both small and large saplings did change over this 22-year period (small: $p = 0.001$, $A = 0.018$; large: $p = 0.034$, $A = 0.009$). Trees, however, were not significantly different between the two sampling periods ($p = 0.996$, $A = -0.005$).

Across all plots, white oak (*Quercus alba*) remains the dominant species in the overstory (IV = 36.8 ± 4.4; Table 3). Oaks taken collectively remain the dominant species in the overstory on southerly slopes (mean IV = 40.1 ± 5.8), and are still important on northerly slopes (IV = 21.1 ± 4.4; Table 3). However, they remain poorly represented in the understory. Red maple saplings are still important on southerly slopes and uplands (Fig. 3). The recruitment of red maple in the large sapling layer has generally increased (Table 4), whereas the density of small red maple saplings mainly decreased (Table 5). American beech saplings have ubiquitously increased in relative density across both size classes except for northeast-facing lower slopes (Fig. 3). However, the relative density of red maple and sugar maple large saplings have changed very little on northerly lower slopes, while sugar maple and American beech small sapling densities decreased. On these northerly lower slopes, spicebush (*Lindera benzoin*) and pawpaw (*Asimina triloba*) small saplings increased (Table 5).

Flowering dogwood (*Cornus florida*), an important component of the sapling strata during the first sampling period, has been virtually eliminated by dogwood anthracnose (*Discula destructiva*) across all sites.

Pielou's evenness decreased on northerly lower slopes in small saplings (0.89 ± 0.02 to 0.77 ± 0.04). In bottomlands, all metrics of diversity decreased between the two sampling events. There were no

Table 3

Mean importance value for trees > 10 cm dbh from plots distributed across the Athens Unit of the Wayne National Forest. Bold values indicate significant changes were tested with the Wilcoxon Rank-Sum test (note there were no significant changes found). ELTPs include uplands, southwest-facing upper slopes (SUS), southwest-facing lower slopes (SLS), northeast-facing upper slopes (NUS), northeast-facing lower slopes (NLS), and bottomlands. Miscellaneous species include *Aesculus* spp., *Celtis occidentalis*, *Cornus florida*, *Juglans nigra*, *Nyssa sylvatica*, *Ostrya virginiana*, *Oxydendrum arboreum*, *Platanus occidentalis*, *Sassafras albidum*, and *Ulmus* spp.

	Uplands		SUS		SLS		NUS		NLS		Bottomlands	
All trees	1994	2016	1994	2016	1994	2016	1994	2016	1994	2016	1994	2016
Acer nigrum	0	0	0	0.3	0.5	0	0.3	1.0	2.9	8.2	1.3	3.0
Acer rubrum	9.6	14.4	7.7	8.3	5.9	7.3	2.4	5.9	3.7	6.2	2.2	4.9
Acer saccharum	4.4	7.9	4.6	7.7	8.1	10.8	22.6	27.8	25.0	25.5	12.1	17.4
Carya spp.	13.1	10.4	15.8	12.4	7.1	8.4	7.7	7.8	8.3	2.4	9.7	5.8
Fagus grandifolia	0.8	0	1.7	4.3	7.1	7.2	16.4	18.8	11.4	9.9	9.8	14.6
Fraxinus spp.	1.9	0.9	2.1	2.0	0.8	0.2	9.9	5.6	6.5	2.5	6.9	8.2
Liriodendron tulipifera	0	0	4.7	6.4	2.3	2.4	6.6	7.5	6.6	7.2	13.0	11.9
Miscellaneous	11.3	13.0	3.9	4.6	6.3	4.8	9.2	8.8	11.6	11.1	16.2	16.1
Prunus serotina	3.8	0.6	0.5	0.6	1.9	2.6	2.5	0.9	0.4	0.5	2.0	2.8
Quercus alba	29.6	27.3	35.0	32.8	56.2	49.4	19.1	20.9	20.1	22.6	27.8	15.9
Quercus coccinea	11.6	14.9	8.8	4.6	4.0	7.9	2.3	0	3.0	2.9	0	0
Quercus muehlenbergii	0	0	0	0	0	0	1.5	1.6	2.6	2.8	3.0	4.1
Quercus prunus	16.1	16.4	14.0	11.6	1.8	1.9	1.1	1.3	1.2	1.9	1.7	0
Quercus rubra	4.9	5.8	8.0	8.9	7.6	9.0	15.4	14.1	15.0	14.6	12.6	9.7
Quercus velutina	19.8	15.5	9.4	10.2	8.1	11.3	3.9	5.4	1.9	1.2	2.7	2.8
Tilia americana	0	0.5	0	0	0	0	3.0	1.1	1.9	4.5	13.9	14.5
n	5		14		7		11		8		5	

