

MATURE HARDWOOD FORESTS OF THE CENTRAL PIEDMONT OF NORTH
CAROLINA: LANDSCAPE DISTRIBUTION AND UNDERSTORY CHANGE

By

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ABSTRACT

KRISTIN TAVERNA: Mature Hardwood Forests of the Central Piedmont
of North Carolina: Landscape distribution and Understory Change.
(Under the direction of P.S. White and R.K. Peet)

The natural landscape of the Piedmont region of North Carolina has a complex history of human impact. Past agricultural disturbance, combined with recent development, has greatly reduced the extent of the once dominant oak-hickory (*Quercus-Carya*) hardwood forests. More localized disturbances continue to impact stands long considered the stable endpoint of succession. In order to further understand the distribution and dynamics of remnant hardwood forests, I used a multi-scale approach to examine (1) whether the current landscape distribution of hardwood stands is a biased subset of their original extent that can be predicted using hypothesized drivers of past agricultural use and (2) whether understory composition in mature, unfragmented hardwood stands exhibit stability over time. Results show that the current distribution of hardwood is non-random and stands are strongly predicted by the interaction of soil quality, soil moisture, distance to streams, and slope angle. Hardwood is largely confined to river valleys and upland areas with steep topography or relatively poor soil quality. At the stand-level, hardwood forests are undergoing significant decline of herbaceous species, combined with dramatic increases in understory woody species abundance. Compositional change is occurring largely independent of environmental conditions, showing that the steady state notion for hardwood forests is fundamentally incompatible with human-accelerated environmental change in the Piedmont region.

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CHAPTER 1

INTRODUCTION:

**MATURE HARDWOOD FORESTS OF THE CENTRAL PIEDMONT OF NORTH
CAROLINA: LANDSCAPE DISTRIBUTION AND UNDERSTORY CHANGE**

The natural landscape of the Piedmont region of the Southeastern US has a complex history of human impact, spanning over 10,000 years beginning with Native American use of the land (Delcourt et al. 1993). Intertwined with the historic land-use of the region is the development of the native flora, described in the earliest accounts as principally oak-hickory (*Quercus-Carya*) dominated forests (Ashe 1897, Oosting 1942; 1956, Braun 1950). As the land-use patterns of the region have shifted over time, so has the extent and composition of Piedmont oak-hickory forests.

In the Piedmont of North Carolina, the most extensive alteration of native forestlands occurred with the arrival of Europeans in the 18th century. By 1830, European settlement of the Piedmont was complete and extensive land conversion to agriculture began on a large scale (Trimble 1974). Exploitative land-use often led to severe soil erosion and made it necessary to clear more land for production. This pattern of land-use continued until the 1920's, at which time poor management practices and economic factors forced many agriculturalists to abandon the land and allow it to grow back into forest (Trimble 1974, Peet & Christensen 1980). The sites that were converted to farmland in the 19th century lost their hardwood canopy and are now largely dominated by successional pine species, such as loblolly pine (*Pinus taeda*) and shortleaf pine (*Pinus echinata*), with shade-tolerant hardwood species in the understory.

The large-scale loss of native hardwood stands and re-growth of pine significantly changed the vegetation pattern in the region (Christensen 1989). The once dominant hardwood forests are now remnant patches scattered among a mosaic of different land-uses.

Although they cover a fraction of their original area, these remnant patches are unique in that the forest canopy has remained in hardwood over time, giving them the important attribute of continuity (White 2001). This habitat-type has persisted in the midst of other forms of disturbance, such as selective extraction of timber, understory grazing by domestic livestock, low-intensity ground fires, and hurricane related wind-throw. Previous research has shown that given the long-lasting impacts of historical land-use and the slow migration of certain plant species in the Piedmont (Hans et al. 2001, Matlack 1994, Peterken & Game 1984, Jolls 2003), it behooves us to identify and protect hardwood forest remnants throughout the region.

This thesis is an examination of hardwood forests of the Piedmont of North Carolina at both the landscape scale and the scale of forest communities. This multi-scale approach allows for a broader discussion of how historic land-use and modern management practices continue to shape native hardwood forests today. In the remainder of this Chapter I expand on the discussion of Piedmont hardwood forests and present the general approaches and questions addressed in subsequent chapters.

The study of Piedmont hardwood forests in North Carolina has a long history in ecology, beginning in the 1930s with the establishment of Duke University Forest and the pioneering work on secondary forest succession by Oosting (1942) and his student Catherine Keever (1950). Using a chronosequence approach, Oosting (1942) documented the variation in forest communities following agricultural disturbance to predict that pine forests would eventually yield to hardwood dominated communities in the Piedmont. Oak-hickory forests were considered the predictable end-point of succession to which post-agricultural forests

would, if given enough time (~ 80-100 years), eventually succeed. These hardwood forest communities varied across the landscape as species composition and structure shifted with local moisture and edaphic gradients from mesic, bottomland sites to xeric, exposed ridgetops (Bordeau 1954, Skeen et al. 1993). Additional work by Peet & Christensen (1980, 1981, 1984) provided further support for this model of successional change, as well as a more detailed examination and description of the variation of hardwood forest composition with environmental conditions.

Common throughout the discussions of Piedmont hardwood forests was the recognition that there are relatively few extant mature hardwood stands in the region owing to the early land-use history. In his analysis of Piedmont plant communities, Oosting (1942) noted:

‘Occasional hardwood stands are found which include trees 200-300 years of age and which show little evidence of recent disturbance...but, almost invariably, they occupy sites which for some reason could not be cultivated to the best advantage’.

Oosting, and other authors since then (Coile 1948, Trimble 1974, Healy 1985, Peet & Christensen 1980, Skeen et al. 1993), invoked a number of environmental variables as predictors of whether a site was cleared for agriculture. Examples include; soil quality (nutrient level and texture), soil moisture, topographic position, and local slope angle. The emphasis on certain environmental variables suggests that the hardwood stands remaining on the landscape largely represent a biased subset of the original distribution of oak-hickory forests. The above environmental predictors of land-use change have also been used in the context of agricultural abandonment (Trimble 1974, Healy 1985) with the idea that the least productive areas would have been abandoned first and left to grow into pine, and only the highest-quality agricultural fields would have remained in production over time.

Although studies have highlighted certain environmental variables as important in influencing land-use change and vegetation pattern, the efficacy of these variables for prediction of the resultant modern, spatially discrete, landscape-scale vegetation patterns of the Piedmont has largely remained untested. Knowledge of the current pattern of hardwood forests and associated environmental variables has important implications for regional conservation and future restoration, particularly since species composition is tightly linked to environmental conditions (Peet & Christensen 1980). In Chapter 2, I address this issue using a modeling approach within a Geographic Information System (GIS) for Orange, Durham, and Wake Counties, North Carolina. I begin with the aforementioned theoretical model of landscape change and from that establish specific hypotheses for the landscape environmental variables that should best predict hardwood presence and pine presence. Specifically, I first hypothesize that hardwood stands will largely be located in sites difficult to plow. This includes sites located in wet or seasonally flooded areas near streams, areas with high soil plasticity, areas with a steep slope angle, and areas with a high relative slope position (on hill and ridge tops). Second, with the onset of agricultural abandonment, only the highest-quality agricultural fields would have remained in production over time. The less productive or less easily cultivated areas would have been abandoned first and left to grow back into successional pine stands. I expect to find pine stands in areas further from streams, with an above average slope angle and/or higher soil plasticity.

Classification trees were used to model and test my hypotheses with the following environmental predictor variables: soil plasticity (surrogate for percent 2:1 lattice clay in soil B horizon), distance of stand to stream, relative slope position, slope angle and topographic convergence index (surrogate for soil moisture). In addition, model performance was

compared to a common linear modeling approach to examine possible advantages of using a non-parametric technique, such as classification trees, for ecological data as they can accommodate non-linear relationships and allow for multiple environmental settings for each vegetation type.

Following the landscape-level analysis, I proceed in Chapter 3 to examine long-term change in remnant hardwood stands on the scale of forest communities (a description of the questions addressed in Chapter 3 will follow the discussion below). Previous research has highlighted the importance of understanding the local composition and dynamics of remnant forest stands as they often contain unique species assemblages and different soil composition than forests that were once agricultural fields or pasture (Honnay et al. 1999, Bossuyt et al. 1999). These sites are of significant conservation value for the protection of native flora and fauna and for regional restoration activities, and thus it is important to understand their long-term dynamics and possible shifts in species composition over time.

Ecological theory and observation suggest that following disturbance species composition changes over time toward a dynamic equilibrium wherein compositional fluctuations are largely based on internal dynamics (Peet 1992, Pickett & White 1985). At scales larger than a single tree, local fluctuations in a mature forest should average out, producing a relatively stable composition, with compositional variation reflecting primarily variation in local environment (e.g. Christensen & Peet 1984). In the Piedmont of North Carolina, oak-hickory forests have long been described as the expected late- successional community, owing to observations of extant hardwood forests (Ashe 1897, Oosting 1942) and historical records (Davis 1996). Results from recent observational studies of mature oak-hickory forests, however, do not provide support for this expectation of stability due to

widespread absence of oak regeneration and increases in mesic shade-tolerant species, such as red maple (*Acer rubrum*) and sugar maple (*Acer barbatum*) (Christensen 1977, Peet & Loucks 1977, Lorimer 1984, Abrams 1998, McDonald 2002). Indeed, regional authors have suggested that oak should not be considered a typical dominant in late successional forests, and its stability is probably limited to sites of extreme edaphic or climatic conditions (Abrams 1992).

The dominant hypothesis for the persistence of oak-hickory forest canopies is the historic occurrence of periodic low-intensity surface fires throughout the region (Lorimer 1985, Abrams 1992, White & White 1996). Hardwood forests were periodically burned by aboriginal populations and subsequently by early settlers to suppress woody growth and encourage an herbaceous understory for browse species (Healy 1985, Frost 1998). Fire would have favored oak regeneration over more mesic species because of physiological adaptations such as thick bark, ability to sprout back after fire, and drought tolerance (Lorimer 1985, Abrams 1992). The frequent use of fire in Piedmont forests declined by the early 1900s, and the practice had nearly ceased by 1940 with the modern era of fire suppression (Hatley 1977, White & White 1996, Frost 1998). Understory grazing by domestic livestock could have also served to mimic some effects of low-intensity ground fires by suppressing growth of woody species, but this practice also largely ceased over much of the Piedmont by the mid-1900s (White & White 1996, McDonald et al. 2002).

The elimination of processes that once supported oak regeneration and the increase in additional factors linked to oak decline, such as disease (e.g. Bruhn et al. 2000) and seed predation (Marquis et al. 1976, Strole & Anderson 1992), is thought to have led to the widespread declines of oak populations throughout Eastern forests. Given the changing

composition of hardwood canopy species, we might similarly expect shifts in forest understory species, such as herbs, shrubs, and tree seedlings. The near simultaneous loss of low-intensity fires and domestic grazing might well have led to gradual increases in the density of shrub and tree species in the understory of hardwood forests. Additional causes of understory change could include dramatic increases in white-tailed deer (*Odocoileus virginianus*) populations, exotic species invasions, and progressive fragmentation. Many authors have highlighted the importance of studying the spatial and temporal dynamics of understory flora, stressing the importance of the understory in maintaining the functional integrity of forest ecosystems (see Gilliam & Roberts 2003). From a conservation perspective, understory herbs tend to have a higher risk of extinction than woody plants in forests with human induced disturbance and decreasing patch size (see Jolls 2003).

Remarkably, there has been very little documentation of long-term compositional change in the understory of temperate deciduous forests in Eastern North America. In the few cases where historic data do exist, authors have shown a general pattern of local native herbaceous species decline with accompanying increases in exotic species (Brewer 1980, Davison & Forman 1982, Drayton & Primack 1996, Rooney & Dress 1997, Rooney et al. *in press*). Such local losses in species richness imply possible regional threats to plant diversity, but these studies are often based on species lists from survey data for only one site (see Brewer 1980, Drayton & Primack 1996). Rooney et al. (*in press*) conducted a broader analysis of understory change using data for sixty-two upland forest stands in northern Wisconsin, originally compiled by Curtis (1959). They found significant losses over a 50 year period with native species richness declining an average of 18.5% at the 20m² scale and suggest overabundant deer as a key driver of community change. They also concluded that

most of the changes cannot be related to succession, habitat loss or invasion by exotic species. The analysis improved upon earlier studies of understory change by providing multiple site comparisons, but the resurvey relied on approximations of original plot locations rather than permanently marked and resampled plots (see also Davison & Forman 1982). Studies done without accurate plot replication are limited in their ability to detect regional directional change in understory species composition.

Many authors have stressed the need for long-term permanent plot studies to further our understanding of forest understory communities (Gilliam & Roberts 2003). In Chapter 3, I assess the understory compositional trends in central Piedmont hardwood forests over a 23 year period using data from a recent resurvey of permanent vegetation plots established by Peet & Christensen in 1977-78 in the North Carolina Piedmont. The sites are part of Duke University Forest in Orange and Durham Counties and were originally established to study Piedmont forest succession. The hardwood plots were selected for their mature hardwood canopy and minimal evidence of human disturbance due to logging, fire, or grazing since about 1900 (Peet & Christensen 1980, Christensen & Peet 1984). My main objective is to assess the stability of understory composition in hardwood stands spanning a range of soil types and site conditions for all species $\leq 1\text{m}$ tall at 25m^2 and 1000m^2 . I address this objective by asking three general questions. (1) Is the understory of mature hardwood forest stands in the study area exhibiting compositional change, and if so, is there evidence for consistency in the direction of change across plots? (2) Which species show the greatest rates of gain, loss, and overall variability, and what if any species attributes are typically associated with such trends? (3) Is change in composition or species richness partly correlated with site environmental conditions or with richness of the original vegetation?

Based on the recent evidence presented above, I predicted significant shifts in understory composition over time and expected them to follow two of the aforementioned trajectories: increases in the abundance of shade-tolerant woody seedlings, and declines in abundance and diversity of herbaceous native species. Further, I predicted that rates of change would be highest in more productive stands (higher in soil resources and moisture) because such places (a) have greater resources to support the establishment of new species and (b) higher initial diversity and hence greater potential for loss because of light limitation, deer browsing, and exotic species invasion.

In Chapter 4, I integrate the information from the landscape analysis of hardwood distribution with the results from the community-level analysis of understory change to expand upon broader conservation implications and to assess possible future trajectories of Piedmont hardwood forests in the context of human-accelerated environmental change.

CHAPTER 2

**MODELING LANDSCAPE VEGETATION PATTERN IN RESPONSE TO
HISTORIC LAND-USE: A HYPOTHESIS-DRIVE APPROACH FOR THE NORTH
CAROLINA PIEDMONT**

Introduction

Numerous studies of spatial pattern in vegetation (e.g., Franklin 1995, Guisan & Zimmerman 2000) have shown that for each spatial scale or level of analysis there are many possible explanatory variables. In order to identify the dominant predictors, researchers often use repeated hypothesis testing to eliminate the least significant variables and construct an explanation around the significant predictors. This approach can lead to inappropriate explanatory variables, particularly when linear models are used on ecological data that is strongly non-linear and often contain high-order interactions (Draper 1995).

In this study I approach the modeling of spatial vegetation pattern with specific hypotheses and predictor variables for the Piedmont region of North Carolina. My hypotheses are based on previous work in the region that describes how current vegetation pattern must be considered in the context of environmental conditions and the long history of anthropogenic disturbance (Oosting 1942, Trimble 1974, Christensen & Peet 1981, Healy 1985). The dominant vegetation pattern today is mainly the result of large-scale clearing of hardwood forests for agriculture in the 18th and 19th centuries and subsequent land abandonment and forest regeneration in the late 19th – early 20th century. Most forest stands not cleared for agriculture have retained their hardwood canopy, and most post-agriculture sites are dominated by successional pine forests (Christensen & Peet 1981). Specific predictor variables of land clearing included: soil quality, soil moisture, topographic position, and slope angle (Oosting 1942, Coile 1948, Trimble 1974, Healy 1985). Although studies have highlighted these environmental variables as important in influencing land-use change

and vegetation pattern, the efficacy of these variables for prediction of the resultant modern, spatially discrete, landscape-scale vegetation patterns of the Piedmont has largely remained untested.

I developed two scenarios of the impact of land-use on the resultant contemporary vegetation pattern and formulated testable predictions derived from each. First, during the period of extensive clearance for agriculture, hardwood stands persisted in areas difficult to plow. I expect that hardwood stands will predominantly be located in wet or seasonally flooded areas near streams, areas with high soil plasticity, areas with a steep slope angle, and areas with a high relative slope position (on hill and ridge tops). Second, with the onset of agricultural abandonment, only the highest-quality agricultural fields would have remained in production over time. The less productive or less easily cultivated areas would have been abandoned first and left to grow back into successional pine stands. I expect to find pine stands in areas further from streams, with an above average slope angle and/or higher soil plasticity.

A thorough test of my predictions can not be done using traditional linear classification models since they do not account for the multiple environmental conditions under which both relict hardwood stands (sites not cleared for agriculture) and pine stands could occur given the predictor variables. Instead, I use statistical methods that model multiple topographic and edaphic pathways for a particular vegetation type (Moore et al. 1991, De'Ath & Fabricius 2000, Vayssières et al. 2000). First, I use classification trees (CART) to assess my two hypothesized transitions of landscape change for the North Carolina Piedmont (Oosting 1942, Trimble 1974). Second, a generalized linear model (GLM), a common parametric model employed by ecologists (e.g., Brown 1994), is built for

comparison with the CART model to assess the accuracy of each method in predicting vegetation.

