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Topography and soils-based mapping reveals fine-scale compositional shifts over two centuries within a central Appalachian landscape

James M. Dyer[a,*], Todd F. Hutchinson[b]

[a] Department of Geography, Ohio University, Athens OH 45701, USA
[b] US Forest Service, Northern Research Station, Delaware OH 43015, USA

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ABSTRACT

When public lands were surveyed in the U.S., "witness trees" were often recorded to facilitate the relocation of property boundaries, and these records provide a snapshot of forest conditions prior to Euro-American settlement and land clearing. This study utilizes witness trees and present-day plot data to explore long-term vegetation changes at a regional scale. Landscape classes for a 5000 km^2 study area in Appalachian Ohio were defined by slope, aspect, topographic position, soil pH, and available water capacity. Cluster analysis and ordination revealed topo-edaphic patterns in the presettlement (c. 1800) and present-day forests, based on 5765 witness trees and 3249 contemporary trees occurring on 547 Forest Inventory and Analysis (FIA) subplots. Mesophication is evident, as the oak-hickory presettlement forest is now dominated by maple-poplar. Size-class analysis suggests the presettlement forest also experienced mesophication following xeric conditions of the preceding centuries. In both presettlement and contemporary forests, ridges form distinctive communities compared to slopes and valleys, although topographic distinctiveness is now more prevalent. Several taxa revealed changes in site affinities over the past two centuries; shifts in their realized niches suggest mesophication acts through diverse individualistic responses to a multiple set of interacting drivers. Specifically, regionally documented changes in land use, drought, N deposition, and fire at the time of the original surveys lead to altered competitive relationships.

1. Introduction

"Witness trees" provide an archival source of ecological information, potentially serving as a bridge between paleo- and contemporary ecologies. Prior to Euro-American settlement beginning in the late 18th century, many public lands in the United States were surveyed using a rectangular system. Stakes were set at corners (often at 1.6 km intervals), and nearby trees noted to aid later location of the surveyed boundaries. Unlike tree rings or pollen cores, the record of witness trees provides a snapshot in time of forest composition across the landscape. Though the sampling intensity of witness tree data is low, it is continuous over large areas, enabling landscape-level vegetation analysis that also contains fine-scale spatial resolution for individual trees (Schulte and Mladenoff, 2001). Thus, witness tree point data and current plot data can be used to document long-term changes in vegetation at a regional scale, and understand how compositional changes are manifested along smaller-scale environmental gradients. Witness tree data extend our ability to capture long-term processes of tree-species replacements, which are critical to our understanding of ecosystem functioning and biodiversity patterns.

It is widely established that the deciduous forests of eastern North America are experiencing a shift in composition as mesophytic species such as red maple, sugar maple, and tulip poplar (binomial nomenclature provided in Table 1) are becoming more abundant in oak-dominated forest landscapes. The cause of the observed changes in species' importance has been attributed to several factors, including changes in land use, climate, and fire regime (Abrams, 1992; Lorimer, 1984; McEwan et al., 2011). It is important to recognize that these factors have not changed uniformly over the eastern deciduous forest, nor is species composition uniform throughout this vegetation association. For example, in the oak-hickory region of Missouri and Arkansas, the importance value for oaks is 43.3%, compared to 2.3% for the mesophytes red maple, sugar maple, and tulip poplar. In contrast, for the Mesophytic region centered on the Appalachians, the importance values for the oaks and the three mesophytes are 20.5% and 19.9%, respectively (Dyer, 2006). Climatically, Bishop and Pederson (2015) report that in the oak-hickory region, summer has been the driest season since the mid-twentieth century (22.3% of annual

* Corresponding author.
E-mail addresses: dyer@ohio.edu (J.M. Dyer), thutchinson@fs.fed.us (T.F. Hutchinson).

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Table 1
Trees in order of their abundance in the original land survey records; taxa listed comprise > 1% of all witness trees (n = 5603), or > 1% of FIA trees ≥ 12.7 cm DBH (n = 3148).

Taxon	Surveyors' designations	Combined FIA species	Binomial nomenclature	Percentage of Witness Trees[a]	Percentage of FIA Trees[b]
White oak	White oak		*Quercus alba* L.	34.1	6.8
Hickory	Hickory	Hickory sp. [209], shagbark hickory [10]	*Carya* Nutt., *C. ovata* (Mill.) K. Koch	13.9	7.0
Black oak	Black oak [673], red oak [35], scarlet oak [1], pin oak [1]	Black oak [101], northern red oak [112], scarlet oak [35]	*Quercus velutina* Lam., *Q. rubra* L., *Q. coccinea* Münchh.	12.7	7.9
American beech	Beech		*Fagus grandifolia* Ehrh.	10.3	4.0
Sugar maple	Sugar, sugartree		*Acer saccharum* Marshall	4.6	9.4
Blackgum	Gum, pepperage		*Nyssa sylvatica* Marshall	3.5	1.4
Red maple	Maple		*Acer rubrum* L.	3.4	12.6
Tulip poplar	Poplar		*Liriodendron tulipifera* L.	2.9	11.6
Chestnut oak	Chestnut oak [89], yellow oak [71]		*Quercus montana* Willd.	2.9	3.1
Elm	Elm	Elm sp. [116], American elm [12]	*Ulmus* L., *U. americana* L.	2.0	4.1
Chestnut	Chestnut		*Castanea dentata* (Marshall) Borkh.	1.9	0.0
Ash	Ash [42], white ash [44], black ash [4], blue ash [3], hoop ash [3]	Ash sp. [114], white ash [12]	*Fraxinus* L., *F. americana* L.	1.7	4.0
Silver maple	White maple		*Acer saccharinum* L.	1.4	0.6
American sycamore	Sycamore		*Platanus occidentalis* L.	0.7	1.7
Buckeye	Buckeye	Buckeye sp. [85], yellow buckeye [6]	*Aesculus* L., *A. flava* Aiton	0.6	2.9
Pine[c]	Pine	Virginia pine [53], pitch pine [19]	*Pinus virginiana* Mill., *P. rigida* Mill.	0.6	2.3
Black walnut	Walnut, black walnut		*Juglans nigra* L.	0.5	1.3
Locust	Locust, black locust, honey locust	Black locust [55], honey locust [2]	*Robinia pseudoacacia* L., *Gleditsia triacanthos* L.	0.3	1.8
Black cherry	Cherry, black cherry		*Prunus serotina* Ehrh.	0.2	5.7
Sassafras	Sassafras		*Sassafras albidum* (Nutt.) Nees	0.1	2.2
Sourwood	Sourwood		*Oxydendrum arboreum* (L.) DC.	0.1	1.7
Bigtooth aspen	Aspen		*Populus grandidentata* Michx.,	0.1	4.8
Other[d]				1.1	3.2

[a] Excluding 162 subcanopy-species trees (dogwood, ironwood, laurel, redbud, service, thornbush).
[b] Excluding 101 non-native trees (eastern white pine, tree-of-heaven, loblolly pine, Scotch pine, osage-orange, red spruce).
[c] Excludes 11 "pine" assigned as hemlock; otherwise the percentage would be 0.8%.
[d] In order of abundance, other witness tree taxa include butternut, basswood (lynn), blackjack oak (likely *Quercus imbricaria*), swamp white oak, birch, hackberry, mulberry, oak, boxelder, bur oak, "gray oak," cottonwood, willow. In order of abundance other FIA taxa include American basswood, boxelder, eastern hemlock, river birch, sweet birch, eastern cottonwood, shingle oak, chinkapin oak, sweetgum, post oak, northern catalpa, hackberry, persimmon, butternut, cucumbertree, red mulberry.

precipitation). In contrast, summer has been the wettest season (28.5%) in the central Mesophytic forest region, and the frequency of summer rain events has increased.