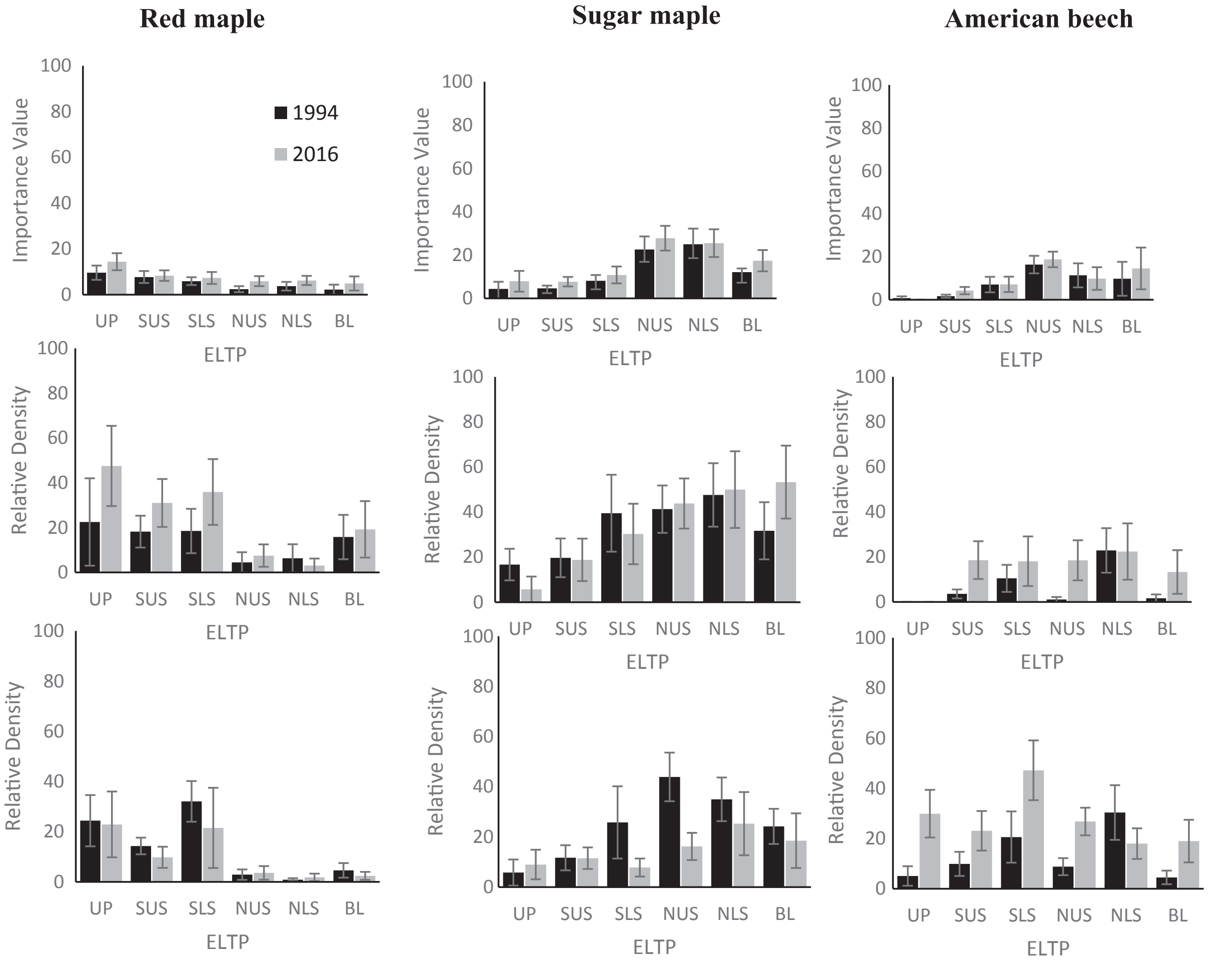

Fig. 3. Changes in abundance, as measured by relative density (for saplings) and importance value (for trees > 10 cm dbh). Top row represents trees (> 10.0 cm dbh); middle row represents large saplings (> 5.0 cm dbh & < 10.1 cm dbh); bottom row represents small saplings (< 5.1 cm dbh). Landscape positions are abbreviated to UP (uplands), SUS (southwest-facing upper slope), SLS (southwest-facing lower slope), NUS (northeast-facing upper slope), NLS (northeast-facing lower slope), and BL (bottomlands).