Study Area

The study was conducted using remotely sensed and GIS-derived data for Orange, Durham, and Wake Counties, North Carolina, located in the eastern portion of the North Carolina Piedmont. The region is characterized by a warm temperate climate, with a mean monthly temperature in July of 26.7°C and a mean of 5.3°C in January. The mean annual precipitation is 1168mm with July and August being the wettest months (North Carolina Climate Office 2003). Topography ranges from flatlands of the Durham Triassic Basin to the rolling hills and occasional steep slopes and bluffs in the adjacent uplands of the Carolina Slate Belt and the eastern felsic crystalline system. The elevation within the study area ranges from 75m to 255m.

Soil parent material varies widely across the study area, forming a complex of metamorphic and igneous rocks along with areas of Triassic basin sedimentary mudstones and sandstones. The soils of the region are all highly weathered, yet differences in lithology and topography have created areas with striking soil differences over relatively short horizontal distances (Daniels et al. 1999). Of importance to this study is the observation that slight differences in soil nutrients and slope can change soil permeability and plasticity, creating areas of high shrink-swell clays and poor drainage that are often less suitable for agriculture (Peet & Christensen 1980, Daniels et al. 1999). The large-scale pattern of soil plasticity is associated with soil parent material and the soils of the Triassic basin system tend to be higher in plasticity compared to rest of the study area. Outside of the Triassic

basin, the Carolina slate belt soils typically have a less permeable B horizon than soils of the felsic crystalline system (Daniels et al. 1999). Also present are scattered intrusions of igneous rock resistant to weathering (high quartz content), creating sites with a rocky soil profile. Additional information on the soil systems in the area can be found in Daniels et al. (1999) and Peet & Christensen (1980).

The vegetation of the study area has a long history of anthropogenic disturbance, with extensive vegetation alteration occurring during the period of European colonization (Peet & Christensen 1980, Healy 1985). The oak-hickory (*Quercus-Carya*) hardwood forests that dominated the landscape prior to European arrival (Ashe 1897, Braun 1950) are now largely scattered fragments among different land-uses. The hardwood stands that persisted during the growth of agriculture were not without disturbance and often used for selective extraction of timber products and domestic livestock grazing (Oosting 1942, Peet & Christensen 1980, White & White 1996). By the late 19th -early 20th century, economic factors and poor land management forced abandonment of much farmland in the region (Peet & Christensen 1980). Mature *Pinus taeda* (loblolly pine) forest now dominates in areas that were initially cleared for agriculture and later abandoned. Some of the oldest (>80 year old) pine stands in the region are now transitioning into the later stages of succession as the pine trees die back and understory hardwood species grow into the canopy (Peet 1992, McDonald et al. 2002).

Methods

Data

Land cover data was based on a July 1999 Enhanced Thematic Mapper (ETM) image at 30m spatial resolution. Maunz (2002) previously classified the image in ERDAS IMAGINE using a supervised classification. Pixels with known land-cover types were

selected based on 1997 digital orthophoto quarter quads (DOQQs) and used as training areas for the image classification (Maunz 2002). The image was initially classified into twelve classes for improved accuracy: Deciduous forest, Pine forest, Field (4 classes), Wet field, Suburban, Urban, Asphalt, Water (2 classes). Areas of mixed forest, comprising hardwood and pine, were split between the two forest classes depending on the percentage of each forest class present. Areas with >50% hardwood were grouped in the hardwood class and areas with >50% pine were grouped with pine. The initial twelve classes were collapsed into 6 classes for the purposes of this study: Hardwood, Pine, Field (includes agriculture land and sparse vegetation), Suburban, Urban and Water. The percentage of total land area covered by each land cover class is listed in Table 2.1.

Predictor variables were selected *a priori* based on the land-use history of the region and the hypothesized model of landscape change. The predictors of hardwood and pine forest include the environmental variables; soil plasticity (surrogate for % 2:1 lattice clay in soil), distance of stand to stream, relative slope position, slope angle and topographic convergence index (surrogate for soil moisture) (Table 2.2).

Topographic variables (slope, relative slope position and topographic convergence index) were derived based on a Shuttle Radar Topography Mission (SRTM) digital elevation model at 28 m spatial resolution (Table 2.2). Slope was calculated in degrees using ArcINFO. Relative slope position (RSP) was calculated for each grid cell of the DEM using ArcINFO and classified into one of seven possible classes (Parker 1982). The classes represent percent distance from slope bottom (0%) to nearest ridge (100%). Each class was ranked according to position, ranging from valley bottom (25) to ridge (0). Relative position along a slope affects the general thermal and hydrologic regime of a site (Parker 1982).

Topographic convergence index (TCI) measures the topographic effects on drainage, taking into account upslope contributing area and local slope angle. It is calculated with the formula: $\ln[A/\tan(\beta)]$, where A is upslope contributing area and β is local slope angle (Wolock and McCabe 1995). The index is used as a surrogate for soil moisture potential, with maximum TCI occurring at the wettest sites. TCI was calculated in grid format using ArcINFO with a spatial resolution of 28m to match the DEM layer.

Simple Pearson correlation analysis led me to discard the RSP variable since it was highly correlated with TCI ($r = 0.71$). I chose TCI over RSP since it is a continuous, rather than categorical variable, and therefore provides a more detailed representation of change across the landscape.

The distance-to-stream variable was calculated for perennial streams and lakes based on the USGS National Hydrology Database (NHD) available at the 1:100,000 scale. The distance measure was calculated in meters in grid format (30m resolution) using the Spatial Analyst extension available in ArcGIS version 8.1.

The plasticity index (PI) was calculated for the B-horizon of each soil series in the study region. The plasticity index is the difference between the plastic limit and liquid limit for a soil and indicates the average water-content range over which the soil has plastic properties (Brady & Weil 2002). Soils with a high PI (>25) are generally expansive clays with a high percentage of 2:1 lattice clay, giving it high shrink-swell capacity.

PI was derived using the County digitized soil survey maps (SSURGO data) and associated attribute databases available via the USDA Natural Resources Conservation Service (NASIS 2003). Mapping scales generally range from 1:12,000 to 1:63,360. The PI for each soil series was calculated by the NRCS using the formula: $PI = \text{plastic limit} - \text{liquid}$

limit. The average value of the range for the liquid limit and plastic limit was used for each soil series. Each County soil data layer was converted to raster format with 30m spatial resolution to match the land-cover layer. The PI value was assigned to each raster cell for the soil series.

Spatial sampling

All environmental variables and hardwood or pine presence/absence were sampled within a geographic information system (GIS) to create four data sets from which the vegetation models were generated. The four data sets were based on the following land cover categories:

- (1) All hardwood stands ≥ 15 ha
- (2) All sites, excluding hardwood or water
- (3) All pine stands ≥ 1 ha
- (4) All sites, excluding pine, hardwood and water

Since hardwood is the dominant land cover in the study region (31.4% of total land area), I restricted my sampling to sites ≥ 15 ha to exclude individually scattered hardwood pixels and smaller hardwood patches that have a higher probability of being mixed forest or planted vegetation in urban/suburban areas.

I generated 1000 random sample points throughout each of the four land cover layers. Five hundred random samples were selected from each data set for use as training data sets. The training data sets were merged to create two final datasets for model development. The first dataset was comprised of land cover categories (1) and (2), listed above. This dataset was used to test my first hypothesis of hardwood presence on the landscape via a comparison

with all other land sites, given that the region was dominated by hardwood prior to extensive agriculture (Ashe 1897, Oosting 1942, Christensen and Peet 1981).

The second dataset consisted of land cover categories (3) and (4) and was used to test my second hypothesis of where pine exists relative to all other non-forested sites. It is important to note that ‘non-forested sites’ includes agricultural fields, sparse vegetation and urban sites. A more precise test of my second hypothesis would have been a comparison of pine stands to strictly agricultural sites, but mixed classifications in the 1999 land-cover map prevented me from making such a comparison. For example, agricultural fields and sparse vegetation are highly reflective and some pixels were incorrectly classified as fields along roadways and in urban areas due to their similarity in spectral characteristics with urban sites. The test of the second hypothesis remains valid with the grouping of ‘non-forested sites’ since many urban sites were potentially in agriculture during the period of extensive cultivation. Two validation data sets were constructed to assess the accuracy of the models developed using the training data, with sample size $n=407$ for the hardwood data and $n=300$ for the pine data.

Classification tree model

Classification tree models (CART) are a non-parametric approach to vegetation modeling that does not try to model a general relationship between response and predictor variables (Moore et al. 1991, De’Ath & Fabricius 2000, Vayssières et al. 2000). Rather the trees are developed by recursively partitioning a dataset into subsets that are increasing homogenous in terms of the response variable (Chambers & Hastie 1992, Urban 2002). Each split in the tree is made at a particular value of the explanatory variable and it allows for the

use of continuous and categorical variables. The path to each terminal node (final classification) in a tree defines a set of environmental conditions under which the splitting rules that lead to that node will apply (Chambers & Hastie 1992, Moore et al. 1991). Because of the recursive algorithm, CART models are especially useful for discovering alternative environmental settings that lead to the same response for data structures that make sense ecologically but are difficult to capture with linear models (Urban et al. 2002, Vayssières et al. 2000). In addition, each path can be implemented into a GIS to graphically display the various habitat positions (Urban et al. 2002).

I developed two separate CART models for both the hardwood and pine data sets using the Tree model option of Splus version 6.0. The first CART model incorporated the five environmental variables listed in Table 2.2, and the second included only those variables determined to be significant by the logistic regression model. The second set of CART models were built solely to compare predictive accuracy with the full CART models. All trees were pruned to eliminate superfluous branches and to avoid over-fitting the data (Breiman et al. 1984). Cross-validation and a cost complexity measure were used to determine the optimum tree, deleting those branches that reduced deviation the least (Franklin 1998, Vayssières et al. 2000).

The first set of CART model predictions were mapped in a GIS to provide a spatial representation of the different habitat conditions predicted for hardwood and pine by the CART analysis. The geographic display of the CART models also allowed me to examine the results in relation to my initial hypotheses of landscape change.

Generalized linear model

Generalized linear models (GLM) are frequently used by plant ecologists to model species response to environmental data (Yee & Mitchell 1991, Franklin 1995). Logits are among the models commonly used to model land use change (e.g., Wear and Bolstad 1998, Morisette et al. 1999, Schneider and Pontius 2001). Logistic regression is a particular form of GLM used for binary response variables. The binary response variable is assumed to be independent and to follow a binomial distribution (Bio et al. 1998, Franklin 1995). I created logistic regression models to examine the probability of hardwood or pine occurring under a given set of environmental conditions. A logistic link function (logit) was employed to convert the linear predictor variables to vegetation type probability values (Brown 1994).

Separate logistic models were developed for the hardwood and pine data sets using the GLM option of Splus version 6.0. A GLM was created for all combinations of the five predictor variables summarized in Table 2.2. A χ^2 -test was performed to test if the coefficients of the fitted model were significantly different from zero, thereby showing the importance of each predictor variable in determining hardwood or pine presence. Only significant variables ($p < .05$) were retained for the final model.

The logit response is a continuous probability value (0-1) specifying the likelihood that a given sample point is hardwood or pine vegetation. In order to collapse this probability into a binary prediction a threshold of 0.50 was set for the training data. All locations with probability ≥ 0.50 were classified as hardwood or pine and assigned a value of 1 (for $p < 0.50$, value=0). This threshold value was assumed reasonable for the training data since the prior probabilities of being classified as hardwood/pine or not was the same (0.5) for both classes in each data set, with sample size $n=500$ for each class (Kutner 1996). The

thresholds for the hardwood and pine validation data were determined separately since the prior probability of hardwood/pine occurrence or non-occurrence was 0.53 and 0.46 for hardwood and 0.25 and 0.75 for pine. I used a receiver operating characteristic (ROC) curve to determine the optimal threshold value for the each validation dataset (Fielding & Bell 1997, Vayssières et al. 2000). ROC curves present the predictive accuracy of a logistic model over the full range of possible threshold values (0-1). A threshold value of 0.50 was chosen for hardwood and 0.47 was chosen for pine to maximize the prediction of hardwood/pine occurrence and non-occurrence (Hosmer & Lemeshow 2000).

Model assessment and comparison of methods

A comparison of CART to GLM models is often difficult because the error rates and goodness-of-fit statistics computed by each method do not provide a common independent criterion. Vayssières et al. (2000) stated that the solution is to compare models based on their ability to correctly classify new cases, or predictive accuracy. I compared the predictive accuracy of each model using both the training data set and the validation data set. The confusion matrix for each model provided information on predictive accuracy for the ‘event’ (hardwood or pine) and ‘non-event’ (non-hardwood or non-pine/hardwood) cases. The confusion matrix is the cross-tabulation of data cases in predicted classes by observed classes, set up as a 2x2 matrix for a binary response variable (Hand 1997).

I further utilized the predictive accuracy information to test whether the observed difference in performance for the two models (CART and GLM) was significant. This was done for the validation data sets using the correlated proportions comparison test developed by Linnet & Brandt (1986). It tests the null hypothesis of no difference in performance

between the two models. The predictive accuracy values of the two models are combined into two additional matrices for calculation of the test statistic (e.g., Vayssières et al. 2000). The Linnet & Brandt test was also used to test the observed difference in performance between the two CART models developed for both hardwood and pine data sets.

Results

Classification tree model

The full CART models generated using the training data had the following form (abbreviations are defined in Table 2.2):

$$\text{Hardwood presence} = f(\text{Dist.stream, PI, Slope, TCI}) \quad (1)$$

$$\text{Pine presence} = f(\text{Dist.stream, PI, Slope, TCI}) \quad (2)$$

The hardwood CART correctly classified hardwood occurrence for 69% of the validation data (accuracy value =0.694; Table 2.4). The pine CART correctly classified pine occurrence for 78% of the validation data (accuracy value=0.776; Table 2.4). The CART model diagrams are presented in Figs. 2.1 and 2.2 for hardwood and pine, respectively. The final pruned classification tree for hardwood had 15 terminal nodes, with 9 terminal nodes classified as hardwood. The final pruned tree for pine had 12 terminal nodes, with 6 classified as pine. Recall that each terminal node represents a separate possible path for classification of a pixel. New locations can be classified by following the appropriate path to a node. The tree is read from top-down and the variables are listed in order of how much deviance they explain. For example, distance-to-stream forms the first split in the hardwood classification tree and therefore is the primary determinant in whether a site is hardwood or not (Figure 2.1). The hierarchical relationships formed in a tree may represent specific

interactions that cannot be captured in a GLM, but the repetition of variables can be difficult to evaluate for their ecological rationality.

Figure 2.1 shows that in areas less than 231.4m but greater than 76m from streams, hardwood occurs predominantly on sites with steeper slopes ($\text{slope} > 1.57$). It also occurs on sites with low slope (< 0.003) and high soil moisture ($\text{TCI} > 3.94$) or at a few sites with low slope and average to low soil moisture. Soil plasticity is not a strong predictor for sites less than 231.4m from streams and the opposite is true for sites far from streams (see Figure 2.1). For sites greater than 231.4m from streams, hardwood occurs on sites with low soil plasticity and high slope ($\text{slope} > 1.97$), sites with soil plasticity ranging from 12.25-15.75, and sites with soil plasticity ranging from 22.75-35.0. The sites with moderate soil plasticity (12.25-15.75) largely represent floodplain soils that experience periodic flooding or upland soils found on slopes and ridge tops outside of the Triassic Basin.

In contrast to the hardwood model, soil moisture (TCI) is the dominant predictor of whether pine occurs at a site or not (Figure 2.2). Distance-to-stream is not used as a predictor variable until further down in the tree, and thus it has lower explanatory power. In drier areas with low TCI (< 5.97), pine predominantly occurs on sites with high soil plasticity ($\text{PI} > 24.25$). It also occurs in dry sites with low soil plasticity and moderately steep slopes ($\text{slope} > 1.86$), and dry sites closer to streams ($< 214.2\text{m}$) with low soil plasticity and low slope. In sites further from streams ($> 214.2\text{m}$), pine occurs in sites with average soil moisture. For the slightly wetter sites displayed on the right-hand side of the tree ($\text{TCI} > 5.97$), pine occurs where there is high soil plasticity ($\text{PI} > 24.25$) and low to moderate increase in slope (> 0.14).

The CART model predictions for hardwood and pine were mapped into a GIS and are displayed in Figures 2.3 & 2.4. The translation of each model into geographic space provides a useful visual interpretation of the model predictions. All grid cells that satisfy the model conditions for each branch of the CART are coded a different color to represent the different locations (and potentially different species and/or community types) for which hardwood and pine are predicted to be located. The numbers in the terminal nodes of each classification tree (Figs.2.1 & 2.2) correspond with the vegetation classes mapped in Figs.2.3 & 2.4.

The map of hardwood predictions (Fig.2.3) clearly shows the strong presence of hardwood along river valleys in areas less than 230m from streams. The majority of these stands are located in areas with higher slope (class 1) or low slope less than 75m from streams (class 2). The other dominant hardwood regions (classes 3-5; Fig.2.3) corresponds with areas further from streams with higher plasticity or slope than the surrounding landscape. The CART model successfully predicted the location of 66% of the actual hardwood in the study area.

The CART pine predictions (Fig.2.4) are more dispersed throughout the study area as compared to the discrete zones of predicted hardwood (Fig.2.3). The presence of pine is not as strongly effected by distance to stream, but rather it is associated with areas of higher soil plasticity and varying soil moisture. For example, pine classes 2-4 in Figure 2.4 represent a strong belt of predicted pine starting in central Durham County and heading south. This region largely corresponds with the location of Triassic basin sediment. The Triassic basin has a history of agricultural use (partially due to a local relief less than surrounding area), but it also contains some of highest soil plasticity in the study area. Figure 2.4 also emphasizes the pine predicted to be in drier sites closer to streams (class 5; Fig.2.4), as well as pine sites

located in upland areas (>214m from streams) with slightly below average soil moisture (class 7). The CART model successfully predicted the location of 72% of the actual pine in the study area.