At a finer spatial scale, vegetation responses to changes in climate, land-use, and disturbance regimes are likely to manifest along environmental gradients (Crimmins et al., 2011). Topography is typically the most obvious environmental gradient in upland forested landscapes. For example, owing to higher solar radiation and greater soil moisture drainage, ridges are often warmer and drier, and valleys are cooler and wetter. Because witness trees are referenced to specific locations, it is possible to establish species' relationships to topographic setting in presettlement forests. By comparing these relationships with those evident in USDA Forest Service Forest Inventory and Analysis (FIA) data, our most comprehensive assessment of contemporary forest conditions, it is possible to assess compositional changes and shifts in species' site affinities within a landscape.

Our objectives were to examine compositional and structural changes since Euro-American settlement (c. 1800) in the forests of southeastern Ohio, through the use of witness tree and FIA data. In a previous study, Dyer (2001) found that these contemporary forests had a higher proportion of early-successional wind-dispersed species, attributable at least in part to land-use changes since settlement. This study expands on the earlier work by using witness tree locations to create presettlement forest association maps. Since witness trees in this dissected landscape were surveyed at a resolution too coarse for simple spatial interpolation, we have developed a topography- and soils-based approach to aggregate individual trees into ecologically meaningful groups, and use multivariate analyses to assess changes in these associations between the presettlement and contemporary forests. Previous research has indicated that at broad spatial scales, presettlement forests revealed a strong imprint of climatic structuring and local hydrology, but that land-use history has resulted in homogenization of contemporary forests (Goring et al., 2016). Our study offers a finer-scale assessment of forest change, by examining compositional changes along environmental gradients within the landscape.

2. Materials & methods

2.1. Study area

The study area is situated in the unglaciated Allegheny Plateau physiographic province of southeastern Ohio. Topography is strongly dissected with steep slopes and typical relief on the order of 50 m. Upland soils are derived from sandstone, siltstone, shale, and limestone (Lucht et al., 1985). Southeastern Ohio falls within the Mesophytic forest region (Dyer, 2006), characterized by high species diversity. At Logan (39.53°N 82.39°W), the normal annual value for precipitation is 107.9 cm and 10.4 °C for temperature, with monthly temperature ranging from −2.3 °C in January to 22.3 °C in July (NOAA, 2010). Climatically, the region is located at the border of Köppen's Humid

Subtropical and Humid Continental zones.

Native American land use pressures in the temperate forests of eastern North America were localized and heterogeneous (Munoz et al., 2014). In southeastern Ohio, habitation by native peoples extends back over 12,000 years (Lepper, 2009). At the time of European contact, native cultures practiced farming supplemented with wild food resources (Wagner, 1996), with farming apparently limited principally to bottomlands (Loskiel, 1794). There are several written accounts by early travelers and settlers in Ohio that described burning by Native Americans in the 18th century, e.g., Joseph Barker, near Marietta Ohio, wrote "The Indians, by burning the Woods every Year, kept down the undergrowth and made good pasture for the deer and good hunting for himself" (Barker [1790], 1958). However, the extent of burning across the study area is unknown. Despite the long history of habitation, there is little record of forest characteristics within the study area prior to the early Euro-American settlement period. The witness tree record, sampled at a low intensity over an extensive area, therefore serves as the baseline condition for the region's forests for this study. Approximately 70% of the study area is now forested (Hansen et al., 2013), a similar percentage to what was reported in the 1850 U.S. Census. Later Censuses and Annual Reports of the Secretary of State indicate widespread clearing from 1850 to c. 1920, when forest cover in southeastern Ohio reached a minimum of only 10–20%. As part of a larger project examining socio-economic drivers of land-use change, this study focuses on a 5088 km^2, five-county area originally surveyed in the late eighteenth century. Perry County and parts of Hocking, Vinton, and Ross Counties were surveyed beginning in 1799 as part of the Congress Lands East of the Scioto River. Athens County and the remainder of Hocking and Vinton Counties were part of the Ohio Company Purchase, whose interior lines were surveyed beginning in 1796 (Fig. 1). The Ohio Company Purchase land comprises about 40% of the total study area, and its witness tree record was included in an earlier study of the entire Ohio Company Purchase (Dyer, 2001). The Ohio Company Purchase and Congress Lands were both conducted under the same congressional ordinance (Sherman, 1925). Townships (9.7 × 9.7 km, or 6 × 6 miles) were delineated, and divided into 36 sections (1.6 × 1.6 km, or 1 × 1 mile). Lot corners were marked with wooden posts and "witnessed" by (usually) two trees, to facilitate relocation of the boundaries. The record of these witness trees serve as an unintentional vegetation survey before widespread forest clearing.

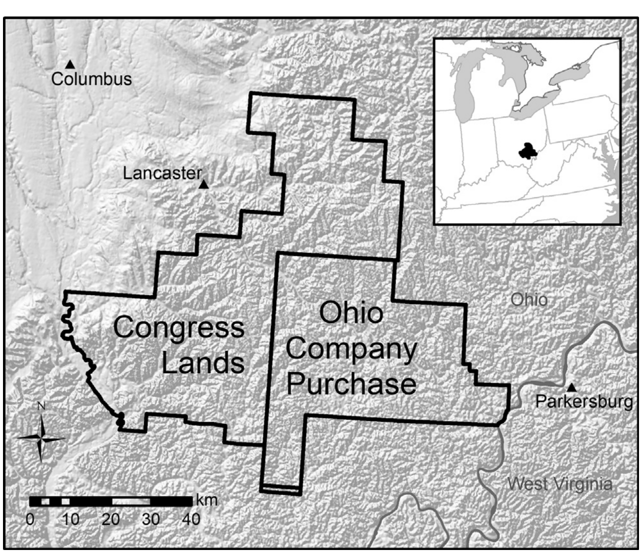

Fig. 1. Study area showing Ohio Company Purchase and Congress Lands East of the Scioto River.

