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Succession of an Upland Oak/Hickory Forest in the Central Hardwood Region

By

Nathan M. Hoover

B.S., Illinois State University, 2011

A Thesis
Submitted in Partial Fulfillment of the Requirements for the
Master of Science Degree

Department of Forestry
In the Graduate School
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THESIS APPROVAL

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A Thesis Submitted in Partial
Fulfillment of the Requirements
For the Degree of
Master of Science
In the Field of Forestry

Approved by:
Dr. Eric Holzmueller, Chair
Dr. John Groninger
Dr. Charles Ruffner

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AN ABSTRACT OF THE THESIS OF

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TITLE: Succession of an Upland Oak/Hickory Forest in the Central Hardwood Region

MAJOR PROFESSOR: Dr. Eric Holzmueller

For the last 9,000-10,000 years the Central Hardwood Region (CHR) has been primarily composed of a mosaic of mesophytic communities in climax and communities of successional forest types dominated by oak (*Quercus* Linnaeus) and hickory (*Carya* Nuttall). Shade intolerant oak/hickory dominated forest types have been maintained by natural disturbance processes in synergy with anthropogenic causes, resulting in a large composition of communities which are neither at climatic nor edaphic climax. Reduction in fire events, thinning, forest grazing, and other disturbance processes over the last 80-100 years have coincided with decreased regeneration of shade intolerant species due to lack of adequate light availability and recruitment of shade tolerant species of communities dominated by American beech (*Fagus grandifolia* L.) and maple (*Acer saccharum* L.) into the overstory of forests typically dominated by oak/hickory. Forest inventory data at Trail of Tears State Forest was analyzed across two separate time events (1980 and 2014) to determine compositional and structural changes which have occurred. Density, basal area, and community patterns via ordination were compared across six Ecological Land Types (ELTs) to determine topography's effect on composition. .

Community trends were analyzed via NMS Ordination and between ELTs by a Mantel Test. A Multi-Response Permutation Procedures (MRRP) was also used as a nonparametric method for assessing differences between ELTs examined in the NMS. Density and basal area between years for species, ELT, and species*ELT interactions were compared. Across all ELTs, between 1980 and 2014, overstory density decreased from 218 trees/ac in 1980 to 180 trees/ac in

2014 and basal area increased from 98 ft^2/ac in 1980 to 106 ft^2/ac in 2014. Maple basal area increased from 5 ft^2/ac to 12 ft^2/ac while beech increased from 1 ft^2/ac to 8ft^2/ac, signifying progression of these species from the understory up into the canopy. The component of soft masting species within the forest has also decreased sharply in the last 34 years. MRPP analysis of overstory compositional gradients reported distinct species compositions between ELTs, however the trend was weak (MRPP: $p \leq 0.001$, $A = 0.038$). NMDS ordination graphs confirmed MRPP showing little separation among ELTs. The final stress was 18.71146 and instability was ≤ 0.01 after 212 iterations (Table 6). Our research at TTSF is a clear example of oak/hickory succession to beech maple on an upland site among species community types as delineated by topographic moisture gradient (ELTs) within the CHR. Expansion of beech and maple onto xeric ELTs suggests a breakdown of edaphic barriers that have previously been thought to be resistant to encroachment from mesophytic species. Currently oak decline induced by lack of management is likely the number one forest health issue resulting in loss of oak/hickory and other soft masting species.

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My family (Mom, Dad, Chris, Ryan, Kristin, Megan, Kristin, and Jersey), I give them all my love and thanks. Without their support, I would not have completed. Their names deserve to be at the top of this thesis as well.

Lastly, thanks goes to Kristin for everything during our seven years. Her unwavering support is at the heart of this project.

DEDICATION

This work is dedicated to my friends, family, co-conspirators, and colleagues.

Here and gone.

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CHAPTER 1

LITERATURE OVERVIEW

The Central Hardwood Forest

The Central Hardwood Forest (CHR) physiographic region encompasses a large part of the interior eastern United States. Its range extends north into the lake states and upper northeast where it is bordered by the Northern Hardwood Conifer Forest. The Eastern half is separated by the Appalachian Mountains while further south into the upper portions of Alabama and Louisiana, the Southern Hardwood Conifer Forest begins. Regions from Texas to Missouri define the Western border where forest cover begins to transition into the Great Prairie. The CHR is further delineated along the upper Mississippi River into Canada and the Missouri River into Nebraska (Braun 1950, Kuchler 1964, McNab et al 2006).

The genesis of the CHR has been influenced by several variables including edaphic conditions, successional processes, fire, storm events, and wildlife. While all of these variables are interactive and influences species composition and distribution across all spatial scales, climate may be thought of as the most overarching. Regional climate trends are primarily a product of large-scale topography, latitudinal position, and land cover types. All of which effect temperature extremes, precipitation, and the number of growing days plants are susceptible to (Barnes et al 1997). Over the last 18,000 years, the floristic compositions and forest types of the eastern U.S. have shifted contingent with the waxing and waning of glacial periods as well as competition between species (Jackson et al 2000). For the last 9,000-10,000 years the present CHR region has included a large component of deciduous tree species adapted the temperate climate and moderate number of growing days.

Topography, edaphic conditions, and disturbance processes have had an effect on regional distributions of forest types. While Government Land Office (GLO) records and other historical data show oak/hickory have been the dominating species on upland and southern exposures, they have also occurred on mid slope and northern aspect sites for the duration of the Holocene epoch (Hanberry 2013). Paradoxically, microclimate conditions on these exposures favor dominance of mesic species (Thompson and Dessecker 1997, Dyer 2001). The prevalence of oak/hickory species is explained by examining fire scar data and historical reports of other disturbances that show a repeated pattern of periodic historical disturbances have maintained these pyrogenic communities (Ruffner and Groninger 2006). Higher frequency of fire occurred on refugee upland sites occasionally extending into more mesic sites during extreme disturbance events or appropriate environment conditions, supporting the expansion of shade intolerant species (Guyette et al 2004). Currently oak/hickory forests located on high site index sites (50-80, height in ft, base age 50) are ubiquitous across the region (Oswalt et al 2014). As such the transition from oak/hickory to maple/beech dominated stands facilitated by removal of disturbance will influence the entirety of the CHR and a large area of the Eastern United States (Ebinger 1986, Abrams 1998, Zaczek et al 2002, Holzmueller et al 2011). To fully understand this process, it is first important to complete a more depth examination into the historic disturbance regimes which played a role in shaping the CHR.

Historical Disturbances

In combination with climate, topography, and edaphic conditions, the episodic destruction of forest communities has played a powerful role in shaping the CHR. Disturbances have been both natural and anthropogenic, occurring heterogeneously across site conditions, and affecting subsequent successional processes (Abrams 2010 &Abrams 2005). Among upland communities, fire has been the essential disturbance process in maintaining oak/hickory (Abrams

2003). Analysis of historic pollen concentrations and carbon dating of woody species' charcoal through the use of soil cores have been used to estimate historic species composition as well as the pervasiveness of fire (Hart and Buchanan 2012). Data from the GLO and current overstory species has also be used to determine forest composition over the last 200 years (Hanberry 2013). Fire scar data issued to predict fire return rate (Smith and Sutherland 1999, Guyette et al 2004) and research in this area has confirmed the variable nature in which fire changes a landscape. However, it has also been conclusive in recording the cumulative decrease in fire affecting the entire region over the last century (Ruffner and Groninger 2006).

Other historical accounts have also been very important in cataloguing the disturbance regime affecting the region, such as documented logging practices and natural storm events (Beilmann and Brenner 1951, Steyermark 1959). The discrepant nature between estimated historic fire return rates and estimated lighting strikes during the Holocene suggests Native Americans were the primary ignition source for fire in this era (Guyette et al 2004). Post-settlement European activity had similar ecological effect on the environment as Native Americans (Nelson 2010). Other disturbance processes also have had huge effects on species distribution such as flooding, drought, storm events, earthquakes, and intense browse/soil disturbance from wildlife. However, historical impacts from these processes have been much less well studied.

Presettlement: The pre-1810 CHR was a mosaic of disturbance patters largely created by anthropogenic forces (McEwan et al 2011). Native Americans intensely used the land for agriculture, firewood collection, irrigation, and hunting (Denevan 1992). Low intensity fires were commonly implemented to maintain grazing forage, regenerate desirable herbaceous species, and for hunting purposes (Van Lear 2004, Donovan and Brown 2007). Intervals between fire events varied across the CHR depending on litter, soil saturation, and topography. For example, historical mean fire intervals reported for the Central Hardwoods range between 2 years in the central till plain of Illinois (McClain et al 2010) to 12 years in the Allegheny Plateau of eastern Kentucky (McEwan et al 2007) to 30 years for a glade located in the Missouri Ozarks (Guyette and Cutter 1997). For the topographically variant Ozark Hills, fire return rates are especially variant over small spatial ranges as shown by (Stambaugh and Guyette 2008). They found site topographic roughness had a positive correlation with mean fire return interval. Fire return rate ranged from 1-39 years. As mentioned above, Native Americans are theorized to be the primary ignition source in the eastern U.S during the presettlement era as lighting strikes are too infrequent to explain historical fire intervals (Kay 2007,Yang et al 2006). Primary disturbances by natural sources included storm events (such as tornadoes, microbursts, and derechos), and intense but ephemeral grazing by bison.

1810-1920: Post-1810 until the 1920s marks a change in the disturbance regime of the CHR. In the early 19th century, several large earthquakes occurred along the Madrid Seismic Fault which felled vast tracts of forest (Fuller 1912). European settlers extensively cleared land and ran livestock within the forest. Large areas of forest where logged in what is known as the "19th Century Great Cutover" for use in railroads, mines, the rising coal industry, and for buildings (Hicks 1997). Fire was a common tool throughout this period as a general land clearing tool for use by farmers, as well as caused by accidental ignitions (Abrams 2010). Populations of American bison (*Bison bison* L.) dropped dramatically due to over-hunting and climatic shifts (Isenberg 2001). As well, chestnut blight (*Cryphonectria parasitica* (Murrill) Barr) affected the region during the 19th century (Paillet 2002), creating canopy openings that were predominately filled by oak and hickory (Diamond et al 2000). It is important to note, even with the increase in disturbance intensity it is still estimated that eastern forests during this time returned to pre-settlement composition, with some exceptions, most notably being the loss of American chestnut (*Castanea dentata* (Marshall) Borkh) (Whitney 1996).

1920-Present: Where post European settlement up until 1920 had been noted for its increased disturbances, post 1920 has been defined by removal of disturbance processes (Nowacki and Abrams 2008). Fire suppression became the official policy of the Forest Service with the establishment of the "10 a.m. policy" (Donovan and Brown 2007). It was the culmination of public perception and professional opinion towards fire suppression and held sway for the next 35 years. Livestock was removed from the forest due to overexploitation in the early 20th century and subsequent "fence laws" were put into place in a successful movement to improve water quality (Hursh 1951). Timber harvesting decreased in the 19th century where it was estimated 99% of the original forest was removed (Abrams 2010). However, some public land has also undergone a significantly greater reduction in harvesting/thinning do to public concern over environmental effects, such as in the Shawnee National Forest (Kessler 1993). Disturbance from white tail deer (*Odocoileus virginianus* Zimmerman) has seen an eventual increase across the 20th century, however increased populations have been shown to decrease stand diversity through preferential browsing of oak (McGarvey et al 2013). On public lands in the CHR the lack of disturbances over the last 80 years has led to a decrease in shade intolerant to intermediate shade intolerant species and an increase in shade tolerant individuals (Zaczek et al 2002, Gould et al 2003, Schmidt and McWilliams 2003, Pierce et al 2006, Holzmueller et al 2011).

