A DENDROCHRONOLOGICAL APPROACH FOR ANALYZING THE GEOGRAPHIC RANGE STRUCTURE OF TREE SPECIES

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DEDICATION

This dissertation is dedicated to the memory of my father, John Sakulich (1931 – 2005).

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ABSTRACT

The purpose of this dissertation research was to investigate the spatial patterns of abundance, growth, and stand structure across the geographic ranges of tree species using dendroecological methods. I assessed whether the biogeographic paradigms of the abundant center hypothesis and the principle of ecological amplitude adequately characterize spatial patterns of tree abundance, climate response, and stand composition. The abundant center hypothesis is a longstanding, yet rarely tested assumption that the centers of geographic ranges represent ideal conditions where species can achieve their greatest abundance, and abundance declines with increasing distance from the range center. A corollary to the abundant center hypothesis is the concept of ecological amplitude, which predicts that species will be subject to greater environmental stress near range margins, and thus, will be more sensitive to environmental variability and occupy restricted sites in peripheral locations.

To investigate ecological amplitude predictions regarding tree species of North America, I analyzed: (1) the abundance of red fir to directly test the abundant center hypothesis, (2) the response of longleaf pine growth to monthly climate variables at peripheral and interior sites, (3) the spatial pattern of annual growth sensitivity to climate in networks of tree-ring data for two widely-distributed species, and (4) the composition and structure of pine-oak stands at a central and a peripheral location within the ranges of several dominant tree species.

The analyses presented here demonstrate that the abundant center hypothesis and ecological amplitude principle do not accurately characterize spatial patterns of

abundance, growth, or stand composition among North American tree species. Lack of support for the abundant center/ecological amplitude paradigm suggests that current models of forest change and species' range dynamics should be reconsidered, and new models should be developed based on empirical analysis of range structure and dynamics.

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CHAPTER 1

INTRODUCTION

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INTRODUCTION

1.1 Purpose

This dissertation research investigates the spatial pattern of abundance, growth, and stand structure across the geographic ranges of several dominant North American tree species using dendrochronology and forest inventory methods. The major goal of this research is to gain increased understanding of patterns of abundance and vegetation dynamics relative to the geographic range boundaries of species. This study investigates long-standing and untested assumptions about the variability of range structure by testing hypotheses about spatial variability in annual growth and community dynamics. Understanding the mechanisms that influence patterns of abundance and limits to species distributions is of paramount importance in addressing many contemporary conservation challenges, such as maintaining biodiversity, controlling the spread of exotic species, and predicting biological responses to climate change.

1.2 Geographic Ranges

No species is found everywhere on Earth. All species have a geographic range that represents areas where they occur as opposed to areas where they are absent (Brown and Lomolino 1998). The identification of species' ranges and the investigation of controls that determine their structure and dynamics form the foundation of the science of biogeography (Brown and Lomolino 1998, Hengeveld et al. 2004). Furthermore, determining the factors that affect species distributions is essential to understanding the processes that contribute to patterns

of biological and genetic diversity, and is thus vital to the fields of ecology and evolutionary biology (Holt and Keitt 2005).

Geographic ranges are determined by environmental conditions as well as attributes of organisms themselves (Hengeveld et al. 2004). Many early biogeographical inquiries focused on range boundaries and sought to explain the abiotic and biotic factors that limited or facilitated the spread of species (e.g., Merriam 1894, Griggs 1914, Grinnell 1917). The most common abiotic factors thought to determine species' range limits are physical barriers and climate (Gaston 2003). Physical features such as coastlines, mountain chains, and rivers can present barriers to the dispersal of organisms and result in coincident range edges for many taxa in the same location (Rapoport 1982).

A vast amount of literature regarding range limits invokes climate as an explanatory control on the distribution of species (Gaston 2003). The focus on climate as a determinant of range limits is likely due to the perceived correlations between climatic variables (especially temperature) and the distributional limits of species (Grinnell 1917, Hutchinson 1918, Halliday and Brown 1943). However, MacArthur (1972) argued that climatic conditions are rarely lethal to species near range boundaries, and are unlikely to be a direct cause of range limits. Additionally, the successful introduction of many species to new locations beyond their range limits with more extreme climatic conditions suggests that climate-induced mortality is not an explanation of most distributions, and climatic controls on species are more likely to be indirect, such as limitation of reproductive capacity (Salisbury 1926, MacArthur 1972, Gaston 2003).

In addition to abiotic controls on the distribution of species, biotic factors in the form of species' attributes and interspecific interactions are often invoked as explanations of geographic range limits (Hengeveld et al. 2004). Attributes of species themselves determine, in part, whether a barrier constitutes a true range edge. For example, a physical barrier, such as a mountain chain, may not be an obstacle for species with high dispersal ability and physiological capacity to withstand a broad range of climatic conditions, but it may become a range boundary for species with limited dispersal ability and restricted climatic tolerance. Additionally, interactions with other taxa, including predators, prey, competitors, pathogens, or pollinators, can influence the shape of species' range boundaries (Case et al. 2005, Gaston 2009, Price and Kirkpatrick 2009).

Investigations into the pattern and process of range limits continue to be an active area of research, particularly in recent decades because of the urgent need to understand biological responses to global change. Rapid climate change, biological invasions, pollution, and habitat fragmentation are affecting the distribution of many species (Parmesan et al. 2000, Gaston 2003, Parmesan et al. 2005, Gaston 2009). Mitigating the undesirable consequences of these factors requires refined understanding of geographic range dynamics. However, despite the long history and abundant body of research on geographic range limits, systematic investigations into the structure of geographic ranges within range boundaries have only gained traction as an area of research in the last three decades (MacArthur 1972). Additionally, long-held paradigms of within-range species abundance have been based on largely untested assumptions (Sagarin and Gaines 2002, Gaston 2003).

1.3. The Abundant Center Hypothesis

The concept that species are most abundant near their range centers and abundance gradually declines toward range margins is often referred to as the abundant center hypothesis and has long been considered a general ecological paradigm (Shelford 1911, Wulff 1943, Andrewartha and Birch 1954, Hengeveld and Haeck 1982, Hengeveld 1990). This assumption is based on a multi-dimensional niche concept, where patterns of abundance are thought to vary along multiple environmental gradients, and centers of high and low population density within a species' range are the result of how closely environmental conditions meet that species' optimal requirements (Wulff 1943, Brown 1984, Brown and Lomolino 1998). Therefore, the point of intersection of a species' multiple niche axes would be the optimal habitat for that species, where it could reach its greatest abundance and occupy the widest range of sites (Brown 1984). Additionally, environmental conditions are assumed to be spatially autocorrelated and near sites will be more likely to meet a species' requirements than distant sites (Brown et al. 1995). Consequently, a species would be less likely to find its niche requirements met at greater distances from its optimal habitat and population density will gradually decline to zero (the range boundary) when conditions are completely unsuitable.

Several modifications and extensions of the abundant center distribution have been proposed. For example, Gaston (2003) contended that the simple hump-shaped model (Figure 1.1A) of abundance is incorrect because no species has a continuous distribution across its entire range, and proposed that a more realistic model of the abundant center distribution would characterize the degree of variance within the abundances of local populations

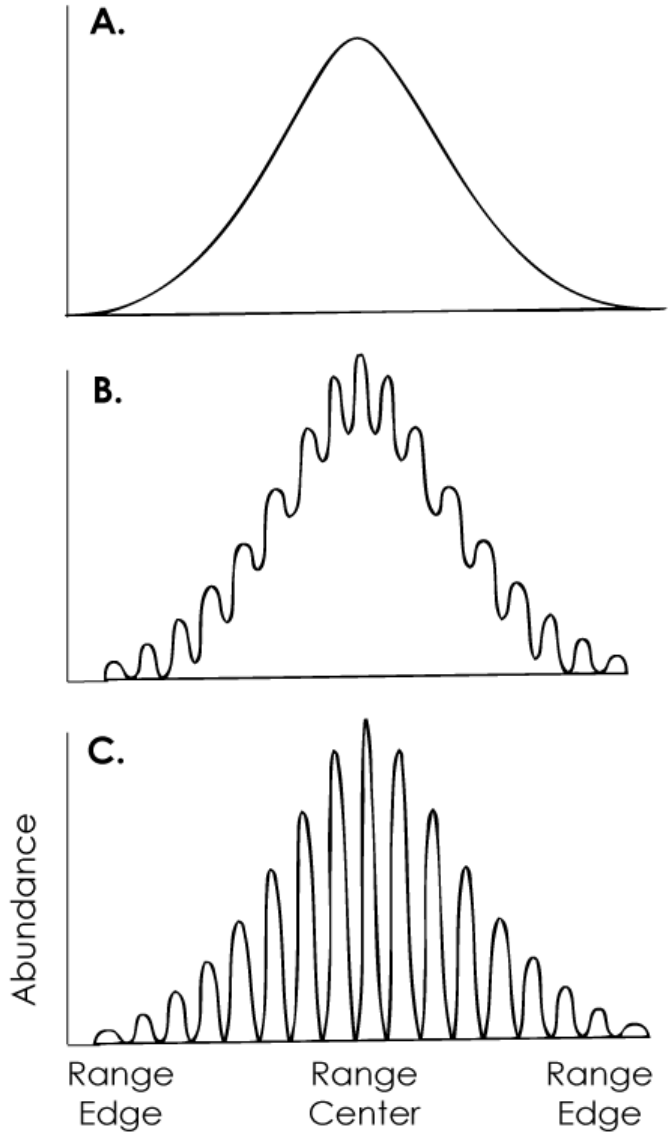

Figure 1.1. Hypothetical representations of the abundant center distribution. Abundance is plotted along a transect from one edge of a species' range to another through the center of the range. The models show a continuous distribution (A), a distribution with low variance (B), and high variance (C), which accounts for a species being absent at locations across its range. Figure redrawn from Gaston (2003).

(Figures 1.1B and 1.1C). Additionally, temporal variability of environmental conditions that alters the suitability of habitat has been theorized to affect abundance most strongly at the margins of species' ranges resulting in expansions, contractions, and shifts in geographic ranges (Andrewartha and Birch 1954) (Figure 1.2).

Numerous studies of a wide variety of taxa have claimed to support the abundant center hypothesis, but many of these analyses have shortcomings. Hengeveld and Haeck (1982) analyzed hundreds of species of insects, birds, and plants in northern Europe and correlated the abundance of each species with its distance from range edge. They concluded that a trend toward lower abundance exists as range edges are approached. However, other studies have shown that this indirect approach to testing the abundant center hypothesis may lead to spurious relationships because the extent to which abundance data fit a trend is related to the area over which the data are collected and the range sizes of the species (Blackburn et al. 1999).

Brown (1984) concluded that abundance data from breeding bird surveys in North America fit an abundant center pattern when mapped. He analyzed abundance along radial transects from the center to the edge of species' ranges, but did not conduct any tests to assess the statistical significance of the pattern. Additionally, reliance on relatively few data points and under-sampling of edges relative to range center limit the robustness of this analysis (Sagarin and Gaines 2002, Gaston 2003).

Brown et al. (1995) argued that the shape of spatial autocorrelation functions of breeding bird census data indicates an abundant center pattern. Plots of spatial autocorrelograms

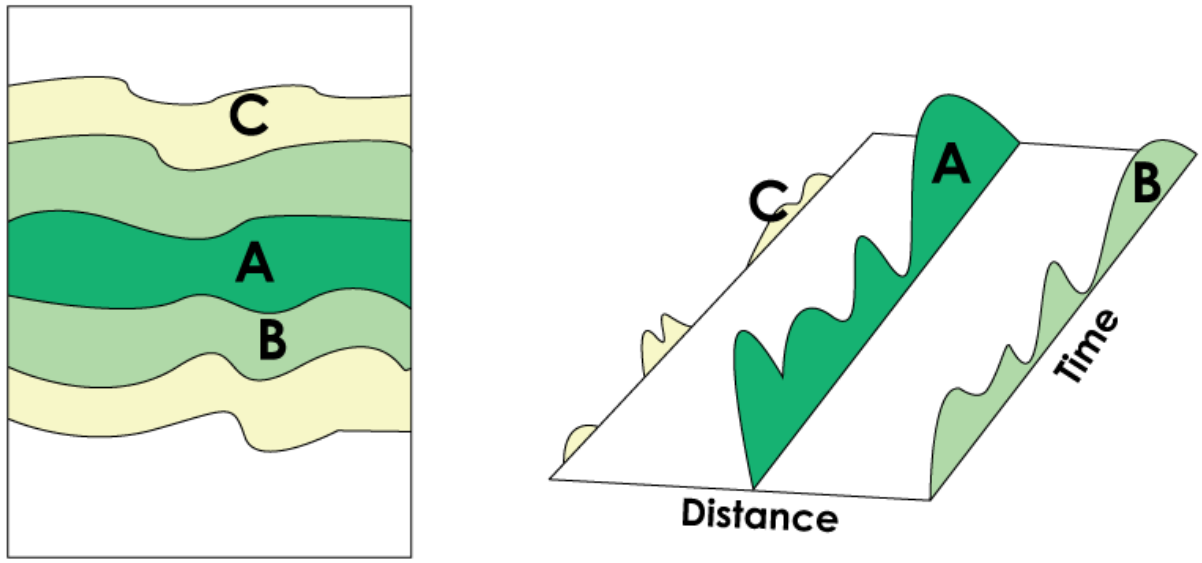

Figure 1.2 Visualization of hypothetical species abundance. The left panel shows areas of high abundance at the range center (dark green) to uninhabited area outside the range (white). The right panel shows variation of abundance through time in areas of (A) high relative abundance, (B) low abundance, and (C) temporary abundance. Figure redrawn from Andrewartha and Birch (1954).

(Moran's I) were typically U-shaped, indicating high spatial autocorrelation among very near and very distant sites (Figure 1.3). Brown et al. (1995) contended this pattern emerged because sites near the range center are in close proximity and have similarly high abundances while sites near range margins are distant from each other and have similarly low abundances. Examination of maps of the distribution of abundance derived from the same data, however, reveals that few species exhibit a single, central peak of abundance, and a U-shaped autocorrelogram can be generated by multiple distant peaks of high abundance (Price et al. 1995, Gaston 2003).

During the past decade, reviews of the literature regarding the abundant center distribution found very few studies that have directly tested the abundant center hypothesis, and fewer still that have supported it (Sagarin and Gaines 2002, Gaston 2003, Sexton et al. 2009). In a comprehensive literature review, Sagarin and Gaines (2002) found only 22 studies that directly tested the abundant center hypothesis, and of the 145 hypothesis tests conducted within those studies, only 39% reported an abundant center pattern in the organisms under analysis. Additionally, many of the studies that reported support for the hypothesis had insufficient data to make reliable conclusions. The lack of empirical support for the abundant center hypothesis as a model for geographic range structure has led recent researchers to investigate whether geographically peripheral populations are in fact ecologically or climatically peripheral, and nearly all recent studies concluded that the abundant center distribution is not a general rule (Samis and Eckert 2007, Yakimowski and Eckert 2007, Duffy et al. 2009, Jarema et al. 2009, Gerst et al. 2011).

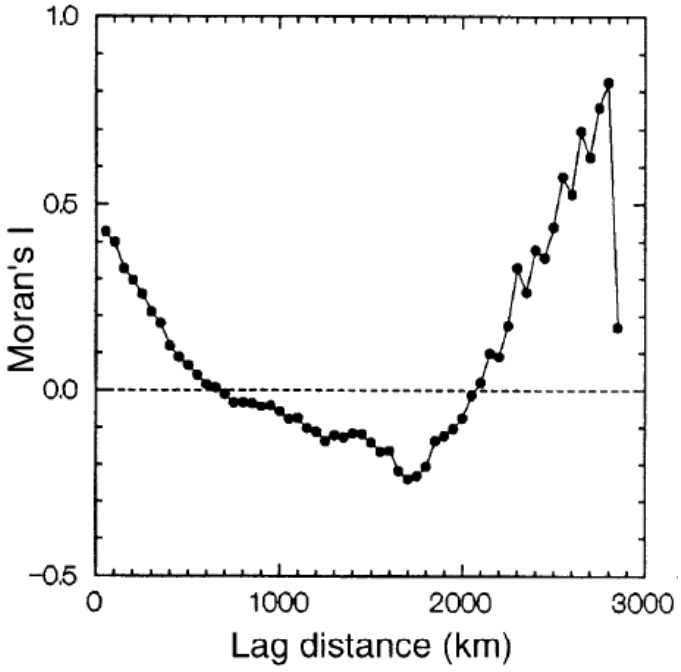

Figure 1.3. Spatial autocorrelation of abundance of Carolina wren (*Thryothorus ludovicianus*) from North American Breeding Bird Survey census routes. Figure from Brown et al. (1995).

Despite the lack of much empirical support, many ecological hypotheses with important conservation implications are based on an abundant center range structure. For example, Hengeveld (1990) noted that abundance or density is but one measure of species vitality, and hypothesized that many processes (e.g., growth, reproductive rates, ratio of sexual to vegetative reproduction) should also vary in a spatial pattern similar to the abundant center distribution. Furthermore, he proposed that population dynamics of range edges are more variable, and that extinction is more likely at range margins. Conversely, Safriel et al. (1994) suggested that edge populations are more resistant to climate change. Predictions based on the abundant center hypothesis have thus led to contradictory proposals that biological reserves should be preferentially located at range centers (Brown et al. 1995) and at range edges (Safriel et al. 1994).

1.4 Predicting Species' Responses to Climate Change

The abundant center paradigm assumes that species' ranges represent optimal response surfaces, where the vital attributes of species (abundance, growth, etc.) vary in response to environmental conditions (Gaston 2003). The optimal response surface concept underlies many attempts to explain relationships between species' distributions and climate, as well as efforts to project future species distributions under novel climatic conditions. The earliest investigations of optimal response were simply approaches that overlaid the geographic range of a species with environmental data, such as an isotherm map of temperatures, to find coincident patterns (Grinnell 1917, Halliday and Brown 1943, Hutchins 1947). More recently, advances in

multivariate techniques for statistical analysis, GIS for spatial data manipulation, and computing power have enabled the analysis of suites of climatic and environmental data to create bioclimatic envelope models of species range dynamics (Parmesan et al. 2005).

Predicting the future distribution of trees is crucial for understanding the consequences of global climate change for forest ecosystems and carbon cycle dynamics (Iverson and Prasad 2001, Ellison et al. 2005, van Mantgem et al. 2009). Most predictive efforts are based on a climate envelope approach carried out by modeling the association between climate and species distributions, and assessing the influence of various climate change scenarios on the resulting modeled distributions (Iverson et al. 1999, McKenney-Easterling et al. 2000, Parker et al. 2000, Schwartz et al. 2001). Prasad et al. (2007) developed one of the most comprehensive databases of modeled distributions of species under climate change scenarios, modeling range shifts for 134 eastern U.S. tree species in their Climate Change Tree Atlas (Figure 1.4).

Unfortunately, this modeling approach has many shortcomings and makes vital assumptions that are likely to be violated. For example, modeling future species distributions based on correlations between current distributions and climatic conditions assumes a causal relationship between climate and range limits. This assumption is unlikely to hold in all situations because many other factors can affect species occurrence, such as dispersal ability, competition, resource availability, predation, pathogens, and disturbance events (Gaston 2003). Moreover, species are likely to respond to climate change in very complex ways because they will be responding not only to changes in climate variables, but also to climate-induced population dynamics of predators, competitors, pollinators, and pathogens (Schmitz et al. 2003).

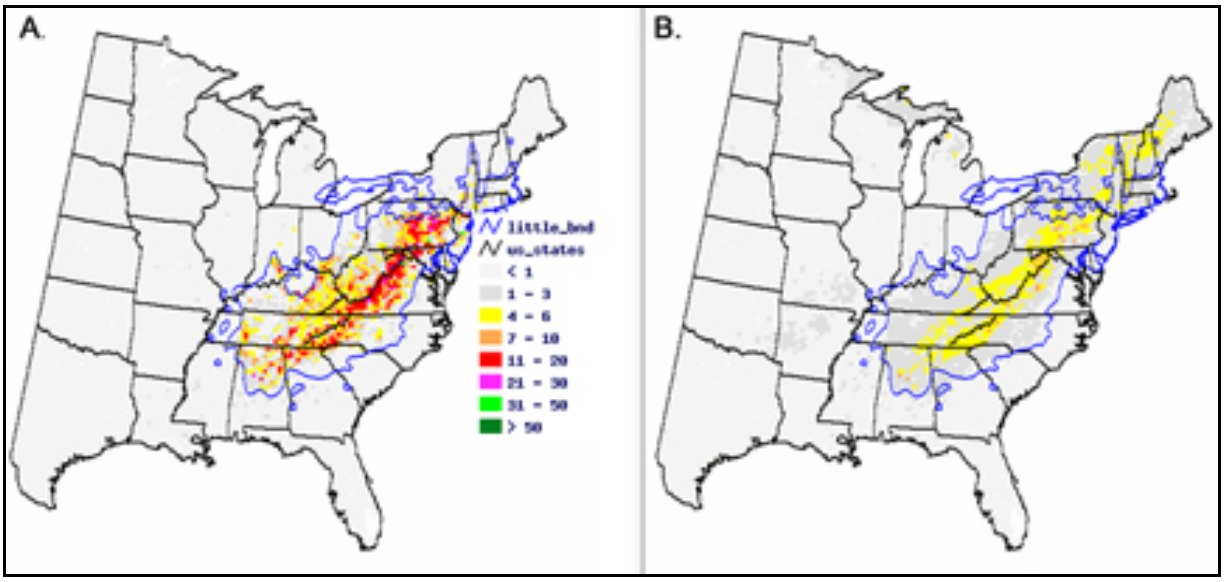

Figure 1.4. Current abundance (A) and projected abundance within modeled suitable habitat (B) of chestnut oak (*Quercus montana* Willd.) Current abundance data categories are ranges of species importance values from the USDA Forest Inventory and Analysis Program. Potential suitable habitat and associated importance values are as projected for the year AD 2100 under Hadley HADCM3 climate model high-emissions scenario. Figure from Prasad et al. (2007).

Additionally, changes in climate are likely to have indirect effects on organisms by altering the frequency and intensity of disturbance events (Taylor and Beaty 2005, Trouet et al. 2010). Current modeling approaches also assume that organisms have no physiological capacity to persist beyond the prevailing climatic conditions within their current distributional limits. Empirically based studies have demonstrated that this is not the case (Spicer and Gaston 1999, Sagarin et al. 2006). Understanding the environmental controls on species distributions, and how distributions will change over time and space, requires comprehensive investigation of species population dynamics and variability of biological processes across the range of habitats where they are found. This understanding will aid and refine attempts at modeling potential species distributions under new climatic or disturbance regimes.

1.5. Ecological Amplitude

A concept closely related to the abundant center distribution and optimal response surfaces is the principle of ecological amplitude. The ecological amplitude concept assumes that species occupy a narrower range of sites, are more likely to occupy sites with low environmental suitability, and are exposed to higher levels of environmental stress near geographic range limits (Fritts 1976, Holt and Keitt 2005). Increasing environmental stress should then lead to lower rates of growth and reproduction, and these lower physiologically vital rates may provide an explanatory mechanism for abundant center distributions of species (Hengeveld 1990).

Griggs (1914) was one of the first researchers to articulate this pattern by distinguishing between stations (local populations) and the overall geographic ranges of plants. In a study of 123 plant species in Ohio, he found few species that become gradually less abundant in stations closer to their range edge, but many species that occur in fewer stations as range limits are approached. He noted, "…whereas a species may be ubiquitous in the centre of its range occurring in all sorts of habitats because highly favored, at its areal limits it will be closely limited to those conditions which are most favorable to it." It follows that one prediction of the ecological amplitude principle is that species will occupy only restricted sites near their geographic range limits.

Additional studies have supported the ecological amplitude prediction that habitat availability is the proximate cause of range limits. In a survey of prickly lettuce (*Lactuca serriola*) at its northern distributional limit, Prince et al. (1985) found that the density of plants in local populations did not decrease as the range edge was approached, but the number of populations decreased near the range edge. They concluded that available habitat was the limiting factor to the expansion of the species' range.

Results from investigations of trees at their geographic range limits have supported the ecological amplitude paradigm (Hutchinson 1918, Boyko 1947, Beschel et al. 1962), and such studies may have influenced the field of dendrochronology, for which ecological amplitude has been considered a guiding principle (Fritts 1976). While working almost exclusively with trees in the arid southwestern United States, Fritts (1976) advocated sampling trees at their

elevational and geographic range limits to maximize the detection of a climate signal in tree-ring chronologies and enable better reconstruction of past climate.

1.6 Data from Trees and Tree Rings

Trees and tree rings provide an excellent source of data to investigate the related paradigms of abundant center and ecological amplitude. The importance of trees as a structural component of forest ecosystems, the implications of tree distributions for carbon sequestration, and the ever-increasing availability of forest inventory data at broad spatial scales have enabled numerous recent investigations of the geographic range structure of tree species (Neilson and Wullstein 1983, Murphy et al. 2006, Rehfeldt et al. 2008, Purves 2009, Woodall et al. 2009).

Networks of tree-ring data have an additional advantage over basic demographic data because they allow for the analysis of temporal as well as spatial patterns. Dendrochronology has existed as a distinct field of inquiry for over a century, and the primary focus of the discipline has been analysis of the relationship between climate and tree growth (Douglass 1920, Fritts 1976). This bioclimatic focus and the increasing amount of publically available tree-ring data have led to several recent investigations of variability of tree growth over geographic and elevational gradients (Cook and Cole 1991, Carrer et al. 2007, LeBlanc and Terrell 2009, Carrer et al. 2010, Goldblum 2010, Miyamoto et al. 2010). However, relatively few dendrochronological investigations have analyzed tree growth or stand structure across broad spatial scales (such as the geographic ranges of species), and even fewer have specifically

sought to answer the question of whether ecological amplitude is a useful paradigm for dendroecology.

1.7 Research Objectives

This research investigates spatial and temporal variability in the structure and dynamics of geographic ranges of tree species using a combination of forest inventory and dendroecological methods. The overall goal of the research is to evaluate how tree growth, establishment, stand composition, and stand structure vary across the geographic ranges of tree species and environmental gradients. This research also seeks to address whether ecological amplitude is a useful, general paradigm for characterizing growth and abundance of trees across broad spatial scales.

The related concepts of abundant center and ecological amplitude form a paradigm regarding the structure of geographic ranges and lead to several predictions about the distribution and biological responses of species. This research aims to address several of these predictions including the following hypotheses:

(1) Tree species will attain their highest levels of abundance near the center of their geographic ranges and abundance will gradually decline toward range edges.

(2) Tree growth–climate relationships will vary spatially across the geographic ranges of species, and the influence of climatic variables on growth will be stronger near range margins.

(3) Tree growth will be more sensitive to climatic conditions at peripheral sites, and inter-annual variability of growth will be higher at peripheral sites.

(4) Species will occur only on specialized sites (*e.g.*, north-facing slopes) near their southern range limit, but they will occupy a wider range of habitats in the interior of their ranges.

(5) Establishment and recruitment rates of trees will be higher toward range interiors and lower at peripheral sites.

Four research objectives are used to test the above hypotheses:

(1) Analyze the abundance of tree species across geographic ranges.

(2) Quantify spatial variability in climate–growth relationships at peripheral and interior sites within the distribution of tree species.

(3) Analyze spatial patterns of sensitivity of tree growth to climate across the geographic ranges of tree species.

(4) Quantify stand structure and dynamics (patterns of establishment, recruitment, and stand composition) near the interior and the margins of species' ranges.

1.8 Justification

For decades, biogeographers and ecologists have assumed that species distributions were characterized by the abundant center distribution, in which species are most abundant at the center of their geographic ranges, and gradually decline in density toward range margins. Despite very little empirical evidence that species' ranges fit the abundant center hypothesis, many ecological theories and models concerning range dynamics have been developed based

on the assumption of an abundant center distribution. Many theories of ecological amplitude stem from the abundant center hypothesis and presuppose that organisms near the margins of their geographic ranges will be limited by unfavorable environmental conditions to a greater degree than organisms near their range centers. Consequently, it has been hypothesized that species occupy a narrower range of sites near their range margins. Fritts (1976) suggested that trees growing near their altitudinal and latitudinal range limits would occupy only restricted sites, and tree growth would be more sensitive to climate at these sites. He further stated that sampling trees based on ecological amplitude was a basic principle of dendrochronology. Although many ecological theories with far-reaching conservation implications are based on the assumption of the abundant center distribution, relatively few direct tests of range structure have been conducted.

This research will explicitly test several hypotheses based on common ecological assumptions in an effort to refine concepts of range structure and dynamics. My results will provide information about the influence of climate variability on tree growth through geographic ranges of several species and will inform future research that focuses on the determinants of geographic range limits, population dynamics, and migration potential of North American tree species. Additionally, I compare patterns of tree establishment, recruitment, and growth rates at study sites near the center and margins of the geographic ranges of several Appalachian tree species. Analysis of these forest compositional and structural data will allow for the detection of spatial and temporal variability in species'

responses to environmental change, and inform efforts that aim to predict patterns of vegetation change in forests of the eastern U.S.

Understanding the patterns and processes associated with range dynamics of tree species is especially important because trees are foundation species in many ecosystems, and changes in the distribution of a major tree species can have far-reaching implications for biological diversity and ecological health of the world's forests (Keever 1953, Allen and Breshears 1998, Ellison et al. 2005, van Mantgem et al. 2009). Previous studies of the range dynamics of eastern forests employed very general models of species distributions with little or no inputs of actual forest structural or compositional data (Iverson and Prasad 2002). While many studies have investigated climatic influences on tree growth, relatively few have analyzed spatial variability in growth–climate relationships (Cook and Cole 1991, LeBlanc and Terrell 2009, Goldblum 2010, Hart et al. 2010). Additionally, very few analyses have been conducted comparing patterns of stand composition and structure across broad spatial scales such as the geographic range extents of tree species. My research aims to address these shortcomings by conducting analyses of abundance, establishment, recruitment, and growth in forest stands across broad geographic gradients. I seek to provide the framework for new models of the distribution of tree species based on empirical investigations of range structure and dynamics.

A major motivation to conduct this research is the urgent need to understand biological responses to global environmental change. Research on a wide variety of species has shown that recent climate change has affected terrestrial biological systems and resulted in latitudinal and altitudinal shifts of species' ranges (Stenseth et al. 2002). Moreover, rapidly increasing

temperatures that have characterized recent decades are projected to continue, with potentially dramatic implications for ecosystems (IPCC 2007). Among the predicted consequences are large shifts in species distributions as well as local and global extinctions over a broad range of taxa (IPCC 2007). Changes in species' distributions and extinction events will not only have profound world-wide ecological impacts, but also economic impacts by affecting agriculture and forestry. Mitigating and responding to rapidly changing ecosystems hinges upon accurate predictions of the effects of environmental changes on biota. A need exists for detailed assessments of current ecosystem change and understanding of the ecological relationships between species and their environment to ensure accurate models of global change. The results of my research will inform such efforts by providing detailed analysis of tree species' responses to environmental change, as well as spatial and temporal variability of these responses.

1.9 Organization of the Dissertation

The remainder of this dissertation consists of five chapters. In each of the next four chapters, I present an analysis of spatial variability in tree abundance, growth, or stand structure. The chapters are intended to be stand-alone studies and have been written as manuscripts for submission to peer-reviewed journals. In chapter 2, I present a simple test of the abundant center hypothesis using abundance data for red fir. Red fir is an ideal tree species to test the hypothesis because the shape of its geographic range is nearly one-dimensional, and the forestry literature contains a large number of studies that report abundance data in plots. In chapter 3, I analyze climate–growth relationships of longleaf pine at a unique range-edge site,

and compare the climate response to several other sites throughout the range of the species. I focus on the response of longleaf pine annual radial growth to monthly precipitation, temperature, and drought. In chapter 4, I employ networks of tree-ring data for two widely-distributed species in North America—eastern hemlock and white oak—and investigate spatial variability in the sensitivity of each species to climate. Chapter 5 investigates stand composition, structure, and dynamics in pine-oak stands in the southern Blue Ridge physiographic province. I compare stand structure and tree establishment in two study sites, one located near the southern range limit of several dominant pine and oak species, and one near the interior of those species' ranges. Finally in chapter 6, I summarize key findings and suggest areas for future research.

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CHAPTER 2

DISTRIBUTION OF RED FIR (*ABIES MAGNIFICA*) ABUNDANCE: A TEST OF THE ABUNDANT CENTER HYPOTHESIS

CHAPTER 2

DISTRIBUTION OF RED FIR (*ABIES MAGNIFICA*) ABUNDANCE: A TEST OF THE ABUNDANT CENTER HYPOTHESIS

In this chapter, I conduct a simple test of the abundant center hypothesis using demographic data for a narrowly-distributed tree species in western North America. A paucity of plot-based abundance data precludes direct tests of the hypothesis in many other tree species, but the geographic range characteristics and data availability for red fir make this species suitable for this analysis. In subsequent chapters, I explore the relationship between geographic location and other biological processes (e.g., growth and tree establishment) using tree-ring data for widely-distributed species in eastern North America.

Abstract

The geographic ranges of species have long been thought to fit the abundant center hypothesis, which holds that species will be most abundant at the center of their ranges and gradually decline in abundance toward range edges. Despite very little empirical evidence, many biogeographic and ecological models and hypotheses have been developed assuming the abundant center hypothesis accurately characterizes the distribution of abundance within geographic ranges. A few recent reviews of the abundant center hypothesis contend that very few studies have been adequately designed to directly test the hypothesis, and fewer still have supported it. Here, I test the abundant center hypothesis by examining the distribution of abundance of red fir (*Abies magnifica* A. Murr.). I use plot level abundance data throughout the natural range of the species and statistically test the association between tree abundance and distance from range center. No significant relationship exists between the abundance of red fir and distance from the center of its range. A lack of empirical support for the abundant center

hypothesis in this analysis agrees with other studies that conclude it is inappropriate to consider this hypothesis a biogeographical rule.