Generalized linear model

The logistic regression (GLM) models developed for hardwood and pine forest for comparison with the CART models are presented below (Equation 3 and 4). Abbreviations for the independent variables are defined in Table 2.2.

$$P(\text{Hardwood}) = \alpha + \beta_1 \text{Dist.stream} + \beta_2 \text{TCI} + \beta_3 \text{Slope}, \quad (3)$$

$$P(\text{Pine}) = \alpha + \beta_1 \text{TCI} + \beta_2 \text{PI} + \beta_3 \text{Dist.stream} \quad (4)$$

The values of the model coefficients are listed in Table 2.3. Although it was hypothesized that all four original variables (Table 2.2) are important predictors for determining hardwood or pine presence, soil plasticity index (PI) was not significant in the hardwood GLM according to the χ^2 -test and slope was not significant in the pine GLM (Table 2.3).

The hardwood GLM correctly classified hardwood occurrence for less than 50% of the validation data (accuracy value = 0.420, Table 2.4) with a threshold value of 0.50. The pine model correctly classified less than 20% of the pine occurrences in the validation data (accuracy value = 0.180, Table 2.4) with an optimum threshold value of 0.47. The pine GLM had considerably higher classification success with the non-pine/hardwood locations (accuracy value = 0.654, Table 2.4).

Model comparison

Model comparisons based on predictive accuracy of ‘event’ cases indicate that the CART models produced the most accurate classification for both the hardwood and pine data (Table 2.4). The predictive ability of a GLM was higher only for the ‘non-event’ cases of the pine data (accuracy value = 0.654 vs. 0.460 for CART). Predictive ability was consistently lower for validation data since it was not used to build the models.

The results of Linnet & Brandt’s test were also included in Table 2.4. Recall that this tests the null hypothesis of no difference in performance between the two models. I tested for differences in predictive ability between GLM and CART on the validation data sets. CART models were significantly better predictors for both hardwood and pine ($p < .001$).

The results of the second set of CART models built for hardwood and pine are also included in Table 2.4 (CART2). These models were built using the significant variables identified in the GLM’s (Table 2.3) to examine whether they improve predictive accuracy. The models were pruned to 20 terminal nodes for hardwood and 14 terminal nodes for pine following the same procedure as the original CART models. Predictive accuracy only slightly increased for the ‘non-event’ cases in each model. The results of Linnet & Brandt’s test were not significant for either hardwood or pine, meaning there was no significant difference in predictive ability between the two CART models.

Discussion

Model predictions

The CART models developed for the hardwood and pine datasets show the relative importance and hierarchical relationships of the environmental predictor variables on

vegetation pattern in the North Carolina Piedmont. Yet the significance of each predictor variable cannot be understood solely based on environmental controls. They are only relevant in the context of historic land-use patterns, showing that the dominant pattern of vegetation across the landscape remains strongly tied to past agricultural use.

Piedmont agriculturalists tended to avoid areas too difficult to farm, thereby allowing some forest stands to remain in hardwood over time (Oosting 1942, Trimble 1974, Peet & Christensen 1980). The current distribution of hardwood is strongly predicted (69% accuracy) by the variables initially hypothesized as being important in determining whether a site is easily cultivated. The primary determinant of hardwood presence/absence in the study area is distance to stream, but additional (interacting) factors are needed to explain hardwood presence near vs. far from streams. Not surprisingly, hardwood stands near streams are predominantly found in areas with higher soil moisture, as these sites would have often flooded and been inhospitable for most agricultural crops. Hardwood stands near streams are also present in areas with steeper slope (Fig.2.1), as these areas would have been more difficult to cultivate than surrounding level topography.

For hardwood sites further from streams, the model did not provide strong support for my initial hypothesis that hardwood would be found on dry ridge-tops. Lack of support could be due to the moderate topography of the study area combined with the resolution of the analysis. The dry ridge-tops known to support remnant hardwood stands (Peet & Christensen 1980) are likely not extensive enough to have been included and sampled in this analysis. Rather the model associated hardwood further from streams with areas of steep slopes or mid to above-average soil plasticity. Soils with a high soil plasticity index generally have poor water drainage and increased shrink-swell capacity, making them

difficult to cultivate under higher moisture regimes and potentially leading to extended anaerobic soil conditions (Brady & Weil 2002). The Carolina Slate Belt system in the northwest portion of the study area contains a higher proportion of plastic soils than the surrounding region (excluding the Triassic basin), as well as areas of sharp topographic variation (Daniels et al. 1999). The moderately high soil plasticity, combined with the irregular topography, likely helped maintain hardwood dominance along the Carolina Slate Belt and the majority of the predicted hardwood sites located >231m from streams are associated with this soil system (Fig.2.3; Class 4-5). Some additional hardwood is predicted to run along the Triassic basin in western Wake County due to higher soil plasticity (Fig.2.3; Class 5), but as I will discuss below, the low slopes and high plasticity of the Triassic basin proved to be more predictive of pine forests.

Pine forest did not become a dominant vegetation type of the North Carolina Piedmont until the decline in agriculture, beginning around the late 19th century (Peet & Christensen 1980, Healy 1985). Early successional pine grew into forest canopy as fields were abandoned throughout the study area. The pine CART model provides some support for my second hypothesis in that the chief determinants of pine presence were soil moisture (low and high) and high soil plasticity, as well as drier sites with above-average slope. It is likely that agriculturalists initially exploited these areas for cultivation, but high soil plasticity or above-average slopes could have rendered them less productive or less easily cultivated, thus leading to early abandonment. Poor management practices in the Piedmont often led to severe soil erosion (Trimble 1974), and in regions such as the Triassic Basin, topsoil erosion would have exposed a plastic B horizon and provided less favorable growing conditions (Daniels et al. 1999). While the data presented in the study do not provide

specific evidence for a causal relationship, the strong belt of predicted pine in the Triassic Basin region, through central Durham and western Wake Counties, provides support for this assertion (Fig.2.4; Class 2-4).

The additional predictions of pine presence in drier sites closer to streams, as well as upland sites with slightly above average soil moisture highlights an important transition in land-use patterns for the study area. The region no longer has a broad agricultural economy, primarily due to increased urban development, and the results reflect that more than just the least productive agricultural sites have been abandoned and grown into successional pine forest. An additional factor that could have led to greater dispersion of pine predictions is the lack of a mixed-forest class in the 1999 land cover map. A mixed-forest class would have further discriminated among hardwood and pine for each model and provided more accurate predictions for each type. Instead sites that could be mixed-forest were grouped as either hardwood or pine in the land-use map (Maunz 2002). The pine models were more likely effected by this grouping since I sampled all stands ≥ 1 ha (vs. hardwood stands ≥ 15 ha), and this would have included more scattered pixels that should be classified as mixed-forest.

Model performance

The CART and GLM model comparisons indicate that on the basis of proportion of accurately classified pixels and the Linnet and Brandt test statistic the CART model produced the most accurate classification (Table 2.4). It is well understood that ecological data often does not conform to a specific functional form, and thus methods such as CART that allow for non-linearity and interactions often improve predictive ability over linear models (Vayssières et al. 2000). This is particularly true in my study where alternative

environmental settings lead to the same response (hardwood or pine presence/absence). In contrast, the logistic GLM models imposed a structure on the response data that could not capture the multiple relationships between predictor variables.

The reduced set of predictor variables (identified by the GLM models) analyzed in the second set of CART models were as effective at predicting hardwood or pine presence in the study area. This result shows that ecologists can benefit from using both methods of analysis when modeling species response to the environment (Vayssières 2000). A GLM model often provides a useful summary of relationships and a measure of variable significance, while CART allows for an easier and more meaningful interpretation of ecological contingencies. Breiman et al. (1984) also suggests that researchers initially use CART with ecological data to identify interaction terms which may then be used in the development of a parametric model, such as a GLM.

Conclusion

This study provides an example of how a hypothesis-driven approach to vegetation modeling can allow researchers to move beyond simple pattern recognition to develop a greater understanding of how historic disturbance and environmental factors affect landscape-level vegetation pattern. This approach is particularly relevant in regions that have a history of anthropogenic disturbance, as vegetation distribution is not solely controlled by relationships along primary environmental gradients. Rather, these patterns are governed by compensatory relationships that yield similar outcomes for various environmental settings or contingencies. Future work will build on the vegetation CART models developed in this study, to describe how recent development has interacted with environmental and anthropogenic variables to create the broader land-use pattern in the region. The

incorporation of social drivers of land-use change will support additional hypotheses and further refine model predictions of vegetation-environment relationships.

Table 2.1. Land cover classes for the study area and the percentage of total area occupied by each class.

Land Cover	% of Total
Hardwood	31.4
Pine	9.3
Field	24.1
Suburban	17.6
Urban	11.2
Water	6.3

Table 2.2. Names and descriptions of environmental variables sampled for analysis. Variables marked with an asterisk were used in the final analysis (the discarded variable was highly correlated with TCI).

Variable	Description	Mean	Std.dev	Min	Max	Variable
Dist.stream*	Distance to nearest stream (m)	328.57	269.17	0	3222.45	Continuous
PI*	Plasticity Index	22.25	13.77	1.17	57.5	Continuous
Slope*	Maximum slope(°)	0.91	0.70	0	41.77	Continuous
RSP	Relative slope position Topographic Convergence	NA	NA	0	25	Categorical [±]
TCI*	Index	5.76	2.29	0.242	22.44	Continuous

[±] Seven slope position categories were calculated for RSP

Table 2.3. GLM coefficients for hardwood and pine models. Coefficients correspond to the variables listed in Equations 3& 4. * variables significant from χ^2 -test at $p < (.05)$. **variables significant from χ^2 -test at $p < (.001)$.

Variables	Hardwood	Pine
Dist.stream	0.0015**	0.0010**
TCI	-0.0169*	0.2550**
Slope	-0.4711**	-0.1415
PI	-0.0001	-0.0202**

Table 2.4. Comparison of predictive accuracy of the generalized linear model (GLM), classification tree model (CART), and classification tree model built using information from the corresponding GLM model (CART2) for each land cover. Accuracy values are reported for the training and validation datasets. Predictive accuracy is the proportion of correctly classified pixels for the entire scene. *L&B test statistic is the statistic for the Linnet and Brandt test (1986) comparing the performance of CART and GLM models.

Land cover	Hardwood			Non-hardwood		
	CART	GLM	CART2	CART	GLM	CART2
Training data	0.748	0.440	0.658	0.672	0.444	0.728
Validation data	<u>0.693</u>	<u>0.420</u>	0.569	0.593	0.365	0.561
L&B test statistic*	7.292					
p-value	<0.001					

Land cover	Pine			Non-pine/hardwood		
	CART	GLM	CART2	CART	GLM	CART2
Training data	0.778	0.360	0.718	0.576	0.397	0.642
Validation data	<u>0.776</u>	<u>0.180</u>	0.632	0.460	0.654	0.513
L&B test statistic*	5.385					
p-value	<0.001					

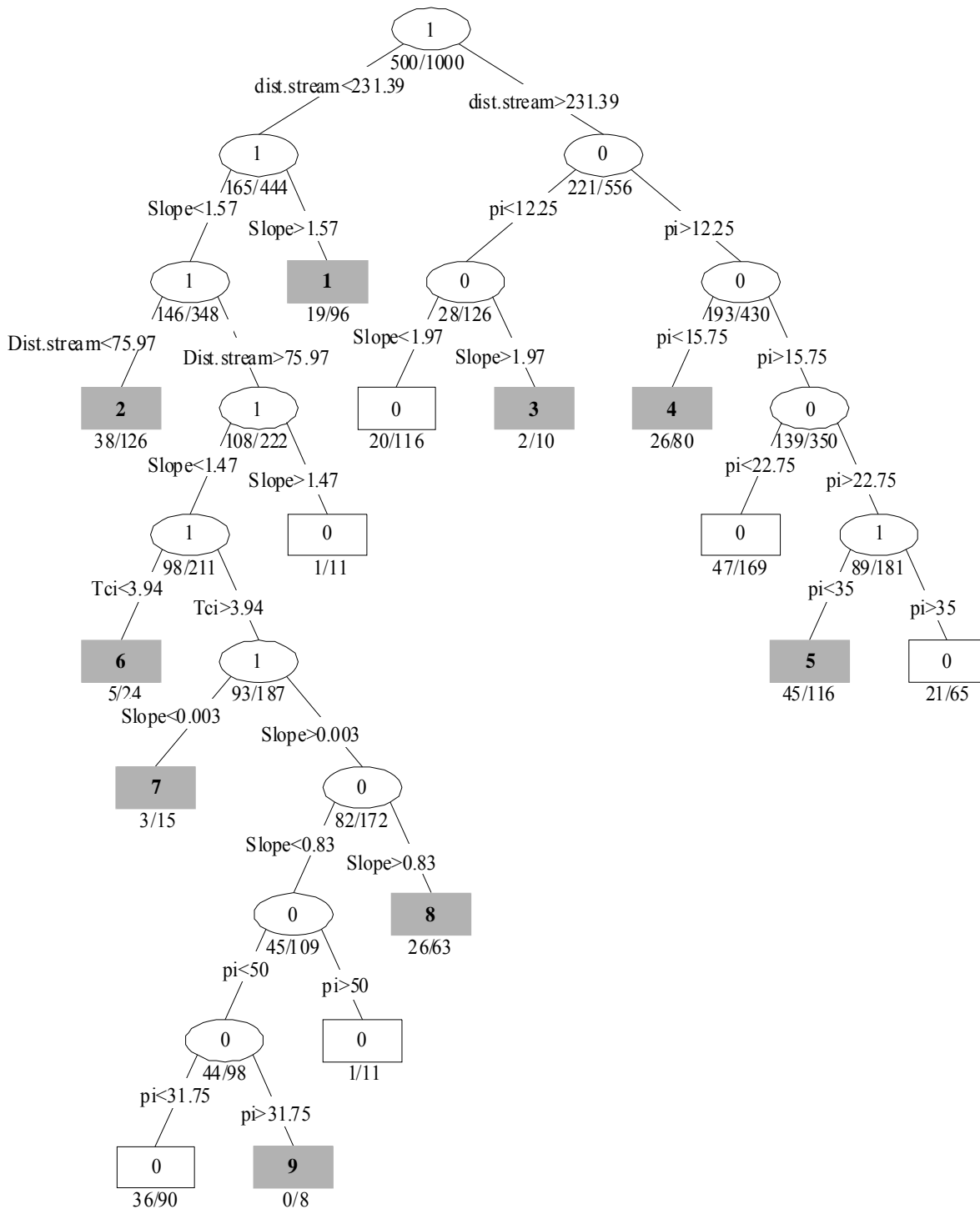


Figure 2.1. CART model for hardwood based on environmental variables (see Equation 3). Abbreviations used for variables are defined in Table 2.2. The circles represent internal nodes and rectangles terminal nodes of the final pruned tree. The terminal nodes with numbers 1-9 are predicted to be hardwood (numbered to represent different hardwood types). Terminal nodes with '0' represent absence of hardwood. Ratio below each node is the proportion of observations misclassified at that node.

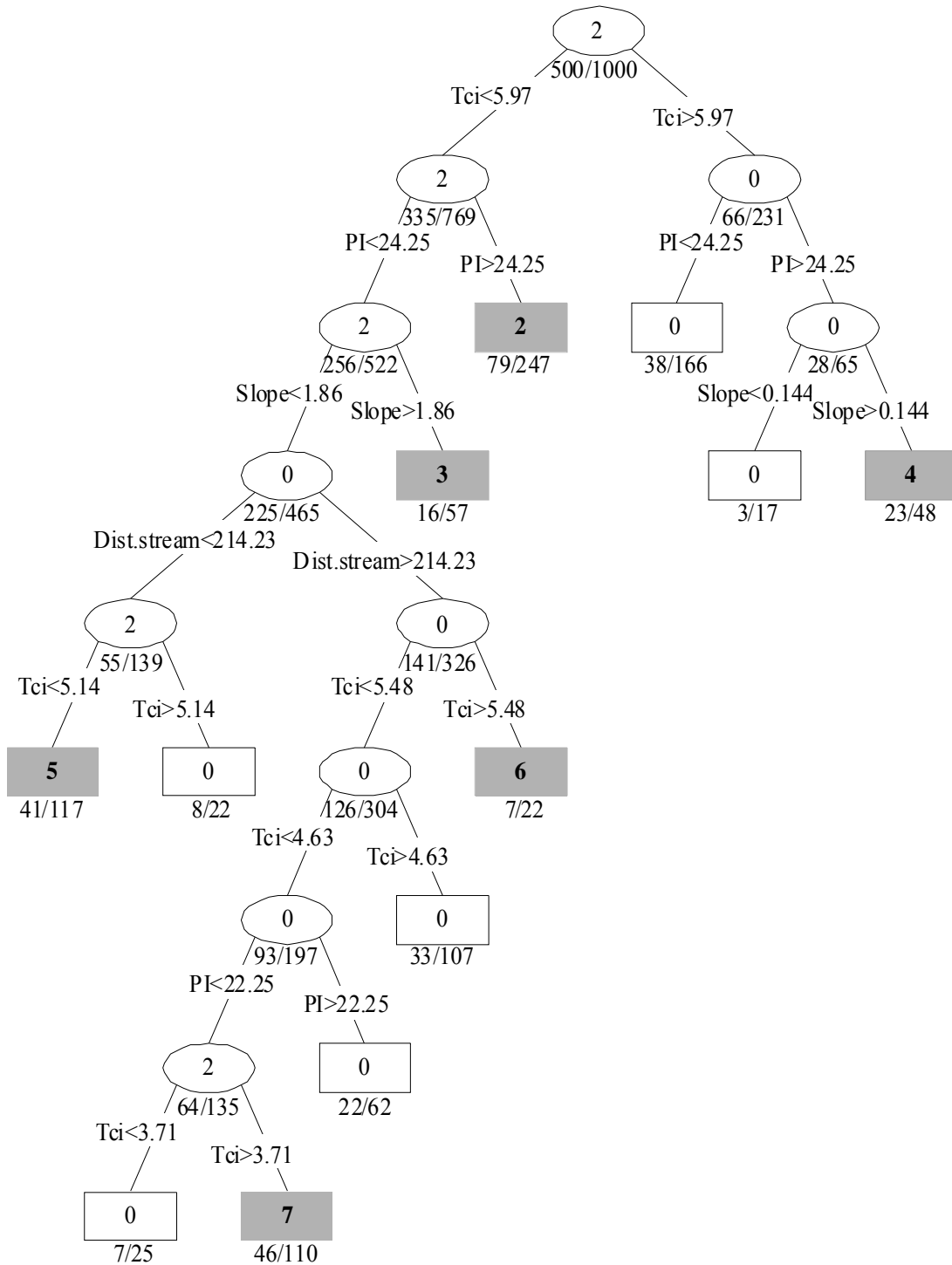


Figure 2.2. CART model for pine based on environmental variables (see Equation 3). Abbreviations used for variables are defined in Table 2.2. The circles represent internal nodes and rectangles terminal nodes of the final pruned tree. The terminal nodes with numbers 1-7 are predicted to be pine (numbered to represent different pine site conditions). Terminal nodes with '0' represent absence of pine. Ratio below each node is the proportion of observations misclassified at that node.