Upland Oak/Hickory Forests

Upland oak and hickory species are intermediate to shade intolerant, requiring ample light throughout their life cycle to germinate and reach maturity (Carvell and Tryon 1961). These species respond well to large disturbance events which increase light on the forest floor, low intensity fire events, and after drought periods which cause mortality of competitors (Arthur et al 2012, Clark et al 2016). Ecophysiological attributes include thicker bark, a capacity to stump sprout, rot resistance, and high gas exchange rates under drier conditions (Kubiske and Abrams 1994, Larsen and Johnson 1996). While upland oak seedlings may be top-killed by fire, they are adapted for regenerating following a burn (Brose and Van Lear 2004). Both oak and hickory are especially adapted for early and robust root growth (Abrams 1996). Their nuts contain two large cotyledons that provide adequate energy stores for root development without the immediate need for a large photosynthetic crown. This allows hard mast seedlings regenerate after fire although acorns must be protected by mineral soil to effectively germinate (Iverson et al 2007). Deep rooting is also a characteristic of mature individuals which allows them to survive draught conditions (Abrams 1996).

Oak species leaves, bark, and acorns contain tannins, which aid in fire, insect, and disease resistant as well as decreasing acorn edibility by seed predators due to their bitter taste and digestive interference (Shimada and Saitoh 2006, Vander Wall 2001). A high lignin content also increase flammability of litter by delaying decomposition of senesced leaves and improving air circulating within the litter layer (Nowacki and Abrams 2008). Maple, beech, and other species are shade tolerant and capable of growing under the low light conditions associated with continuous canopy cover. Given adequate nutrient availability and water resources, they will frequently outcompete upland oak/hickory species, especially in more mesic environments

However, on more xeric environments, oak/hickory may still hold the competitive advantage and may achieve an edaphic climax (Palus 2017).

Forest Succession

Succession is the ecological process describing the dynamic changes in vegetation composition and structure in a given area over time. There is no doubt the progressive replacement of plant species by one another has been known by man throughout history; however, the first precise recording of species replacement patterns was completed by Durea De La Malle in 1825. De La Malle recorded changes in plant communities in the meadows and woodlands of France, proposing a theory of succession which he compared to crop rotation. In 1881, Finish botanist, Ragnar Hult, was the first to introduce the idea of pioneer-adapted species transition into climax community. However, his focus was much less on ecology than plant physiology and it was not until Henry Cowles publication on succession of Indiana sand dunes that the theory began to be more fully developed. Cowles' greatest contributions to theory of plant succession include his detailed description of succession of the Indiana dunes as well his recognition of regional influences, topographic changes, and biotic factors' influence on successional processes.

In 1916, Frederick Clements, who also set the standard for current methods of vegetation sampling, published his first article on succession which was paramount in the development of current theory. Clements described important methods of seed dispersal, environmental conditions affecting germination and growth, and biotic interactions, all of which influence succession. In addition, he described many other relevant theories of ecology such as the important role of dominant species in defining the growing environment which other species must persist under. Clements' definition also had several flaws; however, they were primarily not in his descriptions of phenomena, which were largely comprehensive, but rather in his interpretation of them. Clements' stressed the existence of homogenous self-reproducing climax communities defined by climatic regions and placed less emphasis on other intervening factors such as fire, disease, insects, animals, natural disturbances, and human disturbances. Succession theory as developed by Clements was further modified by Tansley (1935), Whittaker (1953), and most famously by Gleason (1926). Whereas Clements stressed the homogeneity of communities and successional stages, Gleason stressed complexity and heterogeneity as described by his "Individualistic concept". Gleason reasoned fortuitous dispersal events and fluctuating environmental conditions where the main determinants of succession. Conditions affecting these processes are dynamic and unique to every specimen. These criticisms have led to the current definition of succession which is better described as vegetation dynamics.

The current state of succession theory describes several main causes of succession including site availability, species availability, and species performance (Pickett et al 2009). Succession is also divided into primary succession, which occurs when vegetation establishments in a previously unoccupied area, and secondary succession in which a plant establishes in an area already occupied, though these types are many times impossible to distinguish (van der Maarel 2012). The potential for a species to persist on a site is determined by chance establishment events, the microenvironment it is subjected, and recourses available to it (Bakker et al 1996). Once again, climate is the dominating factor controlling the initial availability of a site to a specific species. Simply, only those individuals evolutionarily adapted to the climatic conditions of an environment will be capable of propagating there. Disturbances, such as fire and storm events, also play an important role in clearing land via mortality and altering recourse availability that further influences the dynamic succession of vegetation in an area (Walker and

Moral 2009).

Succession is influenced by a species' capacity to propagate itself, which is related to quantity of seed production, seed viability, and vectors for dispersal (Nathan and Muller-Landau 2000). Additionally, species capable of regenerating (Abrams 1996) or persisting within the seed bank (Clark et al 2007) after disturbance have an additional advantage in populating a site. After initial establishment, secondary succession proceeds variably depending on an individual's performance, interactions with other organisms, and the abiotic environment.

Within the CHR light is the prominent selecting factor for successional pathways, followed by availability of water on xeric ridgetop sites. Successional pathways transition from shade intolerant species to shade tolerant species where those species are capable of maturation (Wang et al 2015). Upland oak/hickory communities exist in two successional site types because of this (Nowacki and Abrams 2008). On south, southwest, upland, and ridgetop sites, soil conditions limit the available water content of the stratum (Boerner 2006). Fire intervals are also shortened (Stambaugh and Guyette 2008), favoring xeric species. Physiologically, oak/ hickory species are draught resistant, deep rooted and intermediate to extremely shade intolerant becoming slightly more shade intolerant as they mature (Burns and Honkala 1990). These conditions may create a climax community of oak/ hickory due to their ability to proliferate under the limiting factors of the environment. Under more mesic site conditions oak/hickory undergo greater competition from hydrophilic species that are capable of outgrowing and shading out slower growing species. Disturbances are necessary to establish and maintain these successional communities of oak/hickory (Hanberry et al 2014). For disturbances to recruit an oak/hickory component, they must create large enough gap openings in the forest to allow shade intolerant individuals to undergo advanced regeneration or invade from refugee sites on xeric low productivity sites (Loftis 2004). Fire plays an additional role in sustaining shade intolerant pyrogenic communalities by causing mortality in the seedling/sapling size class of mesophytic species within the understory. Size class, fire intensity, and fire frequency, litter composition, and environmental stressors are important factors in determining the effect fire will have on modifying species composition via mortality (Albrecht and McCarthy 2006, Iverson et al 2007).

Topographical Effects

Topographic heterogeneity (percent slope, slope position, and aspect) may increase species diversity in a landscape through the creation of differing microenvironments (Beckage and Clark 2003). In itself, topographic positions are products of geological processes and are associated with specific soil types generated from parent material and further modified by a variety of environmental conditions (Jenny 1941). Growth conditions under topographic position are additionally affected by varying amount of light, precipitation, nutrients, disturbance, and competition from other species (Boerner 2006). In turn, vegetation also alters abiotic factors affecting the site and soil conditions (Alexander and Arthur 2010). In culmination, these factors can create several different microenvironment conditions within a forest (Rentch and Hicks 2005). As these conditions are very specific to location they will be discussed broadly and in relation to the study region in the Ozark Hills.

Soils are formed by an interaction between climate, plants and wildlife, percent slope, parent material, and time (Jenny 1941). Topographically, the downslope movement of sediment generally creates deeper soils on lower slope position and thinner soils on upper slope positions (Gabet et al 2003). There are exceptions to this such as in the Ozark Hills where loess caps generated from millennia of deposits from the Mississippi have increased the soil depth heterogeneously on some ridgetops. As well, clay fragipans exist which further accentuate xeric conditions (Seifert et al 2009). Lower slope positions in the Ozark Hills usually contain more organic matter, more exchangeable ions, thicker horizons, higher base saturation, and pH values (Ware et al 1992). South, Southwest, and West soils usually have a higher surface sand content and more clay within the B-horizon. These aspects are commonly associated with lower productivity. Soils on North, Northeast, and East aspects usually have higher organic matter, thicker soil strata, higher base saturation, and pH values. These aspects are commonly associated with higher productivity sites (Fekedulegn et al 2002).

Light exposure, precipitation, nutrients, and disturbance also play a significant role in defining vegetation distribution in a community (Boerner 2006). North, Northeast, and Eastern aspects receive less exposure to solar radiation, which decreases evapotranspiration rates and cools and dampens the forest floor. Eastern aspects also receive the added benefit of early sun exposure during the cool morning and reprieve from the sun earlier in the day as humidity levels drop (Dubayah and Rich 1995). South, Southwest, and West aspects are generally more xeric. They experience a higher degree of solar radiation and light intensity, which in turn increases air temperature and decreases moisture (Martin et al 2011). Due to decreased soil depth, upper slope positions have a decreased capacity to retain precipitation, accentuating xeric conditions. (Downs 1976) concluded drought conditions could cause soil water to drop below the permanent wilting point (-1.5 MPa) in all rooting zones of oak/hickory stands. Upper slope positions also experience greater solar radiation and wind exposure, increasing evapotranspiration rates. Low slope positions have an increased protection from exposure due to shading from adjacent ridges. The result is a wetter and cooler environment with decreased rates of evapotranspiration. Cool air drainage also affects the temperature of low slope position potentially creating an environment 5-10 °F lower than S slopes (Daly et al 2008)

Topography has a mediating effect on disturbances processes across the landscape. Low slope positions, valley bottoms, and windward aspects are vulnerable to uprooting due to windthrow, however, ridgetops may also remain vulnerable, however resulting in stem breakage instead (Lin et al 2004). Low slope positions are also more vulnerable to frost damage due to cool air drainage (Jones and Hellman 2003). Fire occurs more frequently on upper slope positions, which remain drier, and along draws that create convection currents funneling fire upward on these sites (Stambaugh and Guyette 2008).

Soft Mast

Declining soft mast production has been reported across the CHR (Schmidt and McWilliams 2003, Rentch and Hicks 2005). Heterogeneous forests created by variable and periodic disturbance have resulted in a mosaic of species, forest types, and perpetuated mid-successional forests. While this is the cornerstone of oak/hickory regeneration many co-occurring species such as black cherry (*Prunus serotine* Ehrh.), sassafras (*Sassafras albidum* (Nuttall) Nees), persimmon (*Diospyros virginiana* L.), redbud (*Cercis canadensis* L.), ash, tulip poplar, elm, and basswood (*Tilia americana* L.) also rely on these disturbance patterns for reproduction (Thompson and Dessecker 1997). Management of mid-successional oak/hickory forests can increase the biodiversity of these stands increasing their soft mast potential (Holzmueller et al 2009). However many soft masting species are shorter lived than the oak/hickory overstory and “last minute” regeneration efforts of oak/hickory still may lose their diverse soft mast component (Perry et al 1999).

Soft mast is imperative for wildlife species as they provide varying and additional sources of nutrition. Additional species also serve to hedge nutritional production across years in the case of hard mast failure in oak/hickory stands (Short 1975). This is especially important in winter when these species may be a main source of nutrition. This loss in diversity has been shown to have negative effects on resident wildlife including several priority CHR songbird species (Greenberg et al 2011), white-tailed deer (McShea and Schwede 1993), as well as other small mammal populations (Kellner et al 2013). These species are especially important during winter migration of wildlife when they may be the sole food source (McCarty et al 2002). However while soft mast is a successful technique to hedge bets during hard mast failure, these species also provided variable nutrient composition to a variety of wildlife species (Short 1975). This includes many species of bees, flies, and other species that feed on the nectar and pollen of these species. However, in the absence of large scale disturbance associated with oak/hickory regeneration, these pollinator species have been shown to decline (Proctor et al 2012).

Forest Health

Healthy forests support the maximum production of desirable species and services as determined by a community's goals (Rapport et al 1998). Forest health encompasses many variables such as species distribution, environmental conditions, and disturbance return intervals all of which impact succession (Hagle et al 1995). Forest health also includes the study of invasive plants, insects, and disease. Native pathogens are an important piece of the successional process as they are typically the mortality inducing agents, important in nutrient cycling, participate in many trophic interactions, and in themselves often result in landscape disturbance patterns. Simply, they are an important piece of the complex feedback process of ecological succession and forest dynamics (Holdenrieder et al 2004).

