THE ROLE OF CANOPY TREE DIVERSITY ON UNDERSTORY PLANT RICHNESS AND TREE SEEDLING ABUNDANCE IN A *PINUS STROBUS* FOREST IN THE SOUTHEASTERN U.S.

by

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DEDICATION

E.O. Wilson, U.S. Capitol,1998:

> "Now when you cut a forest, an Ancient Forest in particular, you are not just removing a lot of big trees and a few birds fluttering around in the canopy. You are removing or drastically imperiling a vast array of species even within a few square miles of you. The number of these species may go to tens of thousands. Many of them, the very smallest of them, are still unknown to science, and science has not yet discovered the key role undoubtedly played in the maintenance of that ecosystem, as in the case of fungi, microorganisms, and many of the insects."

I dedicate my paper to the early pioneers of ecology and biodiversity research, many whose words went unheeded and unacknowledged until very recently. We owe you a debt.

ACKNOWLEDGEMENTS

I am grateful to my parents, who gave me the freedom to explore both nature and libraries to my heart's content.

I am indebted to the LRES program graduate professors of Montana State University. Most especially, I want to thank Dr. Lisa Rew: her kind words of encouragement, limitless patience, and attention to detail made this paper possible.

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ABSTRACT

The goal of my project was to determine whether diversity in the canopy layer of a *Pinus strobus* dominated, mixed mesic forest in the piedmont of North Carolina showed a relationship to 1) understory richness and 2) tree seedling abundance. Forty plots were randomly selected at White Pines Nature Preserve, in Sanford, North Carolina for the study. For each plot, understory, species and tree seedling richness and density were recorded. Explanatory variables included canopy tree species richness, density and cover, total diameter at breast height (dbh) and environmental data including soil type, distance to nearest trail, and elevation. Diversity was calculated using the Simpson Index of Diversity (1-D) to show the effect of dominance in the canopy. Understory richness showed a decreasing pattern with increasing canopy diversity ($p= 0.0783$), suggesting a negative effect of canopy diversity on understory richness. Likewise, tree seedling abundance showed a significant negative response to canopy richness ($p= 0.0146$) and to all soils types (both positive and negative response). Total canopy tree basal area (diameter of tree at breast height) showed a positive relationship ($p= 0.0514$) to canopy species diversity (with functional similarity), which supports research showing complementarity between functionally-similar canopy tree species. Overall, results for this study suggest that, in a historically *Pinus strobus*-dominated forest, although greater canopy tree basal area is related to higher canopy diversity, understory richness is negatively affected by higher canopy diversity, and tree seedling abundance is negatively affected by higher canopy species richness.

CHAPTER ONE

INTRODUCTION

Forest Biodiversity

A forest is a complex network of individuals in which those individuals both compete and collaborate to maximize available resources. The more complex and diverse the environmental mosaic, the greater the number of niches are available. Nuances within these niches represent opportunities for subtle adaptations to provide existential advantages to different species (Hutchinson, 1959). Environmental constraints such as precipitation, light and temperature all fashion the environmental mosaic and resulting species composition, but they are also buffered by it. Over time, as regions in a forest gradient become fully inhabited by life, the processes of living, including mineralization, decomposition, nutrient exchange, and chemical flux, shape the landscape further across spatial scales, creating more niches, and even redundancies (Chapin et al, 2011; Deng & Shangguan, 2017; Zang et al., 2018; Raiesi & Salek-Gilani, 2018). These redundancies form the backbone of biological diversity by providing overall community resilience to perturbations (Tilman, 1996; Hooper and Vitousek, 1998).

Biological diversity (or biodiversity) is the total variety of all living things inhabiting a shared space, including species both closely and widely related, and encompassing a vast range of traits and characteristics (Gaston & Spicer, 2004). Biodiversity is strongly related to measures of ecosystem functioning, and therefore, ". .

.changes in biodiversity can have significant impacts on ecosystem and landscape processes, both on a day-to-day basis and during extreme events" (Chapin et al., 1998). Functional diversity, likewise, is positively correlated with measures of resilience (Tilman, 1996; Hooper and Vitousek, 1998; Allan et al., 2011; Gazol & Camarero, 2016). As Thomas E. Lovejoy, arguably the "Godfather of Biodiversity", stated succinctly: "In other words, biological diversity integrates the effects of all environmental problems affecting an ecosystem" (Lovejoy, 2000).

Diversity is often measured using sample comparisons of total cover for each species and/or plant functional group. Richness, a measure of 1) the total number of species represented in a given area (for example, a 1-m x 1-m plot containing 12 species would equal a total richness of 12), and 2) evenness (how evenly numbers of each species are represented in a given area), are considered together to find overall diversity using a diversity index, such as the Shannon Index of Diversity (which accounts well for rare species), or Simpson's Diversity Index (a better measure of dominance).

