LONG-TERM TEMPORAL DYNAMICS OF THE DUKE FOREST

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ABSTRACT

Christopher Joseph Payne: Long-term temporal dynamics of the Duke Forest
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In this dissertation, I describe a series of permanent sample plots in the North Carolina Piedmont used to examine near-century forest processes and to evaluate how observed trends can inform existing conceptual models. Specifically, 80 years of tree growth and forest composition were recorded across all succession phases in a series of successional *Pinus taeda* stands and second-growth *Quercus-Carya* and *Liriodendron-Liquidambar* hardwood stands in the Duke Forest. I use these long-term data to scrutinize classical theories of community dynamics and growth trends in Piedmont forests that have served as a model system for successional research for nearly 100 years. Specifically, using a suite of multivariate statistics I examine whether old-field pine forests have succeeded toward putative climax compositions or whether deviations in successional trajectories have occurred owing to shifts in species composition and disturbance events. I additionally examine whether biomass of successional stands can be predicted based on canopy mortality and lags in regeneration and whether growth rates of later-stage forests have increased more than expected over the last century. 80-year biomass and growth trends in successional plots confirm the importance of canopy density and mortality in driving these patterns, but lag patterns in post-hurricane regeneration are not yet formally discernible. In contrast, second-growth hardwood plots demonstrate consistent biomass accumulation and continued increases in growth rate, despite having achieved biomass levels found in more static old-growth forests. Community analyses indicate that successional stands experienced shifting compositional trajectories that were accelerated by Hurricane Fran and resulted in replacement of upland-associated hardwood species (e.g., *Cornus florida*) with species associated with more mesic stands (e.g., *Acer rubrum, Liquidambar styraciflua*, and *Fagus grandifolia*). A similar replacement of putative climax species (e.g., *Quercus alba*) with *A. rubrum* occurred in understories of late-successional hardwood stands. In contrast with accepted successional models, these results are in line with mounting evidence of unanticipated and less predictable forest dynamics over the last century. Such changes could be the result of changing climate patterns or anthropogenic impacts. Regardless, more mechanistic experiments must be developed to determine the cause of these seemingly-widespread patterns to better inform global change and forestry models.

In loving memory of my grandfather, Joseph A. Bugica, who provided me with so many early outdoor experiences and countless scientific conversations. You truly cultivated my curiosity for science, and these experiences helped shape my fascination with the environment.
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LIST OF ABBREVIATIONS AND SYMBOLS

(d/c/m) m	(deci/centi/milli) meters
°C	Degrees Celsius
AIC	Akaike Information Criterion
BA	Basal Area
BH	Breast height (1.37 m)
BIC	Bayesian Information Criterion
CC	Condition code
CO_2	Carbon dioxide
COS	Cosine
DBH	Diameter at breast height
Ft.	Foot (US Standard unit of length)
(M) g	Grams
GIS	Geographic Information System
h	Height
ha	Hectares
ID	Identification number

MAP	Mapped permanent sample plot
n	Sample size
NMDS	Nonmetric Multidimensional Scaling
PCA	Principle Components Analysis
Ppm	Parts per million
PSP	Permanent Sample Plot
r	Radius
R^2	Explanatory Power (coefficient of determination)
SG	Specific Gravity
SPEC	Species code (4-letter)
SPEI	Standardized Precipitation-Evapotranspiration Index
T_{asp}	Transformed Aspect
TEC	Total Exchange Capacity (cation + anion exchange capacities)
USDA	United States Department of Agriculture
USGS	United States Geological Survey
V_p	Parabolic Volume
WD	Wood Density (g/cm^3)

CHAPTER 1: INTRODUCTION

For more than a century, succession has been a focal point in plant ecology and has proven useful as an organizational scheme, as a context for generating and testing numerous ecological concepts, and as a predictive tool (Peet & Christensen 1980, Peet 1992). The predictive ability is increasingly pertinent for understanding the ecological consequences of global change.

Early successional observation and research (e.g., Cowles 1899, 1901, 1911, Clements 1916, 1928, Gleason 1926, Wells 1942, Egler 1954, Odum 1969) – including extensive work in the North Carolina Piedmont (e.g., Billings 1938, Oosting 1942, Kozlowski 1949, Keever 1950, Bormann 1953) – established general successional trends and theories for the field. However, more recent work (e.g., Drury & Nisbet 1973, Pickett 1976, Connell & Slatyer 1977, Pickett et al. 1987a, 1987b, Pickett & McDonnel 1989, van der Maarel & Sykes 1993, and various papers by Peet and Christensen: Christensen 1977, Peet & Christensen 1980, 1988, Christensen & Peet 1981, 1984, Peet 1981, 1992, Peet et al. 2014) have focused instead on empirically and experimentally examining and building on early theories and models in search for underlying mechanisms of succession. These more recent efforts revealed succession to be more complex than the foundational work suggested. Further, this contribution of reductionist, mechanistic-focused research – along with alternative mechanistic concepts proposed by Grime (1977, 1979), Tilman (1985), Huston & Smith (1987), and Smith & Huston (1989) – directed the field toward reevaluating concepts of classical succession in search for a more unifying and generalizable theory of succession. Peet and Christensen (e.g., Peet & Christensen 1980 and Peet 1992) effectively captured the efforts of many of the reductionist approaches that came out of this mid-to-late century work in their reductionist, population-based approach to understanding succession. Specifically, their approach was to explain successional change at the community (or even ecosystem) level as a consequence of population processes in which variation in rates of reproduction, establishment, growth and mortality of individuals strongly influence community-level properties of succession.

Peet (1992) further broke this down by theorizing that secondary succession can be understood as a combination of two sets of linked processes: as a gradient-in-time (*sensu* Whittaker 1953; also see Pickett 1976, 1982) of physiological and life-history characteristics adapting to variable environments, and as a community undergoing competitive-sorting (*sensu* Margalef 1963, 1968) to produce a temporal gradient of increasing community organization and predictability. Although these processes can result in a "climax" community, both short-term and long-term environmental change can impact what that community looks like. This is made evident, for example, by pollen deposit studies (e.g., Davis 1981 and Huntley & Birks 1983) and climate change studies (e.g., Kullman 1987, 1988) that document long-term changes in regional vegetation.

Disturbance events (both local events such as tree mortality and larger events such as wind storms, fire, drought, ice, etc.) can both drive and reinitiate successional sequences (e.g., Bormann & Likens 1979, Turner et al. 2008). Large, episodic events are more likely to initiate drastic changes in a successional sequence, while more continuous events (e.g., individual tree mortality) are likely to expedite the current successional trajectory. However, as both can impact the short-term and long-term environmental characteristics experienced by succeeding plant communities, all scales of disturbance should be considered when analyzing plant community dynamics.

Although new approaches and models proposed as a result of the pulse of mid-to-late-twentieth century research (see Peet & Christensen 1980 for a summary) predicted significant changes and variations in eastern forests, research completed in the last 30 years has demonstrated further complexities in understanding succession. Some of this research has improved our understanding of the effects of land-use history (Dupouey et al. 2002, Taverna 2004, Flinn & Vellend 2005), latitudinal variation (Wright and Fridley 2010) and both small-scale (Palmer 1990) and large-scale (Fridley & Wright 2012) variations in soil properties on patterns of plant dynamics.

Additional research in the last 30 years has demonstrated novel changes in eastern forests that are not inherent in previous models or descriptions of climax communities. Specifically, some studies have shown unprecedented compositional changes and decreases in putative climax species (Abrams & Downs 1990, Abrams 1998, Golubiewski & Urban 1998, Shumway et al. 2001, McDonald et al. 2002, 2003, Abrams 2003, Taverna et al. 2005, Schwartz 2007, Woods 2007, Israel 2011, Peet et al. 2014; including those owing to more than a century of fire suppression: Abrams & Nowacki 1992 and Nowacki & Abrams 2008), shifts in biomass and productivity trends (Myneni et al. 1997, Boisvenue & Running 2006, McMahon et al. 2010 – though see Foster et al. 2010 – , Phillips & Lewis 2014, and Pontius et al. 2016), increasing populations of white-tailed deer (*Odocoileus virginiana*) and subsequent impacts on plant communities (Stromayer & Warren 1997, Abrams 1998, Russell et al. 2001, Horsely et al. 2003, Côté et al. 2004, Keyser et al. 2005, Rossell et al. 2005, Israel 2011, Kribel et al. 2011, White 2012, J. Clark pers. comm.), increases in exotic species and their impacts on native flora (Lovett et al. 2006, Israel 2011, and Luken 2014), and multi-year impacts due to major disturbances (e.g., hurricanes; see Xi et al. 2008, 2012, Xi & Peet 2011).

It is unclear from this recent research whether additional successional mechanisms need to be considered, whether roles of disturbances and human land-use in successional timelines need to be reevaluated, or whether global change has and will continue to alter vegetation dynamics in unpredictable ways. Further, recent research (Israel, 2011) suggests that a number of these changes, at least those occurring in the southeastern U.S., are occurring at an increasing rate as compared to just a decade ago. Consequently, it is imperative to develop a better understanding of these recently-recognized complexities, which are potentially arising from the interaction of successional processes with novel exogenous factors, including those resulting from global change. These complexities, however, are difficult to parse without long-term, frequent examination of forests.

Long-term studies

To understand succession, it is necessary to first identify the underlying patterns of community change through time (Cadenasso et al. 2008). Any subsequent understanding of underlying mechanisms and potential applications (e.g., use as a predictive tool for management) rely on a clear understanding of these patterns. The traditional method for determining patterns of change, still widely used today, is examination of chronosequences employing a space-for-time substitution. However, these studies make a series of assumptions (e.g., see Pickett 1989, Pickett et al. 2001, Cadenasso et al. 2008) that, if not met, preclude the ability to accurately predict successional change. In fact, there was recognition over thirty years ago that this approach can provide limited or misleading information concerning the nature of successional change and effectively no information concerning the extent and nature of variability in the process (Christensen & Peet 1981). More recent empirical work also calls into question the validity of assumptions derived from chronosequence research (see Johnson & Miyanishi 2008). The continued use of chronosequences has been necessary for successional studies due to the paucity of long-term resampling data. However, future work will have to rely more on such long-term resampling efforts (including those that integrate many fields of study; Kampe et al. 2010) to effectively understand the complexities of succession and long-term ecological dynamics in general (Franklin 1989 and Rees et al. 2001).

Long-term resampling studies are unique in that they can track forest change directly instead of inferring change from stand characteristics or dendrochronological studies. These types of studies can incorporate fine-scale spatio-temporal structure, heterogeneity, and spatially-explicit processes (aspects that chronosequences, as well as other often-utilized approaches such as model simulations and idealized theoretical models, lack or ignore; Pickett et al., 2001). Long-term resampling studies further benefit from their ability to capture periodic events or system shifts (e.g., hurricanes and droughts) that may play a significant role in forest dynamics (Woods 2004, Cadenasso et al. 2008, Xi & Peet 2011). Without extensive pre- and post-disturbance data, it is almost impossible to understand the long-term impacts of unpredictable, mid-successional disturbances that otherwise play an important role in creating a mosaic of early and late successional communities throughout forest regions (Pickett & White 1985). Finally, long-term resampling efforts can allow for improved understanding of decadal climate variation on successional trajectories. This understanding is imperative for a successional framework to be truly useful as a predictive tool, especially in the face of significant impacts due to a changing climate (IPCC 2014).

Although ideal for successional studies, long-term resampling projects are difficult and expensive to establish and maintain. Some exceptions include federally-funded programs such as the Long-Term Ecological Research (LTER) program, Long Term Research in Environmental Biology (LTREB) program, National Ecological Observatory Network (NEON), Smithsonian Center for Tropical Forest Science (CTFS), and the Forest Inventory and Analysis Program (FIA) of the U.S. Forest Service. Additional government-funded programs include networks in Australia (the Australian SuperSite Network; Karan et al. 2016) and China (Chinese Ecosystem Research Network; Fu et al. 2010). Ryan et al. (2017), however, acknowledge that a truly useful network of long-term studies must expand beyond a small number of large programs and include a much more extensive network driven by the work of college professors and amateur scientists (e.g., individual researchers, students, citizen scientists, etc.).

Another historical barrier that has impeded the existence of more long-term studies to date is that benefits of such studies can only be realized as the result of insight from research initiatives taken place before many of today’s successional complexities were well known or understood. As a result, those long-term studies that do exist rarely span greater than 20-30 years. Moreover, many of the longer-running long-term studies have involved few (< 5) resampling efforts, potentially resulting in an inability to capture both fine-scale and longer-term dynamics. Some such existing long-term studies include: Bartlett Experimental Forest permanent plots (established 1931; Filip et al. 1960, Leak 1970, Leak & Filip 1977), Bartlett Experimental Forest inventory plots (est. 1931; Pontius et al. 2016), Porcupine Mountains permanent plots (1981; Frelich and Lorimer 1991, Lorimer et al. 2001, Lorimer & Halpin 2014, Halpin & Lorimer 2016), Lady Park Wood permanent transects (est. 1945; Peterken & Jones 1987, 1989), NYBG Forest inventory surveys (est. 1930’s; Rudnicky & McDonnell 1989), Heart’s Content plots (est. 1929; Lutz 1930, Whitney 1984, Rooney & Dress 1997), T.T. Munger Research Natural Area plots (est. 1947; Franklin & DeBell, 1988), Harvard Forest hurricane-damaged permanent plots (est. 1940; Hibbs 1983), and a series of permanent plots associated with the H. J. Andrews LTER program (est. 1910-1989; see Acker et al. 1998 and Acker et al. 2000).

A few quantitative, plot-based studies spanning greater than 30 years with a greater number of sampling efforts do exist. These few extant studies span early stages of post-disturbance succession (Buell-Small Succession Study; est. 1958; see Cadenasso et al. 2008 for examples of previous work), aggrading, transitional and intermediate stages of succession (Duke Forest permanent sample plots; est. 1933 and later; see Xi et al. 2008 for list of previous publications), and dynamics of old-growth forests (Huron Mountains study site; est. 1962; Woods 2000a and Dukes Research Natural Area; est. 1935; Woods 2000b, 2004, 2007).

One of the longest spanning resampling projects examining individual tree growth in temperate forests consists of a series of permanent sample plots in the Duke Forest of the North Carolina Piedmont (with many plots established in the 1930's). The Duke Forest and the adjacent Piedmont landscape have long been used as a model system to study and explain secondary succession, so it is of no surprise that projects associated with these data have generated a substantial quantity of significant literature (e.g., see Xi et al. 2008 for examples), including work that has examined more than 50 years of resampled data (e.g., Christensen & Peet 1981, Golubiewski & Urban 1998, Peet et al. 2014). However, there are still no studies that have tracked forest dynamics of individual temperate forest stands across the entire successional sequence from old-field to mature hardwood forest. Specifically, there is still a lack of population data from a continual resampling study through the later stages of the successional transition phase (see Bormann & Likens 1979, Peet & Christensen 1987, and Peet 1992 for description of phases). Access to such continuous, extensive data is necessary for parsing out long-term successional dynamics from external factors while simultaneously examining the effects of disturbances on successional patterns and processes.

Current study

This dissertation is unique in that I have extended the long-term dataset of the Duke Forest used by Peet, Christensen, Xi and others to now span 80 years of resampled forest growth data for stands across a broad range of initial ages and site conditions. The dataset now spans the successional sequence through the transition phase of a number of successional pine plots and includes upwards of 80 years of data for later-stage hardwood ("climax") dynamics as well. Given this data opportunity, I am equipped to examine the complex compositional and community trends of these Piedmont forest plots in the context of a nearly complete successional trajectory that captures the transition of these stands from young even-aged pines to mixed hardwood communities. Further, I can examine these trends within the backdrop of a century marked by significant climatic, environmental, and ecosystem change.

The objectives of this dissertation, therefore, are to examine the long-term temporal dynamics of successional and late-stage eastern deciduous forests in the Piedmont of the southeastern United States and to determine whether these trends conform to traditional theoretical and observational theories or whether they appear to corroborate novel changes observed throughout eastern forests during the last 30 years. Specifically, this dissertation examines long-term trends in forest composition structure and growth patterns across all stages of succession in the Duke Forest through the exploration of the following key questions:

1. What are the long-term patterns of biomass accretion and forest growth rate in successional pine forests, and do these patterns conform to existing theoretical models

that predict mortality, pine density, and lag in forest regeneration as major drivers of successional trends?

2. Do biomass accretion trends in established, mixed-age hardwood forests dispute equilibrating patterns expected by theoretical models and continue to aggregate similar to recently published trends, and, if so, do the observed patterns seem to be driven by increasing forest growth rates?
3. What is the long-term trend of tree species community composition throughout the course of secondary succession, and do successional trajectories conform to the predictions of classical, early-20th-century models or reflect more recently published trends?
4. What species-specific and environmental patterns appear to be driving larger community trends observed in the Duke Forest, and how do these drivers inform future study of forest dynamics in a changing world?

Questions 1 and 2 are addressed in Chapter 5 of this dissertation. Specifically, Chapter 5 examines the trends in biomass accretion, accretion rate, and growth rate of successional and hardwood forests in the Duke Forest and explores through the use of mixed models what characteristics of the forest best explain the trends observed. Questions 3 and 4 are addressed in Chapter 6. The analyses in Chapter 6 employ a suite of visual and multivariate statistical approaches to characterize the complex forest systems and explore underlying explanations of the dynamics observed. The remaining chapters are dedicated to characterizing the unique Duke Forest permanent sample data used to address this dissertation’s research questions.

Long-term research initiatives are innately linked to the system in which the study was established. Further, long-term research is unavoidably marked by a rich and complex history of sampling efforts, data intricacies, protocol nuances, personnel changes, and countless ancillary occurrences and objectives that arise with unforeseen natural circumstances. As such, a thorough characterization and understanding of the Duke Forest is necessary in guiding this dissertation's analyses. Chapter 2 serves the primary role in this dissertation of documenting and describing in detail the long-term permanent sample plot data from the Duke Forest (and nearby G. W. Hill Forest) that inform most of this dissertation's analyses. Chapter 3 provides a similar role for a second Duke Forest dataset containing larger permanent plots that served as a validation dataset in this dissertation's analyses and could be used to extend the analyses described in Chapters 5 and 6. Chapter 4 introduces an interactive web application I built to explore the complex data in Chapters 2 and 3 in the context of ecological community analyses and which helped to inform the questions asked in subsequent chapters described above.

Overall, this dissertation utilizes the unique longevity of individual tree-growth data present in the Duke Forest (and nearby associated forests) to explore long-term forest dynamics that have been traditionally characterized using less direct approaches such as chronosequences and predictive computer models. In this way, this dissertation provides directly-resampled, long-term evidence to inform our understanding of forest dynamics within the context of a growing body of literature that questions traditional hypotheses in the face of global change.

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CHAPTER 2: LONG-TERM PERMANENT SAMPLE PLOTS IN DUKE FOREST, NORTH CAROLINA: 80 YEARS OF INDIVIDUAL TREE GROWTH DATA

Summary

I describe a data set of tree inventory and growth collected across 80 years in mapped permanent sample plots in the Duke Forest and nearby Hill Forest both located in the northeastern North Carolina Piedmont, USA. The purpose of these data is to document long-term trends in forest composition and dynamics. There are thirty-seven extant plots (405 – 1940 m^2) that were established in the 1930s (n = 34) and 1940s (n=3) that have each been sampled 12 – 16 times with between-sample periods ranging from 2 – 23 years. Twenty-eight plots represent successional old-field pine (primarily *Pinus taeda*) stands with known age and stem density at plot establishment. These stands vary in age since initial post-abandonment pine growth (9 – 30 years) and initial stem density (600 – 29000 stems/ha) and are currently at varying levels of transition to hardwood forests. The remaining nine plots represent relatively “mature” hardwood forests that have been mixed-aged hardwood stands since plot inception 70 – 80 years ago. Two of the plots represent bottomland hardwood communities, while the remaining are representative of upland oak-hickory stands with various soil properties. Diameter and height measurements of stems individually identified to species allows for direct quantification of stand growth and development. Additionally, records of tree condition permit accounting for tree damage and mortality, especially in relation to experimental manipulations in some plots prior to 1960 and damage that resulted from two hurricanes (Hurricane Hazel in 1954 and Hurricane Fran in 1996) that variously impacted plots. Soils were collected for each plot in 2016 and analyzed for nutrients, pH, soil texture and organic matter. The described data have previously been used to examine tree population processes, predictability and convergence in composition, mechanisms of tree competition, patterns of mortality, changes in biomass and production, changes in genetic structure, impacts of land use legacies, and impacts of hurricanes and wind events on long-term forest dynamics. The unprecedented temporal length of the data will continue to be critically important for investigation of long-standing, unconfirmed theories regarding succession and for parsing novel trends in Piedmont forest dynamics from theoretical predictions.

Key words

Permanent sample plots, longitudinal study, secondary succession, Piedmont, North Carolina, forest, tree growth.

Introduction

Individual tree growth data have been methodically collected from permanent sample plots (PSPs) in North Carolina Piedmont forests for periods of up to 80 years. Specifically, these data document long-term forest growth and dynamics in the Duke Forest and the nearby G. W. Hill Forest in Orange and Durham Counties, North Carolina, USA from 1933 through 2013. This data chapter serves to explain and document these data, which are available in supplementary files included with this dissertation with file names provided throughout this chapter.

Professors Clarence F. Korstian and Theodore. S. Coile of the Duke School of Forestry initially directed the Duke Forest PSPs project and established 87 plots between 1933 and 1936 of which 34 are still actively sampled and included as part of these data. Korstian established the plots to monitor tree growth and species composition changes within stands of various age and site condition and subject to various silvicultural management practices. To achieve these goals, some Duke Forest plots were experimentally manipulated in the 1930s through 1950s, primarily in the form of various thinning treatments. The three Hill Forest plots included in this data set were established in 1946 and 1947 and underwent no documented experimentation or other manipulation. Robert K. Peet and Normal L. Christensen relocated and resurveyed the plots between 1977 – 1984, and they turned the focus of the plots towards long-term observation of forest dynamics. Peet & Christensen directed the project from 1977 through 1993, and Peet and Dean L. Urban directed the project from 1997 onward. Plots were resurveyed approximately every five years during these periods. Weimin Xi recorded damage from Hurricane Fran (1996) during the 1997 – 1998 resurveys. Xi resurveyed the Duke Forest plots again in 2000 – 2001, and I resurveyed the plots again in 2012 – 2013. Hill Forest plots were last sampled in 2001. I collected soil data in the winter of 2015–16 and prepared all data for publication and archiving. All plots are expected to be resampled in the future.

The data presented in this chapter represent one of the longest-running permanent sample plot studies of individually-sampled forest communities currently in existence. The unprecedented temporal length of the data and the coverage of data across all stages of succession are critical for examining long-standing, unconfirmed theories regarding trends in successional biomass, growth and community dynamics. Further, the frequent resampling of these forest data in the context of unprecedented environmental and ecosystem changes (e.g., climate change, fire suppression, and shifting herbivory pressure) allows for parsing of novel trends in Piedmont forest dynamics from successional dynamics. As such, these data are used extensively to answer a suite of questions regarding long-term successional trends in the analytical chapters of this dissertation (see Chapters 5 and 6).

Site description

Geology and history

The Piedmont is a physiographic province (Fenneman 1916, 1928) and Level III Ecoregion (Wiken et al. 2011 and U.S. EPA 2013) that comprises a plateau between the Atlantic Coastal Plain and the Blue Ridge Mountains of the eastern United States. The Piedmont extends as far North as New Jersey with the majority of the province spanning the central portion of the Southeastern states of Virginia, North Carolina, South Carolina, Georgia, and Alabama. The widest portion of the Piedmont, located in North Carolina, has elevation typically between 60–210 m (Golubiewski & Urban 1998) and has a gently rolling to flat topography with a few steep-sided peaks of greater elevation. The Duke Forest and nearby G. W. Hill Forest are located in the northeastern portion of the North Carolina Piedmont. The study areas are in Orange and Durham Counties, which rest primarily on two major geologic formations: the Carolina Slate Belt and the Triassic Basin. These parent rocks have largely weathered to low-nutrient soils that physically vary from sandy to silty to heavy clays.

The Triassic Basin bedrock is composed mainly of shales, sandstones, and siltstones. Soils are predominately heavily weathered Ultisols and Alfisols with high clay content in the subsoil. Higher fertility sandy or silty sediment overlies alluvial areas. The Slate Belt bedrock consists mainly of fine-grained felsic metamorphic rocks (i.e., bedded argillites, felsic and mafic volcanics and schists) predominated by Carolina slate but with occasional diabase or basalt intrusions (Bain 1966 and Daniels et al. 1999; which also occur in the Triassic Basin). Most soils in the Slate Belt have deep silt loam surfaces containing high concentrations of silt (~30%) and sand, with numerous soil types having red clay subsoil dominated by kaolinite clays and mica. The soils, though difficult to work, have relatively higher native fertility in lower topographic positions (Schwartz 2007). The basalt and diabase intrusions weather to plastic, shrink-swell soils containing montmorillonite clays. Information pertaining to specific soil series can be found in the Orange and Durham County Soil Surveys (USDA 1976, 1977). Overall, the soils in this region are spatially heterogeneous at the meter scale reflecting underlying geologic variation, and small-scale vegetation composition reflects the associated variation in soil type (Peet & Christensen 1980a and Palmer 1990).

The study area has a warm temperate climate, and the moderate temperatures and ample precipitation throughout the year result in a 200-day growing season (Daniel 1994). The 80-year (1934 – 2014) local mean annual temperature is 14.9 °C (with mean monthly temperatures in January and July being 4.2 °C and 25.4 °C, respectively), and the 80-year local mean annual precipitation is 1185 mm (State Climate Office of North Carolina). Average rainfall is greatest in summer except in instances of severe drought, and there are typically one to two snowfall events per year (McDonald & Urban 2006a). Since 1930, Duke Forest and the surrounding study area have experienced at least three major ice storms, two hurricanes (Hazel in 1954 and Fran in 1996), a tornado and three extreme droughts (Cook et al. 1998, Weaver 2005, Cook et al. 2010).

Extreme weather events have influenced the Duke Forest study plots differentially. Damage from Hurricane Hazel in 1954 can be inferred from the data, and W. Xi (2005) directly measured damage from 1996 Hurricane Fran in 1997 – 2001. Overall, 24 of 37 still extant plots suffered some degree of damage in one or both hurricanes, with the most severe impacts leading to losses of almost 50% of total plot basal area in a few plots. A 1947 glaze storm likewise had significant negative impacts on total basal area in about a quarter of the study plots as did a storm prior to the 1977 sampling year. Although a quarter of the plots still have diminished plot basal area compared to pre-Fran conditions, the majority of damaged plots had recovered in basal area following the earlier disturbances.

Humans have heavily altered North Carolina Piedmont vegetation since at least the time of European settlement. Although the North Carolina Piedmont had been home to several Native American tribes (Peet & Christensen 1980 and Schwartz 2007) that kept forests open using fire (Peet & Christensen 1980, Frost 1998, Taverna et al. 2005b), it was not until the late 18th century that European settlers began clearing the majority of relatively flat land for agriculture (Trimble 1974). By the mid-nineteenth century, most of the arable land was under cultivation, and most land deemed less amenable to agriculture was exploited for wood, grazed by domestic stock, or both (Peet & Christensen 1980). However, poor farming practices and economic hardship resulted in sporadic land abandonment starting in the late 19th century and which has continued through today (Christensen & Peet 1981).

Abandoned agricultural fields became dominated by a canopy of fast-growing pines. Primary among these pines was *Pinus taeda* (loblolly pine), which is an early-successional pioneer species with a typical lifespan on these upland sites of 80 – 100 years (Oosting 1942). Although *Pinus echinata* (shortleaf pine) was more typic of abandoned fields on the Carolina Slate Belt, loblolly had become the dominant old-field in that region as well by the 1930s. Additional information on early succession species can be found in Peet & Christensen (1980). Many of these pine forests continue to be maintained and managed for timber through periodic cutting, while unmanaged stands have begun to transition to hardwood forests following senescence of canopy pines.

Meanwhile, areas often less suitable for cultivation have remained as hardwood-dominated forests with histories of selective cutting and domestic livestock grazing (Healy

1985). The vegetation on these relatively undisturbed sites never fully cleared for agriculture is traditionally a temperate deciduous forest dominated by *Quercus* (oaks) and *Carya* (hickories) species with numerous other hardwood species such as *Liriodendron tulipifera* (tulip poplar) and *Liquidambar styraciflua* (sweetgum) interspersed (Ashe 1897, Oosting 1942, Braun 1950, Christensen & Peet 1984, McDonald et al. 2002). However, some previously less abundant hardwoods such as *Acer rubrum* (red maple) and *Fagus grandifolia* (American beech) have increased in dominance in recent decades (Lorimer 1984, Abrams 1998, McDonald et al. 2002, 2003) as oaks have declined, likely owing, in part, to reductions in low-intensity ground fires (Abrams & Nowacki 1992 and Nowacki & Abrams 2008). Peet (1980) and Peet & Christensen (1980) provide a more detailed description of the previously ascribed steady-state vegetation and its variation with site conditions.

The resulting landscape now consists of a mosaic of fields and forests in different stages of secondary succession, with the pieces representing various edaphic conditions and land-use histories. This mosaic landscape is floristically diverse with greater than 80 tree species identified within the study plots. High regional human population growth rates and increased urban sprawl over the last 30 years have led to further fragmentation of this mosaic landscape (McDonald & Urban 2006b) and present a myriad of novel drivers of vegetative change (e.g., see White et al. 2002, McDonald & Urban 2006a, Duguay et al. 2007, and McKinney 2008).

In addition to this changing mosaic landscape, the North Carolina Piedmont, along with much of the Eastern United States, has additionally seen the return of significant herbivore pressure in forests (Côté et al. 2004, Taverna et al. 2005b, Israel 2011). Herbivore browse has been on the rise as *Odocoileus virginianus* (white-tailed deer) densities have quadrupled since 1980 throughout North Carolina (unpublished data from the NC Wildlife Resources

Commission; see Osborne 1993 for published estimates from 20 years ago). Regionally, deer populations have increased to 12 – 20 deer per km^2 (unpublished data from the NC Wildlife Resources Commission and an internal Duke Forest report). Deer browse has undoubtedly increasingly inhibited forest understory regeneration and altered species composition throughout North Carolina and across the Eastern United States the last 30+ years. However, deer culling programs have been increasingly utilized to decrease browsing pressure. Duke Forest initiated such a program beginning in 2008 to reduce herbivore load throughout the forest, which resulted in deer densities dropping below 10/km^2 (unpublished internal Duke Forest report).

Research plot history and description

Founded in 1931, the Duke Forest (~36.020 N, ~78.983 W) has served as a teaching and research forest for Duke University for over 85 years. G. W. Hill Demonstration Forest (~36.201N, ~78.889W) was founded nearby in 1929 as a teaching laboratory for forestry students attending North Carolina State University in Raleigh, NC. While the almost 1,000-hectare Hill Forest has been primarily utilized for demonstration purposes, the Duke Forest has importantly served as a model system for studying community dynamics and has led to a wealth of significant studies of the subject (e.g., Billings 1938, Oosting 1942, Keever 1950, Bormann 1953, Christensen 1977, Christensen & Peet 1981, 1984, Peet & Christensen 1980, 1987, 1988, see reviews by Peet 1992 and Peet et al. 2014). The Duke Forest, which comprises about 2,800 hectares primarily in Orange and Durham counties in the Piedmont of North Carolina, retains significant research value due, in part, to the availability of three long-term monitoring data sets: large, mapped permanent sample plot data (described in Chapter 3), floristic composition plot data (Peet & Christensen 1980, Taverna et al. 2005, Israel 2011) and the 80-year-old permanent sample plot data described here. Prominent stand types that have been the foci of these data include even-aged successional *Pinus taeda* (loblolly pine) and *Pinus echinata* (shortleaf pine) stands that resulted from the abandonment of old agricultural fields prior to the 1930's and more "mature," uneven-aged deciduous hardwood stands that have been relatively undisturbed anthropogenically in the last century (Xi et al. 2008a) following near-certain selective timber harvesting and livestock grazing prior to 1900. More detailed descriptions of site conditions, site histories, community types and successional dynamics can be found in previous publications (e.g., Oosting 1942, Bormann 1953, Peet 1992, Peet & Christensen 1987, 1988, Knox et al. 1989, McDonald et al. 2003, Taverna et al. 2005a, 2005b, Palmer et al. 2007).

Clarence Korstian of the Duke Forestry School established 51 permanent sample plots (PSPs, 405 – 1012 m^2) with individually marked trees throughout the now-titled Durham and Korstian Divisions of the Duke Forest during the 1930's. An additional 35 plots (numbers 52-86) were subsequently established during the 1930s and 40s, but these did not have individually tracked trees and are not addressed here. Thirty-four of the original 51 Korstian PSPs remain extant and have been resampled 12 – 15 times. Some of these plots have changed size due to enlarging efforts post-1980, and, as a result, the extant PSPs now range from 405 – 1940 m^2. Although Korstian established the plots to monitor tree growth and species composition changes within stands of various age, site condition and silvicultural management practices (Xi et al. 2008), the plots have proven useful for a number of purposes he did not anticipate. Examples of some of these uses include examination of tree population processes (Peet & Christensen 1980b and 1987), predictability and convergence in composition (Christensen & Peet 1981 and 1984), mechanisms of tree competition (Peet & Christensen 1987 and Knox et al. 1989), patterns of mortality (Peet & Christensen 1987), changes in biomass and production (Peet 1981 and 1992), changes in genetic structure (Baker-Brosh 1996), impacts of land use legacies (Golubiewski &

Urban 1998) and impacts of hurricanes and wind events (DeCoster 1996, Xi & Peet 2008a, 2008b, 2011, Xi et al. 2008a, 2008b). Some of the PSPs were experimentally manipulated in the 1930s through 1950s to modify tree density and size structure for assessment of silvicultural practices, but many served as controls as well, and overall there is little contemporary legacy of the density manipulations. Plot descriptions and manipulation histories are available in the associated data file, "psp_plot_histories.csv," located in the supplementary materials (S1).

Twenty-eight of the thirty-four extant plots consist of successional old-field stands that were even-aged pine stands at the time of plot establishment. At the time of establishment, these stands varied in age since initial post-abandonment pine growth (9 – 30 years) and initial stem density (25 – 1172 stems per plot; 600 – 29000 stems/ha). *Pinus taeda* (loblolly pine) is overwhelmingly the dominant pine in these plots, whereas *P. echinata* (shortleaf pine) exists to a much lesser degree in about half of the plots, particularly those with older trees. *Pinus virginiana* (Virginia pine) is near absent with only a few individuals present in successional plots throughout the entire data set.

The successional pine plots are dispersed non-randomly throughout the Durham and Korstian Divisions of the Duke Forest, with various clusters of plots having shared physical location and experimental purposes. PSPs 4 – 7 were established as a cluster of 9-year-old, quarter-acre (1012 m^2) plots on Georgeville clay loam to examine various pruning effects on growth and development of thinned pine stands. PSPs 12 – 23 consist of a suite of tenth-acre (405 m^2) plots at various elevations along a short, sandy hill in the Durham Division of the Duke Forest. PSPs 12 – 23 (which represented 8-year-old stands at plot establishment) varied in initial stocking density (25 – 1172 stems per plot) to examine effects of initial densities on tree and forest growth and development. PSPs 24 – 26 are a cluster of quarter-acre plots that were established as 19-year-old stands on Georgeville silt loam soils with varying manipulations to examine thinning effects on forest growth and development. PSPs 28 – 29, PSPs 39 – 40, and PSPs 41 – 42 represent three different groups of spatially-clustered plots (each being a fifth acre (810 m^2) and 15-years-old at plot establishment) on various soil types that were established to examine degree of thinning (PSPs 28 – 29) and various cutting methods (PSPs 39 – 42) on forest growth and development. PSPs 49 – 51 represent a final cluster of successional pine stands that were established as 30-year-old, fifth-acre (810 m^2) stands at various topographic positions along a shallow valley to examine different methods of thinning on forest growth and development.

The resampling of the successional pine plots has spanned early growth of even-aged pine forests, the thinning of these pine stands, and various stages of transitioning of these stands to a mixed uneven-aged hardwood forest. Senescing and fallen pines are being replaced primarily by early-successional and gap-specialist species such as (in order of decreasing abundance): *Liquidambar styraciflua, Liriodendron tulipifera, Oxydendrum arboreum*, and *Fraxinus* (ash) species. Shade-tolerant *Acer rubrum* (red maple), which is expected to become dominant in future mature forests due in part to more than a century of fire suppression, has become an abundant species throughout all sub-canopy strata. Historically late-successional species such as oaks (e.g., *Quercus rubra, Q. velutina,* and *Q. falcata*) and hickories (e.g., *Carya tomentosa*, *C. carolinae-septentrionalis*, C. *glabra,* and *C. ovata*) have likewise begun entering the higher strata of the forest, and stems of *Nyssa sylvatica, Ulmus alata,* and *Fagus grandifolia* have begun filling the sub-canopy. Species such as *Ostrya virginiana*, *Prunus serotina*, *Cercis canadensis, Juniperus virginiana, and Viburnum rafinesquianum* remain relatively abundant in the mid-story and shrub layers (with *V. rafinesquianum* only in the shrub-layer, though *V. rafinesquianum* levels have diminished in recent years due to increased browsing pressure from deer). *Cornus florida*, which was previously the third most abundant species in these stands, has declined precipitously throughout Duke Forest in the last two decades likely owing to dogwood anthracnose disease.

The remaining six plots of the thirty-four Duke Forest PSP data set consist of uneven-aged deciduous hardwood stands. These stands are located on a range of site conditions in both upland (n = 4) and bottomland (n = 2) forests in the Korstian and Durham Divisions of Duke Forest. Unlike the old-field successional plots, these hardwood stands have all been relatively undisturbed by humans for at least 100 years. However, it should be noted that each plot, like many hardwood stands throughout the North Carolina Piedmont, likely has some history of selective timber harvesting, livestock grazing, and low-intensity ground fires. Regardless, any of these practices preceded the acquisition of the Duke Forest land by Duke University in the 1920s (McDonald et al. 2002).

The bottomland hardwood sites (plots 43 and 44) are uneven-aged *Liquidambar styraciflua – Liriodendron tulipifera* forests that have primarily been withheld from experimental manipulation, save for an improvement cutting performed in PSP 43 in 1950. These two plots are geographically very close and are located on opposite sides of Sandy Creek near Duke University campus. Schafale (2012) classifies this community type as Piedmont Alluvial Forest (CEGL004418). *Fraxinus spp.*, *Carpinus caroliniana*, *Ostrya virginiana*, and *Cornus florida* existed in relatively high volume in plot 44, but the *Carpinus* and *Cornus* have seen significant decreases since plot establishment while *Acer floridanum*, *Fagus grandifolia*, and three non-native shrub species (*Elaeagnus pungens*, *Ligustrum japonicum*, and *Ligustrum sinense*) have all substantially increased in abundance in this plot. Plot 43 experienced similar decreases in *Carpinus caroliniana* and *Cornus florida* and increases in *Fagus grandifolia* and *Elaeagnus* *pungens*, but this plot has more dominant oaks and hickories (specifically *Quercus alba* and *Carya glabra*) and a near absence of *Ostrya virginiana* and *Acer floridanum* as compared to plot 44.

The extant upland hardwood sites are all relatively undisturbed second-growth oak-dominated stands that were primarily withheld from any prominent or ongoing experimental manipulation. Plot 35, which lies on a shrink-swell clay hardpan on an intrusive diabase dyke, is equivalent to Schafale's (2012) Piedmont Xeric Hardpan Forest (CEGL003714). This plot, which serves as a stark contrast to nearby PSPs 36 and 37, was originally described as being typical of a post oak - blackjack oak forest type frequently found on poorly drained soils of the lower Piedmont and composed mainly of *Quercus stellata* (post oak), *Quercus marilandica* (blackjack oak), *Juniperus virginiana*, *P. taeda* and *P. echinata*. However, *Q. marilandica* has been absent from the plot for more than 25 years (a trend seen throughout much of the Duke Forest), while *Acer rubrum*, and to a lesser and more recent extent *Carya ovata* and *Fagus grandifolia*, have increased in abundance.

The remaining upland hardwood plots (PSPs 10, 36 and 37) are all of the white oak - black oak - red oak type and represent examples of Schafale's (2012) Piedmont Dry-Mesic Oak-Hickory Forest (CEGL008475). Plots 36 and 37, which are located nearby to PSP 35, have canopies dominated by oaks (primarily *Q. alba* along with *Q. coccinea* and *Q. velutina*) and hickories (primarily *C. tomentosa* along with *C. carolinae-septentrionalis*). *Acer rubrum, Oxydendrum arboreum, Juniperus virginiana, Liriodendron tulipifera*, *Nyssa sylvatica*, *Cornus florida* and *Ostrya virginiana* are also abundant in these two plots. Additionally, about half-a-dozen pines (*P. taeda* and *P. virginiana*) that invaded the eastern half of Plot 37 following damage from Hurricane Hazel in October 1954 have also now reached the canopy. The hurricane damage received by PSP 37 and not by PSP 36 provided a natural experiment between these near-adjacent plots which has resulted in higher small tree diversity in PSP 37.

Plot 10, the final upland hardwood plot, is in an upland flat in the Triassic Basin (compared to the Carolina Slate Belt location of plots 35 – 37) that is topographically lower than the other upland hardwood sites. This plot has higher levels of soil calcium and magnesium than either Plot 36 or 37, and it also has a higher preponderance of hickories, particularly a number of dominant *C. carolinae-septentrionalis* and *C. tomentosa*. The preponderance of *C. carolinae-septentrionalis*, along with an abundance of *Viburnum rafinesquianum* in the understory, is likely a result of mafic parent rock (see Peet & Christensen 1980a), which is consistent with the magnesium-rich soil.

Three additional upland hardwood plots (each an acre in area, or 4047 m^2) located in G.W. Hill Demonstration Forest (36.201N, 78.889W) near Bahama, NC supplemented these six hardwood plots beginning in the late 1940s. These three plots were established by William D. Miller and North Carolina State University forestry classes as permanent sample plots in 1946 (plot H23) and 1947 (plots H24 and H25). These Hill Forest plots were dominated by *Q. alba*, *Quercus* subgenus *Erythrobalanus* (red oaks), and *L. tulipifera*, with *P. echinata* also being an important component of plot H24. *Carya* species, *A. rubrum*, *N. sylvatica*, and *P. virginiana* exist in relatively high volume on each of these sites as well (Timko 1962). Early plot notes indicate that borings made in dominant and codominant trees suggested that the plots were approximately 33 (plot H23) and 44 (plots H24 and H25) years old in 1947. However, examination of the size distribution of stems suggest the plots are much older. Although the plots are presumed to be located on uncultivated land, the initial presence of a few old and scattered *Pinus virginiana* and *Pinus echinata* suggest that they may have once undergone heavy thinning and are now in the latter stages of ecological succession following land abandonment (Timko 1962). To retain consistency in storage type for plot numbering in the database, I drop the “H” from each plot name and represent the Hill Forest plots as plots 123, 124 and 125 to differentiate them from plots 23 – 25 in Duke Forest.

Each of the 34 extant Duke Forest plots has been periodically resampled for 80 years including most recently in 2012 – 2013. The Hill Forest plots were sampled regularly from 1947 – 2001. Survey efforts occurred at roughly 5-year intervals and involved recording of stem coordinates (1983 – present), species, survival, diameter, height, and tree condition for all woody plant stems >1 cm DBH (diameter at breast height; though it’s unclear if this cutoff was consistently adhered to each sampling period prior to 1978).

Research methods

Tree sampling

Permanent sample plots (or PSPs) were sampled roughly every five years (ranging from 3 – 12 years) typically during the growing season (May – August). However, before 1960, the plots were sometimes sampled in the autumn and even as late as December. Field crews sampled all plots in single years when possible, but most sampling periods required two or more years to complete measurement of all plots. The Hill Forest plots were not established until after the first decade of study in the Duke forest, and they were not sampled during the last decade of the study. Otherwise, few plots were skipped in any given sampling period throughout the course of the study.

Despite 17 original plots now being extinct, the 34 extant Duke Forest plots have retained their original plot and tree numbers based on a consecutive numbering system. Beginning with the 1977 – 1984 remapping efforts, the plots were more formally gridded into transects with an underlying coordinate system. Plots were divided into (typically) 5m-wide transects along the y-axis. These transects were usually assigned numbers consecutively starting with transect “1” at the low end of the y-axis, but in some instances, additional transects were added when plots were enlarged and assigned consecutive numbers less than 1. Although plot corners were marked with metal piping (or replaced by metal conduit if missing after 1975) at the time of plot establishment for remapping purposes, field technicians generally measured transect lines each sampling year using measuring tape. To formalize transect lines, I installed additional metal conduit at each transect corner in 2012 – 13 and made minor adjustments to existing coordinates as needed. As of 2016, 100% of corner pipes and conduits marking transect corners were extant.

The entirety of each plot is mapped using a Cartesian coordinate system. X and Y coordinates are in decimeters (dm) and typically start at zero. If the plot was extended in the zero-direction along either axis during the study, negative coordinates were assigned to those regions. Trees were initially tagged with painted numbers and later metal ID tags. However, tree-marking practices fell out of practice in the 1980s when the plots were formally mapped, and few extant individuals still show signs of these methodologies. As a result, the majority of trees are best located in each plot using their X and Y coordinates. Coordinates are determined using measuring tapes placed along axis and transect lines.

Each tree that was recorded received plot and transect numbers, X and Y coordinates, species code, diameter, height, condition code, and any pertinent notes. Trees that were no longer extant by the mapping efforts in the early 1980s did not receive coordinates. Some trees were additionally assigned a clone number (“CL”) in the field if they were the clone of another individual. During each sampling effort, all previously mapped trees were re-measured and checked for errors and all new ingrowth individuals were assigned coordinates, identified to species, and measured. However, ingrowth was not consistently measured in all plots prior to 1978.

All trees were also automatically assigned a series of identification numbers when entered into the electronic database. These numbers include sequential identification numbers for trees in the same plot (“ID”), a sequential ID number for identification of specific individuals across the entire data set (“StaticLineID”), and a unique identification number for each individual in each year (“YearlyLineID”).

The species code (or SPEC) is a four-letter code representing each species. Each code usually consists of the first two letters of the genus and the first two letters of the specific epithet. However, the first four letters of the genus are used when the species name is not known (rarely), and in some instances, other patterns must be used to avoid duplicates (e.g., CACA = *Carya carolinae-septentrionalis* and CACR = *Carpinus caroliniana*). I maintained full species identifications for most taxa and grouped to genus only those species considered particularly difficult to split from related taxa based on vegetative characteristics (e.g., *Fraxinus* and *Crataegus* species). Leaf samples of species that could not be identified in the field were used to identify these individuals to minimize unknowns in the data.

Trees (and woody shrubs) were only tallied and measured if their height achieved or exceeded 1.37 m (i.e., “breast height”). Further, trees had to be a minimum of 1 cm in diameter to historically be considered for measurement, though this may have been somewhat less consistent prior to 1978. Plot notes indicate that early sampling efforts were only to measure trees with DBH ≥ 0.5 inches (~1.25 cm; or sometimes > 1 inch or ~2.5 cm), but the data indicate that some trees at or near 1 cm were measured during these early years anyway. Additionally, trees of smaller diameters (< 1 cm) were measured with more frequency beginning in 1991, and, by 2012, all trees achieving breast height were measured regardless of diameter size.

The diameter at breast height (DBH) of each tree was determined by measuring the circumference of the main stem of each individual at breast height (1.37 m) using a diameter tape. These tapes automatically convert circumference to diameter by dividing by pi and reporting in centimeters. Breast height was based on height of the stem and not by distance of the stem to the ground. Because of this, the diameter of leaning trees, trees growing on inclines and fallen trees were measured 1.37 m from their base. Note, however, that this approach was formalized in the 1970s and that the details of the methodologies used prior to 1970 are not as well known.

From 1978 onward, measurement of trees with split or branched stems followed a strict protocol. If a tree stem split above 50 cm, then only the largest stem was recorded and measured. However, if the stem of the tree split below 50 cm, then all such stems were recorded and measured as separate entities and identified as clones. In these instances, the field technician made a note and recorded a clone number for the split stems. If two stems of a tree were previously recorded as separate, they remained separate even if the split between stems grew to occur above breast height. On rare occasions, separate stems fused, and two measurements were no longer possible. Typically, in these instances, the larger or older stem was maintained in the dataset, while a note was given to the final measurement of the fused stem. Finally, in any instance where a tree split exactly at breast height (1.37 m), the DBH was measured just below the split. This slight downward (or sometimes upward) adjustment in diameter measurement was likewise employed when a large knot or other unusual protrusion existed exactly at breast height.

The height (in meters) of each individual was also typically measured during sampling efforts and followed the same rules for determining individuals as described above for measuring DBH. Prior to 1978, height was recorded in feet, and diameter was recorded in inches. However, all measurements made prior to 1978 were subsequently converted to metric units. Although the methodology for measuring height is undocumented prior to 1970, subsequent protocol required that a telescoping, graduated height pole be used to measure trees shorter than 10 m. The pole was extended upward until the top of the pole matched the height of the tree being measured as sighted by a nearby field technician. Taller trees were measured using a mechanical Blume-Leiss altimeter (or alternatively an Abney level) from 1975 through 2001, but a laser hypsometer (Nikon Forestry 550 model) was employed for tall (>10m) trees beginning in 2012.

Two additional height variables were measured prior to 1984 through use of the same instruments employed to measure general tree height. "Crown" represented the crown height of measured trees and was calculated by measuring the stem height from the ground to the base of the crown. "Clear" was a variable indicating clear bole height and was calculated by measuring stem height from the ground to the height of the lowest significant branch or visible defect (such as a knot). These two silvicultural variables were dropped from sampling protocols in the early 1980s with the shift in focus away from examining silvicultural practices to understanding long-term ecological change.

One of six condition codes (CC) was assigned to each tree in each sampling period (or was retroactively assigned to trees measured before 1970 based on sampling notes). CC = 1 was assigned to all living trees in good health as well as the majority of new ingrowth individuals. CC = 2 was assigned for all dead trees defined as having no living leaves and still standing or that had fallen and could be definitively identified. CC = 3 was assigned to all missing trees, which were typically assumed to be dead but without a standing stem for verification. Neither dead nor missing trees received diameter or height measurements. CC = 4 was assigned to trees that had a significant loss of height, experienced major die back, or were strongly leaning. Early on in the study, this code was reserved for trees that shrunk to below breast height, but later, all trees that shrunk to any degree received this code. In most of these instances, diameter and height measurements were taken if possible, and the tree was given a note describing the field technician's best guess as to the cause of the change. If the height had been reduced to below 1.37 m, then no measurement was taken and a note indicating so was often reported. CC = 5 was assigned to trees that were cut by humans, which only rarely occurred early in the study. Finally, in the resurveys of 1997 – 1998, hurricane damage codes were assigned to indicate the impact of the 1996 Hurricane Fran. Although a system of more detailed codes (see below and Xi et al. 2008) was developed to describe these damages, these trees received a CC = 6 to indicate whether there was any type of tree damage from the hurricane.

Four ordinal stem damage codes were used in 1997 – 1998 to summarize the overall damage to trees following Hurricane Fran in 1996. These four codes, represented individually in the data as "F1" through "F4," were integrated to easily represent overall damage to stems (Xi et al. 2008). F1 represents uprooting status with a value of 1 indicating no uprooting, 2 indicating a partial uproot and 3 indicating the tree was completely uprooted. F2 codes for "breakage" with values ranging from 1 – 4 signifying 10% canopy loss, 10 – 35% canopy loss, 35 – 90% canopy loss and >90% canopy loss, respectively. F3 indicates the degree to which a tree was leaning because of the hurricane and likewise ranged from 1 – 4. F3 values represent no lean, leaning free with lean >10%, being supported by another tree, and having completely fallen on the ground. Finally, F4 codes for the degree to which other damaged trees were impacting the tree of interest, particularly by leaning on said tree. Again, this code ranged from 1 – 4 with codes indicating whether the tree of interest was not leaned-on (free), was upright and supporting a tree (DBH >30% size of host), was bent or leaning (crown displaced at least 10%), or was pinned. In addition to these four damage codes, field technicians also determined the azimuth (“AZI”) of all fallen stems using a compass in the 1997 – 1998 sampling period.

Finally, I assigned two additional digital categorical variables to each tree in the PSP database to better track tree histories. I used the first of these, “Ingrowth,” which ranged from 0 – 3, to indicate a tree’s sampling status in each given year. An Ingrowth code of 0 indicates that a tree was old growth in that particular year (i.e., the stem had previously been recorded), while a value of 1 indicates that a tree was ingrowth (i.e., a newly measured tree) in that year. An Ingrowth value of 2, on the other hand, indicates that a tree is new but specifically because that tree is in its plot’s initial sampling year. Finally, an Ingrowth code of 3 indicates that a tree was included as ingrowth but only due to an increase in the dimensions of the plot that sampling year.

I applied the second categorical variable, “Phase,” as a descriptor to indicate which area each tree is located in within its specific plot. Because most PSP plots changed size at least once throughout their history (i.e., they changed “phases”), the Phase variable allows one to determine each tree’s location in order to include or exclude certain trees from future analyses sensitive to changes in plot area. I defined phase changes individually for each plot if and when each plot changed in shape or area, and I assigned “Phase” codes based on a tree’s permanent location within its plot. Specifically, a Phase value of 0 indicates that a tree is located in an area of its plot that was present in that plot’s initial sampling year. In contrast, a Phase value of 1 indicates that a tree is located in an area added to its plot when the plot was remapped or enlarged. Higher phase values would be assigned to trees in areas of additional plot enlargements, but this scenario has yet to occur as no plot has been enlarged more than once.

Nomenclature

Nomenclature follows the USDA PLANTS database (USDA, NRCS 2017).

Error correction and data standardization

With almost 157,000 data entries (~139,000 in extant plots) across 80 years in the PSP data set, errors and various other issues were unavoidable. The number of different field technicians, data entry personnel, and database versions only served to compound these issues. Although some issues were clearly generated due to errors in the field (e.g., skipping trees or poor handwriting), the majority of errors in the data seemed to have been generated during electronic data entry and shifts in database versions or coding. I diligently checked for such errors for all data across all years.

Project personnel had previously visually proofed tree data and matched written data sheet records with computer files. Subsequently, I methodically searched for and examined outliers, inconsistencies, irregularities, and potentially problematic scenarios involving tree data and then addressed these issues as described below. I additionally checked all tree metadata, plot history information, soil data, site data, and additional ancillary data (e.g., wood density) for inconsistencies and unlikely values.

I corrected all unknown, blank, misspelled, and invalid species codes (SPECs) by examining a list of unique SPECs in the database and ensuring that each conformed to the spelling of known species codes. I examined individual trees with changing SPECs across time (often due to the changing opinion of field technicians), trees with ecologically or geographically unlikely assigned SPECs, and trees determined to still be misidentified during the 2012 – 2013 sampling period (most commonly *Carya*, *Viburnum* and *Celtis* species). I did so by examining original data sheets, inspecting known range maps of species and through examination of extant individuals. When I could not confirm a definitive species, I opted for a genus-level SPEC code (rarely) or added a note to the database to suggest the best SPEC to use moving forward. I also corrected any blanks and typographical errors for plot numbers, plot types, and year using original plot notes to adjust non-valid entries in the electronic database.

Trees marked as being dead or missing two sampling periods in a row were automatically removed from subsequent sampling field data sheets. However, some of these trees survived in diminutive form; as re-sprouts from stumps, trunks or branches; or, in the case of numerous redbuds (*Cercis canadensis*) knocked over in Hurricane Fran in 1996, as horizontally growing trees with major branches turned upward as vertical growth. Often, this regrowth was not made apparent until numerous sampling periods after the tree had last been marked as dead or missing. As a result, subsequent field crews identified the revived growth from some of these trees as new individuals (“ingrowth”). This was only appropriate if the new growth developed below 50cm up the trunk of the previously recorded individual (as described previously for designation of split trees as distinct individuals). Otherwise, these new recordings had to be included as new growth for an existing individual that typically had previously been marked dead or missing and removed from field sampling sheets. I accounted for these revived trees by inspecting old data sheets to properly identify which individual was found. I updated the identification numbers of these trees to match the old individual, and I removed the newer tree ID from the database.

I examined all instances in which trees were given notes indicating their missing status as questionable (e.g., due to coordinate inaccuracies), instances in which ingrowth individuals were outliers in their DBH or height, and most instances of damaged or killed trees following

Hurricane Fran. I then compared the SPEC, size, condition, and available notes of each questionable ingrowth (or missing) tree as defined in the previous sentence to that of the closest missing (or ingrowth) tree. I made an individual assessment of each situation to determine if the ingrowth tree was in fact new. In instances where I felt confident the tree had previously been recorded, I corrected the ID values and removed the ingrowth tree ID from the database. In all instances, I added a note indicating the solution. I also noted that some exceptionally large ingrowth individuals that were not determined to be regrowth individuals were likely skipped in previous sampling periods, and I marked them as such. Often, these trees were located along plot or transect perimeters.

In some instances, prior data entry personnel failed to transfer some trees from the hand-recorded data sheets from the field to the electronic database. This resulted in subsequent data sheets lacking an entry for these trees. As a result, subsequent field technicians unknowingly recorded these individuals, often with larger than expected sizes, as ingrowth. To determine if questionable individuals had simply not been electronically recorded, I identified ingrowth trees that were large outliers in DBH or height or that contained notes questioning their size or prior status. I then examined hand-recorded datasheets from previous sampling periods for these trees to look for candidates that had been hand-recorded but never electronically entered. Again, in instances where I felt confident the tree had previously been recorded, I corrected the ID values and removed the newer tree ID from the database.

I also examined possible duplicates of individual trees. This issue seemed to arise most often along perimeter lines between adjacent transects or in dense patches of homogeneous sapling growth. However, I could only recognize the latter if notes for individuals or observation of extant individuals left obvious clues. I was able to examine possible perimeter duplicates more methodically. I examined each individual tree that grew within 5 cm of each transect perimeter and compared those trees to each nearby individual within 5 cm of the shared perimeter line of the adjacent transect. I made decisions on an individual basis by noting the distance of each tree from the line and comparing the SPEC, size, condition, and available notes of each tree in question. In instances where trees were determined to be measured in one transect but later marked as missing and measured subsequently in the adjacent transect, I eliminated the duplicate and updated the tree in the transect that seemed most appropriate based on plot coordinates or observation of extant individuals in the field.

I next methodically checked for blanks and outliers in the numerical data: static tree ID (“StaticLineID”), yearly tree ID (“YearlyLineID”), tree ID in plot (“ID”), transect number, X and Y coordinates, condition code (CC), diameter (DBH), and height. Most issues involving ID errors or transect errors were either easily identifiable typographical errors or corrected through the methods described above. I filled in missing coordinates when the data existed to do so or through verification in the field. However, trees missing coordinates in the database often existed prior to 1978 when the plots were first fully mapped and therefore could no longer be assigned coordinates. I left the coordinates for these trees as NA.

I accounted for DBH, height, and CC outliers and blanks by examining previous data sheets when possible, but overall these and related errors for DBH, height, and CC were more difficult to fix. Trees missing diameter were often attributable to data entry errors or typographical errors and could be adjusted, but 15 trees lacked both DBH and height and therefore lacked any method to account for diameter. These trees’ measurements were left blank but given notes explaining why. Thousands of trees lacked a height measurement, but only very few of these were due to similar reasons as the missing DBH info. Most of the trees lacking a height measurement actually never had their heights measured. I used regression modeling to predict these missing heights using methods described later in the “Height prediction” section of this chapter. I retained original, field-collected height measurements (or lack of measurements) as an additional variable in the database called “OrigHT.”

There were diverse issues pertaining to the condition code (CC) of numerous individuals in the data set. I changed all CC values less than 1 or greater than 6 by using previous CC values, past and present measurement values, sample notes, and nearby trees as guides. I fixed most of the trees marked as living (CC=1) that lacked measurement data by examining old data sheets for typographical errors or through methods described for fixing DBH and height. Often, trees with CC > 3 had written notes that helped to confirm or update many CC values. All trees with CC = 5 (cut) after 1978 required a written note indicating they had been cut to confirm the condition code, and only trees measured immediately after Hurricane Fran (1997 – 1998) were allowed to be assigned CC = 6 (if appropriate). All other trees after 1978 assigned CC = 5 or 6 were changed to 3 or 4 based on available evidence of past, present, and subsequent measurements and notes. For example, previous field technicians erroneously applied condition-code methodologies from a concurrent study to about 30 trees by assigning CC = 5 to indicate “damage to the tree (e.g., by insects, by clumsy field crew member, etc.).” Using available data, I updated and changed all of these trees’ condition codes to conform to the present methodologies, and I made a note indicating this process for each updated tree.

Issues pertaining to trees with CC = 2, 3, or 4 were often more complicated and involved close examination of time between sampling periods, tree size, relative growth rates, SPEC, and presence of hurricane damage. Some trees were assigned a CC = 2 (dead) or 3 (missing) but then measured again in a subsequent sampling period (sometimes due to corrections I had made pertaining to missing tree issues described above). In cases when the subsequent sampling effort assigned the tree as CC = 4, I kept the initial CC as it was. This is because the tree likely validly received a CC = 2 or 3 because it died or was damaged to the point that it was not there or not visible at breast height (BH). The following sampling year it was given a CC = 4 if that year's field crew saw regrowth, resprouting, or evidence of a living tree that was either still below BH or clearly growing up from below BH. I likewise kept the condition codes as they were for the similar scenario in which missing or dead trees were later assigned a CC = 1 but clearly had grown back above BH following severe damage. I often placed a note indicating this had occurred if a note did not already exist. Trees that were recorded as missing (CC = 3) in 1997 following Hurricane Fran but then grew back (CC = 1) by 2000 were also kept as is because it was likely that damaged debris were crushing or obscuring these trees.

About fifty trees that had been assigned as dead or missing but later relocated were deemed to have been skipped, overlooked, or wrongly assigned a CC = 2 or 3. In the majority of these instances, I reassigned the CC from 2 or 3 to CC = 1 and calculated new DBH and height measurements for each individual using calculated growth rates for each individual. I did so by determining the change in size from the sampling period before the period in question to the period the tree was next measured, dividing by the length of the time interval to calculate a yearly growth rate, and multiplying that value by the length of time from the previous sampling period to the period in question. I added a note to each of these updated entries.

In the remaining instances (n = 6) of the wrongly assigned dead or missing trees, the measurement of the trees was smaller in the sampling period in which they returned as compared to when they had last been given measurements. As a result, I assumed the trees had been damaged in the interval they were missing. However, I concluded that the damage was likely not severe enough to warrant a CC = 2 or 3 because of the relatively large size of each tree when it was remeasured. Therefore, in these instances I opted to assign each tree a CC = 4 in the period under question (instead of CC = 2 or 3). Because the size of each of these trees was large enough in the following sampling period to assume that each tree had not been damaged below breast height during the misreported period, I assigned each tree an appropriate height value for the period under question. However, calculating the missing height using the above growth rate method would not be appropriate given that the tree was smaller in the more recent sampling period, so I instead opted to assign these trees height (and DBH) values from the sampling year when they were remeasured.

Finally, although previous stewards of the Duke Forest data had left notes pertaining to plot areas and maps indicating purposeful changes in plot areas during remapping in the 1970s, I found that these area data were not always accurate. I also found evidence that some changes in plot areas were not properly recorded or accounted for. To address any possible inaccuracies, I examined the existing plot notes, data sheets, maps, and any existing geo coordinates for each plot in each sampling year. Further, I examined the maximum assigned X and Y coordinates for trees in each plot in each year to determine whether an abundance of trees existed beyond the assumed plot dimensions or if there was clear indication that a plot was not being sampled to its full extent. Additionally, I took plot measurements and laid conduit posts to mark permanent transect lines during the 2012-13 sampling period to confirm current sizes of each plot. Using these data, I added a database column for plot area (in m^2) so that each tree record was given the area of its plot in each row's given sampling year.

Height prediction

I estimated heights for PSP trees with living condition codes (CC = 1) and that lacked a height measurement (*n* = 17,769). I used regression analyses comparing height to diameter (see Henry & Aarssen 1999 and Hulshof et al. 2015 for discussions about height-diameter allometry) to estimate heights for these missing trees. See below for my methodologies for accounting for any remaining trees with a CC > 1 that were still lacking heights.

Training data for the regression models included all trees from the 37 extant Duke Forest and Hill Forest PSP plots that were not missing height or DBH measurements. These training data were refined slightly by eliminating graphical outliers (here defined as trees with DBH > 25 cm and height < 5 m); these outliers were almost entirely trees with condition codes (CC) of 4 or 6 that had experienced large degrees of height damage and therefore were undesirable to include in the model. Regardless, I further limited the training data to include only living trees (CC =1) that had never previously received recorded damage (CC = 4 or 6) or lost greater than 50% of their recorded height over the two previous sampling periods. I added these final stipulations to further reduce the impact of damaged trees on the model predictions. The resulting training data contained approximately 89,000 samples and 65 unique species.

I developed and compared the performance of various models to optimize height predictions. Using root mean square error (RMSE) as a metric to compare models, I determined that a mixed effects model estimating heights based on unique individuals, species and plots was most appropriate. Specifically, I used the lme4 package (Bates et al. 2015) in R (R Core Team 2016) to create a mixed model with diameter and diameter squared as fixed terms to predict missing height values. The model incorporated both a random slope and intercept term based on each individual tree ("StaticLineID") to account for unmeasured variation between individuals.

Additionally, I incorporated random effects for intercepts, slopes and quadratic curve for both species and the plot in which each tree was located. These terms allowed for variation in the height-diameter relationship due to underlying physiologic differences and impacts from variation in soil and site characteristics. I performed manual 5-fold cross-validation to determine whether this model achieved a mean RMSE of 1.4 meters, which is comparable to similar studies (e.g., Zhang 1997, Petráš et al. 2014 and Corral-Rivas et al. 2014). However, the model made a few predictions below breast height, the study's minimum threshold for measured trees. I modified these four trees (all *P. taeda* saplings) to have a height equal to that of breast height (1.37m).

I next turned to address the hundreds of trees that had been assigned a condition code indicating damage (CC = 4 or 6) and given a diameter measurement (indicating a minimal height of 1.37m) but that lacked a height measurement. I examined each of these trees individually to determine the best estimate of height in these instances. I assigned about 460 of these trees a height equal to 1.37 m (breast height; BH) because they appeared to have dropped to or below BH. I based this assumption on the fact that the height measurement in the subsequent year of many of these trees was suddenly near breast height or was much lower than in the sampling period prior to the one in question. I also made this assumption for trees that did not receive a height measurement the following year due to the condition code being assigned as 2 – 4.

Thirty-one additional damaged trees fell under the scenario of having a diameter measurement but lacking a height value. In all of these instances, there was no sign of decreased height in the subsequent sampling period as compared to the sampling period prior to the one in question. Based on the size of the trees following the year in question, I assumed in these instances that the trees had not dropped to or below breast height, and therefore needed to have estimated heights. I opted to take advantage of the individual growth rates of these individuals rather than plugging them into my more generalized height-estimating regression model. I did so by determining the change in size from the sampling period before the period in question to the period the tree was next measured, dividing by the length of the time interval to calculate a yearly growth rate, and multiplying that value by the length of time from the previous sampling period to the period in question.

Trees with notes indicating that the damage brought the trees below breast height (often due to being severely crushed by other downed trees) and that were lacking a diameter measurement were left with blank height values.

Site analyses

Plot locations were estimated using old Duke Forest and Hill Forest plot maps, USGS Quadrant maps, and GIS elevation maps. I confirmed or adjusted some of these plots based on actual GPS readings at plot corners. Using these plot location data, I overlaid PSP plot shapefiles on an NCOneMap LIDAR-derived 20 ft. digital elevation model (DEM) using ArcMAP 9.3.1 (Esri 2006). Water features and roads were also added to this map. I then used tools in ArcMap to calculate various site-level variables

I used ArcMap's built-in tools to measure each plot's elevation, each plot's distance to the nearest body of permanent flowing water in the same watershed, and the elevation of that water body. I also used a built-in tool to calculate the aspect of each pixel within each given plot, which I then averaged across all pixels in each given plot to calculate overall plot aspect. Following a modified model of Beers et al. (1966), I next converted aspect to transformed aspect, or T_{asp}, using the equation: - COS(45 – Aspect). T_{asp} is a linear transformation of aspect with SW facing slopes having a value of 1.0, NE facing slopes having a value of -1.0 and intermediate aspects having values ranging from 1.0 to -1.0 according to the cosine function above. I chose this modification of Beers et al.'s model to assign SW slopes the greatest T_{asp} value because this direction receives the maximum heat load (McCune & Keon 2002).

Although ArcMap's built-in tools performed well for calculating the site-level variables described in the last paragraph, I did not find the built-in tool for calculating slope satisfactory for the purposes of this data. This was because, by accounting for each pixel of a given plot, the tool was too greatly impacted by slopes of within-plot regions that were not indicative of the overall slope of the plot. As a result, I instead used a method similar to that of McNab (1989). I manually measured the elevation of the pixel under each plot corner, measured the difference in elevation between each pairwise combination of plot corners, divided those differences by the distance between each pair, and then averaged the six slopes to determine the overall slope of each plot. I then compared this to actual field measurements taken with a clinometer in some of the plots and found strong alignment between the two methods' values.

After calculating the geographic values for each plot, I next calculated potential solar radiation for each plot. I used each plot's latitude, slope and aspect to look up values in Frank & Lee's (1966) potential solar radiation tables to determine appropriate values.

Next, I used USGS Quadrangle maps, the DEM and personal knowledge of the plots to designate two categorical variables for each plot: topographic position and exposure. Topographic position is a scalar that ranges from valley bottom (=1) through concave and convex slope to ridge and finally hilltop (=5). Exposure is a scalar that varies from sheltered draws (=1) through open hillsides and sheltered hilltops to exposed ridgetops (=5).

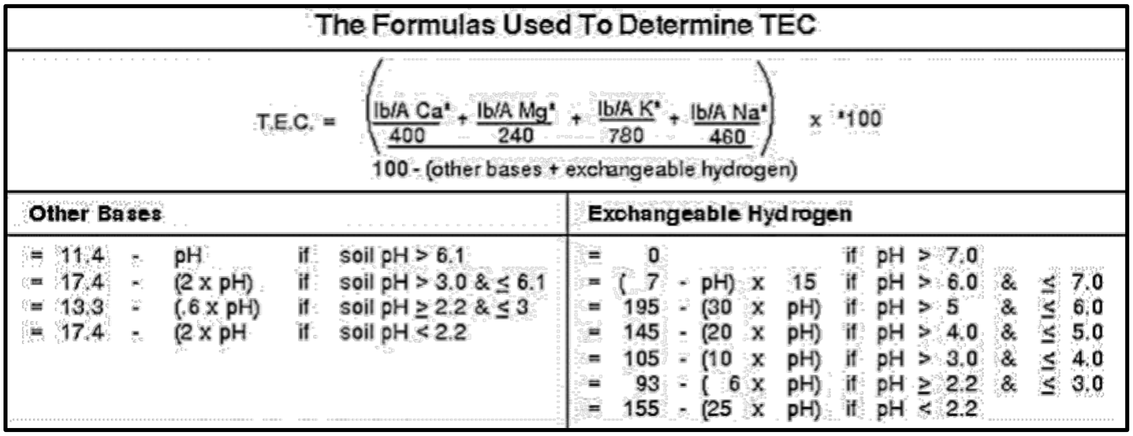
The resulting site variables include: slope (degrees), elevation (m), distance to closest permanently-flowing water (m), elevation of the water body (m), potential solar radiation, T_{asp}, and the categorical topographic position and exposure variables.

Soil methods

I collected soils from each of the 37 extant Duke Forest and Hill Forest PSP plots in 2015 – 2016. In order to compensate for the well-known small-scale heterogeneity in soil characteristics of the region (Palmer 1990), I collected five soil samples from each plot. I removed the litter and humus layers and extracted a 10 cm deep mass of mineral soil (A horizon) from locations near each corner and in the center of the plot. In addition, I took a sample of the B horizon near the center location (variable in depth, but typically 35 – 50 cm) using a manual screw auger. I dried each of these samples in drying ovens set to 55°C for 48 hours, crushed the dried soil with hammers and pestles and then passed each sample through a 2 mm sieve. Due to financial limitations, I was only able to process two samples (one A horizon and one B horizon sample) from each plot. For each plot, I measured out 100 g of each of the five sieved A horizon samples and then combined them to form a 500 g composite sample. The B horizon samples consisted of 250 – 400 g for each individual plot.

Brookside Laboratories, Inc. (New Bremen, OH 45869) processed my soils and reported nutrient, texture, and bulk density data for each sample. Soil texture was determined by calculating the percentage each of sand, silt and clay. Brookside used the hydrometer method (ASTM Standard D422 2002) to determine clay percentage and a #270 (0.053 cm) sieve to determine sand percentages, and they determined silt percentages from the difference. They did not remove organic matter for this process.

Brookside determined both the absolute (ppm) and relative (%) available amounts of various soil nutrients using the Mehlich III extraction method (Mehlich 1984). These nutrients included S, Ca, Mg, K, Na, B, Fe, Mn, Cu, Zn, Al, and P. The lab calculated total exchange capacity (TEC) by summation of exchangeable cations (Ca, Mg, K, and NA) and by accounting for other bases and exchangeable hydrogen using the equation and conditional statements in Figure 2.1 (Ross & Ketterings 1995 and Ross 1995).



The Formulas Used To Determine TEC

$$\text{T.E.C.} = \frac{\left(\frac{\text{lb/A Ca}^{*}}{400} + \frac{\text{lb/A Mg}^{*}}{240} + \frac{\text{lb/A K}^{*}}{780} + \frac{\text{lb/A Na}^{*}}{460}\right)}{100 - (\text{other bases} + \text{exchangeable hydrogen})} \quad \text{x} \;\; {}^{*}100$$

Other Bases

$= 11.4 - \text{pH}$ if soil $\text{pH} > 6.1$
$= 17.4 - (2 \text{ x pH})$ if soil $\text{pH} > 3.0\ \&\ \leq 6.1$
$= 13.3 - (.6 \text{ x pH})$ if soil $\text{pH} \geq 2.2\ \&\ \leq 3$
$= 17.4 - (2 \text{ x pH}$ if soil $\text{pH} < 2.2$

Exchangeable Hydrogen

$= 0$ if $\text{pH} > 7.0$
$= (7 - \text{pH}) \text{ x } 15$ if $\text{pH} > 6.0\ \&\ \leq 7.0$
$= 195 - (30 \text{ x pH})$ if $\text{pH} > 5\ \&\ \leq 6.0$
$= 145 - (20 \text{ x pH})$ if $\text{pH} > 4.0\ \&\ \leq 5.0$
$= 105 - (10 \text{ x pH})$ if $\text{pH} > 3.0\ \&\ \leq 4.0$
$= 93 - (6 \text{ x pH})$ if $\text{pH} \geq 2.2\ \&\ \leq 3.0$
$= 155 - (25 \text{ x pH})$ if $\text{pH} < 2.2$

Figure 2.1 Equations and rules used by Brookside Laboratories, Inc. for determining interpolated soil property values. T.E.C. (total exchange capacity) was calculated as 100 times the sum of the pounds per acre (lb./A) of calcium (Ca), magnesium (Mg), potassium (K) and sodium (Na) ions in soil samples divided each by the constants 400, 240, 780 and 460, respectively, and all divided by 100 minus the sum of "other bases" and exchangeable hydrogen. The value for "other bases" and for exchangeable hydrogen were each determined using the conditional statements provided.

The lab determined the percentage of organic matter in each sample using the loss-on-ignition method (Schulte & Hopkins 1996) at 360°C, and they calculated estimated nitrogen release based on this loss-on-ignition procedure as well. I converted estimated nitrogen release from the reported units of lbs. / acre to ppm. Brookside additionally measured soil pH by combining one-part soil with one-part water and measuring with an electrode (McLean 1982), and they determined Bray II P using the method found in Bray & Kurtz (1945). Finally, Brookside calculated bulk density (in g/cm^3) by weighing a portion of each soil sample and dividing by the volume of that sample portion. I adjusted all values that Brookside reported as "less than" a given value in the following manner: < 0.2 ppm of Boron to 0.1 ppm, < 0.4 ppm of Zinc to 0.2 ppm, and < 0.2 ppm of BrayII P to 0.1 ppm. Lastly, I calculated percent base saturation for each sample as 100 minus the sum of percent exchangeable hydrogen and percent other bases (i.e., not Ca, Mg, K, or Na).