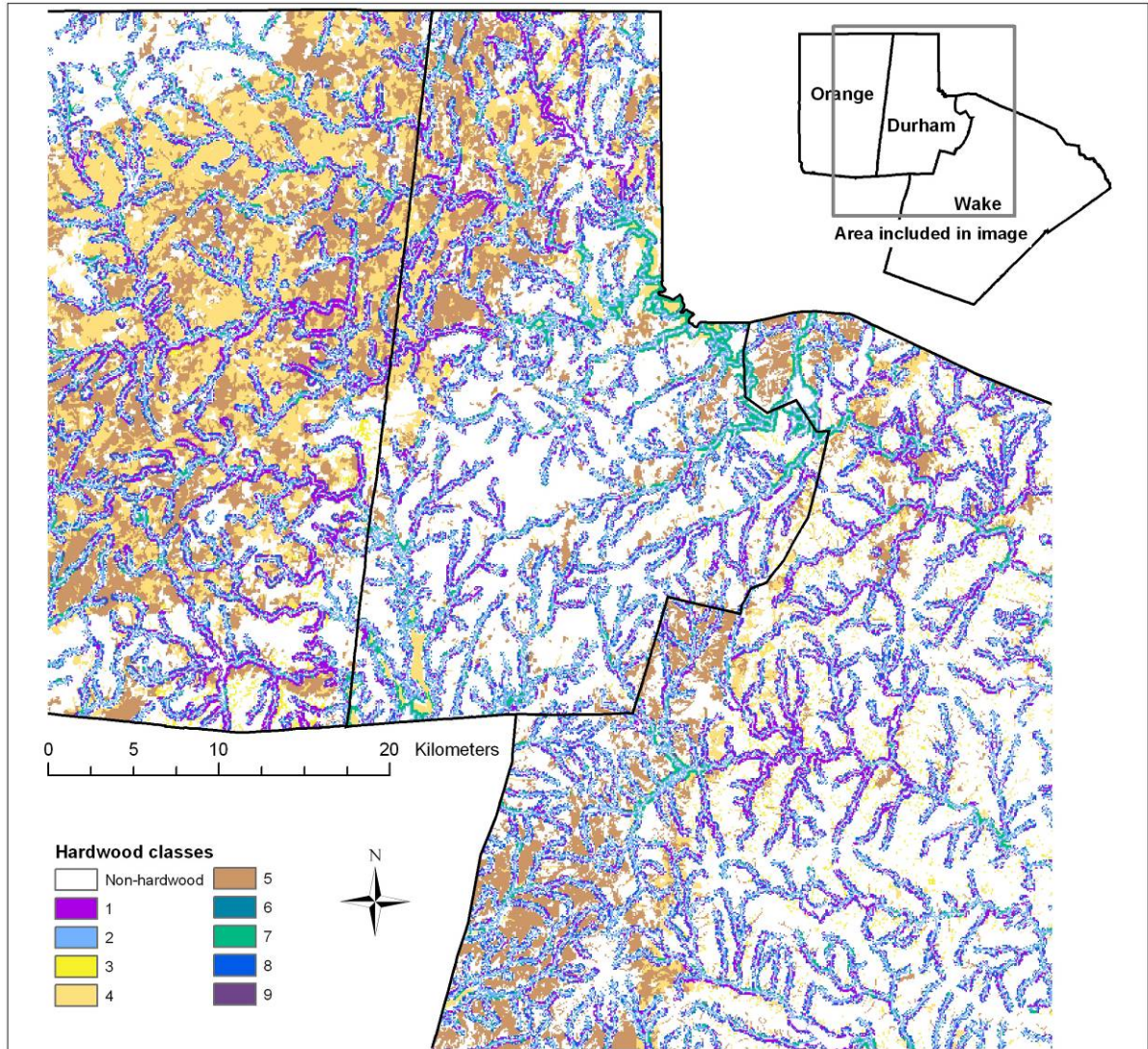


Figure 2.3. CART model predictions of hardwood forest mapped into geographic space. All grid cells that satisfy the model conditions for each branch of the CART (Fig. 2.1) are coded a different color to represent the different locations predicted to be hardwood forest. The vegetation classes correspond with the numbers in the terminal nodes of the hardwood classification tree (Fig.2.1).

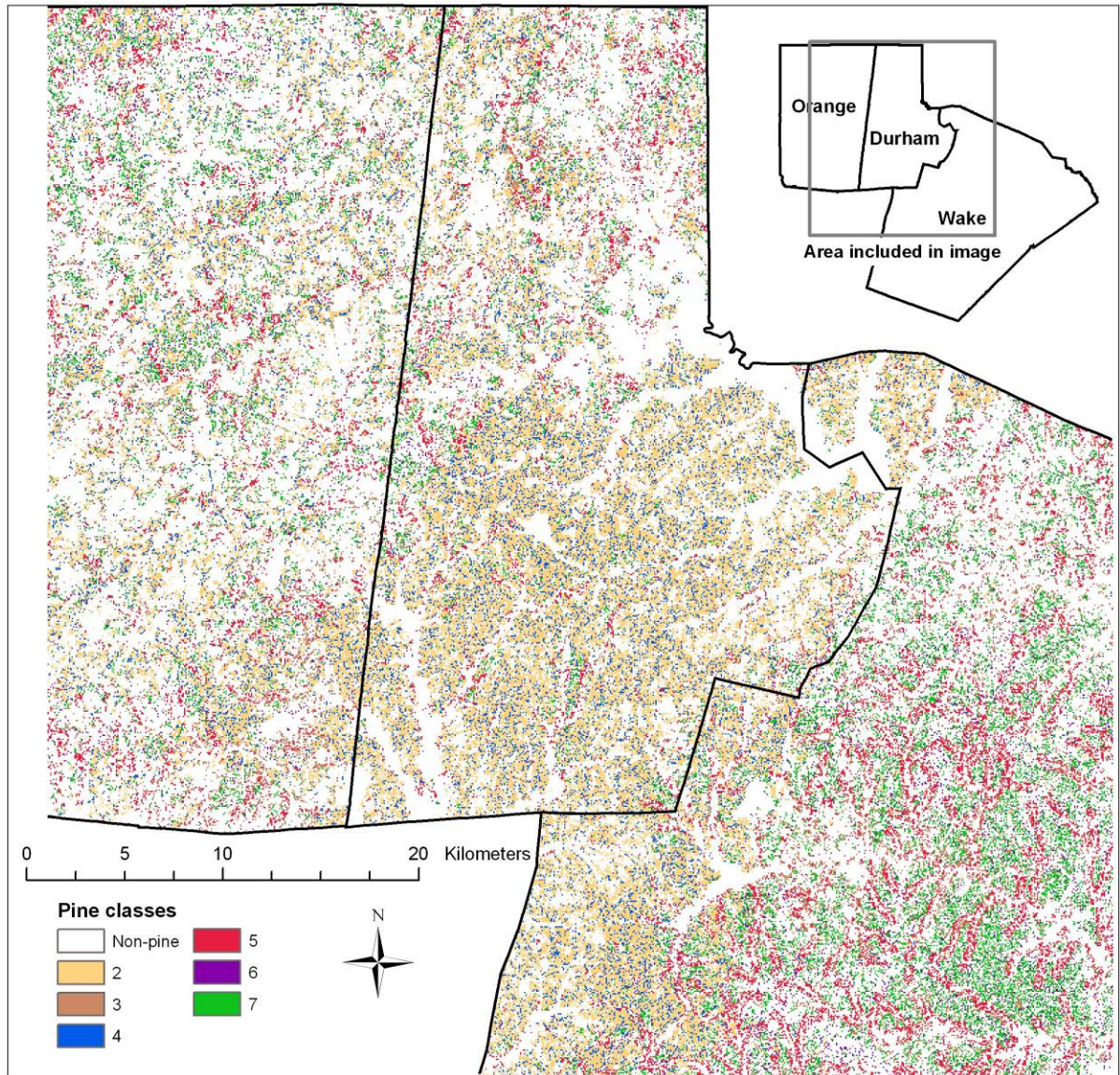


Figure 2.4. CART model predictions of pine forest mapped into geographic space. All grid cells that satisfy the model conditions for each branch of the CART (Fig. 2.2) are coded a different color to represent the different locations predicted to be pine forest. The vegetation classes correspond with the numbers in the terminal nodes of the hardwood classification tree (Fig.2.2).

CHAPTER 3

MATURE HARDWOOD FORESTS IN THE CENTRAL PIEDMONT OF NORTH

CAROLINA: LONG-TERM UNDERSTORY CHANGE

Introduction

Ecological theory and observation suggest that following disturbance species composition changes over time toward a dynamic equilibrium wherein compositional fluctuations are largely based on internal dynamics (Peet 1992, Pickett & White 1985). At scales larger than a single tree, local fluctuations in a mature forest should average out, producing a relatively stable composition. The mature hardwood forests of the Piedmont region of the Southeastern United States have long been assumed to represent the stable endpoint of succession in this region (e.g. Ashe 1897, Oosting 1942, Braun 1950, Peet & Christensen 1980, Delcourt & Delcourt 2000), with compositional variation reflecting primarily variation in local environment (e.g. Christensen & Peet 1984). However, in the contemporary mature hardwood forests of the Piedmont the expectation of stability is open to question due to several potential causes of ongoing change. Among these are long-term fire suppression, increases in deer populations, exotic species invasions, and ongoing recovery from past anthropogenic disturbance (logging, grazing by livestock). Some species, particularly understory herbs, may be slow in equilibrating following disturbance events and environmental change (Christensen 1977, Brewer 1980, Peet & Christensen 1988).

Each of the above processes could effect different subsets of the understory flora and lead to directional change in species composition. For example, fire suppression might increase the abundance of shade-tolerant woody saplings (Lorimer 1985, Abrams 1992, 2003) and eliminate light-demanding herbaceous species originally associated with open woodlands, increases in local deer populations could decrease density and diversity of

understory herbs (Bratton 1979, Rooney & Dress 1997, Waller & Alverson 1997), and increases in aggressive exotic species could restrict overall native species diversity (Richardson et al. 1989, Alvarez & Cushman 2002, Gorchov & Trisel 2003, Jolls 2003). In addition, large infrequent disturbances, such as hurricanes, affect these forests. Hurricane disturbance could lead to transient increases in local (stand-level) richness due to enhanced establishment in newly formed forest patches (Marks 1974, White 1999). Hurricane disturbance may also accelerate the regeneration and growth of shade-intolerant species in forest stands due to increased light availability (Parker et al. 1985, Peet & Christensen 1980).

In studies of long-term species change, researchers in Eastern forests have nearly always focused on canopy species. Interestingly, this work has revealed trends even in older stands, such as a decrease in oak dominance and increase in shade-tolerant species, such as *Acer rubrum* or *Acer barbatum* (Christensen 1977, Peet & Loucks 1977, Lorimer 1984, Abrams 1998, McDonald 2002). Previous work on understory composition in temperate forests have shown patterns of local native species decline with accompanying increases in exotic species (Brewer 1980, Davison & Forman 1982, Drayton and Primack 1996, Rooney and Dress 1997, Rooney et al. *in press*), but these studies have been based on approximations of original plot locations rather than permanently marked and resampled plots or, more often, species lists from survey data for only one site. Studies done without accurate plot replication and multiple site comparisons have limited ability to detect regional directional change in understory species composition.

In 1977 Peet & Christensen established a series of permanently marked vegetation plots in the North Carolina Piedmont. The Piedmont region has served as a model system for work on succession (e.g., Oosting 1942, Keever 1950), and their vegetation data have been

used to define the trajectory of forest composition and structural convergence toward the mature hardwood forests of the region (Christensen & Peet 1984). Additional work showed how understory herb composition of hardwood forests is tightly correlated with soil pH, nutrient status and soil moisture conditions (Peet & Christensen 1980, 1988), and thus any analysis of hardwood stability requires consideration of variation with site characteristics.

A subset of the Peet & Christensen plots were resampled to evaluate the 23-year shift in species abundance and composition in temperate hardwood forests spanning a range of soil types and site conditions. My general objective was to assess the stability of understory composition for all species ($\leq 1\text{m}$ tall). Specifically, I predicted that shifts in understory composition occurred over time and predominantly followed two of the aforementioned trajectories: increases in the abundance of shade-tolerant woody species, and declines in abundance and diversity of herbaceous native species. Further, I predicted that rates of change would be highest in more productive stands (higher in soil resources and moisture) because such places (a) have greater resource availability to support the establishment of new species and (b) higher initial diversity and hence greater potential for loss because of light limitation, deer browsing, and exotic species invasion. I addressed my objective through examination of several specific questions, each examined at 25m^2 and 1000m^2 , to highlight possible differences based on scale (Palmer 1990). First, is the understory of mature hardwood forest stands in the study area exhibiting compositional change, and if so, is there evidence for consistency in the direction of change across plots? Second, which species show the greatest rates of gain, loss, and overall variability, and what if any species attributes are typically associated with such trends? And, third, is change in composition or species

richness partly correlated with site environmental conditions or with richness of the original vegetation?

Methods

Study Area

This study uses data collected from Piedmont hardwood forest stands in or near Duke University Forest located in Orange and Durham Counties, North Carolina. The region is characterized by a warm temperate climate, with a mean monthly temperature in July of 26.7°C and in January of 5.3°C. The mean annual precipitation is 1168mm with July and August being the wettest months (North Carolina Climate Office 2003). Topography is predominantly rolling hills with gentle slopes (<5%), and occasional steep slopes and bluffs along river valleys and hillsides. The elevation within the study area ranges from 75m to 255m.

The landscape is ancient and the soils reflect the long history of leaching in their low nutrient status and high clay content. Soil parent material varies widely across the study area and includes areas of Triassic basin sedimentary mudstones and sandstones, metamorphic Carolina slate, and igneous mafic and felsic intrusions (Daniels et al. 1999). Soils derived from diorite or diabase tend to be more fertile, or on the highly weathered uplands have weathered to shrink-swell clays. The more typical Carolina slate (a highly metamorphosed volcanic ash) weathers to infertile soil dominated by red kaolinitic clays. Differences in parent material often are responsible for strong soil differences over horizontal distances of less than a meter, and hardwood forest composition varies in response to these conditions (Peet & Christensen 1980, Palmer 1990). Further details on hardwood vegetation variation

in relation to soil conditions can be found in Peet & Christensen (1980). The hardwood plots used in this study cover a range of soil types and are representative of conditions typically found throughout the North Carolina Piedmont.

The North Carolina Piedmont has a long history of anthropogenic disturbance and much of the current landscape is dominated by successional pine forest growing on sites abandoned from agriculture. Those areas less suitable for cultivation are predominantly the ones that have remained in hardwood forest, but these sites have not been without disturbance and have a history of selective cutting and domestic livestock grazing (Healy 1985). In addition, hardwood forests were periodically burned by the original aboriginal populations and subsequently by the early settlers to suppress woody growth and encourage an herbaceous understory favorable for livestock, but the use of fire has largely been suppressed since the early 20th century (Hatley 1977, Frost 1998). Grazing could have served to mimic some effects of low-intensity ground fires by suppressing woody growth, and it persisted in the hardwood forest stands of Duke Forest up until its establishment in the 1930s (McDonald 2002). The plots used in this study were originally selected in 1977 for their mature hardwood canopy and minimal evidence of human disturbance due to logging, fire, or grazing since about 1900 (Peet & Christensen 1980, Christensen & Peet 1984).