2.2. Forest composition and structure

Forest Inventory and Analysis (FIA) data for the study area were downloaded from http://www.fia.fs.fed.us. We selected the FIA data collected during the most recent five-year measurement cycle, 2006–2011. There were 162 FIA plots in the study area, the great majority of which consisted of four 168.1 m^2 circular subplots within a 0.61 ha area. Fewer subplots are measured if non-forested conditions are present (FIA, 2016). In all, there were 547 subplots within our study area. Species and DBH (diameter at breast height, 1.37 m) data are available for each tree ≥2.54 cm DBH. Since 97.5% of witness trees were ≥12.7 cm diameter, we used this as a DBH cutoff for the FIA trees to facilitate comparison. Furthermore, we removed 101 individuals of non-native species, resulting in a total sample size of 3249 FIA trees.

Species and diameter for each witness tree were transcribed from archival sources (Ohio Company: Digital Collections at Marietta College, http://digicoll.marietta.edu/; Congress Lands: photocopies from the Ohio Historical Society, Columbus Ohio). The Ohio Company Purchase portion comprises 37% of the study area reported in Dyer (2001). Since additional archival data were used in the present analysis (distance and direction from survey corner, Section 2.3.2), transcriptions were performed anew in the present study. Since surveyors operated under nearly identical instructions, witness trees from the two surveys (n = 6233) were combined for subsequent analysis. At the time of the original land surveys, field notes were transcribed into official survey books. These books are organized by township, with witness tree data provided for each surveyed corner. We therefore searched for and removed duplicate witness trees, recorded at common corners for contiguous surveyed sections. After plotting witness trees in GIS (described below), duplicate records were also identified by searching all trees occurring within five meters of another tree. Transcription errors in the original survey books were also identified by looking for "close matches" for witness trees at each surveyed corner, that is, trees at common corners but entered differently in survey books (e.g. a shared corner might list an 11-in. beech on one page and a 14-in. beech on another, or a 14-in. beech on one page and a 14-in. buckeye on another, though both trees occupy the same location). It was remarkable that out of 6233 witness trees, 7.5% were discarded as duplicates, resulting in a sample size of 5765 trees.

Surveyors did not consistently differentiate species among some genera (e.g., hickory, ash), though this is also the case with the contemporary FIA surveys. More challenging was the failure to consistently discriminate among species in the red oak group (subgenus *Erythrobalanus*), which surveyors usually referred to as "black oak;" a similar situation occurs in the land survey records of New England (C.V. Cogbill, personal communication, 2011). For comparative purposes, three species were combined in the FIA data: northern red oak, black oak, and scarlet oak. The witness trees chestnut oak and yellow oak were combined into a single species; the latter designation was preferentially applied in the Congress Lands, the former in the Ohio Company Purchase. Given the relative abundances, we concluded that this was one and the same species. Surveyors did not distinguish between conifers, so the two native pines included in the FIA data were combined (Virginia and pitch pines). Eleven "pine" witness trees were reclassified as hemlock since they occurred within present-day hemlock stands (Stump, 2008). Table 1 orders witness trees in order of their abundance, along with corresponding FIA percentages.

Given the objective of this study, to examine compositional changes since Euro-American settlement, it is important to address potential witness-tree selection bias by the surveyors: whether species selection reflected their relative abundance, or some subjective criterion. Bourdo (1956) points out that although the choice of species adjacent to a corner was limited, surveyors may have purposefully chosen trees that were further away from the corner. We therefore applied the selection bias test proposed by Kronenfeld (2015), based on relative distances to trees at each survey corner. The ANOVA-based approach tests the null hypothesis that all taxa share the same mean relative distance.

2.3. Forest associations

Given the highly dissected topography of the study area and the coarse spatial resolution of sampled witness trees (approximately two trees per 1.6 km), it is not feasible to create a continuous forest region map by interpolation of individual witness trees. In order to create fine-scale maps of presettlement and contemporary forest associations, we assume that tree species respond to environmental gradients that can be captured by variation in topography and soils. Our general approach was to define "landscape classes" using digital elevation models (DEMs) and soil surveys, then assign each tree (witness or FIA) to the appropriate class based on its location. Composition within landscape classes then enabled us to define forest associations using cluster analysis. Specifics of this methodology are described below.

2.3.1. Landscape classes

Using a 0.7-m resolution DEM (OGRIP, 2010), slope and aspect were computed for the study area using ArcGIS (v. 9.3; ESRI, 2009). To smooth out any fine-scale topographic variation that might be uncharacteristic of the tree's setting, slope and aspect grids were aggregated (using mean value) to 10-m resolution. (Exploratory analysis revealed high correlation between the two DEMs at witness tree locations: r = 0.96 for slope, and 0.90 for aspect.) Two classes were created for slope: steep (≥15°, about one-third the study area) and low-moderate (< 15°, about two-thirds of the area). Two classes were also created for aspect: "warm" (90–270°) and "cool," acknowledging the symmetry of radiation load about the north-south axis. The final DEM-based class was topographic position. The 10-m resolution DEM was classified into ridge, slope, and valley using the Benthic Terrain Modeler (Wright et al., 2005), parameterized to the study area based on trial-and-error and visual inspection of results. The three categories of topographic setting (slope, aspect, topographic position) resulted in 12 possible combinations, which were the landscape classes to which each witness and FIA tree was assigned.

In addition to topographic variables, analysis also included one physical and one chemical soil variable, derived from SSURGO digital soil data (NRCS, 2010). Soil Available Water Capacity (AWC) of the top 100 cm was used to create two classes: low (< 117 mm) and moderate-high (≥117 mm). The low cut-off corresponded to the 25th percentile of study area, and included about one-quarter of the witness trees. pH was used to quantify soil fertility, weighted by horizon depth for the top 100 cm of soil. Two classes were created: pH < 5 and pH ≥ 5. Below pH of 5, free and exchangeable soil Al can result in the inhibition of root growth and reduced uptake of key cations, including Ca (Perry and Amacher, 2012). The 100-cm depth was selected for both soil variables since 95% of roots occur within this depth in temperate deciduous forests (Jackson et al., 1996), and soil fertility patterns at this depth would less likely be altered since settlement (J.L. DeForest, personal communication, 2012). The addition of AWC or pH resulted in 24 possible landscape classes, to which witness trees and FIA trees were assigned.

2.3.2. Witness trees

Surveyors typically marked corners with a post, then noted the distance and bearing of witness trees from the post. We used a GIS shapefile produced by the Ohio Department of Natural Resources, Division of Geological Survey, to locate corners, believed to be accurate to within 12 m (McDonald et al., 2006). From these, witness trees were located trigonometrically using distance and bearing measurements. Since surveyors did not account for magnetic declination (Howe, 1890), bearings were adjusted using a historic estimate of declination (NOAA, 2011). Based on their plotted locations, individual witness trees were assigned to the topo-edaphic landscape class in which they occurred.