Project personnel

Professor Clarence F. Korstian established the Duke Forest plots in the 1930s and directed their study along with Professor Theodore. S. Coile and numerous Duke University personnel through the 1960s. Robert K. Peet and Norman L. Christensen resurveyed the plots beginning in 1978, and numerous students, technicians and volunteers resampled plots through the end of the century under the direction of Peet. Particularly prominent among these were Kathleen Baker-Brosh, Emily S. Bernhardt, Brian Bonham, James K. DeCoster, Lawrence L. Frank, Mark Kapolka, Barbara Lutz Hart, Robert I. McDonald, Michael F. Piehler, Rebecca A. Reed, Jon White, and Weimin Xi. W. Xi collected hurricane damage data in 1997 – 2001. Michael T. Lee managed the data from 2000 – 2012. R. K. Peet, W. Xi, M. Lee, M. McClung, H. Meeler, A. Noetzel, S. Snider, E. Bernhardt, K. Baker-Brosh, J. DeCoster and R. Reed all provided data error correction prior to 2010. I performed final data collection, soil collection, error correction, data standardization, database finalization, and archive preparation. Drew W. Chandler, Eric Hill, Kate E. Murphy, Robert Paxton, Alanna G. Marron, Lindsey Bargelt, Rebecca Leloudis, William Balton, Scott B. Parker, Christopher R. Hakkenberg, Sierra C. Woodruff, Kellyn McNulty, Catherine L. Alves, Spencer C. Snider, Abigail G. Henderson, M. T.

Lee, and R. K. Peet assisted me with 2012 – 2016 tree and soil data collection. Megan McClung (née Faestel), Hannah E. Meeler, Alexandra Q. Noetzel and S. C. Snider also assisted with data entry and error correction for 2012 – 2013 data.

Data set status and accessibility

The data were last updated June 2018 for the final format of all files. Metadata were last updated June 1, 2018; these metadata are complete for this period and are stored with the data. Original tree and plot data are available both digitally and as paper data forms. All digital data exist as supplemental files stored with the electronic copy of this dissertation in the ProQuest LLC Dissertations & Theses Database (PQDT). Any analytical use of the data described in this dissertation should be reported to the Duke Forest Office.

Archiving

All physical forms for tree data and plot metadata currently reside in Robert Peet's lab at University of North Carolina at Chapel Hill. These data will eventually be deposited in the Duke University Archives and made accessible via electronic request to the Duke University Archives.

The data

File identities

psp_dat_all.csv (contains all relevant tree data from extant PSP plots).

psp_extinct_dat.csv (contains historical tree data for extinct PSP plots).

psp_spec_codes.csv (contains species codes and species names).

psp_env.csv (contains site and soil data for all extant PSP plots).

psp_area_changes.csv (details changes in plot areas through time).

psp_plot_history.csv (contains tabulated disturbance histories prior to 1970 for all PSPs).

File sizes

psp_dat_all.csv – 138352 lines (36 columns), not including header row.

psp_extinct_dat.csv – 18275 lines (222 columns), not including header row.

psp_spec_codes.csv – 86 lines (7 columns), not including header row.

psp_env.csv – 37 lines (70 columns), not including header row.

Psp_area_changes.csv – 37 lines (19 columns), not including header row.

Psp_plot_history.csv – 54 lines (45 columns), not including header row.

File comments

psp_dat_all.csv:

I made a number of predictions and updates for missing and inaccurate height measures, condition codes and (to a lesser extent) diameters. These are described in detail under "Research methods." The original, non-modified values (including all of the missing values) for height, condition code and diameter are available as the variables OrigHT, OrigCC and OrigD, respectively. It should be noted that these "original" data values do reflect modifications made to the data prior to 2010, and so may not match all paper data sheets exactly. Additionally, the variable Htype is not well defined anywhere in the metadata, but I included it in the data for completeness sake.

psp_extinct_dat.csv:

This file contains tree growth data for all PSP plots that were no longer extant in 2012–13. The majority of these plots were destroyed, harvested or abandoned prior to 1980, with the two most recently extant plots (plots 32 and 33) last being sampled in 1984. As a result, none of these plots were mapped or resampled in the 1980s. These data were not as meticulously re-examined for errors in 2013, nor did they undergo the height predictions, post-processing procedures, or site and soil analyses mentioned in the research methods section above. I include these data here for the sake of maintaining the PSP data set's long history as completely as possible, but I do not encourage the use of these data under most analysis scenarios. Their plot histories were included in "psp_plot_histories.csv" in the supplemental files (Appendix S1) when such information was available.

psp_spec_codes.csv:

Scientific names follow the nomenclature of USDA NRCS PLANTS database (2017).

psp_env.csv:

This file contains both site and soil (A and B horizon) data for all extant PSP plots.

psp_area_changes.csv:

About one-half of plots have remained constant in size since the beginning of the study. The majority that changed in size or shape did so between 1978 and 1984 when R.K. Peet and N.L. Christensen remapped the plots to include X and Y coordinates for each tree. I placed permanent posts at each transect corner in 2012–13 to formalize plot layouts. Plot 49 is listed as changing plot area in its initial year because plot notes indicate the plot was to be 810 m^2, but trees were always measured in a slightly larger area of approximately 850 m^2.

psp_plot_history.csv:

The plot histories table lists general location information for each plot, the experimental purpose of each plot (when applicable) and any major manipulations or major disturbances experienced by each plot prior to 1980. Note that numerous plots were additionally modified when remapped after 1978, and many plots experienced major damage from Hurricane Fran in

1996. Remapping is detailed in “psp_area_changes.csv,” and Hurricane damage is addressed more quantitatively using hurricane damage codes found in “psp_dat_all.csv” found in the supplementary appendix (S1).

Format and storage mode

The data are saved as ASCII text that is comma delimited (i.e., they’re saved as comma separated values (.CSV files)). No compression schemes were used.

Authentication procedures

For the “psp_dat_all.csv” data, the sum of all StaticLineID values is 2014350643, and there are 138352 unique YearlyLineID values. Additionally, the SPEC code for line 100005 is “LIST” in Year 1992. There are 18275 unique YearlyLineID values in “psp_extinct_dat.csv”, all StaticLineID in these extinct data sum to 850884651 and the SPEC code for line 13000 is “PITA” in Year 1946. The SPEC code present in the fifteenth line of “psp_spec_codes.csv” is “CAOV,” and “*Sassafras albidum* (Nutt.) Nees” is present in row 71, column 5 with associated SPEC code “SAAL” in column 1. The eighteenth line (excluding header information) of “psp_env.csv” contains information for Plot 24 with a Dist.to.H2O value of 121.92 and a BS_B value of 50.8. The sum for all 37 values of TEC_A is 281.16. Column 5 (area_update1) of line 34 (associated with plot 51) of “psp_area_changes.csv” is 816, and the sum of all original max x-axis values (“x_max_orig” in column 13) is 1038.75. The sum of all plots in column 2 of “psp_plot_history.csv” is 1698, and the twenty-second column of the sixth row of this file reads “Second crown thinning. This plot had sufficient basal area / acre to permit an economic thinning and still retain approximately 100 square feet of basal area per acre as growing stock.”

Variable definitions

Table 2.1 Variable definitions for Duke Forest PSP tree growth data stored in "psp_dat_all.csv."

Variable Name	Variable Definition	Units	Storage	Range	Missing Value Codes
YearlyLineID	Unique database identifier number for each tree in each sampling year across entire data set. Assigned in order of increasing Year in increasing order of StaticLineID for trees 1933–2001 and in order of tree entry into database for trees from 2012–2013.	N/A	Integer	1–161015	No missing data
StaticLineID	Unique database identifier number for each tree across entire data set that remains static across sampling years.	N/A	Integer	1–77732	No missing data
Year	Year the stem was observed in yearly data	Calendar years	Integer	1933–2013	No missing data

PSPType	Forest location; “P” is for Duke Forest PSP and “H” is for Hill Forest plot	N/A	String	P or H	No missing data
Plot	Plot identification number	N/A	Integer	4–125	No missing data
TR	Transect on which stem was observed; typically 5m-wide contiguous divisions of plot along Y-axis	N/A	Integer	-1–12	NA
ID	Unique identifier number for each tree within a given plot	N/A	Integer	1–17694	No missing data
X	X-coordinate within given plot	Decimeters (dm)	Integer	-70–640	NA
Y	Y-coordinate within given plot	Decimeters (dm)	Integer	-73–807	NA
SPEC	Species Code (unique four-letter identifier for each species); typically the first two letters of genus and species. For full list, see psp_spec_codes.csv	N/A	String	N/A	No missing data

D	Diameter at Breast Height (1.37 m from base of main stem)	Centimeters (cm)	Floating point	0–89.5	NA
HT	Tree height. Measured as length of stem from base to highest point	Meters (m)	Floating point	0–49.2	NA

CC	Condition Code to categorize general condition of tree during sampling: 1: alive and reasonably intact 2: dead (confirmed by the presence of a dead stem) 3: missing (presumed dead, but no stem could be found for verification) 4: die back to below breast height or significant loss of height. A marginal note was usually made indicating the possible cause of damage. 5: cut (sawed down by humans) 6: damage from Hurricane Fran – see special hurricane codes, F1 through F4. *Missing value*: not a tree or not observed.	N/A	Integer	1–6	NA

Ingrowth	Code categorizing the ingrowth status of each stem in each sampling year: 0: old growth (stem previously recorded) 1: ingrowth 2: originally in plot (stem in plot’s initial year) 3: added due to increase in the dimensions of the plot	N/A	Integer	0–3	No missing data
Phase	Area associated with phase changes in plots. Phases change individually for each plot if and when the plot changes in shape or area. Trees are assigned a phase based on their location: 0: in original plot area (i.e., located in area that existed at plot inception) 1: in area added during plot’s first area increase or remapping	N/A	Integer	0–1	No missing data

PlotInitialYear	Year of initial sampling effort for the given plot	Calendar years	Integer	1933–1947	No missing data
PlotInitialAge	Estimated age of forest in initial sampling year for the given plot. Mixed-age hardwood stands arbitrarily assigned as 100.	Years	Integer	8–100	No missing data
PlotAge	Estimated age of forest stand for the given plot (calculated as PlotInitialAge + Years since initial sampling)	Years	Integer	8–179	No missing data
YearOfPreviousSample	Year of previous sampling date for each given tree (StaticLineID)	Calendar years	Integer	1933–2000	NA
TreeInitialYear	Year that specific tree (StaticLineID) was first measured	Calendar years	Integer	1933–2013	No missing data
Area	Extent of the plot	Square meters (m^2)	Integer	405–4047	No missing data
Species	Latin name of tree species	N/A	String	N/A	NA

OldTR	Indicates former transect number if plot was reshaped or trees were updated in location necessitating the transect be renumbered	N/A	Integer	-1–11	NA
OrigD	DBH recorded in field (prior to adjustments but checked for entry errors)	Centimeters (cm)	Floating point	0–89.5	NA
OrigHT	Tree height recorded in field (prior to predicted and adjusted values; checked for entry errors)	Meters (m)	Floating point	0–49.2	NA
OrigCC	Tree condition code recorded in field (prior to adjustments but checked for entry errors)	N/A	Integer	1–6	NA
CL	Indicates a clonal relationship with this ID. This is typically not applicable and so most often assigned NA.	N/A	Integer	63–3867	NA

Htype	Height quality code indicating source of height data prior to 2012. Values of 1 – 3 indicate that height was interpolated or obtained by regression because height measurements were missing, whereas a value of 4 indicates that the reported height value represents the actually recorded value from the field.	N/A	Integer	1–4	NA
F1	1997-98 Hurricane Fran stem damage code #1. Uprooting status (1 = OK, 2 = partial uproot, 3 = complete uproot)	N/A	Integer	1–4	NA
F2	1997-98 Hurricane Fran stem damage code #2. Breakage (1 = less than 10% canopy loss, 2 = 10-35% canopy loss, 3 = 35-90% canopy loss, 4 = more than 90% canopy loss)	N/A	Integer	1–4	NA

F3	1997-98 Hurricane Fran stem damage code #3. Leaning (1 = OK, 2 = leaning free, with lean over 10%, 3 = supported by another tree, 4 = down (on ground))	N/A	Integer	1–4	NA
F4	1997-98 Hurricane Fran stem damage code #4. Leaned on (1 = free, 2 = upright, supporting a tree (DBH >30% size of host), 3 = bent or leaning (crown displaced at least 10%), 4 = pinned)	N/A	Integer	1–4	NA
AZI	Azimuth of each fallen bole following Hurricane Fran in 1996. True North = 0°, East = 90°, South = 180° and West = 270°.	Degrees	Integer	8–345	NA
Crown	Crown height. Height from ground to base of crown. [Last sampled in 1984]	Meters (m)	Floating point	0.1–29.0	NA

Clear	Clear bole height. Height from ground to height of lowest branch (or visible defect) [Last sampled in 1978]	Meters (m)	Floating point	0–26.5	NA
NotesDba	Combination of some field notes and database notes. Typically database notes are surrounded by brackets “[ ]”	N/A	String	N/A	No missing data, but a blank indicates no note recorded

Table 2.2 Variable definitions for Duke Forest PSP extinct plot tree growth data stored in "psp_extinct_dat.csv."

Variable Name	**Variable Definition**	**Units**	**Storage**	**Range**	**Missing Value Codes**
YearlyLineID	Unique database identifier number for each tree in each sampling year across entire data set.	N/A	Integer	132856–151130	No missing data
StaticLineID	Unique database identifier number for each tree across entire data set that remains static across sampling years.	N/A	Integer	27001–74021	No missing data
Year	Year the stem was observed in yearly data	Calendar years	Integer	1933–1984	No missing data
PSPType	Forest location; "P" is for Duke Forest PSP and "H" is for Hill Forest plot	N/A	String	H or P	No missing data
Plot	Plot identification number	N/A	Integer	1–48	No missing data

TR	Transect on which stem was observed; typically 5m-wide contiguous divisions of plot along Y-axis	N/A	Integer	N/A	NA
ID	Unique identifier number for each tree within a given plot	N/A	Integer	1–1061	No missing data
X	X-coordinate within given plot	Decimeters (dm)	Integer	N/A	NA
Y	Y-coordinate within given plot	Decimeters (dm)	Integer	N/A	NA
SPEC	Species Code (unique four-letter identifier for each species); typically the first two letters of genus and species. See psp_spec_codes.csv for full list.	N/A	String	N/A	No missing data
D	Diameter at Breast Height (1.37 m from base of main stem)	Centimeters (cm)	Floating point	0–74.4	NA
HT	Tree height	Meters (m)	Floating point	0–39.3	NA

CC	Condition Code to categorize general condition of tree during sampling: 1: alive and reasonably intact 2: dead (confirmed as such by the presence of a dead stem) 3: missing (presumed dead, but no stem could be found for verification) 4: die back to below breast height or significant loss of height. A marginal note was usually made indicating the possible cause of damage. 5: cut (sawed down by humans) 6: damage from Hurricane Fran – see special hurricane codes, F1 through F4. *Missing value*: not a tree or not observed.	N/A	Integer	1–5	No missing data

PlotInitialYear	Year of initial sampling effort for the given plot	Calendar years	Integer	1933–1935	No missing data
PlotInitialAge	Estimated age of forest in initial sampling year for the given plot	Years	Integer	3–11	No missing data
PlotAge	Estimated age of forest stand for the given plot	Years	Integer	3–61	No missing data
YearOfPreviousSample	Year of previously sampling date for each given tree (StaticLineID)	Calendar years	Integer	1933–1978	NA
TreeInitialYear	Year that specific tree (StaticLineID) was first measured	Calendar years	Integer	1933–1984	No missing data
CL	Indicates a clonal relationship with this ID. This is typically not applicable and so most often assigned NA.	N/A	Integer	N/A	NA
Crown	Crown height. Stem height from ground to the base of the crown.	Meters (m)	Floating point	0–29.6	NA

Clear	Clear bole height. Stem height from ground to the height of the lowest branch (or visible defect, such as a knot)	Meters (m)	Floating point	0–24.7	NA
NotesDba	Combination of some field notes and database notes. Typically database notes are surrounded by brackets “[ ]”	N/A	String	N/A	No missing data, but a blank indicates no note was recorded

Table 2.3 Variable definitions for Duke Forest PSP species descriptions stored in "psp_spec_codes.csv."

Variable Name	Variable Definition	Units	Storage	Range	Missing Value Codes
SPEC	Species Code (unique four-letter identifier for each species).	N/A	String	N/A	No missing data.
Scientific Name	Latin name of species	N/A	String	N/A	No missing data, but "NA" indicates "not applicable."
Common Name	English (vernacular) name of species	N/A	String	N/A	No missing data.
Original Name	Variant of Latin name if obsolete name previously used in dataset; otherwise same as "Latin Name."	N/A	String	N/A	No missing data, but "NA" indicates "not applicable."
Scientific Name with Author	Latin name and Authority	N/A	String	N/A	No missing data, but "NA" indicates "not applicable."

USDA Code	United State Department of Agriculture abbreviated species symbol.	N/A	String	N/A	No missing data, but “NA” indicates “not applicable.”
NC Code	North Carolina Vegetation Survey abbreviated species code.	N/A	String	N/A	No missing data, but “NA” indicates “not applicable.”

Table 2.4 Variable definitions for Duke Forest PSP site and environmental data stored in "psp_env.csv." These data include geographic attributes, categorical topographic descriptors, and soil nutrients and texture data for each plot.

Variable Name	Variable Definition	Units	Storage	Range	Missing Value Codes
Plot	Plot identification number	N/A	Integer	4–125	No missing data
UTME	Universal Transverse Mercator Easting of plot center	Meters (m)	Floating point	676848.5379–690114.3329	No missing data
UTMN	Universal Transverse Mercator Northing of plot center	Meters (m)	Floating point	3983688.711–4008816.341	No missing data
Zone	Alphanumeric UTM grid zone defining longitudinal (numeric) and latitudinal (alphabetic) projection zones in which transverse Mercator projections (UTME and UTMN) are defined	N/A	String	17S	No missing data

Datum	Point of reference used by the Universal Transverse Mercator projection	N/A	String	NAD_1983	No missing data
Slope	Slope of plot	Degrees	Integer	0–7	No missing data
Aspect	Aspect of plot	Degrees	Integer	73–352	No missing data
Tasp	Transformed aspect. Calculated as: - COS(45 – Aspect)	N/A	Floating point	-0.99859–0.99437	No missing data
Position	Topographic position is a scalar that ranges from valley bottom (=1) through concave and convex slope to ridge and finally hilltop (=5)	N/A	Integer	1–5	No missing data

Exposure	Scalar that varies from sheltered draws (=1) through open hillsides and sheltered hilltops to exposed ridgetops (=5)	N/A	Integer	2–4	No missing data
PotSolar	Potential solar radiation; reported as "radiation index" (Frank & Lee 1966) or the ratio of the total annual potential insolation to the maximum potential insolation at the site.	Ratio	Floating point	0.4928–0.5351	No missing data
Elevation	Elevation of plot	Meters (m)	Floating point	89.916–161.544	No missing data
ElevClosestH2O	Elevation of closest body of permanent flowing water in the same watershed	Meters (m)	Floating point	80.772–137.16	No missing data

DistToH2O	Distance from plot to nearest body of permanent flowing water in the same watershed	Meters (m)	Floating point	3.048–290.1696	No missing data
TEC_A	Total Exchange Capacity - A Horizon	MEQ / 100g	Floating point	3.94–20.28	No missing data
pH_A	pH - A Horizon	pH units	Floating point	4–6.3	No missing data
OM_A	Organic Matter - A Horizon	%	Floating point	2.1–11.35	No missing data
N_A	Estimated Nitrogen Release - A Horizon	ppm	Floating point	31–63	No missing data
S_ppm_A	Sulfur (Mehlich III) - A Horizon	ppm	Floating point	8–25	No missing data
P_ppm_A	Phosphorus (Mehlich III) - A Horizon	ppm	Floating point	5–17	No missing data
P_BrayII_A	Phosphorus (Bray II) - A Horizon	ppm	Floating point	0.1–8	No missing data
Ca_ppm_A	Calcium (Mehlich III) - A Horizon	ppm	Floating point	182–1988	No missing data

Mg_ppm_A	Magnesium (Mehlich III) - A Horizon	ppm	Floating point	52–351	No missing data
K_ppm_A	Potassium (Mehlich III) - A Horizon	ppm	Floating point	29–133	No missing data
Na_ppm_A	Sodium (Mehlich III) - A Horizon	ppm	Floating point	11–29	No missing data
Ca_per_A	Saturation of calcium - A Horizon	%	Floating point	17.93–63.51	No missing data
Mg_per_A	Saturation of magnesium - A Horizon	%	Floating point	4.94–18.84	No missing data
K_per_A	Saturation of potassium - A Horizon	%	Floating point	0.8–8.53	No missing data
Na_per_A	Saturation of sodium - A Horizon	%	Floating point	0.43–2.36	No missing data
Other_bases_per_A	Saturation of other bases - A Horizon	%	Floating point	5.1–9.4	No missing data
H_per_A	Saturation of exchangeable hydrogen (H^+) - A Horizon	%	Floating point	10.5–65	No missing data

B_A	Boron (Mehlich III) - A Horizon	ppm	Floating point	0.1–0.87	No missing data
Fe_A	Iron (Mehlich III) - A Horizon	ppm	Floating point	84–376	No missing data
Mn_A	Manganese (Mehlich III) - A Horizon	ppm	Floating point	21–298	No missing data
Cu_A	Copper (Mehlich III) - A Horizon	ppm	Floating point	0.49–4.68	No missing data
Zn_A	Zinc (Mehlich III) - A Horizon	ppm	Floating point	0.94–11.98	No missing data
Al_A	Aluminum (Mehlich III) - A Horizon	ppm	Floating point	384–1428	No missing data
Bulk_den_A	Bulk density of soil - A Horizon	Grams / cubic centimeter (g/cm^3)	Floating point	0.64–1.26	No missing data
Clay_A	Percentage clay particles - A Horizon	%	Floating point	1.32–16.73	No missing data
Silt_A	Percentage silt particles - A Horizon	%	Floating point	8.52–34.97	No missing data
Sand_A	Percentage sand particles - A Horizon	%	Floating point	53.86–88.57	No missing data

BS_A	Base Saturation - A Horizon	%	Floating point	25.6–84.4	No missing data
TEC_B	Total Exchange Capacity - B Horizon	MEQ / 100g	Floating point	3.53–20.19	No missing data
pH_B	pH - B Horizon	pH units	Floating point	4.7–5.9	No missing data
OM_B	Organic Matter - B Horizon	%	Floating point	0.97–4.52	No missing data
N_B	Estimated Nitrogen Release - B Horizon	ppm	Floating point	19.5–47.5	No missing data
S_ppm_B	Sulfur (Mehlich III) - B Horizon	ppm	Floating point	5–81	No missing data
P_ppm_B	Phosphorus (Mehlich III) - B Horizon	ppm	Floating point	1–24	No missing data
P_BrayII_B	Phosphorus (Bray II) - B Horizon	ppm	Floating point	0.1–15	No missing data
Ca_ppm_B	Calcium (Mehlich III) - B Horizon	ppm	Floating point	119–1529	No missing data
Mg_ppm_B	Magnesium (Mehlich III) - B Horizon	ppm	Floating point	37–688	No missing data
K_ppm_B	Potassium (Mehlich III) - B Horizon	ppm	Floating point	17–160	No missing data

Na_ppm_B	Sodium (Mehlich III) - B Horizon	ppm	Floating point	12–183	No missing data
Ca_per_B	Saturation of calcium - B Horizon	%	Floating point	13.49–53.83	No missing data
Mg_per_B	Saturation of magnesium - B Horizon	%	Floating point	4.42–31.16	No missing data
K_per_B	Saturation of potassium - B Horizon	%	Floating point	0.28–8.14	No missing data
Na_per_B	Saturation of sodium - B Horizon	%	Floating point	0.36–4.32	No missing data
Other_bases_per_B	Saturation of other bases - B Horizon	%	Floating point	5.6–8	No missing data
H_per_B	Saturation of exchangeable hydrogen - B Horizon	%	Floating point	18–51	No missing data
B_B	Boron (Mehlich III) - B Horizon	ppm	Floating point	0.1–1.3	No missing data
Fe_B	Iron (Mehlich III) - B Horizon	ppm	Floating point	40–302	No missing data

Mn_B	Manganese (Mehlich III) - B Horizon	ppm	Floating point	18–367	No missing data
Cu_B	Copper (Mehlich III) - B Horizon	ppm	Floating point	0.45–2.22	No missing data
Zn_B	Zinc (Mehlich III) - B Horizon	ppm	Floating point	0.2–3.52	No missing data
Al_B	Aluminum (Mehlich III) - B Horizon	ppm	Floating point	554–1894	No missing data
Bulk_den_B	Bulk density of soil - B Horizon	Grams / cubic centimeter (g/cm^3)	Floating point	0.93–1.27	No missing data
Clay_B	Percentage clay particles - B Horizon	%	Floating point	4.47–33.62	No missing data
Silt_B	Percentage silt particles - B Horizon	%	Floating point	2.46–49.37	No missing data
Sand_B	Percentage sand particles - B Horizon	%	Floating point	20.54–76.34	No missing data
BS_B	Base Saturation - B Horizon	%	Floating point	41–76.4	No missing data

Table 2.5 Variable definitions for Duke Forest PSP area and mapping information and changes stored in “psp_area_changes.csv.”

Variable Name	Variable Definition	Units	Storage	Range	Missing Value Codes
plot	Plot identification number	N/A	Integer	4–125	No missing data
plot_type	Forest location; "P" is for Duke Forest PSP and "H" is for Hill Forest plot	N/A	String	N/A	No missing data
year_orig	Year that plot was originally established	Calendar years	Integer	1933–1947	No missing data
area_orig	Area of plot at establishment	Square meters (m^2)	Integer	405–4047	No missing data
area_update1	New area of plot after being remapped or enlarged	Square meters (m^2)	Integer	440–1940	NA
year_changed1	Year that plot was remapped or enlarged	Calendar years	Integer	1936–2012	NA
area_2012-2013	Current plot area (as of 2012–13 sampling period)	Square meters (m^2)	Integer	405–4047	No missing data
x_min	Current minimum X-coordinate in plot	Meters (m)	Floating point	-7–0	No missing data

x_max	Current maximum X-coordinate in plot	Meters (m)	Floating point	20–50.15	No missing data
y_min	Current minimum Y-coordinate in plot	Meters (m)	Floating point	-7.5–0	No missing data
y_max	Current maximum Y-coordinate in plot	Meters (m)	Floating point	20.1–80.7	No missing data
x_min_orig	Original minimum X-coordinate in plot	Meters (m)	Floating point	-7–2.6	No missing data
x_max_orig	Original maximum X-coordinate in plot	Meters (m)	Floating point	20.1–50.15	No missing data
y_min_orig	Original minimum Y-coordinate in plot	Meters (m)	Floating point	-6.6–3.3	No missing data
y_max_orig	Original maximum Y-coordinate in plot	Meters (m)	Floating point	20.1–80.7	No missing data
x_min_update1	Minimum X-coordinate after plot was enlarged	Meters (m)	Floating point	-7–0	NA
x_max_update1	Maximum X-coordinate after plot was enlarged	Meters (m)	Floating point	20–44.4	NA
y_min_update1	Minimum Y-coordinate after plot was enlarged	Meters (m)	Floating point	-7.5–0	NA
y_max_update1	Maximum Y-coordinate after plot was enlarged	Meters (m)	Floating point	20.1–56	NA

Table 2.6 Variable definitions for Duke Forest PSP plot history and experimental status information and changes stored in “psp_plot_histories.csv.”

Variable Name	Variable Definition	Units	Storage	Range	Missing Value Codes
Series	Range of plots that are experimentally grouped	N/A	String	N/A	No missing data
Plot	Plot identification number	N/A	Integer	1–125	No missing data
Forest	Forest location	N/A	String	N/A	No missing data
Division	Forest division name (if in Duke Forest)	N/A	String	N/A	NA
Compartment	Forest compartment number (if in Duke Forest)	N/A	Integer	2–64	NA
Stand	Forest stand number (if in Duke Forest)	N/A	Integer	1–28	NA
Established	Year (and usually month) plot was established.	Year (or month & year)	String	N/A	No missing data

Status	Current plot status: extinct (no longer sampled) or extant.	N/A	String	N/A	No missing data
YearLastSampled	Year that plot was most recently sampled. For Status = "extinct" plots, this is the last year the plot was sampled.	Calendar year	Integer	1945–2013	No missing data
StandDetail	Brief description of plot ecology and age	N/A	String	N/A	NA
Soil	Soil series description	N/A	String	N/A	NA
Purpose	Purpose for plot or plot series establishment	N/A	String	N/A	NA
ExperimentalRole	Role that given plot had in initial purposeful experiment among plot series plots	N/A	String	N/A	NA
Method1	First experimental manipulation (or noted disturbance) experienced by plot	N/A	String	N/A	NA
Method1Date	Date (typically month and year) of first plot manipulation	N/A	String	N/A	NA

Method2	Second experimental manipulation (or noted disturbance) experienced by plot	N/A	String	N/A	NA
Method2Date	Date (typically month and year) of second plot manipulation	N/A	String	N/A	NA
Method3	Third experimental manipulation (or noted disturbance) experienced by plot	N/A	String	N/A	NA
Method3Date	Date (typically month and year) of third manipulation	N/A	String	N/A	NA
Method4	Fourth experimental manipulation (or noted disturbance) experienced by plot	N/A	String	N/A	NA
Method4Date	Date (typically month and year) of fourth plot manipulation	N/A	String	N/A	NA

Method5	Fifth experimental manipulation (or noted disturbance) experienced by plot	N/A	String	N/A	NA
Method5Date	Date (typically month and year) of fifth plot manipulation	N/A	String	N/A	NA
Method6	Sixth experimental manipulation (or noted disturbance) experienced by plot	N/A	String	N/A	NA
Method6Date	Date (typically month and year) of sixth plot manipulation	N/A	String	N/A	NA
Method7	Seventh experimental manipulation (or noted disturbance) experienced by plot	N/A	String	N/A	NA
Method7Date	Date (typically month and year) of seventh plot manipulation	N/A	String	N/A	NA

Method8	Eighth experimental manipulation (or noted disturbance) experienced by plot	N/A	String	N/A	NA
Method8Date	Date (typically month and year) of eighth plot manipulation	N/A	String	N/A	NA
Method9	Ninth experimental manipulation (or noted disturbance) experienced by plot	N/A	String	N/A	NA
Method9Date	Date (typically month and year) of ninth plot manipulation	N/A	String	N/A	NA
Method10	Tenth experimental manipulation (or noted disturbance) experienced by plot	N/A	String	N/A	NA
Method10Date	Date (typically month and year) of tenth plot manipulation	N/A	String	N/A	NA

Method11	Eleventh experimental manipulation (or noted disturbance) experienced by plot	N/A	String	N/A	NA
Method11Date	Date (typically month and year) of eleventh plot manipulation	N/A	String	N/A	NA
Method12	Twelfth experimental manipulation (or noted disturbance) experienced by plot	N/A	String	N/A	NA
Method12Date	Date (typically month and year) of twelfth plot manipulation	N/A	String	N/A	NA
Method13	Thirteenth experimental manipulation (or noted disturbance) experienced by plot	N/A	String	N/A	NA
Method13Date	Date (typically month and year) of thirteenth plot manipulation	N/A	String	N/A	NA

Method14	Fourteenth experimental manipulation (or noted disturbance) experienced by plot	N/A	String	N/A	NA
Method14Date	Date (typically month and year) of fourteenth plot manipulation	N/A	String	N/A	NA
Method15	Fifteenth experimental manipulation (or noted disturbance) experienced by plot	N/A	String	N/A	NA
Method15Date	Date (typically month and year) of fifteenth plot manipulation	N/A	String	N/A	NA
Method16	Sixteenth experimental manipulation (or noted disturbance) experienced by plot	N/A	String	N/A	NA
Method16Date	Date (typically month and year) of sixteenth plot manipulation	N/A	String	N/A	NA

Publications and results

These data have been used in the following publications:

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CHAPTER 3: LARGE MAPPED PERMANENT SAMPLE PLOTS IN NORTH CAROLINA PIEDMONT FORESTS: MULTI-DECADAL INDIVIDUAL TREE GROWTH DATA

Summary

I describe a data set of tree inventory and growth collected across various time spans of up to 60 years in large mapped permanent sample plots in the Duke Forest and nearby Big Oak Woods both located in the northeastern Piedmont of North Carolina, USA. The purpose of these data is to allow observation of long-term successional trends in forest dynamics with the large plot sizes enabling examination of spatial patterns in gap dynamics and tree demographics through time. There are nine large mapped plots (5250 – 65536 m^2) that were established between 1951 and 1990 that have each been sampled 3 – 7 times with between-sample periods ranging from 2 – 22 years. Two of the plots consist of mid-successional old-field even-aged pine (*Pinus taeda*) stands that have near-fully transitioned to hardwood forests. The remaining seven plots consist of uneven-aged deciduous hardwood stands located over a range of site conditions, relative topographic positions and underlying soil nutrient conditions. Diameter (and sometimes height measurements) of individual stems allows for direct quantification of stand growth. Additionally, records of tree condition permit accounting for tree damage and mortality, especially in relation to damage from Hurricane Fran in 1996 that variously impacted plots. These data have previously been used to examine spatial and temporal patterns of species composition and diversity, seedling dynamics, tree regeneration, scale-dependence of vegetation-environment correlations and impacts of major wind disturbance on long-term forest dynamics.

Key words

Permanent sample plots, longitudinal study, secondary succession, Piedmont, forest, tree growth.

Introduction

Multiple decades of repeatedly resampled individual tree growth data were collected from large, mapped permanent sample plots (“MAPs”) in North Carolina Piedmont forests. Specifically, these data consist of the products of a long-term examination of forest growth and dynamics in the Duke Forest, North Carolina, and nearby Mason Farm Biological Reserve at the North Carolina Botanical Garden. The relatively large-scale plot sizes enable examination of spatial patterns in gap dynamics and tree demographics through time. These plots were established by various researchers including Robert K. Peet, Norman L. Christensen, Frank H. Bormann, Patricia Carlisle, and Michael W. Palmer.

Period of study

The period of study for the mapped plots was within the interval of 1952 – 2014. Plots were established in 1952 (plot 13), 1978 (plots 4, 7 and 12), 1984 (plots 91 and 92), 1986 (plots 14 and 93) and 1990 (plot 97). Five plots were designated for intensive study in 1989 and received both seedling and sapling subplot transects that were resampled through 2001 (not described in this chapter). Weimin Xi recorded damage from Hurricane Fran (1996) during the 1997 – 1999 resurveys. Plot 93 (“Bryan Center”) was not sampled after 1998 owing to developmental activities on the Duke University campus where it resided. I resampled all extant plots in 2014 and prepared data for archiving. All plots except 93 are expected to be resampled in the future.

Site description

Duke Forest and nearby Mason Farm Biological reserve are located in the northeastern portion of the North Carolina Piedmont in Orange and Durham Counties. Soils in these counties are primarily heavily weathered, physically-varying, low-nutrient soils formed from Carolina Slate and Triassic Basin sediments. These soils are spatially heterogeneous at the meter scale, which is reflected in the composition of overlaying vegetation (Peet & Christensen 1980, Palmer 1990). The study area has a warm temperate climate with 200-day growing season (Daniel 1994), mean annual temperature of 14.9 °C, and mean annual rainfall of 1185 mm (State Climate Office of North Carolina). Since 1930, the regional area has experienced at least three major ice storms, two hurricanes (Hazel in 1954 and Fran in 1996), a tornado, and two extreme droughts (Cook et al. 1998, Weaver 2005, Cook et al. 2010).

Humans have heavily altered North Carolina Piedmont vegetation since the time of European settlement. By 1850, most of the arable land was under cultivation, and less suitable land was typically exploited for wood or grazed (Peet & Christensen 1980). However, continued land abandonment that began in the mid nineteenth century (Christensen & Peet 1981) has led to significant reforestation throughout the area. Fast-growing pioneer tree species, especially *Pinus taeda*, dominated abandoned agricultural fields, and often continue to do so under modern forest management. Unmanaged stands have begun to transition to hardwood forests following senescence of canopy pines. The resulting landscape now consists of a mosaic of fields and floristically diverse forests in different stages of secondary succession with composition driven by edaphic conditions and land-use histories. In addition, high regional human population growth rates since the 1980s has led to further fragmentation of this mosaic landscape (McDonald & Urban 2006), and significant increases in herbivore pressure from *Odocoileus virginianus* (white-tailed deer; Osborne 1993) has further altered these forests over the last thirty years (Côté et al. 2004, Taverna et al. 2005, Israel 2011).

Founded in 1931, Duke Forest (~36.020 N, ~78.983 W) is a 2,800-hectare teaching and research forest that has served Duke University for over 85 years. The forest retains significant research value for many reasons, among them being the availability of three long-term monitoring data sets that include permanent sample plot data (described in Chapter 2), floristic composition plot data (Peet & Christensen 1980, Taverna et al. 2005, Israel 2011) and the large, mapped permanent sample data described here. Prominent stand types that have been the foci of these data collection efforts include even-aged successional *Pinus taeda* (and *Pinus echinata*) stands that resulted from the abandonment of old agricultural fields prior to the 1930's and uneven-aged deciduous hardwood forest stands that have been relatively undisturbed anthropogenically since prior to 1900 (Xi et al. 2008a).

Big Oak Woods (35.884 N, 79.014 W) is a 26-hectare bottomland hardwood forest located in the southeastern portion of Mason Farm Biological Reserve of the North Carolina Botanical Garden. The Mason family farm land was given to the University of North Carolina by bequest of Mary Elizabeth Morgan Mason in 1894 and officially established as a biological reserve in 1984. Big Oak Woods has been continuously forested since before European settlement, and 300+ year-old *Quercus alba* (white oak) trees have been located in the woods. Big Oak Woods has never been clear-cut or plowed, but, like most of the older forests of the Piedmont, the woods have been used as a woodlot and for cattle grazing. The forest experiences some degree of annual flooding owing to its proximity to Morgan Creek and the adjacent Triassic Basin.

Research plot history and description

Nine large mapped forest stands (MAPs; 3200 – 65536 m^2) with individually mapped trees were established in Durham and Orange Counties, North Carolina as permanent sample plots to track tree stem growth and community dynamics. Seven of these plots are located in one of three Divisions of Duke Forest: the Durham Division in western Durham County and the Korstian and Blackwood Divisions located in eastern Orange County. The eighth plot, Plot 97, is located in the Oosting Natural Area (35.976N, 79.057W), which is a part of Duke Forest due west of the Korstian Division in Orange County. The ninth plot (Plot 14, 23550 m^2) is located in nearby Big Oak Woods (Mason Farm Biological Reserve) in southeastern Orange County. Some of these plots have changed size due to remapping or enlarging, and, as a result, the extant MAPs now range from 5250 – 65536 m^2. Other than Plot 13 ("Bormann Plot"), which was established by F.H. Bormann in 1951 – 1952 (Borman 1953) and resampled beginning in 1974 by N.L. Christensen (Christensen 1977), all other MAP plots were established between 1978 – 1990 by R. K. Peet, N. L. Christensen and colleagues to supplement other small-scale permanent sample plots (PSPs; 405 – 1940 m^2) established by Professor Clarence Korstian of Duke University in the 1930s (see Chapter 2).

The larger size of the mapped plots allows for more detailed studies of spatial patterns, gap dynamics and demographic investigations and allows such analyses to be generalized to more than just a few dominant species. In addition to monitoring tree growth, five of these plots were designated for intensive study in 1989 and received both seedling and sapling subplot transects that were resampled through 2001. The plots have been used in a series of studies examining spatial pattern (Bormann 1950, 1953, Christensen 1977, Reed et al. 1993, Palmer & White 1994, Palmer et al. 2007), species diversity (Christensen 1977, Peet & Christensen 1987), seedling establishment, growth and survival (Philippi et al. 1993, 1994), trajectory of species composition (McDonald et al. 2002), spatial pattern of tree regeneration (McDonald et al. 2003), scale-dependence of vegetation-environment correlations (Palmer 1990, Reed et al. 1993) and impacts of disturbance (Xi & Peet 2008a, 2008b, 2011, Xi et al. 2008a, 2008b, 2012).

Two of the MAP plots consist of mid-successional even-aged pine stands that were agricultural fields prior to abandonment and subsequent plot establishment. Plot 4 (“Graveyard Plot”) was a 62-year-old *Pinus taeda* stand when established in 1978 and Plot 7 (“Land’s End Plot”) was an 80 – 90-year-old pine stand when established in 1978. Both plots are located in the Durham Division of Duke Forest. *Pinus taeda* (loblolly pine) is overwhelmingly the dominant pine in these plots, whereas *P. echinata* (shortleaf pine) exists to a much lesser degree in Plot 7. *Pinus virginiana* (Virginia pine) is near absent with only five individuals present in successional plots throughout the entire data set. The resampling of these successional pine stands has spanned the thinning of these pine stands and the transitioning of these stands to a mixed, uneven-aged hardwood forest.

Senescing and fallen pines are being replaced primarily by early-and mid-successional species such as (in order of decreasing abundance): *Liquidambar styraciflua, Liriodendron tulipifera, Acer rubrum, Oxydendrum arboreum,* and *Fraxinus spp*. Late-successional species such as oaks (e.g., *Quercus velutina, Quercus alba* and *Quercus rubra*) and hickories (e.g., *Carya tomentosa*, *Carya glabra,* and *Carya ovata*) have likewise begun entering the canopy, and stems of *Ulmus alata, Ulmus rubra, Ulmus americana* and *Acer floridanum* have begun filling the sub-canopy. Species such as *Ostrya virginiana, Cercis canadensis, Juniperus virginiana, and Carpinus caroliniana* remain relatively abundant in the mid-story and shrub layers. This is owing to these plots’ relatively more base-rich soils as compared to other old-field pine plots elsewhere in the Duke Forest. *Cornus florida*, which was previously a fairly abundant species in these stands, has declined precipitously throughout Duke Forest over the last three decades likely owing to the arrival of the dogwood anthracnose disease.

The remaining seven plots in the MAP data set consist of uneven-aged deciduous hardwood stands. These stands are located across a range of site conditions, relative topographic positions and underlying soil nutrients.

Plot 12 (“Rocky Plot”), located in the Korstian division of Duke Forest, is an upland mixed hardwood stand on rocky, high-calcium soil and is equivalent to Schafale’s (2012) Dry-Mesic Basic Oak–Hickory Forest (Piedmont Subtype; CEGL007232). The canopy is dominated by oaks (predominantly *Q. alba*, *Q. velutina*, Q. *rubra* and *Q. stellata*), hickories (e.g., *C. ovata*, *C. tomentosa* and *C. glabra*), *Fraxinus* species and to a lesser degree *Nyssa sylvatica* and *A. rubrum*. *Cercis canadensis*, *Fraxinus* species, *Chionanthus virginianus* and other basic indicator species are greatly abundant in the understory. A number of successional and pioneer species such as *Juniperus virginiana*, *U. alata* and *P. taeda* (along with understory species such as *C. canadensis* and *P. serotina*) have grown quickly in gaps created by Hurricane Fran in 1996.

Plot 13 (“Bormann Plot”) is an upland mixed hardwood stand on acidic, low-calcium soil in the Durham Division of Duke Forest. Infrequent presence of drier canopy oaks (e.g., *Quercus stellata* and *Quercus falcata*) indicates that this stand represents a forest type that is on the drier range of Schafale’s (2012) Dry-Mesic Oak–Hickory Forest (Piedmont Subtype; CEGL008475). Plot 13 contains numerous oaks typical of CEGL008475 (e.g., *Q. alba*, *Q. rubra* and *Q. velutina*), along with other typical species such as *O. arboreum*, *A. rubrum* and a number of hickories (e.g., *C. tomentosa*, *C. glabra*, *C. ovata* and *Carya carolinae-septentrionalis*). *L. tulipifera* has become more prevalent in the canopy following destruction and subsequent gap formation from Hurricane Fran in 1996, and numerous stems of *Prunus serotina*, *L. styraciflua* and *Viburnum prunifolium* have likewise increased in abundance since Hurricane Fran. *Cornus florida*, which was previously a very abundant species in this plot, has declined significantly (likely owing to dogwood anthracnose disease), as is the case throughout the Duke Forest.

Plot 14 ("Big Oak Woods Plot") is located in the Mason Farm Biological Reserve, Chapel Hill, NC. Plot 14 represents an alluvial hardwood stand situated in a flat floodplain with evidence of regular flooding. More specifically, Schafale (2012) describes this community type as a Piedmont Bottomland Forest (Typic Low Subtype; CEGL007356). *Quercus pagoda*, *Quercus phellos*, *Quercus michauxii*, *Q. alba*, and *L. styraciflua* dominate the canopy of this plot along with *C. ovata*, *N. sylvatica*, *A. rubrum*, *Fraxinus* species and three species of elms (*U. alata*, *U. rubra* and *U. americana*).

Plot 91 ("Whitfield Plot") is a mix of mesic hardwoods with some *Pinus taeda* indicating possible past disturbance. This community is equivalent to Schafale's (2012) Mesic Mixed Hardwood Forest (Piedmont Subtype; CEGL008465), and it occurs on an acidic north-facing slope in the Korstian Division of Duke Forest. *Fagus grandifolia* dominates the canopy of Plot 91, but is joined by numerous stems of *A. rubrum*, *P. taeda*, *L. tulipifera* and *Q. alba*. *Quercus coccinea*, *Q. rubra*, *C. glabra* and *C. tomentosa* are represented in the canopy to a lesser degree, and they have all declined in abundance since plot inception. *Oxydendrum arboreum* has thriven in the canopy and subcanopy in the last 20 years, especially following Hurricane Fran.

Plot 92 ("Bald Mountain Plot") represents a relatively high-elevation monadnock *Quercus montana* stand. Plot 92 is located on the south slope of Bald Mountain in the Blackwood Division of Duke Forest. Schafale (2012) defines the forest type representative of Plot 92 as Piedmont Monadnock Forest (Typic Subtype; CEGL006281). Dominant canopy species in this plot originally included *Q. montana*, *Q. alba* and *A. rubrum*. *O. arboreum* existed as a dominant subcanopy species. However, Plot 92 suffered extensive damage from Hurricane Fran in 1996, which opened a significant portion of the canopy in the plot. *A. rubrum*, *O. arboreum*, *Q. montana*, *L. tulipifera* and *P. serotina* have proliferated throughout the understory along with *Juniperus virginiana* and *Q. velutina* since 1999.

Plot 93 ("Bryan Center Plot") is an upland hardwood stand mixed with both *P. taeda* and *P. echinata*. The plot is located on Duke University campus and, as a result, the plot is in the most urban setting of the MAP plots. This forest stand appears to be most similar to Schafale's Dry Basic Oak–Hickory Forest (CEGL007773). *Q. alba* dominates the canopy of this plot along with *A. rubrum*, *Q. stellata*, numerous hickories (*C. tomentosa*, *C. glabra*, *Carya pallida* and *C. ovata*), *L. tulipifera*, *L. styraciflua*, *Fraxinus* species and *P. echinata*.

Plot 97 ("Oosting Plot") is a second-growth Piedmont hardwood forest dominated by *L. tulipifera*, *L. styraciflua*, *Quercus* species (particularly *Q. alba* and *Q. rubra*), *Carya* species (primarily *C. tomentosa*) and two *Pinus* species (*P. taeda* and *P. echinata*). The underlying basic soils (Palmer et al. 2007) and a suite of basic species (e.g., *Fraxinus* species, *Cercis canadensis*, *Carya ovata* and *Acer floridanum*) suggest that this forest represents Schafale's (2012) Dry-Mesic Basic Oak–Hickory Forest (Piedmont Subtype; CEGL007232). However, a number of trees uncommon to this forest type, such as *Oxydendrum arboreum*, *L. tulipifera*, *Fagus grandifolia*, and *Quercus falcata* also dominate in the canopy in certain regions of the plot. This suggests that the plot, which is over 6.5 ha in area, spans two forest types: CEGL007232 and CEGL008475 (Dry-Mesic Oak–Hickory Forest (Piedmont Subtype)). Palmer et al. (2007) provide a more detailed description of Plot 97.

Each of these plots received some damage from Hurricane Fran in 1996. Plots 4, 13, 92 and 93 were hit particularly hard and each received substantial damage from the storm.

Research methods

Tree sampling

Permanent mapped plots (or “MAPs”) were sampled generally every three to seven years (ranging from 2 – 22 years) typically during the growing season (May – August). Field crews sampled all plots generally in a single year when possible, but most sampling periods required two or more years to complete measurement of all extant plots. Plot 93 was not resampled in 2014 due to significant plot damage and construction on the Duke University campus where the plot resides.

Plots are divided into typically 10 m wide transects (though 8 m in MAP 97 and 12.5 m in MAP 14) along the X-axis (sometimes Y-axis). Transects are numbered consecutively starting from 1 or 0. Plot corners were marked with metal piping early in the plots’ histories for remapping purposes. Metal conduit was additionally added at regular intervals along transect lines throughout each plot, though the intervals are also variable between plots. As of 2016, 100% of conduits marking transect corners were extant.

The entirety of each plot is mapped using a Cartesian coordinate system. X and Y coordinates are in decimeters (dm) in plots 4, 7, 12, 91 and 92 and in meters in Plots 13, 14, 93 and 97. Coordinate lines typically start at zero in each plot, but if the plot was extended in the zero-direction along either axis during the study, negative coordinates were assigned to those extended regions. Very few trees were ever physically marked in this study. As a result, the majority of trees are best located in each plot using their X and Y coordinates. Coordinates are determined in the field using measuring tapes placed along axis and transect lines.

Each tree that was recorded received plot and transect numbers, X and Y coordinates, species code (“SPEC”), diameter measurement, condition code (“CC”), and any pertinent notes. In some instances, as in Plot 12 in 1985, Plot 91 in 1991 and 1998 and Plot 92 in 1991 and 1999, a height measurement was also recorded for some trees. Some trees (n ~ 880) were additionally assigned a clone number (“CL”) in the field if they were the clone of another individual. During each sampling effort, all previously mapped trees were re-measured and checked for errors and all new ingrowth individuals were assigned coordinates, identified to species, and measured. All trees were also automatically assigned a series of identification numbers when entered into the electronic database. These numbers include a sequential identification number for trees in the same plot (“ID”), a sequential ID number for identification of specific individuals across the entire data set (“StaticLineID”), and a unique identification number for each individual in each year (“YearlyLineID”).

The species code (or SPEC) is a four-letter code representing each species. Each code usually consists of the first two letters of the genus and the first two letters of the specific epithet. However, the first four letters of the genus are used when the species name is not known (rarely), and in some instances, other patterns were used to avoid duplicates (e.g., CACA = *Carya carolinae-septentrionalis* and CACR = *Carpinus caroliniana*). I maintained full species identifications for most taxa and grouped to genera only those species considered particularly difficult to split from related taxa based on vegetative characteristics (e.g., *Fraxinus* and *Crataegus* species). Leaf samples of species that could not be identified in the field were used to identify these individuals to minimize unknowns in the data.

Trees were only tallied and measured if their height achieved or exceeded 1.37 m (breast height). Further, trees had to be a minimum of 1 cm in diameter at breast height (DBH) to be considered for measurement, though this was not entirely consistent. Plot notes indicate that initial sampling efforts in Plot 14 (in 1986) and Plot 97 (in 1990) only measured trees with DBH ≥ 2 cm. Trees of smaller diameters (< 1 cm) were measured sporadically throughout the study, but, in 2014, all trees achieving breast height were measured regardless of diameter size.

The diameter at breast height (DBH) of each tree was determined by measuring the circumference of the main stem of each individual at breast height (1.37 m) using a diameter tape. Breast height was based on height along the stem and not by distance of the stem to the ground. Because of this, the diameter of leaning trees, trees growing on inclines, and fallen trees was measured 1.37 m from their base.

Measurement of trees with split or branched stems followed a strict protocol. If a tree stem split above 50 cm from the base, then only the largest stem was recorded and measured. However, if the stem of the tree split below 50 cm, then all such stems were recorded and measured as separate entities and identified as clones. In these instances, the field technician made a note and recorded a clone number for the split stems. If two stems of a tree were previously recorded as separate, they remained separate even if the split between stems grew to occur above breast height. On rare occasions, separate stems fused, and two measurements were no longer possible. Typically, in these instances, the larger or older stem was maintained in the data set, while a note was given to the final measurement of the fused stem. Finally, in any instance where a tree split approximately at breast height (1.37 m), the DBH was measured just below the split. This slight downward (or sometimes upward) adjustment in diameter measurement was likewise employed when a large knot or other unusual protrusion existed at breast height.

The height (in meters) of some trees was measured in Plot 12 in 1985, Plot 91 in 1991 and 1998 and Plot 92 in 1991 and 1999. Measurement of tree height followed the same rules for determining individuals as described above for measuring DBH. A telescoping, graduated height pole was used to measure most trees shorter than 10 m. The pole was extended upward until the top of the pole matched the height of the tree being measured as sighted by a nearby field technician. Taller trees were measured using a mechanical Blume-Leiss altimeter (or alternatively an Abney level).

One of six condition codes (CC) was assigned to each tree in each sampling period. CC = 1 was assigned to all living trees in good health as well as the majority of new ingrowth individuals. CC = 2 was assigned for all dead trees defined as having no living leaves and still standing or that had fallen and could be definitively identified. CC = 3 was assigned to all missing trees, which were typically assumed to be dead but without a standing stem for verification. Missing trees never received diameter or height measurements, and dead trees only rarely received any growth measurement. CC = 4 was assigned to trees that had a significant loss of height, experienced major die back, or was strongly leaning. Early on in the study, this code was reserved for trees that shrunk to below breast height, but later, all trees that shrunk received this code. In most of these instances, diameter and height measurements were taken if possible, and the tree was given a note describing the field technician’s best guess as to the cause of the change. If the height had been reduced to below 1.37 m, then no measurement was taken and a note indicating so was often reported. CC = 5 was assigned to trees that were cut by humans, which only rarely occurred early in the study. Finally, in the resurveys of 1997 – 1999, hurricane damage codes were assigned to indicate the impact of Hurricane Fran in 1996. Though a system of more detailed codes (see below and Xi et al. 2008) was developed to describe these damages, these trees received a CC = 6 to indicate whether there was any type of tree damage from the hurricane.

Four ordinal stem damage codes were used in 1997 – 1999 to summarize the overall damage to trees following Hurricane Fran in 1996. These four codes, represented individually in the data as “F1” through “F4,” were integrated to easily represent overall damage to stems (Xi et al. 2008). F1 represented uprooting status with a value of 1 indicating no uprooting, 2 indicating a partial uproot, and 3 indicating the tree was completely uprooted. F2 coded for “breakage” with values ranging from 1 – 4 signifying 10% canopy loss, 10 – 35% canopy loss, 35 – 90% canopy loss, and >90% canopy loss, respectively. F3 indicated the degree to which a tree was leaning because of the hurricane and likewise ranged from 1 – 4. F3 values represented no lean, leaning free with lean >10%, being supported by another tree, and having completely fallen on the ground. Finally, F4 coded for the degree to which other damaged trees were impacting the tree of interest, particularly by leaning on said tree. Again, this code ranged from 1 – 4 with codes indicating whether the tree of interest was not leaned-on (free), was upright and supporting a tree (DBH >30% size of host), was bent or leaning (crown displaced at least 10%), or was pinned. In addition to these four damage codes, field technicians also determined the azimuth (“AZI”) of all fallen stems using a compass in the 1997 – 1998 sampling period.

Nomenclature

Nomenclature follows the USDA PLANTS database (USDA, NRCS 2017).

Error correction and data standardization

With more than 216,000 data entries across almost 65 years in the MAP data set, errors and various other issues in the data were unavoidable. The number of different field technicians, data entry personnel, and database versions only served to compound these issues. Although some issues were clearly generated due to errors in the field (e.g., skipping trees or poor handwriting), the majority of errors in the data seemed to have been generated during electronic data entry and shifts in database versions or coding. I diligently checked these errors for all data across all years.

Various project personnel had previously visually proofed tree data and matched written data sheet records with computer files. Subsequently, I methodically searched for and examined outliers, inconsistencies, irregularities, and potentially problematic scenarios involving tree data and then addressed these issues as described below. I additionally checked all tree metadata and plot history information for inconsistencies and unlikely values.

I corrected all unknown, blank, misspelled, and synonymized species codes (SPECs) by examining a list of unique SPECs in the database and ensuring that each conformed to the spelling of known species codes in the study. I examined individual trees with changing SPECs across time (often due to the changing opinion of field technicians), trees with ecologically or geographically unlikely assigned SPECs, and misidentified trees (most commonly *Carya*, *Viburnum* and *Celtis* species). I did so by examining original data sheets, inspecting known range maps of species and using plant samples from extant individuals. When I could not confirm a definitive species, I opted for a genus-level SPEC code (rarely) or added a note to the database to suggest the best SPEC to use moving forward. I also corrected any blanks and typographical errors for plot numbers, plot types, and year using original plot notes to adjust non-valid entries in the electronic database.

Trees marked as being dead or missing two sampling periods in a row were automatically removed from subsequent sampling field data sheets. However, some of these trees survived in diminutive form; as re-sprouts from stumps, trunks or branches; or, in the case of numerous redbuds (*Cercis canadensis*) knocked over in Hurricane Fran in 1996, as horizontally growing trees with major branches turned upward as vertical growth. Often, this regrowth was not made apparent until numerous sampling periods after the tree had last been marked as dead or missing. As a result, subsequent field crews identified revived growth from some of these trees as new individuals ("ingrowth"). This was only appropriate if the new growth developed below 50cm up the trunk of the previously recorded individual (as described previously for designation of split trees as distinct individuals). Otherwise, these new recordings had to be included as new growth for an existing but no-longer searched for individual that had been removed from field sampling sheets. I accounted for these revived trees by inspecting old data sheets to properly identify which individual was found. I updated the identification numbers of these trees to match the old individual, and I removed the newer tree ID from the database.

I examined all instances in which trees were given notes indicating their missing status as questionable (e.g., due to coordinate inaccuracies), instances in which ingrowth individuals were outliers in their DBH or height, and most instances of damaged or killed trees following Hurricane Fran. I then compared the SPEC, size, condition, and available notes of each questionable ingrowth (or missing) tree as defined in the previous sentence to that of the closest missing (or ingrowth) tree. I made an individual assessment of each situation to determine if the ingrowth tree was in fact new. In instances where I felt confident the tree had previously been recorded, I corrected the ID values and removed the ingrowth tree ID from the database. In all instances, I added a note indicating the solution. I also noted that some exceptionally large ingrowth individuals that were not determined to be regrowth individuals were likely skipped in previous sampling periods, and I marked them as such. Often, these trees were located along plot or transect perimeters.

In some instances, prior data entry personnel failed to transfer some trees from printed data sheets to the electronic database or failed to do so accurately. As a result, subsequent field technicians unknowingly recorded these individuals, often with larger than expected sizes, as ingrowth. To determine if questionable individuals had simply not been electronically recorded, I examined hand-recorded datasheets from previous sampling periods for all trees that were large outliers in DBH or height or that contained notes questioning their size or prior status. Again, in instances where I felt confident the tree had previously been recorded, I corrected the ID values and removed the newer tree ID from the database.

I also examined possible duplicates of individual trees. This issue seemed to arise most often along perimeter lines between adjacent transects or in dense patches of homogeneous sapling growth. However, I could only recognize the latter if notes for individuals or observation of extant individuals left obvious clues. I was able to examine possible perimeter duplicates more methodically. I examined each individual tree that grew within 5cm of each transect perimeter and compared those trees to each nearby individual within 5 cm of the shared perimeter line of the adjacent transect. I made decisions on an individual basis by noting the distance of each tree from the line and comparing the SPEC, size, condition, and available notes of each tree in question. In instances where trees were determined to be measured in one transect but later marked as missing and measured subsequently in the adjacent transect, I eliminated the duplicate and updated the tree in the transect that seemed most appropriate based on plot coordinates or observation of extant individuals in the field.

I next methodically checked for blanks and outliers in the numerical data: static tree ID (“StaticLineID”), yearly tree ID (“YearlyLineID”), tree ID in plot (“ID”), transect number, X and Y coordinates, condition code (CC), diameter, and height. Most issues involving ID errors or transect errors were either easily identifiable typographical errors or corrected through the methods described above. I filled in missing coordinates when the data existed to do so or through verification in the field.

I accounted for DBH, height, and CC outliers and blanks by examining previous data sheets when possible, but overall these and related errors for DBH, height, and CC were more difficult to fix. Trees missing diameter were often attributable to data entry errors or typographical errors and could typically be adjusted. However, I left blank measurements for trees lacking both diameter and height measurements as well as any indication of their status, but I provided notes explaining why no correction could be made for these trees. Tens of thousands of trees lacked a height measurement, but only very few of these were due to similar reasons as the missing DBH info. Most of the trees lacking a height measurement actually never had their heights measured. These non-existent height measurements were assigned as NA in the data.

There were assorted issues pertaining to the condition code (CC) of numerous individuals in the data set. I changed all CC values less than 1 or greater than 6 by using previous CC values, past and present measurement values, sample notes, and nearby trees as guides. I fixed most of the trees marked as living (CC=1) that lacked measurement data by examining old data sheets for typographical errors or through methods described above for fixing diameter. Often, trees with CC > 3 had written notes that helped to confirm or update many CC values. I examined notes for trees marked as CC = 5 (cut) to see whether they had in fact been cut to confirm the condition code, and only trees measured after Hurricane Fran (1997 – 1999) were allowed to be assigned CC = 6 when appropriate. I updated all other trees assigned as CC = 5 or 6 to CC = 3 or 4 based on available evidence of past, present, and subsequent measurements and notes. For example, previous field technicians erroneously applied condition-code methodologies from a concurrent study to some trees by assigning CC = 5 to indicate “damage to the tree (e.g., by insects, by clumsy field crew member, etc.).” Using available data, I updated and changed all of these trees’ condition codes to conform to recent methodologies, and I made a note indicating this process for each updated tree.

Issues pertaining to trees with CC = 2, 3, or 4 were often more complicated and involved close examination of time between sampling periods, tree size, relative growth rates, SPEC, and presence of hurricane damage. Some trees were assigned a CC = 2 (dead) or 3 (missing) but then measured again in a subsequent sampling period (sometimes due to corrections I had made pertaining to missing tree issues described above). In cases when the subsequent sampling effort assigned the tree as CC = 4, I kept the initial CC as it was. This is because the tree likely validly received a CC = 2 or 3 because it died or was damaged to the point that it was not there or not visible at breast height (BH). The following sampling year it was given a CC = 4 if that year's field crew saw regrowth, resprouting, or evidence of a living tree that was either still below BH or clearly growing up from below BH. I likewise kept the condition codes as they were for the similar scenario in which missing or dead trees were later assigned a CC = 1 but clearly had grown back above BH following severe damage. I often placed a note indicating this had occurred if a note did not already exist. Trees that were recorded as missing (CC = 3) in 1997 following Hurricane Fran but then grew back (CC = 1) by 2000 were also kept as is because it was likely that damaged debris were crushing or obscuring these trees.

Numerous trees that had been assigned as dead or missing but later relocated were deemed to have been skipped, overlooked, or wrongly assigned a CC = 2 or 3. In most of these instances, I reassigned the CC from 2 or 3 to CC = 1 and calculated new DBH measurements for each individual using calculated growth rates for each individual. I did so by determining the change in size from the sampling period before the period in question to the period the tree was next measured, dividing by the length of the time interval to calculate a yearly growth rate, and multiplying that value by the length of time from the previous sampling period to the period in question.

In the remaining instances of the wrongly assigned dead or missing trees, the measurement of the trees was smaller in the sampling period in which they returned as compared to when they had last been given measurements. As a result, I assumed the trees had been damaged in the interval they were missing. However, I concluded that the damage was likely not severe enough to warrant a CC = 2 or 3 because of the relatively large size of each tree when it was remeasured. Therefore, in these instances I opted to assign each tree a CC = 4 in the period under question (instead of CC = 2 or 3). Because the size of each of these trees was large enough in the following sampling period to assume that each tree had not been damaged below breast height during the misreported period, I assigned each tree an appropriate diameter value for the period under question. I opted to assign these trees DBH values from the sampling year when they were first remeasured following assignment of CC = 2 or 3.

Project personnel

F. Herbert Bormann established plot 13 (now called the "Bormann plot") in 1952, and Robert K. Peet and Patricia Carlisle established plots 4, 7 and 12 in 1978. Robert Peet established plot 92 on Bald Mountain in 1984. All of these plots came from or were under the direction of Robert K. Peet and Norman L. Christensen in the 1980s, who subsequently established plot 91 (1984) and plots 14 and 93 (1986). Michael W. Palmer established plot 97 (the "Oosting Plot") in 1989, which was also subsequently placed under the direction of Peet and Christensen. However, trees stems were first recorded for plot 97 in 1990 by Rebecca A. Reed.

Numerous students, technicians and volunteers resampled plots through the end of the century under the direction of Peet. Particularly prominent among these were Kathleen Baker-Brosh, Emily Bernhardt, Brian Bonham, James K. DeCoster, Lawrence L. Frank, Mark Kapolka, Michael Lee, Barbara Lutz, Robert I. McDonald Jr., Michael F. Piehler, Rebecca A. Reed, Jon White, Rickie D. White and Weimin Xi. W. Xi collected hurricane damage data in 1997 – 1999. Michael T. Lee managed the data from 2000 – 2012. I performed final data collection, error correction, database finalization and archival preparation. Meghan L. Cooper, Natalie R. Lynch, Francesca Marsh, Emily R. Adams, S. Shouvik Saleh, Alopi A. Modi and Scott B. Parker assisted me with 2014 tree data collection. Alexandra Q. Noetzel and Spencer C. Snider assisted with data entry and error correction for 2012 – 2013 data.

Data set status and accessibility

The data were last updated November 2016 for the final format of all files. Metadata were last updated December 1, 2016; these metadata are complete for this period and are stored with the data. Original tree and plot data are available both digitally and as paper data forms. All digital data exist as supplemental files (Appendix S2) stored with the electronic copy of this dissertation in the ProQuest LLC Dissertations & Theses Database (PQDT). All physical forms for tree data and plot metadata are available via Robert Peet's lab in the University of North Carolina at Chapel Hill Biology Department. All other data are available strictly in digital format.

Archiving

All physical forms for tree data and plot metadata are expected to be deposited in the Duke University Archives for long-term storage and made accessible via electronic request to the University Archives.

The data

File identities

map_dat_all.csv (contains all relevant tree data from extant PSP plots).

map_spec_codes.csv (contains species codes and species names).

map_area_changes.csv (details changes in plot areas through time).

File sizes

map_dat_all.csv – 216347 lines (53 columns), not including the header row.

map_spec_codes.csv – 88 lines (7 columns), not including the header row.

map_area_changes.csv – 9 lines (40 columns), not including header row.

File comments

map_dat_all.csv:

Initial plot ages for mixed-age hardwood stands were arbitrarily assigned as 100.

map_spec_codes.csv:

Scientific names follow the nomenclature of USDA NRCS PLANTS database (2017).

map_area_changes.csv:

No comments.

Format and storage mode

The data are saved as ASCII text that is comma delimited (i.e., they're saved as comma separated values (.CSV files)). No compression schemes were used.

Authentication procedures

For the “map_dat_all.csv” data, the sum of all StaticLineID values is 6696155164, and there are 216347 unique YearlyLineID values. Additionally, the SPEC code for line 100005 is “LIST” in Year 1997 and Plot 14. The SPEC code present in the fifteenth line (excluding header) of “psp_spec_codes.csv” is “CARY,” and “Sassafras albidum (Nutt.) Nees” is present in row 71, column 5 with associated SPEC code “SAAL” in column 1. The twelfth column of the eighth row (excluding header) of “map_area_changes.csv” contains “185x40 + 200x60 (with section b/w 80-200 X & 80-100 Y not sampled).”

Variable definitions

Table 3.1 Variable definitions for Duke Forest MAP plot tree growth data stored in “map_dat_all.csv.”

Variable Name	Variable Definition	Units	Storage	Range	Missing Value Codes
YearlyLineID	Unique database identifier number for each tree in each sampling year across entire data set	N/A	Integer	1–279086	No missing data
StaticLineID	Unique database identifier number for each tree across entire data set that	N/A	Integer	1–80389	No missing data

	remains static across sampling years.				
Year	Year the stem was observed in yearly data	Calendar Years	Integer	1952–2014	No missing data
PlotType	Type of Duke Forest permanent sample plot. "MAP" designates a mapped permanent sample plot.	N/A	String	N/A	No missing data
Plot	Plot identification number	N/A	Integer	4–97	No missing data
TR	Transect on which stem was observed. Typically 5 – 12.5 m wide contiguous divisions of plot typically along X-axis (but sometimes along Y-axis).	N/A	Integer	0–20	No missing data
ID	Unique identifier	N/A	Integer	1–31362	No missing

	number for each tree within a given plot				data
X	X-coordinate within given plot. (Absolute X-coordinates).	Decimeters (dm) or meters (cm)	Floating point	-295–2571	No missing data
Y	Y-coordinate within given plot. (Absolute Y-coordinates).	Decimeters (dm) or meters (cm)	Floating point	-0.1–2560	NA
SPEC	Species Code (unique four-letter identifier for each species); typically the first two letters of genus and species. See map_spec_codes.csv for full list.	N/A	String	N/A	No missing data
D	Diameter at Breast Height (1.37 m from base of main	Centimeters (cm)	Floating point	0–105.7	NA

	stem)				
HT	Tree height. Measured as length of stem from base to highest point	Meters (m)	Floating point	0–57	NA
CC	Condition Code to categorize general condition of tree during sampling: 1: alive and reasonably intact 2: dead (confirmed as such by the presence of a dead stem) 3: missing (presumed dead, but no stem could be found for verification) 4: die back to below breast height or significant loss	N/A	Integer	1–6	NA

	of height. A marginal note was usually made indicating the possible cause of damage. 5: cut (sawed down by humans) 6: damage from Hurricane Fran – see special hurricane codes, F1 through F4. *Missing value*: not a tree or not observed.				
Ingrowth	Code categorizing the ingrowth status of each stem in each sampling year: 0: old growth (stem previously recorded)	N/A	Integer	0–3	No missing data

	1: ingrowth 2: originally in plot (stem in plot's initial year) 3: added due to increase in the dimensions of the plot				
Phase	Code for the area associated with phase changes in plots. Phases change individually for each plot if and when the plot changes in shape or area. Trees are assigned a phase based on their location: 0: in original plot area (i.e., located in area that existed at	N/A	Integer	0–2	No missing data

	plot inception) 1: in area added during plot's first area increase or remapping 2: in area added during plot's second area increase or remapping				
CO	Column number. 16 m-wide transects along X-axis. For MAP 97 only.	N/A	Integer	0–15	No missing data, but entries outside of MAP plot 97 are recorded as NA
RW	Row number. 16 m-wide transects along Y-axis. For MAP 97 only.	N/A	Integer	0–15	No missing data, but entries outside of MAP plot 97 are recorded as NA

BX	Field X coordinates within a grid block. For MAP 14, X coordinates relative to Haven Wiley's 25 x 25 m grid system throughout Big Oak Woods. For MAP 97, X coordinates within each 16 x 16 m grid cell. These are the coordinates printed on MAP 97 data sheets.	Decimeters (dm) or meters (cm)	Floating point	0–210	NA
BY	Field Y coordinates within a grid block. For MAP 14, Y coordinates relative to Haven Wiley's 25 x 25 m grid system throughout Big Oak Woods.	Decimeters (dm) or meters (cm)	Floating point	-0.1–670	NA

	For MAP 97, Y coordinates within each 16 x 16 m grid cell. These are the coordinates printed on MAP 97 data sheets.				
PlotInitialYear	Year of initial sampling effort for the given plot	Calendar Years	Integer	1952–1990	No missing data
PlotInitialAge	Estimated age of forest in initial sampling year for the given plot	Years	Integer	80–100	NA
PlotAge	Estimated age of forest stand for the given plot	Years	Integer	80–136	NA
YearOfPreviousSample	Year of previously sampling date for each given tree (StaticLineID)	Calendar Years	Integer	1952–2001	NA
TreeInitialYear	Year that specific tree (StaticLineID)	Calendar Years	Integer	1952–2014	No missing data

	was first measured				
Area	Extent of the plot	Square meters (m^2)	Integer	3200–65536	No missing data
XYUnits	Unit of measurement used for plot coordinates for given plot. Either decimeters (dm) or meters (m).	N/A	String	N/A	No missing data
PlotDimensions	Description of plot dimensions (and layout when pertinent).	N/A (but dimension descriptions are in meters (m))	String	N/A	No missing data
MinimumStemSize	Smallest stem diameter that was sampled in the given plot in the given year.	Centimeters (cm)	Floating point	0.1–2.0	No missing data
BLK	Grid cell within Haven Wiley's 25 x 25 m grid system throughout Big Oak	N/A	String	N/A	NA

	Woods.				
OX	Old (superseded) X coordinates	Decimeters (dm)	Integer	-50–1225	NA
OY	Old (superseded) Y coordinates	Decimeters (dm)	Integer	-50–869	NA
NX	"New" X coordinate adjusted from field X coordinate to account for topographic curvature and other spatial errors in plot layout. For MAP 97 Only. See Palmer et al. (2007) for details.	Decimeters (dm)	Integer	0–218	NA
NY	"New" Y coordinate adjusted from field Y coordinate to account for topographic	Decimeters (dm)	Integer	0–670	NA

	curvature and other spatial errors in plot layout. For MAP 97 Only. See Palmer et al. (2007) for details.				
AID	Archived id number now superseded by current ID	N/A	Integer	0–7141	NA
OldSPEC	Species code previously assigned to tree if the tree's SPEC had been updated, changed or fixed in database.	N/A	String	N/A	NA
YearlySPEC	Species code assigned to each tree each year. Useful for tracking species changes as errors, opinions, evidence or keys changed throughout	N/A	String	N/A	No missing data

	time for individual trees.				
OrigCC	Tree condition code recorded in field (prior to adjustments but checked for entry errors)	N/A	Integer	1–6	NA
CL	Indicates a clonal relationship with this ID. This is typically not applicable and so most often assigned NA.	N/A	Integer	6–28953	NA
F1	1997-98 Hurricane Fran stem damage code #1. Uprooting status (1 = OK, 2 = partial uproot, 3 = complete uproot)	N/A	Integer	1–4	NA
F2	1997-98 Hurricane Fran stem damage	N/A	Integer	1–4	NA

	code #2. Breakage (1 = less than 10% canopy loss, 2 = 10-35% canopy loss, 3 = 35-90% canopy loss, 4 = more than 90% canopy loss)				
F3	1997-98 Hurricane Fran stem damage code #3. Leaning (1 = OK, 2 = leaning free, with lean over 10%, 3 = supported by another tree, 4 = down (on ground))	N/A	Integer	1–4	NA
F4	1997-98 Hurricane Fran stem damage code #4. Leaned on (1 = free, 2 = upright, supporting a tree (DBH >30% size of host), 3 = bent or leaning	N/A	Integer	1–4	NA

	(crown displaced at least 10%), 4 = pinned)				
AZI	Azimuth of each fallen bole following Hurricane Fran in 1996. True north is equal to 0°, east equal to 90°, south equal to 180° and west equal to 270°.	Degrees	Integer	20–359	NA
InitialEcology	Description of initial ecology of plot	N/A	String	N/A	No missing data
Composition	Description of plot community type	N/A	String	N/A	No missing data
PlotUTME	Easting coordinate (UTM) of plot center	Meters (m)	Floating point	680386.9–680386.9	NA
PlotUTMN	Northing coordinate (UTM) of plot center	Meters (m)	Floating point	3987934.6–3987934.6	NA

PlotUTMZone	UTM zone number	N/A	Integer	17–17	NA
LocationAccuracy	Accuracy of GPS reading	Meters (m)	Floating point	N/A	NA
PlotNotes	Notes pertaining to entire plot that tree lies within	N/A	String	N/A	No missing data, but a blank indicates no note was recorded
StaticDbaNotes	Database notes added to static tree identification information	N/A	String	N/A	No missing data, but a blank indicates no note was recorded
NotesDba	Combination of some field notes and database notes. Typically database notes are surrounded by brackets "[ ]"	N/A	String	N/A	No missing data, but a blank indicates no note was recorded

Table 3.2 Variable definitions for Duke Forest MAP plot species descriptions stored in "map_spec_codes.csv."

Variable Name	Variable Definition	Units	Storage	Range	Missing Value Codes
SPEC	Species Code (unique four-letter identifier for each species).	N/A	String	N/A	No missing data.
Scientific Name	Latin name of species	N/A	String	N/A	No missing data, but "NA" indicates "not applicable."
Common Name	English (vernacular) name of species	N/A	String	N/A	No missing data.
Original Name	Variant of Latin name; otherwise same as "Latin Name"	N/A	String	N/A	No missing data, but "NA" indicates "not applicable."
Scientific Name with Author	Latin name and Authority	N/A	String	N/A	No missing data, but "NA" indicates "not applicable."
USDA Code	United States Department of Agriculture abbreviated species	N/A	String	N/A	No missing data, but "NA" indicates "not applicable."

	symbol.				
NC Code	North Carolina Vegetation Survey abbreviated species code.	N/A	String	N/A	No missing data, but "NA" indicates "not applicable."

Table 3.3 Variable definitions for Duke Forest MAP plot area and mapping information and changes stored in "map_area_changes.csv."

