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Impacts of Laurel Wilt Disease on Native Persea of the Southeastern United States

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IMPACTS OF LAUREL WILT DISEASE ON NATIVE *PERSEA* OF THE SOUTHEASTERN UNITED STATES

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ABSTRACT

Laurel Wilt Disease (LWD) has caused severe mortality in native *Persea* species of the southeastern United States since it was first detected in 2003. This study was designed to document the range-wide population impacts to LWD, as well as the patterns of mortality and regeneration in *Persea* ecosystems. I used Forest Inventory and Analysis (FIA) data from the U.S. Forest Service to estimate *Persea borbonia* (red bay) populations from 2003 to 2011 to see if any decline could be observed since the introduction of LWD causal agents. Population estimates from 2003 to 2011 suggest that the population is declining. The population in Georgia significantly decreased from ca. 241.1 ± 11.9 million stems in 2003 to ca. 150.3 ± 7.9 million in 2011. Red bay densities decreased significantly in plots surveyed before and after the reported infection by an average of 89.6 live red bay stems/ha. I developed a logistic regression model to predict the probability of red bay mortality due to LWD. Number of years since LWD infection was the most significant variable, with every increase in 1 year resulting in a 153.7 % increase in odds of death. Diameter was also a significant predictor, with an increase of 1 cm DBH resulting in a 5.0 % increase in odds of death.

To document the stand characteristics of red bay and swamp bay (*Persea palustris*) communities, I analyzed data collected from 1988–2012 by the Carolina Vegetation Survey. We used cluster analyses and species indicator analyses to group 388 plots into distinct communities. Red bay and swamp bay communities were significantly different in species composition. In addition, red bay was almost exclusively limited to

maritime coastal forests, whereas swamp bay had a significantly larger geographical range, extending from near coastal setting inland through the fall-line sandhills.

I surveyed plots from 1 to 10 years post LWD in South Carolina and Georgia. We did not find evidence of invasive species abundance increasing after LWD. Nearly all *Persea* in a plot are killed within the first two years of LWD, with the exception of smaller stems under 2.5 cm in diameter. After 10 years, *Persea* has regained much of the basal area prior to infection, however the structure of the stand is predominantly composed of small diameter stems (1 – 5 cm DBH). Seedling densities remain relatively the same throughout all recovery years.

Contrary to initial fears, this study suggests that the native *Persea* species in the U.S. are not on the immediate verge of extinction from LWD at this time. However, it is still too early to say whether these species will fully recover from the disease.

DEDICATION

This dissertation is dedicated to my family. To my parents, Richard and Patricia Shearman, for their unconditional love and support, making me into the person that I am today. To Laura, Kennedy, and Jocelyn, for always believing in me.

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CHAPTER ONE

INTRODUCTION

The main goal of this dissertation is to examine the impacts of Laurel Wilt Disease (LWD) on native *Persea* species of the southeastern United States. Diseases can impact a species at the individual scale and at a population scale. They can also impact communities and ecosystems by freeing up resources for other species. Diseases target specific species, or closely related species, and can be looked at as biological disturbances. Therefore, this dissertation is a study of forest disturbance. White and Pickett (1985) define a disturbance as any event that "disrupts ecosystem, community, or population structure and changes resources, substrate availability, or the physical environment." Disturbances are not always random, nor are they rare. Many disturbances can be viewed as events to which communities have become well adapted (White 1979), such as the historic fire regime of the longleaf pine ecosystem. Other disturbances however, are less frequent, have a higher magnitude, and result in drastic changes to ecosystems.

1.1. Forest Diseases and Pathogens

The term *disease* is defined as an abnormal state of an organism or part of an organism. Pathogens are the causal agent of disease and although many pathogens are fungal species, they can come in other forms such as bacteria, viruses, and parasites. However, fungi make up the second largest taxonomic group of pathogens that cause emerging infectious diseases in plants, second only to viruses (Anderson et al. 2004,

Desprez-Loustau et al. 2007). Pathogens and diseases occur in all forested ecosystems and, like all disturbances, play a major role in forest dynamics (Castello et al. 1995). Forest pathogens and their resulting diseases differ from abiotic disturbances in that they target specific species in an ecosystem. Native pathogens, those that have an evolutionary history with their host, tend to be smaller magnitude disturbances, removing weaker individuals in an ecosystem and leaving more vigorous individuals (Castello et al. 1995). Thus, native pathogens contribute to the distribution and abundance of species (Dinoor and Eshed 1984, Mordecai 2011), and potentially to the maintenance of species diversity in an ecosystem via Janzen-Connell effects (Janzen 1970, Connell 1971; Mordecai 2011). Non-native diseases are usually a disturbance of a higher magnitude than native diseases, especially if their host species is dominant in the ecosystem. Non-native diseases have increased along with the increase in global transportation by humans, moving pathogens into new areas (Hulcr and Dunn 2011). The new environment can result in novel host-pathogen interactions, often within the same genus or family as hosts in the pathogens native range (Parker and Gilbert 2004, Desprez-Loustau et al. 2007).

Perhaps one of the most well-known examples of a non-native forest disease is chestnut blight. Caused by the fungal pathogen, *Cryphonectria parasitica,* chestnut blight resulted in dramatic mortality of American chestnut, *Castanea dentata,* throughout the eastern United States. First detected in 1904, *C. parasitica* is believed to have been introduced to the U.S. from Asia via nursery stock of Asiatic chestnut species, which were commonly planted in the U.S. (Hepting 1974). In its native range, hosts of *C. parasitica,* such as Japanese and Chinese chestnut (*Castanea crenata* and *C. mollissima*)

are relatively resistant to the fungus (Anagnostakis 2001), presumably due these species co-evolving together (Parker and Gilbert 2004). However, once introduced to the U.S., chestnut blight quickly spread throughout the range of American chestnut, functionally eliminating a species that once occupied 25% of the forest canopy (Hepting 1974, Wang et al. 2013).

Phytophthora ramorum, the oomycete pathogen responsible for sudden oak death (SOD), is a more recent example of a non-native disease. SOD is lethal to both oaks (*Quercus* spp.) and tanoak (*Notholithocarpus densiflorus*). First noticed in the mid 1990's, SOD is a relatively new disease that has reached epidemic levels in the western U.S. as well as in Europe (Rizzo and Garbelotto 2003). Although not a true fungus, *P. ramorum* is a member of the Oomycetes, commonly referred to as water molds. Originally, the disease was thought to be restricted to oaks and tanoak, however it is now known that *P. ramorum* can infect a number of different hosts (over 20 woodland species and over 30 nursery species) with less severity (Davidson et al. 2005).

Dispersal mechanisms play an important role in forest pathogens. *Cryphonectria parasitica* has two mechanism for dispersal: short distance via conidia, and longer distance dispersal through ascospores. Acospores can be discharged continually for up to 14 hours following a light rain (Anagnostakis 1987). Wind then disperses the acospores over long distances. Additionally, while the asexual conidia do not initially disperse far, their long persistence and ability to be transported on the surface of insects, birds, and mammals, adds another dispersal dimension that makes *C. parasitica* a successful pathogen. Similarly, *Phytophthora ramorum*, is thought to be primarily dispersed

through rain and wind. Rain-splash has been documented to spread the pathogen's sporangium (asexual reproductive spores) approximately 10 m in a California mixed evergreen forest, while longer distances (~ 4 km) have been documented via air currents (Davidson et al. 2005, Hansen et al. 2008, Mascheretti et al. 2008, Grünwald et al. 2012). *Phytophthora ramorum* also produces chlamydospores, another asexual spore, which can withstand unfavorable conditions for extended periods of time (Davidson et al. 2005, Tooley et al. 2008, Grünwald et al. 2012).

In contrast to the above dispersal mechanisms, many emerging infectious diseases are facilitated by an insect vector, which transports the pathogen to new hosts. For example, Dutch elm disease (DED), which has multiple fungal pathogens within the genus *Ophiostoma,* is vectored by bark beetles, mainly in the genus *Scolytus*. The initial pathogen in the U.S., *O. ulmi,* was first detected in 1931 and are believed to have been introduced in imported logs infested with beetles, which were used for furniture (Campanella 2003). This symbiosis between fungi and insects has been extremely successful, evolving independently in many different insect taxa (Hulcr and Dunn 2011).

1.2. Dissemination of fungal pathogens by beetles

The evolution of beetle-fungus symbioses are believed to be in response to the evolution of tree defenses against insect herbivores (Hulcr and Dunn 2011). Trees have evolved chemicals, resins, latexes, and allelochemicals, which prevent insects from feeding on bark, phloem, or xylem, even in dead trees (Ma et al. 2010, Hulcr and Dunn 2011). Roughly 60 million years ago, the beetle-fungus association began to arise in

multiple lineages of beetles, circumventing these tree defenses through pre-digestion of wood or tissue (Hulcr and Dunn 2011). Eventually, a mutualism developed in which beetles inoculated newly colonized trees with fungi that are used to feed beetle larvae. For example, southern pine beetle larvae feed almost exclusively on fungi, rather than the phloem consumed by the adults (Barras and Perry 1972, Klepzig and Wilkens 1997). The extreme end of the beetle-fungus symbiosis is found in ambrosia beetles, in which the fungus is "farmed" and is the only food source for both beetle adults and larvae (Hulcr and Dunn 2011). Ambrosia beetles are not a phylogenetic group, rather they have evolved independently in approximately 13 clades of beetles and 11 clades of fungi (Beaver et al. 1989, Farrell et al. 2001, Harrington 2005, Hulcr et al. 2007, Alamouti et al. 2009, Hulcr and Dunn 2011). Many bark and ambrosia beetles have evolved sac-like structures, known as mycangia, which are filled with fungal inoculum. These structures protect the inoculum from desiccation while being transported to new hosts. Mycangium characteristics (location, shape, size) vary in different beetle species and can be used to differentiate certain taxa (Batra 1963).

Anthropogenic activities, such as increased global trade, have increased the spread of bark and ambrosia beetles into new environments. For example, beetles from the sub family Scolytinae, which includes beetles that vector DED and LWD, are the most commonly intercepted insect group at U.S. ports-of-entry, making up 58% of all individuals detected (Hulcr and Dunn 2011). In contrast, scolytine beetles make up less than 0.2 % of all insect species on Earth (Hulcr and Dunn 2011). The increase in use of solid wood crates, dunnage for securing cargo, and wood pallets since the 1980s may be

the reason for bark and ambrosia beetles being introduced more than any other guild of forest pests in recent years (Aukema et al. 2010).

Ploetz et al. (2013) described the recent outbreaks of beetle vectored pathogens as "black swan events", those that are rare, have extreme impacts, and are unpredictable. The rarity of these events is relative. Beetle vectored diseases have increased in the last century, but the majority of beetle-fungus associations (even those that are introduced) are usually benign (Ploetz et al. 2013). Those that are destructively pathogenic in introduced environments are quickly noticed by the high mortality of hosts. Trying to predict which beetle-fungus associated disease will be the next outbreak is likely to be very difficult due the host specificity of the vector and the diversity of beetle-fungus associations. Very little is known about the evolutionary history between beetles, their associated fungi, and host trees.

1.3. Laurel Wilt Disease

Laurel Wilt Disease (LWD), the focus of this dissertation, is a vascular disease caused by the fungal pathogen *Raffaelea lauricola* T.C. Harrington, Fraedrich, & Aghayeva (Fraedrich et al. 2008). Like DED, LWD has a beetle vector which delivers the fungus to a new host. Both the beetle and fungus are native to Asia, and are thought to have been introduced together into the United States through the Port of Savannah sometime around 2002 presumably in wood packing material (Fraedrich et al. 2008). In 2003, reports of high red bay (*Persea borbonia*) mortality began to accumulate, with the original cause of death attributed to drought. In 2004, Fraedrich et al. (2008) examined

dead and dying red bay on Hilton Head Island, SC and recovered two native and one non-native ambrosia beetles from symptomatic red bay stems. The non-native beetle was identified as *Xyleborus glabratus* Eichhoff, and had previously been captured in a monitoring trap in Port Wentworth, GA (near the Port of Savannah) in 2002 (Rabaglia et al. 2006, Fraedrich et al. 2008). Fraedrich et al. (2008) isolated an undescribed fungus both from symptomatic red bay stems and from the mycangia of *X. glabratus* adults emerging from infested red bay logs. This fungus was later described by Harrington et al. (2008) as *Raffaelea lauricola*.

Raffaelea lauricola belongs to family Ophiostomataceae, the same family as other pathogens that are spread by bark and ambrosia beetles such as the DED pathogens (*Ophiostoma ulmi*, *O. himal-ulmi*, and *O. novo-ulmi*), and the pathogen causing Japanese oak wilt (*Raffaelea quercivora*) (Fraedrich et al. 2008; Harrington et al. 2008). *Raffaelea lauricola* exists in a budding yeast form within the mycangia of *X. glabratus*. Once inside a host tree, the fungus produces bundles of asexual conidiophores known as sporodochia, which are consumed by beetle larvae and adults (Harrington et al. 2008).

1.4. Disease Cycle

Only female *X. glabratus* beetles are able to transport spores of the pathogen, *R. lauricola* to new hosts. Male beetles are flightless and remain within infected trees. Female beetles carry the spores in mycangia located near the mandibles. Suitable host trees are located through a combination of visual (Mayfield III and Brownie 2013) and olfactory cues (Hanula and Sullivan 2008, Kendra et al. 2013). Upon landing on a

potential host, the female beetle will attempt to bore into the tree to start a natal gallery. On healthy trees, this first attempt at colonization is usually a failure, as the defenses of the tree prevent further gallery creation (Fraedrich et al. 2008). However, susceptible trees become inoculated with the *R. lauricola* fungus at this time. Spores of *R. lauricola* initiate a reaction from the tree to produce tyloses and gums, which slows the transportation of water through the xylem (Inch and Ploetz 2012, Inch et al. 2012). Within days of inoculation, trees show initial symptoms of LWD, most notably partial wilting of the crown, as well as slight discoloration of vascular tissue. It is believed that the initial partial crown wilting, along with volatiles released by the wounded tree and possibly volatiles released by the fungus itself, attract additional beetles to attack (Hulcr and Dunn 2011, Kuhns et al. 2014, Hughes et al. 2015). As the beetles bore into the tree, wood is removed by the beetle and pushed out of the stem at the point of entry in the form of compacted wood tubes, known as frass (Figure 1.1). This frass is another highly visible, but ephemeral symptom. As the disease progresses, the crown wilts completely. In most species, wilted leaves remain on the tree for some time, however in sassafras (*Sassafras albidum*), leaves fall off more quickly (Cameron et al. 2015). Underneath the bark, extensive black streaking of the sapwood continues as the disease progresses.

Figure 1.1. Wood boring dust (frass) from *X. glabratus* gallery construction

Galleries are constructed within infected red bay stems and are lined with fungal mycelia. Eggs are laid within galleries and the pathogenic fungus is used as a food source for the new population. Unfertilized eggs hatch haploid male beetles with only one set of chromosomes (Hughes et al. 2015). Males then mate with their siblings to produce diploid females. Some female beetles leave the infected stem after mating and the cycle repeats, while others remain in the natal galleries, possibly to ensure continued reproduction in the event that the dispersed beetles fail to find suitable hosts (Maner et al. 2013). Multiple generations of beetles can be produced in a single tree, with initial emergence occurring in less than 40 days after gallery construction in warm months (Hanula et al. 2008, Maner et al. 2013, Brar et al. 2013, Hughes et al. 2015). Galleries can remain active for over a year, with adults emerging on warm days throughout the

year (Hanula et al. 2008, Brar et al. 2012, Maner et al. 2013, Hughes et al. 2015). Infected stems usually break apart within a few years as additional decomposers consume the tree (Cameron et al. 2008).

1.5. Lauraceae

As its name implies, host species for LWD are members of the Lauraceae, including red bay (*Persea borbonia*), swamp bay (*P. palustris*), sassafras (*Sassafras albidum*), as well as economically important species such as avocado (*Persea americana*). LWD has been found in nine naturally infected species: red bay, swamp bay, sassafras, avocado, pondspice (*Litsea aestivalis*), pondberry (*Lindera melissifolia*), silk bay (*Persea humilis*), bay laurel (*Laurus nobilis*), and camphortree (*Cinnamomum camphora*) (Fraedrich et al. 2008, 2011, 2015, Mayfield et al. 2008, Hughes et al. 2011, 2012, 2014). Additionally, inoculation experiments have found five other Lauraceous species to be susceptible: California laurel, Northern spicebush (*Lindera benzoin*), pepperleaf (*Licaria triandra*), *Persea indica*, and lancewood (*Nectandra coriaceae*), although LWD has yet to spread to these specie's ranges (Fraedrich et al. 2008, Ploetz and Konkol 2013, Hughes et al. 2013, 2015). The latest reports on the spread of LWD in Texas place it within 550 km of the Mexican border and an abundance of additional potential lauraceous hosts (Menard et al. 2016).

The Lauraceae are a widespread family of aromatic trees, shrubs, and parasitic vines (*Cassytha*). It is estimated that the Lauraceae are represented by approximately 2500 – 3500 species in 50 genera worldwide (Judd et al. 2008, Weakley 2015). Much of

the diversity of the Lauraceae are located in tropical and subtropical regions such as Southeast Asia and northern South America (Judd et al. 2008). The Lauraceae make up a large portion of the monophyletic order Laurales in the Magnoliid clade (Figure 1.2). Distinguishing characteristics of the Lauraceae include alternate (occasionally opposite) leaves that are simple, entire, and usually not lobed (except, for example in *Sassafras*). Most species have small, pale green, white, or yellow, radial flowers with 6 (or sometimes 3 as in *Persea*) tepals. Flowers in lauraceous species have been described as either perfect, having both stamens and pistils in the same flower, or dioecious, in which individual plants have either male flowers or female flowers. However, many species in the family exhibit heterodichogamy, where flowers temporally alternate between female and male phases. On some individuals, all flowers open in a female phase, with receptive stigmas in the morning, and then reopen 6 – 24 hours later (depending on the species) in a male phase where pollen is released (Judd et al. 2008). On other individuals, all flowers open in the female phase in the afternoon and reopen in the male phase and shed pollen the following morning. This temporal dimorphism encourages outcrossing in populations.

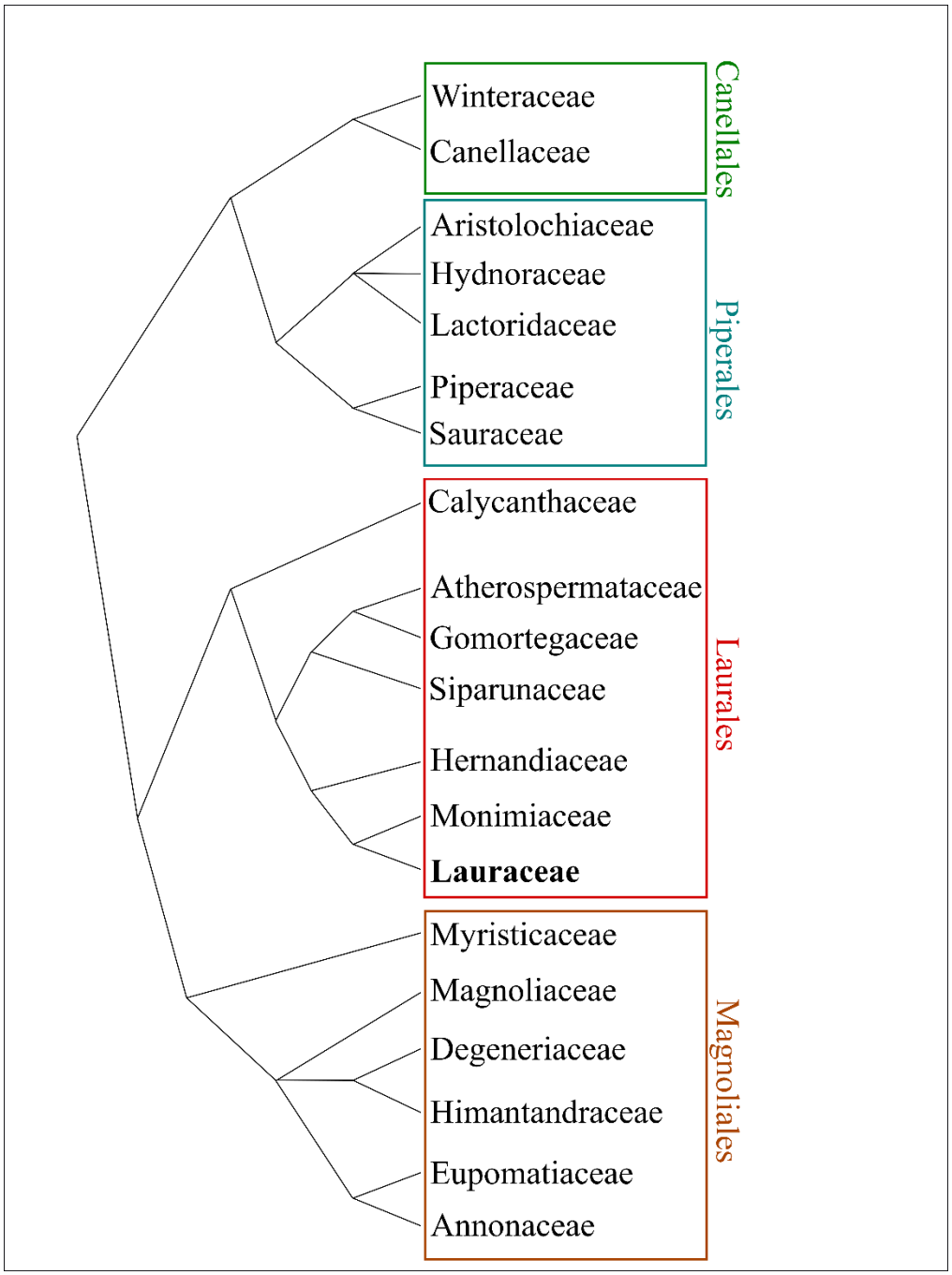

Figure 1.2. Cladogram of the Magnoliid clade showing the relationship of the Lauraceae among the other families. Based on Soltis and Soltis (2004)

Anthers in the Lauraceae open via two or four "flaps", curling upward. Fruit is a drupe, or rarely a one seeded berry (as in avocado, *Persea americana*). Major economical species in the laurel family include bay laurel (*Laurus nobilis*), cinnamon (*Cinnamomum verum*), and avocado. Lauraceae in the southeastern United States include sassafras (*Sassafras albidum*), camphortree (*Cinnamomum camphora*), pondberry (*Lindera melissifolia*), northern spicebush (*L. benzoin*), Bog spicebush (*L. subcoriacea*), as well as avocado, red bay (*Persea borbonia*), swamp bay (*P. palustris*), and silk bay (*P. humilis*).

The genus *Persea* has been revised several times throughout history. First applied in 1601, the word *Persea* was derived from Greek referring to a sacred fruit-bearing tree in Persia and Egypt (Kopp 1966, Coder 2007). Linnaeus incorporated *Persea* into the genus *Laurus* which included the New World species, red bay and avocado, under the names *L. borbonia* and *L. persea* respectively in 1753 (Kopp 1966; Coder 2007). Since that time, the genus has had many names including *Borbonia*, *Farnesia, Menestrata, Tamala,* and *Nothaphoebe* (Coder 2007). Of the roughly 150 – 200 species in the genus *Persea*, only the three bay species, red bay, swamp bay, and silk bay, are native to the southeastern U.S. Catesby (1731) is credited with first describing and illustrating red bay under the name *Laurus caroliniensis* (Sargent 1895, Kopp 1966; Figure 1.3). Catesby's etching of red bay is somewhat ambiguous. His description of the tree suggests that he was actually sketching swamp bay (McMillan et al. 2013, Reveal et al. 2014). However, the leaves in the etching lack the pubescence of swamp bay. Further, the red peduncles and the leaves somewhat resemble lancewood (*Nectandra coriacea*), another lauraceous

species that Catesby described in the Bahamas, suggesting that the red bay illustration may be a composite of all three species (Reveal et al. 2014).

The ambiguity of Catesby's red bay illustration exemplifies the confusion on whether these are indeed three separate species, or varieties of the same species. Swamp bay was first described in 1814 as a variety of red bay by Pursh and is recognized by many authorities as a separate species with ascending (versus appressed) rusty hairs, peduncles 4 – 7cm (versus 1 – 3cm) and more acute leaf blades than red bay (Weakley 2015). Silk bay was noted by Nash in 1895 and described by Kopp (1966) as another variety of red bay and later as a separate species by some authors. Endemic to Florida, silk bay is distinguished by having very dense appressed silky hairs on the underside of the leaves (Weakley 2015). As our study is focused primarily on the Carolinas and Georgia, it is restricted to red bay and swamp bay.

Fernald (1945) expressed the frustration of distinguishing between red bay and swamp bay, writing that he "abandoned the futile attempt to see two species or two varieties in the glabrous-leaved material and that with leaves densely pubescent beneath," and that he "cannot look upon them as anything but glabrous and pubescent forms of one

Figure 1.3. Illustration of red bay by Catesby (1731).

species, *P. borbonia*." Coker and Totten (1945) likewise argued for describing red bay and swamp bay as one species claiming that the distinguishing characteristics between the two are "vague and unsatisfactory", citing an example specimen from North Carolina with short peduncles, suggesting red bay, but with "copiously pubescent" leaves (suggesting swamp bay). However, Wofford and Pearman (1975) conducted a Scanning Electron Microscope (SEM) study on the leaves of native *Persea* species of the southeastern U.S. and found that the pubescence of swamp bay was distinct from red bay. Although hair density was variable, hair length was statistically different from the two species with red bay averaging hairs of 0.16 mm and swamp bay averaging hairs of 0.58 mm (Wofford and Pearman 1975). The SEM study also emphasized the difference between the appressed hairs of red bay and the ascending, or lanate, hairs of swamp bay (Figure 1.4). Wofford (1974) conducted a chemical study on flavonoids in red bay and swamp bay to further separate the species. He suggests that the two are closely related, evolving from a common ancestor, but red bay lacks one unidentified compound and has trace amounts (present in 25% of samples) of three other compounds (orientin, isoorientin, and quercetin 3-O-glucoside) while swamp bay consistently contains these compounds (Wofford 1974). Authorities are increasingly recognizing red bay and swamp bay as different species.

The literature, however, seldom distinguishes between the species. Many studies refer to red bay in their sites, but their site description would suggest that it is actually swamp bay. Once LWD was introduced and mortality of *Persea* species drew attention of

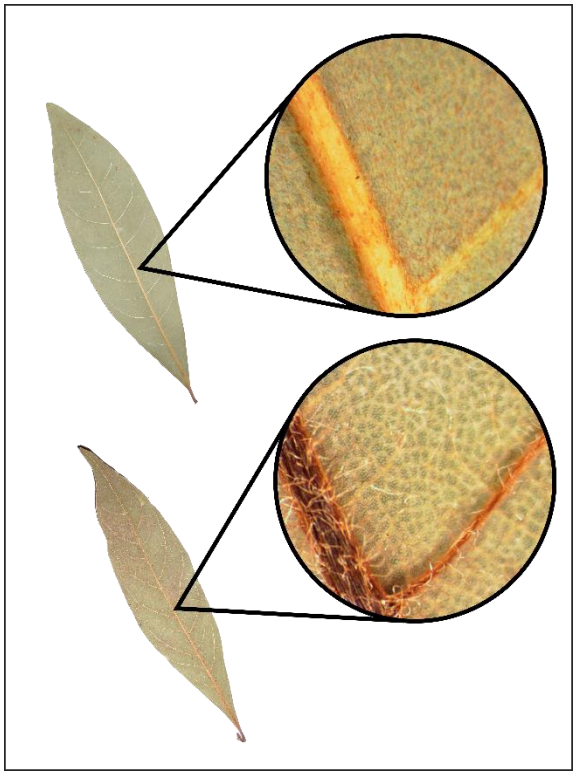

Figure 1.4. Distinguishing characteristics of red bay (top) and swamp bay (bottom).

more researchers, most studies used Brendemuehl's (1990) broader definition of red bay while acknowledging that there may be two different species (for example, Cameron et al. 2008, 2010, 2015, Fraedrich et al. 2008, Spiegel and Leege 2013). No studies have empirically evaluated the differences in red bay and swamp bay communities or whether there are differences in impacts from LWD on these communities.

1.6. Dissertation format

The following chapters document the impacts and implications of LWD on *Persea* communities. Chapters 2 through 5 are independent manuscripts, with literature review, materials and methods, results, and discussion sections. In Chapter 2, I focus on

the impacts of LWD on the entire population of *Persea* species in the U.S., as well as within each state, county, and lastly on individual stems using data from the Forest Inventory and Analysis database of the U.S. Forest Service. In Chapter 3, I look at *Persea* communities, with emphasis on the differences between red bay and swamp bay and the species associated with each. Chapters 4 and 5 detail the aftermath of LWD, in which I discuss the possible fate of *Persea* in the future, as well as potential implications on fire behavior. Lastly, in Chapter 6 I give final conclusions and summary. The objectives of this study were to assess (1) the range-wide changes in *Persea* populations, (2) the patterns of mortality and regeneration, (3) the response of *Persea* communities and possible expansion of invasive plants, and (4) changes in dead woody material and the implications to fire behavior.

1.7. Literature Cited

Alamouti, S. M., C. K. Tsui, and C. Breuil. 2009. Multigene phylogeny of filamentous ambrosia fungi associated with ambrosia and bark beetles. Mycological research 113:822–835.

Anagnostakis, S. L. 1987. Chestnut blight: the classical problem of an introduced pathogen. Mycologia:23–37.

Anagnostakis, S. L. 2001. American chestnut sprout survival with biological control of the chestnut-blight fungus population. Forest Ecology and Management 152:225–233.

Anderson, P. K., A. A. Cunningham, N. G. Patel, F. J. Morales, P. R. Epstein, and P. Daszak. 2004. Emerging infectious diseases of plants: pathogen pollution, climate change and agrotechnology drivers. Trends in Ecology & Evolution 19:535–544.

Aukema, J. E., D. G. McCullough, B. Von Holle, A. M. Liebhold, K. Britton, and S. J. Frankel. 2010. Historical accumulation of nonindigenous forest pests in the continental United States. BioScience 60:886–897.

Barras, S., and T. Perry. 1972. Fungal symbionts in the prothoracic mycangium of Dendroctonus frontalis (Coleopt.: Scolytidae). Zeitschrift für angewandte Entomologie 71:95–104.

Batra, L. R. 1963. Ecology of ambrosia fungi and their dissemination by beetles. Transactions of the Kansas Academy of Science (1903-) 66:213–236.

Beaver, R. A., N. Wilding, N. Collins, P. Hammond, and J. Webber. 1989. Insect-fungus relationships in the bark and ambrosia beetles. Insect-fungus interactions:121–143.

Brar, G. S., J. L. Capinera, P. E. Kendra, S. McLean, and J. E. Peña. 2013. Life Cycle, Development, and Culture of *Xyleborus glabratus* (Coleoptera: Curculionidae: Scolytinae). Florida Entomologist 96:1158–1167.

Brar, G. S., J. L. Capinera, S. Mclean, P. E. Kendra, R. C. Ploetz, and J. E. Peña. 2012. Effect of trap size, trap height and age of lure on sampling Xyleborus glabratus (Coleoptera: Curculionidae: Scolytinae), and its flight periodicity and seasonality. Florida Entomologist 94:1003–1011.

Brendemuehl, R. H. 1990. *Persea borbonia* (L.) Spreng. Red bay. Pages 503–506 *in* R. M. Burns and B. H. Honkala, editors. Silvics of North America. Agriculture Handbook 654, USDA Forest Service, Washington, DC.

Cameron, R. S., C. Bates, and J. Johnson. 2008. Distribution and spread of laurel wilt disease in Georgia: 2006-08 survey and field observations. Georgia Forestry Commission. US Forest Service. http://fhm. fs. fed. us/em/funded/09/so-em-08-02-report. pdf (18 April 2011).

Cameron, R. S., C. Bates, and J. Johnson. 2010. Evaluation of laurel wilt disease in Georgia: progression in red bay and sassafras 2008–2010. Georgia Forestry Commission and US Dep. Agric. Forest Service–Forest Health Protection Region 8.

Cameron, R. S., J. Hanula, S. Fraedrich, and C. Bates. 2015. Progression and Impact of Laurel Wilt Disease within Red bay and Sassafras Populations in Southeast Georgia. Southeastern Naturalist 14:650–674.

Campanella, T. J. 2003. Republic of shade: New England and the American elm. Yale University Press.

Castello, J. D., D. J. Leopold, and P. J. Smallidge. 1995. Pathogens, patterns, and processes in forest ecosystems. Bioscience:16–24.

Coder, K. D. 2007. Taxonomy & Identification: Red bay (*Persea borbonia*). University of Georgia. Warnell School of Forestry & Natural Resources. Outreach Publication SFNR07-2. 10p.

Coker, W. C., and H. R. Totten. 1945. Trees of the southeastern United States. University of North Carolina Press, Chapel Hill.

Connell, J. H. 1971. On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. Dynamics of populations 298:312.

Davidson, J. M., A. C. Wickland, H. A. Patterson, K. R. Falk, and D. M. Rizzo. 2005. Transmission of *Phytophthora ramorum* in mixed-evergreen forest in California. Phytopathology 95:587–596.

Desprez-Loustau, M.-L., C. Robin, M. Buee, R. Courtecuisse, J. Garbaye, F. Suffert, I. Sache, and D. M. Rizzo. 2007. The fungal dimension of biological invasions. Trends in Ecology & Evolution 22:472–480.

Dinoor, A., and N. Eshed. 1984. The role and importance of pathogens in natural plant communities. Annual Review of Phytopathology 22:443–466.

Farrell, B. D., A. S. Sequeira, B. C. O'Meara, B. B. Normark, J. H. Chung, and B. H. Jordal. 2001. The evolution of agriculture in beetles (Curculionidae: Scolytinae and Platypodinae). Evolution 55:2011–2027.

Fernald, M. L. 1945. Botanical specialties of the Seward forest and adjacent areas of southeastern Virginia. Rhodora 47:149–182.

Fraedrich, S. W. 2008. California laurel is susceptible to laurel wilt caused by *Raffaelea lauricola*. Plant Disease 92:1469–1469.

Fraedrich, S. W., T. C. Harrington, R. J. Rabaglia, M. D. Ulyshen, A. E. Mayfield Iii, J. L. Hanula, J. M. Eickwort, and D. R. Miller. 2008. A fungal symbiont of the red bay ambrosia beetle causes a lethal wilt in red bay and other Lauraceae in the southeastern United States. Plant Disease 92:215–224.

Fraedrich, S.W., T.C. Harrington, C. Bates, J. Johnson, L. Reid, T. Leininger, and T. Hawkins. 2011. Susceptibility to laurel wilt and disease incidence in two rare plant species, pondberry and pondspice. Plant Disease. 95:1056–1062.

Fraedrich, S.W., T.C. Harrington, and G.S. Best. 2015. *Xyleborus glabratus* attacks and systemic colonization by Raffaelea lauricola associated with dieback of *Cinnamomum camphora* in southeastern United States. Forest Pathology. 45:60–70.

Grünwald, N. J., M. Garbelotto, E. M. Goss, K. Heungens, and S. Prospero. 2012. Emergence of the sudden oak death pathogen *Phytophthora ramorum*. Trends in microbiology 20:131–138.

Hansen, E. M., A. Kanaskie, S. Prospero, M. McWilliams, E. M. Goheen, N. Osterbauer, P. Reeser, and W. Sutton. 2008. Epidemiology of *Phytophthora ramorum* in Oregon tanoak forests. Canadian Journal of Forest Research 38:1133–1143.

Hanula, J. L., A. E. Mayfield, S. W. Fraedrich, and R. J. Rabaglia. 2008. Biology and host associations of red bay ambrosia beetle (Coleoptera: Curculionidae: Scolytinae), exotic vector of laurel wilt killing red bay trees in the southeastern United States. Journal of economic entomology 101:1276–1286.

Hanula, J. L., and B. Sullivan. 2008. Manuka oil and phoebe oil are attractive baits for *Xyleborus glabratus* (Coleoptera: Scolytinae), the vector of laurel wilt. Environmental entomology 37:1403–1409.

Harrington, T. C. 2005. Ecology and evolution of mycophagous bark beetles and their fungal partners. Insect-fungal associations: ecology and evolution 1:22.