2.1 Introduction

The distribution of abundance within the geographic ranges of species has long been the subject of fundamental biogeographic inquiry. A longstanding and widely accepted assumption concerning the distribution of abundance is the abundant center distribution, or abundant center hypothesis. This hypothesis states that a species will be most abundant at the center of its geographic range, and abundance will gradually decline toward the edges (Wulff 1943, Rapoport 1982, Brown 1984). Throughout the ecological and biogeographic literature several studies claim empirical support for the hypothesis (Hengeveld and Haeck 1982, Brown 1984, Brown et al. 1995). Hengeveld and Haeck (1982) analyzed the distribution of density across the ranges of hundreds of species of carabid beetles, birds, and plants in northwestern Europe. They did not have data on each species from multiple sites across their ranges, but tested the hypothesis indirectly by correlating frequency of occurrence with distance from each species' range center. They concluded that most of the taxa they investigated fit the abundant center distribution and considered this pattern a basic biogeographical rule. Similarly, Brown (1984) asserted that the abundant center pattern not only occurs in local populations, but also across entire geographic ranges of species. He assessed breeding bird survey maps of density over species' ranges, and overlaid four orthogonal transects from the range centers. When he

then calculated mean values for the transects and plotted density as a function of distance, he obtained convex curves that indicated an abundant center pattern.

Brown (1984) further reasoned that the theoretical explanation for the existence of the abundant center pattern is niche-based. He suggested that patterns of abundance vary along multiple environmental gradients, and centers of high and low density within a species' range are the result of how closely environmental conditions meet the optimal requirements for that species. Therefore, the point of intersection of multiple niche axes would be the optimal habitat for that species, where it could reach its greatest abundance. Additionally, he reasoned that environmental conditions are spatially autocorrelated and that near sites will be more likely to meet a species' requirements than distant sites. Consequently, a species would be less likely to find its niche requirements met at greater distances from its optimal habitat and population density will gradually decline to zero (the range boundary) when environmental conditions are completely unsuitable. Others have theorized that differences in birth and death rates across species' ranges as well as migration and dispersal ability are primarily responsible for the abundant center distribution (Hanski 1982, Guo et al. 2005).

Not only have a number of hypotheses been proposed to explain the mechanisms behind the abundant center distribution, but the assumption of the distribution has also been invoked in the development of many ecological models and theories. In their review of the abundant center hypothesis, Sagarin and Gaines (2002a) noted that over 20 hypotheses in ecological literature were formulated based on the assumption that species are most abundant near the center and gradually decline in density toward the edges of their range. These

hypotheses deal with fundamental ecological concepts such as the factors that determine range extents, gene flow through populations, and population dynamics.

Despite its extensive employment in wide-ranging ecological applications, Sagarin and Gaines (2002a) found very few empirical tests that supported the abundant center hypothesis. In a literature survey, they found only 22 studies that directly tested the abundant center hypothesis; and, of the 145 tests conducted within those studies, only 39% supported the hypothesis. Additionally, Sagarin and Gaines (2002a) found numerous limitations of the existing research. Many of the studies did not have adequate data because sampling designs under-sampled the edges of ranges. For example, studies that collect data along multiple transects from the range center, such as Brown's (1984) investigation of breeding birds, inevitably have a greater number of samples near the range center due to the increased sample area near the edges of a range. Also, many studies did not have data from the entire range of the species under consideration, or relied on too few data points to accurately assess patterns of abundance throughout a range. In this instance, a pattern of decreasing abundance may be found from the range center to an edge, but the center may not be the most abundant region of the range, because other edges are not included in the analysis. Furthermore, of the eight studies that Sagarin and Gaines (2002a) determined to have adequate spatial distribution of data, only two used data from throughout the entire geographic range for statistical analysis. Using Brown's (1984) study again as an example, he claimed an abundant center distribution from his plotted curves, but proposed no null expectation and conducted no statistical tests of the significance of this pattern. Finally, Sagarin and Gaines (2002a) pointed out that most tests

of the abundant center hypothesis have been geographically or taxonomically restricted. The vast majority of studies were conducted in Great Britain or the United States, and the taxa under investigation were predominantly birds or insects.

In this study, I conduct a direct test of the abundant center hypothesis using a North American tree species, and take into account many of the shortcomings of previous tests pointed out by Sagarin and Gaines (2002a). Their four main criticisms of the current literature on the abundant center distribution are: 1) few studies directly test the abundant center hypothesis, 2) abundance is often tested in only part of a range, or abundance data in tests of the hypothesis are not adequately distributed throughout entire ranges, 3) distribution of abundance data are seldom tested statistically, and 4) tests of the hypothesis are geographically and taxonomically limited. The goal of my study is to directly test the abundant center hypothesis by compiling abundance data collected in forest plots, measuring the distance between these data points and the range center. Additionally, I use the data to statistically test the abundant center distribution by correlating the relationship between distance from center and abundance and testing for differences in mean abundance between groups of points classified by distance from range center. My analysis focuses on a species in North America, a region where many abundant center studies have been conducted because data are difficult to obtain elsewhere. I conducted my analysis on a tree species, and plant taxa have not been well represented in previous tests of the abundant center hypothesis.

2.2 Methods

2.2.1 Selection of Species

Several characteristics of red fir made it a suitable species for investigating the relationship between geographic position and abundance. Two considerations were especially important when selecting tree species for this analysis: (1) the availability of sufficient abundance data, and (2) the spatial configuration of the species' range. The existence of adequate abundance data is critical for testing the abundant center hypothesis. Only tree species with demographic data available in plots through all or most of their ranges were considered for analysis. Additionally, species with plot data clustered near the center of their ranges were excluded to ensure that the edges of species ranges were not underrepresented relative to the center. The shape of the species range was also taken into account when choosing a species for this analysis. Sagarin and Gaines (2002a) suggested sampling species with nearly one-dimensional ranges (such as intertidal species that inhabit a narrow strip of shoreline) is optimal when assessing the abundant center distribution. Additionally, Sagarin et al. (2006) demonstrated that many difficulties are encountered when trying to determine the center of ranges that are highly irregular in shape. Therefore, trees with linear ranges were preferred. Those with ranges very irregular in shape were excluded.

Red fir was selected to test the abundant center hypothesis because it has a range shape that is predominantly one-dimensional range and plot-level abundance data were readily available from the literature. Red fir is a dominant canopy species that occurs along the north–south axis of the Sierra Nevada and southern Cascades mountain ranges. It is found in nearly

pure stands or mixed with other conifers such as white fir (*Abies concolor* (Gordon) Lindl. ex Hildebr.) and western white pine (*Pinus monticola* Douglas ex D. Don) from the Klamath Mountains in southern Oregon to the southern Sierra Nevada in California at elevations of 1800–2800 m (Barbour and Woodward 1985). Additionally, a great deal of red fir density data exist in the fire history literature because many studies have assessed the increase in tree density in the fire-prone Sierra Nevada during the recent period (1900–present) of anthropogenic fire suppression. Red fir is a suitable species for this study because it has been minimally impacted by direct human manipulation of its inaccessible, high elevation habitat, and because the natural fire regime of infrequent, moderate severity fires that influence stand structure has not been greatly affected by fire suppression activities (Skinner and Chang 1996, Scholl and Taylor 2006).

2.2.2 Abundance and Range Data

I obtained abundance data for red fir from published studies in forest ecology and fire history (Table 2.1). I searched in the title, abstract, and keyword fields on ISI Web of Science for "*Abies magnifica*," and then searched the abstracts for articles that collected stand structural data and reported density of red fir trees in stems per hectare or a unit that could be converted to stems per hectare. Most of the articles were site-based studies and the reported stands were in very close proximity. For these studies, I calculated the mean density of all reported stands and used the latitude and longitude of a central point of the study area as the stand location. An exception was the study by Barbour and Woodward (1985); they collected density in red fir

stands near the northern and southern limits of the species distribution. Several authors did not directly report location in geographic coordinates. I assigned latitude and longitude to these sites by finding landmarks (e.g., peaks, county boundaries) on the authors' study area maps and locating them on topographic maps.

Range extent of red fir used in this analysis was delimited from a digitized version of U.S. Forest Service range maps. The maps from U.S. Forest Service silvicultural publications (Little 1971) were digitized and made available in shapefile format by the U.S. Geological survey as part of the North American Tree Atlas (USGS 2006).

2.2.3 Data Analysis

The range map and point data of abundance were analyzed using a geographic information system (GIS). Manipulation of spatial data and measurements were all performed in ArcGIS version 9.3 (ESRI 2008). The range map was uploaded into the GIS and a shapefile of data points was created from the abundance data reported in published studies. I designated the centroid of each species' range as the range center. A centroid is the mean center of a polygon based on a weighted average of all x and y coordinates contained in it (Ormsby et al. 2004, Sagarin et al. 2006). Brown (1984) defined range centers by the intersection of two perpendicular lines drawn through the widest points of the range, but Sagarin et al. (2006) pointed out that as the range shape deviates from an oval, the center point becomes increasingly skewed toward one side. The calculation of a centroid is an objective and accurate method for

determining range center, but it is still possible to have a skewed centroid position in a range characterized by a highly irregular shape or many disjunct outliers.

All spatial data (i.e., range boundary and plot locations) were projected in the same ArcGIS geodatabase using a conic equidistant projection to minimize map distortion of distances between points. The projection was centered on the range centroid with standard parallels dividing the range into equal thirds, and a standard meridian through the center of the range. Pearson correlation coefficients were calculated between distance from centroid and abundance at each plot, as well as between spatial position (latitude and longitude) and abundance. Additionally, plots were grouped into quartile classes based on their distance from range center, and mean abundance was calculated for each class. For example, 25% of plots that were closest to the range center were grouped into quartile 1. Differences in the means of quartiles were assessed using one-way analysis of variance (ANOVA).

2.3 Results

I found red fir density data reported for 136 stands from 17 publications (Table 2.1), and compiled the stand locations (latitude and longitude) and mean density. All sites were located in California except for two stands in the Carson Range of Nevada. The mean density at the sites was highly variable, ranging from only 14 to 664 trees per hectare. The mean density of red fir at all sites was 301 trees per hectare. The centroid of the range is located in the northern Sierra Nevada approximately 150 km northwest of Lake Tahoe. The plots ranged over nearly five degrees of latitude from just north of the range centroid to the southern extent of the range

in the southern Sierra Nevada (Figure 2.1). All plots are within approximately three degrees of longitude along the axis of the Cascades and Sierra Nevada, with the exception of site 7 located in the Klamath Mountains. Seven of the 18 sites were located north of the centroid and 11 sites were situated to the south. I did not find any published abundance data from the northernmost, disjunct patches of red fir in the southern Cascades in Oregon, but abundance data were found through the range of red fir in the Sierra Nevada. Red fir abundance was not correlated with any of the analyzed measures of spatial distribution (Figure 2.2). No significant relationship was found between tree density and distance from range center ($r = –0.035$, $p = 0.889$). Correspondingly, no spatial gradient in tree abundance was detected. Density of red fir was not correlated with latitudinal ($r = 0.129$, $p = 0.610$) or longitudinal ($r = –0.221$, $p = 0.378$) position.

An abundant center pattern was not detected among forest plots grouped according to distance from range center. When grouped into quartiles, I found no significant differences between quartile means (Figure 2.3). Mean abundance in quartiles ranged from 403.8 trees ha^{-1} in quartile 1 (nearest range center) to 233.5 trees ha^{-1} in quartile 2. Although mean density was highest in the center-most quartile, differences between means were not statistically significant as indicated by a one-way ANOVA test ($F = 0.706$, $P = 0.564$, $DF = 3$). No gradient of abundance was detected among red fir stands grouped in latitude quartiles. Mean abundance in quartiles ranged from 396 trees ha^{-1} in quartile 4 (northernmost quartile) to 193 trees ha^{-1} in quartile 2. Differences between means were not statistically significant as indicated by a one-way ANOVA test ($F = 0.912$, $P = 0.460$, $DF = 3$).

Table 2.1. Literature source, location, number of stands, and density of red fir used in this analysis. All sites are located in California or Nevada, and are listed north to south.

Site	Source	Latitude (° N)	Longitude (° W)	Number of Stands	Mean Density (stems/ha)
1	Bekker and Taylor (2001)	40.68	121.62	5	362
2	Beaty and Taylor (2001)	40.62	121.10	3	196
3	Taylor (2000)	40.57	121.33	4	223
4	Taylor and Solem (2001)	40.50	121.13	5	535
5	Taylor and Halpern (1991)	40.43	121.12	2	664
6	Talley (1977a)	40.08	120.72	4	130
7	Barbour and Woodward (1985) site 1	39.77	122.95	16	410
8	Talley (1977b)	39.50	120.06	9	467
9	Scholl and Taylor (2006)	39.33	119.92	4	280
10	Taylor (2004)	39.12	119.90	4	73
11	Beaty and Taylor (2007)	39.03	120.13	9	96
12	Nagel and Taylor (2005)	38.90	120.08	2	60
13	Talley (1976)	38.08	120.05	11	543
14	Parker (1984)	37.82	119.75	30	364
15	Smith et al. (2005)	36.97	119.03	1	14
16	Griffin (1975)	36.67	118.85	10	289
17	Barbour and Woodward (1985) site 2	36.47	118.50	14	282
18	Pitcher (1981)	36.10	118.37	3	431
			Total	136	301

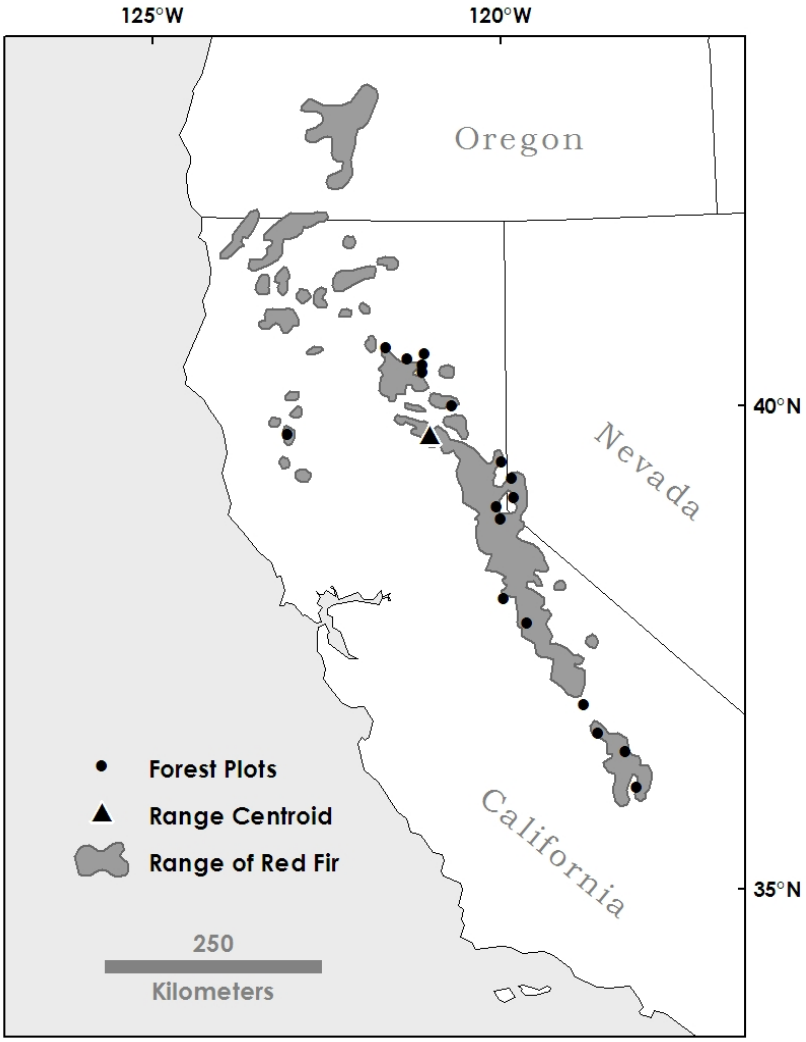

Figure 2.1. Geographic range of red fir, with the range center calculated by a centroid (triangle) and locations of plots (circles) where abundance data were collected.

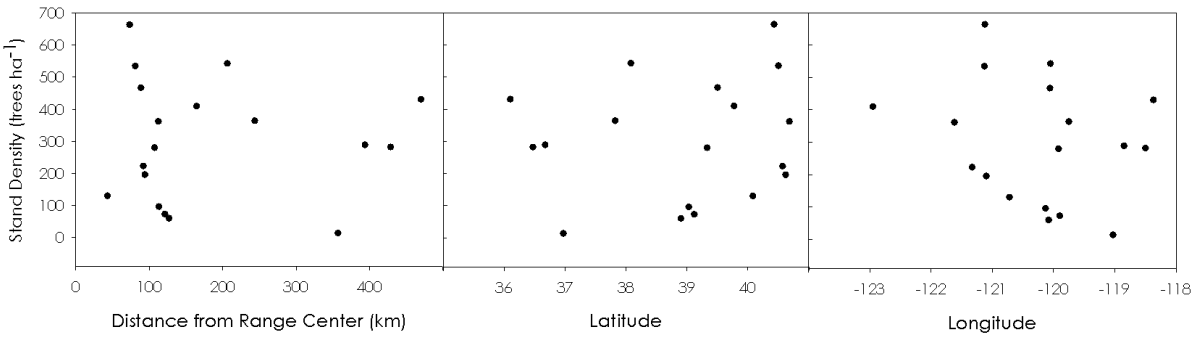

Figure 2.2. Plots of red fir density in trees per hectare versus distance from center of range, latitude, and longitude. No significant correlation exists between abundance of red fir and distance from center ($r = –0.029$, $p = 0.889$), latitude ($r = 0.129$, $p = 0.610$), or longitude ($r = –0.221$, $p = 0.378$).

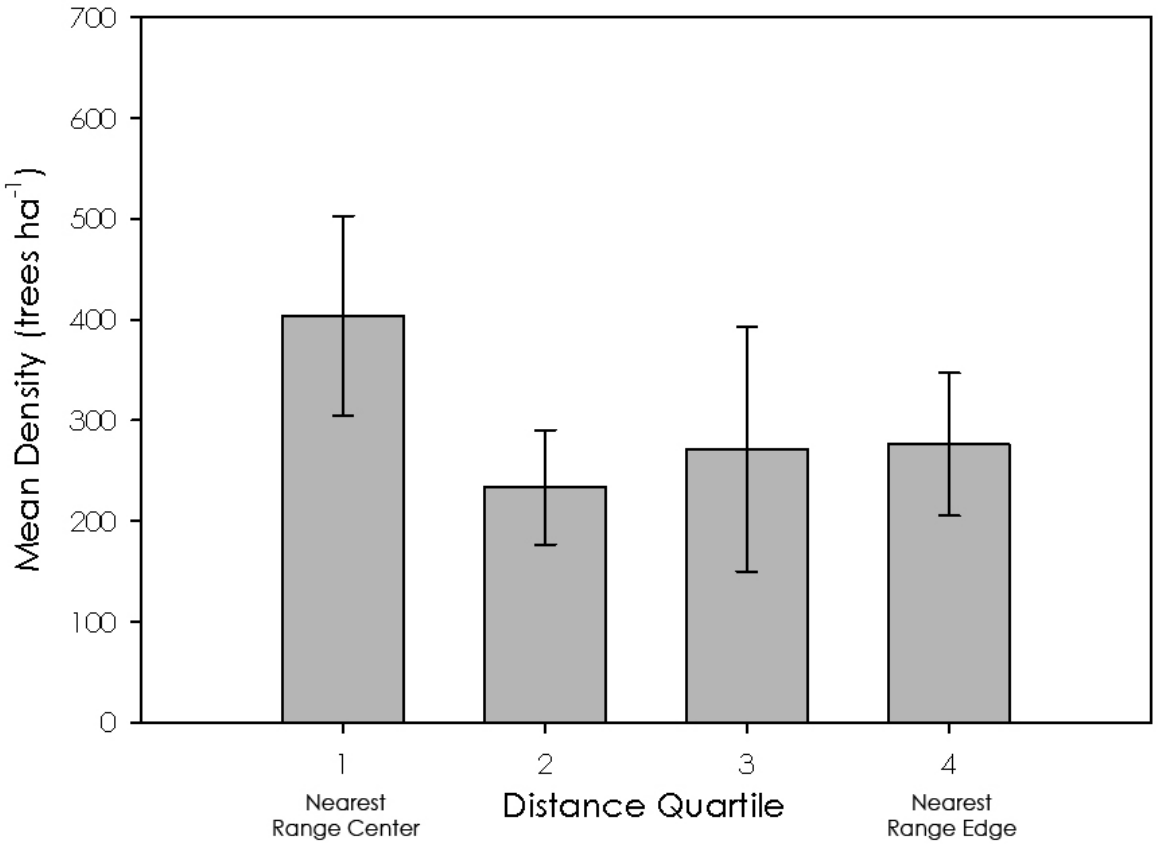

Figure 2.3. Abundance of red fir forest plots grouped in quartiles based on distance from the centroid of the species range. Height of each bar represents quartile mean, and error bars indicate one standard error.

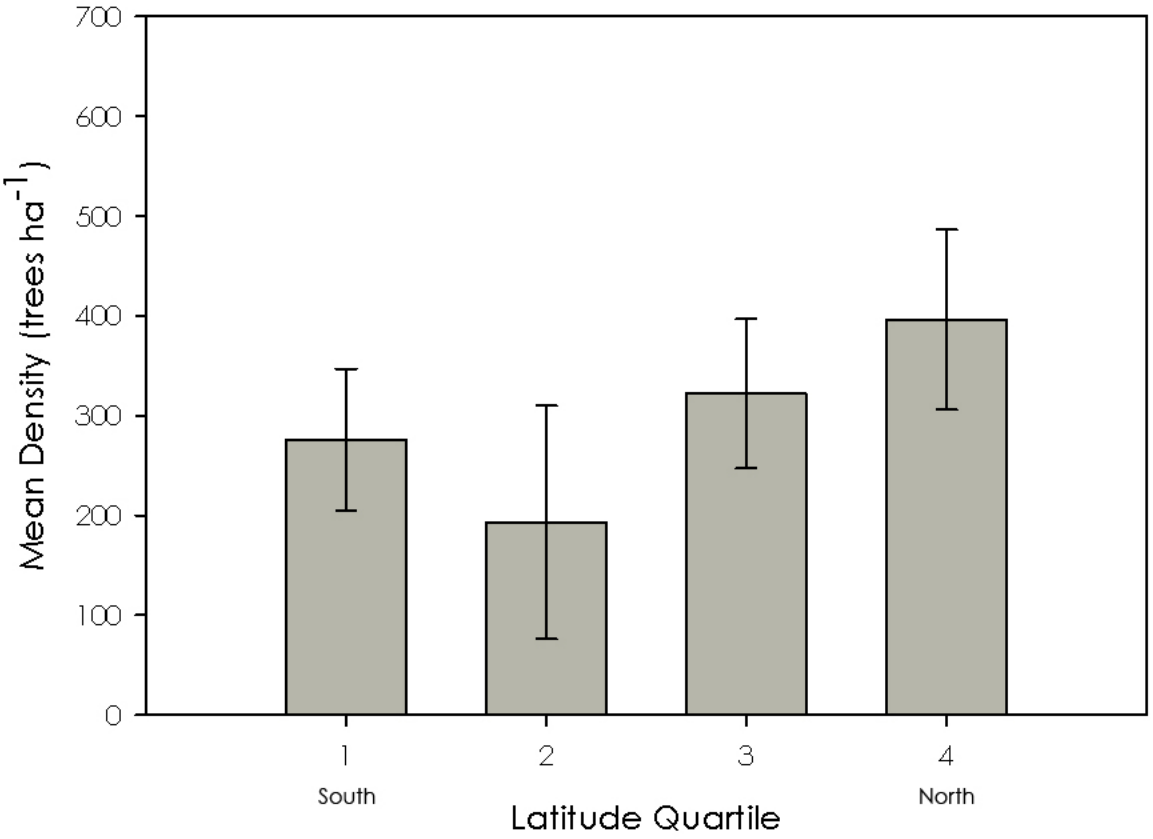

Figure 2.4. As in figure 2.3, but for quartiles of sites based on latitude.

2.4 Discussion

Density within stands of red fir through most of its range is not accurately characterized by an abundant center distribution or an obvious pattern of abundance along its major spatial gradient (latitude). These findings are at odds with early arguments supporting the abundant center hypothesis (e.g., Hengeveld and Haeck 1982, Brown 1984, Brown et al. 1995). However, several of these early studies were based on insufficient data or sampling design, and many did not statistically test their results (Sagarin and Gaines 2002a).

The results presented here do generally agree with several recent studies that found limited or no evidence of abundant center distributions. For example, Jump and Woodward (2003) tested the abundant center hypothesis over the range of three herbaceous perennial plant species (*Cirsium sp.*) in Great Britain and found declining population density and seed production from range center to edge in two of the species, but not in the third. Conversely, Kluth and Brueheide (2005) examined central and peripheral populations of an annual plant in central Europe and found that density, seed production, and seed bank density were higher in the peripheral populations. Additionally, Brewer and Gaston (2002) did not detect an abundant center distribution when examining the geographic range of a phytophagous insect in Europe, but instead found a gradient of declining density across the entire range from north to south.

Adequate data to assess the distribution of abundance of North American tree species are very limited. While assessing the potential for testing the abundant center distribution with plot-based data on North American trees, I surveyed the literature on numerous well-studied

species. For many species, little or no abundance data exists, the data do not cover sufficient portions of the geographic range, or the range shape is too complex, and classification of center and edge regions is ambiguous. This analysis of red fir met many of the criteria suggested by Sagarin and Gaines (2002a) to test the abundant center hypothesis, but some limitations of these data exist. Despite having few sites overall, the red fir data were generally suitable for analyzing the relationship between distribution and abundance because of the data quality, spatial distribution, and range shape. The abundance data for red fir were collected from very detailed demographic surveys of old-growth stands, plots were well distributed throughout most of the species range, and the range is a generally simple, one-dimensional shape.

The red fir plot data are of limited use for assessing abundance of trees at the northern limit, but the plots are well distributed along the species' linear range from north of center to the southern extremity. Many reviews of abundant center literature stress the necessity for abundance data to be collected across the full geographic range (Sagarin and Gaines 2002a, Gaston 2003, Gaston et al. 2008), but they propose no objective criteria for deciding if the data are sufficiently distributed. A method of point pattern analysis could be applied to plots of abundance data, but a decision about the optimal distribution of plots would still be subjective.

Another reason red fir is uniquely suited to test the abundant center hypothesis is because its range is largely one-dimensional. The southern portion of the range of red fir is limited to the axis of the Sierra Nevada and Cascade Range, and is no wider than 100 km east to west, although it stretches nearly 1000 km north to south. Sagarin and Gaines (2002b) asserted that one-dimensional ranges are ideal for testing the abundant center because of the simplicity

of defining range center and edges, and the relative ease of obtaining adequate data from the entire range. The lack of a spatial trend in abundance of red fir is consistent with other studies of the distribution of abundance in one-dimensionally distributed taxa such as coastal dune plants (Samis and Eckert 2007) and intertidal invertebrates (Sagarin and Gaines 2006). Quite a few tree species have generally linear distributions along the axes of major mountain ranges, but very little abundance data are available for most of them.

While a paucity of plot-based absolute abundance data exists across the ranges of many tree species, data on relative abundance can be obtained from inventories such as the United States Forest Service, Forest Inventory and Analysis database. Using these data in an indirect test of the abundant center hypothesis among many widely-distributed species of eastern North American trees, Murphy et al. (2006) did not find conclusive evidence for the abundant center distribution; instead they suggested an "abundant core" region where species are more abundant than at range edges.

One possible problem with abundance data collected over large areas is that the aggregation of many data points may diminish the influence of local variation in species density, producing an abundant center distribution in widely distributed species but not in narrowly distributed ones (Blackburn et al. 1999). Therefore, the method of aggregating abundance data may influence whether or not a species supports the abundant center hypothesis. Data averaged together from broad areas (e.g., a latitudinal band) are more likely to display simple patterns than data at different sites treated independently (Gaston et al. 2008). The restricted range of red fir and limited number of stands may have influenced the observed

patterns of abundance and therefore may not be directly comparable to studies of other species that use highly aggregated data.

The results presented in this and other recent studies suggest that the abundant center hypothesis is, at best, a model limited in applicability to select species. Moreover, because numerous direct, empirical tests do not support the abundant center hypothesis, it would be inappropriate to consider it a general rule of biogeography. Gaston et al. (2008) assert that gradient models, where traits of species change monotonically along geographic gradients, are a better representation of the distribution of species' abundance than peak models. They conclude that the assumption that the peak-based abundant center hypothesis accurately reflects key aspects of the spatial structure of geographic ranges is not well supported. Sagarin et al. (2006) also dispute the utility of the abundant center hypothesis, arguing that relying on simplistic assumptions about distribution of abundance has impeded attempts to progress beyond pattern recognition exercises and test mechanistic hypotheses about species' ranges. Moving from descriptive studies of the distribution of abundance to a more rigorous hypothesis-testing stage of research is of the utmost importance for solving contemporary problems involving aspects of species' distributions such as responses to global climate change.

Although recent studies—including this analysis—conclude that the abundant center hypothesis is unsupported, further research is needed to assess whether abundant center patterns characterize the spatial variability of other biological processes such as growth, reproduction and mortality (Hengeveld 1990). Additionally, if the abundant center is not an adequate model of the spatial variability of biological processes, alternative models need to be

developed and hypotheses need to be tested (Sagarin et al. 2006, Gaston et al. 2008). In the following chapters of this dissertation, I investigate the relationship between spatial location and other vital characteristics of tree species using tree-ring data. Processes I investigate include tree growth response to climatic variables (chapter 4), climatic sensitivity (chapter 5), and regeneration patterns (chapter 6).

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CHAPTER 3

CLIMATE RESPONSE OF LONGLEAF PINE (*PINUS* PALUSTRIS) ACROSS ITS GEOGRAPHIC RANGE: A COMPARISON OF MONTANE AND COASTAL PLAIN SITES

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CLIMATE RESPONSE OF LONGLEAF PINE (*PINUS* PALUSTRIS) ACROSS ITS GEOGRAPHIC RANGE: A COMPARISON OF MONTANE AND COASTAL PLAIN SITES

While the abundant center hypothesis predicts higher abundance of species near the centers of their geographic ranges, the related concept of ecological amplitude predicts higher variability in growth and greater sensitivity to environmental conditions at sites on species' range periphery. In this chapter, I analyze the annual growth of longleaf pine at a range edge site. I quantify the response of radial growth to monthly climate variables, and compare the growth response to several sites from the interior of the species' geographic range. This chapter is the basis for a manuscript that will be submitted to *Plant Ecology*. The use of "we" in this chapter refers also to Grant Harley, Henri Grissino-Mayer, Saskia van de Gevel, and Joseph Henderson who will be co-authors on the manuscript. As the first author, I was responsible for designing the study, obtaining most of the data, performing analyses, and writing the paper.

Abstract

Accurate predictions of future geographic ranges of tree species and mitigation of the undesirable effects of climate change on forest communities require an understanding of the spatial variability of the response of tree growth to climate variables. The principle of ecological amplitude, a long held but largely untested assumption, predicts that trees will be more sensitive to climate near range margins. Here we present an analysis of the climate–growth relationship in an old-growth, montane stand of longleaf pine—a species once extensively distributed in the southeastern United States. We use dendroecological methods to analyze the response of longleaf pine to monthly precipitation, temperature, and Palmer Drought Severity Index (PDSI) at this site on the edge of the species' geographic range. Radial growth at the montane site was influenced by available moisture and precipitation during the growing season, as well as winter temperatures one year prior to growth. Additionally, we compare

climate response and annual growth sensitivity across six sites through the range of the species. High frequency variance of annual growth and climate response across the longleaf pine stands did not vary as predicted by the ecological amplitude theory. Models that predict future distributions of trees based on assumptions of climate response over current ranges should be reconsidered.

3.1 Introduction

Recent increases in global mean annual temperatures and associated changes of precipitation patterns (IPCC 2007) are predicted to have dramatic influences on and feedbacks with ecosystems, especially the world's forests (Iverson et al. 2004, Bonan 2008). Understanding the climate-driven range dynamics of trees is especially important for assessing the response of forest communities to climate change because dominant tree species can act as foundation species that have a major influence on community composition and ecological functions of forests (Ellison et al. 2005). Predicting the consequences of global climate change on forest ecosystems and managing undesirable effects require accurate models of tree species' range dynamics, as well as growth responses to climate.

Detailed understanding of the factors that limit the distribution of tree species and how these factors vary over space and time to influence landscape-scale vegetation patterns are required to predict the effects of climate change on the composition and structure of forest ecosystems. Contemporary research has focused on predicting the responses of species' distributions to global environmental change, especially responses to rapid global warming.

Most of these prediction efforts are carried out by modeling the association between climate and distributions of species, and assessing the influence of various climate change scenarios on the resulting modeled distributions (McKenney-Easterling et al. 2000, Parker et al. 2000, Schwartz et al. 2001, Iverson and Prasad 2002). These climate envelope approaches make assumptions about the relationship between range limits and climate as well as the structure of species ranges.

The climate envelope modeling approach to range dynamics assumes that the prevailing climatic conditions within a species' current range represent suitable habitat, and conditions occurring outside of a species' range represent unsuitable habitat. Climate is therefore assumed to have a direct, causal influence on range limits (Sagarin and Gaines 2002, Gaston 2003). A related assumption is the paradigm that species are most abundant near the center of their geographic range, and abundance declines gradually toward the range edges. This concept is often referred to as the abundant center hypothesis and has been long considered an ecological rule (Wulff 1943, Brown 1984, Hengeveld 1990). The rationale for the abundant center pattern is that range centers represent ideal habitat where all environmental requirements for a species are met. Consequently, a species would be less likely to find its niche requirements met at greater distances from its optimal habitat, and population density gradually declines to zero (the range boundary) where environmental conditions are completely unsuitable. Hengeveld (1990) proposed that, in addition to abundance, other measures of species vitality (e.g., reproductive rates, growth rates) should also follow an abundant center pattern.

In the field of dendrochronology, similar assumptions about range structure of trees have been incorporated into the principle of ecological amplitude. Trees growing near range margins are thought to be restricted to fewer habitats (narrower ecological amplitude) than trees in the interior of a species' range. Reconstructing past climate from tree rings has typically been guided by the ecological amplitude assumption and involved the selection of trees from range edges to enhance the detection of climatic sensitivity, presumably because the annual growth in these trees are more sensitive to inter-annual climatic fluctuations (Fritts 1976).