Variable Name	Variable Definition	Units	Storage	Range	Missing Value Codes
Plot	Plot identification number	N/A	Integer	4–97	No missing data
Name	Plot identification name	N/A	String	N/A	No missing data
Location	Forest that plot is located in	N/A	String	N/A	No missing data
Composition	Brief description of forest type	N/A	String	N/A	No missing data
Establisher	Name of individual that established plot	N/A	String	N/A	No missing data
GridMarkers	X and y dimensions	Meters (m)	String	N/A	No missing data

	indicating spacing of metal grid markers throughout plot				
CoordinateUnits	Units used for plot coordinates. Either meters or decimeters.	N/A	String	N/A	No missing data
InitialYear	First year that plot was sampled	Calendar years	Integer	1952–1990	No missing data
SamplingYears	Range of years that plot was sampled	Calendar years	String	N/A	No missing data
TimesSampled	The number of unique sampling efforts performed for each plot	Count	Integer	3–8	No missing data
OriginalArea	Area of plot at plot inception	Square meters (m^2)	Integer	3200–65536	No missing data
OriginalDimensions	Dimensions of plot at plot inception.	Meters (m)	String	N/A	No missing data
AreaChange1	Area of plot after	Square	Integer	5000–	NA

	first remapping or resizing (if applicable)	meters (m^2)		19400	
Change1Year	Year that first remapping or resizing occurred	Calendar Years	Integer	1982–1991	NA
AreaChange2	Area of plot after second remapping or resizing (if applicable)	Square meters (m^2)	Integer	5600–20400	NA
Change2Year	Year that second remapping or resizing occurred	Calendar Years	Integer	1989–1999	NA
2014Area	Current area of plot as of end of 2014 sampling period	Square meters (m^2)	Integer	5250–65536	No missing data
2014Dimensions	Current dimensions of plot as of end of 2014 sampling period	Meters (m)	String	N/A	No missing data

OrigMinDBH	The minimum diameter tree that was counted and measured as part of the study when plot was first established.	Centimeters (cm)		1–2	No missing data
NewMinDBH	Updated minimum diameter size to be counted and measured in study.	Centimeters (cm)		1–1	NA
YearDBHLowered	Year that the minimum required diameter size to be measured was lowered	Calendar Years		1990–1998	NA
2014MinDBH	The minimum diameter size that was measured in 2014. Note: if	Centimeters (cm)		0.1–0.1	NA

	different from previous values, it was lowered in 2014.				
Xmin	Current minimum X-coordinate in plot	Decimeters (dm)	Floating point	-300–0	No missing data
Xmax	Current maximum X-coordinate in plot	Decimeters (dm)	Floating point	140–2560	No missing data
Ymin	Current minimum Y-coordinate in plot	Decimeters (dm)	Floating point	0–0	No missing data
Ymax	Current maximum Y-coordinate in plot	Decimeters (dm)	Floating point	100–2560	No missing data
XminOrig	Original minimum X-coordinate in plot	Decimeters (dm)	Floating point	0–370	No missing data
XmaxOrig	Original maximum X-coordinate in plot	Decimeters (dm)	Floating point	140–2560	No missing data
YminOrig	Original	Decimeters	Floating	0–200	No missing

	minimum Y-coordinate in plot	(dm)	point		data
YmaxOrig	Original maximum Y-coordinate in plot	Decimeters (dm)	Floating point	100–2560	No missing data
XminUpdate1	Minimum X-coordinate in plot after plot was remapped/enlarged first time	Decimeters (dm)	Floating point	0–330	NA
XmaxUpdate1	Maximum X-coordinate in plot after plot was remapped/enlarged first time	Decimeters (dm)	Floating point	200–1450	NA
YminUpdate1	Minimum Y-coordinate in plot after plot was remapped/enlarged first time	Decimeters (dm)	Floating point	0–150	NA
YmaxUpdate1	Maximum Y-coordinate in plot after plot was	Decimeters (dm)	Floating point	100–1000	NA

	remapped/enlarged first time				
XminUpdate2	Minimum X-coordinate in plot after plot was remapped/enlarged second time	Decimeters (dm)	Floating point	-300–0	NA
XmaxUpdate2	Maximum X-coordinate in plot after plot was remapped/enlarged second time	Decimeters (dm)	Floating point	500–1700	NA
YminUpdate2	Minimum Y-coordinate in plot after plot was remapped/enlarged second time	Decimeters (dm)	Floating point	0–0	NA
YmaxUpdate2	Maximum Y-coordinate in plot after plot was remapped/enlarged second time	Decimeters (dm)	Floating point	750–1200	NA
DisturbanceNotes	Brief notes	N/A	String	N/A	NA

	concerning disturbance history of plot (when available in plot metadata).				
Note	Notes about plot remapping and resizing procedures	N/A	String	N/A	No missing data

Quality assurance/quality control procedures

Data entry errors were methodically examined, noted and corrected after each sampling period. Tree data and plot coordinates were checked in the field for sampling errors each subsequent sampling period. I methodically and exhaustively examined all data following the 2014 sampling period and made all necessary corrections and annotations. See Error Correction section above for details.

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CHAPTER 4: MULTIEDA: AN INTERACTIVE DATA EXPLORATION APPLICATION FOR DUKE FOREST LONG-TERM FOREST DATA

Summary

With the growing size of ecological datasets, it has become operationally difficult to quickly and effectively examine data in exploratory phases of research. This is especially true regarding visual examination of complex data, such as those pertaining to multivariate plot-based inventory studies (e.g., the long-term forest composition data presented in this dissertation). Continuous improvements in computing and statistical technologies have led to the development of numerous programs and tools for analyzing complex data, but few user-friendly interfaces designed specifically for interactive, multi-faceted exploratory visual analyses of large, multivariate community data are available, especially cost-free applications compatible with R.

“MultiEDA” is an interactive web application implemented in the Shiny package of R that provides an extensive yet succinct and user-friendly interface for visually examining trends in multivariate plot-based species data. MultiEDA is designed for use with the permanent plot data presented in Chapters 2 and 3, but the application could be made easily generalizable for most ecological community analyses using the source code provided in the supplementary materials (Appendix S3).

The viewing tool uses a tabular setup to quickly move between linked raw data tables, ordination plots, clustering analysis fits, indicator species tables, size distribution diagrams, and plot layout histories. Each of these functionalities is interactive, with each visual output providing the user the ability to interact with data points directly and providing a series of control

buttons to update visualizations in real time. For example, MultiEDA allows the user to visualize NMDS ordinations with the ability to change input data, select clustering assignment of points, zoom in and out, customize plot labels, reverse axis directions, include change vectors, highlight specific trends, save output as images, generate linked data tables, and interact with the data itself.

A user-friendly and interactive data viewing tool like MultiEDA can make exploratory data analyses for complex ecological community data much quicker and more straightforward. Instead of opening multiple output files or printing various iterations of a plot or graph, MultiEDA lets the user manipulate data output in real time to quickly examine and compare trends. MultiEDA can simplify and expediate exploratory data analyses for a wide range of ecological and environmental multivariate data. This type of exploratory analyses is often key in generating informed hypotheses concerning such complex data as those associated with the Duke Forest. As such, this tool was paramount to generating, investigating and analyzing the hypotheses presented in Chapters 5 and 6 of this dissertation.

Introduction

Exploratory data analysis (or EDA) is an integral phase of all complex ecological community analyses due to such data's inherent multivariate structure. McCune & Grace (2002) define EDA as the "process of probing and exploring the properties and peculiarities of an individual data set until one comes to understand what techniques best reveal the underlying structure." EDA can involve a myriad of techniques including statistical tests, cluster analyses, summary tables, and – perhaps most importantly – data visualization.

Although EDA is used to gain understanding of complex data, the immense amount of output from such exploratory analyses can consist of many iterations of numerous tests and visualizations. This can result in EDA becoming unmanageably complex itself and operationally difficult to use as an inference process. Computer applications can be designed to alleviate this operational difficulty through dynamic graphics displays and multifaceted user interfaces that easily allow a user to move between analyses.

Interactive data visualization allows researchers to move beyond the confines of static data displays towards more dynamic exploration of multivariate data. Dynamic data visualization for exploratory data analysis emerged in the 1960s (Cook & Swayne 2007) and continues to become more popular as technology improves. Various information visualization techniques such as linking, brushing, panning, zooming, and magic lenses (Hearst 1999) have since been developed for users to interact with data tables and graphics. Multi-dimensional graphics viewing via animation have likewise been made possible by the grand tour technique (Asimov 1985, Wickham et al. 2011, Huang et al. 2012) and the application programming interface, Open Graphics Library (OpenGL; Kessenich et al. 2017).

Xie et al. (2014) list a number of stand-alone systems for interactive statistical graphics, such as GGobi (Swayne et al. 2003 and Cook & Swayne 2007). Perhaps most prominent of the contemporary approaches to interactive EDA for ecologists, however, is the fairly robust program PC-ORD (McCune 1986, McCune & Mefford 2011). PC-ORD is both interactive and provides a multifaceted user interface. The program offers a stand-alone graphical user interface (GUI) that allows users to choose among numerous multivariate tools and analyses and to manipulate graphical output using the program's various menus and buttons. PC-ORD, however, comes with a minimum $199 price tag in 2018, resulting in an appeal for cheaper approaches.

R (R Core Team 2017) is a free, open-source statistical environment with software that includes numerous routines and packages for EDA and ecological analyses. Packages relevant to multivariate analyses for community ecologists include vegan (Oksanen et al. 2015), ecodist (Goslee & Urban 2007), labdsv (Roberts 2016a), optpart (Roberts 2016b), cluster (Maechler et al., 2017), ade4 (Dray & Dufour 2007), and MVA (Everitt & Hothorn 2015). Additional packages in R have been developed to allow for complex data visualization. These include an extension of GGobi (rggobi; Wickham et al. 2008 and Lang et al. 2016), cranvas (Xie et al. 2013 and Xie et al. 2014), and rgl (Adler et al. 2017). Although these packages provide effective solutions to viewing multi-dimensional data, each lacks an extensive GUI and ecological focus. They may be used as tools and extensions for ecological EDA, but these R packages do not direct the user toward a workflow typical of ecological community data analysis (e.g., see McCune & Grace 2002 and Peet & Roberts 2013).

In this chapter, “MultiEDA” – an interactive EDA viewing application created using the Shiny (Chang et al. 2017) package in R (R Core Team 2017) and RStudio (RStudio Team 2016) – is introduced. Shiny allows users to build interactive web applications directly from R, which allows for easy integration and application of the various multivariate tools and packages available in the program. The application is run using RStudio, but it can be run via a user’s browser as well. This chapter illustrates the utility of MultiEDA in reference to its initial intended data: long-term forest inventory plots in the Duke Forest located in the central Piedmont in North Carolina, USA. Specifically, the application is used to explore permanent sample plot (“PSP”) data from Chapter 2 and mapped permanent plot (“MAP”) data from Chapter 3 of this dissertation.

Description

The MultiEDA application's user interface uses Shiny's sidebar layout scheme which splits the GUI into a left-aligned toolbar and a primary output region on the right side of the user's screen. The main output region is organized into nine tabs; an introductory tab and eight tabs that contain various tables, graphs, and graphical controls to interact with and manipulate the data shown. This section of the chapter defines each tab in order and describes the types of outputs, linkages, and controls that are available on each tab.

Main control bar

The left tool bar (Figure 4.1), which is fixed across all tabs, is designed to control input data, control clustering assignment, and to manipulate and interact with the ordination output on tab 1, titled "NMDS."

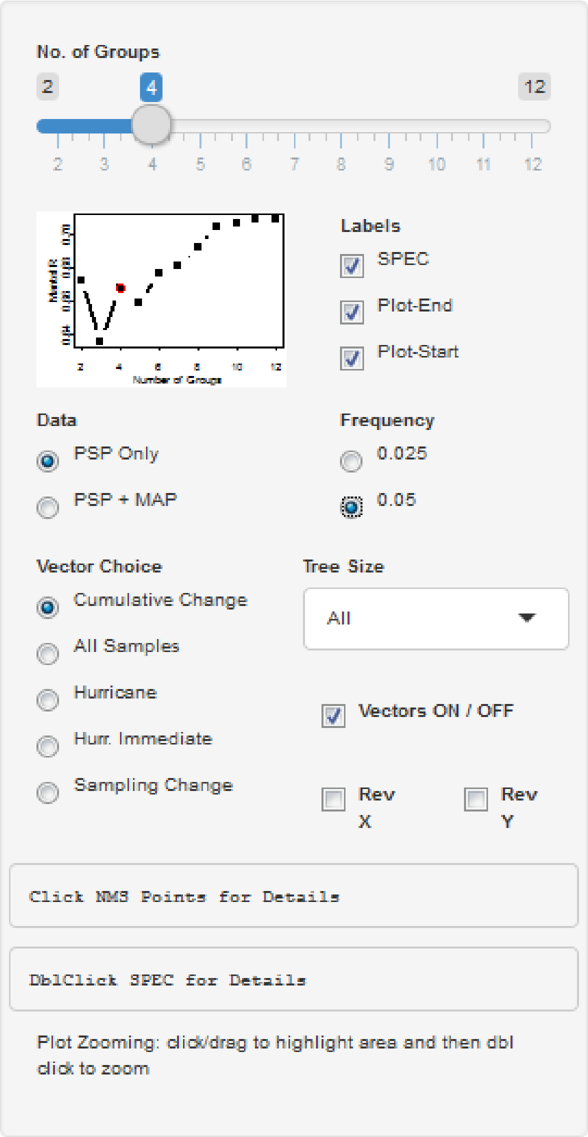
The "Data" section of this toolbar allows the user to modify the data used throughout the EDA process. Because the Duke Forest data consists of two data sets, the user has the option whether to combine them ("PSP + MAP") or simply to go with the more long-term data set ("PSP Only"). Additionally, the user has the option of determining what frequency cutoff to use to eliminate rare species from the analysis. The current version of MultiEDA allows the user to choose between 2.5% or the default 5% cutoff for rare species removal. However, the code can be generalized fairly simply both internal to the application or in the application's set-up code to allow any range of cutoff values as well as a range of relativization approaches and customized data partitions. Finally, a drop-down menu allows the user to select to limit the data based on categorical groupings. In the case of the Duke Forest data, the user can choose between canopy, subcanopy, small-tree/shrub/sapling (called "small"), or all tree sizes to include in the output analyses. The user can define these cutoffs in the set-up code provided as part of the app.

A slider control at the top of the main toolbar allows the user to choose how many groups the clustering analysis divides the data into. Cluster analysis aims to create discrete groups of samples that are ecologically as homogeneous as possible, so it is often important to examine various clustering approaches. The user is aided in his or her decision through the addition of a scree plot showing the Mantel r (dissimilarity in group composition; e.g., see Thompson et al. 2013) for classifications using various number of groups or divisions. The slider tool is linked directly to this scree plot so that the user can easily see the dissimilarity for the selected number of groups highlighted relative to other options. The number of groups defined by the cluster slider is further linked to the graphic display on the “NMDS” tab, the indicator species tables on the “Indicator Spp” tab, the species tables on the “SPEC Data” tab, plot manipulators on the “Spp Density” tab, and finally table output on the “NMDS Data” tab.

The remaining portions of the tool bar are used solely for the NMDS output on the first tab. As such, their functionality will be described in the next section.

NMDS

This initial analysis tab shows a two-axis graphics output for an NMDS ordination (Clarke 1993, McCune & Grace 2002, and Legendre & Legendre 2012; see Figure 4.2). The graph is interactive via various maneuvers with the computer mouse. Single-clicking on a graph point reports in the sidebar menu that datum’s sample (i.e., plot), year of sampling, and the relative group and color assigned based on the selected grouping structure set by the group slider tool in the main sidebar. Clicking and dragging (or “brushing”) the mouse over numerous points reports the same information for all plots located under the highlighted (or brushed) area. Double-clicking the mouse on species weighted average labels reports in an area directly below the plot-info area on the sidebar panel that species’ code and grouping information. This is useful if a label becomes crowded by data points or other labels. Finally, the NMDS output allows the user to recursively zoom by highlighting (brushing) a region of the graphic and then double-clicking the mouse. Again, this is useful in instances where numerous data points seem to overlap at macro scales. Double-clicking in a zoomed-in view resets the zoom.



No. of Groups: 4 (2 – 12)

Labels
☑ SPEC
☑ Plot-End
☑ Plot-Start

Data
● PSP Only
○ PSP + MAP

Frequency
○ 0.025
● 0.05

Vector Choice
● Cumulative Change
○ All Samples
○ Hurricane
○ Hurr. Immediate
○ Sampling Change

Tree Size: All

☑ Vectors ON / OFF

☐ Rev X ☐ Rev Y

```
Click NMS Points for Details
```

```
DblClick SPEC for Details
```

Plot Zooming: click/drag to highlight area and then dbl click to zoom

Figure 4.1 Screenshot of left-tool bar that is available on all screens. This tool-bar manipulates input data, clustering assignment, and ordination output. Text output regions provide ordination plot info when the plot is clicked (to report sample information) or double-clicked (to report species information).

In addition to the data outputs of selected data from the NMDS output, the majority of tools and buttons available on the application’s main toolbar directly manipulate or interact with the NMDS output on this tab. There are checkboxes allowing the user to select which labels (e.g., species weighted averages and plot identifiers) to include or exclude in the output, and there is an additional checkbox to turn successional vectors (see McCune & Grace 2002) on or off. Two additional checkboxes allow the user to reverse the X and/or Y axes by inverting the NMDS values for either or both axes. In this way, the user can orient the ordination output in such a way that might aid ecological interpretation.

The final manipulation tool on the main toolbar is a radio button menu that allows the user to select between a range of successional vector types when the “Vector ON / OFF” checkbox is selected. The user may choose among graphing vectors between all sampling periods for each sample, graphing cumulative change between the first and last years each sample was measured, or by graphing change based on ancillary occurrences relevant to the data. In the case of the Duke Forest data, these other options include graphing change in relation to hurricane occurrences and to protocol changes in the sampling method.

In addition to the sidebar tools, the NMDS tab also provides a series of tools below the NMDS graphic to further manipulate the graph (see bottom of NMDS plot in Figure 4.2). A user may select to highlight successional vectors for an individual plot(s) or groups of plots (i.e., based on cluster assignment). The user is given a drop-down menu to select what type of successional vector(s) (i.e., from the vector choices similarly found in the sidebar menu) to draw in this highlighting process. As such, a user may select to overlap different vector types from those that are portrayed based on the menu selections from the sidebar. The application allows the user to modify the appearance of these overlap vectors through a line-width slider control and a checkbox to control whether line types vary between successional segments (i.e., years). The toolbar is completed by a “Lookup” button that initiates the graphing of the highlighted vectors, a “Reset” button to remove all highlighted vectors, and finally a “Save” button to let the user save the NMDS output as currently viewed. The save button opens a download systems window to let the user select their desired file name and extension.

When highlighted vectors are selected to be drawn, the user will also see a new table appear below this toolbar in the main graphing area of the app (see bottom of Figure 4.2). The table provides the plot, year, cluster analysis group assignment, and both axes’ NMDS scores for each sample (i.e., plot-year combination) that is selected to be highlighted in the “Plot(s)” or “Group(s)” text inputs. The user may elect to have the table show 5, 10, 25, or all rows of the associated data table, and a search box allows the user to search for specific data of interest. Finally, the user may sort the table in ascending or descending order based on any column.

Silhouette

The “Silhouette” tab provides the user further evidence for determining or selecting optimal division of cluster assignments. This tab shows “silhouette plots” (see Figure 4.3) for each possible choice of cluster assignment available in the slider tool on the side toolbar. By default, the plots show silhouette data for clustering assignments dividing the data into 2 – 12 groups. Each plot shows the silhouette width (i.e., goodness of fit of each sample to its own cluster compared to the nearest neighboring cluster; Rousseeuw 1987 and Peet & Roberts 2013) of each sample in each group for a given (i.e., 2 – 12) clustering architecture. In addition, the average silhouette width for each grouping is shown in each graph and an “Average silhouette width” (in this case a *global* average of all groups in the given cluster assignment) is reported below each corresponding graphic.

No. of Groups: 2 – **4** – 12

Labels

☑ SPEC

☑ Plot-End

☑ Plot-Start

Data

● PSP Only

○ PSP + MAP

Frequency

○ 0.025

● 0.05

Vector Choice

● Cumulative Change

○ All Samples

○ Hurricane

○ Hurr. Immediate

○ Sampling Change

Tree Size: All

☑ Vectors ON / OFF

☐ Rev X

☐ Rev Y

```
Click NMS Points for Details
```

```
DblClick SPEC for Details
```

Plot Zooming: click/drag to highlight area and then dbl click to zoom

Cumulative

44

1 – **5** – 6

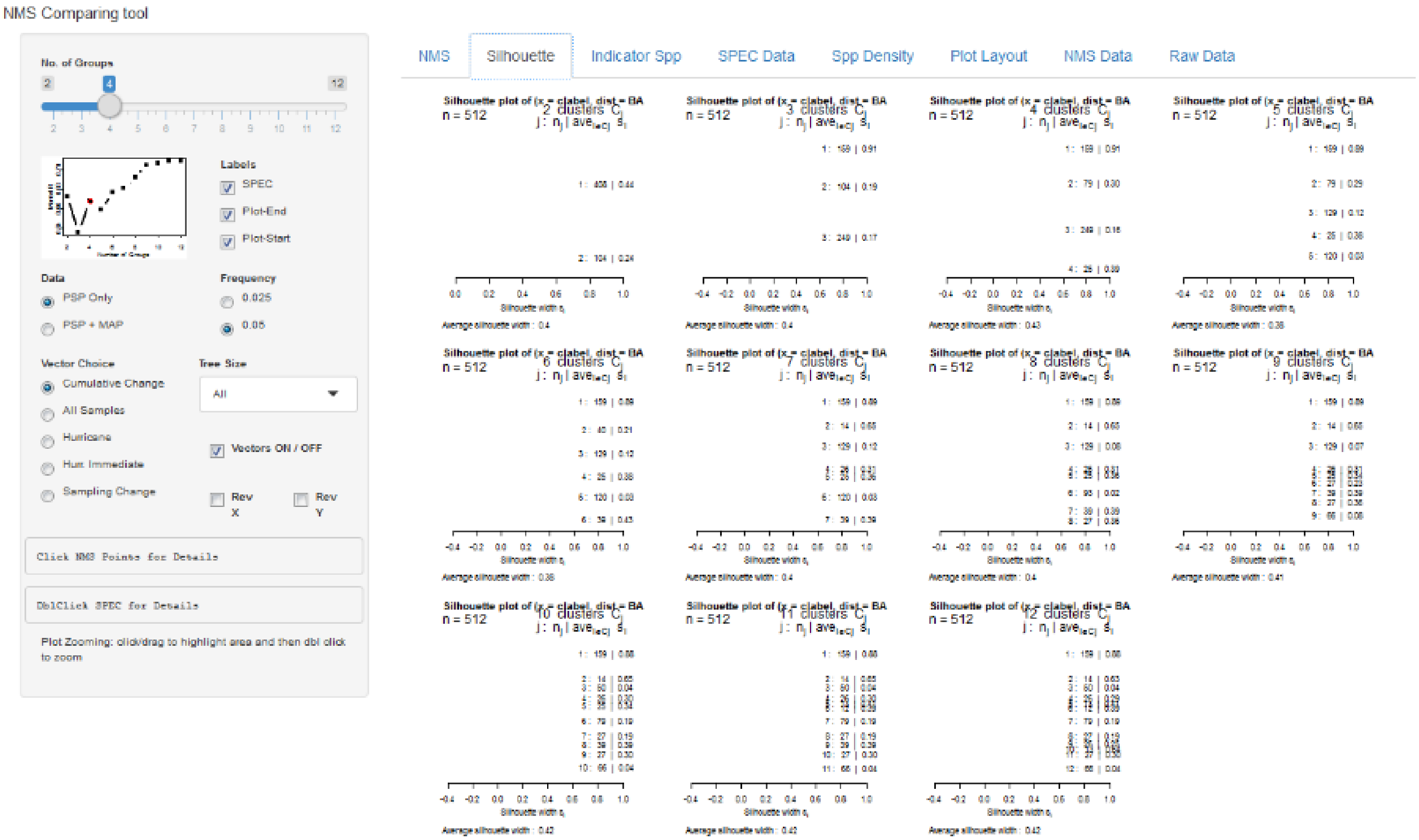
☐ Lty?

Show 10 entries

Search:

plot	Year	NMS1	NMS2	clabel
44	1935	0.667813048826324	-0.423755029577373	4
44	1939	0.661247544855816	-0.443487343912509	4
44	1945	0.657368273049837	-0.447839735533388	4
44	1950	0.653758216092721	-0.459672662239153	4
44	1954	0.587429217254967	-0.54527568440921	4

Figure 4.2 Screenshot of the NMDS ordination page on the second-tab. The main graphic shows an interactive (i.e., clickable and zoomable) NMDS ordination with adjustable labels and trajectory vectors. The point colors are dictated by the group selection slider in the left tool-bar. Customizable controls for individual plots and additional plot manipulation tools are available below the ordination graphic, and selected data output is displayed at the bottom of the main output region.



NMS Comparing tool

No. of Groups: 4

Labels

☑ SPEC

☑ Plot-End

☑ Plot-Start

Data

● PSP Only

○ PSP + MAP

Frequency

○ 0.025

● 0.05

Vector Choice

● Cumulative Change

○ All Samples

○ Hurricane

○ Hur. Immediate

○ Sampling Change

Tree Size: All

☑ Vectors ON / OFF

☐ Rev X

☐ Rev Y

`Click NMS Points for Details`

`DblClick SPEC for Details`

Plot Zooming: click/drag to highlight area and then dbl click to zoom

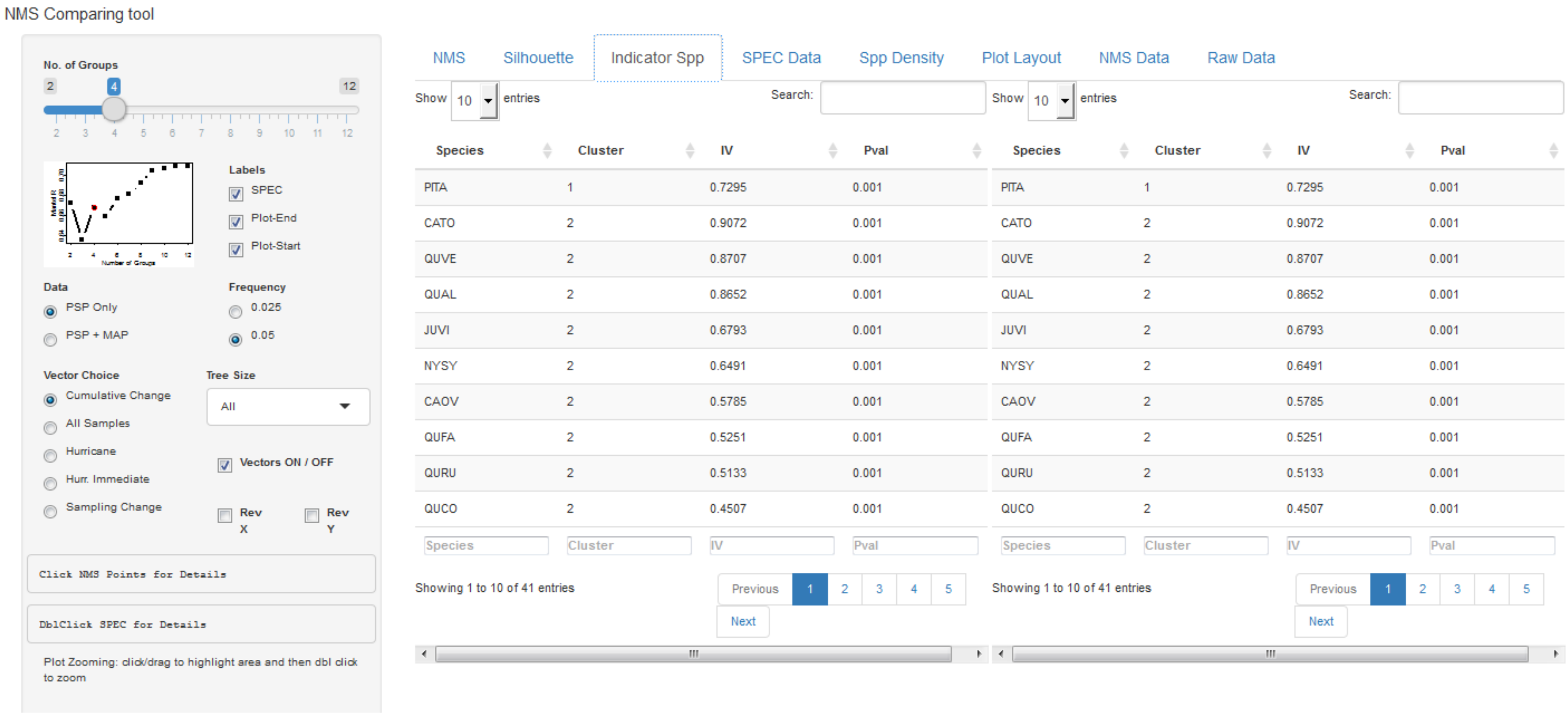
Figure 4.3 Screenshot of the “Silhouette” tab showing the silhouette widths for each clustering approach (i.e., for each variation in the “no. of groups” slider tool on the left toolbar). These plots provide an additional resource for examining clustering analyses.

Indicator Spp

The “Indicator Spp” tab shows the tabular output of an indicator species analysis (Dufrene & Legendre 1997) using the indval function in labdsv package (Roberts 2016a) in R. The table (seen in Figure 4.4) is linked to the data input and cluster-assignment tools on the sidebar menu, and it is useful for determining indicator species for each cluster in the currently-selected clustering architecture. The table includes a column for species, cluster assignment, indicator value and a p value for the indicator value. The user may elect to have the table show 10, 25, 50 or all rows of associated data, and a search box allows the user to search for specific data of interest. Finally, the user may sort the table in ascending or descending order based on any column.

SPEC Data

Like the indicator species tab, the “SPEC Data” tab provides a tabular output for species assignments based on weighted averages and the clustering architecture assigned (see Figure 4.5). This table is to serve as a reference for species information from the NMDS output graphic on the first tab. The table in this tab includes columns for the species code, group assignment and the color assigned to that group assignment. Again, the user may elect to have the table show 10, 25, 50 or all rows of associated data, and a search box allows the user to search for specific data of interest. Finally, the user may sort the table in ascending or descending order based on any column.



NMS Comparing tool

No. of Groups: 4 (2–12)

Labels
☑ SPEC
☑ Plot-End
☑ Plot-Start

Data
● PSP Only
○ PSP + MAP

Frequency
○ 0.025
● 0.05

Vector Choice
● Cumulative Change
○ All Samples
○ Hurricane
○ Hurr. Immediate
○ Sampling Change

Tree Size: All

☑ Vectors ON / OFF

☐ Rev X
☐ Rev Y

Plot Zooming: click/drag to highlight area and then dbl click to zoom

Show 10 entries Search:

Species	Cluster	IV	Pval
PITA	1	0.7295	0.001
CATO	2	0.9072	0.001
QUVE	2	0.8707	0.001
QUAL	2	0.8652	0.001
JUVI	2	0.6793	0.001
NYSY	2	0.6491	0.001
CAOV	2	0.5785	0.001
QUFA	2	0.5251	0.001
QURU	2	0.5133	0.001
QUCO	2	0.4507	0.001

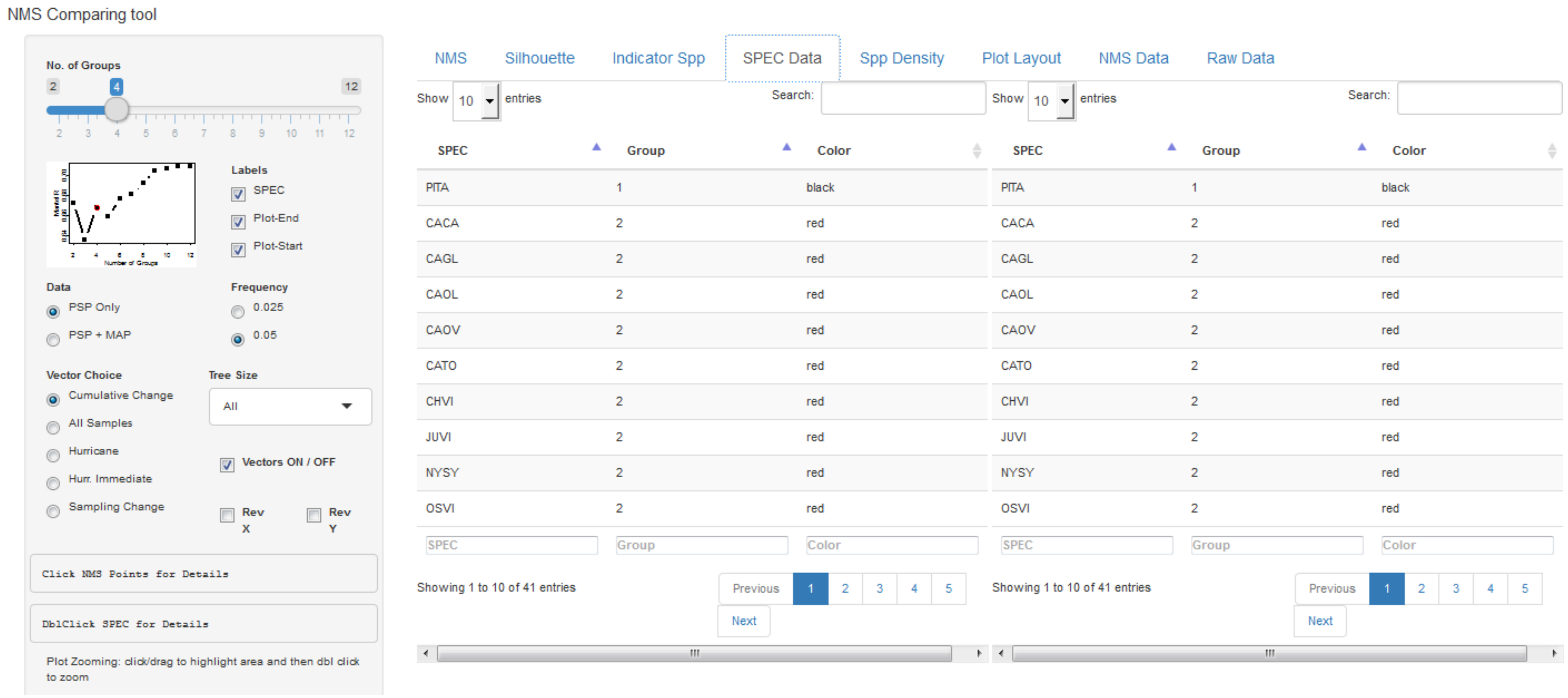
Showing 1 to 10 of 41 entries

Show 10 entries Search:

Species	Cluster	IV	Pval
PITA	1	0.7295	0.001
CATO	2	0.9072	0.001
QUVE	2	0.8707	0.001
QUAL	2	0.8652	0.001
JUVI	2	0.6793	0.001
NYSY	2	0.6491	0.001
CAOV	2	0.5785	0.001
QUFA	2	0.5251	0.001
QURU	2	0.5133	0.001
QUCO	2	0.4507	0.001

Showing 1 to 10 of 41 entries

Figure 4.4 Screenshot of the "Indicator Spp" tab showing table output for Dufrene & Legendre's (1997) indicator species analysis. The table shows species, cluster assignment, indicator value and a p-value for the indicator value of each species. This table is sortable.


NMS Comparing tool

No. of Groups: 4 (2–12)

Labels: ☑ SPEC ☑ Plot-End ☑ Plot-Start

Data: ● PSP Only ○ PSP + MAP

Frequency: ○ 0.025 ● 0.05

Vector Choice: ● Cumulative Change ○ All Samples ○ Hurricane ○ Hurr. Immediate ○ Sampling Change

Tree Size: All

☑ Vectors ON / OFF

☐ Rev X ☐ Rev Y

Click NMS Points for Details

DblClick SPEC for Details

Plot Zooming: click/drag to highlight area and then dbl click to zoom

SPEC	Group	Color
PITA	1	black
CACA	2	red
CAGL	2	red
CAOL	2	red
CAOV	2	red
CATO	2	red
CHVI	2	red
JUVI	2	red
NYSY	2	red
OSVI	2	red

Showing 1 to 10 of 41 entries

SPEC	Group	Color
PITA	1	black
CACA	2	red
CAGL	2	red
CAOL	2	red
CAOV	2	red
CATO	2	red
CHVI	2	red
JUVI	2	red
NYSY	2	red
OSVI	2	red

Showing 1 to 10 of 41 entries

Figure 4.5 Screenshot of the "SPEC Data" tab showing the cluster assignment of the weighted averages of each species code (SPEC). Th group number coincides with groups assigned on the "no. of groups" slider tool on the left toolbar, and the colors match those assigned and used on the NMDS plot on the 2nd tab.

Spp Density

The “Spp Density” tab allows the user to produce a diameter distribution plot for selected species, plots, and years. Specifically, the main graphic on this tab shows stems per hectare of each diameter size for the selected species, plot(s) and sampling years for the selected plots (see Figure 4.6). Distribution curves for different sampling periods are colored from warm to cool colors (i.e., red to purple) for earlier to more recent periods.

The main entry tools on this tab are text inputs for group(s), SPEC, data, plot(s), and period that impact what data is included in generating the graphic. The group(s) selector lets the user choose to include only data points with the assigned group number(s). These group numbers are based on the cluster assignment dictated by the slider tool on the sidebar menu. The species input lets the user enter species codes (“SPEC”; multiple species can be included by separating codes with a comma) to choose which species are included in the graphic. The third text input tool allows the user to determine whether all data are considered (“All”) or just data from either PSP or MAP data sets. The plot input tool establishes which plot(s) will be sampled for generating the distribution graphs. Again, multiple plots can be included by separating plot numbers with a comma. The plot and group tools can be used concurrently to allow refinement or extension of the data included in determining diameter distributions compared to using either on its own. Finally, the user may determine which sampling periods should be included for the final distribution output. The default is to include all sampling years available for any plots included in the graphic via the group or plot input choosers, but the user may choose to limit these outputs using this period choosing tool. Since sampling years are not consistent between plots, sampling years are grouped into “periods” which coincide with project-wide sampling efforts. The user may enter the sampling period number (e.g., 1 – 14) which is ordered from earliest to latest sampling efforts.

The final tool available on this tab is a slider tool which allows the user to apply various smoothers to the diameter distribution plot. These distributions were calculated using kernel density estimation via the density function in the stats package of R (R Core Team 2017). This slider tool changes the bandwidth value in this function between 0 (a stand-in for "SJ" bandwidth; Sheather & Jones 1991) and bandwidth values of 0.1 – 1.0. Higher bandwidth values provide smoother curves, while the SJ bandwidth is a reliable data-based bandwidth selection method created by Sheather & Jones (1991) that also provides a smoothed distribution curve.

Two remaining action buttons are also on this tab. The first, the "Plot" button, initiates the plotting of whichever data are selected in the aforementioned tools. The distribution plot's title and subtitle are updated with each change in the plot or group selected in the entry tools, and the bandwidth choice is likewise included in the final subtitle of the plot based on the selection made in the bandwidth slider tool. There is also a "Reset" button to clear the plot for the use to start over.

Plot Layout

Because many community data are either spatially explicit or longitudinal (or both), it is useful for a data analyst to explore both the spatial distribution of species data within samples (i.e., plots) and the change in those individuals through time. The highly-interactive graphic and manipulative tools on this tab provide the user just that functionality.

NMS Comparing tool

No. of Groups: 4

Labels: ☑ SPEC ☑ Plot-End ☑ Plot-Start

Data: ● PSP Only ○ PSP + MAP

Frequency: ○ 0.025 ● 0.05

Vector Choice: ● Cumulative Change ○ All Samples ○ Hurricane ○ Hurr. Immediate ○ Sampling Change

Tree Size: All

☑ Vectors ON / OFF

☐ Rev X ☐ Rev Y

`Click NMS Points for Details`

`DblClick SPEC for Details`

Plot Zooming: click/drag to highlight area and then dbl click to zoom

PITA

sample.period	sample.years	grp1.area	grp2.area	grp3.area	grp4.area	total.area	grp.succ.area
1	1933-1936	17210	3036	6927	2024	29197	24137
2	1937-1939	12350	3036	6927	2024	24337	19277
3	1943-1947	11338	15177	7939	2024	36478	19277
4	1948-1950	11338	15177	7939	2024	36478	19277
5	1952-1955	8302	15177	10975	2024	36478	19277

Figure 4.6 Screenshot of the "Spp Density" tab showing manipulative diameter distribution plots for the tree data. Each color curve represents the diameter distribution of the selected species (or multiple species) for the selected group (or a specific plot) in a given sampling period. Curves transition from red (1930s) to purple (2010s). a table output is included to provide summed area for the groups being viewed.

The “Plot Layout” tab uses a vertical structure to provide the user a graphics output, manipulative tools, linked data output, and table output (see Figure 4.7). The main graphic on this tab shows individuals (trees in the case of Duke Forest data) within a two-axis spatial orientation, where the axes may represent, for example, UTM, latitude/longitude, or – in the case of spatially-mapped sample plots such as those used in Duke Forest – X and Y coordinates within a sampling space.

Similar to the NMDS graph on MultiEDA’s first tab, various mouse maneuvers allow the user to interact with the data in the plot layout graphic. Single-clicking on a graph point reports that datum’s database identification number(s), year of sampling, plot identifier, location within the plot, species identifier, specimen measurements (e.g., diameter, height and basal area), specimen condition, and other variables drawn from an initial raw data table. Brushing the mouse over numerous points reports the same information for all plots located under the brushed area. These data are reported in a text output area below the toolbar on the main graphics region of this tab. Brushing a region of the graphic and double-clicking the mouse within that brushed area allows the user to recursively zoom. This is useful in instances where numerous data points seem to overlap at macro scales. Double-clicking in a zoomed-in view resets the graphics view.

There are a number of interactive tools to manipulate this plot layout graphic. The two most important tools are for selecting which plot sample and which sampling period of that plot to graph. The user selects the plot via a text input tool which accepts only single plot identifiers at a time. The sampling period is selected using a slider tool. The slider tool is linked to the plot input, and as a result, the selection points on the slider tool change relative to the number of sampling periods that exist for the selected plot. The default sampling period is period 1, or the first year the given plot was sampled. The user may also choose to select a sampling period of

“0,” which simultaneously displays data from all sampling periods for the selected plot. Once the user selects a plot and sampling year, he or she clicks the “Plot” button to display the data in the layout graphic. The graphic’s title and subtitle are automatically updated to include the plot identifier and sampling year(s) associated with the selected sampling period(s). The user must select the “Reset” button and re-click the “Plot” button anytime they wish to change the sampling plot being displayed.

Four additional interactive tools on this tab provide visual manipulation of the data displayed. A radio-button “Sizing” tool allows the user to dictate the relative sizing of the data points in the graphic. The current options are to scale the points relative to basal area, diameter at breast height (DBH; the default), height, or a fourth option to not scale the points at all. A “Sizing” slider tool allows the user to fine-tune the sizing of the points within these relative scales by changing the scale multiplier.

Although the data are displayed as consistent black points in the graphic by default, the user may choose to de-select a “Uniform Color” checkbox, which will assign one of eighteen colors to each species. The colors are established based on alphabetical order of potential species in the plot using a cyclic pattern palette of 18 unique colors. A more nuanced text input tool (“SPEC Highlight”), allows the user to color points associated with only select species. The user may enter multiple species codes (each separated by a comma) into this text input tool, which will color the species one of the eighteen possible colors available in the palette in the order that they are entered. The species codes and their generated colors are inserted as a horizontal key below the graphs subtitle as each species is entered into the text input.

The remaining tools on this tab all allow the user to subset the data being displayed using the pre-set plot-year setting. Two of these tools, a diameter range slider-tool and a height range slider-tool, are linked to the plot-selection input and can be reset when the “Reset” button is clicked by the user. These two tools are range sliders, and they allow the user to set the minimum and maximum diameters and heights of tree samples plotted in the graphic. By default, these ranges automatically set themselves as the minimum and maximum values for diameter and height for all individuals ever recorded in the selected plot. Neither of these slider tools perform their desired function unless a third tool, the “Limit Tree Size” dropdown select tool, is changed appropriately from “No limit” to one of “By D” (by diameter), “By HT” (by height), or “By Both.”

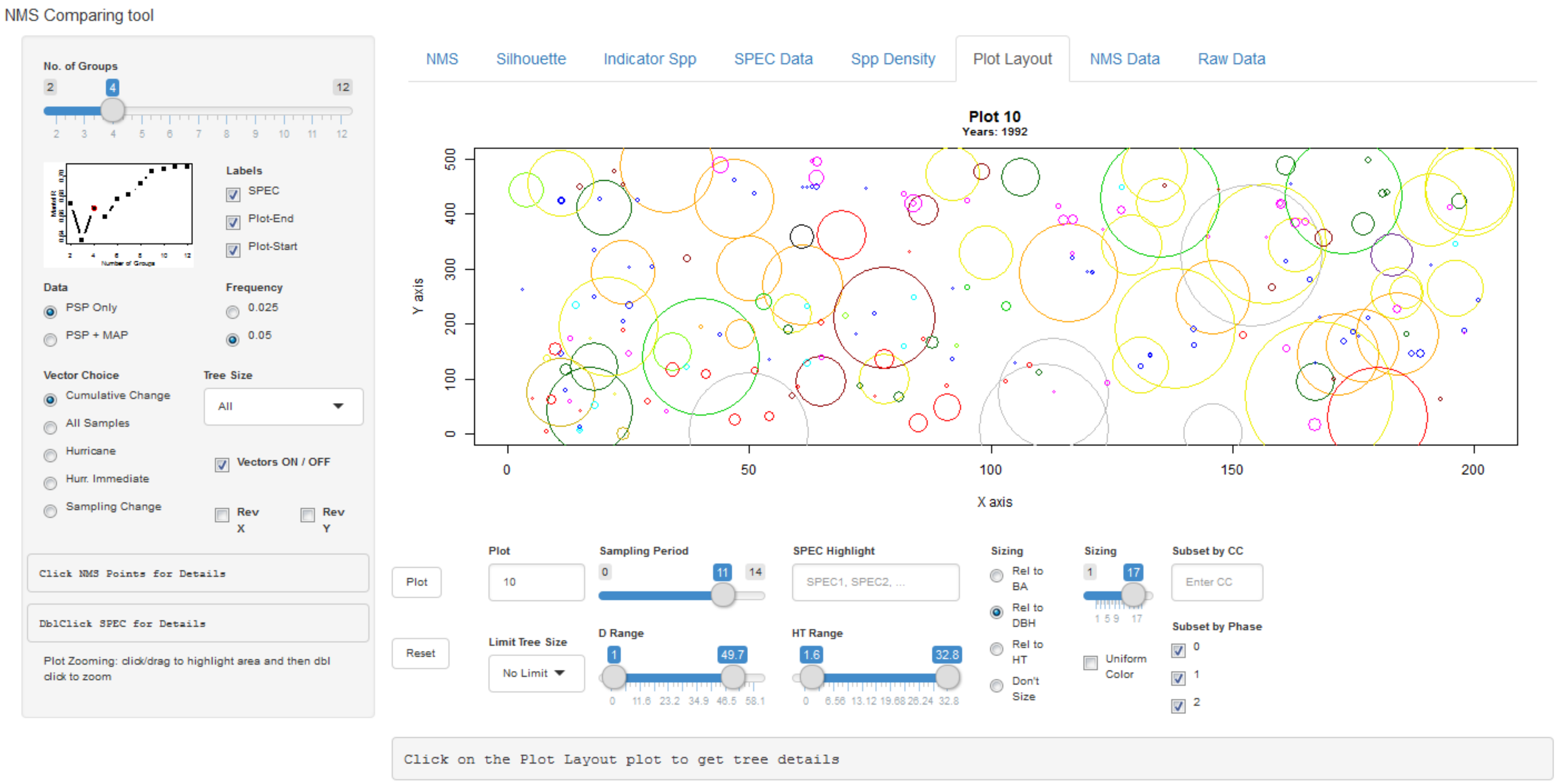
The last two tools that subset the data used for plot input allow the user to subset by tree condition code (CC; alive: 1, dead: 2, missing: 3, height damaged: 4; cut: 5 or 6: damaged by hurricane) or project phase (i.e., designated regions of expanded plots based on sampling history and trees on those areas). A text input tool allows the user to enter one or more CC’s separated by commas, which will automatically update the layout output without need to press the Reset or Plot buttons. The second tool, a group checkbox tool, allows the user to include or exclude trees associated with different phases of the long-term sampling project. The default is to include all trees (i.e., all boxes are checked), but the user may check or uncheck any combination of phases to include or exclude trees as he or she sees fit. This tool is especially helpful for visualizing trees that were added due to plot dimension enlargements.

Below the interactive sub-graph toolbar on this tab is a text output region that reports the data described in the mouse maneuver paragraph earlier in the “Plot layout” section of the chapter. If no plots have been selected using a mouse maneuver, the text output region below the plot layout graph simply prints text that instructs the user to “Click on the Plot Layout plot to get tree details.”

Finally, because some individual trees never received complete or any spatial data (i.e., were not mapped within an x-y cartesian plane), they cannot be included in the graphic on this tab. To avoid simply ignoring these data, a table is produced under the text output region just described to list all of the trees that are unable to be plotted on the layout graphic. This table, which is a subset of the raw tree data, is linked to the interactive tools used to manipulate the plot layout graphic. Specifically, the table is influenced by the plot, sampling period, diameter range, height range, CC limiter, and phase limiter tools. The user may elect to have the table output show 5, 10, 25, or all rows of the associated data table, and a search box allows the user to search for specific data of interest. Finally, the user may sort the table in ascending or descending order based on any column, and he or she may also filter each column by entering a filter value.

NMDS Data

This tab provides a table with NMDS and classification data. Specifically, the table (see Figure 4.8) provides the plot, year, cluster analysis group assignment, and both axes' NMDS scores for each sample (i.e., plot-year combination) that is selected to be highlighted in the "Plot(s)" or "Group(s)" text inputs from the NMDS tab. Again, the data are split into the number of groups dictated by the group-selection slider tool in the sidebar menu. The user may elect to have the table show 25, 50, 100 or all rows of associated data, and a search box allows the user to search for specific data of interest. Finally, the user may sort the table in ascending or descending order based on any column.



NMS Comparing tool

No. of Groups: 2 — 4 — 12

Labels: ☑ SPEC ☑ Plot-End ☑ Plot-Start

Data: ● PSP Only ○ PSP + MAP

Frequency: ○ 0.025 ● 0.05

Vector Choice: ● Cumulative Change ○ All Samples ○ Hurricane ○ Hurr. Immediate ○ Sampling Change

Tree Size: All

☑ Vectors ON / OFF

☐ Rev X ☐ Rev Y

`Click NMS Points for Details`

`DblClick SPEC for Details`

Plot Zooming: click/drag to highlight area and then dbl click to zoom

Plot: 10

Sampling Period: 0 — 11 — 14

SPEC Highlight: SPEC1, SPEC2, ...

Sizing: ○ Rel to BA ● Rel to DBH ○ Rel to HT ○ Don't Size

Sizing: 1 — 17

☐ Uniform Color

Subset by CC: Enter CC

Subset by Phase: ☑ 0 ☑ 1 ☑ 2

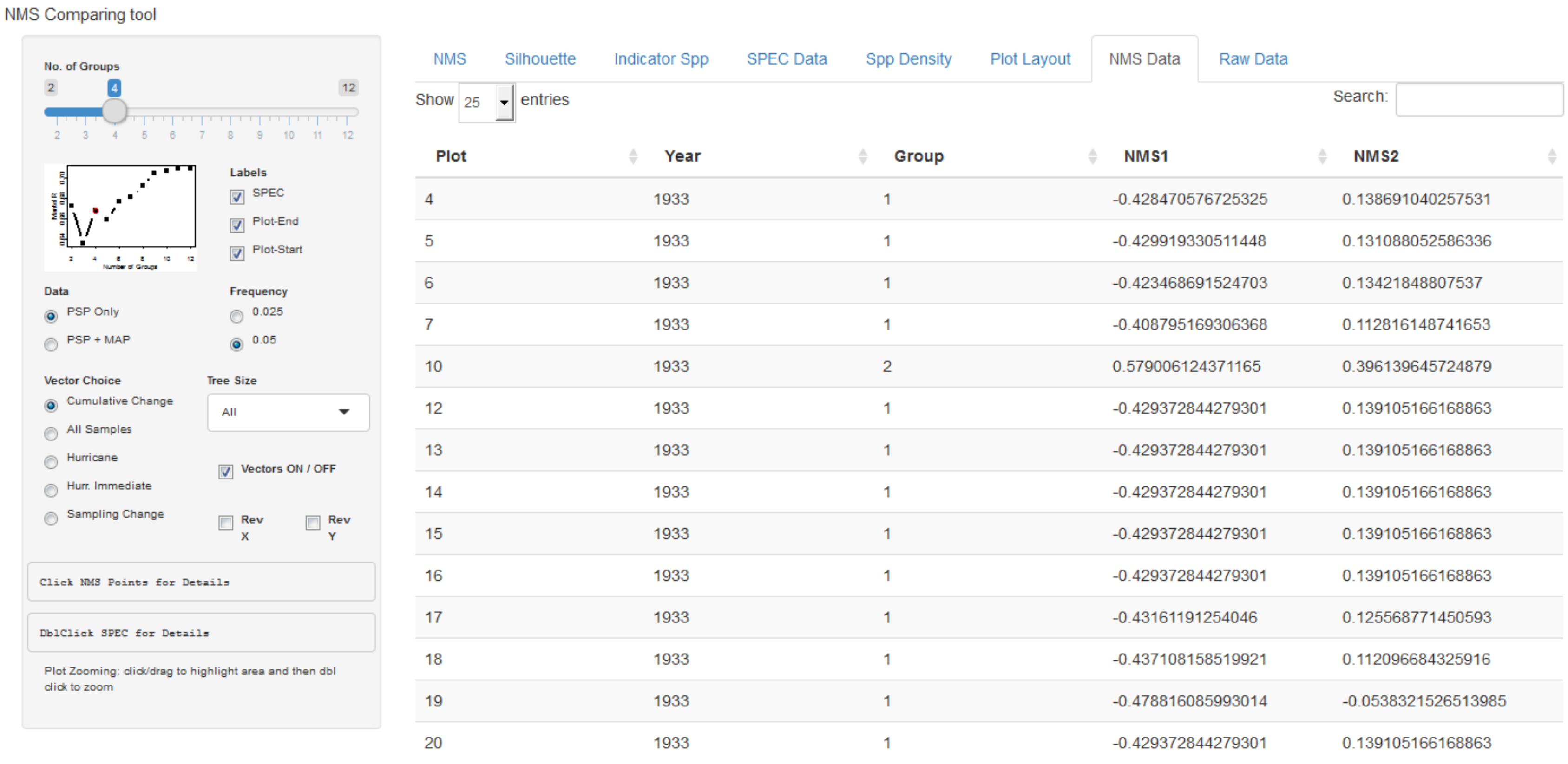
Limit Tree Size: No Limit

D Range: 1 — 49.7

HT Range: 1.6 — 32.8

`Click on the Plot Layout plot to get tree details`

Figure 4.7 Screenshot of the "Plot Layout" tab showing the physical orientations and locations of each tree within each study plot. Controls allow the user to modify relative sizing of trees, differentially color different species, and limit the size ranges of trees or sampling areas of plots to include. A slider tool allows the user to change sampling year to visualize changes in size and orientation of trees. This graphic is interactive and allows the user to click graphic points (i.e., trees) for more data (printed below) or to zoom for closer examination.



No. of Groups: 4 (2–12)

Labels
☑ SPEC
☑ Plot-End
☑ Plot-Start

Data
● PSP Only
○ PSP + MAP

Frequency
○ 0.025
● 0.05

Vector Choice
● Cumulative Change
○ All Samples
○ Hurricane
○ Hurr. Immediate
○ Sampling Change

Tree Size: All

☑ Vectors ON / OFF
☐ Rev X
☐ Rev Y

Plot Zooming: click/drag to highlight area and then dbl click to zoom

Show 25 entries

Search:

Plot	Year	Group	NMS1	NMS2
4	1933	1	-0.428470576725325	0.138691040257531
5	1933	1	-0.429919330511448	0.131088052586336
6	1933	1	-0.423468691524703	0.13421848807537
7	1933	1	-0.408795169306368	0.112816148741653
10	1933	2	0.579006124371165	0.396139645724879
12	1933	1	-0.429372844279301	0.139105166168863
13	1933	1	-0.429372844279301	0.139105166168863
14	1933	1	-0.429372844279301	0.139105166168863
15	1933	1	-0.429372844279301	0.139105166168863
16	1933	1	-0.429372844279301	0.139105166168863
17	1933	1	-0.43161191254046	0.125568771450593
18	1933	1	-0.437108158519921	0.112096684325916
19	1933	1	-0.478816085993014	-0.0538321526513985
20	1933	1	-0.429372844279301	0.139105166168863

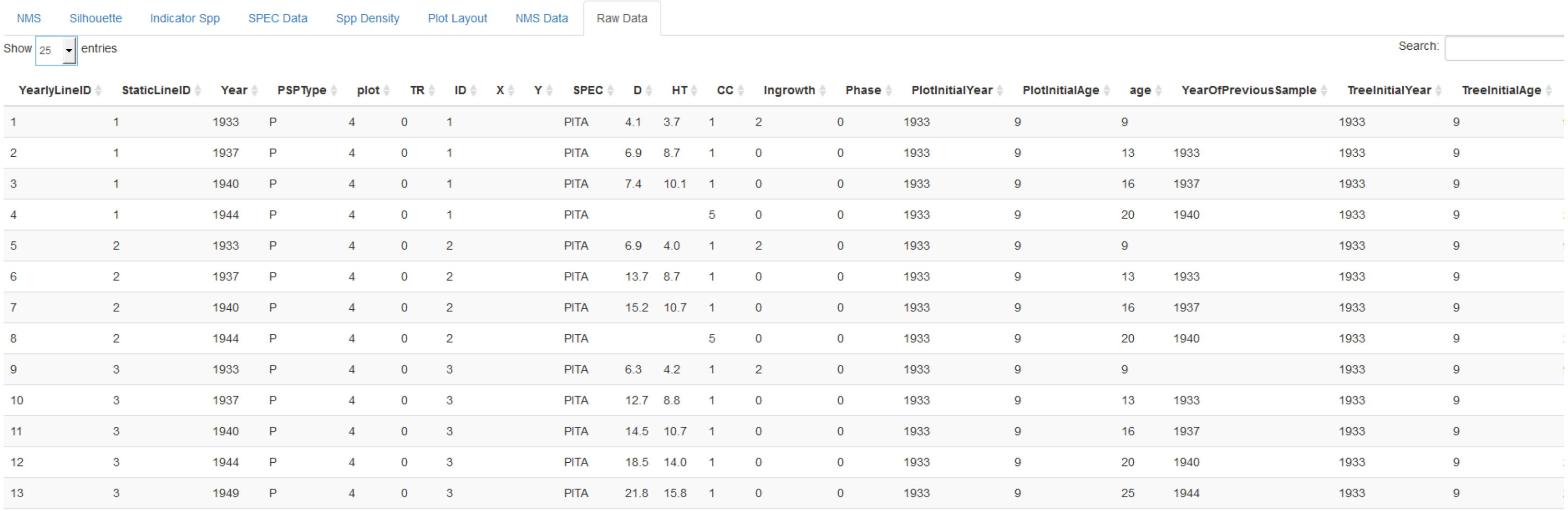
Figure 4.8 Screenshot of the "NMS Data" tab showing the first- and second-axis NMDS scores used to build the NMDS graphic on the "NMDS" tab. Each score is in a row with the sample (i.e., plot and year) found at the given coordinates along with the clustering analysis group assignment (determined by slider tool in left toolbar).

Raw Data

This final tab contains a table for the raw data. The initial sampling data used to generate the NMDs ordinations, cluster analyses, indicator species analyses, plot layout graphics, and species density diagrams are incorporated in this table along with all ancillary variables from the original raw dataset (see subset of table in Figure 4.9). The user may elect to have the table show 25, 50, 100 or all rows of associated data, and a search box allows the user to search for specific data of interest. Finally, the user may sort the table in ascending or descending order based on any column, and he or she may also filter each column by entering a filter value. This raw data is not linked to any other functionality in the MultiEDA tool and is simply included for ease of reference.

Input

In version 1.52 of MultiEDA, the user must supply properly-named input files (see Table 4.1). This is most easily accomplished by loading the RData file “MultiEDA_setup_psp.RData” that can be created using the setup code in “MultiEDA_setup_code.txt,” which is included in Appendix S3 submitted with this dissertation. The set-up code generates six major object types for various partitions of the PSP and MAP data (Table 4.1; see next paragraph) using the raw data files included in appendices for Chapters 2 and 3 of this dissertation. The different data partition variants include no partition (i.e., all data from PSP and MAP datasets) and data subsamples that include only canopy trees, subcanopy trees, or just small woody stems (i.e., those less than or equal to 10 cm diameter). Each of these four data partitions is duplicated – one iteration uses data with a 2.5% sample frequency cutoff to remove rare species while the other uses a 5% cutoff. These eight data partitions are duplicated conceptually once more, but this time by isolating just the PSP data. The result is 16 different partitions of the data (Table 4.1).



YearlyLineID	StaticLineID	Year	PSPType	plot	TR	ID	X	Y	SPEC	D	HT	CC	Ingrowth	Phase	PlotInitialYear	PlotInitialAge	age	YearOfPreviousSample	TreeInitialYear	TreeInitialAge
1	1	1933	P	4	0	1			PITA	4.1	3.7	1	2	0	1933	9	9		1933	9
2	1	1937	P	4	0	1			PITA	6.9	8.7	1	0	0	1933	9	13	1933	1933	9
3	1	1940	P	4	0	1			PITA	7.4	10.1	1	0	0	1933	9	16	1937	1933	9
4	1	1944	P	4	0	1			PITA			5	0	0	1933	9	20	1940	1933	9
5	2	1933	P	4	0	2			PITA	6.9	4.0	1	2	0	1933	9	9		1933	9
6	2	1937	P	4	0	2			PITA	13.7	8.7	1	0	0	1933	9	13	1933	1933	9
7	2	1940	P	4	0	2			PITA	15.2	10.7	1	0	0	1933	9	16	1937	1933	9
8	2	1944	P	4	0	2			PITA			5	0	0	1933	9	20	1940	1933	9
9	3	1933	P	4	0	3			PITA	6.3	4.2	1	2	0	1933	9	9		1933	9
10	3	1937	P	4	0	3			PITA	12.7	8.8	1	0	0	1933	9	13	1933	1933	9
11	3	1940	P	4	0	3			PITA	14.5	10.7	1	0	0	1933	9	16	1937	1933	9
12	3	1944	P	4	0	3			PITA	18.5	14.0	1	0	0	1933	9	20	1940	1933	9
13	3	1949	P	4	0	3			PITA	21.8	15.8	1	0	0	1933	9	25	1944	1933	9

Figure 4.9 Screenshot of the "Raw Data" tab showing raw input data for the Duke Forest permanent plots. These are the data that inform the rest of the application. The data can be sorted and searched. This image has been cropped to remove the side-bar menu so that more detail can be viewed in the main window containing the raw data table. When using the app, additional columns that extend beyond the screen limits can be viewed by scrolling sideways (not shown).

The six object types utilized by MultiEDA (and created in the setup code provided in the supplementary materials) are duplicated for each unique data partition, so there are 16 variants of each of the six primary input object types (or 96 unique input objects). A general description of each of the six object types is given next. “BA.flex.cl” is a data-frame containing cluster analysis results with columns associated with number of cluster groups, Mantel R, and p-values for each clustering architecture. “BA.flex.levels” extends the clustering analysis output from “BA.flex.cl” and contains cluster level (i.e., group assignment) values for each sample (i.e., plot-year combination). “BA.matrix.nrel” contains non-relativized basal area data, whereas “BA.matrix.nrel” contains relativized basal area data. In both objects, the data-frames are arranged with the first two columns containing the plot number and sampling year, while each additional column is labeled with each unique species found in the data. Each cell in the third and greater columns of these data-frames is the summed basal area for that cell’s species (column) in the given plot-year (i.e., sample) row. “BA.nms2” is a two-column data-frame that contains PCA-rotated first and second axis NMDS ordination values for each sample. Finally, “BA.wa” contains the weighted average scores for each species in the NMDS ordination space. Each row name contains the species codes in alphabetical order, while the two columns contain the first- and second-axis weighted average scores.

The following table (Table 4.1) presents the names of the necessary data objects to run Version 1.52 of MultiEDA.

Table 4.1 Grid showing the names of all the data objects currently utilized by MultiEDA Version 1.52 to present output data. The six object types are shown as column headings while the 16 partitions of the Duke Forest data are shown in the far-left column. Percentages represent cutoff value for rare species.

	BA.flex.cl	BA.flex.levels	BA.matrix.nrel	BA.matrix.rel	BA.nms2	BA.wa
PSP+MAP All (5%)	BA.flex.cl.all	BA.flex.levels.all	BA.matrix.nrel.all	BA.matrix.rel.all	BA.nms2.all	BA.wa.all
PSP+MAP All (2.5%)	BA.flex.cl.all.25	BA.flex.levels.all.25	BA.matrix.nrel.all.25	BA.matrix.rel.all.25	BA.nms2.can	BA.wa.can
Canopy (5% cutoff)	BA.flex.cl.can	BA.flex.levels.can	BA.matrix.nrel.can	BA.matrix.rel.can	BA.nms2.psp.all	BA.wa.psp.all
PSP+MAP Canopy (2.5%)	BA.flex.cl.can.25	BA.flex.levels.can.25	BA.matrix.nrel.can.25	BA.matrix.rel.can.25	BA.nms2.psp.can	BA.wa.psp.can
PSP+MAP Subcanopy (5%)	BA.flex.cl.sub	BA.flex.levels.sub	BA.matrix.nrel.sub	BA.matrix.rel.sub	BA.wa.sml.25	BA.wa.sml.25
PSP+MAP Subcanopy (2.5%)	BA.flex.cl.sub.25	BA.flex.levels.sub.25	BA.matrix.nrel.sub.25	BA.matrix.rel.sub.25	BA.wa.sub.25	BA.wa.sub.25
PSP+MAP Small stem (5%)	BA.flex.cl.sml	BA.flex.levels.sml	BA.matrix.nrel.sml	BA.matrix.rel.sml	BA.wa.psp.sml.25	BA.wa.psp.sml.25
PSP+MAP Small stem(2.5%)	BA.flex.cl.sml.25	BA.flex.levels.sml.25	BA.matrix.nrel.sml.25	BA.matrix.rel.sml.25	BA.wa.psp.sub.25	BA.wa.psp.sub.25
PSP Only All (5%)	BA.flex.cl.psp.all	BA.flex.levels.psp.all	BA.matrix.nrel.psp.all	BA.matrix.rel.psp.all	BA.nms2.psp.sml	BA.wa.psp.sml
PSP Only All (2.5%)	BA.flex.cl.psp.all.25	BA.flex.levels.psp.all.25	BA.matrix.nrel.psp.all.25	BA.matrix.rel.psp.all.25	BA.nms2.psp.sub	BA.wa.psp.sub
PSP Only Canopy (5%)	BA.flex.cl.psp.can	BA.flex.levels.psp.can	BA.matrix.nrel.psp.can	BA.matrix.rel.psp.can	BA.nms2.sml	BA.wa.sml
PSP Only Canopy (2.5%)	BA.flex.cl.psp.can.25	BA.flex.levels.psp.can.25	BA.matrix.nrel.psp.can.25	BA.matrix.rel.psp.can.25	BA.nms2.sub	BA.wa.sub
PSP Only Subcanopy (5%)	BA.flex.cl.psp.sml	BA.flex.levels.psp.sml	BA.matrix.nrel.psp.sml	BA.matrix.rel.psp.sml	BA.wa.all.25	BA.wa.all.25
PSP Only Subcanopy (2.5%)	BA.flex.cl.psp.sml.25	BA.flex.levels.psp.sml.25	BA.matrix.nrel.psp.sml.25	BA.matrix.rel.psp.sml.25	BA.wa.can.25	BA.wa.can.25
PSP Only Small stem (5%)	BA.flex.cl.psp.sub	BA.flex.levels.psp.sub	BA.matrix.nrel.psp.sub	BA.matrix.rel.psp.sub	BA.wa.psp.all.25	BA.wa.psp.all.25
PSP Only Small stem (2.5%)	BA.flex.cl.psp.sub.25	BA.flex.levels.psp.sub.25	BA.matrix.nrel.psp.sub.25	BA.matrix.rel.psp.sub.25	BA.wa.psp.can.25	BA.wa.psp.can.25

Conclusion

MultiEDA can be used to conduct exploratory data analyses through the examination of ordinations, species tables, size-class distributions, and temporally-changing, spatially-explicit data structure visualization. The application's many linked and interactive outputs along with their diverse control tools and an overall compact GUI design allow users to explore multivariate community data quickly and effectively. These qualities resulted in the application being paramount for generating and exploring many of the hypotheses associated with the Duke Forest data discussed in the analytical chapters of this dissertation.

Because of the ease of modifying R code, which this Shiny app is built using, most intermediate R users would be capable of editing this application themselves to customize or add functionality to fit their specific needs. In this way, this free application provides ecologists an efficient and attractive interface to explore their data.

Version 1.52 was created specifically for analyzing Duke Forest data, but the underlying code is reproduced as a supplemental file to this dissertation (see Appendix S3) so that interested users can generalize the code to allow for analysis of a broader set of generated data objects in the application. The format and structure of the application would be readily applicable to a range of longitudinal, multivariate data, especially those with mapped forest stem data. Although Version 1.52 requires users to reference output objects made external to MultiEDA in R, the source code could additionally be modified to include a menu with functionality to create data directly within MultiEDA. Interested users could also extend the provided application code to overlay environmental correlation vectors on ordination plots or to provide additional interactive tools to hide and manipulate the resulting joint plot. Finally, Shiny capabilities would allow future interested users to extend the application to include hover instructions over each tool, input, and graphic to help guide novice users. Overall, these potential updates, along with endless customizations and generalizations that could be generated by manipulating the source code in the supplemental files, add to the potential utility of MultiEDA for multivariate exploratory data analyses of a diverse range of ecological data.

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CHAPTER 5: LONG-TERM BIOMASS AND FOREST GROWTH TRENDS IN THE DUKE FOREST, NORTH CAROLINA

Summary

Long-term permanent plot studies provide a unique and valuable opportunity to examine forest processes that occur on time scales of decades and to evaluate how observed trends can confirm and inform existing theoretical models. In this study, 80 years of forest growth was recorded across all phases of succession in a series of thinning even-age *Pinus taeda* stands and aggrading second-growth *Quercus-Carya* and *Liriodendron-Liquidambar* hardwood stands in the Duke Forest (and nearby G. W. Hill Forest) in the Piedmont of North Carolina. Examination of increasing but slowing 80-year biomass and growth rate trends in successional plots supported prior models, and results confirmed the importance of canopy stem density and mortality in driving these patterns. Mortality in these plots due to Hurricane Fran in 1996 resulted in variable losses of biomass. The synchronous mortality of canopy stems from Hurricane Fran in some plots led to lags in hardwood regeneration that have yet to result in formally discernible late-stage patterns. In contrast, mixed-age second-growth hardwood plots demonstrated consistent biomass accumulation and continued increases in growth rate, despite achieving biomass levels found only previously in more static old-growth forests. In contrast with frequently-cited developmental models, these results are in line with mounting evidence for higher-than-expected growth patterns in late-stage forests. Such changes could be the result of changing climate patterns or due to anthropogenic impacts, but regardless, more mechanistic-oriented models must be developed to determine the cause of these newly apparent, seemingly-widespread patterns.

Introduction

Various successional trends in forest biomass have been theorized and observed (see Peet 1981a and Peet 1992 for summary). Early theories of forest succession suggested that forest biomass would increase monotonically across time until slowing and leveling to some asymptote (Odum 1969 and Sprugel 1985). This logistic accretion model has received some support, particularly in the tropics (e.g., Silver et al. 2000), northwestern pine forests (MacLean & Wein 1976 and Forcella & Weaver 1977), various temperate forests in the northern United States (Holt & Woodwell in Whittaker 1975, Sprugel 1984, Caspersen et al. 2000) and for unfavorable temperate sites with low establishment rates (Peet 1978, 1981b).

Although some data have provided support for asymptotic biomass trends, biomass is also frequently observed peaking prior to a forest patch reaching a mature, steady-state stage. In these instances, stand biomass reaches a mid-successional maximum followed by a loss in biomass. This loss either progressively continues through forest climax (e.g., in boreal sites; Bloomberg 1950, Strang 1973), drops to an intermediate asymptotic biomass level (i.e., Bormann & Likens's (1979) "shifting mosaic" model; support from Loucks 1970, Botkin et al. 1972, Peet 1981b, and throughout the forestry literature), or drops and then recovers to an equilibrium via dampening oscillations (e.g., see Ilvessalo 1937, Siren 1955, Plochmann 1956, and Peet 1981a, 1981b). Although some young forest stands may demonstrate a logistic increase during thinning phases of succession (e.g., Switzer et al. 1966, Kinerson et al. 1977, Acker et al. 2000), these forests are likewise expected to experience biomass decline during maturation and subsequently fall under one of the aforementioned rise-then-fall models.

No definitive consensus has emerged regarding which trends are associated with which conditions. However, Peet (1981a, 1992) attempted to unify these different patterns via a population-based model that asserts that biomass dynamics can be understood in terms of time lags in regeneration and in terms of the synchrony of mortality of individuals in the stand. This model incorporates a wide range of pattern outcomes that include those mentioned already. Specifically, the degree of time lag in regeneration can change the pattern of biomass accumulation from a simple logistic curve (no lag) through a peak-and-fall (moderate lag) to damped oscillations around a climax asymptote (long lag). The model posits that synchronous tree mortality serves to amplify the initial drop in biomass and any subsequent oscillations.

Population processes are not the only mechanisms that drive successional biomass dynamics. Changes in resource availability through succession have also been shown to drive biomass trends (see Peet 1992 for examples). Improvements in soil characteristics (e.g., increased organic matter and nutrients) from early species can facilitate subsequent biomass growth (e.g., Pugnaire et al. 1996). Further, Fridley and Wright (2012; also Wright & Fridley 2010) demonstrated that variations in soil fertility (and temperature; Fridley & Wright 2018) can impact establishment and growth rates of tree seedlings, thus impacting the rate of biomass growth in initial successional stages as well. In contrast, soil leaching and tying up of nutrients in dead organic matter can both decrease the availability of needed resources as succession continues resulting in decreased biomass in later successional stages (e.g., Bloomberg 1950 and Strang 1973).

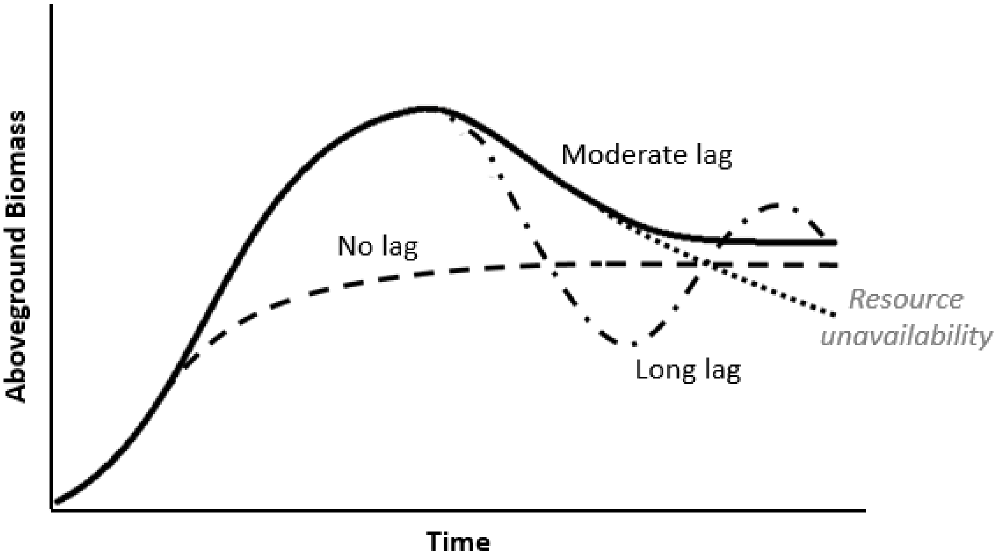

Figure 5.1 Modified conceptualization of Peet's (1981a, 1992) lag model of successional biomass trends. After logistic growth, stands dominated by single, even-aged species are theorized to either slow to an asymptote, peak and fall to an equilibrium, or peak then undershoot and oscillate in a damped manner around a long-term equilibrium depending on the degree of lag in regeneration following canopy mortality. Synchronous mortality is expected to accentuate the magnitude of drop and oscillation, and finally, a total decline in biomass is expected if nutrients become unavailable.

Recent work examining later-stage, mature and old-growth forests has brought into question the generalizability of the conventional biomass accumulation models described above. Some stands have demonstrated earlier leveling off (e.g., Fahey et al. 2005 and Siccama et al. 2007) in biomass than expected based on estimates of Bormann & Likens (1979), whereas others have peaked later (e.g., Tyrrell & Crow 1994, Keeton et al. 2011, Foster et al. 2014, and Eisen & Plotkin 2015) or demonstrated continuing increases through maturation with little evidence of asymptotic relationships or declines in centuries-old stands (e.g., Ziegler 2000 and Pontius et al. 2016). Biomass accumulation rates also have been found to be higher than expected (e.g., McMahon et al. 2010 – though see Foster et al. 2010) and to be increasing across the last century (Salzer et al. 2009 and Pontius et al. 2016). Although biomass is expected to increase as forests develop, these less-expected positive trends in accumulation rates could be due to centuries-long trends in increased growth rates of common canopy species (e.g., Pederson et al. 2004) that might be responding to improved conditions brought about by climate change or increased CO_2 or nitrogen availability.