2.3.3. FIA subplots

Since precise locations of FIA subplots are unavailable to the public due to privacy law, linking trees to topo-edaphic classes involved additional steps. We provided our GIS landscape class layers to the USFS Northern Research Station FIA unit, along with a spreadsheet for determining three subplot centers trigonometrically, as measured from the centrally-located and georeferenced subplot center. The FIA analyst created a circular buffer around each point representing the four subplots, and extracted the percentage of each subplot that fell within each landscape class. All trees within a subplot were placed in a single landscape class if the class comprised > 50% of the subplot; trees were excluded from landscape analysis if no class exceeded 50% of the subplot.

2.3.4. Cluster analysis

Each witness and FIA tree was assigned to the landscape class within which it occurred, and a cluster analysis was performed separately on topography-only (12 classes of slope, aspect, and topographic position), topography + AWC (24 classes), and topography + pH (24 classes). We treat the landscape classes as the "sample units" (McCune and Grace, 2002). Taxa with fewer than five individuals were dropped from analysis, since it would be difficult to reliably assign them to groups (McCune and Grace, 2002). Each landscape class had sufficient trees to retain in the analyses (following guidelines suggested in Mooi and Sarstedt, 2011). The relative density of each tree taxon was computed for each landscape class, and a cluster analysis performed on the landscape classes, creating hierarchical groupings based on similarities in species composition. For example, steep warm slopes may have a similar witness tree composition compared to steep cool slopes, and these two landscape classes would be combined into a "steep slope" group. The clustering method (PC-ORD v. 6, McCune and Mefford, 2011) selected was flexible beta (β = −0.25) using the Sørensen distance measure, which is generally recommended for community analysis (McCune and Grace, 2002). The hierarchical nature of the clustering procedure is evident in the resulting dendrogram, as existing groups combine to form new groups at each iteration. Indicator Species Analysis (Dufrêne and Legendre, 1997) was deemed unsuitable as an aid to determine final number of clusters to retain, since the "lumping" of individual species (e.g., ash, hickory, black oak), and the dominance of witness trees by a few species, meant that a taxon restricted to one group was unlikely. Instead, we sought to identify "natural groups" in the clustering procedures, which provided a compromise between an interpretable summary of results and maximum information retained. Dendrograms and plots of clusters vs. distance aided in this decision.

2.3.5. Ordination

To further explore topographic patterns in both presettlement and contemporary forests, a non-metric multidimensional scaling (NMS) ordination was performed on a combined dataset containing both FIA and witness trees, retaining only those species that occurred in > 1 landscape class. Community resemblance among the samples was expressed by Sørensen distances using relative density in each landscape class. Analysis was performed using the 'slow-and-thorough' autopilot mode of PC-ORD, assuming a random starting configuration. A Monte Carlo test of significance was performed using 250 runs with the real data along with 250 runs with randomized data. Scree plots recommended a two-dimensional solution, and the NMS was then re-run specifying two dimensions and the best starting configuration; the final stress was 5.82 after 52 iterations. The amount of explained variance was expressed by the coefficient of determination between Sørensen distance in species space and Euclidean distance in ordination space.

2.3.6. G-test of association

G-tests (Sokal and Rohlf, 1995) were performed to determine if individual taxa demonstrated an association with topographic position, pH, or available water capacity. Observed occurrences were compared to expected values, based on the proportion of all trees occurring in a particular class. To minimize errors associated with small sample sizes, analysis was restricted to those taxa that accounted for ≥2% of all trees.

3. Results

3.1. Forest composition and structure

Witness tree records suggest the propensity of surveyors to "eyeball" tree diameters, with a high percentage of even numbers recorded (especially 10, 12, 14, 18, 20, 24, 30, and 36 in.). Size-class distribution also suggests that surveyors preferentially selected trees ≥30.5 cm (12 in.). In the presettlement forest, trees larger than 50 cm (20 in.) diameter comprised 30.6% of trees ≥25 cm (10 in.); with the FIA data the percentage has dropped to 10.5%. Selection-bias tests suggest that witness trees reflect their relative abundance in the presettlement forest. No statistical difference was found in mean relative distance to survey corners among any of the presettlement taxa listed in Table 1, nor when all understory species were collapsed into a single taxon. The species' abundances recorded in the witness and FIA trees (Table 1) clearly show the "oak-hickory to maple-poplar transition," with white oak in particular exhibiting a dramatic decrease in abundance. White oak comprised 34.1% of witness trees but only 6.8% of FIA trees ≥12.7 cm (and only 2.6% of FIA trees < 12.7 cm). Pronounced decreases are also observed in the black oak and hickory groups. Overall, oaks and hickories decreased from being 64% of trees in the presettlement forest to 25% in the contemporary forest (13.8% of FIA trees < 12.7 cm). The mesophytic species American beech also experienced a marked decrease, but in contrast three other mesophytic species – sugar maple, red maple, and tulip poplar – have increased in the last two centuries, from 10.9% of witness trees to 33.5% of FIA trees. In addition, nine taxa that were rare in the presettlement forest (each < 1% of witness trees: sycamore, buckeye, pine, black walnut, locust, black cherry, sassafras, sourwood, and bigtooth aspen) have all become more abundant in the contemporary forest. Together these nine taxa comprised only 3.2% of witness trees but now are 24.4% of FIA trees.

3.2. Forest associations

3.2.1. Topographic forest associations

Cluster analysis of witness trees performed with "topography only" variables (slope, aspect, topographic position) revealed two primary associations: Ridges, and Slopes + Valleys (Figs. 2A and 3A). Two similar associations were also revealed using the FIA data (Fig. 2B). (Ridges comprise 18% of the five-county study area, slopes and valleys together comprise 82%.) White oak, hickory, and beech were among the most abundant species in the presettlement forest, and all exhibited very similar relative densities across topographic positions. Black oak, chestnut oak, and chestnut were more abundant on ridges, whereas sugar maple, red maple, elm and ash were more prevalent on slopes and valleys. For some species, topographically-driven differences apparent in the witness trees are now more pronounced in the FIA data (e.g., chestnut oak on ridges, tulip poplar in valleys; Table 2). In contrast, white oak had an "equitable" distribution across topographic positions in the presettlement forest, but now demonstrates an association with ridges. Red maple reversed its pattern, being more prevalent in valleys in the presettlement forest, but now is more strongly associated with slope and ridge positions (Table 2).