Harrington, T. C., S. W. Fraedrich, and D. N. Aghayeva. 2008. *Raffaelea lauricola*, a new ambrosia beetle symbiont and pathogen on the Lauraceae. Mycotaxon 104:399–404.

Hepting, G. H. 1974. Death of the American chestnut. Journal of Forest History 18:61–67.

Hughes, M.A., J.A. Smith, A.E. Mayfield III, M. Minno, and K. Shin. 2011. First report of laurel wilt disease caused by *Raffaelea lauricola* on pondspice in Florida. Plant Disease. 95:1588

Hughes, M.A., K. Shin, J. Eickwort, and J.A. Smith. 2012. First report of laurel wilt disease caused by *Raffaelea lauricola* on silk bay in Florida. Plant Disease. 96:910.

Hughes, M.A. 2013. The evaluation of natural resistance to laurel wilt disease in red bay (*Persea borbonia*). Ph.D. dissertation, University of Florida, Gainesville, FL.

Hughes, M.A., G. Brar, R.C. Ploetz, and J.A. Smith. 2013. Field and growth chamber inoculations demonstrate *Persea indica* as a newly recognized host for the laurel wilt pathogen, Raffaelea lauricola. Plant Health Progress doi:10.1094/PHP-2013-0814-02-BR.

Hughes, M.A., A. Black, and J.A. Smith. 2014. First report of laurel wilt, caused by *Raffaelea lauricola*, on bay laurel (*Laurus nobilis*) in the United States. Plant Disease. 98:1159.

Hughes, M. A., J. A. Smith, R. C. Ploetz, P. E. Kendra, A. E. Mayfield III, J. L. Hanula, J. Hulcr, L. L. Stelinski, S. Cameron, J. J. Riggins, and others. 2015. Recovery plan for laurel wilt on red bay and other forest species caused by *Raffaelea lauricola* and disseminated by *Xyleborus glabratus*.

Hulcr, J., and R. R. Dunn. 2011. The sudden emergence of pathogenicity in insect–fungus symbioses threatens naive forest ecosystems. Proceedings of the Royal Society B: Biological Sciences 278:2866–2873.

Hulcr, J., M. Kolarik, L. R. Kirkendall, and others. 2007. A new record of fungus-beetle symbiosis in Scolytodes bark beetles (Scolytinae, Curculionidae, Coleoptera). SYMBIOSIS-REHOVOT- 43:151.

Inch, S. A., and R. C. Ploetz. 2012. Impact of laurel wilt, caused by *Raffaelea lauricola*, on xylem function in avocado, *Persea americana*. Forest Pathology 42:239–245.

Inch, S., R. Ploetz, B. Held, and R. Blanchette. 2012. Histological and anatomical responses in avocado, *Persea americana*, induced by the vascular wilt pathogen, *Raffaelea lauricola*. Botany 90:627–635.

Janzen, D. H. 1970. Herbivores and the number of tree species in tropical forests. American naturalist:501–528.

Judd, W. S. C., C. S. Kellogg, E. A. Stevens, P. F. W. S. Judd, C. S. Campbell, E. A. Kellogg, and P. F. Stevens. 2008. Plant systematics: a phylogenetic approach.

Kendra, P. E., W. S. Montgomery, J. Niogret, and N. D. Epsky. 2013. An Uncertain Future for American Lauraceae: A Lethal Threat from Red bay Ambrosia Beetle and Laurel Wilt Disease (A Review). American Journal of Plant Sciences 4:727–738.

Klepzig, K. D., and R. T. Wilkens. 1997. Competitive interactions among symbiotic fungi of the southern pine beetle. Applied and Environmental Microbiology 63:621–627.

Kopp, L. E. 1966. A taxonomic revision of the genus *Persea* in the Western Hemisphere (*Persea*: Lauraceae). Revisión taxonómica del género Persea en el hemisferio occidental (*Persea*: Lauraceae). Memoirs of the New York Botanical Garden. 14:1–120.

Kuhns, E. H., Y. Tribuiani, X. Martini, W. L. Meyer, J. Peña, J. Hulcr, and L. L. Stelinski. 2014. Volatiles from the symbiotic fungus *Raffaelea lauricola* are

synergistic with manuka lures for increased capture of the red bay ambrosia beetle *Xyleborus glabratus*. Agricultural and Forest Entomology 16:87–94.

Ma, L.-J., H. C. Van Der Does, K. A. Borkovich, J. J. Coleman, M.-J. Daboussi, A. Di Pietro, M. Dufresne, M. Freitag, M. Grabherr, B. Henrissat, and others. 2010. Comparative genomics reveals mobile pathogenicity chromosomes in Fusarium. Nature 464:367–373.

Maner, M. L., J. L. Hanula, and S. K. Braman. 2013. Gallery productivity, emergence, and flight activity of the red bay ambrosia beetle (Coleoptera: Curculionidae: Scolytinae). Environmental Entomology 42:642–647.

Mascheretti, S., P. J. P. Croucher, A. Vettraino, S. Prospero, and M. Garbelotto. 2008. Reconstruction of the sudden oak death epidemic in California through microsatellite analysis of the pathogen *Phytophthora ramorum*. Molecular ecology 17:2755–2768.

Mayfield III, A.E., J.A. Smith, M. Hughes, and T.J. Dreaden. 2008. First report of laurel wilt disease caused by *Raffaelea* sp. on avocado in Florida. Plant Disease. 92:208–216.

Mayfield III, A. E., and C. Brownie. 2013. The Red bay Ambrosia Beetle (Coleoptera: Curculionidae: Scolytinae) uses Stem Silhouette Diameter as a Visual Host-Finding Cue. Environmental Entomology 42:743–750.

McMillan, P. D., A. H. Blackwell, C. Blackwell, and M. A. Spencer. 2013. The vascular plants in the Mark Catesby collection at the Sloane Herbarium, with notes on their taxonomic and ecological significance. Phytoneuron 7: 1–37.

Menard, R.D., S.C. Clarke, S. Fraedrich, and T. Harrington. 2016. First report of Laurel Wilt, caused by *Raffaelea lauricola*, on red bay (*Persea borbonia*) in Texas. Plant Disease. http://dx.doi.org/10.1094/PDIS-01-16-0038-PDN

Mordecai, E. A. 2011. Pathogen impacts on plant communities: unifying theory, concepts, and empirical work. Ecological Monographs 81:429–441.

Parker, I. M., and G. S. Gilbert. 2004. The evolutionary ecology of novel plant-pathogen interactions. Annual Review of Ecology, Evolution, and Systematics:675–700.

Ploetz, R.C., and J. Konkol. 2013. First report of gulf licaria, *Licaria triandra*, as a suscept of laurel wilt. Plant Disease. 97:1248.

Ploetz, R.C., J. Hulcr, M.J. Wingfield, and Z.W. de Beer. 2013. Destructive tree diseases associated with ambrosia and bark beetles: Black swan events in tree pathology? Plant Disease 95:856–872.

Rabaglia, R. J., S. A. Dole, and A. I. Cognato. 2006. Review of American Xyleborina (Coleoptera: Curculionidae: Scolytinae) occurring north of Mexico, with an illustrated key. Annals of the Entomological Society of America 99:1034–1056.

Reveal, J. L., K. N. Gandhi, and C. E. Jarvis. 2014. Epitypification of the name *Laurus borbonia* (Lauraceae). Taxon 63:918–920.

Rizzo, D. M., and M. Garbelotto. 2003. Sudden oak death: endangering California and Oregon forest ecosystems. Frontiers in Ecology and the Environment 1:197–204.

Sargent, C. S. 1895. The silva of North America. vol. 8. Houghton Mifflin, Boston, MA.

Soltis, P.S., and D.E. Solits. 2004. The origin and diversification of angiosperms. American Journal of Botany. 91: 1614–1626.

Spiegel, K. S., and L. M. Leege. 2013. Impacts of laurel wilt disease on red bay (*Persea borbonia* (L.) Spreng.) population structure and forest communities in the coastal plain of Georgia, USA. Biological Invasions 15:2467–2487.

Tooley, P. W., M. Browning, and D. Berner. 2008. Recovery of *Phytophthora ramorum* following exposure to temperature extremes. Plant Disease 92:431–437.

Wang, G. G., B. O. Knapp, S. L. Clark, B. T. Mudder, and others. 2013. The silvics of *Castanea dentata* (Marsh.) Borkh., American chestnut, Fagaceae (beech family). Gen Tech Rep SRS-173. USDA Forest Service, Southern Research Station, Asheville, NC p 18.

Weakley, A. S. 2015. Flora of the southern and mid-Atlantic states. University of North Carolina Herbarium, North Carolina Botanical Garden, University of North Carolina, Chapel Hill.

White, P. S. 1979. Pattern, process, and natural disturbance in vegetation. The botanical review 45:229–299.

White, P. S., and S. Pickett. 1985. Natural disturbance and patch dynamics: an introduction. In S.T.A. Pickett and P.S. White (Eds.), The ecology of natural disturbance and patch dynamics. (pp. 3-13). Academic Press.

Wofford, B. E. 1974. The systematic significance of flavonoids in Persea of the southeastern United States. Biochemical Systematics and Ecology 2:89–91.

Wofford, B. E., and R. W. Pearman. 1975. An SEM study of leaf surface pubescence in the southeastern taxa of Persea. SIDA, Contributions to Botany 6:19–23.

CHAPTER TWO

POPULATION DYNAMICS OF RED BAY (*PERSEA BORBONIA*) AFTER LAUREL WILT DISEASE: AN ASSESSMENT BASED ON FOREST INVENTORY AND ANALYSIS DATA

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2.1. Introduction

Laurel wilt disease (LWD) is a lethal vascular infection in trees in the laurel family (Lauraceae) caused by the fungus *Raffaelea lauricola* (Fraedrich et al., 2008; Harrington et al. 2008). The fungus is vectored by a non-native ambrosia beetle (*Xyleborus glabratus* Eichhoff), which was first recorded in the U.S. in 2002 (Rabaglia et al. 2006). Laurel wilt disease was first reported in 2003 in red bay (*Persea borbonia* [L.] Spreng.), and has since spread throughout red bay populations in South Carolina, Georgia, and Florida, as well as parts of North Carolina and small pockets of Mississippi and Alabama (Figure 2.1). Mortality of red bay stems on the infected sites is nearly 100% (Fraedrich et al. 2008; Riggins et al. 2010). Koch and Smith (2008) modeled LWD spreading at a rate of 54.8 km/year and predicted that LWD would spread throughout the entire range of red bay in less than forty years. However, possible anthropogenic activities such as reintroductions and spreading through firewood transportation may accelerate this process (Cameron et al. 2008, 2010). The susceptibility of additional Lauraceous hosts will likely spread the disease beyond the range of red bay (Fraedrich 2008; Gramling 2010; Peña et al. 2012). There is evidence that this may have already

happened in Alabama, where LWD was confirmed in Sassafras 160 km away from the nearest documented infected red bay (Bates et al. 2013).

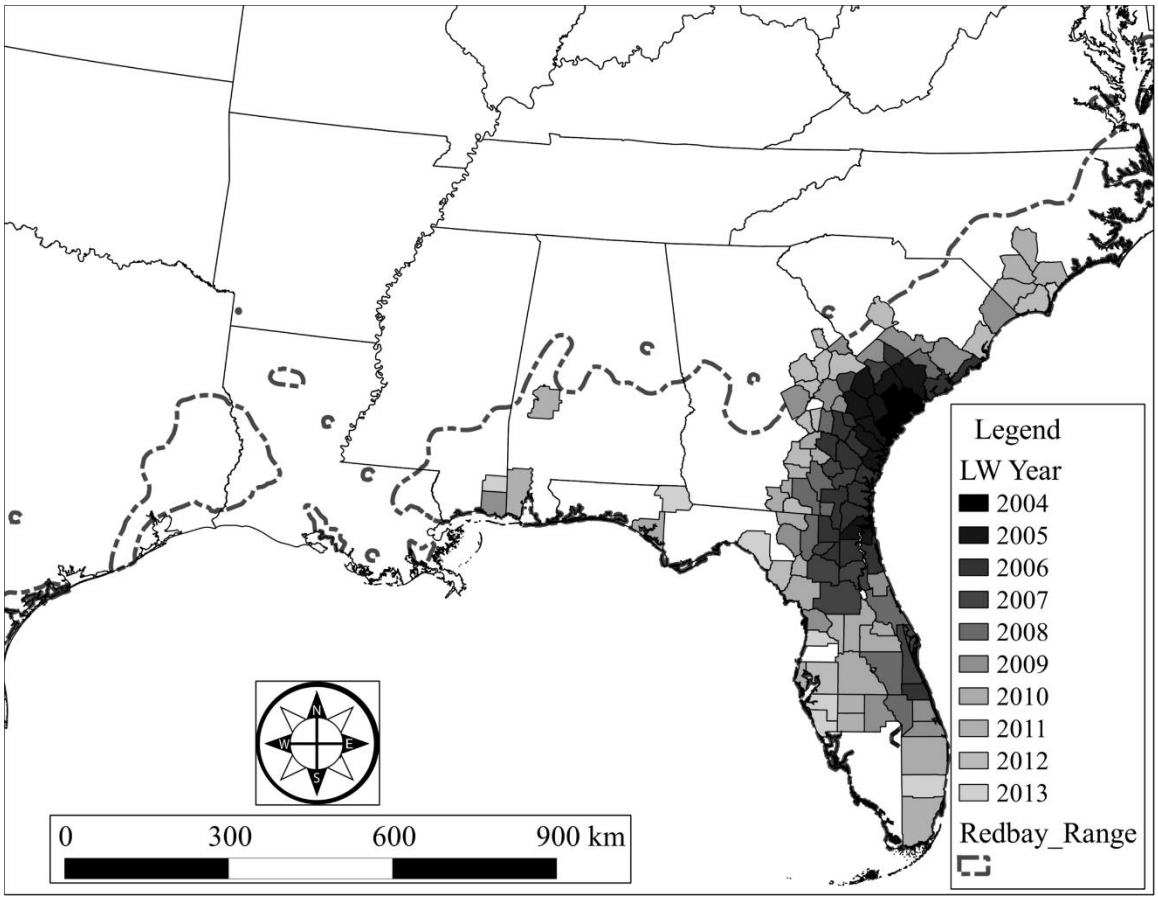

Figure 2.1. Geographic range of red bay (dashed line) in the Southeastern United States (Brendemuehl, 1990). Shaded counties represent the spread of Laurel Wilt Disease as of August, 2013 (USDA, 2013). Darker shades indicate earlier years of reported infection.

Red bay is a medium sized, evergreen broadleaf tree native to the lower coastal plain of the southeastern United States (Brendemuehl 1990). Common along the edges of swamps, coastal hammocks, and wet, well-drained sites, red bay is usually found in mixed stands with species such as loblolly pine (*Pinus taeda* L.), pond pine (*P. serotina*

Michx.), slash pine (*P. elliottii* Engelm.), live oak (*Quercus virginiana* Mill.), water oak (*Q. nigra* L.), black tupelo (*Nyssa sylvatica* Marsh.), and sweetgum (*Liquidambar styraciflua* L.) (Brendemuehl 1990). Red bay can be a major component of the overstory, but is rarely the sole dominant species.

There is debate among taxonomists as to whether red bay and two other closely related congeneric taxa, Swamp bay (*Persea palustris* [Raf.] Sarg.) and silk bay (*P. humilis* Nash), should be split into three separate distinct species or subspecies. Swamp bay is sometimes considered a separate species from red bay, with shorter average height, longer flower stalks and dense bent trichomes on the leaves (Coder 2007). Silk bay is found only in Florida and parts of Texas and flowers about later than red bay (Coder 2007). All three species are susceptible to LWD (Fraedrich et al. 2008; Hughes et al. 2012). The Forest Inventory and Analysis (FIA) database does not distinguish between the three species; therefore this study refers to red bay *sensu lato*.

Most studies on LWD and red bay to date have focused on short-term, stand level impacts. Many studies have recognized a pattern of higher mortality in larger red bay stems (Fraedrich et al. 2008; Shields et al. 2011; Spiegel and Leege 2013). For example, Kendra et al. (2013) found that larger red bay stems had higher numbers of beetle entrance holes and exhibited later stages of the disease than smaller diameter stems. They suggest that the beetles attack larger stems preferentially, which may account for the higher mortality in these larger stems (Kendra et al. 2013). Mayfield and Brownie (2013) used artificial stem silhouettes baited with essential oils to show that *X. glabratus* use visual as well as olfactory cues to locate host trees, with larger silhouettes attracting

more beetles and thus increasing the probability of attack for larger stems. To our knowledge, there have not been any studies on larger scale impacts of LWD on red bay. This study sought to determine whether data collected by the FIA program could be used to verify whether observations made on the smaller scales hold over larger scales.

Starting in 1929, the FIA program was designed to identify long-term trends in U.S. forests on both public and private lands (Smith 2002). For the first five decades of its existence, the FIA program was primarily used for the timber industry (Smith 2002). Over the past 30 years, the program has expanded to increase its role in ecosystem monitoring (Smith 2002). The methodology of the FIA has changed over the years. Originally, inventories were conducted periodically, with states being surveyed on a rotating basis. This resulted in in some states taking as much as 18 years between surveys (Gillespie 1999). In 1999, states began switching to an annual inventory, where 10 to 20 percent of each state was surveyed every year (O'Connell et al. 2013). In addition to providing data in a timelier manner, the new systematic grid design allowed for a representative group of plots to be available for analysis for any area of interest (Smith 2002).

The primary objectives of this study were: (1) to determine if the FIA database could be used to see changes in red bay populations after LWD; (2) to develop a logistic model to predict red bay mortality using individual tree data sampled through the FIA program.

2.2. Materials and Methods

The Forest Inventory and Analysis Program

The current FIA program consists of two main phases (a third phase is also being implemented in some states). Phase 1 consists of remote sensing the extent of forest cover. Millions of points were remotely sensed using satellite imagery or aerial photography. These Phase 1 points are stratified (mainly as either forest or nonforest) to reduce variance in population estimates (Reams et al. 2005).

Phase 2 includes field visits to a subset of Phase 1 plots. Plots were systematically placed using a hexagonal frame design used by the U.S. Environmental Protection Agency's Environmental Monitoring and Assessment Program and later by the Forest Health Monitoring Program (Reams et al. 2005). For this design, a large hexagon was projected over the continental United States, which was then divided into smaller hexagons of approximately 2403 ha each (Reams et al. 2005). A Phase 2 plot was randomly placed in each of the smaller hexagons and assigned to a five panel rotation so that 20% could be surveyed each year (Reams et al. 2005; Smith 2002). Panels were assigned systematically in a uniform distribution (Reams et al. 2005). Plots consist of a cluster of four circular subplots (168 m^2 each). The first subplot is in the center of the plot, while the other three are located 37 m from the first at azimuths of 0, 120, and 240 degrees (Bechtold and Scott 2005). In each subplot, all trees that are 12.7 cm or larger in diameter at breast height (dbh) were measured. Each subplot also contains a 13.5 m^2 microplot which is offset from the center of the subplot by 3.7 m at an azimuth of 90 degrees (Bechtold and Scott 2005). All trees between 2.5 and 12.7 cm dbh were

measured in each microplot. Data obtained from these plots are freely available in the FIA database at: www.fia.fs.fed.us.

Data Analysis

To study range-wide changes in red bay population, we used the Microsoft Access version of the FIA database (version 5.1). The database includes an SQL query to obtain population estimates on trees greater than 2.5 cm in diameter on all forestland. We modified the SQL query in the database to obtain the estimates of all live red bay stems on forestland from 2003–2011. Doubling of the sampling errors approximated a 95% confidence interval of the population estimate (Scott et al. 2005). For any given inventory year, the population of interest is estimated by a moving mean determined from the phase 2 plot inventories multiplied by the extent of forest cover determined by phase 1 plots. The moving mean is an average of the plots that were measured in the current inventory year (~20% of all plots in each state) along with the remaining plots that have been measured in the previous years (~80%) of the inventory cycle (about five years). Population estimates for each state were then summed to estimate a range-wide population. In years where states did not have inventories, populations were estimated by the mean of the previous and subsequent inventories. In cases where there were no previous inventories, populations were assumed to be equal to the next available inventory. We ran least squares regressions of population size versus years on both the total population estimates and the individual state population estimates. To correct for possible errors in the regression estimates due to the nature of the data set, two additional

steps were included in the regression analysis. First, because the population estimates in different states and in different years had different levels of precision, the standard errors of the population estimates were included as a weighting factor in the regressions. The regression results were not altered. Second, because the population estimates were accumulated across years and resulted in a time series, a check for significant auto-correlation was performed. The results indicated that no significant autocorrelation existed.

To see changes in red bay density on the county level, we ran a new query in the FIA database for each state within the native range of red bay. We restricted our results to plots with live red bay stems that have been surveyed since the year 2000 (using the measured year, not the inventory year) and were sampled with the annual inventory methodology. In some instances in the FIA data, trees are measured in earlier years and not in subsequent years and vice versa. In these instances a reason is given for the change. We excluded trees that were tallied in previous inventories, but not in the second inventory due to procedural changes because these trees do not have information on whether they are alive or dead (just that they are no longer being measured). Red bay stems that were reported as missed in the previous inventory were included because if they are alive in the second year of measurement, then they were clearly alive in the first even though they were not directly measured. County data on the first reported year of detection of LWD was obtained from the USDA Forest Service, Region 8, Forest Health, Laurel Wilt website: http://www.fs.fed.us/r8/foresthealth/laurelwilt/. All plots did not have LWD reported in the county during the first measure year. We grouped plots based

whether LWD was reported in the county during the second measure year. We used a paired sample *t*-test to compare red bay density in plots surveyed before and after LWD (n = 229), and also to compare red bay density in plots surveyed twice where no infection was reported (n = 382). The differences in densities between surveys did not meet the assumption of normality, being highly leptokurtic. However, due to the high sample size, we felt the *t*-test was still appropriate. A non-parametric test (Wilcoxon rank-sum) yielded the same results.

For the individual scale, we identified all red bay stems that were surveyed twice and were alive the first time they were surveyed. The FIA database does identify cause of death for a tree, so we filtered out all trees that died for any reason other than "insect" or "disease". We used these data to construct a logistic regression, where the response variable was '1' if the tree was dead in the second survey and '0' if it was alive. For predictor variables, we used diameter at breast height (dbh), and years since infection (based on when LWD was first recorded in the county and the year the actual measurement occurred). We randomly divided our dataset in half and built the model from one half of the dataset (n = 828). The other half (n = 883) was used to validate the accuracy of the model using a confusion matrix. A summary of the two datasets is given in Table 2.1. A Receiver Operator Characteristic (ROC) curve was constructed to evaluate the utility of the model. We used the Hosmer-Lemeshow Goodness of Fit (GOF) test to verify the model fitness.

Table 2.1. Summary of datasets used in a logistic regression to predict the probability of death by laurel wilt disease (LWD). The Model dataset was used to create the regression while the Sample dataset was used to validate the accuracy of the model. The data are individual red bay stems from the Forest Inventory and Analysis (FIA) database. All red bay stems were alive during the first survey.

	Model	Sample
Total stems	828	883
Live stems	697	745
Dead stems	131	138
Stems with LWD in county	259	281
Stems without LWD in county	569	602
Smallest stem dbh (cm)	2.54	2.54
Largest stem dbh (cm)	53.59	62.74
Years of infection		
1	43	38
2	27	42
3	55	65
4	46	43
5	23	23
6	63	62
7	2	7

All analyses were conducted in R version 3.0.1 (R core team 2013). Figures were created using the ggplot2 package (Wickham 2009). The ROC curve was constructed using the Deducer package (Fellows 2012). The confusion matrix utilized the SDMTools

package (VanDerWal et al. 2012). The Hosmer-Lemeshow GOF test was conducted using the ResourceSelection package (Lele et al. 2013).

2.3. Results

Population estimates for red bay by state varied from 3 million to more than 300 million stems and occurred in 0.9 to 5.3 percent of total plots (Table 2.2). As expected, the states in the center of red bay distribution range, including North Carolina, South Carolina, Georgia and Florida, had much larger populations. The range-wide population estimate in 2003 was about 862.2 ± 89.8 million red bay stems, increasing to 951.8 ± 87.1 million in 2011 (Fig. 2.2A). The best-fit regression line was a second order quadratic equation: $\hat{y} = -1.165e+7 + 1.160e+04\ x - 2.886\ x^2$, which explained about 95% of the variation in the data ($p = 0.0001$, Fig. 2.2A). We chose a quadratic equation for our models as opposed to an exponential equation (which would yield a similar fitted line) because it allowed for an eventual decrease in population instead of an upper asymptote. Regression coefficients varied by individual state (Table 2.3). The red bay population in Georgia declined from 241.1 ± 11.9 million stems in 2003 to 150.3 ± 7.9 million stems in 2011 (Fig. 2.2B). Population estimates for all other states increased during the period, with the exception of Texas, which decreased by 6.8 million (Fig. 2.2B). The best-fit regression equations for Georgia, Mississippi, and Texas were linear, indicating a linear decline in Georgia and Texas but a linear increase in Mississippi, whereas Alabama, Florida, North Carolina, South Carolina were best fit by quadratic equations with negative curvatures (Fig. 2.2B, Table 2.1) and Virginia was best fit by a quadratic

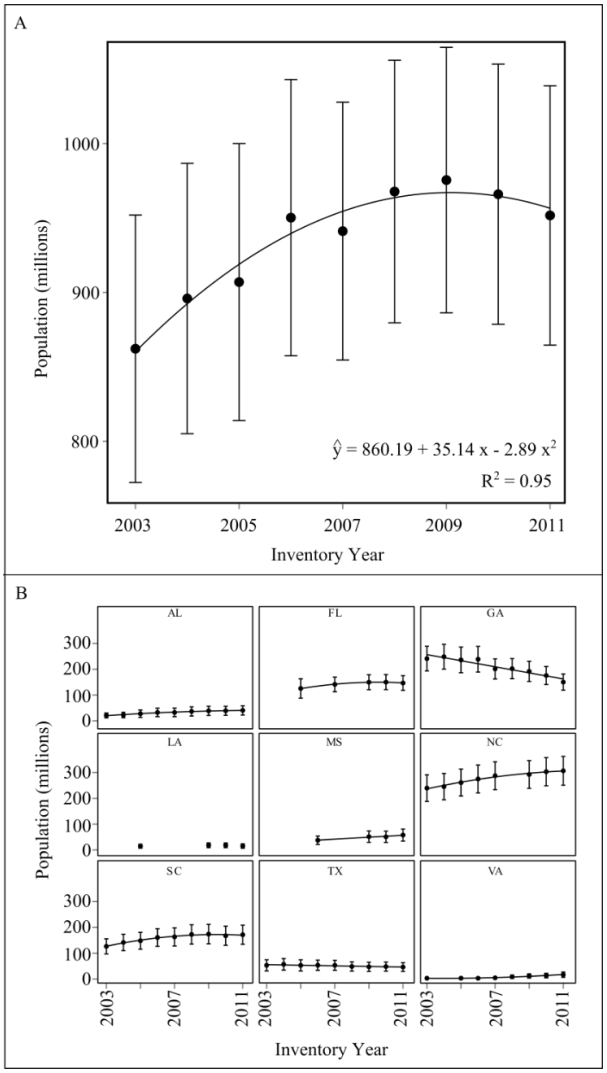

Figure 1.2. Number of live red bay (*Persea borbonia*) stems with diameter at breast height greater than 2.54 cm on forestland across the entire range (A) and by individual states (B). Data are from the Forest Inventory and Analysis database and cover the years 2003 – 2011 (coded as 0 – 8 in the regression analyses). Error bars represent 95% confidence. Trend lines are the best fit least square regressions. See Table **2.**1 for individual state regression equations.

Table 2.2. Population estimates and 95% confidence (millions of stems) of red bay (*Persea borbonia*) for each state in each inventory year. Estimates are from Forest Inventory data. Total population is the sum of each state. In years where states did not have inventories, populations were estimated by the mean of the previous and subsequent inventories. In cases where there were no previous inventories, populations were assumed to be equal to the next available inventory.

	Inventory Year								
State	2003	2004	2005	2006	2007	2008	2009	2010	2011
AL	21.2 ±4.6	22.8 ±5.2	27.9 ±7.2	32.8 ±8.1	32.9 ±8.2	36.7 ±8.9	38.9 ±8.9	39.2 ±8.8	40.6 ±8.9
FL			125.5 ±18.7		141.2 ±14.1		149.8 ±14.6	150.1 ±14.6	146.7 ±14.2
GA	241.1 ±23.9	248.5 ±23.9	236.1 ±24.8	238.7 ±24.8	201.2 ±19.4	202.3 ±19.4	191.8 ±19.5	175.6 ±17.4	150.3 ±15.8
LA			14.5 ±3.8				18.2 ±4.6	18.0 ±4.5	15.2 ±4.2
MS				37.6 ±8.1			51.5 ±10.9	50.8 ±10.9	57.8 ±11.6
NC	239.4 ±25.8	245.3 ±25.5	261.0 ±26.1	274.9 ±26.9	287.4 ±27.0		292.3 ±26.9	303.0 ±27.2	306.5 ±27.9
SC	126.5 ±14.5	141.6 ±15.9	148.1 ±16.3	160.8 ±17.1	163.2 ±17.5	172.6 ±18.7	173.9 ±18.9	167.7 ±18.4	171.5 ±18.5
TX	53.2 ±10.8	56.9 ±11.2	52.9 ±10.8	53.6 ±9.9	53.2 ±9.6	48.6 ±8.8	47.3 ±8.8	48.2 ±8.6	46.3 ±8.3
VA	3.2 ±1.8		3.3 ±1.8	3.1 ±1.7	4.6 ±2.0	8.7 ±3.2	11.9 ±4.1	13.4 ±4.4	16.9 ±5.2
Total	862.2 ±89.8	895.9 ±90.8	907.0 ±93.0	950.3 ±92.8	941.2 ±86.6	967.8 ±88.2	975.5 ±89.2	966.0 ±87.4	951.8 ±87.1

equation but with a slightly positive curvature. No significant trend in population change was detected for the Louisiana data.

Red bay density decreased significantly in plots that were surveyed before and after LWD was reported in that county, while plots without LWD had no significant change (Fig. 2.3). Plots before and after LWD had a mean difference of 89.6 live red bay stems/ha greater than 2.54 cm in diameter (t = 3.356, df = 228, $p < 0.001$). The mean difference in plots without LWD was -0.8 stems/ha, which was not significantly different than zero (t = -0.054, df = 381, p = 0.96).

The logistic regression model, $P_{(\text{dead})} = \frac{e^{-4.398+0.931\,x1+0.049\,x2}}{1+e^{-4.398+0.931\,x1+0.049}}$, where x_1 is years since LWD has been reported in the county and x_2 is diameter at breast height, shows that years since LWD and stem size were highly significant predictors of death by disease or insect ($p < 0.001$ and p = 0.005, respectively) in the sample data (Table 2.4). When holding stem size constant, the model suggests that each additional year since LWD results in a 153.7% increase in the odds of death (Table 2.4). Likewise, when holding time since LWD constant, an increase of 1 cm in stem diameter results in a 5.0% increase in the odds of death (Table 2.4).

The ROC curve resulted in an area under the curve (AUC) of 0.905 (Fig. 2.4). The ROC curve compares the model's predictive abilities with that of random guessing (the straight line in the figure) across all ranges of thresholds. The curve plots the probability of predicting a true positive (sensitivity) against the probability of predicting a false positive (1-specificity). The threshold is the adjustable value at which the model calls a stem dead or alive. High threshold settings (for example 0.95), result in fewer false

positives, however this also results in fewer true positives. A higher AUC values result in a more accurate model for any given threshold and thus makes the AUC a good measure of model adequacy.

Table 2.3. Regression equations for each state describing the change of the number of live red bay (*Persea borbonia*) stems with diameter at breast height greater than 2.54 cm ($\hat{y}$) over time (x). Data are from the Forest Inventory and Analysis database and cover the years 2003 – 2011 (coded as 0 – 8).

State	Regression Equation	*P*-value	R^2
AL	$\hat{y} = 20.27 + 4.34\,x - 0.23\,x^2$	<0.001	0.98
FL	$\hat{y} = 98.99 + 15.49\,x - 1.18\,x^2$	0.004	0.99
GA	$\hat{y} = 256.67 - 11.79\,x$	<0.001	0.91
LA	No significant model could be fit.		
MS	$\hat{y} = 26.40 + 3.84\,x$	0.025	0.95
NC	$\hat{y} = 236.45 + 14.43\,x - 0.72\,x^2$	<0.001	0.98
SC	$\hat{y} = 126.87 + 14.02\,x - 1.08\,x^2$	<0.001	0.98
TX	$\hat{y} = 55.81 - 1.17\,x$	0.002	0.78
VA	$\hat{y} = 2.84 - 0.42\,x + 0.28\,x^2$	<0.001	0.97

When the model was applied to the second dataset, as expected, high proportions of live stems were observed in early years since LWD, while low proportions of live stems were observed in late years since LWD, all of which were in the 2.5 – 12 cm range

after seven years since LWD (Fig. 5). The model had an overall accuracy of 95%, with 826 out of 883 correct predictions with a prediction threshold of 0.5. However, the accuracy of predicting dead stems was only 74% with 102 out of 138 correct predictions (Table 5). The overall accuracy was greatly increased by the accuracy of predicting live stems (97%, with 724 accurate predictions out of 745). The Hosmer-Lemeshow GOF test failed to reject the null hypothesis that there was no significant lack of fit in the model ($X^2 = 7.757$, $df = 8$, $p = 0.458$; Table 2.5).

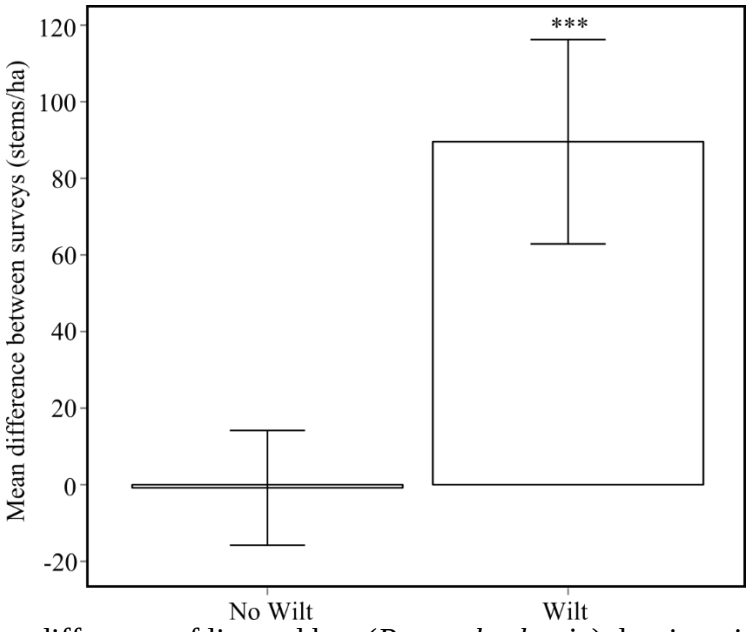

Figure 2.2. Mean difference of live red bay (*Persea borbonia*) density with diameter at breast height greater than 2.54 cm between plots in the Forest Inventory and Analysis Database that were surveyed twice. All plots had no recorded laurel wilt disease (LWD) in the county during the first survey. Plots were grouped into those that had no reports of LWD in the county during the second survey (n = 382) and those that did have LWD reported in the county (n = 229). Error bars represent one standard error; *** represents significance at the 0.001 level (t = 3.356, df = 228).