Many of the theories regarding long-term trends in biomass were developed from chronosequences and tree ring studies (e.g., Loucks 1970, Peet 1978, 1981b, Peet & Christensen 1988, Pederson et al. 2004, Salzer et al. 2009, Keeton et al. 2011, Foster et al. 2014) or model iterations (e.g., Bormann & Likens, 1979 and Foster et al. 2014). In contrast, there is a paucity of studies that have tracked growth rates and biomass accretion of individual temperate forest stands more directly across time across the entire successional sequence. Although Peet (1981a) tracked biomass changes of North Carolina pine forests across 50 years, few studies have observed biomass accretion through the transition stage and beyond (though see Acker et al. 2000, Eisen & Plotkin 2015, and Pontius et al. 2016), with no contemporary work representing the Southeastern United States. Such studies will be necessary to examine proposed theories of mid-to-late-successional biomass trends and to interpret contemporary findings regarding actual forest dynamics.

The objective of this chapter is to examine long-term patterns of biomass accretion (i.e., the net biomass accumulated across time) and accretion rates (i.e., the rate of change in biomass through time) across each stage of succession. The chapter extends the work of Peet (1981a) by examining 80 years of long-term dynamics in a series of permanent sample plots in the Duke Forest and nearby Hill Forest in the North Carolina Piedmont (which is collectively referred to as the “Duke Forest data” throughout this chapter). These data are ideal for this study because the growth and mortality of individual trees has been recorded continuously through each stage of succession, with the consequence that a directly-informed characterization of long-term trends can be described.

In addition to reporting general long-term trends, this chapter seeks to determine whether the Piedmont forests of the southeastern United States, which have served as a model system for successional research for almost 100 years, conform to the patterns predicted by successional biomass theory (i.e., that of Peet 1981a and 1992). Specifically, this chapter explores to what degree mortality, pine density, and lag in forest regeneration impact transitional-stage biomass trends in even-aged pine stands. Additionally, the chapter examines 80 years of biomass trends in later-stage, uneven-aged hardwood stands to determine if these stands appear to be reaching an equilibrium or whether they show trends consistent with following suit of other recently-described aggrading late-stage forests. The accretion rates of these hardwood forests are additionally examined to determine if hypothesized biomass gains appear to be occurring at a stable, increasing or decreasing rate. Finally, forest growth rates (herein defined as plot-level accretion rates corrected for mortality) are examined to determine whether forests are in fact growing faster as time goes on. Such a trend would suggest that a change in resource availability or forest structure itself could be responsible for hypothesized biomass increases in hardwood plots.

Methods

Study area and site description

Thirty-seven permanent sample plots (PSPs) from the Duke Forest (n=34) and the G. W. Hill Forest (n=3) that had been resampled every 5 – 18 years for in most cases 80 years were used for this study. Reference to the Duke Forest data throughout this chapter implicitly includes Hill Forest plot data unless otherwise specified. Although some plots were expanded in size following initial establishment, only original plot areas were utilized in this study (i.e., only trees associated with a “Phase” value of 0 in the data), with plots ranging in area from 405 – 1012 m^2. See Chapter 2 for details.

Twenty-eight of these plots are successional old-field, even-aged pine (primarily *Pinus taeda*) stands with known age and stem density at plot establishment. These plots vary in stand age at establishment (8 – 30 years) and in initial stem density (25 – 1172 stems), and they are currently at varying levels of transition to hardwood forests. The remaining 9 plots are relatively later-stage hardwood forests that were identified as mixed-aged hardwood stands 70 – 80 years ago at establishment. Two of the plots represent bottomland, alluvial hardwood communities, while the remaining plots are representative of upland oak-hickory stands with variable soil properties. Of these upland sites, PSP 35 is the most edaphically (and floristically) distinctive due to its underlying soil which is characterized by magnesium-rich, shrink-swell (montmorillonitic) clay (see Figure 5.2). Subsets of plots are spatially clumped based on shared experimental histories (see Chapter 2 and Supplemental Appendix S1 for details).

Diameter and height measurements of individually-identified stems allows for direct quantification of stand growth. Additionally, records of tree damage (i.e., diameter or height reductions) and mortality permit accounting for losses in biomass, especially in relation to experimental manipulations in some plots prior to 1960 and damage from Hurricane Fran in 1996 that variously impacted plots (see Figure 5.3).

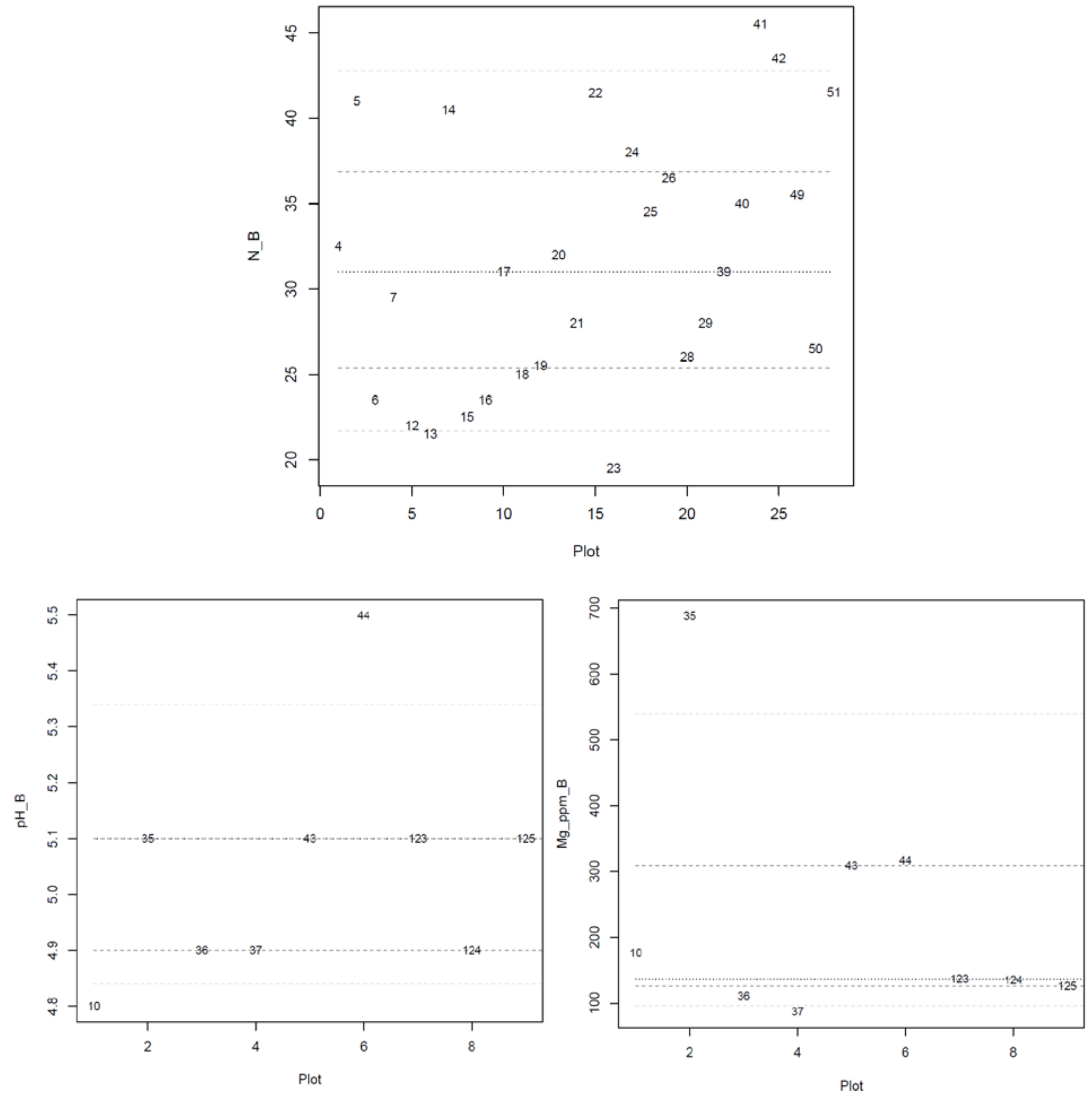

Figure 5.2 Relative relationships of noteworthy soil characteristics for permanent sample plots. a. shows the concentration of B Horizon soil nitrogen (ppm) for all successional plots. b. shows relative B Horizon pH and c shows B Horizon magnesium (ppm) for hardwood plots. The dotted lines represent the median value for each respective graph, while dashed lines represent the 25% and 75$^{\%}$ quantile (dark grey) and 5% and 95% quantile values.

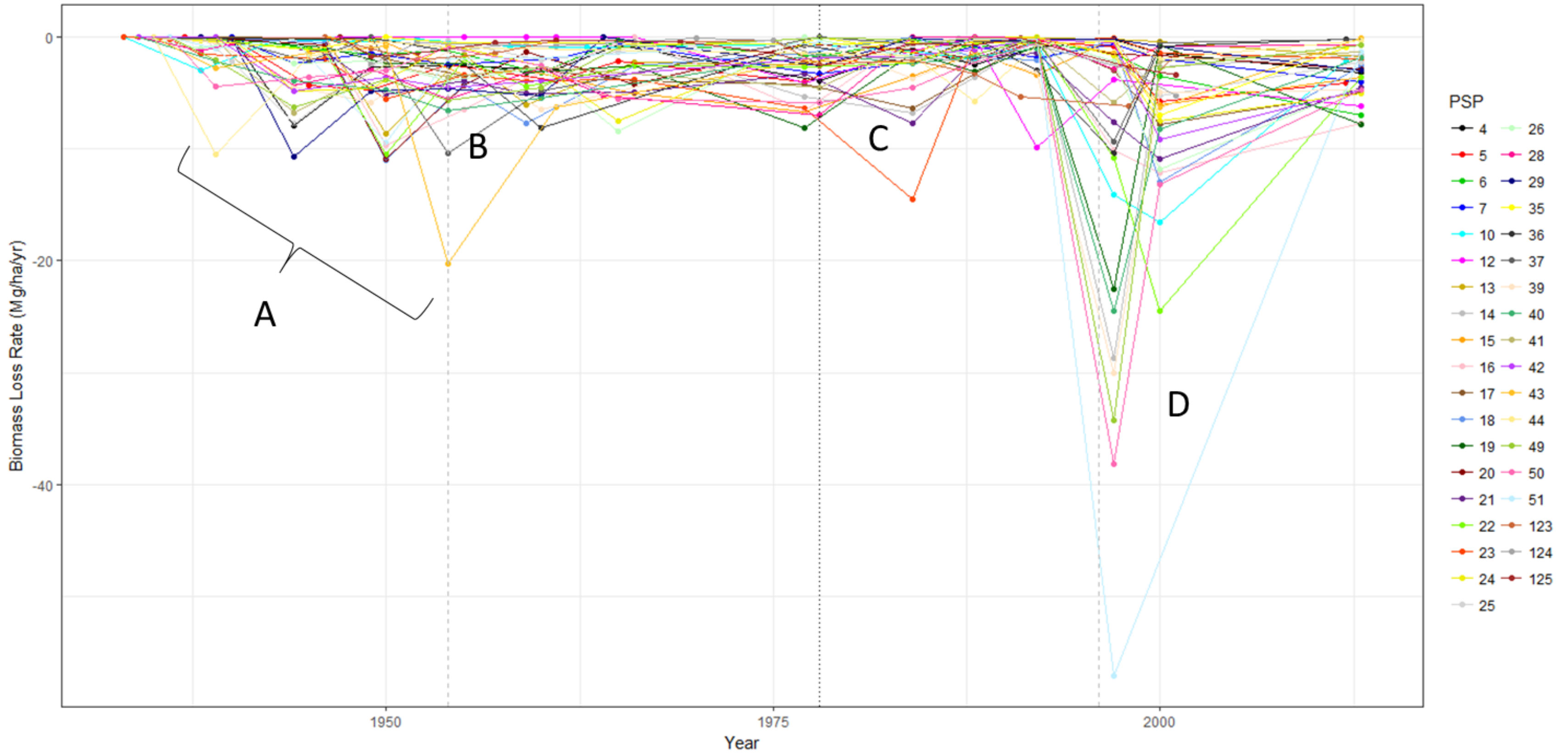

Figure 5.3 Biomass loss (in terms of annual loss rates) for all Duke Forest PSPs. Biomass loss rates has typically been around -3 Mg/ha/year (-2 Mg/ha/year if excluding years in which plots were decimated by Hurricane Fran). Notable causes of plot mortality include: A. Experimental manipulation and cutting; B. Hurricane Hazel damage and salvage (1954); C. Ice storm damage; and D. Hurricane Fran damage (1996). The vertical dotted line indicates year of change in sampling protocol to more consistently measured ingrowth; two vertical dashed lines represent the timing of Hurricane Hazel (1954) and Hurricane Fran (1996). Each line represents an individual PSP and is coded with a unique color and point shape.

Data post-processing

Because the Duke Forest PSP dataset contains both directly-measured diameter and height measurements for each individual tree, an approach incorporating both size parameters was utilized for estimating biomass of each tree. First, the volume of each tree was estimated by calculating each tree's parabolic volume (Newbould 1967, Whittaker & Woodwell 1968, Rochow 1974, Knox et al. 1989) using the following equation:

$$\mathbf{V_p = (0.5 * \pi * r^2 * h)}$$

where *r* is tree radius and *h* is tree height. Diameter measurements from the field were converted to radii (still in cm), and recorded height (m) measurements were converted to centimeters to produce a volume measurement in cubic centimeters (cm^3). Although a parabolic estimation more reasonably approximates the volume of excurrent species such as pines compared to hardwood trees with decurrent growth habits, application of this parabolic approach to estimating biomass of temperate hardwoods has been found to be reasonably accurate (Siccama et al. 1994).

Next, published species averages for wood density (WD) were determined for all species in the PSP data set measured as the oven dry mass divided by green volume in g/cm^3. Although some sources that were referenced reported specific gravity (SG) values instead of WD, these sources all provided "Basic SG" values (oven dry mass / green volume / H_2O density) and therefore could be equated to WD with little consequence (Williamson & Wiemann 2010). Species averages provided by Jenkins et al. (2004) were used for the majority of the species in the data. WD or SG values were also acquired from Davis (1889), Alden (1995), USDA Forest Service (1999), Martínez-Cabrera et al. (2009), Zanne et al. (2009) and Chave et al. (2009), Miles & Smith (2009), Hoffmann et al. (2011), the World Agroforestry Centre (2012) Wood Density Database, Coyle et al. (2014), and Nate Swenson (unpublished data); see Table 5.1.

Because wood density is highly conserved among species within a genus (Swenson & Enquist 2007), genus means were applied to species lacking available wood density data (see Table 5.1 for specific species). This was done by using means for reported genera or by manually calculating averages from available congeneric species. If data for only a single con-generic species of a species missing data was available, that single species value was used for all missing congenerics. Lastly, in a few instances, specific "stand-in" species with available data were selected to inform values of missing species (e.g., the value for closely-related *Carya glabra* was used for *Carya ovalis*).

Finally, the wood biomass of each individual was calculated by multiplying parabolic volume and wood density (or specific gravity) for each individual and is reported in grams. Biomass was aggregated for each species in each plot in each year and then formed into a wide-format matrix with sample units (plot-year combinations) as rows and individual species as columns. Biomass was also summed across all species for each sample (plot and year combination). Final biomass values were scaled by plot area and converted so that each value represented Mg/ha.

A biomass accumulation rate (or change in biomass between sampling periods; Mg/ha/year) was calculated as the difference in biomass between a given sampling year and the prior sampling year divided by the length of time (in years) between each sampling effort. In this way, accumulation rate is synonymous with "biomass increment" from the literature (Clark et al. 2001 and Foster et al. 2014). In addition to accumulation rate, two additional rates were quantified. Because the condition (or "CC") of each tree (i.e., whether it was alive, dead, missing or damaged) was recorded in the PSP data, biomass loss due to mortality or trunk damage and biomass gain due to forest growth could both be quantified. Biomass lost due to mortality and trunk damage was calculated by summing biomass of dead trees and loss of biomass from previous sampling periods for missing trees and damaged trees (i.e., based on decreased height and sometimes decreased diameter of broken stems). A biomass loss rate (Mg/ha/year) was calculated by dividing biomass lost for a given sampling period by the number of years since the previous sampling period. Finally, growth rate (Mg/ha/year) was calculated as the sum of net biomass change and biomass lost divided by the period length. In this way, growth of the forest could be quantified by controlling for biomass losses due to mortality and damage. By accounting for mortality, the growth rate metric avoids potential biases previously identified (Malhi et al. 2004, Foster et al. 2010, Brienen et al. 2012, Foster et al. 2014) in growth studies that ignore mortality-driven biomass losses. Each plot's initial sampling period was dropped from all models incorporating accumulation or growth rate due to the inability to accurately calculate biomass levels prior to initiation of plots.

Table 5.1 Species-average wood density values and literature sources

Species	**WD**	**Notes**	**Data type reported**$^{+}$	**Source***
Acer sp.	0.52	Average of *A. rubrum* & *A. floridanum*	SG	4
Acer floridanum	0.54		SG	4
Acer rubrum	0.49		SG	4
Aesculus sylvatica	0.33		WD	7
Ailanthus altissima	0.33		SG	4
Albizia julibrissin	0.52		WD	7
Alnus serrulata	0.37	Used values for *Alnus spp.*	WD	7
Amelanchier arborea	0.66		SG	2
Asimina triloba	0.47		SG	4
Betula nigra	0.56		SG	4
Calycanthus floridus	0.52		WD	5
Carpinus caroliniana	0.58		SG	4
Carya carolinae-septentrionalis	0.73		WD	11
Carya cordiformis	0.60		SG	4
Carya glabra	0.66		SG	4
Carya ovalis	0.66	Used closely related *C. glabra* as substitute	SG	4
Carya ovata	0.64		SG	4
Carya pallida	0.70		WD	11
Carya sp.	0.62	Avg. from all species as calculated by source	SG	4

Carya tomentosa	0.64		SG	4
Celtis laevigata	0.47		SG	4
Celtis occidentalis	0.49		SG	4
Cercis canadensis	0.58		SG	4
Chionanthus virginicus	0.57		WD	8
Cornus florida	0.64		SG	4
Crataegus marshallii	0.72	Used values for Crataegus spp.	WD	10
Crataegus sp.	0.62	Avg. from all species as calculated by source	SG	4
Diospyros virginiana	0.64		SG	4
Elaeagnus pungens	0.45	Avg. of two China *E. angustifolia* entries	WD	6
Elaeagnus umbellata var. parvifolia	0.45	Avg. of two China *E. angustifolia* entries	WD	6
Euonymus americanus	NA	No data could be found. Only 6 entries in data	--	--
Fagus grandifolia	0.56		SG	4
Fraxinus sp.	0.51	Avg. from all species as calculated by source	SG	4
Gleditsia triacanthos	0.60		SG	4
Hamamelis virginiana	0.56		SG	2
Ilex ambigua	0.50	Avg. of available *Ilex* species	SG	2
Ilex decidua	0.50	Avg. of available *Ilex* species	SG	2
Ilex opaca	0.50		SG	4
Juglans nigra	0.51		SG	4
Juniperus virginiana	0.44		SG	4
Ligustrum japonicum	0.64	Avg. of available species (*L. lucidum* & *L. vulgare*)	WD	6
Ligustrum sinense	0.64	Avg. of available species (*L. lucidum* & *L. vulgare*)	WD	6
Lindera benzoin	0.44	Avg. of reported range of values (400 - 480)	WD	9
Liquidambar styraciflua	0.46		SG	4
Liriodendron tulipifera	0.40		SG	4
Lonicera maackii	NA	No data could be found. Only 1 entry in data	--	--
Magnolia grandiflora	0.46		SG	4
Magnolia tripetala	0.42		WD	8
Morus rubra	0.59		SG	4
Nyssa sylvatica	0.46		SG	4
Ostrya virginiana	0.63		SG	4
Oxydendrum arboreum	0.50		SG	4
Paulownia tomentosa	0.28		WD	6
Pinus echinata	0.47		SG	4
Pinus taeda	0.47		SG	4
Pinus virginiana	0.45		SG	4
Platanus occidentalis	0.46		SG	4
Prunus serotina	0.47		SG	4
Quercus alba	0.60		SG	4
Quercus coccinea var. coccinea	0.60		SG	4
Quercus falcata	0.52		SG	4
Quercus lyrata	0.57		SG	4
Quercus marilandica	0.56		SG	4
Quercus michauxii	0.60		SG	4
Quercus montana	0.57		SG	4
Quercus pagoda	0.61		SG	4
Quercus phellos	0.56		SG	4
Quercus rubra	0.56		SG	4
Quercus sect. Lobatae	0.57	Avg. of all red oak species found in Duke Forest	SG	4
Quercus shumardii	0.56		SG	4
Quercus sp.	0.56	Avg. from all species as calculated by source	SG	4
Quercus stellata	0.60		SG	4

Quercus velutina	0.56		SG	4
Rhus copallinum	0.51		WD	5
Salix nigra	0.36		SG	4
Sassafras albidum	0.42		SG	4
Styrax grandifolius	0.42	Avg. of all Asian species' values	WD	6
Ulmus alata	0.57		SG	4
Ulmus americana	0.46		SG	4
Ulmus rubra	0.48		SG	4
Vaccinium arboreum	0.47		SG	4
Vaccinium corymbosum	0.47	*V. arboreum* only species available	SG	4
Vaccinium sp.	0.47	*V. arboreum* only species available	SG	4
Vaccinium stamineum	0.47	*V. arboreum* only species available	SG	4
Viburnum acerifolium	0.65		WD	8
Viburnum prunifolium	0.83		SG	1
Viburnum rafinesquianum	0.67		WD	8
Viburnum rufidulum	0.83	Used similar-growing *V. prunifolium*	SG	1
Viburnum sp.	0.66	Avg. values of available species	WD	8

+WD is wood density (g/cm3); SG is specific gravity (in each case "Basic SG") *Sources: 1. Davis (1889), 2. Alden (1995), 3. USDA Forest Service (1999), 4. Jenkins et al. 2004, 5. Martínez-Cabrera et al. (2009), 6. Zanne et al. (2009) and Chave et al. (2009), 7. Miles & Smith (2009), 8. Hoffmann et al. (2011), 9. the World Agroforestry Centre (2012) Wood Density Database, 10. Coyle et al. (2014), and 11. Nate Swenson (unpublished).

Analysis

Visual characterization of temporal (for both mixed-age hardwood stands and successional pine stands) and age-based (for pine plots only) biomass accretion patterns were used to examine conformity of Duke Forest plots to theorized trends. Quantification of pine stem densities was also performed for pine stands to characterize the degree of transition from even-aged pine forest to mixed-age hardwood forest.

Mixed effects models were used to quantify linear trends in biomass, accumulation rates, and growth rates of plots and to quantify the predictive ability of stem density, mortality, and between-plot variation in environmental (e.g., soil) characteristics on these trends. Modelling was performed using the lme4 package (version 1.1-13; Bates et al. 2015) in R (R Core Team 2016). Model selection was based primarily on parsimonious inclusion of predictors of interest (e.g., stem density, degree of mortality, etc.), whereas inclusion of ecologically-relevant complexities (e.g., variable soil nutrients) or random-slopes were added to models only if guided by substantial decreases in both the Akaike Information Criterion (AIC; Sakamoto et al. 1986) and Bayesian Information Criterion (BIC; Schwarz 1978). After optimizing information criteria, final models were scrutinized once more by ensuring that all predictors were significant (characterized using bootstrapped 95% confidence intervals). Centering of predictors in the models was accomplished by subtracting predictor means, and scaling of predictors was achieved by dividing centered data by the standard deviation of that centered data. All analyses were performed using R (R Core Team 2016).

Results

Successional pine plots

Biomass trends

Successional plots that consisted of less-than-30-year-old stands at plot establishment had an average of 29.282 ± 30.029 (SD) Mg/ha of biomass at the start of the study. Mean biomass of pine stands around age 30 (the first age shared by all successional plots) was 142.909 ± 38.56 (SD) Mg/ha. Successional PSPs not strongly damaged by Hurricane Fran in 1996 held between 300 – 500 Mg/ha of biomass in the last sampling period, whereas plots severely damaged by Fran maintained a lower range of approximately 100 – 200 Mg/ha of biomass in 2012 – 2013 (Figure 5.4 and Figure 5.5). The average pine stand increased by almost a full order of magnitude (mean factor of change = 8.6 ± 7.6) at its measured peak with multiple plots increasing 10, 20, and even 30 times over initial biomass levels. The mean maximum recorded biomass across successional plots was 355.698 ± 81.175 (SD) Mg/ha, although a number of plots still appear to be actively aggrading biomass.

In the majority of successional plots, plot-level biomass has increasingly been divided across a greater number of species than at plot establishment, resulting in biomass from historical canopy dominants making up a smaller proportion of total plot biomass across time. Specifically, *Pinus taeda* biomass dropped from 98.2 ± 2.2 (SD) % of plot biomass in all successional plots at stand-age 30 to accounting for only about 75.2 ± 14.7 (SD) % of plot biomass in the most recent survey (or near or below 50% in plots most severely damaged from hurricane Fran in 1996). This drop is due to major losses of pine stems in successional plots through thinning and disturbance.

Across successional plots, successional hardwoods such as *Liriodendron tulipifera* and *Liquidambar styraciflua* experienced the largest increases in species-specific plot biomass (Figures 5.4 and 5.5). These two species increased from less than 1 Mg/ha each in 30-year-old stands to 18.274 ± 17.768 (SD) Mg/ha and 17.684 ± 11.484 (SD) Mg/ha, respectively, by the time stand ages approached 85 – 94 years post-pine-establishment. *Oxydendrum arboreum* and *Acer rubrum* likewise experienced noteworthy increasing proportions of plot biomass across the length of the study (with mean biomass magnitudes of 4.363 ± 6.659 Mg/ha and 9.412 ± 8.047 Mg/ha, respectively, by the time stands reached 85 – 94 years post-pine-establishment). Oaks and hickories still accounted for less than 1 Mg/ha per species on average across plots by this stand age (with the exception of *Quercus rubra* with a mean of 1.76 ± 3.492 Mg/ha), while early-to-mid-century mid-story dominant *Cornus florida* began experiencing precipitous decline in the 1990s and 2000s likely due to anthracnose disease (but potentially also influenced by deer browse). Overall, hardwood biomass increased from a mean of about 1.955 ± 2.476 (SD) Mg/ha around stand-age 30 to almost 60 Mg/ha (59.326 ± 21.449) by the time stands reached their late 80s or 90s. The oldest stands (immediately adjacent PSPs 49, 50, and 51 that each experienced severe damage from Hurricane Fran in their 91st year) achieved a mean of 76.500 ± 5.220 (SD) Mg/ha of hardwood biomass by the time they reached 107 years post-pine-establishment (and 15 years post-Fran).

No successional plots that were experimentally manipulated (see plot history table found in Appendix S1 for experimentation details) prior to 1970 show any significant long-term differences due to treatments, suggesting that the treatments only hastened natural self-thinning processes. However, minor, short-term biomass losses due to experimental manipulation are apparent for almost all manipulated plots (PSPs 4, 13, 16, 18, 20, 22, 24, 25, 29, 41, 42, 49, 51 – all but 6 and 7; Figures 5.4 and 5.5). Of these, PSP 41 experienced a decline in biomass that persisted through 1978, whereas PSPs 16 and 50 both experienced reduced growth following experimental manipulation that continued through the middle of the study.

In 2013 (the final sampling year) the Duke Forest PSPs ranged in age from about 90 – 110 years since initial post-abandonment pine growth, and the plots had between 2 and 33 *Pinus taeda* stems remaining (average of 15 ± 9 (SD); or 224 ± 98 (SD) stems per hectare; see Figure 5.6a&c). Plots have experienced an average reduction of 23.8 ± 14.8 (SD) % in proportion of pine to total plot biomass with an average of only 9.9 ± 9.2 (SD) % of initial numbers of *P. taeda* stems still present in plots (see Figure 5.6b). *P. taeda* stem counts have dropped significantly (t = 5.2979, df = 30, p-value = 1.004e-05) from an average of 4319 ± 5536 (SD) stems per hectare to 224 ± 98 (SD) stems per hectare (with the current range between 37 and 370 stems per hectare).

These data suggest that, overall, the successional plots have entered the theoretical transition phase of succession. However, not all the plots have demonstrated a leveling or drop in biomass as might be expected based on theoretical models (e.g., Bormann & Likens 1979 and Peet 1981a, 1992). As can be seen in Figures 5.4 and 5.5, biomass accumulation trends varied across successional plots from continuously increasing (PSPs 4, 7, 13, 15, 18, 20, 21, 23, 25, 26,

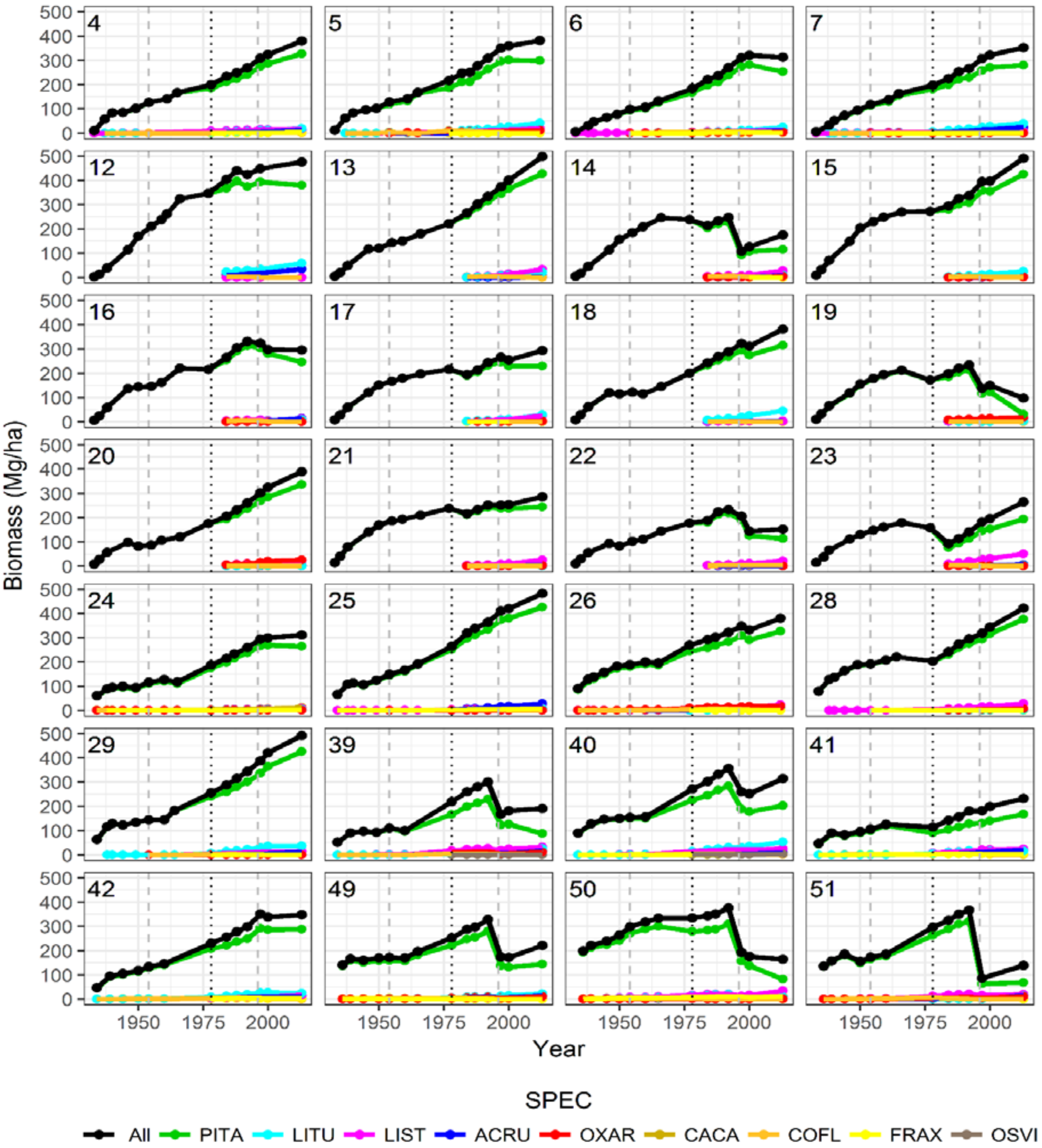

Figure 5.4 Biomass (Mg/ha) trends for all Duke Forest successional *Pinus taeda* plots across time. Thick black line represents whole-plot biomass values, while colored lines represent the most biomass-rich species in descending order of cumulative (across sampling-period) biomass (PITA = *Pinus taeda*, LITU = *Liriodendron tulipifera*, LIST = *Liquidambar styraciflua*, ACRU = *Acer rubrum*, OXAR = *Oxydendrum arboreum*, CACA = *Carya carolinae-septentrionalis*, COFL = *Cornus florida*, FRAX = *Fraxinus spp.*, and OSVI = *Ostrya virginiana*). The vertical dotted line indicates year sampling protocol changed to more consistently measure ingrowth; two vertical dashed lines represent Hurricanes Hazel (1954) and Fran (1996). See Table A.2 for biomass data.

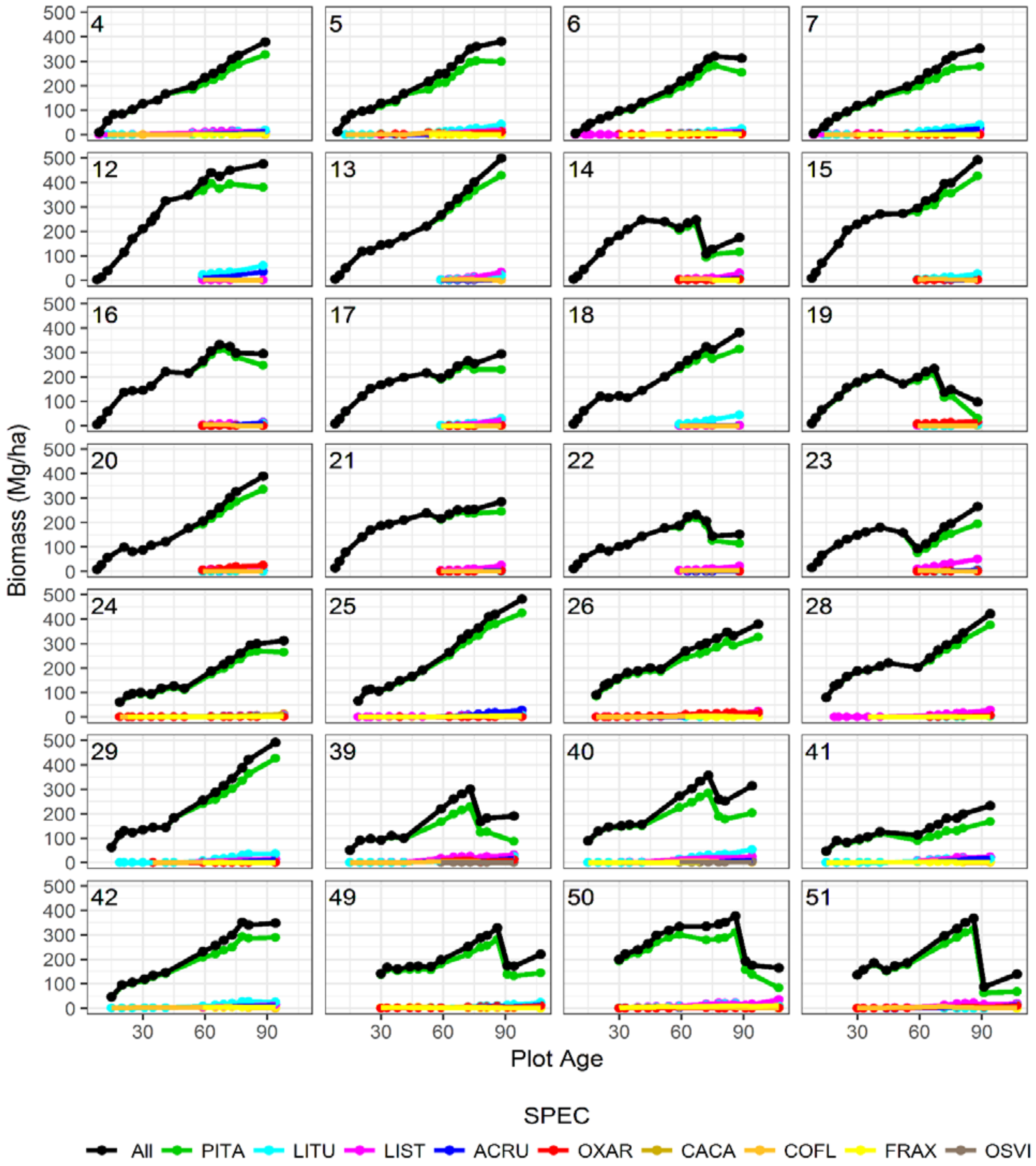

Figure 5.5 Biomass (Mg/ha) trends for all Duke Forest successional *Pinus taeda* plots across stand age. Thick black line represents whole-plot biomass values, while colored lines represent the most biomass-rich species in descending order of cumulative biomass (PITA = *Pinus taeda*, LITU = *Liriodendron tulipifera*, LIST = *Liquidambar styraciflua*, ACRU = *Acer rubrum*, OXAR = *Oxydendrum arboreum*, CACA = *Carya carolinae-septentrionalis*, COFL = *Cornus florida*, FRAX = *Fraxinus spp.*, and OSVI = *Ostrya virginiana*). Plot numbers are shown in the top left.

28, 29), slowing (PSPs 5, 12, 17, 41), levelling off (PSPs 6, 16, 24, 42), increasing post-disturbance (PSPs 14, 22, 39, 40, 49, 51) and declining post-disturbance (PSPs 19, 50). Plots with initial stand ages below 30 were represented by each trend pattern, while stands established 30 years after field abandonment (i.e., PSPs 49, 50 and 51) suffered the most prominent damage from Hurricane Fran in 1996 (when stand ages were approximately 90) and therefore experienced precipitous biomass loss (Figure 5.5). Although plots 49 – 51 are in close proximity to each other and therefore cannot themselves represent trends throughout the entire Duke Forest, additional plots (i.e., PSPs 14, 19, 22, 39 and 40) likewise suffered great losses (> 30% of pre-disturbance biomass) as a consequence of Fran, even though each of these stands was less than 80 years post-abandonment in 1996.

A closer inspection of stem density trends indicates that plots that are still aggrading biomass at a consistent pace (which range in current age from about 90 – 100 years old) have significantly higher (Kruskal-Wallis, chi-squared = 17.123, df = 1, p-value < 0.0001) density of *P. taeda* stems remaining in their canopies compared to plots showing other trends. As shown in Figure 5.6, the majority of these aggrading plots have retained a density of greater than 250 (mean of 304 ± 36) stems per hectare. This suggests that these plots are still in the initial stages of transition. The remaining PSPs, in contrast, each experienced a slowing, levelling or decline in biomass. These plots (which range in age from about 90 – 110 years old) have progressed further in the transition process with an average of 48% less canopy pine stems remaining (163 ± 86 stems per hectare) compared to aggrading plots. Further, the average ratio of hardwood to pine biomass in the more-progressed plots is significantly higher (Kruskal-Wallis, chi-squared = 13.793, df = 1, p-value = 0. 0002): 24.3 ± 27.1 (SD) % compared to 12.3 ± 6.3 (SD) % in aggrading stands. Plots with declined biomass trends all had biomass loss driven by synchronous mortality from Hurricane Fran in 1996. Overall, similar to Smith & Long (2001), stem density seemed to be more important than stand age when predicting trends.

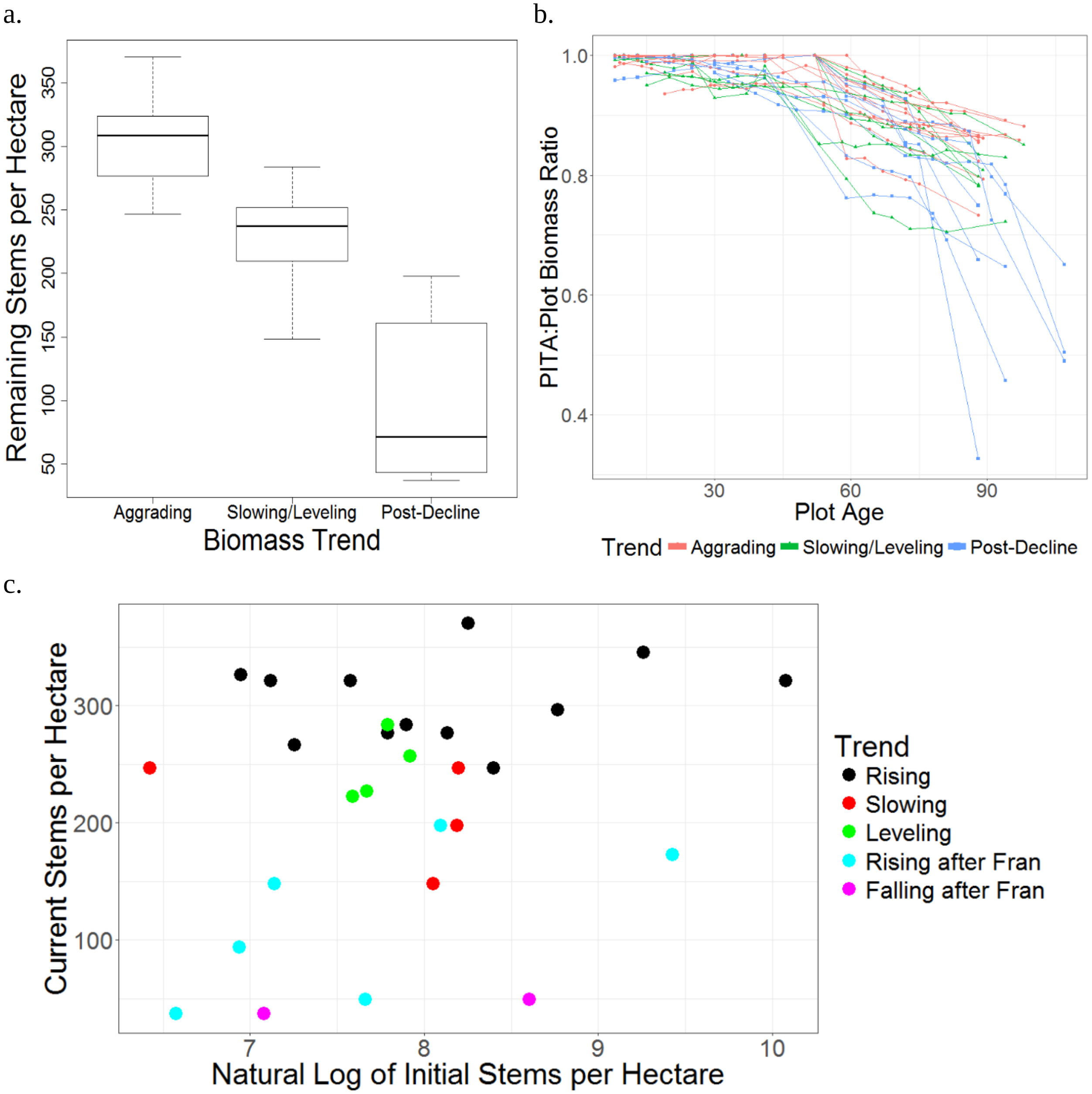

Figure 5.6 Diagnostic plots demonstrating Duke Forest successional plot trends in regard to *Pinus taeda* stem density and plot biomass. Aggregating plots were shown to have a significantly greater number of remaining *Pinus taeda* stems compared to plots that experienced other trends (a and c) and to have a significantly higher percentage of their biomass accounted for by *P. taeda* (b).

A more formal examination of biomass trends in the Duke Forest data using mixed effects models demonstrated that biomass accretion generally increased across age in the successional PSPs and that that increase was significantly dependent on the number of canopy stems and loss of biomass due to damage and mortality. In fact, approximately 71% of the variance (marginal R^2; Nakagawa & Schielzeth 2013 and Johnson 2014; see Figure 5.7 for performance) in the data can be explained by a random slope and intercept model with stand age, number of canopy stems in each plot (here defined as number of stems greater than or equal to the 70th percentile of plot-specific tree heights across all sampling periods), the interaction of age and canopy density, and biomass loss rate (i.e., total biomass of dead, missing, or damaged portions of trees divided by years between sampling efforts) as fixed effects. Specifically, as shown in Table 5.2, the model indicates that the number of canopy stems had a substantial positive impact on biomass levels (0.0645 [95% CI 0.057 – 0.072] Mg/ha per canopy stem, after un-scaling; see methods for scaling protocol) with the impact of canopy trees increasing as stand ages increased (0.002 [95% CI 0.002 – 0.002] Mg/ha more per year). Meanwhile, the model demonstrated that damage and mortality had a significant negative impact on net biomass levels (-1.984 [95% CI -1.407 – -2.571] Mg/ha per Mg/ha/year of biomass lost). Unsurprisingly, plots with large amounts of biomass loss (due to major damage or declines to canopy trees) experienced massive drops in plot biomass levels following Hurricane Fan in 1996.

Examination of the plots most strongly damaged by Hurricane Fran in 1996 (i.e., PSPs 14, 19, 22, 39, 40, 49, 50, 51) demonstrated that there was no trend regarding the proportion of hardwood biomass in a plot at the time of the hurricane and the degree of damage or subsequent recovery in that given plot. A linear model comparing the change in biomass in 1997 to the total biomass of all non-pine species was strongly non-significant for all plots ($F(1,26) = 0.9616$, $p =$

.334, $R^2 < 0.001$) and for just plots suffering significant canopy damage (F(1,6) = 0.0049, p = .947, $R^2 < 0.001$). Similarly, a linear model comparing post-Fran biomass change (i.e., change from 1997 to the 2012 – 2013 sampling effort) to hardwood biomass was also non-significant (F(1,6) = 0.9902, p = .358, $R^2 = 0.142$). Further, adding hardwood biomass as a predictor to the aforementioned mixed model made no substantial improvement either, which suggests that plot-level hardwood biomass is not a significant predictor of biomass trends in any successional plots.

Although the actual data for all but one plot (PSP 12) fall within the 95% bootstrapped confidence intervals for the model predictions, the model's mean prediction consistently underpredicts (e.g., in PSP 15) and overpredicts (e.g., in PSP 23) in a handful of plots. This indicates that additional variables (e.g., those relating to gradients in site quality) could improve the model (as is reflected in the marginal R^2 value of 71%). However, the limited sample size and observational nature of the data limits the statistical power needed for examining much more intricate models.

Table 5.2 Mixed effect model for successional plot biomass trends. The final model was a random slope and intercept model grouped by plot that incorporated centered age, scaled canopy density (of the 70% largest trees across each given plot; see methods for scaling protocol), the loss rate of biomass (in Mg/ha/year) and an interaction between centered age and scaled canopy density as fixed effects. The model was built using the lmer function in the lme4 package of R and used Restricted Maximum Likelihood (REML) to estimate the variance component. The table shows model estimates and upper and lower 95% bootstrapped confidence intervals for each estimate.

	Estimate	Lower	Upper
(Intercept)	214.4929	195.8327	232.9538
(Age - 51)	4.178451	3.733365	4.613557
scale(CanStems70.Ha)	87.31396	77.3046	97.32258
LossRate	-1.983783	-1.406766	-2.570872
(Age - 51):scale(CanStems70.Ha)	2.604278	2.249268	2.956703

Accumulation rate

Model selection criteria (AIC and BIC) indicated that age, in contrast to year, was the better predictor of biomass accumulation trends and that a random intercept model (without random slopes) performed best. The selected mixed model showed that biomass accumulation rates for successional pine plots decreased negligibly, and non-significantly, as plots aged (model estimate of -0.009 [95% CI -0.019 – 0.000] Mg/ha/year; see Figure 5.8. The model, which explained about 90% of the variation in the data (marginal R^2; Nakagawa & Schielzeth 2013 and Johnson 2014) indicated that year-to-year trends were driven significantly by biomass loss due to damage and mortality (model estimate of -1.110 [95% CI -1.074 – -1.146] Mg/ha/year per Mg/ha/year of biomass lost; see Table 5.3) and the density of *Pinus taeda* stems in the plot (with the model showing a change in 0.177 [95% CI 0.104 – 2.500] Mg/ha/year per every 1000 stems/ha of *P. taeda*).

Table 5.3 Mixed effect model for successional plot biomass accumulation rate trends. The final model was a random intercept model grouped by plot that incorporated centered age, scaled *Pinus taeda* ("PITA") density, and the loss rate of biomass (in Mg/ha/year) as fixed effects. The model was built using the lmer function in the lme4 package of R and used Restricted Maximum Likelihood (REML) to estimate the variance component. The table shows model estimates and upper and lower 95% bootstrapped confidence intervals for each estimate.

	Estimate	Lower	Upper
(Intercept)	7.520456	7.153898	7.887737
(Age - 51)	-0.00938	-0.01859	0.00013
LossRate	-1.109604	-1.072758	-1.14647
scale(StemsHa.PITA)	0.60182	0.354564	0.848563

Growth rate trends

Model selection criteria (AIC and BIC) indicated that age was a better predictor of biomass growth trends than year and that a random intercept model (without random slopes) performed best. Further, the information criteria indicated that stems/ha of all species was a better predictor of successional stand growth rates than predictors based on *Pinus taeda* alone (i.e., either stems/ha of all *P. taeda* stems or stems/ha of canopy *P. taeda*). The selected model (see Table 5.4) indicated that growth rates of the Duke Forest successional pine stands experienced a significant downward trend as stands aged (model estimate of -0.025 [95% CI -0.033 – -0.017] Mg/ha/year; see Figure 5.9). The model further demonstrated that denser stands tended to have higher growth rates (0.120 [95% CI 0.075 – 0.166] Mg/ha/year per 1000 stems after unscaling the estimate; see Table 5.4) while stands with higher levels of soil nitrogen had lower growth rates (-0.069 [95% CI -0.111 – -0.028] Mg/ha/year per ppm of nitrogen). All predictors were significant based on 95% confidence intervals. The model, however, only explains 21% of the variation in the data (marginal R^2; Nakagawa & Schielzeth 2013 and Johnson 2014).

Table 5.4 Mixed effect model for successional plot growth rate trends. Growth rates are calculated as the sum of the biomass increment and biomass lost to mortality and damage. The final model was a random intercept model grouped by plot that incorporated centered age, scaled stem density, and the concentration of nitrogen in the B horizon of plot soil as fixed effects. The model was built using the lme4 package of R and used Restricted Maximum Likelihood (REML) to estimate the variance component. The table shows model estimates and upper and lower 95% bootstrapped confidence intervals for each estimate.

	Estimate	Lower	Upper
(Intercept)	9.329545	8.003758	10.64803
(Age - 51)	-0.02476	-0.03288	-0.01662
scale(StemsHa)	0.567339	0.354754	0.784821
N_B	-0.06921	-0.1108	-0.02797

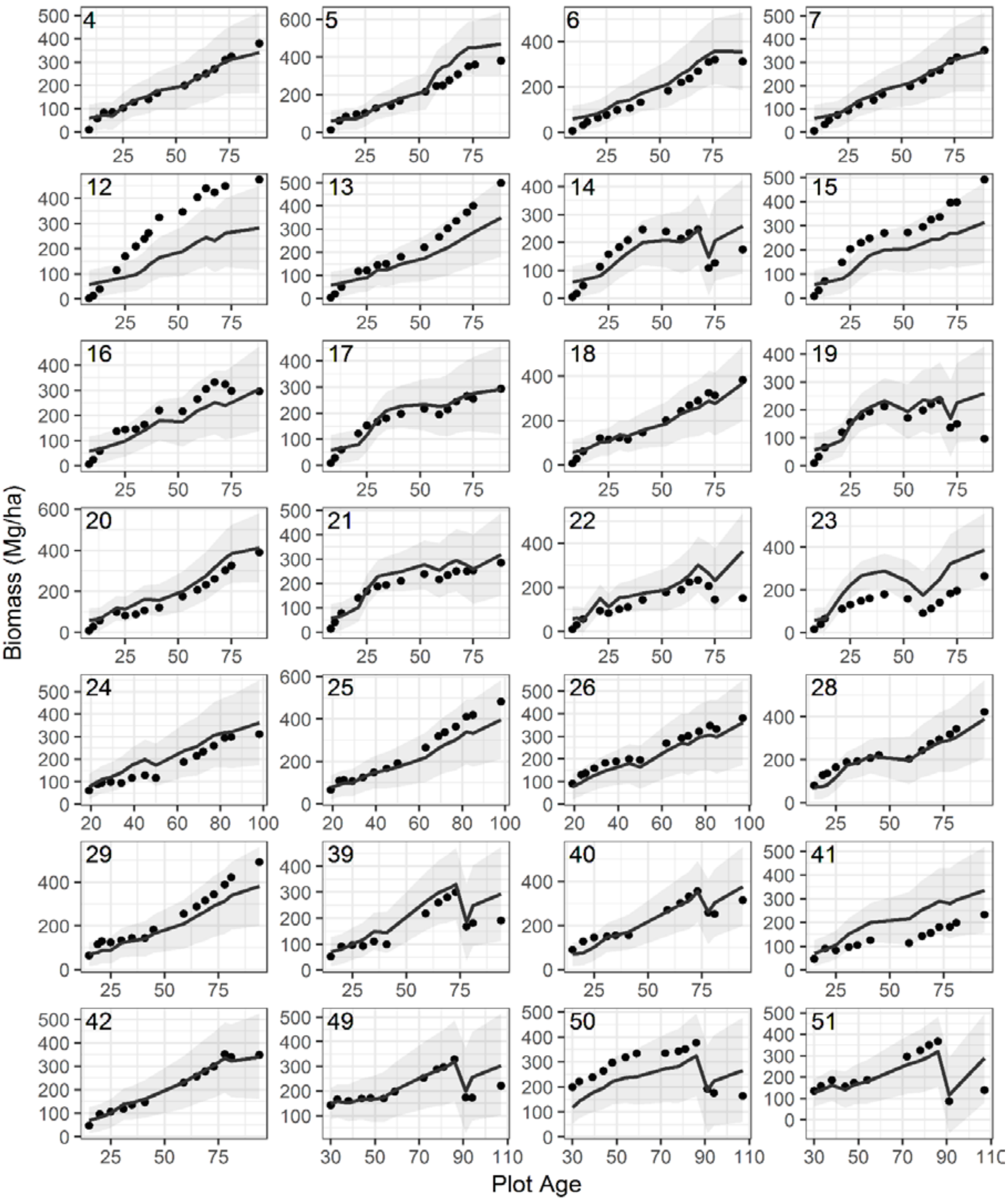

Figure 5.7 Panel graph showing per-plot predictions of the mixed model (Table 5.2) for successional Biomass (Mg/ha) trends. Black dots represent the recorded data, while the black line represents the model predictions. The gray ribbon represents the bootstrapped 95% confidence region for the mean model prediction. The model explained 71% of the variation in the data, though trends seen in PSPs 12 – 23 (which had increasing initial stocking levels) seem to indicate that stocking density would have improved the performance of the model in these plots . Plot numbers are shown in the top left.

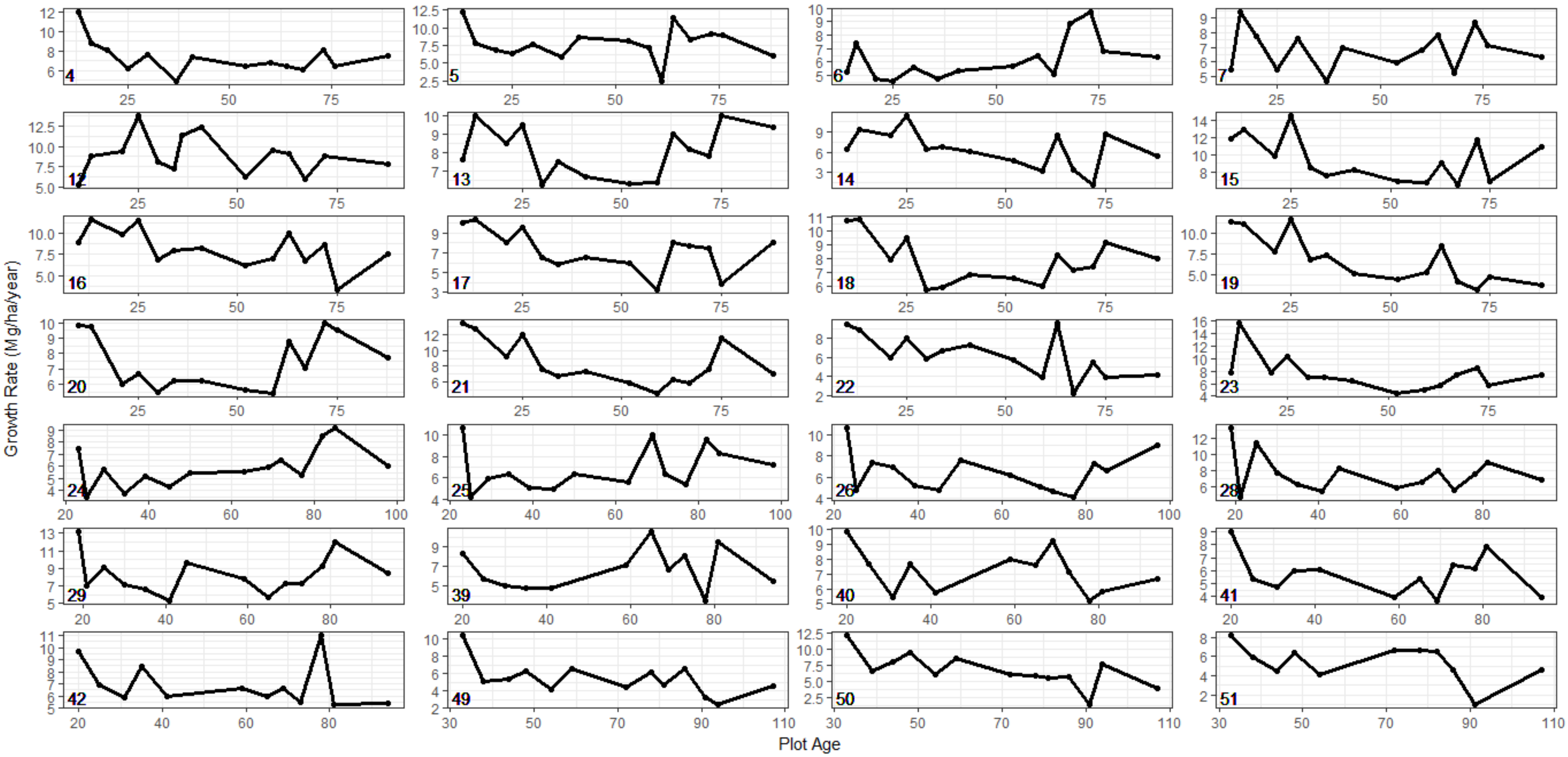

Figure 5.8 Raw growth rate trends for successional pine plots. There appears to be ample fluctuation even after controlling for biomass loss due to mortality, but overall the mixed model (see Table 5.4) demonstrated that stands experienced a significant downward trend as stands aged (model estimate of -0.025 [95% CI -0.033 – -0.017] Mg/ha/year). The model also showed that that denser stands tended to have higher growth rates (0.120 Mg/ha/year per 1000 stems) while stands with higher levels of soil nitrogen had lower growth rates (-0.069 Mg/ha/year per ppm of nitrogen).

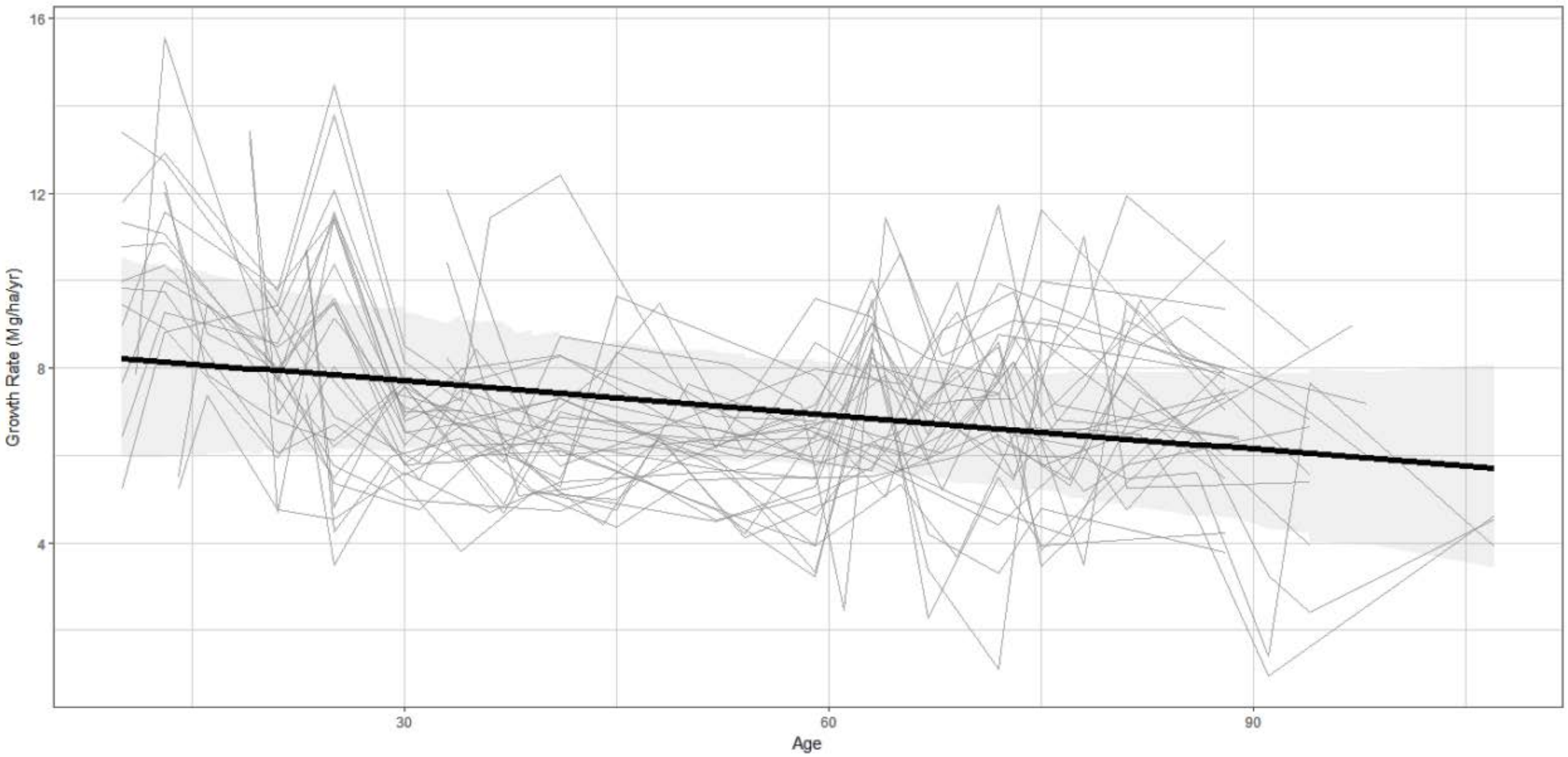

Figure 5.9 Mean growth rate trend (surrounded by 95% bootstrapped confidence region) for successional plots across stand age. Faint lines represent actual plot trends. The mixed model (see Table 5.4) demonstrated that successional plots overall experienced a significant downward trend as stands aged (model estimate of -0.025 [95% CI -0.033 – -0.017] Mg/ha/year).

Hardwood plots

Biomass trends

Other than variable drops in biomass due to hurricane damage to some plots in 1954 (PSPs 36, 37 and 43) and 1996 (PSPs 10, 35, 36, 37, and 123), Duke Forest hardwood plots all increased relatively consistently in biomass following plot inception. PSP 10, which suffered the largest biomass loss amongst hardwood plots due to Hurricane Fran in 1996, is the only hardwood plot not currently at peak biomass across the 80-year study, but it is aggrading post-Fran. Biomass in all hardwood plots has more than doubled on average (mean factor of change = 2.5 ± 0.6 SD) compared to initial levels, and multiple plots have near or more than tripled in biomass. Specifically, upland plots increased from approximately 100 Mg/ha (mean = 98.9 ± 26.9 Mg/ha; SD) to over 200 Mg/ha (mean = 230.4 ± 42.7 Mg/ha; SD), while lowland sites (PSPs 43 and 44) increased from approximately 200 Mg/ha (189.9 ± 13.5 Mg/ha; SD) to more than 400 and 600 Mg/ha, respectively. Although PSPs 43 and 44 had relatively equal biomass at plot inception, PSP 43's lower biomass accretion is likely owing to removal of approximately 1/3 of the plot's basal area in 1950 as part of a silvicultural improvement cutting. This cutting, however, does not seem to have negatively impacted PSP 43's long-term rate of growth. PSP 35, which has shrink-swell clay, had the lowest peak biomass (approximately 200 Mg/ha) of all hardwood PSPs (though it also had the lowest initial biomass among hardwood plots).

Biomass trends were largely driven by growth of canopy dominants (mostly *Quercus alba* in the upland sites and *Liriodendron tulipifera* and *Liquidambar styraciflua* in the lowland sites). The more edaphically unique upland sites, PSPs 35 and 10, had slightly different patterns with canopy *Quercus stellata* and aging *Pinus taeda* driving trends in PSP 35 and a more diverse suite of hickories and oaks driving biomass trends in PSP 10 (see Figure 5.10).

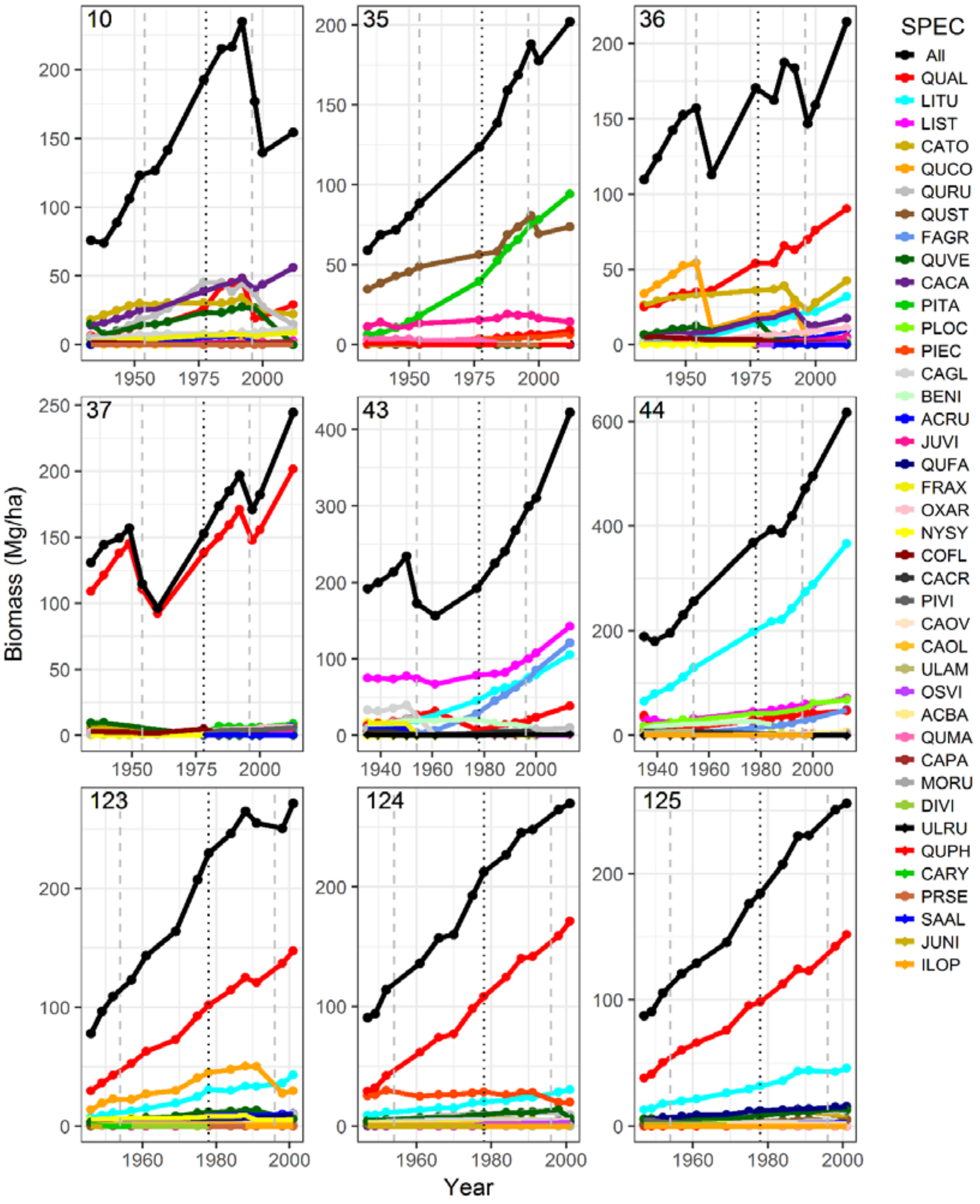

Figure 5.10 Biomass (Mg/ha) trends for all Duke Forest mixed-age hardwood forests. The thick black line represents whole-plot biomass values, while colored lines represent the most biomass-rich species in descending order of cumulative biomass (QUAL = *Quercus alba*, LITU = *Liriodendron tulipifera*, LIST = *Liquidambar styraciflua*, CATO = *Carya tomentosa*, QUCO = *Quercus coccinea*, QURU = *Quercus rubra*, QUST = *Quercus stellata*, FAGR = *Fagus grandifolia*, and QUVE = *Quercus velutina*; see Chapter 2 for a full list species code definitions. Vertical dotted line indicates year of change in sampling protocol to more consistently measure ingrowth; two vertical dashed lines represent Hurricane Hazel (1954) and Hurricane Fran (1996). The plot number is printed in the top right of each panel. See Table A.3 for species-specific biomass data.

In the majority of plots, plot-level biomass has increasingly been divided among a greater number of species than at plot establishment. Put differently, biomass from historical canopy dominants (e.g., *Q. alba* in upland plots and *L. tulipifera* in bottomland plots) in each plot has made up a smaller proportion of total plot biomass across time. *Liquidambar styraciflua* was the largest non-oak accumulating species in oak hickory plots, while *Fagus grandifolia* experienced significant biomass increases in the bottomland plots.

A mixed effects model with random slope and intercept for individual plots (Table 5.5) formally demonstrated that hardwood plots increased in biomass since sampling began 80 years ago. The mixed model, which divides the bottomland and upland sites, incorporates a centered year term, a scaled predictor for the density of canopy stems, an interaction between year and canopy density, yearly loss of biomass due to mortality and tree damage, and soil B horizon magnesium and pH. The model shows that hardwood sites increased in biomass an average of 1.757 [95% CI 0.7134 – 2.823] Mg/ha per year, with basic sites (i.e., PSP 44) having higher biomass (16.658 [95% CI 9.573 – 23.965] Mg/ha) and sites high in soil magnesium (i.e., PSP 35) having lower levels of biomass (-19.680 [95% CI -24.665 – -14.612] Mg/ha) than the average. Density of the 85% tallest trees in each plot had an increasingly (0.726 [95% CI 0.514 – 0.935] Mg/ha per year) positive (33.031 [95% CI 27.621 – 38.303] Mg/ha per unit change in scaled canopy density) effect on stand biomass while biomass loss had a significant negative impact on biomass levels (-1.988 [95% CI -1.048 – -2.923] Mg/ha).

Table 5.5 Mixed effect model for hardwood plot biomass trends. The final model was a random slope and intercept model grouped by plot that incorporated centered year, scaled canopy stem density (of the 85% largest trees in each given plot), the interaction of year and canopy density, a categorical variable differentiating upland and mesic bottomland hardwood plots, the loss rate of biomass (in Mg/ha/year), and scaled concentration of B Horizon soil magnesium (Mg) and pH as fixed effects. The model was built using the lmer function in the lme4 package of R and used Restricted Maximum Likelihood (REML) to estimate the variance component . The table shows model estimates and upper and lower 95% bootstrapped confidence intervals for each estimate.

	Estimate	Lower	Upper
(Intercept)	161.8805	142.1026	182.0237
(Year - 1970)	1.757144	0.713373	2.822635
scale(CanStems85.Ha)	33.03132	27.62062	38.30271
factor(PlotType2)Mesic	89.08865	72.61684	105.0241
LossRate	-1.98724	-1.04802	-2.92329
scale(Mg_ppm_B)	-19.6804	-24.6654	-14.6121
scale(pH_B)	16.65838	9.572879	23.96541
(Year - 1970):scale(CanStems85.Ha)	0.726384	0.514485	0.935456

Accumulation rate

A random intercept model that included annual loss rate of biomass due to mortality and damage as a secondary predictor explained 73% of the variation (marginal R^2; Nakagawa & Schielzeth 2013 and Johnson 2014) in the yearly trend in biomass accumulation rate in hardwood plots. The model showed that accumulation rates marginally (though significantly) increased an average of 0.030 [95% CI 0.015 – 0.045] Mg/ha/year each year of the study resulting in a 2013 mean rate of accumulation of 5.922 [95% CI 4.230 – 7.629] Mg/ha/year. Large biomass loss (especially due to hurricanes in 1954 and 1996) explained most of the negative variation in the accumulation rate. See Table 5.6.

Table 5.6 Mixed effect model for hardwood plot biomass accumulation rate trends. The final model was a random intercept model grouped by plot that incorporated centered year and the loss rate of biomass (in Mg/ha/year as fixed effects. The model was built using the lmer function in the lme4 package of R and used Restricted Maximum Likelihood (REML) to estimate the variance component. The table shows model estimates and upper and lower 95% bootstrapped confidence intervals for each estimate.

	Estimate	Lower	Upper
(Intercept)	4.632323	3.590384	5.696684
(Year - 1970)	0.029985	0.014883	0.044927
LossRate	-1.054774	-0.960635	-1.15269

Growth rate trends

Model selection criteria (AIC and BIC) indicated that a random intercept model (without random slopes) performed better than a more complicated random slope and intercept model when predicting growth rates of hardwood stands. The final model (see Table 5.7) incorporated a centered time variable and a categorical variable for bottomland versus upland hardwood sites. Again, model selection criteria indicated that different slopes for plot type (via an interaction term) did not improve the model, which suggests that all hardwood plots in the study followed similar growth rate trends. Specifically, the model demonstrated that growth rates in hardwood plots significantly increased an average of 0.029 [95% CI 0.014 – 0.044] Mg/ha/year for each year of sampling. Upland plots increased from an average of 3.043 [95% CI 2.665 – 3.450] Mg/ha/year in 1940 to 5.179 [95% CI 3.695 – 6.664] Mg/ha/year in 2013, while bottomland plots averaged 2.662 [95% CI 0.894 – 4.392] Mg/ha/year greater growth rate across the length of the study compared to the upland sites.

Table 5.7 Mixed effect model for hardwood plot growth rate trends. The final model was a random intercept model grouped by plot that incorporated centered year and a categorical variable differentiating upland and mesic bottomland hardwood plots as fixed effects. The model was built using the lmer function in the lme4 package of R and used Restricted Maximum Likelihood (REML) to estimate the variance component. The table shows model estimates and upper and lower 95% bootstrapped confidence intervals for each estimate.

	Estimate	Lower	Upper
(Intercept)	3.920675	3.088329	4.770894
(Year - 1970)	0.029262	0.014114	0.044034
factor(PlotType2)Mesic	2.662164	0.89442	4.392466

Finally, a mixed model including all plot types was developed to compare annual growth rate trends between successional pine stands and later-stage hardwood forests. This combined mixed model (results in Table 5.8; Figure 5.11) showed that the mean growth rate of successional plots has decreased from approximately 8.052 [95% CI 7.330 – 8.764] Mg/ha/year in 1935 to 6.132 [95% CI 5.347 – 6.915] Mg/ha/year in 2013. The annual rate of decline (which matched the estimate from the age model above; Table 5.4) was -0.025 [95% CI -0.033 – -0.016] Mg/ha/year. In contrast, the mean annual growth rate of hardwood plots increased significantly through the span of the study at a rate of 0.029 [95% CI -0.002 – 0.058] Mg/ha/year. This combined model suggested that mean growth rate of all hardwood plots increased from approximately 2.64 [95% CI 2.19 – 3.09] Mg/ha/year in 1940 to 5.772 [95% CI 3.302 – 8.299] Mg/ha/year in 2013. This model, therefore, suggests that growth rates in these piedmont forests are converging around 6.0 Mg/ha/year, regardless of forest type.

Table 5.8 Mixed effect model describing growth rate trends for both successional and hardwood plots. The final model was a random intercept model grouped by plot that incorporated centered year, a categorical variable differentiating successional and hardwood plots, and an interaction between these two predictors as fixed effects. The model was built using the lmer function in the lme4 package of R and used Restricted Maximum Likelihood (REML) to estimate the variance component. The table shows model estimates and upper and lower 95% bootstrapped confidence intervals for each estimate.