Typically, forests pathogens are thought of as primary or secondary damaging agents. Primary damaging agents are capable of successfully attacking vigorous trees and overcoming their natural defenses. Even so primary forest pests usually only cause significant damage during large population outbreaks. As an example of a primary pest, forest tent caterpillar (*Malacosoma disstria* Hubner) usually causes marginal damage throughout its range; however, in outbreak it may cause mass defoliation across the affected area (Cooke and Lorenzetti 2006). Secondary damaging agents are more common and attack already weakened or damaged trees (Wainhouse 2005). This might include any number of native insects such as native bark or borer beetles; fungus including leaf spots, cankers, and leaf scorch; or bacteria such as bacteria leaf scorch (*Xylella fastidiosa* (Wells et al 1987)) or slime flux (*Pectobacterium carotovorum* (Jones 1901, Waldee 1945)).

Increases in international trade over the 20th and 21st century have resulted in increasing pathways for introduction of forest health threats from non-native invasive species. This includes many species, many of which are harmless, a portion of which may be defined as minor pests, and the minority that are significant invasive pests (Kiritani and Yamamura 2003). To name a few of concern to oak/hickory in the CHR they include the following plants: amur honeysuckle (*Lonicera maackii* (Ruprecht) Maxmovich), Japanese honeysuckle (*Lonicera japonica* Thunberg), Japanese privet (*Ligustrum japonicum* Thunb.), Chinese lespedeza (*Lespedeza cuneate* (Dumont de Courset) Don), oriental bittersweet (*Celastrus orbiculatus* Thunb.), princess tree (*Paulownia tomentosa* (Thunb.) Steudal), and tree of heaven (*Alianthus altissima* (Miller) Swingle); insects: Asian longhorned beetle (*Anoplophora glabripennis* Motschulsky 1853), emerald ash borer (EAB) (*Agrilus planipennis* Fairmaire 1888), spotted lantern fly (*Lycorma delicatula* White 1845), European gypsy moth (*Lymantria dispar L.*), and gold spotted oak borer (*Agrilus coaxalis Waterhouse 1889*); and disease: Dutch elm disease (*Ophiostoma ulmi* (Buisman) Melin and Nannfeldt 1934), chestnut blight, thousand cankers disease (*Geosmithia morbida* Kolark et al 2010), dogwood anthracnose (*Discula destructiva*

(Fr.) Munk ex H. Kern 1955), laurel wilt (*Raffaelea lauricola* Fraedrich et al 2008), and sudden oak death (*Phytophthora ramorum* Werres et al 2001). These invasive species often cause unprecedented impacts to successional processes (Pimentel et al 2005).

Invasive plants are already widely distributed throughout the CHR due to accidental introduction or their desired utility as wildlife species, in erosion control, and as ornamentals (Reichard et al 2001). These species increase forest cover shading further driving mesophication processes and favoring multi aged stands. There aggressive growth strategy allows them to rapidly occupy gap openings, potentially resulting in arrested succession where they achieve a homogenous cover (Hejda et al 2009). Along with these plants, several invasive insect and disease have also impacted the CHR such as the chestnut blight (discussed above) and the Dutch elm disease (Potter et al 2011).

Species such as EAB have not yet impacted the entire CHR. It is expected complete mortality of ash across the region will result in increased gap openings and increased rate of succession to shade tolerant species (Kashian and Witter 2011). Other species such as the gold spotted oak borer (Seybold and Coleman 2015) or European gypsy moth (Morin and Liebhold 2016) stand to significantly decrease oak/hickory populations and have the potential to produce non-analogous forest types across the CHR (Flower and Gonzalez-Meler 2015).

The Ozark Hills

Research on the composition and structural changes in the Ozark Hills of Illinois, both in comparison to historical records and in recent composition/structural changes has shown a general trend towards the replacement of oak/hickory dominated communities to stands dominated by beech/maple (Ozier et al 2006). While this trend is ubiquitous across the CHR, this trend is potentially more advanced in the Ozark Hills (Wang et al 2016). An excellent body of research is available documenting the change in forest composition in and surrounding the Ozark hills (van de Gevel 2006, Hanberry et al 2014)

Ozier et al (2006) analyzed 238 permanent plots established in 1980 at Trail of Tears State Forest (TTSF). The inventory was repeated in 2000, with additional sampling of the regenerative age classes. Data collected for species, DBH, and height were used to calculate overall and species density and basal area. Tree age classes were split into seedlings/saplings, pole size, immature, and mature. Age classes were then compared across slope position and aspect. Overall, basal area increased 93 ft^2/ac to 107 ft^2/ac, mostly due to growth in the mature age class. Overall density decreased from 137 trees/ac to 118 trees/ac. Oak basal area and density decreased in every age class except the mature age class, and especially within the seedling/sapling and pole age classes. Hickory density and basal also changed from 27 trees/ac to 23 tree/ac. Basal area changed from 10 ft^2/ac to 11 ft^2/ac following the same trend as reported for oak species. Sugar maple and beech showed both increases in basal area and density, most significantly in the seedling/sapling age class. Sugar maple basal area and density increased from <1 tree/ac to 1 tree/ac and 226 ft^2/ac to 448 ft^2/ac respectively. Beech basal area and density increased from <1 trees/ac to 1 trees/ac and 87 ft^2/ac to 202 ft^2/ac respectively.

Both white oak and red oak showed the same general trend of increasing basal area and decreasing density in mature age classes irrespective of aspect. Black oak changed similarly with exception including a stable density on bottom aspects and a decrease in basal area on north and south aspects. Hickory density decreased on bottomlands, north, and west aspects. However, there was no change in hickory basal area across any aspect.

White oak and red oak densities decreased across slope positions except on the top-mid position. White oak basal area increased across all slope positions while red oak showed no change. Black oak density also decreased across slope positions however basal area also decreased on the mid, mid-bottom, and bottom slope positions. Hickory showed no change in density or basal area across slope positions.

Sugar maple basal area and density increased on every aspect and slope position. Beech density increased on every aspect except northwest and basal area increased on east, north, northeast, south, and southwest aspects. Beech density increased on every slope position except on top-mid and basal area increased on mid, mid-bottom, and bottom slope positions. Inventory data from the 2000 understory showed pawpaw as the most prevalent species in the seedlings class while beech and sugar maple were the most common in the sapling class. White oak seedlings were only recorded on southwest and west aspect and top and bottom slope positions. Black oak was recorded primarily on Southwest aspects and mid slope positions. Red oak was not inventoried in the 2000 understory data. Hickory within the seedling/sapling age classes also occupied more xeric sites consistent with the general trends reported with oak species.

Site conditions where further characterized by (Fralish and McArdle 2009) who analyzed forest dynamics in the Ozark Hills over three centuries. Separate Ecological Land Type positions (ELTs) designated by agglomerative clustering and percent similarity of species importance values were defined and then further used to interpret past and present forest composition as well as to predict future forest composition dependent on topographic variation. Six ELTs were identified by slope position, slope percentage, and aspect as shown in the following Table 1.

Table 1.
Ecological Land Type Positions as defined by (Fralish and McArdle 2009)

Ecological Land Type Position	Characteristics
Ridgetop	Above contour line Top to high slope position/ <10% slope
Southwest Mid-High	203°-270° aspect high to mid slope position
South Mid-High	135°-203° aspect 270°-315° aspect high to mid slope position
North Mid-High	315°-135° aspect high to mid slope position
Low	mid to low slope position regardless of aspect
Low-Bottom	<5% slope

GLO records were used to generate approximated presettlement species Importance Values for the Ozark Hills. (Fralish and McArdle 2009) predicted oak, hickory, and other successional species had a high Importance Value (IV=73.9-80.9) across all ELTs. Beech was shown to range from a low importance value (IV=10.8) on Southwest ELTs to a high Importance Value (IV=35) on Low Slope and Terrace ETLs. Sugar maple was only recorded as a notable stand component on Terrace ELTs (IV=15). Currently oak and hickory have both maintained relatively High Importance values (IV=51.5-70.7 and IV=7.7-93.7 respectively). Late successional species were found to have higher importance values (IV=36.3) on the North and Low Slope ELTs. Terrace ELTs were shown to be dominated by primarily early successional bottomland species including American sycamore (*Platanus occidentalis* L.), sweetgum (*Liquidambar styraciflua* L.), boxelder (*Acer negundo* L.), and other minor species with a combined Importance Values of (IV=56.1). Future forest composition was predicted from understory data on the assumption that the understory will eventually proliferate into the overstory. Across all ELTs, late successional mesophytic species Importance Values were greater than early successional species. The Southwest ELT was an exception where Importance Values (IV=46.7-76.5) of shade intolerant species are predicted to remain high. Oak and hickory Importance Values (IV=29.1-37.9) were predicted to remain highest on Southwest, South, and Ridgetop ELTs.

CHAPTER 2

STUDY OBJECTIVES

The CHR is experiencing major shifts in forest composition. Historically, forests of the CHR have regenerated in a landscape punctuated by periodic disturbances, natural and anthropogenic. Even aged stands have developed from single regeneration events including fire and large-scale timber harvesting resulting in the high percentage of mid-successional shade intolerant oak/hickory forests in the contemporary CHR. Current forests experience reduced intensity and frequency of disturbance events that results in the successional devolution of the even aged structure of many upland forests through increases in competitor species, prevention of regenerating events, and subsequent alterations to the forest environment.

Researches have well documented oak/hickory forest senescence, failed regeneration, and development of shade tolerant beech/maple understories across the CHR. However, less research has studied finer scale topographic specific changes in oak/hickory forest composition and structure. Biases towards the study of dominant species have also overshadowed related changes in soft masting tree species over the last century. It is the goal of our study to document these successional processes in the CHR. Results are discussed in terms of contributing factors to successional pathways via forest health trends. Specific objectives of our study were to:

I) **Objective 1-** Determine compositional and structural shifts from dominant oak/ hickory species to beech/maple forest-wide and by ELT in the CHR.

II) **Objective II-**Determine corresponding compositional and structural changes in soft masting species in the CHR

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CHAPTER 3

STUDY INTRODUCTION

In the past 75 years, the Ozark Hills physiographic region of the Shawnee National Forest has undergone rapid shifts in dominant species composition at rates only comparable to several other areas in the CHR (Wang et al 2016). The Ozark Hills are located east of the Mississippi River along much of Central and Southern Illinois. Primary factors in the development of the Ozarks Hills were uplift of cherty or siliceous limestone bedrock during the Devonian period, erosion, as well as alluvial deposits of loess from the Mississippi (Williams and Indorante 2005). These formative processes as well as historic disturbances affecting the region have created oak/hickory forests with variable components of bottomland pioneering species, successional shade intolerant species, and shade tolerant species (McNab et al 2007).

In 2006, Ozier et al. analyzed 1980 and 2000 inventory data for compositional and structural changes at Trail of Tears State Forest (TTSF), located in the southern section of the Ozark Hills. They reported a decrease in the density of oak and hickory species' seedlings and saplings, a substantial increase in shade tolerant seedlings and saplings, and a decrease in oak and hickory in mature age classes. They also reported variable rates of succession depending on topographic position with north, east, and bottomland positions in the most advanced state of succession. South, west, and upper slopes position were in a moderate state of succession. Ridgetops were reported progressing slowest to an increased maple and beech dominance. These results are conclusive with other studies in the eastern United States (Dyer 2001, McEwan and Muller 2006, Galbraith and Martin 2005, McDonald et al 2002). Due to the advanced state of maple⁄beech succession in the Ozark Hills, it stands as a paramount example of oak/hickory forests transitioning to beech/maple in the CHR. In addition, the increased prevalence of nonnative invasive forest associated plants, insects, and disease stand to further alter CHR forest dynamics (Hejda et al 2009). Analysis and discussion of 1980 and 2014 sampling data at TTSF were used to exemplify this pattern.