Despite the longstanding and widely accepted assumption that the abundant center distribution accurately characterizes the structure of geographic ranges, few tests have been conducted on the abundance of organisms across their ranges, and little empirical evidence supports the assumption (Sagarin and Gaines 2002, Gaston 2003). Even fewer tests of species' vitality across their geographic ranges, such as tests of ecological amplitude, have been conducted (Hart et al. 2010). The latter are especially crucial for understanding variability in growth rates of trees and related carbon sinks of forest ecosystems.

Networks of tree-ring data provide an opportunity to test ecological amplitude assumptions by analyzing spatial patterns of variability in tree responses to climate. Patterns of annual radial growth can be assessed over long environmental gradients and in some cases across the entire geographic range of a tree species. Although some studies have demonstrated that tree responses to climate varies spatially, relatively few have analyzed networks of tree-ring data to quantify this spatial variability or to test the assumed abundant center pattern of growth sensitivity to climate (LeBlanc and Terrell 2009, Hart et al. 2010, Miyamoto et al. 2010).

Increasing our understanding of the variability and spatial pattern of climate response is especially crucial for species, such as longleaf pine, that are of conservation concern and targeted for ecological restoration activities.

Longleaf pine is a formerly widely distributed, dominant species in the southeastern United States. The natural range of longleaf pine prior to European settlement is estimated at 37 million hectares (Frost 2006). Most of the pre-settlement forests were composed of nearly pure stands of longleaf pine with a grass understory, and were distributed on the Coastal Plain of the United States along the Atlantic Ocean and Gulf of Mexico (Henderson and Grissino-Mayer 2009). Human-caused destruction of longleaf pine ecosystems began as early as the 17th century (Frost 2006). Harvesting of trees for naval stores and timber coincided with European settlement of North America, and continued until the first half of the 20th century. Other aspects of land-use history, such as intensive livestock grazing and agricultural clearing, have also dramatically reduced the range and dominance of this species, and left few living trees to provide dendroecological information (van de Gevel et al. 2009). Several studies estimate that longleaf pine has been eliminated from 97% of its original range since the beginning of European settlement (Simberloff 1993, Outcalt and Sheffield 1996, Frost 2006).

In addition to the vast pre-settlement longleaf pine forests of the Coastal Plain, as many as 14 million hectares of pre-settlement longleaf pine existed in mixed-species stands in the Piedmont region of the southern Appalachians (Frost 2006). In these settings, longleaf pine shared dominance with other fire-tolerant species, such as shortleaf pine (*Pinus echinata* Mill.) and loblolly pine (*Pinus taeda* L.), as well as several hardwood taxa, such as oaks (*Quercus spp.*)

and hickories (*Carya spp.*). These mixed-species stands represented a transition from longleaf pine forests of the Coastal Plain to the oak-hickory communities of the Appalachian Mountains. Frost (2006) noted that very few descriptions of these mixed longleaf pine communities have been documented, and that this diverse community type has been overlooked because of the (historically) extensive pure stands of longleaf pine in the region.

Here, we present a 250-year tree-ring chronology developed from an old-growth stand of longleaf pine from a montane site situated near the northwestern margin of the species' geographic range. This record of annual growth from a mixed species stand on a montane site provides an excellent opportunity to analyze ecological amplitude of longleaf pine. The objectives of this paper are to: (1) analyze the growth response of longleaf pine to monthly climate variables and identify the climatic controls on tree growth, and (2) compare climate response and climatic sensitivity of tree growth from this site to other published longleaf pine tree-ring chronologies from sites on the Coastal Plain. Based on the assumptions of ecological amplitude, we hypothesize that this range edge, montane site represents a niche edge habitat for longleaf pine, and therefore tree growth will be more sensitive to climate variability than longleaf pine in the interior of its range on the Coastal Plain.

3.2 Study Areas

3.2.1 Marshall Forest Preserve

We collected tree cores from longleaf pines located in Marshall Forest Preserve (MFP). This preserve consists of approximately 120 ha of minimally-disturbed old-growth forest located in

the city of Rome, Georgia in the northwest part of the state (34° 15′ N, 85° 12′ W) (Figure 3.1). MFP is located in the southern portion of the Ridge and Valley physiographic province of the Appalachian Mountains, which is characterized by folded layers of sedimentary rock forming long parallel ridges of sandstone interspersed with valleys of shale or limestone (DeSelm 1984). MFP is located on Horseleg Mountain, a ridge underlain by Armuchee chert and Conasauga shale (DeSelm 1984). Soils at MFP are shallow, well-drained, shaly silt loams formed from shale residuum (Soil Survey Staff 2010). Elevations within MFP range from 200–300 m above sea level.

The study area has a humid continental climate with mild winters and hot summers. Mean monthly temperatures in this region range from 5° C in January to 25° C in July. Mean annual precipitation is approximately 1100 mm, and is evenly distributed throughout the year (NOAA 2010) (Figure 3.2).

The vegetation along the main ridge in MFP is primarily pine-oak forest dominated by shortleaf pine and chestnut oak (*Quercus montana* Willd.). Mockernut hickory (*Carya tomentosa* Sarg.), shagbark hickory (*Carya ovata* (Mill.) K. Koch.), northern red oak (*Quercus rubra* L.), southern red oak (*Quercus falcate* Michx.), sourwood (*Oxydendrum arboretum* (L.) DC.), white oak (*Quercus alba* L.), and tulip poplar (*Liriodendron tulipifera* L.) also occur in the canopy, especially in more mesic locations lower on the north-facing slope of the ridge. In the understory, red maple (*Acer rubrum* L.) and black gum (*Nyssa sylvatica* Marsh.) are common, and flowering dogwood (*Cornus florida* L.) and black cherry (*Prunus serotina* Ehrh.) are occasionally found. The

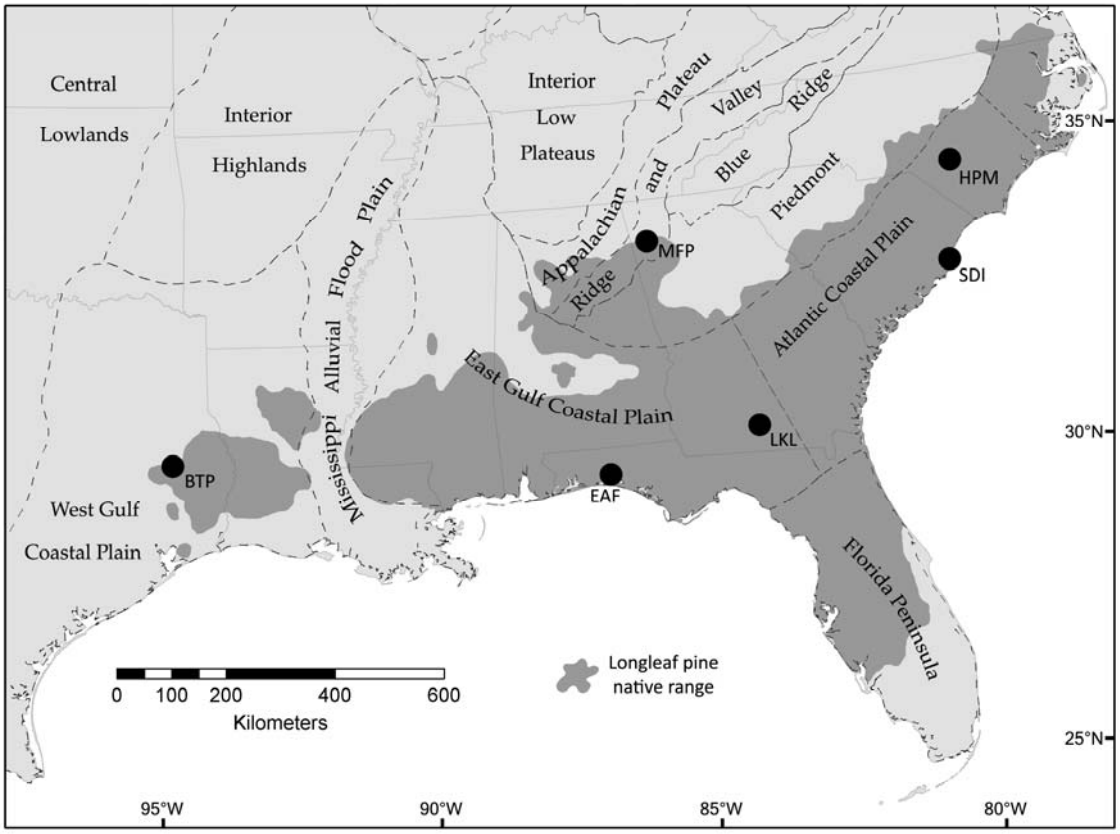

Figure 3.1. Locations longleaf pine tree-ring chronologies used in this study. Dashed lines delineate physiographic provinces. Site location labels are: SDI = Sandy Island, HPM = Hope Mills, EAF = Eglin Air Force Base, MFP = Marshall Forest, BTP = Big Thicket, LKL = Lake Louise. Modified from Henderson and Grissino-Mayer (2009).

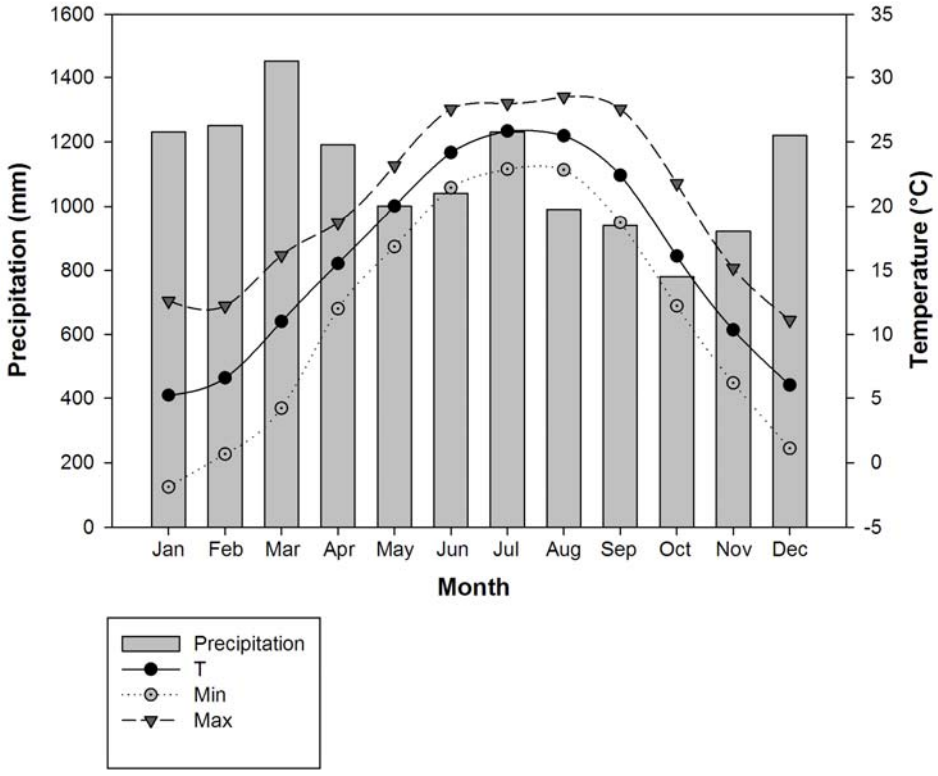

Figure 3.2. Mean, minimum, and maximum temperature and monthly precipitation for NOAA Georgia climate division 1 over the period 1895–2009.

longleaf pine in MFP is primarily interspersed in the canopy with shortleaf pine and chestnut oak near the ridgetop on the southwest-facing slope. However, a few individual longleaf pines are scattered in other moist locations. In addition to large, mature longleaf pine in the canopy, several smaller individuals occur in the subcanopy beneath larger longleaf pines. We observed no longleaf seedlings or saplings during our sampling.

Commercial logging did not occur in Marshall Forest Preserve (DeSelm 1984), but evidence of some timber harvest is discernable from remnant stumps scattered mostly along the southern boundary of the preserve. MFP was designated a National Natural Landmark by the U.S. federal government in 1966 and the property is currently managed by The Nature Conservancy.

3.2.2 Coastal Plain Longleaf Pine Stand

We compared mean sensitivity and climate response between the MFP site and five previously published longleaf pine chronologies from other sites (Figure 3.1; Table 3.1). Data for these additional sites were obtained by retrieving and reanalyzing specimens from the archives of the Laboratory of Tree-Ring Science at the University of Tennessee. These additional chronologies were all developed from longleaf pine growing on the Coastal Plain. The Atlantic Coastal Plain is a belt 160–320 km wide consisting of little topographic relief and is less than 90 m above sea level (Henderson and Grissino-Mayer 2009). Climate along the Coastal Plain is also humid subtropical with mean annual temperatures ranging from 16° C to 23° C,

and annual rainfall ranging from 1170–1650 mm (Henderson and Grissino-Mayer 2009, van de Gevel et al. 2009).

3.3 Methods

3.3.1 Marshall Forest Chronology Development

We obtained annual growth data at the northwestern range limit of longleaf pine by coring all mature longleaf pine individuals present in Marshall Forest Preserve (n = 24) using an increment borer. Two cores were extracted from each tree 30 cm above the root collar on opposite sides of the stem. To minimize the probability of sampling reaction wood, we extracted cores from the sides of trees parallel to the contour of the slope (Fritts 1976, Grissino-Mayer 2003). Additionally, the diameter at breast height (DBH) of each tree was measured, and the position of each tree was recorded using a GPS receiver.

In the laboratory, cores were glued into wooden core mounts so that the transverse plane of the wood was visible, and then sanded to a high polish to ensure clear visibility of annual ring boundaries and wood cellular structure (Orvis and Grissino-Mayer 2002). Annual rings of all cores were dated to the exact calendar year of their formation using both visual and statistical crossdating. Increment cores were examined under 10X magnification using a stereozoom microscope, and lists of narrow marker years were compiled for all samples. Lists of marker years were then matched between samples to ensure correct dating of annual rings (Yamaguchi 1991). Ring widths of all samples were then measured to the nearest 0.001 mm using a Velmex measuring stage and Measure J2X software. We measured earlywood width

(EW) and latewood width (LW), from which we obtained total ring width (TRW) for each annual ring in all increment cores. We used the criteria specified by Stahle et al. (2009) to distinguish the intra-annual boundary between earlywood and latewood. Crossdating accuracy was verified using the program COFECHA to compute time-series correlation coefficients between 50-year segments (25 year overlap) of each tree-ring series (i.e., each core) and the remaining series (Holmes 1983, Grissino-Mayer 2001). Segments with correlation coefficients below the 0.05 level of significance were re-examined under the microscope, and errors in crossdating (if any) were corrected.

The three sets of raw ring-width measurements were detrended and standardized to develop three separate chronologies: EW, LW, and TRW. The program ARSTAN (Cook 1985) was used to remove age-related growth trends in the tree-ring series and combine series into standardized tree-ring chronologies. Each series was detrended by fitting a negative exponential or negative slope linear curve to the raw ring-width measurements. Each ring-width measurement was divided by the corresponding value of the fitted curve to produce a standardized index. All EW, LW, and TRW indices were averaged to create an index for each set of measurements. Autoregressive models were applied to each measurement series to remove autocorrelation, and the series were averaged to create the residual chronology. Residual chronologies are used here for all subsequent growth–climate analyses.

3.3.2 Climate Data

The radial growth of longleaf pine was analyzed as a response to monthly climate. We selected mean monthly temperature, monthly total precipitation, and Palmer Drought Severity Index (PDSI) as climatic variables. PDSI is a monthly index of soil moisture used by the National Weather Service to quantify drought conditions. Monthly climate data were obtained from the National Climatic Data Center (NOAA 2010) for Georgia climate division 1, the northwest portion of the state. Divisional data average climate observations from all climate stations within that division of the state, giving equal weight to each station. Additionally, station data that are incorporated into divisional data are corrected to account for variable effects of elevation and topography. Divisional data therefore reduce the effects of micro-site climate variation, and are well-suited for tree-ring analysis (Blasing et al. 1983).

3.3.3 Response Function Analysis

We analyzed the relationship between the tree-ring chronologies and monthly climate variables using response function analysis (RFA) in the program Dendroclim 2002 (Biondi and Waikul 2004). Response function analysis produces coefficients that are multivariate estimates from a principal component regression model that predicts ring width from monthly climate variables (Fritts et al. 1971). Response functions were computed for EW, LW, and TRW chronologies developed at the Marshall Forest Preserve. We used a 19-month window (April of the year prior to tree growth to October of the current growing year) to analyze the response of tree growth to monthly climate variables. Response functions were developed for the period

1895–2008. The temporal ranges of climate analyses were restricted by the availability of divisional climate data (no divisional data were available prior to 1895).

3.3.4 Comparisons with other longleaf pine chronologies

To assess the variability in growth–climate relationships across the geographic range of longleaf pine, we obtained and re-analyzed data from other tree-ring based studies of this species on the Coastal Plain (Table 3.1). Each Coastal Plain chronology contained between 39 and 125 dated series. The chronologies ranged in length from 251 to 548 years and spanned nearly the entire geographic range of longleaf pine on the Coastal Plain. The climatic response of longleaf pine from these additional five sites located in other parts of its geographic range were made using Pearson product-moment correlation analysis and RFA on the EW, LW, and TRW chronologies from these sites. RFA was conducted in the same manner as for the MFP site. Divisional climate data were also used for climate-growth analyses of the Coastal Plain sites. We used data from Florida climate division 1 for Eglin Air Force Base (EAF), South Carolina division 4 for Sandy Island (SDI), Texas division 4 for Big Thicket Preserve (BTP), North Carolina division 6 for Hope Mills (HPM), and a composite of Alabama division 7 and Georgia division 8 for Lake Louise (LKL).

Table 3.1. Summary statistics of six longleaf pine tree-ring chronologies used in this analysis. Note: average mean sensitivity for the common period (1875–1999) was used in the ANOVA comparison of total ring-width mean sensitivity. Other mean sensitivity values are reported for the entire length of each chronology.

Site Code	Site Name	No. Series	Time Span	Latitude (deg. N)	Longitude (deg. W)	Elev. (m)	Average Mean Sensitivity	Avg. Mean Sensitivity (1875–1999)	EW Mean Sensitivity	LW Mean Sensitivity
SDI	Sandy Island	105	1455–2003	33.57	79.15	3	0.274	0.274	0.270	0.429
EAF	Eglin Air Force Base	49	1716–2004	30.52	86.53	27	0.300	0.283	0.297	0.508
MFP	Marshall Forest Preserve	47	1757–2008	34.25	85.20	300	0.290	0.293	0.310	0.509
BTP	Big Thicket Preserve	125	1629–2004	30.43	94.10	35	0.352	0.349	0.336	0.566
HPM	Hope Mills	39	1597–2003	34.97	78.95	33	0.288	0.277	NA	NA
LKL	Lake Louise	94	1421–1999	30.72	83.26	49	0.360	0.393	NA	NA

We also compared mean sensitivity between all the longleaf pine chronologies. We quantified the mean sensitivity of each longleaf pine tree-ring chronology to test the hypothesis that longleaf pine is more sensitive to climate near the edge of its geographic range, and less sensitive near the range center. Mean sensitivity is the sum of the absolute value of the difference between consecutive annual growth rings expressed as a proportion of total tree growth (Biondi and Qeadan 2008). We calculated mean sensitivity for all longleaf pine TRW chronologies for the 125-year common period 1875–1999. We compared differences in mean sensitivity averaged across all tree-ring series at each site (average mean sensitivity) using a one-way analysis of variance. Pairwise comparisons between all sites were conducted using Tukey tests (Zar 1999).

3.4 Results

3.4.1 Marshall Forest tree-ring chronology development

We located and sampled 24 longleaf pine trees at MFP, and successfully crossdated 47 cores (one core was too badly rotted for adequate measurement of ring widths). We examined 267 50-year segments of the TRW series using the program COFECHA for statistical verification of crossdating accuracy. Only 19 segments (7.1%) failed to reach the 95% significance level when correlated with the master tree-ring series. Upon visual re-examination of these low-correlation segments, it was determined that they were all correctly dated. The average interseries correlation for the entire site was 0.577, and the average mean sensitivity was 0.291.

Variability of latewood width was a larger contributor to total ring-width variability than earlywood width. Average interseries correlation and mean sensitivity of the latewood width series were higher than the total ring width series. The interseries correlation of the LW measurement series was 0.615, and mean sensitivity was 0.508. Conversely, earlywood width (EW) measurement series had a lower average interseries correlation (0.521) and mean sensitivity (0.291).

The tree-ring record covered 252 years from 1757 to 2008. We truncated the tree-ring record at the year 1784 for chronology development and climate analyses to ensure that sample size was at least five crossdated series. We detrended and standardized all three raw measurement series (TRW, EW, and LW) to create composite chronologies (Figure 3.3). Notable features of the TRW standard chronology include a sustained period of below average growth from 1779 to 1812, as well as a minimum ring width in 1960. The minimum ring width coincides with a destructive ice storm in March of 1960 that caused extensive structural damage to the longleaf pine trees at MFP (DeSelm 1984).

3.4.2 Climate–growth relationship

Annual growth of longleaf pine at MFP is primarily influenced by precipitation and available moisture during the growing season. Response function analysis of total ring width to monthly climate data revealed that precipitation in May of the current growing season had a significant influence on ring width (Figure 3.4). Additionally, available soil moisture as

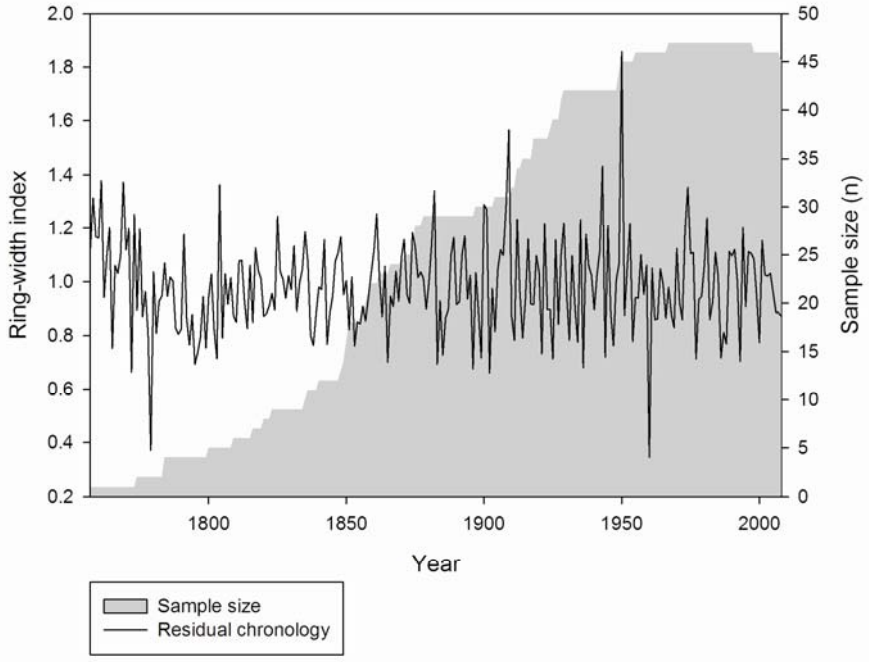

Figure 3.3. Residual longleaf pine tree-ring chronology and sample depth from Marshall Forest Preserve in northwest Georgia.

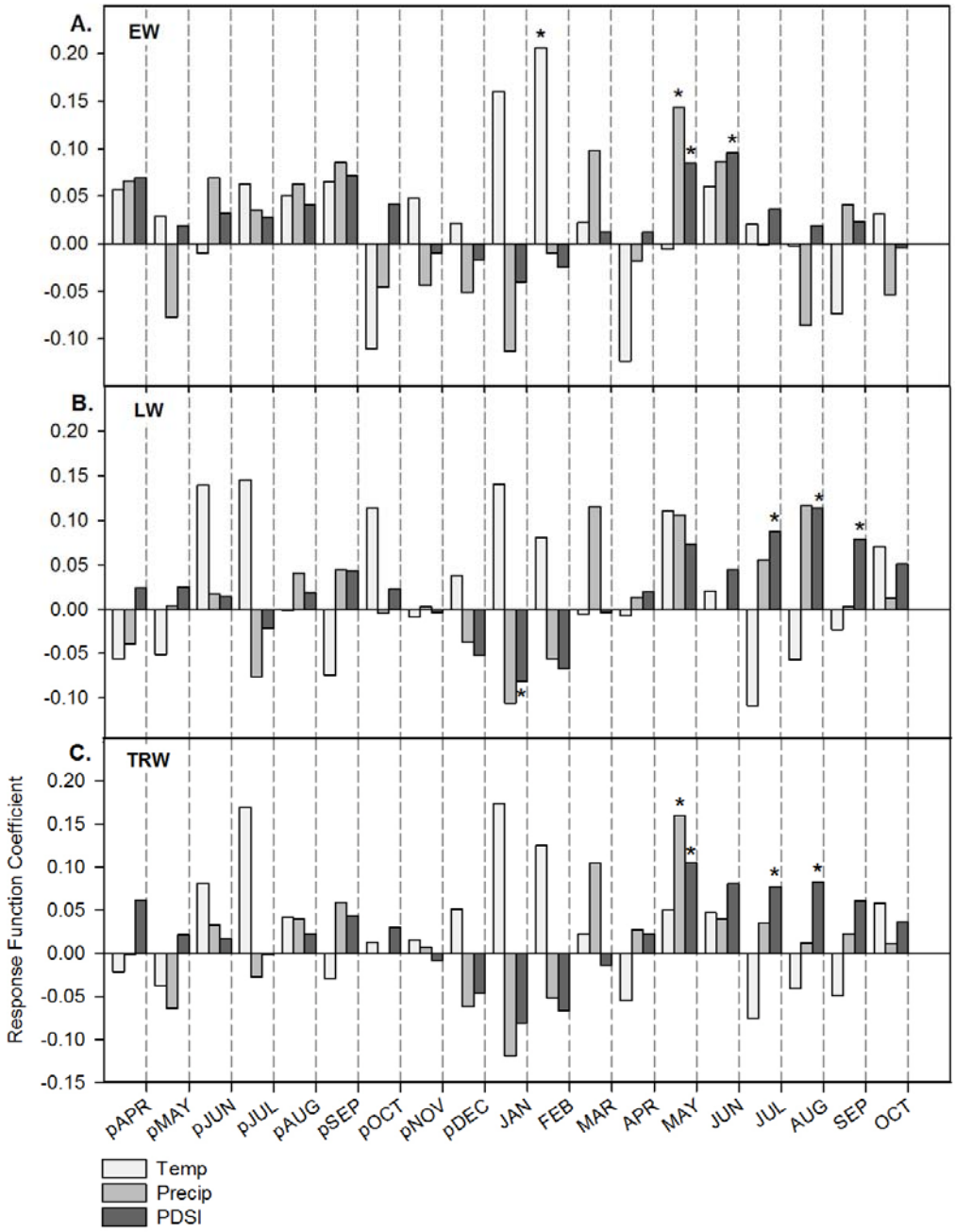

Figure 3.4. Response of Marshall Forest longleaf pine annual growth to monthly climate variables. Response function coefficients are calculated for precipitation and temperature from April (pAPR) of year prior to growth to October (OCT) of current growing year. (A) is response of earlywood width, (B) is latewood width, and (C) total ring width. Significant coefficients ($p < 0.05$) are denoted by an asterisk (*) above each bar.

characterized by PDSI is an important determinant of annual growth. May, July, and August PDSI for the current growing season contribute to annual growth at the 95% confidence level. Mean monthly temperature did not have a significant influence on tree growth for any of the months analyzed in the response function analysis. However, correlation analysis between monthly temperature and the residual tree-ring chronology found significant negative correlations between total ring width and current year summer (June, July, and August) temperatures. This negative relationship between summer temperature and tree growth is likely a signal of moisture stress, as higher temperatures result in higher rates of evapotranspiration.

3.4.3 Intra-annual climate response

Monthly precipitation and available moisture were also the most important controls on the formation of earlywood and latewood. May precipitation as well as May and June PDSI of the current growing season are significantly related to earlywood growth (Figure 3.4). Additionally, earlywood growth is significantly influenced by mean February temperature for the current growing year. Monthly climate for the year prior to annual ring formation did not significantly influence earlywood formation. Monthly PDSI for late summer (July, August, and September) of the current growing year were the only climate variables tested that had a significant influence on latewood growth. No significant relationship was found between mean monthly temperature or monthly precipitation from April of the year prior to growth to

October of the current year of latewood formation. Lag effects of climate from the previous year's growing season did not have any significant influence on radial growth.

3.4.4 Comparisons with Coastal Plain sites

Average mean sensitivity varied significantly between some of the longleaf pine chronologies (Figure 3.5). One-way analysis of variance indicated significant differences between tree-ring chronologies ($F = 29.96$, $P < 0.001$). Pairwise Tukey tests revealed that the average mean sensitivity of the montane longleaf pine site (MFP) was similar to that of some of the Coastal Plain sites (SDI, HPM, and EAF), but lower than others (BTP and LKL). BTP, located on the western edge of the range, had significantly higher average mean sensitivity than the montane site and all Coastal Plain sites except LKL. LKL, located near the center of the species geographic range in southern Georgia, had significantly higher average mean sensitivity than all other sites.

Current year growing season precipitation was an important influence on annual radial growth of longleaf pine at all sites. Each of the six chronologies had either significant correlation (Figure 3.6) or significant response function (Figure 3.7) coefficients between February and September of the current year. The timing of significant relationships between growth and precipitation differed by site. Radial growth at LKL near the center of the species range was strongly associated with February–April precipitation in both correlation and response function analyses. Similar correspondence between correlation and response function coefficients was observed between MFP and May precipitation. Annual growth at the BTP site

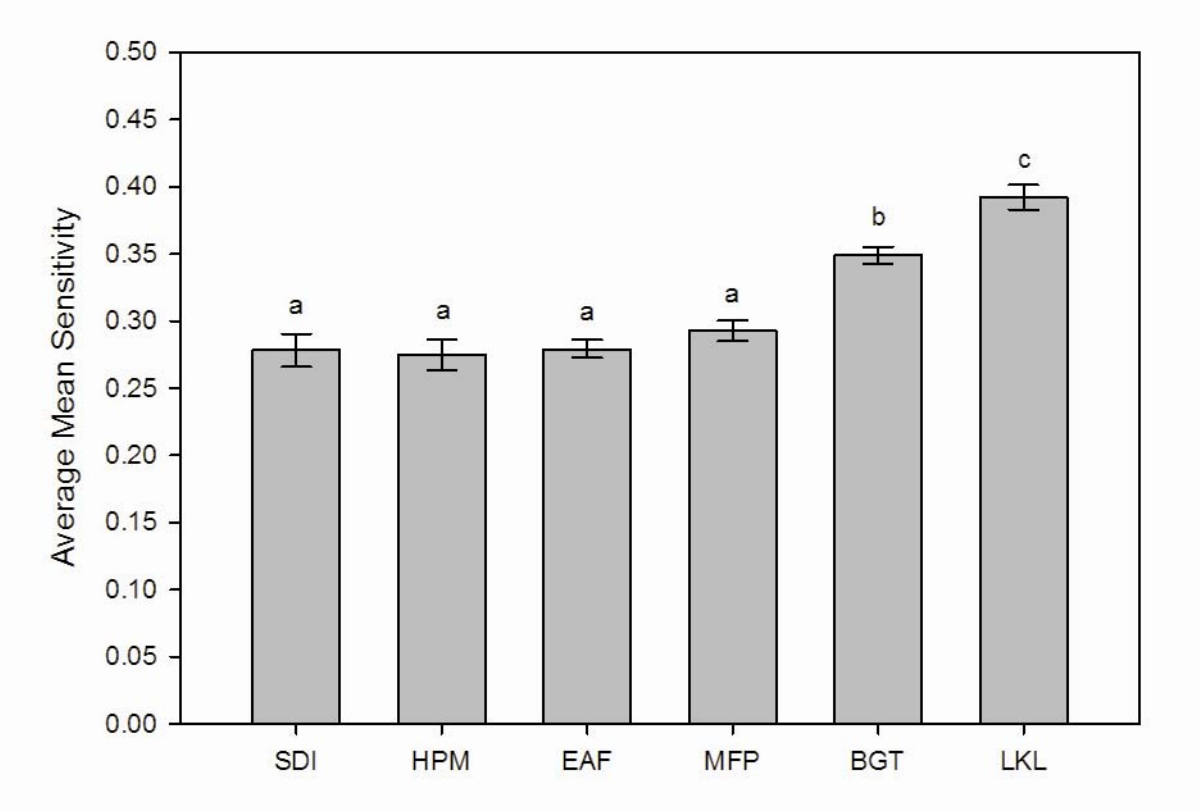

Figure 3.5. Average mean sensitivity and standard errors for the six longleaf pine chronologies. Site codes on the x-axis are: SDI = Sandy Island, HPM = Hope Mills, EAF = Eglin Air Force Base, MFP = Marshall Forest, BTP = Big Thicket, LKL = Lake Louise. Different letters above each bar represent significant differences ($p < 0.001$) between group means as indicated by one-way ANOVA and pairwise Tukey tests.

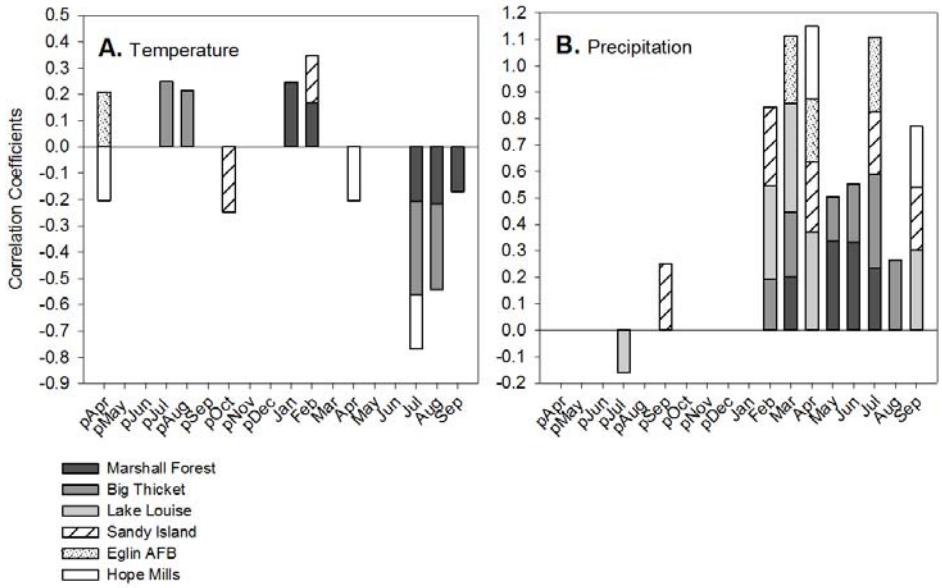

Figure 3.6. Correlations between tree growth and monthly mean temperature (A), and monthly precipitation (B). Only significant coefficients ($p < 0.05$) are shown. Note: axes are not cumulative coefficient values. The height of each bar section corresponds to the absolute value of the coefficient for each site. Maximum and minimum values are different for each panel, but increment scales for each pair of correlation and response function axes are identical.