Abiotic and Biotic Influences on Biodiversity

How do patterns of biodiversity emerge? Some researchers have chosen to focus on one of two drivers: the environment or the organism. E. Lucy Braun (1889-1971) was a prominent botanist and ecologist known for her book on forest ecology, *Deciduous Forests of Eastern North America* (1950), and for her assessment of the relationships between topographical factors and the distributions of plant species in mature deciduous

landscapes (Braun, 1942)—an effect known today as "environmental filtering" (Chapman & McEwan, 2018). Her explanation of how geomorphological features influence plant communities, as well as her pioneering work in phytogeography, earned her several conservation and botanical awards during her lifetime; as well, she was the first woman to preside over the Ecological Society of America. Braun divided eastern deciduous forests into nine "associations" according to floristic factors and dominant species, physiographic processes, and geologic history. Her observations of comparatively high levels of species richness (and a noted increase in canopy species richness) in southern Appalachian cove forests (forests located along streams in mountain valleys) led her to postulate that these areas had served as biological refugia during various glacial periods (Chapman & McEwan, 2018). Although this particular assertion was controversial, Braun published more than 180 widely accepted studies, many of which accounted for patterns of plant diversity and richness through the use of her unique perspective of environmental determinism (Chapman & Bolen, 2015). In contrast to Braun, J. Phillip Grime, in 1977, proposed the "stress-dominance hypothesis" and the C-S-R Triangle to explain patterns of species diversity. He theorized that plants evolved survival mechanisms (traits) based on trade-offs between the tactics of growth ("C", for *competitive strategy*), persistence ("S", for *stress tolerance*), or reproduction ("R", or *ruderal strategy*). From this perspective, geologic processes take a backseat to functional roles: here, interspecific interactions (especially competition for resources) determine the distribution of species across a landscape. Specifically, establishment in a given area can only occur if a given species can successfully outcompete other species for the niche

using one of these strategies. Although Grime's individual publications have focused more on grassland ecosystems than forests, his pioneering theories continue to drive research into the broader aspects of functional diversity and its effects (Thompson et al., 2005). Not insignificant, however, are the basic tenets of overarching forest successional processes—predictable and specific changes that occur over time in a forest ecosystem and include the effects of stochasticity. These processes might ultimately direct species distribution and diversity (Cowles, 1899; Gleason, 1926). Through succession, geology and biology can work concurrently. In this sense, the successional approach can help integrate environmental and species-driven theories of biodiversity.

Trees and the Canopy

Larger organisms often play outsized roles in ecosystems. For vertebrates, "keystone" species, including top-tier predators or very large herbivores and omnivores, can modify habitats and significantly affect biogeochemical processes (including biomass conversion, nutrient turnover, and serving as nutrient sources) such that the maintenance of that ecosystem becomes dependent on their presence. In the plant communities of grasslands, species with widely lateral and very deep root networks tend to acquire nutrients more efficiently, distribute more moisture laterally, better stabilize soil while also creating significant pore space, and maintain greater viability following fire (Weaver, 1968). Although their ability to draw moisture from extreme depths is less certain (Helzer, 2019), dominant grassland species can use resources efficiently through

very site-specific root development (lateral or deep), which helps to stabilize the larger grassland ecosystem: “the soil contains stored-up energy and becomes the abode of bacteria, fungi, actinomycetes, and many other microorganisms” (Weaver, 1968).

Similarly, in a forest, trees perform a variety of services for other species; for example, they can cycle enormous quantities of nitrogen (Vituosek, 1981). As trees die or when they are removed, vast quantities of nutrients may be released into the watershed until those trees are replaced by adequate quantities of biomass. Trees also provide structural heterogeneity to a forest; in this way they can be considered “keystone structures” (McGee, 2018). As senescence approaches, arboreal species, including invertebrates and epiphytes, take advantage of a large, old tree’s fissured bark, wide canopy spread, high-nutrient bark leachate, and significantly higher levels of moisture in the bark (McGee, 2018). In addition, large diameter trees—which have also been shown more likely to be common tree species—store disproportionately higher carbon via biomass compared to higher numbers of smaller, more abundant, yet frequently rarer tree species (Lutz et al., 2018; Köhl et al., 2017).

Canopy trees also influence understory species, through effects upon several important variables including light availability, litter type and amount, and soil effects, including moisture availability, pH, and nutrient retention. Exactly how the forest canopy influences overall understory diversity is less clear. Simard (2018) has shown how the *Rhozopogan*-Douglas fir mycorrhizal network in a boreal forest contributes to overall forest functioning, including resilience and defense, and resource allocation. Mestre et al. (2017) found that in Chilean temperate forests, understory functional

diversity was similar between mixed and evergreen forests, but dissimilar at the level of species richness. Alternatively, deciduous and mixed forests were similar at the level of species, but less so in terms of functional diversity. The greatest understory richness was observed in stands of only deciduous forest (and not, as the authors predicted, in mixed stands of evergreen and deciduous). In this study, the type of forest was used to predict understory richness, but the total diversity of the canopy layer was not considered (Mestre et al., 2017). Huo et al. (2014) found that in a coniferous (evergreen) forest, although dominant species appeared to affect understory species composition significantly, topographical variables (primarily elevation) had a more significant influence.

It is possible that the canopy diversity *per se* has relatively low importance in regard to understory diversity when compared to variables such as stand size, functional type of the canopy (evergreen or deciduous), resource heterogeneity, topographical features, and mineral soil composition (McIntosh et al., 2016). In fact, biodiversity at large has been shown to impact ecosystem function relative to the level of heterogeneity in an system (Tylianakis et al., 2008), although this effect could actually be due to the overarching effects of environmental resource limitations (Yang et al., 2015). However, it may also be possible that diversity in the canopy does impact understory richness, or that particular patterns of diversity, such as patterns of co-dominance, influence overall forest functioning. Madrigal-González et al. (2016) showed a positive effect of tree species functional diversity on overall forest productivity in boreal and high latitude forests, although the effects of functionally-diverse mixtures were compared only with

