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Urban Forest Dynamics: Untangling Ecosystem Patterns at Harbison State Forest

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URBAN FOREST DYNAMICS: UNTANGLING ECOSYSTEM PATTERNS AT HARBISON STATE FOREST

by

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ABSTRACT

As expansion continues to push the wildland-urban interface farther into the suburbs and the landscape which surrounds cities, it will become more important to understand the factors that influence species composition in remaining green spaces. Harbison State Forest, an ~890-hectare urban forest provides a convenient setting to analyze species composition patterns within a multipurpose urban green space.

The factors that can create these patterns include environmental (topography, soil nutrient content, light, temperature, and precipitation), naturally occurring disturbances that alter these factors (e.g., fire, windthrow), and anthropogenic disturbances such as logging and prescribed burning.

I measured basal area by species on 74 randomly distributed plots. These data were complemented by measures of logging history and burn history along with environmental measures of slope angle, elevation, and slope orientation taken *in situ*. Soil samples were taken at each plot and analyzed by an outside lab for chemical make-up and nutrient content. I then used NMS, MRPP, and ISA to analyze the distribution of species.

NMS created gradients of soil structure differences between floodplain and upland soils while MRPP found significant ($p < 0.05$) differences between plots with differing histories. Soil proved to be the main determining factor in relation to woody species composition. Forest succession in Harbison is mostly influenced by environmental factors and represents a natural ecosystem existing in a suburban landscape.

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LIST OF ABBREVIATIONS

ASL .... Above Sea Level
AUC .... Area Under the Curve
BA .... Basal Area
CEC .... Cation Exchange Capacity
CHM .... Canopy Height Model
DBH .... Diameter at Breast Height
DEM .... Digital Elevation Model
GIS .... Geographic Information Science
GLM .... Generalized Linear Model
GPS .... Global Positioning System
HSF .... Harbison State Forest
ISA .... Indicator Species Analysis
LiDAR .... Light Detection and Ranging
MRPP .... Multi-response Permutation Procedure
NMS .... Nonmetric Multidimensional Scaling
SCFC .... South Carolina Forest Commission
SPSS .... Statistical Package for the Social Sciences
TIN .... Triangulated Irregular Network

CHAPTER 1

INTRODUCTION

1.1 Introduction

Expansion of urban and suburban areas is a common process globally and in the Southeastern United States, where models predict a 101-192% increase in urban sprawl over the next 50 years (Terando, et al., 2014). The retention of urban green spaces, undeveloped areas of natural vegetation that provide potential habitat and movement pathways within human-dominated areas (Chin and Kupfer, 2019), during such expansion has implications for wildlife, vegetation, and humans. For example, green spaces may provide key landscape elements for maintaining populations of species in an increasingly urbanized region. It is thus important to understand factors structuring plant and animal communities in landscape features and the ways in which urban forest management influences the natural environment of urban green spaces and the quality of life therein (Chin and Kupfer, 2020).

Urban green spaces are highly diverse in form, history, setting, intended purpose(s), and management intensity. They provide a range of potential benefits in urban environments, serving as habitat for plants and animals and providing ecosystem services such as carbon sequestration (Nowak and Crane, 2002), noise abatement (Nowak and Crane, 2002) and air purification (Dorney, et al., 1984). They also provide places of recreation, solitude, and respite from the stresses of urban life (Kaplan, 1983). These

benefits will be more important as heavily urbanized and suburbanized environments fragment landscapes and as the lines between suitable habitat patches and those that are inadequate blur.

The species composition of urban forests should be viewed as a function of a city's size, development history, patterns of land ownership, preferences, and natural setting (Sanders, 1984). Direct human disturbances and management in the form of various practices of intervention alter a range of environmental conditions within urban forests (e.g., temperature, light, moisture) and can change successional patterns and the composition of forest stands. Humans have found ways to manage these habitats for their own variety of complex reasons, for example, by using prescribed burns that favor certain species of trees and eliminate others. However, the consequences are as varied as the management strategies.

Plant biogeography includes an understanding of natural processes in a forest community as responses to environmental gradients and anthropogenic forces. This study will explore forest ecology, human influence on that ecology or lack thereof, and how the two interact in an urban setting. Urban green spaces are important and will become more common with expansion; therefore, understanding the basis of why a forest may be the way it is and how an ecosystem's structure and composition are shaped by intrinsic and extrinsic forces should be at the forefront of forest research. More specifically, the goal of this research is to quantify how forest composition varies across gradients of environmental conditions and historical anthropogenic disturbances at Harbison State Forest (HSF), a large green space located within the city limits of Columbia, South Carolina.

Managed by the South Carolina Forest Commission (SCFC) since 1951, HSF contains forest stands that occupy conditions ranging from floodplains to well-drained uplands and that have experienced varied disturbance histories, including forest clearing, fire, and insect outbreaks. My hypothesis is that environmental factors (e.g., moisture gradients, sunlight exposure and soil composition) will play the larger role but that anthropogenic influences (prescribed fire, and logging) also help to explain forest community composition because individuals respond to and interact with a spectrum of conditions for survival and reproduction based on species-specific adaptations (Mckenzie, et al., 2003). Observing how these factors interact at HSF will serve as a baseline for understanding why the forest is composed the way we see today.

Using Nonmetric Multidimensional Scaling (NMS), Multiresponse Permutation Procedure (MRPP), and Indicator Species Analysis (ISA), I investigate the compositional gradients in HSF and the environmental factors behind them. These analyses are complemented by an analysis of factors shaping biodiversity measures (species richness and species evenness) to explore how species-level patterns and controls are shaped at the level of community assemblages.

1.2 An Overview of Biogeography and Landscape Ecology

Biogeography is the study of the distribution of species and ecosystems in geographic space and through geological time. At the scale of human-perceived landscapes, the spatial pattern of organisms reflects spatial variability in environmental conditions and the response of individual organisms to those conditions based on the species-specific adaptations that serve to define their niche. The most important

constraints on vegetation generally are climate (including microclimate), landforms, and soils (Forman, 2016). Varied conditions can promote or inhibit the establishment, dispersal, and reproduction of certain plant species, leading to spatial patterns based on species niches but subject to stochastic processes (Matthews and Whittaker, 2014). Conversely, the idea that spatial landscape patterns are not simply a reflection of ecological processes but recursively affect them is the basis of landscape ecology.

The heterogenous arrangement of species and ecosystems across a landscape has been conceptualized in the form of a landscape mosaic consisting of 'patches' (e.g., of habitat) arranged in a matrix (the predominant habitat or landcover), with elements that can be described as corridors, barriers, and edges (Forman, 1995). A landscape that has a variety of small to medium patches of natural vegetation and corridors for migration provides a level of heterogeneity that can be useful in maintaining a level of rich biodiversity (Forman, 1995). A habitat patch that is larger and closer to a mainland source is going to be more diverse than a smaller and more isolated one (Kupfer, 1995). Rates of migration due to distance will decrease while rates of local extinction will increase from competition for resources and space. This, in general, is the theory of island biogeography. While it eventually became normal to apply island biogeography to forest fragments and while it makes sense for marine environments, there are too many assumptions with the theory for it to work perfectly in a terrestrial landscape (Kupfer, et al., 2006), particularly in urban landscapes that often contain an exceptionally broad range of habitat conditions.

1.3 The Landscape Mosaic in Urban Systems

Forman (2016) explored the idea of urban landscape ecology, focusing on a few key areas: land/water use and management, built structures, permeating anthropogenic flows, noise/light pollution, and contemporary human decisions and those of the past societies. The commonality of these foci is that the anthropogenic source of a disturbance can affect the surrounding ecosystem. The structure and composition of urban forests, for example, are the products of two dominant ecological processes: disturbances and forest succession. To understand and predict urban forest patterns, these regular and repetitive processes must also be understood, including the ways in which humans have affected them.

A disturbance can be defined as any relatively discrete event that disrupts the structure of an ecosystem, community, or population and changes resource availability or the physical environment (White and Pickett, 1985). Vegetation patterns in urban forests are a reflection of successional recovery following disturbances such as windthrow, logging, insect outbreaks, the regular intervention in these processes by anthropogenic factors, and intentional or goal-oriented land and vegetation management practices (Sanders, 1984). Natural disturbances are an inherent part of most ecosystems, but humans have had increasingly greater impacts on disturbance regimes, often resulting in rapid and novel conditions. The things that have changed are the character of the disturbance (from marine to aquatic to terrestrial), the nature of the disturbance (anthropogenic or 'natural'), the intensity of the disturbance, and the anthropogenic response to the disturbance (Turner, 2010). Disturbances interact with other key drivers

of global change and strongly affect ecological systems and, in return, humans living in association with urban green spaces (Turner, 2010).