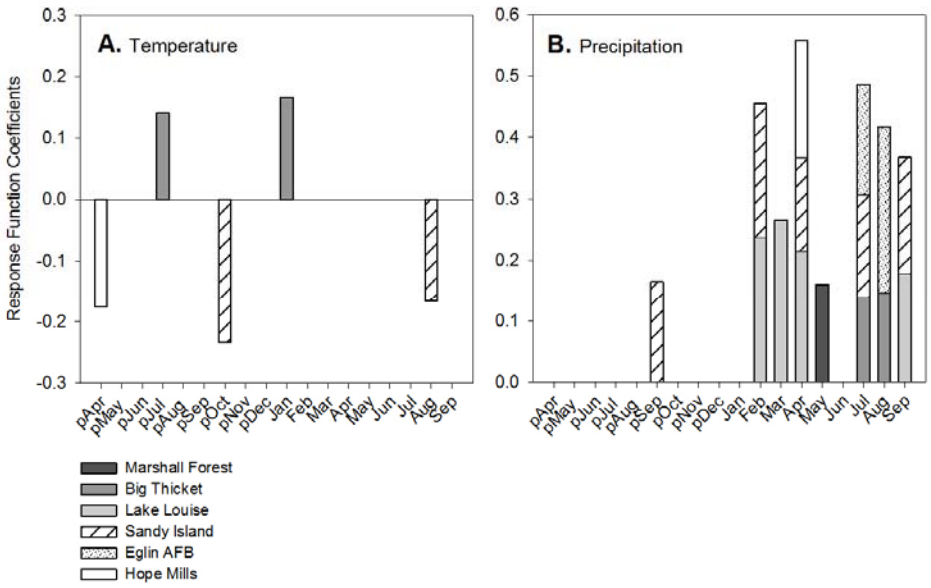

Figure 3.7. As in Figure 3.6, but for response function analysis.

was most strongly related to July and August precipitation. SDI and EAF sites had positive associations with precipitation across a wider range of growing season months. Few significant relationships between previous year precipitation and annual growth were detected.

Inverse associations between late growing season temperature (July–September) and tree growth were identified at several sites. Significant negative correlations with late summer temperature were observed at MFP, BTP, and HPM. Response function analysis revealed a significant negative coefficient for SDI and current August temperature. These negative relationships between summer temperatures and radial growth are likely caused by increased moisture stress from higher temperatures during the growing season.

Three of the longleaf pine sites had positive associations with winter temperatures prior to the growing season. Radial growth at MFP was positively correlated with January and February temperature, SDI was positively correlated with February temperature, and BTP had a significant positive response to January temperature.

3.5 Discussion

The patterns of sensitivity and response to monthly climate variables in longleaf pine across its geographic range are not consistent with the predictions of the ecological amplitude hypothesis. Despite being located on a marginal site near the northwestern limit of its geographic range and near the upper limit of elevation for the species, longleaf pine at Marshall Forest Preserve exhibit similar values of average mean sensitivity and show similar responses to monthly climate observed in the other longleaf pine stands we examined on the Coastal Plain.

Average mean sensitivity at MFP was not significantly different from average MS at three Coastal Plain sites (SDI, HPM, and EAF), and average mean sensitivity was lower at MFP than at two Coastal Plain sites (BTP and LKL). Additionally, the site with the highest average mean sensitivity was LKL, near the center of the geographic range of longleaf pine. The spatial pattern of mean sensitivity, based on ecological amplitude assumptions, would predict high mean sensitivity at a montane site near the range edge, such as MFP, and low mean sensitivity at a Coastal Plain site near the center of the species' range, such as LKL.

High mean sensitivity at the BTP site near the western limit of the species' range on the Western Gulf Coastal Plain may indicate a response to limited precipitation or available soil moisture. Mean sensitivity at BTP was significantly higher than at the montane site at MFP, or at some of the Coastal Plain sites. The concept of ecological amplitude suggests that mean sensitivity should be higher at locations where climate is more limiting to tree growth (Fritts1976), and the western edge of the range of longleaf pine may represent such a location because it is located on the dry side of a gradient of decreasing precipitation from east to west. The Western Gulf Coastal Plain is generally warmer and drier than the rest of the geographic range of longleaf pine (Boyer 1990, PRISM 2004). The high mean sensitivity in longleaf pine growth at BTP is possibly a result of limitation of annual radial growth from lower precipitation. Leblanc and Terrell (2009) similarly found a greater sensitivity to monthly precipitation in the radial growth of white oak (*Quercus alba* L.) on the western (drier) edge of the east-to-west North American precipitation gradient.

While high mean sensitivity values at the BTP site seemingly support the ecological amplitude concept, the highest mean sensitivity values at LKL are difficult to explain. LKL is located near the center of the natural range of longleaf pine in southern Georgia. The average mean sensitivity of the LKL longleaf pine chronology is significantly higher than all other sites analyzed, both montane and Coastal Plain sites. LKL is not on the edge of a climatic gradient of either annual precipitation or temperature, such as BTP. In fact, higher and lower values of annual precipitation, maximum and minimum temperatures over the period 1971–2000 can be found in other areas of the range of longleaf pine, not at LKL (PRISM 2004). The occurrence of highest mean sensitivity at LKL, which is not near the species range edge or a climatic outlier, contradicts the ecological amplitude concept.

Similarly, the pattern of growth response to monthly climate variables does not seem to be related to geographic position within the range of longleaf pine. Although MFP was located in a very different physiographic setting than the other sites, the longleaf pine stand at MFP had a similar climate response. Precipitation during the growing season was important to longleaf pine growth throughout its range, but preconditioning effects from the previous growing season were only important at one site (SDI). The strength of correlation between monthly precipitation and radial growth was not higher at MFP compared to any Coastal Plain sites. The strongest correlations between climate variables and growth were at LKL near the center of the species' range, and SDI on the Atlantic Coastal Plain. The pattern of climate response across the range of longleaf pine does not match the predictions of an ecological amplitude model, or a

monotonic latitudinal or longitudinal gradient found in some hardwood species (Pederson et al. 2004, LeBlanc and Terrell 2009).

Annual growth of longleaf pine at Marshall Forest Preserve is primarily influenced by water availability during the growing season, as indicated by significant relationships between radial growth and monthly moisture-related climate variables (precipitation and PDSI). May precipitation is the most important predictor of total ring width as indicated by RFA. PDSI throughout the entire growing season (May–September) is an important predictor of radial growth, with May–June PDSI being important for earlywood growth, and July–September PDSI strongly associated with latewood growth. Precipitation falling in the growing season or winter prior to the current year's growth was not significantly associated with longleaf pine radial growth. Both the importance of current year growing season precipitation and the seasonal relationship between monthly PDSI and earlywood/latewood growth are consistent with studies of longleaf pine climate–growth relationships in other locations of the species' range (Lodewick 1930, Meldahl et al. 1999, Henderson and Grissino-Mayer 2009).

Winter temperatures prior to the growing season were significantly associated with radial growth of longleaf pine at MFP and some Coastal Plain sites. January and February temperatures were significantly correlated with total ring width, and RFA indicated a significant effect of February temperature on earlywood width. Bhuta et al. (2009) also used RFA and identified a significant relationship with February temperature and longleaf pine growth at two sites near the species' northern latitudinal range margin on the Coastal Plain of Virginia. Henderson and Grissino-Mayer (2009) reported no correlation between winter

temperatures and longleaf pine growth at three sites along the Gulf coast (SDI, EAF, and BTP). However, our reanalysis of their data using RFA indicated a significant positive relationship between January temperature and annual growth at the BTP site at the western range limit of this species on the Coastal Plain.

The significant relationship between annual growth at MFP and winter temperatures supports the hypothesis of Bhuta et al. (2009) that winter temperatures are an important limiting factor to growth of temperate conifer species along their northern range margins. However, the significant relationship between January temperatures and growth at BTP refutes their speculation that winter temperatures are only important to growth of longleaf pine near northern range limits. The spatial pattern of climate response of longleaf pine to winter temperatures does not follow a north–south gradient through its geographic range, as positive relationships between winter temperatures and annual growth were detected at MFP, BTP, and SDI sites. Fine-scale variability of site characteristics may be more important in influencing temperature sensitivity in longleaf pine than broad-scale latitudinal gradients. The positive relationship between previous winter temperatures and annual radial growth is similar to the response of other temperate conifer tree species in North America. Biermann (2009) identified a significant growth response of shortleaf pine to winter temperatures in the Great Smoky Mountains of Tennessee. Pederson et al. (2004) found differing sensitivity to winter temperature among several species in the Hudson River Valley. They found Atlantic white cedar and pitch pine to be more sensitive to temperature (especially winter and spring temperatures) than oak and hickory. Tardif et al. (2006) found that white oak radial growth was

not limited by winter temperatures at its northern range limit. Several studies have illustrated the differential response of evergreen and deciduous tree growth to increases in temperature, and emphasized various physiological explanations for differences, such as contrasting strategies for carbon allocation between hardwoods and conifers (Way and Oren 2010).

The discrepancy between the pattern of climate response predicted by theory, such as the ecological amplitude hypothesis and the observed patterns of annual growth, have important implications for studies that attempt to predict the future distribution of longleaf pine. Variable climate–growth responses will also impact efforts aimed at restoring this species to its native range. Many models of future tree species distributions assume that current ranges represent suitable habitat, and that climate has a direct, causal influence on range limits (Gaston 2003). Our analysis of variability of annual radial growth at several sites through the range of longleaf pine suggests that climate response does not vary along predictable geographic gradients. Models of the future distribution of this species need to incorporate empirical estimates of climate response across many geographic locations, as well as other parameters such as competition and disturbance regimes. Additionally, models of the interactions between temperate forests and carbon cycles need to incorporate not only future projections of species' abundance, but also projections of future growth rates and carbon assimilation. While annual growth of longleaf pine across its geographic range does not seem to fit the predictions of ecological amplitude theory, further research is needed on rates of regeneration, recruitment, stand structure, disturbance histories, and competition to understand spatial variability of ecological processes, and how these processes may be altered by a changing climate.

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CHAPTER 4

MODELING SPATIAL VARIABILITY OF CLIMATE SENSITIVITY IN ANNUAL GROWTH OF TREE SPECIES IN EASTERN NORTH AMERICA

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The previous chapter examined variability in the response of a tree species to specific climate variables (monthly temperature and precipitation) at several sites across the geographic range of the species. In this chapter, I employ a much larger network of tree-ring data and examine the climatic response of two widely distributed tree species in eastern North America, eastern hemlock and white oak. I examine spatial variability in tree growth by modeling mean sensitivity (a measure of growth response to inter-annual climate variability) in relation to spatial location within the geographic range of each species. This chapter is the basis for a manuscript that will be submitted to *Journal of Biogeography*. The use of "we" in this chapter refers also to Henri Grissino-Mayer, Nicholas Nagle, Justin Hart, and Saskia van de Gevel, who will be co-authors on the manuscript. As the first author, I was responsible for designing the study, obtaining and processing most of the data, performing the analyses, and writing the paper.

Abstract

We analyzed the pattern of climate sensitivity in annual growth of eastern hemlock (*Tsuga canadensis*) and white oak (*Quercus alba*), two widely distributed, long-lived species that have been extensively used for dendrochronological research in eastern North America. We modeled the pattern of annual growth variability across the geographic ranges of both tree species using tree-ring records and examined the influence of distance from range edge, as well as latitudinal and longitudinal position. We hypothesized that variability of annual growth (mean sensitivity) would be higher near the edges of species' ranges and lower at interior range locations. Additionally, we predicted that eastern hemlock sensitivity would be less variable than white oak because hemlock has a highly restricted topographic distribution. Despite the fact that a very flexible model was fit to the tree-ring data, distance from range edge was not a

significant predictor of average mean sensitivity for either tree species and did not influence the pattern of sensitivity in the model predictions. Model output predicted a broad-scale trend of increasing sensitivity along a southeast to northwest gradient through each species' range. Trends in ring-width sensitivity were instead significantly correlated with gradients of annual temperature range and mean annual precipitation.

4.1 Introduction

The paradigm that species are most abundant near their geographic range centers and become gradually less abundant toward their range margins is referred to as the abundant center hypothesis. The abundant center hypothesis has long been considered an ecological rule and, as such, it provides the basis for number of ecological models (e.g., range contraction and range shape models among others) (Wulff 1943, Hengeveld 1990, Brown et al. 1995). This theoretical framework is based on a multi-dimensional niche concept, in which patterns of abundance vary along multiple environmental gradients, and centers of high and low population density within a species' range are the result of how closely environmental conditions match the optimal requirements for that species. Therefore, the point of intersection of multiple niche axes would be the optimal habitat for that species, where it could reach its greatest abundance and locally occupy a high number of sites. Additionally, because environmental conditions are spatially autocorrelated, near sites will be more likely to meet a species' requirements than distant sites (Brown 1984). Consequently, a species would be less likely to find its niche requirements met at greater distances from its optimal habitat, and

population density will gradually decline to zero (the external range boundary) where environmental conditions are completely unsuitable.

Hengeveld (1990) noted that abundance or density is but one measure of species vitality, and hypothesized that many processes (e.g., growth, reproductive rates, ratio of sexual to vegetative reproduction) should also vary in a spatial pattern similar to the abundant center distribution. If species occupy less than optimal habitat, then they should be subject to greater environmental stress closer to their geographic range limits. Increasing environmental stress should, in turn, lead to lower rates of growth and reproduction, and these lower physiologically vital rates may explain demographic patterns such as abundant center (Hengeveld 1990).

The relationship between tree growth and climate has been investigated by dendrochronologists for nearly a century (Douglass 1920), and a guiding principle of dendrochronology has been the paradigm that range edges are locations where climatic conditions contribute to environmental stress for trees. Stressed trees are thought to be most suitable for detecting climatic influences on growth, and this long-held assumption in the analysis of tree rings is often referred to as the principle of ecological amplitude because trees are assumed to occupy restricted sites near range limits and a wider variety of sites at range interiors where environmental conditions are presumably more favorable for growth (Fritts 1976, Fritts and Swetnam 1989). Because climate-induced variability in ring widths forms the basis of crossdating and makes dendrochronology possible, Fritts (1976) advocated sampling near elevational and external geographic range margins to maximize the possibility of trees being sensitive to climate variability, and this sampling strategy has generally been followed by

dendrochronologists ever since (e.g., Cook and Briffa 1990, Makinen et al. 2000, Carrer et al. 2007, Leonelli et al. 2008, Carrer et al. 2010).

Despite the longstanding and widely accepted assumption that the abundant center distribution and ecological amplitude principle accurately characterize the structure of geographic ranges, very few empirical tests of the hypothesis have been successfully conducted, and many tests do not support the hypothesis (Sagarin and Gaines 2002). Understanding the structure of geographic ranges and the processes that influence range limits is crucial for addressing many urgent ecological concerns, such as controlling the spread of alien invasive species, conserving biodiversity, and mitigating climate-induced range migrations (Gaston 2003). Many recent studies have focused on refining knowledge of range structure and have used newly available networks of demographic data to develop new models of the distribution of abundance of many organisms (Sagarin et al. 2006, Gaston et al. 2008), yet relatively few investigations of variability of growth rates or other vital biological processes have been conducted across the geographic ranges of species (LeBlanc and Terrell 2009).

Because of the wide acceptance of ecological amplitude assumptions in the field of dendrochronology, an examination of radial growth sensitivity across the geographic ranges of tree species is overdue. Previous studies have investigated the spatial structure of abundance of tree species (Murphy et al. 2006, Iverson et al. 2008), and a few investigations have examined spatial variability in the response of tree growth to specific climatic variables (Cook and Cole 1991, LeBlanc and Terrell 2009, Chen et al. 2010, Goldblum 2010, Miyamoto et al. 2010). However, research focused on variability of the overall sensitivity of tree growth to climate

across the entire geographic ranges of tree species is lacking (Hart et al. 2010). Variability in tree growth across continental scales has potentially important consequences for range dynamics, future forest composition, climate-induced mortality, and carbon sequestration (Parmesan et al. 2000, Tardif et al. 2006, van Mantgem et al. 2009).

In this study, we analyzed the spatial pattern of climate sensitivity in annual radial growth variability in eastern hemlock (*Tsuga canadensis* (L.) Carr.) and white oak (*Quercus alba* L.), two widely distributed, relatively long-lived species that have been extensively used for dendrochronological research such as climate reconstruction (e.g., Cleveland and Duvick 1992, Leblanc and Foster 1992, Black and Abrams 2005). We modeled the pattern of annual growth variability across the geographic ranges of both species using existing tree-ring records and examined the influence of distance from range edge and geographic position within each species range on annual growth sensitivity to explicitly test the ecological amplitude theory. Specifically, our objectives were to: (1) analyze the relationships between geographic position variables and mean sensitivity of both species through correlation analysis, (2) model the spatial pattern of sensitivity of tree growth to climate variability across the geographic ranges of each species, (3) document the relationship between growth variability and climate through correlation analysis between annual growth sensitivity and climatic variables across the species' ranges. Our results combined with recent investigations allow us to test the assumption that sensitivity to climate increases from a minimum at the range center to a maximum at range edges.

4.2 Methods

4.2.1 Tree Species: Eastern hemlock and white oak

Eastern hemlock is a slow-growing, long-lived conifer tree species native to eastern North America. Its current range extends from northern Michigan and Wisconsin east to the maritime provinces of Canada, New England and the Mid-Atlantic States, and south along the Appalachian Highlands (Figure 4.1). This extensive geographic range occurs over a wide range of climatic conditions. In northern portions of the eastern hemlock range, January temperatures average –12° C and mean July temperatures are ca. 16° C. In the southern regions, January average temperatures may be as high as 6° C. Additionally, precipitation throughout the range of eastern hemlock generally follows an increasing gradient from west to east with annual precipitation ranging from less than 740 mm to over 1520 mm (Godman and Lancaster 1990). Despite occurrence across this wide range of climatic conditions, the microclimate of eastern hemlock stands is remarkably similar. Dense evergreen foliage inhibits understory insolation, thus creating a cool, moist microclimate that can be quite different from prevailing conditions immediately outside hemlock-dominated stands (Cook and Cole 1991). The shade tolerance of eastern hemlock seedlings and saplings allows the species to dominate sites (often in pure stands) and self perpetuate where environmental conditions are suitable (Godman and Lancaster 1990).

White oak is a long-lived, moderately shade tolerant, angiosperm tree widely distributed throughout eastern North America. The native range of white oak encompasses

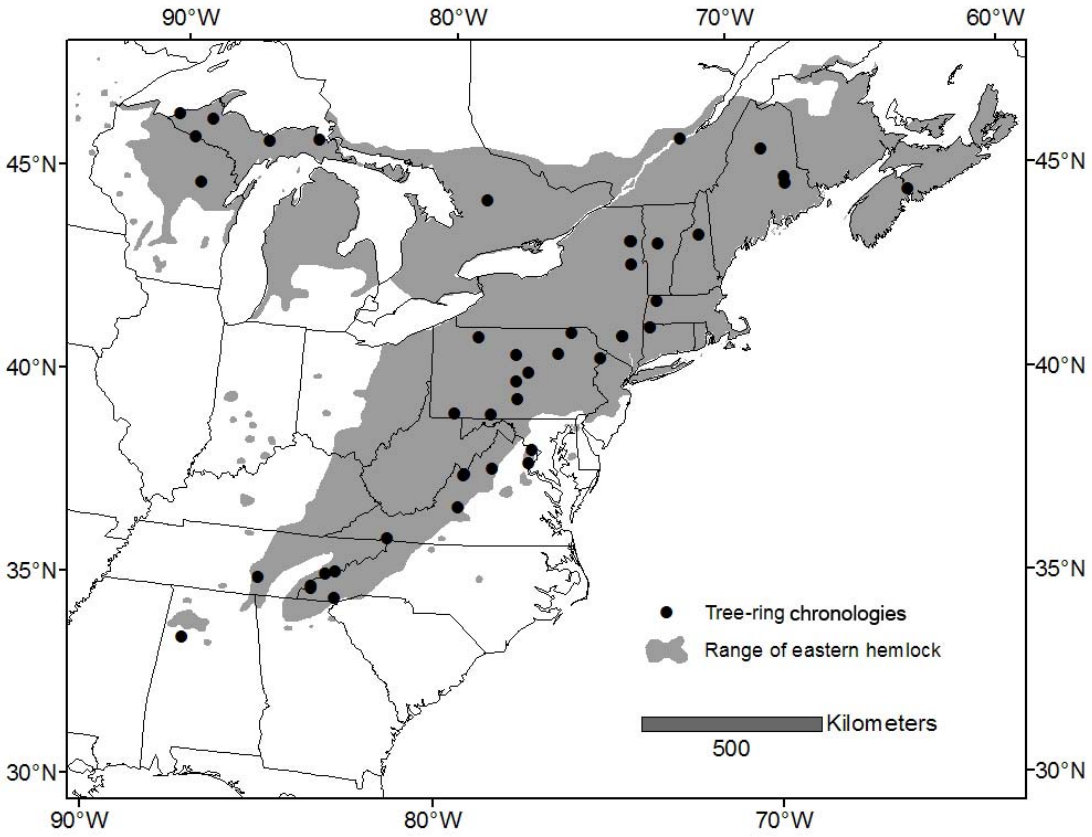

Figure 4.1. Native range of eastern hemlock and locations of tree-ring chronologies.

nearly all of the eastern United States from southern Maine west across southern Quebec and Ontario to Minnesota; south through western Iowa and eastern Kansas to the Gulf of Mexico (Figure 4.2). This expansive geographic range spans a wide variety of climates. Mean annual temperature ranges from 7° C along the northern range limit to 21° C at the southern boundary. Minimum temperatures range from –46° C in Wisconsin and Minnesota to –18° C in northern Florida (Rogers 1990). Mean annual precipitation ranges from 760 mm in southern Minnesota to nearly 2200 mm in the southern Appalachian Mountains (Rogers 1990). White oak occurs in a wide variety of habitats from mesic to xeric, and can tolerate all but the driest sites due to several morphological and physiological adaptations to drought (Abrams 1990). Because white oak is long-lived and annual rings crossdate well, it is one of the most widely used eastern tree species in dendrochronology (Cleveland and Duvick 1992, Leblanc and Foster 1992, Rubino and McCarthy 2000, Tardif et al. 2006, LeBlanc and Terrell 2009).

4.2.2 Tree-Ring Data

The extensive spatial distribution and long length of established eastern hemlock and white oak tree-ring chronologies combined with their documented radial growth responses to climate variables (Cook and Cole 1991, LeBlanc & Terrell 2009, Goldblum 2010) make them ideal species to investigate broad-scale variability in sensitivity to climate. Fifty-two eastern hemlock and 71 white oak tree-ring chronologies were downloaded from the International Tree-Ring Data Bank (ITRDB) (NOAA 2009). Eastern hemlock chronologies were typically over 300

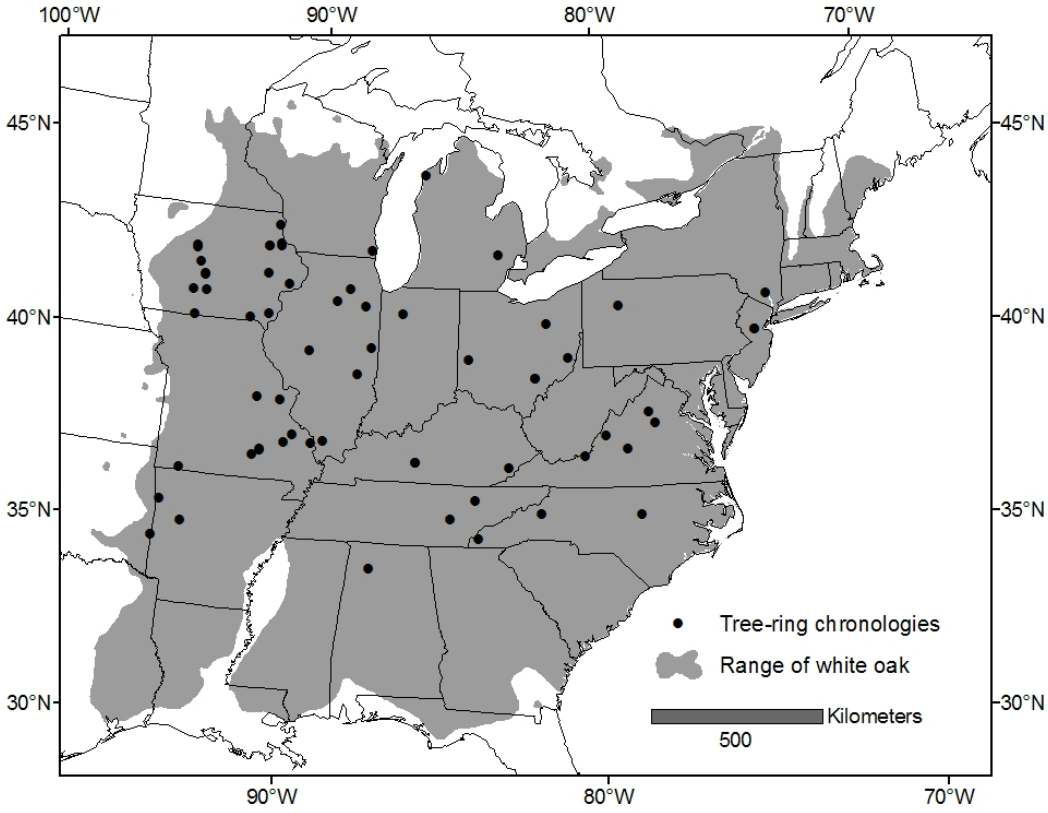

Figure 4.2. Native range of white oak and locations of tree-ring chronologies.

years in length, and white oak chronologies were generally over 250 years. Chronologies of both species were relatively well distributed across their respective geographic ranges (Figures 4.1 and 4.2). The spatial distribution of the chronologies allowed for the assessment of variability in tree growth and sensitivity across a wide range of latitude and longitude, as well as investigation of the relationships between tree growth and position within the geographic ranges. The generally contiguous shapes of both species' ranges minimize the effects that irregular and discontinuous edge shapes can have on investigations of variability within species' ranges (Sagarin and Gaines 2002). Additionally, the long length of the chronologies permitted analysis of mean sensitivity between sites over a long common period, thus capturing low-frequency variability in climate. Tree-ring chronologies submitted to the ITRDB do not constitute a true random sample of all available tree-ring data. However, these chronologies were developed by numerous researchers for a variety of purposes including climate reconstruction, archeological dating, and investigations of forest dynamics, and most of the sites were targeted not because they met any systematic criteria but simply because they contained old trees (Cook and Cole 1991, LeBlanc and Terrell 2009).

The primary metric we used to assess tree growth response to climate was average mean sensitivity, a measure that quantifies the strength of common climatic signal in a tree-ring chronology. The sensitivity of a tree-ring series refers to the absolute differences in ring width between consecutive rings. The mean sensitivity (MS) statistic was first developed by Douglass (1920), and later refined by Schulman (1956) as the average of these first differences expressed as a ratio of the mean ring width, and is defined by the following equation:

$$MS = \frac{n}{n-1} \frac{\sum_{t=2}^{n} |w_t - w_{t-1}|}{\sum_{t=1}^{n} w_t}$$

where w_t = ring width in year t, and n = the length of the tree-ring series. MS has a theoretical minimum of 0 and maximum of 2, but typical observed MS values for tree-ring chronologies vary between 0.1 and 0.6 (Biondi and Qeadan 2008). MS was developed to quantify the strength of response of growth to high-frequency climate variability, and has been shown to co-vary with climatically limiting factors such as soil moisture availability and precipitation (Schulman 1945, Fritts 1976, Strackee and Jansma 1992, Makinen et al. 2000, Carrer and Urbinati 2004, Liang et al. 2010). Because MS is a temporal measure of dissimilarity that incorporates only first-order relationships, it is strongly influenced by inter-annual environmental variability, such as climate, and less affected by low-frequency environmental variables.

Ring-width measurement data were downloaded for all available eastern hemlock and white oak chronologies in the ITRDB. The data from each site were then inspected using the dendrochronology quality-control program COFECHA (Holmes 1983, Grissino-Mayer 2001). COFECHA verifies the accuracy of tree-ring dating by computing time-series correlation coefficients between 50-year segments (25 year overlap) of each tree-ring series (specimen) and the remaining series. Chronologies that contain numerous segments with correlation coefficients below the 0.05 level of significance may be incorrectly dated. Chronologies were excluded from further analysis if they lacked geographic coordinates, contained possible crossdating errors, or showed insufficient chronology length. The remaining chronologies

(46 eastern hemlock and 63 white oak) used for analysis all had precise latitude and longitude provided in the metadata and had a sample depth of at least 10 series spanning the years 1800 to 1975. All measurement series in each chronology were then truncated to this 176-year common period, and the average mean sensitivity for each site was calculated as the average of the mean sensitivity values for all tree-ring series (specimens) included in the chronology.

4.2.3 Spatial Analysis

Geographic ranges of eastern hemlock and white oak were obtained from digitized versions of the United States Forest Service range maps (Little 1971). A collection of these maps for most North American tree species are available online from the United States Geological Survey (USGS 1999). All spatial data (i.e., digital range maps and point locations of tree-ring chronologies) were analyzed using ArcGIS software (ESRI 2008). Points were projected using an equidistant projection centered on the centroid of each species' range, and Euclidean distances between each tree-ring site and the nearest location along the species' range boundary were measured.

We developed a generalized additive model (GAM) (Wood 2004, 2008) to assess the relationship between spatial position within each species' range and mean sensitivity of tree growth. Models were developed and analysis conducted using R and associated packages (Wood 2004, R Development Core Team 2009, Keitt et al. 2010). Using the existing tree-ring chronologies, we modeled average mean sensitivity with two predictor variables: (1) distance from range edge (DIST) and (2) a flexible spatial term (G), which includes the geographic

position of each tree-ring site (projected x,y coordinates from latitude and longitude). We specified a GAM with a Gaussian distribution and an identity link function. The generalized model allows a great deal of flexibility in the spatial predictor term because smoothly varying functions can be fit to model predictors instead of coefficients. The spatial term (G) is permitted to vary smoothly in two dimensions across the spatial extent of the species' ranges. The GAM is summarized by the following equation:

$$Y_s = \beta_{0s} + X_s\beta_1 + G_s + \varepsilon$$

where Y is the predicted average mean sensitivity at spatial location s, X is the distance to the nearest edge of the species geographic range, G is a two-dimensional geographic spline, and ε is an error term.

If the ecological amplitude paradigm were correct, we would expect DIST to be a significant predictor of mean sensitivity regardless of the underlying structure of the spatial component (G) of the model. We therefore interpret the significance of the DIST coefficient to evaluate the presence of an ecological amplitude pattern of mean sensitivity in the tree-ring chronologies. We used the output of the model to generate a continuous map of predicted mean sensitivity to examine the spatial structure (G) of mean sensitivity. Predicted mean sensitivity was mapped across the entire range of each species on a raster grid with 30 x 30 km cells.

To investigate the relationship between climate variability and annual growth sensitivity, we conducted correlation analysis between average mean sensitivity and climate variables. We obtained minimum and maximum monthly temperature and monthly precipitation averaged over the period 1971–2000. For each tree-ring site, we obtained data from the nearest 30 arc second (approximately 1 km) grid cell from the PRISM gridded climate dataset (PRISM 2004). Correlation coefficients were calculated between MS and monthly climate variables.

4.3 Results

Average mean sensitivity of tree growth for both eastern hemlock and white oak was significantly correlated with latitude and longitude (Figure 4.3). MS values for eastern hemlock ranged from 0.19 to 0.34, with the highest values occurring mostly in the northwest region of the species range. Eastern hemlock MS was significantly correlated with latitude ($r = 0.58$, $P < 0.001$) with a trend of increasing MS from south to north. White oak MS values ranged from 0.16 to 0.34 and showed a similar pattern of significant correlations between MS and latitude ($r = 0.35$, $P = 0.005$) as well as longitude ($r = –0.28$, $P = 0.029$). No significant correlation was found between distance from range edge and either eastern hemlock ($r = –0.13$, $P = 0.377$) or white oak ($r = –0.06$, $P = 0.636$) mean sensitivity.

Despite the fact that a very flexible model was fit to the tree-ring data, distance from range edge was not a significant predictor of average mean sensitivity for either tree species, and distance to range edge did not influence the pattern of sensitivity in the model predictions.