CHAPTER 4

METHODS

Study Area

Trail of Tears State Forest (TTSF) (37.509998,-89.349947) encompasses 5,162 ac and is located in Union County, IL (Figure 1). It is part of the Ozark Plateau physiographic region, which covers an expansive area of the central and western CHR. The Union County area is characterized by hot and dry summers and moderate winters. Temperate ranges from an average of 46°F to 69°F with an average annual temperature over the last ten years of 52°F. Average annual precipitation is approximately 49 inches. (NOAA 2014). TTSF is typified by narrow ridges 148-197' high, which lead into ephemeral streams. The dendritic pattern of ridgetops was created in the Pennsylvanian Period with the uplifting of the Devonian-age cherty bedrock (Helmig et al 2011). Soils include Stookey and Hosmer soils types on ridgetops, Goss and Baster soils typically found on mid to lower slopes, and Elsah and Wakeland soils found along stream terraces (National Cooperative Soil Survey 2001). Generally, soils are more productive in lower slope position with exception of sporadic ridgetops where loess caps provide an added benefit in available water content gained from millennia of drift from the Mississippi alluvial valley. Fragipans also occur sporadically across ridgetops increasing heterogeneity (National Cooperative Soil Survey 2001).

TTSF has shared a similar disturbance regime to most other public lands in the CHR. Pre-1810 the forest was used by several Native American tribes, most notably being the Mississippian Cahokia. After 1830, the forest underwent several major harvesting operations for timber, the barrel industry, and by the Illinois Central Railroad. Other events of note include the temporary encampment of 10,000 Cherokee, Creek, and Chickasaw in the winter of 1838 during their march on the “Trail of Tears” to a reservation in Oklahoma. In 1929, 1,306 acres of the now TTSF was purchased by the Illinois Department of Conservation with the remainder purchased in subsequent years. Up until 1989 when the last cutting operation occurred, the forest was managed in 26 compartments with two compartments per year harvested to 60 % residual stocking. The forest has not been managed since except for several prescribed fires in recent years (van de Gevel et al 2003).

Ecological Land Types

Unique community types were delineated by species composition and topographic variation (azimuth, slope, and slope position) by using agglomerative clustering and percent similarity analysis of species importance values (Fralish and McArdle 2009). Based on these values, six Ecological Land Types (ELTs) were developed: Ridgetops, Southwest Mid-high slopes, South mid-high slopes, North mid-high slopes, Lowlands, and Bottomlands (Table1). Our study focused on the direction of succession of these communities.

Forest Inventory

Inventory data was used across two years (1980 and 2014) at TTSF. Data for present forest composition was collected in 2014. Variable radius plots (504) were stratified across ELTs over a 925 acre area on the north end of TTSF. This area has been identified by the Illinois DNR as a demonstration area for future management activities within TTSF. Forest data for 1980 was collected from fixed area permanent plots established on a 924 x 924 ft. grid across the entire forest. Only 54 of the plots which overlapped with the current inventory area were used in this study. In all inventory years, species and DBH were recorded. Stems above 3.3’ and greater than 3” in DBH were included in overstory plots. From these initial tallies, density and basal area were calculated. ELT was also determined for each plot utilizing azimuth, slope, and slope position data collected in the field (Table 1.). In addition, four nested regeneration plots were inventoried in 2014. Regeneration plots were $5_{1/2}$ ft. radius circular plots established 26 ft. in the cardinal directions, from the overstory plot. Seedlings were recorded as any stem less than 3.3 ft. while saplings were any stem above 3.3 ft. and between 1”-3” in diameter.

Statistical Analysis

Several possibilities were considered for statistical analysis of forest communities at TTSF including non-metric multidimensional scaling (NMS), a repeated measures ANOVA design, and a repeated measures Mixed Model and Trend Analysis design. However NMS was chosen due to its efficiency at analyzing spatial and temporal trends in community structure. NMS also tolerates missing values (McCune et al 2002). Plots with missing values are removed in other statistical techniques including profile analysis (multivariate repeated measures) and repeated measures ANOVA which reduces sampling size and statistical power. PC-ORD version 6 was used to visualize community trends via NMS Ordination test and a Mantel Test was used to determine significant correlations among the land types for each year (McCune and Mefford 1999). A Multi-Response Permutation Procedures (MRRP) was also used as a nonparametric method for assessing differences between ELTs examined in the NMS. These results were further confirmed by a Mantel test using a Bray-Curtis dissimilarity index. Inventory data was used to compare density and basal area between years for species, ELT, and species*ELT interactions.

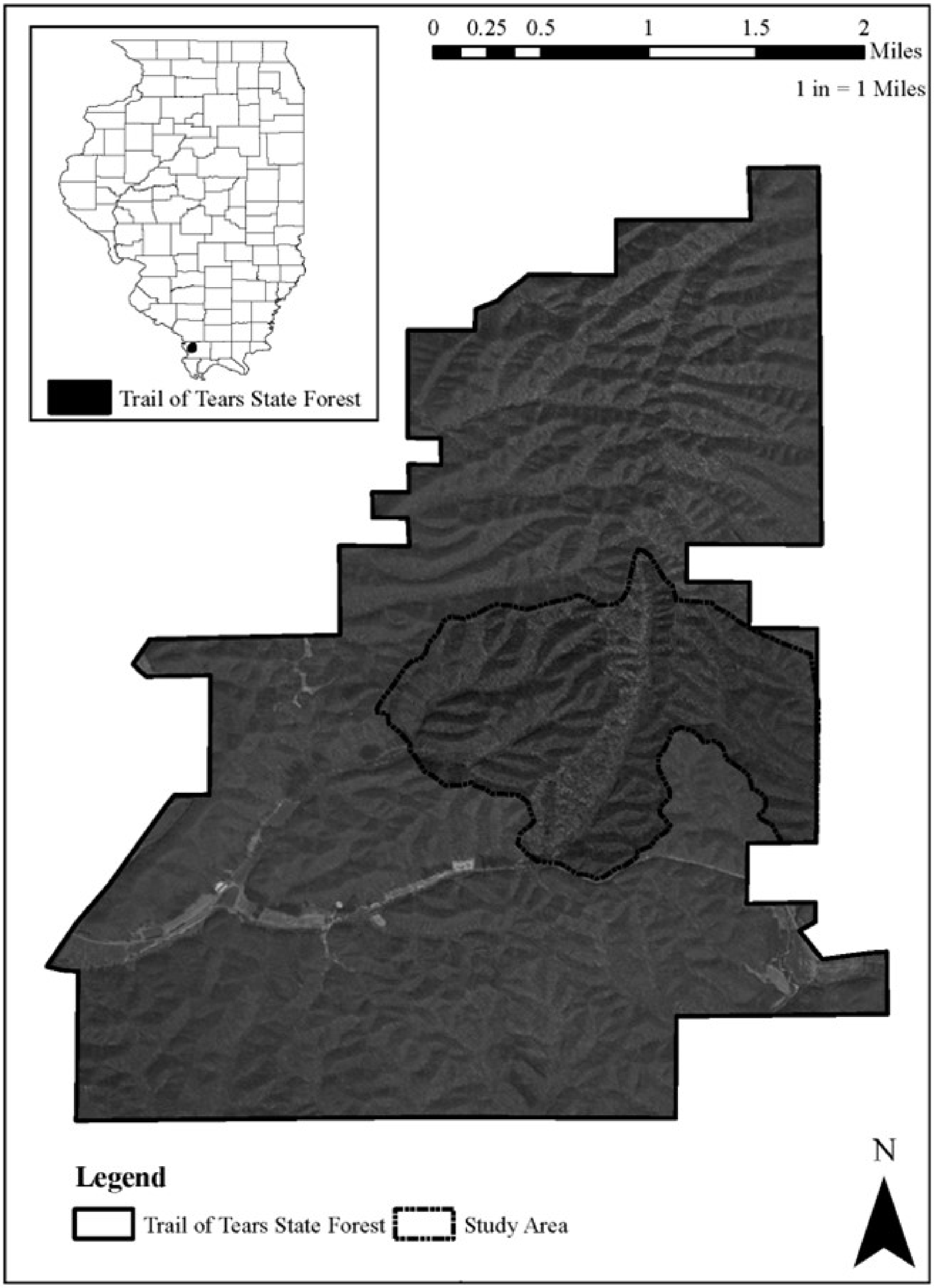

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Figure 1. Study Area at Trail of Tears State Forest in Union County, IL

CHAPTER 5

RESULTS

Species Composition

Across all ELTs, between 1980 and 2014, ovestory density decreased from 218 trees/ac in 1980 to 180 trees/ac in 2014 and basal has area increased from 98 ft^2/ac in 1980 to 106 ft^2/ac in 2014 (Table 2). The largest decline in species density was in oak species which decreased from 78 trees/ac to 37 trees/ac followed by hickory species which decreased from 26 trees/ac to 18 trees/ac. Conversely, maple species increased from 31 trees/ac to 46 trees/ac ($p \leq 0.01$) and beech from 8 trees/ac to 37 trees/ac. Maple basal area increased from 5 ft^2/ac to 12 ft^2/ac while beech increased from 1 ft^2/ac to 8ft^2/ac, signifying progression of these species from the understory up into the canopy. Both oak and hickory species showed unsubstantial shifts in basal area with the exception of black oak which has declined from 22 ft^2/ac to 12 ft^2/ac.

Oak has undergone the greatest decrease in density on sites where it was once most prevalent including Ridgetops, Southwest, South, and North ELTs. Most notably white oak decreased from 79 trees/ac to 38 trees/ac on the South ELT. Meanwhile Lowland and Bottomland ELTs have also declined with only a marginal oak component reported in 2014. Hickory trends population dynamics were variable on upland sites increasing on Ridgetops from 34 trees/ac to 43 trees/ac and decreasing on Southwest ELTs from 29 trees/ac to 20 trees/ac, though the results were unsubstantial. However, hickory declined on lowland and bottomland ELTs. Beech increased on all ELTs most notably on South ELTs where it increased from 4 trees/ac to 54 trees/acand Southwest ELTS where it increased from 4 trees/ac to 45 trees/ac. Maple also increased steadily between 10-19 trees/ac on all ELTs.

The component of soft masting species within the forest has also decreased sharply in the last 34 years (Table 2). The greatest declines in density were seen in flowering dogwood from 10 trees/ac to 2 trees/ac and sassafras which decreased from 19 trees/ac to 8 trees/ac. Cucumber tree (*Magnolia acuminata* L.) and mulberry (*Morus* spp. L.) have been extirpated during the study period. Little change was seen in black cherry, black gum (*Nyssa sylvatica* Marsh.), or hackberry (*Celtis occidentalis* L.). All three were reported at <4 trees/acre in all survey ELTs and years.

The most common sapling species in the regeneration layer at TTSF was pawpaw (*Asimina triloba* (L.) Dunai) at 2,126 stems/ac, followed by beech at 1,596 stems/ac, maple at 461 stems/ac, ironwood at 313 stems/ac, and ash at 107 stems/ac (Table 4). Meanwhile oak saplings comprised 78 stems/ac and hickory 90 stems/ac. The most common seedlings species was pawpaw at 2,648 stems/ac, followed by ironwood at 517 stems/ac, beech at 387 stems/ac, oak at 369 stems/ac, and maple at 339 stems/ac (Table 5). Beech dominated across all ELTs, with the highest sapling density reported on South ELTs at 1,910 stems/ac with only slight marginal dips on Ridgetops (Table 4) and Bottomland ELTs. Maple reported sapling and seedling densities between 400-650 stems/ac on Ridgetop, South, North, and Southwest ELTs (Tables 10-13) with proportionally lower numbers on Lowland and Bottomland ELT (Tables 14-15). Oak regeneration was limited on Southwest, South, and North ELTS and marginal on Lowland and Bottomland ELTs (Table 3-4). Comparatively, while hickory regeneration was most prominent on Ridgetop ELTs at a sapling density of 149 stems/ac and a seedling density of 458 stems/ac (Table 4), it still hold a relatively well distribution on Lowland and Bottomland ELTs (Tables 3-4).