Table 4

Mean relative density for large saplings > 5.0 cm and < 10.0 cm dbh from plots distributed across the Athens Unit of the Wayne National Forest. Bold values indicate significant changes were tested with the Wilcoxon Rank-Sum test. ELTPs include uplands, southwest-facing upper slopes (SUS), southwest-facing lower slopes (SLS), northeast-facing upper slopes (NUS), northeast-facing lower slopes (NLS), and bottomlands. Miscellaneous species include *Aesculus* spp., *Celtis occidentalis*, *Cercis canadensis*, *Nyssa sylvatica*, *Osrtya virginiana*, *Oxydendrum arboreum*, and *Sassafras albidum*.

	Uplands		SUS		SLS		NUS		NLS		Bottomlands	
Large Saplings	1994	2016	1994	2016	1994	2016	1994	2016	1994	2016	1994	2016
Acer rubrum	22.5	47.5	18.2	31.0	18.5	35.9	4.5	7.5	6.3	3.1	15.8	19.2
Acer saccharum	16.7	5.7	19.7	18.8	39.5	30.3	41.3	43.8	47.6	50.0	31.7	53.3
Carya spp.	0	0	0.8	0	0	0	0	0	0	0	0	0
Cornus florida	**39.2**	**0**	**16.7**	**0**	11.9	0	0	0	13.9	0	5.8	0
Fagus grandifolia	0	0	3.6	18.6	10.5	18.1	**1.1**	**18.5**	22.9	22.4	1.7	13.3
Fraxinus spp.	0	2.9	9.3	2.1	0	0	5.3	0	0	0	1.7	5
Liriodendron tulipifera	0	0	0.9	0	0	0	0	0	0	0	0	0
Miscellaneous	37.5	53.4	21.0	16.8	25.6	6.1	33.3	36.8	18.8	10.4	30.0	27.5
Nyssa sylvatica	5	2	0.9	3.2	1.8	2.0	1.5	7.0	0	0	2.5	5
Prunus serotina	0	0	2.5	0	0	0	0	0	0	0	0	0
Quercus spp.	10.0	0	6.1	10.3	7.1	0	0	0	4.2	0	0	0
Tilia americana	0	0	0	0	0	0	4.5	4.5	0	0	20.0	0
n	5		14		7		11		8		5	

landscape positions that experienced declines across all metrics of diversity of large saplings. Southwesterly upper slopes experienced declines in Shannon diversity and richness; southerly lower slopes declined in Pielou's evenness; northerly upper slopes increased in richness; northerly lower slopes decreased in Shannon and Simpson diversity and richness; and bottomlands increased in Pielou's evenness, but decreased in richness. Tree diversity indices changed very little overall.

4. Discussion

Few studies of forest succession and mesophication evaluate change among different geomorphic positions (Arthur et al., 2017, Keyser et al., 2017, Murphy and McCarthy, 2017). While authors have repeatedly predicted oak regeneration to be more successful in areas of low moisture (Arthur et al., 2015, Nowacki and Abrams, 2008), this has only been demonstrated on truly xeric sites (Olson et al., 2014).

4.1. Change in structure

The maturation of these southeastern Ohio forests is illustrated by the consistent decrease in stem density and increase in mean basal area of overstory trees. In comparison to a selected sample of old-growth oak forests in the eastern U.S., the forests we studied have mean basal area (26.1 ± 0.8 m^2) and stem density (158 ± 6.2 m^2) values that are very similar to those reported for old-growth mesic oak forests (Tyrrell et al., 1998). From the positively skewed diameter distribution of all tree across all our plots, we would infer an overall single-cohort age structure. The overall stem density—of all trees and saplings—has increased as a result of increasing red maple and American beech in the understory. This trend is consistent with other studies of mesophication (Nowacki and Abrams, 2008).