Although the hardwood plots have remained free of overt anthropogenic disturbance for over 100 years, other forms of disturbance have occurred over time. Of particular importance is the increase in white-tailed deer (*Odocoileus virginianus*) populations throughout the region. Studies in North American temperate forests have shown that deer are responsible for a significant decline in richness and cover of understory vegetation (Waller & Alvenson 1997, Rooney et al. *in press*). The state of North Carolina began using deer harvest

statistics to estimate deer populations in the mid 1980's (Downing 1980) and the data indicate that deer populations in the northern Piedmont of North Carolina have increased considerably over the past 25 years, Figure 3.1.

An additional notable disturbance is the occurrence of hurricanes. In particular, Hurricane Fran passed through the region in September, 1996. The eye of Fran passed 15 miles east of Duke Forest and the strong winds (up to 35meters/second) caused severe damage, labeling it as the most destructive natural disaster ever to strike North Carolina (Carpino 1998). Research done following the hurricane found that most damage in Duke Forest occurred in mature hardwood forests located along river bottoms due to flooded soil conditions, as well as hardwood stands located on exposed ridge slopes and tops (Carpino 1998). The 2000 resurvey of the Peet & Christensen hardwood plots identified nine plots (out of 36) as experiencing some level of hurricane damage, as evidenced by down trees. In addition, 10 stands were so badly damaged by Hurricane Fran that they were impossible to resample.

Field Methods

Peet and Christensen established a series of 105 permanent hardwood forest plots in 1977 as part of their research on Piedmont secondary succession (1981, 1984, 1988) and hardwood forest vegetation (1980). Thirty-six of these plots were precisely relocated and resampled during the interval of 1999-2001 (referenced as 2000) using the same methodology as 1977, except for leaf cover scale (see description below). The basic sampling unit was a 0.1ha (20 x 50m) plot with a 50m transect running the length of the plot down the centerline. The frequency and cover of all understory species (vascular plants <1m tall) were recorded in twenty-five 0.5 x 2m contiguous subplots arranged along the center

transect. All understory species present in the 0.1 ha plot, but absent in the subplots, were recorded. Multiple environmental, soil nutrient and soil texture variables were measured for each plot in 1977 (Table 3.1; see also Peet & Christensen 1980). These data were not recollected in the 2000 resurvey and are assumed to have been constant over time.

In the original 1977 survey, leaf cover was estimated to the nearest percent for each species per subplot. In the 2000 resurvey, leaf cover was estimated using the protocol of the North Carolina Vegetation Survey, which assigns cover based on a ten-point scale (see Peet et al. 1998). To allow comparison across years, the ten-point cover scale was converted to percentages using the geometric mean of each cover class (Oksanen 1976). The average percent cover for each species per plot was calculated as the average cover across subplots. Species present in the 0.1 ha plot, but absent in the subplots were assigned a cover of 0.02 percent.

To ensure accurate comparisons of species richness and composition between the 1977 and 2000 data sets, I updated all species nomenclature to conform to Kartesz (1999). In addition, I created two separate datasets for each year for calculations of richness and composition to control for possible taxonomic problems across years due to misidentification or species identified only to genus. For comparison of species richness, I maintained full species identifications for most taxa and grouped to genera only those species considered difficult to split from related taxa based on vegetative characteristics. For comparison of species composition, all potentially problematic species were grouped to genus and all family-level and unknown designations were removed. The final species list for richness contained 331 taxa, 314 identified to species, 11 to genus and 6 to family or above. The final species list for composition contained 302 taxa, 285 identified to species and 17 to genus.

All woody (shrub and tree) species were assigned a shade tolerance value of low, mid, or high, following USDA (2002).

Data Analysis

Change in understory composition and variation based on taxa

I first compare changes between 1977 and 2000 in total species richness at each site at both the subplot (25m²) and plot (1000m²) scales. I also compare changes in richness at 25m² and 1000m² for species grouped by growthform (tree, shrub, and herb). I tested the significance of changes in richness between survey periods (1977-2000) using paired exact randomization tests with 1000 randomizations and plots serving as replicates (null hypothesis: difference in richness across years is equal to zero; see Manly, 1997, for a description of methods for paired randomization tests). In addition, I qualitatively compared change in richness for plots that were noted to have experienced hurricane damage in 1996 (9 out of 36) with all remaining plots.

To assess changes in understory composition between 1977 and 2000, I first ran a block multi-response permutation procedure (MRPP) to test the null hypothesis of no change in understory composition within plots at 25m² and 1000m² between survey periods. Block MRPP is a multivariate permutation procedure for use with paired-plot compositional data. Two groups were defined to represent the two sample periods and each pair of plots, one for each time period, was considered a block (36 total). Tests of significance are based on random permutations across groups of within block differences of species composition, calculated using a Euclidean dissimilarity measure and species presence/absence (Mielke & Berry 2001). Tests were performed in PC-ORD version 4.24 (McCune & Mefford 1999). Further details of the method can be found in Mielke (1984) and Mielke & Berry (1982).

Consistency in the direction of compositional change across plots at 1000m² was assessed using nonmetric multidimensional scaling with varimax rotation (NMS; Mather 1976, Kruskal 1964) as implemented in PC-ORD version 4.24 (McCune & Mefford 1999). This analysis was limited to 1000m² since species cover data is only available at the plot level. NMS ranks plots based on dissimilarity, calculated using a Bray-Curtis dissimilarity measure and average species cover. NMS was run with a random starting configuration and 25 runs of the real data. To reduce noise from rare species, those occurring in fewer than two plots were deleted from the dataset prior to the NMS ordination. Appropriate dimensionality was assessed using a Monte Carlo test and a configuration with the minimum stress level was used. The direction of compositional change over time between each pair of plots was examined by drawing vectors between each pair of plots on the two-dimensional ordination (McCune & Grace 2002). The lengths of each vector represent the amount of compositional change based on dissimilarity between plots. The relative position of 1977 plots and 2000 plots on an ordination axis were compared with a two-sample t-test (Peterson & McCune 2001). Plots that experienced hurricane damage were identified separately in the ordination diagram to examine the direction and extent of compositional change in relation to other hardwood plots.

An indicator species analysis (Dufrene & Legendre 1997) was performed in PC-ORD to examine individual species relationships to the two sample periods (1977 and 2000). The test provides a method for assessing which species have the strongest affinity to one time period, thereby emphasizing species with the strongest influence on compositional change over time in the NMS ordination. The indicator value for each species is calculated by combining the relative abundance and relative frequency of each species in each group

(year), and the highest indicator value (IV_{\max}) across groups is used as the overall indicator value for each species. The statistical significance of IV_{\max} for each species is evaluated using a Monte Carlo test with 1000 randomizations (null hypothesis: IV_{\max} no larger than would be expected by chance).

Change in association with environmental variables

I conducted a simple correlation analysis to examine the environmental factors correlated with change in richness at 25m² and 1000m² for species grouped by growthform (herb, shrub, tree). I did not test for correlations with the full dataset as growthform data is nested within this dataset and would provide redundant results. A correlation analysis was also used to examine the change in diversity for each growthform in relation to the original 1977 richness at each scale. Spearman's ranked correlations were used to avoid assumptions about normality of the data. Environmental variables are listed in Table 3.1.

To assess change in species composition in relation to environment, I compared the length of the paired plot vectors to environmental variables in the NMS ordination. The relationships between individual environmental variables and plot scores were initially overlaid on the ordination with a vector biplot. The angles of each environmental vector indicate the direction of highest correlation and the lengths represent the strength of the correlation. A varimax rotation was used to improve the alignment of environmental variables with one primary ordination axis (Mather 1976). Correlations between the ordination axes and environmental variables were calculated with Pearson's r^2 . I correlated the length of the paired-plot vectors with 1977 plot positions on the primary environmental

ordination axis using Spearman's rank correlation to test if the extent of compositional change between plots varied with environment.

Results

Change in understory species richness

Across all sites, I observed decreases in regional species richness with much of the loss driven by decreases in herb species. Peet & Christensen (1980) recorded a total of 272 species throughout the hardwood plots in 1977 and the 2000 resurvey recorded 252 species for a net loss of 21 species, 18 of which were herb species (see Appendix A for full list of species lost and gained). Native species richness exhibited greater declines with a net loss of 28 species (23 herb) due to the 7 new exotic species recorded in 2000 (Appendix A). Total loss of native species was 70 species (58 herbs).

In addition to overall herb loss, another important trend is the decline in the number and abundance of regionally rare native herb species over time. Sixty-one percent (89 out of 145) of herb species occurring in 10 or fewer plots in 1977 declined in plot frequency, and more than half of those that declined (52 species) were not recorded at all in 2000. There were 123 infrequent native herb species (10 or fewer plots) in 2000, and 25 of these species (20.3%) maintained the same plot frequency over time.

The loss in overall regional diversity contrasts with the change observed at the subplot (25m²) and plot (1000m²) scales for paired plots. At 25m² there was no significant change in total or native species richness (Table 3.2). Total richness and native richness predominantly increased at 1000m² (22 out of 36 plots), but only total species richness showed significant increases ($p \leq 0.05$) due to a slightly higher mean difference in richness

from the new exotic species recorded in 2000 (Table 3.2). Plots damaged by the hurricane had some of the greatest increases in total species richness; 8 out of 9 hurricane plots increased in total richness (increases range from 10-25 species per plot) at 1000m². Seven of the hurricane plots increased in total species richness at 25m².

The analysis of change in richness by growthform provides insight on which species are influencing the shift in richness patterns from regional to local scales. Change in herb richness per plot conforms to the regional pattern in that richness showed significant declines at both 25m² and 1000m² for all herbs and native herbs (Table 3.2). This contrasts with the change in tree richness, which showed strong increases at the subplot and plot scales (Table 3.2), but no regional increases in richness (net loss of 2 species, Appendix A). Shrub richness did not significantly change at 25m² ($p= 0.227$), but there were significant increases in richness at 1000m² ($p= .011$). Eight hurricane plots increased in total richness at 1000m² across all growthforms (results vary for 25m²), and the greatest increases were largely for tree species (increases range from 4-11 species per plot).

Change in understory composition

Understory composition exhibited significant change between 1977 and 2000 at both 25m² and 1000m² (blocked MRPP 25m²: $p= 0.001$, $R= 0.003$; 1000m²: $p= 0.013$, $R= 0.002$; R measures within-group agreement). There is also strong evidence of directional change in composition across all plots at 1000m² based on the NMS paired-plot vectors (Fig.3.2). Plots show significant separation by year (group) along the vertical ordination axis ($n= 72$, $t= 5.00$, $p= 0$; Fig. 3.3). These results imply there was a dominant trend in shifts of species composition across the majority of plots between 1977 and 2000. Hurricane damaged plots did not exhibit strong differences in extent or direction of compositional change in

comparison to other plots (Fig.3.2). The horizontal axis of the ordination accounts for 39.2% of the variation in the data while the vertical axis accounts for 10.8%.

Based on the results of the indicator species analysis, the directional change in understory species composition evident in the NMS ordination is predominantly due to decreases in herb frequency and abundance and increases in tree frequency and abundance over time. Fourteen species (7 herb, 5 shrub and 2 tree species) were highly indicative of plot composition in 1977 ($p < .05$), and nearly all (10 out of 14) decreased in subplot and plot frequency over time (Table 3.3). Only one herb, *Polygonatum biflorum*, showed an increase in subplot or plot frequency (+1 increase in plot frequency). Additional 1977 indicator herb species that exhibited high declines in plot frequency (≥ 4 plots) and relatively high subplot declines include: *Chimaphila maculata*, *Desmodium sp.*, *Prenanthes altissima*, *Chrysogonum virginianum*, *Silene virginica*, *Epifagus virginiana*, *Tephrosia virginiana*, and *Chamaelirium luteum* (Table 3.3). One exotic vine species, *Lonicera japonica*, declined in subplot and plot frequency over time (-12 and -2, respectively).

Seven species are highly indicative of plot composition in 2000 ($p < .05$; Table 3.3), including four trees and only one herb, *Phytolacca americana* (Pokeweed), which is commonly found in disturbed sites throughout North Carolina (Radford et al. 1968). *Phytolacca americana* was not found in 1977 and it exhibited the highest increase in total plot frequency for herbs (+8plots; Table 3.3). *Microstegium vimineum* had the next highest increase (+7 plots; Appendix A). *Microstegium* is an exotic species found in low woods of the Piedmont (Radford et al. 1968). Expanding the significance level for the 2000 indicator species to $p < 0.165$ (arbitrary cutoff value) includes seven additional tree species (including the exotic species, *Paulownia tomentosa*) and one shrub, *Asimina parviflora* (Table 3.3). In

contrast, the additional indicator species for 1977 includes ten herb species and three tree species (Table 3.3).

Of the tree species that increased in plot frequency (≥ 2 plots) over time, 10 are classified as highly shade tolerant, 18 are mid-shade tolerant, and 3 have low shade tolerance (Appendix A). The highly shade-tolerant tree species showing the greatest increases in subplot and plot frequency that are also indicative of plot composition in 2000 ($p < 0.165$) include; *Carpinus caroliniana*, *Acer barbatum*, and *Ostrya virginiana* (Table 3.3). Some historically dominant (and less shade tolerant) oak and hickory species also exhibited increases in frequency over time. *Quercus falcata*, *Quercus alba*, and *Carya ovata* showed the greatest increases at both the subplot and plot scale (Table 3.3). The only oak or hickory species that declined in plot frequency or had strong declines in subplot frequency are *Quercus coccinea*, *Quercus marilandica*, *Quercus michauxii*, *Carya glabra*, and *Carya pallida* (Appendix A).

The shade intolerant tree species that increased in subplot and plot frequency are *Liriodendron tulipifera*, *Liquidamber styraciflua* and *Quercus phellos*. *Liriodendron* is highly indicative of plot composition in 2000 ($IV_{\max} p < 0.05$) and showed the highest increase in subplot occurrences (+105; +6 in plot frequency) across all tree species. *Liquidamber* increased in subplot frequency by 26 and plot frequency by 2, *Quercus phellos* increased by 1 and 8 for subplot and plot frequency, respectively (Appendix A).

Change in species richness and composition with environment

Relationships between change in species richness and environmental variables varied with growthform at 25m² and no significant relationships were found at 1000m² (Table 3.4).

Herb species had the strongest correlations with environment, with positive correlations associated with pH and soil cation variables (Ca, Mg, K) (Table 3.4). A positive correlation implies that species richness tended to increase along the environmental gradient over time. This suggests that herb richness was more likely to increase at 25m² in nutrient rich sites (sites with higher pH and soil cations). It is important to note that soil cation variables and pH are positively correlated with each other ($0 < p < .01$), which explains some portion of the correlation. This is also true of the soil texture variables ($p = 0$ for all soil texture correlations), with %sand negatively correlated with %silt and %clay, and all three together adding to 100. Change in herb species richness is positively correlated with %sand ($p < .01$) and negatively correlated with %silt and %clay ($p < .01$ and $p < .05$, respectively).

Change in tree species richness showed no relationship with pH or soil cations and was only moderately correlated with %silt ($r = -0.35$; $p = 0.04$). Tree and herb richness are both negatively correlated with elevation ($p < .01$). Elevation is often considered a surrogate for soil moisture (Peet & Christensen 1980), and thus a negative correlation means low, wet sites tended to increase in species richness over time, while higher, dry sites generally decreased. Change in shrub richness was not correlated with any examined environmental variables. Only change in herb richness showed a relationship with the original (1977) plot richness ($r = 0.43$; $p < .01$), which is also partly explained by the relationship with soil pH and nutrients as overall richness tends to increase with soil fertility (see Peet & Christensen 1980).

Change in overall species composition at 1000m² is moderately correlated with environment (Spearman's rank correlation: $r = 0.38$, $p = 0.023$), based on the analysis of paired-plot vector length with 1977-plot position along axis 1 of the NMS ordination

(Fig.3.2). A positive correlation means that vector length increased from left to right along axis 1, and thus plots with higher soil cations, pH, and %sand exhibited greater compositional change over time (Fig.3.2-3.3). Yet it is important to note that the overall coefficient of determination (r^2) of plot vector length with axis 1 is 0.103 (Table 3.5). This relatively low r^2 value (only 10% of variation explained) implies that although there is some relationship with environment, species change at 1000m² is predominantly occurring across all plots, largely independent of the measured environmental factors. This is also represented by the nearly orthogonal position of the ‘group’ (year) vector to the primary environmental vectors in the NMS vector biplot (Fig.3.3).

Discussion

The understory composition of mature hardwood forests in Duke Forest does not provide support for the ‘steady-state’ paradigm of successional theory; these plots are not stable. Although species fluctuations are to be expected in late-successional stands due to natural dynamics (Pickett & White 1985), current successional theory does not explain the larger directional change that appears to be occurring across all hardwood plots, apart from any apparent hurricane effect. The apparent shift in species composition could be the result of different factors that have persisted or increased over time. I discuss the results in the context of the mechanisms initially described as common for eastern hardwood forests: recovery from an earlier regime of chronic fire or grazing, increases in white-tailed deer populations, exotic species invasion, and small-scale variation due to hurricane disturbance.

On a regional scale, I found an overall decline in understory native species richness with herbaceous species showing the strongest decreases. These results support the findings

of other studies that show widespread regional losses of species diversity (e.g. Tilman et al. 1994, Pimm et al. 1995), and highlight a potential trend towards increased species loss in mature hardwood forests over time (see Gilliam & Roberts 2003). My results differ from other studies of temperate forests in that a similar pattern of overall understory species loss is not observed at smaller scales (Davison & Forman 1982, Kwiatkowska 1994, Drayton & Primack 1996, Rooney et al. *in press*). The Duke Forest hardwood plots have not yet exhibited significant change in understory native species richness at the subplot (25m²) or plot (1000m²) scale. The apparent stability of understory species richness is due to the combined effect of decreasing herb richness and increasing tree seedling richness at both scales.