	Estimate	Lower	Upper
(Intercept)	7.19094	6.765298	7.616542
(Year - 1970)	-0.02462	-0.03603	-0.01326
factor(PlotType)Hard	-2.68229	-3.55995	-1.80209
(Year - 1970):factor(PlotType)Hard	0.053327	0.028877	0.077895

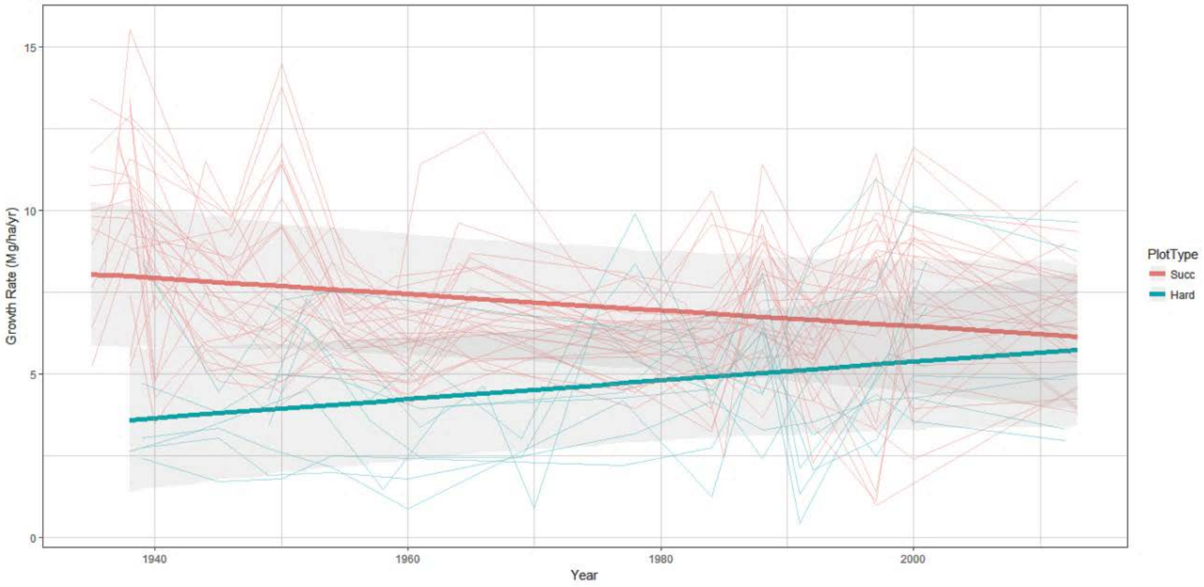

Figure 5.11 Mean growth rate trend (surrounded by 95% bootstrapped confidence region) for successional (red) and hardwood (blue) plots across time. Faint lines represent actual plot trends. The mixed model (see Table 5.8) demonstrated that growth rates in successional plots has decreased from approximately 8.052 Mg/ha/year in 1935 to 6.132 Mg/ha/year in 2013 at an annual rate of -0.025 Mg/ha/year. In contrast, the mean annual growth rate of hardwood plots increased significantly from 2.64 Mg/ha/year in 1940 to 5.772 Mg/ha/year in 2013 at a rate of 0.029 Mg/ha/year. This combined model suggested that growth rates in Duke Forest are converging around 6.0 Mg/ha/year, regardless of forest type.

Discussion

Successional pine plots

Although all successional plots in the Duke Forest are older than 90 years since initial post-abandonment pine growth, only half of the plots have experienced a leveling or decline in plot-level biomass. The remaining plots are – based on the relatively high remaining density of canopy *Pinus taeda* and relatively low ratio of hardwood to pine biomass in these plots – still in the earliest stages of the transition phase. As such, these plots are adhering to the expectations of theoretical models (e.g., Borman & Likens 1979, Peet 1981a, 1992) and continuing to aggrade biomass for the time being and likely for many more years in the absence of another major wind disturbance (Peet & Christensen 1987). The remaining plots, in contrast, are more advanced in successional age.

Overall, the density of canopy stems (which consisted primarily of *Pinus taeda* in all successional plots until the last few sampling periods) and loss in biomass due to mortality and damage explain most of the variation in the successional plot biomass data. The importance of canopy dominants as drivers in biomass trends reflect previous findings (e.g., Smith & Long 2001 and Li et al. 2018). The importance of mortality likewise coincides with previous conclusions (e.g., Peet & Christensen 1987, Acker et al. 2002, Coomes et al. 2012, Zhang et al. 2012, and Foster et al. 2014). These results are not surprising given that more than 50% (and usually 70 – 90%) of all stand biomass in the Duke Forest successional plots is held within canopy pines (primarily *P. taeda*) and that Xi et al. (2008) showed *P. taeda* to be highly susceptible to wind damage and uprooting (especially as they increased in diameter).

Unlike Acker et al. (2000), the Duke Forest successional plots were primed for examining the impacts of synchronous mortality and lag of regeneration on post-peak biomass trends given the ample recruitment of hardwood ingrowth and variable response of these plots during and after Hurricane Fran. Synchronous mortality caused by Hurricane Fran in 1996 led to precipitous drops in biomass for all Duke Forest successional plots that experienced a declining biomass trend, and the magnitude of the drop was directly related to the number of canopy stems destroyed in the storm. However, the successional plots have not progressed far enough in succession to observe the long-term impacts of this synchrony on potential oscillatory late-successional trends in biomass.

Although the data support impacts of synchronous mortality, the analyses did not sufficiently demonstrate that a lag (here defined as the biomass of hardwood trees in relation to whole-plot biomass at the time of canopy mortality) significantly impacted post-mortality trends as theorized by Peet (1981a, 1992). It appears that variability between plots was too great given the small sample size of the Duke Forest data to ascertain definitive formal trends. However, visual inspection of biomass trends suggest that the impact of rising hardwood biomass might simply be outweighed by the post-disturbance trends in canopy pine biomass at this point in time. Specifically, hardwood impacts were likely preponderated by aggrading biomass from surviving canopy pines in plots that recovered and by further significant delayed loss of canopy pine biomass in plots that continued to lose canopy biomass post-Fran.

The delayed loss of canopy pine biomass in hurricane-damaged plots does suggest that there is opportunity for greater hardwood biomass to lessen biomass losses and recover overall plot biomass to some degree. However, the degree to which hardwoods can do so appears to be limited in the Duke Forest successional plots given the small percentage of biomass such trees account for in each stand. Specifically, only three successional plots had hardwoods achieve greater than 50% of total plot biomass, and, in each of these cases, this milestone was only reached more than a decade after near-complete canopy destruction from Fran. Of these plots, PSP 39 (which doubled in hardwood biomass after Hurricane Fran) does provide strong visual evidence that regenerating hardwoods diminished the decline of this plot’s total biomass due to canopy pine mortality. Overall, however, the limited ratio of hardwood biomass in damaged plots suggests that these plots appear to have substantial (in regard to biomass recovery) lags in hardwood regrowth that exceed spans of fifteen years (as opposed to ten-year lags estimated for coastal Oregon *Picea-Tsuga* forests; Acker et al. 2000). As such, given the long lag in recovery observed in these plots, the time scale needed to examine lag effects on late-stage successional biomass trends needs to be extended beyond the scope of this study’s currently sampled timeline.

Hardwood plots

Initial biomass levels for the Duke Forest hardwood plots were all lower than both peak and post-Fran regrowth levels of all but the most damaged successional pine plots. This seems to suggest one or more of three scenarios: 1) successional plots have increased in accretion levels relative to historical expectation, 2) successional plots will potentially suffer further biomass loss events to more closely match initial hardwood plot biomass magnitudes, or 3) the Duke Forest hardwood plots have below expected biomass because they have either undergone prior modification (e.g., wood harvesting) or have suffered substantial disturbance in recent pre-study history.

Scenario one is not supported by the Duke Forest data as both biomass acquisition rate and forest growth rate have experienced marginal and significant declines, respectively, across all successional pine plots since plot inception (see Tables 5.3 and 5.4 and Figures 5.7 and 5.8). These results coincide with similar reductions in growth following canopy closure observed in numerous even-aged cohort systems (e.g., Bormann & Likens 1979, Ryan et al. 1997, 2004, Smith & Long 2001, and Foster et al. 2014). Scenario two receives credence from the final recorded biomass levels of the successional plots most damaged by hurricane Fran (i.e., PSPs 19, 39, 50, and 51). These plots have minimal canopy pines remaining (a state potentially shared historically by all hardwood plots in the data), and their remaining hardwood biomass is around the mean initial biomass for hardwood plots (approximately 100 Mg/ha). Scenario three likewise is credible given the substantial grazing and exploitative practices that have been historically practiced throughout the region and broader North Carolina Piedmont (Peet & Christensen 1980 and Healy 1985). Additionally, the center of an unnamed Category 1 hurricane passed within 15 km of the Duke Forest in 1896 (along with two additional Category 1 hurricanes that passed within a 70 km radius in the 1890s; Knapp et al. 2010), which potentially could have caused similar damage as Hurricane Fran in 1996 (or Hurricane Hazel in 1954). The substantial presence of mid-successional *L. tulipifera* in many of the hardwood plots further adds credibility to potential pre-study disturbance in these plots.

The diameter sizes of dominant canopy trees (primarily *Q. alba* as well as *Q. stellata* and *Quercus falcata*) and known histories of the Duke Forest upland hardwood plots place the hardwood plots' ages beyond any potential plot-clearing disturbance by at least 100 years at establishment. However, the lack of extraordinarily large diameter (i.e., > 70 cm; Brown et al. 1997) trees at plot establishment – given the probable potential for both selective timber harvesting and reoccurring hurricanes in the region through the late 19th century – suggest that these plots did suffer some degree of canopy loss and therefore were below steady-state biomass levels at inception. This is further corroborated by comparing the mean biomass levels in initial sampling periods of upland Duke Forest sites (90 ± 23 Mg/ha) to biomass levels in known eastern forest old-growth stands (typically 220 – 260 Mg/ha; Brown et al. 1997, though

Whittaker 1966 described an oak-hickory forest reaching 370 Mg/ha). These data suggest that the aggrading trends observed in these plots can likely be attributed to their lack of maturity at the start of the study (and that they are in fact aggrading from some disturbed state).

Regardless of initial stand immaturity, the Duke Forest upland hardwood sites have achieved a maximum mean biomass of approximately 242 (± 27) Mg/ha, which place them squarely within the ranges Brown et al. (1997) found in old-growth eastern forests (and substantially greater than typical oak-hickory forests sampled throughout the eastern United States as part of the U.S. Forest Service's long-running Forest Inventory Analysis; Brown et al. 1997). The hardwood plot biomass is also similar to levels observed in mature 170-year-old (Pontius et al. 2016) and 300+ year-old (Keeton et al. 2001) northern hardwood-conifer forests in New Hampshire, USA. These data suggest, along with the relatively constant (Peet & Christensen 1987) contemporary portions of each plot's density depletion curve illustrated in Figure 5.12, that the Duke Forest upland hardwood plots can sufficiently be compared to mature stands at present time (though see Eisen & Plotkin 2015 for a much younger stand showing similar growth rates in Massachusetts, USA and see Busing & White 1993 for a discussion about area-effects on perceived biomass trends and deviations about mean trends). As such, the plots are expected to be leveling in biomass and decreasing in growth rate (Bormann & Likens 1979 and Peet 1981a, 1992). However, biomass and both the accumulation and growth rates are still significantly increasing in all upland plots similar to the findings of Ziegler (2000), Salzer et al. (2009), Keeton et al. (2011) and Pontius et al. (2016). Increasing growth rates (along with peak loss rates coinciding with relatively recent Hurricane Fran in 1996) suggest that, unlike Caspersen et al.'s (2000) conclusions about North Carolina forests, increasing growth is driving accumulation rate changes more prominently than trends in decreased mortality in these relatively late-stage hardwood forests.

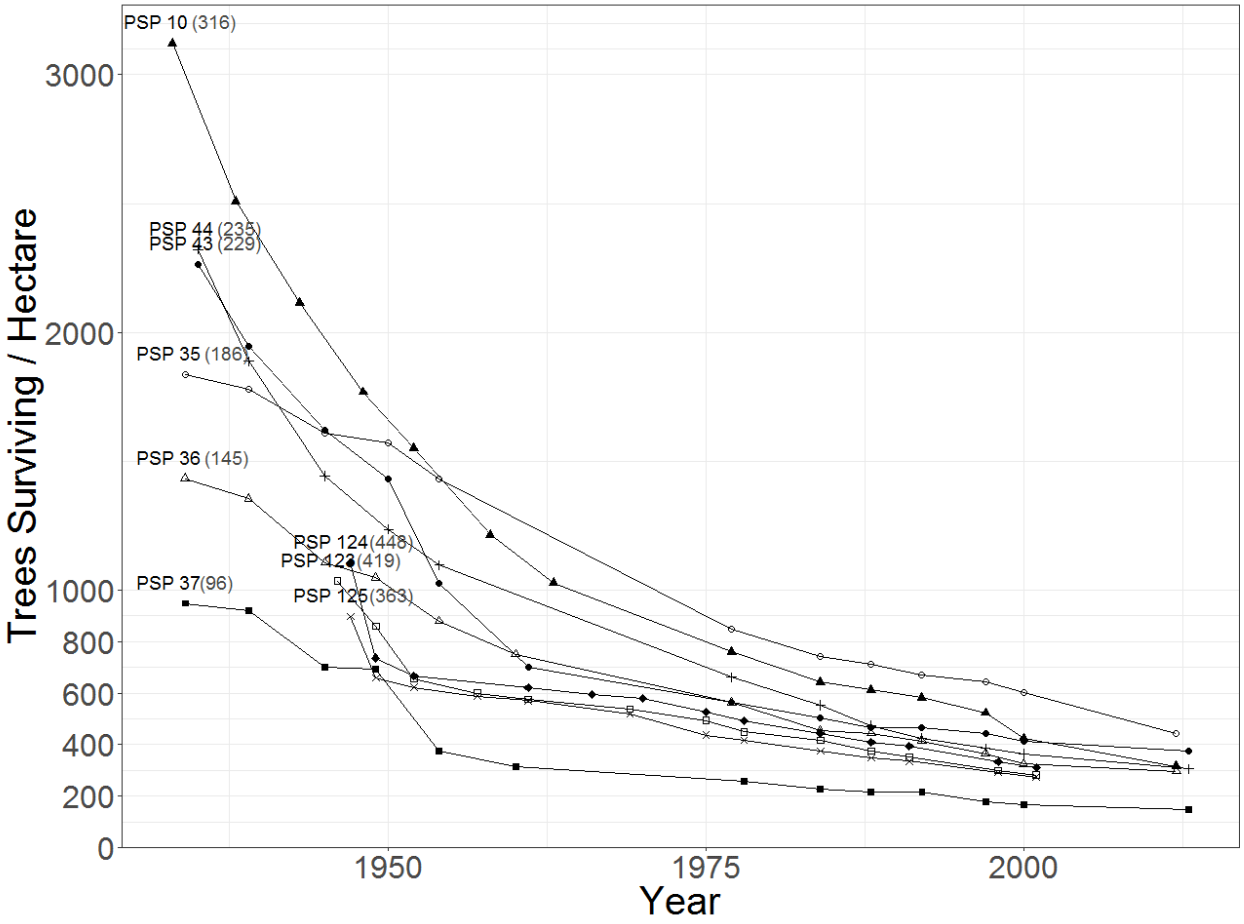

Figure 5.12 Depletion curves illustrating mortality trends of all stems alive in initial sampling periods for each mixed-age hardwood plot. Greater depletion rates may indicate earlier successional age in which thinning processes are more extensive (Peet & Christensen 1980). Leveling and convergence of the curves indicate plot maturity. Actual initial stem counts are provided in parentheses next to each plot's initial sampling point.

The greater number of large-diameter trees and greater initial biomass (approximately 200 Mg/ha) in the bottomland plots suggest that these plots were less affected by earlier disturbances and human manipulation in recent history compared to the upland Duke Forest sites. In fact, presence of multiple canopy dominants (especially *L. tulipifera* and *L. styraciflua*) exceeding 60 (and even 80) cm diameter suggest that these lowland sites have not undergone any major manipulation or disturbance in over 100 years. Current biomass levels in these late-successional lowland plots (mean of 519 Mg/ha) surpass the values compiled by Whittaker (1966), Brown et al. (1997), and Keith et al. (2009) for eastern forests, with PSP 44 (617 Mg/ha) surpassing even the greatest documented biomass in each of these publications. Despite their mid-to-late-successional status, both PSP 43 and 44 not only continue to aggrade biomass, but they are doing so at an ever-quicker rate similar to the majority of upland sites (and mean trend for hardwood plots overall). The lowland sites experienced accumulation rates exceeding 8.6 and 9.3 Mg/ha/year, respectively, leading up to the most recent sampling period.

Together, the Duke Forest hardwood plot data suggests that these Piedmont forests are continuing and increasing their rate of net carbon uptake via biomass aggradation even as they mature. Although the lack of large (i.e., DBH > 70 cm) trees and presence of mid-successional species such as *L. tulipifera* and *L. styraciflua* suggests these plots are all aggrading from a disturbed state, the still-linearly-increasing growth rates suggest that the plots will continue to aggrade biomass into the future. These results do not yet portray the late-stage equilibrating hypotheses of Peet (1981a; possibly owing to small plot size; Busing & White 1993) and instead align well with a growing recognition for such late-development growth in temperate forests globally (Pregitzer & Euskirchen 2004, Luyssaert et al. 2008, Keith et al. 2009, Lichstein et al. 2009, Rhemtulla et al. 2009, Foster et al. 2014, Pontius et al. 2016, among others) and mounting evidence of increased productivity across the major temperate regions of the world (Boisvenue & Running 2006 and Salzer et al. 2009).

Foster et al. (2014) posited that such continued aggradation trends could be attributed to increased recruitment and subsequent growth of shade-tolerant cohorts underneath canopies, especially canopies that had suffered mortality. However, this does not seem to be the case in the Duke Forest hardwood stands. Although biomass of shade tolerant and intermediately tolerant species (USDS 2018) doubled on average in the last 40 years, these species still consistently accounted for less than half of total plot biomass (which is about the same amount they accounted for 40 years ago). It is also possible that some degree of the sustained growth rates could be due to mortality-driven growth during hurricane recovery, but this does not explain the nearly-as-fast or faster growth rates observed in most plots before Hurricane Fran nor the unchanging growth rates experienced by less-damaged plots (e.g., PSPs 43, 44, 124, and 125).

Multiple publications (e.g., Myneni et al. 1997, Salzer et al. 2009, McMahon et al. 2010, Zhang et al. 2012, Peters et al. 2013, Pontius et al. 2016) theorize that these trends might be related to changes in climate, atmospheric conditions, and pollutant inputs (e.g., rising temperature, precipitation, atmospheric CO_2, and nitrogen deposition). Although weather station data from nearby the Duke Forest (unpublished analyses; data from State Climate Office of North Carolina) indicate that the last 60 years have been marked by an increase in temperature and wetness (based on the Standardized Precipitation-Evapotranspiration Index, or SPEI; Vicente-Serrano et al. 2010) and national data (see Solomon 1986 for examples) suggest that atmospheric CO_2 and nitrogen deposition have significantly risen this past century, the current study was not designed to examine these larger environmental trends. As such, no formal claims regarding their impacts can be made, but suffice it to say that all of these factors could alone or in combination be altering forest biomass and growth trends both locally and at larger spatial scales. In the case of the Duke Forest data, evidence of increasing growth rates throughout multiple strata of the forest (i.e., both in canopy stems and small-stemmed strata; analyses not shown) suggest that each of these environmental and ecosystem variables could very well be at play. Long-term, mechanistic analyses continue to be needed to parse out the effects of these potential drivers of change.

Conclusion

The Duke Forest successional even-aged pine permanent sample plots demonstrate various trends along 80 years of biomass accretion, but these trends are reflective of those previously theorized by Peet (1981a and 1992). Peet, however, developed his theory based on change driven by population processes in the absence of disturbance, whereas most of the observed patterns in this study were driven by major disturbance. This does not contradict Peet, but rather, it suggests that trends observed across landscapes are more complicated than a theory developed solely on population-processes and that other factors need to be considered.

Overall, biomass accumulation rates (and loss-corrected growth rates) have and continue to decline in these successional pine plots as is expected, and overall biomass trends are best explained by surviving canopy stems and biomass lost due to both mortality and damage. Specifically, the data definitively show synchronous mortality from Hurricane Fran negatively impacted canopy stems and drove significant losses in plot biomass. These losses appear to be somewhat mitigated by the magnitude of hardwood regeneration, which lags canopy mortality by at least fifteen years in these plots. Continued observation of the successional plots will be required to determine the longer-term impacts of synchrony of mortality and to better characterize lagged regeneration times on late-stage successional patterns.

Late-successional secondary hardwood stands in the Duke and Hill Forests continue to aggrade biomass 80 years after plot establishment. Current biomass levels of upland permanent sample sites are well-within the range of previously measured old-growth stands from the literature, and biomass levels in the bottomland plots exceed many published maxima previously recorded throughout eastern forests. The hardwood plots' already substantial and unanticipated accretion levels appear to be driven by significantly increasing accumulation and growth rates, and mixed models demonstrate that these rates continue to increase through the end of the study. Although growth trends can be partially explained by initial understocking in these plots due likely to selective harvesting of timber or damage from historical tropical storms, the plots' continued growth is less expected. Given the mounting evidence of similar unexpected late-succession growth trends throughout the temperate regions of North America and across the globe, this study must be taken as characteristic of at least a subset of a suite of now-to-be-expected growth-rate patterns in temperate forests. Understanding these late-successional growth trends as a norm instead of an exception is necessary as they must inform updates to forestry and global change modelling.

Understanding the rates of and controls on biomass accumulation in forests across succession has important implications for optimizing economic returns in forestry as well as estimating the effect of reforestation on global carbon cycling and carbon sequestration. This has become increasingly pertinent given consistent evidence like the present study that suggests current models under-characterize some late-growth temperate forests. As a result, a clearer understanding of temporal trends and the mechanisms driving them, especially those informed by long-term resampling data, can have immediate value and utility.

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CHAPTER 6: 80 YEARS OF FOREST DYNAMICS IN THE NORTH CAROLINA PIEDMONT: REVISITING A MODEL SYSTEM FOR STUDY OF FOREST SUCCESSION

Summary

Long-term permanent sample plot studies provide a unique and valuable opportunity to examine forest processes that occur on the timescale of decades or longer and to evaluate how observed long-term trends can confirm and inform existing conceptual models. In this study, 80 years of forest community dynamics was observed in a series of thinning even-age *Pinus taeda* stands and aggrading second-growth *Quercus-Carya* and *Liriodendron-Liquidambar* hardwood stands in the Piedmont of North Carolina, USA. Analyses indicated that successional *Pinus taeda* stands experienced changing compositional trajectories, first gradually, and then accelerated by hurricane damage during the course of the study. Specifically, successional plots experienced a replacement of species associated with upland *Quercus-Carya* hardwood sites (e.g., *Cornus florida*) with species associated with more mesic hardwood stands (e.g., *Acer rubrum*, *Liquidambar styraciflua*, *Fraxinus spp.* and *Fagus grandifolia*), causing successional communities to be more similar to bottomland hardwood sites than the characteristic climax *Quercus-Carya* community type. Putative climax species (e.g., *Quercus alba* and various hickory species) remain unabundant in successional plots, and these species have actually declined in hardwood stands. Additionally, the same mesic species that have increased in successional plots (most predominantly *A. rubrum*) have also increased in hardwood stands. The shared compositional changes between plot types despite variation in edaphic characteristics

suggests that some novel region-wide driver might be responsible for observed changes. Such changes could be the result of changing climate patterns, increasing browsing pressure from deer, anthropogenic influences (e.g., fire exclusion or nitrogen deposition), or – more likely – a result of many of these factors. Regardless, more mechanistic-oriented models must be developed to determine the cause of these newly apparent seemingly-widespread patterns.

Introduction

Floristic succession in North Carolina Piedmont abandoned agricultural fields has long served as the model system for studying secondary succession of temperate forests of eastern North America. This is because of the rich history of classical studies performed in this system (e.g., Wells 1932, Crafton & Wells 1934, Billings 1938, Oosting 1942, Keever 1950, Bormann 1953), the apparent generalizability of post-disturbance forest dynamics concepts (see Peet & Christensen 1987 for examples), and the continued monitoring of long-term resampling plots in the northeastern Piedmont of North Carolina (Peet & Christensen 1980, 1987, Peet 1981).

Classical studies posited that old agricultural fields become invaded by herbs within a year, transition to perennial herbs and grasses over the first 5 years post-abandonment, and are followed by an influx of primarily pine (e.g., *Pinus taeda* or *Pinus echinata*) and sparse fast-growing shade-intolerant tree species such as *Liriodendron tulipifera* and *Liquidambar styraciflua*. The pines form a highly competitive even-aged stand that rapidly form a closed canopy (5-15 years) and eliminate less-competitive individuals via a natural thinning process that spans an average of 60-80 years post-canopy closure (Peet & Christensen 1987). The dense pine stand precludes growth of all but a few shade-tolerant understory species and excludes shade-intolerant pines from regenerating without the formation of large, disturbance-mediated gaps. Due to this shading, when pines die and fall out of the canopy, they are subsequently replaced by understory hardwood species that grow to fill in the gaps during a transition stage. According to Billings (1938) and Oosting (1942), mature stands succeed toward a mosaic of mixed-age hardwoods with oaks (*Quercus*) and hickories (*Carya*) as canopy dominants and a variable suite of shade-tolerant hardwood species in the understory that are determined by individual site conditions (e.g., see Peet & Christensen 1980 and Palmer 1990).

Although the classic predictions of Billings (1938) and Oosting (1942) appeared to reflect the mature forests described in the early 20th century, recent evidence suggests that the successional sequence in these old-field forests is not transpiring as was predicted 70+ years ago. Specifically, studies have demonstrated unprecedented compositional changes in successional and maturing forests throughout eastern forests in the United States, including in the North Carolina Piedmont (Golubiewski & Urban 1998, Taverna et al. 2005, Schwartz 2007, Israel 2011, Peet et al. 2014). These deviations include novel changes brought on by increasing populations of *Odocoileus virginiana* (white-tailed deer; Stromayer & Warren 1997, Abrams 1998, Russell et al. 2001, Horsely et al. 2003, Côté et al. 2004, Keyser et al. 2005, Rossell et al. 2005, Israel 2011, Kribel et al. 2011, White 2012), increasing impacts of exotic species on native flora (Lovett et al. 2006, Israel 2011, Luken 2014), rises in atmospheric CO_2 and nitrogen deposition (e.g., Bobbink et al. 2010, Peters et al. 2013), and multi-year impacts due to major disturbances (e.g., hurricanes; Woods 2004, Xi et al. 2008, 2012, Xi & Peet 2011). Chief among the observed compositional changes is growing evidence of successional replacement of putative climax oaks (especially *Quercus alba*) by more mesophytic assemblages of hardwoods, especially *Acer rubrum* (Abrams 1998, 2003, Abrams & Downs 1990, Abrams & Nowacki 1992, Shumway et al. 2001, McDonald et al. 2002, 2003, Nowacki & Abrams 2008). Although 20th century suppression of low-intensity surface fires likely has played a major role in this compositional shift from oaks to more mesophytic species (e.g., see Abrams & Nowacki 1992 and Shumway et al. 2001), additional drivers such as selective logging, land clearing and herbivory (especially from increased populations of *O. virginiana*; Whitney 1994) could potentially be exacerbating changes, while high-intensity, low-frequency disturbances such as hurricanes may be accelerating the observed compositional changes (Abrams & Scott 1989, Arévalo et al. 2000, White & Jentsch 2004, Xi 2005). Examination of these patterns is further complicated by apparent variation in trends due to environmental and edaphic heterogeneity (McDonald et al. 2002, 2003), as well as probable impacts due to past human land-use (Taverna et al. 2005, Dupouey et al. 2002) and impacts of continuing global and regional climate change.

Historically, much of the field's understanding about succession (e.g., work by Billings and Oosting) was primarily based on indirect approaches such as those attained from chronosequences, which have been questioned for their validity and generalizability (Pickett 1989, Pickett et al. 2001, Cadenasso et al. 2008, Johnson & Miyanishi 2008, Lorimer & Halpin 2014). Further, such studies are not able to disentangle many of the aforementioned complexities that may impact successional dynamics. More contemporary work, meanwhile, has increasingly relied on directly-sampled data from permanent sample plots (e.g., Woods 2007, Israel 2011, and many others listed previously), which are better able to parse patterns and rates of forest dynamics and associated drivers of change (e.g., disturbance events and both environmental and climate change). However, there are still no long-term monitoring studies that have tracked forest dynamics of individual stands across the entire successional sequence (specifically while observing the transition of forests from pine to hardwood).

This chapter builds on the long-term permanent-sample data from the Duke Forest (North Carolina, USA; and associated data from the nearby G. W. Hill Forest) first reported on by Peet

& Christensen (1980, 1987) over 30 years ago, and it extends the observation of these data through mid-to-late-stage transition of multiple successional old-field pine stands to mixed-aged hardwood forests. The unique longevity of this frequently-sampled, individual-tree-growth dataset allows for direct comparison of realized long-term trends in these Piedmont forests to classical successional theory. Further, the concomitant sampling of hardwood stands in the Duke and Hill Forests allows for both the examination of shared convergence in community structure between successional and relatively mature stands, as well as examination of near-century dynamics in the context of changing environmental (e.g., changing climate) and ecosystem (e.g., increased herbivory) conditions.

The objective of this chapter is to examine long-term patterns of community dynamics across each stage of succession. Specifically of interest are whether the Piedmont forests of the southeastern United States that have served as a model system for successional research for almost 100 years conform to the patterns predicted by classical, early-20th-century successional models or reflect more recently published trends. A suite of multivariate techniques is used to compare changing community composition of old-field successional plots with later-stage successional hardwood stands in the region to determine how similar plot types have become in 80 years. Examination of successional trajectories of these old-field plots is also performed to determine if any substantial shifts in mid-successional species composition have occurred. The hardwood sites are likewise examined for evidence of compositional change to determine if there is consistency in the direction of change across plots. Additionally, the chapter seeks to determine what underlying species-specific and environmental patterns appear to be driving larger community trends observed in the Duke Forest. For example, the abundance of putative climax species such as *Quercus alba* and mesophytic species such as *Acer rubrum* and *Fagus* *grandifolia* is examined for various forest strata to determine to what degree mesophication appears to be occurring in Duke Forest. The basal area of individual species is examined to determine the general patterns of gains and losses in specific community components and to what degree each is associated with observed whole-plot compositional trends.

Methods

Study area and data

Thirty-seven permanent sample plots (PSPs) from the Duke Forest (n=34) and the G. W. Hill Forest (n=3) that had been resampled every 5 – 18 years for a maximum of 80 years (1933 – 2013) were used for this study (see Supplementary Appendix S1 for the data). Reference to the Duke Forest data throughout this chapter implicitly includes Hill Forest plot data unless otherwise specified. All trees and shrubs in each of the sample plots were spatially mapped, and their diameters at breast height (DBH) and heights were recorded. Because of inconsistencies between years and plots (see Chapter 2), data were filtered so that only trees achieving a DBH greater than or equal to 1 cm were included. Additionally, although numerous plots were expanded in size subsequent to their establishment, only original plot areas (indicated by a "Phase" value of 0 in the PSP data) and trees growing in those original areas were utilized for this study to retain consistency through time for each plot. The resulting plots areas ranged from 405 – 1012 m^2 (tenth acre to quarter acre). Overall, the plots are generally spatially clumped based on shared experimental histories (e.g., adjacent PSPs 12 – 23 underwent treatments to ensure various initial stocking densities). See Chapter 2 and Supplemental Appendix S1 for details.

Twenty-eight of the PSPs are successional old-field, even-aged pine (primarily *Pinus taeda*) stands with known age and stem density at plot establishment. These stands vary in age since initial post-abandonment pine growth (8 – 30 years) and initial stem density (25 – 1172 stems), and they are currently at varying levels of transition to hardwood forests. The remaining 9 plots are mixed-age hardwood stands. Two of the hardwood plots represent bottomland, small-stream alluvial hardwood communities, while the remaining hardwood plots are representative of drier upland oak-hickory stands with variable soil properties. Of these upland sites, PSP 35 is the most edaphically (and floristically) distinctive due to its underlying shrink-swell (montmorillonitic) clay. Initial NMDS ordination results corroborated the floristic uniqueness of PSP 35 as compared to all other plots based on proportions of relativized species abundances. As a consequence, PSP 35 acted as an outlier that obscured long-term trends in and between the other plots. As a result, PSP 35 was removed from all subsequent analyses.

Geomorphic site descriptors (e.g., slope, aspect, elevation, elevation of closest water, distance to water, and topographic position) were determined and soil samples were collected for each plot in order to characterize the environmental conditions of the plots. Soil analyses provided data on nutrients, acidity, texture, and bulk density for both A and B horizons for each plot. Topographical position is characterized by a categorical scalar that ranges from valley bottom (=1) through concave and convex slope to ridge and finally hilltop (=5). More information regarding methods, descriptions, and a list of soil variables can be found in Chapter 2.

Post-processing forest growth data

Because the Duke Forest PSP data contain directly-measured DBH measurements for individual trees, basal area (BA; m^2) was calculated for each tree from DBH (cm) using the following equation adapted from Husch et al. (2003):

$$\mathbf{BA = \pi * (DBH/200)^2} \text{ or } \mathbf{BA = 0.00007854 * DBH^2}$$

Plot BA data were aggregated for each species (SPEC) in each plot in each year and then merged into a samples-by-species abundance matrix with sample units (plot-year combinations) as rows, individual SPECs as columns, and each cell representing the aggregated plot-level basal area for the cell's given species in the given sample. Rare species were next removed by eliminating all species that occurred in less than 5% of all sample units (i.e., across all sampling years of all plots; see Gauch 1982 and McCune & Grace 2002), and then the data were relativized using the Wisconsin Double Standardization approach (Bray & Cutis 1957, Peet & Roberts 2013). This approach first standardizes by column (species) maximum to allow for equal treatment of all species regardless of abundance (i.e., BA) and then by row sum (sample total) to make all plots equal in terms of total abundance so that comparisons are based on differences in species compositions alone. The resulting transformation yielded values that were proportions of relative abundances.

Multivariate analyses

Distance matrix

A Bray-Curtis dissimilarity (or distance) matrix (Bray & Cutis 1957, Legendre & Legendre 2012) was calculated from the aggregated relativized basal area data using the Ecodist package (Goslee & Urban 2007) in R (R Core Team 2016). The Bray-Curtis dissimilarity matrix was chosen because it is a compositional dissimilarity approach that down-weights the preponderance of joint absences in pairwise sample comparisons common in species abundance data (Orlóci 1978). Next, a step-across procedure was performed on the distance matrix using the Vegan package (Oksanen et al. 2015) in R to apply an extended dissimilarities approximation (De'ath 1999) to pairwise samples that exhibited complete dissimilarity (i.e., had no species in common).

NMDS ordination

The stepped-across Bray-Curtis distance matrix was used to perform nonmetric multidimensional scaling (NMDS; Clarke 1993, McCune & Grace 2002, and Legendre & Legendre 2012) ordination to view the complex data. The ordination was performed using the nmds function of the Ecodist package (Goslee & Urban 2007) in R (R Core Team 2016). The goal of NMDS is to map samples into a reduced-dimension ordination space while preserving the rank order of ecological distances among samples. More specifically, NMDS is used to ordinate a set of points in a specified (often 2D) number of dimensions such that the rank order agreement between the distances of a distance matrix and of the dissimilarity values themselves are maximized (Minchin 1987). The resulting ordination should have points placed such that more similar objects are located closer together and more dissimilar objects are spaced farther apart (Legendre & Legendre 2012). NMDS is a powerful and useful ordination technique because it employees few assumptions (Minchin 1987, Clarke 1993, McCune & Grace 2002, Legendre & Legendre 2012) which allows the technique to be generally unbiased when summarizing data.

Unlike other ordination techniques (e.g., PCA), NMDS requires that the number of dimensions of the ordination be specified *a priori*. The appropriate number of axes was determined by repeating several configurations of ordinations with varying number of dimensions and using a scree (stress vs. dimensionality) plot to visually inspect which number of axes resulted in no major decrease in stress (or no major increase in explanatory power, R^2). The appropriate number of axes, then, was one less than this number. According to McCune & Grace (2002), stress is a "measure of departure from monotonicity in the relationship between the dissimilarity (distance) in the original *p*-dimensional space and distance in the reduced *k*-dimensional ordination space" and is essentially an "inverse measure of fit to the data." Due to inherent characteristics of the steepest-descent numerical algorithms used in NMDS, “jittering” of points within each ordination can lead to slight variations in stress. To ensure the minimal stress for any given dimensionality, a number of iterations of each ordination were also performed to determine the orientation that resulted in the objective function reaching a tolerable lack-of-fit level or converging (Legendre & Legendre 2012). For these analyses and all others in this chapter, the program’s seed value was set to a consistent value of 62218 to ensure reproducible results.

A scree plot from the step-down process indicated that 2 axes optimized the explanatory power of the ordination. An additional 1000 random starts resulted in an optimized ordination with low stress. A Principle Components Analysis (PCA) was performed on the resulting NMDS solutions themselves in order to rotate the axes and distribute the newly aligned axes in order of decreasing magnitude of variance explained (Legendre & Legendre 2012). These resulting rotated NMDS values were used to create the NMDS graphic for visualization of trends. Finally, R^2 values were calculated using Mantel correlations to quantify the amount of variance that each NMDS axis (and the ordination overall) explained.

The above process was repeated three more times with various partitions of the data in order to examine trends in various size-classes of stems. Specifically, in addition to the unpartitioned data, the ordination process (and all subsequent multivariate analyses described below) was repeated for canopy trees, subcanopy trees, and small-stemmed trees. Canopy and subcanopy trees were partitioned by finding the 70% quantile of all diameters for all species in a given plot across all sampling years and assigning all stems greater than or equal to 70% of stem measurements in that plot as canopy trees and all stems less than that 70% quantile (including below 10 cm DBH) as subcanopy. This partitioning was applied to each plot individually since plots had a range of diameter distributions and achieved canopy heights. The small tree partition of the data was constructed by analyzing only trees equal to or below 10 cm DBH, as these trees were the most representative of rapid changes in forest dynamics, especially those accelerated or driven by hurricane disturbance. For the remainder of the chapter, the full data set that was not partitioned by diameter is referred to simply as “unpartitioned data.”

Joint plot

Following graphing of abundance data in the NMDS ordination, the wascores function in the Vegan package (Oksanen et al. 2015) of R (R Core Team 2016) was used to calculate weighted averages of species abundances (i.e., basal areas) for the unpartitioned and each of the partitioned datasets’ species so that associations of each species with different groups of samples in the species (ordination) space could be visualized via a joint plot (McCune & Grace 2002). These weighted averages were further utilized for informed visual investigation of cluster characteristics (see next section).

Cluster analysis

Cluster analysis was performed using the stepped-across distance matrix to corroborate NMDS sorting and to aid in the description of various community-types identified through the previously-described analyses (i.e., grouping of samples in the NMDS ordinations and the associated weighting of species in each grouping region of the ordination) for unpartitioned and partitioned forms of the data. Although various cluster assessment approaches and various numbers of clusters were examined, agglomerative hierarchical clustering with a flexible beta linkage ($\beta = -0.25$) with four groups created the best grouping of PSP samples in regard to alignment to NMDS results. This clustering assignment was generated using the agnes function in the Cluster package (Maechler et al. 2015) in R (R Core Team 2016). The distinction of being the best clustering approach was formally determined by selecting for a clustering outcome that had a locally high Mantel R correlation between groups using the mantel function in the Ecodist Package (Goslee & Urban 2007) of R. Clustering outcomes were additionally scrutinized by calculating average silhouette widths for each cluster outcome using the optpart package (Roberts 2016b) in R. In this case, clustering outcomes with the highest average silhouette width, or the average goodness of fit of each sample to its own cluster compared to the nearest neighboring cluster (Rousseeuw 1987, Peet & Roberts 2013), were prioritized, as were more parsimonious grouping assignments (i.e., those with fewer groups). Finally, the chosen clustering outcome was visually inspected by examining the clustering assignments in NMDS space to see how well they overlapped with the organization of sample points generated by the ordination.

Successional change vectors

Finally, to examine how specific plots changed through time, compositional change vectors were plotted in the NMDS ordination space (McCune & Grace 2002). The trajectory of each plot was examined both by plotting change vectors between consecutive sampling years of each plot and by plotting cumulative change vectors from the first to last sampling period of each plot. The direction of change in species space each sampling year was determined by observing the angle and direction of vectors in NMDS space.

Environmental correlations and biplot

The vf function in the ecodist package of R was used to determine the correlations of environmental (i.e., soil and topography) variables with the ordination axes. Function vf generated p-values via randomization procedures and only variables with a $p \leq 0.05$ were considered when plotting the resulting correlation vectors onto the NMDS space. Each vector's direction indicates the direction of correlation with the given axes, while the length of each vector represents the magnitude of correlation and the angle is representative of the relative correlation of the variable with both axes. In instances in which multiple environmental variables were correlated or redundant, the most ecologically-relevant of these variables were selected to include in the analyses while the others were dropped. Correlations between the ordination axes and environmental variables were calculated with Pearson's r^2.

Species trends

Species-level trends driving community shifts were examined via three methods: NMDS, diameter distribution plots, and relative abundance plots. The NMDS approach was achieved by enlarging sample points in NMDS space based on relative abundances of species of interest in each sample and observing patterns. Diameter distributions graphics allowed a more nuanced examination of these trends. Diameter distributions were created for each species of interest in each sampling period for each of the plot types (i.e., successional pine plots, upland hardwood plots, and bottomland hardwood plots). These distributions were scaled by plot area so that they represented stems per hectare, then smoothed by binning diameters into 2 cm size classes, and finally graphed using the ggplot2 package (Wickham 2009) in R (R Core Team 2016). Relative abundance plots were also generated using ggplot2 for each partition of the data by summing total abundance (i.e., basal area) of all species in each sample and determining the percentage of the total each individual species comprised.

Results

NMDS

The results of 1000-iterations of a 2-dimensional NMDS using all unpartitioned data resulted in an optimized ordination with a stress of 0.224. After rotating the ordination axes using PCA, the first and second axes had R^2 values of 0.589 and 0.239 respectively and collectively explained 83% of the variation among the samples (Mantel r = 0.910, p-val = 0.001). The ordination (Figure 6.1) demonstrates that successional pine plots have remained distinct compositionally from hardwood stands and that upland and bottomland hardwood stands likewise remained distinct overall throughout the course of the study.

Examination of the NMDS output for the partitioned data suggested that these distinctions are driven primarily by canopy trees in the plots, as the NMDS for canopy stems (stress = 0.160; axes R^2 = 0.782 and 0.152; total R^2 = 0.934; Mantel r = 0.966, p-val = 0.001; Figure 6.2) showed similar grouping as the unpartitioned-data NMDS trends. However, NMDS output for subcanopy (stress = 0.304; axes R^2 = 0.459 and 0.152; total R^2 = 0.611; Mantel r = 0.782, p-val = 0.001; Figure 6.3) and small stems (stress = 0.320; axes R^2 = 0.411 and 0.165; total R^2 = 0.576; Mantel r = 0.759, p-val = 0.001; Figure 6.4) demonstrated increasing convergence of community composition between stand types as stem size decreased. Specifically, the smaller size classes of stems in successional pine stands have become very similar in composition (in relativized NMDS space) to similar size classes of stems in bottomland hardwood stands (Figure 6.9). Further, the most disturbed upland hardwood stand (i.e., PSP 10) also experienced converging composition with both successional plots and bottomland hardwood plots following significant damage from Hurricane Fran in 1996.

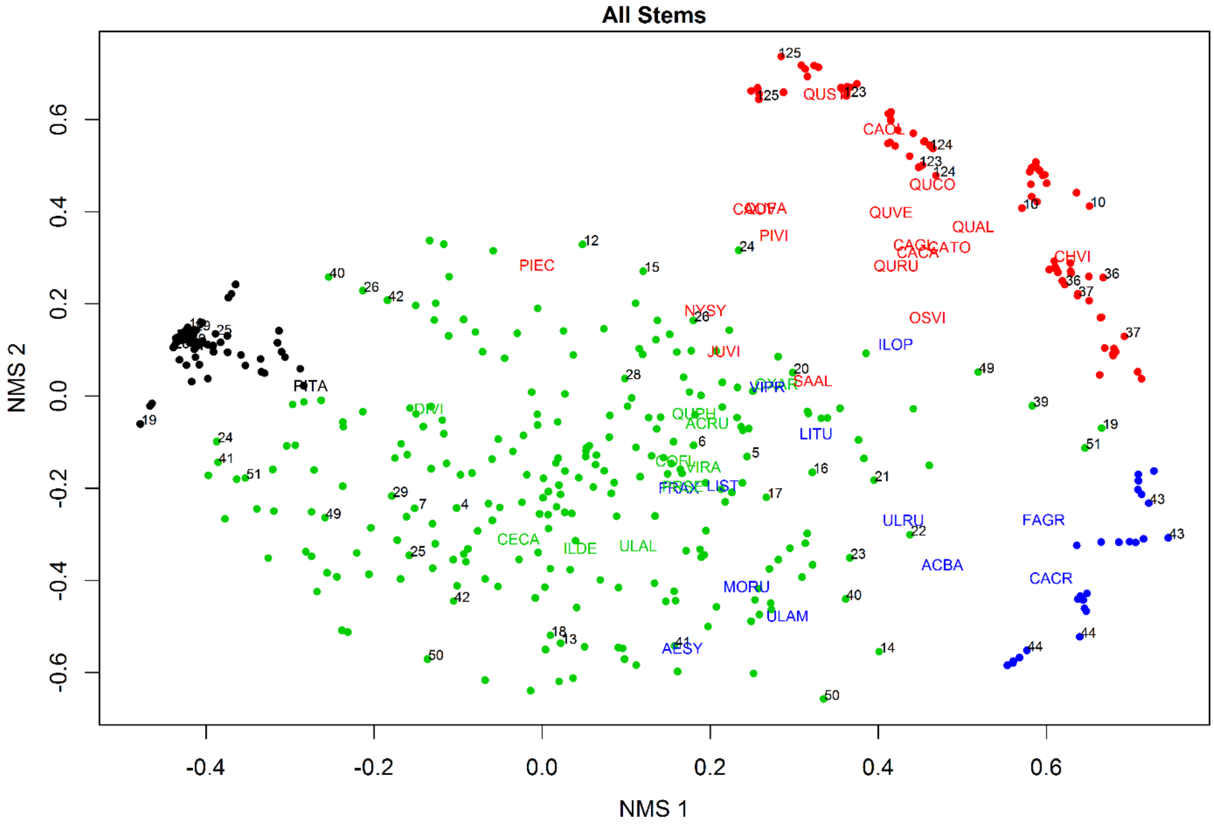

Figure 6.1. Nonmetric multi-dimensional scaling (NMDS) ordination of unpartitioned PSP data set. The first two axes account for 83% of the variation among the samples (Mantel r = 0.910, p-val = 0.001). Each point represents the community characteristic of an individual sample (i.e., plot-year combination). Four-letter species codes (SPECs) were added to the plot using weighted averaging, and colors of points were dictated by cluster analyses using the full data. Groups roughly equate to: black (1) = near-monocultures of *Pinus taeda*; green (3) = successional pine stands, red (2) = upland hardwood stands; blue (4) = bottomland hardwood stands. PSP plot numbers were also added adjacent to the NMDS points that represents each plot's initial and final sampling year.

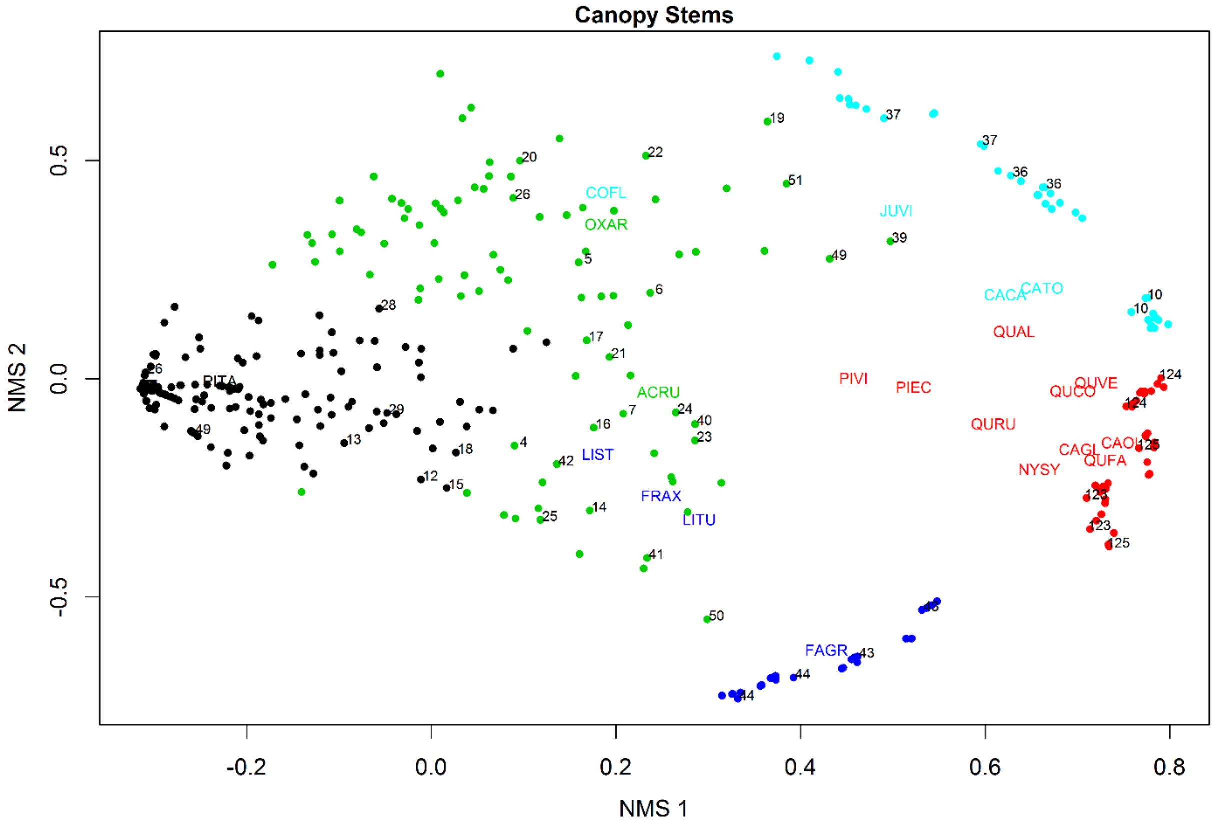

Figure 6.2. Nonmetric multi-dimensional scaling (NMDS) ordination of canopy stems. The first two axes account for 93% of the variation among the samples Mantel r = 0.966, p-val = 0.001). Each point represents the community characteristic of an individual sample (i.e., plot-year combination). Four-letter species codes (SPECs) were added to the plot using weighted averaging, and colors of points were dictated by cluster analyses based on a subdivision of the data containing only canopy stems. Groups roughly equate to black (1) = near-monocultures of *Pinus taeda*; green (3) = successional pine stands; red (2) = upland hardwood stands in Hill Forest; cyan (5) = upland hardwood stands in Duke Forest; blue (4) = bottomland hardwood stands. PSP plot numbers were also added adjacent to the NMDS points that represents each plot's initial and final sampling year.

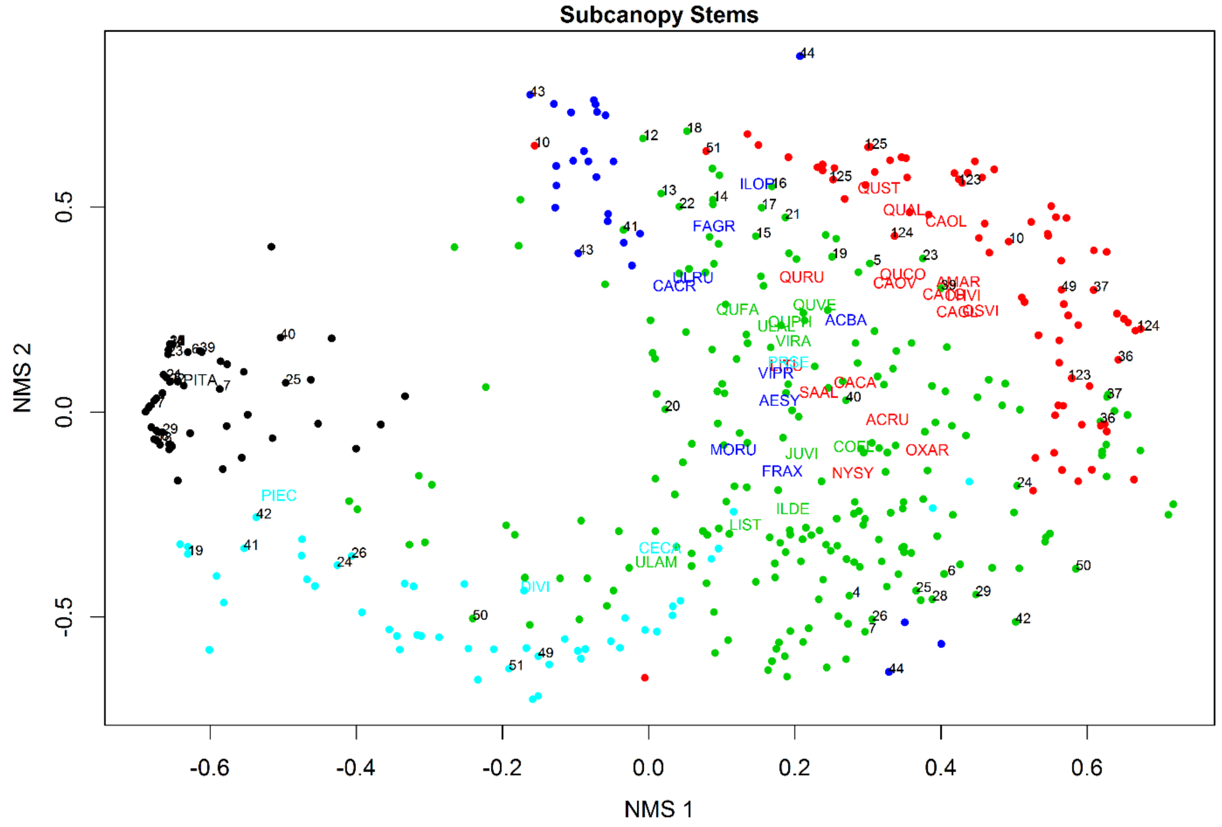

Figure 6.3. Nonmetric multi-dimensional scaling (NMDS) ordination of subcanopy stems. The first two axes account for 61% of the variation among the samples Mantel r = 0.782, p-val = 0.001). Each point represents the community characteristic of an individual sample (i.e., plot-year combination). Four-letter species codes (SPECs) were added to the plot using weighted averaging, and colors of points were dictated by cluster analyses based on a subdivision of the data containing only subcanopy stems. Groups roughly equate to black (1) = near-monocultures of *Pinus taeda*; cyan (5) = early successional plots with high abundance of *Diospyros virginiana*; green (3) = successional pine stands, red (2) = upland hardwood stands; blue (4) = bottomland hardwood stands. PSP plot numbers were also added adjacent to the NMDS points that represents each plot's initial and final sampling year.

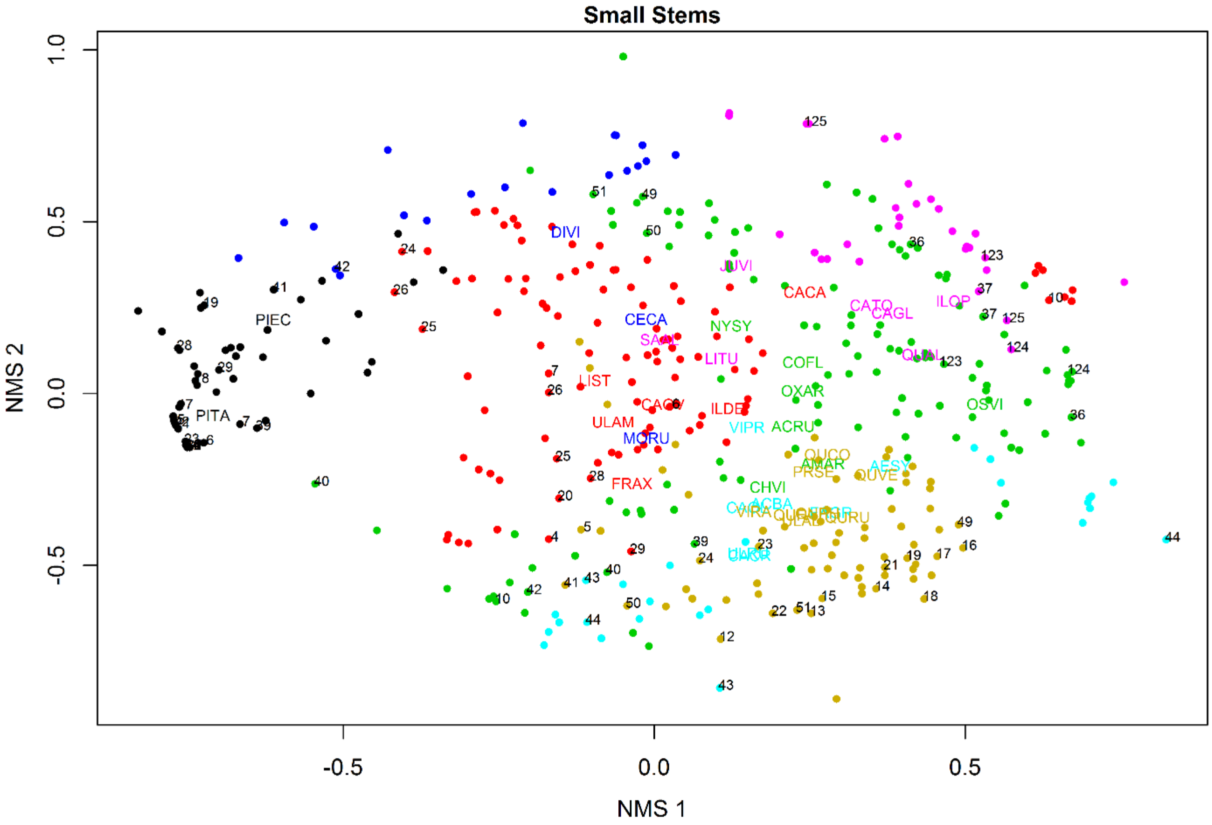

Figure 6.4. Nonmetric multi-dimensional scaling (NMDS) ordination of small (i.e., ≤ 10 cm DBH) stems. The first two axes account for 58% of the variation among the samples Mantel r = 0.759, p-val = 0.001). Each point represents the community characteristic of an individual sample (i.e., plot-year combination). Four-letter species codes (SPECs) were added to the plot using weighted averaging, and colors of points were dictated by cluster analyses based on a subdivision of the data containing only small-stem trees. Groups roughly equate to: black (1) = near-monocultures of *Pinus taeda*, red (2) = samples with basic/rich indicator species; green (3) = samples with species tolerant of lower pH; (4) blue = early successional plots with high abundance of *Diospyros virginiana*; cyan (5) = mesic bottomland plots; magenta (6) = samples with relatively-xeric hardwoods (e.g., *Quercus alba*); gold (7) = samples with a suite of variable and relatively-mesic hardwoods and oaks. PSP plot numbers were also added adjacent to the NMDS points that represents each plot's initial and final sampling year.

Classifying community types: Cluster analysis, species weighted averages and indicator species analyses

Based primarily on parsimony and a local maximum in Mantel r (0.67; see Figure 6.5), cluster analyses indicated that the unpartitioned data were best clustered into four groupings. Descriptions were assigned to each of the four clusters of samples using plot histories, dominant species types, and indicator species analyses (Dufrene & Legendre 1997; using the indval function in labdsv package; Roberts 2016a). Specifically, cluster analyses using all stem sizes (i.e., the unpartitioned data) indicated that the plots cluster into groups that corroborate their actual plot types (i.e., successional pine stands and upland and bottomland hardwood stands; see Figure 6.1). Group 1 samples represented young even-age pine stands. Each of the plots in Group 1 quickly (within 30 years) transitioned to Group 3 samples, which represented successional pine forests with hardwood ingrowth. Group 2 consisted of established dry oak-hickory samples, and Group 4 consisted of mixed-age, bottomland hardwood stands.

Weighted averaging (see Figure 6.1), relative species abundances (see Table A4.1) and indicator species analysis (see Table A5.1) demonstrated similar results regarding community assignment. Pine plots were most represented by *Pinus taeda* early on, but as they progressed to successional plots (i.e., Group 3) the significant indicator species shifted to a suite of shade-tolerant hardwood species (chief among them being *Ulmus alata*, *Cornus florida*, *Acer rubrum*, *Oxydendrum arboreum*, *Cercis canadensis*, and *Diospyros virginiana*). Hardwood plots had many more indicator species than the successional plots. The species with highest indicator status in upland hardwood sites included primarily oaks and hickories (especially *Carya tomentosa, Quercus velutina, Quercus alba, Carya ovata, Quercus falcata*, and *Quercus rubra*) as well as *Juniperus virginiana* and *Nyssa sylvatica*. Significant indicator species for bottomland hardwood plots consisted primarily of mesic species (e.g., *Carpinus caroliniana*, *Fagus* *grandifolia*, and *Ulmus rubra*), species indicative of prior disturbance (e.g., *Liquidambar styraciflua* and *Liriodendron tulipifera*), and species associated with more basic and rich soil conditions (e.g., *Fraxinus spp., Morus rubra, Aesculus sylvatica, Acer floridanum, and Ostrya virginiana*).

The species assignments for canopy analyses (see Tables A4.2 and A5.2) were fairly similar to (though less speciose than) unpartitioned data analyses except that Hill Forest upland plots were separated from Duke Forest upland sites in both NMDS space and cluster analysis (see Figure 6.2). Duke Forest upland hardwood sites were moved into a 5th group. Hill Forest sites retained the "upland hardwood plot" compositional characteristics (i.e., high abundance of a suite of oaks and hickories) from the unpartitioned-data analyses, while *Carya carolinae-septentrionalis*, *Carya tomentosa*, *Cornus florida*, and *Juniperus virginiana* shifted from this community type to being more indicative of Duke Forest upland hardwood plots (see Tables A4.2 and A5.2).

Species associations for the small-stem (i.e., ≤ 10 cm DBH) tree partition of the data were more complex (see Figure 6.4 and Table A4.4) and appeared to be best characterized using 7 groups based on Mantel r (0.551, p-value = 0.001; Figure 6.5) and indicator species analysis (see Table A5.4). Group 1, as with the unpartitioned data, was representative of early-stage, pine stands with *Pinus taeda* as the strongest indicator. Group 2 was composed of species associated with more rich and basic soil conditions (see Table A5.4), with *L. styraciflua* and *Fraxinus* species being the strongest indicator species. Group 3 consisted of species generally more tolerant of acidic edaphic conditions (e.g., *Nyssa sylvatica, Oxydendrum arboreum, Cornus florida,* and *Amelanchier arborea*) as well as *Acer rubrum* and *Chionanthus virginicus*. Presence of *C. virginicus*, which is usually associated with more basic sites, with these otherwise acid-tolerant species in Group 3 samples suggests that perhaps deer browse or some other ecosystem driver is affecting the competitive abilities of some acidic species. Group 4 was most strongly associated with *Diospyros virginiana* (IV = 0.566). Group 5 was representative of a bottomland community of species associated with moist, rich soil and included similar species as Group 4 from the unpartitioned data groupings. Finally, Groups 6 and 7 consisted of dryer (Group 6) and mixed or more mesic (Group 7) oak-hardwood communities. The strongest indicator species for Group 6 were *Juniperus virginiana, Quercus alba, Carya tomentosa, Carya glabra, and Liriodendron tulipifera,* whereas the strongest indicators in Group 7 consisted of *Ulmus alata,* numerous oaks (e.g., *Q. phellos, Q. rubra, Q. falcata, Q. velutina,* and *Q. coccinea*), *Viburnum rafinesquianum,* and *Prunus serotina*. Although each of these groups were best represented by the aforementioned species, multiple species were fairly ubiquitous across group types. The most ubiquitous species (i.e., those that had significant abundance in each of the 7 groups) included *A. rubrum, C. florida, Fraxinus spp., J. virginiana, L. tulipifera,* and *Morus rubra*.

Successional change

Overall, when examining cumulative change of the unpartitioned-data ordination (Figure 6.6), successional pine plots changed much more dramatically compared to more mature hardwood plots. This was anticipated based on their progressing successional transition from near-monocultures of pines to increasingly speciose hardwood forests. More specifically, the composition of most successional plots moved away from even-aged monocultures of pines in a direction that suggests they are becoming most compositionally similar to the bottomland hardwood plots. Plots that suffered the most significant canopy pine damage from Hurricane Fran in 1996 (i.e., PSPs 39, 49, 50, and 51; see Figure 5.3) have progressed farthest along NMDS axis 1 in a positive direction toward hardwood community types.

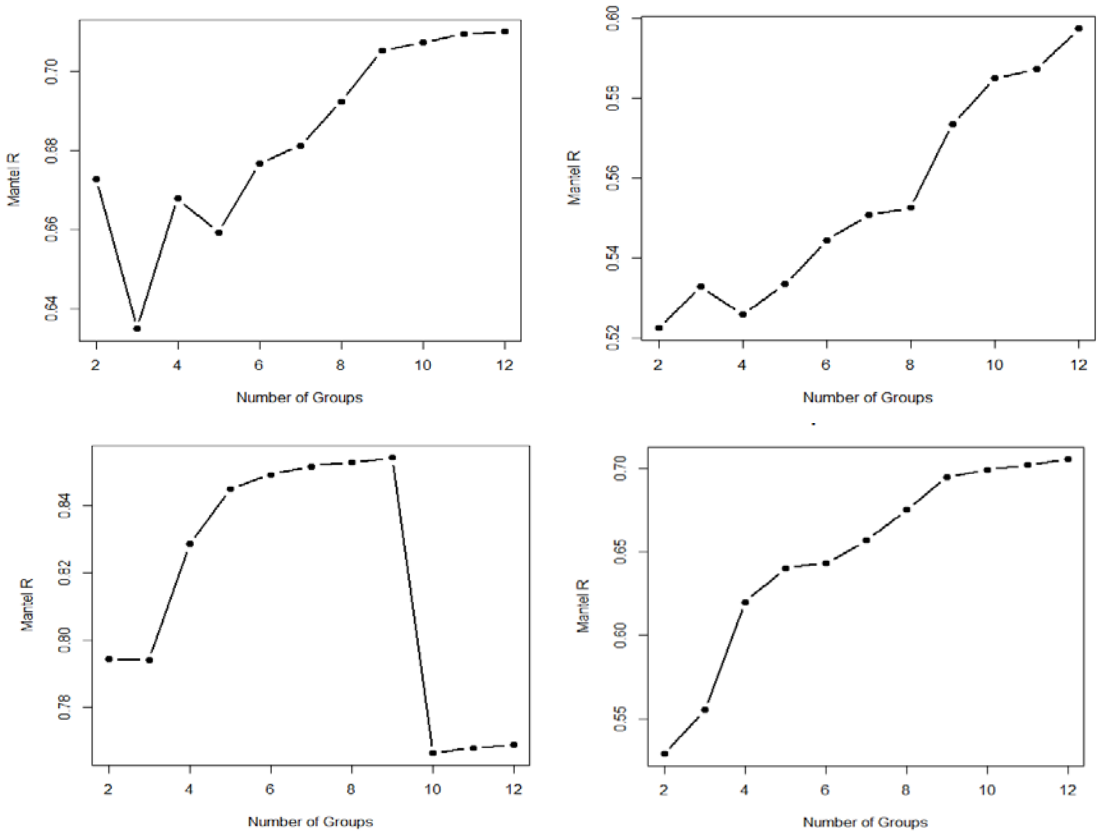

Figure 6.5. Scree plots showing mantel r for possible cluster analysis grouping outcomes. Groupings include, clockwise from top left: all-data; small-stem data; subcanopy data; and canopy data. For this analysis, 4 groups were selected for all-data, 7 groups were selected for small-stem data, and 5 groups were used to group both the canopy and subcanopy data.

All hardwood plots except for PSP 124 likewise moved farther in the positive NMDS 1 direction, with PSPs 123 and 37 having moved specifically closer to the bottom right corner of the NMDS space during the study. This expansion in a positive NMDS1 direction suggests that these samples' distinctive community types are increasingly diverging though time from successional plots. However, examination of PSPs 123 and 37 of the unpartitioned-data NMDS provides indication that some upland sites have become more similar to the bottomland plots overall.

Examination of cumulative temporal canopy trends (Figure 6.6) again demonstrates that successional plots changed more drastically than hardwood plots. Again, the composition shifted positively along NMDS 1 for successional plots, but overall this progression was less pronounced as compared to the unpartitioned-data analyses. Additionally, the canopy compositions of successional plots seemed not to be all directed toward bottomland hardwood community sample points. Rather, successional plots appeared to be diverging with some plots moving toward bottomland community points as before, but with others (especially plots heavily damaged by Hurricane Fran in 1996; PSPs 19, 39, 49, and 51) being directed toward upland hardwood ordination points associated with PSPs 36 and 37. Interestingly, unlike the unpartitioned data, the canopy data suggests that hardwood plots are mostly transitioning in the negative NMDS 1 direction, as opposed to the positive change direction that successional plot communities are transitioning toward (though see the bottom of Figure 6.6 for evidence that some plots such as PSP 37 have a net negative movement along NMDS 1 despite a trend toward the positive direction of NMDS 1 in recent sampling periods).

Cumulative compositional change of the subcanopy data-partition (Figure 6.8) suggests significantly more convergence of plots through time. Two thirds of all plots, regardless of plot type, have shifted toward the top right corner of the subcanopy ordination space. Again, successional plots have experienced the greatest amount of change, but PSP 10 (which was the most severely damaged hardwood plot following Hurricane Fran) also shifted relatively dramatically in this NMDS space. Although most plots appear to be converging as mentioned, about one third of successional plots have diverged and are transitioning toward the bottom right corner of the ordination space. These divergent plots include PSPs 4, 6, 7, 25, 26, 28, 29, 42, and 50. However, given the back-and-forth movement of the bottomland hardwood plot samples (see bottom of Figure 6.8) in and out of the top and bottom regions of the ordination space (i.e., between the two divergent clusters of plot endpoints), this divergence is much more likely due to the NMDS jittering process not finding an optimized (i.e., lowest stress) configuration and not any significant difference in species compositions between seemingly-diverged groups of plots. This assumption is questionable, however, given the robust number (i.e., 1000) of random starts used to generate the NMDS currently included in this chapter.

Examination of the per-sampling-period successional vectors for the subcanopy stems (Figure 6.8) reveled that many successional plots were initially directed toward NMDS space associated with upland hardwood communities. However, these trajectories all changed direction toward NMDS regions associated with bottomland plots within the last few sampling periods. In fact, this transition overwhelming occurred following Hurricane Fran in 1996, which suggests that the hurricane either initiated or accelerated a shift in sub-canopy species composition in successional plots.

Finally, the successional vectors for the small-stem data (Figure 6.9) suggests significant amounts of convergence of the smallest size-classes of woody stems in these forests. Specifically, other than two semi-outliers (PSPs 5 and 7), all successional pine plots are succeeding toward the bottom (or bottom right) of the ordination space, regardless of initial site conditions. The bottom-right trend of most of these successional plots mirrors that of the bottomland hardwood plots, which originated near that region of the NMDS space and continued to transition further toward the bottom right of the NMDS space. PSP 10 (which was the most severely damaged hardwood plot following Hurricane Fran) appears to have strongly shifted in community structure following the hurricane, and it now has a small-stem community type similar to both bottomland hardwood stands at earlier stages in the study and to some current successional plots (i.e., PSPs 40, 41, and 42). Upland PSPs 36, 123 and 124 have additionally progressed toward the NMDS space where the other plots are converging, though these upland sites have not progressed as far. Only PSPs 37 and 125 have had their small-stem stratum progress away from the otherwise ubiquitous convergence area in the lower region of the NMDS space.

Examination of per-sampling-period change vectors for the small-stem data (bottom of Figure 6.9) suggests that the convergence of plot compositions is relatively recent. Most successional plots appear to curve from some initial successional trajectory aimed toward distinct upland hardwood samples around mid-to-late 20th century and instead begin to succeed toward the convergence area of the NMDS space near the bottomland hardwood points. This redirection appears to also be accelerated in sampling periods following Hurricane Fran in 1996 (and to a lesser degree, following Hurricane Hazel in 1954; see Figure 6.10 for example plots) as was seen in the subcanopy data.

Species trends

Successional plots have experienced a decline in *Pinus taeda* stems as they have matured and grown (Figure 6.11), including a complete drop-off of small stems (Figure 6.17 and top left box of Figure 6.24) that resulted in almost no understory *P. taeda* stems by the 1980s (Figures 6.30 and 6.31). Plots most damaged by Hurricane Fran in 1996 have the lowest relative abundance of pines still remaining in the canopy (e.g., PSPs 19, 39, 49, 50, and 51; see Figure 6.12), which explains their relatively-long successional vectors that extend closest to hardwood samples. Regardless, *P. taeda* still made up the largest percentage of each successional plot's basal area as of the most recent sampling period. The high abundance of *P. taeda*, along with the near absence of pine in most hardwood stands, is likely the main reason that successional plots are still distinct from hardwood sample points in the unpartitioned-data and canopy-stem NMDS spaces. *Cornus florida*, *Diospyros virginiana*, *Nyssa sylvatica*, and *Juniperus virginiana* were once fairly abundant in successional plots (especially *C. florida*), but each of these species has been greatly reduced in both density and total basal area over the last 20 – 30 years (Figures 6.13, 6.14, 6.24, and 6.31). Each of these species has little or no presence in bottomland hardwood plots, but each is relatively abundant in the drier upland hardwood sites. As such, the loss of abundance of these species in successional plots has very likely played a role in the compositional shift away from upland hardwood plots in NMDS space through time. For example, this can be visualized by the shift in successional change vectors away from upland sites belonging to successional plots that once had high abundance of canopy *C. florida* (e.g., PSP 23; Figure 6.13).

In the time that the once-abundant hardwoods mentioned above have declined, *Acer rubrum* has become dramatically more abundant in successional plots (Figure 6.24) as has *Ulmus alata* and numerous species otherwise most abundant in bottomland hardwood stands: *Liquidambar styraciflua*, *Fraxinus spp.*, *Ulmus americana*, and *Acer floridanum*. Of these species, *A. rubrum*, *L. styraciflua*, and *Fraxinus spp.* experienced the greatest expansion into successional plot canopies (see Figure 6.15). Only a few species associated with upland hardwood stands experienced significant increases in abundance in any successional plots during the course of the study: *Oxydendrum arboreum, Carya tomentosa, Carya glabra, Quercus rubra*, and (in PSP 24 only) *Carya carolinae-septentrionalis*. These species became most abundant in successional plots with the greatest amount of Hurricane Fran damage following 1996, with *O. arboreum* and – to a much lesser degree – *C. tomentosa* reaching higher vertical strata in some plots (see Figure 6.15). *Prunus serotina* likewise became more abundant in successional plots that experienced sizeable canopy damage in 1996. PSP 15 experienced the most significant increase in oak species (namely, *Q. rubra, Q. velutina*, and *Q. falcata*), which it began experiencing in the last 20 years (bottom row of Figure 6.16).

Smaller size-classes of stems changed much more dramatically than canopy stems in successional plots (compare Figures 6.29, 6.30, and 6.31 to Figures 6.27 and 6.28). Mirroring the shifts in direction of successional plot change-vectors described in the last section, most successional plots have experienced a progressive transition in common understory plants as the plots have aged. *P. taeda* plummeted in abundance in successional plot understories relatively quickly during the study (Figure 61.7), and plots containing *Diospyros virginiana* likewise saw significant decline in this species decades ago. Most successional plots experienced a shift in species composition part-way through the study. The plots with plants associated with more basic and rich conditions (i.e., those grouped into Group 2 using the small-stem-informed cluster analysis) experienced a rise and subsequent fall in *L. styraciflua, Fraxinus spp., C. ovata, C. carolinae-septentrionalis, J. virginiana, A. rubrum*, and other species abundances (Figure 6.18). At the same time, the seemingly more acid-tolerant communities associated with the small-stem Group 3 experienced a rise and fall in significant understory abundance of *N. sylvatica*, *C. florida*, *A. rubrum,* and *O. arboreum* (Figure 6.19). A number of these Group 3 plots have more recently experienced an increase in *Morus rubra* abundance (Figure 6.23); the presence of relatively large-diameter *M. rubra* in bottomland hardwood plots (Figure 6.26) likely has played a role in redirecting successional plots that contain these increasing *M. rubra* abundances in species space.