Attention to disturbances increased in the 1980s and 1990s as more major disturbances were being observed while changes were occurring on a global scale (Turner, 2010). By interacting with landscapes, disturbances create vegetation patterns which form the basis for any ecosystem processes that will carry forward on the landscape. The first effect of a disturbance is to remove organisms (Reice, 1994). Disturbances can kill off organisms, disturb nutrient distribution, and introduce novel conditions to an ecosystem which all lead to responses from both vegetation and wildlife. Disturbance also creates a heterogeneity of conditions (Whittaker, et al., 1973) that facilitates the co-existence of species with varied adaptations (e.g., shade tolerance) across a landscape. Understanding disturbances and how they create or maintain heterogeneity in a landscape is informative of how the ecosystem operates at that landscape level. Fire can benefit or harm species and is also a process that occurs naturally and has been harnessed (and suppressed) by humans over the course of the evolution of civilization. In this way, it is a dynamic disturbance that we are still working to understand and manage today.

1.4 Disturbances and the Landscape Mosaic

Fire has been a common disturbance throughout the Southeast for thousands of years, leading to the evolution of distinct, fire-maintained ('pyrophyllic') ecosystems (Fowler and Konopik, 2007). Fires were once started and spread by the Native American populations and by lightning from thunderstorms (e.g., Lafon, 2010). The combination of

fires started by weather and native populations on the landscape is even thought to have served as a "stabilizing disturbance" (Brose, et al., 2001) in mixed oak forests, favoring the perpetuation of oak (*Quercus*) and pine (*Pinus*) forests.

During the Industrial Revolution, fire was seen as an undesirable and destructive force that had to be controlled (Brose, et al., 2001), and fire suppression became common in many regional ecosystems, including those dominated by Longleaf pine (*Pinus palustris*). Suppression led to denser than normal stands with mid stories and understories made up of fire sensitive, shade tolerant shrubs and trees, especially on mesic upland sites. The future of the oak/pine complex forest is being threatened, and it seems the problem needs to be fought with fire to clear out mesic competitors and allow these trees back in (Abrams, 1992).

Fire regimes (the seasonality, severity, frequency, and size of fires in an area) develop and emerge over long periods of time; as a result, they are a strong natural selection factor that influences the evolution and distribution of species and thereby greatly affect the composition of species that can survive in a forest (Lafon, 2010). Fire regimes vary with region/climate and are important for growth and development of species like Longleaf pine through the critical grass stage and onward into maturity (Garren, 1943). Typically, moderately wet climates are the most fire prone as they have enough precipitation for heavy fuel production but with enough dry spells that allow burning (Lafon, 2010). When fire regimes are altered by human actions, populations, communities, and ecosystems (along with the services they provide) can be affected.

Beyond fire, logging and forest conversion are common disturbances that shaped the landscape mosaic in many southeastern forests. Timber harvesting may vary in

intensity with different consequences for vegetation in the affected area of harvest. Clear-cut logging results in the removal of all trees within a given area for harvest (Blair, et al., 2016), and typically results in the greatest amount of change to site conditions (both biotic and abiotic). Forest thinning is the process of reducing competition between trees by removing a percentage of the overstory or understory, thereby increasing the competitive advantage of some selected species. Overcrowding can lead to decreased productivity from shading and a lack of physical growing space. Finally, salvage logging refers to the process of going into a recently disturbed forest and clearing out living and damaged trees (Blair, et al., 2016). This allows managers to "salvage" some of the economic value and/or prevent pest outbreaks following an event, such as an intense windstorm or fire.

In South Carolina, the vast majority (80%) of logging firms have become more mechanized since 2008 (Conrad, et al., 2018), which can result in greater impacts on tree composition. As Hatchell, et al. (1970) explored in their work, tree harvesting equipment (typically with treads for locomotion) create trails of compacted earth material. This can occur through machinery transiting a space before any logging takes place. Compaction of soil leads to decreased rates of infiltration of water and can lead to standing water and runoff. Depending on the type of woody vegetation, this can impede growth and establishment. Hatchell, et al. (1970) found that these were long lasting effects and that compacted soils showed decreased infiltration and stronger soil levels nearly two decades later.

When comparing different logging scenarios and their effects on woody plant composition, the results are dynamic. The ecological consequences of salvage logging for

example, are not fully understood (Emery, et al. 2020). The removal of dead and damaged trees modifies the composition of an area's fuel bed, which can lead to changes in fire regime and changes in nutrient recycling (Emery, et al. 2020). As Blair, et al. (2016, p 1) describe, "Understanding biotic responses to various disturbance regimes is becoming increasingly important around the world given the extent and frequency of human disturbance such as logging."

In many areas, logging has been a pre-cursor to habitat transformation. For example, forest ecosystems dominated by longleaf pine once covered roughly 25 million ha from Virginia to Texas and south Florida (Frost, 2007; Outcalt, and Sheffield, 1996). However, it is estimated that less than 5% of the original extent of longleaf pine forest remains due to agriculture, timber operations, and fire suppression (Oswalt, et al., 2012), and little of what is left is in reference condition. Human population density, rates of land use conversion, and extent of urban systems in the Southeast are all projected to increase dramatically in upcoming decades, resulting in further habitat loss, degradation, and fragmentation (Wear and Greis, 2013; Terando, et al. 2014).

In addition to the impacts of habitat loss and fragmentation, forest transformation leads to the creation of forest edges and the occurrence of edge effects (Murcia, 1995). The interaction between two adjacent ecosystems is especially pronounced when separated by an abrupt transition (Murcia, 1995). As a forest is cut for timber or transitioned into a suburban matrix, the amount of edge the remaining forest has increases. Edge effects manifest in the form of altered microclimate regimes that can persist for some distance into the forest away from the actual edge; as patches of forest become smaller, the ability to escape the edge becomes more difficult (Kupfer, 1995).

1.5 The Interactive Effects of Environmental Gradients and Disturbance Regimes

There is extensive research that explores the concepts and principles discussed thus far (McDonald, et al., 2008, Lafon, et al., 2017, Turner, 2010), and even some research that explores the dynamics between multiple disturbances, such as Blair et al. (2016) and Bowd, et al. (2018), who both look at forests in Australia. The interplay of logging and fire is nothing new, as they are both standard practices that are known quite well in forest management. As Turner (2010) put it, the interactions of disturbances are poorly understood, as prior disturbance can exert a strong effect on ecosystem response to a subsequent disturbance. An understanding of these interactions can be used by resource managers to better understand what is working and what is not *in situ*. Vegetation response to disturbance can be a key indicator of what direction an ecosystem is being driven by natural and anthropogenic disturbances. HSF presents a chance for all these processes to be explored in an urban landscape.

CHAPTER 2

STUDY AREA AND METHOD

2.1 Study Area

The study was conducted at Harbison State Forest, near Columbia, SC. The land included in HSF was purchased by the South Carolina Forestry Commission in 1951 and is now bounded by: 1) busy roads leading to dense subdivisions to its south, southwest, west, and northwest, 2) the South Carolina Criminal Justice Academy campus to the southeast and east, and 3) the Broad River to the north and northeast. Since its establishment as a State Forest, it has been set aside and managed as a recreational green space and a place of education on the many ecosystem services provided by regional forested ecosystems. At nearly 890 ha, HSF provides continuous areas of forested habitat surrounded by development, thereby providing an ideal setting for studying urban forest dynamics (Fig. 2.1).

Figure 2.1 Study locations: Harbison State Forest (Google Earth Pro, 2021)

The study area is in the humid subtropical climate zone and has mild winters and hot, humid summers. Rainfall averages 106-119 cm a year, with average daily temperatures of 10 and 25.5 ^{o}C in the winter and summer, respectively (South Carolina State Climatology Office). Elevation ranges from 54 m asl on the bottomlands near the Broad River to 106 m asl on the upland area of the forest, and slopes can exceed 25-30^{o}. It is also a heavily gullied landscape in large part due to past land uses, with dried up and active creek beds throughout. The forest transitions from upland habitat with well-drained loamy sand/loam with a high sand percentage to lowland floodplain with silt loam (Soil Survey of Richland County, 1978).

The Forestry Commission is self-funded (Harbison Management Plan, 2017), so choices must be made between timber harvest, recreation value, and habitat preservation. The quick growth of pine, particularly Loblolly (*Pinus taeda*), makes it attractive for timber uses, and logging has been carried out in HSF since at least 1918 (Aiken, 1981). More recently, thinning of trees in some areas has been carried out, while other areas have been clear-cut for timber harvest purposes. HSF contains areas of existing or potential habitat for longleaf and loblolly pines, so the maintenance of a regular fire interval is important. Prescribed fires, defined as the application of fire under environmental and meteorological conditions that will allow that fire to be confined to a prescribed area and to burn at a desired intensity (Barbour, et al., 1987), have thus become an important tool for managing pine habitat to meet goals for conservation at HSF (Harbison Management Plan, 2017).