I predicted overall declines in herb diversity and abundance, largely due to the growing evidence of the detrimental impacts of white-tailed deer populations on forest understory flora (Anderson 1994; 1997, Kelley 1994, Waller et al. 1997, Rooney et al. *in press*). Although I did not specifically test for deer effects, the significant decline in herbs and the estimated 100% increase in white-tailed deer populations in the northern Piedmont of North Carolina since 1985 provides support for herbivory as a possible causal factor of decline. Research by Kelley (1994) found that deer browsing on forest herbs is generally concentrated in the spring (April and May) when many understory plants are available and before agricultural crops begin to provide food (see also Roberts & Gilliam 2003). Nearly all of the herb species that exhibited relatively high decreases in plot frequency (≥ 4 plots) are primarily woodland herbs present in the spring, either vegetatively or in flower (Radford et al. 1968). Deer herbivory could also be a reason for the decline in the exotic species, *Lonicera japonica* (Japanese honeysuckle), as it is considered an important regional food

item for Piedmont populations of white-tailed deer (Osborne 1993). *Lonicera japonica* is the only exotic species that decreased in frequency at the subplot and plot level.

Increases in white-tailed deer populations have been suggested to contribute to the decline of oak and hickory species in hardwood forests due to their high preference and browsing intensity on *Quercus alba* (white oak) and *Carya ovata* (shagbark hickory) seedlings and saplings (Strole & Anderson 1992; see also Marquis et al. 1976, Tilghman 1989). Such a factor would further exacerbate the oak and hickory decline often attributed to fire suppression (Lorimer 1985, Abrams 1992) and competition with shade-tolerant species (Lorimer et al. 1994, McDonald et al. 2003). My results run contrary to this expectation as over half of the oak and hickory species present in 1977, including *Quercus alba* and *Carya ovata*, increased in subplot and plot frequency over time. Oak and hickory species are indeed reproducing in the understory, but other factors appear to be preventing them from surviving into older age-classes in Duke Forest (see McDonald et al. 2002) and the Piedmont region (Abrams 2003). The overall increase in tree seedling richness combined with the significant declines in herbaceous species richness highlights the need for further research on deer effects in the Piedmont region.

Although not supporting a deer effect, the strong increase in tree seedling richness across nearly all plots provides support for my initial hypothesis of increases in woody species abundance due to recovery from past fire and grazing disturbance. The cessation of ground-level disturbance from low-intensity fires and understory grazing in hardwood forests since the early 1900s has facilitated the recruitment of woody species throughout Eastern forests (Abrams 2003). This recruitment has largely supported shade tolerant species, such as *Acer rubrum* and *Acer barbatum*, since they tend to be faster growing and more

competitive in the understory and numerous studies have documented their increase in hardwood forest canopies (Christensen 1977, Anderson & Adams 1978, Lorimer 1984, 1994, McDonald et al. 2002). I observed strong increases in a number of shade tolerant species at both the subplot and plot scale (Appendix A), but significant change in abundance was not restricted to species with high shade-tolerance.

The strong increase in abundance of the shade-intolerant species, *Liriodendron tulipifera* and *Liquidamber styraciflua* at both scales suggests that localized plot disturbance from Hurricane Fran is an additional factor effecting woody species density in Duke Forest. White (1999) found that *Liriodendron* and *Liquidamber* seedlings greatly increased in damaged Piedmont hardwood forests one year following Hurricane Fran. Additional species that significantly increased in White's (1999) study plots and which also show increases in the present analysis include: *Pinus spp.*, *Paulownia tomentosa*, *Phytolacca americana*, and *Erechtites hieraciifolia*. All of these species are known to colonize disturbed sites with high-light conditions and three (*Paulownia*, *Phytolacca* and *Erechtites*) did not occur at all in 1977. The consistent increase in richness across all growthforms (at 1000m²) in hurricane damaged plots runs contrary to the larger trends in the data and suggests that plot-level effects from the hurricane persisted over the 3-4 years following the storm. Localized increases in richness could be due to increased light and water availability from the opening up of new sites for colonization following the disturbance (Pickett & White 1985, White 1999). Since none of the studied plots experienced large-scale hurricane damage, I expect that with time the early-successional species will decline and be replaced by the mid and late-successional species present in the stands (Pickett & White 1985).

The disturbance and creation of forest patches due to Hurricane Fran could also have contributed to the moderate increase in exotic species abundance and diversity over time. Each of the five exotic species that occurred in greater than one plot in 2000 (*Ligustrum sinense*, *Microstegium vimineum*, *Verbascum thapsus*, *Paulownia tomentosa*, and *Glechoma hederacea*) was found to have invaded at least one hurricane damaged plot. These species are easily dispersed and are commonly found in roadsides and disturbed sites throughout much of North Carolina (Radford et al. 1968). I initially did not expect the hardwood forests of Duke Forest to experience strong increases in exotic species as they have remained relatively intact and isolated from regional anthropogenic disturbances, such as habitat fragmentation, over at least the last 70 years. However, given the predominant trend towards increased exotic species presence throughout Eastern forests (Rooney et al. *in press*) and the habitat disturbance that continues surrounding Duke Forest, I anticipate that their abundance and diversity will increase in the future.

Change in species richness and composition with environment

The significant correlations between change in herb richness and environmental variables at 25m² suggests there are local patterns of species change along primary environmental gradients, with the drier, less fertile sites showing little change (or loss) in herb composition and the mesic fertile sites the greatest increase. These results add a temporal perspective to the earlier work by Peet & Christensen (1980) where they found that herbs show stronger variation in richness in response to multiple environmental variables than shrubs and trees. Some authors have also suggested that rate of succession is a function of site (Peet & Loucks 1977, Fralish et al. 1991), and my results (for herbs and trees) support

the expectation that mesic sites show the greatest change over time. Soil cation (Ca, Mg, K) concentrations appear to be an important factor in the amount of change in herb richness over time, but it is unclear whether this is because of limitations in soil nutrients or if herb species experience less competition with other understory species (such as trees and shrubs) in sites with higher soil cations. There could also be a hurricane effect as plots with higher soil cations includes some of the sites most damaged by the hurricane (plots 505-509, Fig. 3.3). The hurricane effect could additionally explain some of the significant increase in herb and tree seedling richness at lower elevations as hardwood stands in lower areas sustained more hurricane damage in Duke Forest (Carpino 1998).

The moderate positive correlation between change in overall species composition (as represented by plot vector length) and environmental variables provides some support of my initial prediction of greater overall species change in areas of higher soil fertility and lower elevation due to increased availability of resources. This result differs from the above discussion of richness in that it pertains to change based on the entire species assemblage within a plot, rather than just measures of richness. Viewed together, the results suggests that increases in species richness in low elevation, fertile plots contributed to greater species turnover over time, whereas the decreases in richness in drier, less fertile plots did not cause as much overall compositional change. I interpret this result with some reservation given the weak coefficient of determination ($r^2 = .103$) for the correlation of plot vector length with the primary environmental axis of the NMS ordination. It instead seems that directional compositional change is occurring over time across all plots, largely independent of environmental conditions.

The systematic declines in herbaceous species richness, coupled with the dramatic increases in woody seedling abundance signal important shifts in mature hardwood forests of the Piedmont. The past legacy of human disturbance in the forest stands and current disturbance regimes continue to upset the dynamic equilibrium thought to have existed in mature oak-hickory hardwood forests. Some authors have suggested that the current shift toward a more mesic hardwood forest is more typical of late-successional stands and the historic dominance of oak-hickory forests was primarily a consequence of higher fire frequency (Abrams 2003, White & White 1996). Whether fires should be reintroduced to the ecosystem is a matter of debate, but indeed, important to consider in order protect the hardwood stands from future species loss. Loss of fire could explain some of our species losses, but many are species typically associated with mesic closed forest, and these are much more likely the victims of increased deer pressure. Loss of herbaceous species highlights yet another alarming trend, particularly since their reduction cannot be attributed to the mechanisms commonly associated with species extinction, such as habitat fragmentation and invasive species (Wilcove 1998, Jolls 2003). This implies that more research is needed to understand the mechanisms responsible for the decline as well as more active management and long-term monitoring to help prevent further loss of native understory flora.

Table 3.1. Environmental variables recorded for each hardwood plot in 1977. Data were not recollected in 2000 and are assumed to have been constant over time.

Variable	Description	Mean	Std.dev	Min	Max
pH	Soil pH in topsoil	4.76	0.586	3.62	5.92
Ca	Ca in topsoil (ppm)	418.59	404.128	37.40	1268.80
Mg	Mg in topsoil (ppm)	101.32	92.633	6.48	306.02
K	K in topsoil (ppm)	67.37	22.911	25.74	117.32
PO ₄	PO ₄ in topsoil (ppm)	3.38	2.134	0.78	12.98
%Sand	Sand in A horizon (%)	56.39	11.015	36.00	75.00
%Silt	Silt in A horizon (%)	33.61	7.572	21.00	46.00
%Clay	Clay in A horizon (%)	10.56	4.644	4.00	22.00
Slope	Local slope angle (°)	8.78	8.642	0.00	32.00
Elevation	Plot elevation (m)	143.44	36.134	79.30	253.15

Table 3.2. Summary statistics for change in species richness at the subplot (25m²) and plot (1000m²) scale from 1977-2000 (n= 36 paired plots). Data listed are for all species (Total), species separated by growthform (Herb, Shrub, Tree), and native species of each species group (labeled with N.).

*Plots w/ + change = Total number of plots (out of 36) that increased in species richness.

**Plots w/ - change = Total number of plots (out of 36) that decreased in species richness.

	Growthform	Total	N.Total	Herb	N.Herb	Shrub	N.Shrub	Tree	N.Tree
25m² (n=36)	Plots w/ + change*	19	15	11	10	12	13	26	26
	Plots w/ - change **	15	15	21	22	16	17	6	6
	Mean richness difference	0.14	-0.06	-1.50	-1.80	-0.30	-0.25	1.97	1.97
	Permutation test statistic	93	86	40	33	26	28	86	86
	p-value	0.460	0.530	0.036	0.014	0.227	0.290	0.0001	0.0001
	<hr/>								
1000m² (n=36)	Plots w/ + change	22	22	12	9	22	21	30	30
	Plots w/ - change	13	13	22	24	10	10	5	5
	Mean richness difference	3.17	2.11	-2.06	-2.86	1.11	0.97	4.11	4.00
	Permutation test statistic	204	173	61	44	62	57	161	157
	p-value	0.030	0.093	0.041	0.006	0.011	0.019	0	0

Table 3.3. Indicator values (percent of perfect indication) and frequency statistics of species associated with 1977 plots or 2000 plots, listed in order of statistical significance (p -value) by year. The p -value is based on the proportion of 1000 randomized trials (Monte Carlo test) with indicator value equal to or exceeding the observed indicator value. All species with p -value ≤ 0.165 were included to show trends between years. Year: 1= 1977, 2= 2000. Growthform: 1=Tree, 2=Shrub, 3=Herb. Nativity: N=Native, I= Introduced (exotic).

Species name	Nativity	Growthform	Indicator value				Change in frequency	
			1977	2000	Year	p-value	25 subplots	Plot
<i>Chimaphila maculata</i>	N	3	72	18	1	0.001	-52	-4
<i>Desmodium spp.</i>	N	3	82	11	1	0.002	-66	-4
<i>Viburnum rafinesquianum</i>	N	2	72	24	1	0.002	-3	-2
<i>Vitis aestivalis</i>	N	2	52	4	1	0.013	-28	-8
<i>Goodyera pubescens</i>	N	3	35	4	1	0.014	-9	-7
<i>Euphorbia corollata</i>	N	3	39	5	1	0.015	-7	-9
<i>Euonymus americana</i>	N	2	56	16	1	0.027	10	-1
<i>Aureolaria virginica</i>	N	3	35	1	1	0.029	-8	-8
<i>Lonicera japonica</i>	I	2	53	7	1	0.038	-12	-2
<i>Polygonatum biflorum</i>	N	3	57	24	1	0.038	-13	1
<i>Carya glabra</i>	N	1	59	27	1	0.039	-37	0
<i>Nyssa sylvatica</i>	N	1	66	10	1	0.044	-14	4
<i>Sambucus nigra</i>	N	2	14	0	1	0.044	-16	-5
<i>Houstonia caerulea</i>	N	3	14	0	1	0.046	-3	-5
<i>Prenanthes altissima</i>	N	3	41	9	1	0.086	-16	-5
<i>Celtis laevigata</i>	N	1	14	0	1	0.102	-8	-4
<i>Pinus taeda</i>	N	1	40	8	1	0.104	-19	-3
<i>Chrysogonum virginianum</i>	N	3	14	1	1	0.112	-4	-4
<i>Lespedeza spp.</i>		3	23	3	1	0.124	-16	-3
<i>Silene virginica</i>	N	3	11	0	1	0.128	-1	-4
<i>Epifagus virginiana</i>	N	3	11	0	1	0.13	-6	-4
<i>Dioscorea villosa</i>	N	3	32	4	1	0.133	-7	0
<i>Tephrosia virginiana</i>	N	3	11	0	1	0.133	-2	-4
<i>Viburnum prunifolium</i>	N	2	49	13	1	0.134	-18	2
<i>Solidago spp.</i>	N	3	36	3	1	0.14	-25	-1
<i>Juniperus virginiana</i>	N	1	72	13	1	0.153	-3	4
<i>Maianthemum racemosum</i>	N	3	34	5	1	0.157	-17	0
<i>Chamaelirium luteum</i>	N	3	13	1	1	0.164	-1	-4
<i>Rubus spp.</i>	N	2	2	47	2	0.003	29	13
<i>Phytolacca americana</i>	N	3	0	22	2	0.004	7	8

<i>Vitis rotundifolia</i>	N	2	22	74	2	0.015	150	2
<i>Quercus falcata</i>	N	1	3	30	2	0.026	18	11
<i>Carpinus caroliniana</i>	N	1	5	40	2	0.028	102	8
<i>Liriodendron tulipifera</i>	N	1	16	55	2	0.037	105	6
<i>Fraxinus americana</i>								
+ <i>pennsylvanica</i>	N	1	18	54	2	0.041	88	9
<i>Ulmus alata</i>	N	1	8	35	2	0.071	49	6
<i>Asimina parviflora</i>	N	2	0	15	2	0.096	2	5
<i>Pinus virginiana</i>	N	1	3	17	2	0.096	0	6
<i>Ostrya virginiana</i>	N	1	7	32	2	0.097	60	4
<i>Paulownia tomentosa</i>	I	1	0	11	2	0.111	0	4
<i>Quercus alba</i>	N	1	32	58	2	0.125	37	4
<i>Acer barbatum</i>	N	1	6	35	2	0.142	56	5

Table 3.4. Environmental variables correlated with change in species richness at 25m² from 1977 to 2000. Data listed are for species separated by growth form (Herb, Shrub, Tree). Only correlations with $p < 0.05$ are shown below. No factors were significantly correlated with change in richness at 1000m². Symbol is: * $p < 0.01$.

Variables	25m ²		
	Tree	Shrub	Herb
pH			0.44*
Ca			0.52*
Mg			0.54*
K			0.41
PO4			
Sand			0.47*
Silt	-0.35		-0.42*
Clay			-0.39
Slope			
Elevation	-0.46*		-0.49*
Full 1000m ² richness			0.43*

Table 3.5. Coefficients of determination for the correlations between NMS ordination axes and measured environmental variables. Environmental variables were measured in 1977 and are assumed to have been constant over time.

NMS Axis	r^2		
	1	2	3
Group	0.001	0.263	0.039
Vector length	0.103	0.006	0.089
pH	0.624	0.001	0.027
Ca	0.497	0.016	0.085
Mg	0.554	0.000	0.039
K	0.149	0.009	0.002
PO4	0.018	0.012	0.018
%sand	0.470	0.052	0.000
%silt	0.602	0.053	0.000
%clay	0.355	0.038	0.003
Slope	0.023	0.011	0.078
Elevation	0.312	0.022	0.025

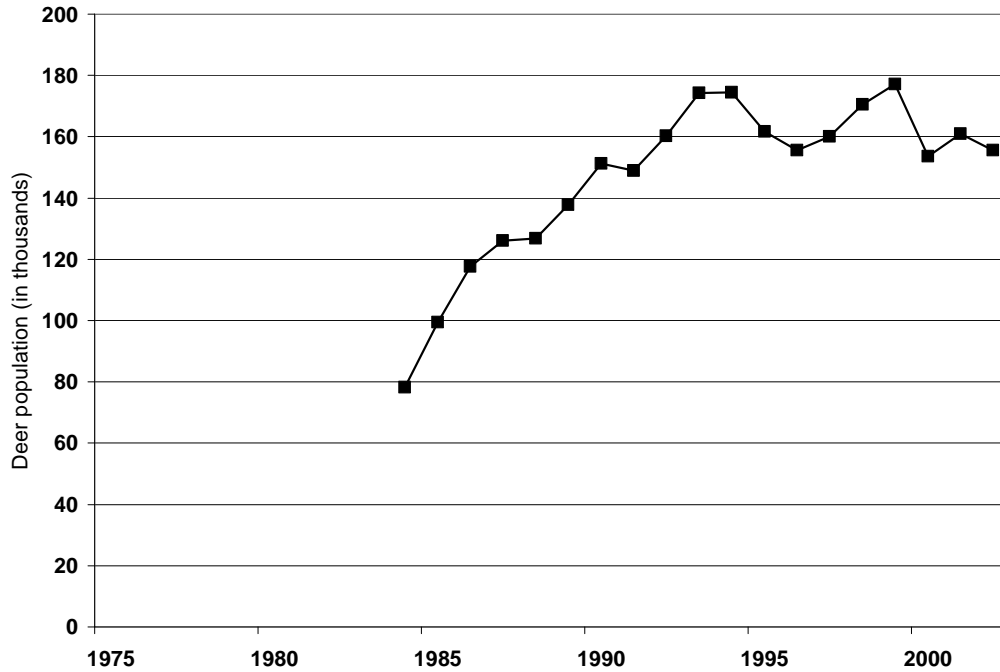


Figure 3.1. Total deer population in the northern Piedmont management zone between 1984-2002. Population density is based on the population reconstruction model of Downing (1980) compiled by the North Carolina Wildlife Resources Commission (unpublished data). Understory surveys were conducted in 1977 and 2000.