ELT Overstory Composition

NMS ordination (Figure 2) and MRPP (Table 6) analysis were used to determine whether overstory species composition was significantly different between ELTs. MRPP analysis of overstory compositional gradients reported distinct species compositions between ELTs, however the trend was weak (MRPP: $p \leq 0.001$, A = 0.038). NMDS ordination graphs confirmed MRPP showing little separation among ELTs. The final stress was 18.71146 and instability was ≤ 0.01 after 212 iterations (Table 6). Upland ELTs (ridgetop, southwest slopes, south slopes, and north slopes) have remained marginally distinct with the exception of southwest slopes vs south slopes and ridgetops vs southwest slopes which have homogenized.

A Mantel Test using a Bray-Curtis dissimilarity index was used to confirm these results. While comparison of ELTs in 2014 showed significantly different communes, individual indices between 1980 and 2014 were subtracted to determine the percent change in ELTs between years (Table 7). Values are presented as percentages with negative values reporting a decrease in similarities between years while positive values report an increase in similarity between years. Comparisons of percent dissimilarity calculated using the Bray-Curtis method between 1980 and 2014 showed increasing similarity between species compositions on SW mid-high slopes, S mid-high slopes, N mid-high slopes, and lowlands (Table 6). Ridgetop percent similarity to other land types decreased, with the exception of North mid-high slopes, which increased 3% in similarity. Bottomlands also decreased in similarity to other land types, with the exception of lowlands which became 6% more similar.

Table 2.
TTSF forest inventory data for all species' density in 1980 and 2014. Standard error is calculated for all values.

	Ridgetop				**South**				**Southwest**				**North**				**Lowland**				**Bottomland**				**Across all ELTs**			
Species	**1980**		**2014**		**1980**		**2014**		**1980**		**2014**		**1980**		**2014**		**1980**		**2014**		**1980**		**2014**		**1980**		**2014**	
Ash spp.	7	(6.2)	1	(0.4)	11	6.2	4	(0.4)	7	(4.3)	2	(0.3)	8	(1)	4	(0.4)	14	(1)	3	(0.4)	10	(4.4)	3	(0.2)	9	(2.4)	3	(0.4)
Basswood	0	(N/A)	0	(<0.01)	0	(N/A)	0	(N/A)	0	(N/A)	0	(N/A)	0	(N/A)	<1	(<0.01)	0	(N/A)	<1	(0)	0	(N/A)	<1	(0.1)	0	(N/A)	<1	(<0.01)
Beech	0	(N/A)	20	(3.9)	4	(4)	54	(2.8)	4	(5.2)	45	(2.2)	12	(2)	25	(1.9)	19	(9)	37	(2.4)	10	(9)	36	(2.6)	8	(4.3)	37	(2.6)
Black Cherry	0	(N/A)	<1	(<0.01)	0	(N/A)	<1	(0.2)	0	(N/A)	0	(N/A)	0	(N/A)	<1	(0)	1	(2.8)	<1	(0)	1	(1.8)	<1	(0.1)	<1	(0.5)	<1	(0.1)
Black Gum	2	(2.7)	3	(0.3)	2	(2.8)	4	(1.2)	3	(4.4)	3	(0.3)	3	(6)	4	(0.5)	3	(5.6)	4	(0.7)	6	(3.9)	<1	(0.9)	3	(1.5)	3	(0.8)
Cucumber Tree	0	(N/A)	0	(N/A)	0	(N/A)	0	(N/A)	0	(N/A)	0	(N/A)	<1	(1.5)	0	(N/A)	0	(N/A)	0	(N/A)	1	(1.4)	0	(N/A)	<1	(0.4)	0	(N/A)
Dogwood	6	(4.2)	3	(0)	7	(5.1)	1	(0.5)	7	(2.7)	8	(0.62)	20	(4)	<1	(0.9)	14	(2)	0	(N/A)	9	(6.1)	0	(0.6)	10	(3)	2	(0.65)
Elm spp.	2	(3.9)	1	(0.8)	1	(2.2)	3	(0.6)	0	(N/A)	<1	(0.7)	<1	(1.5)	1	(0.6)	6	(6)	7	(0.8)	5	(5.6)	6	(0.7)	3	(1.8)	3	(0.7)
Hackberry	0	(N/A)	0	(<0.01)	0	(N/A)	0	(N/A)	0	(N/A)	0	(N/A)	0	(N/A)	<1	(<0.01)	0	(N/A)	1	(<0.01)	0	(N/A)	0	(N/A)	0	(N/A)	<1	(0.3)
Hickory spp.	34	(1)	43	(1.6)	16	(9.2)	22	(2.1)	29	(1)	20	(1.2)	28	(2)	16	(2.1)	37	(1)	9	(1.5)	22	(7.3)	10	(0.9)	26	(5.5)	18	(1.7)
Ironwood	13	(9.7)	5	(0.3)	3	(3.5)	5	(0.9)	2	(2.7)	2	(0.6)	4	(7.3)	7	(0.7)	12	(1)	0	(0.5)	4	(4.2)	<1	(2.1)	6	(2.6)	4	(1)
Maple	27	(5)	45	(2.8)	23	(4)	39	(2.4)	17	(3)	27	(2.7)	36	(8)	48	(3.2)	42	(3)	58	(2.3)	40	(9)	59	(2.1)	31	(7.2)	46	(2.7)
Mulberry	0	(N/A)	0	(N/A)	1	(1.6)	0	(N/A)	0	(N/A)	0	(N/A)	0	(N/A)	0	(N/A)	0	(N/A)	0	(N/A)	<1	(0.8)	0	(N/A)	<1	(0.4)	0	N/A
Black Oak	25	(6)	12	(0.3)	22	(9.8)	9	(0.5)	26	(3)	8	(0.3)	8	(4.5)	4	(0.4)	11	(0)	2	(0.5)	7	(6.5)	<1	(0.3)	16	(4.5)	6	(0.4)
Red Oak	14	(7)	4	(0.3)	9	(4.5)	6	(0.5)	9	(7.1)	8	(0.4)	17	(9.6)	6	(0.5)	8	(7.2)	2	(0.3)	10	(8.6)	1	(0.4)	11	(3.3)	5	(0.4)
White Oak	57	(6)	38	(1.3)	79	(9)	38	(1.4)	74	(3)	36	(2)	28	(2)	22	(1.5)	26	(5)	13	(1.3)	27	(3.1)	4	(0.7)	48	(6)	25	(1.4)
Other Oak Spp.	3	(6.5)	6	(0.4)	3	(2.3)	2	(0.6)	13	(1)	2	(0.67)	0	(N/A)	<1	(0.4)	1	(2.8)	<1	(0.1)	0	(N/A)	5	(0.2)	3	(2.8)	2	(0.45)
Pecan	0	(N/A)	<1	(<0.01)	0	(N/A)	0	(N/A)	0	(N/A)	0	(N/A)	0	(N/A)	<1	(0.1)	0	(N/A)	0	(N/A)	0	(N/A)	0	(0.1)	0	(N/A)	<1	(0.1)
Persimmon	1	(2.6)	0	(<0.01)	0	(N/A)	0	(N/A)	0	(N/A)	0	(N/A)	2	(4.5)	1	(0.3)	0	(N/A)	<1	(0.1)	<1	(0.8)	0	(0.8)	<1	(0.7)	<1	(0.3)
Redbud	0	(N/A)	0	(<0.01)	0	(N/A)	0	(N/A)	0	(N/A)	0	(0.3)	0	(N/A)	0	(N/A)	1	(2.8)	0	(N/A)	0	(N/A)	3	(<0.01)	<1	(0.2)	<1	(0.2)
Sassafras	19	(1)	18	(2.4)	17	(4.1)	7	(1.3)	13	(1)	7	(1.1)	26	(1)	6	(0.9)	26	(7)	7	(1.3)	18	(3.1)	7	(1.2)	19	(5.5)	8	(1.3)
Sweetgum	<1	(1.3)	3	(1.9)	3	(4.4)	3	(0.9)	0	(N/A)	2	(1.2)	1	(3)	7	(1.2)	13	(7)	12	(0.5)	33	(0.3)	29	(0.9)	11	(8.4)	9	(1.1)
Sycamore	0	(N/A)	<1	(0.1)	0	(N/A)	<1	(0.2)	0	(N/A)	0	(0.1)	0	(N/A)	<1	(0.1)	0	(N/A)	<1	(0)	<1	(1.1)	2	(0.1)	<1	(0.3)	<1	(0.1)
Tulip Poplar	<1	(1.3)	5	(0.9)	1	(3.1)	4	(1.4)	3	(6.5)	2	(0.3)	2	(3.1)	7	(0.9)	13	(1)	9	(1.3)	34	(7.1)	19	(0.6)	11	(4)	7	(1)
Walnut	1	(2.6)	0	(0.1)	<1	(1)	<1	(0.2)	0	(N/A)	0	(0.1)	0	(N/A)	<1	(0.1)	1	(2.8)	0	(0.2)	1	(1.7)	3	(0.1)	<1	(0.6)	<1	(0.2)
Total	**212**	**(9)**	**209**	**(5.7)**	**202**	**(1)**	**201**	**(4.7)**	**205**	**(8)**	**172**	**(4)**	**197**	**(2)**	**162**	**(4.2)**	**251**	**(9)**	**167**	**(3.6)**	**240**	**(5)**	**190**	**(3.8)**	**218**	**(8)**	**180**	**(4.3)**

Table 3.
TTSF forest inventory data for all species basal year in 1980 and 2014. Standard error is calculated for all values.