monospecific stands, and effects were seen to decease in significance as tree communities matured. Another study (Poznanovic et al., 2014) suggested the existence of a particular ectomycorrhizal fungi-sharing relationship between birch and hemlock seedlings in Michigan (U.S.), although findings could not be extrapolated to a similar relationship in the canopy. Most interestingly, Collet et al. (2014) found over a 12-year study that mixtures of two functionally similar species (*Fagus* and *Acer* spp.) at the same density showed a significant effect for increased diameter growth compared to pure stands of either species: "when pooling trees from the two species, average diameter was highest in the 50/50 mixture plots and lowest in the almost pure plots." A positive effect of *Fagus* was shown for height growth for both species in mixed plots. However, at different densities, diameter growth of neighboring trees of the same species showed a significantly greater negative effect than seen in neighboring trees of different species (Collet et al., 2014). Overall, these studies suggest that complementarity could exist between tree species as seedlings as well as in the canopy, but understandings about their effects on other layers of the forest, such as the understory, are lacking. Information about these effects could help us better understand forest resiliency and patterns of transition during periods of environmental variability. This study examines the response of understory richness and tree seedling abundance to canopy species diversity, in order to help clarify how the canopy relates to these measures of forest functioning.

The *Pinus strobus*-Dominant Forest

Eastern white pine, *Pinus strobus L.,* is a large pine native to North America. Tall specimens can grow as high as 57 meters. It extends from Newfoundland, Canada in the north, west to Ontario, south to Georgia and east through North Carolina through the northeastern states into Canada (Figure 1).

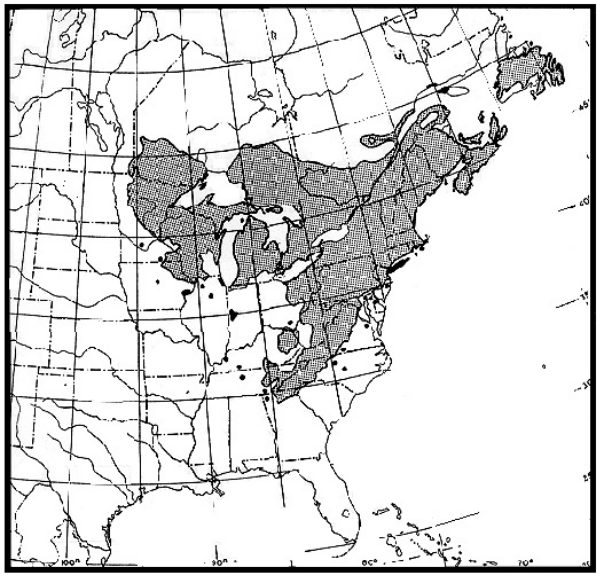

Figure 1: Range of *Pinus strobus L.*, Hall & Braham, 1998.

Pinus strobus is a long-lived pine (up to 450 years), with medium shade tolerance and a wide range of soil tolerances, although competing most successfully in low to medium-fertility soils. Even and uneven-aged stands of *P. strobus* occur; it can serve as a pioneer species, or as a long term member in a climax-forest community. Some *P. strobus*-dominated stands in Canada have persisted over 700 years: these old-growth

homogenous stands may be relicts left over from a cooler post-glacial period between 12,000 and 7,000 years ago (Barton, 2018). Other pure, even-age stands have been found to occur in old fields with intact sod (Carey, 1993).

In a climax or near-climax mid-latitude forest, *P. strobus* typically associates with northern red oak (*Quercus rubra*), red maple (*Acer rubrum*), and hemlock (*Tsuga canadensis*; Hall & Braham, 1998). Common understory species include blueberries (*Vaccinium* spp.), wintergreen (*Gaultheria procumbens*), and bracken fern (*Pteridium aquilinum*) on drier sites; wood sorrel (*Oxalis* spp.), partridgeberry (*Mitchella repens*), and sarsaparilla (*Aralia nudicaulis*) on moist sites (Carey, 1993). Due to the heavy pine litter, dense shade and acid soils, understory growth in pure *P. strobus* stands tends to be sparse. In the canopy, more shade-tolerant species are able to succeed *P. strobus*, including paper birch (*Betula papyrifera*), white cedar (*Thuja occidentalis*), white spruce (*Picea glauca*), and balsam fir (*Abies balsamea*) in northern/high-altitude regions (Carey, 1993).

Pinus strobus seeds are a food source for songbirds and small mammals, including squirrel, mouse, and vole; the foliage and bark is consumed by rabbit, deer, beaver, porcupine and other mammals, and gophers consume the roots and seedlings. Carey (1993) showed that black bear mothers with cubs spend over 95% of their time within 180 m of mature *P. strobus*, which are used as climbing routes to escape danger. For human use, *P. strobus* has been shown to be an effective species for strip-mine restoration due to a tolerance for degraded and acid soils (Carey, 1993). Large *P. strobus* are anecdotally known to effectively draw groundwater up to the forest floor and release

the moisture via transpiration, creating a cooling effect for the entire forest during the summer, and a warming effect during the winter (Penny, personal communication, November 15, 2019; Penny, 1997); this effect is probably not due to a central taproot, as *P. strobus* have been shown to use three to five large radial roots, with long, downward-branching sinker roots in coarser soils (Wendel & Smith, 1990).

Pinus strobus seeds are wind-dispersed over large distances, as far as 210 m in the open (60 m in a stand). Underground caches can contain as many as 30 seeds and serve to place seeds in direct contact with mineral soils beneath the pine litter. Fertilization takes as many as 13 months after pollination; another 2 years pass before cones ripen and seeds disperse. Mast seeding occurs every 3-5 years. Although young *P. strobus* stands can be decimated by fires, seedlings are surprisingly tolerant of needle scorch (Carey, 1993). Needles have low resin content and are relatively resistant to fire. Due to a thick bark and branch-free lower trunks, *P. strobus* more than 18.3 m tall (or 50 years old) shows significant resistance to moderate severity fires, with crowns that typically escape lethal levels of scorching.