Although successional PSPs 12 – 23 (represented by the gold Group 7 sample points in small-stem NMDS space; Figures 6.4 and 6.9) appear to not have experienced the same meandering transition early on in the study, this is an artifact of inconsistent measurement of small stems prior to 1978 in these plots. Specifically, the data for these plots consisted primarily of the canopy *P. taeda* measured at plot inception for the first 30 years of the study, so the additional inclusion and measurement of ingrowth after 1978 resulted in the community characteristics shifting drastically. However, interestingly, these plots represent the lone examples of successional plots that have picked up relatively high abundances of species in their understories that are associated with mature oak-hickory forests: namely, *Q. rubra, Q. falcata,* and *Q. velutina* (Figure 6.22). These small-stem oaks have been maintaining strong presence as seedlings (and sprouts) while also expanding into mid-story canopy classes (see Figure 6.24). Finally, *Fagus grandifolia* – which is otherwise most abundant in bottomland hardwood stands – has also become increasingly more prevalent throughout the small-stem size class of all successional plots (Figures 6.24, 6.29, 6.30, and 6.31) at the same time that *A. rubrum* has increased in the understory of all successional plots.

Although the canopies of hardwood stands have remained relatively stable in relative abundances of dominant species (e.g., *Q. alba* and *L. tulipifera* and to a lesser degree *C. tomentosa*, *Q. rubra,* and *N. sylvatica* in upland sites and *L.* styraciflua, *L. tulipifera, F. grandifolia,* and to a lesser degree *Q. alba* and *Platanus occidentalis* in bottomland sites; Figure 6.27), hardwood plot understories have changed dramatically since sampling began. These changes have primarily been in the form of decreased oak and hickory regeneration in upland hardwood stands. PSP 10, which experienced sizeable destruction from Hurricane Fran in 1996, experienced almost a complete removal of *Carya carolinae-septentrionalis* in its understory over the last 20 years, and PSPs 10, 37, and 123 all experienced declines in small-stem *Carya ovata* abundance during the course of the study (Figure 6.18). The abundances of numerous oaks and hickories (e.g., *Q. alba, C. tomentosa, C. glabra, Q. rubra,* and *Q. velutina*) in the understory have likewise decreased in upland hardwood plots (Figure 6.21 and Figure 6.22). These low regeneration rates are additionally reflected in the diameter distribution plots in Figure 6.25, which show near-zero abundance of small-diameter *Q. alba*, *C. carolinae-septentrionalis,* and *Q. coccinea* stems, along with reducing regeneration and little growth of *N. sylvatica*, *C. florida*, and *Q. velutina* stems. However, the diameter distribution plots in figure 6.25 show that *C. tomentosa* and *C. glabra* have seen a resurgence in the understory following Hurricane Fran in 1996. Other species less historically associated with these oak-hickory stands have also increased in abundance over the last few decades; these include species commonly associated with mesophication of forests (i.e., *A. rubrum* and *F. grandifolia*) as well as *Ostrya virginiana*, *Fraxinus spp.*, and *Viburnum rafinesquianum* (Figure 6.25 and Figure 6.31). However, the increase in *V. rafinesquianum* is primarily restricted to PSP 10.

The greatest transition in species abundance for bottomland hardwood stands is by far the substantial increase in understory *Fagus grandifolia*. The increase in *F. grandifolia* (and simultaneous decrease in understory *Carpinus caroliniana*) can be seen by the increasing (decreasing for *C. caroliniana*) point sizes in Figure 6.20 as well as widening (shrinking for *C. caroliniana*) proportions in relative abundances shown in Figures 6.29, 6.30, and 6.31. As in all other plot types, *Cornus florida* and *Juniperus virginiana* experienced reductions in abundance in bottomland hardwood plots, though *C. florida* (along with *Betula nigra*) has been essentially eliminated (Figures 6.26 and 6.31) from all strata of the bottomland stands. Unlike in all other plot types, *Acer rubrum* has never been abundant in the bottomland plots and has declined in these plots over the last 30 years (Figures 6.29, 6.30 and 6.31). *Liquidambar styraciflua* has likewise decreased in understory abundance, despite its relatively unchanging abundance in bottomland plot canopies. Meanwhile, as can be seen in Figure 6.26, *Acer floridanum* (ACBA), along with *Ostrya virginiana*, *Aesculus sylvatica*, *Viburnum rufidulum* and the invasive *Elaeagnus pungens* (ELPU) have all increased dramatically in understory abundance in the last few decades (though increases in woody shrubs might, in part, reflect a known shift toward more rigorous sampling of shrubby species in the late 1980s).

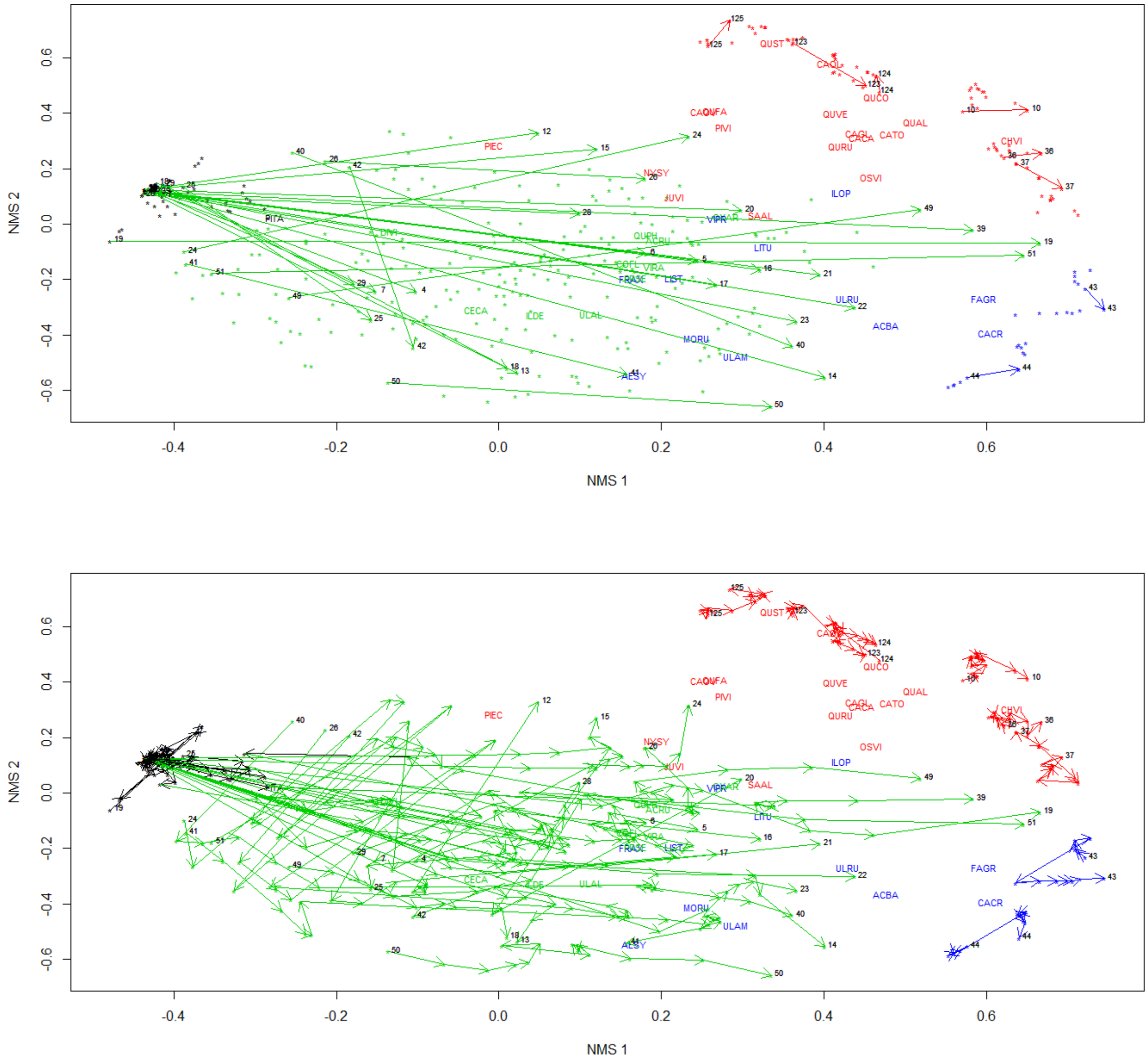

Figure 6.6. Successional compositional change of plots in NMDS space using unpartitioned PSP data. Cumulative (top) and per-sampling-period (bottom) change vectors tracing change in community composition in NMDS space of each plot across the length of the study. These plots represent change in NMDS space based on full inclusion of the PSP data. Each point represents the community characteristic of an individual sample (i.e., plot-year combination). Four-letter species codes (SPECs) were added to the plot using weighted averaging, and colors of points were dictated by cluster analyses using the full data. PSP plot numbers were also added.

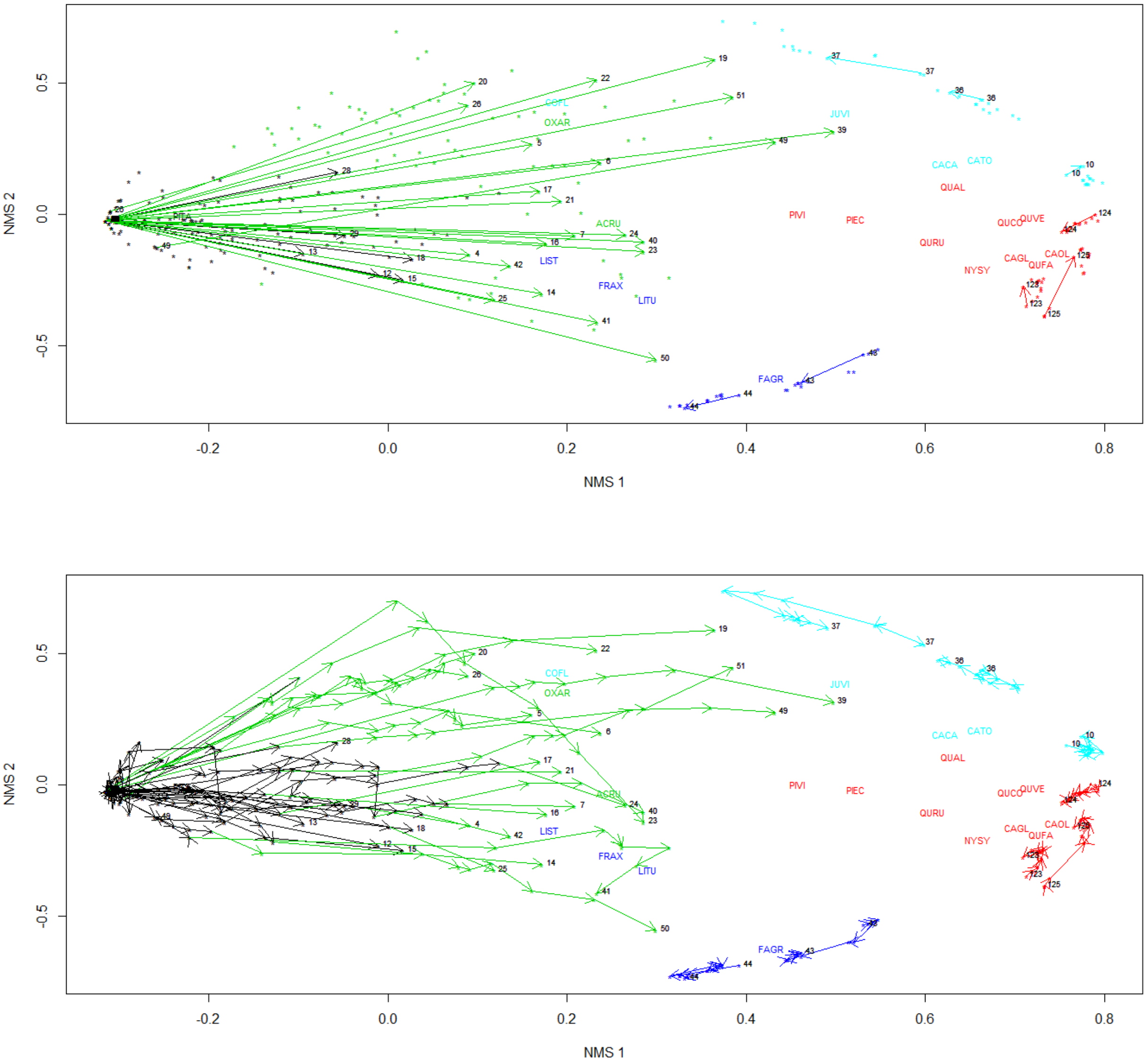

Figure 6.7. Cumulative (top) and per-sampling-period (bottom) change vectors tracing change in canopy community composition in NMDS space of each plot across the length of the study. These plots represent change in NMDS space based on a subdivision of PSP data that only included canopy stems. Each point represents the community characteristic of an individual sample (i.e., plot-year combination). Four-letter species codes (SPECs) were added to the plot using weighted averaging, and colors of points were dictated by cluster analyses based on a subdivision of the data containing only canopy stems. PSP plot numbers were also added.

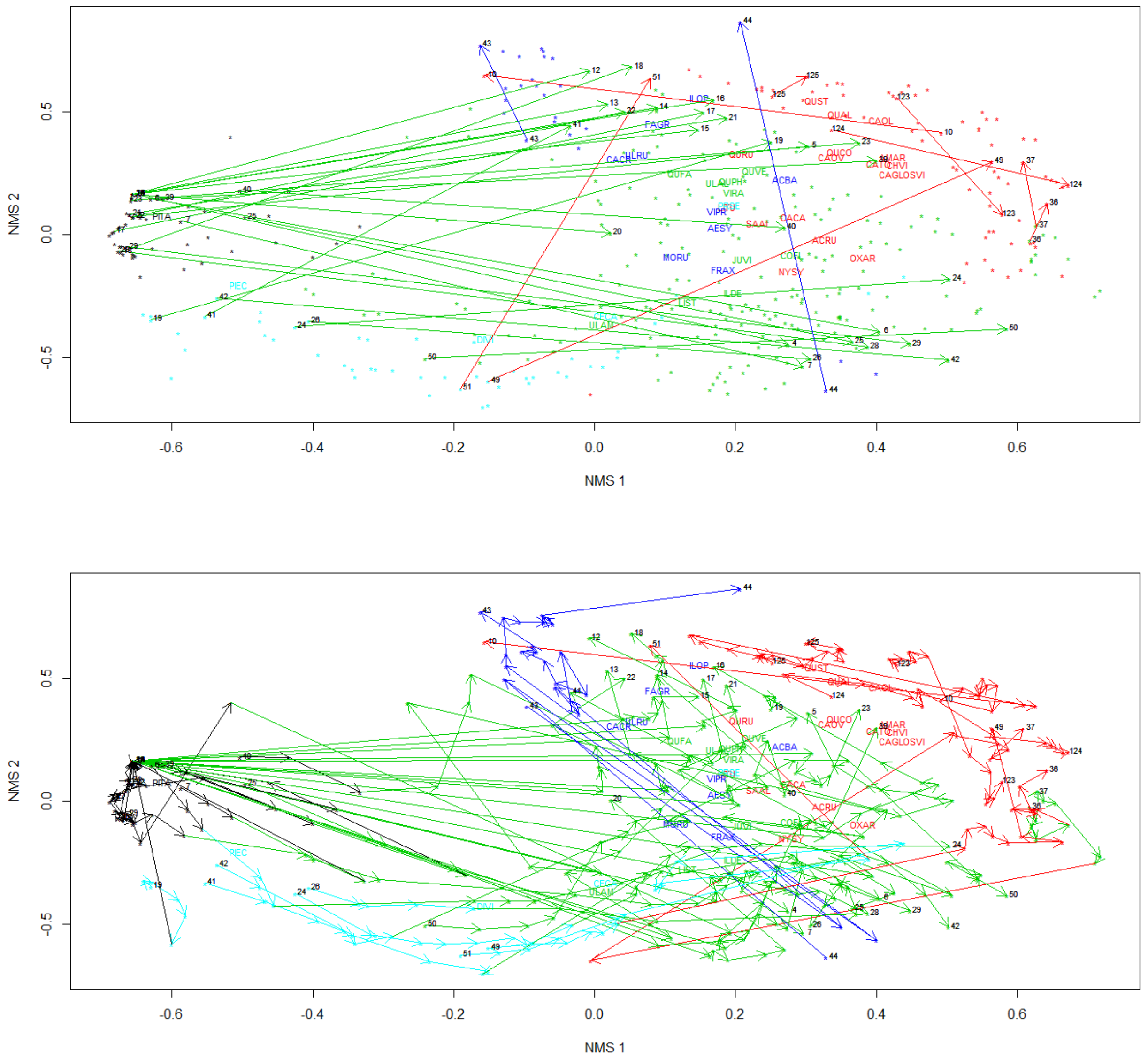

Figure 6.8. Cumulative (top) and per-sampling-period (bottom) change vectors tracing change in subcanopy community composition in NMDS space of each plot across the length of the study. These plots represent change in NMDS space based on a subdivision of PSP data that only included subcanopy stems. Successional plots changed trajectories drastically following Hurricane Fran in 1996 resulting in successional plots (green arrows) typically moving away from upland sites (red points) in the last few sampling periods in the graphic. Each point represents the community characteristic of an individual sample (i.e., plot-year combination). Four-letter species codes (SPECs) were added to the plot using weighted averaging, and colors of points were dictated by cluster analyses based on a subdivision of the data containing only subcanopy stems. PSP plot numbers were also added.

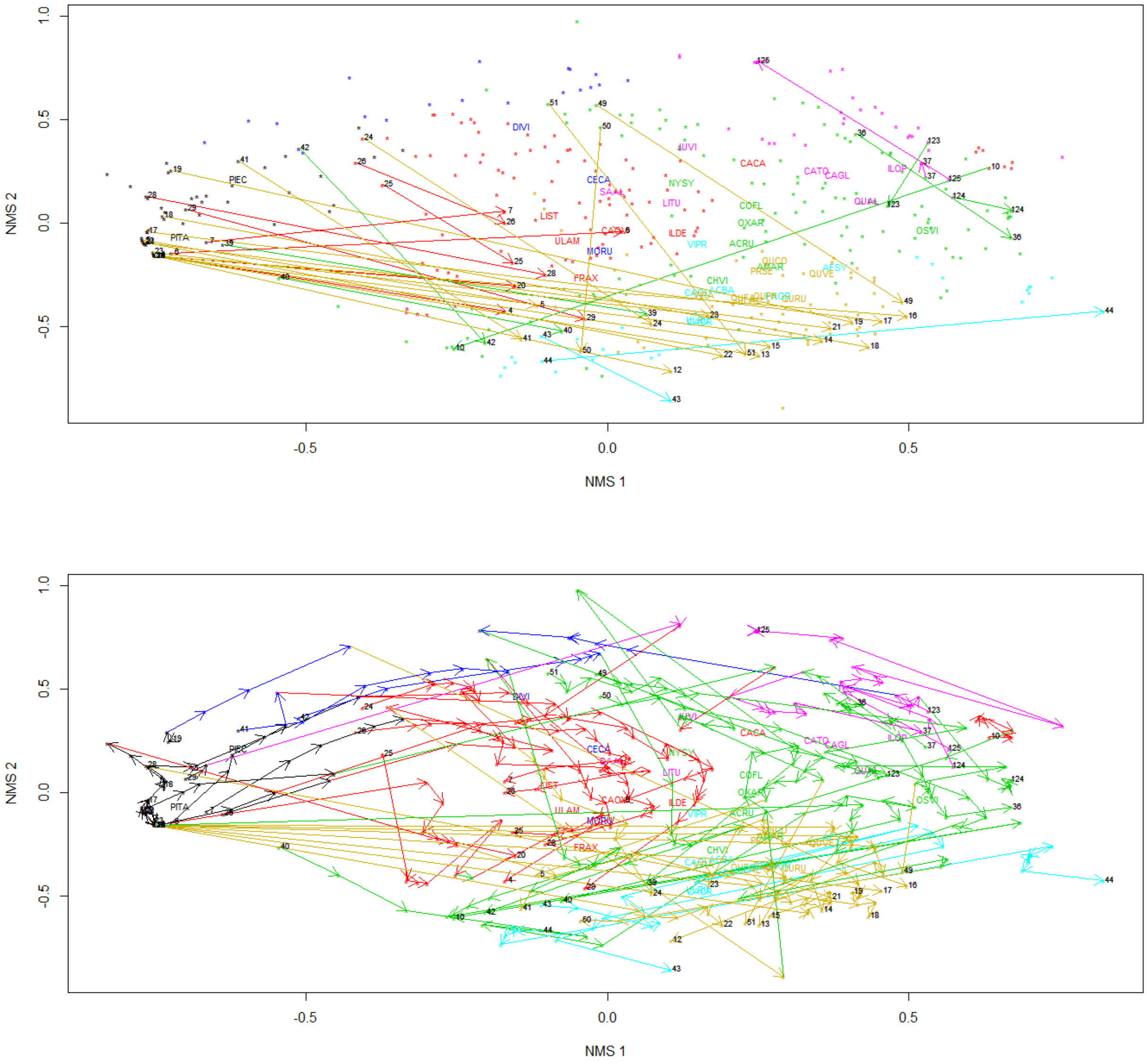

Figure 6.9. Cumulative (top) and per-sampling-period (bottom) change vectors tracing change in small-stem stratum community composition in NMDS space of each plot across the length of the study. These plots represent change in NMDS space based on a subdivision of PSP data that only included small (DBH ≤ 10 cm) stems. Each point represents the community characteristic of an individual sample (i.e., plot-year combination). Four-letter species codes (SPECs) were added to the plot using weighted averaging, and colors of points were dictated by cluster analyses based on a subdivision of the data containing only small-stem trees. PSP plot numbers were also added.

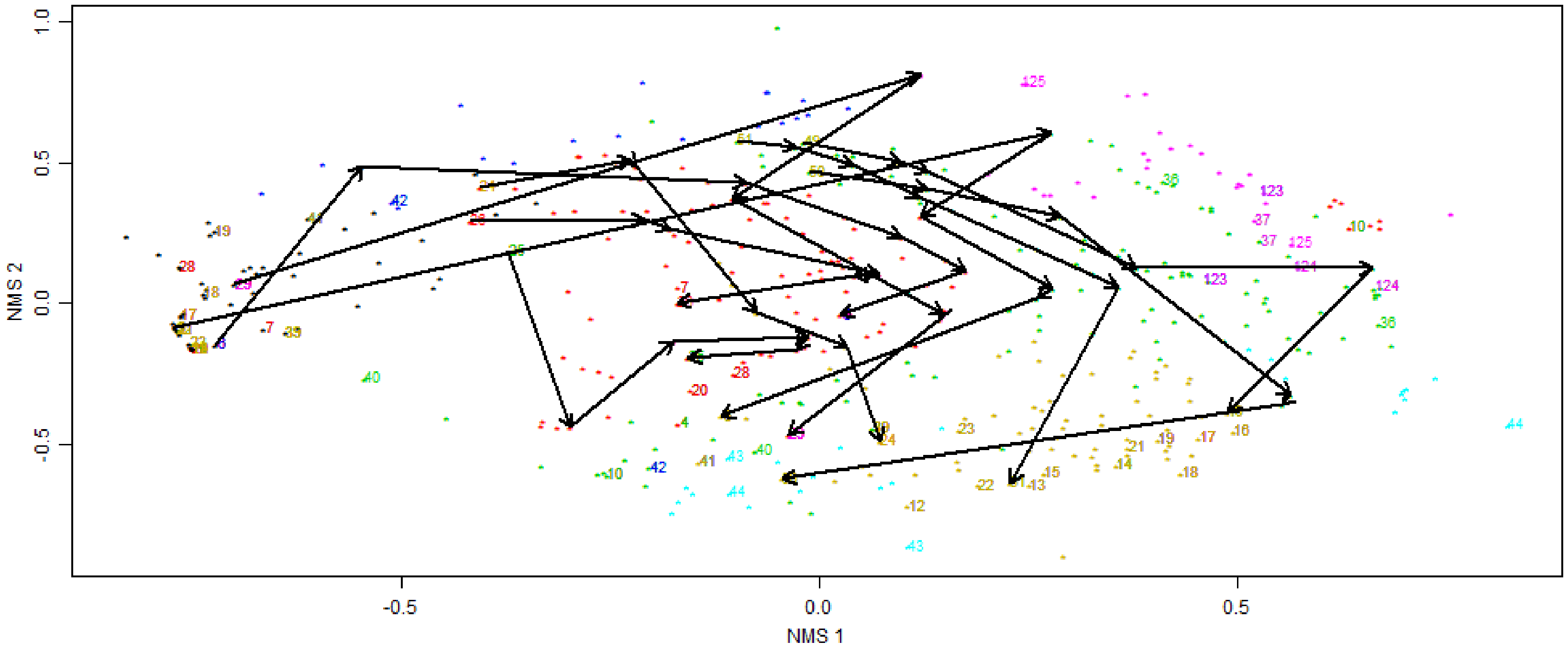

Figure 6.10. Change vectors demonstrating the direction and magnitude of community composition change (in NMDS space) before and after two major hurricanes (Hurricane Hazel in 1954 and Hurricane Fran in 1996). Vectors are just shown for a subset of PSPs (5, 6, 24, 25, 26, 29, 49, and 51) to demonstrate the change in direction caused by hurricane damage and the acceleration of this direction change following Fran in 1996. The subset of plots was chosen at random from those that showed similar trends. NMDS constructed from small-stem partition of PSP data.

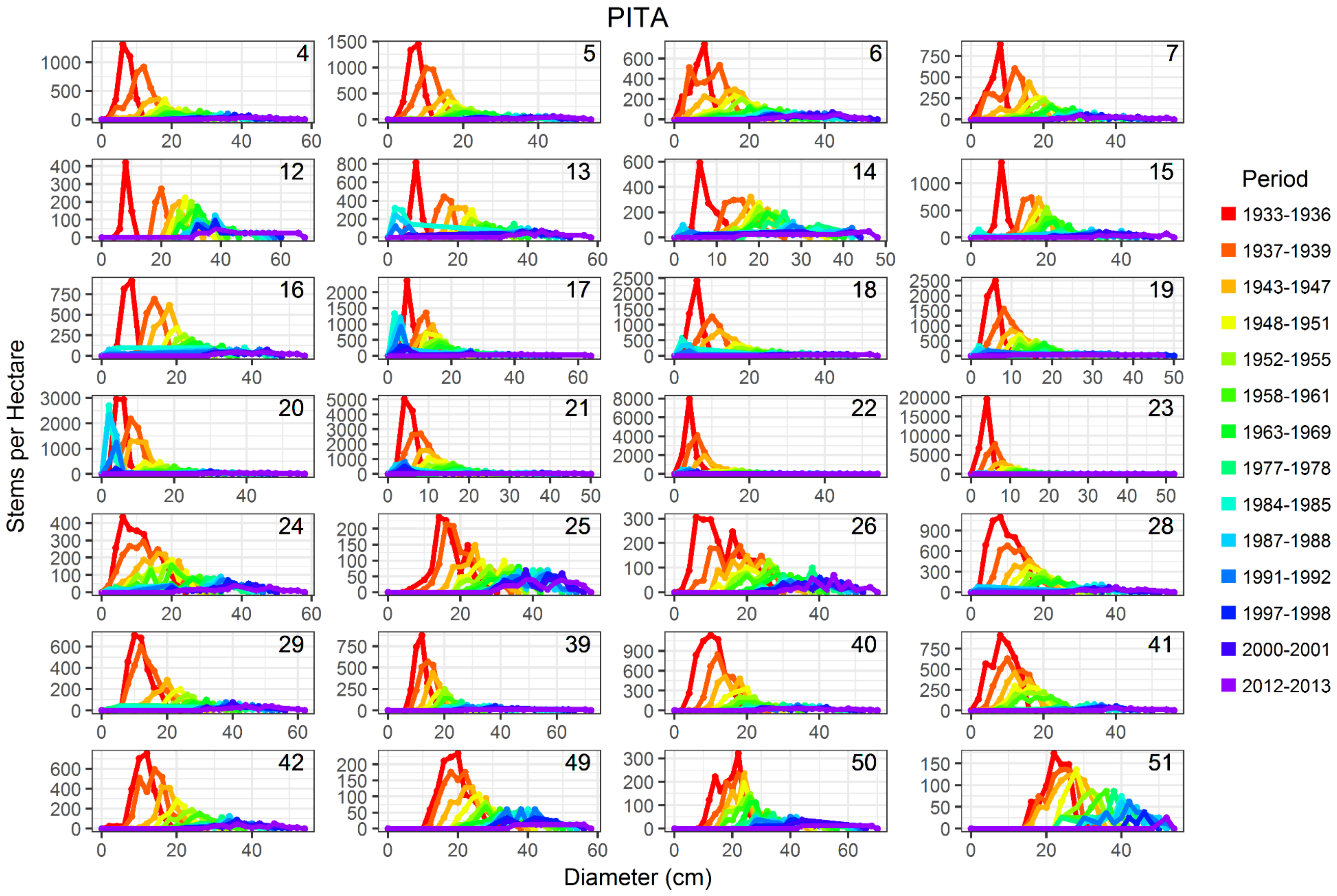

Figure 6.11. Diameter distribution of *Pinus taeda* (PITA) in each sampling period in each successional PSP.

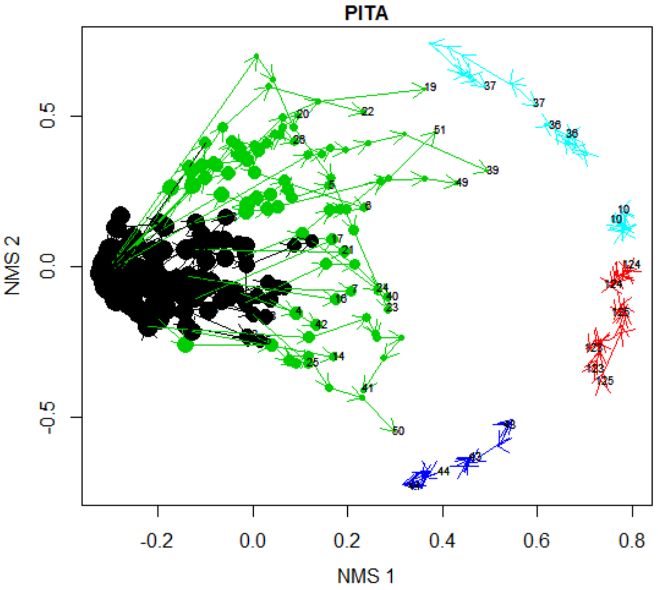

Figure 6.12. Canopy NMDS ordinations with point size weighted by *Pinus taeda* (PITA) abundance. PITA canopy abundance has declined significantly in all plots that have community types most similar to hardwood stands. Change vectors are included in each graphic to help direct the reader to the temporal flow of each plot.

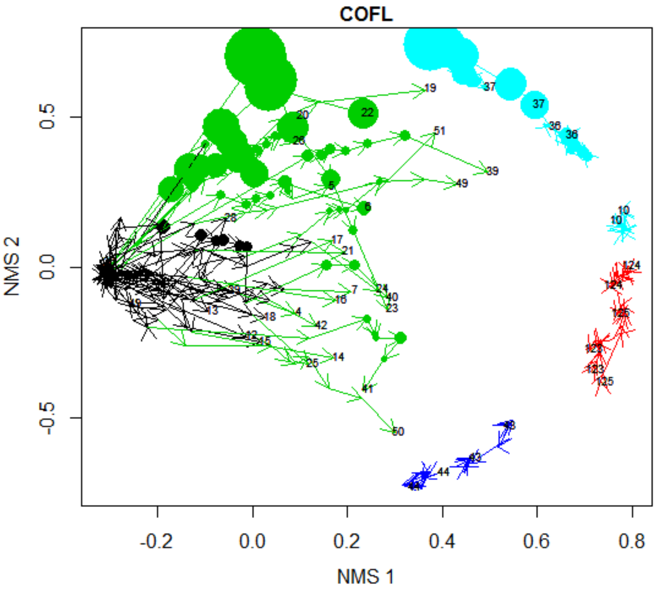

Figure 6.13. Canopy NMDS ordinations with point size weighted by *Cornus florida* (COFL) to demonstrate the decline in large individuals of COFL that once drove successional plots toward NMDS space occupied by upland hardwood plot samples.

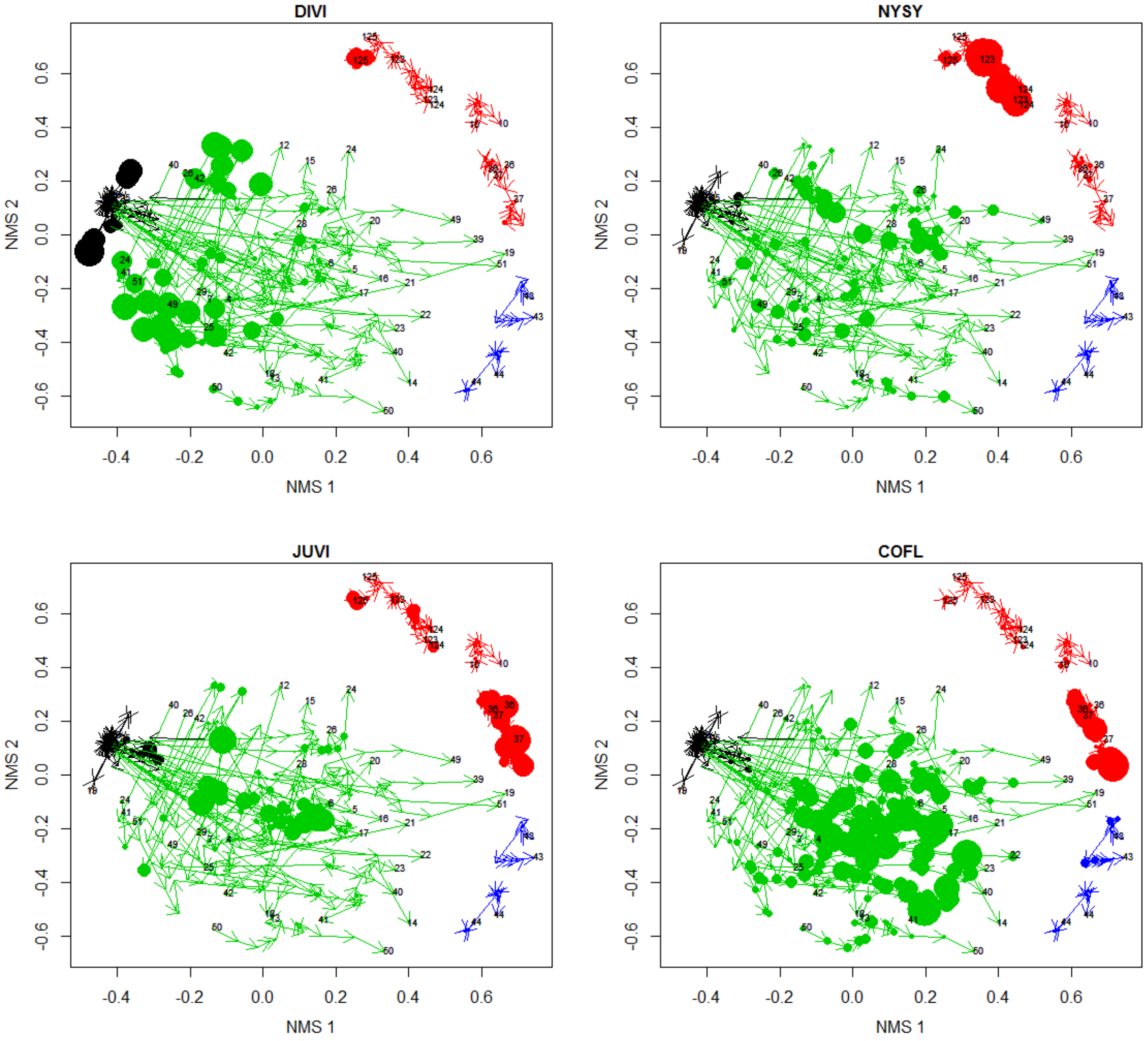

Figure 6.14. Unpartitioned-data NMDS ordinations with point size weighted by hardwood species that were once prominent in successional pine plots but that have significantly declined in successional pine plots in recent decades. Each of these species is relatively abundant in upland hardwood stands. Change vectors are included in each graphic to help direct the reader to the temporal flow of each plot.

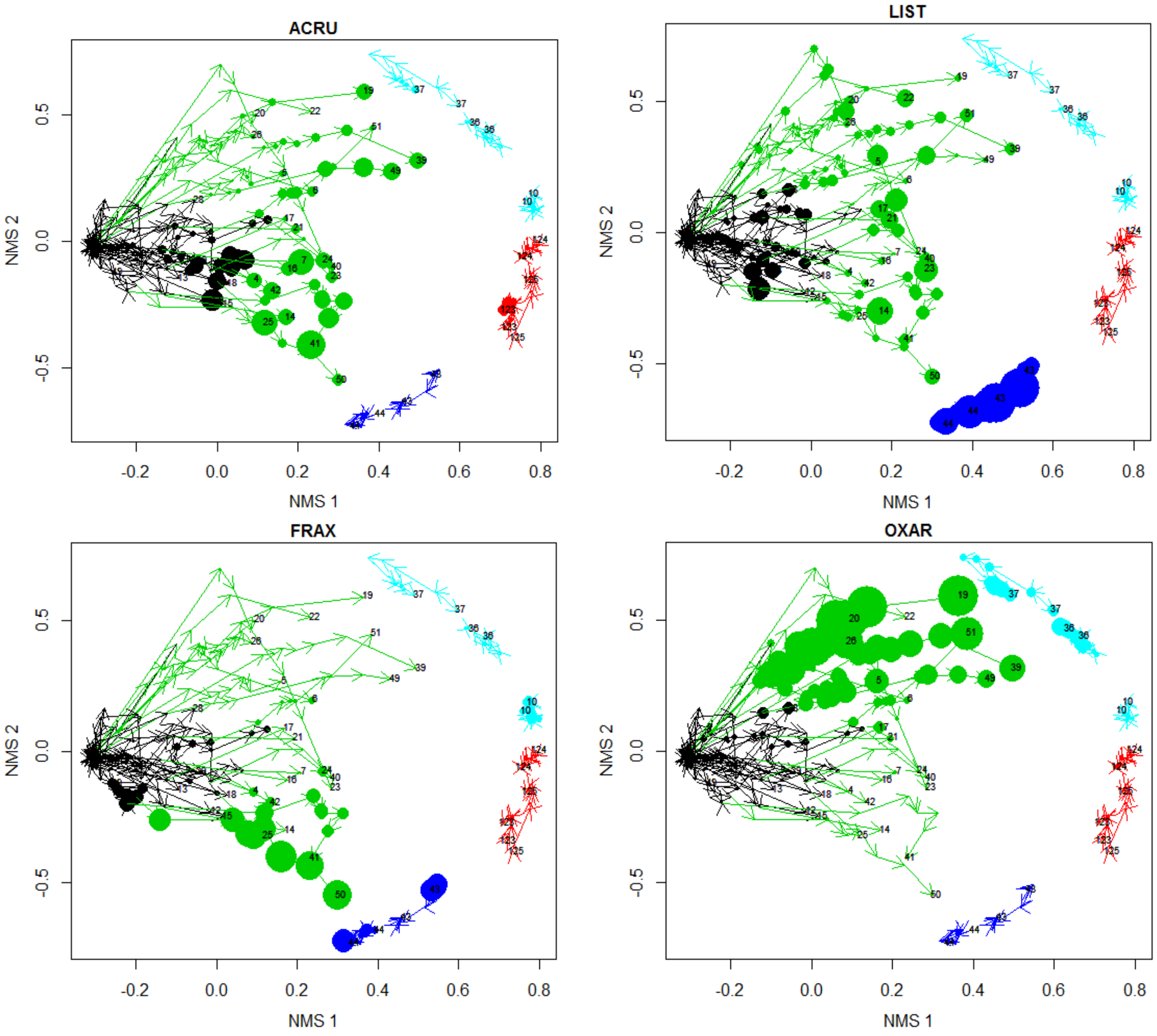

Figure 6.15. Canopy-tree NMDS ordinations with point size weighted by hardwood species that have become increasingly more abundant in the canopies of successional pine stands. Most of these species (i.e., ACRU, LIST, and FRAX) tend to be more common toward bottomland hardwood sample points, while OXAR is an uncommon canopy species in successional plots that is shared by a subset of the upland hardwood stands. Change vectors are included in each graphic to help direct the reader to the temporal flow of each plot. Species code definitions can be found in Appendix 1.

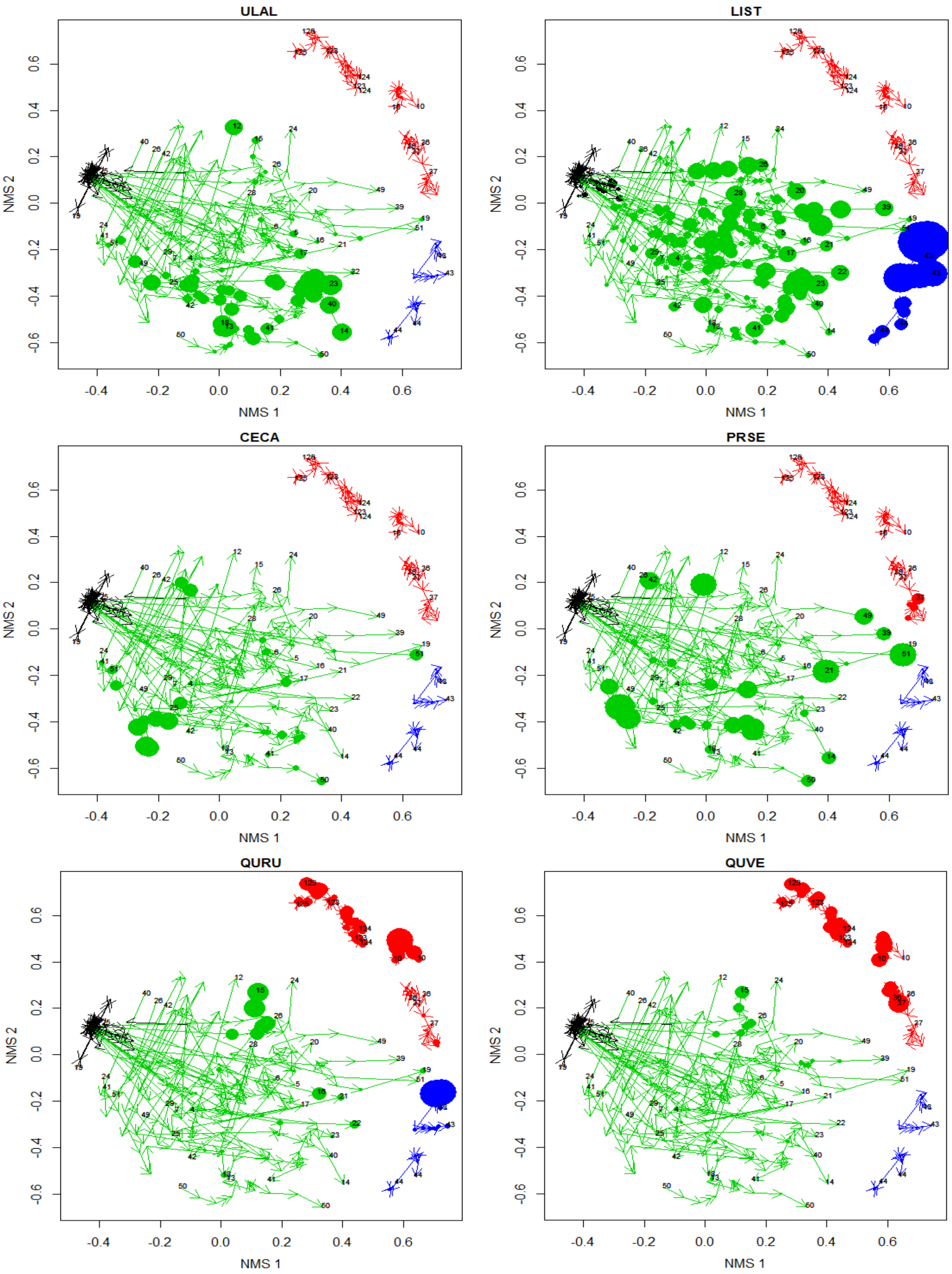

Figure 6.16. Unpartitioned-data NMDS ordinations with point size weighted by successional hard-wood species that tend to be more common toward bottomland hardwood sample points (top row), that tend to have increased following major disturbance (middle row), and tend to be more abundant in upland hardwood sites (e.g., oaks; bottom row). Change vectors are included in each graphic to help direct the temporal flow of each plot. Species code definitions can be found in Appendix 1

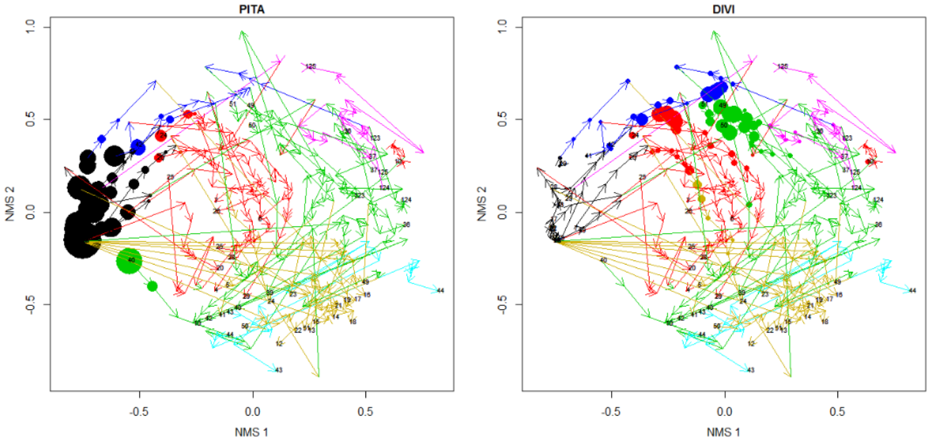

Figure 6.17. Small-stem NMDS ordinations with point size weighted by prominent species in small-stem Group 1 (PITA, left) and Group 4 (DIVI, right). These graphs are to demonstrate the decline of regrowth in these species in their respective plot types.

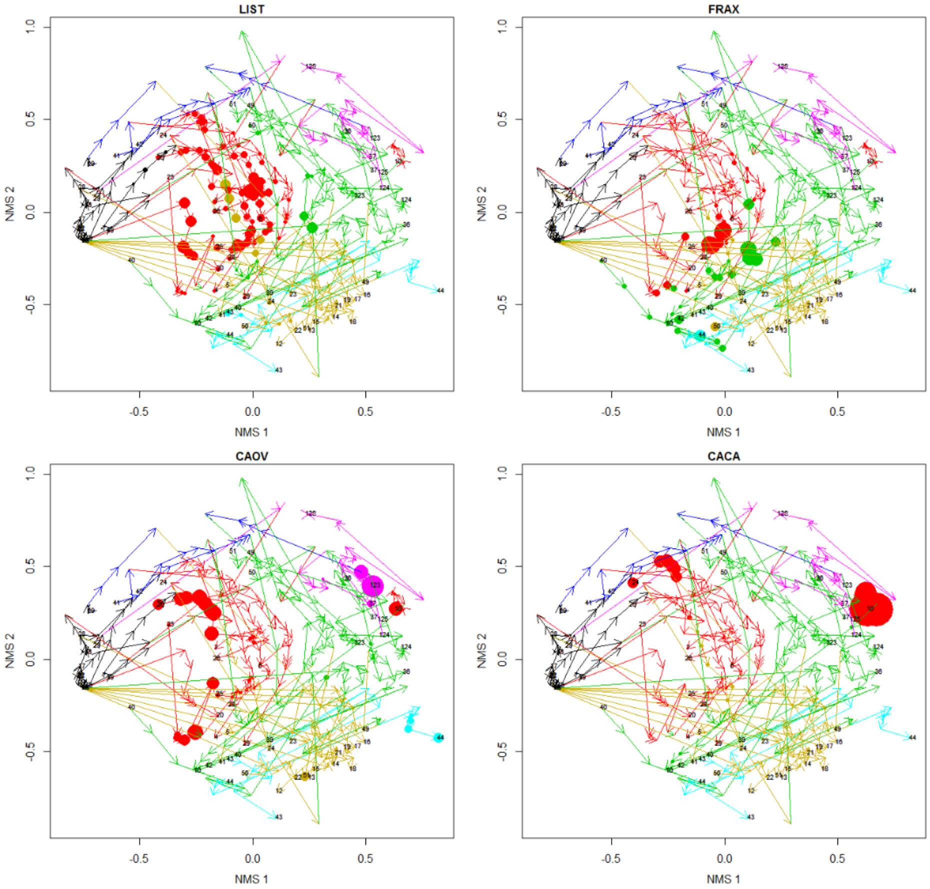

Figure 6.18. Small-stem NMDS ordinations with point size weighted by prominent species in small-stem Group 2 (LIST, FRAX, CAOV, & CACA). These graphs are to demonstrate the decline of regrowth in these once-abundant species in Group 2 in the last few decades.

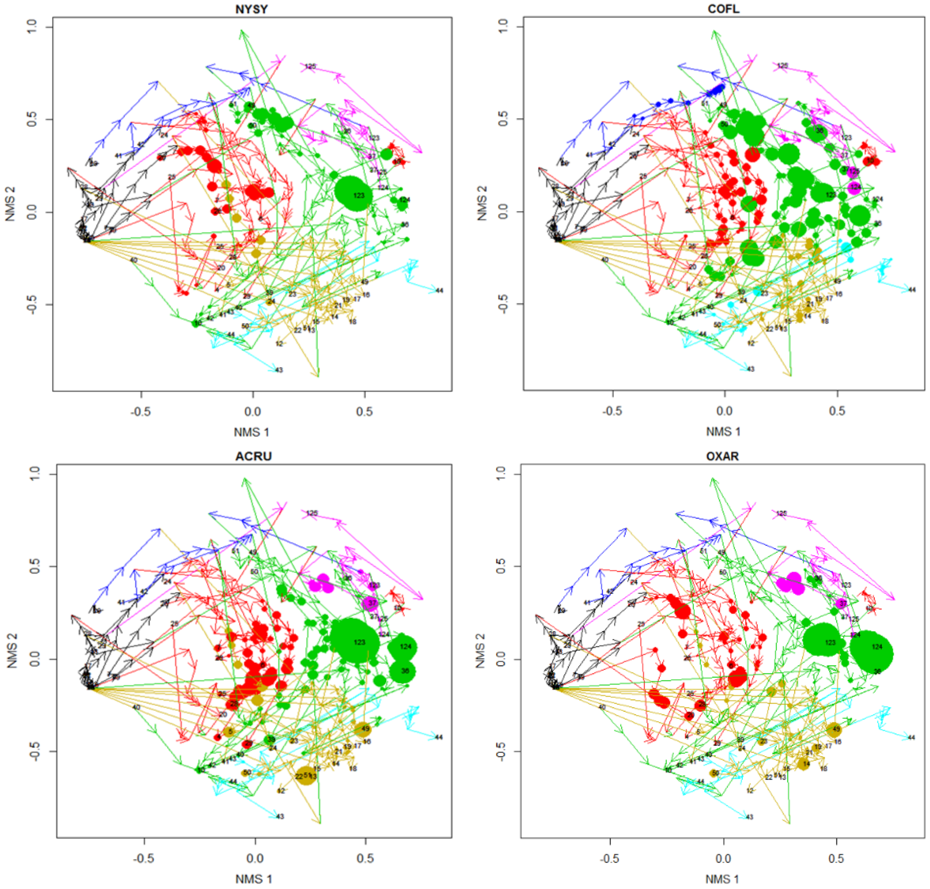

Figure 6.19. Small-stem NMDS ordinations with point size weighted by prominent species in small-stem Group 3 (NYSY, COFL, ACRU, & OXAR). These graphs are to demonstrate the decline of regrowth in these once-abundant species in Group 3 in the last few decades.

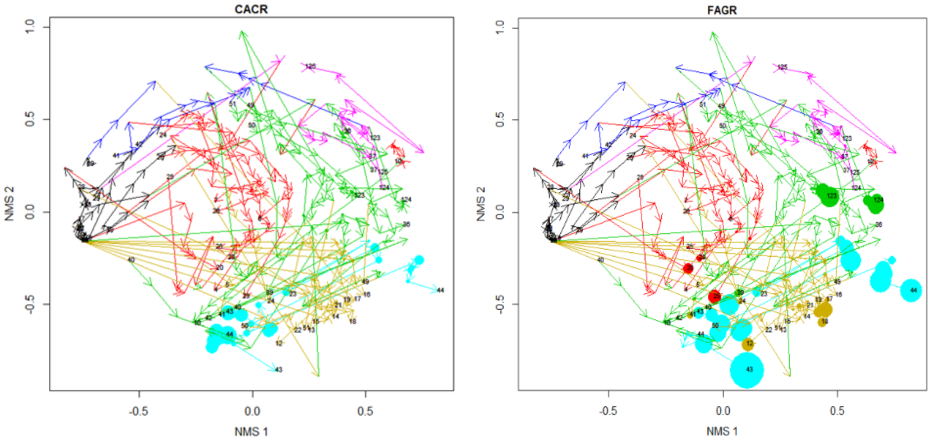

Figure 6.20. Small-stem NMDS ordinations with point size weighted by prominent species in small-stem Group 5 (CACR and FAGR). These graphs demonstrate the unique relative high abundance of these species in small-stem stratum of bottomland plots and how only recently other plot types (e.g., Group 7, gold) have experienced increases in these species.

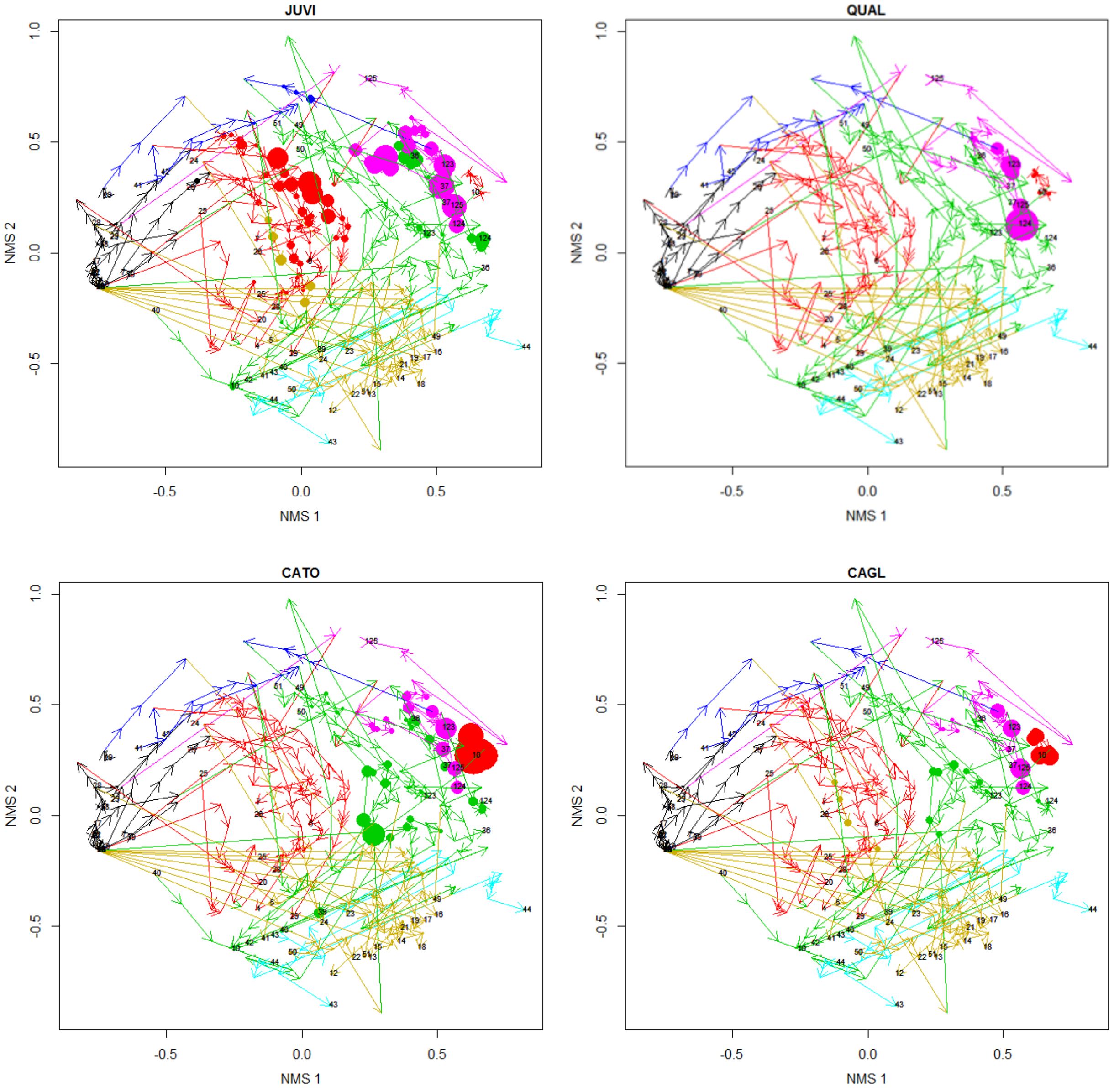

Figure 6.21. Small-stem NMDS ordinations with point size weighted by prominent species in small-stem Group 6 (JUVI, QUAL, CATO, and CAGL). These graphs demonstrate that these once-abundant species in Group 6 are both uncommon in the lowest strata of other forest types and becoming less abundant in upland hardwood plots (PSPs 10, 36, 37, 123, 124, and 125). The decline in upland sites can be visualized by tracing the declining point size along successional vectors for each sample plot. Species code definitions can be found in Appendix 1.

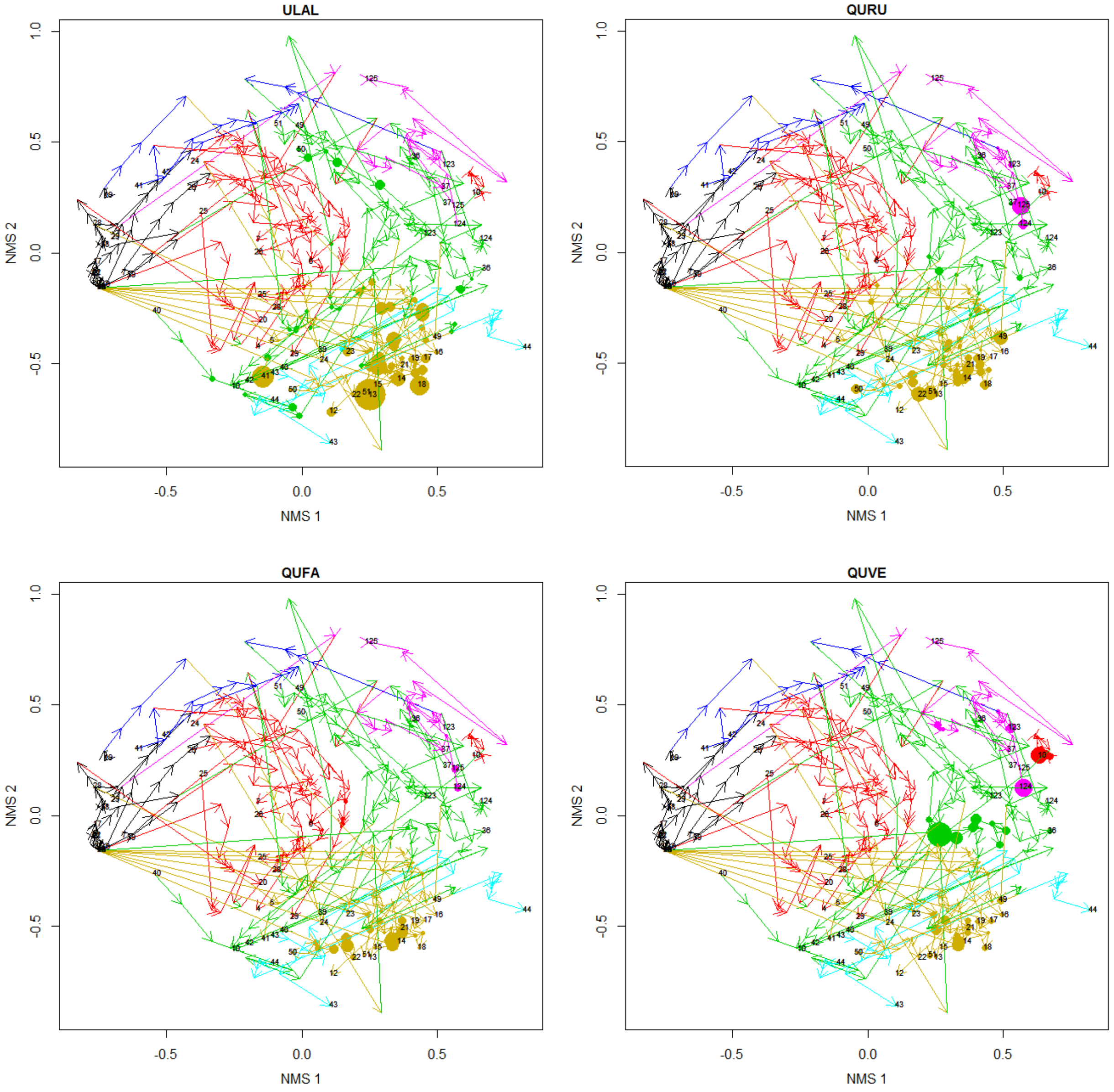

Figure 6.22. Small-stem NMDS ordinations with point size weighted by prominent species in small-stem Group 7 (ULAL, QURU, QUFA, and QUVE). These graphs demonstrate that the most prominent regrowth of many oak species is occurring in this geographically clustered suite of successional pine plots. The top left graphic shows that a species uncommon in other plot types, ULAL, has simultaneously become abundant in Group 7 (gold) plots. Species code definitions can be found in Appendix 1.

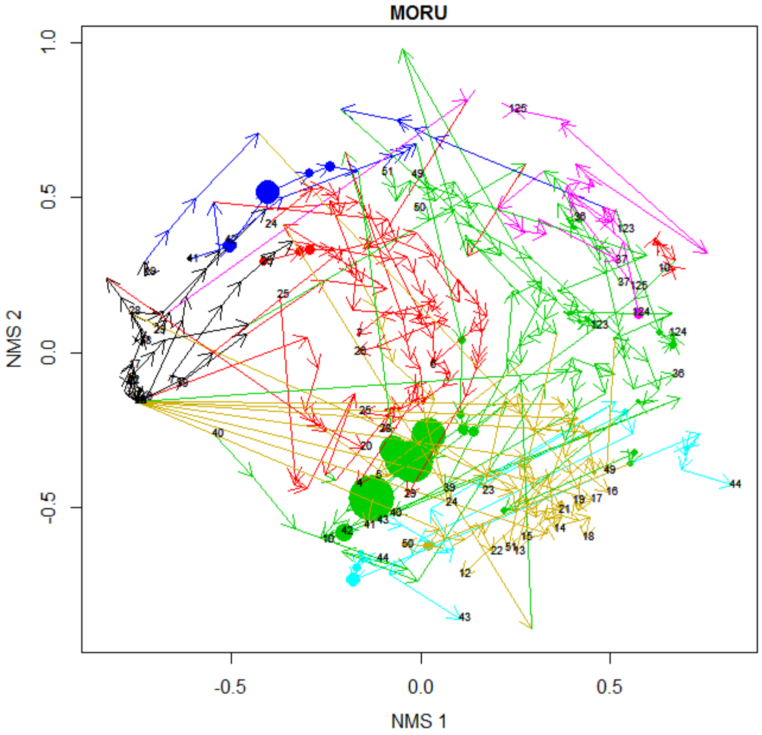

Figure 6.23. Small-stem NMDS ordinations with point size weighted by *Morus rubra* (MORU), which has become more prevalent in the understory of Group 3 successional plots in recent decades. The abundance of MORU in these plots is unique to this region of the NMDS space where many plots in the study have succeeded toward as of the final sampling period in 2013.

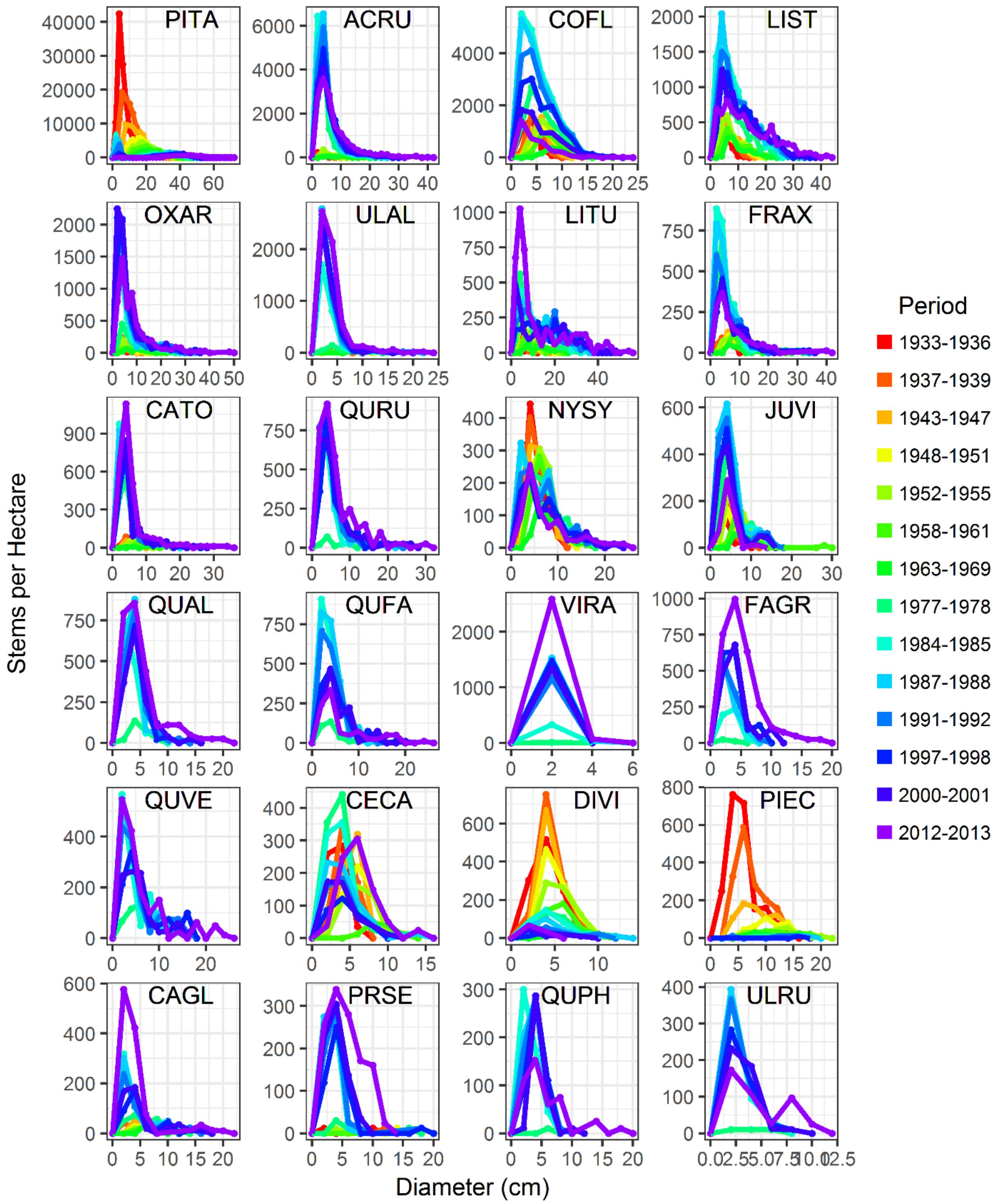

Figure 6.24. Diameter distribution of the 24 most cumulatively abundant (across all sampling periods) species in each sampling period aggregated across all successional pine plots. Species code definitions can be found in Appendix 1.

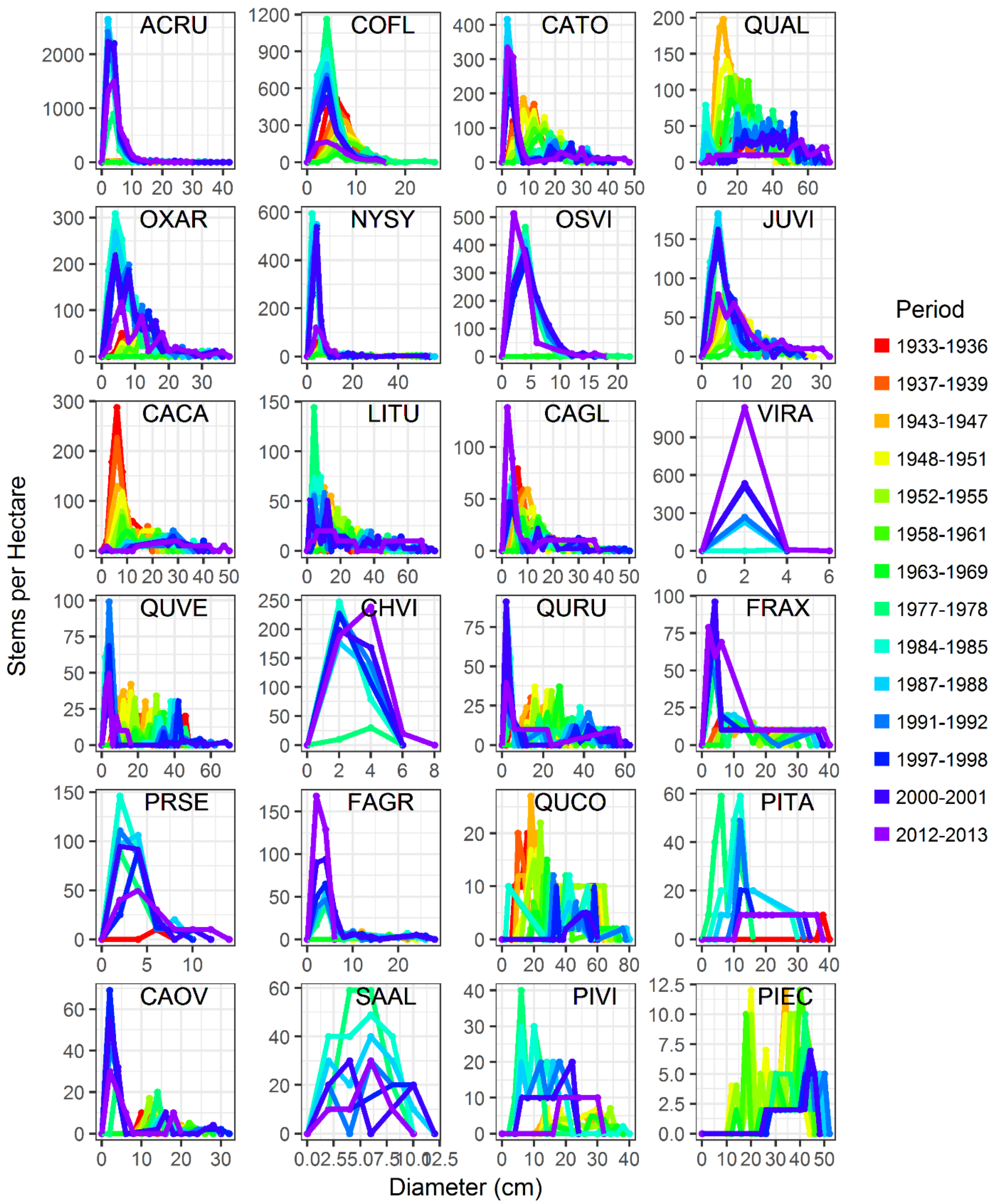

Figure 6.25. Diameter distribution of the 24 most cumulatively abundant species across all sampling periods shown for each sampling period aggregated across all upland hardwood plots (PSPs 10, 36, 37, 123, 124, & 125). Species code definitions can be found in Appendix 1.

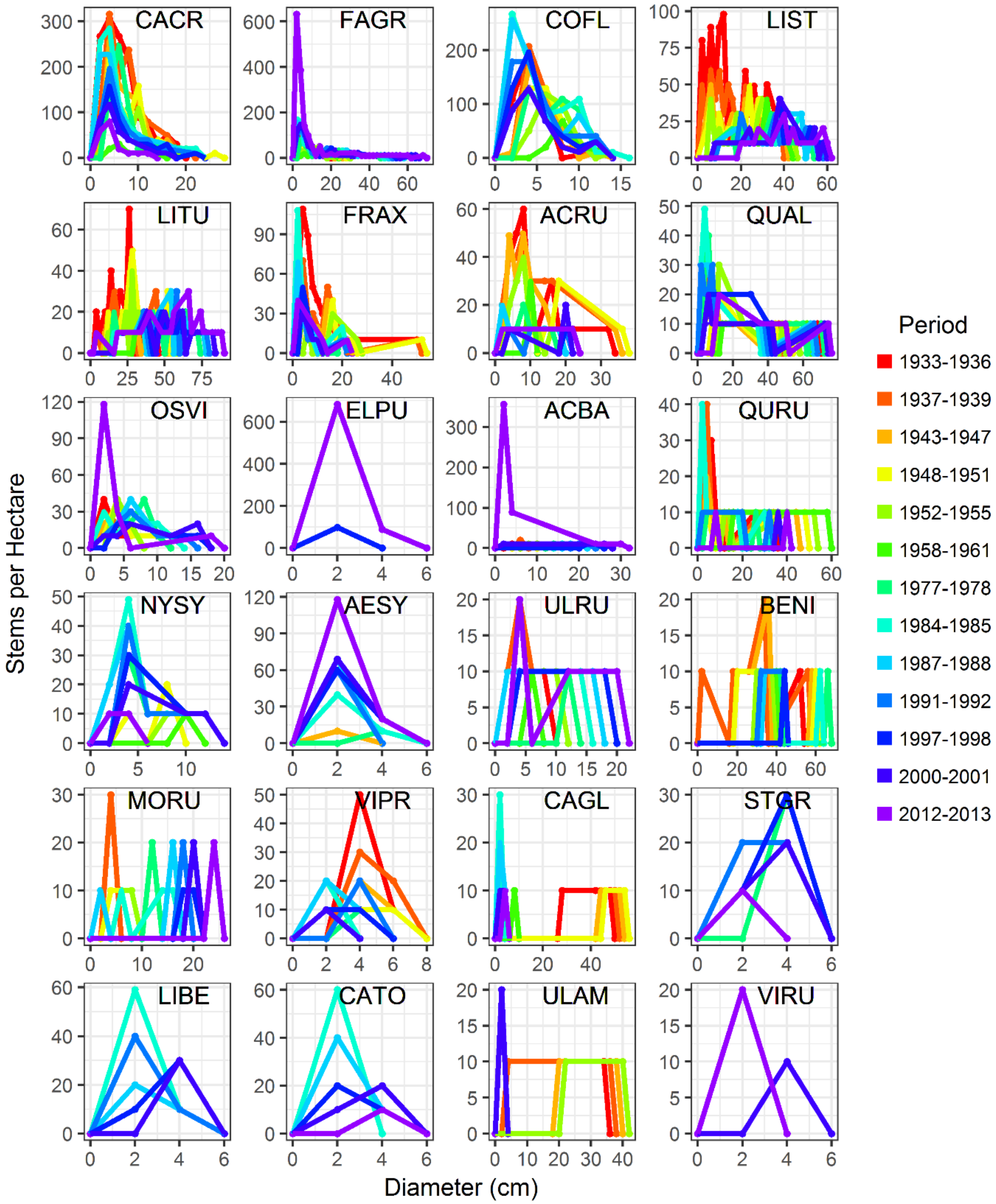

Figure 6.26. Diameter distribution of the 24 most cumulatively abundant species across all sampling periods shown for each sampling period aggregated across both bottomland hardwood plots (PSPs 43 & 44). Species code definitions can be found in Appendix 1.