Even with the anthropogenic forces that act on HSF discussed thus far (e.g., prescribed fire, logging), it is expected that the main contributors to species composition within the forest are environmental factors such as topography, soil structure and composition, moisture, and sunlight exposure. Human impacts will then be superimposed on those basic biophysical gradients. There may, for example, be extreme cases of heavily disturbed plots which show departures from the compositional norm and plots that have never been disturbed naturally or anthropogenically and differ in composition accordingly.

2.2 Species Data

To address these themes, I collected data on the composition of woody species in 74 plots distributed across HSF. Plots were randomly located using a stratified random approach after acquisition of the official HSF boundary from the South Carolina Forestry Commission Geographic Information Systems (GIS) division. I began by overlaying a 300 m by 300 m grid on the HSF boundary using ArcMap 10.8.1. Grid squares with 50% or more of their surface outside of the boundary were dismissed. Within the remaining grid squares, a point was randomly assigned using ArcMap to serve as a sample plot center.

After navigating to the coordinates of a designated plot center with a GPS, I collected data on species composition using circular plots due to their ease of set up. All woody plants with a diameter at breast height (DBH; 1.37 m) > 2.5 cm and within 6.91 m in radius of the center were measured and identified to species. This yielded species records in a plot of 150 m^2. Prior to analysis, individuals were classified into two categories: 1) saplings (2.5 cm ≤ DBH < 10 cm), and 2) trees (DBH ≥ 10 cm). Individual diameters were transformed into measures of basal area (BA) for use in subsequent analyses. Individuals < 2.5 DBH but with a height > 1 m were tallied and recorded as seedlings. Seedlings were represented in the full dataset by adding a 0.1 to a plot's total BA for a species if it contained them as seedlings.

2.3 Environmental Data

Along with the vegetation data, I recorded the slope angle and orientation of each plot using a Brunton compass. These variables served as proxies for hydrological regime

and amount of sun exposure, respectively. Elevation was extracted from a Digital Elevation Model (DEM) with 10-meter resolution acquired from the South Carolina Department of Natural Resources. Within Arcmap, the distance of a plot's center from a stream and from a road was extracted using the Euclidean Distance tool and SCFC GIS data on HSF attributes.

Soil characteristics serve as important controls on forest diversity and composition (Swanson, et al., 1988). Therefore, I took 7-10 soil samples from 10-15 cm deep holes dug randomly throughout each plot after clearing away any present layers of duff. The samples were sent to the Clemson Soil Lab and analyzed for cation exchange capacity (CEC), amount (lbs/acre) of various nutrients (P, K, Ca, Mg, and total %), acidity and soil pH.

Soil class and accompanying structure can also be useful predictors of vegetation distribution (Forman, 2016). Therefore, I extracted the specific soil class of each plot from SoilWeb (https://casoilresource.lawr.ucdavis.edu/gmap/) and verified soil class characteristics through the 1978 Richland County Soil Survey. Soils fell into six categories, ranging from well drained uplands to the flat Broad River floodplain. These categories were defined from the Richland County Soil Survey (1978) as follows:

> Soil Class 1: Wedowee (We). There were 21 plots (28.4%) on this soil type, which consists of deep, well-drained and moderately permeable soils on slopes ranging 2-30%;
>
> Soil Class 2: Congaree (Co). There were 5 plots (6.8%) on this soil type, which is a well-drained soil associated with floodplains on slopes from 0-2%
>
> Soil Class 3: Chewacla (Ce). There were 4 plots (5.4%) on this poorly drained soil, which is also associated with floodplains;
>
> Soil Class 4: Nason (Na). The greatest number of plots, 39 (52.7%), fell on this widely distributed well-drained soil, which is associated with ridges and slopes ranging from 2-30%;

Class 5: Herndon (He). There were 5 plots (5.4%) on this well-drained soil associated with ridges and slopes of 2-10%;

Class 6: Orange (Oab). There was only one plot (1.4%) on this somewhat poorly drained, relatively flat (0-4%) soil type. .

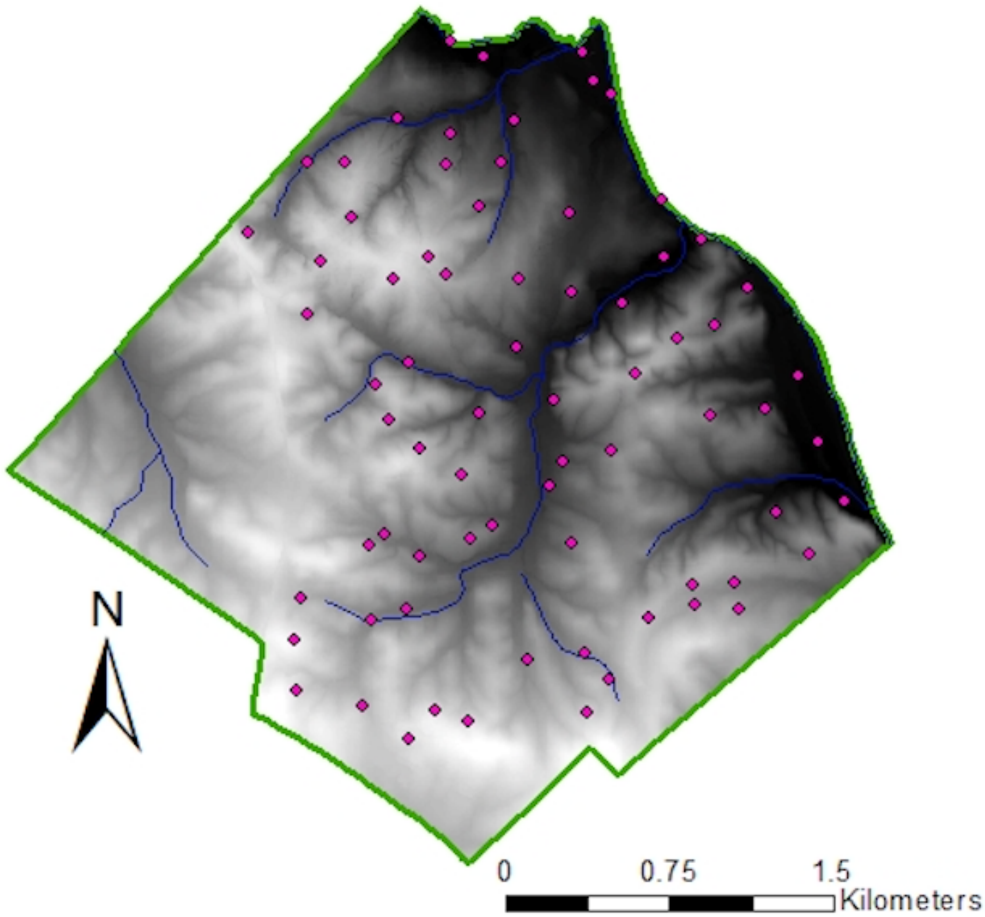

Figure 2.2, Harbison State Forest elevation (USGS DEM Layer) and plot points (Arcmap 10.8.1)

The two main disturbances for which I was able to obtain data were fire history and logging. Unfortunately, there is no long-term database of fire history available for HSF, but I was able to obtain an Arcmap layer of prescribed fires for the years 2009-2020 from the SCFC. I also recorded evidence of recent fires (e.g., ash, scorched trunks) during vegetation sampling to help discern burned from unburned sites. This information was used to assign each plot a ‘yes’ or ‘no’ (1/0) value for recent burn history indicating whether a plot was likely burned since 2009. The same ‘yes’ or ‘no’ (1/0) coding was used for logging history, which was ascertained through in the field observations. As an active forest and source of income through timber sales, HSF has been logged since at least 1918 (Aiken, 1981), with operations as recent as Summer 2021. Air photos dating from 1951-1981 obtained through the University of South Carolina Library were also used to assess logging history of plots in Arcmap in cases when field observations were insufficient.

Another aspect of forest structure that I explored in HSF is the overall height of the forest overstory. The forest canopy is the first barrier to sunlight for midstory and understory trees. As such it is a major factor in the growth and colonization of the forest by new species (Hart and Kupfer, 2011). The shade tolerance of a particular understory tree plays a large role in colonization success (Chin and Kupfer, 2020). It is difficult to get a height measurement of a tree from the forest floor. When taking various angle readings around a particular tree with a laser, obstructions, and operator error can lead to inaccurate measurements. Measurements can be taken from above using Light Detection and Ranging (LiDAR) data. Using an airplane or drone, a device can take readings of the ground surface by repeatedly and rapidly shooting a laser pulse and measuring the time it

takes that pulse to return. This data can and has been used to measure canopy height as the laser is bounced off obstructions such as leaves and tree branches. Combined with ground measurements, this data can be used to create a Canopy Height Model (CHM). Information on the specific LiDAR metadata can be found in the Appendix A.

