

Topographic, edaphic, and stand structural factors associated with oak and hickory mortality and maple and beech regeneration in mature forests of Appalachian Ohio

THESIS

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Abstract

Oak (*Quercus* spp.) and hickory (*Carya* spp.) trees are failing to replace themselves in forests of the eastern U.S., likely due to fire suppression and a moister climate during the past century. Our study explored the implications of this mesophication process for future forest composition in southeastern Ohio. In 2016-2018 we resampled permanent plots first established in 1993-1995, in mature forests of the Athens and Marietta Units of the Wayne National Forest. We used mixed logistic regression models to characterize mortality patterns of five oak and one hickory species, and generalized linear mixed models to characterize sapling density patterns of three common shade-tolerant tree species that are likely to dominate future forest composition. For both the mortality and sapling models, we chose a set of *a priori* topographic, edaphic, and stand structural variables, and used the full set of *a priori* covariates for analysis of each species. Our mortality data revealed relatively high mortality rates for all species of the red oak subgenus (*Erythrobalanus*). Models indicated that chestnut oak (*Quercus montana*) and pignut hickory (*Carya glabra*) mortality were positively associated with competition, while white oak (*Quercus alba*) mortality was negatively associated with competition. Northern red oak (*Quercus rubra*) mortality was associated with mesic topographic positions and older stand age. Our sapling data showed that American beech (*Fagus grandifolia*) nearly doubled in density between the two sampling periods (217 trees per hectare[tph] 1990s, 429 tph 2010s), while both red maple (*Acer*

rubrum) and sugar maple (*Acer saccharum*) nearly halved in density (red maple 441 tph 1990s, 216 tph 2010s; sugar maple 608 tph 1990s, 298 tph 2010s). Models indicated that soil acidity was positively related with red maple sapling density, and negatively associated with sugar maple sapling density. Higher slope positions were positively related with red maple sapling density and negatively associated with American beech sapling density. Overall, these results indicated that stand structural variables are more important than soil characteristics and topographic position in explaining mature tree mortality of most common oak and hickory species, and that topographic and acidity gradients will likely partially explain future relative dominance patterns of red maple, sugar maple, and American beech.

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Fields of Study

Major Field: Environment and Natural Resources

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Chapter 1

Red maple, sugar maple, and American beech sapling regeneration in mature hardwood forests of southeastern Ohio, as affected by landscape, edaphic, and stand structural factors

Abstract

Oak (*Quercus* spp.) and hickory (*Carya* spp.) trees are failing to replace themselves in forests of the eastern U.S., likely due to fire suppression and a moister climate during the past century. Oak restoration is not widely applied across large areas of eastern forest. Thus, competitive interactions between saplings of shade-tolerant species in mature oak-hickory forests have substantial potential to drive future forest compositions. We studied several factors driving sapling density patterns of three common shade-tolerant tree species in southeastern Ohio: red maple (*Acer rubrum*), sugar maple (*Acer saccharum*), and American beech (*Fagus grandifolia*). In 2016-2018, we resampled 167 1/100th hectare plots from a long-term study established in 1993 - 1995 on the Wayne National Forest of southeastern Ohio, and thus we were able to evaluate changes in sapling density patterns between the two time periods over 21-25 years. We used generalized linear mixed models with a negative binomial distribution to characterize each focal species' relationship with selected topographic, edaphic, and

stand structural factors. We found that American beech sapling density nearly doubled between the two sampling periods (217 trees per hectare[tph] 1990s, 429 tph 2010s) while both maple species declined in sapling density by more than half (red maple 441 tph 1990s, 216 tph 2010s; sugar maple 608 tph 1990s, 298 tph 2010s). Our models showed that soil acidity was an important factor associated with maple saplings; sugar maple was positively associated with high pH, red maple with low pH. Slope position was also important for multiple species; red maple was positively associated with upper slopes while American beech was positively associated with lower slopes. Overall, these results indicated that stand structural variables are more important than soil characteristics and topographic position in explaining mature tree mortality of the most common oak and hickory species, and that topographic and acidity gradients will likely partially explain future relative dominance patterns of red maple, sugar maple, and American beech.

1 Introduction

Many studies over the past few decades have found that oak and hickory trees are being replaced by shade-tolerant mesophytic species such as red maple (*Acer rubrum*), sugar maple (*Acer saccharum*) and American beech (*Fagus grandifolia*; hereafter beech) (Brose et al. 2014; Nowacki and Abrams 2008). This process perpetuates itself through a positive feedback loop, in which the mesophytic species shed leaf litter that holds more moisture and decomposes faster than the litter of more xeric tree species like oaks and hickories (*Carya* spp.) (Alexander and Arthur 2014; Kreye et al. 2013), and they cast deeper shade than more xeric tree species (Canham et al. 1994). The combined effect is a cooler, moister understory, with more fertile soil and leaf litter with greater resistance to

fire. This changing of site conditions is called “mesophication” (Nowacki and Abrams 2008). Oak seedlings and saplings tend to fare poorly in the more mesic conditions, especially relative to maple and beech seedlings and saplings, and fire becomes less likely. In many cases it is likely that the stable state of the entire ecosystem will eventually change from the former oak-hickory type and to a maple or maple-beech type (Nowacki and Abrams 2008). Due to the positive feedback cycle of mesophication, reversing these trends becomes increasingly difficult with time (Abrams 2005). Many researchers have attributed mesophication to fire suppression in the past century (Nowacki and Abrams 2008), and other potential contributing factors include greater precipitation and a steady increase in the whitetail-deer (*Odocoileus virginianus*) populations and resulting herbivory during the past century (McEwan et al. 2011; Pederson et al. 2015). Other factors may have overinflated modern expectations for oak dominance on the landscape, by increasing oak regeneration to extremely high levels in the early 20th century. These include wide-scale forest harvesting and subsequent unintentional forest burning, and the near-extinction of American chestnut (*Castanea dentata*), both of which were likely competitively advantageous for some oak species (McEwan et al. 2011; Whitney 1994).

Relatively little research has focused on the effect of landscape-scale dynamics on mesophication (Palus et al. 2018). Three studies have provided information about differences in tree species compositions on discrete landscape positions, including two reporting changes over two “snapshots” in time (Olson et al. 2014; Palus et al. 2018), and one reporting species composition in a single snapshot (Jose and Gillespie 1997). Among other questions, these studies addressed the hypothesis that oak regeneration could be

more successful than mesophytic regeneration on drier landscape positions. Olson et al. (2014) found that oak could be successfully recruited into the sapling layer of mature forests of the Missouri Ozarks, on most landscape positions. However, Missouri has markedly drier forests compared with other regions of the eastern U.S. (Hanberry and Nowacki 2016). Studies in southern Indiana (Jose and Gillespie 1997), and southeastern Ohio (Palus et al. 2018) found that oak saplings and small trees were numerically outcompeted by red maple, beech, and sugar maple, even on drier landscape positions.

This led us to ask which factors are influencing the successful regeneration of these three mesophytic trees species in mature central hardwoods forests. If oaks will not dominate future undisturbed forests, what tree species will? The question is critical because in recent decades a “hands-off” approach has been a dominant management strategy in eastern U.S. forests (Widmann 2016), and sugar maple, red maple and beech each provide different ecosystem services and face different future threats. Sugar maple is the most economically valuable of the three, both for lumber (Dey et al. 2017; Ray 2018), and for syrup (Matthews and Iverson 2017). In contrast, beech bark disease has degraded the quality of beech lumber over much of eastern North America (Cale et al. 2017). Beech provides hard mast crops if healthy, and thus an increase in beech would likely be beneficial to wildlife that also consume acorns and hickory nuts (Gysel 1971; Jakubas et al. 2004). Maples are generally seen as undesirable for wildlife when compared with oaks (McShea et al. 2007). Red maple often has lower commercial value than sugar maple and oaks (Ray 2018), although its increasing commonness lends potential to use it in low-value wood products (Alderman et al. 2005). Both maple species face potential threats from Asian long-horned beetle (*Anoplophora glabripennis*)

(Dodds and Orwig 2011) and spotted lanternfly (*Lycorma delicatula*) (Dara et al. 2015).

In addition to beech bark disease, beech faces a new potential threat from beech leaf disease, the full ramifications of which are yet unknown (Ewing et al. 2018). Climate change will also have different impacts on our focal species; severe climate change scenarios are projected to decrease basal area and density of sugar maple and beech by 2100 in the central Appalachians, while slightly increasing the same metrics for red maple (Butler et al. 2015).

1.1 Purpose, Questions, and Hypotheses

Our study sought to increase understanding about the drivers of the regeneration patterns for the three most common mesophytic species in southeastern Ohio: red maple, sugar maple, and beech. We sampled two units of the Wayne National Forest (hereafter the Wayne), in two time periods: the 1990s and 2010s. Using these data, we explored three questions:

- 1) How is the relative dominance of each of our three focal species changing over time?
- 2) What are the relationships of regeneration of our focal species with topographic position (slope and aspect), stand structural characteristics (stand age and basal area), and soil characteristics (pH and depth)?
- 3) Will our ability to predict sapling composition with landscape variables decrease over time as mesophication changes the edaphic conditions?

Our hypotheses are:

- 1) Beech will be more common relative to red maple and sugar maple in the 2010s sampling period.
- 2) Red maple saplings will be associated with upper slopes and drier aspects. Sugar maple and beech saplings will both be associated with lower slopes and more moist aspects. Saplings of all three species will be associated with lower overstory basal area and with older stands. Red maple saplings will be more associated with shallower soils and lower pH. Sugar maple saplings will be associated with deeper soil textures and higher pH. Beech saplings will be associated with deeper soil textures and lower pH.
- 3) The performance of our sapling-species abundance models will decrease with time, as judged by r^2 values and model coefficients.

2 Methods

2.1 Study Area

Our study area is the Wayne National Forest of southeastern Ohio, specifically the Athens Unit and the Marietta Unit. Southeastern Ohio is unglaciated, strongly dissected by steep hills, heavily forested, and has a long history of intensive and extensive land use, settlement, and land abandonment by both Native American groups and European descendants (Hutchinson et al. 2003; Kern and Wilson 2014) (see Appendix A for more information on southeastern Ohio land-use history).

2.1.1 Climate

Southeastern Ohio has a continental climate with cold winters and warm, humid summers. It receives precipitation (mostly rainfall) relatively evenly throughout the year, although rainfall is slightly lower in fall and winter than in spring and summer (NOAA 2018). The Marietta Unit is likely slightly moister and warmer than the Athens Unit; the average annual rainfall for the Marietta Wastewater Treatment Plant weather station was 42.70 inches from 1981-2010, 3.33 inches more than the 39.37 inch average for the Athens Ohio University weather station (NOAA 2018). Additionally, the average temperature for the Marietta Station was 1.2°F higher than that of the Athens Station for the same period (NOAA 2018).

2.1.2 Bedrock and Soil

The Athens Unit and Marietta Unit are both located on the unglaciated Allegheny Plateau Province (Lessig et al. 1977; Lucht et al. 1985). The Athens Unit is primarily located on slightly older bedrock, from the Pennsylvanian Era of 302-318 million years ago, formed from multiple cycles of advance and retreat of prehistoric seas and swamp forests. Most of the bedrock of the Marietta Unit is from the Permian Era of 298-302 million years ago, formed from sediment accumulation in a prehistoric coastal swamps, with some Pennsylvanian bedrock in modern valleys (Kern and Wilson 2014; Ohio Division of Geological Survey 2017). Common rock types of both units include sandstone, shale, siltstone, limestone, and coal (Lessig et al. 1977; Lucht et al. 1985). Most soils in the region are of the order Alfisol, suborder udalf, and small areas in each unit are the soil order Ultisol, suborder udult (Brady and Weil 2010). The udic

designation of both suborders indicates a relatively wet moisture regime, adequate for plant growth year round (Brady and Weil 2010).

The physiography of both the Athens Unit and Marietta Unit is greatly dissected with steeply sloping ravines, and level bottomlands and ridgetops. There are frequently two to three relatively flat structural benches along the length of a typical hillslope. These benches are artifacts of the multi-layered nature of the bedrock, and the differential erosion rates of the layers (Hix and Percy 1997).

2.1.3 Vegetation

Southeastern Ohio is within the Central Hardwoods region, Appalachian Mountain section of (Fralish 2003), the mixed-mesophytic forest region of (Braun 1950), and the mesophytic forest region of (Dyer 2006). It is characterized by a high diversity of primarily deciduous tree species. The most common species by importance value in Dyer's mesophytic forest region are red maple (10.9%) and white oak (*Quercus alba*) (5.3%), based on Forest Inventory and Analysis (FIA) data cited in (Dyer 2006, page 347). In presettlement land surveys of a portion of southeastern Ohio, oaks comprised 60.7% of witness trees, while red maple, sugar maple, and beech combined made up 18.3% of witness trees (Dyer and Hutchinson 2019, page 34). In southeastern Ohio areas studied by (Hutchinson et al. 2003), these three mesic species were mostly limited to bottomlands, and red maple in particular was uncommon. Modern surveys on the Athens Unit of the Wayne National Forest (Palus et al. 2018), and in other areas of southeastern Ohio (Dyer and Hutchinson 2019) have found sugar maple, red maple, and beech have much greater abundance and more widespread distribution than was indicated by the presettlement land surveys.

2.2 Field Methods

2.2.1 Study Design

This study is a continuation of the Wayne National Forest Ecological Classification System project, a long-term research project that examines ecosystem structure and dynamics through the development of a hierarchical ecosystem typing framework (Hix and Chech 1993; Hix and Pearcy 1997). Researchers originally established 128 permanent plots along 58 transects in the Marietta Unit in 1993 – 1995 (Hix and Pearcy 1997). We resampled 83 of these plots over the summers of 2017 and 2018; the remainder were lost due to access issues or forest harvesting, which disqualified them from the current study. Researchers also established 108 permanent plots along 51 transects in the Athens Unit in 1993-1995 (Hix and Chech 1993), and we resampled 84 of these plots in 2016 (Palus et al. 2018).

The original researchers selected these stands to represent mature, relatively undisturbed second-growth forests (at least 70 years old at the original time of sampling, and at least 93 years old at time of first resampling, based on U.S. Forest Service Vegetation Management Information System data and visual inspection). The stands were originally chosen on the basis of five criteria: “(1) no obvious evidence of major anthropogenic disturbance within the past 40 years (e.g., no stumps), (2) no dominance of early successional tree species, (3) no evidence of recent fire, significant windthrow, or unexplainable mortality, (4) stand is ‘fully stocked’ relative to the upland central hardwoods stocking chart (Gingrich 1967), and (5) no extensive (multiple-tree) gaps in the canopy” (Hix and Pearcy 1997, page 1118-1119). Within a random subset of each stand that met these criteria, the original researchers established one or two transects

running roughly through the center of the stand. Each transect contained two to five plots running parallel with elevational contours. Each plot was located at least 30 meters from the next plot on the transect.