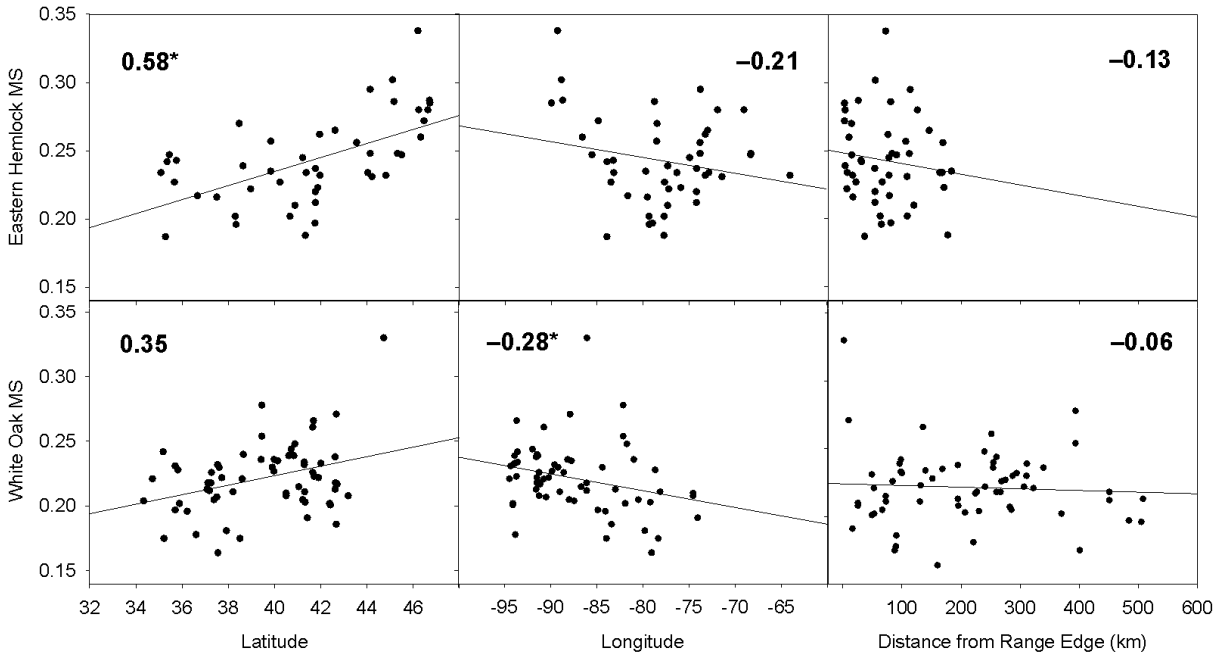

Figure 4.3. Relationship between average mean sensitivity (MS) of eastern hemlock and white oak and spatial location of tree-ring chronologies. Latitude and longitude units are degrees, and distance from geographic range edge is measured in kilometers. The number in the corner of each plot is the Pearson correlation coefficient. Asterisks (*) denote significant relationships ($P < 0.05$).

The regression coefficients for distance from range edge were not significant in either linear (not shown) or generalized additive models that were fit to the tree-ring data. In the GAM of eastern hemlock sensitivity the *t*-value of DIST was –0.44 (P = 0.661). The *t*-value of DIST was 1.0 (P = 0.317) in the GAM of white oak sensitivity. Spatial location (latitude and longitude) was an important predictor in the models of mean sensitivity of both species. The spatial term (G) in the generalized additive models was a significant predictor of MS in both eastern hemlock (F = 19.99, P < 0.001, df = 2.03) and white oak (F = 9.254, P < 0.001, df = 2.0).

A gradient of increasing mean sensitivity from southeast to northwest was evident in the map of sensitivity values predicted by the generalized additive model for eastern hemlock (Figure 4.4). The highest predicted MS values were in the northwestern portion of the range in Wisconsin and the upper peninsula of Michigan. Sensitivity decreased gradually eastward with moderate MS values predicted along the northern range limit. Sensitivity of eastern hemlock decreased rapidly to the south with the lowest values occurring in the southern Appalachian Highlands.

The spatial pattern of average mean sensitivity of white oak was similar to that of eastern hemlock. Predicted sensitivity of white oak increased from southeast to northwest, with the highest values occurring in Wisconsin and Minnesota and the lowest values in southern Georgia and northern Florida (Figure 4.5). In addition to a similar spatial pattern, the range of sensitivity values of white oak was similar to eastern hemlock, although the values are generally lower overall.

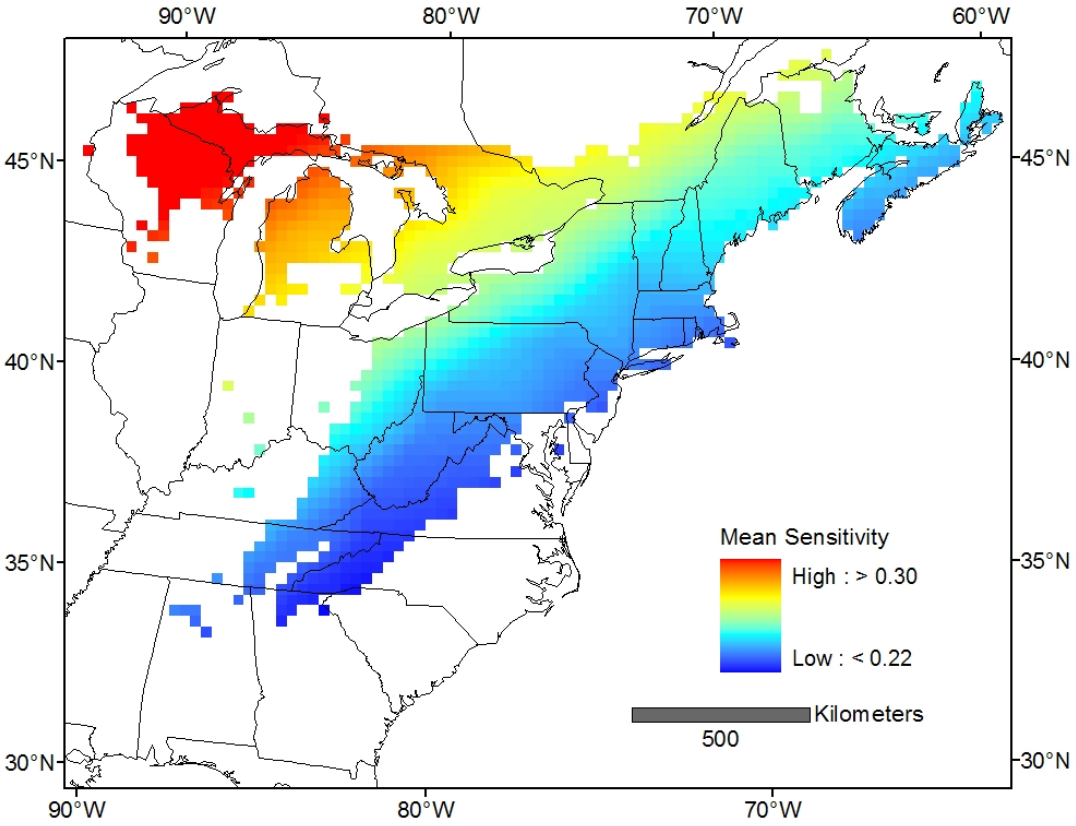

Figure 4.4. Predicted mean sensitivity of eastern hemlock throughout its range as predicted by the generalized additive model of average mean sensitivity generated from existing tree-ring chronologies. Predicted values are for each 30 km grid cell in the species range. Predictor variables are distance from range edge and a smoothly varying 2-dimensional spline of latitude and longitude.

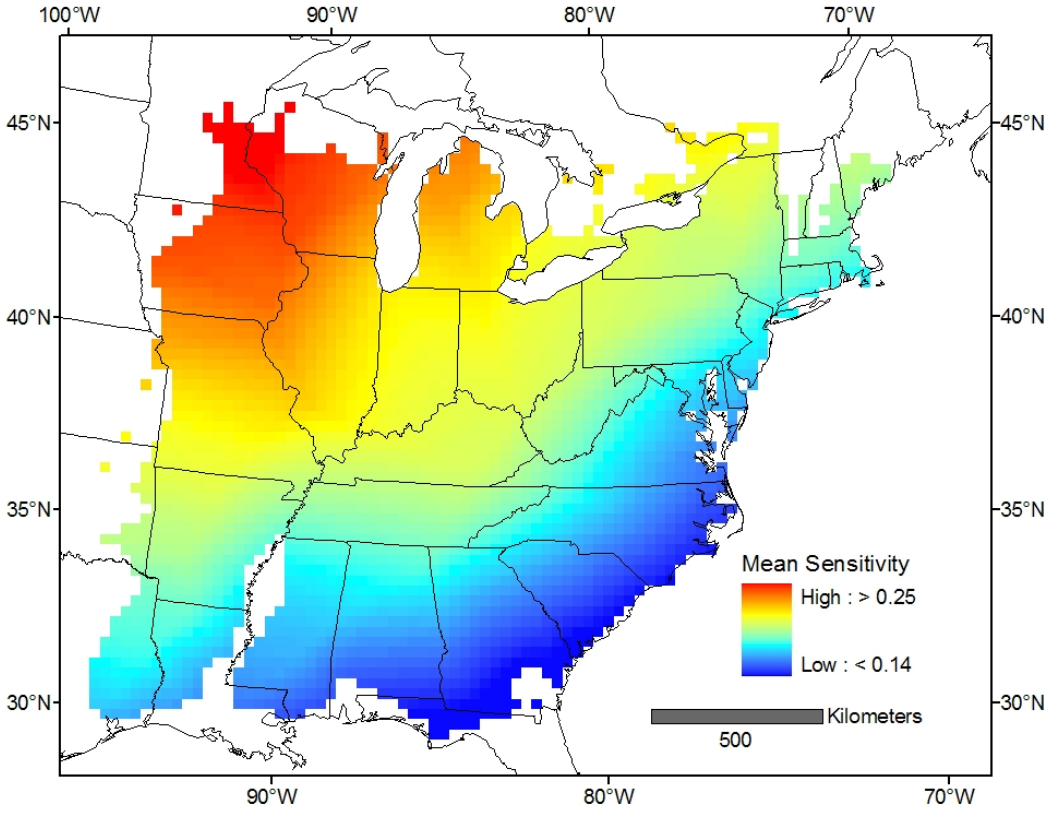

Figure 4.5. As in Figure 4.4, but for white oak.

High mean sensitivity in tree-ring chronologies was associated with sites with low precipitation and a wide temperature range, and these sites were typically located in the northwestern portion of each species' geographic range. The spatial gradient in predicted mean sensitivity followed trends of decreasing precipitation, decreasing annual temperatures, and increasing annual temperature range across eastern North America. Annual temperature range (the difference between July and January temperatures of the same year) (Figure 4.6a) and mean temperature of the coldest month (Figure 4.6b) were significantly correlated with average mean sensitivity of eastern hemlock. Mean sensitivity was positively correlated with temperature range ($r = 0.56$, $P < 0.001$) and negatively correlated with temperature of the coldest month at a site ($r = –0.54$, $P < 0.001$). No significant relationship was found between mean annual temperature and eastern hemlock MS. Mean sensitivity of eastern hemlock chronologies was also correlated with mean annual precipitation ($r = –0.46$, $P = 0.002$) and average precipitation of the driest month ($r = –0.55$, $P < 0.001$) (Figure 4.6c and 4.6d). Increased precipitation during the growing season (May, June, July) was also significantly related to lower MS ($r = -0.46$, $P = 0.002$).

Mean sensitivity of white oak was related to the same climate variables as eastern hemlock, but correlations were not as strong. Mean sensitivity of white oak increased with higher temperature range and lower monthly temperatures (Figures 4.7a and 4.7b). White oak MS was positively correlated with mean annual temperature range ($r = 0.34$, $P = 0.007$) and negatively correlated with coldest month temperature ($r = –0.29$, $P = 0.023$). No significant relationship existed between mean annual temperature and MS. The strongest associations

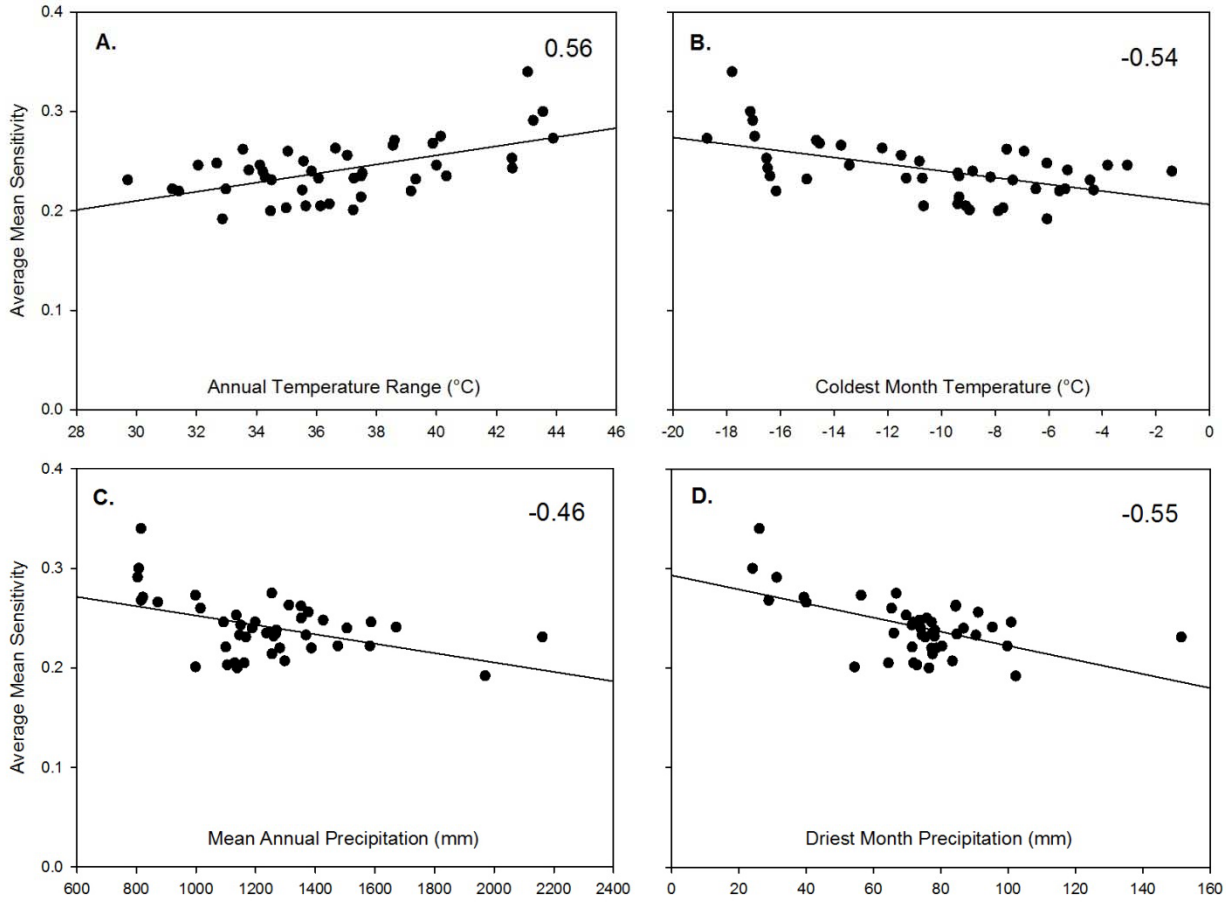

Figure 4.6. Relationship between mean sensitivity of eastern hemlock tree-ring chronologies and climate. Climate variables are derived from the 1971–2000 PRISM gridded monthly normals. Annual temperature range (A.) was calculated as the difference between mean July and mean January temperature. Coldest month (B.) for each site was January. The most common driest month (D.) was February. Numbers in the corner of each plot are Pearson correlation coefficients. All correlations are significant ($P < 0.05$).

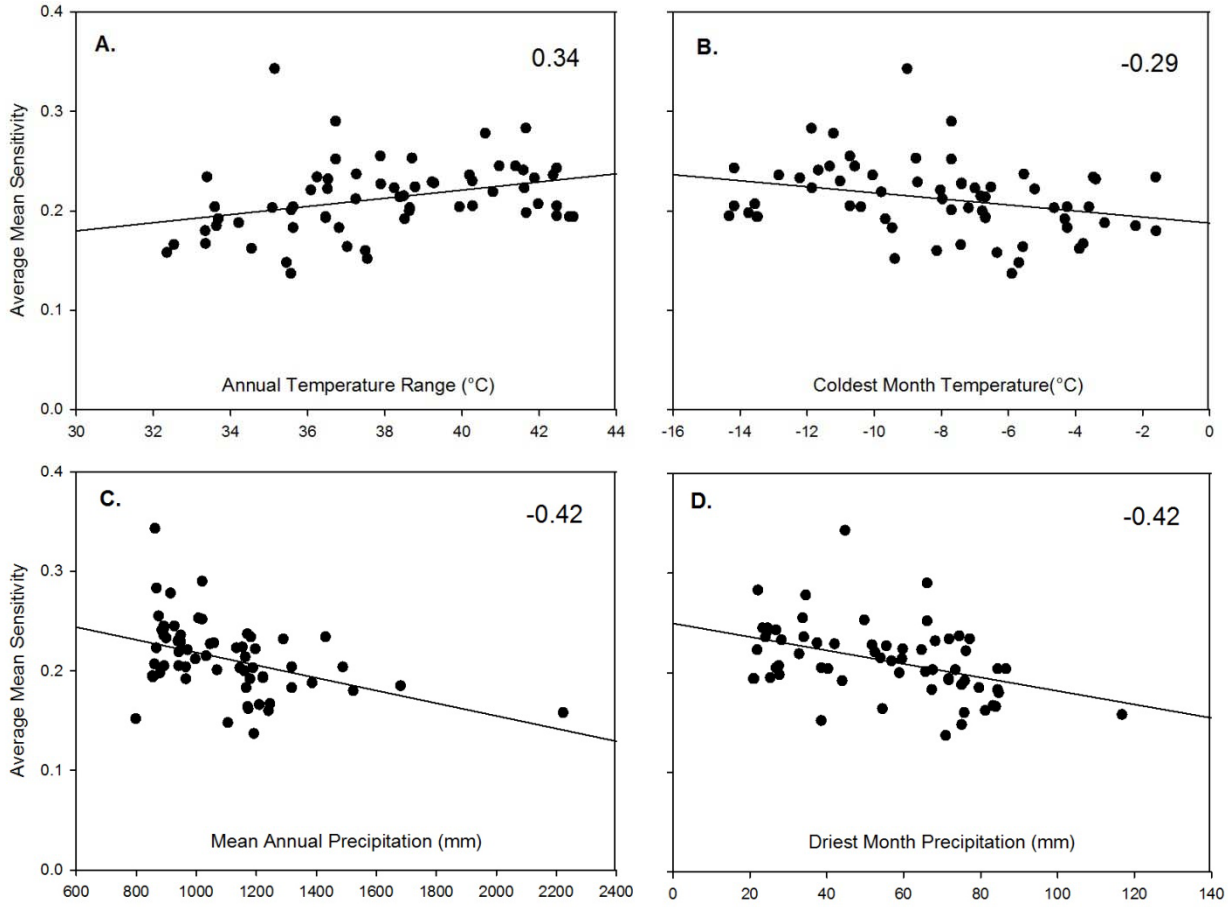

Figure 4.7. Relationship between mean sensitivity of white oak tree-ring chronologies and climate. Climate variables are derived from the 1971–2000 PRISM gridded monthly normals. Annual temperature range (A.) was calculated as the difference between mean July and mean January temperature. Coldest month (B.) for each site was January. The most common driest months (D.) were January and February. Numbers in the corner of each plot are Pearson correlation coefficients. All correlations are significant ($P < 0.05$).

between white oak MS and climate were negative correlations with mean annual precipitation ($r = –0.42$, $P < 0.001$) and driest month precipitation ($r = –0.42$, $P < 0.001$). White oak MS was also negatively correlated with growing season (May, June, July) precipitation ($r = –0.31$, $P = 0.013$).

4.4 Discussion

Broad-scale geographic trends in variability of tree growth were observed in the modeled predictions of mean sensitivity of both eastern hemlock and white oak, but we found no evidence of an ecological amplitude pattern in the sensitivity of annual radial growth of either species. At the scale of an entire geographic range, we found no significant correlation between MS of tree-ring chronologies of either species and the distance from range edge. Also, distance from range edge was not a significant predictor of mean sensitivity in any spatial model we fit to the tree-ring data networks. Although it is theoretically difficult to prove the absence of a relationship, highly flexible generalized additive models of mean sensitivity were not sensitive to variation in distance from geographic range edge. Taken together, our results suggest that all external range limits do not necessarily represent stressful environmental conditions where growth will be highly variable. However, we acknowledge that some range edges may indeed represent climate-induced stressful conditions where trees may be near their physiological limits. The spatial pattern of predicted MS generated by our models visually illustrates this concept.

A gradient of increasing mean sensitivity from southeast to northwest was the most conspicuous spatial pattern in models of predicted MS for both species. Mean sensitivity was

highest along the northern range edge, and especially in the northwest portion, of both eastern hemlock and white oak, suggesting these range edges may be maintained by climate-driven limiting factors on tree growth. Correspondingly, range edges in other locations of each species' range are likely to be limited by factors other than climate (e.g., Shankman and Hart 2007). The pattern of growth sensitivity generally conforms to the ecological explanation of range limits proposed by Loehle (1998), in which trees face a tradeoff between height and radial growth rate. Tree range limits in the northern hemisphere may be determined by northern environments favoring slow-growing, cold-adapted species, and southern environments favor fast-growing trees that can out-compete neighboring individuals for resources (Loehle 1998). The similar gradient of MS in both species suggests broad-scale climatic factors may have an important influence on annual growth near the northern range limits, but competition may be much more important to delimiting southern range boundaries.

Our results showing a clear latitudinal trend in climatic sensitivity of tree growth is consistent with other recent studies. For example, Falcon-Lang (2005) analyzed chronology statistics of all species in the ITRDB and examined possible correlations using a climate index that incorporated annual temperature and precipitation. He found a weak trend of higher MS values among conifers growing in cold-dry environments, but no clear trend among angiosperms using the same climate index. Variability that weakened spatial patterns in both sets of correlations was likely due to differential responses of numerous species included in the analysis.

Liang et al. (2010) found a trend of increasing mean sensitivity and stronger response of tree growth to monthly climate variables among 16 tree-ring chronologies on the Tibetan Plateau. They found significant correlations between MS and latitude, longitude, and altitude along a gradient of decreasing precipitation and available soil moisture. Additionally, they found an increasing strength of growth response to climatic variables with increasing aridity along this gradient.

A gradient of increasing MS was also reported along an elevational gradient among high-elevation, old growth beech forests in the Eastern Alps (Di Filippo et al. 2007). MS was also significantly correlated with latitude and longitude, with the highest sensitivity values occurring in the most continental locations of their study area. These areas had the lowest minimum temperatures and the greatest difference in intra-annual temperature variability.

Chen et al. (2010) developed climate-growth models for 129 Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco) tree-ring chronologies in western North America, and modeled annual radial growth using a heat-moisture index of monthly growing season temperatures and precipitation. They found a significant negative correlation between the slope of their regression equations and latitude, which they interpreted as a decrease in climate sensitivity at higher latitudes. Sites at lower latitudes in Mexico had a weaker growth-climate relationship than sites in the Central Rockies. The authors attributed this pattern to a possible genetic adaptation to drought stress by populations of trees occurring in the more drought-prone environment of Mexico.

In this study, we found strong relationships between MS and climate variables that indicate a degree of continentality (e.g., range of intra-annual temperatures and minimum monthly temperatures). In light of previous findings (Di Filippo et al. 2007) as well the results presented here, it is possible that the pattern of increasing sensitivity with latitude reported by Chen et al. (2010) is related to the gradient of increasing continentality (greater temperature range and lower minimum temperatures) from Mexico to the Central Rockies. Continentality may possibly have an influence on mean sensitivity by altering tree phenology and exacerbating the effects of drought even if temperature has no direct relationship with growth.

Despite broad-scale spatial variability in mean sensitivity to climate, response of tree growth to monthly climate variables is remarkably consistent. Previous studies have investigated the climate response of eastern hemlock and white oak across large spatial extents and found the same monthly climate variables influencing growth across their entire geographic ranges. For example, Cook and Cole (1991) investigated the response of eastern hemlock growth to monthly climate and found spatially coherent patterns of annual growth response to previous July and current March temperatures. They found eastern hemlock annual growth was negatively correlated with previous July temperatures, and detected significant positive correlations between tree growth and March temperatures in 33 of 42 tree-ring chronologies spanning the entire range of the species. Despite the wide range of macroclimatic conditions and variability of site characteristics (e.g., hydrology, topographic position), the spatial pattern of climate–growth relationships was consistent. Moreover, the strongest correlations between monthly climate variables and annual growth occurred in the

northwestern part of the range. The average mean sensitivity values of the chronologies analyzed by Cook and Cole (1991) were not reported, but many of those same chronologies were included in our analysis. The spatial pattern of high mean sensitivity values in the northwestern portion of the range predicted by our model coincides with the strongest climate–growth correlations presented by Cook and Cole (1991).

Investigations of the relationship between climate and annual growth of white oak have also shown that trees respond to the same climate variables across their geographic ranges (LeBlanc and Terrell 2009, Goldblum 2010). White oak radial growth is influenced by growing season moisture conditions across its entire geographic range. Two recent analyses of white oak climate response reported significant positive correlations between radial growth and current growing season precipitation and negative correlations with growing season temperature (LeBlanc and Terrell 2009, Goldblum 2010). Both studies also detected a trend of stronger growth-climate correlations in the northwestern portions of the species range, a finding that is supported by our analyses of mean sensitivity. Neither study of climate response reported any influence of winter temperatures limiting growth of white oak at any part of its range.

Although the strength of climatic response and inter-annual growth variability each reach a maximum along the northern range limits of eastern hemlock and white oak, little direct evidence exists to suggest that climate, especially temperature, is responsible for limiting the spatial distribution of either species. Analysis of the influence of climate on annual growth of white oak at its northern range limit in Quebec demonstrated that radial growth is limited by growing season precipitation while previous winter temperatures had no influence (Tardif et al.

2006). Similarly, in an analysis of patterns of tree establishment across topographic positions, Kavanagh and Kellman (1986) suggested that the northern range extent of eastern hemlock at its latitudinal range edge in Ontario was not limited by temperatures. While annual growth may not be directly limited by temperature at northern distributional limits, climate may exert influence on other biological processes such as seed production, seedling establishment, or recruitment of juvenile trees to the canopy. Further research is necessary to test such hypotheses, and models attempting to relate distributional limits of trees to broad climate variables such as annual or monthly temperatures should be carefully scrutinized before employing them to predict future range extents as a result of climate change.

Models projecting future tree growth, tree species distributions, and primary productivity of forests will be vital for management and conservation of forests in response to a changing climate, as well as for understanding feedbacks between the global carbon cycle and climate change. Here we have shown that common assumptions of forest dynamics models are not reasonable for two dominant tree species of eastern North America. Eastern hemlock and white oak do not exhibit a uniform sensitivity to climate across their geographic ranges, and the spatial pattern of growth variability does not conform to a response predicted by the ecological amplitude paradigm. Current models of climate-driven tree migrations that use a climate envelope approach generally predict range contractions along southern range limits (Prasad et al. 2007), but our findings suggest that trees in southern portions of their ranges may not be at risk of rapid range contraction. Future models of forest dynamics should explicitly include information on the spatial variability of the response of tree growth to climate.

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CHAPTER 5

STAND STRUCTURE AND COMPOSITION IN PINE-OAK STANDS AT TWO SITES IN THE SOUTHERN BLUE RIDGE PHYSIOGRAPHIC PROVINCE

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Previous chapters of this dissertation focused on applications of dendrochronology to understand spatial variability of tree growth. In this chapter I use plot-level dendroecological and forest inventory techniques to understand spatial variability in stand structure, species composition, and regeneration of trees by comparing sites at the northern and southern edges of the southern Blue Ridge physiographic province. Study sites were selected because they represent locations near the center and southern range edge of several species that dominate these pine-oak forests. This chapter is the basis for a manuscript that will be submitted to *Journal of Vegetation Science*. The use of "we" in this chapter refers to Henri Grissino-Mayer and me who will be co-authors on the manuscript. As the first author, I was responsible for designing the sampling strategy, leading data collection, performing the analyses, and writing the paper.

Abstract

Understanding spatial and temporal variability of stand structure and composition of forests is crucial to accurately projecting vegetation dynamics in response to changing environmental conditions such as rapid climate change. This study investigated stand dynamics in pine-oak forests of the southern Appalachian Mountains. We compared stand composition, structure, and tree regeneration in two sites at the interior and periphery of the geographic ranges of several dominant tree species and tested the assumption that range interior represents ideal habitat where species can attain higher abundance, dominance, and rates of regeneration. Both study sites contained stands undergoing a compositional shift from several species of pine and oak to shade-tolerant hardwoods, especially red maple. The shift from pine-oak to maple began 80 to 100 years ago in interior stands and 60 to 80 years ago in stands near the southern limit of the pine-oak community type. Few differences in tree

regeneration or stand composition existed between interior and peripheral stands. The similarity of structure and composition in range interior and range periphery sites suggests that geographic range edges do not necessarily represent ecological range edges, and processes of forest dynamics do not change along a range-wide spatial gradient in pine-oak stands. The relative proportion of pine-oak forests in the southern Appalachian Mountains is likely to be greatly reduced without intervention by forest management, but pine-oak stands near their southern range limit may not be at greater risk of replacement than interior sites.

5.1 Introduction

Pine-oak forest communities in the southern Appalachian Mountains form distinct stands that contrast sharply with surrounding forest composed solely of deciduous tree species (Braun 1950). These forest communities are valued for wildlife habitat, watershed protection, and timber resources, and are recognized for the contribution they make to the compositional and structural diversity of landscapes of the eastern deciduous forest (Brose and Waldrop 2010, Brose et al. 2010). Pine-oak forests are closely associated with xeric sites within the oak-chestnut forest type of the Ridge and Valley and Blue Ridge physiographic provinces of the southern Appalachian Mountains (Braun 1950, Zobel 1969, Williams 1998). The principal tree species of these communities are Table Mountain pine (*Pinus pungens* Lamb.), pitch pine (*Pinus rigida* P. Mill.), shortleaf pine (*Pinus echinata* P. Mill.), Virginia pine (*Pinus virginiana* P. Mill.), and chestnut oak (*Quercus montana* Willd.) (Zobel 1969, Williams 1998). Pine-oak communities are found from Pennsylvania to northern Georgia, and their southern distributional limit coincides

with the southern geographic range limit of three principal species: chestnut oak, pitch pine, and Table Mountain pine (Williams 1998, Brose et al. 2010).

Previous dendroecological research on Appalachian pine-oak forests and oak forests throughout eastern North America generally has examined patterns of tree regeneration and recruitment over time. Many of these studies have documented a succession of forest composition from oak or pine-oak to shade-tolerant hardwood species, especially red maple (e.g., Lorimer 1984, Goebel and Hix 1996, DeWeese 2007). Furthermore, many dendroecological investigations have focused on the role of changing fire regimes as the main driver of compositional change in oak forests (Abrams 1992, Abrams et al. 1997, Williams 1998, Brose and Waldrop 2006, Nowacki and Abrams 2008, Brose and Waldrop 2010). While the literature on structural and compositional change in these forests is extensive, nearly all previous studies are site-specific and variability of forest conditions within similar communities is often overlooked.

Climate change, disturbance, and forest dynamics are likely to have influences on forest composition and species distributions due to the differential responses of individual species to environmental change (Parker et al. 2000, Prasad et al. 2007, Iverson et al. 2008). However, relatively little empirical research has focused on the spatial variability of stand structure and composition within forest communities. Moreover, most models aimed at predicting compositional change in forests assume that climate has a direct and causal effect on species' range limits and that species will have a simple spatial response to climate change (Iverson et al. 2004b, a).

Many projections of future species' distributions and community composition are based on the abundant center paradigm, in which the center of a species' geographic range is considered to be ideal habitat and therefore supports greater abundances than sites closer to range edges (Wulff 1943, Brown 1984, Guo et al. 2005). A paucity of direct empirical tests as well as a number of taxa documented to be exceptions to the abundant center model call into question the generality of this paradigm (Sagarin and Gaines 2002, Gaston 2003).

Although recent research has examined variability of abundance across the geographic ranges of species and refined models of range structure (Sagarin and Gaines 2006, Samis and Eckert 2007, Gaston et al. 2008, Gerst et al. 2011), little is known about spatial variability of other measures of species' vitality such as growth rates, reproduction, and mortality, which may also be expected to vary according to an abundant center paradigm (Hengeveld 1990). Moreover, most studies of geographic variability have been limited to individual species, and comparative investigations of community-level responses across geographic gradients are lacking.

This study seeks to increase understanding of the spatial variability of stand composition and structure of pine-oak communities, especially in relation to the southern distributional limit of important tree species. We use dendroecological techniques to compare the structural and compositional characteristics of stands at an interior position within the geographic ranges of pine-oak species and compare them to stands at the southern range edge of those species. We also compare patterns of tree regeneration and assess the relationship between stand composition and environmental gradients. Specifically, the objectives of this study were to: 1) quantify temporal variability in stand structure and species' composition of

pine-oak stands at the northern and southern edges of the southern Blue Ridge physiographic province, 2) identify any differences in contemporary stand characteristics between the two sites (i.e., density, basal area, and regeneration of trees), and 3) investigate the association between forest composition and environmental gradients at both sites.

5.2 Study Area

To investigate variability of stand structural characteristics in relation to geographic range boundaries, we quantified forest stand structure in pine-oak stands in the southern Blue Ridge physiographic province of the Appalachian Mountains. Two study sites were selected to represent the range interior and southern range edge of several important species of Appalachian pine-oak communities, and these study sites were located near the northern and southern edges of the southern Blue Ridge physiographic province (Figure 5.1). The northern site was located on the Jefferson National Forest in southwestern Virginia. Sample plots were located in the southeastern region of the forest surrounding the intersection of Smyth, Wythe, and Grayson Counties (36.76°N, 81.26°W). The southern site was located on the Chattahoochee National Forest in northeastern Georgia. Sample plots were located in and around Warwoman Wildlife Management Area in Rabun County (34.95°N, 83.25°W).