To create a CHM, the LiDAR data from 2019 was downloaded from the USGS 3DEP online application and opened in Arcmap using the LP360 application. Seven data tiles were needed to cover the entire forest. Using the "LAS dataset to TIN" (Triangulated Irregular Network) tool allowed me to create two TINs, one with last returns of the laser (the ground surface) and another of first returns (the canopy). The TIN was generated and converted into a Raster to subtract one from the other using raster math. The result was a map of the height of the trees across the forest. Maximum height values were then extracted for each of the 74 plot locations.

2.4 Data Analysis

To assess patterns and potential controls of species composition at HSF, I used an ordination method (non-metric multidimensional scaling: NMS), multi-response permutation procedure (MRPP), and Indicator Species Analysis (ISA). NMS is a "numerical, repeatable system of organizing vegetation data which then graphically illustrates similarities and differences between stands" (Hobbs, 1988, p 140) that determines the best position of *n* entities (sample sites) in a *k* dimensional mathematical space based on a measure of their similarity in species composition (Hobbs, 1988; McCune and Grace, 2002). The graphical output of ordination is intuitive in that similar stands are closer together along a gradient and more dissimilar as they get further apart.

Because NMS is a nonparametric ordination, it has been shown to be well suited to nonnormal data and works well for ecological data with fewer assumptions about the data increased robustness to noise (McCune and Grace, 2002). It is widely used in ecology to understand gradients of composition (Chin and Kupfer, 2020; Hart and Kupfer, 2011).

Prior to performing NMS, I removed species that occurred on less than three plots to avoid negative influences of rare species. I attempted several different data transformations including using the raw data, a logarithmic transformation, and a square root transformation to the BA data. The square root transformation yielded the lowest stress values and best fit to the composition data (*see discussion on stress below*) so results throughout this thesis will be from analyses using that transformation.

Ordinations were performed in the same manner using 50 iterations for three different species matrices: 1) an overstory matrix using only tree data, 2) an understory matrix using only sapling data, and 3) a combined matrix using data from the tree-, sapling- and seedling layers. Ordinations were based on plot-level measurements of species basal area; for the combined matrix, each seedling was assigned a nominal value of 0.1.

Results of all ordinations were interpreted using a secondary matrix comprised of burn history (0/1), logging history (0/1), slope angle (degrees), slope orientation, year established, floodplain (0/1) soil pH, soil CEC (meg/100g), soil acidity (meg/100g), measures (lbs/acre) of: Phosphorus (P), Calcium (Ca), Magnesium (Mg), Potassium (K), total % base saturation, distance from stream (meters), distance from road (meters), drainage class, elevation, and soil series. The overstory (Tree only) layer also included

the addition of the canopy height variable. Ordination graphs were rotated by the elevation variable to facilitate the interpretation of ordination results. Rotating an ordination does not impact geometry of the results or the cumulative variance (McCune and Grace, 2002).

To evaluate the fit of an ordination, I plotted the Kruskal stress value and the correspondence between the ordination and the actual data, which show the stability of the solution. Stress values range from 0 to 100, but typically values greater than 20 are considered unstable solutions with interpretation being cautioned against (McCune and Grace, 2002). The pair-wise dissimilarities were calculated using the Bray-Curtis coefficient (McCune and Grace, 2002; Hart and Kupfer, 2011). The number of species and plots included in the analyses were: a) tree data = 21 species and 74 plots, b) sapling data = 20 species and 66 plots, and c) the full data = 31 species and 74 plots. Ordinations and other multivariate analyses were conducted with PCORD v5.0.

Along with the ordination, PCORD calculates the Pearson's correlation coefficient (*r*) between axis values in the ordination and environmental variables. Pearson's *r* ranges in values between -1 and +1 with significance being tested using a null hypothesis to find independence among all descriptors (Legendre and Legendre, 2012).

Beyond understanding how environmental factors structure forest composition, differences in diversity between plots can be indications of important drivers of a range of forest processes. Here, I examined two measures of diversity: species richness, which is "simply the number of species in some area within a community" (Barbour, et al., 1987, p 162), and species evenness, which is the distribution of species within that community. Evenness (also sometimes called equitability) shows how well represented

different species are within an area and can show inequalities in distribution. If one species dominates, evenness will be low but if all species have similar counts then the evenness will increase.

I used General Linear Modeling (GLM) to examine relationships between each biodiversity measure (species richness, species evenness) and three categorical predictors: burn history, logging history and soil series. Each model was initially fit with all three predictor variables; variables were removed from the model if they did not contribute significantly to the model and if their removal did not significantly change the Corrected Akaike Information Criteron (AICc) to create the best model. I fit models for four datasets (tree richness and evenness; sapling richness and evenness) using SPSS v. 28.0.

MRPP and Indicator Species Analysis (ISA) were used to quantify differences in species composition between groups of key predictor variables and to identify species that were key indicators of associated with specific disturbance histories or soil classes MRPP is "a nonparametric procedure for testing the hypothesis of no difference (in composition) between two or more groups of entities" (McCune and Grace, 2002). MRPP provides a test statistic, which becomes more negative with stronger separation, a p-value, and the agreement statistic which describes within-group homogeneity (McCune and Grace, 2002). MRPP values were calculated for burn history, logging history and soil class. Analyses were based on rank transformed Sorensen distance values, which use proportions of the maximum distance possible.

Indicator species analysis is often used as a complement to MRPP to determine the relationship between species occurrence or abundance values from a set of sampled sites and the classification of the same sites into site groups that represent things such as habitat types, community types, or disturbance states. Specifically, ISA identifies a representative species for subgroups of predictor variables. The values range from 0 for a species that occurs over a range of predictors / groups to 100 for a species that only and consistently occurs in a single category (Chin and Kupfer, 2020).

CHAPTER 3

RESULTS

3.1 Plot Conditions

Plots varied in slope from 0 to 16 degrees and though unequally, faced in all 4 cardinal directions, resulting in different amounts of daily radiation and hydrological regimes. A transition from ridgetops to moist floodplains along the Broad River can also be observed through elevation and soil composition/structure. Plots ranged from having thick underbrush while others were sparse and easy to traverse. Prescribed burns had been conducted on 18 (24%) of the plots while 48 (64%) of the plots had a history of logging. LiDAR data revealed a canopy with a minimum of 11.0 meters (39 feet), maximum of 39.3 meters (129 feet) and overall average (among the plot sites) of 25.1 meters (82.2 feet). Summaries of soil conditions and other variables can be found in Appendix Table A.2.

3.2 Forest Composition

I recorded 43 woody species, with six species accounting for 78.4% of the 2,246 individuals measured (see Appendix Table A.1). Loblolly Pine (*Pinus taeda*) was the most dominant species by BA, followed by Sweetgum (*Liquidambar styraciflua*), Longleaf pine, White Oak (*Quercus alba*), Cherrybark Oak (*Quercus pagoda*) and Red Maple (*Acer rubrum*) (Table 3.1). Two nonnative species were recorded, Autumn Olive (*Elaeagnus umbellata*) and Japanese Privet (*Ligustrum japonicum*), although each occurred on only one plot. Both species are known ornamentals that may have escaped cultivation or may have been established anthropogenically.

Table 3.1. Dominant Species Basal Area Totals (m^2/ha)

	Total BA (3,157.8)	% of Total
Loblolly pine	1,089.3	35.4
Sweetgum	522.8	16.5
Longleaf pine	398.5	12.6
White Oak	174.5	5.5
Cherrybark Oak	134.2	4.2
Red Maple	127.8	4.0
All Other Species	680.2	21.6

The overstory was dominated by Loblolly Pine and Sweetgum. Together these two species occurred on 47 and 46 plots respectively (approx. 62% of plots). Longleaf Pine (59,744 cm^2) and White Oak (25,917 cm^2) also had majorities of the total BA of the overstory even though they only occurred on just 22 and 17 plots each. The large BAs recorded for White Oak and Longleaf were often due to single, large trees in the overstory. Species that were present in the overstory on only one plot included Eastern Red Cedar (*Juniperus virginiana*), Black Cherry (*Prunus serotina*), Laurel Oak (*Quercus*

laurifolia) and Sourwood (*Oxydendrum arboreum*). These species were also represented in the understory.