	Ridgetop				South				Southwest				North				Lowland				Bottomland				Across all ELTs			
Species	**1980**		**2014**		**1980**		**2014**		**1980**		**2014**		**1980**		**2014**		**1980**		**2014**		**1980**		**2014**		**1980**		**2014**	
Ash spp.	2	(0.48)	2	(0.17)	2	(0.13)	2	(0.13)	<1	(0.27)	<1	(0.23)	2	(0.34)	3	(0.24)	3	(0.47)	3	(0.27)	3	(0.44)	3	(0.24)	2	(0.38)	2	(0.23)
Basswood	0	(N/A)	0	(<0.01)	0	(N/A)	0	(N/A)	0	(N/A)	0	(N/A)	0	(N/A)	<1	(0.04)	0	(N/A)	<1	(0.05)	0	(N/A)	<1	(0.06)	0	(N/A)	<1	(0.03)
Beech	0	(<0.01)	3	(0.24)	2	(0.08)	9	(0.55)	<1	(0.76)	7	(0.51)	2	(0.48)	8	(0.47)	3	(0.49)	11	(0.52)	1	(0.43)	11	(0.6)	1	(0.48)	8	(0.51)
Black Cherry	0	(<0.01)	<1	(0.07)	0	(N/A)	<1	(<0.01)	0	(N/A)	0	(N/A)	0	(<0.01)	<1	(0.07)	<1	(0.06)	<1	(0.05)	<1	(0.15)	<1	(0.1)	<1	(0.08)	<1	(0.06)
Black Gum	<1	(0.27)	<1	(0.09)	<1	(0.07)	<1	(0.14)	<1	(0.07)	<1	(0.13)	<1	(0.09)	2	(0.23)	<1	(0.19)	1	(0.19)	1	(0.37)	1	(0.16)	<1	(0.24)	1	(0.17)
Cucumber Tree	0	(<0.01)	0	(N/A)	0	(N/A)	0	(N/A)	0	(N/A)	0	(N/A)	<1	(0.34)	0	(N/A)	0	(N/A)	0	(N/A)	1	(0.4)	0	(N/A)	<1	(0.25)	0	(N/A)
Dogwood	<1	(0.08)	<1	(0.07)	<1	(0.03)	<1	(0.14)	<1	(0.09)	<1	(0.04)	3	(0.38)	<1	(0.04)	1	(0.22)	0	(N/A)	<1	(0.15)	0	(N/A)	1	(0.21)	<1	(0.06)
Elm spp.	<1	(0.09)	<1	(0.07)	<1	(<0.01)	<1	(0.05)	0	(N/A)	<1	(0.09)	<1	(0.05)	<1	(0.11)	2	(0.52)	3	(0.32)	1	(0.54)	3	(0.28)	<1	(0.32)	1	(0.19)
Hackberry	0	(N/A)	0	(<0.01)	0	(N/A)	0	(N/A)	0	(N/A)	0	(N/A)	0	(N/A)	<1	(<0.01)	0	(N/A)	<1	(<0.01)	0	(N/A)	0	(N/A)	0	(N/A)	<1	(0.04)
Hickory spp.	17	(2.01)	21	(0.82)	4	(1.24)	9	(0.56)	11	(0.48)	9	(0.48)	17	(1.44)	10	(0.62)	10	(1.18)	7	(0.41)	10	(1.22)	7	(0.4)	11	(1.42)	10	(0.57)
Ironwood	1	(0.17)	<1	(0.09)	<1	(0.03)	<1	(0.07)	<1	(0.08)	<1	(0.11)	<1	(0.1)	<1	(0.15)	2	(0.27)	0	(N/A)	<1	(0.09)	<1	(0.06)	<1	(0.14)	<1	(0.1)
Maple	5	(0.62)	12	(0.61)	3	(0.24)	10	(0.45)	2	(0.36)	7	(0.49)	5	(0.74)	12	(0.56)	11	(1.06)	14	(0.57)	7	(1.02)	16	(0.65)	5	(0.8)	12	(0.56)
Mulberry	0	(<0.01)	0	(N/A)	<1	(<0.01)	0	(N/A)	0	(N/A)	0	(N/A)	0	(N/A)	0	(N/A)	0	(N/A)	0	(N/A)	<1	(0.02)	0	(N/A)	<1	(0.03)	0	(N/A)
Black Oak	35	(3.76)	23	(0.89)	27	(3.06)	18	(0.82)	33	(2.4)	15	(0.84)	9	(1.19)	11	(0.61)	24	(4.02)	5	(0.5)	11	(2.59)	2	(0.22)	22	(3.06)	12	(0.74)
Red Oak	8	(1.38)	8	(0.47)	7	(1.15)	10	(0.6)	6	(1.02)	10	(0.83)	9	(0.89)	11	(0.63)	13	(2.07)	5	(0.42)	8	(1.27)	4	(0.41)	8	(1.23)	8	(0.61)
White Oak	30	(3.65)	33	(1.02)	42	(2.54)	43	(1.24)	35	(2.37)	46	(1.11)	38	(3.45)	29	(0.91)	18	(2.74)	20	(0.82)	14	(1.52)	8	(0.51)	29	(2.99)	31	(1.11)
Other Oak Spp.	2	(0.84)	4	(0.46)	2	(1.76)	2	(0.39)	6	(0.57)	4	(0.28)	0	(N/A)	1	(0.23)	1	(0.33)	2	(0.27)	0	(N/A)	4	(0.3)	2	(0.74)	3	(0.31)
Pecan	0	(N/A)	<1	(0.07)	0	(N/A)	0	(N/A)	0	(N/A)	0	(N/A)	0	(N/A)	<1	(0.08)	0	(N/A)	0	(N/A)	0	(N/A)	0	(N/A)	0	(N/A)	<1	(0.05)
Persimmon	<1	(0.07)	0	(<0.01)	0	(N/A)	0	(N/A)	0	(N/A)	0	(N/A)	<1	(0.06)	<1	(0.09)	0	(N/A)	<1	(0.11)	<1	(0.02)	0	(N/A)	<1	(0.04)	<1	(0.07)
Redbud	0	(<0.01)	0	(<0.01)	0	(N/A)	0	(N/A)	0	(N/A)	0	(N/A)	0	(N/A)	0	(N/A)	<1	(<0.01)	0	(N/A)	0	(N/A)	<1	(<0.01)	<1	(<0.01)	<1	(0.03)
Sassafras	2	(0.2)	3	(0.37)	2	(0.32)	1	(0.14)	1	(0.36)	1	(0.16)	4	(0.79)	2	(0.18)	4	(0.35)	2	(0.29)	3	(0.59)	2	(0.23)	3	(0.49)	2	(0.23)
Sweetgum	<1	(0.05)	<1	(0.21)	<1	(<0.01)	2	(0.17)	0	(N/A)	1	(0.28)	<1	(0.13)	4	(0.39)	5	(1.07)	8	(0.66)	9	(1.99)	23	(0.94)	3	(1.18)	6	(0.59)
Sycamore	0	(<0.01)	<1	(0.07)	0	((N/A))	<1	(<0.01)	0	(N/A)	0	(N/A)	0	(N/A)	<1	(0.04)	0	(N/A)	<1	(0.05)	<1	(0.15)	3	(0.34)	<1	(0.08)	<1	(0.13)
Tulip Poplar	<1	(0.05)	3	(0.3)	2	(0.24)	2	(0.3)	<1	(1.05)	2	(0.3)	3	(0.88)	9	(0.72)	4	(0.8)	17	(0.77)	19	(4.08)	27	(1.29)	6	(2.37)	10	(0.78)
Walnut	<1	(0.13)	0	(<0.01)	<1	(<0.01)	<1	(<0.01)	0	(N/A)	0	(N/A)	0	(N/A)	<1	(0.06)	2	(0.68)	0	(N/A)	<1	(0.35)	2	(0.21)	<1	(0.28)	<1	(0.09)
Total	**107**	**(3.71)**	**116**	**(<0.01)**	**96**	**(<0.01)**	**109**	**(<0.01)**	**97**	**(3.02)**	**105**	**(1.32)**	**96**	**(<0.01)**	**103**	**(1.18)**	**103**	**(3.43)**	**100**	**(<0.01)**	**92**	**(11.54)**	**115**	**(1.27)**	**98**	**(26.92)**	**106**	**(1.25)**

Table 4.

TTSF all ELTs forest inventory data for all species' sapling density in 2014. Standard error is calculated for all values.

Species	Ridgetop		South		Southwest		North		Lowland		Bottomland		Across all ELTs	
Ash Spp.	130	(38.7)	121	(13.5)	73	(10.5)	92	(12.9)	145	(10)	81	(10.5)	107	(16.2)
Basswood	0	(N/A)	0	(N/A)	0	(N/A)	0	(N/A)	5	(<0.1)	0	(N/A)	<1	(0.9)
Beech	1126	(56.5)	1910	(58.1)	1650	(50.5)	1569	(63.8)	1717	(60.9)	1227	(75.9)	1596	(61.5)
Black Cherry	0	(N/A)	0	(N/A)	0	(N/A)	0	(N/A)	0	(N/A)	0	(N/A)	0	(N/A)
Blackgum	0	(N/A)	31	(9.8)	18	(6)	7	(1.8)	14	(2.1)	0	(N/A)	14	(5.2)
Dogwood Spp.	50	(8.3)	54	(7.3)	98	(6.2)	40	(7.5)	51	(10.8)	7	(5.6)	51	(7.9)
Elm Sp.	30	(11.3)	90	(10.2)	110	(9.2)	51	(8.7)	5	(8.6)	52	(7.1)	57	(9.3)
Hackberry	0	(N/A)	0	(N/A)	6	(2.5)	0	(N/A)	0	(N/A)	0	(N/A)	<1	(0.9)
Hickory Spp.	149	(22.8)	144	(13.8)	171	(10.5)	55	(8.8)	23	(10.8)	37	(9.4)	90	(12.4)
Ironwood	458	(26.9)	422	(35.2)	403	(15.5)	260	(19.4)	192	(22.8)	214	(34.8)	313	(26.5)
Maple Spp.	598	(32.6)	593	(36.7)	642	(27.6)	495	(29.8)	253	(28.9)	185	(30.6)	461	(31.2)
Mulberry Spp.	0	(N/A)	0	(N/A)	0	(N/A)	7	(2.6)	0	(N/A)	0	(N/A)	2	(1.3)
Black Oak	130	(24.6)	31	(15.6)	6	(3.5)	29	(6.5)	9	(5.1)	22	(0)	31	(10.9)
Red Oak	0	(N/A)	18	(17.6)	37	(<0.1)	51	(6.5)	14	(8)	52	(28.6)	31	(11.5)
White Oak	30	(3.1)	13	(2)	24	(4.2)	7	(1.8)	0	(N/A)	0	(N/A)	11	(3.4)
Other Oak Spp.	0	(N/A)	0	(N/A)	6	(4.9)	0	(N/A)	0	(N/A)	37	(2.6)	5	(2.6)
Pawpaw	279	(122.6)	822	(184.2)	978	(172.1)	2501	(134.9)	3934	(159.5)	3416	(202.4)	2126	(164.2)
Pecan	0	(N/A)	0	(N/A)	0	(N/A)	0	(N/A)	0	(N/A)	0	(N/A)	0	(N/A)
Persimmon	0	(N/A)	4	(2)	0	(N/A)	0	(N/A)	28	(2.1)	0	(N/A)	6	(4.7)
Redbud	0	(N/A)	4	(2.8)	18	(2.5)	4	(2.6)	5	(<0.1)	7	(0)	6	(2.4)
Sassafras	438	(29.9)	328	(23.5)	238	(12.9)	121	(34)	80	(24)	104	(18.9)	199	(25.7)
Sweetgum	0	(N/A)	13	(4.9)	55	(7.4)	18	(4.1)	65	(4.6)	30	(10.9)	32	(11.7)
Sycamore	0	(N/A)	0	(N/A)	0	(N/A)	0	(N/A)	5	(<0.1)	0	(N/A)	<1	(0.9)
Tulip Poplar	0	(N/A)	9	(4.5)	6	(<0.1)	59	(12.4)	51	(9)	15	(10.1)	29	(8.7)
Walnut	0	(N/A)	0	(N/A)	0	(N/A)	0	(N/A)	0	(N/A)	0	(N/A)	0	(N/A)
Total	**3418**	**(195.8)**	**4611**	**(182.3)**	**4547**	**(169.8)**	**5368**	**(141)**	**6595**	**(158.6)**	**5486**	**(216.3)**	**5169**	**(173.1)**

Table 5.
TTSF all ELTs forest inventory data for all species' seedling density in 2014. Standard error is calculated for all values.