2.2.2 Vegetation Sampling

Each “plot” consisted of two circular subplots, nested and concentric, of 100 m² and 500 m² sizes. Within the 100-m² subplot, we tallied by species each individual woody plant with a diameter at breast height (1.37 m; dbh) of 0.1-10.0 cm. We refer to these plants as the “sapling layer.” Within the 500-m² subplot, we recorded the species and dbh to the nearest tenth-centimeter of each woody plant with a dbh of 10.1 cm or more, alive or dead. We also recorded the crown class for each of the live stems (overtopped, intermediate, codominant, or dominant (Smith 1986)). We refer to these plants as the “tree layer,” including those that are overtopped or intermediate.

2.2.3 Environmental Variables and Soils

The first crews to measure the plots in the 1990s recorded the environmental variables that we used as covariates in our models. These variables are slope percent, aspect, and percent distance to ridge. The latter was determined by mapping the slope’s length from ridgetop to bottomland, in a line that passed through each plot and was perpendicular to the slope at the point of the plot, and then dividing the distance of the plot from the ridge by the total length of the slope. One soil pit per transect was excavated and the following measurements were determined by subhorizon: texture, pH, depth, and thickness.

2.3 Data Analysis

To model sapling abundance, we used generalized linear mixed models with negative binomial distribution assumptions. The negative binomial distribution is commonly used for count data like ours, and we chose it over the Poisson distribution because of observed overdispersion of variance with our three focal species, better model fits with negative binomial assumptions, and better visual fits of our data with the negative binomial distribution. We used transect as a random effect, in order to control for potential pseudoreplication caused by grouping our plots in space (Zuur et al. 2009). We ran our models using the “glmer.nb” function in the lme4 package (Bates et al. 2019) in R version 3.4.4.

For model evaluation, we selected a set of *a priori* variables and then compared the common model with each *a priori* variable included for each unit and each sampling period. We chose this approach because keeping the same set of variables in each final model afforded more direct comparison of effect sizes between different species and time periods. We used seven covariates spanning three distinct types: landscape variables (transformed slope aspect, percent distance to ridge, and the interaction factor of the two), edaphic (solum depth, acidity of B horizon), and stand structure (basal area of the plot, stand age). We also included management unit of the Wayne as a covariate, in order to test for differences that couldn't be accounted for by our *a priori* variables. Variable justification, relevant literature, our hypothesized relationships, and further explanation of the units chosen are contained in Table 1. All variables were screened for covariance, with a threshold of 0.7. Importance of individual covariates was measured with both partial coefficient significance from model outputs with a *p* value threshold of 0.05. The

overall predictive ability of each model was assessed using the trigamma r^2 value, which is a preferred method for generalized linear mixed models with a log link (Barton 2018). We calculated these using the function “r.squaredGLMM” in the MuMIn package (Barton 2018).

3 Results

In the 1990s, sugar maple had the highest sapling density (608 trees per hectare [tph]), followed by red maple (441 tph) and beech (217 tph). In the 2010s, beech had the highest sapling density (429 tph), followed by sugar maple (298 tph) and red maple (216 tph) (Table 2). Sugar maple decreased relatively evenly across both units (Figure 1). Our three focal species combined decreased in density by about 25% between sampling periods. Overall, our focal species made up 42.31% of sapling relative density for all species in both sampling periods and Wayne management units. They were the only species with relative density values above 10% (Table 3).

Model coefficients, standard errors, and significance levels are shown in Table 4. Landscape variables showed several significant interactions with density, including percent distance to ridge for the red maple 2010s model (-1.819 ± 0.862 , $P = 0.03$), percent distance to ridge for both beech models (1990s: 1.847 ± 0.836 , $P = 0.03$; 2010s: 2.149 ± 0.701 , $P = 0.002$), transformed aspect for beech 2010s (0.849 ± 0.332 , $P = 0.01$), and the interaction factor of transformed aspect and percent distance to ridge with beech 2010s (0.849 ± 0.332 , $P = 0.02$). Of the soil variables, pH of the B horizon exhibited significant interactions with density for both red maple models (1990s: -0.744 ± 0.329 , $P = 0.02$; 2010s: 0.844 ± 0.321 , $P = 0.009$) and sugar maple 1990s (0.532 ± 0.196 , $P = 0.007$), while depth of solum did not display any significant interactions. The only significant

interaction for stand structure variables was stand age for red maple 2010s (0.024 ± 0.011 , $P = 0.03$). Wayne management unit did not show significant interactions for any of the models, and standardized confidence intervals of management unit spanned several standard deviations.

The predictive ability of each model, measured by conditional r^2 value, is shown in Figure 2 and Table 5. It was highest for red maple (1990s: 0.73, 2010s: 0.84), followed by beech (1990s: 0.54, 2010s: 0.53) and sugar maple (1990s: 0.10; 2010s: 0.84). Patterns of marginal r^2 values between time values were variable for our models (Figure 2). Coefficient estimates of transformed slope aspect and percent distance to ridge were closer to zero in the sugar maple model from the more recent sampling period. For the same two landscape coefficients, estimates moved further from 0 in the 2010's for both the beech and the red maple models, with overlap in confidence intervals (Figure 3).

4 Discussion

4.1 Relative abundance patterns

A recent pattern of increasing beech abundance in the regeneration layer over time has been noted in several studies of northern hardwoods (Duchesne and Ouimet 2009; Gravel et al. 2011). Possible explanations include beech's shade tolerance giving it a competitive advantage as many forests advance in successional development, increasing whitetail deer populations harming sugar maple more than beech, and increasing soil acidity from beech leaf litter negatively affecting sugar maple. However, the most common explanation is decreasing availability of base cations and increasing soil acidity caused by atmospheric deposition, which can incite sugar maple decline and

open gaps for possible beech expansion (Duchesne and Ouimet 2009; Gravel et al. 2011). Unlike in northern hardwoods forests where most beech-maple research has long been conducted, beech is typically not indicated as the major species benefitting from mesophication in central hardwoods oak ecosystems (McEwan et al. 2011; Nowacki and Abrams 2008). Our results, along with those of Palus et al. (2018) and those from canopy gaps in Hutchinson et al. (2012), indicate that beech is the most common species in the regeneration layer of undisturbed southeastern Ohio oak-dominated forests, although *Acer* as a genus has higher density than *Fagus*. Similar results were found by Richards and Hart (2011), who recorded beech as the most common species in the sapling layer (1 meter height to 5 cm dbh) in canopy gaps of a forest in Appalachian Alabama, followed by sugar maple, blackgum (*Nyssa sylvatica*), and red maple. This study was in similarly aged forest, suggesting that beech regeneration is abundant in many undisturbed mature second-growth central hardwoods stands.

The observed trend of increasing beech sapling density is likely to continue; Palus et al. (2018) divided sapling data into two size classes, which showed that both maple species were more common than beech in the larger class (5.1-10.0 cm dbh), but that beech was more common in the smaller class (0.1-5.0 cm dbh). Additionally, beech sapling importance on south-facing slopes in southeastern Ohio was shown to increase in older stands of a chronosequence study (Goebel and Hix 1996). Furthermore, we expect that current estimates of relative beech density in the sapling layer are conservative for estimates of future relative beech density within these cohorts, because beech saplings have been shown to have higher survival and a higher rate of canopy layer ingrowth than sugar maple saplings in a northern hardwoods forest (Gauthier et al. 2015). An important

caveat is that beech bark disease may reach our study area within several decades. The resulting “aftermath forest” is likely to still contain beech, but mostly in thick clusters of relatively small root suckers rather than mature trees. Additionally, beech leaf disease is an emerging threat presently found in northern Ohio and adjacent states and Canadian provinces (Ewing et al. 2018).

4.2 Landscape-scale results

Our finding that red maple saplings were significantly more abundant closer to the ridgetops was consistent with our hypothesis and with studies that provide red maple abundance data broken down into landscape categories and size classes, in southeastern Ohio (Palus et al. 2018), in western Kentucky (Arthur et al. 2015), and in southern Indiana (Jose and Gillespie 1997). These results are also consistent with red maple classification as a stress tolerator with low resource requirements (Abrams 1998). However, they don’t reflect the commonly-observed bimodal pattern of red maple abundance on both xeric sites and bottomland sites (Abrams 1998). This is likely because sugar maple saplings were outcompeting red maple saplings on bottomland sites (Palus et al. 2018).

We had expected but did not find that sugar maple was associated with lower slope positions and more mesic slope aspects. Greater sugar maple abundance on lower slopes was found in southern Indiana by (Jose and Gillespie 1997) and in southern Ohio by (Palus et al. 2018), and greater sugar maple abundance on mesic sites in western Kentucky was recorded by (Arthur et al. 2015). McCarthy et al. (2001) found sugar maple sapling abundance was much higher on the north-facing slope of an old growth

oak stand in southeastern Ohio. Cleavitt et al. (2014) found that sugar maple seedlings had very low survival at higher elevations in New Hampshire, St Clair and Lynch (2005) found that sugar maple seedlings grew more slowly in upper slope soil, which was nutrient-poor and acidic, and Horsley et al. (2000) found that mature sugar maples were declining primarily on ridges and upper slopes in northern Pennsylvania, and not on adjacent lower slopes and unglaciated soil.

Some studies have speculated that atmospheric deposition may affect upper landscape positions more than lower positions, thus explaining why sugar maple often declines on upper slopes in areas where it was historically an important component of the forest (Bailey et al. 2004). Additionally, atmospheric deposition levels are high in southeastern Ohio, and this is a likely cause of observed topographic shifts in tree species of the region (Dyer and Hutchinson 2019). Thus, our controlling for pH, a variable affected by atmospheric deposition and one that affects calcium availability (Ellis and Mellor 1995), could be an explanation of our inability to find significant interactions between sugar maple abundance and landscape-scale variables. However, our observed correlation of percent distance to ridge with pH was low (0.09), and small sugar maples appear to be surprisingly ubiquitous in relation to topographic features, as shown by categorical analysis of saplings in the Athens Unit (Palus et al. 2018) and diameter distributions of canopy trees in the Marietta Unit (Appendix A). We speculate that our soils could be less acidic than those in studies cited above, thus reducing adverse effects on sugar maples regenerating on higher landscape position.

The complicated pattern of beech significance with both our landscape covariates and their interaction factor could be explained as beech being able to colonize all but the

driest landscape positions: ridgetops and southwest-facing upper slopes. This would be consistent with findings that beech regeneration is limited by soil moisture (Arii and Lechowicz 2002). The pattern may partially due to the ability of beech to regenerate in adverse conditions via asexual production of root suckers, which it has been shown to do on southwest-facing aspects (Held 1983) and upper-slope positions (Takahashi et al. 2010), while regenerating sexually on northeast facing aspects (Held 1983). On our study plots, mature beech trees were present on southwest lower, northeast upper, and northeast lower slope positions (Appendix A), so it is possible that beech saplings regenerated asexually in these areas.

4.3 Stand Structural Variables

We were surprised to find red maple density to be associated with older stands, because there was no significant interaction of stand age with either sugar maple or beech, it is the least shade tolerant of our focal species (Canham et al. 1994), and it decreased over time on both management units. We surmise that our study plots have become and will continue to become more deeply shaded over time, because more maples have been reaching the smaller canopy size classes in more recent sampling periods (Appendix B), and they are likely to cast a deeper shade as they become more dominant. This is corroborated by the increased importance of beech, the most shade tolerant of our focal species (Canham et al. 1994), in the most recent sampling period. A chronosequence study in our area found a similar pattern of increased red maple sapling abundance in the oldest stands (greater than 150 years), despite a general decrease before that age (Goebel and Hix 1996). We speculate that large pockets of canopy mortality may be more common in our older stands (Chapter 2), which could be advantageous to

red maple if they occur on upper landscape positions, where both canopy oaks and regeneration-layer red maples are more common. Our Chapter 2 analysis gives more weight to this explanation; mortality rates in the tree layer of the Marietta Unit are relatively high for species of the red oak subgenus (*Erythrobalanus*) (Chapter 2), which tend to have higher importance values on upper landscape positions (Palus et al. 2018).

Several studies have shown that beech has an advantage in growth and/or survival in closed-canopy locations, while sugar maple can have a growth advantage in canopy gaps as small as single-tree size (Canham 1988; Canham et al. 1994; Kobe et al. 1995). These observations have also held true at a stand level; Nolet et al. (2008) argued that minor canopy disturbances favored beech saplings while major disturbances favored sugar maple saplings in northern hardwoods forests of Quebec, and Poulson and Platt (1996) argued that beech-maple codominance in an old-growth forest of southwestern Michigan was maintained by fluctuations in disturbance levels and resulting changes in light levels. Based on these studies and our observations of our plots spanning a gradient of gap dynamics, we expected to find a relationship between basal area, a proxy for light, and abundance of our focal species. We believe the absence of this result may have been due to lag effects between overstory tree mortality and establishment into our sapling-size class; we used the current sampling period basal area for our models of both sampling periods. Thus, a large tree could have died shortly before we visited a plot and the seedling layer would not have had time to respond to the opening before we measured the saplings on the plot. Additionally, basal area as a metric likely under-represented the shade cast by the numerous smaller maple and beech in the tree layer (Appendix B). Another explanation could be that a different factor such as soil or climate was mediating

competition (Boisvert-Marsh et al. 2019; Murphy and Mccarthy 2017; Takahashi and Lechowicz 2007).

4.4 Edaphic Variables

The relationship of sugar maple with soil acidity has been well studied in the northeastern U.S. and eastern Canada, and our results are consistent with this literature, which shows a negative relationship between survival and growth of sugar maple with increasing acidity across the life stages of the tree (Bal et al. 2015). This is often attributed to the decreasing availability of calcium and the increasing availability of aluminum with decreasing pH, although many other nutrients important for sugar maple become less available with decreasing pH (Bal et al. 2015; St.Clair et al. 2008). Many studies have found that pH can mediate the competitive balance between sugar maple and red maple and sugar maple and beech. Bigelow and Canham (2002) studied a transition oak-northern hardwood forest in Northwest Connecticut, and found that red maple saplings had higher growth rates in soils with lower pH, and they suggested that atmospheric deposition may be contributing to observed recent increases in red maple regeneration. St Clair and Lynch (2005) found in a greenhouse experiment that red maple seedlings displayed little negative response to being grown on nutrient-poor soils vs. nutrient rich soils, especially when compared to the significant negative growth responses of sugar maple. Our stand level results agreed with these studies, since red maple had a significant negative relationship with pH in both our sampling periods.