Composition in the sapling and seedling layers were relatively similar. Loblolly Pine and Sweetgum again dominate both BA measurements and seedling counts across the forest. Two species that were prominent as seedlings but largely absent as sapling were Pawpaw (*Asimina triloba)* in floodplain plots and Sparkleberry (*Vaccinium arboreum*) in upland plots.

3.3 Ordination Results

The ordination of overstory individuals produced a solution with 3 axes that accounted for 82.7% of the variation in the original species matrix (Axis 1 = 30.6%; Axis 2 = 19.8%; Axis 3 = 32.3%) and had a stress value of 15.9, which indicates a reasonable capture of variation between plots.

Figure 3.1, Overstory data NMS run scatterplot (Axis 1 and 3) with soil series as the grouping variable. Floodplain associated soils are shown in green while non-floodplain soils are in red. Correlations also plotted. NMS rotated by elevation variable. Plus marks (+) indicate species distribution.

Low Axis 1 and 3 values were associated with floodplain plots, greater concentration of nutrients, and were closer to streams, while high Axis 3 values were higher elevation plots and greater slope (Fig. 3.1). Species more commonly associated with floodplains (American Elm (*Ulmus americana*), Ironwood (*Carpinus caroliniana*), Sweetgum, Water Oak (*Quercus nigra*) and Swamp Chestnut Oak (*Quercus michauxii*)) were represented at lower Axis 3 values while upland species had higher Axis 1 values (Fig. 3.1) which had a positive correlation with elevation.

Table 3.2. Pearson's *r* values between environmental variables and NMS Axis values summarizing overstory composition. Nutrients measured in lb/acre. Correlations > 0.25 are highlighted in bold.

Variable	Axis 1	Axis 2	Axis 3
Angle(degrees)	0.147	-0.35	-0.092
Orient	0.068	-0.147	-0.03
pH	-0.256	0.046	**0.277**
CEC(meg/100g)	-0.164	**0.266**	0.171
Acidity	0.107	0.219	**-0.343**
Total %	-0.133	0.025	**0.381**
Dist_Stm (m)	0.224	0.073	-0.38
Dist_Rd (m)	-0.166	-0.122	0.159
Elev (m asl)	**0.332**	0.005	**-0.525**
Rad	-0.011	0.129	0.084
Canopy (m)	0.078	0.059	-0.045
P	**-0.296**	0.069	0.203
K	-0.075	-0.043	**0.292**
Ca	-0.211	0.2	0.3
Mg	-0.204	0.022	0.411

The understory run produced a 3 axes solution which was able to account for 66.4% of the variation in the species matrix (Axis 1 = 23.1%; Axis 2 = 19.1%; Axis 3 = 24.2%), but with a stress value of 19.6, which indicates caution should be used with further analysis.

NMS Axis 2 values for the sapling layer showed high Pearson's *r* values for individual soil characteristics including pH ($r = 0.405$), CEC ($r = 0.377$), and overall nutrient base saturation ($r = 0.458$), suggesting these variables are important at the sapling stage. The ordination showed no pattern among burned plots and only minor patterns among logging history with logged plots. The ordination also showed a strong gradient between nutrient dense plots and high elevation plots (Fig. 3.2).

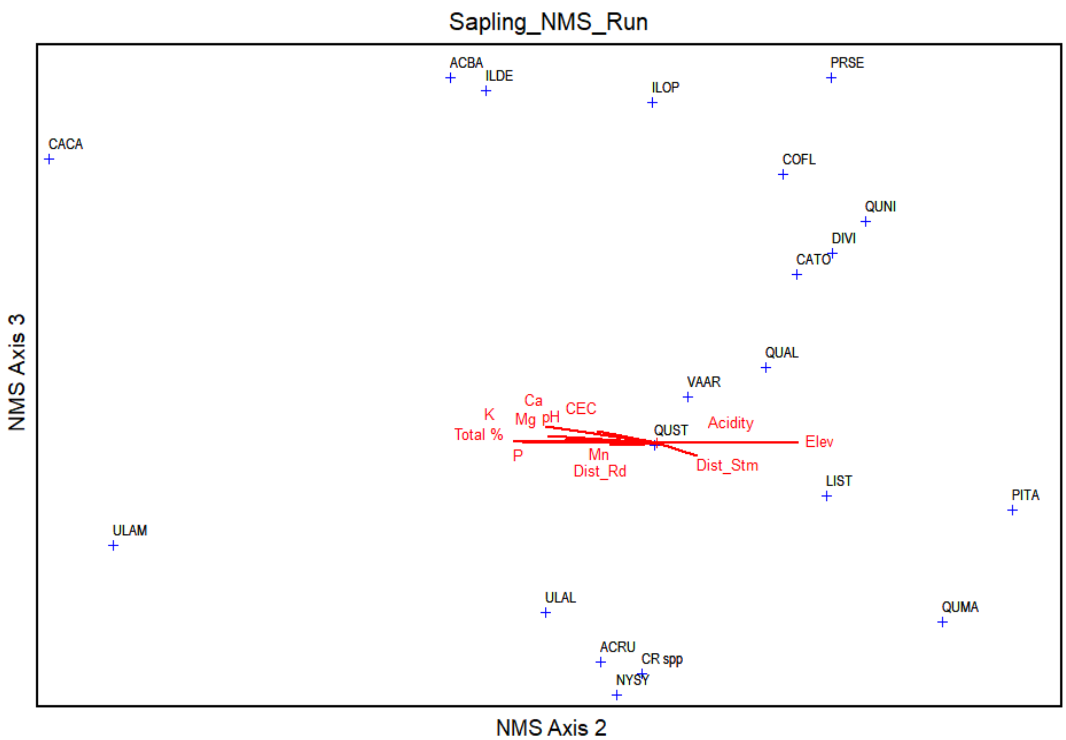

Figure 3.2, Understory data run NMS scatterplot (Axis 2 and 3) with soil series as the grouping variable. Plots removed for clarity. NMS rotated by elevation variable. Plus marks (+) indicate species distribution.

Table 3.3. Pearson's *r* values between environmental variables and NMS Axis values summarizing understory composition. Nutrients measured in lb/acre. Correlations > 0.25 are highlighted in bold.

Variable	Axis 1	Axis 2	Axis 3
Angle (degrees)	0.21	-0.013	-0.094
Orient	**0.285**	-0.126	-0.054
pH	**-0.432**	0.003	0.217
CEC (meg/100g)	-0.37	-0.098	0.109
Acidity	0.202	0.011	-0.173
Total %	**-0.449**	-0.119	0.217
Dist_Stm (m)	**0.268**	0.258	-0.063
Dist_Rd (m)	-0.155	0.026	0.203
Elev (m asl)	**0.467**	0.011	**-0.346**
Rad	-0.087	0.057	-0.04
P	**-0.373**	**-0.282**	**0.334**
K	**-0.469**	-0.148	**0.298**
Ca	**-0.501**	-0.09	0.172
Mg	**-0.339**	-0.152	**0.261**

The ordination of the full dataset produced a solution with 3 axes which accounted for 83.7% of the species variation between plots (Axis 1 = 21.1%; Axis 2 = 32.6%; Axis 3 = 30.0%). The solution had a stress value of 15.6 suggesting a reasonable capture of the variation between plots.