Ordination of the combined FIA and witness tree data, classified by "topography only" into the 12 landscape classes each, explained 96.5% of the variance in species composition. Fig. 4 presents the two axes of the NMS ordination; Axis 1 accounted for 82.9% of the variation, and Axis 2, 13.6%. Axis 1 shows a wide separation in species composition between presettlement and contemporary forests. Within the presettlement forest, ridge sites are distinct but not widely separated from

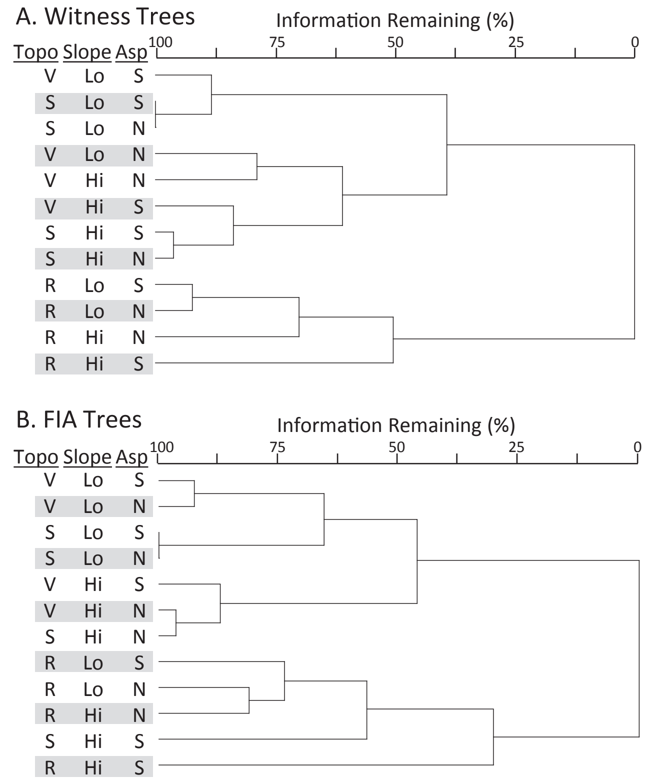

Fig. 2. Cluster analysis results using 12 "topography only" classes, for (A) Witness Trees and (B) FIA Trees. Topographic Position ("Topo"): R (Ridge), S (Slope), V (Valley); Slope: Lo (low, < 15°), Hi (high, ≥15°); Aspect ("Asp"): N (0–90, 270–360°), S (90–270°).

slope and valley. In contrast, Axis 2, though explaining much less compositional variation, does further segregate FIA landscape classes by topographic position.

3.2.2. Topo-edaphic forest associations

Spatial covariance was observed among pH and AWC classes, with high-pH sites corresponding with moderate-high AWC sites. Although low-pH cells were equally distributed among the low and moderate-high AWC sites, 90% of high-pH cells occurred within the moderate-high AWC class. Similarly, three-quarters of low-AWC cells were low-pH, and three-quarters of high-AWC cells were high-pH. G-tests indicated that more trees showed a significant association with pH compared to AWC classes; this held true for both witness trees and FIA data (Table 3). A number of taxa that experienced a decrease since the presettlement period have shifted their associations to more "favorable" sites in the contemporary forest, now occurring preferentially on high-pH sites (white oak, hickory, black oak) or moderate-high AWC sites (hickory). In contrast, some species that have increased since settlement have expanded beyond the most favorable sites. Sugar maple is no longer statistically associated with high-pH, high-AWC sites, and red maple now exhibits an association with low-pH, low-AWC sites.

Interactive effects of topographic and soil factors on species composition were evident when soil variables were included in the cluster analysis. Adding pH as a soil fertility category (resulting in 24 topo-edaphic landscape classes) revealed two associations in the presettlement forest: low-pH slopes clustered with ridges, and high-pH slopes clustered with valleys (Fig. 3B). With the FIA data, three forest associations were present: Ridges still remained a distinctive association, but the Slopes + Valleys association segregated into high- and low-pH clusters.

Whereas 40% of the study area was classified as low-pH, only 25%

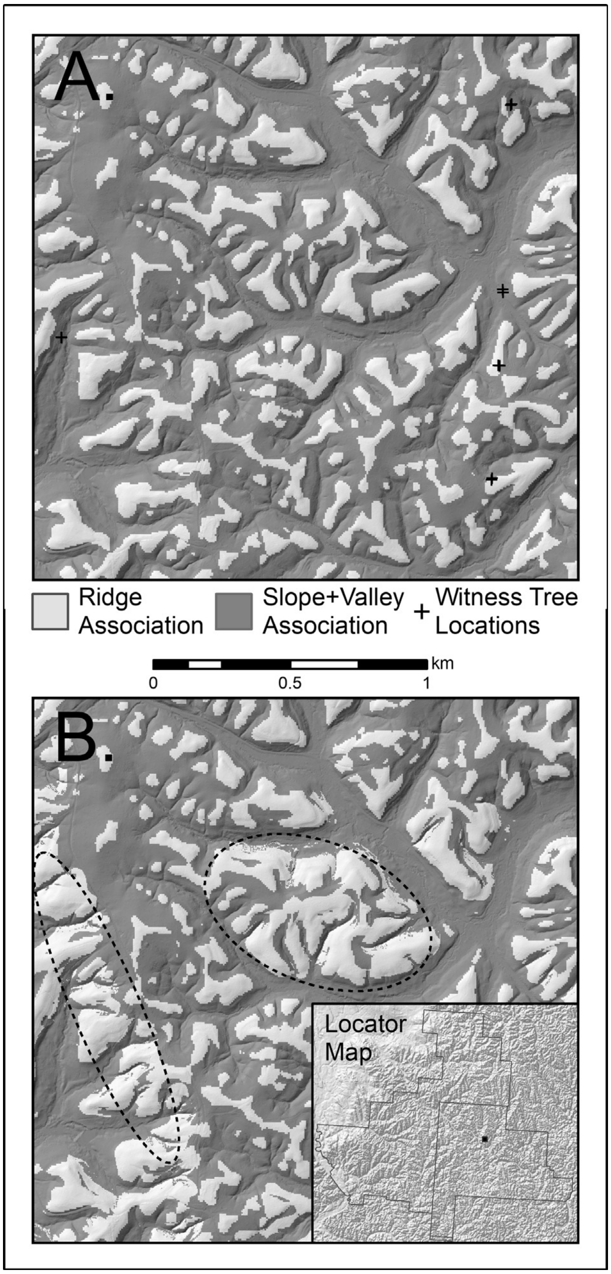

Fig. 3. Presettlement forest regions. (A) Results of "topography only" cluster analysis (slope, aspect, topographic position). (B) Inclusion of pH results in low-pH slopes clustering with ridges (area within dashed lines).

was classified as low-available water capacity. Cluster analysis performed with this more unbalanced division is more challenging with smaller initial group sizes. (Three landscape classes had to be dropped from the FIA analysis because they had few trees.) But when soil available water capacity was included with the topographic variables, interactive effects were again noted. With the witness trees, three forest associations can be discerned: high-AWC slopes and valleys, low-AWC ridges and steep slopes, and high-AWC ridges. With the exception of segregating low-AWC ridges, AWC was not as an important factor in distinguishing forest clusters with the FIA data.