Beech is also often associated with lower pH and lower calcium sites (Duchesne and Ouimet 2009), but our findings did not corroborate this. Some studies have found

evidence that beech grows on lower pH sites due to competitive exclusion by sugar maple on higher pH sites, rather than effects on growth. For example, Bigelow and Canham (2002) found that beech saplings grew fastest on higher pH soils, but were more common on low pH soils, and Long et al. (1997) found that calcium fertilization in the form of dolomitic lime had little effect on overstory beech growth in northern Pennsylvania, while it did affect overstory sugar maple positively. On both stand and regional levels, beech in Quebec forests has been found to be negatively related to pH (Arii and Lechowicz 2002; Nolet et al. 2008) and calcium concentration (Duchesne and Ouimet 2009). Additionally, calcium concentration had a stronger signal when predicting beech density relative to sugar maple density than it did when predicting absolute beech density (Duchesne and Ouimet 2009). We believe the lack of a relationship between beech sapling abundance with pH, in combination with our finding that topography had several significant interactions with beech sapling abundance, suggest that soil moisture is more important than pH in influencing regeneration of beech in our study area. This agrees with the findings of Arii and Lechowicz (2002), that soil moisture was the most important factor mediating the success of beech and sugar maple in Quebec.

For all our focal species, our study is unique in testing sapling relationships with soil pH in southern Ohio, which is south of the primary regions of sugar maple decline and research into sugar maple-acidity relationships (Bal et al. 2015). More southern soils have greater base cation availability and thus sugar maples in the southern portion of their range are likely more buffered against the negative effects of increasing acidity (Bal et al. 2015); therefore, it is notable that we found pH interactions with our focal species that are similar to those found in many studies of northern hardwoods ecosystems.

4.5 Trends in Mesophication Over Time

Contrary to the hypothesis of mesophication being a positive feedback loop (Nowacki and Abrams 2008), we did not find evidence that mesophication affected the ability of landscape level covariates to predict sapling abundance over time, as judged by changes in marginal r^2 values and coefficient sizes over time. We believe the most likely explanations for this lack of evidence of mesophication as a positive feedback loop is that our study did not span a long enough time to capture the effect, and that interactions with topographic variables may be confounded with competition between species. We based our hypothesis on Hanberry et al. (2012), who found that the influence of topographic variables over mesic tree species distributions in Missouri weakened over time. Additionally, Dyer and Hutchinson (2019) found similar patterns of change in relation to topographic variables in southeastern Ohio, near our study area. However, both these studies compared modern Forest Inventory and Analysis data with reference data from General Land Office surveys in the early 19th century, well before the advent of modern fire suppression, so both the timespan and ecological dynamics between “snapshots” were much different than our work spanning just over two decades. These studies suggest that our study period may have started too late to detect the weakening control of topographic variables over mesic tree regeneration, as this phenomenon likely already happened. However, ridgetops in many areas still contain relatively low densities of mesophytic regeneration, particularly for sugar maple and beech (Jose and Gillespie 1997; Olson et al. 2014; Palus et al. 2018). Thus, if Nowacki and Abrams (2008)’s hypothesis of mesophication as a positive feedback loop is true, then researchers on long-term studies may observe increasing sugar maple and/or beech regeneration on the drier

sites as mesophication continues. An important caveat applies: interspecific competition between mesic tree species may inhibit changes from being apparent at the species level. For example, overstory beech trees in some areas appear to inhibit sugar maple regeneration underneath, potentially through deep shading or allelopathic properties of the leaf litter (Arii and Lechowicz 2002; Hane et al. 2003). It is possible that greater density stands of red maple could grow on ridgetops in the future and that they would inhibit sugar maple and/or beech regeneration in a way currently unknown. For example, Alexander and Arthur (2014) found in eastern Kentucky that red maple leaf litter immobilized nitrogen for longer periods of time than oak leaf litter. It is thus a plausible hypothesis that high concentrations of red maple leaf litter could slow the growth of sugar maple, which thrives in high nitrogen environments (Boggs et al. 2005), even though red maple leaf litter increases the moisture in the forest floor (Alexander and Arthur 2014), which would likely favor sugar maple, all else being equal. Thus, careful thought needs to be applied to testing relationships between topographic variables and mesophication in central hardwoods forests.

5 Conclusions

We found that the major factors influencing the abundances of red maple, sugar maple, and American beech saplings in our study area included slope aspect, slope position, soil pH, and stand age. Our results suggest that the practice of delineating silvicultural management units using topographic variables will be useful in predicting mesophication trajectory of mature Ohio forests, but that other factors, especially soil pH, would strengthen the predictions. It also suggests that future competition between red

maple and sugar maple in central hardwoods stands will likely be affected by distribution of atmospheric deposition that acidifies the soil.

Importantly, we found a pattern of increasing beech regeneration over time, especially on the Athens Unit, while we also found a pattern of decreasing maple regeneration, as maple grew out of our sapling size class and into our tree size class. This pattern should be of interest to those concerned with forest and wildlife health in the central hardwoods region, given the differential ecosystem services that maples and beeches provide, and for the different threats they face. Beech will not likely provide valuable ecosystem services or commercial products in southeastern Ohio if beech bark disease (Cale et al. 2017) or beech leaf disease (Ewing et al. 2018) reach the area.

The expense of oak restoration (Brose et al. 2014), combined with the low extent of modern forest management and timber harvesting (Widmann 2016), make it likely that shade-tolerant species such as red maple, sugar maple, and beech will be the dominant species of the future in many oak forests. Managers and scientists investigating mesophication should conduct more research into the competition of the species replacing oak and hickory, so that they may better predict future composition of our eastern forests.

Table 1: Justification and rationale for covariates used in sapling density modeling

Variable	Justification	Studies with importance for our focal species	Notes on units of measure
Plot basal area (meters squared per hectare)	Used as proxy for subcanopy light in absence of direct measure	Canham 1988 (sugar maple and beech, response to canopy gaps), Poulson and Platt 1996 (sugar maple and beech, response to indirect light indicator)	
Stand age (years)	Important factor in determining successional status and regeneration dynamics of shade tolerant species		Age is stand age, not individual tree age, and was determined from Forest Service Vegetation Management Information System
Solum depth (centimeters)	Determines area available for root growth, and thus important factor in site productivity	(Hix and Pearcy 1997) (thickness of A horizon significant for determining canopy composition).	Solum used because fine roots in forests are likely located in upper portions of soil (Schenk and Jackson 2002), late-successional tree species have relatively shallow roots (Gale and Grigal 1987; Pallardy and Rhoads 1993), and more nutrients in upper horizons because they are transported upwards by plants (Jobbágy and Jackson 2001)
Soil acidity (pH of B horizon)	Predicts availability of important plant nutrients, especially calcium	(Bailey et al. 2004) (mature sugar maple, B horizon), (Bigelow and Canham 2002) (all three focal species, saplings, first 10 cm of soil), (Arii and Lechowicz 2002) (sugar maple and beech saplings, first 10 cm of soil), (St Clair and Lynch 2005) (red maple and sugar maple seedlings, O+A and B horizons).	B horizon used because it was found most significant in study of sugar maple decline (Bailey et al. 2004) and because it is less susceptible to erosion over time than A horizon (Kreznor et al. 1989).
Cosine-Transformed Aspect (TASP)	Important determinate of temperature and moisture dynamics	Palus et al. 2018 (all three focal species, multiple life stages, the Wayne); (Hix and Pearcy 1997) (predicting overstory composition, the Wayne)	Slope aspect was cosine transformed ($\cos(45^\circ - \text{aspect}) + 1$), to make the metric change continuously rather than breaking between 0° and 360° . TASP maximizes at 2 for a 45° aspect, and minimizes at 0 for a 225° aspect (Beers et al. 1966).
Percent Distance to Ridge (PDR)	Important determinate of temperature and moisture dynamics	Palus et al. 2018 (all three focal species, multiple life stages, the Wayne); Horsley et al. 2000 (mature sugar maple), Cleavitt, Fahey, & Battles, 2011 (sugar maple seedlings)	Percent distance to ridge is maximized at the bottom of a slope; positive correlation is higher mortality on lower slopes.
TASP:PDR interaction	May capture topographic dynamics that TASP or PDR alone cannot		High values of the interaction factor indicate upper slopes and northeast facing aspects.
Management Unit (Marietta)	Will help us understand if unmodeled factors drive sapling-density differences across the two management areas	Seeley et al. 2019 (pre-settlement beech abundance explained by different environmental and climatic variables in Wisconsin and Michigan)	The hypothesized relationships are with the Marietta Unit, as that is the additional term in our model.

Table 2: Sapling density (tph) of the focal species, 1990s and 2010s, on the Athens and Marietta Units

Species	1990s	2010s
Red maple	441	216
Sugar maple	608	298
American beech	217	429
Total	1265	943

Table 3: Relative density values for all sapling species, Athens and Marietta Units. “Other” row includes all taxa with a relative density value of less than one: *Acer negundo*, *Aesculus flava*, *Aesculus glabra*, *Betula lenta*, *Carya cordiformis*, *Castanea dentata*, *Carya glabra*, *Carya laciniosa*, *Carya ovata*, *Carya ovalis*, *Carya spp.*, *Carya tomentosa*, *Cercis canadensis*, *Celtis occidentalis*, *Corylus americana*, *Cornus racemosa*, *Crataegus spp.*, *Diospyros virginiana*, *Elaeagnus umbellata*, *Fraxinus quadrangulata*, *Juglans cinerea*, *Kalmia latifolia*, *Liriodendron tulipifera*, *Lonicera japonica*, *Magnolia acuminata*, *Morus rubra*, *Oxydendrum arboreum*, *Pinus strobus*, *Pinus virginiana*, *Prunus americana*, *Prunus serotina*, *Quercus alba*, *Quercus coccinea*, *Quercus spp.*, *Quercus montana*, *Quercus rubra*, *Quercus velutina*, *Rosa multiflora*, *Rubus spp.*, *Sassafras albidum*, *Sambucus canadensis*, *Staphylea trifolia*, *Tilia americana*, *Tsuga canadensis*, *Ulmus americana*, *Vaccinium stamineum*, *Viburnum acerifolium*, *Viburnum dentatum*, *Viburnum spp.*, and *Vitis spp.*

Species	Athens 1990s	Athens 2010s	Marietta 1990s	Marietta 2010s	Average
<i>Acer saccharum</i>	16.99	10.49	19.41	15.64	15.63
<i>Acer rubrum</i>	13.86	12.55	16.86	10.21	13.37
<i>Fagus grandifolia</i>	5.37	19.15	8.54	20.18	13.31
<i>Lindera benzoin</i>	2.85	8.29	6.29	15.64	8.27
<i>Cornus florida</i>	14.47	0.63	13.64	0.41	7.29
<i>Ostrya virginiana</i>	8.93	8.04	3.30	3.32	5.90
<i>Asimina triloba</i>	2.85	7.16	2.82	1.94	3.69
<i>Carpinus caroliniana</i>	3.95	3.33	2.99	3.57	3.46
<i>Hamamelis virginiana</i>	1.21	2.45	4.53	4.86	3.26
<i>Viburnum prunifolium</i>	4.16	4.02	0.13	0.08	2.10
<i>Ulmus rubra</i>	2.49	1.07	3.92	0.49	1.99
<i>Fraxinus pennsylvanica</i>	2.19	2.57	0.70	1.62	1.77
<i>Amelanchier arborea</i>	2.24	2.51	1.19	0.97	1.73
<i>Fraxinus americana</i>	0.44	1.76	1.32	2.92	1.61
<i>Nyssa sylvatica</i>	1.10	1.07	2.16	1.30	1.41
Other	16.9	14.91	12.2	16.85	15.21

Table 4: Mixed effects model coefficients (\pm standard error), p values indicated by asterisks (** $p < 0.01$, * $p < 0.05$, . $p < 0.1$). Coefficients untransformed from model output, generalized linear mixed model with negative binomial distribution assumption and log link

Covariate	Red Maple 1990s	Red Maple 2010s	Sugar Maple 1990s	Sugar Maple 2010s	Beech 1990s	Beech 2010s
Intercept	2.358 (± 2.08)	0.497 (± 2.034)	-0.445 (± 1.380)	-0.153 (± 1.240)	-2.080 (± 1.679)	-1.453 (± 1.412)
Transformed Aspect (TASP) (0-2)	0.049 (± 0.399)	0.338 (± 0.329)	-0.484 (± 0.297)	-0.341 (± 0.283)	0.560 (± 0.389)	0.849 (± 0.332)*
Percent Distance to Ridge (PDR) (0-1)	-1.745 (± 0.995).	-1.819 (± 0.862)*	0.153 (± 0.643)	-0.281 (± 0.601)	1.847 (± 0.836)*	2.149 (± 0.701)**
TASP:PDR ((0-2):(0-1))	0.123 (± 0.648)	0.048 (± 0.518)	0.366 (± 0.452)	0.415 (± 0.431)	-1.089 (± 0.581).	-1.180 (± 0.488)*
Acidity of B Horizon (pH)	-0.744 (± 0.329)*	-0.844 (± 0.321)**	0.532 (± 0.196)**	0.320 (± 0.173).	0.072 (± 0.248)	-0.008 (± 0.200)
Depth of Solum (cm)	0.004 (± 0.007)	0.010 (± 0.007)	-0.002 (± 0.004)	-0.002 (± 0.004)	-0.005 (± 0.005)	-0.007 (± 0.005)
Stand Age (years)	0.007 (± 0.011)	0.024 (± 0.011)*	-0.010 (± 0.007)	-0.004 (± 0.006)	0.007 (± 0.008)	0.013 (± 0.007).
Basal Area of Plot (m ² /ha)	0.022 (± 0.013).	0.004 (± 0.010)	0.014 (± 0.010)	0.003 (± 0.009)	0.004 (± 0.012)	-0.001 (± 0.010)
Unit (Marietta)	0.778 (± 0.481)	-0.374 (± 0.462)	0.077 (± 0.286)	-0.167 (± 0.260)	0.079 (± 0.361)	-0.575 (± 0.299).

