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

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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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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