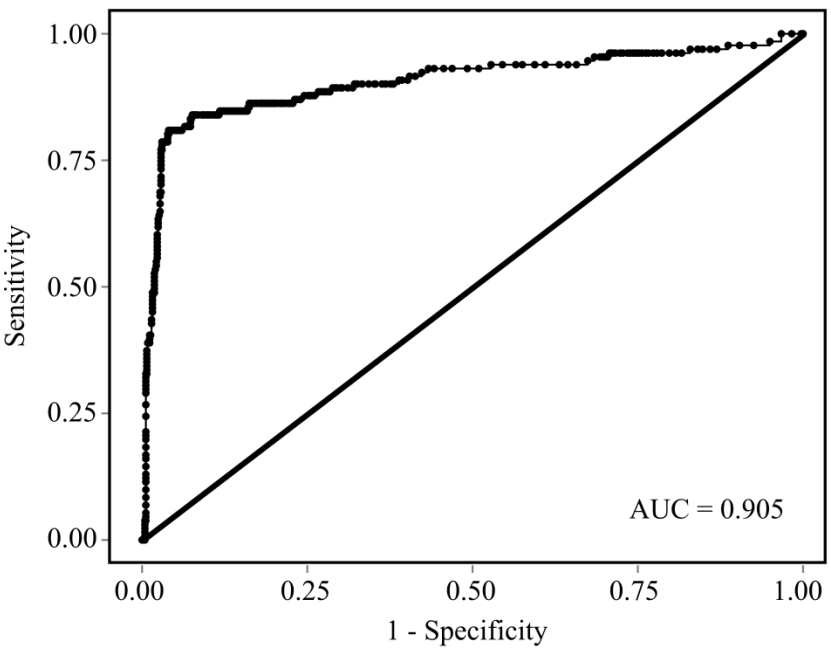

Figure 2.3. Receiver Operating Characteristic (ROC) curve for the logistic model predicting the probability of death by laurel wilt disease in red bay (*Persea borbonia*). The curve plots the probability of making true positive predictions (Sensitivity) against the probability of making false positive predictions (1 – Specificity) over a continuum of threshold values. The resulting area under the curve (AUC) can be used as a measure of the models usefulness compared to random guessing (the straight line) or when comparing other models.

Table 2.4. Parameter estimates and their corresponding *p*-values for the logistic regression model of probability of death by laurel wilt disease (LWD) for red bay (*Persea borbonia*). The model was fitted to 828 red bay stems in the Forest Inventory and Analysis database. Change in odds represents the change in odds of death by LWD for each change in one unit of the parameter, holding the other parameter constant (found by the equation: change = (exp(β) - 1) * 100, where β is the parameter estimate).

	Parameter Estimate	95% CI	Z	*p*	Change in odds (%)
Intercept	-4.398		-11.846	<0.001	
Years of Wilt	0.931	[0.806,1.07]	13.953	<0.001	153.70
Diameter (cm)	0.049	[0.02,0.08]	2.806	0.005	5.02

Table 2.5. Accuracy of the logistic regression model in predicting live and dead red bay (*Persea borbonia*) stems. The model: $P(\text{dead}) = \exp(-4.398 + 0.931\ x_1 + 0.049\ x_2)/[1+\exp(-4.398 + 0.931\ x_1 + 0.049\ x_2)]$, where x_1 is years since LWD has been in the county and x_2 is diameter at breast height. The model was made to 828 red bay stems. The other half of the dataset consisting of 883 red bay stems was used to validate model predictions with a threshold of 0.5 probability of death. The Hosmer-Lemeshow Goodness of fit tests the null hypothesis (there is no significant lack of fit) against the alternative (there is significant lack of fit).

	Observed		
Predicted	Live	Dead	Total
Live	724	36	
Dead	21	102	
Accuracy	0.97	0.74	0.94

Hosmer-Lemeshow Goodness of fit: $X^2 = 7.757$, $df = 8$, $p = 0.458$

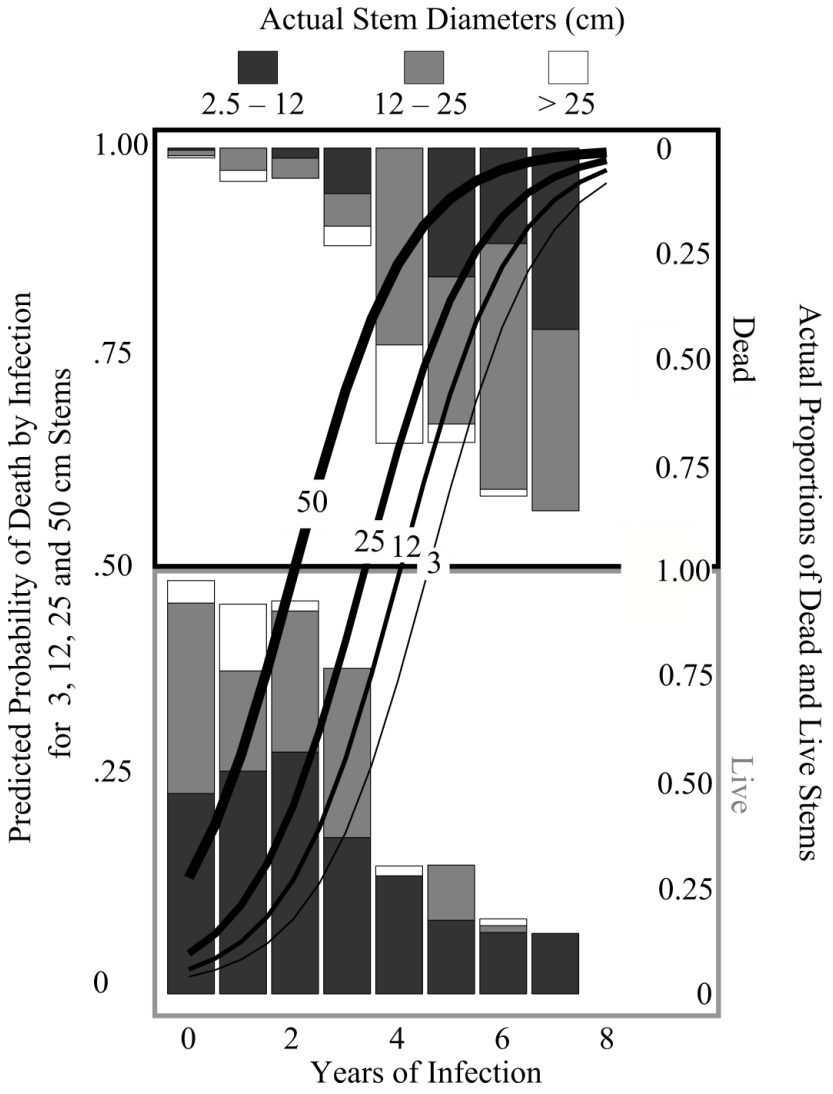

Figure 2.4. Probability curves for hypothetical 3, 12, 25, and 50 cm red bay (Persea borbonia) stems (left axis) over Years of Infection of laurel wilt disease (LWD) in the county. Curves are a result of the logistic model: $P(dead) = \exp(-4.398 + 0.931\ x_1 + 0.049\ x_2)/[1+\exp(-4.398 + 0.931\ x_1 + 0.049\ x_2)]$, where x_1 is years since LWD has been in the county and x_2 is diameter at breast height. The model was fitted to 828 red bay stems. Bars represent actual proportions (right axis) of live (bottom) and dead (top) stems from an additional dataset of n = 883.

2.4. Discussion

Our range-wide and state-level estimates of red bay populations at different years had mostly overlapping confidence intervals, which would suggest no significant population change over the study years. However, this result might be somewhat misleading due to the methods used for FIA data collection and in calculating the estimates for each year. Because each year only about 20% of the FIA plots were measured, our estimates are calculated as moving averages. More precisely, about 80% of the data used in the population estimate of any given year are the same as that of the previous year (for example, see Westfall et al. 2013). Thus, the data from year to year are not entirely independent, which makes using the overlapping confidence intervals inappropriate for determining significance (Schenker and Gentleman 2001). The positive covariance between any two inventory years would make the standard error smaller so the error bars presented here are too large to accurately represent the 95% confidence (Westfall et al. 2013). Unfortunately, we cannot easily separate the standard errors that are dependent from those that are independent using this FIA estimation. Red bay density is highly variable in the field, so error bars at this scale are likely to be large regardless. Furthermore, there is going to be some degree of lag in any observation of population decline since only ~20% of new plots are measured from year to year. Compounding the issues cited above, inventory years are not always the same as the actual year that plots were measured and plots were not always measured every 5 years consistently (Table 2.6).

Table 2.6. Results of a simple query of red bay trees on one plot in the Forest Inventory and Analysis database for Florida. Reconcile code provides a reason why the tree was not tallied in the previous inventory. In this case, code 1 represents ingrowth. P2 Panel is the Panel designation (1–5) that indicates the position of the plot in the 5-year sampling rotation of the state. Inventory Year represents the inventory where the plot is used for estimations, while Measure Year is the actual year the plot was measured

Tree	Reconcile Code	P2 Panel	Inventory Year	Measure Year	State	County
1		1	2002	2004	FL	Collier
2		1	2002	2004	FL	Collier
3		1	2002	2004	FL	Collier
4		1	2002	2004	FL	Collier
1		3	2009	2009	FL	Collier
2		3	2009	2009	FL	Collier
3		3	2009	2009	FL	Collier
4		3	2009	2009	FL	Collier
5	1	3	2009	2009	FL	Collier
6	1	3	2009	2009	FL	Collier

Despite the above limitations on the estimation of red bay population in each study year, the range-wide red bay population did show some evidence of decline in recent years, as indicated by the negative curvature of the fitted regression. At the level of the state, Georgia has shown the most pronounced decline in red bay population, probably due to being the state where LWD was first detected (Fraedrich et al. 2008). All other states that have been reported as having LWD also displayed a trend of recent decline as indicated by the negative curvature of the fitted regression, with the exception of Louisiana and Mississippi where LWD was only recently detected within a small area.

Red bay population appears to have increased in the years prior to 2009, where it begins to decline. There could be few explanations for this increase. Some of the increase could be missed trees tallied in later inventories but not in earlier ones. It is possible that a tree that was killed by LWD (or other reason) has resprouted and those resprouts are counted as new individuals. However, this could only happen if the resprouts were also located within the microplot (or have grown to 12.7 cm dbh between measurements, which is unlikely). The addition of new plots over the years could also increase the population estimate by raising the average number of trees and by increasing the estimated forest area with red bay.

For population dynamics of red bay over this relatively short time period, the FIA data is more reliable at the level of county. We have shown that counties with reported LWD presence had significantly reduced red bay populations. Our result suggests that as LWD spreads to more counties, a significant decline in the state and subsequently the range-wide population should be clearly manifested in future inventories. Since the majority of red bay stems are located in FL, GA, NC, and SC, these states will play pivotal roles in the future of the range-wide population decline.

Our logistic model agrees with observations and studies such as Fraedrich et al. (2008) and Mayfield and Brownie (2013) that larger diameter stems have higher probability of attack. Although it is not clear whether *X. glabratus* attacks smaller stems once the larger ones are depleted (Shields et al. 2011), our model does predict an increased probability of death with time since LWD regardless of diameter. Maner et al. (2014) found that beetle populations remained low after all larger stems were dead. They

confirmed in the laboratory that *X. glabratus* can successfully breed in smaller stems, but these small stems produced few adults and took longer than that of larger (over 3 cm) stems (Maner et al. 2014). They suspect that it is these small stems that allow for beetle populations to persist in such low densities as far as 9 years after the initial invasion (Maner et al. 2014).

Given the patchiness of red bay throughout its range, we questioned whether red bay density would also aid *X. glabratus* in locating host trees. However, plot density was not identified as a significant predictor in our model, which may suggest that encounters with red bay are due to chance after beetles emigrate from infected areas. Mayfield and Brownie (2013) stated an additional hypothesis for the preference of *X. glabratus* for large diameter stems. Since *X. glabratus* uses the xylem of its host for the construction of egg galleries and the cultivation of fungi (Harrington et al. 2010), larger diameter stems equates to larger egg galleries and increased brood size (Brar et al. 2013; Mayfield and Brownie 2013).

Our model performed better when predicting live trees. This is likely due to the large amount of uninfested plots in the dataset, which led to low probabilities of death. Incorrect predictions could be due to a number of factors. Having LWD in the county does not necessarily mean that it was in the plot when measured. This could lead to the model predicting a higher probability of death.

Although LWD results in a high mortality rate, some red bay stems may survive the infestation as indicated by our model and our assessment made at the level of county. For example, in our validation dataset, approximately 12% of stems in the 2.5 to 12 cm

dbh range were alive after 7 years of LWD in the county. Cameron et al. (2010) found several large stems up to 14 cm in diameter near Savannah, GA, in areas that have had the disease for a number of years. We have also observed that relatively large stems remained alive in infected stands after nine years on both Hunting Island, in the 15 – 20 cm class, and Hilton Head Island, in the 5 – 10 cm class (Shearman, personal observation). These survivors may be important seed sources for future generations of red bay. It is unknown whether these survivors are simply overlooked by *X. glabratus*, or convey some type of immunity to beetle attacks or the subsequent fungal infection. Resistance to LWD in red bay is currently being studied (see Hughes and Smith 2014).

We have shown that FIA database can be used to evaluate population dynamics of red bay. However, long term, range wide dynamics will likely be more evident after LWD has progressed throughout the range of red bay and more inventory cycles have been completed. Querying the FIA database on a plot and tree basis can be used to see short term population dynamics at the county and individual scale.

Attempts at preventing the spread of LWD to date have been largely unsuccessful. Carrillo et al. (2013) found that insecticides such as malathion and z- cypermethrin + bifenthrin were highly toxic to *X. glabratus* and significantly reduced the number of beetle entrance holes in avocado. However, all of the insecticides tested by Carrillo et al. (2013) had low persistence, requiring numerous applications for long-term prevention. Mayfield et al. (2008a) found that macroinfusions of the fungicide propiconazole successfully prevented symptoms of LWD in inoculated red bays for at least 7.5 months. Red bays would need to be retreated on a yearly basis to keep the concentrations of

propiconazole at effective levels (Mayfield et al. 2008a; Ploetz et al. 2011). Perhaps this, along with a focus on larger diameter red bay stems could be a potential, albeit costly (both monetarily and in the detrimental effects of yearly injections), preventative measure.

The only available management option may be to let the disease run its course. Hanula et al. (2008) found that beetle populations significantly declined after all red bays in the area have been killed. There is evidence of regeneration of red bay in some infected stands (Shearman personal observation), so it is possible that by the time these stems grow large enough to be attacked, the beetle population may be extirpated (either on its own or through management). Any decline in red bay population may therefore be a shift to lower diameter classes as seen by Spiegel and Leege (2013), rather than complete loss of the species, provided that other species do not increase in abundance and prevent red bay from returning (Goldberg and Heine 2009), or browsing by herbivores does not impede regeneration (Evans et al. 2013). How red bay regenerates and how the communities respond to LWD is a topic of our future study.

2.5. Literature Cited

Bates CA, Fraedrich SW, Harrington TC, Cameron RS, Menard RD, Best GS (2013) First report of laurel wilt, caused by *Raffaelea lauricola*, on Sassafras (*Sassafras albidum*) in Alabama. Plant Dis 97:688.

Bechtold WA, Scott CT (2005) The forest inventory and analysis plot design. In: Bechtold WA, Patterson PL (Eds) The enhanced Forest Inventory and Analysis program–National sampling design and estimation procedures. U.S. Department of Agriculture Forest Service, Southern Research Station. Gen Tech Rep SRS-80 Asheville NC 85 pp.

Brar GS, Capinera JL, Kendra PE, McLean S., Peña JE (2013) Life cycle, development, and culture of *Xyleborus glabratus* (Coleoptera: Curculionidae: Scolytinae). Fla Entomol 96:1158–1167.

Brendemuehl RH (1990) *Persea borbonia* (L.) Spreng. Red bay. In: Burns RM, Honkala BH (Eds.), Silvics of North America. Agriculture Handbook 654, USDA Forest Service, Washington, DC, pp. 503–506.

Cameron RS, Bates C, Johnson J (2008) Distribution and spread of laurel wilt disease in Georgia: 2006-08 survey and field observations. Georgia Forestry Commission, Georgia.

Cameron RS, Bates C, Johnson J (2010) Evaluation of laurel wilt disease in Georgia: Progression in red bay and sassafras – 2008–2010. Georgia Forestry Commission. Georgia.

Carrillo D, Crane JH, Peña JE (2013) Potential of contact insecticides to control *Xyleborus glabratus* (Coleoptera: Curculionidae), a vector of laurel wilt disease in avocados. J Econ Entomol 106:2286–2295.

Coder KD (2007) Taxonomy & identification: red bay (*Persea borbonia*). Univ Ga Warn Sch For Nat Resour Outreach Publ SFNR07-2 10p.

Evans JP, Scheffers BR, Hess M (2013) Effects of laurel wilt invasion on red bay populations in a maritime forest community. Biol Invasions 15, Online First 8p.

Fellows I (2012) Deducer: A data analysis GUI for R. J Stat Soft 49(8):1-15. URL http://www.jstatsoft.org/v49/i08/.

Fraedrich SW (2008) California laurel is susceptible to laurel wilt caused by *Raffaelea lauricola*. Plant Dis 92:1469–1469.

Fraedrich SW, Harrington TC, Rabaglia RJ, Ulyshen MD, Mayfield III AE, Hanula JL, Eickwort JM, Miller, DR (2008). A fungal symbiont of the red bay ambrosia beetle causes a lethal wilt in red bay and other Lauraceae in the southeastern United States. Plant Dis 92:215–224.

Gillespie AJ (1999) Rationale for a national annual forest inventory program. J For 97:16–20.

Goldberg N, Heine J (2009) A comparison of arborescent vegetation pre-(1983) and post-(2008) outbreak of the invasive species the Asian ambrosia beetle *Xyleborus glabratus* in a Florida maritime hammock. Plant Ecol Divers 2:77–83.

Gramling JM (2010) Potential effects of laurel wilt on the flora of North America. Southeast Nat 9:827–836.

Hanula JL, Mayfield AE, Fraedrich SW, Rabaglia RJ (2008) Biology and host associations of red bay ambrosia beetle (Coleoptera: Curculionidae: Scolytinae), exotic vector of laurel wilt killing red bay trees in the southeastern United States. J Econ Entomol 101:1276–1286.

Harrington TC, Aghayeva DN, Fraedrich SW (2010) New combinations in *Raffaelea*, *Ambrosiella*, and *Hyalorhinocladiella*, and four new species from the red bay ambrosia beetle, *Xyleborus glabratus*. Mycotaxon 111:337–361.

Harrington TC, Fraedrich SW, Aghayeva DN (2008) *Raffaelea lauricola*, a new ambrosia beetle symbiont and pathogen on the Lauraceae. Mycotaxon 104:399–404.

Hughes MA, Shin K, Eickwort J, Smith JA (2012) First report of laurel wilt disease caused by *Raffaelea lauricola* on silk bay in Florida. Plant Dis 96:910–911.

Hughes MA, Smith JA (2014) Vegetative propagation of putatively laurel wilt-resistant red bay (Persea borbonia) Native Plants 13:42–50.

Kendra PE, Montgomery WS, Niogret J, Epsky ND (2013) An uncertain future for American Lauraceae: A lethal threat from red bay ambrosia beetle and laurel wilt disease (a review). Am J Plant Sci 4:727–738.

Koch FH, Smith WD (2008) Spatio-temporal analysis of *Xyleborus glabratus* (Coleoptera: Circulionidae: Scolytinae) invasion in eastern US forests. Environ Entomol 37:442–452.

Maner ML, Hanula JL, Horn S (2014) Population trends of the red bay ambrosia beetle (Coleoptera: Curculionidae: Scolytinae): Does utilization of small diameter red bay trees allow populations to persist? Fla Entomol 97:208–216.

Mayfield III AE, Barnard EL, Smith JA, Bernick SC, Eickwort JM, Dreaden TJ (2008a) Effect of propiconazole on laurel wilt disease development in red bay trees and on the pathogen in vitro. Arboric Urban For 34:317–324.

Mayfield III AE, Smith JA, Hughes M, Dreaden TJ (2008b) First report of laurel wilt disease caused by a *Raffaelea* sp. on avocado in Florida. Plant Dis 92:976–976.

Mayfield III AE, Brownie C (2013) The red bay ambrosia beetle (Coleoptera: Curculionidae: Scolytinae) uses stem silhouette diameter as a visual host-finding cue. Environ Entomol 42:743–750.

Lele SR, Keim JL, Solymos P (2013) ResourceSelection: resource selection (probability) functions for use-availability data. R package version 0.2-3. http://CRAN.R-project.org/package=ResourceSelection.

O'Connell BM, LaPoint EB, Turner JA, Ridley TR, Boyer D, Wilson AM, Waddell KL, Conkling BL (2013) The Forest Inventory and Analysis Database: Database description and user manual version 5.1.5 for Phase 2. USDA Forest Service. 531 p. http://www.fia.fs.fed.us/.

Peña JE, Carrillo D, Duncan RE, Capinera JL, Brar G, McLean S, Arpaia ML, Focht E, Smith JA, Hughes M (2012) Susceptibility of *Persea* spp. and other Lauraceae to attack by red bay ambrosia beetle, *Xyleborus glabratus* (Coleoptera: Curculionidae: Scolytinae). Fla Entomol 95:783–787.

Ploetz RC, Pérez-Martínez JM, Evans EA, Inch SA (2011) Toward fungicidal management of laurel wilt of avocado. Plant Dis 95:977–982.

R Core Team (2013) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/. Accessed: November 4, 2013

Rabaglia RJ, Dole SA, Cognato AI (2006) Review of American Xyleborina (Coleoptera: Curculionidae: Scolytinae) occurring north of Mexico, with an illustrated key. Ann Entomol Soc Am 99:1034–1056.

Reams GA, Smith WD, Hansen MH, Bechtold WA, Roesch FA, Moisen GG. 2005. The forest inventory and analysis sampling frame. In: Bechtold WA, Patterson PL (Eds) The enhanced Forest Inventory and Analysis program–National sampling design and estimation procedures. U.S. Department of Agriculture Forest Service, Southern Research Station. Gen Tech Rep SRS-80 Asheville NC 85 pp.

Riggins JJ, Hughes M, Smith JA, Mayfield III AE, Layton B, Balbalian C, Campbell R (2010) First occurrence of laurel wilt disease caused by *Raffaelea lauricola* on red bay trees in Mississippi. Plant Dis 94:634–634.

Schenker N, Gentleman JF (2001) On judging the significance of differences by examining the overlap between confidence intervals. Am Stat 55:182–186.

Scott CT, Bechtold WA, Reams GA, Smith WD, Westfall JA, Hansen MH, Moisen GG (2005) Sample-based estimators used by the Forest Inventory and Analysis national information management system. In: Bechtold WA, Patterson PL (Eds) The enhanced Forest Inventory and Analysis program–National sampling design and estimation procedures. U.S. Department of Agriculture Forest Service, Southern Research Station. Gen Tech Rep SRS-80 Asheville NC 85 pp.

Shields J, Jose S, Freeman J, Bunyan M, Celis G, Hagan D, Morgan M, Pieterson EC, Zak J (2011) Short-term impacts of laurel wilt on red bay (*Persea borbonia* [L.] Spreng.) in a mixed evergreen-deciduous forest in northern Florida. J For 109:82–88.

Smith JA, Dreaden TJ, Mayfield III AE, Boone A, Fraedrich SW, Bates C (2009a) First report of laurel wilt disease caused by *Raffaelea lauricola* on sassafras in Florida and South Carolina. Plant Dis 93:1079–1079.

Smith JA, Mount L, Mayfield III AE, Bates CA, Lamborn WA, Fraedrich SW (2009b) First report of laurel wilt disease caused by *Raffaelea lauricola* on Camphor in Florida and Georgia. Plant Dis 93:198–198.

Smith WB (2002) Forest Inventory and Analysis: a national inventory and monitoring program. Environ Pollut 116:S233–S242.

Spiegel KS, Leege LM (2013) Impacts of laurel wilt disease on red bay (*Persea borbonia* (L.) Spreng.) population structure and forest communities in the coastal plain of Georgia, USA. Biol Invasions 15:2467–2487.

USDA, United States Department of Agriculture, Forest Service, Forest Health Protection, Southern Region (2013) Distribution of counties with laurel wilt disease by year of initial detection. http://www.fs.fed.us/r8/foresthealth/laurelwilt/dist_map.shtml.

VanDerWal J, Falconi L, Januchowski S, Shoo L, Storlie C (2012) SDMTools: Species distribution modelling tools: Tools for processing data associated with species distribution modelling exercises. R package version 1.1-13. http://CRAN.R-project.org/package=SDMTools.

Westfall JA, Pugh SA, Coulston JW (2013) Conducting tests for statistically significant differences using forest inventory data. U.S. Department of Agriculture Forest Service, Northern Research Station. Research Paper NRS-22. Newton Square PA 14 pp.

Wickham H (2009) ggplot2: elegant graphics for data analysis. Springer New York.

CHAPTER THREE

A COMMUNITY ANALYSIS FOR FOREST ECOSYSTEMS WITH NATURAL GROWTH OF *PERSEA* IN THE SOUTHEASTERN UNITESD STATES

3.1. Introduction

Red bay (*Persea borbonia*) and swamp bay (*P. palustris*) are evergreen broadleaf tree species in the Lauraceae native to the southeastern United States. Their taxonomic status has been debated, with some authors placing both species, along with *P. humilis* of Florida, in one broadly circumscribed *Persea borbonia*. Both species are highly susceptible to Laurel Wilt Disease (LWD), a fungal infection vectored by a non-native ambrosia beetle (Fraedrich et al. 2008).

First introduced around 2002 in Port Wentworth, GA, LWD has been spreading rapidly throughout the southeastern US (Fraedrich 2008). Koch & Smith (2008) predicted that LWD would spread throughout the range of red bay and swamp bay in under 40 years, reaching Texas by the year 2035. Although they were correct in their under 40 year prediction, LWD has spread much faster than Koch and Smith (2008) expected and has already been found (as of 2015) in all states within the range of red bay and swamp bay, with the exception of Virginia. Human transport of infested firewood is thought to have increased the rate of spread of LWD (Cameron et al. 2008; Cameron et al. 2010). The rapid spread of LWD may lead to region-wide extinction of red bay and swamp bay populations, altering the composition, structure and function of the red bay/swamp bay

ecosystems of which it was once a significant component (Evans et al. 2014; Spiegel & Leege 2013).

In addition to red bay and swamp bay, several other Lauraceae species native to the Carolinas are susceptible to LWD, including sassafras (*Sassafras albidum*), spicebush (*Lindera benzoin*), pondspice (*Litsea aestivalis*), pondberry (*Lindera melissifolia*) and bog spicebush (*Lindera subcoriacea*), as well as such introduced species as avocado (*Persea americana*), and to a lesser extent camphor tree (*Cinnamomum camphora*) (Fraedrich et al. 2008; Mayfield III et al. 2008; Smith, Mount, et al. 2009; Smith, Dreaden, et al. 2009). However, the ambrosia beetle that vectors LWD, *Xyleborus glabratus*, seems to preferentially attack red bay and swamp bay over other possible hosts (Hanula et al. 2008; Kendra et al. 2013). Red bay and swamp bay populations (collectively) have declined significantly in counties with documented LWD present, and populations range-wide are declining (Shearman et al. 2015).

The dominance of red bay or swamp bay in a forest community may affect the susceptibility of the community to LWD. Larger-diameter stems have a higher probability of being attacked by *X. glabratus* (Fraedrich et al. 2008; Mayfield III & Brownie 2013; Shearman et al. 2015) as well as a higher initial mortality immediately following infection (Fraedrich et al . 2008; Shields et al. 2011). Ambrosia beetles construct egg galleries in the xylem of their host. Large diameter stems likely result in longer galleries and higher brood production (Harrington et al. 2010). It is also possible that larger stems reduce competition with other wood-boring insects (Harrington et al. 2010). Because *X. glabratus* targets larger stems, LWD is likely to impact communities

that support larger red bay or swamp bay individuals than communities where these species are relatively small. Additionally, the loss of larger trees is a greater disturbance in these communities than in communities with small-diameter stems, which may in turn have greater impacts on the overall community composition and dynamics. Therefore, distinguishing ecologically and compositional distinct communities with significant red bay or swamp bay populations can be useful for understand the risk presented by LWD, as well as their responses after LWD outbreak.

Little has been published on the ecology of red bay and swamp bay. Brendemuehl (1990) states that red bay (*sensu lato*) is commonly found in mixed stands along swamps, hammocks, and wet, well drained sites. Common associates include loblolly pine (*Pinus taeda*), pond pine (*P. serotina*), slash pine (*P. elliottii*), live oak (*Quercus virginiana*), black tupelo (*Nyssa sylvatica*) and sweetgum (*Liquidambar styraciflua*) (Brendemuehl 1990). No studies have empirically shown which communities have higher abundance of red bay or swamp bay. With the recent and extensive mortality of *Persea*, along with its uncertain future due to LWD, it is important to document the characteristics of red bay and swamp bay communities to guide any future conservation and restoration efforts for these communities. Therefore, our objectives were to (1) determine whether red bay and swamp bay are associated with different communities, (2) identify distinct communities where these species occur, and (3) determine which communities have higher importance of either red bay or swamp bay and are, therefore, at higher risk of being impacted by LWD.

3.2. Materials and Methods

Carolina Vegetation Survey

The Carolina Vegetation Survey (CVS) uses a specific protocol for documenting the composition and structure of vegetation (Peet et al. 1998; Peet et al. 2012). Vegetation is measured in 10 m by 10 m modules, which can be combined to accommodate a variety of plot sizes depending on the extent of homogenous vegetation. A full CVS plot consists of 10 modules arranged in a 50 m by 20 m plot. In each module, species are tallied and stems are measured in diameter classes. Percent cover is estimated for all species in each of 4 contiguous modules, as well as for the entire plot.

Taxonomic Resolution

When the CVS protocol was first implemented in the 1980s, Radford et al. (1968) was the standard taxonomic reference. In these early years, all *Persea* were identified as *P. borbonia* (R. Peet, personal communication). Later, Weakley's flora was adopted, which split *Persea* into *P. borbonia* and *P. palustris*. In response to this change, some plots from before the split were updated as needed based on geography (Peet, personal communication).

Data Analysis

We analyzed data collected using the CVS protocol between 1988 and 2012 to describe stand characteristics of red bay and swamp bay communities, primarily in the Carolinas, with additional plots in Virginia, Florida, and Georgia. We restricted our

analysis to plots where red bay or swamp bay were present as measurable stems (at least 1.4 m in height). Plots ranged in size from 100 m^2 to 1000 m^2. Because larger plots tend to have more species (Peet & Roberts 2013), as well as higher constancy for species than smaller plots (Dengler et al. 2009), we removed plots smaller than 300 m^2 so that all plots were within a factor of four as recommended by Peet & Roberts (2013) and Otypková & Chytry (2006). Species cover in CVS plots are estimated using a standard cover class scale: 1 = trace, 2 = 0 – 1%, 3 = 1 – 2%, 4 = 2 – 5%, 5 = 5 – 10%, 6 = 10 – 25%, 7 = 25 – 50%, 8 = 50 – 75%, 9 = 75 – 95%, 10 = > 95%. Plots of low taxonomic quality were removed from the analysis. We identified those plots by calculating the relative cover of flora identified above the species level: $\frac{Cov_L}{Cov_T}\ X\ 100\%$, where Cov_L is the sum of cover values (the midpoints of the cover class ranges) of flora identified above the species level, and Cov_T is the sum of cover values for all flora in the plot. Plots in which more than 10% of the relative cover were identified above the species level were removed. Of the remaining plots, only species that occurred in at least two plots and were identified to their specific epithet were included in the analysis. Different varieties of a species were grouped together as one species. The resulting species matrix consisted of 984 species in 388 plots. Botanical nomenclature follows Weakley (2015).

We classified plots following the methods of Matthews et al. (2011). Plots were compared by calculating the Bray-Curtis (BC) dissimilarity index using the function "vegdist" from the "vegan" package (Oksanen et al. 2015) in R (version 3.2.2, R Core Team 2015). The abundance values used to compare plots were the original cover class scale for each species.

To test whether red bay and swamp bay are associated with different communities, we first visualized the data in a non-metric multidimensional scaling (NMS) ordination using the BC dissimilarity matrix. The NMS ordination was conducted using the "metaMDS" function in the "vegan" package (Oksanen et al. 2015). Environmental variables collected for each plot, including latitude, longitude, distance from the Atlantic Coast, elevation, average soil pH, percent soil organic matter, exchangeable nutrients (N, P, K, Na, etc.), base saturation, the percent of base saturation occupied by cations (%H, %Ca, %Na, %Mg, %K, and %Other), micronutrients (B, Fe, Mn, Cu, Zn, and Al), and soil texture (percent sand, silt, and clay), were fit to the ordination using the "envfit" function in the "vegan" package. Soil samples were analyzed either by Brookside Laboratories Inc. (www.blinc.com) or by the North Carolina Department of Agriculture (www.ncagr.gov). We tested for differences among groups (red bay, swamp bay, or both species present) with an Analysis of Similarity (ANOSIM) using the "anosim" function with the Bray-Curtis distance metric in the "vegan" package (Oksanen et al. 2015). ANOSIM compares the dissimilarity between groups to the dissimilarity within groups and computes a statistic, *R*, which ranges between -1 and 1. An *R* value of 0 indicates completely random groupings (i.e., the dissimilarity between groups is the same as that of within groups), while an *R* value approaching 1 indicates more distinct groups (Clarke 1993; Anderson & Walsh 2013). To conduct multiple comparisons, we repeated the analysis using subsets of the data. For example, to compare the red bay group with the swamp bay group, we removed the group with both species and conducted an ANOSIM on the two remaining groups.

We then conducted a cluster analysis with the "agnes" function in the package "cluster" (Maechler et al. 2015), using a flexible beta ("gaverage" argument) linkage method ($\beta = -0.25$). To determine the appropriate number of groups, we conducted multiple indicator species analyses under different group numbers, selecting the number of groups based on the highest number of significant indicator species for a single cluster, and lowest average *P*-value (Dufrêne & Legendre 1997; McCune et al. 2002; Matthews et al. 2011). The indicator value (IV) is the square root of the product of species specificity, the probability that the given species is in a given cluster when it is found; and species fidelity, the probability of finding the given species in a given group. Thus, a species with an indicator value of 1 will only be found in its associated group and is always found in that group. Once the optimum number of groups was found, we ran another Indicator Species Analysis allowing for species to be indicators of multiple groups using the "multipatt" function in the "indicspecies" package (De Cáceres et al. 2015) with 999 permutations.

Cluster assignments were verified by conducting a bootstrap forest (aka random forest) analysis in JMP (2015, SAS Institute Inc.). We used the groups identified in the cluster analysis as a response variable with the species matrix as predictors to see if the predicted groups agreed with the original cluster groupings. We then ran another bootstrap forest analysis, using the new groupings as the response variable, and the abiotic variables collected for each plot. We used the results of this analysis to identify important abiotic variables associated with each group. Lastly, we compared our groups with those of the US National Vegetation Classification (NVC) groups (see Jennings et

al. 2009, and http://usnvc.org) classified by the researchers that surveyed the plots or by subsequent CVS researchers. Once we identified the appropriate groups, we calculated the basal area (0.00007854 * DBH^2, where DBH is the diameter in cm at 1.4 m height and basal area is in m^2, which was converted to m^2/ha based on the size of the plot), density (stems per hectare) and importance value (relative basal area + relative density) of red bay and swamp bay stems in each plot. We tested for differences in basal area, density, and relative importance among groups using the Kruskal-Wallis test with multiple comparisons (kruskalmc function in the pgirmess package, Giraudoux 2015).

3.3. Results

Red bay and swamp bay plots clustered in distinct groups along axis 1 in the ordination, with plots reporting both species clustering between red bay only plots and swamp bay only plots (Figure 3.1). We chose a three dimensional solution based on a scree plot, which plots the decrease in stress for each increase in dimensionality. The three dimensional solution had a stress value of 0.13, which is an acceptable ordination based on Clarke's (1993) rule of thumb, while also having an interpretable number of dimensions. The red bay plots clustered in areas of higher soil pH, P, %Ca, and base saturation, as well as lower elevation, less distance to the coast, and lower %H (Figure 3.1). In short, they were largely restricted to the coastal fringe. All of the abiotic variables were significantly predicted by the ordination, with the best-fit variables being latitude, exchangeable nitrogen, and soil pH (r^2 = 0.50, 0.47, and 0.42 respectively, Table 3.1). The results of the ANOSIM suggest that there were significant differences in species

composition of plots having red bay, swamp bay, or both species (R =0.37, P < 0.001). Comparisons were also significantly different between red bay and swamp bay plots (R=0.44, P < 0.001), and red bay versus both (R=0.31, P = 0.005).