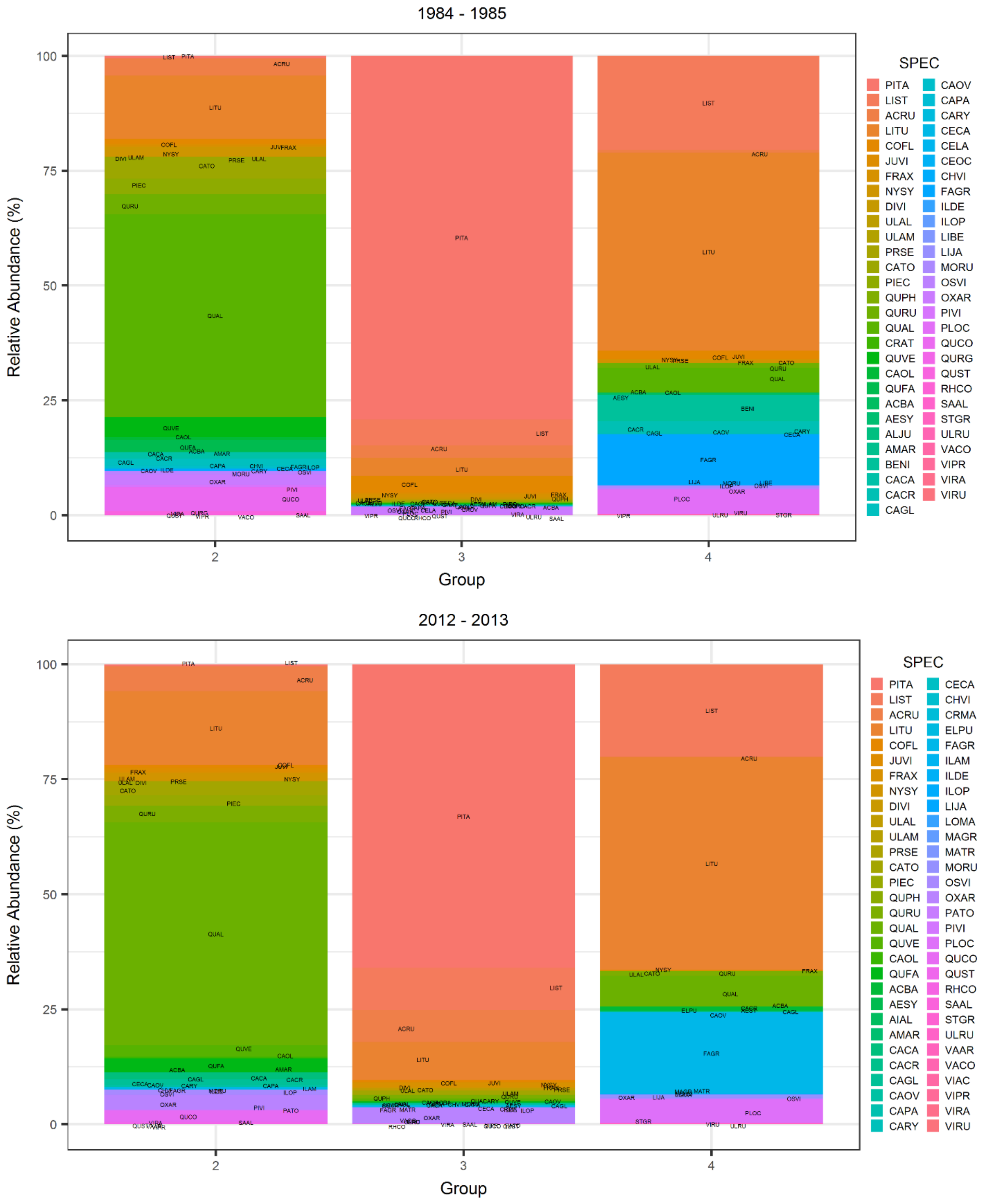

Figure 6.27. Comparing relative abundances (basal areas) of prominent species of all diameter sizes between 1980s and 2010s for plot-types designated by cluster analysis using full data set. Groups roughly equate to 2 = upland hardwood stands; 3 = successional pine stands; 4 = bottomland hardwood stands.

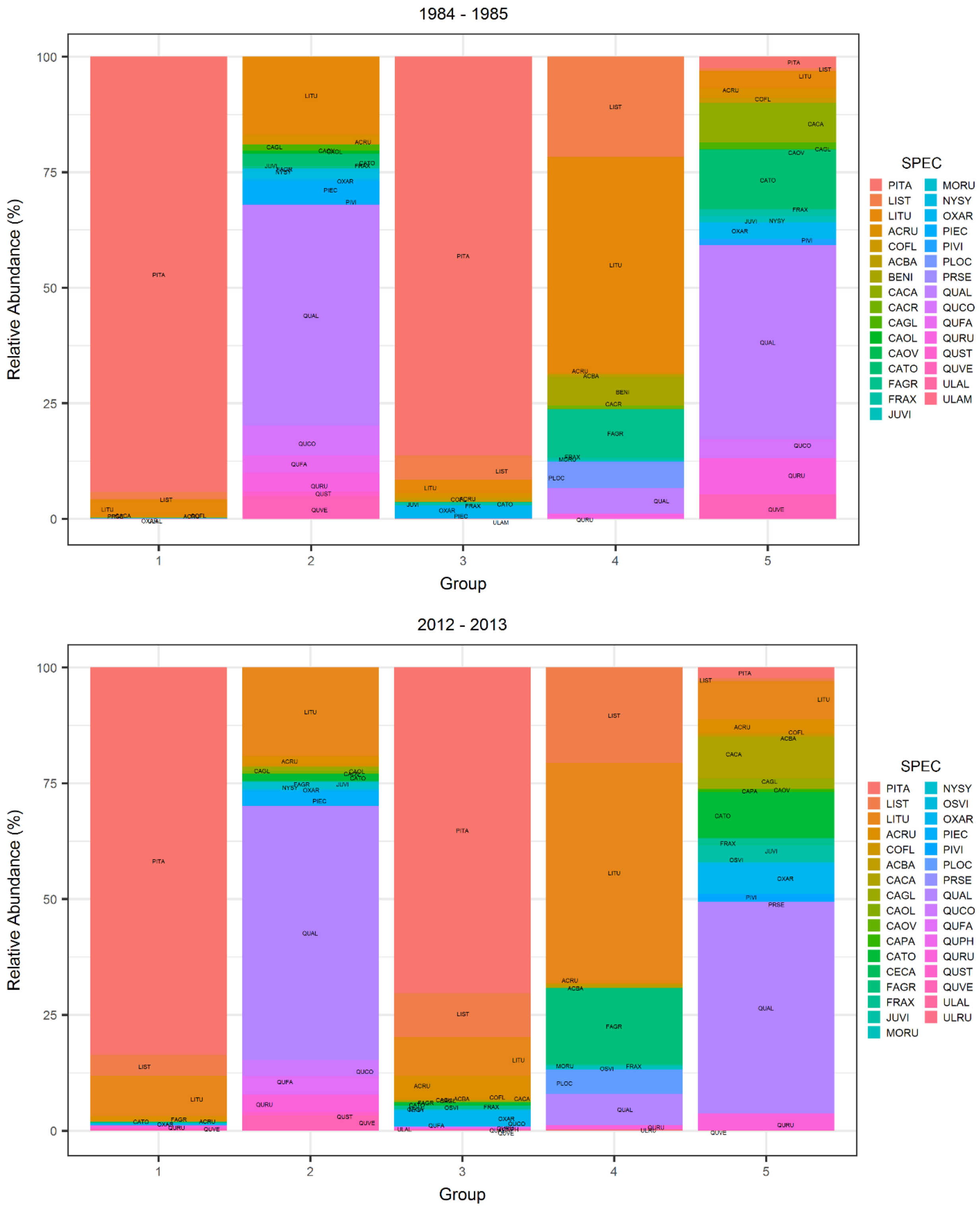

Figure 6.28. Comparing relative abundances of prominent canopy species between 1980s and 2010s for plot-types designated by cluster analysis using canopy trees. Groups equate to 1 = primarily pine; 2 = upland hardwood stands in Hill Forest; 3 = successional pine stands; 4 = bottomland hardwood stands; 5 = upland hardwood stands in Duke Forest.

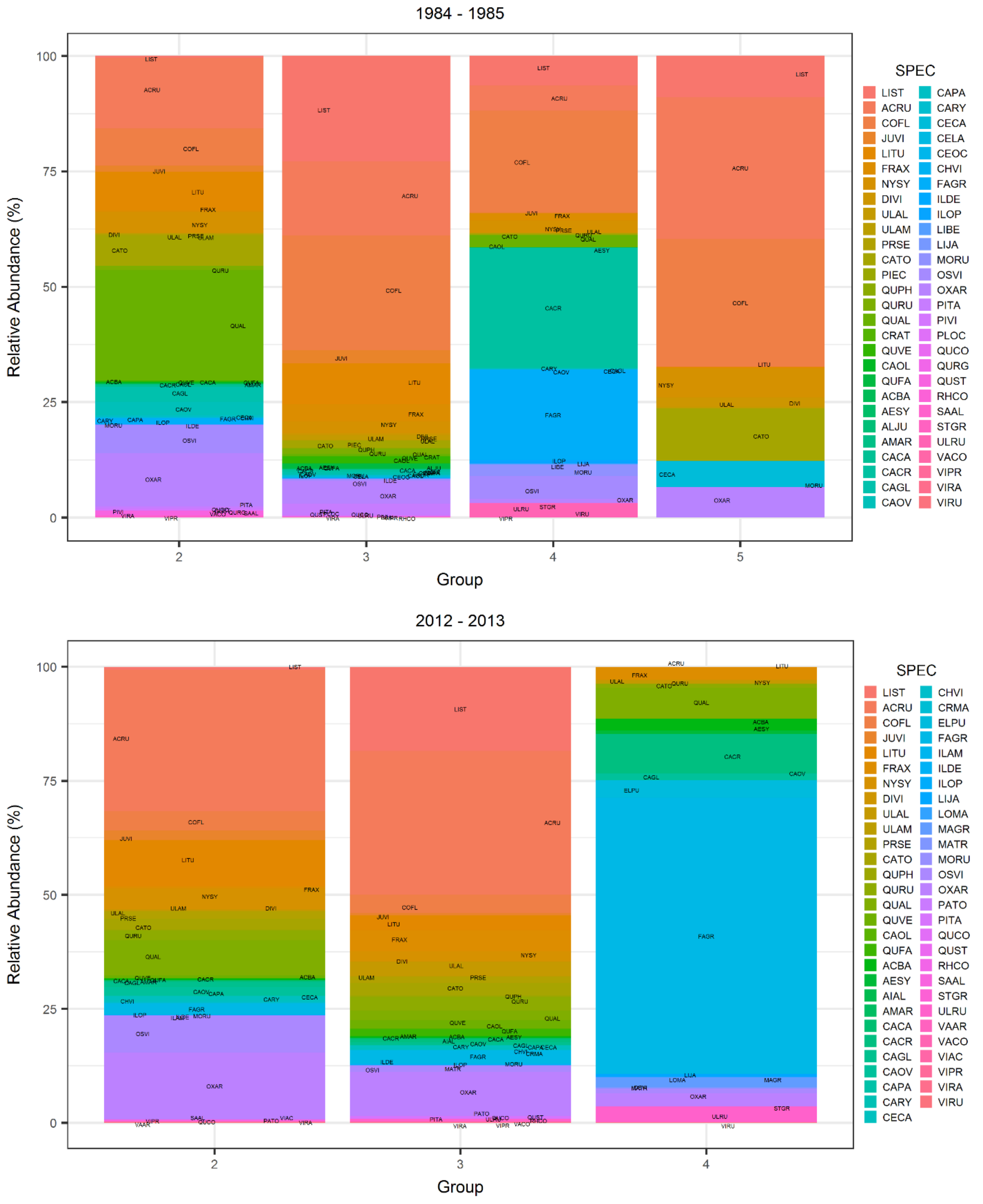

Figure 6.29. Comparing relative abundances of prominent subcanopy species between 1980s and 2010s for plot-types designated by cluster analyses using subcanopy trees. Groups roughly equate to 2 = upland hardwood stands; 3 = successional pine stands; 4 = bottomland hardwood plots; 5 = stands with high abundance of *D. virginiana*.

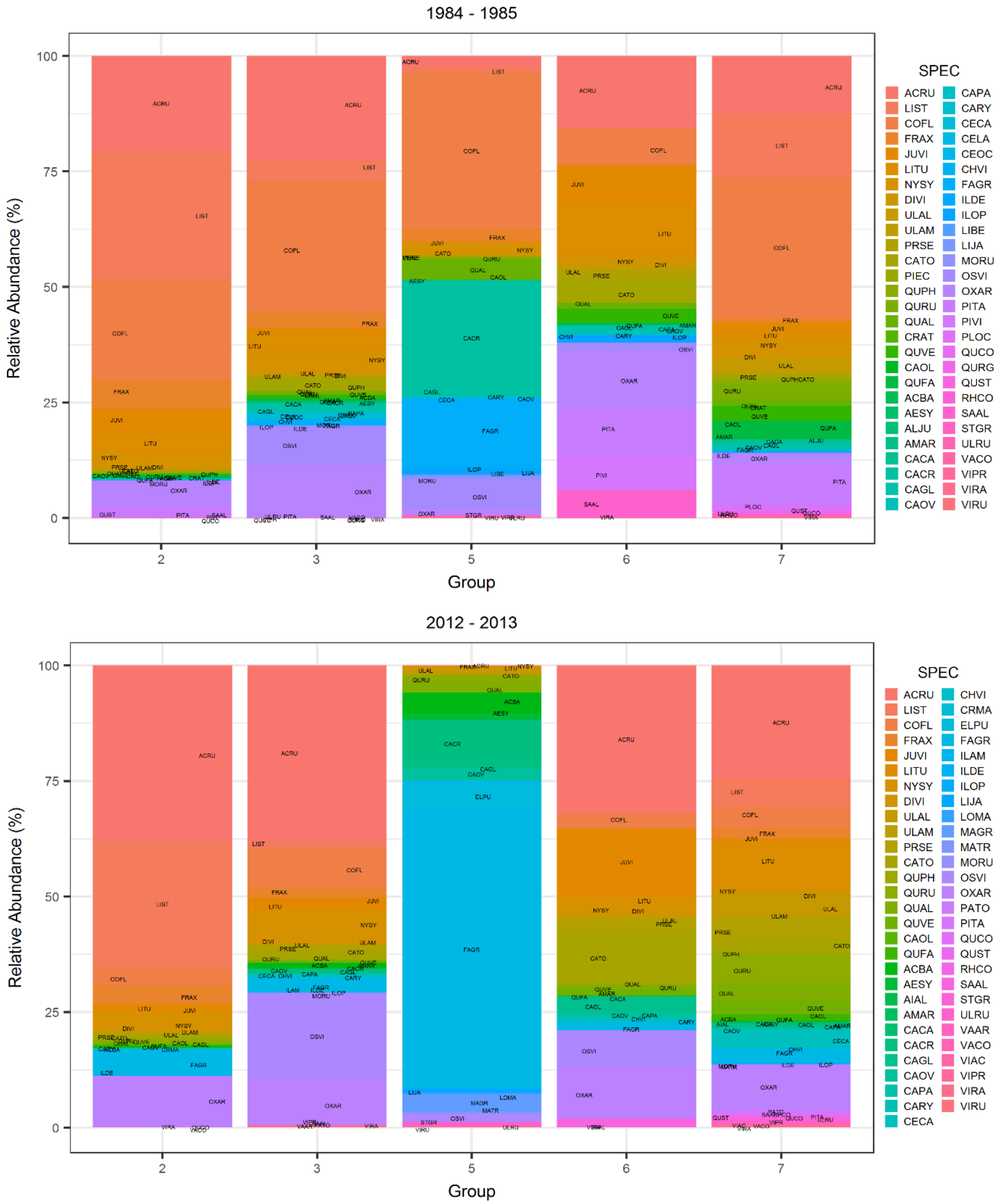

Figure 6.30. Comparing relative abundances of small-stem species between 1980s & 2010s. Groups were designated by cluster analysis using sub-10 cm DBH stems. Groups roughly equate to: 2 = basic/rich; 3 = acidic; 5 = mesic bottomland; 6 = sub-xeric oak; 7 = mesic/mixed oak. Missing group numbers were not present in either sampling period.

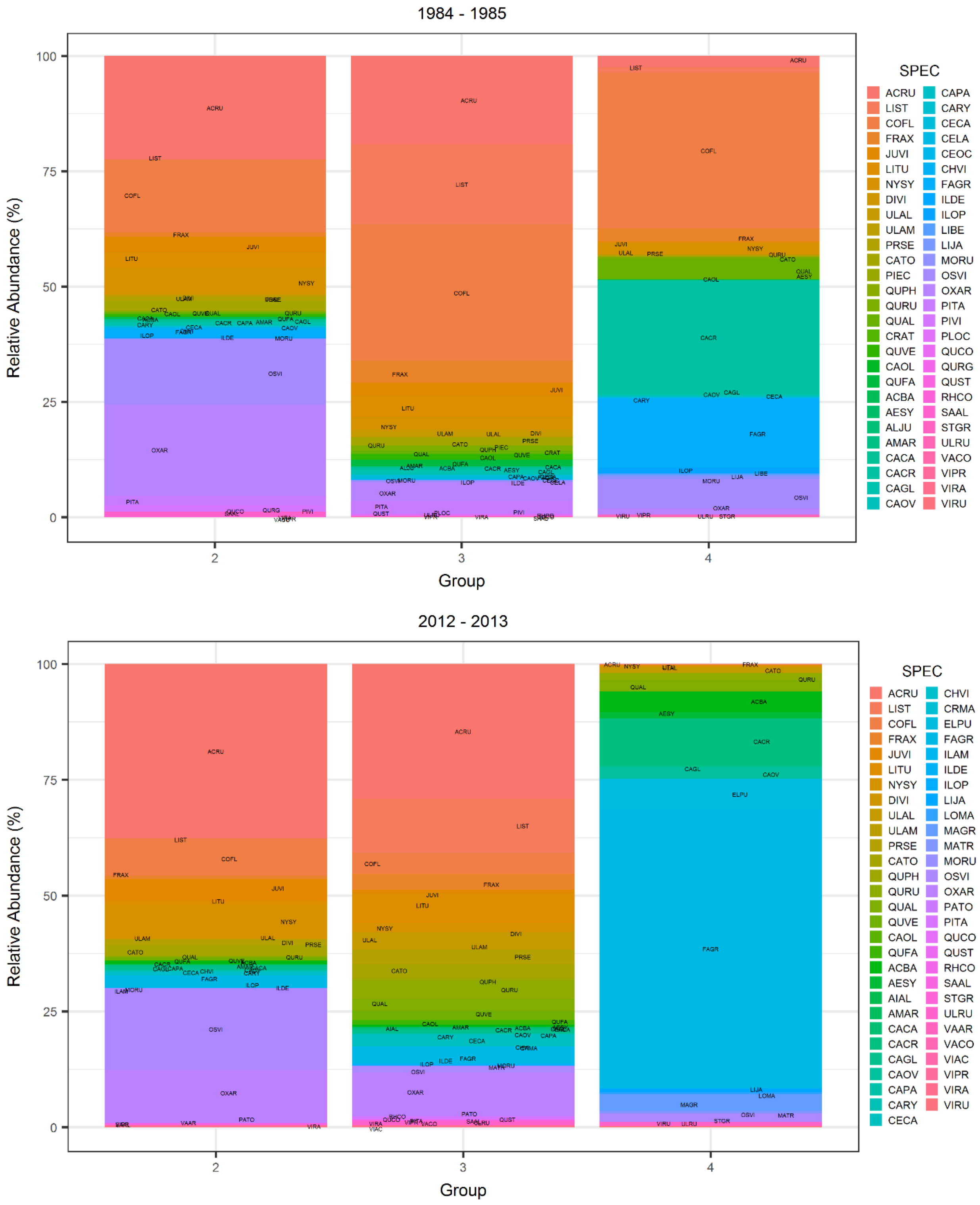

Figure 6.31. Comparing relative abundances of prominent small-stem species between 1980s and 2010s. Groups were designated by real-world plot-type assignments. Groups are: 2 = upland hardwood stands; 3 = successional pine stands; 4 = bottomland hardwood stands.

Environmental correlations

After removing redundant and correlated site-level variables, correlation analyses were performed to determine variable loadings on NMDS axes for the ordination using unpartitioned PSP data. Site variables were much more correlated with NMDS 1 compared to NMDS 2, which is to be expected given the varimax rotation used on the NMDS ordination (Mather 1976). Axis correlations are listed in Table 6.1 and can be visualized as a biplot in Figure 6.32. NMDS 1 was most positively correlated with sulfur, % clay content, potassium, pH, and nitrogen; the axis was most negatively correlated with sodium, bulk density, iron, boron, phosphorous, distance to water, zinc, total exchange capacity, calcium, potential solar radiation, and copper. Sodium, bulk density, iron, boron, phosphorous, zinc, and copper were all positively correlated with NMDS 2, whereas sulfur, potassium, pH, and manganese were negatively correlated with the second NMDS axis. Correlation analyses for the small-stem ordination showed similar, though slightly more variable results as the correlations for the full-data analyses (axis correlations for the small-stem ordination are listed in Table 6.2 and can be visualized as a biplot in Figure 6.33). In both analyses, no single variable had a correlation greater than 30% for either axis and the most correlated variables tended to be secondary nutrients (e.g., sulfur, iron, boron, zinc, etc.).

Specific correlation trends were inspected by observing median trends in the per-plot raw environmental data (analyses not shown). Soil texture trends were driven by high clay content (and associated low sand content) in upland hardwood stands and the reverse trend in numerous successional plots (especially PSPs 12 – 23), which also reflects agricultural soil preferences. However, soil texture in bottomland plots was split: PSP 44 more closely matched successional plots, whereas PSP 43 was more similar to upland sites. Soil pH trends were driven primarily by PSP 44 (bottom right of ordination), which was the only plot with recorded pH greater than 6.0.

The increasing nitrogen vector toward hardwood plots was a result of PSP 10 having the highest nitrogen level across plots and all other upland sites having nitrogen levels above the median concentration. These high nitrogen levels were likely owing to the upland hardwood plot's successional ages and advanced organic matter accumulation. Bottomland hardwood sites had relatively low soil nitrogen, which might be due to the occasional flooding that occurs in these plots and the resulting denuding of topsoil. Higher bulk density of soils in successional pine plots could be due to compaction (Murphy et al. 2006) from their agricultural history. Soil compaction likely led to reduced leaching ability, so nutrients that accumulated due to irrigation practices (i.e., sodium) and fertilization practices (e.g., phosphorus and boron) have lingered in higher concentrations in successional plot soils.

Categorical topographic position centroids were also added to the biplot to determine impacts of site "wetness" on community trends, and they had a goodness of fit of $r^2 = 0.0176$ (p-value = 0.018). These centroids showed that the categorical positions were weighted relatively centrally in the NMDS plot except for position 1 that was positively skewed toward greater NMDS 1 and, to a lesser degree, position 5, which likewise was skewed toward established hardwood-dominated samples. The skew of position 5 is likely owing to PSP 37 (the only plot with a topographic position of 5; ridgetop), and the skew of position 1 is driven by low topographic positions of PSP 43 and 44 represented in the blue sample points, which are the only plots to be described with a topographic position of 1 (valley bottom). The random order placement of position centroids in general suggests that there is no monotonic vertical- or horizontal-axis correlation due to topographic position across samples. However, the skew of both position 1 and 5 toward hardwood samples (i.e., toward a positive NMDS 1) indicates that hardwood plots are located in more extreme topographical positions than successional plots overall. An additional metric, the difference in elevation between each plot and the nearest body of water, did not prove to be significantly correlated with either axis, which provides further evidence that topographic position is likely not driving successional plot community trends.

Overall, the stronger variable loadings on axis 1 compared to axis 2 suggests that the largest environmental variation between plots is between successional pine stands and hardwoods plots. Additionally, most of the variables that are significantly correlated with NMDS 2 actually have between-plot-type relationships that are opposite to their correlation directions when comparing just median sample values between plot types. The NMDS 2 correlations, therefore, are likely just a result of the greater number of samples from successional plots outweighing actual plot-type differences between hardwood stand types. Overall, due to the limited loadings along the vertical NMDS axis, it is clear that additional unmeasured environmental characteristics could be driving observed successional trends. However, when time is used as a correlate, it explains over 51% of the variation in NMDS1. This strong positive correlation with NMDS 1 suggests that succession is a stronger predictor of compositional trends in successional plots than variations in soil characteristics.

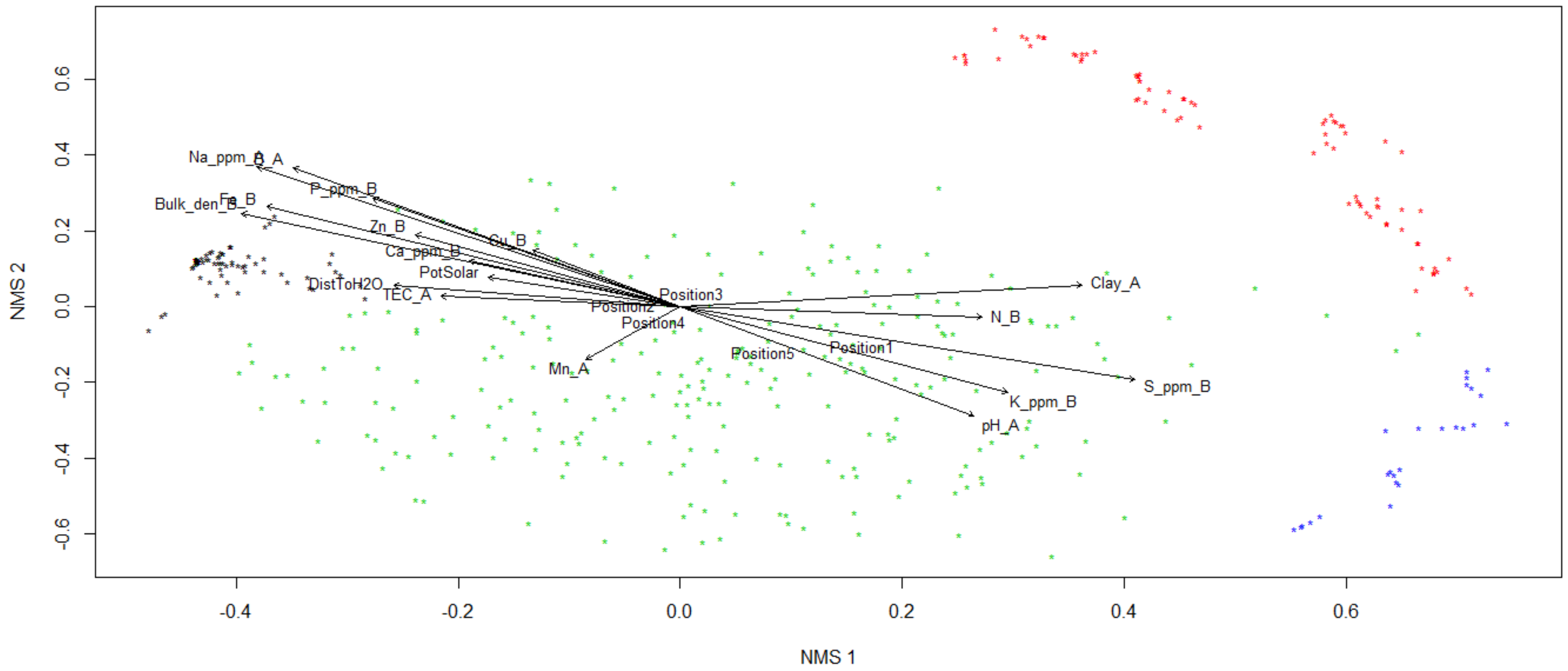

Figure 6.32. Unpartitioned-data NMDS ordination biplot showing correlation vectors for environmental variables. The length of the arrows indicated the magnitude of correlation of each variable with the NMDS axes, whereas the angle of the arrows indicates the relative weighting of correlation with either NMDS axis 1 or NMDS axis 2. Arrow direction indicates whether each environmental variable is positively (up or right) or negatively (down or left) correlated with the ordination axes. Variables include sulfur (S in parts per million; ppm), sodium (Na), bulk density (Bulk_den), iron (Fe), boron (B), % clay content (Clay), potassium (K), phosphorus (P), pH, nitrogen (N), distance to water (DistToH2O), zinc (Zn), total exchange capacity (TEC), calcium (Ca), potential solar radiation (PotSolar), copper (Cu), and manganese (Mn). Categorical centroids for topographic position ("Position" 1 – 5) were also added to the analyses.

Table 6.1. Pearson correlations between environmental variables and both the first (NMDS1) and second (NMDS2) axes of the unpartitioned-data ordination. Only environmental variables that were significantly correlated with unpartitioned-data ordination axes are shown. "_A" and "_B" refer to variables measured from A Horizon and B Horizon soil samples, respectively. Variables include sulfur (S in parts per million; ppm), sodium (Na), bulk density (Bulk_den), iron (Fe), boron (B), % clay content (Clay), potassium (K), phosphorus (P), pH, nitrogen (N), distance to water (DistToH2O), zinc (Zn), total exchange capacity (TEC), calcium (Ca), potential solar radiation (PotSolar), copper (Cu), and manganese (Mn).

Variable	NMDS1	NMDS2
S_ppm_B	0.286	-0.107
Na_ppm_A	-0.283	0.219
Bulk_den_B	-0.281	0.139
Fe_B	-0.268	0.152
B_A	-0.261	0.219
Clay_A	0.245	0
K_ppm_B	0.214	-0.131
P_ppm_B	-0.207	0.170
pH_A	0.199	-0.173
N_B	0.184	0
DistToH2O	-0.175	0
Zn_B	-0.173	0.110
TEC_A	-0.145	0
Ca_ppm_B	-0.135	0
PotSolar	-0.120	0
Cu_B	-0.100	0.090
Mn_A	0	-0.088

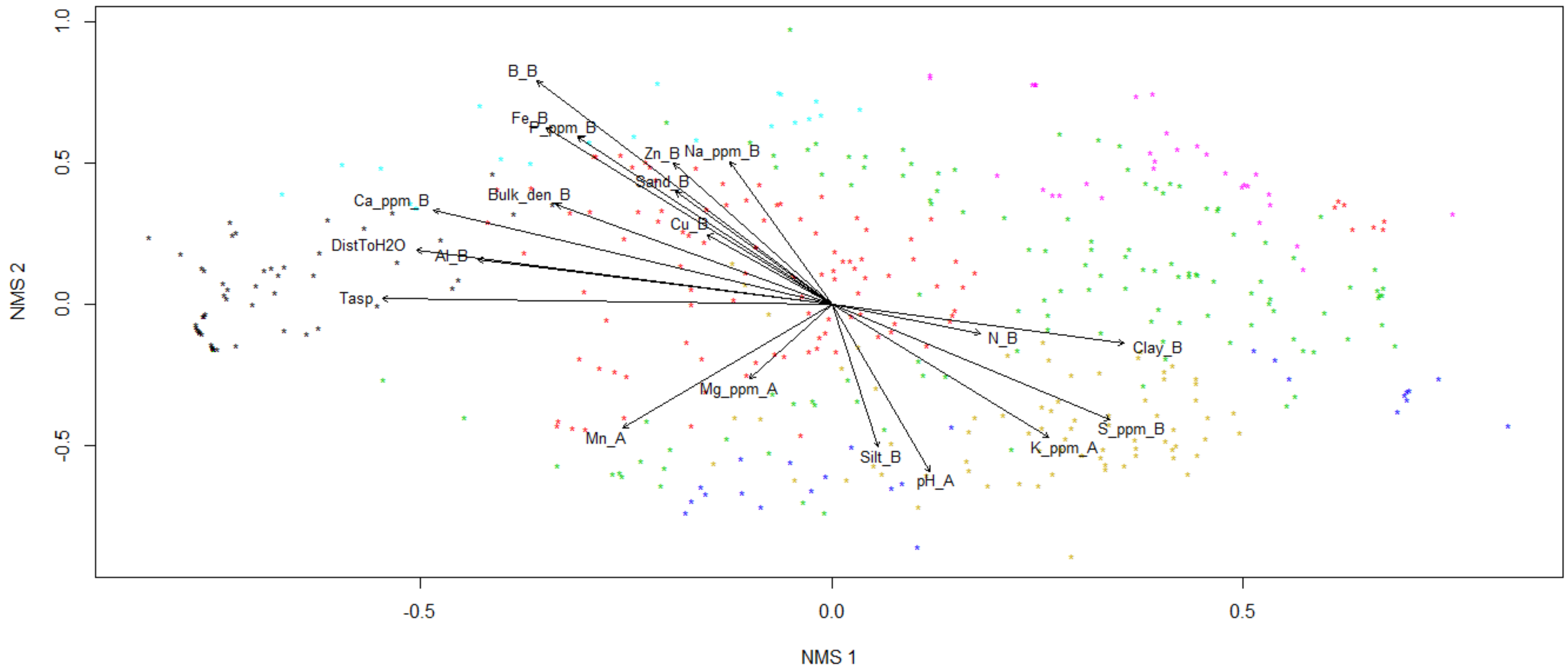

Figure 6.33. Small-stem-data NMDS ordination biplot showing correlation vectors for environmental variables. The length of the arrows indicated the magnitude of correlation of each variable with the NMDS axes, whereas the angle of the arrows indicates the relative weighting of correlation with either NMDS axis 1 or NMDS axis 2. Arrow direction indicates whether each environmental variable is positively (up or right) or negatively (down or left) correlated with the ordination axes. Variables include boron (B), iron (Fe), pH, phosphorus (P), transformed aspect (Tasp), distance to water (DistToH2O), % silt content (Silt), calcium (Ca), sodium (Na), zinc (Zn), potassium (K), aluminum (Al), manganese (Mn), % sand content (Sand), sulfur (S), % clay content (Clay), bulk density (Bulk_den), magnesium (Mg), copper (Cu), and nitrogen (N).

Table 6.2. Pearson correlations between environmental variables and both the first (NMDS1) and second (NMDS2) axes of the small-stem-data ordination. Only environmental variables that were significantly correlated with unpartitioned-data ordination axes are shown. The table was split to fit onto a single page. "_A" and "_B" refer to variables measured from A Horizon and B Horizon soil samples, respectively. Variables include boron (B), iron (Fe), pH, phosphorus (P), transformed aspect (Tasp), distance to water (DistToH2O), % silt content (Silt), calcium (Ca), sodium (Na), zinc (Zn), potassium (K), aluminum (Al), manganese (Mn), % sand content (Sand), sulfur (S), % clay content (Clay), bulk density (Bulk_den), magnesium (Mg), copper (Cu), and nitrogen (N).

Variable	NMDS1	NMDS2
B_B	-0.180	0.349
Fe_B	-0.173	0.273
pH_A	0	-0.266
P_ppm_B	-0.154	0.260
Tasp	-0.247	0
DistToH2O	-0.232	0.077
Silt_B	0	-0.228
Ca_ppm_B	-0.228	0.137
Na_ppm_B	0	0.227
Zn_B	-0.097	0.221
K_ppm_A	0.131	-0.206
Al_B	-0.197	0
Mn_A	-0.126	-0.191
Sand_B	-0.095	0.176
S_ppm_B	0.164	-0.174
Clay_B	0.163	0
Bulk_den_B	-0.162	0.149
Mg_ppm_A	0	-0.117
Cu_B	0	0.108
N_B	0.084	0

Discussion

Compositional trends

Successional pine stands were expected to experience decreasing *Pinus taeda* densities in understory (due to shading out) and both mid-story and canopy strata (due to thinning). The successional trajectories and diameter distributions for successional plots match those expectations (Figures 6.11, 6.12 and 6.17). The dying out of canopy *P. taeda* indicates that these plots are each progressing through the transition stage of succession, which is corroborated by increasing relative abundances of hardwood species (Figure 6.27) and an increase in hardwood indicator species in these plots (Tables A5.1).

Non-pine species composition of successional plots initially began to reflect components of upland hardwood communities, especially pioneer and seral species found to persist in upland hardwood stands. This is evident from mid-study abundances of *Cornus florida*, *Juniperus virginiana*, *Nyssa sylvatica*, *Carya ovata*, *Carya carolinae-septentrionalis*, *Oxydendrum arboreum*, and *Diospyros virginiana* in understory strata (Figures 6.14, 6.18 and 6.19) and larger stems of some of these species (e.g., *O. arboreum* and *C. florida*; Figures 6.13 and 6.15) present in more recent sampling periods that drove successional trajectories toward upland sample communities. However, abundances of each of these species declined dramatically in lower strata and only *O. arboreum* remains abundant in the canopy of select successional plots. Losses of these species began around mid-century and continued in earnest through the 1990s; most of these species continue to become less common in successional plots. The losses of these species in the first half-century of the study sometimes resulted in stark trajectory changes following Hurricane Hazel in 1954 (PSPs 6 and 7; Figure 6.34), but usually these losses coincided with the start of a gradual, mid-century shift in direction of successional trajectories in the small-stem stratum (Figure 6.9 and Figure 6.34) away from upland hardwood plots. This shift was likely accentuated by near-simultaneous increases of species more associated with bottomland plots (*Liquidambar styraciflua*, *Fraxinus spp.*, *Ulmus americana*, *Acer floridanum*, and more recently *Fagus grandifolia*) in these sites, which drew communities toward bottomland hardwood stands. Finally, most successional plot trajectories experienced large, reversing trends following Hurricane Fran damage in 1996 (Figure 6.34), which have thus far changed the direction of composition change in these plots (typically farther away from upland community types; Figure 6.8; similar to Woods 2004 and White et al. 2015). Closer examination revealed that continued loss of *C. florida* is a major factor resulting in this shift.

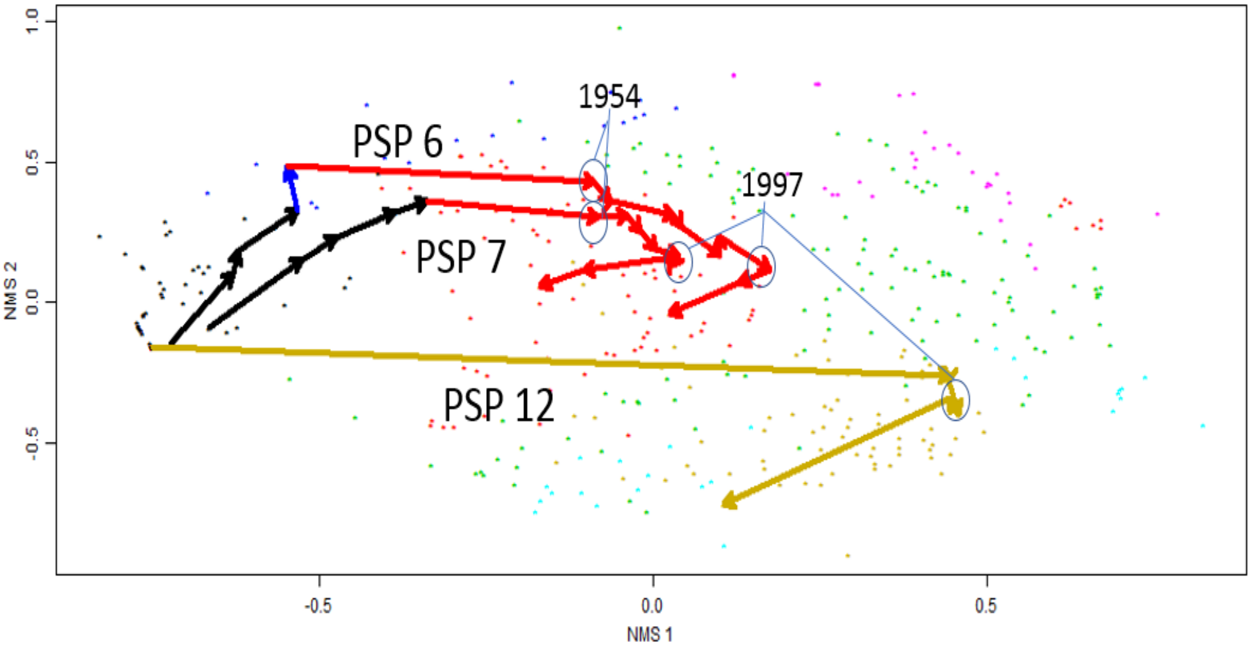

Figure 6.34. Successional trajectories of sample PSPs to demonstrate how gradual changes in composition began occurring in the 1960s (i.e., following 1954) and how hurricane impacts (Hazel in 1954 and Fran in 1996) accelerated compositional change. The plot shows an NMDS ordination of small-stem trees for all PSP data overlaid by successional vectors for PSPs 6, 7, and 12.

Cornus florida, which is found in both old-growth understories and as an important component of secondary growth forests (Orwig & Abrams 1994, Goebel & Hix 1996), has declined throughout eastern forests (Hiers & Evans 1997, Jenkins & White 2002, Pierce et al. 2008, Suchecki & Gibson 2008) primarily as a result of anthracnose caused by *Discula destructiva* that arrived in the United States in the 1970s (Hibben & Daughtrey 1988). Like in many previous studies, *C. florida* has declined in all plot types in Duke Forest and Hill Forest. Loss of *C. florida* examined by other studies has been associated with increases in *A. rubrum, L. tulipifera, O. virginiana*, and *Sassafras albidum* stems and losses in *Q. alba* and both *Quercus* and *Carya* seedlings in general (Suchecki & Gibson 2008; Pierce et al. 2008). While the upland hardwood sites in the present study have followed these additional trends, successional plots only experienced sizeable increases in *Acer rubrum* (and to a lesser degree *L. tulipifera*) with only a few successional plots having experienced any significant growth of oaks or hickories at any level. Losses of *N. sylvatica* observed in the Duke Forest data contrast trends seen elsewhere in eastern forests (Hiers & Evans 1997 and Martin 1989), while the persistence of *O. arboreum* mirrors climate-influenced predictions made by Iverson & Prasad (1998).

Successional plots, overall, appear to have begun accumulating greater abundances of early-establishment hardwoods such as *L. styraciflua, L. tulipifera, A. rubrum*, and *O. arboreum* (Peet & Christensen 1980), but the successional plots contain few putative upland climax species, with oaks and hickories being all but absent in many successional plots. Due to the low-shade tolerance of oak seedlings (Larsen & Johnson 1998), failure of these seedlings to establish in these plots suggests that they will not play a major role in these communities without additional disturbance (Rentch et al. 2003) and instead will be substituted by more shade-tolerant species (similar to Christensen 1977, Lorimer 1984, Nowacki et al. 1990, Abrams & Downs

1990). Although this low oak abundance could potentially be due to the early stages of transition of many of these plots, oak abundance in successional plots does not seem to be related to stand age or successional progress. Instead, greater abundance of oaks in plots with select characteristics suggest that oaks have otherwise lost a competitive edge in many stands (likely due to removal of fire; Abrams & Nowacki 1992 and Shumway et al. 2001). Specifically, an exception to the paucity of oaks includes a cluster of 10 geographically-close PSPs on a sandy, relatively-acidic slope that have experienced recent increases in small-stemmed *Q. rubra, Q. falcata, Q. velutina*, and to a lesser and more recent extent *Q. alba* (Figures 6.24 and 6.30). These plots contain the sandiest soils in the dataset, which might explain the growth of these oak species (especially *Q. velutina*; Gysel 1957) that are common on well-drained sandy loams. Perhaps the lower water retention (Brady & Weil 1996) of the exceptionally sandy soils in these plots restrict more mesic, faster-growing, shade-tolerant species from competing as strongly against more dry-tolerant oaks (Abrams 1990). This hypothesis is somewhat supported given relatively lower abundances of *A. rubrum*, *L. styraciflua*, and *Fraxinus* species in these plots compared to successional plots as a whole. Further, this trend reflects contrasting dynamics of these suites of species as seen by McDonald et al. (2003) and supports McDonald et al.'s (2002) observation that *A. rubra* had the slowest rate of increase on sandy and acidic soils. *Carya tomentosa* has likewise begun appearing in the small-stem stratum of these plots and others with large canopy damage following Hurricane Fran (e.g., PSP 39, 49 and 51), and *C. ovata* has persisted in PSP 26 and recently entered the small-stem stratum of additional plots (e.g., PSPs 14, 22, and 51). These data show that, unlike oaks, the abundance of some species of hickories have increased as plot successional stage (i.e., advanced transition from pines) has advanced.

Hardwood stands have also experienced shifts in community characteristics, though typically to a much smaller degree than transitioning pine stands and more restricted to smaller tree sizes. Observed dynamics could be partially explained by the fact that the upland hardwood plots in the study appear to still be maturing from prior natural disturbance or wood-harvesting (see chapter 5; also note the abundance of species associated with disturbance such as *J. virginiana*). However, similar to previous reports (Christensen 1977, Lorimer 1984, Suchecki & Gibson 2008) recruitment of the putative climax oak species (especially *Q. alba*) has decreased throughout upland plots across this study (see Figure 6.25). However, unlike the oaks, multiple hickory species (e.g., *C. tomentosa* and *C. glabra*) have increased in small-stem abundance, possibly owing to their young stems' greater tolerance for shade (e.g., see Smalley 1990).

Acer rubrum has increased dramatically across both successional plots and upland hardwood plots (Figures 6.24, 6.25), especially in plot subcanopies (Figure 6.29 and 6.30). The concurrent decline of oaks and rise of *A. rubrum* reflect findings found throughout the literature regarding increased *A. rubrum* abundance in eastern forests (Abrams 1998, 2003, Abrams & Downs 1990, Abrams & Nowacki 1992, Shumway et al. 2001, McDonald et al. 2002, 2003, Nowacki & Abrams 2008, Pontius et al. 2016). Further, *A. rubrum* increased most in hardwood stands following Hurricane Fran. The hurricane appeared to accelerate rate of *A. rubrum* increase similar to White et al. (2015) and similar to patterns observed from human-mediated disturbance (e.g., logging impacts; Abrams & Downs 1990, Abrams & Nowacki 1992). Although to a lesser degree and more constrained to smaller size-classes (except in PSP 124), *Fagus grandifolia* likewise increased in abundance across successional and upland hardwood plots despite these plots not being especially mesic in nature. Overall, the decrease in oak and hickory abundance and increase in *A. rubrum* and *F. grandifolia* abundance across non-bottomland plots suggests that the Duke Forest is experiencing mesophication as predicted by Nowacki and Abrams (2008) for North American temperate forests under fire suppression and as shown by additional work in the NC Piedmont (Christensen 1977, McDonald et al. 2002, Israel 2011).

Environmental drivers

Soil characteristics showed no convincing trends relating successional trajectories of successional plots to upland or bottomland hardwood stands. Although a number of soil characteristics were correlated with ordination axes, most were relatively low correlations and seemed to reflect differences in successional plots from hardwood stands instead of similarities of successional stands to one type of hardwood stand or the other. One exception was soil pH, which was positively correlated with the NMDS axis demonstrating the difference in hardwood plots (as was shown by Christensen & Peet 1984). However, it seems apparent based on the topographic positions and community types of the hardwood plots that these communities are along a moisture gradient. Unfortunately, water availability was not a directly recorded metric for these plots, so no formal examination could be made. Regardless, categorical topographic position centroids indicated that both types of hardwood plots exist at more extreme topographic positions than the successional plots, which suggests that the successional plots would be intermediate in this moisture gradient. Future work could compare a topographic moisture index for all plots to quantify this gradient more thoroughly.

Perhaps of greater interest is whether external factors such as increased deer herbivory, human land-use, or changing climate conditions have had an impact on the community dynamics described in this chapter. Local weather station data from nearby the Duke Forest (unpublished analyses; data from State Climate Office of North Carolina) does indicate that the last 60 years have been marked by an increase in temperature and wetness (based on the Standardized

Precipitation-Evapotranspiration Index, or SPEI; Vicente-Serrano et al. 2010), and national data suggest that atmospheric CO_2 and nitrogen deposition have significantly risen this past century (Huang et al. 1999, Houghton et al. 2001, Keeling & Whorf 2002). Changes in climatic conditions have been shown to impact species differentially (e.g., Lindroth et al. 1993, Battipaglia et al. 2013, Boisvenue & Running 2006), and gradually increasing levels of atmospheric CO_2 and soil nitrogen have also been shown to impact temperate plant communities (e.g., Rainey et al. 1999, Gilliam 2006, Bobbink et al. 2010, Peters et al. 2013). Additionally, herbivore browse has been on the rise as *Odocoileus virginianus* (white-tailed deer) densities have quadrupled since 1980 throughout North Carolina (unpublished data from the NC Wildlife Resources Commission; see Osborne 1993 for published estimates from 20 years ago), and deer populations have increased regionally to 12 – 20 deer per km^2 (unpublished data from the NC Wildlife Resources Commission and an internal Duke Forest report). As with the changing climate variables, deer populations have also been shown to differentially impact species, including both maples and oaks (see Russell et al. 2001 for examples). Observed deer impacts on these two species are not consistent and highly variable in both time and space, however, with evidence for no impact (Inouye et al. 1994), reduced regeneration (Rossell et al. 2007), reductions in seedlings (Stange & Shea 1998) and saplings (Healy 1997), and reduced rates of height growth (Inuoye et al. 1994) in oaks and both increased mortality (though, variable depending on season of browse; Canham et al. 1994) and underrepresentation of saplings (Marquis 1981, Trumbull et al. 1989, Tilghman 1989) of *A. rubrum*. The gradual change of the listed climatic, human-initiated, and deer-related variables could help explain the otherwise unexplained gradual changes in community composition experienced by successional plots starting mid-century prior to accelerated change brought on by Hurricane Fran. Shifts in competitive abilities due to a backdrop of century-long fire exclusion (e.g., Shumway et al. 2001) are also potentially occurring. Unfortunately, all these variables are highly correlated with time, which, unlike the soil variables already discussed, explains more than 50% of the compositional trends in Duke Forest. As such, this project does not have the required scope to disentangle observed patterns and formally conclude to what degree these changing conditions explain the observed changes in forest dynamics.

Although formal conclusions about environmental drivers cannot be made, observation of the long-term compositional trends made possible by the unique permanent sample data in the Duke Forest and the Hill Forest hint toward the potential importance of some drivers. For example, greater changes and greater degrees of convergence in composition were observed in smaller-stem strata compared to canopy stems throughout the study, which suggests that the drivers of these changes began after canopy individuals were established and that the drivers continue to impact these forests through present time. Additionally, significantly less *Acer rubrum* and *Fagus grandifolia* and greater relative abundance of *Quercus alba* existed in the subcanopies of upland hardwood stands in the 1940s (see Figure 6.35) compared to today, suggesting that competitive differences between these suites of species had not yet (or only relatively recently beforehand) begun shifting toward contemporary conditions (see Figure 6.29). This suggests that fire exclusion, which was fairly ubiquitous by 1900, very well may have set the stage for compositional shifts in these forests as suggested by Abrams & Nowacki (1992) and Shumway et al. (2001). Alternatively, low intensity grazing of domestic stock could have substituted for fire throughout the 1800s. The wetter conditions experienced by the region since the mid-20th-century likely have further enabled this transition to occur.

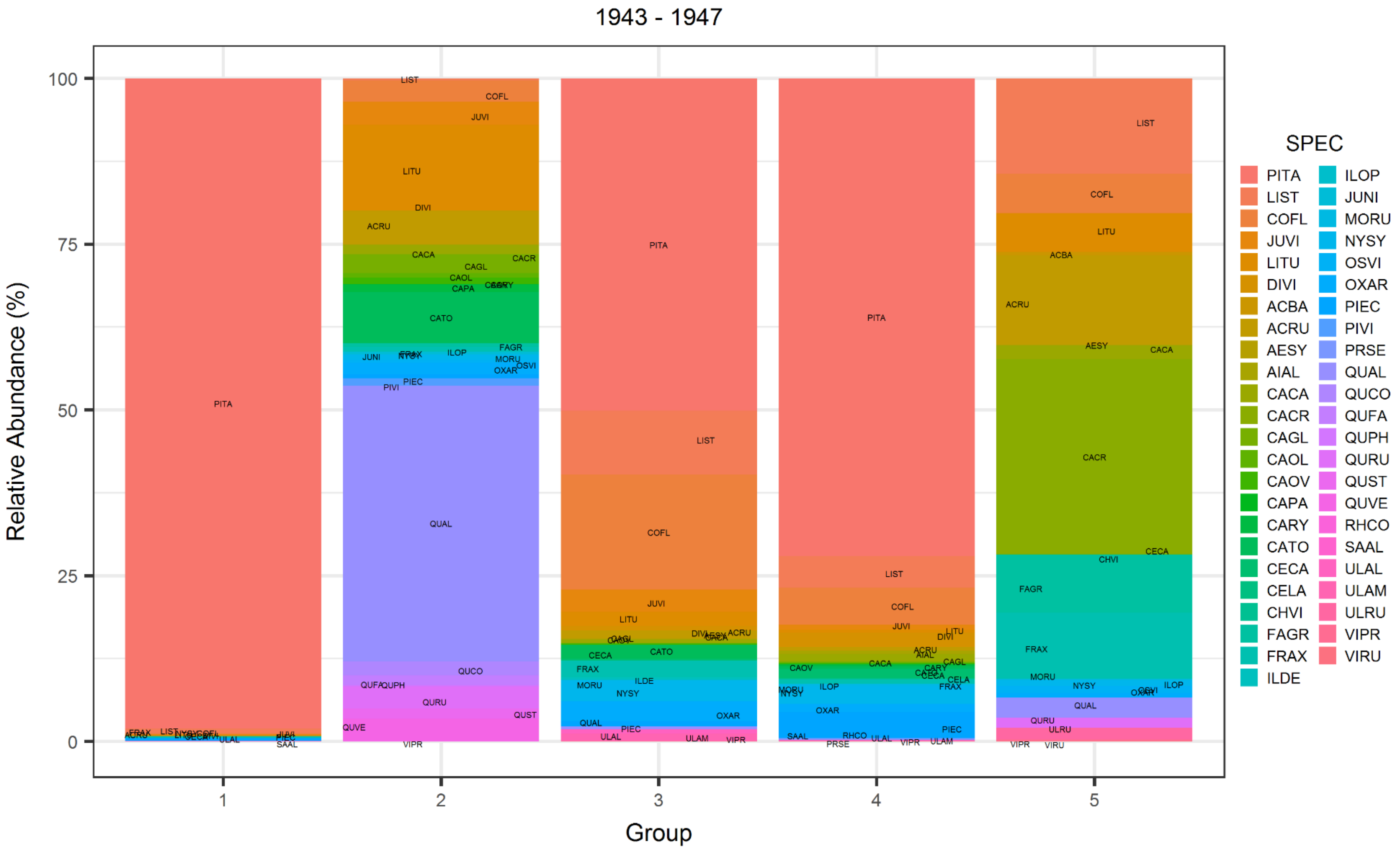

Figure 6.35. Relative abundances of prominent subcanopy species in the 1940s for plot-types designated by cluster analyses using subcanopy trees. Groups roughly equate to: 1 = near-monoculture of *Pinus taeda*; 2 = upland hardwood stands; 3 = successional pine stands; 4 = bottomland hardwood plots; 5 = stands with high abundance of *D. virginiana*.

The near-absence of *Oxydendrum arboreum* in upland hardwood sites in the 1940s (Figure 6.35) compared to the much greater relative abundance of *O. arboreum* in these sites by the 1980s (Figure 6.29) potentially suggests that human land-use practices were also directly impacting community composition. *O. arboreum*, which typically develops a slender, crooked stem as it seeks canopy gaps, has little value as a timber species and was likely actively removed from these forests to promote growth of more robust timber species (e.g., oaks and hickories) or for the use as tool handles when still young and straight. The selective management of these forests ended before plot inception, which likely has enabled *O. arboreum* stems to grow more actively to achieve contemporary abundance levels.

Anecdotal observation from the current study's plots and direct quantification in nearby permanent plots (Christensen 1977, Taverna 2005, Israel 2011) reveals very few herbs growing in the understory of the Duke Forest or surrounding forests. Conversely, nitrogen deposition would be expected to increase herb cover (Gilliam 2006; mostly of select species). Failure to see this trend (and in fact, evidence of the opposite observation through time) – though not telling of the impacts of nitrogen deposition – demonstrates the magnitude of impact that elevated deer herbivory has had on these forests. White-tailed deer have additionally been found to decrease abundance of various oak and hickory seedlings (Rossell et al. 2005) as has been seen in the Duke Forest data reported here, adding further support for the importance of deer for novel dynamics. However, deer have also been found to decrease abundance of species that have increased in abundance in the Duke Forest data (e.g., *A. rubrum* and *P. serotina*; Rossell et al. 2005), suggesting further complication to these trends. Israel (2011), however, showed a significant decline in maples and beeches in regional forest herb-layers, suggesting that the observed increases in these species are due to a shift in competitional ability to reach larger size classes (perhaps owing to the fire exclusion already mentioned). Similar complication is demonstrated regarding potential impacts of carbon fertilization from elevated atmospheric CO_2. Although substantial increases of *Ulmus alata* in the understory of successional plots in the Duke Forest seemingly corroborates findings by Mohan et al. (2007) that showed *U. alata* responded with the greatest increase in growth rates to elevated CO_2 conditions, declines in *Q. alba* contradict Mohan et al.'s (2007) results for seedlings of that species. These findings and the trends mentioned in the preceding paragraphs support the notion that multiple drivers are concurrently changing the composition of these Piedmont forests, and thus demonstrates the need for future successional research to consider many drivers of change simultaneously. Permanent plot studies such as this are necessary to parse out the resulting trends from these various interacting drivers that are clearly playing out over multiple decades.

Conclusion

Community dynamics in NC Piedmont forests are complex and changing, and the changes in Duke Forest (and Hill Forest) continue (see Abrams 1998, Taverna 2005, and Israel 2011) to call into question the concept of stable climax communities in eastern forests. Clearly, the assumptions of Billings (1938), Oosting (1942), and others regarding successional trajectories of Piedmont forests do not represent current trends. Species associated with upland sites have been largely replaced by more mesic species in successional old-field plots. The relatively later-stage hardwood sites have likewise shifted in community structure that mirrors that of successional plots, including declines in oak and hickory abundance (especially in smaller size classes) and increases in *Acer rubrum* and *Fagus grandifolia* abundance as seen throughout temperate forests of the eastern United States (e.g., Nowacki & Abrams 2008). The seemingly ubiquitous changes in forest communities between forest types suggests that either changed land-use practices (e.g., decades of fire suppression only now made apparent by accelerated compositional change due to major wind disturbance) or novel conditions (perhaps changing climate, fertilization effects from increasing atmospheric CO_2 or nitrogen deposition, or increased deer herbivory) are driving region-wide changes shared by plots. Interestingly, small-stem strata across forest types appear to be converging to a greater extant relative to canopy stems, which suggests that the novel changes observed are being driven by characteristics that outweigh, at least to a degree, between-plot edaphic variation. The greater compositional shifts experienced by small-stemmed plants and greater convergence of species composition between plot types in the small-stem strata compared to canopy individuals also suggest that the most prominent drivers of novel compositional change began occurring after canopy establishment and continue to be driving trends in the forest system.

Although disease can explain some species trends (e.g., decline of *Cornus florida*) and hurricanes demonstrably accelerated community shifts, a large portion of the novel variability and changed successional trajectories remains unexplained. It seems likely, however, that fire exclusion followed by significant increases in herbivory, regional mean temperatures, wetness, atmospheric CO_2, and nitrogen deposition could all at least in part be driving some of these trends. Results from this study also indicate that predicted increases in severe weather systems likely will continue to have a dramatic impact on eastern forest dynamics. Overall, a better understanding of these novel changes is required to parse out drivers of forest change, which will benefit both global change model predictions and forest stewardship and management.

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APPENDIX A1: SPECIES CODE DEFINITIONS

Table A1.1. Species codes (“SPEC”) and associated species names.

SPEC	Scientific Name	Common Name
ACBA	*Acer floridanum*	Southern Sugar Maple
ACER	*Acer sp.*	Maple
ACRU	*Acer rubrum*	Red Maple
AESY	*Aesculus sylvatica*	Painted Buckeye
AIAL	*Ailanthus altissima*	Tree Of Heaven
ALJU	*Albizia julibrissin*	Silktree
AMAR	*Amelanchier arborea*	Common Serviceberry
BENI	*Betula nigra*	River Birch
CACA	*Carya carolinae-septentrionalis*	Southern Shagbark Hickory
CACO	*Carya cordiformis*	Bitternut Hickory
CACR	*Carpinus caroliniana*	American Hornbeam
CAFL	*Calycanthus floridus*	Eastern Sweetshrub
CAGL	*Carya glabra*	Pignut Hickory
CAOL	*Carya ovalis*	Red Hickory
CAOV	*Carya ovata*	Shagbark Hickory
CAPA	*Carya pallida*	Sand Hickory
CARY	*Carya sp.*	Hickory
CATO	*Carya tomentosa*	Mockernut Hickory
CECA	*Cercis canadensis var. canadensis*	Eastern Redbud

CELA	*Celtis laevigata*	Sugarberry
CEOC	*Celtis occidentalis*	Common Hackberry
CHVI	*Chionanthus virginicus*	White Fringetree
COFL	*Cornus florida*	Flowering Dogwood
CRAT	*Crataegus sp.*	Hawthorn
CRMA	*Crataegus marshallii*	Parsley Hawthorn
DIVI	*Diospyros virginiana*	Common Persimmon
ELPU	*Elaeagnus pungens*	Thorny Olive
ELUM	*Elaeagnus umbellata var. parvifolia*	Autumn Olive
EUAM	*Euonymus americanus*	Strawberry Bush
FAGR	*Fagus grandifolia*	American Beech
FRAX	*Fraxinus sp.*	Ash
GLTR	*Gleditsia triacanthos*	Honeylocust
HAVI	*Hamamelis virginiana*	American Witchhazel
ILAM	*Ilex ambigua*	Carolina Holly
ILDE	*Ilex decidua*	Possumhaw
ILOP	*Ilex opaca var. opaca*	American Holly
JUNI	*Juglans nigra*	Black Walnut
JUVI	*Juniperus virginiana*	Eastern Redcedar
LIBE	*Lindera benzoin*	Northern Spicebush
LIJA	*Ligustrum japonicum*	Japanese Privet
LISI	*Ligustrum sinense*	Chinese Privet
LIST	*Liquidambar styraciflua*	Sweetgum

LITU	*Liriodendron tulipifera*	Tuliptree
LOMA	*Lonicera maackii*	Amur Honeysuckle
MAGR	*Magnolia grandiflora*	Southern Magnolia
MATR	*Magnolia tripetala*	Umbrella-Tree
MORU	*Morus rubra var. rubra*	Red Mulberry
NYSY	*Nyssa sylvatica*	Blackgum
OSVI	*Ostrya virginiana*	Hophornbeam
OXAR	*Oxydendrum arboreum*	Sourwood
PATO	*Paulownia tomentosa*	Princess Tree
PIEC	*Pinus echinata*	Shortleaf Pine
PITA	*Pinus taeda*	Loblolly Pine
PIVI	*Pinus virginiana*	Virginia Pine
PLOC	*Platanus occidentalis*	American Sycamore
POST	*NA*	Corner post of plot
PRSE	*Prunus serotina*	Black Cherry
PSPM	*NA*	PSP marker post
QUAL	*Quercus alba*	White Oak
QUCO	*Quercus coccinea var. coccinea*	Scarlet Oak
QUER	*Quercus sp.*	Oak
QUFA	*Quercus falcata*	Southern Red Oak
QULY	*Quercus lyrata*	Overcup Oak
QUMA	*Quercus marilandica*	Blackjack Oak
QUPH	*Quercus phellos*	Willow Oak

QURG	*Quercus sect. Lobatae*	Red Oak Section Oak
QURU	*Quercus rubra*	Northern Red Oak
QUST	*Quercus stellata*	Post Oak
QUVE	*Quercus velutina*	Black Oak
RHCO	*Rhus copallinum*	Flameleaf Sumac
SAAL	*Sassafras albidum*	Sassafras
SEED	*NA*	Seedling transect marker post
STGR	*Styrax grandifolius*	Bigleaf Snowbell
ULAL	*Ulmus alata*	Winged Elm
ULAM	*Ulmus americana*	American Elm
ULRU	*Ulmus rubra*	Slippery Elm
UNKN	*NA*	Unknown
VAAR	*Vaccinium arboreum*	Farkleberry
VACC	*Vaccinium sp.*	Blueberry
VACO	*Vaccinium corymbosum*	Highbush Blueberry
VAST	*Vaccinium stamineum*	Deerberry
VIAC	*Viburnum acerifolium*	Mapleleaf Viburnum
VIBR	*Viburnum sp.*	Viburnum
VIPR	*Viburnum prunifolium*	Blackhaw
VIRA	*Viburnum rafinesquianum*	Downy Arrowwood
VIRU	*Viburnum rufidulum*	Rusty Blackhaw

APPENDIX A2: BIOMASS TABLES (SUCCESSIONAL PLOTS)

Table A2.1. Tables showing plot-level biomass of all individual species that achieved a cumulative, across-sampling-period (1933 – 2013) sum of 1 Mg/ha or greater in a given plot for each of the 28 successional pine plots. Species-specific biomass is shown for each sampling period for each plot. Species are sorted by decreasing cumulative biomass. Included species that achieved < 0.001 Mg/ha in a given sampling year are reported as "<0.001." Species are represented by 4-letter species codes (i.e., "SPEC"), whereas "All" signifies cumulative, whole-plot biomass for a given year. Definitions of species codes (SPEC) can be found in Appendix 1

PSP 4

SPEC	1933	1937	1940	1944	1949	1954	1961	1965	1978	1984	1988	1992	1997	2000	2013
All	9.704	57.733	84.033	84.74	102.037	126.701	140.427	166.884	199.898	234.077	249.619	269.799	309.371	324.165	379.425
PITA	9.702	57.625	83.811	83.809	100.273	126.572	140.427	166.884	184.204	211.201	223.661	240.578	273.829	286.892	326.964
LIST	<0.001	0.087	0.164	0.617	1.059	0	0	0	8.706	10.237	11.505	12.984	15.044	13.971	16.779
LITU	0	<0.001	<0.001	0.025	0.074	0	0	0	3.17	5.285	6.01	7.534	10.766	12.493	18.924
ACRU	0	0	0	0	0	0	0	0	1.502	3.313	3.712	4.933	6.274	7.178	12.226
COFL	0	<0.001	0.025	0.183	0.408	0.129	0	0	1.211	2.352	2.646	1.713	1.543	1.421	0.581
FRAX	0	0	0	0	0	0	0	0	0.279	0.56	0.795	1.025	1.419	1.791	3.766
JUVI	0	<0.001	0.024	0.092	0.207	0	0	0	0.724	0.933	1.058	0.822	0.277	0.227	0

PSP 5																
SPEC	**1933**	**1937**	**1940**	**1945**	**1949**	**1954**	**1961**	**1965**	**1977**	**1982**	**1985**	**1988**	**1992**	**1997**	**2000**	**2012**
All	12.557	61.523	84.483	96.301	102.481	128.546	141.977	168.06	217.027	247.207	249.877	277.889	308.939	350.136	359.525	381.442
PITA	12.506	61.264	84.14	95.87	101.581	119.399	132.932	165.062	184.98	211.449	211.726	236.772	263.252	295.686	301.513	299.087
LITU	0	<0.001	0.018	0.138	0.397	2.073	0.753	0.89	8.194	9.825	12.202	14.128	17.637	22.59	26.439	41.648
LIST	0	0.017	0.047	0.181	0.331	1.592	1.511	0	5.437	7.2	7.545	9.563	10.826	13.547	14.575	19.674
OXAR	0	0	0	0	0	0.342	2.612	1.135	6.963	5.304	5.75	6.252	7.306	8.189	9.424	11.408
COFL	0	<0.001	<0.001	0.051	0.129	3.598	0.968	0.304	9.7	10.399	9.511	6.788	4.87	3.875	0.832	0.048
ACRU	0	0	0	0	0	0.146	0	0	1.31	2.153	2.333	3.731	4.299	5.307	5.91	8.794
JUVI	0	0	0	0	0	0.543	2.532	0	0.168	0.522	0.478	0.266	0.267	0.312	0.292	0
ULAL	0	0	0	0	0	0	0	0	0.182	0.273	0.233	0.282	0.396	0.534	0.443	0.597
NYSY	0	<0.001	<0.001	0.028	0.043	0.623	0.668	0.669	0.032	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001

PSP 6

SPEC	1933	1938	1940	1945	1949	1954	1960	1965	1978	1984	1988	1992	1997	2000	2013
All	5.693	31.786	46.523	64.738	76.77	98.181	107.24	132.44	183.284	220.641	237.04	270.008	311.147	320.94	313.251
PITA	5.677	31.447	45.843	63.304	75.774	93.849	102.161	125.629	166.857	197.244	211.11	238.828	273.9	281.899	253.332
LITU	0	0	0	0	0	0.138	0.297	0.505	2.376	4.286	5.229	7.604	10.974	12.562	24.457
LIST	0.014	0.217	0.404	0.967	0.523	1.343	1.629	2.241	4.132	5.735	6.206	7.695	8.82	10.046	14.612
COFL	0	0	0	0	0	1.345	1.897	2.559	5.483	6.649	6.487	6.208	6.852	5.432	2.279
ACRU	0	0	0	0	0	0.027	0.02	0.037	0.689	1.488	1.944	2.856	3.859	4.811	10.724
OXAR	0	0	0	0	0	0.044	0.087	0.131	0.997	1.723	2.132	2.623	3.342	3.514	4.321
JUVI	0	0	0	0	0	0.702	0.417	0.531	1.24	1.634	1.767	1.863	1.291	1.116	0.253
FRAX	0	0	0	0	0	0.022	0.047	0.077	0.39	0.607	0.843	1.027	1.292	1.543	3.176
PIEC	<0.001	0.109	0.24	0.384	0.33	0.465	0.474	0.51	0.861	1.02	1.06	1.057	0.807	0	0
DIVI	0	0.014	0.036	0.083	0.144	0.193	0.211	0.221	0.257	0.248	0.252	0.24	0	0	0

PSP 7															
SPEC	**1933**	**1938**	**1940**	**1944**	**1949**	**1954**	**1961**	**1965**	**1978**	**1984**	**1988**	**1992**	**1997**	**2000**	**2013**
All	5.803	33.243	52.043	73.463	93.706	118.969	137.807	163.339	197.859	225.061	253.039	266.382	306.909	322.521	352.538
PITA	5.735	32.638	50.898	70.877	91.224	113.083	130.056	155.598	181.512	199.688	221.94	228.87	258.723	270.103	279.679
LITU	0	<0.001	<0.001	0.068	0.213	0.743	0.978	1.547	5.787	11.223	14.234	18.521	24.489	27.821	39.776
ACRU	0	0	0	0	0	0.163	0.38	0.617	2.9	5.518	7.894	9.552	13.661	15.313	24.606
LIST	0.055	0.416	0.84	1.962	1.762	3.207	4.09	3.794	4.633	4.743	5.434	5.598	6.29	6.435	6.706
COFL	0	<0.001	0.013	0.063	0.07	1.003	1.466	1.265	1.983	2.357	1.675	1.714	1.43	0.613	0.118
JUVI	0	0.03	0.068	0.218	0.312	0.546	0.555	0.405	0.599	0.615	0.685	0.606	0.605	0.437	0.042
OXAR	0	0	0	0	0	0.015	0.041	0.037	0.197	0.562	0.678	1.031	1.077	1.084	0.436
FRAX	0	0	0	0	0	<0.001	0.022	0.034	0.145	0.222	0.369	0.35	0.468	0.557	1.037
PIEC	0.013	0.152	0.216	0.275	0.125	0.18	0.196	0.013	0	0	0	0	0	0	0

PSP 12															
SPEC	**1933**	**1935**	**1938**	**1946**	**1950**	**1955**	**1959**	**1961**	**1966**	**1977**	**1984**	**1988**	**1992**	**1997**	**2013**
All	2.618	13.061	39.485	114.84	169.949	210.618	239.559	262.404	324.508	346.699	404.535	440.761	424.798	449.191	475.745
PITA	2.618	13.061	39.485	114.84	169.949	210.618	239.559	262.404	324.508	346.699	366.293	396.96	373.819	393.962	379.449
LITU	0	0	0	0	0	0	0	0	0	0	23.207	26.51	30.632	34.292	59.095
ACRU	0	0	0	0	0	0	0	0	0	0	9.52	11.673	15.163	18.192	34.494
COFL	0	0	0	0	0	0	0	0	0	0	3.14	2.824	2.689	1.221	0.131
PLOC	0	0	0	0	0	0	0	0	0	0	1.243	1.368	1.14	0.489	0
ULAL	0	0	0	0	0	0	0	0	0	0	0.77	0.929	0.885	0.5	0.856
FAGR	0	0	0	0	0	0	0	0	0	0	0.103	0.181	0.204	0.332	1.363

PSP 13

SPEC	1933	1935	1938	1946	1950	1955	1959	1966	1977	1984	1988	1992	1997	2000	2013
All	4.829	20.123	50.102	117.864	120.976	144.067	149.617	180.011	221.919	266.636	302.574	334.624	372.335	400.794	498.524
PITA	4.829	20.123	50.102	117.864	120.976	144.067	149.617	180.011	221.919	258.059	289.25	315.283	344.028	365.662	427.627
LIST	0	0	0	0	0	0	0	0	0	2.334	4.269	6.538	10.587	15.041	33.368
LITU	0	0	0	0	0	0	0	0	0	1.579	2.57	4.533	7.571	9.825	21.184
COFL	0	0	0	0	0	0	0	0	0	3.012	3.647	3.915	4.305	3.125	0.393
QUFA	0	0	0	0	0	0	0	0	0	0.479	0.895	1.285	1.888	2.359	5.746
QUVE	0	0	0	0	0	0	0	0	0	0.712	0.989	1.689	1.643	2.044	3.292
QURU	0	0	0	0	0	0	0	0	0	0.082	0.181	0.345	0.639	0.856	2.232
CATO	0	0	0	0	0	0	0	0	0	0.113	0.197	0.286	0.441	0.601	1.49
ULAL	0	0	0	0	0	0	0	0	0	0.15	0.303	0.334	0.507	0.574	1.133
ACRU	0	0	0	0	0	0	0	0	0	0.027	0.104	0.213	0.467	0.439	1.669

PSP 14														
SPEC	**1933**	**1935**	**1938**	**1946**	**1950**	**1955**	**1959**	**1966**	**1977**	**1984**	**1988**	**1992**	**1997**	**2000**	**2013**
All	4.9	17.722	45.52	113.286	157.546	184.02	208.608	246.476	239.236	214.055	233.534	246.815	108.743	126.476	174.968
PITA	4.9	17.722	45.52	113.286	157.546	184.02	208.608	246.476	239.236	203.67	220.608	228.134	92.86	107.627	115.312
LIST	0	0	0	0	0	0	0	0	0	4.038	5.402	8.31	7.639	10.237	28.816
COFL	0	0	0	0	0	0	0	0	0	5.217	5.512	6.71	5.544	3.121	0.363
ACRU	0	0	0	0	0	0	0	0	0	0.501	0.734	1.381	0.982	1.669	8.509
LITU	0	0	0	0	0	0	0	0	0	0.154	0.354	0.906	0.672	1.489	9.406
OXAR	0	0	0	0	0	0	0	0	0	0.285	0.592	0.885	0.663	1.142	5.052
ULAL	0	0	0	0	0	0	0	0	0	0.017	0.035	0.064	0.112	0.404	2.804
QURU	0	0	0	0	0	0	0	0	0	0.054	0.099	0.153	0.094	0.225	2.136

PSP 15															
SPEC	**1933**	**1935**	**1938**	**1946**	**1950**	**1955**	**1959**	**1966**	**1977**	**1984**	**1988**	**1992**	**1997**	**2000**	**2013**
All	8.924	32.495	71.191	148.788	204.301	229.929	248.159	270.268	272.415	294.857	324.871	337.078	394.898	397.138	491.363
PITA	8.924	32.495	71.191	148.788	204.301	229.929	248.159	270.268	272.415	279.855	302.289	307.946	357.192	354.753	425.799
LITU	0	0	0	0	0	0	0	0	0	3.583	5.383	8.566	11.543	14.091	25.623
QURU	0	0	0	0	0	0	0	0	0	3.914	6.219	7.23	9.527	12.705	15.678
QUVE	0	0	0	0	0	0	0	0	0	1.877	3.109	3.923	5.411	6.27	13.867
COFL	0	0	0	0	0	0	0	0	0	3.184	4.31	4.52	4.605	2.237	0.965
QUFA	0	0	0	0	0	0	0	0	0	0.998	1.421	1.845	2.351	2.447	3.095
LIST	0	0	0	0	0	0	0	0	0	0.865	1.002	1.114	1.148	1.216	1.62
OXAR	0	0	0	0	0	0	0	0	0	0.087	0.248	0.62	1.091	1.194	2.066
CATO	0	0	0	0	0	0	0	0	0	0.151	0.244	0.399	0.708	0.849	0.81
QUAL	0	0	0	0	0	0	0	0	0	0.204	0.369	0.543	0.625	0.483	0.871
ACRU	0	0	0	0	0	0	0	0	0	0.034	0.081	0.197	0.482	0.665	0.642

PSP 16														
SPEC	**1933**	**1935**	**1938**	**1946**	**1950**	**1955**	**1959**	**1966**	**1977**	**1984**	**1988**	**1992**	**1997**	**2000**	**2013**
All	6.16	24.04	58.766	136.851	143.754	145.793	162.588	220.644	215.86	265.037	305.088	331.724	324.153	298.059	295.459
PITA	6.16	24.04	58.766	136.851	143.754	145.793	162.588	220.644	215.86	254.756	291.002	313.08	303.93	281.465	246.721
LIST	0	0	0	0	0	0	0	0	0	4.088	5.588	7.494	8.674	4.937	11.916
ACRU	0	0	0	0	0	0	0	0	0	1.042	1.761	3.341	3.598	4.697	13.978
COFL	0	0	0	0	0	0	0	0	0	4.363	5.381	5.919	5.015	1.849	0.057
QURU	0	0	0	0	0	0	0	0	0	0.197	0.402	0.506	1.117	1.934	9.032
LITU	0	0	0	0	0	0	0	0	0	0.127	0.237	0.555	0.982	2.158	8.883
QUAL	0	0	0	0	0	0	0	0	0	0.14	0.237	0.317	0.244	0.349	2.052
OXAR	0	0	0	0	0	0	0	0	0	0.066	0.176	0.249	0.418	0.416	0.224
CATO	0	0	0	0	0	0	0	0	0	0.031	0.032	0.034	0.033	0.054	0.842