The Blue Ridge province is a region of the Appalachian Mountains characterized by steep ridges extending from southern Pennsylvania to northern Georgia (Fenneman 1938). The province is subdivided into northern and southern regions at Roanoke Gap, Virginia, where the northern portion is a narrow strip of lower ridges (sometimes a single ridge), and the southern

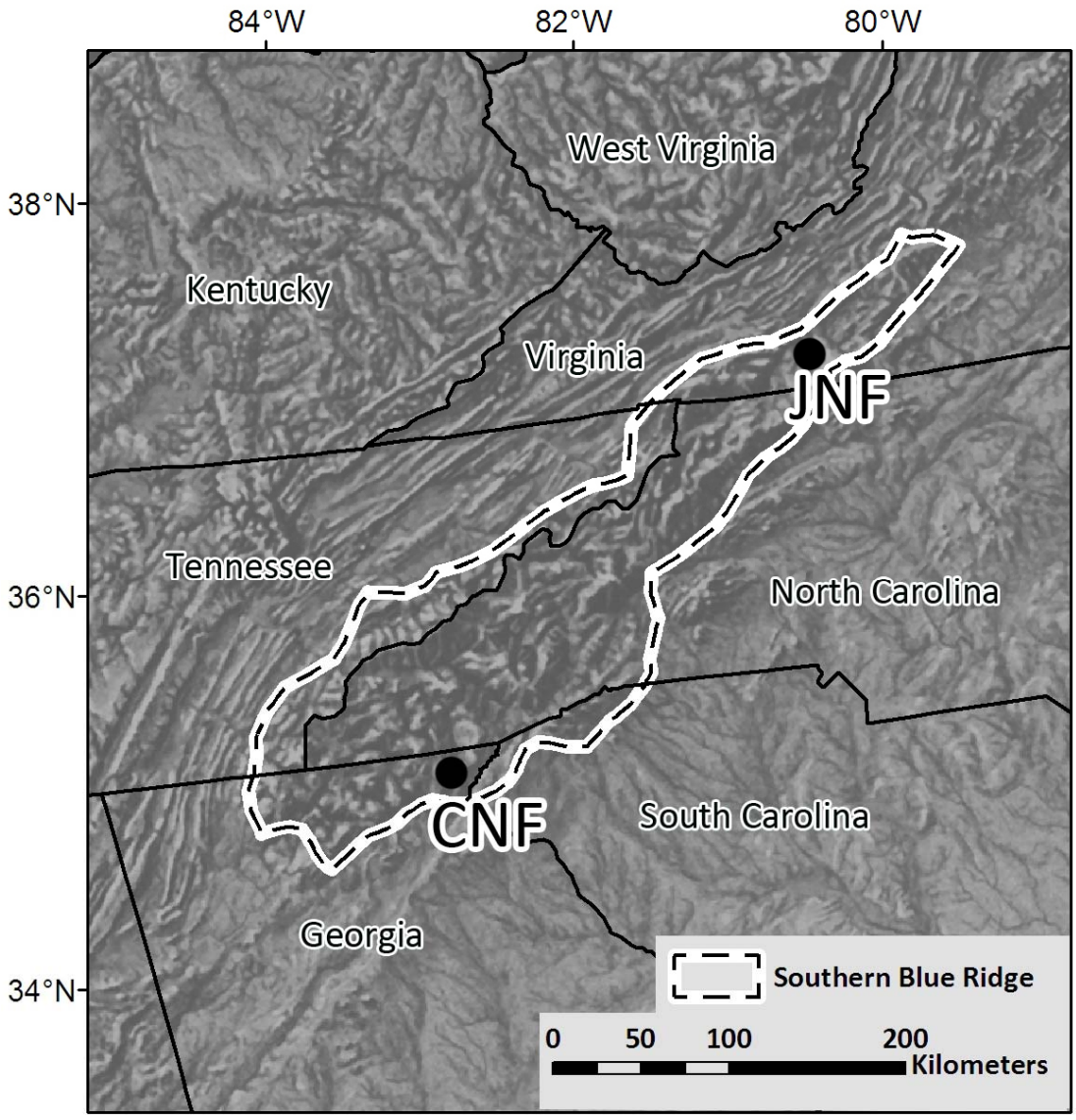

Figure 5.1. Location of study sites in the southern Blue Ridge physiographic province. Pine-oak stands were located in the Jefferson National Forest (JNF) in Virginia and the Chattahoochee National Forest (CNF) in Georgia.

portion is much wider (reaching 100 km at its widest point) and consists of higher ridges (Fenneman 1938, Braun 1950). The southern Blue Ridge is underlain by Paleozoic metamorphic rocks (predominantly metamorphosed igneous formations of gneiss and schist) that have a complex history of deformation associated with the late Paleozoic Appalachian orogeny (Hatcher 1976, Yurkovich 1984). Soils at both study sites are typically well drained to excessively well drained sandy to very stony loam formed from residuum of granite and gneiss (Soil Survey Staff 2010).

A humid continental climate prevails in the region with hot summers and cool winters. At the Virginia study site, average minimum January temperature is –7 °C and average maximum July temperature is 26 °C. Annual precipitation is 1194 mm and is evenly distributed throughout the year (PRISM 2004). At the Georgia study area, average minimum January temperature is –3 °C and average maximum July temperature is 28 °C. Annual precipitation is 1988 mm and average precipitation exceeds 150 mm in each month (PRISM 2004).

Several species of pine and oak have geographic ranges in the Appalachian Mountains that partially overlap to varying degrees (USGS 1999). These species collectively form the pine-oak communities that are found throughout the oak-chestnut forest association of the Blue Ridge and Ridge and Valley provinces of the Appalachian Mountains. These communities are composed of pitch, Table Mountain, and shortleaf pine, as well as several oak species, especially chestnut oak (Braun 1950). The understory of these stands usually contain several shade-tolerant hardwood species, including blackgum (*Nyssa sylvatica* Marsh.), red maple (*Acer rubrum* L.), and sourwood (*Oxydendron arboretum* (L.) DC.). Several Appalachian pine and oak species,

including pitch pine, Table Mountain pine, and chestnut oak, approach their southern distributional limit at the southern edge of the Blue Ridge province near our study area in Georgia.

Forests of the southern Blue Ridge have experienced a range of human land-use activity over several centuries. Native American populations fluctuated widely throughout history, and the intensity of their land use varied accordingly (Fogelson 2004, DeWeese 2007, Abrams and Nowacki 2008, Springer et al. 2010). European settlement began in the region as early as the late 18th century, and involved clearing land for farming, livestock grazing, and timber harvest (Cowell 1995, SAMAB 1996). The regenerated second-growth forests of the region experience a variety of natural disturbances including wind storms (Williams 1998), ice storms (Lafon and Speer 2002), beetle infestations (Lafon and Kutac 2003), and fire (Lafon et al. 2005, DeWeese 2007, Lafon and Grissino-Mayer 2007, Brose and Waldrop 2010). Additionally, a major compositional shift occurred in the region when the once-dominant American chestnut (*Castanea dentata* Marsh.) was all but eliminated from the landscape by chestnut blight (*Chryphonectria parasitica* (Murill) Barr), an invasive fungal pathogen (Braun 1950, Keever 1953).

5.3 Methods

5.3.1 Site Selection

We selected individual stands to sample from the US Forest Service FSVEG database (FSVEG 2010). This database contains georeferenced polygons of all stands on each national forest along with attribute data of estimated stand age and species composition. Stands in

Virginia and Georgia were selected by querying the FSVEG databases for the Jefferson and Chattahoochee National Forests, respectively. Two criteria were established to qualify stands for sampling. First, stands had to have an estimated age of at least 100 years. Second, only stands classified as pitch pine/mixed oak (FSVEG forest type 15) or Table Mountain pine/mixed oak (FSVEG forest type 20) were considered for analysis. At each national forest, we randomly selected 20 stands that met our criteria and created a list of the UTM coordinates of the geographic centroid of each stand. This list of coordinates was used for field navigation to the stands. All spatial data analysis for stand selection was conducted in ArcGIS 9.3 (ESRI 2008).

5.3.2 Field Methods

Navigation to selected pine-oak stands was accomplished with the aid of a hand-held GPS receiver and topographic map. Each stand was visually assessed to ensure that it was indeed composed of typical pine-oak tree species and that the canopy structure was indicative of an old stand with no evidence of recent disturbance (i.e., a heterogeneous assemblage of tree sizes and crown heights) (Oliver and Larson 1996). Any stand that was misidentified in the FSVEG dataset— because it had a species composition that was not pine-oak, did not show characteristics of an old stand, or was recently logged or burned—was not sampled and a replacement stand was selected from the dataset.

We established one 400 m^2 fixed-area plot at or near the center of each selected stand. In each plot, all live trees (stems >5 cm dbh), standing dead trees, and downed logs that were rooted in the plot were identified by species and their diameters were measured at breast height

(dbh). Live saplings (stems >1.4 m tall and <5.0 cm dbh) and seedlings (<1.4 m tall) within the plots were tallied. We also recorded the elevation, slope aspect, slope steepness, slope configuration (concave, straight, or convex) and topographic position (valley bottom to ridge-top) of each plot. The last four of these measurements were used to calculate the topographic relative moisture index (TRMI). TRMI is a scalar index ranging from 0 to 60, and indicates relative moisture at specific locations in complex terrain (Parker 1982).

Stand age structure and tree recruitment patterns were determined by collecting increment cores from all trees and analyzing annual growth rings. A single core was obtained from each tree using an increment borer at a height of 30 cm above the ground (Grissino-Mayer 2003). To avoid coring through distorted rings associated with reaction wood, all trees were cored on a side of the stem parallel to the contour of the slope. Most trees were cored to the pith whenever possible; however, in some cases trees contained heart rot and only incomplete cores were collected. Increment cores were placed into labeled straws in the field and transported back to the laboratory.

5.3.3 Laboratory Methods

Increment cores were processed in the laboratory using standard techniques (Stokes and Smiley 1968, Speer 2010). All increment cores were air dried, glued to wooden mounts, and sanded to a high polish using progressively finer-grit sandpaper until cell structure of growth rings was clearly visible (Orvis and Grissino-Mayer 2002). Cores were examined under magnification using a stereo zoom microscope, and annual rings were visually crossdated using

the list method (Yamaguchi 1991). For cores that included the pith, the calendar year of the pith subtracted from the year of the outermost growth ring was considered the pith age of the tree. Pith ages for cores that reached the center of the tree but did not include the pith were assigned by overlaying a transparent ring annulus on the innermost rings of the core to estimate missing interior rings, and then subtracting this correction factor from the calendar year of the innermost ring on the core (Villalba and Veblen 1997). More than 95% of cores reached the center of trees. For the remaining cores that were incomplete due to interior rot, tree ages were estimated using a linear regression of tree age regressed on tree diameter (dbh) for each species. Additionally, to account for the time necessary for trees to grow to coring height (30 cm), 5 years were subtracted from all pith ages (Brose and Waldrop 2010). Once these corrections were made to all pith ages, we considered them establishment dates.

5.3.4 Statistical Analyses

Species composition of each study site was quantified by calculating the importance value of all surveyed tree species. Importance value is an index of abundance based on relative density and relative dominance. Importance value is calculated by adding relative density (trees per hectare) and relative basal area (the combined cross sectional area of all tree stems of that species in m^2 per hectare), then multiplying this sum by 100. Importance values can thus reach a maximum of 200 in a pure stand of a single species (Husch et al. 2003).

Cluster analysis was used to identify stands of similar species composition. A data matrix of species importance values was created for Virginia and Georgia stands. Cluster

analysis on these importance value matrices was conducted using Ward's method as a group linking measure, and relative Euclidean distance as the distance measure. Ward's method is a hierarchical agglomerative clustering strategy that maximizes between-group variance and minimizes variance within groups (Gauch 1982). Cluster analysis was performed using the R language and environment for statistical computing (Maechler et al. 2005, R Development Core Team 2009).

Stand structure was summarized for the groups of plots identified by cluster analysis. Distribution of tree diameters was summarized for all groups by aggregating diameter data by species into 10-cm diameter classes. Histograms of size classes were constructed to provide a visual assessment of structural diversity of groups and to allow comparisons of stand structure between groups. Similarly, tree ages within compositional groups were aggregated into 20-year age classes. These age structure data reflect patterns of tree establishment and survivorship that may be related to endogenous and exogenous stand disturbances, as well as processes of ecological succession (Taylor 2000).

Differences in regeneration and abundance between the interior and southern edge study sites were tested by comparing density of seedlings, saplings, and overstory trees. Density of seedlings, samplings, and dominant trees did not meet the normality assumption necessary for conducting t-tests, therefore non-parametric Mann-Whitney rank-sum tests were used to test for significant differences between sites.

Ordination was used to identify patterns of variation in forest composition that may be related to environmental gradients. We used detrended correspondence analysis (DCA) as our

ordination method. Correspondence analyses such as DCA were developed for use with ecological data as an alternative to principal components analysis—and the associated linearity restrictions (Jackson and Somers 1991). DCA is an ordination method based on reciprocal averaging that arranges species scores along multiple orthogonal axes (Gauch 1982). Additionally, a detrending procedure is used to remove systematic distortions of data projected along axes and facilitate visual interpretation of output (Hill and Gauch 1980). We ran DCA on matrices of importance values using R (R Development Core Team 2009, Oksanen et al. 2010). Additionally, we conducted correlation analyses to determine if DCA axes were significantly associated with environmental variables that we measured at each plot (i.e., elevation, slope aspect, slope steepness, slope configuration, topographic position, and TRMI).

5.4 Results

5.4.1 Distribution of Plots

Pine-oak forest plots were primarily distributed on slopes with south and west-facing aspects at elevations between 800 and 1000 m, but plots in Georgia were distributed across a slightly wider range of landscape positions (Figures 5.2 and 5.3). Mean elevation of Virginia stands was 930 m with an elevational range from 754 to 1,059 m. Mean elevation of plots in Georgia was 813 m, with a range of 588 to 1,017 m. Only one plot in Virginia was situated at an elevation below 800 m, but eight plots in Georgia were located at a lower elevation. Additionally, 11 Virginia plots were located on south-facing slopes (aspects ranging from 135 to 225 degrees from North), while only eight plots in Georgia were south-facing. No plots in

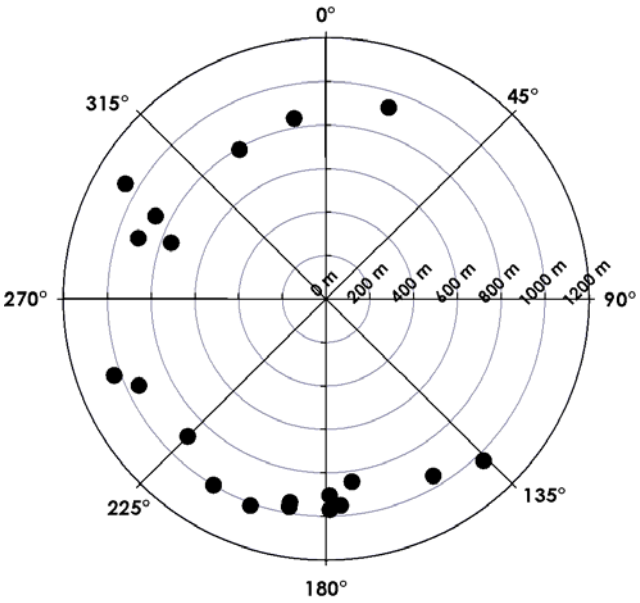

Figure 5.2. Distribution of sample plots in Virginia. Plots (points) are displayed on radial axes of elevation in meters above sea level, and angular position representing slope aspect in degrees from North.

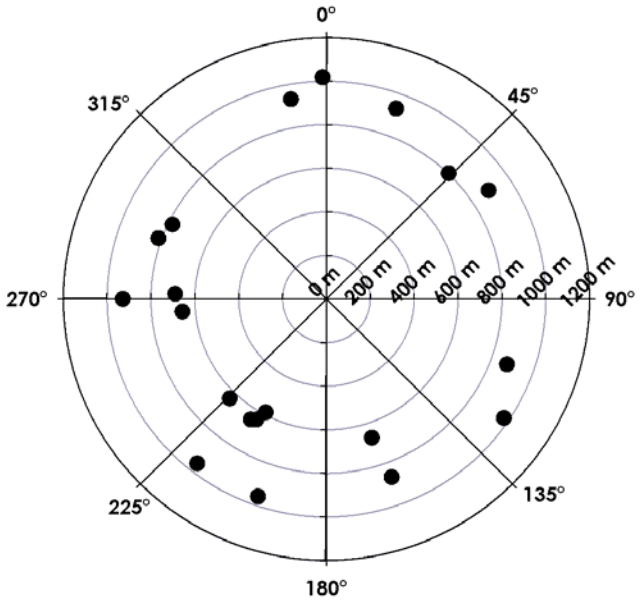

Figure 5.3. As in Figure 5.2, but for sample plots in Georgia.

Virginia were located on slopes with eastern aspects, but three Georgia plots were east-facing. Mean TRMI values were similar at both study sites. Mean TRMI for Virginia stands was 22, with index values ranging from 9 to 43, while mean TRMI in Georgia was 21.3, with a range of values from 10 to 27.

5.4.2 Species Composition

The canopies of pine-oak stands in Virginia were dominated by several species of pine and oak with shade-tolerant hardwood species, especially red maple, attaining high abundance in the understory. The most important species across all Virginia stands were chestnut oak and Table Mountain pine (Table 5.1). Red maple was also an important species, and attained the highest density among all species present (145 trees/ha). Scarlet oak and pitch pine were also important associates in most stands. Several other shade-tolerant species, notably sourwood, eastern white pine, and blackgum were important components of the understory. Overall, 16 tree species were present in sampled stands in Virginia.

Hardwood species generally had higher importance values in pine-oak stands in Georgia compared to stands in Virginia (Table 5.2). Red maple had the highest importance value among Georgia species due to high density of trees (217.5 trees/ha). Blackgum, a shade-tolerant hardwood, was also a very important stand component, and co-occurred with chestnut oak and pitch pine. Table Mountain pine was relatively less important in Georgia stands compared to Virginia stands. Table Mountain pine was the eighth most important species in

Table 5.1. Density, basal area, and Importance Value for all trees (> 5.0 cm dbh) surveyed in Virginia.

Species	Common Name	Density (stems/ha)	Basal Area (m^2/ha)	Importance Value
Quercus montana	Chestnut oak	145.0	158.1	37
Pinus pungens	Table Mountain pine	106.3	133.0	30
Acer rubrum	Red maple	197.5	49.5	26
Quercus coccinea	Scarlet oak	112.5	96.0	25
Pinus rigida	Pitch pine	73.8	124.0	26
Oxydendrum arboreum	Sourwood	131.3	37.1	18
Pinus strobus	Eastern white pine	108.8	24.7	14
Nyssa sylvatica	Blackgum	93.8	19.6	12
Ostrya virginiana	Hop hornbeam	31.3	3.7	4
Quercus rubra	Northern red oak	18.8	11.7	4
Pinus echinata	Shortleaf pine	3.8	10.1	2
Betula lenta	Sweet birch	3.8	2.5	1
Castanea dentata	American chestnut	7.5	0.7	1
Quercus alba	White oak	2.5	1.8	1
Acer pensylvanicum	Striped maple	1.3	0.1	0
Tsuga canadensis	Eastern hemlock	1.3	0.1	0
Total Virginia		**1038.8**	**672.8**	**200**

Table 5.2. Density, basal area, and Importance Value for all trees (> 5.0 cm dbh) surveyed in Virginia.

Species	Common Name	Density (stems/ha)	Basal Area (m^2/ha)	Importance value
Acer rubrum	Red maple	217.5	51.6	30
Quercus montana	Chestnut oak	100.0	143.5	29
Nyssa sylvatica	Blackgum	198.8	59.2	29
Pinus rigida	Pitch pine	73.8	150.5	27
Quercus rubra	Northern red oak	53.8	68.5	15
Oxydendrum arboreum	Sourwood	87.5	41.0	15
Pinus strobus	Eastern white pine	53.8	61.6	14
Pinus pungens	Table Mountain pine	37.5	62.4	12
Pinus echinata	Shortleaf pine	30.0	52.9	10
Quercus coccinea	Scarlet oak	30.0	32.8	7
Quercus alba	White oak	16.3	27.3	5
Carya glabra	Pignut hickory	15.0	4.9	2
Sassafras albidum	Sassafras	15.0	2.0	2
Pinus virginiana	Virginia pine	2.5	6.1	1
Cornus florida	Flowering dogwood	7.5	1.4	1
Magnolia fraseri	Fraser magnolia	5.0	0.4	1
Liriodendron tulipifera	Yellow poplar	2.5	0.3	0
Quercus stellata	Post oak	1.3	0.8	0
Tsuga canadensis	Eastern hemlock	1.3	0.5	0
Castanea dentata	American chestnut	1.3	0.1	0
Total Georgia		**950.0**	**768.1**	**200**

Georgia with an importance value of only 12, while the species was second most important, with a value of 30, in Virginia. A total of 20 species were identified in Georgia.

In Virginia, five compositional groups were identified by cluster analysis of importance values (Figure 5.4a). Group 1 contains six stands and is dominated by chestnut oak, while red maple and Table Mountain pine are minor associates. The average importance value of chestnut oak is 80.3 in group 1 stands. Group 2 consists of four stands and is dominated by Table Mountain pine (average IV = 68.6) with pitch pine of secondary importance. Group 3 contains only two stands dominated by high density of eastern white pine (average IV = 62.9). Chestnut oak, scarlet oak, and red maple are also major components of group 3. The most important species of group 4 is pitch pine (average IV = 62.1). Red maple, chestnut oak, and scarlet oak are also relatively abundant in group 4. Dominance in group 5 is shared by scarlet oak and red maple with average importance values of 47.8 and 40.4, respectively. Groups 4 and 5 consist of four stands each.

Four compositional groups were identified by cluster analysis among stands in Georgia (Figure 5.4b). Group 1 consists of five stands and is dominated by chestnut oak (average IV = 65.4). Northern red oak and red maple are also important in this group. Group 2 is composed of four stands and is dominated by Table Mountain pine (average IV = 58.7), with chestnut oak and blackgum being minor associates. Group 3 is made up of five stands, and pitch pine (average IV = 56.9) is the most important species of the group. Group 4 consists of six stands that are dominated by red maple (average IV = 44.4). Sourwood and pitch pine also contribute to the stand composition, with average importance values of 30.6 and 25.1, respectively.

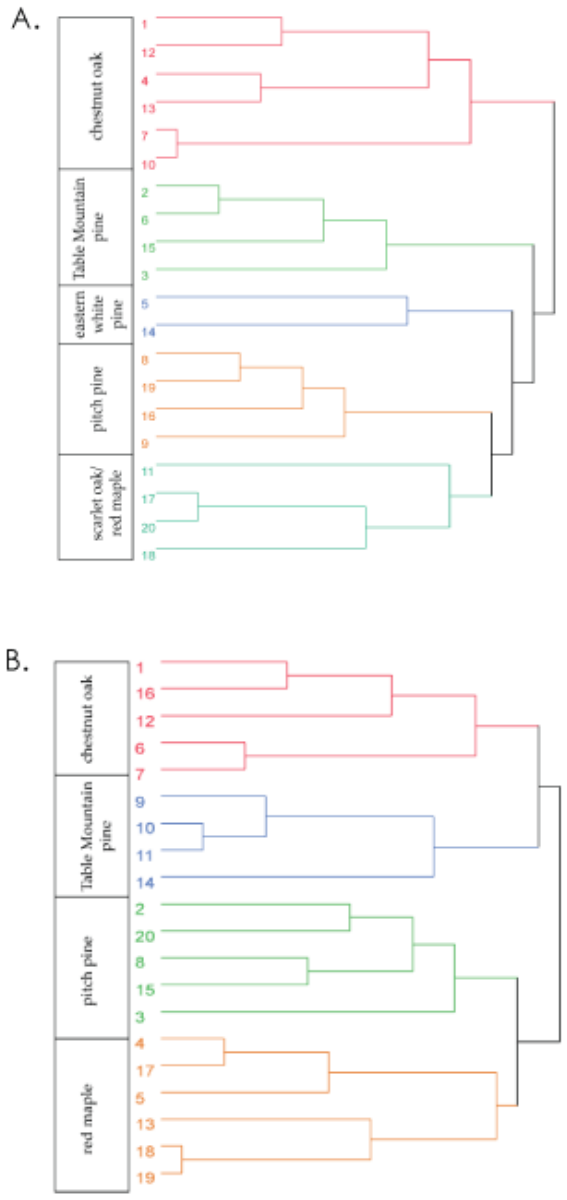

Figure 5.4. Dendrograms of groups of plots identified by cluster analysis of stand composition in Virginia (A.) and Georgia (B.). Compositional groups are coded by color, and boxes to left denote the most important species in each group. Length of lines joining two plots represents relative similarity of species composition. Numerals represent stand identification numbers.

5.4.3 Stand Structure

The diameter distributions of pine-oak stands at both sites are indicative of structurally diverse stands with high levels of regeneration (Figures 5.5 and 5.6). Size class histograms of all compositional groups display some form of a reverse J-shaped distribution, in which the greatest number of individuals occur in the smallest diameter class and abundance decreases with diameter (Oliver and Larson 1996). Size class distributions are generally similar between study sites but major distributional differences are apparent between species. The smallest diameter classes are dominated by shade-tolerant hardwood species (red maple, blackgum, and sourwood) and these species show a skewed reverse J-shaped distribution. Oak and pine dominate the larger size classes, and usually have a unimodal distribution. Pine is absent from the smallest diameter category in three of five compositional groups in Virginia and two of four compositional groups in Georgia. Additionally, the modal distributions of pine and oak in Georgia are more platykurtic than the peaked modal distributions in the Virginia stands.

5.4.4 Stand Age Structure and Establishment Dates

The distribution of tree ages in all groups indicates a shift in composition from mostly pine and oak to hardwoods such as red maple, blackgum, and sourwood (Figures 5.7 and 5.8). Similar to the diameter distributions, pine and oak have unimodal age distributions across all compositional groups at both study sites. In both Virginia and Georgia, pine and oak establishment reached a peak 80 to 100 years ago. In Virginia, this peak of oak and pine establishment coincided with a peak in the establishment of shade-tolerant hardwoods. In

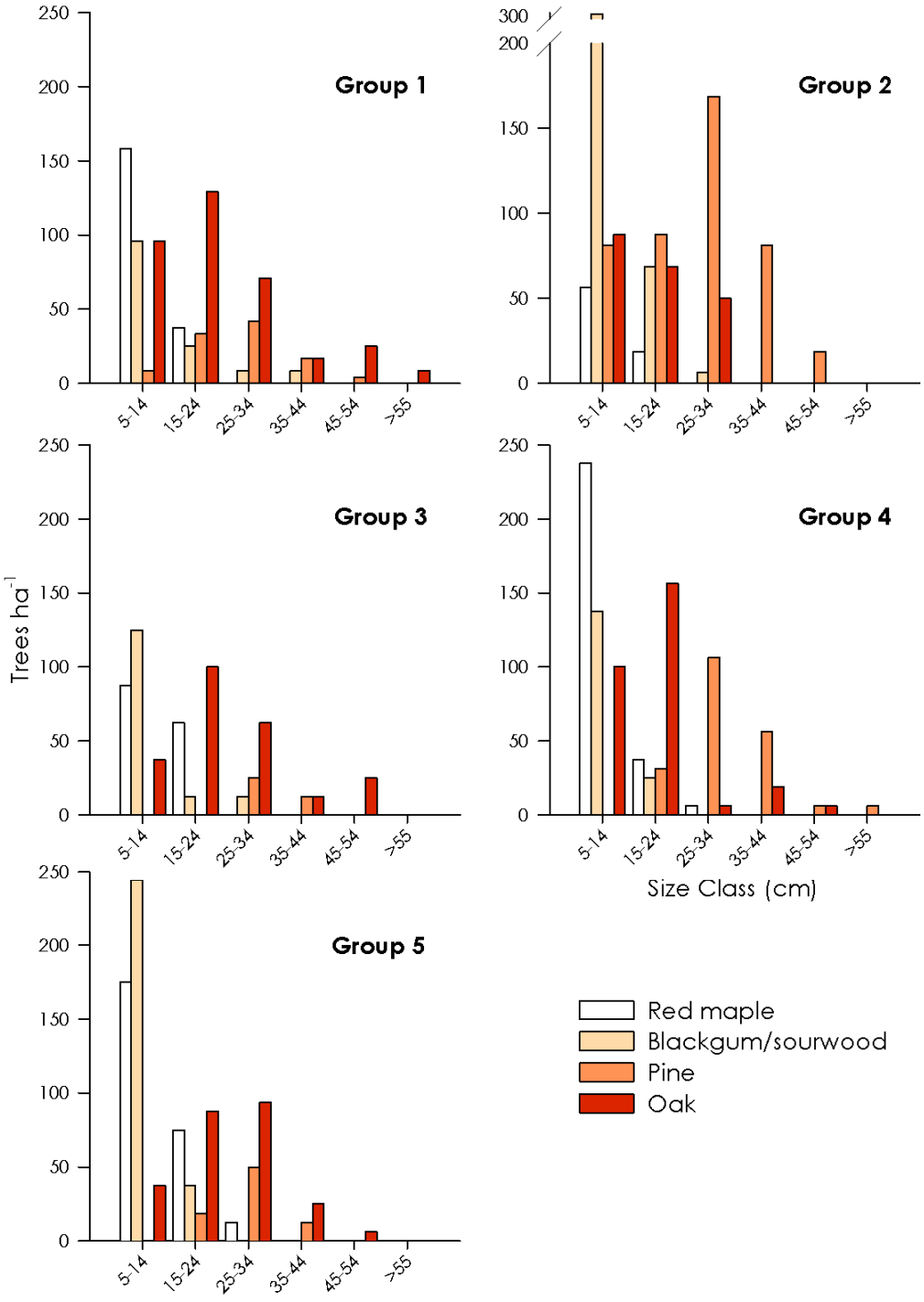

Figure 5.5. Diameter distribution of important tree species by compositional group in Virginia. Height of each bar indicates number of trees (> 5.0 cm dbh) per hectare of each species in 10-cm diameter classes.

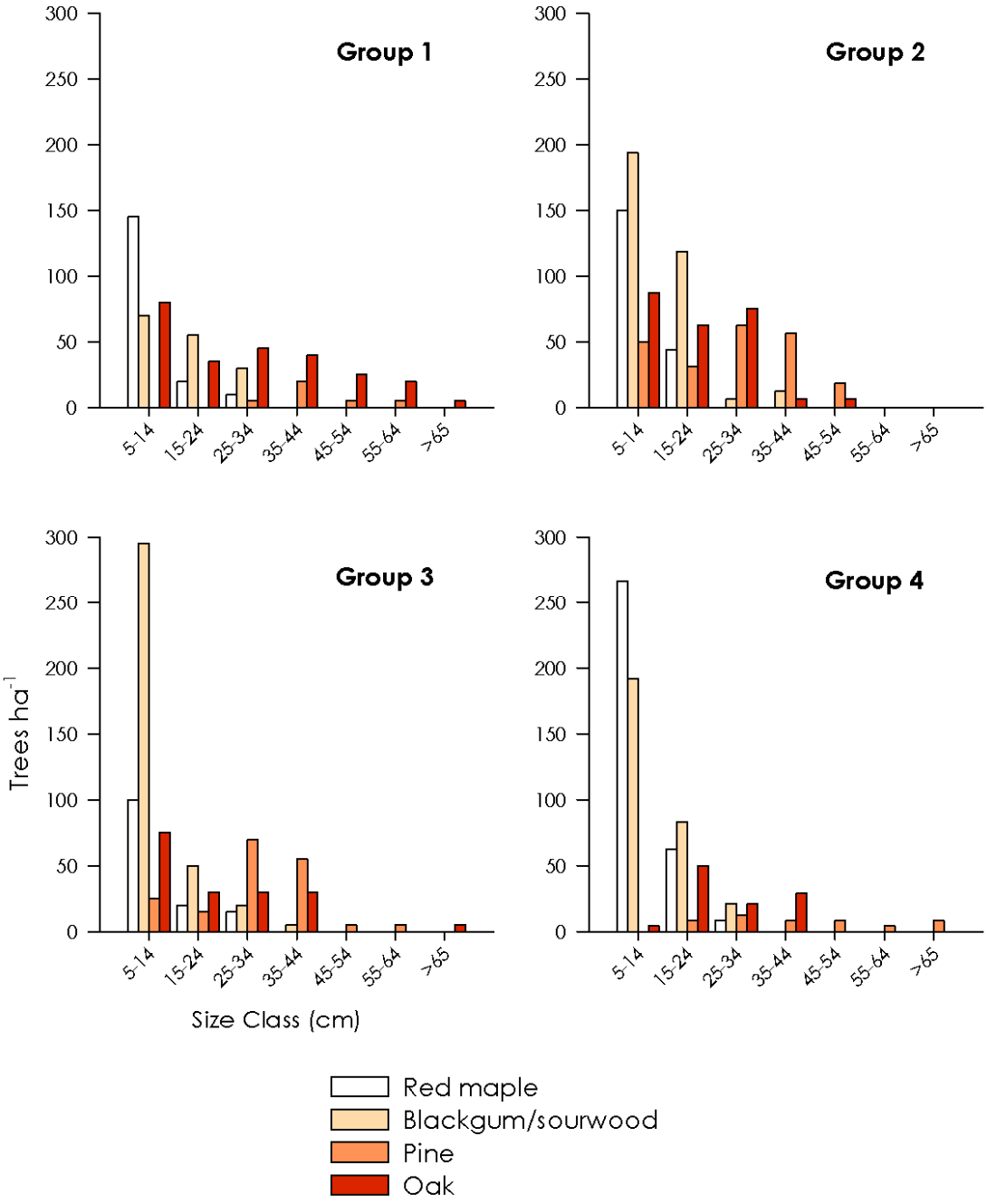

Figure 5.6. Diameter distribution of important tree species by compositional group in Georgia. Height of each bar indicates number of trees (> 5.0 cm dbh) per hectare of each species in 10-cm diameter classes.