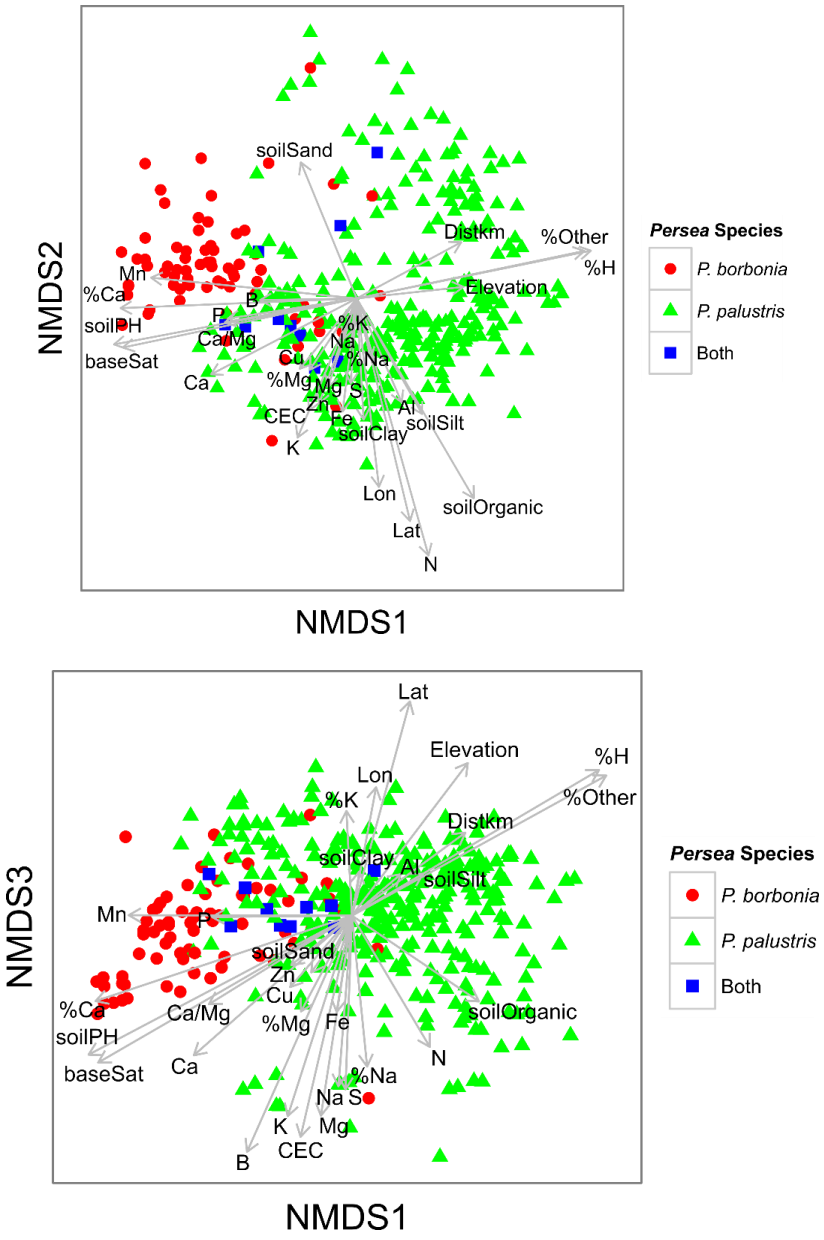

Figure 3.1. NMDS ordination of 388 CVS plots where red bay or swamp bay occur as measurable stems. Red circles indicate plots where red bay was recorded, green triangles indicate plots with swamp bay, and blue squares indicate that both species were present. Vectors show magnitude and direction of environmental variables. The final ordination was a 3-dimensional solution with axes 1 and 2 (top) and axes 1 and 3 (bottom).

Table 3.1. Environmental variables fit to a 3-dimensional NMDS ordination of 388 CVS plots and 984 species and a bootstrap forest analysis of the same 388 plots in seven groups identified in a hierarchical cluster analysis. Only plots where red bay or swamp bay were present as measurable stems were included. NMDS1-3 are axes scores for each variable in the ordination. The goodness of fit statistic, r^2, is the squared correlation coefficient. Number of splits is the number of times the variable defined a split in a random forest tree. G2 is the likelihood-ratio chi-square statistic.

	Ordination					**Bootstrap Forest**	
Variable	**NMDS1**	**NMDS2**	**NMDS3**	**r^2**	***P* -value**	**Number of Splits**	**G^2**
Latitude	0.17667	-0.7358	0.65375	0.50	0.001	1278	85.76
N	0.24506	-0.8769	-0.4135	0.47	0.001	710	44.34
soil pH	-0.8721	-0.1651	-0.4607	0.42	0.001	508	25.89
base sat.	-0.8513	-0.1785	-0.4934	0.41	0.001	508	26.07
%Other	0.86202	0.17562	0.47548	0.40	0.001	435	20.19
%H	0.84768	0.17669	0.50021	0.39	0.001	500	23.42
%Ca	-0.9479	-0.0389	-0.3162	0.34	0.001	403	13.08
soil Organic	0.47871	-0.8161	-0.3237	0.33	0.001	714	46.89
K (ppm)	-0.2478	-0.5823	-0.7743	0.31	0.001	395	12.63
B (ppm)	-0.4056	-0.007	-0.914	0.31	0.001	427	10.48
CEC	-0.1993	-0.4712	-0.8592	0.31	0.001	467	16.88
Longitude	0.09953	-0.8424	0.52966	0.27	0.001	843	41.45
Ca (ppm)	-0.698	-0.3633	-0.6172	0.24	0.001	521	23.25
Mn (ppm)	-0.9949	0.10046	0.002	0.23	0.001	461	14.89
Mg (ppm)	-0.1385	-0.4277	-0.8933	0.23	0.001	387	12.46
S	-0.0328	-0.4668	-0.8837	0.18	0.001	455	16.20
Elevation (m)	0.60308	0.06504	0.79503	0.17	0.001	755	32.68
Na (ppm)	-0.0765	-0.245	-0.9665	0.14	0.001	298	7.86
Ca/Mg	-0.8402	-0.1513	-0.5207	0.13	0.001	337	7.25
soil Sand	-0.363	0.88343	-0.2963	0.13	0.001	381	9.60
%Na	0.09187	-0.3949	-0.9141	0.13	0.001	298	7.86
Fe (ppm)	-0.0975	-0.7824	-0.6151	0.11	0.001	503	15.51
Distance (km)	0.74004	0.39782	0.54229	0.11	0.001	1053	66.91
soil Silt	0.4736	-0.8352	0.27956	0.10	0.001	321	8.34
P	-0.988	-0.1541	-0.0093	0.09	0.001	417	15.31
soil Clay	0.05428	-0.9462	0.3191	0.09	0.001	329	6.15
Zn (ppm)	-0.3047	-0.8523	-0.4251	0.08	0.001	332	8.14
%Mg	-0.3819	-0.5806	-0.7191	0.08	0.001	300	6.77
Al (ppm)	0.37664	-0.8693	0.32019	0.08	0.001	577	20.08
Cu (ppm)	-0.5083	-0.6285	-0.5887	0.07	0.001	343	7.11
%K	-0.05	-0.297	0.95357	0.06	0.003	338	8.09

However there was no significant difference in composition between swamp bay and plots with both species (R = 0.01, P =0.44).

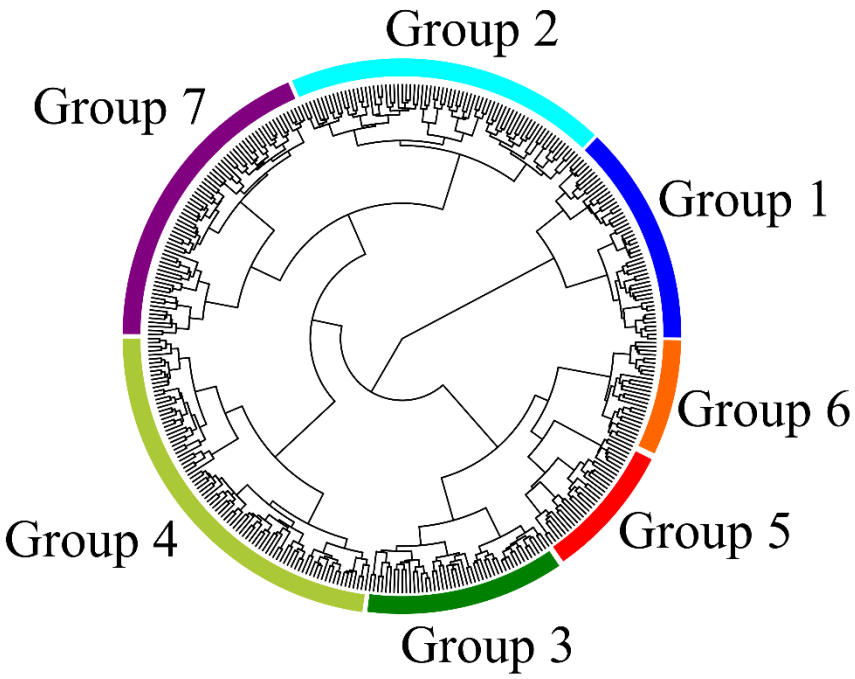

Figure 3.2. Cluster dendrogram of 388 CVS plots in seven community groups.

The indicator species analysis suggested that seven groups provided the highest number of significant indicator species per cluster, along with the lowest average *P*-value. Plots in Cluster 1 were consistent with maritime live oak communities. The most common NVC group for Cluster 1 was the Live Oak – Pignut Hickory – Cabbage Palmetto Coastal Forest Group (G798, Table 3.2), which made up approximately 70% of

the plots clustered in Cluster 1. The remaining plots in Cluster 1 included 4 NVC groups, mostly the Sand Laurel Oak – Sand Live Oak – Water Oak Coastal Plain Forest Group (22% of plots in the group, Table 3.2, Appendix A.). Significant indicator species for Cluster 1 include red bay (IV = 0.86), yaupon (*Ilex vomitoria*, IV = 0.83), devilwood (*Cartrema americanum*, IV = 0.73), live oak (*Quercus virginiana*, IV= 0.73), and Darlington oak (*Quercus hemisphaerica*, IV= 0.71) (Table 3.3).

Cluster 2 was largely composed of temperate deciduous forest plots. Approximately 18% of the plots in Cluster 2 were assigned to the American Beech – Southern Sugar Maple – White Oak Forest Group (G166), with another 16% assigned to the Pitch Pine – Oak Species / Northern Bayberry Forest Group (G495, Table 3.2). The remaining plots were spread among 12 NVC groups with 15% unclassified (Appendix A.1). The most significant indicator species in Cluster 2 were little brown jug (*Hexastylis arifolia*), American beech (*Fagus grandifolia*), white oak (*Quercus alba*), and strawberry bush (*Euonymus americanus*) with indicator values of 0.63, 0.61, 0.60, and 0.57 respectively (Table 3.3).

Cluster 3 and Cluster 5 were similar in terms of NVC Groups, consisting primarily of longleaf pine (*Pinus palustris*) communities. The majority of plots in these clusters (49% in Cluster 3 and 32% in Cluster 5) were classified as members of the Longleaf Pine / Inkberry – Saw Palmetto Woodland Group (G596, Table 3.2). In our analysis, Cluster 3 and 5 are separated based on location, with Cluster 3 occurring in more northern latitudes, and group 5 being more typical of southern latitudes (Figure 3.3). Indicator species also separate the two groups, with the top indicator species of

Table 3.2. US National Vegetation Classification (NVC) groups for CVS plots where red bay and swamp bay occur as measurable stems. NVC Groups are arranged by the results of an agglomerative hierarchical cluster analysis of all 388 plots cut into seven groups. NVC counts are the number of plots classified for a particular association in each cluster. Only the three most frequent associations are shown. A complete list of all associations is in Appendix A.1.

Cluster	n	NVC Group	NVC Counts	Description
1	50	G798	35	Live Oak - Pignut Hickory - Cabbage Palmetto Coastal Forest Group
		G790	11	Sand Laurel Oak - Sand Live Oak - Water Oak Coastal Plain Forest Group
		G034	2	Swamp Chestnut Oak - Laurel Oak - Sweetgum Bottomland Forest Group
2	73	G166	13	American Beech - Southern Sugar Maple - White Oak Forest Group
		G495	12	Pitch Pine - Oak species / Northern Bayberry Forest Group
		G798	9	Live Oak - Pignut Hickory - Cabbage Palmetto Coastal Forest Group
3	47	G596	23	Longleaf Pine / Inkberry - Saw Palmetto Woodland Group
		G009	6	Longleaf Pine / Sand Post Oak / Three-awn species Woodland Group
		G154	4	Longleaf Pine / Turkey Oak Xeric Woodland Group
4	89	G037	34	Sweetbay - Loblolly-bay - Pond Pine Forest Group
		G038	15	Swamp Tupelo - Ogeechee Tupelo - Bald-cypress Hardwood Basin Swamp Group
		G186	7	Shining Fetterbush - Inkberry - Swamp Titi Shrubland Group
5	31	G596	10	Longleaf Pine / Inkberry - Saw Palmetto Woodland Group
		G009	6	Longleaf Pine / Sand Post Oak / Three-awn species Woodland Group
		G190	4	Longleaf Pine - Slash Pine - Pond Pine Woodland Group
6	27	G036	18	Pond-cypress / Holly species Depression Forest Group
		G111	4	Beaksedge species - Spikerush species - Yellow-eyed-grass species Wet Prairie Group
		G037	2	Sweetbay - Loblolly-bay - Pond Pine Forest Group
7	71	G033	31	Bald-cypress - Water Tupelo Floodplain Forest Group
		G034	9	Swamp Chestnut Oak - Laurel Oak - Sweetgum Bottomland Forest Group
		G759	7	Green Ash - American Elm - Black Willow Floodplain Forest Group

Cluster 3 being southern blueberry (*Vaccinium tenellum*, 0.82), pineland three-awn (*Aristida stricta*, 0.82), Piedmont staggerbush (*Lyonia mariana*, 0.79), creeping blueberry (*Vaccinium crassifolium*, 0.75), and blue huckleberry (*Gaylussacia frondosa*, 0.73). In contrast, Cluster 5 indicator species include Beyrich threeawn (*Aristida beyrichiana*, 0.74), long stalked aster (*Symphyotrichum dumosum*, 0.65), and saw palmetto (*Serenoa repens*, 0.63) (Table 3.3). Indicator species for both groups include longleaf pine, dwarf huckleberry (*Gaylussacia dumosa*, 0.78), and bracken fern (*Pteridium aquilinum*, 0.68) (Table 3.4).

Cluster 4 has the highest proportion of plots from the Sweetbay – Loblolly-bay – Pond Pine Forest Group (G037, 38%, Table 2). Only four species, Atlantic white cedar (*Chamaecyparis thyoides*), smooth winterberry (*Ilex laevigata*), leatherleaf (*Chamaedaphne calyculata*), and wild ginger (*Hexastylis minor*), were significant indicator species for Cluster 4 alone (IV = 0.48, 0.35, 0.25, and 0.24 respectively, Table 3.3). However, Cluster 4 shared several highly significant indicator species with other groups, such as swamp tupelo (*Nyssa biflora*, IV = 0.83, groups 4+5+6+7), netted chain fern (*Lorinseria areolata*, IV = 0.67, groups 2+4+6+7), shining fetterbush (*Lyonia lucida*, IV = 0.61, groups 3+4+5+6), and Virginia-willow (*Itea virginica*, IV = 0.61, Clusters 4+7) (Table 3.4). Cluster 6 had the fewest number of plots, with 27 of the 388 total plots (Table 3.2, Figure 3.2). Approximately 67% of the plots in Cluster 6 were classified as members of the Pond-Cypress / Holly species Depression Group (G036, Table 3.2). Pond cypress (*Taxodium ascendens*), maidencane (*Hymenachne hemitomon*), and Virginia chain fern (*Anchistea virginica*) had the highest indicator values for this

Table 3.3. Indicator species associated with seven community clusterss where red bay or swamp bay are present as measurable stems. Species specificity (A) is the probability that the given spieces is in a given cluster when it is found. Species fidelity (B) is the probability of finding the given species in a given cluster. Only the top five species are listed. The full list can be found in Appendix A.2.

Cluster	Family	Species	A	B	Indicator Value	*P* -value
1	Lauraceae	*Persea borbonia*	0.75	0.98	0.86	0.001
	Aquifoliaceae	*Ilex vomitoria*	0.71	0.96	0.83	0.001
	Oleaceae	*Cartrema americanum*	0.73	0.74	0.73	0.001
	Fagaceae	*Quercus virginiana*	0.76	0.70	0.73	0.001
	Fagaceae	*Quercus hemisphaerica*	0.63	0.80	0.71	0.001
2	Aristolochiaceae	*Hexastylis arifolia*	0.91	0.44	0.63	0.001
	Fagaceae	*Fagus grandifolia*	0.97	0.38	0.61	0.001
	Fagaceae	*Quercus alba*	0.89	0.40	0.60	0.001
	Celastraceae	*Euonymus americanus*	0.64	0.51	0.57	0.001
	Araceae	*Arisaema triphyllum*	0.80	0.37	0.55	0.001
3	Ericaceae	*Vaccinium tenellum*	0.82	0.83	0.82	0.001
	Poaceae	*Aristida stricta*	0.93	0.72	0.82	0.001
	Ericaceae	*Lyonia mariana*	0.91	0.68	0.79	0.001
	Ericaceae	*Vaccinium crassifolium*	0.90	0.62	0.75	0.001
	Ericaceae	*Gaylussacia frondosa*	0.59	0.89	0.73	0.001
4	Cupressaceae	*Chamaecyparis thyoides*	0.75	0.30	0.48	0.001
	Aquifoliaceae	*Ilex laevigata*	0.90	0.13	0.35	0.002
	Ericaceae	*Chamaedaphne calyculat*	0.94	0.07	0.25	0.014
	Aristolochiaceae	*Hexastylis minor*	1.00	0.06	0.24	0.019
5	Poaceae	*Aristida beyrichiana*	1.00	0.55	0.74	0.001
	Asteraceae	*Symphyotrichum dumosu*	0.87	0.48	0.65	0.001
	Arecaceae	*Serenoa repens*	0.72	0.55	0.63	0.001
	Ericaceae	*Vaccinium myrsinites*	0.81	0.48	0.63	0.001
	Pinaceae	*Pinus elliottii*	0.81	0.48	0.63	0.001
6	Cupressaceae	*Taxodium ascendens*	0.78	0.85	0.81	0.001
	Poaceae	*Hymenachne hemitomon*	0.92	0.63	0.76	0.001
	Blechnaceae	*Anchistea virginica*	0.57	0.89	0.71	0.001
	Iridaceae	*Iris tridentata*	0.98	0.48	0.69	0.001
	Polygalaceae	*Polygala cymosa*	1.00	0.44	0.67	0.001
7	Cupressaceae	*Taxodium distichum*	0.83	0.56	0.68	0.001
	Saururaceae	*Saururus cernuus*	0.70	0.65	0.67	0.001
	Osmundaceae	*Osmunda spectabilis*	0.59	0.73	0.66	0.001
	Araceae	*Peltandra virginica*	0.88	0.46	0.64	0.001
	Hypericaceae	*Hypericum walteri*	0.78	0.44	0.59	0.001

Table 3.4. Indicator species associated with more than one community Cluster where red bay or swamp bay are present as measurable stems. Species specificity (A) is the probability that the given spieces is in a given cluster when it is found. Species fidelity (B) is the probability of finding the given species in a given cluster. Only the top five species are listed. The full list can be found in Appendix A.2.

Cluster	Family	Species	A	B	Indicator Value	*P* -value
1+2	Smilacaceae	*Smilax bona-nox*	0.77	0.80	0.78	0.001
	Cornaceae	*Cornus florida*	0.90	0.53	0.69	0.001
	Juglandaceae	*Carya glabra*	0.99	0.43	0.65	0.001
	Betulaceae	*Carpinus caroliniana*	0.83	0.44	0.61	0.001
	Apiaceae	*Sanicula canadensis*	0.91	0.26	0.49	0.001
1+5	Smilacaceae	*Smilax auriculata*	0.86	0.36	0.56	0.001
	Rubiaceae	*Galium pilosum*	0.89	0.17	0.39	0.002
	Fabaceae	*Erythrina herbacea*	0.79	0.14	0.33	0.003
	Smilacaceae	*Smilax pumila*	0.68	0.15	0.32	0.004
2+3	Nyssaceae	*Nyssa sylvatica*	0.67	0.51	0.58	0.001
	Fagaceae	*Quercus nigra*	0.59	0.57	0.58	0.001
	Lauraceae	*Sassafras albidum*	0.71	0.38	0.51	0.001
	Fagaceae	*Quercus stellata*	0.85	0.08	0.27	0.021
2+4	Magnoliaceae	*Liriodendron tulipifera*	0.87	0.31	0.52	0.001
	Annonaceae	*Asimina triloba*	0.95	0.07	0.25	0.029
2+5	Poaceae	*Dichanthelium laxiflorum*	0.88	0.14	0.36	0.001
	Fagaceae	*Castanea pumila*	0.95	0.13	0.34	0.002
	Acanthaceae	*Ruellia caroliniensis*	0.86	0.12	0.32	0.002
	Ulmaceae	*Ulmus alata*	0.78	0.09	0.26	0.048
	Poaceae	*Piptochaetium avenaceum*	0.80	0.08	0.25	0.02
2+6	Asteraceae	*Solidago rugosa*	0.93	0.07	0.26	0.01
2+7	Hydrangeaceae	*Decumaria barbara*	0.83	0.40	0.58	0.001
	Ulmaceae	*Ulmus americana*	0.96	0.33	0.57	0.001
	Fagaceae	*Quercus laurifolia*	0.76	0.40	0.55	0.001
	Urticaceae	*Boehmeria cylindrica*	0.83	0.35	0.54	0.001
	Bignoniaceae	*Campsis radicans*	0.87	0.30	0.51	0.001
3+4	Ericaceae	*Kalmia carolina*	1.00	0.07	0.27	0.004
3+5	Pinaceae	*Pinus palustris*	0.88	0.82	0.85	0.001
	Ericaceae	*Gaylussacia dumosa*	0.96	0.63	0.78	0.001
	Dennstaedtiaceae	*Pteridium latiusculum*	0.79	0.58	0.68	0.001
	Xyridaceae	*Xyris caroliniana*	1.00	0.45	0.67	0.001
	Melastomataceae	*Rhexia alifanus*	0.96	0.44	0.65	0.001
3+6	Asteraceae	*Eupatorium album*	0.85	0.08	0.26	0.01
4+5	Theaceae	*Gordonia lasianthus*	0.91	0.27	0.49	0.001
	Anacardiaceae	*Toxicodendron vernix*	0.81	0.13	0.32	0.004
4+6	Ericaceae	*Zenobia pulverulenta*	0.89	0.13	0.34	0.001
4+7	Iteaceae	*Itea virginica*	0.83	0.44	0.61	0.001

Table 3.4. Continued

Cluster	Family	Species	A	B	Indicator Value	*P* -value
5+6	Poaceae	*Andropogon capillipes*	0.94	0.48	0.67	0.001
	Eriocaulaceae	*Eriocaulon decangulare*	0.99	0.43	0.65	0.001
	Haemodoraceae	*Lachnanthes caroliniana*	0.94	0.36	0.58	0.001
	Poaceae	*Panicum verrucosum*	0.94	0.33	0.55	0.001
	Poaceae	*Aristida palustris*	1.00	0.21	0.46	0.001
5+7	Asteraceae	*Mikania scandens*	0.77	0.31	0.49	0.001
	Asteraceae	*Baccharis halimifolia*	0.89	0.25	0.48	0.001
	Poaceae	*Dichanthelium dichotomum*	0.75	0.18	0.36	0.002
6+7	Smilacaceae	*Smilax walteri*	0.69	0.40	0.53	0.001
	Iridaceae	*Iris virginica*	0.90	0.23	0.46	0.001
	Pontederiaceae	*Pontederia cordata*	1.00	0.12	0.35	0.001
1+2+3	Poaceae	*Chasmanthium laxum*	0.75	0.24	0.42	0.001
1+2+5	Lamiaceae	*Callicarpa americana*	0.97	0.38	0.60	0.001
	Poaceae	*Dichanthelium commutatum*	0.81	0.34	0.53	0.001
	Ericaceae	*Vaccinium arboreum*	0.88	0.29	0.50	0.001
	Aristolochiaceae	*Endodeca serpentaria*	1.00	0.21	0.46	0.001
	Vitaceae	*Vitis aestivalis*	0.93	0.20	0.43	0.001
1+2+7	Vitaceae	*Parthenocissus quinquefolia*	0.82	0.80	0.81	0.001
	Rubiaceae	*Mitchella repens*	0.86	0.64	0.74	0.001
	Bignoniaceae	*Bignonia capreolata*	0.91	0.44	0.63	0.001
	Arecaceae	*Sabal minor*	1.00	0.26	0.51	0.001
	Rhamnaceae	*Berchemia scandens*	0.79	0.30	0.49	0.001
1+3+5	Fabaceae	*Clitoria mariana*	0.93	0.10	0.31	0.005
2+3+5	Hypericaceae	*Hypericum hypericoides*	0.78	0.29	0.48	0.001
	Fagaceae	*Quercus falcata*	0.93	0.23	0.46	0.001
2+3+7	Rosaceae	*Rubus pensilvanicus*	0.80	0.16	0.36	0.003
2+4+7	Ericaceae	*Leucothoe axillaris*	1.00	0.09	0.31	0.007
2+5+7	Cornaceae	*Cornus stricta*	1.00	0.20	0.45	0.001
	Ericaceae	*Vaccinium elliottii*	0.87	0.10	0.29	0.018
	Vitaceae	*Vitis cinerea*	1.00	0.08	0.28	0.008
2+6+7	Caprifoliaceae	*Lonicera japonica*	0.80	0.24	0.44	0.001
	Juncaceae	*Juncus effusus*	0.95	0.06	0.25	0.036
	Aquifoliaceae	*Ilex decidua*	1.00	0.06	0.24	0.039
	Dryopteridaceae	*Onoclea sensibilis*	1.00	0.05	0.23	0.042
3+4+5	Aquifoliaceae	*Ilex coriacea*	0.87	0.50	0.66	0.001
	Myricaceae	*Morella caroliniensis*	0.88	0.26	0.48	0.001
3+4+6	Ericaceae	*Vaccinium formosum*	0.77	0.53	0.64	0.001
3+4+7	Ericaceae	*Eubotrys racemosus*	0.86	0.37	0.57	0.001

Table 3.4. Continued

Cluster	Family	Species	A	B	Indicator Value	*P* -value
3+5+6	Aquifoliaceae	*Ilex glabra*	0.79	0.82	0.80	0.001
	Poaceae	*Andropogon virginicus*	0.92	0.43	0.63	0.001
	Poaceae	*Andropogon glaucopsis*	0.99	0.34	0.58	0.001
	Droseraceae	*Drosera capillaris*	1.00	0.13	0.37	0.002
	Campanulaceae	*Lobelia nuttallii*	1.00	0.10	0.32	0.001
4+5+7	Adoxaceae	*Viburnum nudum*	0.79	0.26	0.45	0.001
4+6+7	Cyperaceae	*Dulichium arundinaceum*	1.00	0.06	0.25	0.034
5+6+7	Cyperaceae	*Cladium jamaicense*	1.00	0.09	0.29	0.005
	Haloragaceae	*Proserpinaca palustris*	1.00	0.07	0.26	0.01
	Alismataceae	*Sagittaria lancifolia*	1.00	0.07	0.26	0.007
1+2+3+6	Ericaceae	*Vaccinium pallidum*	0.92	0.11	0.31	0.007
1+2+6+7	Bromeliaceae	*Tillandsia usneoides*	0.90	0.50	0.67	0.001
2+3+4+5	Symplocaceae	*Symplocos tinctoria*	0.95	0.22	0.45	0.001
2+3+5+6	Ebenaceae	*Diospyros virginiana*	0.87	0.34	0.55	0.001
2+4+6+7	Blechnaceae	*Lorinseria areolata*	0.93	0.48	0.67	0.001
3+4+5+6	Ericaceae	*Lyonia lucida*	0.83	0.63	0.72	0.001
	Clethraceae	*Clethra alnifolia*	0.83	0.57	0.69	0.001
	Rosaceae	*Aronia arbutifolia*	0.89	0.47	0.65	0.001
	Pinaceae	*Pinus serotina*	0.90	0.45	0.63	0.001
	Ericaceae	*Lyonia ligustrina*	0.86	0.24	0.45	0.001
3+4+5+7	Cyrillaceae	*Cyrilla racemiflora*	0.94	0.32	0.55	0.001
	Ericaceae	*Rhododendron viscosum*	1.00	0.14	0.37	0.002
4+5+6+7	Nyssaceae	*Nyssa biflora*	0.88	0.78	0.83	0.001
	Asteraceae	*Erechtites hieraciifolius*	0.95	0.09	0.30	0.018
1+2+3+4+7	Aquifoliaceae	*Ilex opaca*	0.97	0.69	0.82	0.001
1+2+3+6+7	Pinaceae	*Pinus taeda*	0.88	0.59	0.72	0.001
1+2+4+5+7	Vitaceae	*Muscadinia rotundifolia*	0.93	0.70	0.80	0.001
1+2+4+6+7	Anacardiaceae	*Toxicodendron radicans*	0.93	0.75	0.83	0.001
	Smilacaceae	*Smilax rotundifolia*	0.94	0.53	0.71	0.001
2+3+4+5+7	Poaceae	*Arundinaria tecta*	0.99	0.24	0.49	0.002
2+3+4+6+7	Altingiaceae	*Liquidambar styraciflua*	0.93	0.61	0.75	0.001
3+4+5+6+7	Smilacaceae	*Smilax laurifolia*	0.92	0.76	0.84	0.001
1+2+3+4+5+7	Gelsemiaceae	*Gelsemium sempervirens*	0.99	0.44	0.66	0.001
1+2+3+5+6+7	Myricaceae	*Morella cerifera*	0.95	0.65	0.79	0.001
2+3+4+5+6+7	Lauraceae	*Persea palustris*	0.99	0.93	0.96	0.001
	Sapindaceae	*Acer rubrum*	0.99	0.75	0.86	0.001
	Magnoliaceae	*Magnolia virginiana*	0.98	0.62	0.78	0.001
	Ericaceae	*Vaccinium fuscatum*	0.96	0.40	0.62	0.002
	Osmundaceae	*Osmundastrum cinnamomeum*	0.99	0.33	0.57	0.001

group (0.81, 0.76, and 0.71 respectively, Table 3.3). In addition, Cluster 6 shared many of the indicator species with Cluster 4 listed above.

The last cluster, Cluster 7, consisted mainly of plots assigned to the Bald-cypress – Water Tupelo Floodplain Forest Group (G033, 44% of plots, Table 3.2). Bald-cypress (*Taxodium distichum*) had the highest indicator value for this group (IV = 0.68) along with lizard's-tail (*Saururus cernuus*, IV = 0.67), American royal fern (*Osmunda spectabilis*, 0.66), and green arrow-arum (*Peltandra virginica*, 0.64) (Table 3.3).

A total of 222 species were associated with more than one group (Appendix A.1). The species with the highest indicator values for multiple groups are listed in Table 4. Our results show that although red bay was associated with Cluster 1 alone (Table 3.3), swamp bay was a significant indicator species for all other groups (0.96, Table 3.4). Plots in Cluster 1 also were found to be restricted to the coast of NC and SC, whereas plots in other groups were found more inland (Figure 3.4).

The bootstrap forest analysis agreed with our hierarchical clusters. Using the species matrix as predictors resulted in a low misclassification rate (0.04) and high R^2 values (Entropy $R^2 = 0.75$, Generalized $R^2 = 0.96$) suggesting a model with good fit (Table 3.5). The results were similar using abiotic variables as predictors for the seven groups (Entropy $R^2 = 0.69$, Generalized $R^2 = 0.95$, Misclassification Rate = 0.09). To check if we could lower the misclassification rate, we reassigned plots that were misclassified to different clusters and conducted the analyses again. Because this only slightly improved the biotic model and worsened the abiotic model, we retained our initial seven group clusters.

Table 3.5. Results of the bootstrap forest analyses using 7 clusters identified in a hierarchical cluster analysis of 388 plots where red bay and swamp bay were present as measurable stems as a categorical response variable. The analyses were conducted using biotic predictors (species cover code matrix), as well as abiotic predictors (see Table 3.1 for list of variables).

Predictors	N	Entropy R^2	Generalized R^2	RMSE	Misclassification Rate	Trees in Forest	Terms sampled per split	Number of Terms
Biotic	388	0.75	0.96	0.38	0.04	500	246	984
Abiotic	388	0.69	0.95	0.45	0.09	500	7	31

Red bay and swamp bay basal area, density, and relative importance were highly variable within groups. The results of the Kruskal-Wallis test rejected the null hypothesis that basal area (χ^2=106.77, *df* = 6, *P*<0.001), density (χ^2=69.88, *df* = 6, *P*<0.001), and importance (χ^2=19.21, *df* = 6, *P*=0.004), were the same among all groups. In pairwise comparisons, Clusters 3 and 5 had significantly lower basal area of *Persea* when compared to most other groups (Clusters 1, 2, 3, and 4; Figure 3.5). Median basal area was highest in groups 1, 4, and 7 (0.32, 0.29, and 0.23 m^2/ha respectively). Lowest basal area was in groups 5 and 3 (0.001 and 0.002 m^2/ha respectively). Median density was highest in groups 4, 7, 1, and 2 (360, 280, 215, 130 stems/ha respectively). Lowest density was in Cluster 3 (30 stems/ha) and Cluster 5 (40 stems/ha). Clusters 3 and 5 had significantly lower density compared to Clusters 4, 7, and 1, but were not different than Clusters 2 or 6 (Figure 3.6). Median relative importance was highest in Clusters 1 and 7 (9.4 and 9.0 respectively). Lowest median importance was in Clusters 3 and 6 (1.8 and 3.2 respectively), however the only significant differences were between Clusters 1 and 3, and Clusters 7 and 3 (Figure 3.7).

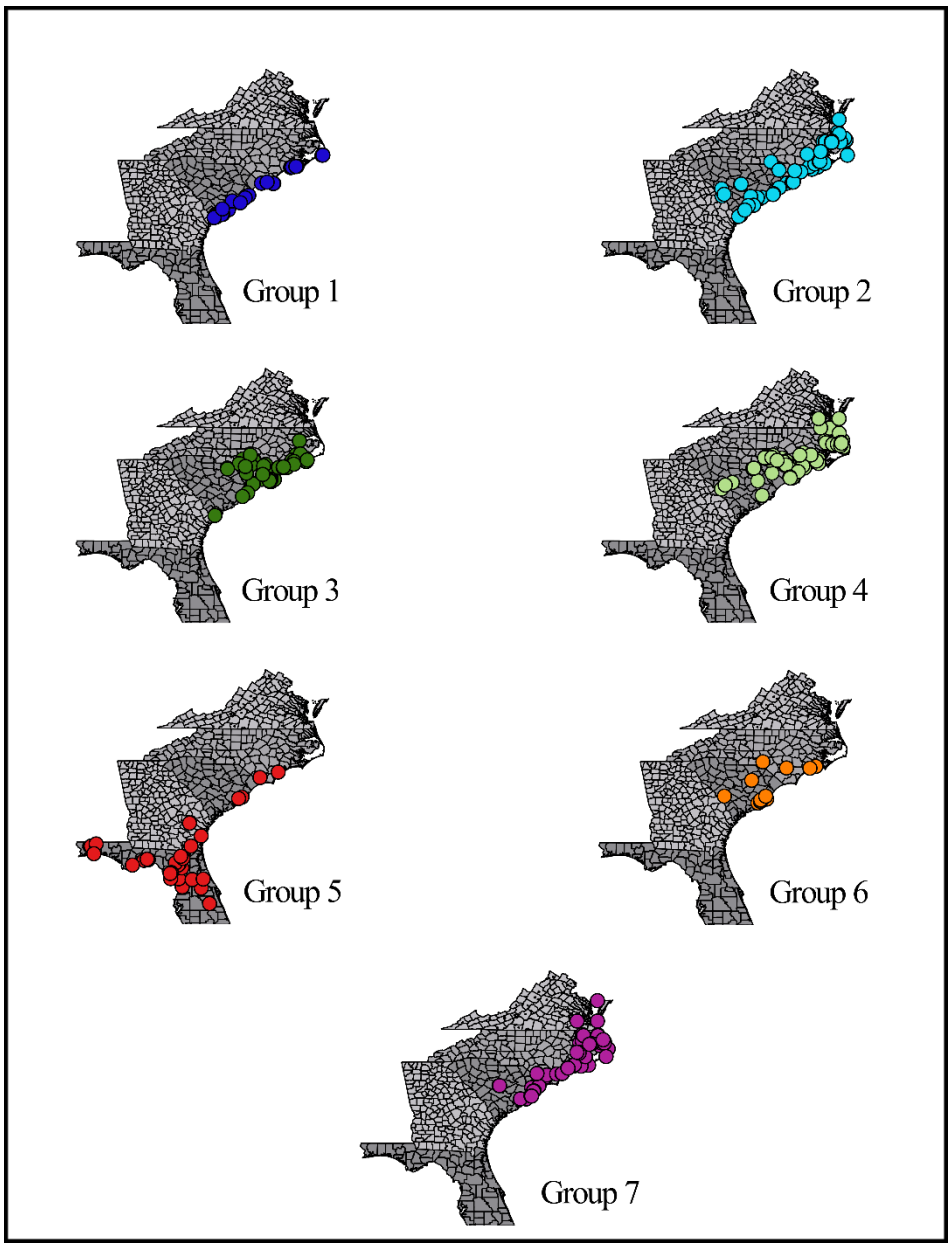

Figure 3.3. Approximate locations of 388 CVS plots in VA, NC, SC, FL, and GA. Plots were grouped into seven community types using cluster analysis.