Table 5: r^2 values for generalized linear mixed models of sapling abundance, trigamma method

Model	Marginal r^2	Conditional r^2
Sugar Maple 1990s	0.10	0.45
Sugar Maple 2010s	0.03	0.34
Red Maple 1990s	0.16	0.73
Red Maple 2010s	0.25	0.84
American Beech 1990s	0.05	0.54
American Beech 2010s	0.12	0.53

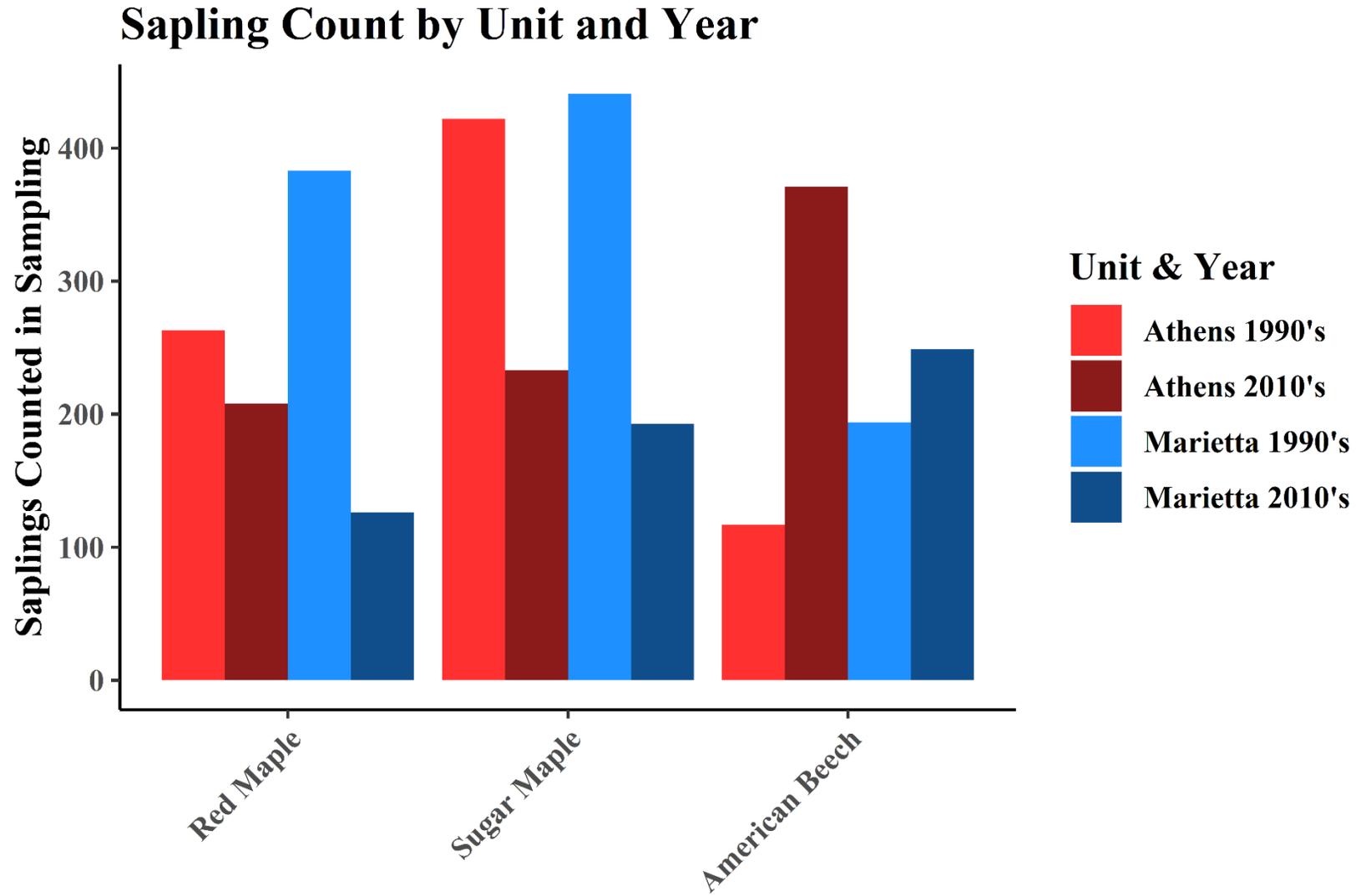


Figure 1: Saplings counted in sampling effort, by unit and sampling period (84 plots Athens Unit, 83 plots Marietta Unit)

GLMM r^2 Values (Trigamma Method)

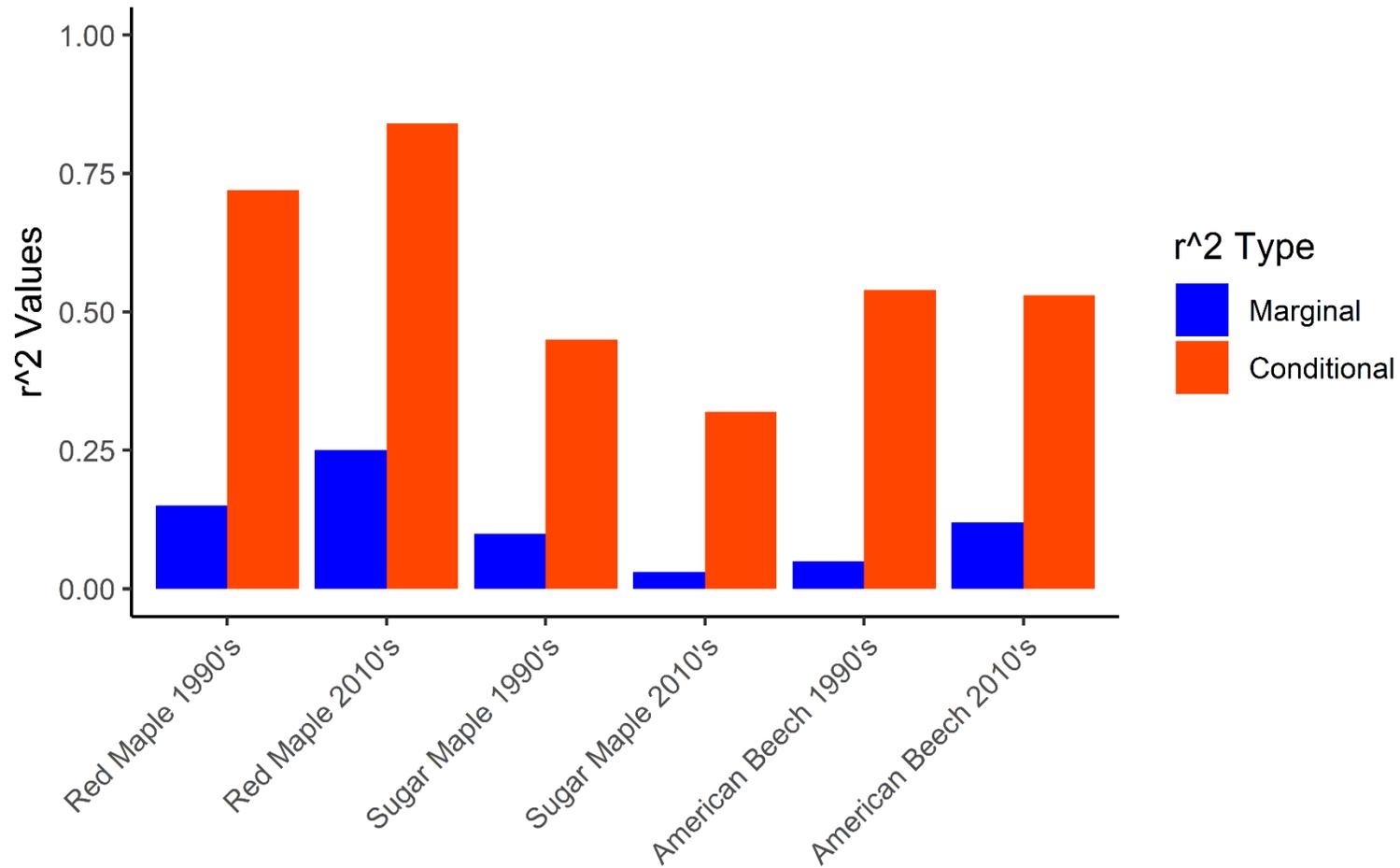


Figure 2: r^2 values for generalized linear mixed models of sapling abundance, trigamma method. Values from `r.squaredGLMM {MuMIn}`, R version 3.5.2

Sapling Abundance GLMM Coefficients

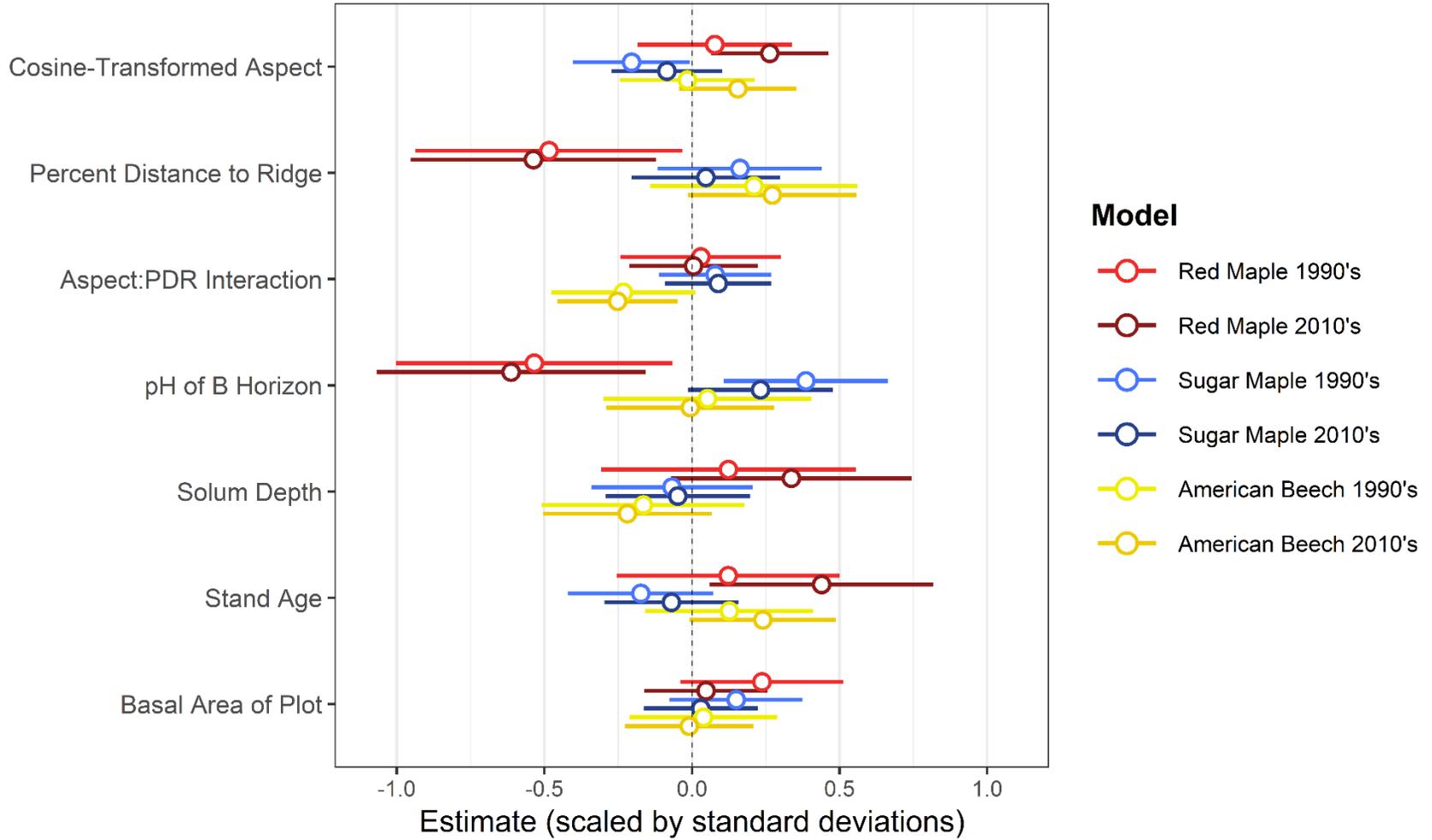


Figure 3: 95% confidence intervals of sapling model coefficients. Management unit was omitted because the confidence intervals were wider than other coefficients and thus distorted the scale

Chapter 2

Predisposing factors' effects mortality of oak (*Quercus*) and hickory (*Carya*) species in mature hardwood forests undergoing mesophication in Appalachian Ohio

Abstract

Mature oak (*Quercus* spp.) and hickory (*Carya* spp.) trees across the eastern U.S. are gradually being replaced by more shade tolerant tree species, likely due to fire suppression and a relatively moist climate during the past century. Oaks and hickories are highly valuable to wildlife; therefore, studying their mortality patterns can provide information on the longevity of habitat quality for many animal species. Using a permanent plot network designed for ecological classification in mature second-growth forests, we studied background mortality rates of five oak and one hickory species. We sampled 86 1/20th hectare plots on the Marietta Unit of the Wayne National Forest in southeastern Ohio, first in 1993-1995, and then again in 2018, providing a 23-25 year time window for the analyses. We calculated mortality rates for white oak (*Quercus alba*), chestnut oak (*Quercus montana*), northern red oak (*Quercus rubra*), black oak (*Quercus velutina*), scarlet oak (*Quercus coccinea*), and pignut hickory (*Carya glabra*). For each of these species other than scarlet oak, we also modeled the relationships of mortality probability with *a priori* landscape, edaphic, stand structural, and individual

tree covariates, using mixed logistic regression. We found that the red oak subgenus (*Erythrobalanus*) had higher mortality rates (41.0% of stems) than the white oak subgenus rate (22.2%). The species with the highest mortality rate was scarlet oak (61.3%), followed by northern red oak (41.4%), black oak (26.7%), pignut hickory (23.9%), white oak (23.4%), and chestnut oak (19.1%). In our models, red oak mortality was associated with more mesic slope positions, shallower solum, and older stand ages. Pignut hickory and chestnut oak mortality was associated with higher basal area on the plot, while white oak mortality was associated with lower basal area on the plot. Our data suggest that red oak subgenus tree in mature forests of our area will become increasingly uncommon relative to white oak subgenus trees, as the result of dying at higher rates. Overall, our models suggest that stand structural variables are important for more species than topographic variables. Additionally, our northern red oak models suggest that silvicultural interventions may best be targeted to areas of mature forests where northern red oak tends to have a shorter life span, such as more mesic slope aspects and positions.