Pinus strobus is threatened by various factors throughout its range: “White Pine Blister Rust”, *Cronartium ribicola*; overall decline from high soil pH, compacted soil and too little root space; “White Pine Root Decline”, *Leptographium procerum*; *Phytophthora* root rot disease; ozone damage; White Pine Cone Beetle, *Conophthorus coniperda*; White Pine Weevil, *Pissodes strobi*; and “Brown Spot Needle Blight”, *Mycosphaerella dearnessii*.

Although *P. strobus* shows genetic adaptions to local and regional environmental conditions, reduced growth has been found to result from high temperature stress, freeze events (or cold periods) at the beginning or end of the growing season, inadequate moisture during periods of high temperatures, and higher than normal precipitation events during the spring and fall (Chhin et al., 2018). These findings are particularly relevant for *P. strobus* in the era of anthropogenic climate change.

The understory layer of the forest, while contributing less biomass overall to the forest ecosystem, is a component of forest resilience and an important reservoir of species for forest regeneration due to higher levels of overall richness. Further, the understory helps determine the trajectory of forest successional processes—a future forest of tree seedlings waits in the understory for release from environmental constraints. However, in degraded landscapes, such as degraded agricultural landscapes, the understory is typically the last area to recover (Flinn & Vellend, 2005). By clarifying how forest community factors, such as canopy species diversity, relate to understory species functioning, we might gain a fuller picture of the *in situ* influences on forest resiliency, and later perhaps, response to stressors such as climate change.

Therefore, to better understand how the forest understory relates to the canopy, my study evaluated how 1) understory species richness and 2) tree seedling abundance were affected by canopy layer richness, diversity, and soil type in an established, deciduous forest historically dominated by *P. strobus*. In addition, I considered the effect of canopy diversity on total basal area (measured by diameter at breast height) of canopy species, as well as the future trajectory of *P. strobus* in the study area by comparing *P.*

strobus seedling numbers to numbers of mature individuals. My expectations were that 1) understory species richness would increase with increased tree canopy richness and diversity, 2) numbers of tree seedlings in the understory would increase in response to higher canopy richness and higher canopy diversity, and 3) tree diversity in the canopy would show a positive relationship to total basal area of canopy species. More specifically, I expected a co-dominant canopy species pattern (expressed as medium dominance, or medium diversity, using Simpson's Index of Diversity) to be related to higher numbers of tree seedlings in the understory and higher richness in the understory.

CHAPTER TWO

METHODS

Study Area

White Pines Nature Preserve is a 152-ha privately managed conservation area located at the junction of the Deep River (a 80.5-km, class WS IV/ water source with protected critical areas) and the Rocky River (a 49.9-km, class C river with critical areas) in the Cape Fear watershed of North Carolina. The rivers form the north, east, and southeast boundaries of the preserve. Areas of the preserve that are adjacent to the river are characterized by a sharp rise in elevation (a difference in elevation of 403 ft between the river bank and the plateau areas of the preserve). There are several trails in the preserve, which are gently used; the preserve is typically visited by approximately 4-7 visitors per day.

The forest canopy is comprised typically of mature white pine (*P. strobus*), poplar (*Liriodendron tulipifera*), sweet gum (*Liquidambar styraciflua*), beech (*Fagus grandifolia*), hickory (*Carya spp.*) and oak trees (*Quercus spp.*); the understory is composed of rhododendron (*Rhododendron ferrugineum*), blood-root (*Sanguinaria canadensis*), *Trillium* species, trout lily (*Erythronium americanum*), Jack-in-the-pulpit (*Arisaema triphyllum*), *Acer* species, beech (*F. grandifolia*), black gum (*Nyssa sylvatica*), and sparse areas of forbs and small bushes. White Pines Preserve also hosts a mountain disjunct population of Dutchman's breeches (*Dicentra cucullaria*). The mesic forest

floor is primarily shaded and moist, and is dominated by tree litter (pine needles dominate). Fires are infrequent and rarely intense; the most likely fire regime for this area is once every 150 to 350 years (Carey, 1993).

In mature mesic forests, reproduction occurs mainly within canopy gaps. In the well-shaded plots of this study, *P. strobus, Oxydendrum arboretum, F. grandifolia, Acer* and *Quercus* spp. were the dominant canopy species (see Appendix A). Most of the mature *P. strobus* individuals were of similar age and size (large and mature). Plots that included *P. strobus* in the canopy typically included silky willow (*Salix sericea*), greenbrier (*Smilax bona-nox*), striped wintergreen (*Chimaphila maculate*), and strawberry bush (*Euonymus americanus*) in the understory. A small number of *P. strobus* saplings and young trees were present. Pine seedlings were infrequent when compared to seedlings of other species.

Soil type for the study plots included BaE (Badin-Nanford complex, 15-30% slopes), NaD (Nanford-Badin complex, 10-15% slopes), and NaB (Nanford-Badin complex, 2-6% slopes). The Nanford soil series are deep and well-drained, with moderate permeability, and have parent material of fine-grained metavolcanic rocks. These soils are found on the ridges and slopes of the piedmont uplands of North Carolina. They are silty loams of the fine, kaolinitic, thermic typic Kanhapludults taxonomic class (order: Ultisol), and are strongly acid throughout the solum portion (USDA, 2015).

Soils of areas adjacent to the study plots included NaC (Nanford-Badin complex, 6-10% slopes), GkE (Georgeville-Badin complex, 15-30% slopes), GeB2 (Georgeville silty clay loam, 2-6% slopes, moderately eroded), ChA (Chewacla and Wehadkee soils,

0-2% slopes, frequently flooded), and RvA (Riverview silt loam, 0-3% slopes, frequently flooded; USDA, 2015).