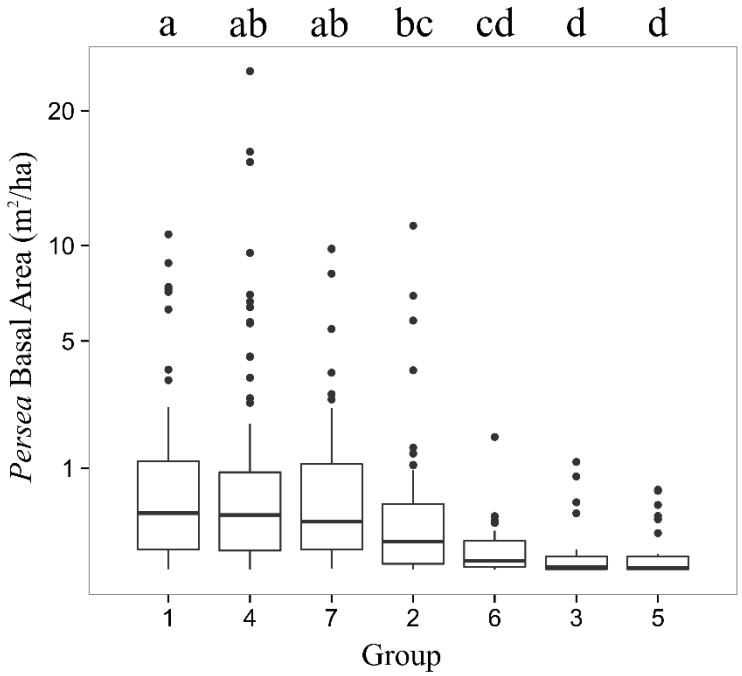

Figure 3.4. Boxplots showing basal area of *Persea* species among different community groups. Groups were identified using cluster analysis. Boxes represent the interquartile range. Horizontal bars are the median basal area for all plots in that group. Groups with the same letter are not significantly different at $\alpha = 0.05$ in a Kruskal-Wallis multiple comparison test.

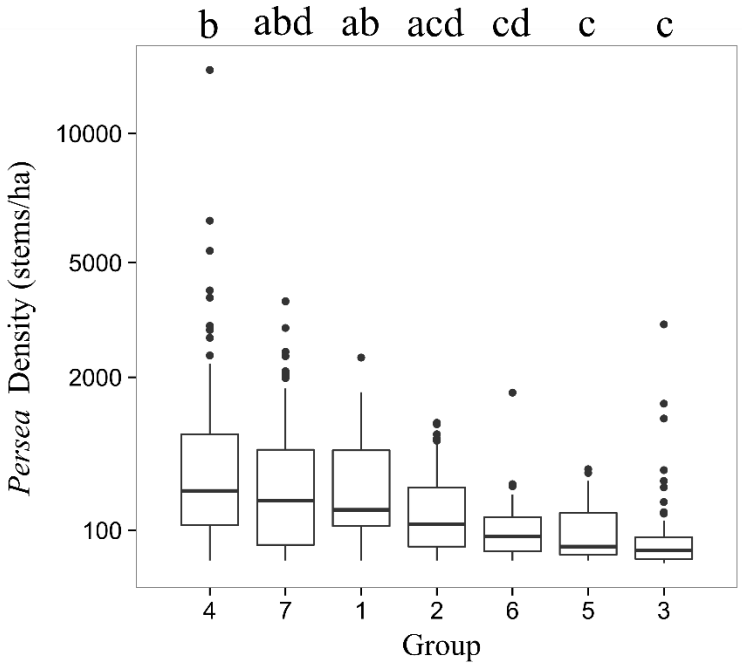

Figure 3.5. Boxplots showing density of *Persea* species among different community groups. Groups were identified using cluster analysis. Boxes represent the interquartile range. Horizontal bars are the median basal area for all plots in that group. Groups with the same letter are not significantly different at $\alpha = 0.05$ in a Kruskal-Wallis multiple comparison test.

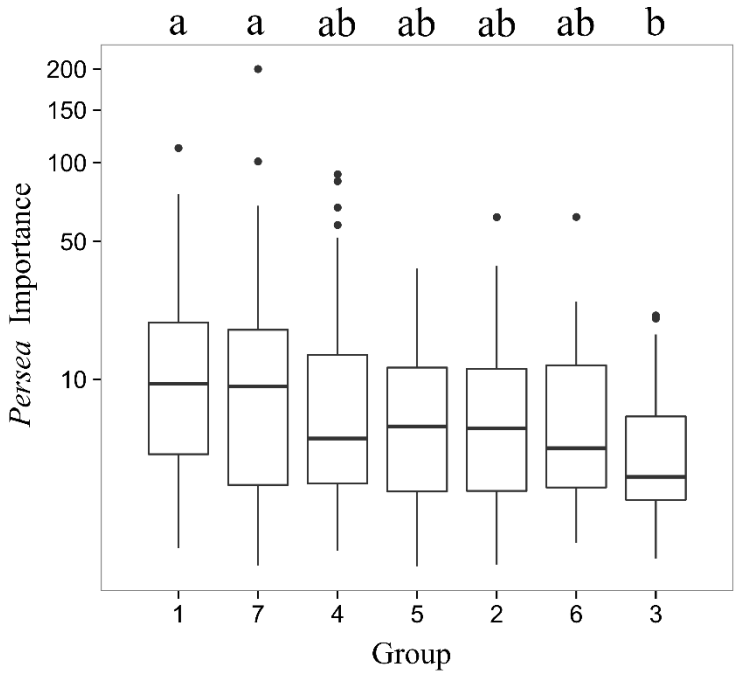

Figure 3.6. Boxplots showing relative importance (relative density + relative basal area) of *Persea* species among different community groups. Groups were identified using cluster analysis. Boxes represent the interquartile range. Horizontal bars are the median basal area for all plots in that group. Groups with the same letter are not significantly different at $\alpha = 0.05$ in a Kruskal-Wallis multiple comparison test.

3.4. Discussion

Our study clearly demonstrates that red bay and swamp bay are members of different communities. Red bay is restricted to coastal communities, whereas swamp bay has a larger geographic distribution, with a slight overlap in the two species as suggested by Kirkman et al. (2007). Plots reportedly as having both species were not significantly different than plots having swamp bay alone, but were different from those having red bay alone, indicating that the overlap between the two species occurs in environments where swamp bay is more prevalent. Another possibility is that the red bay reported in these plots may be less pubescent swamp bay. For some swamp bay individuals, it is difficult to see the ascending trichomes without magnification, although both species have been observed in the same plot near the coast (Shearman personal observation). Weakley (2015) suggests that reports of red bay north of North Carolina are likely to be misidentified swamp bay individuals with less dense trichomes or including swamp bay in a larger definition of red bay. It is possible that these misidentifications also occur in reports of red bay further inland. The higher pH, calcium, and phosphorus concentrations in the soils of red bay plots close to the Atlantic coast is possibly caused by shell middens, deposits of mollusk shell and cultural detritus created by native peoples (Sawbridge & Bell 1972), and is consistent with previous studies reporting high pre-wilt red bay density on soils with high pH and phosphorus concentrations (Smith et al. 2015). Perhaps these soil conditions favor red bay establishment over swamp bay.

We identified seven community groups in which red bay and swamp bay occur. That the bootstrap analyses using both biotic and abiotic predictors largely agreed with

the hierarchical cluster analysis is convincing evidence for our seven groups. The indicator species analysis supports the results of the NMS ordination, showing red bay as an indicator species of Cluster 1 only, while swamp bay was an indicator for all of the other groups, indicating a wider geographical distribution but a less distinctiveness for those communities containing swamp bay.

Among the seven groups, red bay and swamp bay were least important in the longleaf pine communities (Clusters 3 and 5), with the lowest density and basal area. This pattern is likely due to the frequent fires that occur in the longleaf pine ecosystem. Without fire, it is likely that *Persea* basal area, density, and importance would increase in these communities. For example, Menges et al. (1993) studied changes in vegetation in south-central Florida over a period of 20 years in areas that had not been burned in over 60 years. They found that the flatwoods, the community with the shortest historic fire return interval (3 – 10 years), shifted towards bayhead community vegetation, which contains swamp bay, loblolly bay (*Gordonia lasianthus*), and sweet bay (*Magnolia virginiana*). *Persea* increased in basal area (0.13 to 0.55 m^2/ha) and in density (67 to 178 stems/ha) in the flatwood/bayhead complex from 1969 – 1989 (Menges et al. 1993). Although plots in our Clusters 3 and 5 were assigned to the same NVC Groups, our analysis split them largely along the "wiregrass gap" in South Carolina, with plots to the north including the northern wiregrass species, *Aristida stricta*, and plots to the south including the southern species, *A. beyrichiana* (Peet 1993).

The pond cypress communities (Cluster 6) also had low *Persea* basal area, density and importance. These communities are also maintained by disturbance, mainly flooding,

which allows for few species other than *Taxodium ascendens* to establish (Schafale 2012). Pond cypress woodlands may also require fire during dry seasons to maintain their open savanna structure (NatureServe 2015).

The increase in *Persea* density and basal area in the absence of disturbance suggests that the two *Persea* species are "later successional" species. Several other authors have arrived at the same conclusion. Buell and Cain (1943) found that, in the absence of fire, southern white cedar swamps were replaced by *Persea-Magnolia* swamps, with swamp bay being the most abundant. Monk (1968) suggested that bayhead forests (those dominated by *Magnolia virginiana*, *Persea palustris*, and *Gordonia lasianthus*) can be considered "climax" communities and can result from the elimination of fire in wet sites. Duever and Riopelle (1983) reported that red bay (or more likely, swamp bay) was found on older tree islands in the Okefenokee Swamp, but was not found on younger islands, where it would otherwise be expected. Bratton and Miller (1994) found that *Persea* frequency on Cumberland Island, GA, was highest in the understory in areas that had no history of agriculture use. *Persea* frequency in the overstory, however, was highest in cotton fields that were abandoned prior to 1870. They found that land use history and soil moisture were significant covariates in red bay frequency (Bratton and Miller 1994). All of these studies, as well as the results of our analyses, suggest that red bay and swamp bay are sensitive to frequent disturbances. *Persea* basal area, density, and importance were seen to be highly variable in all groups. Perhaps one reason we did not detect significant differences in *Persea* basal area, density,

or importance among Clusters 1, 2, 3, and 5 is that plots within these groups have had different land use histories and disturbances.

Implications of Laurel Wilt Disease

Because of their large difference in *Persea* abundance, the seven communities identified in our study will likely be impacted differently by LWD. Communities in Clusters 1, 2, 4, and 7 are likely the most susceptible to attack by *X. glabratus*, because these communities support the highest basal area of *Persea*. Red bay, being restricted to coastal communities (Cluster 1), has a potentially higher risk of extirpation. Similarly, the consequences of the loss of mature *Persea* in these communities will also vary among communities or even on a stand by stand basis. Communities or stands where *Persea* has high importance will likely see more impacts. Spiegel and Leege (2013) suggested that co-dominant species such as sweet bay (*Magnolia virginiana*) and loblolly bay (*Gordonia lasianthus*) will increase in dominance following the loss of *Persea*. This increase in dominance would likely be more pronounced in stands where dead *Persea* left large gaps. Goldberg and Heine (2009) compared vegetation on Little Talbot Island in Florida after LWD, with surveys from 1983 done by Stalter and Dial (1984). They found that eastern redcedar (*Juniperus virginiana*) replaced red bay as the third most abundant species in the overstory, although red bay did increase in abundance in the understory along with oaks (*Quercus* spp.), cabbage palms (*Sabal palmetto*), and holly (*Ilex opaca* and *I. vomitoria*). This suggests that although overstory structure will change in stands

with a large *Persea* component, the future status of red bay and swamp bay communities remains uncertain.

Our study is the first that attempted to characterize *Persea* communities in its core distribution range. Since our study was based on data collected before the introduction of LWD, our analyses provides valuable information on these communities, which should be useful in any future restoration efforts. Our study supports that *Persea* is very sensitive to disturbance because the groups with low *Persea* basal area and density are also those that are typically maintained by frequent disturbances. Therefore, rapid land development in coastal forests could also negatively impact *Persea* communities that are already facing the devastating LWD. The threats from LWD and disturbances are extremely acute for red bay communities. Among the seven community types classified in the study, red bay is almost entirely restricted to one community type in coastal areas, and thus facing higher risk of extirpation should make red bay communities a conservation priority.

3.5. Literature Cited

Anderson, M.J., & Walsh, D.C. 2013. PERMANOVA, ANOSIM, and the Mantel test in the face of heterogeneous dispersions: What null hypothesis are you testing? *Ecological Monographs* 83: 557–574.

Bratton, S.P., & Miller, S.G. 1994. Historic field systems and the structure of maritime oak forests, Cumberland Island National Seashore, Georgia. *Bulletin of the Torrey Botanical Club*

Brendemuehl, R.H. 1990. Persea borbonia (L.) Spreng. Red bay. In Burns, R.M. & Honkala, B.H. (eds.), *Silvics of North America*, pp. 503–506. Agriculture Handbook 654, USDA Forest Service, Washington, DC.

Buell, M.F., & Cain, R.L. 1943. The Successional Rôle of Southern White Cedar, Chamaecyparis Thyoides, in Southeastern North Carolina. *Ecology* 24: 85–93.

Cameron, R.S., Bates, C., & Johnson, J. 2008. Distribution and spread of laurel wilt disease in Georgia: 2006-08 survey and field observations. *Georgia Forestry Commission. US Forest Service. http://fhm. fs. fed. us/em/funded/09/so-em-08-02-report. pdf (18 April 2011)*

Cameron, R.S., Bates, C., & Johnson, J. 2010. Evaluation of laurel wilt disease in Georgia: progression in red bay and sassafras 2008–2010. *Georgia Forestry Commission and US Dep. Agric. Forest Service–Forest Health Protection Region* 8.:

Clarke, K.R. 1993. Non-parametric multivariate analyses of changes in community structure. *Australian journal of ecology* 18: 117–117.

De Caceres, M., Jansen, F., & De Caceres, M.M. 2015. Package "indicspecies."

Dengler, J., Löbel, S., & Dolnik, C. 2009. Species constancy depends on plot size–a problem for vegetation classification and how it can be solved. *Journal of Vegetation Science* 20: 754–766.

Duever, M.J., & Riopelle, L.A. 1983. Successional sequences and rates on tree islands in the Okefenokee Swamp. *American Midland Naturalist*

Dufrêne, M., & Legendre, P. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecological monographs* 67: 345–366.

Fraedrich, S.W., Harrington, T.C., Rabaglia, R.J., Ulyshen, M.D., Mayfield Iii, A.E., Hanula, J.L., Eickwort, J.M., & Miller, D.R. 2008. A fungal symbiont of the red bay ambrosia beetle causes a lethal wilt in red bay and other Lauraceae in the southeastern United States. *Plant Disease* 92: 215–224.

Giraudoux, P. 2015. Package "pgirmess."

Goldberg, N., & Heine, J. 2009. A comparison of arborescent vegetation pre-(1983) and post-(2008) outbreak of the invasive species the Asian ambrosia beetle Xyleborus glabratus in a Florida maritime hammock. *Plant Ecology & Diversity* 2: 77–83.

Hanula, J.L., Mayfield, A.E., Fraedrich, S.W., & Rabaglia, R.J. 2008. Biology and host associations of red bay ambrosia beetle (Coleoptera: Curculionidae: Scolytinae), exotic vector of laurel wilt killing red bay trees in the southeastern United States. *Journal of economic entomology* 101: 1276–1286.

Harrington, T.C., Aghayeva, D.N., & Fraedrich, S.W. 2010. New combinations in Raffaelea, Ambrosiella, and Hyalorhinocladiella, and four new species from the red bay ambrosia beetle, Xyleborus glabratus. *Mycotaxon* 111: 337–361.

Jennings, M.D., Faber-Langendoen, D., Loucks, O.L., Peet, R.K., & Roberts, D. 2009. Standards for associations and alliances of the US National Vegetation Classification. *Ecological Monographs* 79: 173–199.

Kendra, P.E., Montgomery, W.S., Niogret, J., & Epsky, N.D. 2013. An Uncertain Future for American Lauraceae: A Lethal Threat from Red bay Ambrosia Beetle and Laurel Wilt Disease (A Review). *American Journal of Plant Sciences* 4: 727–738.

Koch, F.H., & Smith, W.D. 2008. Spatio-temporal analysis of Xyleborus glabratus (Coleoptera: Circulionidae: Scolytinae) invasion in eastern US forests. *Environmental entomology* 37: 442–452.

Maechler, M., Rousseeuw, P., Struyf, A., Hubert, M., Hornik, K., Studer, M., & Roudier, P. 2015. *Package "cluster."*

Matthews, E.R., Peet, R.K., & Weakley, A.S. 2011. Classification and description of alluvial plant communities of the Piedmont region, North Carolina, USA. *Applied Vegetation Science* 14: 485–505.

Mayfield III, A.E., & Brownie, C. 2013. The Red bay Ambrosia Beetle (Coleoptera: Curculionidae: Scolytinae) uses Stem Silhouette Diameter as a Visual Host-Finding Cue. *Environmental entomology* 42: 743–750.

Mayfield III, A.E., Smith, J.A., Hughes, M., & Dreaden, T.J. 2008. First report of laurel wilt disease caused by a Raffaelea sp. on avocado in Florida. *Plant Disease* 92: 976–976.

McCune, B., Grace, J.B., & Urban, D.L. 2002. *Analysis of ecological communities*. MjM software design Gleneden Beach, OR.

Menges, E.S., Abrahamson, W.G., Givens, K.T., Gallo, N.P., & Layne, J.N. 1993. Twenty Years of Vegetation Change in Five Long-Unburned Florida Plant Communities. *Journal of Vegetation Science* 4: 375–386.

Monk, C.D. 1968. Successional and environmental relationships of the forest vegetation of north central Florida. *American Midland Naturalist*

Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Wagner, H., & others. 2015. Package "vegan." *Community ecology package, version 2.3-5*

Otypková, Z., & Chytry, M. 2006. Effects of plot size on the ordination of vegetation samples. *Journal of Vegetation Science* 17: 465–472.

Peet, R.K. 1993. A Taxonomic study of *Aristida stricta* and *A. beyrichiana*. *Rhodora* 95: 25–37.

Peet, R.K., & Roberts, D.W. 2013. Classification of Natural and Semi-natural Vegetation. In derarel, E. van & Franklin, J. (eds.), *Vegetation Ecology*, pp. 28–70. John Wiley & Sons, Ltd.

Peet, R.K., Wentworth, T.R., & White, P.S. 1998. A flexible, multipurpose method for recording vegetation composition and structure. *Castanea*

Radford, A.A., Ahles, H.E., & Bell, C.R. 1968. *Manual of the vascular flora of the Carolinas*. University of North Carolina Press.

Sawbridge, D.F., & Bell, M.A.M. 1972. Vegetation and Soils of Shell Middens on the Coast of British Columbia. *Ecology* 53: 840–849.

Schafale, M.P. 2012. Guide to the natural communities of North Carolina, fourth approximation. *North Carolina Natural Heritage Program, North Carolina Department of Environment and Natural Resources, Raleigh, North Carolina*

Shearman, T.M., Wang, G.G., & Bridges, W.C. 2015. Population dynamics of red bay (Persea borbonia) after laurel wilt disease: an assessment based on forest inventory and analysis data. *Biological Invasions* 17: 1371–1382.

Shields, J., Jose, S., Freeman, J., Bunyan, M., Celis, G., Hagan, D., Morgan, M., Pieterson, E.C., & Zak, J. 2011. Short-term impacts of laurel wilt on red bay (Persea borbonia [L.] Spreng.) in a mixed evergreen-deciduous forest in northern Florida. *Journal of Forestry* 109: 82–88.

Smith, J.A., Dreaden, T.J., Mayfield III, A.E., Boone, A., Fraedrich, S.W., & Bates, C. 2009. First report of laurel wilt disease caused by Raffaelea lauricola on sassafras in Florida and South Carolina. *Plant Disease* 93: 1079–1079.

Smith, C.K., Landreaux, E., Steinmann, H., McGrath, D., Hayes, C., & Hayes, R. 2015. Red bay Survival Eleven Years after Infection with an Exotic Disease on St. Catherines Island, Georgia, USA. *Environment and Natural Resources Research* 6: 27.

Smith, J.A., Mount, L., Mayfield III, A.E., Bates, C.A., Lamborn, W.A., & Fraedrich, S.W. 2009. First report of laurel wilt disease caused by Raffaelea lauricola on Camphor in Florida and Georgia. *Plant Disease* 93: 198–198.

Spiegel, K.S., & Leege, L.M. 2013. Impacts of laurel wilt disease on red bay (Persea borbonia (L.) Spreng.) population structure and forest communities in the coastal plain of Georgia, USA. *Biological Invasions* 15: 2467–2487.

Stalter, R., & Dial, S.C. 1984. Hammock vegetation of Little Talbot Island State Park, Florida. *Bulletin of the Torrey Botanical Club* 111: 494–497

CHAPTER FOUR

RECOVERY OR EXTINCTION? INSIGHT FROM *PERSEA* RESPONSE TO LAUREL WILT DISEASE DURING THE FIRST 10 YEARS

4.1. Introduction

Laurel wilt disease (LWD), caused by the non-native fungus, *Raffaelea lauricola* T.C. Harr., Fraedrich & Aghayeva., is responsible for heavy mortality in the Lauraceae of the southeastern United States (Fraedrich et al. 2008, Harrington et al. 2008). The fungus is vectored by a non-native ambrosia beetle (*Xylaborus glabratus* Eichhoff), which entered the U.S. around 2002 (Rabaglia et al. 2006, Fraedrich et al. 2008). Laurel wilt disease was first reported in 2003 in red bay (*Persea borbonia* [L.] Spreng.) and is now present in eight states, with near complete mortality of red bay stems in the infected stands (Fraedrich 2008, Riggins et al. 2010). In addition to dissemination by beetle, the spread of LWD has been facilitated by anthropogenic activities such as transportation of firewood (Cameron et al. 2008, 2010). Additional lauraceous hosts are also susceptible and will likely spread the disease beyond the range of red bay (Fraedrich et al. 2008, Smith et al. 2009a, 2009b, Gramling 2010, Peña et al. 2012).

Red bay is native to the lower coastal plain of the southeastern United States (Brendemuehl 1990). Swamp bay (*Persea palustris* [Raf.] Sarg.) is sometimes considered a separate species from red bay, with smaller stature and longer flower stalks and dense bent trichomes on the leaves (Coder 2007). Chapter 3 found that red bay and swamp bay are members of different communities, with red bay almost exclusively inhabiting the

coastal fringe maritime forests and swamp bay having a much wider distribution. Despite this, most studies on LWD include swamp bay in a larger definition of red bay.

Many studies have recognized a pattern of higher mortality in larger *Persea* stems (Fraedrich et al. 2008, Shields et al. 2011, Spiegel and Leege 2013, Cameron et al. 2015). For example, Kendra et al. (2013) found that larger red bay stems had higher number of beetle entrance holes and suggest that the beetles attack larger stems first, which may account for the higher mortality in these larger stems. Mayfield and Brownie (2013) used artificial stem silhouettes baited with essential oils to show that *X. glabratus* use visual as well as olfactory cues to locate host trees, with larger silhouettes attracting more beetles. Shearman et al. (2015) used data from the Forest Inventory and Analysis (FIA) database to show that stem diameter significantly increased the odds of death of *Persea* stems in counties where LWD was present. Larger stems are believed to provide larger egg galleries, although Maner et al. (2014) found that *X. glabratus* can feasibly sustain low populations on small diameter stems (2 – 3 cm), only producing a few adults per stem. It is unknown how long *X. glabratus* can maintain these low populations. Maner et al. (2014) found beetle populations dropped to low levels (<1 captured per day) 5 years after invasion and dropped even further 8 – 9 years post invasion. Similarly, Cameron et al. (2015) found that post-epidemic (~7 years) *X. glabratus* populations averaged approximately 0.03 beetles trapped/day, whereas advanced-active sites averaged 5.70 beetles trapped/day. It is possible that, given enough time, *X. glabratus* could be removed from the system allowing *Persea* to re-establish.

Although many studies have documented the initial decline of *Persea* in stands infected with LWD (for example Fraedrich et al., 2008; Shields et al., 2011; Spiegel and Leege, 2013), there have been few studies documenting recovery of *Persea* after LWD. Evans et al. (2014) monitored plots on St. Catherine's Island, GA from 2004 to 2009 and found that after 98% mortality of initial red bay stems, subsequently resprouting stems also suffered 79% mortality. They also observed that there was no regeneration of red bay or any hardwood species in their plots. They suggest that deer browse on the island is preventing regeneration of hardwoods and, along with a lack of seed production, is contributing to the decline of red bay (Evans et al. 2014). Smith et al. (2015) also studied red bay on St. Catherine's Island. They observed stands 11 years post infection, using standing dead stems (snags) and logs as indicators of pre-wilt red bay density. They found that, although different plot locations (maritime forest, hammock, and old field) had different red bay density prior to LWD, all sites were similar in terms of density (29 – 51 average stems/ha) and diameter (3.1 – 3.8 cm average diameter at breast height) of red bay after 11 years (Smith et al. 2015). Much like Evans et al. (2014), Smith et al. (2015) did not find any red bay seedlings among their study sites. However, they noted that deer browse on red bay sprouts was low and many sprouts were above the browse line. Additionally, they found several red bay trees with fruits, which suggests that the post-LWD seed regeneration of *Persea* requires further study.

In this study, the primary objectives were: (1) to identify the patterns of *Persea* mortality and regeneration; and (2) determine the plant community response to the loss of *Persea* and any possible expansion of invasive plants that may hinder regeneration.

Additionally, this study sought to determine whether there are any differences in these previous objectives between stands dominated by red bay or swamp bay.

4.2. Methods

Study Site

Our study took place at multiple locations along the coast of South Carolina and Georgia (Figure 4.1). We chose locations along the gradient of disease progression so that we had stands sampled in a range of "recovery years", the number of years that have passed since LWD was detected in the stand. Laurel Wilt Disease was first reported from 2004 – 2012 among sites. Sites were sampled during the growing season in 2013 and 2014, resulting in a range of 1 – 10 recovery years over the 61 sampled plots (Table 4.1). Most plots consisted of either red bay or swamp bay alone, although two plots contained both species. In both of these cases, the plot was predominantly one of the two species with a single individual of the other.

Sampling Methods

At each site, plots were chosen based on high density of either living or dead *Persea*. We used a modified version of the Carolina Vegetation Survey (CVS) protocol to record the vegetation on our plots (Peet et al. 1998). Plots were 400 m^2 (20 x 20 m) in size which were divided into four 10 m by 10 m modules (Figure 4.2). Five to ten plots were sampled at each site, except for Francis Marion where only three suitable sites were found. Percent cover was estimated for all species in each plot according to a standard

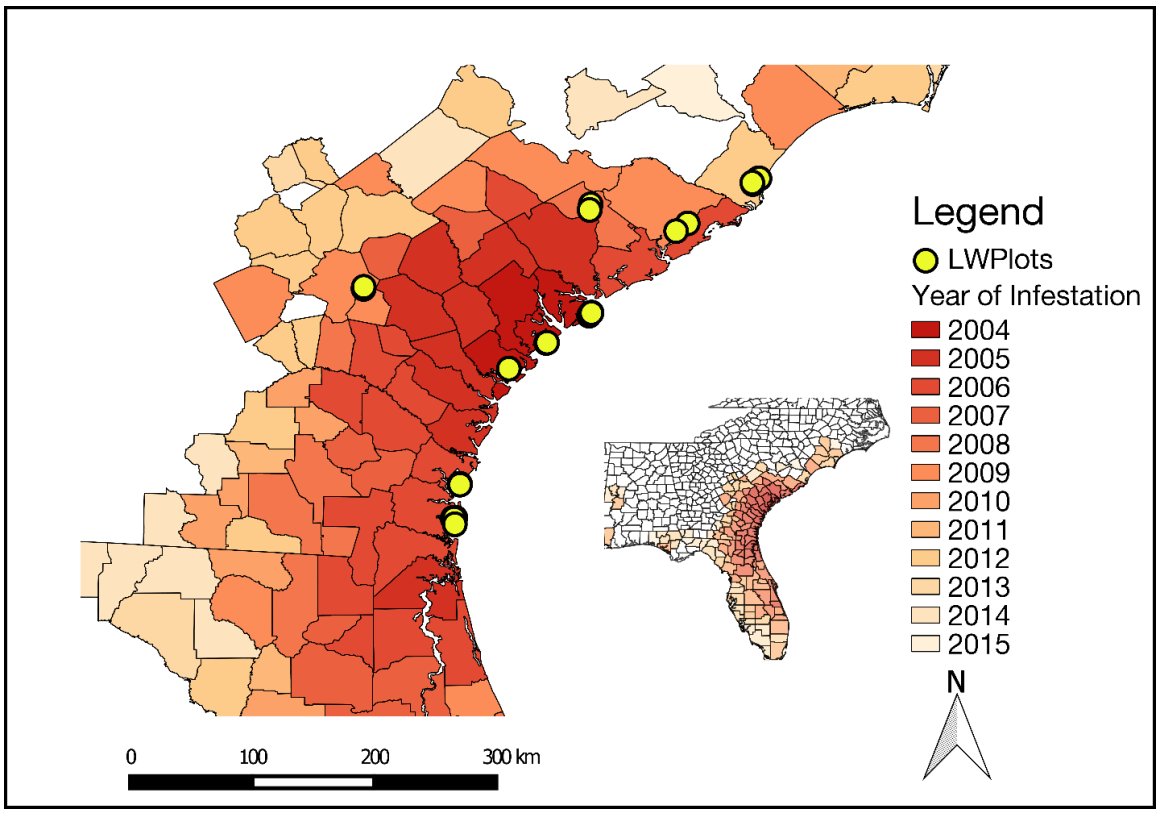

Figure 4.5. Location of 61 sampled plots in 9 sites along the coast of South Carolina and Georgia. Infestation data obtained from Hughes et al. (2015).

cover class scale: 1 = trace, 2 = 0 – 1%, 3 = 1 – 2%, 4 = 2 – 5%, 5 = 5 – 10%, 6 = 10 – 25%, 7 = 25 – 50%, 8 = 50 – 75%, 9 = 75 – 95%, 10 = > 95%. Woody stems with a measurable diameter at breast height (DBH) were recorded for all species in diameter classes. *Persea* stems were recorded in three categories: live, wilted (leaves still on), or snag (standing dead). Dead stems that had fallen over were measured on the ground or, in some instances, the highest measurable point along the stump and counted as snags. In each module, nested quadrats were located in two corners (10 m^2 in area each, Figure

3.2). In each quadrat, *Persea* seedlings were counted and measured in three size classes (<30, 30–60, >60 cm).

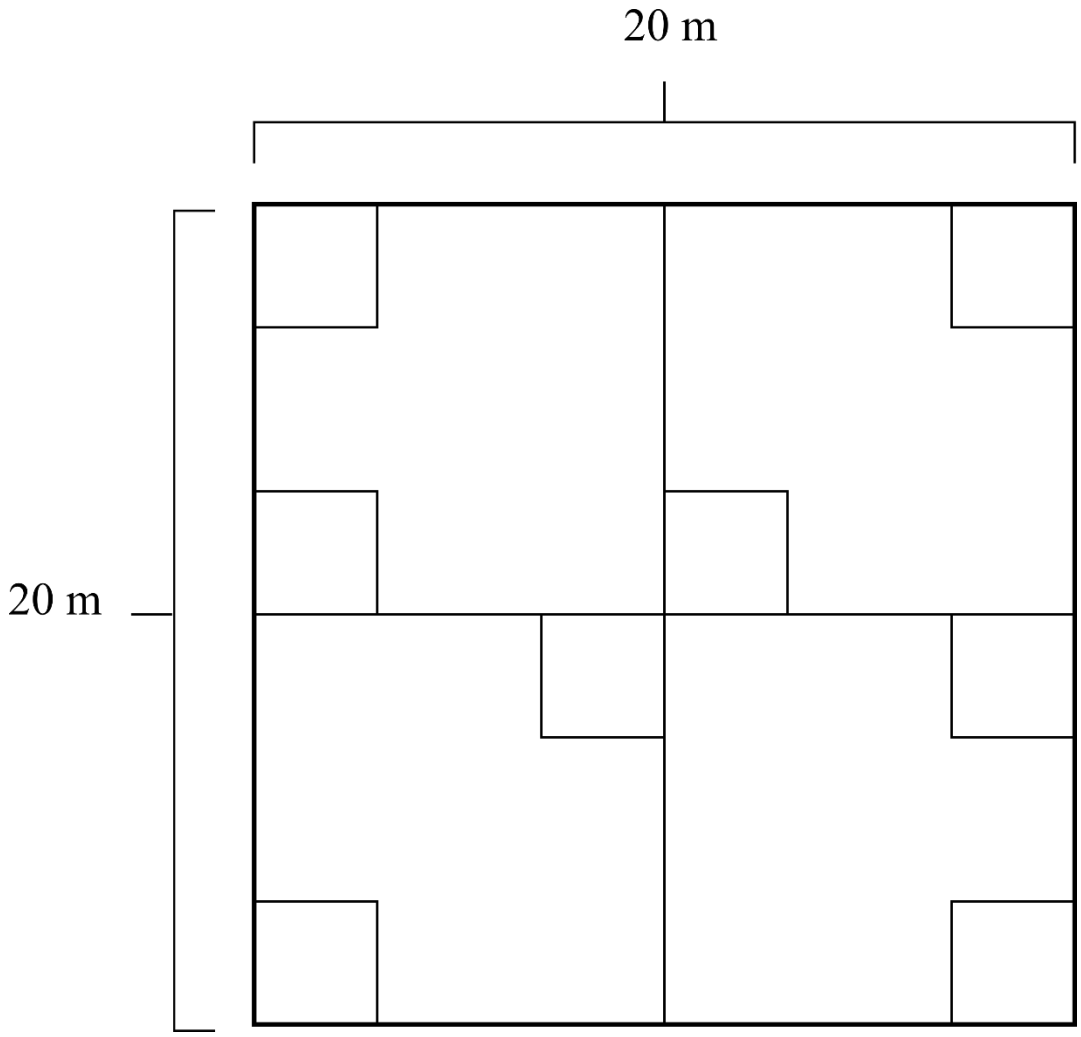

Figure 4.6. Plot design showing 20 x 20 m plot made up of four 10 x 10 m modules. Each module has two 10 m^2 seedling subplots.

Data Analysis

We removed plots from Francis Marion from the analyses because they were primarily longleaf pine woodlands that are subject to frequent prescribed burns. These woodlands typically have low *Persea* abundance to begin with, which could mask any observable *Persea* recovery. We calculated the basal area of all species including *Persea* snags using the formula: $BA = DBH^2 * 0.00007854$, where DBH is the midpoint of the

Table 4.1. Number of plots surveyed for each location. LW Year is the year that laurel wilt disease (LWD) was first reported at the site. Recovery Years is the number of years since LWD was reported and when the site was sampled. Overstory plots are 400 m^2 modified CVS plots (see methods). Seedling plots are 10 m^2 subplots nested within each overstory plot (eight per plot). Either red bay (*Persea borbonia*) or swamp bay (*P. palustris*) was the dominant *Persea* species in each site.