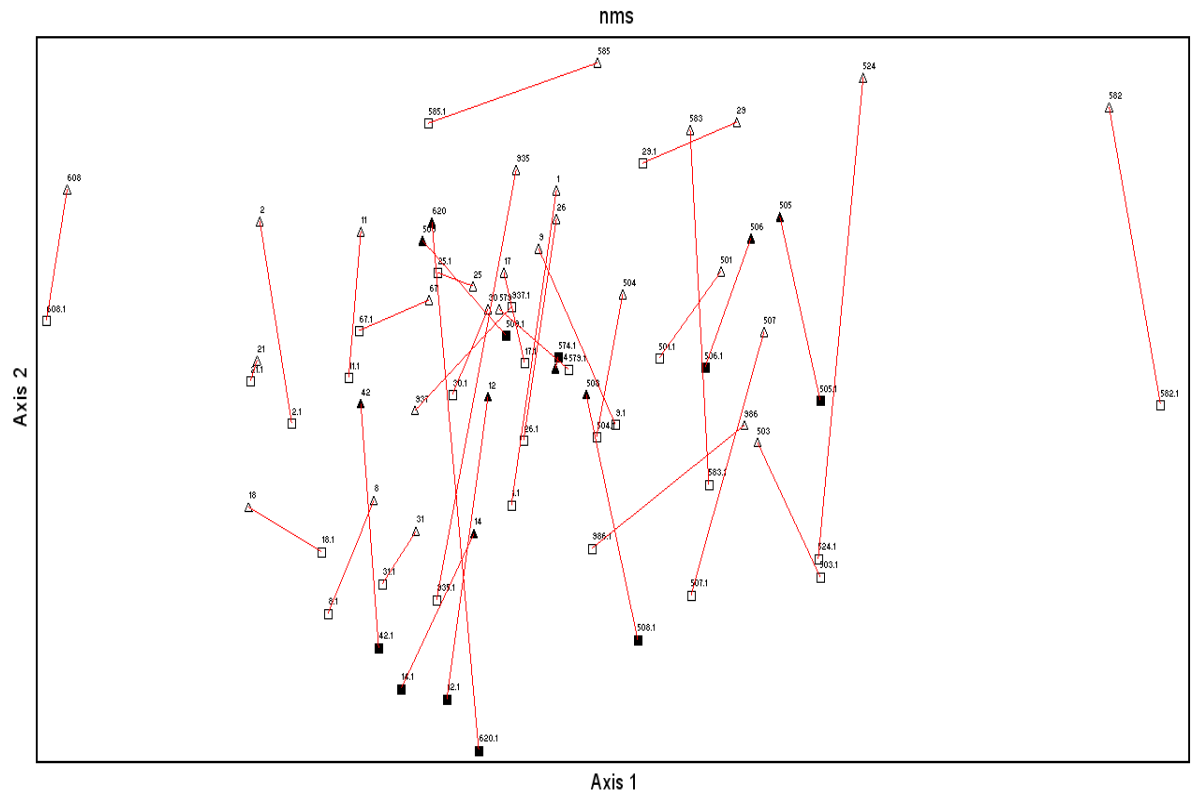


Figure 3.2. NMS ordination of plots in species space with paired-plot vectors drawn from 1977 to 2000 plot, showing direction of compositional change over time. Ordination is based on the 226 species that occurred in no fewer than two hardwood plots. Symbols are plots coded for year (triangle= 1977, square = 2000), filled symbols represent the plots with hurricane damage.

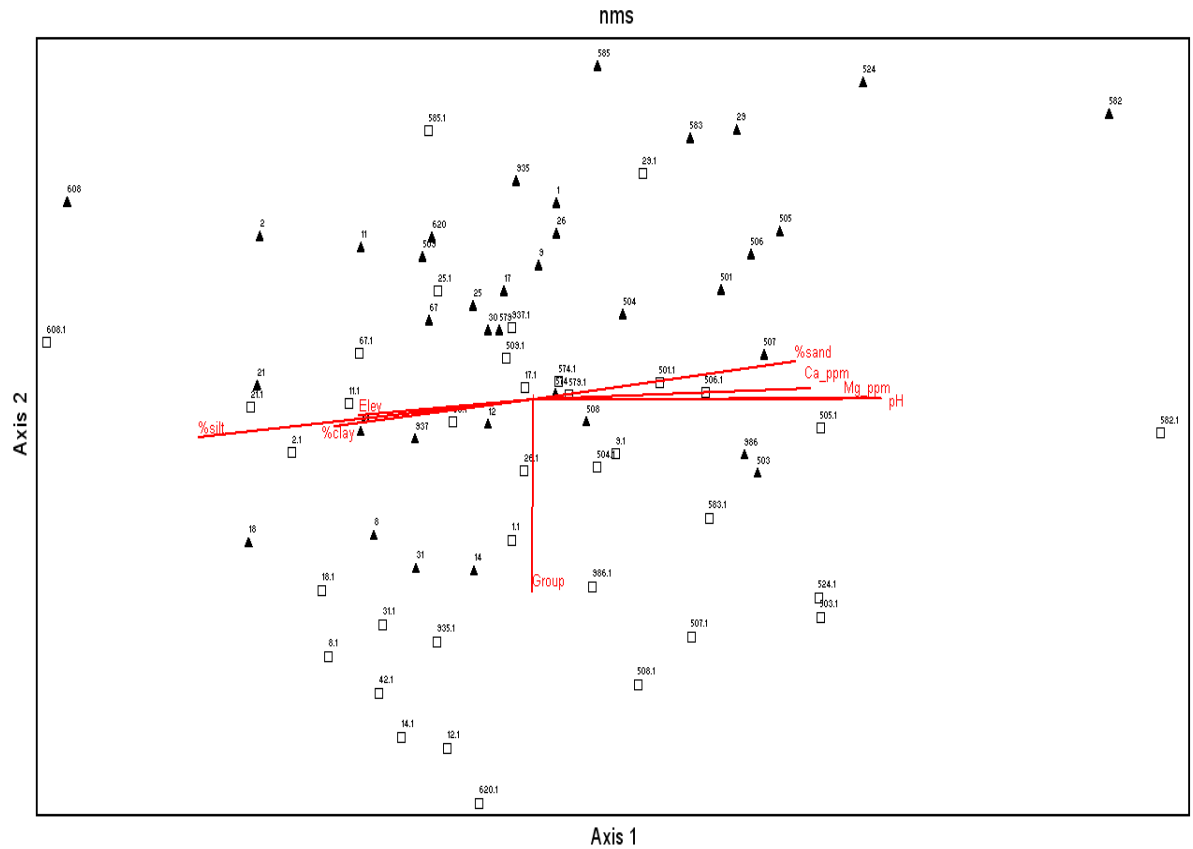


Figure 3.3. NMS ordination of plots in species space with correlation vectors of environmental variables (radiating from center) with the ordination. Ordination is based on the 226 species that occurred in no fewer than two hardwood plots. Environmental variables were measured in 1977 and are assumed to have been constant over time. All correlation vectors have $r^2 \geq .250$. Length of correlation vectors represents the strength of the correlation and angle indicates direction of highest correlation. Symbols are plots coded for year (triangle= 1977, square = 2000). (Group) is a categorical variable for year (1977 or 2000). All other environmental variables are defined in Table 3.1.

CHAPTER 4
CONCLUSIONS

This study has demonstrated how both the landscape distribution and local dynamics of hardwood stands in the North Carolina Piedmont are shaped by the interaction of environmental factors with historic and present disturbance regimes. Oak-hickory hardwood forests are no longer present at their original extent and their biased distribution suggests that we may never know the full range of species assemblages that once existed in association with the forests of this region. Given the lack of early records on hardwood forests, it is difficult to assess the species loss that has already occurred as a result of previous agricultural disturbance and habitat fragmentation.

The understory analysis in mature hardwood forests (Chapter 3) highlights an additional trend of recent herbaceous species decline occurring separate from the above threats. The Duke Forest hardwood stands have remained relatively intact during the study period and the significant species decline cannot be strongly attributed to the mechanisms commonly associated with species extinction, such as habitat loss and fragmentation, direct exploitation, and exotic species invasion (Wilcove 1998, Jolls 2003). These results echo the findings of the long-term analysis conducted by Rooney et al. (*in press*) in which they conclude that similar patterns of species loss suggest a major and largely unacknowledged trend of biotic impoverishment occurring in temperate forests throughout North America. Indeed, it is not unreasonable to assume that the recent pattern of herbaceous species decline in unfragmented hardwood forests of the Piedmont would have remained undetected for some time without the baseline data collected by Peet & Christensen.

The observation that historically ‘steady-state’ hardwood stands of the Piedmont exhibit understory and overstory (Christensen 1977, McDonald 2002, 2003) directional change and remain only as patches on the landscape by no means reduces their conservation value. These forests will likely never fit the traditional definition of old-growth (*sensu* Martin 1992, see also White & White 1996), but as a regional resource they have important attributes that have yet to be fully recognized. Hardwood stands that have remained continuously forested and free of severe soil disturbance since European settlement, even in the presence of other disturbances, likely support regional rare flora and are important for the protection of biological diversity.

Given the projected increases in population for the Piedmont region, which will place an even greater demand on forested areas, it is crucial that greater effort is put towards studying the mechanisms important in effecting change, along with increased support for the protection of remaining remnant hardwood stands. Future research on mechanisms of hardwood compositional change could entail combining field experiments (such as deer exclosures) with structural equation modeling. Structural equation modeling is a useful technique for hardwood forest research in this region since it is a method for evaluating complex hypotheses involving multiple causal pathways among variables (McCune & Grace 2002). This modeling framework would allow us to compare the relative strengths of different variables, such as deer herbivory and fire suppression, in effecting species change and examine how they interact to cause shifts in understory composition. It would also be useful for future analyses to be expanded to include the understory as well as higher strata (e.g., shrub and overstory layers) since success in the understory is clearly linked to overstory development.

Knowledge of the distribution of mature hardwood stands and their shifting composition has important implications for conservation planning. We need to know what species are being lost and why in order to take proper management actions to preserve the ecological integrity of the stands. Programs such as the Nature Conservancy and the North Carolina Natural Heritage program have identified a number of unique stands of Piedmont hardwood, but these areas are not all currently protected and nor is there any ongoing systematic monitoring program. Inadequate monitoring can lead to a lack of detection of regional threats on native species and result in the continued loss of flora.

More proactive measures for the protection and monitoring of remnant hardwood stands will not only support the stands themselves, but also contribute to regional restoration efforts in post-agriculture or other disturbed forest sites. Previous research has shown that it may take tens to hundreds of years for some forest plant species to recolonize secondary forests due to factors such as seed limitation and slow dispersal capabilities (e.g., Peterken & Game 1984, Whitney & Foster 1988, Bossuyt et al. 1999). If remnant stands do indeed support a distinct flora in comparison to more heavily disturbed sites, introductions into potentially suitable but unoccupied sites should be considered. Regional restoration efforts should also aim to support the reintroduction of natural disturbance regimes, such as low-intensity ground fires.

Without active monitoring, protection and restored natural disturbance regimes, I forecast a continued decline in the extent of oak-hickory hardwood forests in the North Carolina Piedmont, along with a shift towards a more overall mesic species composition. Indeed, it has been suggested that, even for sites that remain protected, upland oak-hickory will become a rare ecosystem type in the future (Fralish et al. 1991, Abrams 2003). In

addition, understory trends will likely include an increased loss of sensitive herb species along with the further spread of exotic species. Proactive measures to monitor changes in diversity and to identify and respond to particular threats would greatly help reduce the impact of anthropogenic disturbance on native forests in the future.

**APPENDIX A. FULL SPECIES LIST FOR DUKE FOREST HARDWOOD
PLOTS FROM 1977 TO 2000**

Number of species =319. Change in frequency reflects absolute change.

L/G: New species gained (+) or species lost (-) between 1977 and 2000

GF: Growthform, 1=Tree; 2=Shrub; 3=Herb

Nativity: N=Native; I=Introduced (exotic)

ShadeT: Shade tolerance, High; Medium (Mid); Low

1977 Subplot Occurrence: Total number of subplots species occurred
in across all plots in 1977

Scientific name	L/G	GF	Nativity	ShadeT	1977 Subplot	Change in frequency	
					Occurrence	Subplot	Plot
<i>Acer barbatum</i>		1	N	High	42	56	5
<i>Acer rubrum</i>		1	N	Mid	516	37	1
<i>Amelanchier arborea</i>		1	N	High	7	5	4
<i>Betula nigra</i>	-	1	N	Low	0	0	-1
<i>Carpinus caroliniana</i>		1	N	High	39	102	8
<i>Carya alba</i>		1	N	Mid	106	6	2
<i>Carya cordiformis</i>		1	N	Mid	3	13	5
<i>Carya glabra</i>		1	N	Mid	168	-37	0
<i>Carya ovata</i>		1	N	Mid	88	30	12
<i>Carya pallida</i>		1	N	Mid	6	-5	0
<i>Castanea dentata</i>	-	1	N	Low	1	-1	-1
<i>Celtis laevigata</i>		1	N	High	9	-8	-4
<i>Celtis occidentalis</i>		1	N	Mid	1	10	5
<i>Cercis canadensis</i>		1	N	High	93	29	0
<i>Chionanthus virginicus</i>		1	N	High	24	-7	-1
<i>Cornus florida</i>		1	N	High	223	3	3
<i>Crataegus flabellata</i>	-	1	N	Mid	2	-2	-1
<i>Crataegus flava</i>		1	N	Low	0	0	-4
<i>Crataegus marshallii</i>		1	N	High	0	1	1
<i>Crataegus sp.</i>		1	N	Mid	0	0	0
<i>Diospyros virginiana</i>		1	N	Mid	17	-2	2
<i>Fagus grandifolia</i>		1	N	High	53	39	12
<i>Fraxinus americana</i>							
+ <i>pensylvancia</i>		1	N	Mid	33	88	9
<i>Gleditsia triacanthos</i>	-	1	N	Low	0	0	-1
<i>Ilex ambigua</i>		1	N	High	4	-1	1
<i>Ilex decidua</i>		1	N	High	6	-5	1
<i>Ilex opaca</i>		1	N	High	5	0	5
<i>Juglans nigra</i>		1	N	Mid	2	-1	0
<i>Juniperus virginiana</i>		1	N	Mid	40	-3	4
<i>Liquidambar styraciflua</i>		1	N	Low	18	26	2
<i>Liriodendron tulipifera</i>		1	N	Low	27	105	6

<i>Morus rubra</i>		1	N	Mid	9	-2	1
<i>Nyssa sylvatica</i>		1	N	High	69	-14	4
<i>Ostrya virginiana</i>		1	N	High	76	60	4
<i>Oxydendrum arboreum</i>		1	N	Mid	26	18	2
<i>Paulownia tomentosa</i>	+	1	I	Mid	0	0	4
<i>Pinus echinata</i>		1	N	Mid	8	-8	3
<i>Pinus taeda</i>		1	N	High	31	-19	-3
<i>Pinus virginiana</i>		1	N	Mid	1	0	6
<i>Platanus occidentalis</i>	-	1	N	Mid	0	0	-1
<i>Prunus americana</i>	+	1	N	Low	0	0	1
<i>Prunus serotina</i>		1	N	High	146	-3	-2
<i>Quercus alba</i>		1	N	Mid	308	37	4
<i>Quercus coccinea</i>		1	N	Low	2	-2	-4
<i>Quercus falcata</i>		1	N	Mid	7	18	11
<i>Quercus marilandica</i>		1	N	Low	3	-3	-1
<i>Quercus michauxii</i>		1	N	Mid	0	0	-4
<i>Quercus montana</i>		1	N	Low	7	16	4
<i>Quercus phellos</i>		1	N	Low	15	1	8
<i>Quercus rubra</i>		1	N	Mid	85	-9	5
<i>Quercus stellata</i>		1	N	Mid	25	4	2
<i>Quercus velutina</i>		1	N	Mid	71	-8	4
<i>Robinia pseudoacacia</i>		1	N	Low	9	-4	-1
<i>Sassafras albidum</i>		1	N	Mid	29	4	0
<i>Styrax grandifolius</i>	+	1	N	High	0	1	2
<i>Ulmus alata</i>		1	N	Mid	7	49	6
<i>Ulmus rubra</i>		1	N	High	25	7	4
<i>Aesculus sylvatica</i>		2	N	Mid	30	-14	2
<i>Alnus serrulata</i>	-	2	N	High	0	0	-1
<i>Asimina parviflora</i>		2	N	High	0	2	5
<i>Campsis radicans</i>		2	N	Low	9	-5	-2
<i>Castanea pumila</i>		2	N	High	1	-1	0
<i>Ceanothus americanus</i>	-	2	N	High	0	0	-3
<i>Cornus foemina</i>	+	2	N	Mid	0	1	3
<i>Corylus americana</i>		2	N	Mid	3	-3	-3
<i>Elaeagnus umbellata</i>		2	I	Low	3	4	1
<i>Euonymus americana</i>		2	N	Mid	205	10	-1
<i>Gaylussacia baccata</i>	+	2	N	High	0	3	1
<i>Hamamelis virginiana</i>		2	N	Mid	19	-10	-2
<i>Hydrangea arborescens</i>	-	2	N	High	6	-6	-1
<i>Itea virginica</i>	-	2	N	High	0	0	-1
<i>Ligustrum sinense</i>		2	I	High	4	7	2
<i>Lindera benzoin</i>		2	N	Mid	7	1	-1
<i>Lonicera japonica</i>		2	I	High	181	-12	-2
<i>Lonicera sempervirens</i>		2	N	High	43	7	3
<i>Mahonia bealei</i>	+	2	I	High	0	0	1
<i>Parthenocissus quinquefolia</i>		2	N	Mid	121	2	8
<i>Passiflora incarnata</i>	+	2	N	High	0	2	3