Species-specific diameter distributions help elucidate more discrete trends of forest development since the first sampling of these plots. For example, the shape parameter for yellow-poplar is not significantly different from a normal distribution (Fig. 2). As a shade-intolerant species often considered to exhibit early-successional traits, a single

Table 5

Mean relative density ± SE for small saplings < 5.1 cm dbh from plots distributed across the Athens Unit of the Wayne National Forest. Bold values indicate significant changes were tested with the Wilcoxon Rank-Sum test. ELTPs include uplands, southwest-facing upper slopes (SUS), southwest-facing lower slopes (SLS), northeast-facing upper slopes (NUS), northeast-facing lower slopes (NLS), and bottomlands. Miscellaneous species include *Acer nigrum*, *Aesculus* spp., *Amelanchier arborea*, *Cercis canadensis*, *Crataegus* spp., *Magnolia acuminata*, *Nyssa sylvatica*, *Oxydendrum arboreum*, *Sassafras albidum*, and *Ulmus* spp.

Small saplings	Uplands		SUS		SLS		NUS		NLS		Bottomlands	
	1994	2016	1994	2016	1994	2016	1994	2016	1994	2016	1994	2016
Acer rubrum	24.4	22.9	14.3	9.8	32.1	21.5	2.9	3.6	0.9	1.8	4.6	2.4
Acer saccharum	5.8	9.0	11.7	11.5	25.8	7.8	**43.9**	**16.2**	35.0	25.3	24.2	18.5
Asimina triloba	3.2	15.6	0	0	0	1.2	3.5	8.8	5.5	13.7	12.4	11.7
Carpinus caroliniana	2.1	0	2.1	9.3	5.5	5.8	3.9	3.4	8.6	3.5	9.8	2.7
Carya spp.	5.7	16.8	3.6	9.6	2.9	1.9	0	0.9	0.7	1.0	1.8	0.9
Cornus florida	**29.3**	**0.5**	**23.9**	**2.7**	**13.7**	**0.6**	5.9	1.4	8.9	2.4	4.4	0.9
Fagus grandifolia	5.1	29.9	9.9	23.1	20.6	47.2	**8.8**	**26.8**	30.4	18.0	4.5	19.0
Fraxinus spp.	0.5	2.9	3.4	9.7	2.3	10.0	3.3	12.6	0	2.4	5.4	7.6
Hamamelis virginiana	0	0	4.4	4.3	0	0	0	1.1	0	0.8	2.5	14.3
Lindera benzoin	0	0	0	0	0	0	10.6	22.3	11.9	27.0	**8.4**	**33.7**
Liriodendron tulipifera	0	0	0.2	1.4	0	0	0.5	0.5	0	1.2	2.9	1.6
Miscellaneous	23.2	37.9	16.5	24.3	13.5	8.9	12.7	15.8	17.1	12.5	33.2	22.0
Ostrya virginiana	12.9	0	10.7	15.9	9.7	12.5	15.2	8.6	16.4	17.4	5.9	4.2
Prunus serotina	1.1	0	4.0	3.0	1.9	0	1.1	0.2	0	0	0	0
Quercus spp.	4.8	4.4	7.2	10.6	2.8	2.4	0	0	0	0.1	0	0
Tilia americana	0	0	0	0	0	0	2.7	0.2	0	0	2.2	0
Viburnum acerifolium	3.8	1.7	2.4	0	0	1.2	3.6	0.2	0	0.2	0	0
Viburnum prunifolium	0	0	10.4	15.4	0	0	5.3	0.6	0	0	0.6	0
n	5		14		7		11		8		5	

cohort of yellow-poplar would indicate a single, large disturbance event in the past that resulted in open conditions where yellow-poplar would have flourished. In this case, the establishment of yellow-poplar likely coincides with widespread harvesting activities in the early 20th century. The shape parameter for white oak indicates a positively skewed distribution, though its diameter distribution has shifted closer to normal since the initial sampling. This is a consequence of its lack of regeneration. As old individuals die and there is no recruitment of new individuals, the current stand structure will shift with few new individuals to replace the old trees. The strong positively skewed diameter distributions of red maple, sugar maple, and American beech reflect their abundant regeneration. While old-growth forests generally exhibit negative exponential diameter distributions, the diameter distributions for our stands illustrate the transition in tree species composition, rather than a steady-state.

4.2. Changes in species composition

While oak remains the dominant species in the canopy across the forests we studied, their failure to regenerate is consistent with studies across the Central Hardwood Forest Region (Abrams, 2003; Fei et al., 2011; Lowney et al., 2016; Pierce et al., 2006). The abundances of mesophytic species, including red maple, sugar maple, American beech, and American basswood, are increasing, while that of oak is decreasing across all size strata. The changes documented in mesophytes, however, vary by species and strata. The small amount of change in overstory trees is largely due to the longevity of oaks (Loehle, 1988); longer periods than this study will be needed to conclusively observe significant changes. With the abundance of red maple small saplings in 1994, there has been substantial ingrowth of red maple into the large-sapling size class in 2016. The changes observed in red and sugar maple large saplings appear to be nearly inversely related. On dry sites, red maple increased, while sugar maple declined. Changes on mesic sites were more variable, and may be related to the existing abundance of mesophytic species.