Location	LW Year	Recovery Years	Overstory Plots	Seedling Plots	Species
Hobcaw	2012	1	9	72	*P. palustris*
GL Smith SP	2012	2	5	40	*P. palustris*
Francis Marion	2009	4	3	24	*P. palustris*
Brosnan Forest	2008	6	5	40	*P. palustris*
Cumberland Island	2006	8	10	80	*P. borbonia*
Jekyll Island	2006	8	9	72	*P. borbonia*
Hilton Head	2004	9	5	40	*P. palustris*
Hunting Island	2004	9	10	80	*P. borbonia*
Skidaway Island	2004	10	5	40	*P. palustris*

diameter class at 1.4 m height in cm and BA is basal area in m^2, which was converted to m^2/ha. Because *Persea* density and basal area varies widely from location to location and we did not have adequate control plots to compare plots in each recover year, we used *Persea* snags as indicators of the abundance before laurel wilt appeared in each plot. Snags generally break apart a few years after infestation (Cameron et al. 2008), but enough of the stem usually remains (either as a snag, log, or stump) to estimate pre-disease abundance as has been done in other studies (e.g. Smith et al. 2015). We took the difference of live basal area and snag basal area for all plots and regressed them on recovery year. Early in the disease progression, live basal area should be larger than snag basal area, as many large stems have yet to succumb to the disease. In this case, the live-snag difference would be a positive number. As the disease progresses through the stand, snag basal area would increase, eventually to the point where snag basal area is larger than live basal area and the live-snag difference would be a negative number. If recovery is taking place, live basal area should begin to increase after some time, eventually to the point where live basal area equals snag basal area and the difference is zero. To see if red bay recovery differed from swamp bay, we compared the difference in live and snag basal area in the red bay plots with those of swamp bay for similar recovery years using a *t*-test. Seedling density was calculated for each plot. This density was then compared by height classes for groups of recovery years (1 – 2, 6 – 8, and 9 – 10) using Analysis of Variance (ANOVA). *Persea* stem density was calculated in diameter classes and summarized for each recovery year.

Table 4.2. Basal area (m^2/ha) for tree species in nine sites impacted from Laurel Wilt disease. Bro = Brosnan Forest; CI = Cumberland Island; FM = Francis Marion; GL = G. L. Smith State Park; HH = Hilton Head Island; HI = Hunting Island State Park; Hob = Hobcaw Barony; JI = Jekyll Island; SI = Skidaway Island

Species	**Bro**	**CI**	**FM**	**GL**	**HH**	**HI**	**Hob**	**JI**	**SI**
Morella cerifera	0.1	0.0	0.1	0.0	0.4	0.1	0.3	0.0	0.2
Persea snag	4.4	4.5	0.0	6.8	0.9	2.6	0.4	3.9	2.9
Pinus taeda	0.0	2.2	0.1	0.9	9.5	0.0	14.2	1.7	20.6
Persea palustris	1.2	0.0	0.3	0.0	0.3	0.0	5.5	0.0	2.4
Liquidambar styraciflua	2.6	0.0	0.2	0.0	2.9	1.6	4.7	0.0	11.3
Quercus virginiana	0.0	31.9	0.0	0.0	3.8	4.3	1.0	26.5	0.3
Ilex opaca	0.0	0.1	0.0	0.0	0.0	0.0	1.3	0.7	0.1
Quercus hemisphaerica	0.0	0.2	1.1	0.0	1.0	1.7	0.0	9.9	0.0
Quercus nigra	0.0	0.0	0.8	5.7	1.6	0.0	3.5	0.0	2.9
Acer rubrum	8.9	0.0	0.0	0.8	0.0	0.0	0.1	0.0	0.0
Quercus laurifolia	0.0	2.4	0.1	0.0	0.0	0.0	0.0	0.0	0.0
Persea borbonia	0.0	0.2	0.0	0.0	0.0	0.6	0.0	0.4	0.0
Gordonia lasianthus	0.0	0.0	0.0	6.8	0.0	0.0	0.0	0.0	0.0
Pinus elliottii	0.0	0.0	0.0	0.0	17.0	29.8	0.0	1.9	0.0
Nyssa sylvatica	12.1	0.0	0.0	0.7	0.0	0.0	0.0	0.0	0.0
Juniperus virginiana	0.0	3.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Pinus palustris	0.0	0.8	10.1	0.0	0.0	0.0	0.0	0.0	0.0
Pinus serotina	0.0	0.0	1.2	7.9	0.0	0.0	0.0	0.0	0.0
Magnolia virginiana	0.0	0.0	0.0	2.8	0.0	0.0	0.0	0.0	0.0
Liriodendron tulipifera	0.0	0.0	0.0	3.5	0.0	0.0	1.7	0.0	0.0
Sabal palmetto	0.0	0.0	0.0	0.0	1.8	5.2	0.0	0.0	0.0
Cliftonia monophylla	0.0	0.0	0.0	9.0	0.0	0.0	0.0	0.0	0.0
Nyssa biflora	0.0	0.0	0.0	0.0	0.0	0.0	2.0	0.0	0.0
Quercus michauxii	0.0	0.0	0.0	0.0	0.0	0.0	1.2	0.0	0.0
Other	0.0	0.9	0.5	0.9	0.0	0.2	0.9	0.8	0.3
Total	29.3	46.3	14.5	45.7	39.2	46.1	37.0	45.8	41.0

4.3. Results

Woody species composition and basal areas differed among sites (Table 4.2). The most common non-*Persea* species found among sites was wax myrtle, *Morella cerifera*, which occurred as a measurable stem in six of the nine sites and as an understory species in nearly all plots. *Persea* basal area also differed substantially among sites, with Hobcaw having the highest live *Persea* basal area (4.4 m^2/ha) and wilted *Persea* basal area (1.1 m^2/ha) and G.L. Smith State Park (GL) having no live measurable stems (Table 4.2). GL had the highest *Persea* snag basal area (5.9 m^2/ha), with Francis Marion and Hobcaw having the lowest (0 and 0.4 m^2/ha respectively).

We did not find any indication that LWD was facilitating invasive species establishment in our plots. One individual seedling of Chinese tallow (*Triadica sebiferum*) was found in one plot. Other non-native species found include red woodsorrel (*Oxalis rubra*) and Chinese privet (*Ligustrum sinense*), however none of these species had a cover value higher than 0 – 1% in any plot.

A plot of the difference of live *Persea* basal area and *Persea* snags against recovery year indicated that a piecewise regression best fit the data (Figure 4.2). A decline in the difference occurs from year 1 to year 2, followed by an increase in years 2 – 10. The trend line was highly significant ($P < 0.001$), with the first segment having a negative slope (-9.96 m^2/ha/yr +/- 2.3) and the second segment having a positive slope (0.85 m^2/ha/yr +/- 0.59), which explained approximately 61% of the variation in the data (Figure 4.2). We included both species in the regression because we did not find any significant differences in live-dead basal area between red bay and swamp bay among the

years where we had data on both species (mean difference = -0.17, t = -0.18, df =32, P = 0.86, Table 4.3).

Table 4.3. Results of a *t*-test comparing recovery of red bay (*P. borbonia*) and swamp bay (*P. palustris*) in plots 8 - 9 years after infection from Laurel Wilt Disease. Recovery is measured by the difference of live basal area (m^2/ha) and dead snag basal area (m^2/ha).

Species	**N**	**Mean**	**Std Error**	**UCL**	**LCL**	***t*-ratio**	***df***	***P*-Value**
P. borbonia	28	-1.13	0.40	-0.32	-1.93			
P. palustris	6	-1.30	0.86	0.45	-3.04			
Difference		-0.17	0.94	1.75	-2.10	-0.18	32	0.86

Density of *Persea* seedlings (≤ 140 cm tall) was highest in year 1 and year 9 plots for seedlings under 30 cm in height (9792 and 7708 stem/ ha respectively, Table 4.4). All other plots had similar densities for the 0 – 30 cm size class. The 30 – 60 cm and 60 – 140 cm size classes were also similar among plots, with plots in year 10 having the highest density in the 30 – 60 cm size class (3725 stem/ha) and plots in year 6 having the highest density in the 60 – 140 cm size class (5350 stem/ha). Comparing densities in groups of recovery years found no significant differences in the 0 – 30 or 30 – 60 cm size classes. There was a significant difference in seedling density for 60 – 140 cm seedlings ($F_{2,55}$ = 7.7, P = 0.001), with plots in the 6 – 8 year group having slightly higher density

(955, 2598, and 1150 stem/ha, for the 1 – 2, 6 – 8, and 9 – 10 groups respectively, Figure 4.3).

Table 4.4. *Persea* basal area and seedling density (and standard errors) for plots in different years since LWD.

		Basal Area (m^2/ha)			Seedling Density (stems/m^2)		
Recovery Year	n	Live	Wilted	Snag	0 - 30 cm	30 - 60 cm	60 - 140 cm
1	9	4.4 (0.5)	1.1 (0.5)	0.4 (0.08)	9792 (1345)	1125 (130)	514 (99)
2	5	0.01 (0.002)	0.003 (0.003)	5.9 (1.5)	4625 (1452)	2725 (1508)	1720 (532)
6	5	1.1 (0.2)	0.07 (0.05)	4.4 (1.1)	4050 (922)	3225 (505)	5350 (900)
8	19	0.3 (0.05)	0.02 (0.01)	2.1 (0.5)	4711 (1012)	2243 (380)	1875 (272)
9	15	0.5 (0.1)	0.03 (0.01)	0.8 (0.4)	7708 (1713)	3075 (708)	925 (209)
10	5	2.3 (0.5)	0.06 (0.03)	2.9 (1.2)	4000 (1297)	3725 (1835)	1825 (519)

Density of *Persea* saplings and trees (> 140 cm tall) differed among recovery years. In year 1, the highest density of live stems was in the 5 – 10 cm diameter class (291.7 stems/ha) with stems ranging from the 0 – 1 cm class to the 25 – 30 cm class (Table 4.5). Wilted stems and snags were less abundant than live stems. In year 2 plots, live stems were only found in the 0 – 1 and 1 – 2.5 cm classes (75.0 and 25.0 stems/ha respectively). Snags made up the majority of the *Persea* density, with the highest density in the 10 – 15 cm class (80.0 stems/ha). Snags ranged from 0 – 1 cm to 35 – 40 cm (Table 4.5). There was an increase in live stem density in year 6, primarily in the smaller

diameter classes, with the 0 – 1 cm class having the highest live *Persea* density (825.0 stems/ha). *Persea* stems in year 6 ranged from 0 – 1 cm to 10 – 15 cm. The 0 – 1 cm class also had the highest density in year 8 plots (407.9 stems/ha). In years 9 and 10, however, the highest density is in the 1 – 2.5 cm class (535.0 and 1895.0 stems/ha respectively for years 9 and 10). Snags were found in most size classes in years 2 – 10, whereas wilted stems after year 2 were found in the 0 – 1 through 5 – 10 cm classes (Table 4.5).

Table 4.5. Mean density and standard error (stems/ha) of live, wilted, and dead (snag) Persea stems for each diameter class in plots along the coast of South Carolina and Georgia. Plots were located in different years since LWD was first detected.

		Diameter Class (cm)									
Recovery Year	Status	0 - 1	1 - 2.5	2.5 - 5	5 - 10	10 - 15	15 -20	20 - 25	25 - 30	30 - 35	35 - 40
1	Live	166.7 (38.0)	108.3 (50.0)	202.8 (80.5)	291.7 (65.1)	113.9 (20.5)	50.0 (10.2)	2.8 (2.8)	2.8 (2.8)	0.0	0.0
	Wilted	25 (8.3)	19.4 (5.6)	44.4 (18.5)	47.2 (18.8)	33.3 (13.2)	11.1 (8.4)	0 (0)	2.8 (2.8)	0.0	0.0
	Snag	2.8 (2.8)	11.1 (6.1)	38.9 (17.7)	41.7 (9.3)	11.1 (6.1)	0.0	0.0	0.0	0.0	0.0
2	Live	75.0 (47.4)	25.0 (7.9)	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	Wilted	0.0	15.0 (15.0)	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	Snag	25.0 (25.0)	15.0 (15.0)	0.0	25.0 (15.8)	80.0 (21.5)	20.0 (14.6)	25.0 (11.2)	40.0 (17)	5.0 (5.0)	5.0 (5.0)
6	Live	825.0 (164.5)	690.0 (318.2)	365.0 (139.1)	105.0 (47)	5.0 (5.0)	0.0	0.0	0.0	0.0	0.0
	Wilted	30.0 (9.4)	35.0 (6.1)	15.0 (10.0)	10.0 (10.0)	0.0	0.0	0.0	0.0	0.0	0.0
	Snag	15.0 (15.0)	15.0 (10.0)	155.0 (37.4)	315.0 (78.5)	120.0 (26.7)	20.0 (12.2)	5.0 (5.0)	5.0 (5.0)	5.0 (5.0)	0.0
8	Live	407.9 (49.3)	340.8 (43.6)	84.2 (18.5)	14.5 (6.1)	1.3 (1.3)	0.0	0.0	0.0	0.0	0.0
	Wilted	5.3 (2.4)	11.8 (4.8)	6.6 (3.2)	1.3 (1.3)	0.0	0.0	0.0	0.0	0.0	0.0
	Snag	0.0	5.3 (2.4)	13.2 (5.2)	76.3 (17.0)	57.9 (12.1)	50.0 (9.4)	17.1 (4.7)	9.2 (3.4)	3.9 (2.1)	1.3 (1.3)
9	Live	420.0 (65.5)	535.0 (74.0)	118.3 (19.1)	26.7 (9.0)	3.3 (2.3)	1.7 (1.7)	0.0	0.0	0.0	0.0
	Wilted	35.0 (9.7)	45.0 (10.4)	1.7 (1.7)	3.3 (2.3)	0.0	0.0	0.0	0.0	0.0	0.0
	Snag	3.3 (3.3)	0.0	8.3 (4.0)	51.7 (13.2)	60.0 (17.6)	23.3 (7.1)	8.3 (4.0)	0.0	0.0	1.7 (1.7)
10	Live	635.0 (114.2)	1895.0 (509.3)	1025 (306.2)	150.0 (31.6)	5.0 (5.0)	0.0	0.0	0.0	0.0	0.0
	Wilted	30.0 (20.0)	90.0 (25.7)	10.0 (6.1)	5.0 (5.0)	0.0	0.0	0.0	0.0	0.0	0.0
	Snag	80.0 (58.3)	115.0 (108.9)	20.0 (12.2)	10.0 (6.1)	60.0 (24.5)	45.0 (21.5)	25.0 (11.2)	0.0	0.0	0.0

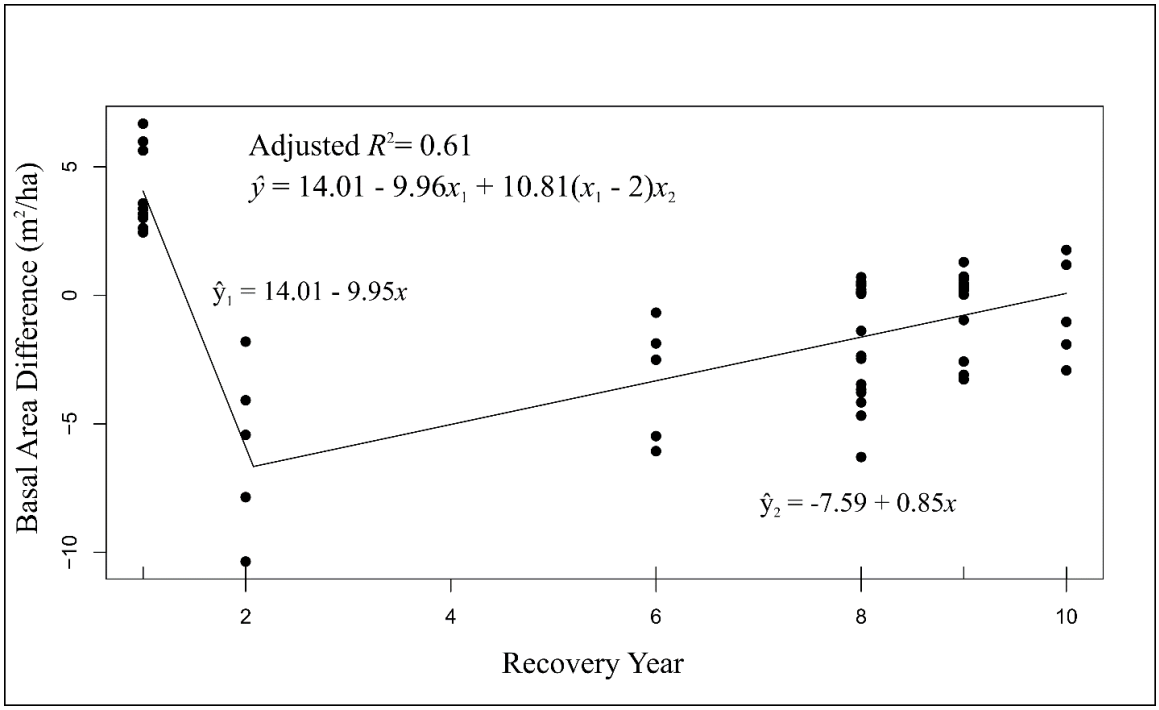

Figure 4.7. Piecewise regression of the difference in live Persea basal area and dead (snag) basal area on years since LWD. The equation for the entire line is indicated by $\hat{y}$, where x_1 is the recovery year and x_2 is a dummy variable ($x_2 = 1$ if $x_1 > 2$ and $x_2 = 0$ if $x_1 \leq 2$). Each piece in the regression is represented by equations $\hat{y}_1$ and $\hat{y}_2$.

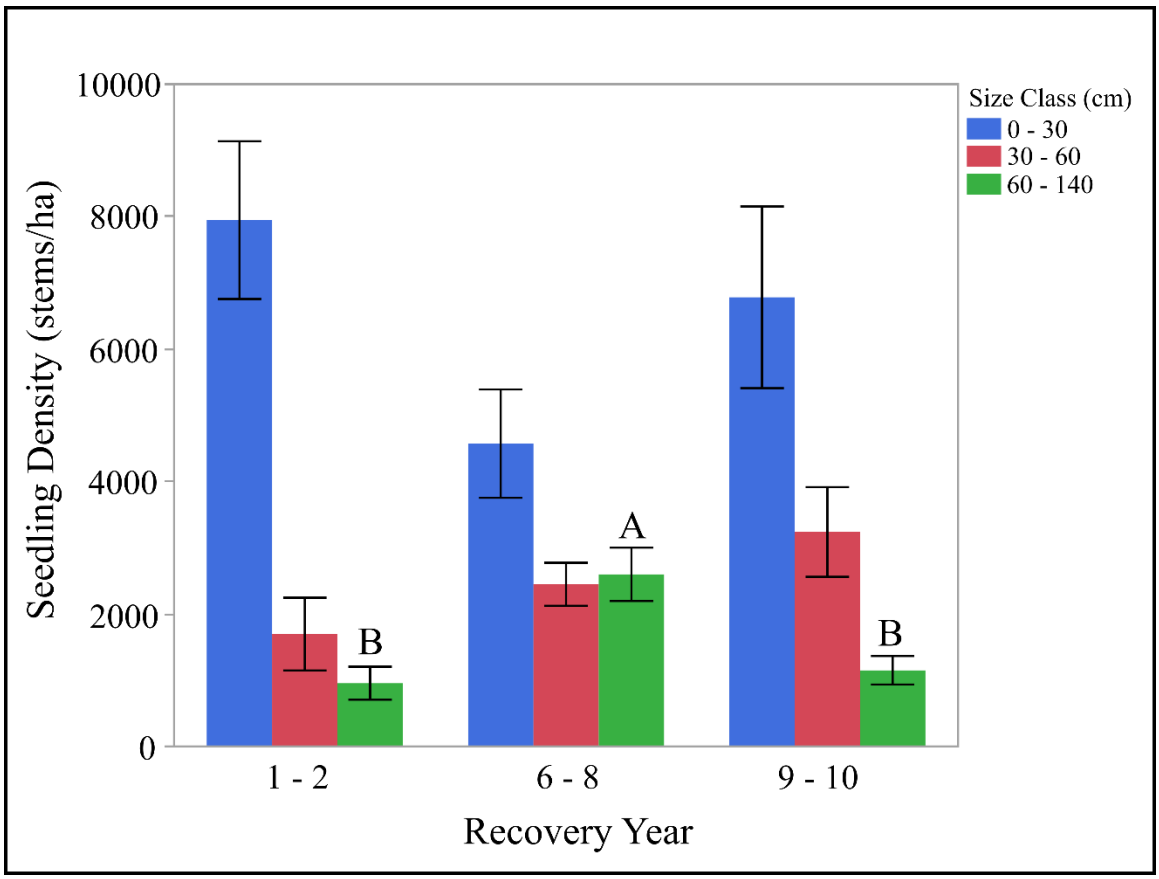

Figure 8.4. Comparison of mean seedling density for different groups of recovery years. Error bars are ± 1 standard error from the mean. Bars with no letters and bars with the same letter are not significantly different ($\alpha = 0.05$) between recovery years.

4.4. Discussion

Due to the nature of the spread of LWD, uninfected control plots were not practical in our study as they would have been located too far from our infected plots to make an adequate comparison. Unfortunately this limits our ability to make inferences on the role of LWD and invasion of non-native species. Disturbances are often thought to

promote invasion by non-native species (Vitousek et al. 1996). However, this idea is overly simplistic as other factors, such as soil fertility, as well as traits of the invading species, influences the dynamics of disturbance and invasion (Lake and Leishman 2004). We did not find any indication that non-native species were being facilitated by LWD. This lack of invasion could be due to the fact that *Persea* is not usually a dominant canopy species. Many invasive species are shade intolerant (Pattison et al. 1998, Knapp and Canham 2000, Valladares and Niinemets 2008). Because removal of *Persea* does not create large canopy gaps, invasive species may not have the opportunity to establish in the low light understory. Goldberg and Heine (2009) suggested the possibility that other native sub-canopy species such as yaupon (*Ilex vomitoria*) may replace *Persea* after LWD. Because species composition was different among our plots, we could not determine for certain if this was occurring, but we found no relationship between yaupon (or other common species such as wax myrtle), recovery year, or snag basal area that would indicate this was the case.

In the first year after infection, the basal area of live trees in our study was still larger than that of snags, and the difference in the number of living versus dead trees (snags) was positive. In the second year, most of the original live trees in the stand were then snags, and the live-snag difference was negative. Several other studies have found similar high mortality in the first few years after infection (Fraedrich et al. 2008; Shields et al. 2011; Cameron et al. 2012; Evans et al. 2014; Spiegel and Leege et al. 2008; Cameron et al. 2015). Shields et al. (2011) found 100%, 30.2%, and 1.8% mortality of *Persea* in the overstory, sapling, and seedling layers one year after initial detection of

LWD in a mixed evergreen-deciduous forest in northern Florida. Fraedrich et al. (2008) reported an increase in mortality from 9.8% to 92.4% of all *Persea* in a 16-month period at Fort George Island, Florida. Our plots in the one year after LWD stage still had a large proportion of live *Persea*, but the majority of these trees died the following year (Shearman personal observation). Our results agree with the results of Cameron et al. (2015), who reported that the average time from initial infection of *Persea* plots to disease inactivity was approximately 2.2 years, but could take up to 3.6 years in stands with larger and more abundant *Persea*. The bend in our piecewise regression also occurs around the second year, after which recovery begins to occur and the slope changes from negative to positive.

Our study is the first to demonstrate evidence of recovery of *Persea* after Laurel Wilt Disease. The recovery of live basal area seen in our study is likely the result of a combination of resprouting stems from dead stumps and small stems that were not attacked (or are resistant) during the initial disease outbreak. Cameron et al. (2015) noted that basal resprouts began in *Persea* within 6 months of showing symptoms of LWD. Although many of these initial sprouts wilt and die, Cameron et al. (2015) found that they were usually replaced by additional resprouts such that the number of sprouts per dead stem increased in the first few years after LWD and remained relatively constant 7 – 11 years post infection. Our study, as well as that of Cameron et al. (2015) are in contrast to Evans et al.'s (2014) study on St. Catherine's Island, GA. They suggested that sprouting was not a means to maintain *Persea* as approximately 79% of the original post infection resprouts (genets) died five years later. Cameron et al. (2015) attribute this contradiction

to the possibility that St. Catherine's Island may be a unique habitat that does not represent the larger *Persea* response to LWD. Regeneration failure has been reported on St. Catherine's Island in all hardwoods on the island (Evans and Keen 2013, Evans et al. 2014), suggesting other factors (for example deer browse) may be at play. Our evidence suggests that resprouts are not only able to persist up to 10 years after initial infection, but are regaining the former basal area occupied prior to LWD. However, if and when the stand recovered from LWD will be re-infested again remains unknown, which requires long-term monitoring beyond 10 years. Such long-term monitoring would be needed to understand the ultimate fate of red bay and swamp bay. We hypothesize four possible outcomes for the future of red bay and swamp bay: (1) the two species continue to decline, failing to regenerate, to the point of extinction; (2) *Persea* recovers, either by *X. glabratus* populations declining due to lack of sufficient host material, or by the propagation of wilt resistant individuals (Hughes and Smith 2014); (3) *X. glabratus* maintain small populations resulting in *Persea* occurring perpetually as small diameter stems; (4) a cyclical pattern emerges as *Persea* recover, are attacked and decimated, and recover again. It is beyond the scope of this study to test these hypotheses, as they will require long-term monitoring. However, our results indicate that red bay and swamp bay are not failing to regenerate, suggesting that the first hypothesis is the least likely to be supported at this time.

Our data suggest that mortality and regeneration is similar between red bay and swamp bay. This information is useful as most studies on LWD do not distinguish between the two species (e.g. Fraedrich et al. 2008; Cameron et al. 2008). Using the

larger definition of red bay (including both species) should not impact the results of these studies.

Resprouts in our plots have been observed to flower and fruit (Shearman, personal observation), which is contrary to other studies on St. Catherine's Island (Evans et al. 2013). Other studies have also noted a lack of *Persea* seedlings (Evans et al. 2013; Smith et al. 2015). In contrast, we found seedlings in every plot, although some were likely to be vegetative sprouts from other stems. We attempted to distinguish between stems originating from sprouts and those from seed, but this was exceedingly difficult (especially in the larger height classes), as *Persea* often spread vegetatively through root suckers, which then decay forming an independent seedling (Titus 1990). It is unknown how far from the parent these underground connections can be. However, some portion of the seedlings in our study have originated from seed as evidence by uprooted seedlings with the seed coat still attached (Shearman personal observation). There was not a strong relationship between recovery year and seedling density, with most plots having similar seedling densities. It is therefore difficult to determine the survival of these seedlings and the relationship to LWD. Because of this, a new study has begun in which we tagged seedlings in our earliest recovery year plots and will follow their survival through time.

Using snags as indicators of pre-infection basal area poses potential problems in that some snags may have fallen and decayed in later recovery years to the point where they were not detected, potentially increasing the slope of the recovery trend line. Early attempts at halting the spread of the disease included removing infected trees (Hughes et al. 2015), although stumps would still remain. Additionally, diameter measurements of

snags were not always measured at the same height and missing portions of bark and wood may have introduced error in the basal area estimates. However, because *Persea* basal area is extremely variable from stand to stand, the use of snags as indicators is a better option than attempting to find an uninfected control stand that may not be representative of pre-wilt conditions in our plots. Live basal area among recovery years showed a similar pattern to that of Figure 3, however there was significant lack of fit among the residuals.

In the tenth year after LWD, the difference in basal area of live stems and snags is approaching zero, indicating that *Persea* is recovering almost all of the basal area prior to the disease. However, this recovery is the result of extremely high densities of lower diameter stems. Although there appears to be progression to slightly larger diameter classes with time, it is still unknown whether there will be a second wave of attacks by *X. glabratus* once these trees reach larger diameters.

Our results indicate that *Persea* is not in danger of extinction at this time. We found no evidence that invasive species were expanding in our plots after LWD, instead *Persea* appears to be regenerating well, both by sprouting and by seed. This suggests that our first hypothesis on the future of red bay and swamp bay is likely rejected, but future studies should be conducted to confirm this. It is still too soon to make decisions on the remaining three hypotheses, however the persistence of *X. glabratus* in small diameter stems (Maner et al. 2014) could make full recovery of *Persea* impossible.

4.5. Literature Cited

Brendemuehl, R. H. 1990. *Persea borbonia* (L.) Spreng. Red bay. Pages 503–506 *in* R. M. Burns and B. H. Honkala, editors. Silvics of North America. Agriculture Handbook 654, USDA Forest Service, Washington, DC.

Cameron, R. S., C. Bates, and J. Johnson. 2008. Distribution and spread of laurel wilt disease in Georgia: 2006-08 survey and field observations. Georgia Forestry Commission. US Forest Service. http://fhm. fs. fed. us/em/funded/09/so-em-08-02-report. pdf (18 April 2011).

Cameron, R. S., C. Bates, and J. Johnson. 2010. Evaluation of laurel wilt disease in Georgia: progression in red bay and sassafras 2008–2010. Georgia Forestry Commission and US Dep. Agric. Forest Service–Forest Health Protection Region 8.

Cameron, R. S., J. Hanula, S. Fraedrich, and C. Bates. 2015. Progression and impact of Laurel Wilt Disease within red bay and sassafras populations in southeast Georgia. Southeastern Naturalist 14:650–674.

Coder, K. D. 2007. Taxonomy & identification: Red bay (*Persea borbonia*). University of Georgia. Warnell School of Forestry & Natural Resources. Outreach Publication SFNR07-2. 10p.

Evans, J. P., and E. M. Keen. 2013. Regeneration failure in a remnant stand of pignut hickory (*Carya glabra*) on a protected barrier island in Georgia, USA. Natural Areas Journal 33:171–176.

Evans, J. P., B. R. Scheffers, and M. Hess. 2014. Effect of laurel wilt invasion on red bay populations in a maritime forest community. Biological Invasions 16: 1581–1588.

Fraedrich, S. W., T. C. Harrington, R. J. Rabaglia, M. D. Ulyshen, A. E. Mayfield III, J. L. Hanula, J. M. Eickwort, and D. R. Miller. 2008. A fungal symbiont of the red bay ambrosia beetle causes a lethal wilt in red bay and other Lauraceae in the southeastern United States. Plant Disease 92:215–224.

Goldberg, N., and J. Heine. 2009. A comparison of arborescent vegetation pre-(1983) and post-(2008) outbreak of the invasive species the Asian ambrosia beetle *Xyleborus glabratus* in a Florida maritime hammock. Plant Ecology & Diversity 2:77–83.

Gramling, J. M. 2010. Potential effects of Laurel Wilt on the flora of North America. Southeastern Naturalist 9:827–836.

Harrington, T. C., S. W. Fraedrich, and D. N. Aghayeva. 2008. *Raffaelea lauricola*, a new ambrosia beetle symbiont and pathogen on the Lauraceae. Mycotaxon 104:399–404.

Hughes, M. A., and J. A. Smith. 2014. Vegetative propagation of putatively laurel wilt-resistant red bay (*Persea borbonia*). Native Plants Journal 15:42–50.

Hughes, M. A., J. A. Smith, R. C. Ploetz, P. E. Kendra, A. E. Mayfield III, J. L. Hanula, J. Hulcr, L. L. Stelinski, S. Cameron, J. J. Riggins, and others. 2015. Recovery plan for laurel wilt on red bay and other forest species caused by *Raffaelea lauricola* and disseminated by *Xyleborus glabratus*.

Kendra, P. E., W. S. Montgomery, J. Niogret, and N. D. Epsky. 2013. An uncertain future for American Lauraceae: A lethal threat from red bay ambrosia beetle and Laurel Wilt Disease (A Review). American Journal of Plant Sciences 4:727–738.

Knapp, L. B., and C. D. Canham. 2000. Invasion of an old-growth forest in New York by *Ailanthus altissima*: sapling growth and recruitment in canopy gaps. Journal of the Torrey Botanical Society:307–315.

Koch, F. H., and W. D. Smith. 2008. Spatio-temporal analysis of *Xyleborus glabratus* (Coleoptera: Circulionidae: Scolytinae) invasion in eastern US forests. Environmental entomology 37:442–452.

Lake, J. C., and M. R. Leishman. 2004. Invasion success of exotic plants in natural ecosystems: the role of disturbance, plant attributes and freedom from herbivores. Biological conservation 117:215–226.

Maner, M. L., J. L. Hanula, and S. Horn. 2014. Population trends of the red bay ambrosia beetle (Coleoptera: Curculionidae: Scolytinae): Does utilization of small diameter red bay trees allow populations to persist? Florida Entomologist 97:208–216.

Mayfield III, A. E., and C. Brownie. 2013. The red bay ambrosia beetle (Coleoptera: Curculionidae: Scolytinae) uses stem silhouette diameter as a visual host-finding cue. Environmental Entomology 42:743–750.

Pattison, R. R., G. Goldstein, and A. Ares. 1998. Growth, biomass allocation and photosynthesis of invasive and native Hawaiian rainforest species. Oecologia 117:449–459.

Peet, R. K., T. R. Wentworth, and P. S. White. 1998. A flexible, multipurpose method for recording vegetation composition and structure. Castanea:262–274.

Peña, J. E., D. Carrillo, R. E. Duncan, J. L. Capinera, G. Brar, S. McLean, M. L. Arpaia, E. Focht, J. A. Smith, M. Hughes, and others. 2012. Susceptibility of *Persea* spp.

and other Lauraceae to attack by red bay ambrosia beetle, *Xyleborus glabratus* (Coleoptera: Curculionidae: Scolytinae). The Florida Entomologist 95:783–787.

Rabaglia, R. J., S. A. Dole, and A. I. Cognato. 2006. Review of American Xyleborina (Coleoptera: Curculionidae: Scolytinae) occurring north of Mexico, with an illustrated key. Annals of the Entomological Society of America 99:1034–1056.

Riggins, J. J., M. Hughes, J. A. Smith, A. E. Mayfield III, B. Layton, C. Balbalian, and R. Campbell. 2010. First occurrence of laurel wilt disease caused by *Raffaelea lauricola* on red bay trees in Mississippi. Plant Disease 94:634–634.

Shearman, T. M., G. G. Wang, and W. C. Bridges. 2015. Population dynamics of red bay (*Persea borbonia*) after laurel wilt disease: an assessment based on forest inventory and analysis data. Biological Invasions 17:1371–1382.

Shields, J., S. Jose, J. Freeman, M. Bunyan, G. Celis, D. Hagan, M. Morgan, E. C. Pieterson, and J. Zak. 2011. Short-term impacts of laurel wilt on red bay (*Persea borbonia* [L.] Spreng.) in a mixed evergreen-deciduous forest in northern Florida. Journal of Forestry 109:82–88.

Smith, C. K., E. Landreaux, H. Steinmann, D. McGrath, C. Hayes, and R. Hayes. 2015. Red bay survival eleven years after infection with an exotic disease on St. Catherines Island, Georgia, USA. Environment and Natural Resources Research 6:27.

Smith, J. A., T. J. Dreaden, A. E. Mayfield III, A. Boone, S. W. Fraedrich, and C. Bates. 2009a. First report of laurel wilt disease caused by *Raffaelea lauricola* on sassafras in Florida and South Carolina. Plant Disease 93:1079–1079.

Smith, J. A., L. Mount, A. E. Mayfield III, C. A. Bates, W. A. Lamborn, and S. W. Fraedrich. 2009b. First report of laurel wilt disease caused by *Raffaelea lauricola* on Camphor in Florida and Georgia. Plant Disease 93:198–198.

Spiegel, K. S., and L. M. Leege. 2013. Impacts of laurel wilt disease on red bay (*Persea borbonia* (L.) Spreng.) population structure and forest communities in the coastal plain of Georgia, USA. Biological Invasions 15:2467–2487.

Titus, J. H. 1990. Microtopography and woody plant regeneration in a hardwood floodplain swamp in Florida. Bulletin of the Torrey Botanical Club:429–437.

Valladares, F., and Ü. Niinemets. 2008. Shade tolerance, a key plant feature of complex nature and consequences. Annual Review of Ecology, Evolution, and Systematics:237–257.

Vitousek, P. M., C. M. Antonio, L. L. Loope, and R. Westbrooks. 1996. Biological invasions as global environmental change. American Scientist 84:468.