Temperatures at White Pines Preserve have ranged from an average of -2.7 ^{o}C in January to 31.3 ^{o}C in July (for the period of 1971-2000; USDA, 2015). Average precipitation was 122 cm, with an average snowfall of 10.9 cm, for the same period.

Field Methods

The steep slopes of White Pines Preserve made assessing randomly assigned ecological quadrats a challenge. Further, ecological contrasts between gently and sharply sloped areas were likely to confound data. To accommodate this, the baseline of the survey was assigned longitudinally along a route with minimal variations in elevation and slope (<42 ft change in elevation) and where all possible quadrats would be further than 50 me from a significant body of water.

Along this 600-m baseline, 5 random, 100-m horizontal (east-west) transects were selected. This was done by converting meters along the 600-m baseline into decimal degrees (0.0001 decimal degrees = 11.132m), subtracting these degrees from the northern longitudinal starting point of 35.6180 (35.6180 - 0.0054 = 35.6126), and using a random number generator to generate 5 non-repeating numbers south along this gradient (35.6180 to 35.6126) to the fourth decimal place, assuring that each 10-m x 10-m quadrat would not overlap (0.0001 degree decimals = 11.132 m). The mid-point of each transect was centered on the baseline (at the 50-m marker of the transect).

Below are the (non-repeating) randomized longitudinal locations (from north to south) of the transect lines along the baseline (Figure 2):

35.6173
35.6159
35.6158
35.6145
35.6129

Then, two (non-repeating) randomly generated quadrat locations, situated east to west along each transect, were selected for each transect location.

The number set used to select the quadrat locations (whole integers 1-10) was converted to 10-m intervals so as not to overlap. To achieve this, for each transect location, two unique numbers were generated between 1-10, from which 0.5 was subtracted to find the center point of each quadrat. The numbers were then multiplied by 10 to show their locations (east to west) along the 100-m transects. Finally, distances from the quadrat centers (at transect) were calculated from the transect to make measurement in the field easier (Table 1).

Table 1: Transect locations, organized north to south down the column.

Transect Latitude N to S along -79.155 Longitude	**Random Value (1-10), non-repeating in location pairs**	**Quadrat Center Location E to W**	**Quadrat Location from Transect Midpoint**	**Quadrat Identifier**
35.6173	3	25 meters	25 meters E (**left** of midpoint facing S)	1 (A)
35.6173	5	45 meters	5 meters E (**left**	2 (B)

			of midpoint facing S)	
35.6159	7	65 meters	15 meters W (**right** of midpoint facing S)	3 (C)
35.6159	2	15 meters	35 meters E (**left** of midpoint facing S)	4 (D)
35.6158	1	5 meters	45 meters E (**left** of midpoint facing S)	5 (E)
35.6158	8	75 meters	25 meters W (**right** of midpoint facing S)	6 (F)
35.6145	8	75 meters	25 meters W (**right** of midpoint facing S)	7 (G)
35.6145	2	15 meters	35 meters E (**left** of midpoint facing S)	8 (H)
35.6129	4	35 meters	15 meters E (**left** of midpoint facing S)	9 (I)
35.6129	7	65 meters	15 meters W (**right** of midpoint facing S)	10 (J)

Quadrats were further divided into quarter-quadrat plots, each measuring 5-m x 5-m. The quarter-quadrat plot was the sample size used for all analyses and they were numbered

clockwise facing north to simplify data collection; for example, Quadrat 1, Quarter-Quadrat 1 is designated “1.1”, and so on (Figure 3).

Figure 2: Field placement of 10 quadrats at White Pines Preserve, Sanford, NC. Soil types are identified (Google Earth with SoilWeb Earth overlay, USDA NCSS, 2019).

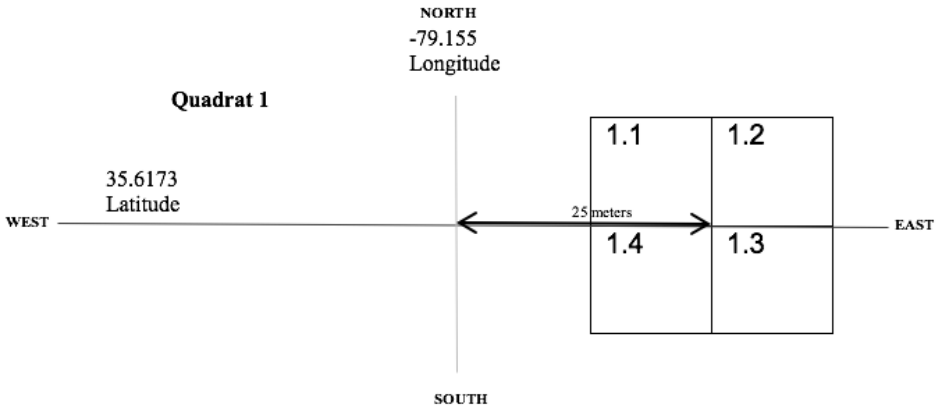

Figure 3: Quarter-quadrat plot layout in the field.

Field Collection

Ten quadrats (four quarter-quadrats each, for a total of 40 plots) were sampled for understory species richness and density (including tree seedlings), canopy species richness and density, total dbh (diameter measured at 1.3 m), canopy cover (using a densitometer), distance to nearest trail, and center of quadrat elevation. All abundance and richness data were collected directly at White Pines Preserve during August, 2019.