However, changes in the small-sapling size class show a different pattern. While red maple and sugar maple small-sapling regeneration has either remained static or decreased in abundance, American beech small saplings have increased across all ELTs, except for northerly lower slopes. We believe fire suppression has facilitated the importance of red maple in these layers, which, in turn, created more mesic conditions suitable for American beech. In the continued absence of fire and minor disturbances, American beech will likely continue to increase in abundance, and may eventually become an important component of the overstory.

4.3. Forest development in the Wayne National Forest

Our results support observations that oak regeneration is primarily restricted to dry sites, albeit in low densities, if present at all. However, based on our results, American beech and red maple were successfully regenerating on dry sites. The only ELT without a clear increase in mesophytic regeneration was the mesic northerly lower slope positions. This trend may be a result of the existing abundance of large sugar maple and American beech saplings, which maintained a combined relative density of roughly 70% over the past 22 years. These northerly lower slopes may be approaching a stable state, with these two late-successional species represented in the sapling layer likely to become dominant in the overstory in the absence of major disturbance. The persistence of oak in the overstory allows it to continue serving as a propagule source, in the event that some major disturbance eliminates much of the competing mesophytic vegetation. However, outside of surface fire, most disturbances disproportionately affect the overstory, thus releasing the mesophytic-dominated understory (Abrams and Nowacki, 1992; Holzmueller et al., 2012).

Studies on the Wayne National Forest have previously shown succession occurring in waves of species-specific mortality, e.g., overstory change on south-facing slopes generally begins with the loss of scarlet oak, and progresses toward dominance of white oak (Goebel and Hix, 1996). With the suppression of most fires, however, this trajectory is changing. The increased establishment of American beech we observed in this study may define a new successional trajectory for these forests. American beech is very tolerant of understory conditions; the small saplings of this species will likely grow into larger size classes in the absence of disturbance (Burns and Honkala, 1990). Further, compared with red maple, suitable habitat for American beech is expected to experience only slight declines under future climate scenarios (Prasad et al., 2007). It is prudent to begin considering the implications for these forests reverting to dominance by American beech—in light of novel stressors such as Beech Bark Disease (Houston, 1994) and a newly discovered disease, Beech Leaf Disease (Hausman, 2017)—and shift management strategies accordingly.

Several models suggest climate change will result in increased summer drought throughout the Central Hardwood Forest Region (Clark et al., 2016; Iverson et al., 2008; Peters et al., 2015). While precipitation may increase in the winter months, this will have little effect on the growth of trees during the dormant season. As a result, forests dominated by species well-adapted to drought—such as oak—are expected to be more resilient to these climatic changes (Butler et al., 2015; Iverson et al., 2018). Suitable habitat for species such as red maple and sugar maple are expected to experience declines under future climate scenarios (Prasad et al., 2007). However, red maple has a wide tolerance of ecological conditions (Abrams, 1998) and is considered to be a warm-based tree (Nowacki and Abrams, 2015). If management activities fail to return these forests to a trajectory of oak dominance, severe long-term droughts may result in large-scale tree mortality with little understory tree species regeneration.

4.4. Conclusions

This study shows that mesophication is occurring independent of landscape position in the Athens Unit of the Wayne National Forest in southeastern Ohio. Not only has red maple increased ubiquitously in the understory, but the abundance of American beech is becoming substantially more abundant. Management regimes should consider the implications of increased American beech dominance in the future. Moreover, we have observed that the driest of sites in the Athens Unit of the Wayne National Forest have not inhibited red maple encroachment through self-regulation. In other words, this study fails to observe evidence of resistance to mesophication based on landscape position. Successful management interventions, as suggested by other authors, will be needed even on the driest sites (Dey, 2014; Hutchinson et al., 2012; Keyser et al., 2017).

Acknowledgements

Research support was provided through state and federal funds appropriated to the School of Environment and Natural Resources, the Ohio Agricultural Research and Development Center (P.I. Hix and Goebel), and the United States Department of Agriculture Forest Service Northern Research Station agreement 15-CS-11242302-122 (P.I. Matthews).

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