4. Discussion

4.1. Forest transition

Not unexpectedly, an oak-hickory to maple-poplar transition was observed, as Paciorek et al. (2016) reported in a "township-level" (8 km grid) analysis extending from Maine to Minnesota. White oak was by far the most dominant species in the southeastern Ohio presettlement forest, as Whitney (1982) also observed in northeastern Ohio. The decrease in white oak abundance from the presettlement forest to the current forest has been documented in many areas of the eastern deciduous forest (Abrams, 2003). Combined, oaks comprised half of witness trees in our study area, but now constitute only 17.7% of trees. Sugar maple and tulip poplar increased significantly over the last 200 years (4.6 to 9.4% and 2.9 to 11.6%, respectively). Red maple is the most abundant tree species in the contemporary forest, comprising 12.3% of stems ≥12.7 cm DBH. Many of these trees are small however; two-thirds of red maple are < 25 cm, and only 1.5% are > 50 cm DBH. As McEwan et al. (2005) noted, presence in the shaded and humid understory does not guarantee eventual canopy dominance on more xeric sites. In 46 Appalachian oak stands in Pennsylvania, Steiner et al. (2018) report a delay in oak dominance over red maple until the fourth decade after clearcut harvest. This pattern is more common in drier physiographic provinces (Blue Ridge, Ridge and Valley) and on more xeric landscape settings; on the more mesic Appalachian Plateau sites, red maple continued to dominate, however.

Besides oak, other hard-mast producing witness tree taxa demonstrated significant declines, which could have a large negative impact on mast-dependent wildlife (McShea et al., 2007). Beech decreased from 10.3% to 4.0%. This post-settlement decrease is in keeping with a pattern observed throughout the deciduous forest, and has been attributed to its low recolonization ability following forest clearing (e.g. Smith et al., 1993; Thompson et al., 2013; White and Mladenoff, 1994). Hickory decreased by half (native species include bitternut, pignut, mockernut, shellbark, shagbark, and red hickories). Chestnut made up less than 2% of witness trees, before extirpation by chestnut blight in the early 20th century.

Through our topo-edaphic mapping, a more nuanced compositional shift is observed at the landscape level. A topographic pattern is evident in the presettlement forest, with ridges compositionally distinct from slopes and valleys. However, these differences in composition were subtle, because most of the dominant taxa (e.g., white oak, hickory, beech) were similar in abundance across the landscape. The NMS ordination shows that this topographic distinctiveness has become more pronounced in the contemporary forest. Furthermore, several taxa reveal changes in site affinities. Although the most abundant species have wide ecological amplitude, some species' abundance patterns have shifted topographically; for example white oak is now more strongly associated with ridges. There is also the suggestion that some taxa that have decreased since settlement (white oak, black oak, hickory) now occur on better quality sites (higher pH or AWC) than expected by chance, and species that have increased (red maple, sugar maple) have expanded into lower quality sites. In the presettlement forest for example, red maple preferentially occurred in valley settings, but now demonstrates an association with ridge and slope positions (Table 2). Furthermore, it now occurs in low-pH and low-AWC sites more often than expected by chance, although no association with pH or AWC was observed in the presettlement forest (Table 3). These results indicate that numerous taxa have shifted their realized niches, perhaps in response to alterations in competitive relationships brought about by changes to the physical environment and/or the disturbance regime. Below, we address land use change, drought, fire, and atmospheric deposition as potential drivers of the observed changes.

Table 2
Percentage of taxa by topographic position, for taxa comprising ≥3% of witness trees or FIA trees, with underlined values indicating a stronger association between the taxon and topographic position than expected by changes (G-test, P ≤ 0.01).

	Witness Trees			FIA Trees[a]		
	Ridge (n = 1035)	Slope (n = 3117)	Valley (n = 1451)	Ridge (n = 591)	Slope (n = 1341)	Valley (n = 969)
White Oak	33.1	34.9	33.3	9.0	6.7	3.8
Black Oak	20.7	11.9	9.4	9.3	8.1	6.1
Hickory	15.4	13.7	13.4	5.6	7.3	6.9
Beech	9.4	10.1	11.4	2.4	5.0	4.1
Chestnut oak	5.7	2.2	2.3	6.9	2.1	2.0
Sugar maple	1.4	5.6	4.7	4.4	9.2	12.7
Blackgum	2.5	3.7	4.0	1.2	1.4	1.4
Red maple	1.8	3.2	4.9	16.6	13.2	9.0
Tulip poplar	2.5	2.3	4.3	4.6	10.7	17.9
Elm	0.6	2.7	1.4	2.9	3.4	5.5
Ash	0.4	2.2	1.5	3.4	3.8	4.6
Cherry	0.0	0.2	0.3	4.4	6.9	5.6
Aspen	0.0	0.1	0.0	11.5	4.8	0.7

Note: Values "by column" provide a summary of species abundance by topographic position, but since topographic positions occupy different areas within the study area, caution must be used in interpreting values "by row".
[a] Trees were excluded from FIA subplots that did not exceed 50% ridge, slope, or valley, resulting in a smaller sample size than reported in Table 1.

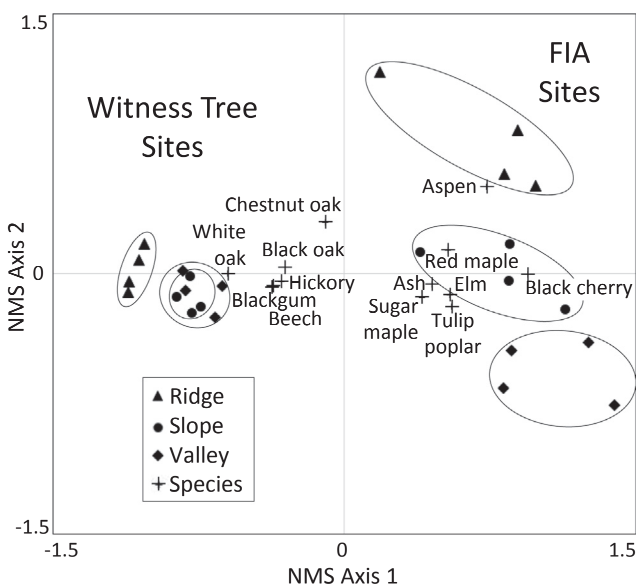

Fig. 4. Graph of NMS ordination on combined dataset of witness and FIA trees, based on relative density of taxa within each topographic class. Axis 1 segregates witness tree classes from FIA classes, and accounts for 82.9% of variation. Axis 2 explains 13.6% of the variation, and segregates FIA classes by topographic position.

4.2. Land use change

Land use changes and subsequent successional patterns have played a major role in compositional shifts since settlement. Most of the study area consists of regrowth following a period of rapid and widespread deforestation and logging 1870–1930. Compared to the presettlement forest, today's forest has smaller-diameter trees, and is dominated by early-successional species. Species that have experienced a significant increase since settlement tend to be small-seeded and wind-dispersed (e.g. sugar maple, red maple, tulip poplar, elm, ash, aspen), whereas most species that have decreased are large seeded and animal dispersed (white oak, hickory, black oak, beech). Dramatic long-term changes in forest composition have been reported from other areas in the eastern U.S. with several notable studies also documenting changes by comparing witness trees with FIA plot data. In the Upper Midwest (Wisconsin, Minnesota, Michigan), the major compositional change from presettlement to current forests has been a large decrease in pines

Table 3
Statistically-significant associations with soil classes (pH and AWC) for both witness tree and FIA taxa (G-test, P ≤ 0.05). All sites fell into one of two pH classes, pH < 5 (poor fertility) or pH ≥ 5 (good fertility). Similarly, all sites fell into one of two AWC classes (available water capacity in the top 100 cm): Low (< 117 mm, corresponding to the 25th percentile of the study area), and Moderate-high (≥117 mm).