The baseline, transect locations and elevation measurements were found using an *eTrex HC series Garmin* GPS locator and Google Earth. A surveyors' measuring wheel was used to count out meters from the center of transects for placing quadrats. Pre-measured ropes served to delineate the quadrat and quarter-quadrat boundaries, and were

held in place with thin tent anchors. Canopy cover was estimated using a spherical densitometer from the center point of each plot and covered each 5 m x 5 m plot area.

In each quarter-quadrat plot, tree canopy individuals > 3-m high were counted, identified to species, and had dbh recorded. Height criteria was evaluated in the field by stacking 2, 1.5-m sticks. Circumferences were found using flexible measuring tape, with a marked reference for breast height at 1.3 m. Circumferences were later converted to diameters. For the understory, individual tree species < 3-m high were counted, recorded to species, and labelled as understory tree seedlings (for simplification purposes, tree saplings < 3-m high were also included). All understory species of vascular plants were identified and counted in each quadrat. The North Carolina Forest Service publication, *Common Forest Trees of North Carolina: How to Know Them* (Holmes, 2012) helped identify species.

Data Analysis

Data analyses were performed using R statistical software (version 3.5.3, 2019). Graphics, including boxplots and graphs, were created using R. Diversity analyses, including total richness and Simpson's Diversity Index (1-D), were performed using the *Vegan* package in R (Oksanen, 2013).

For the main analyses, the response variables were 1) understory richness and 2) tree seedling abundance and the fixed variables were canopy richness and soil type. There was a high correlation between soil type and both distance to trail and elevation,

and therefore only soil type was used. Additional explanatory variables, including total cover and canopy deciduous and evergreen basal area, were also evaluated and removed using a step-wise procedure if not significant to find the most parsimonious model.

Most models used generalized linear modelling with Poisson distribution due to richness and seedling abundance count data. Data using Simpson's Index of Diversity (1-D), with values from 0 to 1, were analyzed using generalized linear models with a Gaussian distribution. All data were tested for homogeneity of variance, and diagnostic plots for all models suggested that data were normally distributed. Alpha was set at 0.05 (5%), but trends were noted when $p < 0.1$.

CHAPTER THREE

RESULTS

Measures of Richness and Diversity

Total species richness (including all vascular plant species) for the area studied (1000 m^2) averaged 8.66 species, ranging from 4 to 14 species, per 5-m x 5-m plot, with an overall species richness of 31. Overall, diversity as measured by the Simpson Index (1-D) ranged from 0.40 to 0.88, with a mean diversity score of 0.71 (a score of 0.71 equals a medium-high level of diversity, and a medium-low level of dominance). Understory species richness averaged 7.5 species, ranging from 3 to 14 species, per 5-m x 5-m plot. Understory diversity as measured by the Simpson Index (1-D) ranged from 0.35 to 0.88, with a mean of 0.69. Tree canopy species averaged 2.45 species, ranging from 0 to 6 species, per 5-m x 5-m plot. Tree canopy diversity as measured by the Simpson Index (1-D) ranged from 0 to 1, with a mean of 0.56.

Pinus strobus represented 10.6% of all canopy individuals, but only 1.9% of all understory tree seedlings. To evaluate the evergreen contribution to measures of tree canopy diversity, a linear regression model relating canopy diversity (Simpson Diversity Index, 1-D) to percentage evergreen basal area in the canopy was used; no significance ($p= 0.895$) for this relationship was found.

Understory species richness showed a decreasing pattern with increasing canopy diversity ($p=0.0783$; Figure 4), although no effect was seen for canopy richness.

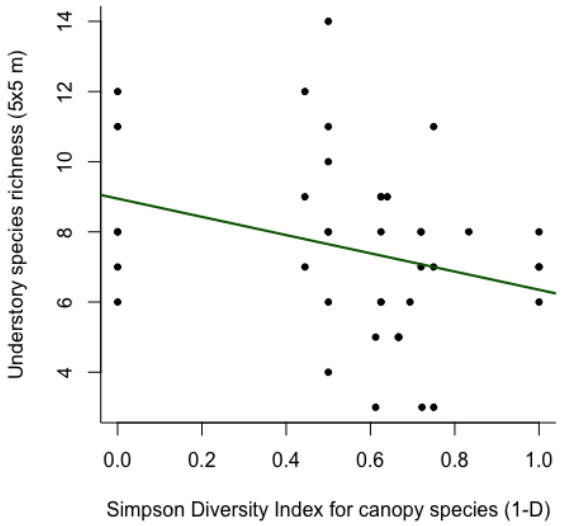

Figure 4: Understory species richness vs. canopy species diversity shows a negative relationship (Simpson Diversity Index, 1-D).

The effect of additional variables, including canopy deciduous basal area and canopy evergreen basal area, was assessed independently and found to have no effect on understory richness.

Measures of Tree Seedling Abundance

Total tree seedling abundance (tree species < 3-m high) for the area studied (1000 m^2) averaged 28.62 individuals, ranging from 8 to 109 individuals, per 5-m x 5-m plot, with a total tree seedling count of 1145 individuals.

Seedling abundance in the understory was explained by canopy richness (p= 0.0146; Figure 5) and soil type, with more seedlings in the BaE soil type than the other two (NaB, $p < 0.0001$; and NaD, $p < 0.0001$; Figure 6).