Introduction

Recent studies have shown that canopies currently dominated by oak and hickory (*Carya* spp.) are gradually being replaced by shade-tolerant mesic tree species, especially maple (*Acer* spp.) (Brose et al. 2014; Nowacki and Abrams 2008). These mesic species slowly change the characteristics of the forest floor, making conditions more favorable for mesic species regeneration and less favorable for oak regeneration over time (Alexander and Arthur 2014; Kreye et al. 2013). This process has been named “mesophication.” (Nowacki and Abrams 2008). The causes are still not fully understood

and are multifaceted; however, the most relevant likely factors are moister climatic conditions over the past century and changing disturbance regimes due in part to fire suppression in the past century (McEwan et al. 2011; Nowacki and Abrams 2015; Pederson et al. 2015). The primary management tools for reversing mesophication and promoting oak regeneration are prescribed burning and thinning; however, these measures are rarely effective without multiple treatments (Brose et al. 2013), which may render oak forest restoration too expensive for application to large areas, in the absence of commercial timber sales. Many forests in the eastern U.S. are currently managed with a “hands-off” approach (Widmann 2016), making it seem unlikely that oak forests will be restored across a large area. Some studies have investigated whether dry landscape positions offer refugia from mesophication, and primarily found that even on the driest landscape positions like ridgetops, oak regeneration is greatly outnumbered by mesic tree regeneration (Palus et al. 2018; Jose and Gillespie 1997). A study from the Missouri Ozarks found that oak regeneration was competitive on dry landscape positions (Olson et al. 2014), but that region is among the driest in the central hardwoods forest region (Hanberry and Nowacki 2016), so the results may not be applicable to other areas in the eastern U.S.

Thus, it seems likely that oak-hickory forests will slowly become more dominated by mesic tree species as mature oak trees die and are replaced by other species. Knott et al. (2019) showed this trend across eastern U.S. forests between the 1980s and the 2010s; *Quercus* declined the most of any genus included in their study, both in stem density and importance value. Anthropogenic climate change is likely to favor oaks over their mesic competitors by the year 2100 (Butler et al. 2015; Iverson et al. 2008). However, it is not

certain if or when the effects of climate change will impede mesophytic regeneration in the next century (Ma et al. 2016). Furthermore, the general pattern of decreasing oak importance (Knott et al. 2019) combined with the sparseness of oak regeneration in mature forests over the past several decades (Jose and Gillespie 1997; Palus et al. 2018) suggest that even if the changing climate eventually tips the competitive balance between oak and maple, there will likely be a period of at least several decades in which mature oak trees are rare in the canopy of eastern U.S. forests, barring major changes in the disturbance regime or devastating forest pest epidemic(s).

Oak and hickory benefits to wildlife

This likely scenario of diminished importance of oak would be a major problem for wildlife, as *Quercus* is arguably the most important tree genus for wildlife (McShea et al. 2007). Acorns are a critical food for many common eastern animals, because they are high in fat, storable through winter, and available in the autumn (Kirkpatrick and Pekins 2002). Oak and hickory leaves are another vital wildlife resource, as they host a high diversity (Sierzega and Eichholz 2019; Narango et al. 2017; Tallamy and Shropshire 2009) and abundance (Butler and Strazanac 2000) of insect taxa (primarily Lepidopteran larvae), relative to the leaves of *Acer* and *Fagus* trees. Accordingly, the majority of insectivorous songbird species studied preferred oak trees over maple trees for foraging (Narango et al. 2017; Wood et al. 2012; Graber and Graber 1983), and oak forests host a greater abundance of songbirds throughout the year than maple forests (Rodewald and Abrams 2002). Hickory is also often foraged by songbirds at higher rates than its availability (Newell et al. 2014; Gabbe et al. 2002).

Different oak species and subgenera vary considerably in the services they provide to wildlife. For example, most songbird species studied preferred to nest and had higher nesting success in white oak (*Quercus alba*) over northern red oak (*Quercus rubra*) (Boves et al. 2013; Newell and Rodewald 2011), and different studies of acorn production rank different oak species as top producers, depending on locality and other factors (Greenberg and Parresol 2002). Oak species diversity provides a natural buffer against interannual food fluctuations, as masting cycles of the two primary subgenera of oak (white oak subgenus, *Leucobalanus* and red oak subgenus, *Erythrobalanus*) are largely independent of one another, and acorn crops of the two subgenera may fail in two different years following spring killing frosts (Koenig and Knops 2002). Intra-genus food supply buffering is also likely to apply to foliage-gleaning birds, which can change relative foraging preferences within the *Quercus* genus between different years (Gabbe et al. 2002; Wood et al. 2012). Additionally, red oak acorns and white oak acorns can be complementary to one another as food sources, because white oak is preferred by many animals likely due to lower tannin content (Kirkpatrick and Pekins 2002; Pekins and Mautz 1987), while red oak is preferred for overwinter storage by some animals such as squirrels (*Sciurus* spp.), likely due to its delaying of germination until spring and greater resistance to pest infection (Fox 1982; Steele et al. 1996). Other attributes of acorns may be critical to some species, for example, blue jays (*Cyanocitta cristata*) preferentially eat small acorns (Moore and Swihart 2006; Scarlett and Smith 1991). These studies of wildlife ecology illustrate that a diversity of oak species is likely crucial for maintaining healthy, stable, and diverse wildlife populations.

Oak and Hickory Mortality

Since many eastern U.S. wildlife species heavily benefit from or possibly are reliant on oak and hickory, and since oak and hickory may not regenerate in many areas, understanding oak and hickory mortality is crucial to understanding the rate of habitat quality decline that many animal species are likely to face in upcoming decades.

Studying mortality of these tree species may help managers estimate how much longer wildlife species will have resources like acorns and prime foraging habitat, and studying landscape patterns of oak mortality could assist in prioritizing areas for management.

The mortality rates of oak species differ in relation to many factors. Species in the red oak subgenus consistently show higher mortality rates than oaks in the white oak subgenus (Kabrick et al. 2008, Starkey and Oak 1989). Scarlet oak (*Quercus coccinea*) in particular is often identified as the oak with the highest mortality rate (Goebel and Hix 1997), followed by northern red or black oak (*Quercus velutina*) (Greenberg et al. 2011; Voelker et al. 2008). This reflects a difference in lifespan, as species from the white oak subgenus tend to live longer than trees in the red oak subgenus (Greenberg et al. 2011; Shumway et al. 2001).

Oak mortality is often framed as an issue of oak decline (Haavik et al. 2015), even in areas with relatively low mortality rates (Greenberg and Parresol 2002). Oak decline is a disease complex in which many abiotic and biotic factors combined gradually kill trees, and is the most commonly studied cause of oak mortality in the eastern U.S., although it is still poorly understood (Haavik et al. 2015). The decline spiral concept of Manion (1991) holds that decline-related tree mortality is caused by interactions of predisposing factors, inciting factors, and contributing factors. Predisposing factors make

a tree less resilient to stressors, inciting factors further weaken a tree's natural defenses against damage, and contributing factors take advantage of the tree's weakened state to finish killing it (Manion 1991). Infestations of wood borers, bark beetles, or root rot fungi are often the ultimate cause of oak death, and are generally considered contributing factors. The most commonly cited inciting factor for oak mortality is drought, although mechanical damage from wind and ice storms or defoliation events from pests like gypsy moth (*Lymantria dispar*) can also act as the initial stressor (Haavik et al. 2015; Morin and Liebhold 2016).

Managers, however, are likely most interested in the effects of predisposing factors, which may help predict which areas may be subject to future tree mortality (Fan et al. 2011; Oak et al. 1996). Some general patterns have arisen from the literature about the predisposing factors. On an individual-tree scale, older age, more suppressed crown condition, and slower growth are often associated with higher oak mortality, and tree size can have either a positive or negative association with oak mortality depending on species (Fan et al. 2011; Shifley et al. 2006). On a stand scale, oak mortality is often positively associated with higher basal area of surrounding oaks, higher basal area of other canopy trees, stand age, and shallower soil (Oak et al. 1996; Oak et al. 1991; Wang et al. 2008). On a landscape scale, researchers often identify oaks on drier topographic positions like upper-slope positions and south or west-facing aspects as being more susceptible to mortality, likely because they are exposed to the most severe effects of drought (Oak et al. 1991; Stringer et al. 1989). However, Kabrick et al. (2008) found that the apparent significance of topography in explaining of red oak subgenus mortality was actually due to higher density red oak subgenus trees on drier landscape positions, when

mortality counts were used rather than rates. In contrast to most studies, Bendixsen, Hallgren, and Frazier (2015) found that oak mortality in Oklahoma was higher on more mesic slope aspects and closer to water. They hypothesized that trees on more mesic topographic positions may have less developed root systems, and thus were not as drought-hardy as their xeric counterparts, or that conditions may have been better for fungal pathogens on more mesic topographic positions.

Despite this rich literature on oak mortality, there are few studies of background oak mortality, which we define as mortality expected to be occurring at relatively low rates (~0.5 – 2% per year, Stephenson and Mantgem 2005), in areas not experiencing severe disturbance events or management practices. It is crucial for researchers to understand background oak (and hickory) mortality rates, because the majority of vulnerable forests do not experience severe oak decline events at any given time (Oak et al. 2004; Oak et al. 1991). We had the opportunity to study background mortality rates in mature second-growth forests of southeastern Ohio, using a permanent plot network that was established in the 1990s for use in developing an ecosystem classification system (Hix and Chech 1993; Hix and Pearcy 1997). We quantified mortality rates for five oak and one hickory species, and modeled the effect of predisposing tree-scale, stand-scale, and landscape-scale factors on mortality rates for all but one of these species. Our primary question was whether topographic variables, which are useful for delineation of oak management units in southeastern Ohio (Iverson et al. 1997, 2018), were predictive of oak and hickory mortality rates in mature second-growth forests, when we controlled for other variables known to affect oak mortality. We also sought to compare species-level patterns of relative background mortality rates with studies of the same species.

Methods

Study Area

Our study area was the Marietta Unit of the Wayne National Forest (hereafter the Wayne) of southeastern Ohio. Southeastern Ohio is a part of the Allegheny Plateau Province, and has heavily dissected topography (Lessig et al. 1977). The area has a long history of land use and subsequent abandonment by both Native American groups and European descendants (Kern and Wilson 2014). It largely proven unfavorable for agriculture, and today is heavily forested (Hutchinson et al. 2003). For more information on southeastern Ohio history, see Appendix A.

Climate

Southeastern Ohio has a continental climate with cold winters and warm, humid summers. It receives precipitation (mostly rainfall) relatively evenly throughout the year, although rainfall is slightly lower in fall and winter than in spring and summer. The average annual rainfall for the weather station in the study area at Marietta Wastewater Treatment Plant was 42.70 inches from 1981-2010. The summer average temperature during that time period was 72.6°F, and the winter average was 32.7° degrees Fahrenheit (NOAA 2018).

Bedrock and Soil

The Marietta Unit is located on the unglaciated Allegheny Plateau Province (Lessig et al. 1977). The main bedrock was formed during the Permian Era of 298-302 million years ago, from sediment accumulation in a prehistoric coastal swamps, with

some Pennsylvanian bedrock in modern valleys (Kern and Wilson 2014; Ohio Division of Geological Survey 2017). Common rock types include sandstone, shale, siltstone, limestone, and coal (Lessig et al. 1977). Most soils in the region are of the order Alfisol, suborder udalf, and small areas are the soil order Ultisol, suborder udult. The udic designation of both suborders indicates a relatively moist climate, adequate for plant growth year round (Brady and Weil 2010). The physiography included steeply sloping hillsides and ravines, along with level bottomlands and ridgetops. There are frequently two to three relatively flat structural benches along the length of a hillslope; these are artifacts of the multi-layered nature of the bedrock, and the differential erosion rates of the rock layers (Hix and Percy 1997).

Vegetation

Southeastern Ohio is within the Central Hardwoods region, Appalachian Mountain section of (Fralish 2003), the mixed-mesophytic forest region of (Braun 1950) and the mesophytic forest region of (Dyer 2006). It is characterized by a high diversity of primarily deciduous tree species. The most common species by importance value in Dyer's mesophytic forest region are red maple (10.9%) and white oak (5.3%), based on Forest Inventory and Analysis (FIA) data cited in (Dyer 2006, page 347). In presettlement land surveys of area, oaks comprised 60.7% of witness trees in southeastern Ohio (Dyer and Hutchinson 2019, page 34), while red maple, sugar maple, and American beech combined made up 18.3% of witness trees. In southeastern Ohio areas studied by Hutchinson et al. (2003), these three mesic species were mostly limited to bottomlands. Modern surveys on the Athens Unit of the Wayne National Forest (Palus et al. 2018), and in other areas of southeastern Ohio (Dyer and Hutchinson 2019) found sugar maple, red

maple, and beech to be much greater in abundance and wide spread in distribution compared to the presettlement land survey data.

Study Design

This study is a continuation of the Wayne National Forest Ecological Classification System project, a long-term research project that examines ecosystem structure and dynamics through the development of a hierarchical ecosystem classification framework (Hix and Chech 1993; Hix and Pearcy 1997). Researchers originally established 128 permanent plots along 58 transects in the Marietta Unit in 1993 – 1995, primarily in 1994 (Hix and Pearcy 1997). We resampled 86 of these plots during the summer 2018; the remainder were lost due to access issues or harvesting, which disqualified them from the current study. The time between data collection “snapshots” was thus 23-25 years, primarily 24 years.

The original researchers selected these stands to represent mature, relatively undisturbed second-growth forests (at least 70 years old at the original time of sampling, and at least 93 years old at time of first resampling, based on U.S. Forest Service Vegetation Management Information System data and visual inspection). The stands were originally chosen on the basis of five criteria: “(1) no obvious evidence of major anthropogenic disturbance within the past 40 years (e.g., no stumps), (2) no dominance of early successional tree species, (3) no evidence of recent fire, significant windthrow, or unexplainable mortality, (4) stand is ‘fully stocked’ relative to the upland central hardwoods stocking chart (Gingrich 1967) and (5) no extensive (multiple-tree) gaps in the canopy” (Hix and Pearcy 1997, page 1118-1119). Within a random subset of each

stand that met these criteria, the original researchers established one or two transects running roughly through the center of the stand. Each transect contained two to five circular 500-m² plots randomly placed along the transect, so that the plots were at least 30 meters apart from one another. Transects ran parallel with elevational contours.