CHAPTER FIVE

MODELING FIRE BEHAVIOR AFTER LAUREL WILT DISEASE

5.1. Introduction

Extensive mortality of red bay (*Persea borbonia*) and swamp bay (*P. palustris*) has occurred since the introduction of *Xyleborus glabratus*, the vector of Laurel Wilt Disease (LWD) (Cameron et al. 2008, 2015, Fraedrich et al. 2008, Shields et al. 2011, Spiegel and Leege 2013). Mortality from LWD can potentially increase the fire risk for ecosystems in which red bay or swamp bay make up a considerable portion of the stand. Areas with a high density or basal area of dead *Persea* may accumulate a high amount of fuel since dead leaves remain on the tree for over a year (Mayfield et al. 2009). Once these leaves fall, the litter can alter nutrient cycling or possibly affect the structure of the ecosystem by reducing seed germination (Xiong and Nilsson 1999). Dead snags often fall apart within a few years of dying due to rapid colonization of the laurel wilt fungus (*Raffaelea lauricola*) as well as other fungi introduced by additional species of ambrosia beetles (Cameron et al. 2008).

The rapid accumulation of woody debris after LWD may be similar to other disturbances that increase fuel loads such as hurricanes or pine-beetle outbreaks. Hurricanes and other weather-related disturbances have an immediate effect of breaking limbs, defoliating branches, and uprooting trees. This disturbance undoubtedly leads to an increase in fuels in impacted stands. For example, Guan (2014) found that damaged stands from hurricanes Hugo, Opal, Katrina, and Ike, had higher fuel loads than nearby

undamaged stands. Biotic disturbances like southern pine beetle (*Dendroctonus frontalis*) outbreaks are possibly more similar to LWD in that the impacts on fuel are less immediate and more species specific. Evans (2012) found that fuel loads were significantly greater in stands impacted by southern pine beetle compared to control stands. Similarly, studies on other pine beetle outbreaks agree that fine fuels increase shortly after outbreaks, returning to pre-outbreak levels multiple decades later, while larger coarse woody debris continues to increase long after the outbreak (Hicke et al. 2012).

Fire behavior is primarily influenced by fuel, weather, and topography. Fuel is a combination of living and dead organic matter that is combustible by fire. Dead fuels can be classified by size, usually described in terms of the time needed to reach equilibrium moisture content (1-hr, 10-hr, 100-hr, and 1000-hr). Spatial arrangement, compactness, chemical content, and moisture all impact the way live and dead fuels burn, however, it is the fine fuels (litter, 1-hr, 10-hr, 100-hr) that primarily impact fire spread (Rothermel 1972). Weather influences fire behavior through wind, humidity, and temperature, while topography mainly influences the speed in which fire spreads (fire moves faster uphill). Predicting fire behavior involves evaluating these factors prior to the fire and calculating the fire intensity and rate of spread based on known models (Rothermel 1983). The BehavePlus software program was developed by the U.S. Forest Service to model fire behavior under different conditions.

Fire is not a frequent occurrence in most *Persea* stands. Red bay and swamp bay are not considered to be fire-adapted species, experiencing high mortality in most fires

(Van Deelen 1991). Although swamp bay is found in longleaf pine (*Pinus palustris*) stands, it usually is restricted to small diameter stems due to the frequent fires that maintain the longleaf ecosystem. In other stands, such as maritime live-oak forests, hardwood swamps, hammocks, and pocosins, red bay and swamp bay reach larger diameters in the absence of disturbances such as fire. There is concern that mortality from LWD in these types of stands may increase the risk of severe fires. Thus, the objectives of this study were to (1) quantify the fuel loads in stands impacted by LWD; (2) model fire behavior in these stands; and (3) determine if LWD affects fuel loads and fire behavior.

5.2. Methods

We sampled the same sites as those used in Chapter 4. A total of 60 plots were sampled for fuel loads. We excluded sites from Francis Marion due to the frequent prescribed burns that would affect the results, leaving 57 plots for the analyses. Originally, we intended to sample plots in nearby healthy and infected stands in order to compare the difference between the two over time. However, we were unable to locate comparable healthy stands within sites.

Dead woody material was sampled using Brown's (1974) planar intersect method (Figure 5.1). Three, 15.2 m transects were installed starting from one randomly selected corner of each plot. The first transect ran along the diagonal of the plot. The other two transects were installed at +22° and -23° from the first transect. Along each transect, downed woody material that intersected the sampling plane was tallied according to

diameter size classes: 0–0.64, 0.64–2.54, 2.54–7.62 cm, for 1-hr, 10-hr, 100-hr fuels respectively. Large debris greater than 7.62 cm in diameter (1000-hr fuels) were recorded separately and measured at the point where the center crossed the sampling plane. Large debris was identified as hardwood or softwood and whether the stem is sound or rotten. For the first 1.83 m along the transect, all size classes were tallied. From 1.83 to 3.66 m., only debris greater than 2.54 cm were tallied. After 3.66 m., only debris greater than 7.62 cm in diameter were recorded. Depths of fuel bed, litter and duff were measured at three equally spaced points along each transect. Dead woody material was sampled before any vegetation sampling occurred to minimize compaction of the litter layer.

Data Analysis

Fuel counts for 1-h, 10-h, 100-h, and 1000-h fuels were converted to dry weights using formulas published by Brown (1974). Live herbaceous and live woody fuel loads were calculated using the regression equations found in Brown and Marsden (1976):

Herbaceous: $Y = -28.14 + 0.001535(x_2^2 x_1) + 8.926\ (x_2) - 0.1256\ (x_2^2)$

Woody: $Y = 109.0 - 2.161\ (x_1) + 0.1078\ (x_1^2)$

Where, x_1 is the estimated percent cover of the herbaceous or shrub layers in each plot and x_2 is the estimated height of the herbaceous layer in cm. These were then converted into tons/ac for use with modeling fire behavior using BehavePlus (version 5.0.5). We ran fire behavior models for each plot and compared them by groups of

recovery year. Our models were initialize from model 7 (Southern Rough) in the BehavePlus model database. We altered the model defaults by changing the parameters

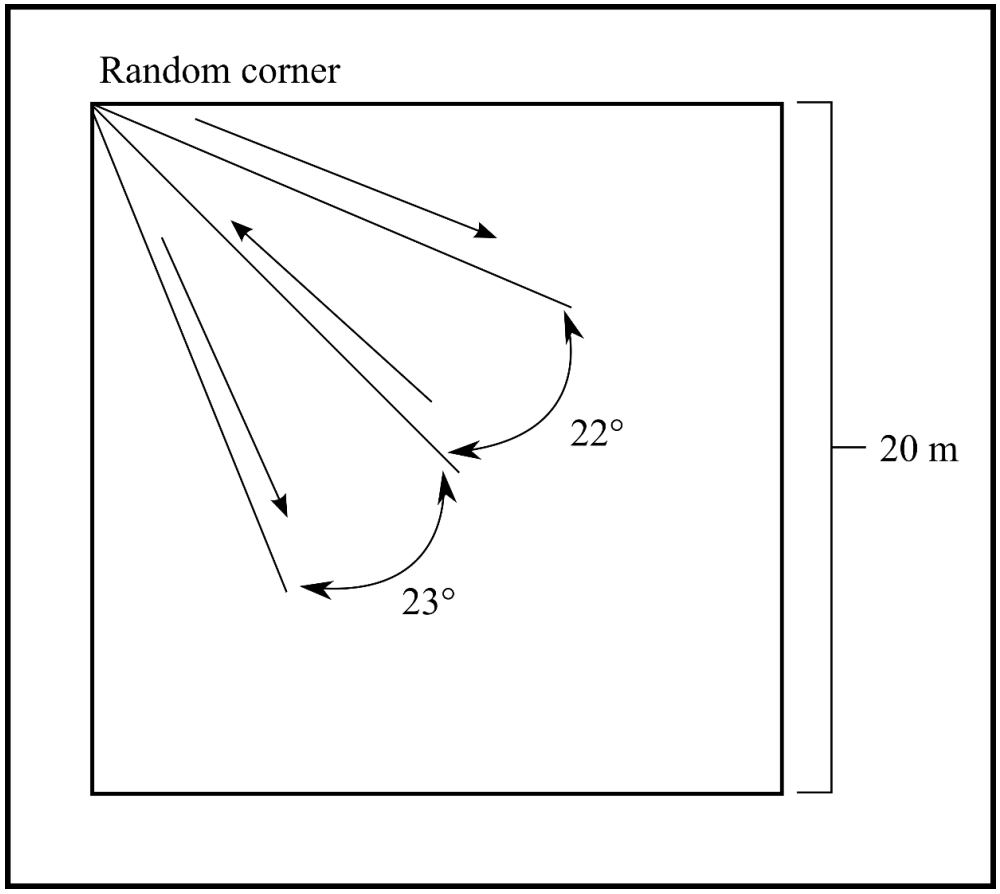

Figure 5.9. Sampling design for woody fuels. In each plot, a random corner was chosen. From this corner, three 15.2 m transects were placed with the first transect running diagonally across the plot and the other two lying 22 and 23 degrees on either side. All fuels were counted for the first 1.82 m. From 1.82 – 3.66 m, only fuels over 2.54 cm in diameter were measured. From 3.66 – 15.2 m, only fuels greater than 7.62 cm in diameter were measured. Litter, duff, and fuel height were measured at three points along each transect (3.66, 7.62, and 12.19 m).

that we had sampled data: fuel loads (1-h, 10-h, 100-h, live herbaceous, and live woody), as well as fuel bed depth (the average fuel height measured in each plot). Model defaults were used for parameters in which we had no data for. Slope and wind speed were held constant (0%, and 6.4 km/h respectively) to compare impacts of just fuel loads on fire behavior. We modeled an extreme moisture scenario, that of a very dry dormant season with very dry dead fuel and fully cured live fuel (Moisture Scenario D1L1), as well as a moderate moisture scenario in which dead fuel had higher moisture levels and live fuel was approximately 66% cured (D3L2), to estimate fire rate of spread and flame length. The percent of cured live fuel represents the proportion of live herbaceous fuel that is transferred to dead fuel in the model. Model parameters are listed in Table 5.1. We then used Analysis of Variance (ANOVA) to test for differences among groups of recovery years (1 – 2, 6 – 8, 9 – 10 years since LWD). Where ANOVA assumptions were not satisfied, we compared groups using Kruskal-Wallis rank sum test. Pairwise comparisons were made using Tukey's HSD or Kruskal multiple comparisons. We also compared fuel and fire behavior variables with snag basal area for each plot to see if there were significant correlations.

5.3. Results

Of the model parameters that were changed, only 1-hr fuel, litter, and duff, showed significant differences among recovery groups (Table 5.2). Later recovery years

(9 – 10) had lower average 1-hr fuel loads compared with 1 – 2 and 6 – 8 recovery year groups as well as significantly lower ranks ($\chi^2 = 28.1$, $DF = 2$, $P < 0.001$). Litter depth

Table 5.1. Parameters used in modeling fire behavior with BehavePlus

Parameter	Units	Value	
Fuel/Vegetation, Surface/Understory			
Fuel Model Type	N/A	Dynamic	
1-hr fuels	tonne/ha	Field measurements[1]	
10-hr fuels	tonne/ha	Field measurements[1]	
100-hr fuels	tonne/ha	Field measurements[1]	
Live herbaceous fuel load	tonne/ha	Field/regression equations[2]	
Live woody fuel load	tonne/ha	Field/regression equations[2]	
1-h SA/V	m^2/m^3	model default	
Live herbaceous SA/V	m^2/m^3	model default	
Live woody SA/V	mt^2/m^3	model default	
Fuel bed depth	m	Field measurements	
Dead fuel moisture of extinction	%	model default	
Dead fuel heat content	kJ/kg	model default	
Live fuel heat content	kJ/kg	model default	
Fuel Moisture Scenario		**D1L1**	**D3L2**
1-hr fuel moisture	%	3	9
10-hr fuel moisture	%	4	10
100-hr fuel moisture	%	5	11
Live herbaceous moisture	%	30	60
Live woody moisture	%	60	90
Weather			
Midflame wind speed (upslope)	km/h	4	
Terrain			
Slope grade	%	0	

[1] Measurement converted to tonne/ha using equations from Brown (1974)

[2] Measurement converted to tonne/ha using equations from Brown and Marsden (1976)

was significantly different among groups ($F_{2,54}$, $P < 0.001$), with the highest average depth in the 9 – 10 year recovery group (6.6 cm), whereas the 1 – 2 and 6 – 8 year groups were not significantly different (4.32 cm for both groups, P = 0.99). Average duff depth was also significantly different among groups ($F_{2,54}$, $P < 0.001$), with the 1 – 2 (4.32 cm) and 9 – 10 (5.08 cm) year plots being higher than the 6 – 8 year plots (2.79 cm) (Table 5.2).

Our model of fire behavior showed no significant differences in flame length ($F_{2,48}$, $P = 0.053$ for D1L1 and $F_{2,48}$, $P = 0.053$ for D3L2) or rate of spread ($F_{2,48}$, $P = 0.12$ for D1L1 and $F_{2,48}$, $P = 0.11$ for D3L2) among recovery groups (Table 5.3). The extremely dry moisture scenario (D1L1) had an average predicted rate of spread of 0.97 – 1.41 m/min and average flame length of 0.46 – 0.79 m. Under the moderate moisture scenario (D3L2) the average rate of spread was 0.4 – 0.8 m/min, and the average flame length was 0.34 – 0.58 m (Table 5.3).

Rate of spread and flame height were weakly, although significantly, correlated with snag basal area under both moisture scenarios (Figure 5.2). Both moisture scenarios had similar fits for rate of spread ($R^2 = 0.12$, $P = 0.01$ for D1L1, and $R^2 = 0.13$, $P = 0.01$ for D3L2) as well as flame length ($R^2 = 0.18$, $P = 0.02$ for D1L1, and $R^2 = 0.18$, $P = 0.02$ for D3L2). Among the parameters used in the models, snag basal area was correlated with average fuel height ($R^2 = 0.15$, $P < 0.01$) (Figure 5.2).

Table 5.2. Means (and standard error) of fuel variables for different recovery years after Laurel Wilt Disease. Years with the same letter are not significantly different at the 0.05 level.

	Recovery Year		
	1 - 2	6 - 8	9 - 10
1-hr fuel (tonne/ha)	0.9 (0.09) A	1.3 (0.16) A	0.5 (0.07) B
10-hr fuel (tonne/ha)	6.3 (0.72) A	6.9 (0.67) A	5.8 (0.49) A
100-hr fuel (tonne/ha)	3.4 (0.54) A	3.6 (0.58) A	2.9 (0.69) A
1000-hr fuel (tonne/ha)	3.4 (1.01) A	5.2 (1.36) A	6.5 (1.88) A
Litter depth (cm)	4.3 (0.2) A	4.3 (0.3) A	6.6 (0.6) B
Duff depth (cm)	4.3 (0.43) AB	2.8 (0.36) B	5.1 (0.51) A
Herb Loading (tonne/ha)	1.3 (0.07) A	1.6 (0.11) A	1.3 (0.09) A
Shrub Loading (tonne/ha)	1.3 (0.31) A	1.3 (0.22) A	1.8 (0.27) A
Average Fuel Ht (m)	0.15 (0.03) A	0.15 (0.02) A	0.09 (0.03) A

Table 5.3. Fire behavior predicted using BehavePlus under different moisture scenarios for different groups of years since LWD. There were no statistical differences between years at the 0.05 level.

Fire Behavior	Moisture Scenario	Recovery Years		
		1 - 2	6 - 8	9 - 10
Rate of Spread (m/min)	D1L1	1.3 (0.30)	1.4 (0.27)	0.7 (0.21)
	D3L2	0.8 (0.17)	0.8 (0.15)	0.4 (0.12)
Flame Length (m)	D1L1	0.8 (0.15)	0.8 (0.10)	0.5 (0.08)
	D3L2	0.6 (0.11)	0.5 (0.08)	0.3 (0.06)

5.4. Discussion

There are many factors that have likely impacted this study. First, woody fuels are highly variable both spatially and by species composition (Fry and Stephens 2010). Because LWD kills nearly all *Persea* in a stand and spreads rapidly from stand to stand (Fraedrich et al. 2008), we did not have control plots in the same stands as infected plots. Although we detected differences in 1-hr fuels, litter, and duff among recovery years, it is likely that these differences are due to factors other than LWD. For example, in 2014, a severe ice storm impacted the southeastern United States (Pile et al. 2016). The storm occurred in February, between the two field seasons of this study, and some of our plots

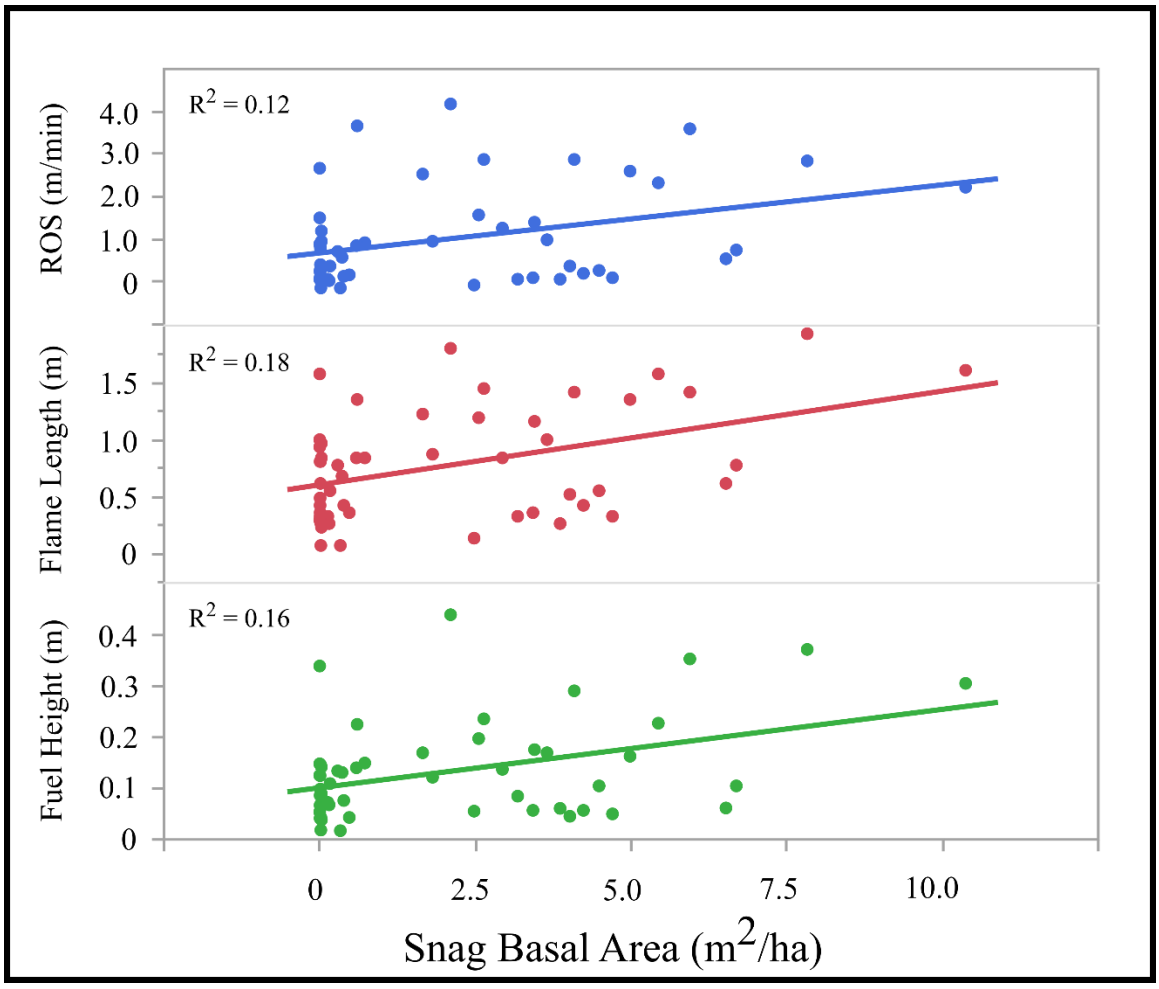

Figure 5.10. Relationship between *Persea* snag basal area and flame rate of spread (ROS), flame length, and fuel height in plots impacted by LWD. Fire behavior was modelled using BehavePlus under an extremely dry moisture scenario (D1L1, see text).

had visible signs of ice storm damage. There is no doubt that damage from this and other storms, has affected the fuels in our plots. Second, initial attempts at preventing the spread of the disease have likely impacted the fuel loadings in our study. For example, shortly after LWD was detected on Jekyll Island, GA, management on the island attempted to stop the spread by removing and burning symptomatic stems (Hughes et al. 2015). Although stumps and litter still remained, the removal of large stems has likely confounded our results.

The two moisture scenarios behaved similarly among recovery years in our fire behavior models, with the D1L1 model having roughly twice the rate of spread and about 25% higher flame length than the D3L2 model. The D1L1 scenario was designed as an extreme case, with both dead and live fuel having very low moisture levels. This is probably an unrealistic scenario in the case of LWD. In the first few years after LWD, wood moisture content remains high (Cameron et al. 2008). By the time *Persea* stems break apart, they are already colonized by multiple species of saprotrophic fungi. Therefore, a moisture scenario with higher dead fuel moisture (such as the D3L2), may be more accurate. Regardless, the models in this study should be taken with care. The fire models are significantly impacted by the base model we used to initialize the parameters (Southern Rough). It is unknown if this base model is an adequate representation of our stands. Extensive field verification would be required to see if the parameters used, such as surface area to volume ratio (SA/V), as well as fuel moisture percentage, are accurate.

Perhaps the most compelling evidence for impacts of LWD on fire behavior is the significant correlation between snag basal area and flame height and rate of spread. This impact is entirely due to the relationship between snag basal area and fuel height in our plots, as this was the only parameter that was significant. Although theoretically it is plausible that stands with high snag basal area would have more intense fires, one would think that this relationship would extend to fuel loads as well. For example, Forrestel et al. (2015) found a significant relationship between tanoak (*Notholithocarpus densiflorus*) snag basal area and fuel loads in stands impacted with Sudden Oak Death (SOD). Perhaps the lack of healthy plots in our study is masking the relationship between fuels and snag basal area in our plots. It appears from the figures in Forrestel et al. (2015) that without including healthy stands, they may not have seen a significant relationship. The very low correlation coefficient in our study also makes any interpretation questionable as does the lack of a significant negative year effect on the relationship.

We cannot conclude that LWD has increased the risk of high intensity fires. Long-term studies are needed, preferably starting in areas where LWD has not yet arrived. High densities of *Persea* are located in areas of North Carolina (Koch and Smith 2008), which have yet to be impacted by LWD. These locations, may be ideal to set up long-term monitoring plots in the event that *X. glabratus* progresses further north as expected.

Literature Cited

Brown, J. K. 1974. Handbook for inventorying downed woody material.

Brown, J. K., and M. A. Marsden. 1976. Estimating fuel weights of grasses, forbs, and small woody plants. Research Note INT-210. US Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station, Ogden, Utah 11.

Cameron, R. S., C. Bates, and J. Johnson. 2008. Distribution and spread of laurel wilt disease in Georgia: 2006-08 survey and field observations. Georgia Forestry Commission. US Forest Service. http://fhm. fs. fed. us/em/funded/09/so-em-08-02-report. pdf (18 April 2011).

Cameron, R. S., J. Hanula, S. Fraedrich, and C. Bates. 2015. Progression and impact of Laurel Wilt Disease within red bay and sassafras populations in southeast Georgia. Southeastern Naturalist 14:650–674.

Evans, J. 2012. Fuel dynamics in southern pine beetle-killed stands and their implication to fire behavior. M.S. Thesis. Clemson University, Clemson, SC.

Forrestel, A. B., B. S. Ramage, T. Moody, M. A. Moritz, and S. L. Stephens. 2015. Disease, fuels and potential fire behavior: Impacts of Sudden Oak Death in two coastal California forest types. Forest Ecology and Management 348:23–30.

Fraedrich, S. W., T. C. Harrington, R. J. Rabaglia, M. D. Ulyshen, A. E. Mayfield III, J. L. Hanula, J. M. Eickwort, and D. R. Miller. 2008. A fungal symbiont of the red bay ambrosia beetle causes a lethal wilt in red bay and other Lauraceae in the southeastern United States. Plant Disease 92:215–224.

Fry, D. L., and S. L. Stephens. 2010. Stand-level spatial dependence in an old-growth Jeffrey pine-mixed conifer forest, Sierra San Pedro Martir, Mexico. Canadian Journal of Forest Research 40:1803–1814.

Guan, S. 2014. Post-hurricane fuel dynamics and forest regeneration of coastal pine stands in southeast United States. M.S. Thesis. Clemson University, Clemson, SC.

Hicke, J. A., M. C. Johnson, J. L. Hayes, and H. K. Preisler. 2012. Effects of bark beetle-caused tree mortality on wildfire. Forest Ecology and Management 271:81–90.

Hughes, M. A., J. A. Smith, R. C. Ploetz, P. E. Kendra, A. E. Mayfield III, J. L. Hanula, J. Hulcr, L. L. Stelinski, S. Cameron, J. J. Riggins, and others. 2015. Recovery plan for laurel wilt on red bay and other forest species caused by *Raffaelea lauricola* and disseminated by *Xyleborus glabratus*.

Koch, F. H., and W. D. Smith. 2008. Spatio-temporal analysis of *Xyleborus glabratus* (Coleoptera: Circulionidae: Scolytinae) invasion in eastern US forests. Environmental Entomology 37:442–452.

Pile, L. S., C. A. Maier, G. G. Wang, D. Yu, and T. M. Shearman. 2016. Responses of two genetically superior loblolly pine clonal ideotypes to a severe ice storm. Forest Ecology and Management 360:213–220.

Rothermel, R. C. 1972. A mathematical model for predicting fire spread in wildland fuels. USDA For. Serv. Res. Pap. INT-115, U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station, Ogden, UT.

Rothermel, R. C. 1983. How to predict the spread and intensity of forest and range fires. The Bark Beetles, Fuels, and Fire Bibliography:70.

Shields, J., S. Jose, J. Freeman, M. Bunyan, G. Celis, D. Hagan, M. Morgan, E. C. Pieterson, and J. Zak. 2011. Short-term impacts of laurel wilt on red bay (*Persea borbonia* [L.] Spreng.) in a mixed evergreen-deciduous forest in northern Florida. Journal of Forestry 109:82–88.

Spiegel, K. S., and L. M. Leege. 2013. Impacts of laurel wilt disease on red bay (*Persea borbonia* (L.) Spreng.) population structure and forest communities in the coastal plain of Georgia, USA. Biological Invasions 15:2467–2487.

Van Deelen, T. R. 1991. Persea borbonia. Fire effects information system,[Online]. US Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory (Producer). Available: http://www. fs. fed. us/database/feis/5 Nov.

Xiong, S., and C. Nilsson. 1999. The effects of plant litter on vegetation: a meta-analysis. Journal of Ecology 87:984–994.

CHAPTER SIX

CONCLUSIONS

It has been over a decade since Laurel Wilt Disease was first detected in the southeastern United States. In that time it has spread to eight states and has caused extensive mortality to *Persea* throughout its range. In this dissertation, we have examined the impacts and implications of LWD on *Persea* ecosystems.

In Chapter 2, we found that the Forest Inventory and Analysis (FIA) database was a useful tool in observing the population dynamics of *Persea*. State and range-wide population estimates show that *Persea* has been declining since 2009. However, due to the moving average method of the population estimates, this decline has likely started prior to 2009 and will likely continue in the next several inventories. County wide plot data shows significant decline of *Persea* after LWD is detected compared with measurements made prior to detection. The speed in which LWD spreads is evident in our logistic model, which suggested that each year following the detection of LWD in a county increases the odd of death of a *Persea* stem in that county by approximately 153.7%. Our model also supported the observation of many studies suggesting that larger diameter stems are more likely to be attacked, with the odds of dying increasing by about 5% for every centimeter.

The FIA database, however, does not distinguish between the native *Persea* species of the southeast. Therefore, in Chapter 3, we analyzed data from the Carolina Vegetation Survey (CVS), to shed light on the differences in communities between red

bay and swamp bay. We show that these two species are members of different communities. The range of red bay appears to be much smaller than that of swamp bay, because it is restricted to the coastal fringe. We were unable to detect differences in *Persea* basal area, density, or importance among most of the communities, due to the high variability in the abundance of *Persea* from plot to plot. However, we did find that highly disturbed communities tend to have a lower abundance of *Persea*. Based on these results, we assessed the risk of LWD to *Persea* communities and concluded that maintaining red bay should be made a conservation priority, although both species remain at high risk through the majority of communities in which they are found.

Chapter 4 studied the aftermath of LWD in South Carolina and Georgia. As other studies have also observed, nearly all *Persea* stems are killed within the first two years after LWD. In the years that follow, we did not find evidence that non-native invasive species were capitalizing on the disturbance. We also did not find evidence that the surrounding vegetation was preventing *Persea* regeneration. Instead, it appears that *Persea* is regaining much of the basal area lost from LWD. Both red bay and swamp bay seem to respond similarly, having no statistical differences in the regeneration. Most other studies have commented on the lack of *Persea* seedlings in the aftermath of LWD. We found this not to be true in our plots, and although a portion of these seedlings are likely to be sprouts, we have documented evidence that some are regenerating from seed (Figure 6.1). We did not find any trend regarding seedling density and recovery year, possibly because resprouting individuals are producing seeds (Figure 6.2). These results suggest that *Persea* is persisting 10 years after LWD.

In Chapter 5, we attempted to see if LWD was affecting fuel loads, which could potentially increase the risk of severe fires. This study was largely unsuccessful as we did not have adequate control plots in uninfected stands that could compare fuel loads. We could not detect differences in fuel loads among recovery years between most fuels, and those that were significantly different were confounded by other variables. The resulting fire models mirrored the results of the fuel data, with no significant differences in flame length or rate of spread among recovery years. We did however, find slight correlations snag basal area and average fuel height, which subsequently resulted in correlations between snag basal area and fire behavior. Long-term studies are needed to support or reject the hypothesis that LWD influences fire behavior.

Unfortunately, it is still too early to determine the fate of *Persea* after the disturbance that is LWD. Whether *Persea* recovers completely hinges on the ability of *X. glabratus* to maintain low populations in the long term. We predict one of four possible futures for swamp bay and red bay *Persea*: (1) the two species will continue to decline, failing to regenerate, to the point of extinction; (2) both species will recover, either by *X. glabratus* populations declining due to lack of sufficient host material, or by the propagation (natural or assisted) of wilt resistant individuals; (3) *X. glabratus* will maintain small populations resulting in *Persea* occurring perpetually as small diameter stems; (4) a cyclical pattern will emerge as *Persea* recover, are attacked and decimated, and recover again. Future long-term studies that monitor recovery in *Persea* species as well as beetle populations will be able to test these hypotheses.

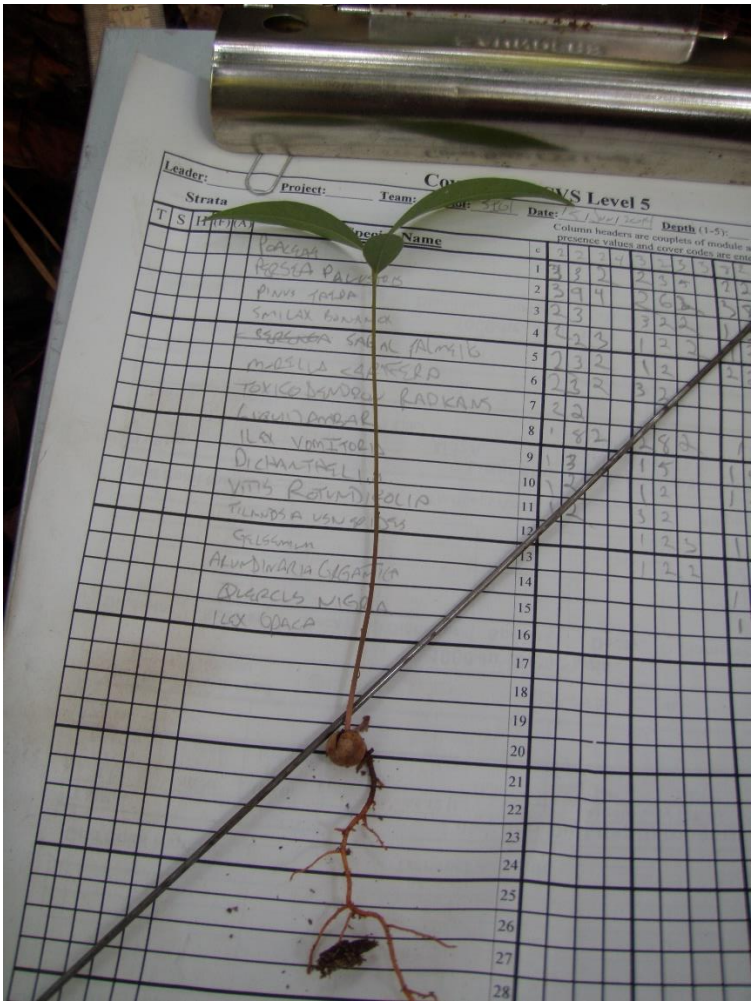

Figure 6.1. *Persea palustris* seedling at Skidaway Island state park, 10 years after LWD.

Figure 6.2. Evidence that resprouting *Persea* can flower.

APPENDICES

Appendix A

Results of a cluster analysis on *Persea* ecosystems

Appendix A.1. US National Vegetation Classification (NVC) groups for CVS plots where red bay and swamp bay occur as measurable stems. NVC Groups are arranged by the results of an agglomerative hierarchical cluster analysis of all 388 plots cut into seven groups. NVC counts are the number of plots classified for a particular association in each cluster.