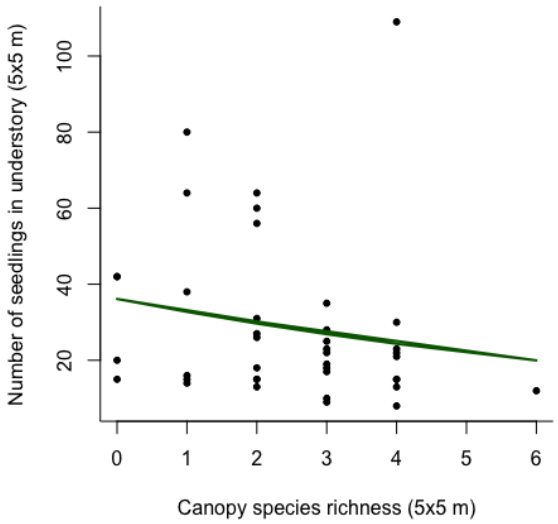

Figure 5: Number of seedlings in the understory vs. canopy species richness shows a negative relationship.

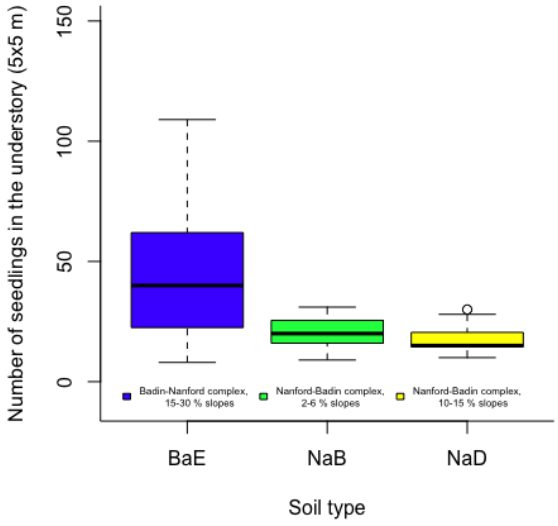

Figure 6: Total number of seedlings in the understory vs. soil type. BaE soil type is found to have a positive relationship with number of seedlings in the understory.

Seedling abundance was not significantly related to canopy species diversity as measured by the Simpson Index (1-D), nor canopy deciduous basal area or canopy evergreen basal area.

Total Basal Area of Canopy Species

Total basal area of canopy species was positively related to canopy diversity (Figure 7) as measured by the Simpson Index (1-D) ($p= 0.0514$) and controlling for soil type. Soil type was not significant for total basal area in canopy.

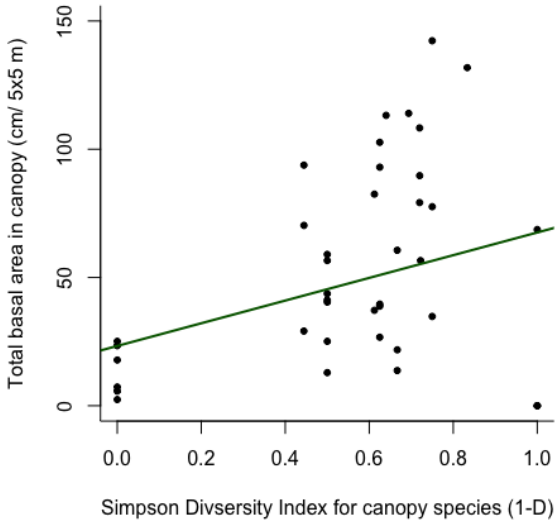

Figure 7: There is a positive relationship between basal area in the canopy and measures of diversity in the canopy (Simpson Diversity Index, 1-D).

CHAPTER FOUR

DISCUSSION

Future Trajectory of *P. strobus* at the Study Site

In this study, *Pinus strobus* represented 10.6% of the canopy individuals, but only 1.9% of all understory tree seedlings. A low seedling-to-mature-specimen ratio is essentially an upside-down replacement stage structure, and suggests a decreased likelihood of sustainable replacement fertility for this species in this forest (Gurevitch et al., 2016). The average dbh of mature *P. strobus* individuals in the study was 31.2 cm (n=10); 2.2 cm was the average dbh of younger trees (n=3) more than 3-m high but less than 10-cm dbh. Very old trees (more than 100 years old) are past reproductive age and young trees are not yet reproducing; therefore, only a specific age range of *P. strobus* can reproduce (Gurevitch et al., 2006). Using dbh values and the growth factor for *P. strobus* of 5 (applied to dbh in inches; see Appendix B), the average age of mature *P. strobus* was 61.2 years for this small sample; however, rates of growth for this species are highly variable, and natural stands (not those established on old field sites or plants) grow more slowly.

It is plausible that a significant portion of the population at this location has surpassed reproductive age, and this could explain the low numbers of younger individuals. In addition, seedlings are typically susceptible to mortality due to

competition from understory associates (Wendel & Smith, 1990). Considering the additional vulnerability of *P. strobus* individuals to the effects of climate change (extreme weather events, hot or cold periods, wet events during dormant seasons, and inadequate precipitation during the growing season), an increase in the reproductive rate of this species at this location seems unlikely, and the current scarcity of *P. strobus* seedlings relative to other canopy species suggests a rapidly declining population for this site (only 1.9% of total seedlings of all species).

White Pines Preserve: Diversity and Tree Seedlings

Understory richness showed a decreasing pattern with increasing canopy diversity. Mestre et al. (2017) suggested that richness in the understory might respond positively with increasing amounts of deciduous relative to evergreen cover (functional dissimilarity); this study suggests that increasing canopy diversity (without regard to functional diversity) may have a negative effect on understory species richness. These findings are potentially compatible in the sense that, in both studies, an increase in diversity (for Mestre et al., 2017, in functional diversity; for this study, higher total richness and higher diversity as measured by the Simpson Index of Diversity, 1-D) showed lower richness in the understory. However, for this study, the increase in diversity could not be explained by a shift in the functional composition of the canopy, as the model relating canopy diversity (Simpson Diversity Index, 1-D) to percentage evergreen basal area in the canopy showed no relationship between functional diversity

and total diversity. Collet et al. (2014) observed a positive (using height and basal area measures), complementary effect between different, yet functionally similar species in the canopy (a type of diversity more similar to that of this study), but did not evaluate the effects on understory richness.