Vegetation Sampling

We relocated plots with GPS coordinates and in spatial relation to two witness trees that were established by the original field crew. The original crew sampled trees in clockwise order starting at due north from plot center, and we relocated trees by cruising in the same order while using a copy of the original data sheets as a reference. We recorded the species and diameter at breast height (dbh) (tree diameter at 4.5 feet aboveground) to the nearest tenth-centimeter of each standing woody plant with a dbh of 10.1 cm (3.98 inches) or more. We also noted whether it was alive or dead. We refer to these individual stems as the “tree layer,” including those that with crown classes that were overtopped or intermediate.

Environmental Variables & Soil Sampling

The first crews to measure the plots in the 1990s recorded the environmental variables that we used as covariates in our models - slope percent, slope aspect, and slope position. Slope percent was measured with a clinometer, and slope aspect was measured with a compass. Slope position was determined by first measuring the slope length from ridgetop to bottomland, in a line that passed through each plot. To calculate the percent distance to the ridgetop, the distance to the ridgetop above the plot was divided by the

total length of the slope. One soil pit per transect was excavated and the following measurements were determined in the field, by horizon: texture, pH, depth, and thickness.

Data Analysis

We modeled the mortality rates of white oak, chestnut oak (*Quercus montana*, formerly *Quercus prinus*), northern red oak, black oak, and pignut hickory (*Carya glabra*). We originally planned to model scarlet oak as well, but small sample size (n = 24) precluded further investigation. We chose nine *a priori* variables, from four types: landscape variables (cosine transformed slope aspect, percent distance to ridge, the interaction factor of the two, and slope percent), edaphic variables (acidity of the B horizon, thickness of the solum), stand structure variables (basal area of the plot in the 1990s, stand age), and individual tree variables (basal area of the tree). These variables are summarized in Table 7, along with selected literature citations and further explanation as needed of each chosen metric.

To characterize the effects of these variables on the probability of tree mortality between sampling periods, we used mixed-effects logistic regression models, which model a binary response variable in relationship to the predictor variables. We set transect as a random variable, to compensate for potential pseudoreplication caused by spatially grouping plots (Zuur et al. 2009). The models were run in R version 3.5.2, using the “glmer” function in the “lme4” package (Bates et al. 2019). For model evaluation, we kept each *a priori* variable in the model for each species. We chose this approach because it afforded direct comparison of effect sizes and confidence intervals between different species. Variables were pre-screened for covariance, with a threshold

of 0.7. Importance of individual covariates was measured with both significance from model outputs with a p-value threshold of 0.1 and with confidence intervals at the 95% level. We used a p-value significance threshold 0.1 rather than the more common 0.05, because our relatively small sample size provided reduced statistical power and because we also rely on distribution of confidence intervals to assess ecological interpretation. We also chose a higher threshold to reduce the chance of committing a type 2 error and the potential negative consequences for management (Lieber 1990). The overall predictive ability of each model was assessed using the delta method of calculating r^2 values for mixed-effects models (Nakagawa et al. 2017), using the function “r.squaredGLMM” in the MuMIn package (Barton 2018).

Results

White oak ($n = 135$) and chestnut oak ($n = 181$) trees were far more common on our study plots than northern red oak ($n = 67$), black oak ($n = 60$), or scarlet oak ($n = 24$). The mortality rates for both white oak subgenus species were lower than the rates for any of the red oak subgenus species. The overall mortality rate of the white oak subgenus was 22.2% by stem count, while the mortality rate of the red oak subgenus was 41.0%. Chestnut oak had the lowest overall mortality rates (19.1% stem mortality), followed by white oak (23.4%). Scarlet oak had the highest mortality rate (61.3% stem mortality), followed by northern red oak (41.4% stem mortality). Pignut hickory had 23.9% stem mortality, which is approximately 1% stem mortality per year (Figure 4). Scarlet oak, pignut hickory, and chestnut oak had higher mortality rates as proportions of basal area than rates as proportions of stem count, implying that some of the larger trees of those species died, while northern red oak, black oak, and white oak had higher mortality rates

by stem count. All study species combined had a mortality rate of 28.1% by stem count, or 1.17% per year (Table 7 and Figure 4).

Predictive ability of the mortality models was highest for northern red oak (0.52 conditional r^2), and lowest for white oak (0.14 conditional r^2) (Table 8 and Figure 5). Despite the relatively small sample size, northern red oak mortality had the most sensitivity to the predisposing factors we modeled; northern red oaks died at higher rates lower on slopes (12.751 ± 4.525 , $P = 0.005$), on northeasterly aspects (4.516 ± 1.720 , $P = 0.009$), on upper northeasterly and lower southwesterly landscape positions (-8.267 ± 3.266 , $P = 0.001$), in older stands (0.055 ± 0.025 , $P = 0.03$), on shallower soils (-0.058 ± 0.023 , $P = 0.01$), and on lower pH soil (0.958 ± 0.576 , $P = 0.096$). White oak mortality had a significant negative relationship with basal area of the plot (-0.021 ± 0.011 , $P = 0.05$). Chestnut oak mortality had the opposite response; it was significantly more likely to die with higher basal area on the plot (0.092 ± 0.045 , $P = 0.04$). Pignut hickory mortality was related with more mesic aspects (0.891 ± 1.256 , $P = 0.07$). Black oak mortality did not show any significant relationships with the covariates (Table 9 and Figure 6).

Discussion

The high rates of red oak subgenus mortality were consistent with results of other studies (Fan et al. 2012; Starkey and Oak 1989). We also found the same relative ranking of mortality rates as in a study of the same four oak species in mature forests of the southern Appalachians: scarlet oak had the highest, followed by northern red oak, black oak, white oak, and chestnut oak, respectively (Greenberg et al. 2011). However, Yaussy et al. (2013) found different relative rankings among the same five oak species in a multi-

state study that included many thinned stands, which indicates that oak mortality in managed forests may be driven by different factors than those affecting background oak mortality. The mortality rate for pignut hickory was intermediate between the white oak subgenus and the red oak subgenus rates, which contrasted with other studies that gave a background mortality rate for a grouping of hickory species, finding them to have the same or higher mortality as northern red oak (Shifley and Smith 1982; Smith and Shifley 1984; Widmann et al. 2014). This could suggest that pignut hickory has a lower mortality rate than other hickory species, that a regional difference exists in hickory mortality relative to oak mortality, or that our results on hickory mortality are specific to mature forests.

Our findings on the relative sensitivity of northern red oak to predisposing factors were consistent with the responses of multiple oak species reported in Keyser and Brown (2016). We did not expect, however, to find northern red oak was more likely to die on more mesic slope positions and aspects. Researchers often find that red oak subgenus trees have higher mortality rates on more xeric sites. Trees on these landscape position are often supposed be more susceptible to drought, a leading predisposing factor in oak decline (Oak et al. 1991; Starkey and Oak 1989). However, Bendixsen, Hallgren, and Frazier (2015) found that oak decline in a xeric area of Oklahoma was more likely on lower slope positions, although the dominant species in that study was post oak (*Quercus stellata*), which is part of the white oak subgenus. We also did not expect to find a relationship between northern red oak mortality and aspect, because several studies were unable to demonstrate this association for the red oak subgenus. However, these were from the Ozark region, which is more xeric relative to Ohio and which has undergone a

severe oak decline episode during the past several decades (Wood et al. 2018; Kabrick et al. 2008; Wang et al. 2008). It is possible that the severity of oak decline in the Ozark region resulted in more widespread red oak subgenus mortality across slope aspects than would occur in our study area, or that the lumping of red oak subgenus species obscured the relationship of northern red oak with aspect. Other possibilities include increased competition from mesic species on more mesic landscape positions (Appendix B), conditions being suitable for fungal pathogens on more mesic aspects, or trees on mesic aspects allocating relatively little carbohydrates to their root systems, thus rendering them less adapted to drought conditions (Bendixsen et al. 2015; Canadell et al. 1999). The importance of soil and root systems was reflected in our finding of a significant negative relationship between solum depth and northern red oak mortality, similar to associations reported in Oak et al. (1996) and Starkey and Oak (1989). Additionally, pH showed a significant negative relationship with northern red oak mortality, which corroborates results from southwestern Pennsylvania (Demchik and Sharpe 2000). Finally, northern red oak mortality showed a significant positive association with stand age. This likely reflects its relatively short lifespan (Greenberg and Parresol 2002), and is similar to the results of (Oak et al. 1991; Wang et al. 2008)

Relatively few studies have focused specifically on black oak mortality, but some have shown that black oak were more likely to die at greater sizes (Fan et al. 2011; John Michael Kabrick 2004). Our model, on the other hand, did not find that black oak mortality rate was affected by tree size or any other variable, despite having a similar sample size to northern red oak. It thus appears that black oak is more resilient to stressors such as drought than northern red oak. This could reflect a more conservative

response to stress; for example, (Keyser and Brown 2016) found that black oak slowed its relative growth rate more than red oak, white oak, or chestnut oak in the two years following drought. Black oak often has lower absolute growth rates than northern red oak, and higher growth rates than white oak or chestnut oak (Burns and Honkala 1990).

Consistent with the literature, both our focal species from the white oak subgenus died at relatively low rates and were relatively insensitive to landscape-scale variables (Greenberg et al. 2011; Kabrick et al. 2008; Keyser and Brown 2016). These two species showed opposite relationships to basal area of the plot, likely reflecting different abilities to survive under competitive stress. It is also possible that the observed relationship is confounded with site productivity, and that white oak health is generally better on more productive sites, although the other covariates in our model such as slope position, aspect, pH, and depth of solum likely represented a large portion of the productivity gradient. Chestnut oak, on the other hand, showed less resilience to competition. This is despite it having similar shade tolerance and nearly as slow growth rates compared with white oak (Burns and Honkala 1990). It is likely that the association of chestnut oak with drier landscape positions (Palus et al. 2018) renders it more sensitive to competition for water in drought. Additionally, we observed anecdotally (Radcliffe personal observation 2018) that a large number of plots had several large chestnut oaks in close proximity, and suspect that the species may have had a clumped distribution that caused it to frequently self-thin. The only study we found with data on chestnut oak spatial pattern showed a uniform spatial distribution, the opposite of clumped. However, these data were from the New Jersey pine barrens, a relatively flat and sandy system (Gill 1975), so chestnut oak dynamics could be different than in our topographically diverse system. Other studies

have found positive relationships of white oak mortality (Kabrick 2004) or white oak subgenus mortality (Bendixsen et al. 2015) with mesic aspects, but our data did not show this association.

We could not find studies modeling species-level hickory mortality rates in relationship to predisposing factors, although Yaussy et al. (2013) modeled the association of genus-level hickory mortality with competition, and found a positive correlation. Our pignut hickory model corroborated these results. Hickory is a relatively understudied tree group, especially on the species level, but we believe that it merits more attention from ecologists, considering its high benefits to wildlife (Fralish 2004).

Conclusion

Our data on oak and hickory abundance and mortality rates in mature forests, in combination with our literature review showing importance of oak diversity for wildlife, suggest that forest managers prioritizing wildlife management in mature forests similar to our study area should consider focusing restoration their efforts on red oak subgenus species. Scarlet oak, black oak, and northern red oak are dying at higher rates than white oak and chestnut oak, and they are less common in our second-growth study forests of at least 93 years old. Our literature review indicated a mix of white oak subgenus and red oak subgenus tree species is beneficial if not essential for many wildlife species; land managers and wildlife ecologists should be aware of the trends of decreasing red oak subgenus importance values we discovered in this study. Foresters may act by harvesting white oak subgenus trees preferentially to red oak subgenus trees, thinning to promote individual red oak tree vigor (Yaussy et al. 2013), or designing regeneration treatments specifically for red oak subgenus species (Crow 1988). However, red oak subgenus trees

are more common than white oak subgenus trees across the state of Ohio (Widmann 2016), and the eastern U.S. (Abrams 2009), so our observed patterns of greater white oak subgenus importance likely apply only to mature, second growth forests.

Our models suggest that competition is the only predisposing factor we tested that significantly predicts mortality rates for any of our focal species other than northern red oak, as it was significant for chestnut oak and near significant for white oak and pignut hickory. In topographically complex landscapes, designing thinning treatments to increase drought resilience (D'Amato et al. 2013) may be more effective in mitigating overall oak and hickory mortality than focusing on landscape positions to manage or leave alone, although our study is not informative about the efficacy of management treatments. Additionally, finding of a negative relationship between white oak mortality rate and competition warrants further consideration and study. Northern red oak, however, was more likely to die on more mesic landscape positions and in older stands, thus suggesting that these areas could be relatively low in protection priority on properties where northern red oak is a species of concern. Black oak on the other hand, appears to be relatively resilient to the predisposing factors we studied. Overall, there is relatively little research into patterns of background oak and hickory mortality in mature forests east of the Ozark Highlands, especially in relation to scales larger than individual tree growth and competition. Thus, managers will need to view our results as locally specific until more studies are conducted.

Table 6: Variables used in mixed logistic regression models of tree mortality, supporting literature, and notes on choice of metric

Variable	Negative correlation with oak mortality	Positive correlation with oak mortality	Notes
Tree basal area (meters ² /hectare)	(Greenberg, Keyser, and Speer 2011[Erythrobalanus]), (Voelker, Muzika, and Guyette 2008[in low mort areas]), (Fan et al. 2012 [Leucobalanus]), (Wood et al. 2018 [white oak]) (Yaussy et al. 2013 [including managed stands])	(Fan et al. 2011[black and scarlet oaks]), (Kabrick 2004 [black and scarlet oaks, dominant/codominant crowns])	Basal area of individual tree chosen because it scales more linearly with sapwood area than diameter (Meinzer et al. 2005)
Total basal area of plot (meters ² /hectare)		(Oak, Huber, and Sheffield 1991), (Wang et al. 2008) (Yaussy et al. 2013[white oak, black oak, scarlet oak])	Competition of all species chosen rather than competition of Quercus as some other studies have, because of the diversity of our study area and the lack of a major oak decline event
Stand age (years)		(Greenberg, Keyser, and Speer 2011 [tree age, Leucobalanus]), (Oak, Huber, and Sheffield 1991), (Wang, He, and Kabrick 2008[tree age][non-linear])	Age is stand age, not individual tree age, and was determined from Forest Service Vegetation Management Information System
Solum depth (inches)	(Oak et al. 1996) (Starkey and Oak 1989[all sampled oaks])		Depth of solum chosen rather than depth of entire soil profile, because some soil pits did not reach the depth to bedrock, and because most fine roots in forest ecosystems are found in upper layers of the soil (Schenk and Jackson 2002).
B horizon acidity (pH)	(Demchik and Sharpe 2000 [northern red oak]),		B horizon chosen because it had greater significance than A horizon in a study of sugar maple mortality (Bailey et al. 2004), displayed different nutrient concentrations with different levels of oak mortality in (Demchik and Sharpe 2000) and because it's more resistant to erosion over time (Kreznor et al. 1989).
Slope percent	(Oak et al. 1996)	(Wang, He, and Kabrick 2008 [non-linear]), (Bendixsen, Hallgren, And Frazier 2015 [primarily post oak])	
Slope aspect (cosine transformed [TASP])	(Bendixsen et al. 2015) (Kabrick 2004 [white oak])		Slope aspect was cosine transformed ($\cos(45^\circ - \text{aspect}) + 1$), to make the metric change continuously in a circular fashion. TASP maximizes at 2 for a 45° aspect, and minimizes at 0 for a 225° aspect (Beers, Dress, and Wensel 1966).
Slope position (percent distance to ridge [PDR])	(Stringer et al. 1989), (Oak, Huber, and Sheffield 1991), (Starkey and Oak 1989 [lumped oaks])	(Bendixsen et al. 2015)	Percent distance to ridge is maximized at the bottom of a slope; positive correlation is higher mortality on lower slopes.
Slope aspect:slope position interaction (TASP:PDR)			High values of the interaction factor indicate upper slopes and northeast facing aspects.
Management Unit (Marietta)			Included to test for differences between management units in factors that drive focal species' abundance other than those we controlled for.