Taxon	Change since settlement (%)[a]	Soil pH: Witness Trees	Soil pH: FIA	Soil AWC: Witness Trees	Soil AWC: FIA
White oak	−27.3	< 5	≥5	–	–
Hickory	−6.9	–	≥5	–	Mod-high
Beech	−6.3	≥5	–	Mod-high	–
Black oak	−5.0	< 5	≥5	Low	–
Blackgum	−2.1	< 5	< 5	–	Low
Chestnut oak	+0.2	< 5	< 5	–	Low
Elm	+2.1	≥5	≥5	Mod-high	Mod-high
Sugar maple	+4.8	≥5	–	Mod-high	–
Tulip poplar	+8.7	< 5	< 5	Low	–
Red maple	+9.2	–	< 5	–	Low

[a] Abundance difference in witness trees vs. FIA plots, as reported in Table 1.

and a concomitant increase in maples and aspens (Schulte et al., 2007); due to compositional changes and regional homogenization, Goring et al. (2016) report the loss of presettlement forest assemblages and the creation of novel assemblages in these Great Lakes forests, as land-use change synchronizes successional patterns and alters the regional species pool. Maples have also increased substantially in the Northeast, while beech and oaks have exhibited sharp declines in relative abundance (Thompson et al., 2013). As observed in the Upper Midwest, compositional homogenization following widespread clearing has masked broad-scale environmental gradients that spanned numerous ecoregions in the presettlement forests.

However, land use change alone may be insufficient to explain compositional shifts observed here, and throughout the eastern deciduous forest (Pederson et al., 2015). Eastern forests have experienced multiple factors acting in synchrony that could contribute to compositional change (McEwan et al., 2011), with changes in climate and in fire frequency potentially playing prominent roles.

4.3. Drought

The late 20th century is among the wettest periods in the eastern U.S. since 1500 CE (Pederson et al., 2015). Over this time, the American

Northeast and Canadian Southeast have exhibited increases is average daily precipitation, fraction of wet days in a year, and average length of consecutive wet days (Roque-Malo and Kumar, 2017). The Ohio Valley has experienced "garden watering" conditions since the mid-twentieth century, with more frequent summer rain events (Bishop and Pederson, 2015). A broad-scale increase in moisture could favor increased dominance by mesophytic species. However, with the potential for more frequent and severe droughts in the near future (Walsh et al., 2014), there is interest in understanding the effects of drought on forests. Overall, a drier climate could favor oaks, whose growth and mortality rates are less affected by drought (Klos et al., 2009).

The North American Drought Atlas (Cook et al., 2008) indicates central Ohio (39.5–41°N, 81.5–85°W) experienced numerous multi-year droughts (with summer PDSI < -2) in the centuries preceding Euro-American settlement: a five-year drought beginning 1562 (including two years with summer PDSI < -3), three-year droughts beginning in 1575 (with one year < -3) and 1627, and starting in 1698 three consecutive years with summer PDSI < -2 followed by three consecutive years with summer PDSI < -1.5. Multi-year droughts in the western U.S. are linked to tree mortality (Clark et al., 2016), and a severe three-year drought resulted in species-specific patterns of mortality in the southeastern U.S. (Berdanier and Clark, 2016). It seems reasonable to assume that severe droughts in the 16th and 17th centuries would favor drought-tolerant species such as oak in our Ohio study area, relative to drought-sensitive species. Drought-induced mortality, and a possible increase in fire frequency would also favor certain shade- and fire-tolerance traits. The century immediately preceding the survey of witness trees was more mesic, however, with no three-year droughts (summer PDSI < -1.5). This climatic change could be expected to favor different life-history traits, and the size-class distribution of the witness trees may support this supposition. Table 4 presents the abundance of common witness trees in the small size class (25–38 cm DBH) vs. large size class ($>$ 50 cm DBH), which can serve as a surrogate for age classes. Taxa that had higher relative abundance in the large size class (which were more likely to have established prior to the more mesic 18th century) included white oak, black oak, and chestnut oak - taxa tolerant of drought and fire with intermediate shade tolerance. Taxa more prevalent in the small size class (which are more likely to have established after the last major drought 1698–1703) include beech, sugar maple and red maple – shade-tolerant taxa that are intolerant of drought and fire. By contrast, hickories are drought- and fire-tolerant but at the time of the witness tree survey were more abundant in the small size class. In contemporary oak forests, the slow-growing hickories are typically smaller than the oaks, despite being the same age (Cowden et al., 2014). So, it may be that the smaller hickories in the witness tree survey had established with the oaks, but remained subordinate due to slower growth rate. This 18th century "mesophication" is similar to the contemporary pattern observed in the eastern U.S. In central Ohio in the twentieth century there were no droughts (summer PDSI < -1.5) of three or more consecutive years, and there were 31 years with summer PDSI > 1, nearly double the total of each of the previous four centuries. If the study area experiences a return to more frequent and severe droughts (Walsh et al., 2014), how might a vegetation response unfold?

Clark et al. (2016) note that drought effects at the level of individual trees are well established, but that extrapolating to the landscape level presents a challenge. It is likely that topographic-driven variations in water balance can alter competitive relationships under drought conditions, leading to habitat shifts among tree species. Presettlement records do provide a means to explore landscape-level changes under drier climatic conditions. Not only are individual species shifting site preferences, but landscape patterns have also changed. Ridge, slope, and valley settings, an inferred xeric-mesic gradient, have all witnessed major compositional changes since presettlement (Table 2). Such topographic shifts are in accord with observations in two old-growth stands near our study area. From field surveys and dendroecological analysis of Dysart Woods, a white oak-dominated stand c. 100 km from the study area, McCarthy et al. (2001) concluded that with a changing climate, oak abundance and regeneration has shifted to drier upper slopes. A similar observation was made by McEwan et al. (2005) at Lilley Cornett Woods, about 270 km south of our study area. They observed white oak in the overstory across a number of settings, but successful regeneration was restricted to xeric ridge positions.