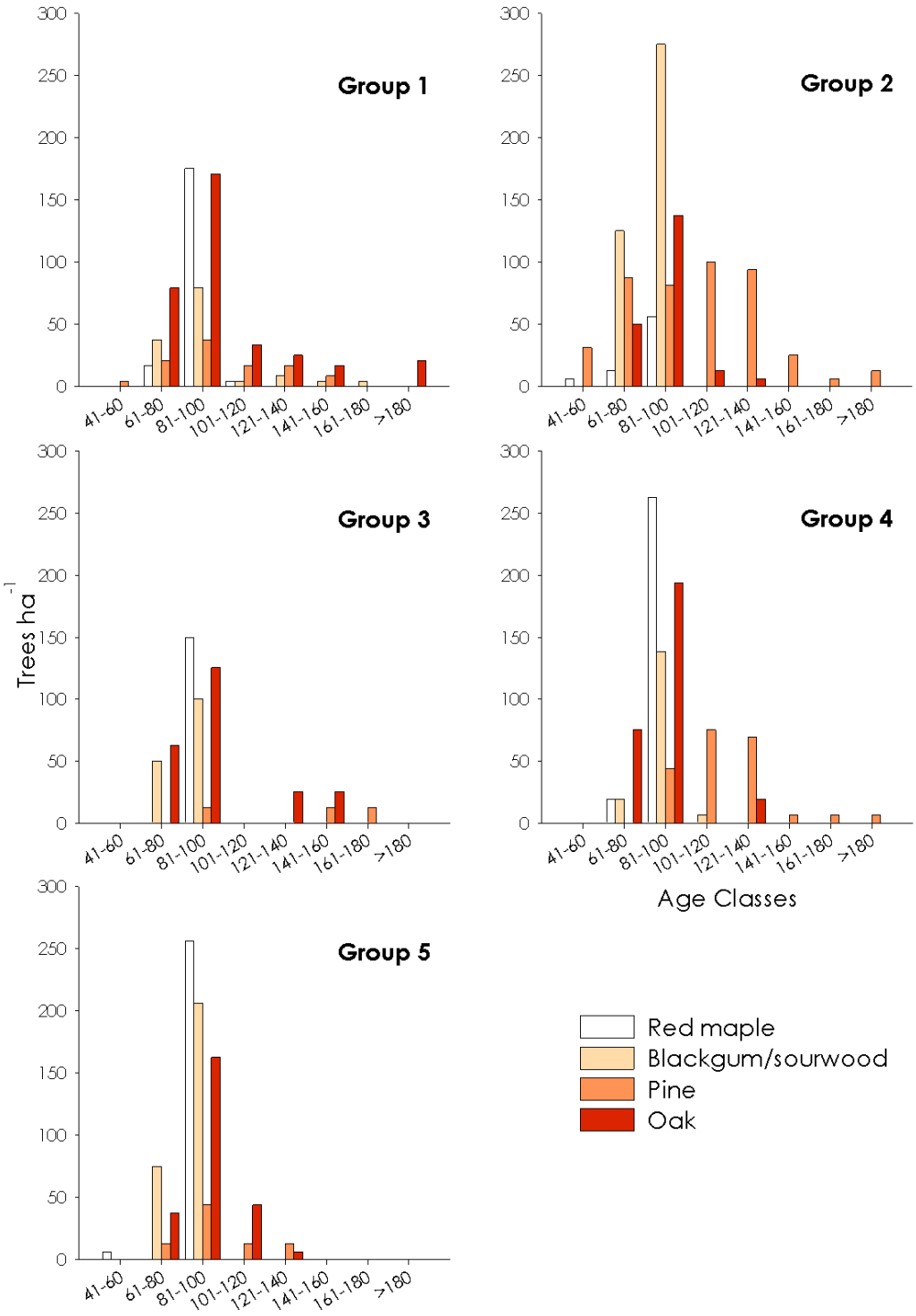

Figure 5.7. Age distribution (20-year age classes) of important tree species by compositional group in Virginia.

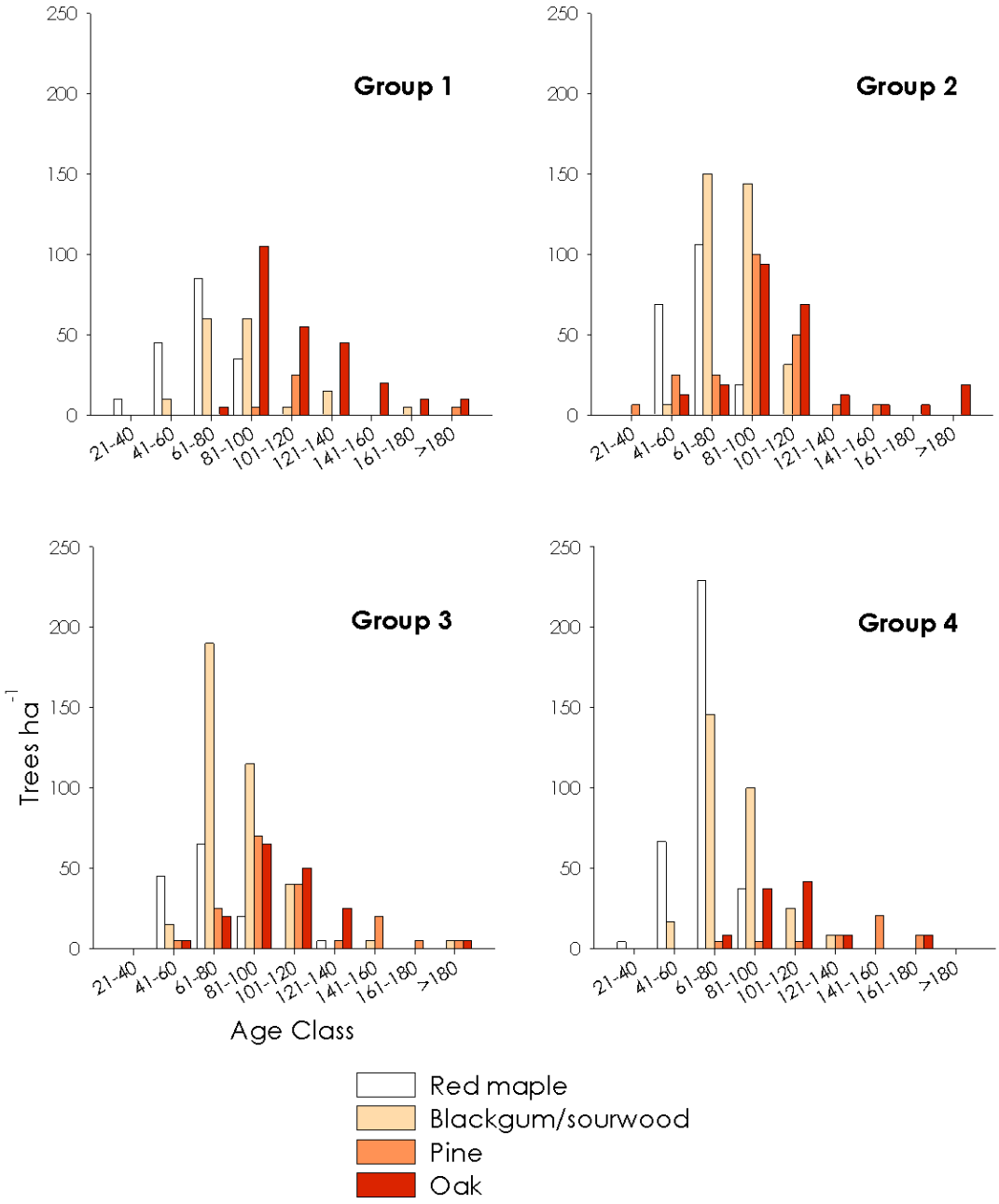

Figure 5.8. Age distribution (20-year age classes) of important tree species by compositional group in Georgia.

Georgia, however, a peak in hardwood recruitment occurred later (60 to 80 years ago) and recruitment of shade-tolerant hardwoods remained higher than oak and pine.

The shift in stand composition caused by differential rates of recruitment and survivorship is apparent when examining the distribution of establishment dates by taxonomic groups (Figures 5.9 and 5.10). Both sites experienced relatively continuous establishment of oak and pine for the past century, but little to no establishment of these species in recent decades. No successful pine establishment occurred in Virginia after 1950 or in Georgia after 1970. Similarly, no oak establishment has occurred since 1940 in Virginia and since 1950 in Georgia (Figure 5.9). Successive peaks of shade-tolerant species have occurred in both sites (Figure 5.10). Blackgum and sourwood were the first to reach a peak, followed closely by red maple, and finally eastern white pine. In each case, peaks of establishment occurred a decade or two earlier in Virginia.

5.4.5 Regeneration and Abundance

Mean values of seedling and sapling density as well as overstory density and basal area varied widely, but some significant differences exist between the study areas (Table 5.3). Abundance of scarlet oak seedlings and saplings as well as blackgum saplings were significantly higher in Virginia. Density of red maple seedlings was significantly higher in Virginia, but abundance of red maple saplings was higher in Georgia. The density and basal area of Table Mountain pine and scarlet oak in the overstory were all significantly higher in

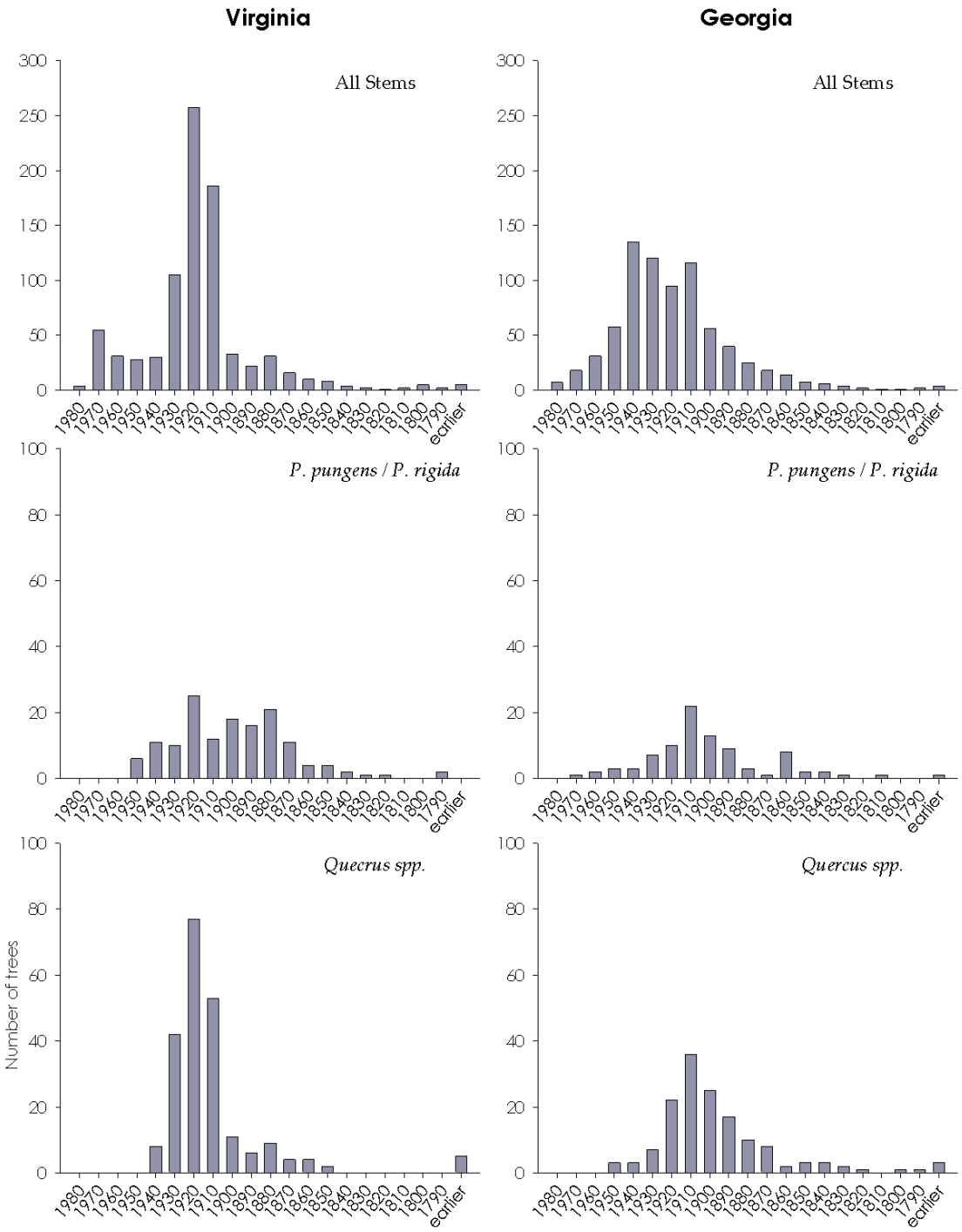

Figure 5.9. Establishment dates for all trees, and shade-intolerant species (yellow pines and oaks) sampled in Virginia (left column) and Georgia (right column). Category labels on the *x*-axis indicate beginning year of each decade.

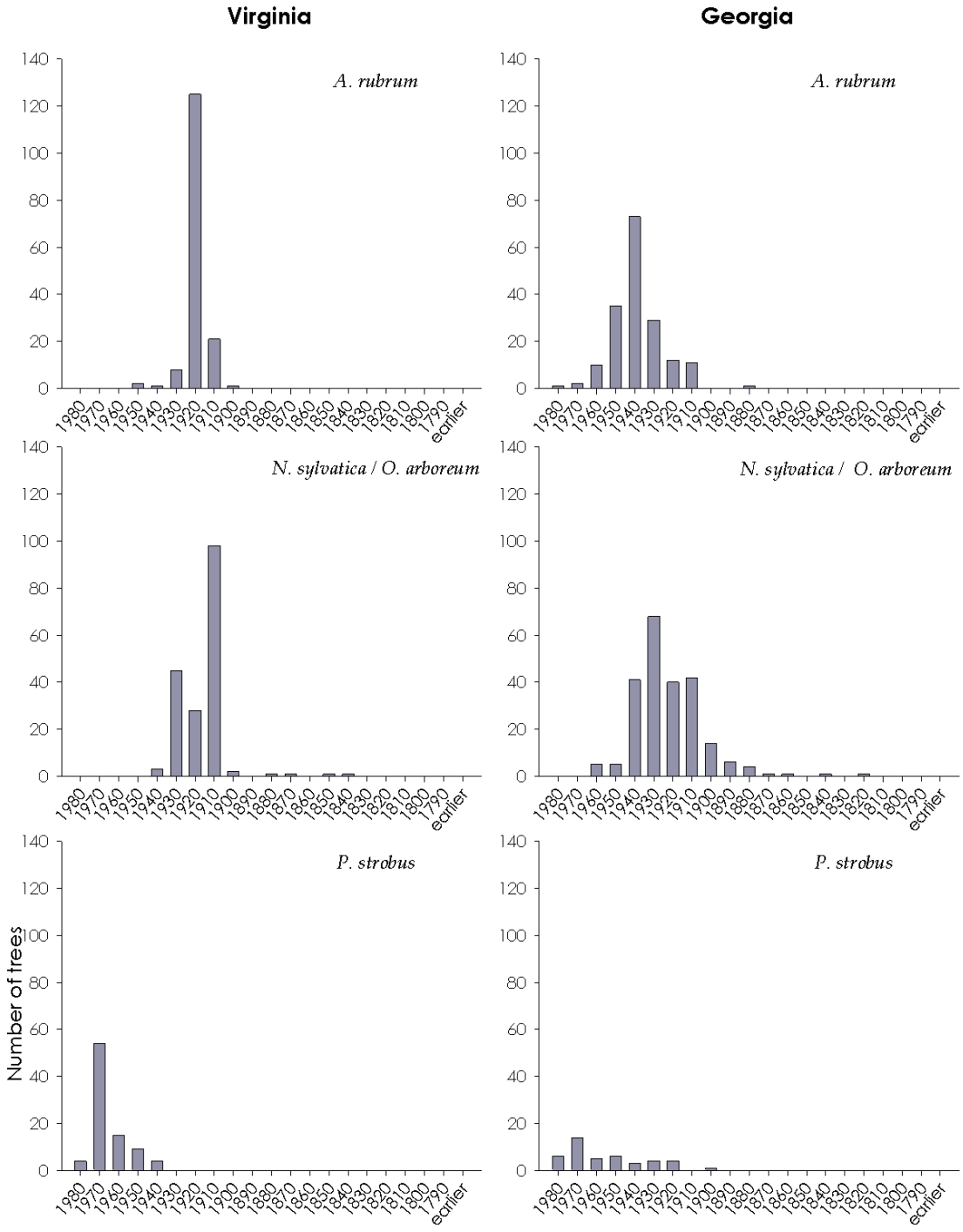

Figure 5.10. Establishment dates for shade-tolerant species sampled in Virginia (left column) and Georgia (right column). Category labels on the x-axis indicate beginning year of each decade.

Table 5.3. Attributes (mean ± one standard error) of seedlings, saplings, and overstory of important species in sampled pine-oak stands.

	Virginia	Georgia
Seedling density (seedlings/ha)		
P. pungens	—	—
P. rigida	2.0 ± 1.4	—
P. strobus	14.0 ± 6.5	35.0 ± 14.4
Q. coccinea	23.0 ± 5.7	— **
Q. montana	181.0 ± 123.4	51.0 ± 18.6
Q. rubrua	24.0 ± 10.3	39.0 ± 14.1
A. rubrum	513.0 ± 180.3	135.0 ± 56.7 **
N. sylvatica	5.0 ± 2.5	6.0 ± 3.3
O. arboreum	—	—
Sapling density (saplings/ha)		
P. pungens	13.0 ± 9.3	—
P. rigida	—	—
P. strobus	152.0 ± 40.8	228.0 ± 104.2
Q. coccinea	20.0 ± 6.3	— **
Q. montana	15.0 ± 6.0	14.0 ± 5.4
Q. rubrua	17.0 ± 9.5	20.0 ± 8.6
A. rubrum	64.0 ± 12.7	246.0 ± 53.2 *
N. sylvatica	91.0 ± 20.6	50.0 ± 16.8 *
O. arboreum	13.0 ± 4.2	18.0 ± 10.2

Items marked with an asterisk are significantly different as indicated by Mann-Whitney rank-sum tests. (* indicates $P < 0.05$, ** indicates $P < 0.01$)

Table 5.3. Continued

	Virginia	Georgia
Overstory density (trees/ha)		
P. pungens	2.9 ± 0.6	1.0 ± 0.4 **
P. rigida	3.1 ± 0.7	2.7 ± 0.6
P. strobus	—	0.6 ± 0.2 *
Q. coccinea	1.8 ± 0.4	0.3 ± 0.1 **
Q. montana	2.4 ± 0.6	1.3 ± 0.4
Q. rubrua	0.2 ± .01	0.8 ± 0.3
A. rubrum	0.4 ± 0.2	—
N. sylvatica	—	—
O. arboreum	—	—
Overstory basal area (m²/ha)		
P. pungens	5.3 ± 1.2	2.5 ± 1.2 *
P. rigida	5.8 ± 1.5	6.8 ± 1.2
P. strobus	—	2.2 ± 0.9 *
Q. coccinea	2.8 ± 0.9	0.9 ± 0.4 *
Q. montana	5.4 ± 1.6	4.8 ± 1.3
Q. rubrua	0.3 ± 0.2	2.1 ± 0.7
A. rubrum	0.3 ± 0.2	—
N. sylvatica	0.3 ± 0.2	—
O. arboreum	—	—

Items marked with an asterisk are significantly different as indicated by Mann-Whitney rank-sum tests. (* indicates $P < 0.05$, ** indicates $P < 0.01$)

Virginia, while density and basal area of eastern white pine in the overstory is significantly higher in Georgia.

5.4.6 Environmental Gradients

Composition of pine-oak stands varies along similar environmental gradients at both study sites. Forest plots of similar species composition were distributed along ordination axes, and axes were significantly correlated with several environmental variables. DCA ordination axis 1 for the Virginia study site (Figure 5.11a) was significantly correlated with slope aspect ($r = 0.48$, $p = 0.03$) with higher axis scores corresponding to north-facing aspects. Axis 1 is negatively correlated with abundance of Table Mountain pine, chestnut oak, and pitch pine. DCA axis 2 is significantly correlated with elevation ($r = –0.52$, $p = 0.02$) and TRMI ($r = 0.49$, $p = 0.03$) with higher axis scores relating to low elevation, moist sites. Axis 2 is positively correlated with abundance of eastern white pine and red maple, and is negatively correlated with abundance of Table Mountain pine. Stands dominated by Table Mountain pine and pitch pine (compositional group 2) occupy the most xeric portion of ordination with the lowest scores on both DCA axes. Stands with a large component of eastern white pine (group 3) occupy the most mesic portion of DCA space.

Ordination axis 1 for the Georgia study site (Figure 5.11b) was significantly correlated with elevation ($r = –0.75$, $p < 0.001$), slope aspect ($r = –0.47$, $p = 0.03$), and slope position ($r = 0.56$, $p = 0.01$). Higher DCA scores along axis 1 are related to low elevations, low slope positions, and northerly slope aspects. Stands dominated by Table Mountain pine (compositional group 2)

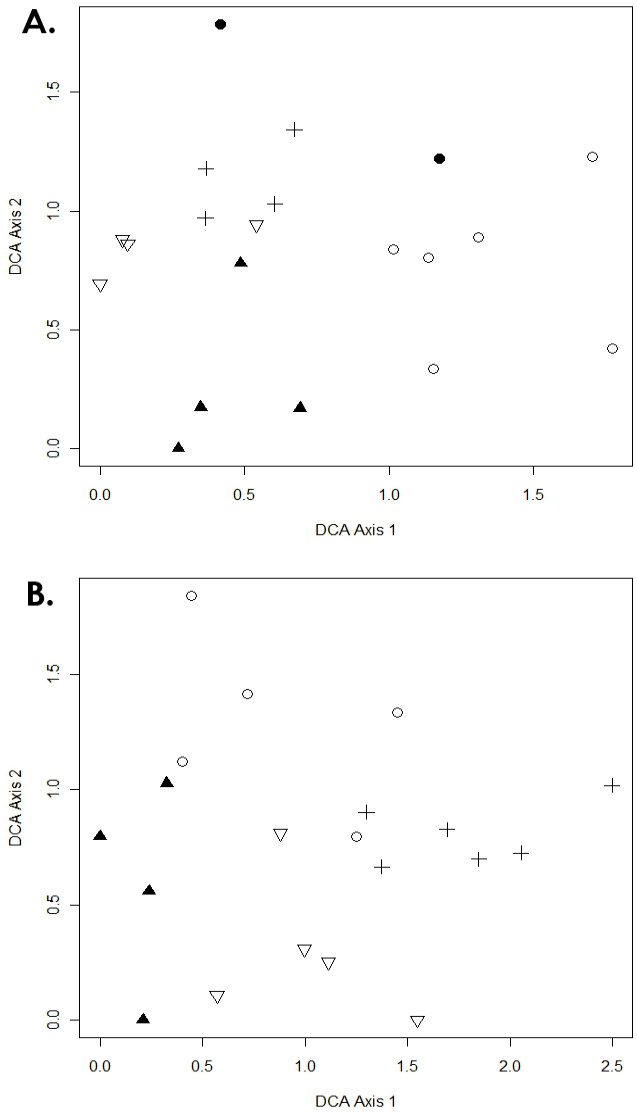

Figure 5.11. Sample (plot) DCA scores by compositional group for pine-oak stands in Virginia (A) and Georgia (B). Point symbols in (A) refer to stands dominated by the following species: open circles = chestnut oak (group 1), filled triangles = Table Mountain pine (group 2), filled circles = eastern white pine (group 3), open triangles = pitch pine (group 4), crosses = scarlet oak (group 5). Symbols in (B) are: open circles = chestnut oak (group 1), filled triangles = Table Mountain pine (group 2), open triangles = pitch pine (group 3), crosses = red maple (group 4).

have the lowest scores along DCA axis 1, followed by chestnut oak stands (group 1), pitch pine stands (group 3), and finally red maple/sourwood stands (group 4). Additionally, abundance of chestnut oak and Table Mountain pine and chestnut oak are negatively correlated with this axis, while white oak, red maple, and sourwood are positively correlated with axis 1. The second DCA axis is not significantly correlated with any measured environmental variables, but it is positively correlated with chestnut oak abundance and negatively correlated with abundance of scarlet oak, pitch pine, and blackgum.

5.5 Discussion

5.5.1 Species Composition

Pine-oak stands in Virginia and Georgia share nearly all important species but some key differences in the relative importance of species are apparent. The two study areas share 13 tree species, and the eight most important species are common to both sites. Shade-tolerant hardwood species (red maple and blackgum) have higher relative importance among dominant species in Georgia than Virginia. Table Mountain pine is the most important conifer species in Virginia, while pitch pine is the most important conifer in Georgia. The other difference between sites is the uniqueness of minor species. Three species (hop hornbeam, sweet birch, and striped maple) are unique to Virginia stands, while seven species occur only in the Georgia stands (pignut hickory, sassafras, Virginia pine, flowering dogwood, Fraser magnolia, yellow poplar, and post oak). This distribution of species leads to higher overall species richness in Georgia (20 versus 16 species). Any support for an abundant center pattern based on the

importance values of species is equivocal. Table Mountain pine has a much lower relative importance at its range edge site, while pitch pine and chestnut oak do not.

Brose et al. (2010) compared importance values of trees in Table Mountain pine stands in Pennsylvania and Tennessee, and they also found minimal differences in the relative importance of species. They found 13 species in each of their study locations, and found that chestnut oak and Table Mountain pine dominated both sites, but the relative importance of red maple was higher in Tennessee.

5.5.2 Stand Structure

The pattern of forest change in pine-oak stands in Virginia and Georgia is similar, but the processes that produce forest structure are different. The size and age structure of all compositional groups in both study areas illustrate a clear pattern of small sizes and young age classes dominated by shade-tolerant hardwood species (e.g., red maple, blackgum, and sourwood) and larger sizes and older age classes dominated by pines and oaks. This type of pattern is regarded as evidence of a future shift in stand composition as it is generally assumed that (in the absence of catastrophic disturbance) small, young understory trees will replace old, overstory trees as they die (Lorimer 1984).

The temporal signature of the replacement of pine and oak with maple and blackgum is different between stands in Virginia and Georgia, and within each study area the pattern is consistent across compositional groups. In both sites, pine and oak establishment peaked 80 to 100 years ago and then began a decline. In Virginia, this peak of oak and pine establishment

coincided with a peak in the establishment of shade-tolerant hardwoods, but in Georgia a peak in hardwood recruitment was offset, occurring more recently (60 to 80 years ago). The distinctly different modes of transition may be related to the collapse of American chestnut. Chestnut was a foundation species throughout much of the Appalachians, and rapid die-back of mature chestnut during the first half of the 20th century created numerous and expansive canopy gaps for the recruitment of other species (Keever 1953, Woods and Shanks 1959). Small chestnut saplings were present in both study areas. However, we observed greater chestnut sprouting from old stumps in Virginia than in Georgia, but we did not design our study to explicitly test for differences in remnant chestnut material. In any case, a greater proportion of chestnut may have contributed to conditions favorable to the establishment of a variety of new species at once.

A transition from pine-oak to maple dominance has been widely documented elsewhere, and the cause of this shift in species composition has most often been attributed to human land-use change resulting in fire exclusion (Abrams 1992, Loftis and McGee 1993, Armbrister 2002, Brose and Waldrop 2006, DeWeese 2007, Nowacki and Abrams 2008, Brose and Waldrop 2010). Both pines and oaks have life history characteristics that enhance their survival and regeneration in environments with frequent fires. Oak and pine have thick bark that insulates stems from fire damage, while maples typically have thin bark and are easily killed by fire (Burns and Honkala 1990, Abrams 1992, Barnes et al. 1998). Additionally, oak species generally allocate a great deal of resources to roots where carbon reserves are safe from fire. This allocation of resources to below-ground growth results in their ability to readily

sprout from root collars after trees are top-killed by fire. Conversely, maples allocate more resources to above-ground growth and do not typically re-sprout after fire (Abrams 1992). Pine species such as Table Mountain pine and pitch pine also successfully regenerate after fire by releasing seeds from serotinous cones. The bracts of serotinous cones are sealed with wax. After exposure to heat from fire, the wax melts allowing cones to open. Pine seeds deposited after fire are more likely to become established due to direct contact with mineral soil, increased light levels, and less competing vegetation (Zobel 1969).

Exclusion of fire from eastern US forests beginning in the early 20th century is often cited as the major factor contributing to a shift in dominance from pine and oak to maple and other shade-tolerant species (Abrams 1992, Abrams and Nowacki 2008). However, recent research points out that this compositional shift also coincides with several other environmental transitions that may be drivers of this ecosystem change. For example, the shift from oak to maple in North America occurs during a shift from a period of frequent, multi-year droughts to an era of high moisture availability (McEwan et al. In Press). Pine and oak species both have morphological and physiological adaptations to drought, such as deep root systems and xerophytic leaves, that give them advantages over other species in environments that experience frequent or severe droughts (Abrams 1990, Barnes et al. 1998). However, the effects of climate and fire are not easily separated because climatic shifts to cooler and wetter conditions often result in a decrease in fire frequency (Abrams 1992).

The shift from pine-oak forests also coincides with population increases of several herbivores, especially white-tailed deer (*Odocoileus virginianus*) (McCabe and McCabe 1997,

McEwan et al. In Press). Increases in deer populations over the past 150 years may have contributed to the decline of oak forests because deer have been observed to preferentially browse oak seedlings over maples (Strole and Anderson 1992). Additionally, increases in deer browsing intensity have resulted in decreasing oak seedling density (Rooney and Waller 2003).

We found similar patterns of compositional shift from pine-oak to red maple in our study sites, but both sites have similar land-use and disturbance histories. A spatial network of plot-level dendroecological data may provide the basis for disentangling the multiple confounding effects of land-use, climate, disturbance history, and loss of foundation species on compositional shifts in forests. However, any such network will need to include a wide range of environmental and historical characteristics so a very large network will likely be necessary.

5.5.3 Tree Regeneration and Overstory Density

Regeneration of pine and oak species was extremely limited in Virginia and Georgia, and few significant differences in seedling or sapling establishment exist between sites. No Table Mountain pine saplings were counted in Georgia, and no pitch pine saplings or Table Mountain pine seedlings were counted at all. Red maple had the most prolific regeneration of any species surveyed. In Virginia, significantly more red maple seedlings established, but significantly fewer saplings were counted. The abundance of red maple regeneration may be of little use for predicting recruitment to the overstory, however, because this species experiences very high mortality during the recruitment process (Woods and Shanks 1959). The high abundance of red maple and other hardwoods in the seedling, sapling, and understory layers,

along with a lack of pine and oak regeneration, suggests that pine and oak importance will decline in the southern Blue Ridge region regardless of the location of stands relative to the range boundaries of pine and oak species.

The lack of Table Mountain pine regeneration in our study sites agrees with the previously documented pattern of decreasing regeneration at southern locations in the geographic range of Table Mountain pine. Brose et al. (2010) found significantly more seedlings of Table Mountain pine near the species' distributional limit in Pennsylvania compared to stands in Tennessee. They attributed the difference to the prevalence of serotinous cones in Tennessee, and many trees lacking cone serotiny in Pennsylvania. Zobel (1969) also noted that genotypes of Table Mountain pine that lack cone serotiny tend to be clustered near the species' northern distributional limit. The limited regeneration we observed in Virginia and Georgia suggests that cone serotiny is likely to be prevalent in these locations.

5.5.4 Stand Composition along Environmental Gradients

Patterns of species composition are generally similar in both study areas, and they are responding to similar environmental gradients. Although not all compositional groups are completely comparable between Virginia and Georgia, stands dominated by certain species tend to occupy similar regions of ordination space. For example, stands with the greatest Table Mountain pine component (Virginia group 2 and Georgia group 2) occupied the same ordination space when plotted along DCA axes that were correlated with variables related to moisture (slope aspect, elevation, TRMI, etc.). For example, Table Mountain pine dominates the

most xeric positions in both study sites. Stands dominated by the other major species also line up in the same relative positions along the axes. After Table Mountain pine, pitch pine stands tend to occupy the next driest locations, followed closely by chestnut oak and distantly by red maple and eastern white pine.

One interpretation of the ecological amplitude paradigm is that species near their range limits may preferentially occupy sites that are less stressful (Griggs 1914, Kavanagh and Kellman 1986). For example, species near their southern distributional limit may be found on increasingly north-facing slope aspects because southerly aspects may be associated with warmer, drier local conditions. Our analyses of pine-oak stands, however, do not support such a prediction. The relative positions of dominant tree species along environmental gradients are similar at distant sites at both the interior and periphery of the range of pine-oak species. Taken together, these analyses suggest that the structure, composition, and regeneration of pine-oak stands in the southern Appalachian Mountains do not vary along broad-scale environmental gradients coincident with species' geographic ranges. The southern range limit of this forest community and its dominant species may not be determined by climatic factors, but instead by the lack of suitable habitat on the Appalachian Piedmont and Coastal Plain (Shankman and Hart 2007). Assumptions of ecological amplitude regarding the spatial variability of abundance or stand structure within the geographic ranges of pine-oak species are unsupported. However, dendroecological data collected from a network of stands with greater spatial extent may allow more comprehensive analysis of spatial variability and may further refine understanding of these forests and facilitate preservation of the landscape diversity they provide.

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CHAPTER 6

CONCLUSIONS AND FUTURE RESEARCH

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The overall purpose of this dissertation research was to investigate the spatial patterns of abundance, growth, and stand structure across the geographic ranges of tree species using dendroecological and forest inventory methods. Specifically, I investigated whether spatial patterns of tree abundance, growth, climate response, and establishment conform to the related biogeographic paradigms of abundant center and ecological amplitude. Past ecological applications of dendrochronology have overwhelmingly focused on reconstructing past disturbances (e.g., fire, insect outbreak) in forest ecosystems, or less frequently on changes in forest composition or distribution at the scale of a single stand or landscape. While many researchers have used networks of tree-ring data to reconstruct past climate, relatively few studies have used networks of tree-ring data to test biogeographic theory at broad spatial scales. The analyses presented here aim to begin filling this gap in the literature by demonstrating the applicability of tree-ring data to investigations of biogeographic theory.

6.1 The distribution of abundance of red fir

No abundant center pattern was detected in the analysis of red fir.

Red fir abundance in plots was not correlated with spatial position of those plots within the species' geographic range limits. No significant relationship was found between tree

density and distance from range center (r = –0.035, p = 0.889). Correspondingly, density of red fir was not significantly correlated with latitudinal (r = 0.129, p = 0.610) or longitudinal (r = –0.221, p = 0.378) position. Similarly, no gradient of abundance was detected among red fir stands grouped in quartiles of latitude, longitude, and distance from range center. Mean density was highest in the centermost quartile, but differences between means were not statistically significant as indicated by a one-way ANOVA test (F = 0.706, P = 0.564, DF = 3).

6.2 Growth response of longleaf pine to climate variability

1. Radial growth of longleaf pine at a range edge site was influenced by current-year growing season moisture availability and previous winter temperatures.