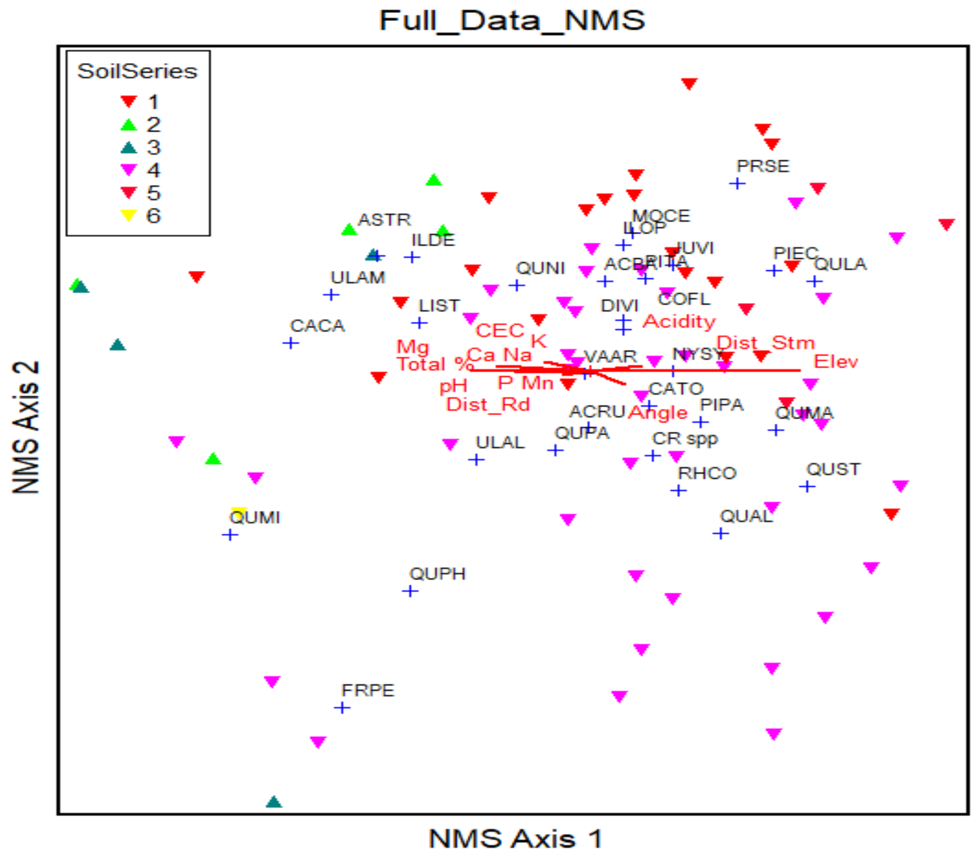

Figure 3.3, Full data run NMS scatterplot (Axis 1 and 2) with soil series as the grouping variable. Floodplain associated soils are shown in green while non-floodplain soils are in red. Correlations also plotted. NMS rotated by elevation variable. Plus marks (+) indicate species distribution.

With increasing Axis 1 values, elevation also increased. Lower Axis 1 values were more likely to be floodplain soils that were closer to streams, less likely to have been logged (Fig. 3.5), and associated with an absence of recent burn history. Species most associated with higher Axis 1 sites were Loblolly Pine, Longleaf, Black Cherry, (White Oak, Blackgum (*Nyssa sylvatica*), American Holly (*Ilex opaca*), and Eastern Red Cedar.

Table 3.4. Pearson's *r* values between environmental variables and NMS Axis values summarizing full data composition. Nutrients measured in lb/acre. Correlations > 0.25 are highlighted in bold.

Variable	Axis 1	Axis 2	Axis 3
Angle (degrees)	**0.267**	-0.192	-0.214
Orient	0.069	-0.016	-0.105
pH	**-0.438**	-0.026	0.013
CEC (meq/100)	**-0.308**	0.163	0.15
Acidity	**0.322**	0.115	0.28
Total %	**-0.416**	0.054	-0.137
Dist_Stm (m)	**0.434**	0.009	0.186
Dist_Rd (m)	-0.233	-0.098	-0.066
Elev (m asl)	**0.653**	0.013	0.175
Rad	-0.082	0.106	0.015
P	**-0.392**	-0.059	0.074
K	**-0.268**	0.017	-0.157
Ca	**-0.436**	0.122	0.065
Mg	**-0.493**	0.05	-0.143

Axis 2 was negatively correlated with slope angle (r = -0.329) but positively correlated with total soil nutrients (r = 0.319). The Axis 1 and 2 results suggest a gradient with more floodplain species (e.g., Ironwood, American Elm and Pawpaw) at higher Axis 2 values and at lower Axis 1 values. These plots also had higher amounts of Ca, Mg and were less acidic.

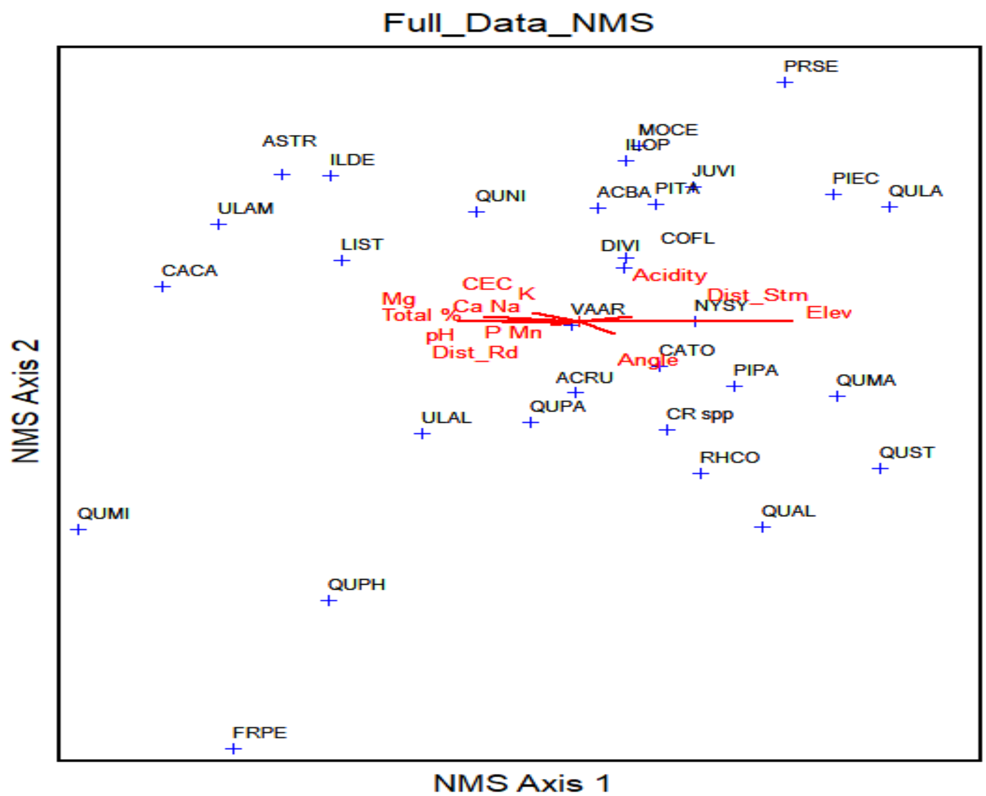

Figure 3.4, Full data run NMS scatterplot (Axis 1 and 2) with plots removed for clarity of species distribution. NMS rotated by elevation variable. Plus marks (+) indicate species distribution.

Plots at the extreme ends of any axis were characterized by having low amounts of seedling cover along the ground and having high BA numbers in the tree layer. Plots that were most easily distinguished in the ordination as floodplain were made up of Ironwood, Winged Elm (*Ulmus alatus*) and Red Maple in the sapling layer, with most of the tree layer dominated by Sweetgum. Floodplain plots were also characterized by thicker overstory with less light penetration and noticeably more herbaceous cover. Meanwhile plots associated with upland sites lacked seedling cover while saplings consisted of Loblolly Pine, Blackgum and Sparkleberry. The tree layer in this space was dominated by White Oak, Longleaf Pine and Loblolly Pine. These plots also had some herbaceous cover with more open canopies.

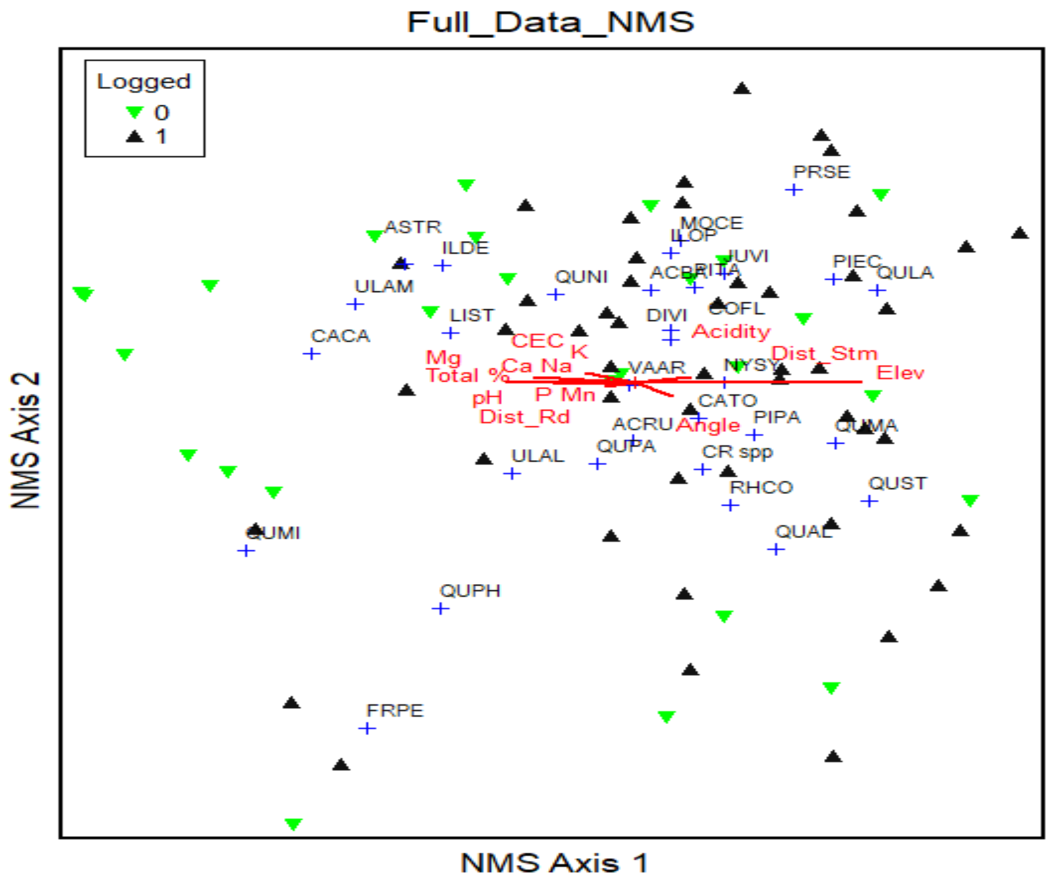

Figure 3.5, Full data run NMS scatterplot (Axis 1 and 2) with logging history as the grouping variable (green = unlogged plot; black = logged plot). Correlations plotted. NMS rotated by elevation variable.