Table 7: Mortality rates by stem count and basal area for focal species and major groupings

Group	Species	Sample Size	Stem Count Mortality (%)	Basal Area Mortality (%)
White Oak Subgenus	White Oak	135	23.4	22.8
	Chestnut Oak	181	19.1	20.4
	Total	316	22.2	21.5
Red Oak Subgenus	Northern Red Oak	67	41.4	32.0
	Black Oak	60	26.7	23.0
	Scarlet Oak	24	61.3	78.8
	Total	151	41.0	39.4
Oak Genus	Total Oaks	467	28.5	28.7
Hickory Genus	Pignut Hickory	52	23.9	30.9
All Trees	Total Trees	519	28.1	27.5

Table 8: r^2 values for mixed effects logistic regression model, delta method.
Values from r.squaredGLMM {MuMIn}, R version 3.5.2

Species	Marginal r^2	Conditional r^2
White Oak	0.14	0.14
Chestnut Oak	0.18	0.34
Northern Red Oak	0.52	0.52
Black Oak	0.23	0.34
Pignut Hickory	0.29	0.29

Table 9: Mixed effects logistic regression model coefficients (\pm standard error), raw output from glmer {lme4}, R version 3.5.2. *P* values denoted with asterisks (** < 0.01, * < 0.05, .<0.1), alpha level 0.05

Variable	White Oak	Chestnut Oak	Northern Red Oak	Black Oak	Pignut Hickory
Intercept	-1.841(\pm 3.680)	-2.677(\pm 4.638)	-16.319(\pm 5.859)**	-12.405(\pm 19.047)	1.940(\pm 6.563)
Basal area of tree 1990s (ft ² /acre)	-0.036(\pm 0.028)	-0.030(\pm 0.175)	-0.264(\pm 0.160)	-0.389(\pm 0.297)	0.802(\pm 0.502)
Basal area of plot 1990s (ft ² /acre)	-0.021(\pm 0.011)	0.092(\pm 0.045)*	0.045(\pm 0.048)	-0.127(\pm 0.109)	0.141(\pm 0.077)
Age (years)	0.023(\pm 0.018)	0.004(\pm 0.019)	0.055(\pm 0.025)*	0.022(\pm 0.038)	-0.034(\pm 0.029)
Depth of solum (inches)	-0.033(\pm 0.028)	0.017(\pm 0.023)	-0.058(\pm 0.023)*	-0.028(\pm 0.025)	0.019(\pm 0.013)
B horizon acidity (pH)	0.379(\pm 0.497)	-0.416(\pm 0.657)	0.958(\pm 0.576)	3.361(\pm 3.491)	-1.272(\pm 0.907)
Slope percent	0.020(\pm 0.019)	-0.024(\pm 0.026)	0.025(\pm 0.025)	-0.017(\pm 0.029)	-0.011(\pm 0.027)
Slope aspect (cosine-transformed, TASP)	0.072(\pm 0.821)	0.019(\pm 0.893)	4.516(\pm 1.720)**	0.148(\pm 1.652)	0.891(\pm 1.256)
Slope position (percent distance to ridge, PDR)	0.277(\pm 1.935)	-2.954(\pm 3.488)	12.751(\pm 4.525)**	-1.512(\pm 3.452)	-1.404(\pm 2.769)
TASP:PDR	-2.154(\pm 1.643)	1.327(\pm 2.237)	-8.267(\pm 3.266)*	-0.492(\pm 3.385)	2.638(\pm 2.740)

Mortality Rates of Focal Species

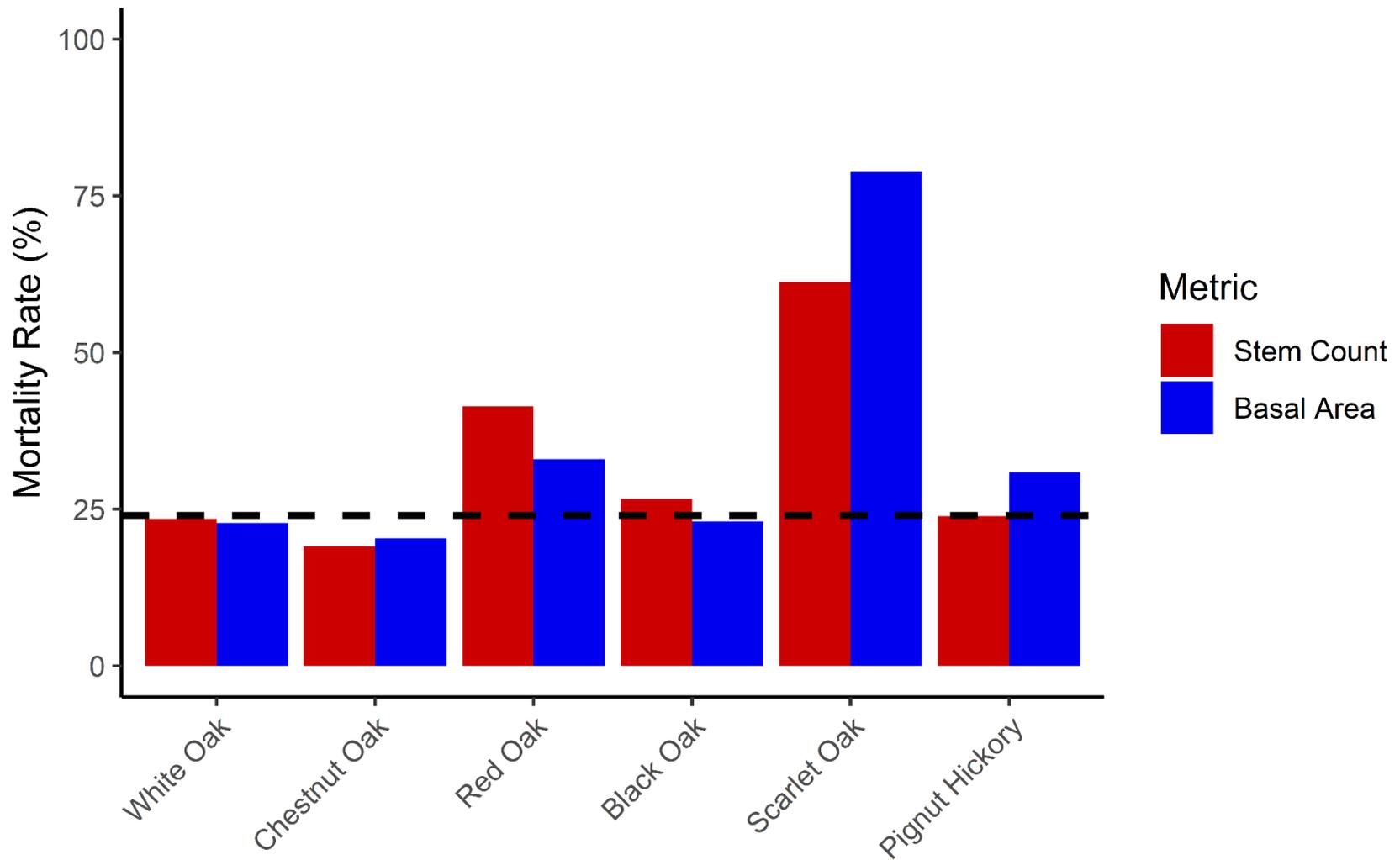


Figure 4: Mortality rate of focal species by stem count and basal area. Dotted line indicates approximately 1% mortality per year, the background mortality rate found in Greenberg et al. (2011)

r² Values by Species, Delta Method

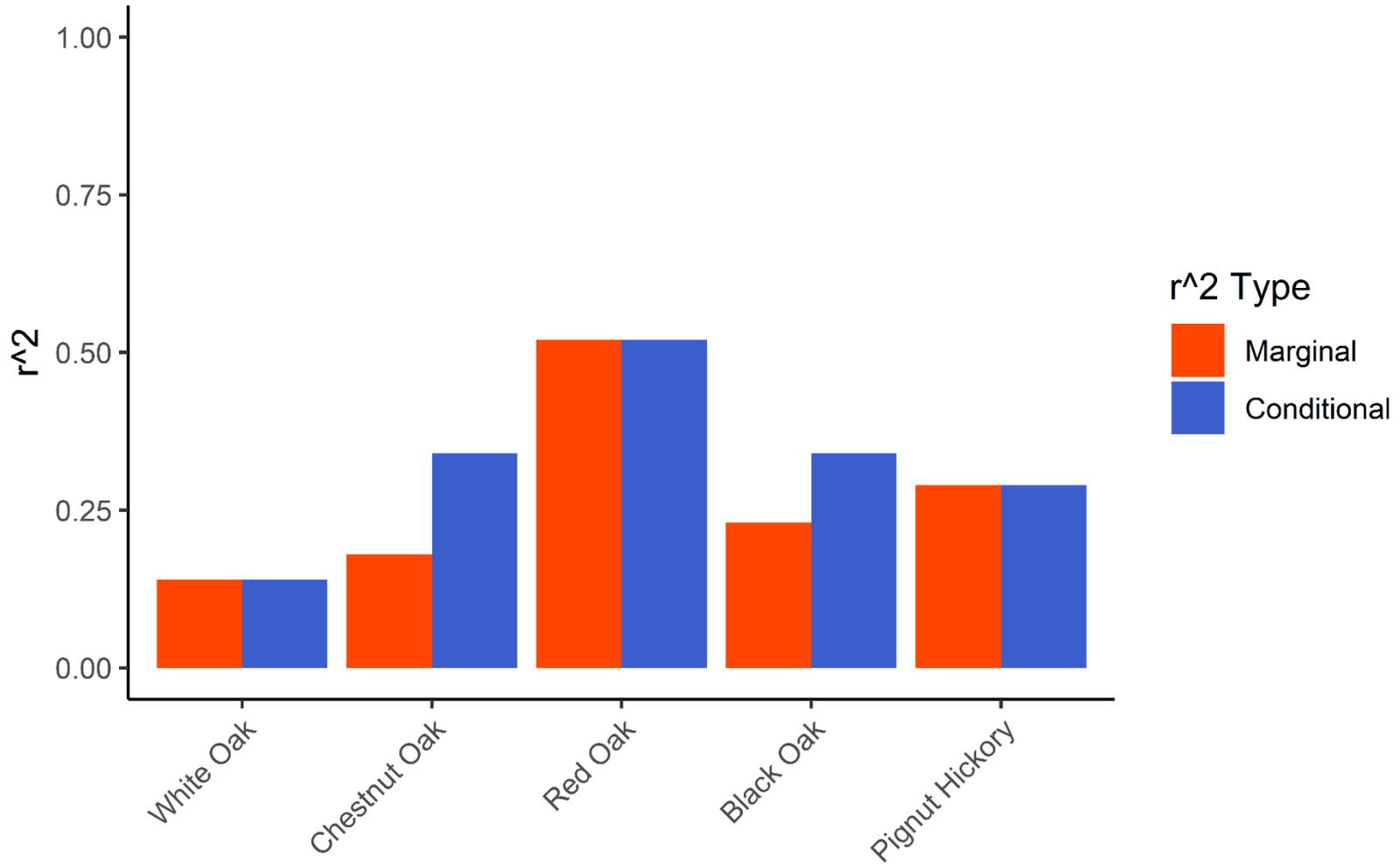


Figure 5: r² values for mixed effects logistic regression models of tree mortality, delta method. Values from r.squaredGLMM {MuMIn}, R version 3.5.2