Tree seedling abundance did not show a pattern with canopy diversity but did show a significant negative response to canopy richness. In this case, soil type was significantly related to seedling totals, with more seedlings on BaE than the other soil types.

Total basal area in the canopy showed a significant relationship to canopy diversity. This is consistent with the tree complementarity study of Madrigal-González et al. (2016), but possibly less directly consistent with the findings of Lutz et al. (2018), who found that more common species tend to make up the bulk of the canopy biomass (although diverse communities can be composed of common species). The model relating canopy diversity (Simpson Diversity Index, 1-D) to percentage evergreen basal area in the canopy showed no relationship between functional diversity (through evergreen percentage) and total diversity for this study site. Therefore, these results are consistent with, but show a difference to, the findings of Madrigal-González et al. (2016) in the sense that *canopy diversity with similarity rather than functional diversity* is showing an effect for increased canopy growth.

For some time, we have understood that overall diversity in forests tends to correlate with measures of resilience (Tilman, 1996; Hooper and Vitousek, 1998; Gazol & Camarero, 2016); therefore, using biodiversity as a proxy for resilience seems to be

reasonable. But, do patterns of canopy species diversity influence overall diversity and species richness in a forest? Allan et al. (2011) found that, in very rich grassland communities in Germany, a high turnover of dominant species was adaptive and increased long-term productivity: "The turnover in the functionally important species within communities was correlated with higher biomass production over time, particularly where functional group diversity was higher."

However, in communities with lower species richness, lower functional diversity among species, and a lower amount of evenness, "the presence of a species in a community with temporally stable high productivity might be sufficient to guarantee function over time, in which case species turnover would not promote high functioning." (Allan et al., 2011). Yet, even viewed as a low-richness and functionally "neutral" (Allan et al., 2011) ecosystem (requiring lower levels of functional complementarity and dominant species turnover to maintain functioning), the current study would have had to have shown *no effect* of canopy diversity on understory richness to have been consistent with the model of Allen et al. (2011). Again, Allan et al.'s findings seem to be contradicted by Collet et al. (2014) who showed a facultative effect of functionally *similar* tree species (vs. identical species). In addition, Felton et al. (2019) saw a significant decrease in the local diversity of all species, as well as a decrease in resilience to disease and disturbance, in forests undergoing rapid species replacement of the dominant canopy species by a *functionally similar species* (from *Pinus sylvestrus* to *Picea abies*, due to intense browsing by herbivores), suggesting effects related to specific dominant canopy species (and related variables) rather than *functional type.*

The overarching goal of diversity research should be to better understand the variables that influence the resilience of forest ecosystems, and to use these understandings to inform practices. With this goal in mind, further research could investigate 1) how different types of forest canopies (with different patterns of functional similarity) relate to patterns of understory and overall diversity, 2) how scale and location affect these relationships (for example, grassland communities vs. forests, or large continuous forests vs. smaller communities), and 3) whether current models suggest a relationship between changes in forest community structure and environmental changes.

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APPENDICES

APPENDIX A

PLANT LIST

Tree species	Common name
Acer rubrum	RED MAPLE
Carya glabra	MOCKERNUT/PIGNUT HICKORY
Cornus florida	FLOWERING DOGWOOD
Fagus grandifolia	AMERICAN BEECH
Ilex opaca	AMERICAN HOLLY
Liquidambar styraciflua	SWEETGUM
Liriodendron tulipifera	YELLOW POPLAR/ TULIP TREE
Oxydendrum arboreum	SOURWOOD
Pinus palustris	LONGLEAF PINE
Pinus strobus	WHITE PINE
Quercus alba	WHITE OAK
Quercus rubra	RED OAK
Ulmus americana	AMERICAN ELM
Carpinus caroliniana	HORNBEAM/ IRONWOOD
Woody shrubs	Common name
Vitis rotundifolia	MUSCADINE
Salix sericea	SILKY WILLOW
Parthenocissus quinquefolia	VIRGINIA CREEPER
Kalmia latifolia	MOUNTAIN LAUREL
Forb species	Common name
Asarum canadense	INVASIVE WILD GINGER
Asplenium platyneuron	SPLEENWORT
Chimaphila maculata	STRIPED WINTERGREEN
Euonymus americanus	STRAWBERRY BUSH
Eurybia divaricata	WHITE WOOD ASTER
Goodyera pubescens	DOWNY RATTLESNAKE PLANTAIN
Hexastylis arifolia	LITTLE BROWN JUG
Hexastylus virginica	VIRGINIA HEARTLEAF
Smilax bona-nox	GREENBRIAR
Toxicodendron radicans	POISON IVY
Zenobia pulverulenta	HONEYCUP
Graminoid species	Common name
Nothoscordum bivalve	FALSE GARLIC
Aletris farinosa	COLIC ROOT/STAR GRASS

APPENDIX B

DIVERSITY INDEX AND GROWTH RATE

Simpson Diversity Index (1-D)	$\tilde{D} = 1 - \sum_{i=1}^{S} p_i^2,$	*P*= the relative percentage of each species With Simpson's Diversity, as the community becomes more even and diverse, the score increases between 0-1.

Approximate age of tree= diameter (in) of tree at breast height (1.3 m) x growth factor