Species	Ridgetop		South		Southwest		North		Lowland		Bottomland		Across all ELTs	
Ash Spp.	628	(17.2)	333	(26.6)	226	(25.3)	194	(26.6)	201	(35.2)	222	(16.4)	271	(17.2)
Basswood	0	(N/A)	0	(N/A)	0	(N/A)	0	(N/A)	9	(3.7)	0	(N/A)	2	(<0.1)
Beech	259	(20.4)	386	(20.4)	409	(20.1)	334	(20.4)	440	(31)	481	(57.4)	387	(63.7)
Black Cherry	0	(N/A)	27	(6)	18	(2.9)	22	(6)	14	(2.6)	15	(7.7)	18	(4.4)
Blackgum	0	(N/A)	9	(5.5)	12	(4.6)	0	(N/A)	9	(<0.1)	15	(4.3)	7	(<0.1)
Dogwood Spp.	60	(3.2)	36	(4.9)	79	(9)	26	(4.9)	19	(5.4)	37	(9.6)	39	(8.5)
Elm Spp.	70	(14)	81	(4.9)	37	(14.4)	55	(4.9)	5	(8.4)	140	(10.2)	60	(11.1)
Hackberry	0	(N/A)	0	(N/A)	0	(N/A)	0	(N/A)	0	(N/A)	0	(N/A)	0	(<0.1)
Hickory Spp.	458	(35.2)	351	(29.1)	403	(24.1)	176	(29.1)	173	(14.2)	170	(30.3)	269	(21)
Ironwood	986	(49.3)	670	(42.3)	623	(40.3)	418	(42.3)	267	(38.7)	384	(27.9)	517	(45.7)
Maple Spp.	558	(34.6)	360	(41.3)	532	(38.4)	389	(41.3)	140	(34.3)	126	(28.3)	339	(35)
Mulberry Spp.	0	(N/A)	0	(N/A)	0	(N/A)	0	(N/A)	0	(N/A)	0	(N/A)	0	(N/A)
Black Oak	389	(19.3)	135	(16)	79	(32.7)	51	(16)	80	(10.1)	15	(9.4)	104	(5)
Red Oak	40	(12)	130	(16.2)	110	(19)	139	(16.2)	70	(15.1)	148	(29.8)	112	(27.4)
White Oak	219	(15.8)	126	(23.3)	92	(13.2)	154	(23.3)	164	(20.8)	74	(27.1)	137	(13.7)
Other Oak Spp.	0	(N/A)	0	(N/A)	18	(6.5)	15	(2.5)	14	(5.5)	59	(2.1)	16	(8.5)
Pawpaw	349	(198)	1528	(160.8)	1760	(168.6)	2780	(160.8)	4270	(210.5)	4443	(193.1)	2648	(165.4)
Pecan	10	(<0.1)	0	(N/A)	0	(N/A)	0	(N/A)	0	(N/A)	0	(N/A)	<1	(<0.1)
Persimmon	0	(N/A)	0	(N/A)	0	(N/A)	0	(N/A)	0	(N/A)	0	(N/A)	0	(N/A)
Redbud	0	(N/A)	4	(<0.1)	12	(2.1)	11	(<0.1)	5	(6.1)	0	(N/A)	6	(<0.1)
Sassafras	508	(15.1)	337	(20.4)	324	(20.5)	231	(20.4)	103	(39.5)	89	(32)	249	(24.6)
Sweetgum	0	(N/A)	9	(17.8)	24	(2.9)	18	(7.5)	42	(9.6)	15	(14.1)	20	(<0.1)
Sycamore	0	(N/A)	0	(N/A)	0	(N/A)	0	(N/A)	0	(N/A)	7	(<0.1)	<1	(2.6)
Tulip Poplar	60	(10.1)	0	(N/A)	0	(N/A)	18	(<0.1)	19	(10)	15	(20.7)	15	(2.6)
Walnut	0	(N/A)	0	(N/A)	0	(N/A)	0	(N/A)	0	(N/A)	0	(N/A)	0	(N/A)
Total	**4594**	**(1353.7)**	**4521**	**(938)**	**4761**	**(1238.4)**	**5031**	**(853.8)**	**6043**	**(992.7)**	**6454**	**(1366.5)**	**5218**	**(435.6)**

Table 6.
NMDS and MRPP Results of TTSF 2014 overstory by species composition and density.

NMDS Results						MRPP Results		
Sample	**Stress**	**Axis 1**	**Axis 2**	**Axis 3**	**Sum**	**T**	**A**	**P Value**
2014 Overstory	22.78	0.25	0.214	0.28	0.71	-25.77	0.04	<0.01

Table 7.
Percent Similarity Change between ELTs at TTSF between 1980 and 2014 using the Bray-Curtis Method. Positive values indicate increasing similarity while negative values indicate decreasing.

	Ridgetop	Southwest	South	North	Lowland	Bottomland
Ridgetop	0.00	-8.90	-3.09	3.21	-7.74	-6.74
Southwest	-8.90	0.00	0.74	7.97	6.01	-1.35
South	-3.09	0.74	0.00	12.79	9.72	-0.68
North	3.21	7.97	12.79	0.00	0.17	-6.69
Lowland	-7.74	6.01	9.72	0.17	0.00	5.64
Bottomland	-6.74	-1.35	-0.68	-6.69	5.64	0.00

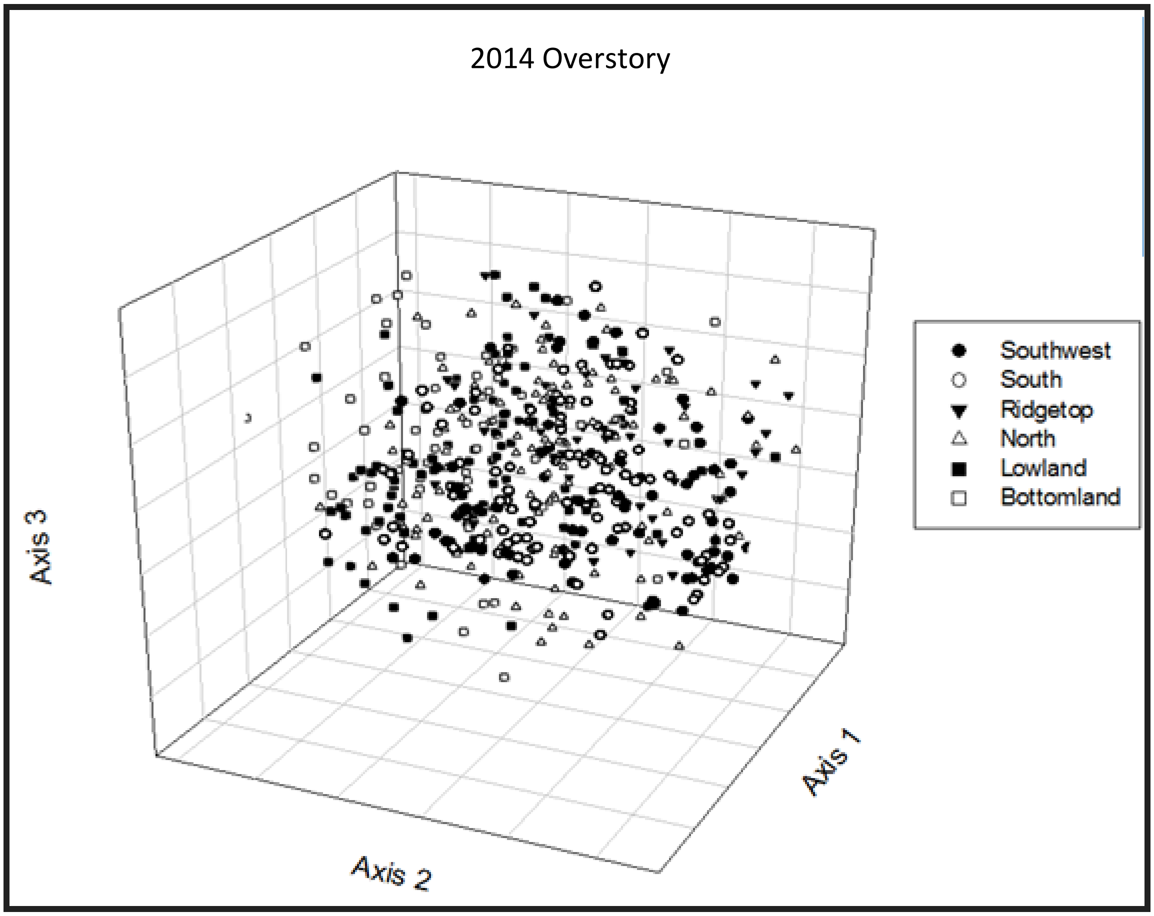

Figure 2. Nonmetric Dimensional Scaling (NMDS) ordination of TTSF overstory species composition and density in 2014.

CHAPTER 6

DISCUSSION

Overstory Succession

Our research at TTSF yields an interesting perspective on the issue of widespread declining oak/hickory forests in the CHR and management of successional forests reliant on disturbance under changing social, economic, and ecological pressures. Our results show a reduction in oak/hickory overstory composition, very low composition of these species in the regeneration layer, and conversion into a multi-aged forest structure populated by primarily beech and maple undergoing recruitment into higher size classes (Table 3). These changes have occurred across ELTs (Table.2-3), suggesting an overall homogenization of species composition within the forest. Weak associations between ELTs in our MRPP analysis confirm these results (Table 6) as well as high percent similarities reported in the Bray-Curtis dissimilarity index analysis of ELTs (Table 7).

TTSF is undergoing succession to a shade tolerant beech/maple climax forests as the present cohort of oak/hickory forest experiences annual mortality. In 1980 oak and hickory species comprised 48% of forest trees while only 31% in 2014 (Table 2). Meanwhile basal area oak and hickory has increased (Table 3). A more in depth analysis shows decreases in overall TPA and increases in BA are substantial on Ridgetop and Bottomland ELTs. This trend is typical of successional forests reliant on periodic disturbance for recruitment of understory stems and mortality associated with over maturation of the overstory. Increasingly across the CHR natural and stochastic senescence processes (e.g. windthrow, disease, pests, natural senescence) decrease oak/hickory stocking while beech and maple have increased exponentially within the shaded understory (McEwan et al 2007, Fei and Steiner 2007, Holzmueller et al 2012). The state of succession of oak/hickory forests to beech/maple in the region is confirmed by several other studies in the Ozark highlands including Shang et al (2007) and Olson et al (2014). Our results are conclusive with the body of literature on successional processes occurring in maturing oak/hickory uplands lacking disturbance in the CHR (Ebinger 1986, Zazcek et al 2002, Galbraith and Martin 2005, DeSantis et al 2010, Fei et al 2011).

Our understory data indicates that while regeneration of oak and hickory seedlings is present, with the exception of black oak, recruitment of these species is absent into the sapling layer. This suggests that the microenvironment conditions for germination and initial growth of shade intolerant species may be adequate, but light conditions are not adequate to bring these species into the overstory. In the case of gap openings where initial light penetration may be high, competitor species are prevalent and shading, especially in single tree gaps, occurs rapidly creating minimal light conditions again. These ephemeral light swings are not conducive for oak recruitment which typical requires prolonged 20% - 30% light exposure to encourage growth and limit overtopping by competitor saplings (Dey et al 2008).

In the case of nominal light conditions consistent with uneven stands oak and hickory will continue to stagnant in the understory while shade intolerant maple, beech, and pawpaw will proliferate. Along with this, the regeneration potential of oak/hickory will decrease with the loss of viable mother trees, seed banking, and stump sprouts.

ELT Overstory Composition

Delimiting of these successional patterns along ELT boundaries showed a substantial increase across all ELTs in beech/maple density and basal area (Table 2-3). Notably, beech expansion into the canopy has occurred from xeric ridgetops to mesic bottomlands. Analysis of ELTs between 1980 and 2014 using the Bray-Curtis dissimilarity index showed dissolving ecological boundaries between all land types and increased in similarity (Table 7). Our results differ to previous research which have hypothesized edaphic restraints to mesic expansion from bottomlands and show successful establishment of these species on all ELTs (Klos et al 2009, Burton et al 2010,Hanberry et al 2014). Further analysis utilizing MRPP and NMDS confirm these results. Our results suggest under a reduced disturbance scenario shade tolerant species composition increased across all ELTS and a homogenization of communities has occurred within the forest.

In regard to oak, three main trends stand out. First, the red oak group has seen the greatest reduction in density at TTSF, dropping from 27 trees/ac to 11 trees/ac. This trend has been reported in other areas of CHR and is tied to its shorter lifespan as well as mechanisms of mortality associated with native pathogens (Fei and Steiner 2007, Wargo et al 1983). Secondly, low and bottomland ELT oak populations have become low to marginal components while beech and maple maintain the highest density on these sites. Oak regeneration is likely not feasible today on lowland bottomland ELTs. This is due to increasing competition from shade intolerant species, including pawpaw. Pawpaw has become increasingly dominate in the understory of all ELTs, ranging from ¼ of stems on xeric ELTs and ¾ of stems on mesic ELTs. Prior research has shown increasing densities of pawpaw to be significant competitors to oak/hickory due to their defensive compounds against herbivory and clonal growth strategy (Slater and Anderson 2014). Lastly, upland ELTs have seen the greatest drop in oak density. Several articles have discussed whether the limited water availability on these sites or the original higher population of oak has caused the present high density of oak (McDonald et al 2002, Iverson et al 2007, McEwan et al 2011). Current research points to the latter suggesting these trends are simply representative of the original population as defined by disturbance patterns (Nowacki and Abrams 2008) and environmental conditions are not solely restrictive (Palus 2017). This further supports the concept that edaphic barriers will not limit progression of mesophytic species onto upland sites (Hanberry et al 2012).