PSP 17															
SPEC	**1933**	**1935**	**1938**	**1946**	**1950**	**1955**	**1959**	**1966**	**1977**	**1984**	**1988**	**1992**	**1997**	**2000**	**2013**
All	8.569	28.552	59.536	122.037	152.409	167.596	179.928	197.862	216.772	194.957	213.77	244.407	266.387	254.334	293.859
PITA	8.501	28.357	59.195	121.655	152.182	167.596	179.928	197.862	216.772	190.406	206.094	231.984	246.658	230.35	229.784
LITU	0	0	0	0	0	0	0	0	0	2.263	3.793	5.453	8.324	10.134	29.866
LIST	0	0	0	0	0	0	0	0	0	1.931	3.139	5.624	8.805	10.513	25.417
OXAR	0	0	0	0	0	0	0	0	0	0	0.025	0.144	0.555	0.897	3.256
ACRU	0	0	0	0	0	0	0	0	0	0.027	0.074	0.185	0.405	0.675	1.894
COFL	0	0	0	0	0	0	0	0	0	0.109	0.172	0.338	0.529	0.515	0.689
FRAX	0	0	0	0	0	0	0	0	0	0.153	0.251	0.305	0.428	0.466	0
QUAL	0	0	0	0	0	0	0	0	0	0.014	0.056	0.11	0.183	0.225	0.679
PIEC	0.068	0.195	0.341	0.382	0.227	0	0	0	0	0	0	0	0	0	0

PSP 18															
SPEC	**1933**	**1935**	**1938**	**1946**	**1950**	**1955**	**1959**	**1966**	**1977**	**1984**	**1988**	**1992**	**1997**	**2000**	**2013**
All	7.994	29.527	61.943	121.143	115.099	122.48	114.874	144.74	201.149	242.813	268.049	288.485	323.599	312.043	382.074
PITA	7.843	29.13	61.377	120.74	115.099	122.48	114.874	144.74	201.149	232.824	253.39	267.749	294.754	275.063	314.758
LITU	0	0	0	0	0	0	0	0	0	7.021	10.08	14.446	19.736	26.068	44.799
LIST	0	0	0	0	0	0	0	0	0	1.032	1.575	2.163	2.99	3.268	1.889
FAGR	0	0	0	0	0	0	0	0	0	0.077	0.197	0.503	1.042	1.706	7.717
ACRU	0	0	0	0	0	0	0	0	0	0.567	0.83	0.964	1.376	1.403	2.689
QURU	0	0	0	0	0	0	0	0	0	0.162	0.289	0.525	0.938	1.549	3.855
COFL	0	0	0	0	0	0	0	0	0	0.678	0.844	1.007	0.985	1.015	0.484
CATO	0	0	0	0	0	0	0	0	0	0.041	0.099	0.176	0.333	0.566	2.985
ULAL	0	0	0	0	0	0	0	0	0	0.136	0.236	0.253	0.345	0.38	1.055
QUVE	0	0	0	0	0	0	0	0	0	0.018	0.052	0.118	0.238	0.354	0.982
PIEC	0.151	0.397	0.566	0.404	0	0	0	0	0	0	0	0	0	0	0
QUFA	0	0	0	0	0	0	0	0	0	0.085	0.17	0.235	0.39	0.25	0.281

PSP 19															
SPEC	**1933**	**1935**	**1938**	**1946**	**1950**	**1955**	**1959**	**1966**	**1977**	**1984**	**1988**	**1992**	**1997**	**2000**	**2013**
All	10.215	32.859	65.957	119.904	156.589	178.546	194.709	212.464	172.182	199.076	220.465	233.937	137.621	149.75	97.059
PITA	9.788	31.587	63.539	116.858	153.218	176.174	192.436	211.26	172.182	185.503	204.271	213.964	116.732	124.173	31.737
OXAR	0	0	0	0	0	0	0	0	0	7.97	9.222	11.256	12.131	13.852	18.538
LIST	0	0	0	0	0	0	0	0	0	1.951	3.108	4.028	5.366	6.295	15.144
ACRU	0	0	0	0	0	0	0	0	0	1.437	2.222	3.002	2.174	3.249	12.265
PIEC	0.363	1.125	2.178	2.709	3.034	2.002	2.273	1.204	0	0	0	0	0	0	0
QUAL	0	0	0	0	0	0	0	0	0	0.066	0.145	0.232	0.382	0.832	7.377
QURU	0	0	0	0	0	0	0	0	0	0.061	0.157	0.269	0.218	0.45	4.965
COFL	0	0	0	0	0	0	0	0	0	1.96	1.121	0.876	0.407	0.441	0.329
LITU	0	0	0	0	0	0	0	0	0	0	<0.001	0.025	0.034	0.091	3.498
QUPH	0	0	0	0	0	0	0	0	0	0.03	0.054	0.086	0.038	0.09	1.554
DIVI	0.064	0.147	0.24	0.337	0.337	0.371	0	0	0	0.034	0.025	0	0	0	0

PSP 20														
SPEC	**1933**	**1935**	**1938**	**1946**	**1950**	**1955**	**1959**	**1966**	**1977**	**1984**	**1988**	**1992**	**1997**	**2000**	**2013**
All	8.147	27.788	56.772	98.911	81.817	87.589	106.935	121.073	175.787	205.586	232.6	260.375	302.247	325.688	389.116
PITA	8.147	27.788	56.772	98.911	81.817	87.589	106.935	121.073	175.787	193.273	215.535	236.236	268.638	285.006	336.287
OXAR	0	0	0	0	0	0	0	0	0	5.272	7.3	10.86	15.643	20.636	25.823
LIST	0	0	0	0	0	0	0	0	0	6.352	8.598	11.171	14.667	16.18	22.93
LITU	0	0	0	0	0	0	0	0	0	0.253	0.468	0.977	1.868	2.264	0.086
ACRU	0	0	0	0	0	0	0	0	0	0.109	0.195	0.352	0.483	0.617	2.354
COFL	0	0	0	0	0	0	0	0	0	0.267	0.394	0.629	0.748	0.709	0.083
FAGR	0	0	0	0	0	0	0	0	0	<0.001	0.018	0.043	0.108	0.159	1.166

PSP 21														
SPEC	**1933**	**1935**	**1938**	**1946**	**1950**	**1955**	**1959**	**1966**	**1977**	**1984**	**1988**	**1992**	**1997**	**2000**	**2013**
All	14.409	41.188	78.911	141.288	168.882	187.098	194.155	210.035	238.324	216.251	233.685	251.273	251.234	253.236	285.402
PITA	14.351	41.053	78.722	141.288	168.882	187.098	194.155	210.035	238.324	212.045	227.498	242.11	238.484	237.316	243.84
LIST	0	0	0	0	0	0	0	0	0	3.341	4.624	6.447	8.779	10.698	25.781
QURU	0	0	0	0	0	0	0	0	0	0.098	0.232	0.404	0.809	1.185	4.514
COFL	0	0	0	0	0	0	0	0	0	0.571	0.823	1.244	1.187	1.054	1.123
ACRU	0	0	0	0	0	0	0	0	0	0.041	0.116	0.245	0.526	0.807	3.522
OXAR	0	0	0	0	0	0	0	0	0	<0.001	0.066	0.309	0.672	1.068	1.843
PRSE	0	0	0	0	0	0	0	0	0	0.034	0.052	0.087	0.161	0.269	0.848
CATO	0	0	0	0	0	0	0	0	0	0.012	0.038	0.065	0.093	0.124	1.034
QUFA	0	0	0	0	0	0	0	0	0	0.027	0.067	0.12	0.096	0.162	0.638
QUVE	0	0	0	0	0	0	0	0	0	<0.001	0.011	0.031	0.084	0.111	0.85

PSP 22

SPEC	1933	1935	1938	1946	1950	1955	1959	1966	1977	1984	1988	1992	1997	2000	2013
All	10.768	29.674	55.933	93.578	83.499	102.067	110.78	143.951	177.611	188.623	224.271	232.757	206.044	144.497	151.985
PITA	10.725	29.542	55.691	93.348	83.499	102.067	110.78	143.951	177.611	181.018	213.279	219.169	191.088	125.862	113.923
LIST	0	0	0	0	0	0	0	0	0	3.724	5.256	7.064	8.862	11.827	21.92
COFL	0	0	0	0	0	0	0	0	0	2.672	3.63	3.596	4.061	3.588	2.874
QUCO	0	0	0	0	0	0	0	0	0	0.472	0.784	0.849	0.619	0.88	3.377
QUAL	0	0	0	0	0	0	0	0	0	0.169	0.361	0.65	0.295	0.677	2.775
QURU	0	0	0	0	0	0	0	0	0	0.19	0.368	0.575	0.5	0.694	2.379
QUFA	0	0	0	0	0	0	0	0	0	0.316	0.474	0.627	0.404	0.532	2.272
FAGR	0	0	0	0	0	0	0	0	0	0.017	0.044	0.108	0.131	0.29	1.667

PSP 23

SPEC	1933	1936	1938	1946	1950	1955	1959	1966	1977	1984	1988	1992	1997	2000	2013
All	15.347	38.201	66.023	111.702	130.842	148.546	160.834	179.729	158.393	92.111	113.296	141.202	182.665	195.495	264.611
PITA	15.33	38.179	65.999	111.702	130.842	148.546	160.834	179.729	158.393	76.243	93.931	113.883	144.825	153.633	193.973
LIST	0	0	0	0	0	0	0	0	0	9.809	14.115	20.978	28.696	32.013	50.854
COFL	0	0	0	0	0	0	0	0	0	5.405	3.78	2.901	2.472	1.647	0.026
ACRU	0	0	0	0	0	0	0	0	0	0.089	0.246	0.686	1.426	1.887	6.223
QURU	0	0	0	0	0	0	0	0	0	0.128	0.243	0.492	0.904	1.093	3.642
ULAL	0	0	0	0	0	0	0	0	0	0.248	0.484	0.774	1.122	1.353	2.183
LITU	0	0	0	0	0	0	0	0	0	<0.001	0.044	0.265	0.895	1.381	3.519
OXAR	0	0	0	0	0	0	0	0	0	0.049	0.2	0.755	1.494	1.449	1.715
NYSY	0	0	0	0	0	0	0	0	0	0.063	0.115	0.24	0.421	0.523	0.911
CATO	0	0	0	0	0	0	0	0	0	0.037	0.086	0.146	0.281	0.385	1.244

PSP 24															
SPEC	**1934**	**1938**	**1940**	**1944**	**1949**	**1954**	**1960**	**1965**	**1978**	**1984**	**1987**	**1992**	**1997**	**2000**	**2013**
All	60.941	89.215	95.97	99.481	94.972	116.963	127.723	117.347	187.992	214.84	233.716	259.779	294.043	299.044	311.4
PITA	59.213	86.09	92.675	95.194	89.864	110.989	121.035	111.219	175.179	198.085	215.249	237.057	265.613	270.043	264.964
CACA	0.907	1.377	1.353	1.57	1.553	1.698	2.444	2.247	3.236	4.222	4.585	5.445	6.712	7.499	12.131
ACRU	0.026	0.063	0.071	0.109	0.17	0.245	0.26	0.343	1.653	2.934	3.502	4.965	6.465	7.043	12.439
LIST	0.267	0.545	0.573	0.88	1.142	1.561	1.6	1.091	2.369	3.179	3.539	4.168	4.958	4.957	7.969
LITU	0	<0.001	0.012	0.023	0.099	0.186	0	0	1.41	2.185	2.148	2.53	3.088	3.344	4.623
FRAX	0	<0.001	0.013	0.029	0.038	0.092	0.08	0.105	0.627	0.862	1.036	1.282	1.699	1.971	3.697
OXAR	<0.001	0.026	0.031	0.05	0.084	0.082	0.207	0.235	0.38	1.064	1.21	1.421	2.029	1.648	0.985
PIVI	0.215	0.317	0.381	0.486	0.621	0.847	1.092	1.333	1.568	0	0	0	0	0	0
NYSY	0.053	0.106	0.115	0.158	0.186	0.257	0.248	0.253	0.378	0.538	0.493	0.573	0.604	0.599	0.79
JUVI	0.065	0.209	0.249	0.417	0.611	0.363	0.28	0	0.255	0.407	0.511	0.663	0.82	0.365	<0.001
CAGL	0.054	0.08	0.08	0.095	0.104	0.111	0.137	0.157	0.189	0.353	0.32	0.377	0.387	0.419	1.028
COFL	<0.001	<0.001	<0.001	0.015	0.032	0.063	0.079	0.108	0.305	0.564	0.661	0.709	0.828	0.254	0
DIVI	0.13	0.329	0.339	0.368	0.389	0.389	0.247	0.255	0.355	0.221	0.128	0.105	0.089	0.044	0
QUPH	0	0	0	0	0	0	0	0	0.017	0.069	0.11	0.171	0.245	0.3	1.206
QURU	0	0	0	0	0	0	0	0	0.012	0.053	0.081	0.141	0.289	0.35	1.069

PSP 25															
SPEC	**1934**	**1938**	**1940**	**1944**	**1949**	**1954**	**1960**	**1965**	**1978**	**1984**	**1987**	**1992**	**1997**	**2000**	**2013**
All	66.547	109.178	113.342	106.257	125.318	149.045	166.491	191.353	264.799	319.486	338.252	364.206	410.368	419.224	482.192
PITA	66.304	108.233	112.231	104.112	121.794	144.108	161.786	188.239	251.436	297.575	311.704	333.323	372.666	380.111	425.235
ACRU	0	0.032	0.041	0.065	0.126	0.357	0.26	0.111	3.601	7.216	8.792	12.046	16.32	18.62	28.593
LIST	0.13	0.455	0.573	1.113	1.789	2.228	2.226	1.228	3.345	4.88	5.67	5.633	6.193	6.604	8.093
FRAX	0.017	0.112	0.146	0.389	0.719	0.843	0.955	0.761	1.99	2.956	3.817	4.27	4.89	5.216	8.632
LITU	0	0	0	0	0	0.017	0	0	0.368	1.267	1.686	2.218	3.571	4.369	7.25
COFL	<0.001	0.066	0.076	0.19	0.342	0.688	0.537	0.424	2.101	2.88	3.561	3.454	3.21	0.492	0.68
NYSY	0.06	0.161	0.13	0.191	0.269	0.367	0.453	0.296	0.865	1.251	1.524	1.658	1.773	1.846	1.23
CAGL	0	<0.001	<0.001	0	0	0	0	0	0.059	0.787	0.86	0.95	1.096	1.409	2.002
CAOV	0.028	0.071	0.073	0.098	0.136	0.189	0.253	0.295	0.528	0.033	0.037	0.046	0.051	0.054	0.063
OXAR	0	0	0	0	0	0.079	0	0	0.282	0.261	0.141	0.186	0.27	0.227	0.276

PSP 26															
SPEC	**1934**	**1938**	**1940**	**1944**	**1949**	**1954**	**1960**	**1965**	**1977**	**1984**	**1987**	**1992**	**1997**	**2000**	**2012**
All	90.922	129.515	138.157	158.384	182.456	188.587	200.262	195.996	269.884	292.324	302.239	322.338	347.861	332.265	380.375
PITA	85.104	122.124	130.355	150.484	173.697	179.749	191.05	186.531	244.29	257.6	269.032	284.318	308.438	290.993	326.777
OXAR	0.059	0.22	0.282	0.648	1.439	3.8	3.291	3.857	10.395	13.462	12.734	14.932	15.991	17.218	18.711
LIST	0.99	1.297	1.38	1.497	1.678	1.636	2.101	2.573	6.56	9.838	9.088	10.513	11.543	13.244	23.186
COFL	0.03	0.087	0.094	0.148	0.319	0.609	1.062	1.249	4.674	6.227	6.47	6.376	5.19	3.251	0.732
PIEC	3.696	4.262	4.45	3.857	3.35	1.371	0.987	0	0	0	0	0	0	0	0
ACRU	0	<0.001	<0.001	0.013	0.038	0.073	0.128	0.23	1.157	1.699	2.113	3.016	3.477	3.793	5.634
NYSY	0.338	0.536	0.569	0.679	0.811	0.974	1.255	1.259	1.927	2.327	1.728	1.806	1.606	1.644	1.962
CAOV	0.101	0.15	0.15	0.181	0.181	0.2	0.221	0.236	0.533	0.787	0.844	1.168	1.5	2.044	3.321
PIVI	0.437	0.572	0.572	0.636	0.717	0	0	0	0	0	0	0	0	0	0

PSP 28															
SPEC	**1934**	**1938**	**1940**	**1944**	**1949**	**1954**	**1960**	**1964**	**1978**	**1984**	**1988**	**1992**	**1997**	**2000**	**2013**
All	79.556	127.931	136.045	164.613	188.601	192.183	208.276	220.76	202.9	242.27	273.852	295.534	318.687	343.344	422.001
PITA	78.446	126.595	134.686	163.229	187.036	190.568	206.286	220.76	202.9	230.618	258.766	275.834	293.5	316.118	376.214
LIST	0	<0.001	0.01	0.058	0.193	0.428	0.679	0	0	7.124	9.249	12.244	15.331	17.485	28.773
OXAR	0	0	0	0	0	0	0	0	0	1.144	1.527	2.492	3.906	4.171	7.227
ACRU	0	0	0	0	0	0	0	0	0	0.609	1.092	1.655	2.543	2.884	6.674
COFL	0	0	0	0	0	0.05	0.07	0	0	2.266	2.585	2.434	2.152	1.116	0.231
PIEC	1.11	1.309	1.326	1.286	1.279	0.983	1.144	0	0	0	0	0	0	0	0
LITU	0	0	0	0	0	0	0	0	0	0.166	0.267	0.516	0.837	1.133	2.089
FRAX	0	0	0	0	0	<0.001	0	0	0	0.097	0.119	0.157	0.181	0.2	0.425

PSP 29															
SPEC	**1934**	**1938**	**1940**	**1944**	**1949**	**1954**	**1960**	**1964**	**1978**	**1984**	**1988**	**1992**	**1997**	**2000**	**2013**
All	62.933	115.72	129.29	123.051	134.239	143.881	143.838	182.339	255.181	287.955	315.369	343.348	387.8	421.091	491.381
PITA	62.152	114.524	127.986	122.612	134.16	143.588	143.352	181.58	240.179	258.475	280.652	301.222	335.591	363.616	426.305
LITU	0	<0.001	<0.001	<0.001	0.037	0.103	0.131	0.248	6.317	14.711	18.039	22.931	29.615	35.376	36.424
LIST	0	0	0	0	0	0.12	0.267	0.366	4.82	7.709	8.994	10.733	12.466	12.888	14.613
ACRU	0	0	0	0	0	0	0	0	0.682	1.869	2.855	4.131	5.813	6.903	12.642
COFL	0	0	0	0	0	0.033	0.058	0.1	2.589	3.799	3.077	2.208	1.98	0.753	0.041
OXAR	0	0	0	0	0	<0.001	0	0	0.109	0.34	0.544	0.824	0.987	0.902	0.513
PIEC	0.768	1.165	1.267	0.393	0	0	0	0	0	0	0	0	0	0	0
JUVI	0.014	0.029	0.033	0.037	0.041	0.031	0.029	0.044	0.404	0.666	0.677	0.754	0.698	0.108	0
FRAX	0	0	0	0	0	0	0	0	<0.001	0.174	0.22	0.215	0.234	0.193	<0.001

PSP 39

SPEC	1934	1939	1944	1949	1954	1960	1978	1984	1988	1992	1997	2000	2013
All	51.61	90.679	96.951	92.368	110.089	99.553	218.97	260.063	280.498	300.215	167.617	181.378	191.235
PITA	51.502	90.346	96.255	90.892	107.692	96.969	166.844	199.419	214.546	228.821	123.404	125.549	87.436
LIST	0.084	0.265	0.527	1.075	1.68	1.419	17.859	22.472	24.64	26.311	18.43	24.824	31.674
OXAR	0	0	0	0	0	0	10.394	11.27	13.425	15.078	5.854	6.549	11.351
ACRU	<0.001	<0.001	<0.001	0.022	0.051	0.167	6.159	7.256	8.93	9.322	6.821	7.897	16.848
LITU	<0.001	0.015	0.028	0.066	0.181	0.346	4.247	5.432	5.832	7.255	4.827	6.902	26.132
CATO	0	0	0	0	0	0	3.097	3.658	3.64	4.082	2.748	3.848	9.705
COFL	0.017	0.045	0.13	0.313	0.484	0.651	5.124	4.98	4.361	4.135	3.097	2.839	0.478
QUVE	0	0	0	0	0	0	3.026	2.96	2.942	3.342	1.593	1.886	2.851
CAGL	0	0	0	0	0	0	0.648	0.886	1.017	1.08	0.699	0.947	2.553
QURU	0	0	0	0	0	0	0.546	0.823	0.661	0.382	0	0	0
CACR	0	0	0	0	0	0	0.578	0.526	0.23	0.142	0.036	0.056	0.271
OSVI	0	0	0	0	0	0	0.194	0.241	0.217	0.248	0.097	0.029	0.725

PSP 40													
SPEC	**1934**	**1939**	**1944**	**1950**	**1954**	**1960**	**1978**	**1984**	**1988**	**1992**	**1997**	**2000**	**2013**
All	89.335	127.652	146.335	150.518	154.711	156.27	270.86	302.244	332.105	356.166	259.513	252.044	314.114
PITA	88.438	126.1	143.964	147.205	149.841	150.3	225.478	245.592	267.841	283.994	188.568	177.354	203.362
LITU	0.055	0.126	0.188	0.315	0.637	1.114	14.374	21.387	25.777	30.768	30.132	34.467	53.481
LIST	0.146	0.461	0.857	1.354	1.997	2.393	14.489	17.516	19.783	21.296	21.778	20.989	24.779
ACRU	<0.001	<0.001	<0.001	0.012	0.022	0	2.712	3.452	3.939	4.409	4.602	5.113	9.438
COFL	0.028	0.105	0.191	0.346	0.544	0.59	5.767	5.557	5.329	5.079	3.931	2.116	1.087
CATO	0	0	0	0	0	0	1.125	1.53	1.602	1.967	2.855	3.628	7.894
ULAL	0.032	0.08	0.204	0.321	0.564	0.607	1.645	1.697	1.785	1.681	2.054	2.223	2.849
OSVI	0	0	0	0	0	0	1.389	1.2	1.391	1.699	1.358	1.739	3.58
QUFA	0	0	0	0	0	0	0.7	0.917	0.789	1.288	1.524	1.701	3.339
QUVE	0	0	0	0	0	0	1.193	1.301	1.689	2.03	1.341	1.196	1.451
FRAX	0.542	0.677	0.825	0.917	1.004	1.143	0.17	0.14	0.144	0	0	0	0
QUAL	0	0	0	0	0	0	0.651	0.581	0.585	0.53	0.465	0.484	0.876
CACR	0	0	0	0	0	0	0.635	0.628	0.534	0.389	0.356	0.399	0.755
ACBA	0	0	0	0	0	0	0.028	0.254	0.337	0.454	0.549	0.636	1.181
QURU	0	0	0	0	0	0	0.28	0.391	0.493	0.582	0	0	<0.001

PSP 41													
SPEC	**1934**	**1939**	**1944**	**1950**	**1954**	**1960**	**1978**	**1984**	**1988**	**1992**	**1997**	**2000**	**2013**
All	46.738	90.05	82.762	96.05	105.397	125.677	113.89	142.033	156.218	180.941	182.114	199.204	232.344
PITA	44.424	86.754	78.655	90.684	99.841	120.907	90.44	104.673	113.915	128.521	129.723	140.492	167.84
LIST	0	0	0	0	0	0	7.192	11.94	13.792	17.052	20.82	21.834	24.024
LITU	<0.001	0.013	0.032	0.047	0.06	0.099	5.449	10.956	12.193	17.191	11.788	16.243	15.228
ACRU	0	0	0	0	0	0	3.364	4.953	6.318	8.333	10.663	13.494	20.023
COFL	0.092	0.55	1.036	1.405	1.473	1.542	3.684	5.041	5.088	4.784	3.741	1.679	0.059
FRAX	0.234	0.517	0.787	1.026	1.254	1.437	2.636	2.749	3.018	3.09	3.195	2.812	3.455
PIEC	1.723	1.558	1.02	0.896	0.649	0.392	0	0	0	0	0	0	0
CECA	0.058	0.294	0.683	1.131	1.136	0.438	0.355	0.498	0.333	0.256	0.153	0.239	0.396
ACBA	0	0	0	0	0	0	0.255	0.463	0.703	0.965	1.349	1.591	0.109
MORU	0.035	0.106	0.209	0.452	0.555	0.426	0.21	0.386	0.436	0.341	0.332	0.382	<0.001
ULAL	0	0	0	0	0	0	0.057	0.099	0.119	0.122	0.125	0.164	0.764
CELA	0.106	0.14	0.187	0.212	0.227	0.303	<0.001	<0.001	0	0	0	0	0

PSP 42													
SPEC	**1934**	**1939**	**1944**	**1950**	**1954**	**1960**	**1978**	**1984**	**1988**	**1992**	**1997**	**2000**	**2013**
All	46.839	95.178	105.345	118.491	133.77	145.997	230.429	256.041	277.8	298.645	350.969	339.28	347.793
PITA	45.427	92.009	101.562	113.686	129.066	141.159	208.26	221.344	236.353	249.102	292.406	285.728	288.611
LITU	0.199	0.608	0.808	1.145	1.461	1.897	8.678	12.788	15.716	20.213	26.397	27.47	24.584
LIST	0	0	0	0	0	0	4.183	6.674	7.765	8.5	10.474	11.012	16.348
ACRU	0	0	0	0	0	0	2.2	4.848	6.358	9.114	10.65	10.029	12.88
COFL	0.26	0.764	1.361	1.782	1.954	1.727	4.281	5.919	6.278	6.454	5.682	1.352	0.048
FRAX	0	0	0	0	0	0	1.284	2.295	3.046	3.279	3.316	3.34	4.918
PRSE	0.14	0.325	0.533	0.677	0.781	0.827	0.969	1.241	1.284	1.302	1.535	0	0
PIEC	0.67	1.094	0.504	0.619	0	0	0	0	0	0	0	0	0
DIVI	0.125	0.277	0.404	0.43	0.397	0.387	0.072	0.072	0.015	<0.001	0	0	0
CECA	0.017	0.082	0.149	0.151	0.11	0	0.257	0.436	0.471	0.243	0.16	0.042	0.019

PSP 49														
SPEC	**1936**	**1939**	**1944**	**1950**	**1954**	**1960**	**1965**	**1978**	**1984**	**1987**	**1992**	**1997**	**2000**	**2013**
All	141.357	166.174	160.062	169.444	171.869	169.528	197.152	252.526	288.112	296.438	328.401	173.405	172.106	220.906
PITA	137.251	160.266	151.881	158.773	159.833	157.846	182.362	221.315	247.91	254.908	280.337	138.294	132.29	143.819
LITU	0.125	0.239	0.368	0.707	1.045	1.522	2.742	6.054	8.733	9.623	10.947	12.932	14.976	22.649
ACRU	0.213	0.365	0.526	0.762	1.313	1.323	2.13	4.996	7.88	8.48	11.081	5.229	7.155	14.176
CATO	0.116	0.186	0.303	0.448	0.614	0.894	1.771	3.981	5.392	5.625	6.821	6.251	6.378	14.1
OXAR	0.062	0.231	0.442	0.729	0.997	1.021	1.535	4.348	5.808	6.082	7.603	4.09	4.447	10.374
LIST	0.087	0.146	0.247	0.458	0.751	1.024	1.716	3.957	4.875	5.405	6.115	4.462	5.033	11.385
COFL	0.586	1.315	2.282	3.499	4.238	3.64	2.695	4.852	4.114	3.255	2.201	0.543	0.481	0.196
NYSY	0.606	0.763	0.988	1.083	1.167	1.04	1.156	1.448	1.568	1.431	1.651	0.843	0.562	0.801
FRAX	1.259	1.455	1.576	1.692	0.626	0.62	0.691	0.696	0.841	0.863	0.886	0	0	0.012
CAGL	0.094	0.088	0.121	0.145	0.191	0.336	0.353	0.823	0.976	0.752	0.745	0.746	0.725	1.535
DIVI	0.362	0.384	0.448	0.368	0.298	0.227	0	0.025	0	0	0	0	<0.001	0.027
CARY	0.124	0.208	0.31	0.41	0.477	0.035	0	0	0	0	0	0	0	0
AIAL	0.387	0.376	0.354	0.133	0.095	0	0	0	0	0	0	0	0	0

PSP 50														
SPEC	**1936**	**1939**	**1945**	**1950**	**1954**	**1960**	**1965**	**1978**	**1984**	**1987**	**1992**	**1997**	**2000**	**2013**
All	199.029	221.722	239.224	263.646	297.875	318.784	333.718	334.855	343.099	350.982	376.48	192.449	175.876	164.1
PITA	193.361	211.906	224.007	241.971	270.691	289.17	300.709	278.655	283.694	287.816	309.621	157.417	137.918	82.698
LIST	0.606	1.652	3.214	5.266	7.1	8.013	10.146	17.107	20.678	20.371	21.595	12.954	16.715	34.782
LITU	0.387	0.923	1.657	2.811	3.793	4.421	6.414	12.366	15.557	18.228	20.293	2.231	3.836	8.578
FRAX	0.931	1.409	2.403	3.329	4.295	4.687	6.051	8.253	10.112	10.158	10.389	11.734	7.539	12.346
ACRU	0.041	0.107	0.252	0.453	0.729	1.087	1.284	3.96	5.012	6.059	7.489	4.275	4.485	10.711
COFL	1.935	3.154	4.332	5.456	6.356	6.373	3.492	4.593	1.808	1.22	1.393	1.048	1.116	0.771
NYSY	0.44	0.715	0.939	1.159	1.347	1.454	1.644	2.265	2.329	2.628	2.676	2.307	2.893	4.309
ULAL	0.13	0.305	0.637	1.151	1.523	1.945	2.277	3.599	1.797	1.98	0.152	0.166	0.385	2.743
ULAM	0.647	0.788	0.942	1.195	1.45	1.52	1.661	1.904	1.992	2.319	2.506	0.135	0.256	0.094
OXAR	<0.001	<0.001	<0.001	0.015	0.018	0.022	0	2.102	0.05	0.076	0.143	0.034	0.098	1.655
CECA	0.057	0.1	0.143	0.164	0.195	0	0	0	0.023	0.055	0.116	0.077	0.352	2.077
DIVI	0.355	0.463	0.422	0.391	0.078	0	0	0	0	0	0	0	0	<0.001
PRSE	<0.001	0	0	0	0	0	0	0	0	0	0	0	0.057	1.392

PSP 51												
SPEC	**1936**	**1939**	**1944**	**1950**	**1954**	**1960**	**1978**	**1984**	**1988**	**1992**	**1997**	**2013**
All	135.94	157.466	185.64	155.507	173.123	186.306	295.744	325.261	350.043	367.336	87.08	139.122
PITA	134.482	155.19	182.122	149.817	165.404	178.071	262.967	288.92	309.325	320.845	63.135	68.11
LIST	0.095	0.256	0.676	1.468	2.502	2.174	13.115	17.826	19.901	22.272	15.195	19.314
OXAR	0.061	0.08	0.087	0.316	0.564	1.086	5.856	5.431	7.308	9.085	5.174	10.981
ACRU	<0.001	<0.001	0.016	0.023	0.019	0	1.847	5.654	6.488	8.063	1.425	15.193
COFL	0.21	0.537	1.093	1.917	2.577	2.951	7.351	3.025	2.347	1.825	0.458	0.163
CATO	0.048	0.078	0.147	0.2	0.321	0.466	2.668	2.876	3.274	4.156	1.5	6.496
LITU	0	0	0	0	0	0	<0.001	0.012	0.022	0.035	0.039	12.425
CECA	0.174	0.326	0.524	0.694	0.91	0.732	0.758	0.498	0.375	0.071	0.03	2.428
NYSY	0.347	0.412	0.443	0.494	0.54	0.491	0.697	0.697	0.648	0.627	0.11	<0.001
DIVI	0.429	0.466	0.494	0.518	0.176	0.174	0.256	0.304	0.328	0.333	0	0
PRSE	0	0	0	0	0	0	0	0	0	0	0	1.685

APPENDIX A3: BIOMASS TABLES (HARDWOOD PLOTS)

Table A3.1. Tables showing plot-level biomass of all individual species that achieved a cumulative, across-sampling-period (1933 – 2013) sum of 1 Mg/ha or greater in a given plot for each of the 9 hardwood plots. Species-specific biomass is shown for each sampling period for each plot. Species are sorted by decreasing cumulative biomass. Included species that achieved < 0.001 Mg/ha in a given sampling year are reported as "<0.001." Species are represented by 4-letter species codes (i.e., "SPEC") , whereas "All" signifies cumulative, whole-plot biomass for a given year. Definitions of species codes (SPEC) can be found in Appendix 1.

PSP 10														
SPEC	**1933**	**1938**	**1943**	**1948**	**1952**	**1958**	**1963**	**1977**	**1984**	**1988**	**1992**	**1997**	**2000**	**2012**
All	75.964	73.85	88.527	105.988	122.909	126.596	141.56	192.5	215.411	216.67	234.785	176.686	139.682	154.399
CACA	14.186	16.139	18.564	21.966	25.228	25.725	29.111	38.888	43.239	45.212	48.286	40.094	43.759	56.126
CATO	18.233	21.834	24.892	28.337	29.948	28.974	30.374	30.405	30.271	31.276	34.279	26.653	24.768	22.151
QURU	5.801	7.513	10.304	13.783	18.538	21.359	26.08	45.403	45.05	38.715	44.082	37.151	27.483	14.75
QUAL	6.383	7.348	9.259	11.707	14.277	14.728	16.566	25.865	42.626	44.379	46.725	19.013	20.399	29.085
QUVE	15.272	7.466	9.608	11.839	14.375	14.756	16.556	23.601	23.197	25.457	27.493	26.44	0	<0.001
CAGL	3.946	4.577	5.386	6.494	7.02	7.314	7.78	7.719	7.533	7.557	8.894	8.637	9.707	12.308
FRAX	2.162	2.552	3.058	3.658	4.043	4.265	5.387	6.777	6.726	7.486	7.317	6.35	6.833	8.908
QUCO	0.856	1.196	1.618	2.025	2.671	2.86	3.505	5.013	6.837	6.238	6.021	6.316	0	0
ACRU	0.563	0.906	1.164	1.557	1.976	2.342	2.632	5.244	5.892	6.035	7.335	1.395	1.787	2.451
LIST	0.598	0.686	0.877	1.04	1.148	1.155	1.416	1.433	1.625	1.598	1.743	1.922	1.626	2.519
CAPA	0.295	0.323	0.436	0.513	0.539	0.604	0.643	0.858	1.004	1.216	1.099	1.223	1.646	2.372
COFL	1.717	1.353	1.278	0.9	0.957	0.472	0.36	0.424	0.344	0.31	0.271	0.162	0.188	0.503
CAOV	0.252	0.326	0.395	0.476	0.492	0.551	0.6	0.688	0.783	0.824	0.783	0.783	0.805	1.022
PIEC	0.695	0.882	0.961	1.012	1.044	0.878	0	0	0	0	0	0	0	0
PITA	3.982	0	0	0	0	0	0	0	0	0	0	0	0	0
JUVI	0.337	0.404	0.443	0.497	0.511	0.52	0.438	0.015	0.02	0.031	0.036	0.052	0.071	0.239
NYSY	0.307	0.305	0.27	0.179	0.132	0.083	0.1	0.141	0.154	0.167	0.188	0.206	0.227	0.56
ACBA	0	0	0	0	0	0	0	0.014	0.042	0.067	0.107	0.189	0.243	0.997

PSP 35

SPEC	1934	1939	1945	1950	1954	1977	1984	1988	1992	1997	2000	2012
All	58.948	68.779	71.965	80.467	88.35	123.564	138.647	159.127	168.802	188.159	177.718	202.03
QUST	34.71	38.541	43.045	45.536	48.941	56.293	58.132	68.816	73.581	80.861	69.274	73.731
PITA	6.228	7.254	10.386	14.263	18.359	39.711	52.416	60.3	65.795	75.416	78.314	94.282
JUVI	11.108	14.028	10.604	11.755	13.288	15.458	16.522	19.235	18.406	18.349	16.467	14.312
QUAL	0.644	0.881	1.058	1.113	1.336	2.925	4.165	4.756	5.422	6.381	6.065	8.87
PIEC	0.407	0.788	0.827	1.547	1.395	3.728	3.76	3.912	4.072	4.896	5.039	6.393
QUMA	3.221	3.916	3.346	3.309	2.422	3.263	1.456	0	0	0	0	0
FRAX	0.615	0.759	0.903	0.986	1.019	0.806	0.477	0.061	0.081	0.126	0.163	0.377
CAOV	0	0	0	0	0	0.13	0.333	0.454	0.573	0.866	1.02	2.13
PIVI	0.618	0.997	0.05	0.108	0.204	1.007	0.924	0.982	0.155	0.169	0.085	0
ACRU	0	0	0	0	0	0.043	0.261	0.411	0.514	0.833	0.965	1.68
CATO	0.674	0.784	0.817	0.833	0.845	0	<0.001	<0.001	<0.001	<0.001	<0.001	0.024
QUPH	0.516	0.605	0.682	0.746	0.277	0	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
DIVI	0.08	0.069	0.073	0.073	0.082	0.157	0.074	0.086	0.081	0.084	0.092	0.088

PSP 36													
SPEC	**1934**	**1939**	**1945**	**1949**	**1954**	**1960**	**1977**	**1984**	**1988**	**1992**	**1997**	**2000**	**2012**
All	109.546	124.103	142.418	152.509	156.981	112.977	170.523	162.28	187.428	183.686	146.748	159.057	214.37
QUAL	24.988	27.087	32.108	34.173	34.968	36.311	54.01	54.285	65.596	62.931	69.858	76.077	90.224
CATO	26.35	29.037	31.797	32.165	33.322	33.793	35.974	36.715	39.097	29.981	22.505	27.958	42.445
QUCO	33.726	39.836	46.437	52.439	54.201	10.695	19.238	20.223	23.04	25.719	1.036	0	0
LITU	2.023	2.555	3.26	4.04	5.303	5.811	13.934	14.864	17.783	19.311	22.054	21.804	31.86
CACA	4.73	5.692	6.658	7.145	7.894	8.523	16.842	18.133	21.001	22.99	12.769	12.514	17.489
QUVE	6.597	7.799	10.315	10.569	12.259	9.223	16.64	4.401	5.839	6.242	<0.001	0.029	0.746
OXAR	4.684	5.078	5.276	5.338	2.788	3.02	6.111	6.399	6.67	7.705	8.398	9.231	11.078
COFL	4.812	5.182	4.509	4.505	3.903	3.18	3.548	2.17	2.076	1.718	1.543	1.739	1.325
ACRU	0.456	0.572	0.663	0.768	0.928	0.891	2.108	2.367	3.024	3.219	3.992	4.298	9.931
JUVI	0.723	0.789	0.882	0.848	0.928	1.057	1.567	1.933	2.36	2.772	3.114	2.973	5.052
NYSY	0.456	0.475	0.512	0.518	0.488	0.473	0.448	0.591	0.731	0.816	0.971	1.607	0.414
QURU	0	0	0	0	0	0	<0.001	0.04	0.036	0.035	0.075	0.242	2.578
OSVI	0	0	0	0	0	0	0.062	0.102	0.122	0.196	0.366	0.495	1.015

PSP 37													
SPEC	**1934**	**1939**	**1945**	**1949**	**1954**	**1960**	**1978**	**1984**	**1988**	**1992**	**1997**	**2000**	**2013**
All	130.86	144.303	149.514	156.88	114.808	96.52	152.622	173.598	184.933	197.217	171.256	182.371	244.452
QUAL	109.134	121.392	137.904	144.914	110.698	92.282	138.116	150.245	159.355	171.011	147.596	155.81	201.646
OXAR	2.156	2.477	1.508	1.691	1.397	1.427	2.483	4.468	5.093	5.348	5.194	6.323	6.932
PITA	0	0	0	0	0	0	2.201	6.925	6.615	6.128	5.968	6.244	8.815
PIVI	0	0	0	0	0	0	0.9	3.593	4.107	4.114	4.428	4.445	6.196
COFL	2.656	2.689	2.58	2.595	2.023	2.046	4.93	1.592	1.669	1.601	1.215	1.022	0.781
CATO	6.21	6.528	5.945	6.039	0	0	0.212	0.282	0.313	0.295	0.227	0.273	0.987
ACRU	0.047	0.053	0.055	0.041	0	0	0.525	1.578	2.191	2.443	2.601	3.386	8.204
QUVE	9.382	9.725	0	0	0	0	0.13	0.239	0.147	0.143	0.062	0.049	0.096
LITU	0	0	0	0	0	0	0.903	1.616	1.858	2.208	1.915	2.108	4.408
JUVI	0.306	0.324	0.324	0.342	0.353	0.386	0.526	0.928	1.102	1.175	1.293	1.716	3.66
QURU	0.564	0.68	0.818	0.906	0.336	0.379	0.901	0.848	1.124	1.345	<0.001	<0.001	0.017
OSVI	0	0	0	0	0	0	0.105	0.253	0.292	0.287	0.126	0.246	0.989
SAAL	0	0	0	0	0	0	0.265	0.419	0.38	0.457	0.096	0.097	0.136
CAGL	0.095	0.091	0	0	0	0	0.076	0.158	0.186	0.176	0.188	0.213	0.45
PRSE	0	0	0	0	0	0	0.115	0.148	0.198	0.193	0.066	0.116	0.477
NYSY	0.071	0.076	0.088	0.096	0	0	0.04	0.08	0.099	0.124	0.117	0.154	0.311
CACA	0.239	0.267	0.293	0.256	0	0	0	<0.001	0	0	0	0	<0.001

PSP 43													
SPEC	**1935**	**1939**	**1945**	**1950**	**1954**	**1961**	**1977**	**1984**	**1988**	**1992**	**1997**	**2000**	**2013**
All	192.001	199.429	213.737	234.221	172.677	156.311	192.357	224.714	240.875	268.178	299.139	310.527	422.058
LIST	75.195	74.416	73.738	77.754	74.308	67.05	78.673	80.51	81.856	91.938	100.019	107.664	142.432
LITU	12.746	13.911	14.712	16.661	20.089	27.157	45.353	58.22	62.643	66.395	75.286	79.719	105.9
FAGR	1.67	2.511	3.65	5.143	3.072	6.542	28.311	44.949	53.516	62.527	74.01	85.415	121.059
QUAL	13.245	15.473	18.27	22.01	26.433	31.564	7.603	11.311	13.916	16.476	20.308	23.845	38.239
BENI	14.518	15.841	17.605	19.698	19.282	19.76	21.681	15.973	14.542	14.953	11.464	0	0
CAGL	33.127	31.412	35.56	39.368	0	0.141	0	<0.001	<0.001	0	<0.001	<0.001	0
QURU	8.906	13.053	17.042	21.898	24.997	0.719	3.057	3.921	5.153	5.547	6.782	8.15	9.882
FRAX	16.249	16.753	16.211	16.062	0.098	0	0.306	0.194	0.272	0.341	0.425	0.32	0.336
CACR	4.913	5.217	4.745	2.868	1.556	1.603	2.977	4.55	4.605	5.094	5.561	1.077	0.231
ACRU	8.456	8.263	9.114	9.446	1.064	0.276	0.806	0.845	0.756	1.197	1.426	1.438	1.857
COFL	0.601	0.882	1.105	1.422	1.637	1.277	2.833	3.022	2.151	1.908	1.774	0.79	0
ULRU	1.228	0.318	0.329	0.013	0.019	0.039	0.247	0.646	0.822	1.209	1.493	1.565	1.629
CACA	1.049	1.26	1.534	1.723	0	0	0	0	0	0	0	0	0
NYSY	0.051	0.066	0.072	0.087	0.111	0.166	0.273	0.378	0.43	0.323	0.322	0.28	<0.001
OXAR	0	0	0	0	0	0	0.073	0.141	0.193	0.256	0.225	0.214	0.197

PSP 44												
SPEC	**1935**	**1939**	**1945**	**1950**	**1954**	**1977**	**1984**	**1988**	**1992**	**1997**	**2000**	**2013**
All	188.827	180.28	195.967	229.685	255.724	368.215	392.909	387.277	418.935	471.722	495.62	616.801
LITU	64.987	79.707	91.771	111.267	128.892	197.581	217.433	221.329	243.041	273.557	288.316	366.498
LIST	33.718	29.305	24.5	27.966	31.619	45.107	48.104	51.015	54.508	59.805	58.493	71.647
PLOC	18.021	21.824	24.731	29.59	29.106	41.441	40.906	44.561	47.781	52.146	60.779	68.632
QUAL	37.747	8.458	9.842	11.741	14.859	29.17	33.519	36.381	36.371	42.896	41.741	46.892
FAGR	1.411	2.089	2.801	3.629	4.232	14.508	16.812	19.306	23.661	29.354	32.434	48.844
BENI	13.801	17.428	19.617	21.238	22.398	27.147	21.922	0	0	0	0	0
CACR	8.243	8.498	7.831	7.965	7.37	4.533	3.154	2.818	1.775	1.442	1.088	0.36
FRAX	3.274	4.144	4.897	5.661	6.27	2.776	3.316	3.372	1.598	1.825	1.498	1.765
ULAM	5.577	6.382	7.184	8.383	8.537	0	0	0	0	0	0	0
ACBA	0.044	0.076	0.128	0.182	0.29	1.513	2.115	2.855	3.66	4.447	4.985	6.944
OSVI	0.323	0.363	0.416	0.429	0.103	0.829	1.167	1.154	1.484	1.92	2.195	1.463
MORU	<0.001	0.026	0.031	0.05	0.083	0.602	0.925	0.984	1.593	1.893	1.795	3.33
ACRU	0.762	1.005	1.187	0.523	0.649	0.952	1.107	0.891	1.037	1.298	1.406	0
QURU	0.359	0.391	0.417	0.517	0.636	1.117	1.21	1.298	1.221	0.073	0.081	0.076
COFL	0.142	0.127	0.193	0.285	0.346	0.833	1.033	1.076	0.875	0.638	0.446	0

PSP 123													
SPEC	**1946**	**1949**	**1952**	**1957**	**1961**	**1969**	**1975**	**1978**	**1984**	**1988**	**1991**	**1998**	**2001**
All	78.105	96.54	109.317	122.995	143.449	163.86	207.539	229.539	246.141	265.065	255.158	250.704	271.691
QUAL	29.668	36.323	42.814	52.76	62.81	72.994	92.772	101.891	114.439	125.194	120.748	137.036	147.443
QUCO	13.777	19.389	22.737	22.436	27.051	29.786	40.674	44.992	47.564	50.507	50.209	27.623	29.559
LITU	7.388	9.274	11.154	12.721	15.108	19.418	24.999	30.667	29.992	33.637	33.336	36.11	42.97
QUVE	3.252	4.173	4.565	5.626	7.039	8.417	10.996	11.721	12.585	13.003	13.467	7.425	6.167
ACRU	4.358	4.974	4.758	5.317	5.801	6.543	7.872	9.193	9.818	10.031	8.781	10.255	10.387
NYSY	5.371	6.193	6.427	6.889	7.082	6.874	7.473	8.63	8.391	9.198	5.109	5.167	5.789
QURU	2.044	2.729	3.168	2.744	2.957	3.666	5.109	5.795	6.153	6.976	7.481	8.829	10.045
QUFA	1.129	1.41	1.9	2.158	2.747	3.24	4.516	4.406	5.724	6.731	7.416	8.894	8.887
CATO	3.862	4.447	4.572	4.862	5.15	5.198	5.183	4.224	3.094	2.082	1.537	1.74	1.824
CAGL	1.135	1.432	1.319	1.598	1.698	1.893	2.209	2.104	2.366	2.454	2.555	2.474	2.678
CAOV	1.087	1.453	1.642	1.894	1.975	1.994	2.345	2.228	2.403	2.238	1.296	1.408	1.669
CAOL	0.881	1.26	1.331	1.461	1.48	1.626	1.871	2.065	2.037	1.273	1.36	1.334	1.589
PIVI	1.706	2.169	2.406	2.068	2.247	2.176	1.521	0	0	0	0	0	0
OXAR	0.035	0.037	0	0	0	0	0	0.884	0.862	1.06	1.146	1.613	1.864
COFL	0	0	0	0	0	0	0	0.651	0.641	0.588	0.59	0.53	0.42
CARY	1.606	0.723	0.1	0.105	0	0	0	0	0	0	0	0	0
JUVI	0.439	0.376	0.366	0.3	0.236	0	0	<0.001	0.011	0.015	0.02	0.041	0.051

PSP 124													
SPEC	**1947**	**1949**	**1952**	**1961**	**1966**	**1970**	**1975**	**1978**	**1984**	**1988**	**1991**	**1998**	**2001**
All	90.617	93.85	114.009	136.275	157.1	160.101	192.749	212.427	226.852	245.071	247.823	264.556	269.827
QUAL	29.064	31.935	41.973	61.637	74.07	77.088	98	108.345	124.603	140.151	141.642	158.929	171.16
PIEC	25.283	26.167	29.775	24.856	26.287	26.594	27.72	28.536	25.996	27.943	28.128	19.833	20.089
LITU	9.044	9.401	11.614	13.327	15.319	15.323	19.367	20.486	21.44	23.921	23.996	28.479	30.429
QURU	4.24	4.751	5.877	7.15	8.693	8.942	10.459	10.219	10.44	11.551	12.226	11.162	9.57
QUVE	4.26	4.531	5.268	6.726	7.613	7.502	9.393	9.801	11.344	11.136	11.95	13.847	6.809
CATO	3.798	3.637	4.173	4.802	5.273	4.894	5.74	6.641	6.618	5.115	5.048	5.009	4.634
CAGL	3.42	3.453	3.975	4.493	5.216	5.115	5.621	5.816	5.511	5.055	5.097	5.126	4.897
OXAR	1.881	1.259	1.427	1.136	1.313	1.227	1.576	2.396	3.072	3.352	3.348	4.246	4.59
NYSY	2.281	2.066	2.249	2.172	2.429	2.287	2.29	2.469	2.473	2.533	2.434	2.537	2.485
QUFA	0.753	0.811	1.023	1.53	1.7	1.814	2.388	2.55	2.847	3.348	3.236	3.795	3.539
ACRU	0.816	0.511	0.617	0.91	1.097	1.256	1.411	2.158	2.531	3.038	2.9	3.497	3.819
CAOL	0.613	0.744	0.905	1.4	1.605	1.582	2.189	2.333	2.757	2.174	2.236	2.522	2.586
QUST	1.488	1.532	1.797	2.208	2.368	2.279	2.577	4.984	2.054	0	0	0	0
FAGR	0.761	0.942	1.12	1.4	1.534	1.618	1.924	2.068	2.061	2.249	2.001	1.821	1.294
OSVI	0.541	0.523	0.469	0.581	0.528	0.556	0.516	1.896	1.992	2.382	2.383	2.974	3.214
JUVI	0.77	0.777	0.939	1.108	1.182	1.192	0.797	0.846	0.418	0.392	0.431	0.451	0.422
FRAX	0.478	0.299	0.337	0.408	0.457	0.442	0.384	0.397	0.427	0.457	0.51	<0.001	<0.001
COFL	0.835	0.235	0.252	0.151	0.147	0.141	0.127	0.244	0.147	0.158	0.148	0.184	0.138

PSP 125

SPEC	**1947**	**1949**	**1952**	**1957**	**1961**	**1969**	**1975**	**1978**	**1984**	**1988**	**1991**	**1998**	**2001**
All	87.563	90.765	105.493	120.814	129.268	145.446	176.113	184.613	207.595	229.757	230.537	250.513	255.815
QUAL	38.147	40.974	50.436	60.339	66.104	76.063	95.525	98.512	112.569	124.479	122.884	142.412	151.737
LITU	12.95	13.994	17.79	20.089	21.38	26.23	29.157	31.796	35.837	43.505	44.011	43.036	45.883
QUFA	5.583	5.787	6.869	7.889	8.853	9.281	11.77	12.275	12.955	13.6	13.85	15.158	15.688
CATO	4.867	4.999	6.064	7.174	7.224	8.088	10.414	10.731	10.795	11.254	11.337	9.115	5.723
QUVE	5.772	6.022	4.646	5.483	5.122	5.75	7.431	8.419	10.21	11.212	11.236	13.417	12.83
QURU	2.727	2.823	3.718	4.587	5.26	6.451	9.154	9.962	10.889	12.031	11.648	11.755	11.965
QUST	1.819	1.833	2.281	2.513	2.836	3.004	3.695	3.893	4.197	4.623	5.461	4.486	4.973
CAGL	2.122	1.919	2.203	2.484	2.309	2.373	3.056	3.281	3.325	3.355	4.183	4.554	0.107
PIVI	4.928	4.775	3.667	2.42	2.4	1.146	1.388	1.352	1.521	0	0	0	0
CAOV	0.834	0.9	1.048	1.219	1.221	1.376	1.641	1.773	1.918	1.975	2.038	2.14	2.119
ACRU	0.851	0.555	0.69	0.789	0.775	1.015	1.364	1.455	1.78	2.146	2.305	2.776	2.896
NYSY	2.317	2.336	2.392	2.46	2.503	2.075	0.487	0.522	0.518	0.544	0.409	0.371	0.451
DIVI	1.272	1.242	1.412	1.493	1.529	1.401	0	0	0	0	0	0	0
COFL	1.118	0.779	0.878	0.77	0.834	0.455	0.206	0.065	0.053	0.064	0.058	0.093	0.082
JUVI	1.421	1.236	0.709	0.344	0.326	0.213	0.216	0.016	0.015	0.017	0.016	0.016	0.016
FAGR	0.183	0.069	0.087	0.116	0.15	0.22	0.298	0.375	0.426	0.476	0.573	0.678	0.685
OXAR	0.142	0.101	0.119	0.148	0.217	0.181	0.181	0.049	0.459	0.442	0.494	0.465	0.608

APPENDIX A4: RELATIVE SPECIES ABUNDANCES IN CHAPTER 6 CLUSTER-ANALYSIS GROUPS

This appendix contains tables of relative abundances (“R. A.”; %) of each species present in all samples of groups assigned by cluster-analyses in Chapter 6. The four tables represent the cluster-analysis-defined groups for the complete, unpartitioned data, and three partitions of the data: canopy stems, subcanopy stems, and small-stems (i.e., DBH ≤ 10 cm). Short descriptions of groups are provided in the caption of each table, and more detailed descriptions are available in the text of Chapter 6. Definitions of species codes (SPEC) can be found in Appendix 1.

Table A4.1. Relative abundances (%) of species in each cluster-analysis group for unpartitioned PSP data. Relative abundances (R. A.) are based on proportions of relativized basal areas of species, and species are sorted in the table by decreasing R. A. Definitions of species codes (SPEC) can be found in Appendix 1. Groups roughly equate to 1 = near-monoculture of *Pinus taeda* stand; 2 = upland hardwood stands; 3 = successional pine stands; 4 = bottomland hardwood stands.

Group 1		Group 2		Group 3		Group 4	
SPEC	**R. A. (%)**	**SPEC**	**R. A. (%)**	**SPEC**	**R. A. (%)**	**SPEC**	**R. A. (%)**
PITA	96.7	CATO	12.19	PITA	35.73	LIST	17.72
DIVI	0.81	COFL	7.53	COFL	13.07	CACR	12.98
PIEC	0.71	QUAL	7.35	OXAR	6.37	LITU	10.16
LIST	0.54	QUVE	7.1	LIST	6.21	FAGR	8.08
JUVI	0.42	QURU	6.83	ULAL	5.9	ULRU	7.87
COFL	0.4	OXAR	5.77	ACRU	4.16	FRAX	6.78
SAAL	0.11	JUVI	5.31	FRAX	3.37	ULAM	4.95
NYSY	0.07	CACA	4.69	CECA	2.44	QURU	4.57
FRAX	0.06	CAGL	4.43	DIVI	2.4	ACBA	4.24
CAOV	0.05	NYSY	3.08	JUVI	1.96	MORU	3.98
ULAM	0.05	CAOV	3.07	ILDE	1.93	COFL	3.8
OXAR	0.04	CAOL	2.87	PRSE	1.88	ILOP	3.32
LITU	0.03	ACRU	2.86	QUPH	1.67	CAGL	3.23
ACRU	0.02	LITU	2.77	LITU	1.59	AESY	2.3
CAGL	<0.01	QUCO	2.52	VIRA	1.37	VIPR	1.62
		QUFA	2.51	NYSY	1.17	ACRU	1.14
		QUST	2.34	AESY	1.08	QUAL	1.12
		SAAL	2.33	CATO	0.9	OSVI	0.65
		CHVI	2.1	QURU	0.89	ULAL	0.31
		PIVI	1.96	ULRU	0.58	NYSY	0.3
		PIEC	1.72	MORU	0.57	PRSE	0.21
		FRAX	1.7	QUVE	0.54	CHVI	0.16
		ILOP	1.14	SAAL	0.49	OXAR	0.15
		DIVI	1.08	CACA	0.47	CACA	0.14
		OSVI	0.93	CAOV	0.46	CAOV	0.12
		PRSE	0.83	ULAM	0.43	CECA	0.04
		VIPR	0.68	CAGL	0.38	QUPH	0.03
		VIRA	0.64	QUFA	0.33	JUVI	0.03
		QUPH	0.63	ACBA	0.33	CAOL	<0.01
		FAGR	0.24	VIPR	0.32	CATO	<0.01
		ACBA	0.2	PIEC	0.24		
		ULAL	0.13	PIVI	0.22		
		PITA	0.12	ILOP	0.14		
		LIST	0.11	CACR	0.13		
		ILDE	0.1	OSVI	0.11		
		CECA	0.09	FAGR	0.11		
		MORU	0.03	QUAL	0.03		
		ULAM	0.03	QUCO	0.03		
		CACR	0.02	CAOL	0.02		
		ULRU	<0.01	CHVI	<0.01		
				QUST	<0.01		

Table A4.2. Relative abundances (%) of species in each cluster-analysis group for PSP canopy stems. Relative abundances (R. A.) are based on proportions of relativized basal areas of species, and species are sorted in the table by decreasing R. A. Definitions of species codes (SPEC) can be found in Appendix 1. Groups roughly equate to 1 = near-monoculture of *Pinus taeda* stand; 2 = upland Hill Forest hardwood stands; 3 = successional pine stands; 4 = bottomland hardwood stands; 5 = upland Duke Forest hardwood stands.

Group 1		Group 2		Group 3		Group 4		Group 5	
SPEC	**R. A. (%)**	**SPEC**	**R. A. (%)**	**SPEC**	**R. A. (%)**	**SPEC**	**R. A. (%)**	**SPEC**	**R. A. (%)**
PITA	92.28	QUVE	12.13	PITA	39.72	LIST	33.66	CATO	19.63
LIST	2.09	QURU	10.12	OXAR	17.26	LITU	25.1	COFL	12.6
ACRU	1.39	QUAL	9.91	LIST	11.22	FAGR	14.35	CACA	10.72
LITU	1.28	NYSY	8.79	COFL	10.59	FRAX	11.43	OXAR	9.67
FRAX	0.82	QUFA	8.66	ACRU	9.16	QURU	6.69	JUVI	8.58
OXAR	0.57	LITU	6.5	FRAX	5.52	CAGL	4.59	QUAL	7.95
PIVI	0.33	CATO	6.46	LITU	2.56	QUAL	2.34	QUVE	7.39
COFL	0.28	PIVI	6.33	CATO	1.57	ACRU	1.79	QURU	7.38
QURU	0.27	CAGL	6.17	QURU	0.71	CACA	0.05	FRAX	4.1
CACA	0.23	CAOL	6.11	JUVI	0.52			CAGL	2.86
PIEC	0.2	PIEC	4.89	NYSY	0.39			PIVI	2.77
JUVI	0.09	ACRU	4.85	QUFA	0.18			ACRU	2.38
QUVE	0.06	QUCO	4.31	QUVE	0.16			QUCO	2.33
NYSY	0.05	JUVI	2.54	CAGL	0.15			LITU	0.72
CATO	0.03	OXAR	1.42	CACA	0.15			PITA	0.39
FAGR	0.02	FRAX	0.41	QUCO	0.07			LIST	0.25
QUFA	<0.01	FAGR	0.4	FAGR	0.03			NYSY	0.19
				QUAL	0.03			PIEC	0.1
				PIEC	0.03				

Table A4.3. Relative abundances (%) of species in each cluster-analysis group for PSP subcanopy stems. Relative abundances (R. A.) are based on proportions of relativized basal areas of species, and species are sorted in the table by decreasing R. A. Definitions of species codes (SPEC) can be found in Appendix 1. Groups roughly equate to 1 = near-monoculture of *Pinus taeda* stand; 2 = upland hardwood stands; 3 = successional pine stands; 4 = bottomland hardwood stands; 5 = DIVI stands.

Group 1		Group 2		Group 3		Group 4		Group 5	
SPEC	**R. A. (%)**	**SPEC**	**R. A. (%)**	**SPEC**	**R. A. (%)**	**SPEC**	**R. A. (%)**	**SPEC**	**R. A. (%)**
PITA	88.11	NYSY	9.14	LIST	19.27	DIVI	32.76	FAGR	26.63
PIEC	6.95	CAGL	8.11	COFL	17.01	PIEC	11.86	CACR	14.65
LIST	1.63	CATO	7.49	ULAL	6.95	PITA	10.41	ULRU	9.87
JUVI	0.67	COFL	6.77	ACRU	6.23	NYSY	8.06	FRAX	7.84
SAAL	0.65	OXAR	6.65	FRAX	5.74	COFL	7.77	ILOP	6.17
COFL	0.51	ACRU	6.54	OXAR	4.55	CECA	7.19	COFL	5.78
FRAX	0.45	CAOV	5.27	NYSY	4.25	LIST	6.6	LIST	5.75
DIVI	0.38	CHVI	5	JUVI	3.07	CACA	2.24	AESY	4.43
NYSY	0.26	SAAL	3.36	QUFA	2.68	MORU	1.93	ACBA	3.68
LITU	0.18	QUAL	3.17	DIVI	2.37	ACRU	1.79	MORU	3.65
ULAL	0.16	CACA	2.72	QUPH	2.24	PRSE	1.73	VIPR	2.36
CAOV	0.04	JUVI	2.69	QUVE	2.11	OXAR	1.31	NYSY	2.31
CECA	0.02	LITU	2.62	ILDE	2.1	FRAX	1.19	ACRU	1.72
ACRU	<0.01	AMAR	2.54	LITU	2.04	CATO	0.92	OSVI	0.99
		FAGR	2.27	VIRA	2	ULAM	0.84	QURU	0.72
		CAOL	2.16	PITA	1.79	JUVI	0.84	LITU	0.49
		QUVE	2.08	FAGR	1.61	VIPR	0.76	ULAL	0.49
		QURU	1.99	QURU	1.56	CAGL	0.6	PRSE	0.44
		FRAX	1.93	PRSE	1.45	CAOV	0.32	CAOV	0.39
		ILOP	1.86	CATO	1.37	SAAL	0.32	CACA	0.39
		PRSE	1.73	AESY	1.32	ULAL	0.22	OXAR	0.34
		ACBA	1.72	MORU	1.21	LITU	0.16	QUAL	0.24
		DIVI	1.67	ACBA	1.15	ULRU	0.08	CHVI	0.2
		OSVI	1.64	ULAM	0.99	ILOP	0.07	ULAM	0.13
		QUST	1.48	PIEC	0.87	QUPH	0.04	CAGL	0.12
		QUFA	1.39	ULRU	0.84	VIRA	0.02	JUVI	0.06
		VIRA	1.35	CECA	0.75	QUST	<0.01	CAOL	0.05
		VIPR	0.86	CAGL	0.6	QURU	<0.01	CECA	0.05
		QUPH	0.6	CAOV	0.48			QUPH	0.04
		LIST	0.58	CACA	0.35			CATO	0.03
		QUCO	0.5	CACR	0.19				
		CECA	0.46	OSVI	0.18				
		MORU	0.41	ILOP	0.18				
		ULAM	0.37	QUAL	0.13				
		PIEC	0.34	QUCO	0.12				
		ULAL	0.34	AMAR	0.08				
		ILDE	0.22	VIPR	0.08				
		CACR	0.03	SAAL	0.06				
		PITA	0.02	CAOL	0.05				
		ULRU	<0.01	QUST	0.01				

Table A4.4. Relative abundances (%) of species in each cluster-analysis group for small-stem (i.e., DBH ≤ 10 cm) PSP data. Relative abundances (R. A.) are based on proportions of relativized basal areas of species, and species are sorted in the table by decreasing R. A. Definitions of species codes (SPEC) can be found in Appendix 1. Groups roughly equate to: 1 = near-monoculture of *Pinus taeda* stand; 2 = basic/rich; 3 = acidic; 4 = DIVI stands; 5 = mesic bottomland; 6 = sub-xeric oak; 7 = mesic/mixed oak.

Group 1		Group 2		Group 3		Group 4		Group 5		Group 6		Group 7	
SPEC	R. A. (%)	SPEC	R. A. (%)	SPEC	R. A. (%)	SPEC	R. A. (%)	SPEC	R. A. (%)	SPEC	R. A. (%)	SPEC	R. A. (%)
PITA	78.61	LIST	25.4	COFL	21.5	DIVI	50.09	CACR	21.27	JUVI	28.62	QURU	13.83
PIEC	11.9	JUVI	9.16	ACRU	6.87	PIEC	10.2	FAGR	20.04	ILOP	15.78	ULAL	12.18
LIST	4.29	COFL	9.13	NYSY	6.86	COFL	9.59	COFL	7.8	CATO	7.95	COFL	9.35
JUVI	2.22	FRAX	5.77	FRAX	5.44	PITA	7.49	ILOP	7.58	CAGL	6.95	QUPH	8.98
DIVI	1.54	DIVI	5.41	DIVI	5.44	CECA	7.11	VIPR	6.12	COFL	5.97	QUFA	7.84
SAAL	0.5	ACRU	5.37	OXAR	4.75	JUVI	6.52	AESY	4.63	QUAL	5.74	ACRU	5.6
LITU	0.38	CAOV	5.03	JUVI	4.22	MORU	3.35	FRAX	4.53	LITU	5.02	LIST	5.1
COFL	0.28	OXAR	4.33	LIST	3.73	CATO	2.24	ULRU	3.64	SAAL	4.51	QUVE	4.82
NYSY	0.12	NYSY	4.28	CATO	3.28	LITU	2.11	LIST	3.62	FAGR	3.01	OXAR	3.14
FRAX	0.07	ULAM	3.52	AESY	3.22	PRSE	0.42	CAOL	3.14	QUVE	2.03	FAGR	2.75
MORU	0.07	LITU	3.47	ULAL	3.04	FRAX	0.42	ACBA	2.92	OXAR	1.93	VIRA	2.71
CECA	0.04	CACA	2.22	LITU	2.88	LIST	0.34	CAOV	2.46	ACRU	1.66	ULRU	2.43
ACRU	<0.01	CAGL	2.11	MORU	2.64	ACRU	0.12	QURU	2.41	CAOV	1.64	QUCO	2.42
		ILDE	1.9	CECA	2.6			NYSY	1.93	DIVI	1.57	PRSE	2.13
		QUFA	1.71	CHVI	2.6			MORU	1.61	QUFA	1.49	LITU	1.98
		CATO	1.61	CAGL	2.52			ACRU	1.19	QURU	1.42	CAOL	1.59
		CAOL	1.57	ACBA	1.91			QUAL	1.17	PRSE	0.99	JUVI	1.59
		VIPR	1.21	QUVE	1.59			ULAL	0.85	AMAR	0.74	FRAX	1.3
		FAGR	1	ILDE	1.54			CAGL	0.52	QUCO	0.74	CATO	1.27
		PITA	0.93	QURU	1.53			OXAR	0.51	CHVI	0.53	NYSY	1.09
		PIEC	0.86	CAOL	1.05			OSVI	0.47	NYSY	0.52	QUAL	1.04
		QURU	0.6	AMAR	0.94			ULAM	0.45	ULAL	0.36	CAGL	0.97
		QUVE	0.49	FAGR	0.91			PRSE	0.28	OSVI	0.32	ILDE	0.93
		ULAL	0.48	OSVI	0.9			LITU	0.26	VIRA	0.17	DIVI	0.79
		VIRA	0.43	VIRA	0.86			CHVI	0.22	FRAX	0.13	CAOV	0.74
		QUCO	0.43	PRSE	0.79			JUVI	0.17	MORU	0.12	PITA	0.63
		ACBA	0.31	PITA	0.76			QUPH	0.1	PITA	0.08	CECA	0.56
		MORU	0.31	SAAL	0.72			CATO	0.06	CACR	0.03	ILOP	0.44
		QUAL	0.29	CAOV	0.69			CECA	0.06	CACA	<0.01	AMAR	0.43
		QUPH	0.27	QUCO	0.66			CACA	0.04			AESY	0.29
		ILOP	0.14	CACR	0.63							ACBA	0.23
		SAAL	0.13	ULAM	0.62							CACA	0.22
		PRSE	0.06	CACA	0.51							MORU	0.2
		ULRU	0.05	VIPR	0.5							SAAL	0.16
		CECA	0.03	QUAL	0.44							ULAM	0.15
				QUFA	0.38							VIPR	0.1
				ILOP	0.35							CHVI	0.01
				ULRU	0.12								
				QUPH	0.03								
				PIEC	0.01								

APPENDIX A5: INDICATOR SPECIES IN CHAPTER 6 CLUSTER-ANALYSIS GROUPS

This appendix contains four tables of indicator species for groups assigned by cluster analyses in Chapter 6. The four tables represent the cluster-analysis-defined groups for the unpartitioned data and three partitions of the PSP data, respectively: canopy stems, subcanopy stems, and small-stems (i.e., DBH ≤ 10 cm). See Chapter 6 for description of partitions. Indicator species analysis (Dufrene & Legendre 1997) was performed (using the indval function in labdsv package (Roberts 2016) in R; R Core Team 2016) on the relativized species abundance (basal area) matrix to produce indicator values as a product of exclusivity (relative abundance across groups) and frequency (the proportion of samples in each group that contain that species) of species. The Monte Carlo method was used to evaluate statistical significance. Table columns include SPEC (species codes), Group (cluster-analysis group assignment), IV (indicator value), and Pval (significance of IV). Short descriptions of groups are provided in the caption of each table, and more detailed descriptions are available in the text of Chapter 6. Definitions of species codes (SPEC) can be found in Appendix 1.

Table A5.1. Indicator species for each cluster-analysis group for unpartitioned PSP data. All significant (i.e., Pval < 0.05) indicator species are shown, and species are sorted in the table by decreasing IV (indicator value). Definitions of species codes (SPEC) can be found in Appendix 1. Groups roughly equate to 1 = near-monoculture of *Pinus taeda* stand; 2 = upland hardwood stands; 3 = successional pine stands; 4 = bottomland hardwood stands.

SPEC	Group	IV	Pval
PITA	1	0.7295	0.001
CATO	2	0.9072	0.001
QUVE	2	0.8707	0.001
QUAL	2	0.8652	0.001
JUVI	2	0.6793	0.001
NYSY	2	0.6491	0.001
CAOV	2	0.5785	0.001
QUFA	2	0.5251	0.001
QURU	2	0.5133	0.001
QUCO	2	0.4507	0.001
CAGL	2	0.4459	0.001
CACA	2	0.3698	0.001
CAOL	2	0.3264	0.001
QUST	2	0.3032	0.001
PIVI	2	0.2728	0.001
CHVI	2	0.2348	0.001
PIEC	2	0.204	0.008
SAAL	2	0.1208	0.004
ULAL	3	0.6206	0.001
COFL	3	0.525	0.001
OXAR	3	0.3627	0.001
CECA	3	0.2904	0.002
DIVI	3	0.2425	0.003
VIRA	3	0.2303	0.003
ILDE	3	0.2292	0.001
PRSE	3	0.2278	0.004
QUPH	3	0.1757	0.005
CACR	4	0.9891	0.001
FAGR	4	0.9581	0.001
ULRU	4	0.7447	0.001
LIST	4	0.721	0.001
LITU	4	0.6985	0.001
FRAX	4	0.5468	0.001
MORU	4	0.4865	0.001
AESY	4	0.4359	0.001
VIPR	4	0.3716	0.001
ILOP	4	0.3173	0.001
ULAM	4	0.2541	0.001
OSVI	4	0.2132	0.002

Table A5.2. Indicator species for each cluster-analysis group for PSP canopy stems. All significant (i.e., Pval < 0.05) indicator species are shown, and species are sorted in the table by decreasing IV (indicator value). Definitions of species codes (SPEC) can be found in Appendix 1. Groups roughly equate to 1 = near-monoculture of *Pinus taeda* stand; 2 = upland Hill Forest hardwood stands; 3 = successional pine stands; 4 = bottomland hardwood stands; 5 = upland Duke Forest hardwood stands.

SPEC	Group	IV	Pval
PITA	1	0.697	0.001
QUFA	2	0.9784	0.001
NYSY	2	0.7661	0.001
CAOL	2	0.641	0.001
QUVE	2	0.6145	0.001
QUAL	2	0.4899	0.001
CAGL	2	0.4023	0.001
QURU	2	0.3709	0.001
PIEC	2	0.3127	0.001
PIVI	2	0.2928	0.001
QUCO	2	0.2144	0.001
OXAR	3	0.4021	0.001
FAGR	4	0.8916	0.001
LIST	4	0.7127	0.001
LITU	4	0.6943	0.001
FRAX	4	0.3284	0.001
CATO	5	0.5494	0.001
JUVI	5	0.4572	0.001
COFL	5	0.3356	0.001

Table A5.3. Indicator species for each cluster-analysis group for PSP subcanopy stems. All significant (i.e., Pval < 0.05) indicator species are shown, and species are sorted in the table by decreasing IV (indicator value). Definitions of species codes (SPEC) can be found in Appendix 1. Groups roughly equate to 1 = near-monoculture of *Pinus taeda* stand; 2 = upland Hill Forest hardwood stands; 3 = successional pine stands; 4 = bottomland hardwood stands; 5 = upland Duke Forest hardwood stands

SPEC	Group	IV	Pval
PITA	1	0.8782	0.001
CAGL	2	0.8147	0.001
CATO	2	0.7533	0.001
QUAL	2	0.668	0.001
CAOV	2	0.5407	0.001
OXAR	2	0.3865	0.001
NYSY	2	0.3552	0.001
LITU	2	0.3438	0.001
QURU	2	0.3298	0.002
JUVI	2	0.3184	0.001
QUVE	2	0.2911	0.001
CHVI	2	0.2687	0.001
AMAR	2	0.2582	0.001
QUST	2	0.2512	0.001
OSVI	2	0.2023	0.001
CAOL	2	0.1914	0.001
SAAL	2	0.184	0.001
PRSE	2	0.138	0.048
CACA	2	0.1082	0.021
ULAL	3	0.5559	0.001
LIST	3	0.5156	0.001
COFL	3	0.4475	0.001
QUFA	3	0.2535	0.001
ILDE	3	0.2461	0.001
VIRA	3	0.2173	0.001
QUPH	3	0.2088	0.001
DIVI	4	0.8638	0.001
CECA	4	0.5832	0.001
PIEC	4	0.2556	0.001
CACR	5	0.9854	0.001
FAGR	5	0.8728	0.001
ULRU	5	0.7317	0.001
AESY	5	0.493	0.001
FRAX	5	0.4208	0.001
VIPR	5	0.3489	0.001
ILOP	5	0.3281	0.001
MORU	5	0.1826	0.003

Table A5.4. Indicator species for each cluster-analysis group for small-stem (i.e., DBH ≤ 10 cm) PSP data. All significant (i.e., Pval < 0.05) indicator species are shown, and species are sorted in the table by decreasing IV (indicator value). Definitions of species codes (SPEC) can be found in Appendix 1. Groups roughly equate to: 1 = near-monoculture of *Pinus taeda* stand; 2 = basic/rich; 3 = acidic; 4 = DIVI stands; 5 = mesic bottomland; 6 = sub-xeric oak; 7 = mesic/mixed oak.

SPEC	Group	IV	Pval
PITA	1	0.8882	0.001
PIEC	1	0.278	0.001
LIST	2	0.5575	0.001
FRAX	2	0.2474	0.001
OXAR	2	0.2094	0.002
CAOV	2	0.1434	0.015
ULAM	2	0.1371	0.003
CACA	2	0.1151	0.017
NYSY	3	0.3913	0.001
COFL	3	0.3352	0.001
MORU	3	0.1382	0.02
CHVI	3	0.0888	0.02
DIVI	4	0.7727	0.001
CECA	4	0.342	0.001
CACR	5	0.97	0.001
FAGR	5	0.723	0.001
VIPR	5	0.4635	0.001
ULRU	5	0.4435	0.001
AESY	5	0.364	0.001
OSVI	5	0.1562	0.008
CAOL	5	0.0855	0.02
JUVI	6	0.5453	0.001
QUAL	6	0.5124	0.001
CATO	6	0.4532	0.001
CAGL	6	0.3774	0.001
LITU	6	0.2312	0.003
ILOP	6	0.2096	0.001
SAAL	6	0.1691	0.002
ULAL	7	0.7106	0.001
QURU	7	0.6608	0.001
QUPH	7	0.6302	0.001
QUVE	7	0.4735	0.001
VIRA	7	0.4724	0.001
QUFA	7	0.414	0.001
PRSE	7	0.2682	0.001
QUCO	7	0.1951	0.001

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