Tree Mortality Model Coefficients

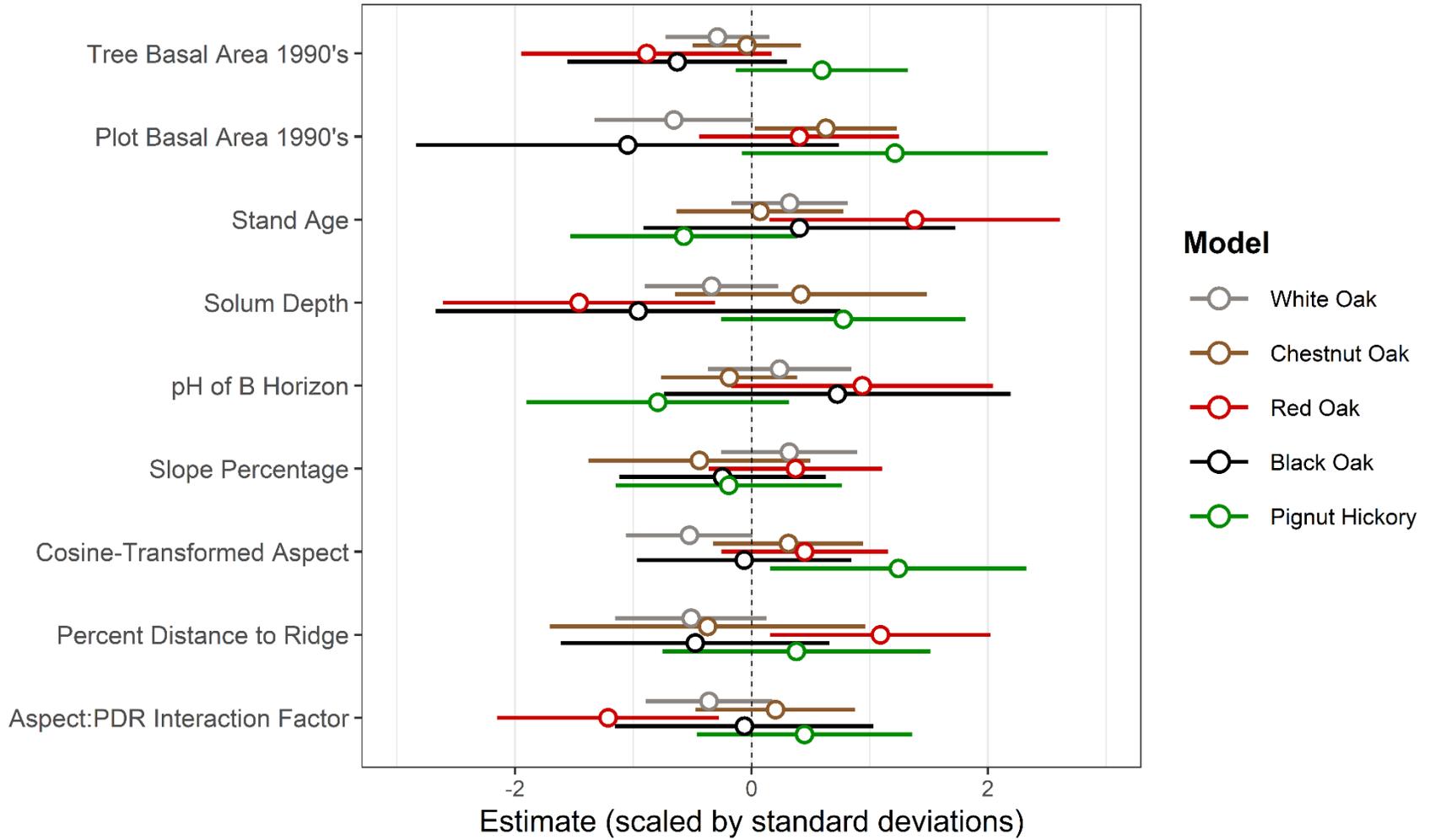


Figure 6: Mixed effects logistic regression model coefficients with confidence intervals, scaled by standard deviations. Output from `plot_summs {jtools}`, R version 3.5.2

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Appendix A: History of Land Use in Southeastern Ohio

Ohio was first inhabited by Native Americans at least 11,000 years ago (Kern and Wilson 2014), and they likely conducted forest burning regularly over the past 3,000 years (Delcourt et al. 1998). Many early settlers described some forest areas as open and relatively devoid of “underbrush,” and attributed this to Native American burning (Hutchinson et al. 2003). The full spatial extent of their land management practices, however, is heavily debated (Guyette et al. 2005; McEwan et al. 2011; Nowacki and Abrams 2008), and was probably limited to 10s or at most 100s of kilometers around settlement areas, at least in more recent prehistoric times (Munoz et al. 2014; Tulowiecki and Larsen 2015). It likely changed often in prehistoric times, as the composition and structure of tribes in the area was dynamic, and the effects were spatially and temporally heterogeneous (Munoz et al. 2014). In general, land use in southern Ohio became more intensive and cultures more complex over time. Some milestones include the embrace of the “Eastern Agricultural Complex” (the deliberate management of wild plants and animals for increased food production) by Adena people around 3,000 years ago, the intensification of ceremonialism and mound building by the Hopewell people around 2,100 years ago, and the move away from the Eastern Agricultural Complex in favor of maize production about 1,100 years ago. In more recent times, the Ohio River was an important line of Native American resistance to European encroachment. Thus southern Ohio was inhabited by many native peoples, most prominently of the Shawnee Tribe, and several U.S. military campaigns were waged against them, resulting in frequently shifting patterns of settlement and land use (Kern and Wilson 2014).

European descendants of the first colonists settled southeastern Ohio early in the history of the United States. The city of Marietta – the namesake of one of our study area units – was established in 1788. It was the first capitol of the Northwest Territory, and the area northeast of the city, including the land that is today the Marietta Unit, was the first area of the U.S. surveyed under the Northwest Land Ordinance of 1785. Early farmers cleared low-lying parcels, but much of the land in unglaciated Ohio went unsold because it was deemed unsuitable for farming (Kern and Wilson 2014). Later in the 19th century, iron mining became southern Ohio’s largest industry, and large areas of forests were cleared for use in processing the ore. Many of these areas were cut multiple times on short rotations, and human-caused fires were common, and other areas were cleared for lumber. The iron industry declined in the late 19th century as better ore deposits were found near Lake Superior. Many of the present mature stands thus date back to the late 19th century (Hutchinson et al. 2003). Other long-time industries in the region include petroleum drilling, salt mining, and coal mining (Kern and Wilson 2014). During the Great Depression of the 1930s, many farmers and landowners on the relatively infertile land of southeastern Ohio were financially ruined, and the United States government began buying tax-delinquent land for a national forest in 1934. The Wayne officially became a national forest in 1951 (USDA Forest Service 2018).

This legacy of land use and abandonment has left the Wayne a patchwork of publicly owned and private land today, primarily in private ownership. Intensive and varied land use continues in across the area, including the continued maintenance of many small oil wells (USDA Forest Service 2005), with many roads and trails maintained for access. There have also been recent controversies about leasing parts of the Wayne for natural gas fracking (Smith 2018),

an industry that has boomed in eastern Ohio in the past decade (ODNR 2019). Additionally, the land is managed for many forms of recreation, as well as some timber harvesting and prescribed burning (USDA Forest Service 2006).

Appendix B: Diameter Distributions by Ecosystem Land Type, Athens and Marietta Units

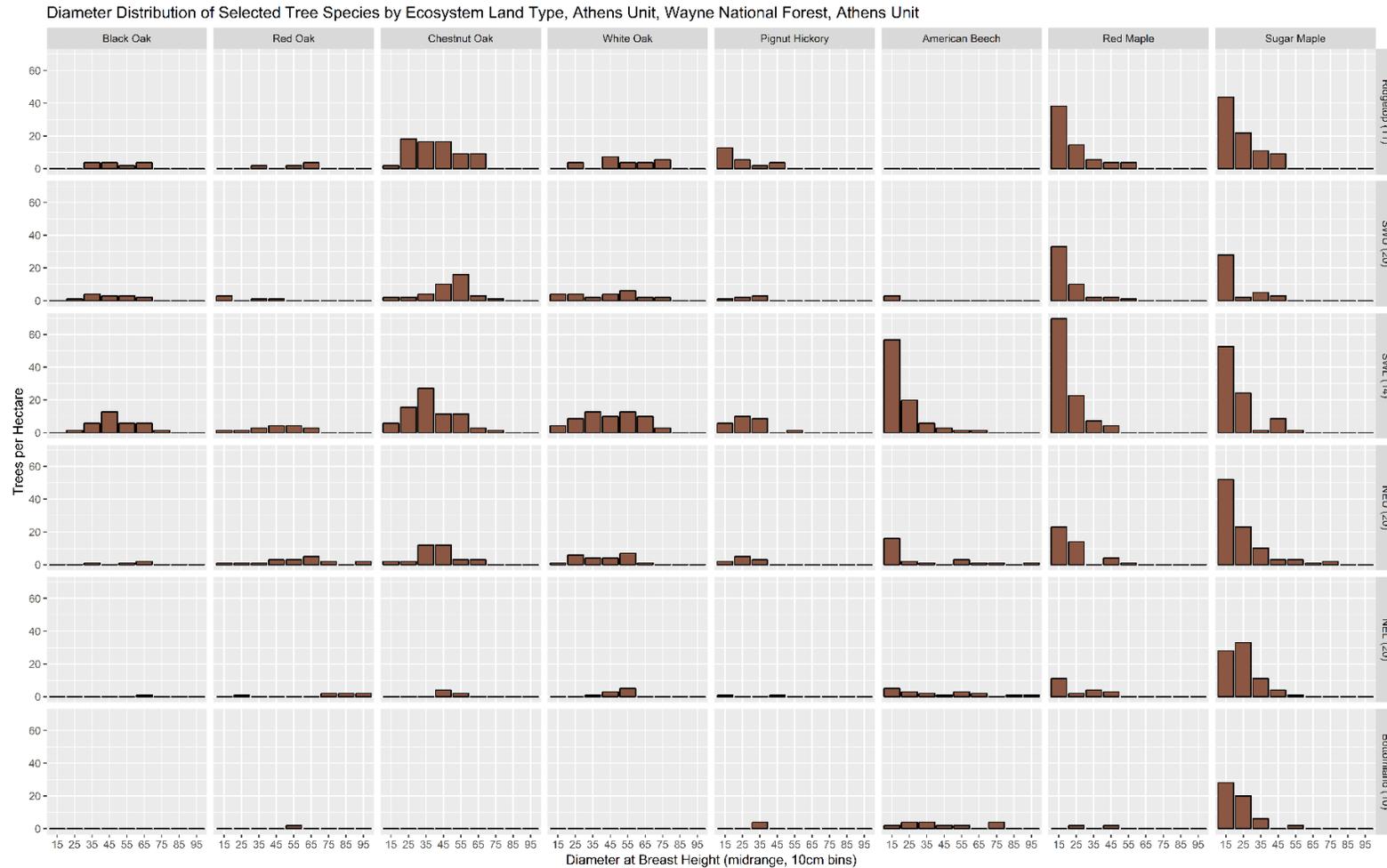


Figure 7: Diameter distribution of eight common tree species on the Athens Unit of the Wayne National Forest, divided by six Ecological Land Types. SWU = Southwest Upper, SWL = Southwest Lower, NEU = Northeast Upper, NEL = Northeast Lower. Ridgetops and bottomlands are separated from the slopes by having less than 15% slope. "Northeast" includes slopes facing aspects of 316-135 degrees, and "Southwest" includes slopes facing aspects of 136-315 degrees. Upper and lower slopes are divided by the 50% distance to ridge mark

Diameter Distribution of Selected Tree Species by Ecosystem Land Type, Marietta Unit, Wayne National Forest

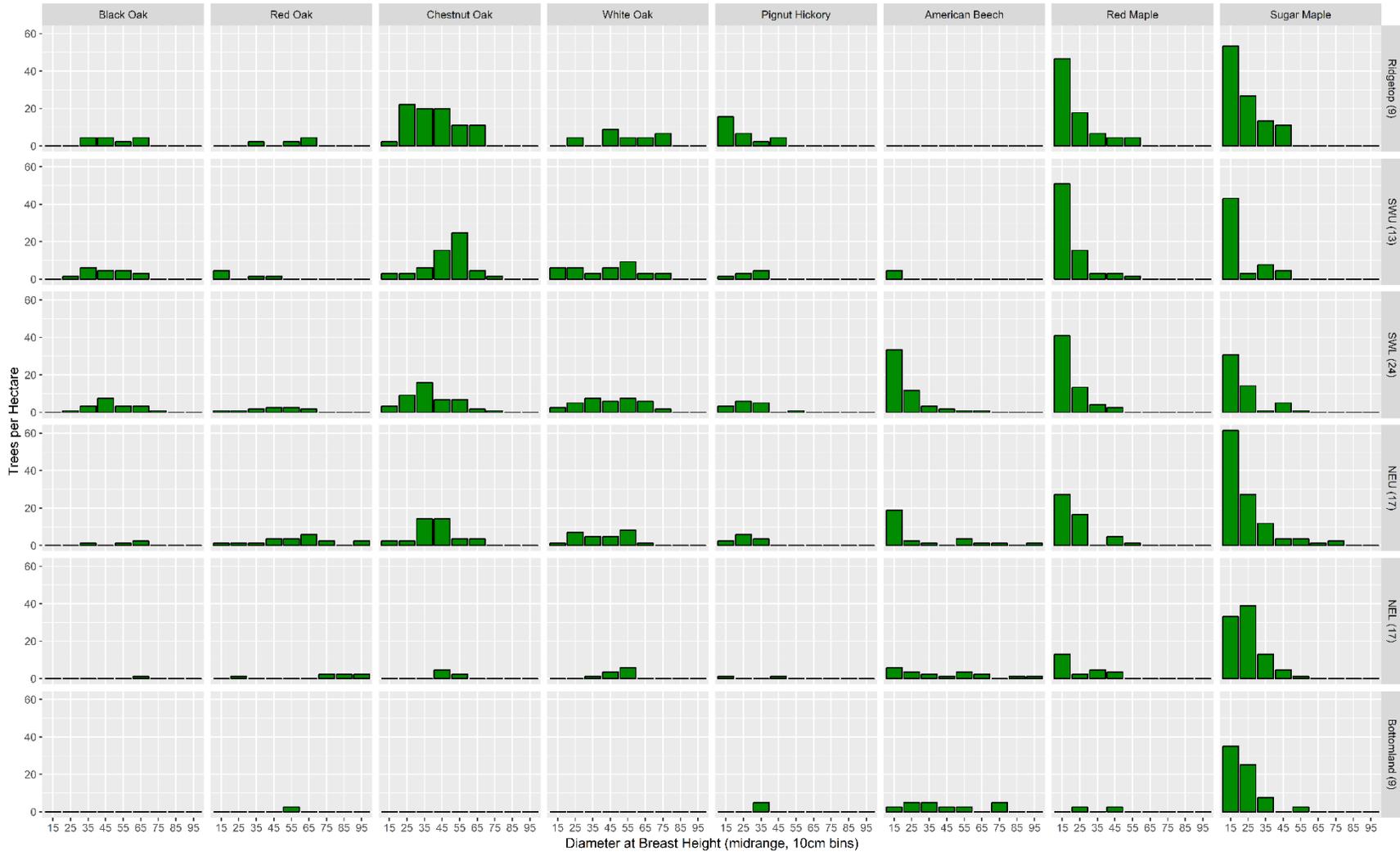


Figure 8: Diameter distribution of eight common tree species on the Marietta Unit of the Wayne National Forest, divided by six Ecological Land Types. SWU = Southwest Upper, SWL = Southwest Lower, NEU = Northeast Upper, NEL = Northeast Lower. Ridgetops and bottomlands are separated from the slopes by having less than 15% slope. "Northeast" includes slopes facing aspects of 316-135 degrees, and "Southwest" includes slopes facing aspects of 136-315 degrees. Upper and lower slopes are divided by the 50% distance to ridge mark