3.4 Patterns and Correlates of Biodiversity

The overstory data produced a GLM for evenness that had significant results (p value < 0.05) when run with just soil series (Table 3.6). Non-significant results in the overstory were expected with burn history and logging because most of the trees are large and mature enough in the overstory to withstand surface fires and have either recovered from or not been influenced by logging operations. Richness in the overstory did not produce a significant GLM.

Table 3.5 Overstory Evenness with Soil Series Variable

Parameter	B	Std Error	Lower	Upper	Wald Chi-Square	df
Intercept	0.878	0.0337	0.812	0.944	677.924	1
Orange	0.091	0.1581	-0.219	0.401	0.334	1
Herndon	0.056	0.0843	-0.109	0.222	0.447	1
Nason	0.003	0.0418	-0.079	0.085	0.006	1
Chewacla	-0.181	0.0843	-0.346	-0.015	4.596	1
Congaree	0.18	0.0769	-0.331	-0.03	5.512	1
Wedowee	0					

In the understory layers, I found burn history and soils interacted differently from the overstory. Logging was found to be insignificant and was removed from the model. Floodplain soils and specifically soil type 5, Herndon series, were found to have lower species richness but had no significance in evenness. Herndon soils are those associated with moderate slopes in upland topography. Burn history lowered species richness significantly ($p < 0.001$) to when run with soil series. Evenness was lower ($p = 0.031$) in burned plots compared to unburned. The GLM for evenness was run with just burn history as soils did not contribute to the model.

Logging did not influence any measures of species richness or evenness which may be due to young age of the trees in this layer and an insufficient amount of data. Species evenness was found to be lower in floodplain soils. Herndon soils which are also upland showed lower evenness. The other upland (Series 1 and 4) soils had higher evenness (Table 3.7).

With burn history of the last decade a lower species richness ($p < 0.001$) and lower species evenness ($p <0.031$) were found on burned plots (Tables 3.7 and 3.8). Burn indicators were to be expected as the intent of prescribed burns are to promote some species while deterring others.

Table 3.6 Understory Richness with Soil Series and Burn History

Parameter	B	Std Error	Lower	Upper	Wald Chi-Square	df
Intercept	4.63	0.3691	3.907	5.354	157.408	1
Orange	1.608	1.7935	-1.907	5.124	0.804	1
Herndon	-1.951	0.9871	-3.886	-0.017	3.908	1
Nason	-0.851	0.4689	-1.77	0.068	3.296	1
Chewacla	-2.821	0.9264	-4.636	-1.005	9.271	1
Congaree	-2.735	0.8586	-4.418	-1.052	10.146	1
Wedowee	0					
Burn	-1.239	0.5068	-2.232	-0.246	5.975	1

Table 3.7 Understory Evenness with Burn History

Parameter	B	Std Error	Lower	Upper	Wald Chi-Square	df
Intercept	0.782	0.0483	0.687	0.876	261.702	1
Burn	-0.0215	0.098	-0.407	-0.23	4.827	1

3.5 MRPP Results

MRPP values were calculated using Sorensen distance for recent burn history, logging history, and soil series. For the overstory, the MRPP indicated that species composition differed as a function of soil history ($T = -8.77$; $p < 0.0000001$), burn history ($T = -3.63$; $p = 0.005$) and logging history ($T = -2.66$; $p = 0.02$).

The understory MRPP values indicated that species composition differed through soil series (T = -8.32; p = 0.00) and logging history (T = -2.36; p = 0.02). MRPP values were insignificant for burn history (T = -1.62; p = 0.07). These results reflect what was shown in ordination (Fig. 3.2; Table 3.3).

MRPP for the Full dataset indicated that species composition differed as a function of soil series (T = -10.048; p = 0.0000001), burn history (T = -4.336; p = 0.002), and logging history (T = -2.628; p = 0.02). The full dataset numbers were like that of the overstory MRPP.

The differences between plots in soil classes in all strata of the forest was therefore higher than expected by chance. Pairwise comparisons between groups showed the clearest distinction between upland soil types and lower elevation floodplain soil types. One soil class, (Orange), was excluded as it was only represented on one plot.

The ISA for burned and for logged plots in the overstory showed patterns that align with the ordination results (Fig. 3.1; Table 3.2). Longleaf Pine was found to be the most characteristic species of burned sites for the overstory while Ironwood, Sweetgum and American Elm, all of which are floodplain associated species, were indicators of unlogged plots (Table 3.6).

Ironwood, Sweetgum and American Elm were found to be most associated with soil layers 2 (Congaree) and 3 (Chewacla), which are the representative floodplain soils of HSF. American Holly was found to be an indicator for soil type 1 (Nason) and Blackgum for soil type 5 (Herndon). The association of Blackgum with soil type 5, which is associated with the sides of sloped uplands, tends to fit its ecological habitat.

Table 3.8. ISA results for the Overstory for Burn, Logging and Soil Type

	Species	IV
Burned	*Pinus palustris*	47
Unlogged	*Carpinus caroliniana*	16.6
	Liquidambar styraciflua	49.8
	Ulmus americana	23.1
Nason	*Ilex opaca*	42.9
Congaree	*Liquidambar styraciflua*	46
Chewacla	*Carpinus caroliniana*	36.8
	Ulmus americana	31.2
Herndon	*Nyssa sylvatica*	39.2

Table 3.9, ISA for the understory for burn, logging and soil type

	Species	IV
Unburned	*Acer rubrum*	47.7
Logged	*Carya tomentosa*	23.7
	Liquidambar styraciflua	41.6
Unlogged	*Carpinus caroliniana*	20.8
	Ulmus americana	23.2
Nason	*Benthamidia florida*	48.8
	Ilex opaca	59.5
Congaree	*Ulmus americana*	55.5
Chewacla	*Carpinus caroliniana*	52.2

The understory ISA also assigned high values species that indicated floodplains along with unlogged plots. Ironwood and American Elm were indicators of floodplain soils and unlogged plots. American Holly and Dogwood (*Benthamidia florida)* were associated with the upland soil series 1 (Wedowee).

For burn history in the understory, Red Maple was assigned a high value as an indicator of an unburned plot. Red Maple has seen an expansion of its range across the Eastern United States (Abrams, 1998). Red Maple is ecologically known to be fire intolerant and fire suppression may have led to its expansion.

CHAPTER 4

DISCUSSION AND CONCLUSIONS

4.1 Ecosystem Patterns in Harbison State Forest

Forest succession at Harbison State Forest is controlled by the influence of multiple environmental variables. Soil conditions, which themselves are reflections of topographic setting and riparian inputs, had the greatest influence, while the history of logging and prescribed burns did have significant influence in measures of richness and evenness. Soil class, which is a general proxy for soil nutrient composition and structure, shows plainly as the most important driver of species distribution in the full forest data.

Woody vegetation analysis indicates that natural mechanisms are mostly responsible for controlling forest succession in HSF. HSF exists in a complex matrix of development and has been managed through anthropogenic means. Despite these influences it has remained in its current composition through relatively natural succession. Anthropogenic disturbances do have small scale effects, but if the current level of disturbance is maintained, the forest may see similar patterns in the years to come. The similarity between overstory composition and understory composition indicates that succession is occurring similarly to succession when it was acquired by the SCFC. HSF as a whole represents natural succession of a forest occurring in the suburban landscape.