4.4. Fire

If the region experienced more severe droughts in the presettlement period (1500s, 1600s), then one could hypothesize that fire would have been more frequent, and potentially result in a more pyrogenic species assemblages (Nowacki and Abrams, 2008). Yet fire-scar studies, which date the occurrence of non-lethal fire on surviving trees, have not revealed a strong link between fire and drought in the Appalachians, either before or after Euro-American settlement. Unfortunately, there remain relatively few fire-scar sites encompassing the presettlement period in the Central Hardwood (Hart and Buchanan, 2012) or Appalachian Plateau (Lafon et al., 2017; Stambaugh et al., 2018) regions. Appalachian fire-scar studies reveal an anthropogenic origin for the majority of fires, which occur primarily in the dormant season when lightning (and drought stress) are uncommon (Lafon et al., 2017). In oak-pine forest of Missouri's Ozark Highlands, Guyette et al. (2002) characterized the environment during the settlement period as ignition saturated; compared to the presettlement period, fires are more frequent and widespread without a strong link to drought. In contrast, during the presettlement period with lower population densities, the fire regime was ignition limited. A fire-drought link would be more likely during this period of more infrequent fires, with the spatial extent and spread of fire limited by topographic roughness. In southern Ohio, fire-scar data are currently limited to the postsettlement period ca.

Table 4
Abundance in small and large size classes for common witness trees, as a percentage of all witness trees.

	Taxon	25–38 cm (10–14.9 in.)	> 50 cm (> 20 in)	Shade tolerance	Drought tolerance	Fire tolerance
Higher percentage in larger size classes	White oak	26.7	52.2	Intermediate	High	High
	Black oak	8.1	18.7	Intermediate	High	High
	Chestnut oak	2.8	3.6	Intermediate	High	High
	Tulip poplar	2.5	3.5	Low	Low	High
	Chestnut	1.2	3.5	Intermediate	Intermediate	Low
	SUBTOTAL	41.3	81.5			
Higher percentage in smaller size classes	Hickory	19.5	4.2	Intermediate	High	Low
	Beech	13.2	5.4	High	Low	Low
	Sugar maple	6.3	1.1	High	Low	Low
	Red maple	4.9	0.6	High	Low	Low
	Blackgum	4.7	0.1	High	Intermediate	High
	SUBTOTAL	48.6	11.4			

Note: Tolerance traits compiled from numerous published and online sources. Fire tolerance considers direct effects on adult individuals, vs. a regeneration response.

1850-present. These data reveal that fires occurred frequently at several sites in southeastern Ohio from ca. 1870 to 1930 (Hutchinson et al., 2008; McEwan et al., 2007) and that the establishment of maples coincided with the cessation of fire (Hutchinson et al., 2008). The closest fire-scar sites to our study extending to the presettlement period also show evidence of increased fire frequency after settlement before the onset of fire suppression efforts in the 20th century: Lilley Cornett Woods Kentucky, 270 km south of our study area (McEwan et al., 2014), Boone Creek watershed Indiana, 400 km southwest (Guyette et al., 2003), and several sites in central Pennsylvania, c. 450 km northeast (Stambaugh et al., 2018). Fire chronologies at these study sites reveal presettlement fire, but also suggest extended fire-free intervals prior to settlement. Stambaugh et al. (2018) report regionally-synchronous fires at their sites, based on their pine chronologies.

Fire was noted by the Ohio Company surveyors in their line descriptions. Some burns were quite extensive ("this mile, and indeed, all this part of the township has been burnt and the timber principally destroyed except the low ground – the hills are covered with thick growth of brush of almost every kind.") One large burned area occurred along the location of a major salt road, suggesting that this area may have already been transitioning from an ignition-limited fire regime stage. In several instances, evidence of burned land was noted when external township lines were first surveyed in 1788–1789, but when the interior lines were surveyed 1796–1797, surveyors did not comment on burned conditions along the resurveyed lines. Instead, they only reported on the type of timber, or they sometimes noted brushy conditions. Since the public land survey represents a snapshot in time, it is difficult to assess the frequency of fires during this period, and our research into disturbance noted in these line descriptions is ongoing.

4.5. Nitrogen deposition

Atmospheric deposition of N may be another potential factor related to the observed changes in forest composition. Globally, it has been estimated that the amount of biologically-available N produced by humans increased 10-fold from 1860 to 1990 (Galloway et al., 2004). Across most of the eastern U.S., N deposition is greater than in most other parts of the country and exceeds the critical load, the level at which it is likely to alter ecosystem structure and function (Pardo et al., 2011). In the Appalachian Plateau Region that includes our study site, total wet atmospheric deposition of N over the last four decades has averaged from 6.2 kg ha^{-1} yr^{-1} in the 1990s to 4.6 kg ha^{-1} yr^{-1} in the 2010s (National Atmospheric Deposition Program, https://nadp.slh.wisc.edu/). FIA data were used to show that red maple, sugar maple, tulip poplar and black cherry growth in the Midwest and northeast U.S. was positively related to levels of N deposition (Thomas et al., 2010). All of these species form arbuscular mycorrhizal (AM) associations. The authors hypothesized that tree species with AM associations could benefit from increased N availability to a greater degree than species with ectomycorrhizal (EM) associations, because EM produce enzymes that can make N available from organic forms, while AM do not. Also, even moderate N addition has been shown to decrease EM diversity and alter EM composition in Illinois oak forests (Avis et al., 2008). The species with the largest long-term declines in abundance in our region, the oaks, hickories, and American beech, all have EM associations (Comas and Eissenstat, 2009). In addition to the positive effects of N deposition on the growth of some species, oak regeneration may be negatively impacted by greater N deposition. In Illinois, planted northern red oak seedlings developed 60% less biomass at a site with higher N deposition compared to a site with lower deposition, while the growth of sugar maple seedlings was not different among sites (BassirRad et al., 2015).

Although speculative, the long-term changes in species composition in our region are consistent with research that indicates species-specific responses to levels of N deposition. In addition to increases in AM species and decreases in species with EM associations, a biogeochemical driver may also be contributing to the observed shifts in realized niches based on soil pH and AWC. Nitrogen deposition may have enhanced seedling competitiveness of red maple on more acidic sites, and sugar maple and beech on all sites (Table 3). Concomitantly, hickory, white oak, and black oak now are associated with well-buffered sites. Although it can be difficult to disentangle drivers since soil pH and AWC covary, white oak and black oak do not demonstrate an association with moderate-high AWC sites in the contemporary forest, but are associated with higher-pH sites.

4.6. Conclusion

Climate change, modifications to the physical environment, and altered disturbance regimes affect competitive relationships and patterns of mortality and establishment; the manifestation of these biotic interactions can be expected to differ along environmental gradients. By adopting a spatially-explicit landscape-level approach, we have observed shifts over the past 200 years in the realized niches of taxa dominant in the eastern deciduous forest. These shifts suggest diverse individualistic responses to a multiple set of interacting drivers, rather than a community-level response to a single driver (e.g., fire, climate). Our analysis also suggests that mesophication is not unique to the twentieth century, but was evident in the presettlement forest as well. Acknowledging geographic variation in both biotic and abiotic factors throughout the eastern temperate forest, we encourage further fine-scale analyses that seek to disentangle drivers of compositional change, to understand forest dynamics under a changing climate.

5. Declarations of interest

None.

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