<i>Rhododendron periclymenoides</i>		2	N	High	17	-11	-3
<i>Rhus aromatica</i>	-	2	N	High	0	0	-1
<i>Rhus copallinum</i>		2	N	Low	0	0	0
<i>Rosa carolina</i>		2	N	Mid	14	-4	0
<i>Rubus spp.</i>		2	N	Mid	4	29	13
<i>Sambucus nigra</i>	-	2	N	Low	16	-16	-5
<i>Smilax bona-nox</i>		2	N	High	28	-9	1
<i>Smilax glauca</i>		2	N	High	10	0	4
<i>Smilax rotundifolia</i>		2	N	Low	11	17	9
<i>Staphylea trifolia</i>		2	N	High	1	-1	1
<i>Toxicodendron radicans</i>		2	N	High	52	-13	2
<i>Trachelospermum difforme</i>	+	2	N	High	0	9	1
<i>Vaccinium fuscatum</i>	+	2	N	High	0	1	1
<i>Vaccinium pallidum</i>		2	N	High	75	-4	1
<i>Vaccinium stamineum</i>		2	N	High	81	10	0
<i>Vaccinium tenellum</i>		2	N	High	32	-19	-1
<i>Viburnum acerifolium</i>		2	N	High	122	79	5
<i>Viburnum dentatum</i>	-	2	N	High	2	-2	-1
<i>Viburnum prunifolium</i>		2	N	High	39	-18	2
<i>Viburnum rafinesquianum</i>		2	N	High	443	-3	-2
<i>Viburnum rufidulum</i>		2	N	High	20	15	4
<i>Vitis aestivalis</i>		2	N	High	55	-28	-8
<i>Vitis rotundifolia</i>		2	N	Mid	127	150	2
<i>Actaea racemosa</i>		3	N		4	2	0
<i>Adiantum pedatum</i>	-	3	N		0	0	-1
<i>Agrimonia pubescens</i>		3	N		18	4	-5
<i>Amphicarpaea bracteata</i>		3	N		24	5	1
<i>Andropogon spp.</i>		3	N		15	-10	2
<i>Anemone virginiana</i>	-	3	N		0	0	-2
<i>Antennaria plantaginifolia</i>		3	N		6	-6	-3
<i>Aplectrum hyemale</i>	-	3	N		1	-1	-1
<i>Arabis canadensis</i>	-	3	N		1	-1	-1
<i>Arisaema dracontium</i>	+	3	N		0	3	1
<i>Arisaema triphyllum</i>		3	N		2	8	1
<i>Aristolochia serpentaria</i>		3	N		22	-8	1
<i>Arnoglossum atriplicifolium</i>	-	3	N		0	0	-1
<i>Asclepias variegata</i>	-	3	N		0	0	-1
<i>Asclepias verticillata</i>	-	3	N		0	0	-1
<i>Asplenium platyneuron</i>		3	N		15	-1	1
<i>Aureolaria virginica</i>		3	N		9	-8	-8
<i>Baptisia sp.</i>	+	3	N		0	0	2
<i>Bignonia capreolata</i>	-	3	N		4	-4	-1
<i>Boehmeria cylindrica</i>		3	N		2	-1	1
<i>Botrychium biternatum</i>		3	N		0	12	2

<i>Botrychium virginianum</i>		3	N	37	-3	-1
<i>Brachyelytrum erectum</i>		3	N	3	1	1
<i>Bromus pubescens</i>		3	N	0	2	-1
<i>Carex spp.</i>		3	N	123	5	-3
<i>Chamaecrista fasciculata</i>	+	3	N	0	0	1
<i>Chamaelirium luteum</i>		3	N	2	-1	-4
<i>Chasmanthium latifolium</i>		3	N	2	-2	1
<i>Chasmanthium laxum</i>	-	3	N	0	0	-1
<i>Cheilanthes lanosa</i>		3	N	18	-6	0
<i>Chimaphila maculata</i>		3	N	129	-52	-4
<i>Chrysogonum virginianum</i>		3	N	4	-4	-4
<i>Circaea lutetiana</i>		3	N	3	16	1
<i>Cirsium vulgare</i>	+	3	I	0	0	1
<i>Clematis viorna</i>		3	N	0	0	-1
<i>Clematis virginiana</i>		3	N	10	-4	0
<i>Clitoria mariana</i>		3	N	8	-5	-1
<i>Commelina communis</i>		3	I	0	0	-1
<i>Conopholis americana</i>	-	3	N	1	-1	-2
<i>Conyza canadensis</i>	+	3	N	0	0	1
<i>Coreopsis major</i>		3	N	4	-4	-1
<i>Coreopsis verticillata</i>		3	N	3	-3	-3
<i>Cryptotaenia canadensis</i>		3	N	3	-3	-1
<i>Cunila origanoides</i>		3	N	1	0	1
<i>Cynoglossum virginianum</i>	+	3	N	0	0	1
<i>Danthonia sericea</i>		3	N	0	1	-1
<i>Danthonia spicata</i>		3	N	34	-15	4
<i>Dennstaedtia punctilobula</i>		3	N	0	0	2
<i>Desmodium laevigatum</i>		3	N	31	-31	-6
<i>Desmodium nudiflorum</i>		3	N	126	-27	-1
<i>Desmodium obtusum</i>	-	3	N	2	-2	-3
<i>Desmodium paniculatum</i>		3	N	2	-2	-3
<i>Desmodium perplexum</i>		3	N	0	1	-4
<i>Desmodium rotundifolium</i>		3	N	7	-6	-6
<i>Desmodium sp.</i>	-	3	N	2	-2	-2
<i>Desmodium viridiflorum</i>	+	3	N	0	0	1
<i>Dichantheium sp.</i>		3	N	48	5	0
<i>Dioscorea villosa</i>		3	N	26	-7	0
<i>Eleocharis sp.</i>	+	3	N	0	1	1
<i>Elephantopus carolinianus</i>		3	N	3	-1	-1
<i>Elephantopus tomentosus</i>	-	3	N	0	0	-3
<i>Elymus hystrix</i>		3	N	15	17	1
<i>Elymus villosus</i>	-	3	N	0	0	-2
<i>Elymus virginicus</i>	+	3	N	0	0	1
<i>Epifagus virginiana</i>	-	3	N	6	-6	-4

<i>Epigaea repens</i>		3	N	2	-2	-1
<i>Erechtites hieraciifolia</i>	+	3	N	0	2	2
<i>Erigeron annuus</i>	-	3	N	0	0	-1
<i>Erythronium americanum</i>	-	3	N	1	-1	-1
<i>Eupatorium capillifolium</i>	+	3	N	0	0	1
<i>Eupatorium fistulosum</i>	+	3	N	0	0	1
<i>Eupatorium hyssopifolium</i>	-	3	N	0	0	-1
<i>Euphorbia corollata</i>		3	N	12	-7	-9
<i>Eurybia divaricata</i>		3	N	2	-2	0
<i>Festuca subverticillata</i>		3	N	2	15	1
<i>Fragaria virginiana</i>		3	N	5	-3	-1
<i>Galactia volubilis</i>	-	3	N	5	-5	-1
<i>Galium aparine</i>	-	3	N	0	0	-1
<i>Galium circaezans</i>		3	N	101	19	-1
<i>Galium obtusum</i>	-	3	N	0	0	-2
<i>Galium pilosum</i>	-	3	N	3	-3	-2
<i>Galium triflorum</i>		3	N	15	-3	-2
<i>Gelsemium sempervirens</i>	-	3	N	0	0	-1
<i>Geum canadense</i>		3	N	17	-7	1
<i>Geum sp.</i>	+	3	N	0	0	1
<i>Geum virginianum</i>	-	3	N	0	0	-1
<i>Glechoma hederacea</i>	+	3	I	0	4	2
<i>Goodyera pubescens</i>		3	N	12	-9	-7
<i>Heliopsis helianthoides</i>	+	3	N	0	0	1
<i>Hepatica nobilis</i>		3	N	23	6	1
<i>Heuchera americana</i>		3	N	0	0	-2
<i>Hexastylis arifolia</i>		3	N	96	60	1
<i>Hexastylis minor</i>		3	N	18	-5	0
<i>Hieracium gronovii</i>	-	3	N	3	-3	-2
<i>Hieracium venosum</i>		3	N	25	-13	0
<i>Houstonia caerulea</i>	-	3	N	3	-3	-5
<i>Houstonia purpurea</i>	-	3	N	0	0	-2
<i>Huperzia lucidula</i>		3	N	1	2	0
<i>Hypericum hypericoides</i>		3	N	0	0	-2
<i>Hypericum nudiflorum</i>	+	3	N	0	0	1
<i>Hypericum prolificum</i>	-	3	N	0	0	-1
<i>Hypoxis hirsuta</i>		3	N	2	0	1
<i>Impatiens capensis</i>		3	N	0	6	0
<i>Ipomoea pandurata</i>		3	N	4	-2	0
<i>Iris cristata</i>		3	N	5	-2	-2
<i>Iris verna</i>		3	N	0	0	0
<i>Juncus coriaceus</i>		3	N	3	-3	0
<i>Juncus tenuis</i>	+	3	N	0	2	1
<i>Lactuca canadensis</i>		3	N	0	0	-1
<i>Lathyrus venosus</i>	-	3	N	1	-1	-1
<i>Leersia virginica</i>		3	N	0	1	1
<i>Lespedeza hirta</i>	-	3	N	7	-7	-4

<i>Lespedeza procumbens</i>	+	3	N	0	1	2
<i>Lespedeza repens</i>		3	N	8	-8	-4
<i>Lespedeza sp.</i>	+	3		0	2	3
<i>Lespedeza violacea</i>		3	N	3	-3	3
<i>Lespedeza virginica</i>		3	N	1	-1	0
<i>Liatris pilosa</i>	-	3	N	1	-1	-1
<i>Ligusticum canadense</i>		3	N	3	-1	-3
<i>Lilium michauxii</i>	-	3	N	1	-1	-3
<i>Liparis liliifolia</i>		3	N	1	-1	-1
<i>Lobelia inflata</i>	+	3	N	0	4	1
<i>Lobelia nuttallii</i>	+	3	N	0	0	1
<i>Lobelia sp.</i>	+	3	N	0	0	1
<i>Luzula acuminata</i>		3	N	1	2	-1
<i>Lycopodium digitatum</i>		3	N	0	0	0
<i>Lycopus virginicus</i>	-	3	N	1	-1	-1
<i>Lysimachia ciliata</i>		3	N	3	-2	-1
<i>Maianthemum racemosum</i>		3	N	59	-17	0
<i>Marshallia obovata</i>	-	3	N	0	0	-1
<i>Matelea carolinensis</i>		3	N	13	-6	0
<i>Medeola virginiana</i>	+	3	N	0	0	1
<i>Melanthium virginicum</i>	+	3	N	0	0	2
<i>Melica mutica</i>		3	N	7	-2	-3
<i>Menispermum canadense</i>		3	N	5	5	1
<i>Microstegium vimineum</i>		3	I	25	16	7
<i>Mitchella repens</i>	+	3	N	0	0	2
<i>Monarda fistulosa</i>	+	3	N	0	0	1
<i>Monotropa hypopithys</i>	-	3	N	0	0	-1
<i>Muhlenbergia schreberi</i>	-	3	N	0	0	-1
<i>Onoclea sensibilis</i>		3	N	3	2	1
<i>Oxalis spp.</i>		3	N	5	25	2
<i>Parthenium integrifolium</i>	-	3	N	15	-15	-2
<i>Passiflora lutea</i>		3	N	0	2	0
<i>Penstemon australis</i>	-	3	N	0	0	-1
<i>Penstemon laevigatus</i>	-	3	N	0	0	-3
<i>Phlox sp.</i>	+	3	N	0	1	1
<i>Phryma leptostachya</i>		3	N	9	13	5
<i>Physalis virginiana</i>	-	3	N	1	-1	-2
<i>Phytolacca americana</i>	+	3	N	0	7	8
<i>Piptochaetium avenaceum</i>		3	N	20	-10	-4
<i>Pityopsis graminifolia</i>	-	3	N	1	-1	-2
<i>Plantago rugelii</i>	+	3	N	0	0	1
<i>Pleopeltis polypodioides</i>		3	N	0	0	-1
<i>Poaceae spp.</i>		3	N	29	35	17
<i>Podophyllum peltatum</i>		3	N	3	-1	0
<i>Polygonatum biflorum</i>		3	N	117	-13	1

<i>Polygonum sp.</i>	+	3		0	1	1
<i>Polygonum virginianum</i>	-	3	N	8	-8	-1
<i>Polypodium virginianum</i>		3	N	2	0	0
<i>Polystichum acrostichoides</i>		3	N	44	-14	4
<i>Porteranthus trifoliatu</i>	-	3	N	0	0	-1
<i>Potentilla canadensis</i>		3	N	10	-3	0
<i>Prenanthes altissima</i>		3	N	38	-16	-5
<i>Prenanthes serpentina</i>	+	3	N	0	6	2
<i>Prunella vulgaris</i>		3	N	0	0	0
<i>Pteridium aquilinum</i>	+	3	N	0	0	1
<i>Pycnanthemum incanum</i>	-	3	N	2	-2	-1
<i>Pycnanthemum tenuifolium</i>	-	3	N	1	-1	-1
<i>Pyrola americana</i>	-	3	N	2	-2	-1
<i>Ranunculus spp.</i>		3	N	1	0	0
<i>Rhus glabra</i>		3	N	0	0	2
<i>Rudbeckia laciniata</i>		3	N	11	-11	-1
<i>Ruellia caroliniensis</i>		3	N	2	6	-5
<i>Salvia lyrata</i>		3	N	1	-1	2
<i>Sanguinaria canadensis</i>		3	N	0	9	2
<i>Sanicula spp.</i>		3	N	30	11	0
<i>Scleria oligantha</i>		3	N	14	19	2
<i>Scrophularia spp.</i>	+	3	N	0	0	1
<i>Scutellaria elliptica</i>		3	N	0	8	2
<i>Scutellaria integrifolia</i>		3	N	2	1	1
<i>Scutellaria serrata</i>		3	N	13	-13	0
<i>Sedum ternatum</i>		3	N	0	0	0
<i>Sericocarpus asteroides</i>		3	N	1	0	-3
<i>Sericocarpus linifolius</i>	-	3	N	0	0	-1
<i>Silene virginica</i>	-	3	N	1	-1	-4
<i>Silphium asteriscus</i>	-	3	N	2	-2	-2
<i>Silphium compositum</i>	-	3	N	0	0	-1
<i>Sisyrinchium angustifolium</i>	-	3	N	16	-16	-1
<i>Smallanthus uvedalius</i>		3	N	5	2	0
<i>Smilax herbacea</i>	-	3	N	0	0	-1
<i>Solidago spp.</i>		3	N	36	-25	-1
<i>Stellaria media</i>	+	3	I	0	0	1
<i>Stellaria pubera</i>		3	N	10	5	2
<i>Stylosanthes biflora</i>	-	3	N	3	-3	-2
<i>Symphyotrichum dumosum</i>	+	3	N	0	0	1
<i>Symphyotrichum undulatum</i>		3	N	16	-14	0
<i>Tephrosia virginiana</i>	-	3	N	2	-2	-4
<i>Thalictrum revolutum</i>		3	N	1	0	-1
<i>Thalictrum thalictroides</i>		3	N	19	2	-2
<i>Thaspium barbinode</i>		3	N	6	0	-1

<i>Thaspium trifoliatum</i>		3	N	1	-1	0
<i>Tiarella cordifolia</i>		3	N	22	-6	-2
<i>Tipularia discolor</i>		3	N	0	0	-2
<i>Tradescantia virginiana</i>	+	3	N	0	0	1
<i>Tragia urticifolia</i>	-	3	N	4	-4	-1
<i>Trifolium pratense</i>	+	3	I	0	0	1
<i>Trillium catesbaei</i>		3	N	16	-16	-2
<i>Uvularia perfoliata</i>		3	N	70	1	4
<i>Uvularia puberula</i>		3	N	0	4	0
<i>Uvularia sessilifolia</i>	-	3	N	1	-1	-2
<i>Verbascum thapsus</i>	+	3	I	0	0	3
<i>Verbesina alternifolia</i>	+	3	N	0	0	1
<i>Verbesina occidentalis</i>		3	N	24	-1	0
<i>Vernonia glauca</i>	-	3	N	0	0	-2
<i>Vernonia sp.</i>	+	3	N	0	0	1
<i>Viola spp.</i>		3	N	39	-1	-5
<i>Zizia aurea</i>	-	3	N	0	0	-1

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