Longleaf pine annual growth in Marshal Forest Preserve was significantly correlated with spring and summer precipitation and soil moisture. Response function analysis of tree growth with monthly climate data revealed that precipitation in May of the current growing season had a significant influence on ring width. Additionally, available soil moisture as characterized by Palmer Drought Severity Index (PDSI) was an important determinant of annual growth. May, July, and August PDSI for the current growing season were significant predictors of annual ring width. Mean monthly temperature did not have a significant influence on tree growth for any of the months analyzed. However, correlation analysis between monthly temperature and the residual tree-ring chronology found significant negative correlations between total ring width and current year summer (June, July, and August) temperatures. This negative relationship between summer temperature and tree growth is

likely a signal of moisture stress, as higher temperatures result in higher rates of evapotranspiration. Additionally, earlywood growth is positively correlated with mean February temperature for the current growing year.

2. The spatial pattern of average mean sensitivity of longleaf pine tree-ring chronologies does not support the ecological amplitude hypothesis.

Despite being located on a marginal site near the northwestern limit of its geographic range and near the upper elevational limit of the species, longleaf pine at Marshall Forest Preserve (MFP) exhibits similar values of average mean sensitivity and shows similar responses to monthly climate observed in other longleaf pine stands on the Coastal Plain. Average mean sensitivity at MFP was not significantly different from that of three Coastal Plain sites, and average mean sensitivity was lower at MFP than at two Coastal Plain sites. Additionally, the site with the highest average mean sensitivity was Lake Louise, located near the center of the geographic range of longleaf pine. The spatial pattern of mean sensitivity based on ecological amplitude assumptions would predict high mean sensitivity at a montane site near the range edge, such as MFP, and low mean sensitivity at a Coastal Plain site near the center of the species range, such as Lake Louise.

3. The response of longleaf pine growth to moisture at a montane, range-edge site is similar to that of sites on the Coastal Plain.

Current year growing season precipitation was an important influence on annual radial growth of longleaf pine at all sites. Each of the six chronologies had either significant correlation or response function coefficients between February and September of the current year. The timing of significant relationships between growth and precipitation differed by site, but positive correlations between growth and precipitation were detected at both montane and Coastal Plain sites. Additionally, inverse associations between late growing season temperature (July–September) and tree growth were identified at several sites. These negative relationships between summer temperatures and radial growth are likely caused by increased moisture stress from higher temperatures during the growing season.

4. Radial growth of longleaf pine at a northern range edge site was influenced by temperature, while growth at most other sites was not.

Three of the longleaf pine sites had positive associations with winter temperatures prior to the growing season. Radial growth at Marshall Forest Preserve was positively correlated with January and February temperature, growth at Sandy Island was positively correlated with February temperature, and longleaf pine at Big Thicket Preserve had a significant positive response to January temperature. The Marshall Forest and Big Thicket sites are located near the northern and western range limits of the species, and Sandy Island is located on the Atlantic Coastal Plain in the northern part of the range. While growth response to moisture appears to

be fairly uniform throughout the geographic range of longleaf pine, sensitivity to temperature may be unique to trees growing near range boundaries.

6.3 Spatial variability of climate response in eastern hemlock and white oak

1. Distance from range edge was not a significant predictor of climate sensitivity in eastern hemlock or white oak.

Despite the fact that very flexible models were fit to tree-ring data, distance from range edge was not a significant predictor of average mean sensitivity for either tree species, and distance to range edge did not influence the pattern of sensitivity in the model predictions. The pattern of mean sensitivity predicted by our model does not support the ecological amplitude prediction of increased inter-annual growth variability caused by greater environmental stress at locations near the range edges. In particular, low mean sensitivity values along the southern geographic range limits of both species indicate that climatic factors are not likely to be a causal determinant of range boundaries.

2. Eastern hemlock and white oak chronologies had trends of increasing sensitivity in radial growth along latitudinal and longitudinal gradients.

A gradient of increasing mean sensitivity (MS) from southeast to northwest is evident in the map of sensitivity values predicted by the generalized additive model for eastern hemlock and white oak. The highest predicted MS values are in the northwestern portion of the geographic range of each species. Sensitivity decreased gradually eastward, with moderate MS

values predicted along the northern range limit. Sensitivity decreases rapidly to the south, with the lowest values occurring in the southeastern portions of the ranges. We conclude that a monotonic increase in sensitivity characterizes the climate–growth relationships of these species. Moreover, an ecological amplitude pattern of lower sensitivity near range interiors and higher sensitivity at range edges is not an accurate model of spatial variability of growth response to climate.

3. Higher mean sensitivity values in both species were related to climate variables that characterize continental climates.

High mean sensitivity in tree-ring chronologies was associated with geographic locations characterized by low precipitation and a wide temperature range, and these sites were located in the northwestern portion of each species' geographic range. The spatial gradient in predicted mean sensitivity follows trends of decreasing precipitation, decreasing annual temperatures, and increasing annual temperature range across eastern North America. Annual temperature range—the difference between July and January temperatures of the same year—and mean temperature of the coldest month were the climatic variables most strongly associated with average mean sensitivity of eastern hemlock and white oak. Correlations between these climate variables and average mean sensitivity for both species were statistically significant, but the strength of the relationship was greater for eastern hemlock than white oak.

6.4 Structure and composition of pine-oak stands

1. Support for an abundant center pattern based on the importance values of species is equivocal.

Table Mountain pine has a much lower relative importance at its range edge site, while pitch pine and chestnut oak do not. Stand composition was similar between pine-oak stands in Virginia and Georgia. The two study areas share 13 tree species, and the eight most important species are common to both sites. Shade-tolerant hardwood species (red maple and blackgum) have higher relative importance among dominant species in Georgia than Virginia. Table Mountain pine is the most important conifer species in the study area in Virginia, while pitch pine is the most important conifer in the study area in Georgia. The other difference between sites is the uniqueness of minor species. Three species (hop hornbeam, sweet birch, and striped maple) are unique to Virginia stands, while seven species occur only in the Georgia stands (pignut hickory, sassafras, Virginia pine, flowering dogwood, Fraser magnolia, yellow poplar, and post oak). This distribution of species leads to higher overall species richness in Georgia (20 versus 16 species).

2. Stands are experiencing a compositional transition from pine-oak to shade-tolerant hardwood species.

The size and age structure of all compositional groups in both study areas illustrate a clear pattern of small sizes and young age classes dominated by shade-tolerant hardwood species (e.g., red maple, blackgum, and sourwood) and larger sizes and older age classes

dominated by pines and oaks. This type of pattern is regarded as evidence of a future shift in stand composition, as it is generally assumed that (in the absence of catastrophic disturbance) small, young understory trees will replace old, overstory trees as they die. The implications of this compositional transition are reduced abundance of pine and oak species, and the elimination of pine-oak stands as a landscape feature in the southern Appalachians.

3. Compositional change is similar at both study sites, but the timing of the shift in species composition differs between sites.

The temporal pattern of transition from pine and oak to maple and blackgum is different between stands in Virginia and Georgia, and within each study area the pattern is consistent across compositional groups. In both sites, pine and oak establishment peaked 80 to100 years ago and then began a decline. In Virginia, this peak of oak and pine establishment coincided with a peak in the establishment of shade-tolerant hardwoods, but in Georgia a peak in hardwood recruitment occurred more recently (60 to 80 years ago). The distinctly different modes of transition may be related to the collapse of American chestnut, a former foundation species in Appalachian forests that experienced a rapid, catastrophic dieback. The difference in chestnut abundance or the timing of dieback between sites may explain the temporal differences in compositional transitions, but this was not explicitly tested by our research.

4. Few differences in seedling/sapling establishment exist between Virginia and Georgia stands.

Regeneration of pine and oak species was extremely limited in Virginia and Georgia, and few significant differences in seedling or sapling establishment exist between sites. No Table Mountain pine saplings were counted in Georgia, and no pitch pine saplings or Table Mountain pine seedlings were counted in either study area. Red maple had the most prolific regeneration of any species surveyed. The pattern of regeneration considered with age distributions of species suggest that the reduction of pine-oak stands in the southern Blue Ridge region is likely.

5. Stand composition along environmental gradients does not reflect an ecological amplitude pattern.

One interpretation of the ecological amplitude paradigm predicts that species near their range limits may occupy less stressful sites (e.g., a species near its southern range limit may be more likely to occupy north-facing aspects). Our results do not support this prediction because species tend to dominate stands with similar landscape positions at both study sites. Patterns of species composition are generally similar in both study areas, and they appear to be responding to similar environmental gradients. Although not all compositional groups are completely comparable between Virginia and Georgia, stands dominated by certain species tend to occupy similar regions of ordination space. For example, Table Mountain pine dominates the most xeric positions in both study sites. After Table Mountain pine, pitch pine stands tend to occupy

the next driest locations, followed closely by chestnut oak and distantly by red maple and eastern white pine.

6.5 Recommendations for future research

This research has demonstrated that tree-ring data are well suited for broad-scale analysis of biogeographic trends related to the variability of tree growth and establishment across space. Additionally, I have shown that very little evidence from these analyses supports the abundant center/ecological amplitude paradigm. Tree growth in response to climate variables was not related to geographic position at the scale of the geographic range of species, and patterns of establishment and stand composition at a range interior and range edge site were similar. Further research in this area is necessary to provide clearer understanding of the spatial variability of climate response and stand structure at broad spatial scales. Future research should particularly address: (1) the development of more refined models of species' range dynamics incorporating more accurate data on species' responses to climate; (2) the confounding effects of climate, land-use history, and disturbance on compositional and structural dynamics of forests; and, (3) the role that tree mortality plays in the range dynamics of individual tree species and changes in stand composition.

In this dissertation, I have shown that both the growth response of trees to monthly climate variables and the overall climate sensitivity of annual tree growth do not conform to the traditional assumptions of ecological amplitude. However, the research presented here focused only on three species—longleaf pine, eastern hemlock, and white oak. To accurately project

changes in the composition of forests throughout North America, research is needed on many other species. Moreover, information on growth and reproduction of trees in relation to climate need to be integrated with models of dispersal, species interactions, and land-use change to project future patterns of potential habitat for tree species. Such integrative models will move beyond the climate envelope approach that makes unsupported assumptions about the causal and direct control that climatic factors exert on species distributions.

Analysis of stand structure and composition can provide valuable insights into the dynamics of species' distributions and community composition. Identification of temporal patterns of tree establishment and recruitment to the canopy facilitates understanding of the biological and environmental processes that shape spatial patterns of forest dynamics. Quantifying changes in stand structure in response to changing climate, the collapse of populations of foundation species, and changes in land-use/land management are essential for accurate projections of future vegetation patterns. Collecting stand structure data is time-consuming and labor intensive, but these data are valuable for the wealth of spatial and temporal information they can provide. Furthermore, much research quantifying stand structure has already been conducted. The next step is to combine these studies in a comparative investigation of stand structure across regions or forest types. A comparison of stand structure across broad spatial scales and a diversity of land-use histories will facilitate the disentangling of confounding factors (e.g., climate, disturbance, land-use) on compositional shifts in forests.

An additional avenue of research that will provide crucial insights into spatial and temporal patterns of range dynamics is the use of dendrochronology to understand tree mortality across broad spatial scales. Tree mortality caused either by a pathogen affecting a single species or by a catastrophic disturbance affecting many species can contribute to rapid yet enduring changes in forest composition and structure. Mortality events near species' range limits can also result in long-lasting shifts in distributions of species. Although dendroecological analysis of tree mortality is not new, future research integrating networks of dendroecological data may enable the analysis of tree mortality and range dynamics over long temporal and spatial scales. Moreover, dendroecological analysis of mortality may provide an efficient complement to labor-intensive, time-consuming research involving censuses of tree mortality in long-term, permanent plots.

In early stages of this research, I attempted to reconstruct tree mortality by crossdating annual rings of remnant wood in study plots. However, the outermost wood of both standing dead trees and logs on the forest floor was too badly decayed to confidently assign dates of death to trees. Although rates of decay in the eastern deciduous forests may be too rapid to allow implementation of such a technique, research in other forest ecosystems (especially in more arid environments) is likely to be successful. Combining information on mortality with conventional stand structure data will enable more sophisticated analysis of spatial and temporal forest dynamics and lead to better understanding of the controls on geographic range limits.

Based on the analyses presented in this dissertation, I conclude that the related paradigms of ecological amplitude and abundant center do not characterize the spatial patterns of abundance and vitality of several dominant tree species of eastern North America. Spatial variability in the response of species to environmental controls is diverse, and accurate projections of future species distributions must account for this diversity of responses. Additionally, dendroecological approaches can provide a wealth of information on spatial and temporal variability of the interactions between trees and their environments. Since the development of the science of dendrochronology more than a century ago, the major contributions of the field have involved the application of dendrochronological techniques and theory to paleoclimatology and forestry. However, dendrochronological techniques can and should be more widely applied to the study of biogeography.

APPENDICES

Appendix A. Summary statistics for Marshal Forest Preserve longleaf pine chronology.

Seq	Series ID	First year	Last year	Number of years	Corr. with master	Mean ring width (mm)	Std. dev.	MS	Auto corr.
1	MFC25a	1758	2009	252	0.429	1	0.489	0.315	0.003
2	MFC25b	1757	2009	253	0.436	1.19	0.618	0.326	-0.029
3	MFC35a	1835	2009	175	0.624	1.1	0.526	0.293	-0.015
4	MFC35b	1823	2009	187	0.445	1	0.531	0.272	-0.01
5	MFC36a	1855	2009	155	0.61	1.64	0.852	0.321	-0.022
6	MFC36b	1856	2009	154	0.574	1.35	0.688	0.351	-0.007
7	MFC37a	1897	2009	113	0.56	0.92	0.406	0.357	0.002
8	MFC37b	1912	2009	98	0.572	0.94	0.403	0.267	0.01
9	MFC38a	1914	2009	96	0.577	2.09	0.967	0.338	-0.008
10	MFC38b	1918	2009	92	0.489	1.43	0.776	0.311	-0.105
11	MFC39a	1954	2009	56	0.538	1.86	0.852	0.349	0.012
12	MFC39b	1967	2009	43	0.483	1.84	0.775	0.32	0.021
13	MFC40a	1836	2009	174	0.515	0.74	0.363	0.267	-0.058
14	MFC40b	1840	2009	170	0.491	0.9	0.489	0.26	-0.022
15	MFC41a	1949	2009	61	0.678	2.6	1.538	0.316	0.022
16	MFC41b	1949	2009	61	0.677	1.57	0.905	0.294	-0.011
17	MFC42a	1816	2009	194	0.62	0.98	0.344	0.225	-0.029
18	MFC42b	1809	2009	201	0.6	1.3	0.566	0.319	-0.032
19	MFC42c	1774	2009	236	0.6	1.22	0.494	0.308	-0.023
20	MFC43a	1850	2009	160	0.66	1.11	0.701	0.349	-0.015
21	MFC43b	1874	2009	136	0.464	1.35	1.323	0.27	-0.018
22	MFC44a	1929	2009	81	0.431	0.74	0.468	0.369	-0.07
23	MFC44b	1948	2009	62	0.49	0.6	0.435	0.373	-0.092
24	MFC45a	1866	2009	144	0.652	0.83	0.447	0.282	-0.097
25	MFC45b	1859	2009	151	0.592	1.15	0.623	0.256	-0.011
26	MFC46a	1928	2009	82	0.502	1.8	0.754	0.323	0.023
27	MFC46b	1927	2009	83	0.568	1.42	0.59	0.321	-0.032
28	MFC47a	1910	2009	100	0.758	1.97	0.828	0.266	0.029
29	MFC47b	1924	2009	86	0.73	1.61	0.766	0.262	-0.05
30	MFC48a	1858	2009	152	0.657	1	0.416	0.274	-0.04
31	MFC48b	1855	2009	155	0.624	1.12	0.474	0.268	0.032
32	MFC50a	1878	2009	132	0.831	1.43	0.637	0.306	0.034

Appendix A. Continued

33	MFC50b	1862	2009	148	0.729	1.2	0.498	0.252	0.023
34	MFC52a	1857	2009	153	0.604	1.41	0.764	0.217	0.006
35	MFC52b	1871	2009	139	0.741	1.22	0.598	0.301	0.002
36	MFC53a	1904	1997	94	0.641	0.75	0.426	0.274	-0.011
37	MFC53b	1911	2009	99	0.488	0.66	0.205	0.254	-0.007
38	MFC54a	1851	2009	159	0.658	1.28	0.682	0.269	-0.028
39	MFC54b	1850	2009	160	0.639	1.5	0.578	0.299	0.012
40	MFC55a	1784	2009	226	0.559	1.02	0.493	0.291	0.027
41	MFC55b	1784	2009	226	0.457	1.01	0.592	0.309	0.013
42	MFC56a	1819	2009	191	0.521	0.78	0.555	0.246	-0.022
43	MFC56b	1818	2009	192	0.534	0.82	0.437	0.281	-0.02
44	MFC57a	1917	2009	93	0.651	1.9	0.926	0.258	0.068
45	MFC57b	1908	2009	102	0.616	2.51	0.939	0.252	0.011
46	MFC51a	1848	2008	161	0.548	0.99	0.571	0.281	-0.033
47	MFC51b	1849	2008	160	0.593	1.09	0.51	0.304	-0.001
Total or Mean				**6598**	**0.577**	**1.2**	**0.599**	**0.291**	**-0.012**

Correlation with master (Corr. with master) is the Pearson correlation coefficient of each individual series to the master chronology created with the remaining series. Other statistics describing tree ring series include standard deviation (Std. dev.), mean sensitivity (MS), and autocorrelation (Auto Corr.).

Appendix B. Location and mean sensitivity (MS) of white oak tree-ring chronologies.

Site Name	First year	Last year	Lat.	Long.	Dist. from range edge (km)	MS (all years)	MS (1800–1975)
Andrew Johnson Woods	1626	1985	40.88	-81.75	239.42	0.248	0.221
Babler State Park	1641	1980	38.60	-90.72	322.32	0.221	0.215
Backbone State Park	1735	1977	42.62	-91.57	194.46	0.238	0.243
Backbone State Park B	1730	1980	42.62	-91.57	194.46	0.213	0.205
Blackfork Mountain	1650	1980	34.72	-94.45	52.50	0.221	0.185
Buffalo Beats North Clay	1681	1995	39.45	-82.15	393.56	0.254	0.252
Buffalo Beats North Ridgetop	1856	1995	39.45	-82.15	393.56	0.278	0.29
Cameron Woods	1845	1980	41.65	-90.73	251.13	0.261	0.278
Cranbrook Institute	1581	1983	42.67	-83.42	90.55	0.186	0.152
Current River Natural Area	1636	1981	37.27	-91.27	268.35	0.226	0.214
Current River Natural Area Rec	1588	1992	37.25	-91.27	266.58	0.218	0.2
Dark Hollow Trail	1648	1977	41.42	-74.08	16.21	0.191	0.16
Davis Purdue-Glen Helen	1662	1985	39.90	-84.40	287.35	0.23	0.212
Dolliver Memorial State Park	1685	1981	42.38	-94.08	52.92	0.202	0.194
Duvick Backwoods	1654	1980	41.68	-93.68	135.49	0.266	0.283
Dysart Woods	1625	1998	39.98	-81.00	339.20	0.236	0.201
Ferne Clyffe State Park	1655	1981	37.53	-89.58	293.97	0.232	0.237
Fire Tower Road Cook Forest	1660	1981	41.32	-79.22	206.55	0.203	0.183
Fox Ridge State Park	1674	1980	39.42	-88.17	253.94	0.236	0.227
Geode State Park	1724	1984	40.83	-91.37	311.22	0.239	0.236
Giant City State Park	1652	1981	37.60	-89.20	310.69	0.23	0.222
Greasy Creek	1777	1982	37.72	-90.20	306.40	0.222	0.223
Hampton Hills	1770	1992	35.82	-78.68	151.22	0.228	0.234
Hutchenson Forest	1674	1982	40.50	-74.57	25.36	0.208	0.194
Hutchenson Forest Long Cores	1620	1982	40.50	-74.57	25.36	0.21	0.193
Jack's Fork	1776	1981	37.12	-91.50	259.77	0.218	0.224
Joyce Kilmer Wilderness	1641	1983	35.22	-83.97	400.77	0.175	0.158
Kankakee River State Park	1686	1980	41.22	-88.00	66.69	0.205	0.204
Kickapoo State Park	1670	1980	40.13	-87.75	168.44	0.235	0.253
Lacey-Keosauqua State Park	1715	1981	40.72	-91.97	259.72	0.244	0.219
Lake Ahquabi State Park	1574	1980	41.28	-93.58	139.59	0.234	0.245
Ledges State Park	1663	1981	42.00	-93.88	97.68	0.233	0.236
Lilley Cornett Tract	1660	1982	37.08	-83.00	507.84	0.213	0.192
Lincoln's New Salem State Park	1671	1980	39.97	-89.85	274.97	0.227	0.229
Linville Gorge	1617	1977	35.88	-81.93	369.66	0.202	0.167
Lower Rock Creek	1728	1982	37.50	-90.50	282.36	0.207	0.203
Magazine Mountain 1	1809	1967	35.18	-93.58	98.22	0.242	0.234
Mammoth Cave	1648	1966	37.18	-86.10	450.66	0.218	0.204

Appendix B. Continued

Mammoth Cave Recollect	1649	1985	37.18	-86.10	450.66	0.212	0.183
Merritt Forest State Preserve	1711	1980	42.70	-91.13	224.05	0.217	0.207
Montpelier Natural Landmark	1713	2000	38.20	-78.15	72.79	0.211	0.203
Mountain Lake Virginia	1552	1983	37.38	-80.50	285.12	0.205	0.166
Nine Eagles State Park	1672	1982	40.62	-93.90	96.02	0.239	0.245
Norris Dam State Park	1633	1980	36.22	-84.08	504.88	0.196	0.188
Palisades Kepler State Park	1770	1983	41.90	-91.50	240.38	0.222	0.233
Pammel State Park	1635	1981	41.28	-94.07	99.71	0.232	0.241
Patty's Oaks Blue Ridge Parkway	1569	1982	37.92	-79.80	220.73	0.181	0.148
Piney Creek Pocket Wilderness	1651	1982	35.70	-84.88	483.89	0.197	0.204
Pinnacle Point/Hawksbill Gap	1612	1981	38.50	-78.35	87.54	0.175	0.137
Platte Plains	1888	2002	44.72	-86.08	1.65	0.33	0.343
Pleasant Prairie	1807	2000	42.67	-87.90	9.46	0.271	0.255
Pulaski Woods	1692	1985	41.05	-86.70	72.48	0.215	0.192
Roaring River	1724	1982	36.60	-93.82	89.70	0.178	0.164
Sandwich	1807	1980	41.65	-88.58	84.08	0.226	0.23
Saylorville Dam	1654	1981	41.72	-93.70	131.74	0.223	0.223
Sipsey Wilderness	1679	1985	34.33	-87.45	230.32	0.204	0.18
Starved Rock State Park	1633	1980	41.30	-89.00	130.30	0.211	0.205
Sweet Briar College	1749	1998	37.55	-79.07	160.13	0.164	0.162
Van Buren	1870	1967	35.70	-94.32	48.97	0.231	0.232
Wegener Woods	1662	1982	38.65	-91.50	254.51	0.24	0.228
White Pine Hollow State Preserve	1631	1980	42.63	-91.13	226.78	0.218	0.198
Woodman Hollow State Preserve	1695	1979	42.42	-94.10	49.05	0.201	0.194
Yellow River State Forest	1651	1980	43.18	-91.25	195.21	0.208	0.195

Appendix C. Location and mean sensitivity (MS) of eastern hemlock tree-ring chronologies.

Site Name	First year	Last year	Lat.	Long.	Distance from range edge (km)	MS (all years)	MS (1800–1975)
Adirondack Mountain Reserve	1608	1981	44.13	-73.78	112.34	0.248	0.235
Alan Seeger Natural Area	1609	1981	40.67	-77.70	108.98	0.202	0.205
Alger County	1652	1983	46.32	-86.62	10.39	0.260	0.266
Bass Lake Peninsula	1595	1983	45.10	-88.88	54.67	0.302	0.300
Bear Run	1641	1981	40.88	-77.32	119.94	0.210	0.207
Bigelow Pond	1659	1985	41.95	-73.22	76.19	0.262	0.256
Bowater-Mersey	1572	1982	44.82	-64.00	16.38	0.232	0.225
Burling Tract	1742	1977	38.97	-77.20	6.80	0.222	0.221
Dale City	1780	1978	38.63	-77.30	3.73	0.239	0.246
Dingman's Falls State Park	1609	1981	41.22	-74.92	77.71	0.245	0.240
East Branch Swamp	1540	1981	41.33	-77.72	177.43	0.188	0.201
Ferncliffe Natural Area	1623	1981	39.83	-79.70	183.72	0.235	0.234
Gibb's Brook	1509	1981	44.22	-71.40	108.44	0.231	0.220
Granville Gulf	1670	1981	44.03	-72.83	164.03	0.234	0.232
Hemlock Cove Sunset Field	1531	1982	37.50	-79.52	16.92	0.216	0.222
Hemlocks Natural Area	1535	1981	40.23	-77.65	66.44	0.227	0.231
Hen Wallow Falls B	1793	1995	35.75	-83.23	30.56	0.243	0.248
Joyce Kilmer Memorial Fore	1784	1997	35.35	-83.92	31.56	0.242	0.241
Kelsey Tract	1560	1983	35.08	-83.18	7.41	0.234	0.231
Kit Springs Branch Nantaha	1660	1992	35.28	-83.93	36.76	0.187	0.192
Loon Lake	1570	1983	46.20	-89.30	72.38	0.338	0.340
Matawaumkeag	1697	1981	45.50	-68.28	90.77	0.247	0.253
Mohawk Trail	1697	1980	42.62	-72.97	146.00	0.265	0.263
Mohonk Lake Talus Slope	1626	1984	41.77	-74.18	54.32	0.212	0.214
Mount Rogers 3 Sites	1645	1982	36.67	-81.67	78.82	0.217	0.220
North Forty Tract	1650	1985	41.97	-73.22	77.93	0.232	0.233
Number Three Pond	1686	1981	45.32	-68.25	83.15	0.248	0.243
Pack Forest	1595	1976	43.55	-73.80	169.41	0.256	0.246
Pot Lake-Northwest Lake	1641	1982	45.17	-78.75	80.92	0.286	0.289
Presque Isle River	1444	1983	46.72	-89.97	2.67	0.285	0.268
Rainbow Falls Trail	1685	1995	35.67	-83.50	22.15	0.227	0.222
Ramseys Draft	1660	1978	38.30	-79.35	63.21	0.202	0.203
Ramseys Draft Recollection	1595	1981	38.33	-79.33	65.20	0.196	0.200
Reed Pond	1639	1986	46.23	-69.00	126.24	0.280	0.273
Reviere du Moulin	1524	1982	46.63	-71.88	3.65	0.280	0.258
Rickett's Glen State Park	1637	1981	41.37	-76.30	167.88	0.234	0.250

Appendix C. Continued

Roaring Brook Keene Valley	1599	1978	44.13	-73.75	113.82	0.295	0.275
Rock Rift Road Mohonk Lake	1658	1986	41.77	-74.17	53.85	0.237	0.238
Salt Point	1510	1983	46.47	-84.87	2.68	0.272	0.271
Salt Springs State Park	1619	1981	41.87	-75.88	171.01	0.223	0.233
Savage Gulf	1610	1985	35.45	-85.57	14.99	0.247	0.246
Shenandoah National Park	1756	1997	38.47	-78.47	14.65	0.270	0.262
Silver River	1635	1983	46.70	-88.75	26.11	0.287	0.291
Sipsey River	1800	2007	33.75	-87.67	23.47	0.240	0.240
Spruce Glen	1511	1984	41.77	-74.18	54.32	0.220	0.235
Sweetroot Natural Area	1612	1981	39.83	-78.52	106.31	0.257	0.260
Tionesta Natural Area	1425	1978	41.75	-78.97	81.33	0.197	0.205

Appendix D. Example R code for conducting cluster analysis and detrended correspondence analysis of tree species' importance values in plots.

```
# Cluster Analysis and DCA ordination on stand structure plots
# from pine-oak stands on Jefferson National Forest, VA
# John Sakulich
# 5 February 2011

# Cluster analysis using Ward's method
setwd('C:/R/StandStructure')
library(cluster)
jnf.iv <- read.table('JNF_IV.txt', row.names=1, header = TRUE)
names(jnf.iv)
jnf.clstr <- agnes(jnf.iv, metric='euclidean', method='ward', stand=TRUE)
names(jnf.clstr)
plot(jnf.clstr, which.plots=2, main='Dendrogram of Plots')


# DCA Ordination
setwd('C:/R/StandStructure')
library(vegan)
jnf.iv <- read.table('JNF_IV.txt', row.names=1, header = TRUE)
names(jnf.iv)

# Specify DCA
jnf.dca <- decorana(jnf.iv)

# Alternate approach: specify DCA with downweighting of rare taxa
jnf.dca.dw <- decorana(jnf.iv, iweigh=1)


# Investigate DCA axes and scores
names(jnf.dca)
summary(jnf.dca)
plot(jnf.dca)

# Extract plot DCA scores from first two axes (1&2)
jnf.dca.scores <- jnf.dca$rproj[ ,1:2]


# Run correlation analysis between environmental
# variables (e.g., slope aspect, position, elevation) and DCA axes
setwd('C:/R/StandStructure')
jnf.envt <- read.delim('JNF_envt_dca.txt', header = TRUE)
names(jnf.envt)
attach(jnf.envt)
cor.mat <- cor(cnf.envt, method = 'pearson')
cor.mat.sig <- cor.test(cnf.envt, method = 'pearson')

# Plot DCA scores with symbols indicating importance value groups
plot(DCA1, DCA2, type="n", xlab="DCA Axis 1", ylab="DCA Axis 2", main="Sample
Scores by Compositional Group")
points(DCA1[Comp_Grp=='1'], DCA2[Comp_Grp=='1'], col=1, pch=1, cex=1.5)
```

Appendix D. Continued

```
points(DCA1[Comp_Grp=='2'], DCA2[Comp_Grp=='2'], col=1, pch=17, cex=1.5)
points(DCA1[Comp_Grp=='3'], DCA2[Comp_Grp=='3'], col=1, pch=16, cex=1.5)
points(DCA1[Comp_Grp=='4'], DCA2[Comp_Grp=='4'], col=1, pch=6, cex=1.5)
points(DCA1[Comp_Grp=='5'], DCA2[Comp_Grp=='5'], col=1, pch=3, cex=1.5)

# Compute correlations and store in correlation matrix, only matrix entries
# above main diagonal is filled in
dca.cor <- matrix(-1,nrow=8,ncol=2) #correlation matrix
dca.sig <- matrix(-1,nrow=8,ncol=2) #correlation significance matrix
x<-cor.test(DCA1,Comp_Grp)
dca.cor[1,1] <- x$estimate
dca.sig[1,1] <- x$p.value
x<-cor.test(DCA1,Elev_m)
dca.cor[2,1] <- x$estimate
dca.sig[2,1] <- x$p.value
x<-cor.test(DCA1,TRMI_config)
dca.cor[3,1] <- x$estimate
dca.sig[3,1] <- x$p.value
x<-cor.test(DCA1,TRMI_pos)
dca.cor[4,1] <- x$estimate
dca.sig[4,1] <- x$p.value
x<-cor.test(DCA1,TRMI_asp)
dca.cor[5,1] <- x$estimate
dca.sig[5,1] <- x$p.value
x<-cor.test(DCA1,TRMI_steep)
dca.cor[6,1] <- x$estimate
dca.sig[6,1] <- x$p.value
x<-cor.test(DCA1,TRMI)
dca.cor[7,1] <- x$estimate
dca.sig[7,1] <- x$p.value
x<-cor.test(DCA1,Pos)
dca.cor[8,1] <- x$estimate
dca.sig[8,1] <- x$p.value
x<-cor.test(DCA2,Comp_Grp)
dca.cor[1,2] <- x$estimate
dca.sig[1,2] <- x$p.value
x<-cor.test(DCA2,Elev_m)
dca.cor[2,2] <- x$estimate
dca.sig[2,2] <- x$p.value
x<-cor.test(DCA2,TRMI_config)
dca.cor[3,2] <- x$estimate
dca.sig[3,2] <- x$p.value
x<-cor.test(DCA2,TRMI_pos)
dca.cor[4,2] <- x$estimate
dca.sig[4,2] <- x$p.value
x<-cor.test(DCA2,TRMI_asp)
dca.cor[5,2] <- x$estimate
dca.sig[5,2] <- x$p.value
x<-cor.test(DCA2,TRMI_steep)
dca.cor[6,2] <- x$estimate
dca.sig[6,2] <- x$p.value
x<-cor.test(DCA2,TRMI)
```

Appendix D. Continued

```
dca.cor[7,2] <- x$estimate
dca.sig[7,2] <- x$p.value
x<-cor.test(DCA2,Pos)
dca.cor[8,2] <- x$estimate
dca.sig[8,2] <- x$p.value

# Convert DCA correlation and significance matrices to data.frames
row.label <- c('Comp_Grp', 'Elev_m', 'TRMI_config', 'TRMI_pos', 'TRMI_asp',
'TRMI_steep', 'TRMI', 'Pos')
col.label <- c( 'plot.var', 'DCA1', 'DCA2')
dca.cor.df <- as.data.frame(dca.cor, row.names=row.label,
col.names=col.label)
dca.sig.df <- as.data.frame(dca.sig, row.names=row.label,
col.names=col.label)
```

VITA

John B. Sakulich earned a Bachelor of Science degree in geography with a concentration in physical and environmental geography from the Pennsylvania State University in 2002. He received a Master of Science degree from the Department of Geography at Penn State in 2004. His thesis research investigated fire history and stand dynamics of high-elevation, mixed-conifer forests of Guadalupe Mountains National Park in west Texas. From 2005 to 2007, he worked as a Senior Research Staff Assistant in the Tree-Ring Laboratory at the Lamont-Doherty Earth Observatory, where he carried out fieldwork and laboratory analysis of tree-ring data from the Indonesian Archipelago to reconstruct variability in climatic variables associated with the Asian Monsoon. In 2011, he was awarded the Doctorate of Philosophy in geography by the University of Tennessee. While pursuing the doctorate, he worked as a Graduate Teaching Associate and Graduate Teaching Assistant in the Department of Geography, served as a Graduate Fellow for the University of Tennessee Earth Project funded by the National Science Foundation, and worked as a Graduate Research Assistant for the Initiative for Quaternary Paleoclimate Research. After graduation, John accepted a job as an assistant professor in the Department of Biology at Regis University in Denver, Colorado.