Changes in Soft Mast

While incurring mortality and dwindling regeneration potential are two primary concerns at TTSF, smaller populations of soft masting species at TTSF have shown even less resiliency to lack of disturbance. Species including dogwood, sassafras, mulberry, and cucumber tree have declined or become extirpated in the forest. Forest management focused on proliferation of longer lived oak and hickory species has the potential to provide inadequate disturbance to these shorter lived shade intolerant species. This is especially true in areas of the CHR, such as TTSF where even short lived oak species such as red and black oak already has already experienced collapsing regeneration potential. This loss in diversity has been shown to have negative effects on resident wildlife including several priority songbird species in other areas (Greenberg et al 2011). These species are especially important during winter migration when they may be the sole food source (McCarty et al, 2002). However while soft mast is a great way of hedging bets during hard mast failure, these species also provided variable nutrient composition to a variety of wildlife species (Short 1975). This is an important factor for successful multi goal forest management (Perry et al 1999) and a tool towards engaging concerned stakeholder groups (Sheppard et al 2005).

These species provide numerous other key ecosystem functions within the CHR other than wildlife value. Dogwood for example, has been documented to serve as calcium pump, absorbing mineralized calcium for its own growth, which later is available to other species as dogwood sheds its leaves in fall (Holzmueller et al 2010). Sassafras stems, which have decreased by half in density at TTSF, also provide valuable wildlife forage via their fruit and buds. Sassafras is an early successional species that often falls out several years after canopy closure. However, sassafras snags serve an importance purpose as wildlife trees and very rarely they reach considerable size in the overstory (Grant and Clebach 1975). At TTSF most trees have been shaded out and clonal pockets of sassafras persist in the understory. The clonal nature of sassafras allows it to persist in shaded environments however; canopy removal is required for a stand to maintain a sassafras component (Guyette and Kabrick 2002).

Mulberry is more tolerant of shade, but a decline in population has been reported across the CHR during the last 50 years (Core 1974). No direct disease or insect has been determined. It is likely there are numerous reason including leaf spot, wood boring insects, habitat loss, and fragmentation (Perry et al 1999). Mulberry was not inventoried in our study and is likely nearly or completely extirpated from the stand. Cucumber tree has suffered the same fate as mulberry at TTSF. As the Ozark population represents an isolated group of cucumber tree it is possible the species is especially vulnerable to the shifting environmental conditions at TTSF. This may include shifting nutrient availability, light conditions, or additional competition from mesophytic species and invasive plants (Binkley and Giardina, 1998).

Forest Health and Succession

Not only does homogenizing forest composition decrease biodiversity in itself and the multitude of benefits that biodiversity provides, it also increases the forests susceptibility to insects and disease (Boyd et al 2013). While it is important to research successional pathways through historical ecological mechanisms, introduction and increased distribution of several invasive non-native diseases, plants, and insects, such as emerald ash borer (EAB), have huge impacts on contemporary forests. These forest health issues have required new management strategies and have a strong potential to drive succession towards non- analogous states (Flower and Gonzalez-Meler 2015).

Some forest health issues, including many species of invasive plants are already prolific across the CHR (Huebner 2006). This includes amur honeysuckle, autumn olive, several species of privet, Japanese honeysuckle, princess tree, and tree of heaven (Webster et al 2006). These species readily invade smaller forested areas, highly recreated areas, and disturbed areas. Larger forested tracts often have heavy populations of invasive plants along edge habitat which pose as staging areas for interior invasion (Hutchinson and Vankat 1997). Invasive species outcompete native species for light, water, and nutrients. Not only does this decrease the regeneration potential of desirable oak and hickory species but also has the potential to disrupt trophic interactions and inhibit the regeneration of even native shade tolerant species, potentially resulting in arrested succession (Hejda et al 2009).

Other pest populations such as EAB are still trending upward across the CHR with many unaffected areas across the North American distribution of ash. However many forests have suffered the impacts of EAB, resulting in 100% mortality of all ash species and white fringe tree in infected areas (Herms and McCullough 2014). In 2015, EAB was detected in Southern Illinois adjacent to TTSF. Ash is a minor component at TTSF composing 3% of stems in 1980 and 2% in 2014. The largest populations are found in low and bottomland ELTs however, a relatively high component can also be found on upland ELTs. South facing ELTs reported a 9% ash component in 1980 and a 2% component in 2014. Small gap openings, created during EAB inflicted mortality, are predicted to accelerate successional shifts to beech/maple over the next 5-10 years (Klooster et al 2014).

Other forest health threats such as Asian longhorned beetle (ALB), laurel wilt, and European gypsy moth, are not currently affecting TTSF. However they have the potential to result in wide spread mortality at TTSF depending on their rate of spread (Venette et al 2014). Asian longhorned beetle infests species within 12 genera of hardwood species in the U.S including maple, ash, willow (*Salix* L.), elm, birch, sycamore, hackberry, mimosa (*Albizia julibrissin* Durazz., 1772 non sensu Baker, 1876), yellow poplar, and mountain-ash (*Sorbus americana* Marsh.). While mulberry, oak, locust, and basswood are all questionable hosts (Hu et al 2009). Currently there are seven infestation sites in the U.S. the closest to TTSF being in Clermont County, Ohio. Eradication of these infestation sites has been successful in some cases however is intensive including massive removal and chipping of infested tress (Haack et al 2010). It is suggested while ALB has typically infested urban areas it has a large potential to outbreak into forested settings (Dodds and Orwig 2011).

Laurel wilt is a recent disease discovered in 2002 in Port Wentworth, GA. All species in the laurel genus, including sassafras, are impacted by the *R. lauricola* fungus (Fraedrich et al 2008). The wilt is spread mainly by redbay ambrosia beetle (*Xyleborus glabratus* Eichhoff 1877); however other ambrosia beetles may play a role as potential vectors (Ploetz et al 2017). Northern movement into the Carolinas and Arkansas over the last several years has resulted in infestation of isolated stands of sassafras (Oswalt et al 2014). This suggests potential movement into the interior CHR and further decrease of the sassafras population at TTSF in the next 20-30 years (Hanula et al 2008).

European gypsy moth, which was introduced in Massachusetts in the latter half of the 19th century, has slowly spread across the Eastern U.S. since its introduction (McManus, and Csóka 2007).. The slowed movement in thanks to well-coordinated state and federal monitoring and eradication programs. However even with current management recourses and efforts, gypsy moth will likely eventually infest all of the CHR, including TTSF (Tobin and Blackburn 2007). Maturing oak stands are particularly vulnerable to defoliations during outbreak status of gypsy moth in quarantined zones. Silvicultural practices promoting health forests and the reduction of native pathogenic stressors is recommended to increase the resilience of oak to these impacts (Waring and O'Hara 2005).

All of the above nonnative insects and disease aggressively populate new hosts shifting forest dynamics and, along with native insect and disease, impact overall forest succession at TTSF. Due to the aging oak overstory the largest native forest health issue of concern at TTSF is oak decline (Kabrick et al, 2008). This complex is an encompassing term for a host of typically secondary insects and disease which have resulted in wide scale mortality of oak species, typically in the red oak group, across the CHR (Bendixsen et al 2015)). Pathogen associates of oak decline are commonly root rot (e.g. Armillaria root rot), other fungal agents such as hypoxylon canker (*Hypoxylon spp.* Bull.)), or insects (e.g.. two-lined chestnut borer (*Agrilus bilineatus* Weber) (Haavik et al 2015). However other species may be present while the above may be absent. Secondary pathogens, such as those involved in oak decline, invariably increase in overmature stands, driving successional pathways (Millar and Stephenson 2015). Our research shows shifting species composition at TTSF representative of these complex interactions. However, it is important to understand the impact of invasive species and there potential to increase the speed, change, or produce non-analogous successional pathways.

Management Implications

TTSF is a representative model for managing mid successional forests that have developed an advanced midstory and understory due to removal of disturbance from the ecosystem. Our results provide sufficient evidence for several recommendations for land management under this scenario. Shifts in overstory and understory composition show a sharply reduced capacity for present oak/hickory overstory regeneration and recruitment.

Before determining management strategies at TTSF (or similar forests), it is first important to weight ecological restrictions, fiscal restrictions, and management objectives. A fundamental questions addressed in the literature is the ecological restrictions behind recruiting oak/hickory. Our research suggests that present management in the CHR should consider accepting a lower composition of oak/hickory than historically observed on Lowland and Bottomland ELTs while focus oak/hickory recruitment on upland ELTs. In addition, our data shows a changing forest structure that requires a midstory removal for adequate recruitment on oak hickory. Prescribed fire is an additional available practice that has a studied history improving forage tonnage as well as decreasing density of pyrophobic species such as beech and maple (Ryan et al 2013). However, fire and midstory removal alone will not sufficiently regenerate oak species (Holzmueller et al 2012), and will likely need to be combined with overstory removal to increase the likelihood of successful oak regeneration (Brose et al 2013). In order to further increase the success of these treatments to regenerate oak they should focus on upland sites rather than lowlands, even where oak had predominated before. Our current assessment of oak/hickory regeneration potential shows these species have very little presence in the understory and are subjected to a high degree of competition from other shade tolerant species, especially on lowland and bottomland ELTs. The above practices focused on regeneration of the overstory should promote co-occurring mid successional soft masting species as well. However, it is important to note the short lived nature and the marginal component maintained by many of these species may inhibit their regeneration even during management.

Periodic surveillance for mortality and forest health issues is also important. Areas with established recreated areas, such as TTSF, have an increased risk of introduction of exotic pests and diseases. Any insect of disease-induced mortality will necessitate focused management in that area. This is especially important as species such as black oak, have very low levels of regeneration in the understory.

CHAPTER 7

CONCLUSION

Senescing oak/hickory forests co-occurring with failed regeneration is a major environmental issue across the CHR. The Ozarks have the highest importance of oak and the second highest importance of hickory in the eastern U.S (Abrams 2010). This region has experienced unprecedented decreases in these species along with the Highland Rim of Tennessee, the central Alleghany Plateau, and the Driftless area of the Upper Midwest (Fei et al 2011).These species have a keystone effect supporting a host of biodiversity and trophic levels. Regional changes in oak/hickory forests are a paramount research area for informing management and land prescriptions.

Our research at TTSF is a clear example of oak/hickory succession to beech maple on an upland site among species community types as delineated by topographic moisture gradient (ELTs) within the CHR. Expansion of beech and maple onto xeric ELTs suggests a breakdown of edaphic barriers throughout the region which have been hypothesized to resist encroachment from mesophytic species. Especially noteworthy is the expansion of beech from mesic refuge sites.

In addition our study shows a corresponding decline in soft masting species in advance of reported declines in oak and hickory. As soft masting species exist at lower stocking levels and have short lifespans they are especially vulnerable to lack of management. Some of the species including mulberry, cucumber tree, and dogwood may be completed extirpated from the forest.

Under a no management scenario stochastic small gap disturbances will likely continue to favor maple/beech expansion across the region. It is likely these processes will be accelerated due to insect and disease attacks on the mature oak/hickory overstory as well as gap mortality of other species by invasive species, such as EAB. Currently oak decline induced by lack of management is likely the number one forest health issue. Introduction of other forest health concerns such as laurel wilt and Asian longhorned beetle may exacerbate these issues in the future.

These results typify shifting forest types across large spatial areas indiscriminant of topographical variation. This is directly related to lack of disturbance in the forest as also shown by previous research. These changes, and their potential to accelerate under imminent forest health threats, are important for direct management and communicating management ideas. It is more important than ever for land managers to communicate all of these ideas (overstory composition, soft mast, and forest health concerns) in order to have an effective impact.

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Thesis Title: SUCCESSION OF AN UPLAND OAK/HICKORY FOREST IN THE CENTRAL HARDWOOD REGION

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