4.2 Gradients of Species Interpreted Through Data Analysis

Accessibility can explain some of the gradients observed in differences in the overstory between plots that had been logged and those that had not. The floodplains are in an area that is more difficult to reach for logging operations. Floodplains also are characterized by inundated soils that are more difficult for logging equipment to traverse without getting stuck, and floodplains, in HSF, are typically located at the bottom of some of the steepest slopes found in the forest.

In the understory, most of the trees that are currently in the sapling size class (2.5< DBH < 10.0) were possibly old enough and therefore large enough to withstand recent (<10 years ago) fires that are managed to be less intense. More intense fires would be needed to clear out saplings of this maturity. Conversely saplings may be too young to have been affected by historical logging in many areas that were surveyed.

Data for prescribed burns have only been recorded from roughly the previous decade. Longleaf Pine being an indicator of burns can be partially attributed to management choices in preferentially burning places that already had Longleaf Pine to begin with rather than being a direct correlation between the two. A lack of burn history for floodplain plots can also be attributed to the fact that floodplains do not serve a habitat role for Longleaf.

Overstory evenness and understory richness decreased in floodplain soils. Lower values for diversity measures could be a result of large overstory trees in nutrient dense soils. A size disparity of dominating trees affects the species composition in the overstory while shading out the understory layer below.

In the understory, burn history was found to be significant to both species' richness and evenness. Burns predominantly take place in areas where pyrophilic pines already exist. Richness decreased in tandem with evenness which is affected by the existence of multiple Pine species. This pattern can most readily be seen in the quickly responding understory (Table 3.10).

4.3 Data and Method Constraints

HSF is a small forest and as such it did not take many plots to cover the entire footprint. We also lost 12 plots due to closure from active logging operations. Randomly assigned plot coordinates made for a completely unbiased layout of points across the forest. We were able to visit many different types of stands and secluded areas in the forest. There was soil and therefore habitat variety within the only 74 plots that served as our main source of data. Selecting one point within each 300 by 300-meter grid square offered a reasonable amount of separation but smaller grid cells (and more plots) could have been used to possibly create larger amounts of variety including more floodplain plots.

A large constraint was a timeline in the data. Burn history only covered roughly the last decade. Air photos and field observations of stumps create a comprehensive understanding of what areas have been logged but "time since" was not perfectly captured in many cases. Older air photos were also difficult to interpret for canopy cover.

LiDAR data for HSF's County (Richland) is complete and dense. It offers a unique and useful way to analyze the canopy structure however with our use of ordination as analysis method it did not provide much difference or influence on the data. Canopy height was used only for the overstory data as it would only apply to that layer but there was no evidence of a canopy influence in the ordination runs.

Throughout the ordination process another theme is clear: the overall data had similar results to the data that contained only the overstory BA. This factor is one of dominance in the data. Trees are larger and have larger BA values. Taking sapling and seedling numbers away from the data should not result in large changes in pattern and did not in this study.

4.4 Future Directions and Conclusion

This study focused on woody vegetation response to various drivers in the environment and of anthropogenic origin. The herbaceous layer may respond to changes in the environment at a finer scale than woody vegetation and may prove to be more indicative of change given the short lens of burn history and the unknowns with logging timeframes.

The oldest trees in HSF were probably already there and situated when the Forest Commission purchased the forest in 1951. The patterns of speciation, at least, had already been set and have been that way with some continuity over the last ~70 years. A burn history of <10 years and a discontinuous logging history may not be well captured in the overstory layer. As has been stated, the overstory makes up most of the BA data collected and may prevent some influences from being seen.

The sapling and seedling data that make up the understory layers could be giving a better picture for the next 50 years of HSF succession. However, the next layer down may have the answers to what patterns will be emerging with a changing climate for the next century of HSF succession. That work will require a floristic inventory looking at the herbaceous layer of HSF using a method aside from DBH measurements.

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APPENDIX A: SPECIES DATA AND ADDITIONAL METADATA

Table A.1. Species List and Total Basal Area (m^2/ha) and Individual Seedling Count

	Overstory	Understory	Seedling Count
ACBA- *Acer barbatum*	17.80	1.76	**3**
ACNE- *Acer negundo*	14.44	0.29	0
ACRU- *Acer rubrum*	103.64	24.24	15
AMCA- *Amelanchier canadensis*	0.00	0.14	0
ASTR- *Asimina triloba*	0.00	0.69	181
CACA- *Carolina carpinus*	19.20	5.08	1
CAAM- *Calicarpa americana*	0.00	0.00	14
CATO- *Carya tomentosa*	41.86	2.50	15
CECA- *Cercis canadensis*	0.00	0.55	0
COFL- *Benthamidia florida*	27.52	12.62	4
CR spp- *Crataegus*	0.00	3.78	8
DIVI- *Diospyros virginiana*	2.57	2.07	27
ELUM- *Eleagnus umbellatum*	0.00	0.00	3
FRPE- *Fraxinus pennsylvanica*	71.69	0.00	0
ILOP- *Ilex opaca*	39.49	8.07	35
ILDE- *Ilex decidua*	0.00	0.27	4
JUVI- *Juniper virginiana*	3.89	0.22	7
LIJA- *Ligustrum japonica*	5.30	0.00	0
LIST- *Liquidambar styraciflua*	495.72	26.93	243
MOCE- *Morella cerifera*	0.00	0.00	36
MORU- *Morus rubra*	4.87	0.00	0
NYSY- *Nyssa sylvatica*	27.41	6.14	2
OSVI- *Ostrya virginiana*	0.89	0.00	0
OXAR- *Oxydendrum arboreum*	0.22	0.14	0
PIEC- *Pinus echinata*	18.63	0.00	0
PIPA- *Pinus palustris*	398.50	0.00	0
PITA- *Pinus taeda*	1066.36	23.00	64
PLOC- *Platanus occidentalis*	0.00	0.21	0
PRSE- *Prunus serotina*	1.99	0.93	1
QUAL- *Quercus alba*	172.87	1.76	3
QULA- *Quercus laurifolia*	1.39	0.87	0

QUMA- *Quercus macrocarpa*	34.54	3.31	8
QUMI- *Quercus michauxii*	27.07	0.00	0
QUNI- *Quercus nigra*	72.73	2.12	1
QUPA- *Quercus pagoda*	134.16	0.19	0
QUPH- *Quercus phellos*	55.69	0.19	0
QURU- *Quercus rubra*	0.00	0.38	0
QUST- *Quercus stellata*	45.94	2.18	3
RHCO- *Rhus copallinum*	0.00	0.09	15
ULAL- *Ulmus alata*	32.90	13.00	20
ULAM- *Ulmus americana*	26.21	4.13	1
VAAR- *Vaccinium arboreum*	8.11	5.98	152
VIRU- *Viburnum rufidulum*	0.00	0.14	0

Table A.2. Soil and Environmental Variable Breakdowns

	Low	Mean	High
pH	4	4.9	6
CEC(meg/100g)	3.1	9.35	17.2
Acidity(meg/100g)	2.4	4.8	9.2
Ca lbs/acre	112	1300.7	4243
Mg lbs/acre	41	262.6	611
K lbs/acre	23	103.1	185
P lbs/acre	4	10.5	23
Total % Base Saturation	12	45	77
Angle(degrees)	0.4	4.7	16
Orientation	n/a	156	n/a
Distance to Stream (meters)	2.9	184	526
Distance to Road (meters)	1	68	236
Elevation (meters asl)	49.3	72	98
Radiation	0.69	0.84	0.92
Canopy Height (meters)	11	24	36

Table A.3. Average Richness (number of species) and Evenness across HSF by strata:

	Tree	Sapling	Overall
Richness	3.7	3.8	7.2
Evenness	0.86	0.82	0.73

LiDAR METADATA:

LiDAR data from the 2019 SC Savannah Pee Dee project comes from the USGS 3DEP LiDAR Explorer app and a specific project flown in leaf off conditions between January 5, 2020, and January 29, 2020. Horizonal datum was NAD83 (2011) State Plane South Carolina (FIPS 3900) in feet (EPSG 6570). The vertical datum was NAVD88, GEOID18 in US survey feet. The collection covering the study area totaled around 5,775 sq miles and was QL2. Resolution was 2 points per meter with 0.71-meter nominal point spacing.

The operating altitude was 3,500m with a maximum rate of 2,000 kHz and a scan angle from 20-40 degrees. Scan width comprised of 70% of the flight altitude with 250 scan lines per second. Up to 15 returns were recorded per pulse. A Leica Flightpro ALS70 was used with a beam divergence of 0.25 mrad, and the unit measured 37cm x 68cm x. 26cm and weighted 47kg. A second sensor, the Optech Galaxy Prime was also used. It operated with a class 4 laser as well with similar divergence and up to 8 returns. Its scan angle was 10-60 degrees and measured 34cm x 34 cm x 25 cm with 27 kg in weight.