Cluster	n	NVC Group	NVC Counts	Description
1	50	G798	35	Live Oak - Pignut Hickory - Cabbage Palmetto Coastal Forest Group
		G790	11	Sand Laurel Oak - Sand Live Oak - Water Oak Coastal Plain Forest Group
		G034	2	Swamp Chestnut Oak - Laurel Oak - Sweetgum Bottomland Forest Group
		G007	1	American Beech - Southern Magnolia - Oak species Forest Group
		G495	1	Pitch Pine - Oak species / Northern Bayberry Forest Group
2	73	G166	13	American Beech - Southern Sugar Maple - White Oak Forest Group
		G495	12	Pitch Pine - Oak species / Northern Bayberry Forest Group
		G798	9	Live Oak - Pignut Hickory - Cabbage Palmetto Coastal Forest Group
		G130	7	Loblolly Pine - Swamp Chestnut Oak - Cherrybark Oak Flatwoods Group
		G034	5	Swamp Chestnut Oak - Laurel Oak - Sweetgum Bottomland Forest Group
		G033	3	Bald-cypress - Water Tupelo Floodplain Forest Group
		G007	3	American Beech - Southern Magnolia - Oak species Forest Group
		G752	2	Northern & Mid-Atlantic Coastal Wetland Group
		G759	2	Green Ash - American Elm - Black Willow Floodplain Forest Group
		G159	2	White Oak - Southern Red Oak - Northern Red Oak Forest & Woodland Group
		G038	1	Swamp Tupelo - Ogeechee Tupelo - Bald-cypress Hardwood Basin Swamp Group
		G031	1	Loblolly Pine - Sweetgum - Chinese Tallow Ruderal Forest Group
		G037	1	Sweetbay - Loblolly-bay - Pond Pine Forest Group
		G165	1	White Oak - Southern Red Oak - Water Oak Forest Group
		Unclassified	11	

Appendix A.1. Continued

Cluster	n	NVC Group	NVC Counts	Description
3	47	G596	23	Longleaf Pine / Inkberry - Saw Palmetto Woodland Group
		G009	6	Longleaf Pine / Sand Post Oak / Three-awn species Woodland Group
		G154	4	Longleaf Pine / Turkey Oak Xeric Woodland Group
		G037	3	Sweetbay - Loblolly-bay - Pond Pine Forest Group
		G190	1	Longleaf Pine - Slash Pine - Pond Pine Woodland Group
		G186	1	Shining Fetterbush - Inkberry - Swamp Titi Shrubland Group
		G036	1	Pond-cypress / Holly species Depression Forest Group
		G776	1	Common Buttonbush - Highbush Blueberry Coastal Plain Shrub Swamp Group
		G187	1	Beaksedge species - Pitcherplant species Seepage Wetland Group
		G790	1	Sand Laurel Oak - Sand Live Oak - Water Oak Coastal Plain Forest Group
		Unclassified	5	
4	89	G037	34	Sweetbay - Loblolly-bay - Pond Pine Forest Group
		G038	15	Swamp Tupelo - Ogeechee Tupelo - Bald-cypress Hardwood Basin Swamp Group
		G186	7	Shining Fetterbush - Inkberry - Swamp Titi Shrubland Group
		G034	5	Swamp Chestnut Oak - Laurel Oak - Sweetgum Bottomland Forest Group
		G036	5	Pond-cypress / Holly species Depression Forest Group
		G033	4	Bald-cypress - Water Tupelo Floodplain Forest Group
		G130	4	Loblolly Pine - Swamp Chestnut Oak - Cherrybark Oak Flatwoods Group
		G044	1	Red Maple - Blackgum - Sweetgum Seepage Forest Group
		G553	1	Red Maple - Loblolly Pine - Sweetgum Ruderal Flooded & Swamp Forest Group
		Unclassified	13	

Appendix A.1. Continued

Cluster	n	NVC Group	NVC Counts	Description
5	31	G596	10	Longleaf Pine / Inkberry - Saw Palmetto Woodland Group
		G009	6	Longleaf Pine / Sand Post Oak / Three-awn species Woodland Group
		G190	4	Longleaf Pine - Slash Pine - Pond Pine Woodland Group
		G033	2	Bald-cypress - Water Tupelo Floodplain Forest Group
		G187	2	Beaksedge species - Pitcherplant species Seepage Wetland Group
		G036	1	Pond-cypress / Holly species Depression Forest Group
		G176	1	Saw Palmetto / Beyrich's Three-awn Shrubland Group
		G154	1	Longleaf Pine / Turkey Oak Xeric Woodland Group
		G111	1	Beaksedge species - Spikerush species - Yellow-eyed-grass species Wet Prairie Group
		Unclassified	3	
6	27	G036	18	Pond-cypress / Holly species Depression Forest Group
		G111	4	Beaksedge species - Spikerush species - Yellow-eyed-grass species Wet Prairie Group
		G037	2	Sweetbay - Loblolly-bay - Pond Pine Forest Group
		Unclassified	3	
7	71	G033	31	Bald-cypress - Water Tupelo Floodplain Forest Group
		G034	9	Swamp Chestnut Oak - Laurel Oak - Sweetgum Bottomland Forest Group
		G759	7	Green Ash - American Elm - Black Willow Floodplain Forest Group
		G037	5	Sweetbay - Loblolly-bay - Pond Pine Forest Group
		G038	4	Swamp Tupelo - Ogeechee Tupelo - Bald-cypress Hardwood Basin Swamp Group
		G130	4	Loblolly Pine - Swamp Chestnut Oak - Cherrybark Oak Flatwoods Group
		G752	2	Northern & Mid-Atlantic Coastal Wetland Group
		G120	2	Southern Cattail - Bulrush species - Awl-leaf Arrowhead Tidal Marsh Group
		G553	1	Red Maple - Loblolly Pine - Sweetgum Ruderal Flooded & Swamp Forest Group
		G031	1	Loblolly Pine - Sweetgum - Chinese Tallow Ruderal Forest Group
		G495	1	Pitch Pine - Oak species / Northern Bayberry Forest Group
		Unclassified	4	

Appendix A.2. Indicator species associated with seven community groups where red bay or swamp bay are present as measurable stems. Species specificity (A) is the probability that the given spieces is in a given group when it is found. Species fidelity (B) is the probability of finding the given species in a given group.

Cluster	Family	Species	A	B	Indicator Value	*P* -value
	Lauraceae	*Persea borbonia*	0.75	0.98	0.86	0.001
	Aquifoliaceae	*Ilex vomitoria*	0.71	0.96	0.83	0.001
	Oleaceae	*Cartrema americanum*	0.73	0.74	0.73	0.001
	Fagaceae	*Quercus virginiana*	0.76	0.70	0.73	0.001
	Fagaceae	*Quercus hemisphaerica*	0.63	0.80	0.71	0.001
	Cupressaceae	*Juniperus virginiana*	0.63	0.78	0.70	0.001
	Arecaceae	*Sabal palmetto*	0.78	0.60	0.69	0.001
1	Rosaceae	*Prunus caroliniana*	0.84	0.54	0.67	0.001
	Sapotaceae	*Sideroxylon tenax*	1.00	0.26	0.51	0.001
	Cyperaceae	*Carex floridana*	0.82	0.14	0.34	0.001
	Rhamnaceae	*Sageretia minutiflora*	1.00	0.10	0.32	0.002
	Rhamnaceae	*Frangula caroliniana*	1.00	0.08	0.28	0.006
	Dioscoreaceae	*Dioscorea floridana*	1.00	0.06	0.25	0.017
	Agavaceae	*Yucca aloifolia*	1.00	0.06	0.25	0.01
	Asteraceae	*Lactuca canadensis*	1.00	0.04	0.20	0.04
	Agavaceae	*Yucca gloriosa*	1.00	0.04	0.20	0.038
	Aristolochiaceae	*Hexastylis arifolia*	0.91	0.44	0.63	0.001
	Fagaceae	*Fagus grandifolia*	0.97	0.38	0.61	0.001
	Fagaceae	*Quercus alba*	0.89	0.40	0.60	0.001
	Celastraceae	*Euonymus americanus*	0.64	0.51	0.57	0.001
	Araceae	*Arisaema triphyllum*	0.80	0.37	0.55	0.001
	Moraceae	*Morus rubra*	0.74	0.37	0.52	0.001
	Hamamelidaceae	*Hamamelis virginiana*	0.73	0.37	0.52	0.001
	Rubiaceae	*Galium uniflorum*	0.89	0.25	0.47	0.001
	Rosaceae	*Prunus serotina*	0.55	0.36	0.44	0.001
2	Ericaceae	*Oxydendrum arboreum*	0.70	0.27	0.44	0.001
	Fagaceae	*Quercus pagoda*	0.78	0.25	0.44	0.001
	Dryopteridaceae	*Athyrium asplenioides*	0.78	0.23	0.43	0.001
	Poaceae	*Dichanthelium boscii*	0.82	0.22	0.42	0.001
	Rubiaceae	*Galium circaezans*	1.00	0.18	0.42	0.001
	Juglandaceae	*Carya cordiformis*	0.86	0.21	0.42	0.001
	Fagaceae	*Quercus velutina*	0.84	0.21	0.42	0.002
	Ericaceae	*Chimaphila maculata*	0.88	0.19	0.41	0.001
	Annonaceae	*Asimina parviflora*	0.91	0.18	0.40	0.001
	Juglandaceae	*Carya tomentosa*	0.74	0.21	0.39	0.001
	Asteraceae	*Solidago caesia*	1.00	0.15	0.39	0.001
	Lauraceae	*Lindera benzoin*	0.92	0.15	0.37	0.001

Appendix A.2. Continued

Cluster	Family	Species	A	B	Indicator Value	*P* -value
	Cornaceae	*Cornus asperifolia*	0.84	0.16	0.37	0.001
	Dryopteridaceae	*Polystichum acrostichoides*	1.00	0.14	0.37	0.001
	Oleaceae	*Fraxinus americana*	0.88	0.15	0.36	0.001
	Fagaceae	*Quercus phellos*	0.53	0.25	0.36	0.001
	Phrymaceae	*Phryma leptostachya*	1.00	0.12	0.35	0.001
	Fagaceae	*Quercus shumardii*	0.80	0.15	0.35	0.001
	Juglandaceae	*Carya pallida*	1.00	0.11	0.33	0.001
	Juglandaceae	*Juglans nigra*	1.00	0.11	0.33	0.001
	Ruscaceae	*Polygonatum biflorum*	1.00	0.11	0.33	0.001
	Betulaceae	*Ostrya virginiana*	0.94	0.11	0.32	0.001
	Cyperaceae	*Scleria oligantha*	0.82	0.12	0.32	0.001
	Magnoliaceae	*Magnolia tripetala*	1.00	0.10	0.31	0.001
	Oxalidaceae	*Oxalis dillenii*	1.00	0.10	0.31	0.003
	Berberidaceae	*Podophyllum peltatum*	1.00	0.10	0.31	0.001
	Styracaceae	*Styrax grandifolius*	1.00	0.10	0.31	0.001
	Polygonaceae	*Persicaria virginiana*	0.86	0.11	0.31	0.002
	Fabaceae	*Cercis canadensis*	0.94	0.10	0.30	0.002
2	Oleaceae	*Ligustrum sinense*	0.68	0.12	0.29	0.004
	Cyperaceae	*Carex digitalis*	1.00	0.08	0.29	0.001
	Theaceae	*Stewartia malacodendron*	1.00	0.08	0.29	0.002
	Fabaceae	*Hylodesmum nudiflorum*	1.00	0.08	0.29	0.002
	Rubiaceae	*Galium triflorum*	0.84	0.10	0.28	0.004
	Pinaceae	*Pinus glabra*	0.69	0.11	0.27	0.008
	Ophioglossaceae	*Botrypus virginianus*	0.90	0.08	0.27	0.004
	Asteraceae	*Verbesina occidentalis*	0.85	0.08	0.27	0.008
	Sapindaceae	*Acer negundo*	1.00	0.07	0.26	0.01
	Cyperaceae	*Carex styloflexa*	1.00	0.07	0.26	0.009
	Papaveraceae	*Sanguinaria canadensis*	1.00	0.07	0.26	0.009
	Iridaceae	*Sisyrinchium mucronatum*	1.00	0.07	0.26	0.009
	Orobanchaceae	*Epifagus virginiana*	1.00	0.07	0.26	0.009
	Rosaceae	*Geum canadense*	0.71	0.10	0.26	0.012
	Asteraceae	*Smallanthus uvedalia*	0.84	0.07	0.24	0.015
	Rosaceae	*Amelanchier arborea*	1.00	0.05	0.23	0.015
	Cyperaceae	*Carex cephalophora*	1.00	0.05	0.23	0.013
	Juglandaceae	*Carya myristiciformis*	1.00	0.05	0.23	0.024
	Lamiaceae	*Collinsonia tuberosa*	1.00	0.05	0.23	0.012
	Violaceae	*Viola affinis*	1.00	0.05	0.23	0.017
	Melanthiaceae	*Chamaelirium luteum*	1.00	0.04	0.20	0.048
	Rosaceae	*Geum virginianum*	1.00	0.04	0.20	0.04
	Ruscaceae	*Maianthemum racemosum*	1.00	0.04	0.20	0.036
	Oxalidaceae	*Oxalis stricta*	1.00	0.04	0.20	0.046
	Thelypteridaceae	*Phegopteris hexagonoptera*	1.00	0.04	0.20	0.039
	Rosaceae	*Prunus americana*	1.00	0.04	0.20	0.047
	Fagaceae	*Quercus coccinea*	1.00	0.04	0.20	0.05

Appendix A.2. Continued

Cluster	Family	Species	A	B	Indicator Value	*P* -value
	Lamiaceae	*Scutellaria elliptica*	1.00	0.04	0.20	0.045
2	Trilliaceae	*Trillium maculatum*	1.00	0.04	0.20	0.047
	Violaceae	*Viola walteri*	1.00	0.04	0.20	0.047
	Ericaceae	*Vaccinium tenellum*	0.82	0.83	0.82	0.001
	Poaceae	*Aristida stricta*	0.93	0.72	0.82	0.001
	Ericaceae	*Lyonia mariana*	0.91	0.68	0.79	0.001
	Ericaceae	*Vaccinium crassifolium*	0.90	0.62	0.75	0.001
	Ericaceae	*Gaylussacia frondosa*	0.59	0.89	0.73	0.001
	Iridaceae	*Iris verna*	1.00	0.36	0.60	0.001
	Asteraceae	*Carphephorus bellidifolius*	1.00	0.23	0.48	0.001
	Fagaceae	*Quercus marilandica*	0.89	0.21	0.44	0.001
	Asteraceae	*Carphephorus tomentosus*	0.86	0.21	0.43	0.001
	Diapensiaceae	*Pyxidanthera barbulata*	1.00	0.17	0.41	0.001
	Asteraceae	*Ionactis linariifolia*	0.85	0.19	0.40	0.001
	Ericaceae	*Rhododendron atlanticum*	0.69	0.17	0.34	0.001
	Gentianaceae	*Gentiana autumnalis*	1.00	0.11	0.33	0.002
	Ericaceae	*Kalmia buxifolia*	1.00	0.11	0.33	0.001
	Asteraceae	*Symphyotrichum walteri*	0.75	0.13	0.31	0.003
	Euphorbiaceae	*Euphorbia ipecacuanhae*	1.00	0.09	0.29	0.002
3	Polygonaceae	*Polygonum polygamum*	1.00	0.09	0.29	0.003
	Asteraceae	*Sericocarpus linifolius*	1.00	0.09	0.29	0.003
	Caryophyllaceae	*Stipulicida setacea*	1.00	0.09	0.29	0.003
	Asteraceae	*Vernonia acaulis*	0.93	0.09	0.28	0.005
	Euphorbiaceae	*Euphorbia curtisii*	0.93	0.09	0.28	0.005
	Fabaceae	*Tephrosia virginiana*	0.73	0.11	0.28	0.007
	Poaceae	*Dichanthelium villosissimum*	1.00	0.06	0.25	0.004
	Fabaceae	*Amorpha herbacea*	0.74	0.09	0.25	0.008
	Rosaceae	*Amelanchier obovalis*	0.70	0.09	0.24	0.02
	Poaceae	*Dichanthelium mattamuskeete*	0.79	0.06	0.23	0.032
	Poaceae	*Danthonia sericea*	0.76	0.06	0.22	0.041
	Asteraceae	*Cirsium repandum*	1.00	0.04	0.21	0.025
	Commelinaceae	*Cuthbertia graminea*	1.00	0.04	0.21	0.03
	Fabaceae	*Lespedeza angustifolia*	1.00	0.04	0.21	0.03
	Cyperaceae	*Rhynchospora pallida*	1.00	0.04	0.21	0.021
	Eriocaulaceae	*Lachnocaulon beyrichianum*	1.00	0.04	0.21	0.026
	Orchidaceae	*Spiranthes lacera*	1.00	0.04	0.21	0.019

Appendix A.2. Continued

Cluster	Family	Species	A	B	Indicator Value	*P* -value
4	Cupressaceae	*Chamaecyparis thyoides*	0.75	0.30	0.48	0.001
	Aquifoliaceae	*Ilex laevigata*	0.90	0.13	0.35	0.002
	Ericaceae	*Chamaedaphne calyculata*	0.94	0.07	0.25	0.014
	Aristolochiaceae	*Hexastylis minor*	1.00	0.06	0.24	0.019
5	Poaceae	*Aristida beyrichiana*	1.00	0.55	0.74	0.001
	Asteraceae	*Symphyotrichum dumosum*	0.87	0.48	0.65	0.001
	Arecaceae	*Serenoa repens*	0.72	0.55	0.63	0.001
	Ericaceae	*Vaccinium myrsinites*	0.81	0.48	0.63	0.001
	Pinaceae	*Pinus elliottii*	0.81	0.48	0.63	0.001
	Poaceae	*Schizachyrium scoparium*	0.79	0.48	0.62	0.001
	Ericaceae	*Gaylussacia nana*	1.00	0.35	0.60	0.001
	Poaceae	*Sorghastrum secundum*	1.00	0.35	0.60	0.001
	Poaceae	*Dichanthelium strigosum*	0.77	0.45	0.59	0.001
	Poaceae	*Dichanthelium angustifolium*	0.95	0.35	0.58	0.001
	Xyridaceae	*Xyris ambigua*	0.72	0.45	0.57	0.001
	Poaceae	*Paspalum setaceum*	0.91	0.35	0.57	0.001
	Poaceae	*Ctenium aromaticum*	1.00	0.32	0.57	0.001
	Rubiaceae	*Houstonia procumbens*	1.00	0.32	0.57	0.001
	Ericaceae	*Lyonia fruticosa*	1.00	0.32	0.57	0.001
	Poaceae	*Coleataenia longifolia*	1.00	0.29	0.54	0.001
	Poaceae	*Dichanthelium columbianum*	1.00	0.29	0.54	0.001
	Xyridaceae	*Xyris platylepis*	1.00	0.29	0.54	0.001
	Rubiaceae	*Oldenlandia uniflora*	1.00	0.29	0.54	0.001
	Fagaceae	*Quercus minima*	0.81	0.35	0.54	0.001
	Poaceae	*Andropogon glomeratus*	0.70	0.39	0.52	0.001
	Asteraceae	*Bigelowia nudata*	0.92	0.29	0.52	0.001
	Poaceae	*Andropogon gyrans*	1.00	0.26	0.51	0.001
	Poaceae	*Coleataenia anceps*	1.00	0.26	0.51	0.001
	Cyperaceae	*Scleria muehlenbergii*	0.89	0.29	0.51	0.001
	Cyperaceae	*Scleria triglomerata*	0.88	0.29	0.51	0.001
	Asteraceae	*Ageratina aromatica*	0.98	0.26	0.50	0.001
	Asteraceae	*Elephantopus elatus*	0.98	0.26	0.50	0.001
	Hypericaceae	*Hypericum crux-andreae*	0.87	0.29	0.50	0.001
	Melastomataceae	*Rhexia petiolata*	0.71	0.35	0.50	0.001
	Cyperaceae	*Scleria ciliata*	0.77	0.32	0.50	0.001
	Apiaceae	*Centella asiatica*	0.96	0.26	0.50	0.001
	Onagraceae	*Ludwigia virgata*	0.92	0.26	0.49	0.001
	Poaceae	*Dichanthelium chamaelonche*	0.91	0.26	0.49	0.001
	Poaceae	*Dichanthelium ovale*	0.91	0.26	0.48	0.001

Appendix A.2. Continued

Cluster	Family	Species	A	B	Indicator Value	*P* -value
	Cyperaceae	*Rhynchospora baldwinii*	0.80	0.29	0.48	0.001
	Poaceae	*Aristida spiciformis*	1.00	0.23	0.48	0.001
	Cistaceae	*Crocanthemum carolinianum*	1.00	0.23	0.48	0.001
	Poaceae	*Sporobolus floridanus*	1.00	0.23	0.48	0.001
	Poaceae	*Aristida virgata*	0.85	0.26	0.47	0.001
	Cyperaceae	*Scleria pauciflora*	0.96	0.23	0.47	0.001
	Cyperaceae	*Rhynchospora chapmanii*	0.94	0.23	0.46	0.001
	Myricaceae	*Morella pumila*	0.80	0.26	0.46	0.001
	Poaceae	*Dichanthelium ensifolium*	0.90	0.23	0.45	0.001
	Poaceae	*Muhlenbergia expansa*	0.90	0.23	0.45	0.001
	Campanulaceae	*Lobelia glandulosa*	0.87	0.23	0.44	0.001
	Poaceae	*Andropogon hirsutior*	1.00	0.19	0.44	0.001
	Acanthaceae	*Dyschoriste oblongifolia*	1.00	0.19	0.44	0.001
	Poaceae	*Eragrostis elliottii*	1.00	0.19	0.44	0.001
	Poaceae	*Erianthus giganteus*	1.00	0.19	0.44	0.001
	Asteraceae	*Helianthus heterophyllus*	1.00	0.19	0.44	0.001
	Hypericaceae	*Hypericum brachyphyllum*	1.00	0.19	0.44	0.001
	Chrysobalanaceae	*Licania michauxii*	1.00	0.19	0.44	0.001
	Acanthaceae	*Ruellia ciliosa*	1.00	0.19	0.44	0.001
	Poaceae	*Sporobolus clandestinus*	1.00	0.19	0.44	0.001
	Xyridaceae	*Xyris jupicai*	1.00	0.19	0.44	0.001
5	Asteraceae	*Helianthus angustifolius*	1.00	0.19	0.44	0.001
	Sarraceniaceae	*Sarracenia minor*	0.74	0.26	0.44	0.001
	Fabaceae	*Galactia regularis*	0.94	0.19	0.43	0.001
	Cyperaceae	*Rhynchospora ciliaris*	0.93	0.19	0.43	0.001
	Eriocaulaceae	*Lachnocaulon anceps*	0.61	0.29	0.42	0.001
	Hypericaceae	*Hypericum cistifolium*	0.75	0.23	0.41	0.001
	Asteraceae	*Erigeron vernus*	0.86	0.19	0.41	0.001
	Asteraceae	*Chaptalia tomentosa*	0.86	0.19	0.41	0.001
	Asteraceae	*Vernonia angustifolia*	0.86	0.19	0.41	0.001
	Fabaceae	*Lespedeza hirta*	0.85	0.19	0.41	0.001
	Poaceae	*Aristida purpurascens*	0.85	0.19	0.41	0.001
	Poaceae	*Dichanthelium longiligulatum*	0.84	0.19	0.40	0.001
	Cistaceae	*Crocanthemum corymbosum*	1.00	0.16	0.40	0.001
	Poaceae	*Digitaria filiformis*	1.00	0.16	0.40	0.001
	Polygonaceae	*Eriogonum tomentosum*	1.00	0.16	0.40	0.001
	Apiaceae	*Eryngium yuccifolium*	1.00	0.16	0.40	0.001
	Fabaceae	*Galactia elliottii*	1.00	0.16	0.40	0.001
	Poaceae	*Hymenachne hemitomon*	1.00	0.16	0.40	0.001
	Ericaceae	*Kalmia hirsuta*	1.00	0.16	0.40	0.001
	Asteraceae	*Liatris spicata*	1.00	0.16	0.40	0.001
	Fagaceae	*Quercus chapmanii*	1.00	0.16	0.40	0.001
	Melastomataceae	*Rhexia lutea*	1.00	0.16	0.40	0.001

Appendix A.2. Continued

Cluster	Family	Species	A	B	Indicator Value	*P* -value
	Cyperaceae	*Rhynchospora grayi*	1.00	0.16	0.40	0.001
	Cyperaceae	*Rhynchospora oligantha*	1.00	0.16	0.40	0.001
	Lamiaceae	*Scutellaria multiglandulosa*	1.00	0.16	0.40	0.001
	Euphorbiaceae	*Stillingia sylvatica*	1.00	0.16	0.40	0.001
	Asteraceae	*Symphyotrichum concolor*	1.00	0.16	0.40	0.001
	Apiaceae	*Tiedemannia filiformis*	1.00	0.16	0.40	0.001
	Euphorbiaceae	*Tragia smallii*	1.00	0.16	0.40	0.001
	Poaceae	*Tridens carolinianus*	1.00	0.16	0.40	0.001
	Xyridaceae	*Xyris difformis*	1.00	0.16	0.40	0.001
	Asteraceae	*Liatris gracilis*	1.00	0.16	0.40	0.001
	Juncaceae	*Juncus scirpoides*	0.70	0.23	0.40	0.001
	Poaceae	*Amphicarpum muhlenbergianum*	0.81	0.19	0.40	0.001
	Asteraceae	*Hieracium gronovii*	0.69	0.23	0.39	0.001
	Fabaceae	*Rhynchosia reniformis*	0.94	0.16	0.39	0.001
	Asteraceae	*Eupatorium compositifolium*	0.51	0.29	0.39	0.001
	Rosaceae	*Rubus cuneifolius*	0.72	0.19	0.37	0.001
	Apiaceae	*Eryngium integrifolium*	0.84	0.16	0.37	0.001
	Poaceae	*Sorghastrum nutans*	0.81	0.16	0.36	0.001
	Euphorbiaceae	*Acalypha gracilens*	1.00	0.13	0.36	0.001
	Poaceae	*Andropogon floridanus*	1.00	0.13	0.36	0.001
	Apocynaceae	*Asclepias verticillata*	1.00	0.13	0.36	0.001
5	Polygalaceae	*Asemeia grandiflora*	1.00	0.13	0.36	0.001
	Fabaceae	*Centrosema arenicola*	1.00	0.13	0.36	0.001
	Poaceae	*Coleataenia rigidula*	1.00	0.13	0.36	0.001
	Euphorbiaceae	*Croton argyranthemus*	1.00	0.13	0.36	0.001
	Cyperaceae	*Cyperus plukenetii*	1.00	0.13	0.36	0.001
	Poaceae	*Dichanthelium portoricense*	1.00	0.13	0.36	0.001
	Poaceae	*Eragrostis spectabilis*	1.00	0.13	0.36	0.001
	Poaceae	*Eustachys floridana*	1.00	0.13	0.36	0.001
	Poaceae	*Gymnopogon ambiguus*	1.00	0.13	0.36	0.001
	Cistaceae	*Lechea sessiliflora*	1.00	0.13	0.36	0.001
	Asteraceae	*Liatris tenuifolia*	1.00	0.13	0.36	0.001
	Lycopodiaceae	*Lycopodiella appressa*	1.00	0.13	0.36	0.001
	Asteraceae	*Oclemena reticulata*	1.00	0.13	0.36	0.001
	Cyperaceae	*Rhynchospora perplexa*	1.00	0.13	0.36	0.001
	Cyperaceae	*Rhynchospora pineticola*	1.00	0.13	0.36	0.001
	Gentianaceae	*Sabatia brevifolia*	1.00	0.13	0.36	0.001
	Lamiaceae	*Salvia azurea*	1.00	0.13	0.36	0.001
	Plantaginaceae	*Sophronanthe hispida*	1.00	0.13	0.36	0.001
	Poaceae	*Sporobolus curtissii*	1.00	0.13	0.36	0.002
	Eriocaulaceae	*Syngonanthus flavidulus*	1.00	0.13	0.36	0.001
	Asteraceae	*Trilisa paniculata*	1.00	0.13	0.36	0.001
	Lentibulariaceae	*Utricularia juncea*	1.00	0.13	0.36	0.001

Appendix A.2. Continued

Cluster	Family	Species	A	B	Indicator Value	*P* -value
5	Hypericaceae	*Hypericum fasciculatum*	0.78	0.16	0.35	0.001
	Melanthiaceae	*Zigadenus glaberrimus*	0.77	0.16	0.35	0.001
	Fagaceae	*Quercus elliottii*	0.77	0.16	0.35	0.001
	Violaceae	*Viola septemloba*	0.95	0.13	0.35	0.001
	Poaceae	*Andropogon ternarius*	0.75	0.16	0.35	0.002
	Asteraceae	*Solidago stricta*	0.91	0.13	0.34	0.001
	Orchidaceae	*Pogonia ophioglossoides*	0.90	0.13	0.34	0.002
	Convolvulaceae	*Stylisma patens*	0.72	0.16	0.34	0.001
	Lamiaceae	*Scutellaria integrifolia*	0.89	0.13	0.34	0.001
	Rosaceae	*Rubus trivialis*	0.51	0.23	0.34	0.002
	Violaceae	*Viola primulifolia*	0.50	0.23	0.34	0.002
	Poaceae	*Aristida lanosa*	0.87	0.13	0.33	0.002
	Rubiaceae	*Galium bermudense*	0.87	0.13	0.33	0.001
	Fabaceae	*Desmodium ciliare*	0.86	0.13	0.33	0.001
	Cistaceae	*Lechea minor*	0.86	0.13	0.33	0.001
	Fabaceae	*Tephrosia spicata*	0.84	0.13	0.33	0.001
	Melanthiaceae	*Stenanthium densum*	0.67	0.16	0.33	0.001
	Asteraceae	*Marshallia graminifolia*	0.82	0.13	0.33	0.001
	Poaceae	*Dichanthelium oligosanthes*	0.81	0.13	0.32	0.002
	Xyridaceae	*Xyris elliottii*	0.80	0.13	0.32	0.001
	Fabaceae	*Desmodium lineatum*	0.78	0.13	0.32	0.002
	Juglandaceae	*Carya tomentosa*	0.78	0.13	0.32	0.001
	Violaceae	*Viola lanceolata*	0.78	0.13	0.32	0.001
	Poaceae	*Andropogon tracyi*	1.00	0.10	0.31	0.002
	Annonaceae	*Asimina incana*	1.00	0.10	0.31	0.003
	Poaceae	*Axonopus furcatus*	1.00	0.10	0.31	0.002
	Asteraceae	*Balduina angustifolia*	1.00	0.10	0.31	0.001
	Asteraceae	*Bidens mitis*	1.00	0.10	0.31	0.002
	Asteraceae	*Carphephorus corymbosus*	1.00	0.10	0.31	0.001
	Asteraceae	*Cirsium nuttallii*	1.00	0.10	0.31	0.002
	Poaceae	*Coleataenia tenera*	1.00	0.10	0.31	0.003
	Fabaceae	*Dalea albida*	1.00	0.10	0.31	0.002
	Euphorbiaceae	*Euphorbia exserta*	1.00	0.10	0.31	0.002
	Poaceae	*Eustachys glauca*	1.00	0.10	0.31	0.002
	Cyperaceae	*Fuirena breviseta*	1.00	0.10	0.31	0.001
	Cyperaceae	*Fuirena scirpoidea*	1.00	0.10	0.31	0.002
	Lamiaceae	*Hyptis alata*	1.00	0.10	0.31	0.002
	Cistaceae	*Lechea torreyi*	1.00	0.10	0.31	0.002
	Poaceae	*Mnesithea rugosa*	1.00	0.10	0.31	0.001
	Poaceae	*Muhlenbergia capillaris*	1.00	0.10	0.31	0.003
	Poaceae	*Paspalum bifidum*	1.00	0.10	0.31	0.002
	Turneraceae	*Piriqueta caroliniana*	1.00	0.10	0.31	0.001
	Tetrachondraceae	*Polypremum procumbens*	1.00	0.10	0.31	0.002
	Fagaceae	*Quercus myrtifolia*	1.00	0.10	0.31	0.001

Appendix A.2. Continued

Cluster	Family	Species	A	B	Indicator Value	*P* -value
5	Fabaceae	*Rhynchosia cinerea*	1.00	0.10	0.31	0.002
	Asteraceae	*Rudbeckia hirta*	1.00	0.10	0.31	0.001
	Poaceae	*Setaria corrugata*	1.00	0.10	0.31	0.003
	Poaceae	*Setaria parviflora*	1.00	0.10	0.31	0.001
	Iridaceae	*Sisyrinchium nashii*	1.00	0.10	0.31	0.003
	Asteraceae	*Solidago virgata*	1.00	0.10	0.31	0.002
	Asteraceae	*Sphagneticola trilobata*	1.00	0.10	0.31	0.003
	Poaceae	*Sporobolus junceus*	1.00	0.10	0.31	0.002
	Fabaceae	*Tephrosia florida*	1.00	0.10	0.31	0.001
	Xyridaceae	*Xyris baldwiniana*	1.00	0.10	0.31	0.003
	Xyridaceae	*Xyris floridana*	1.00	0.10	0.31	0.001
	Osmundaceae	*Osmunda spectabilis*	0.57	0.16	0.30	0.003
	Asteraceae	*Balduina uniflora*	0.90	0.10	0.30	0.001
	Fabaceae	*Chamaecrista nictitans*	0.90	0.10	0.30	0.001
	Droseraceae	*Drosera brevifolia*	0.90	0.10	0.30	0.003
	Tofieldiaceae	*Triantha racemosa*	0.67	0.13	0.29	0.002
	Solanaceae	*Physalis walteri*	0.87	0.10	0.29	0.002
	Anacardiaceae	*Toxicodendron pubescens*	0.64	0.13	0.29	0.005
	Poaceae	*Dichanthelium caerulescens*	0.85	0.10	0.29	0.004
	Poaceae	*Dichanthelium sphaerocarpon*	0.84	0.10	0.29	0.004
	Asteraceae	*Solidago fistulosa*	0.84	0.10	0.29	0.003
	Cyperaceae	*Rhynchospora latifolia*	0.84	0.10	0.29	0.003
	Fabaceae	*Desmodium strictum*	0.82	0.10	0.28	0.004
	Xyridaceae	*Xyris flabelliformis*	0.82	0.10	0.28	0.004
	Poaceae	*Anthaenantia villosa*	0.79	0.10	0.28	0.006
	Apocynaceae	*Asclepias pedicellata*	0.79	0.10	0.28	0.004
	Fabaceae	*Lespedeza repens*	0.78	0.10	0.28	0.004
	Cyperaceae	*Rhynchospora chalarocephala*	0.76	0.10	0.27	0.008
	Asteraceae	*Lactuca floridana*	0.76	0.10	0.27	0.007
	Fabaceae	*Indigofera caroliniana*	0.73	0.10	0.27	0.007
	Lamiaceae	*Salvia lyrata*	0.70	0.10	0.26	0.006
	Poaceae	*Andropogon arctatus*	1.00	0.06	0.25	0.017
	Poaceae	*Anthaenantia rufa*	1.00	0.06	0.25	0.014
	Poaceae	*Aristida condensata*	1.00	0.06	0.25	0.014
	Asteraceae	*Arnoglossum ovatum*	1.00	0.06	0.25	0.017
	Annonaceae	*Asimina reticulata*	1.00	0.06	0.25	0.011
	Ericaceae	*Bejaria racemosa*	1.00	0.06	0.25	0.01
	Orchidaceae	*Calopogon pallidus*	1.00	0.06	0.25	0.014
	Asteraceae	*Carphephorus pseudoliatris*	1.00	0.06	0.25	0.013
	Rhamnaceae	*Ceanothus americanus*	1.00	0.06	0.25	0.016
	Fabaceae	*Chamaecrista deeringiana*	1.00	0.06	0.25	0.015
	Cyrillaceae	*Cliftonia monophylla*	1.00	0.06	0.25	0.01

Appendix A.2. Continued

Cluster	Family	Species	A	B	Indicator Value	*P* -value
5	Asteraceae	*Coreopsis floridana*	1.00	0.06	0.25	0.01
	Euphorbiaceae	*Croton glandulosus*	1.00	0.06	0.25	0.016
	Cyperaceae	*Cyperus polystachyos*	1.00	0.06	0.25	0.011
	Fabaceae	*Desmodium fernaldii*	1.00	0.06	0.25	0.009
	Fabaceae	*Desmodium floridanum*	1.00	0.06	0.25	0.012
	Rubiaceae	*Diodella teres*	1.00	0.06	0.25	0.011
	Cyperaceae	*Eleocharis flavescens*	1.00	0.06	0.25	0.011
	Cyperaceae	*Eleocharis microcarpa*	1.00	0.06	0.25	0.015
	Eriocaulaceae	*Eriocaulon lineare*	1.00	0.06	0.25	0.02
	Cyperaceae	*Fuirena squarrosa*	1.00	0.06	0.25	0.01
	Fabaceae	*Galactia erecta*	1.00	0.06	0.25	0.018
	Ericaceae	*Gaylussacia mosieri*	1.00	0.06	0.25	0.013
	Plantaginaceae	*Gratiola ramosa*	1.00	0.06	0.25	0.011
	Hypericaceae	*Hypericum microsepalum*	1.00	0.06	0.25	0.013
	Hypericaceae	*Hypericum suffruticosum*	1.00	0.06	0.25	0.014
	Hypericaceae	*Hypericum tetrapetalum*	1.00	0.06	0.25	0.012
	Hypoxidaceae	*Hypoxis sessilis*	1.00	0.06	0.25	0.016
	Convolvulaceae	*Ipomoea sagittata*	1.00	0.06	0.25	0.011
	Asteraceae	*Iva microcephala*	1.00	0.06	0.25	0.014
	Juncaceae	*Juncus trigonocarpus*	1.00	0.06	0.25	0.014
	Cistaceae	*Lechea pulchella*	1.00	0.06	0.25	0.008
	Asteraceae	*Liatris laevigata*	1.00	0.06	0.25	0.006
	Onagraceae	*Ludwigia lanceolata*	1.00	0.06	0.25	0.014
	Onagraceae	*Ludwigia maritima*	1.00	0.06	0.25	0.015
	Onagraceae	*Ludwigia microcarpa*	1.00	0.06	0.25	0.013
	Lamiaceae	*Lycopus amplectens*	1.00	0.06	0.25	0.013
	Vitaceae	*Nekemias arborea*	1.00	0.06	0.25	0.013
	Onagraceae	*Oenothera filipes*	1.00	0.06	0.25	0.015
	Boraginaceae	*Lithospermum virginianum*	1.00	0.06	0.25	0.009
	Oxalidaceae	*Oxalis corniculata*	1.00	0.06	0.25	0.016
	Plantaginaceae	*Penstemon australis*	1.00	0.06	0.25	0.015
	Polemoniaceae	*Phlox nivalis*	1.00	0.06	0.25	0.01
	Asteraceae	*Phoebanthus grandiflorus*	1.00	0.06	0.25	0.006
	Solanaceae	*Physalis arenicola*	1.00	0.06	0.25	0.012
	Lentibulariaceae	*Pinguicula lutea*	1.00	0.06	0.25	0.013
	Polygalaceae	*Polygala cruciata*	1.00	0.06	0.25	0.017
	Polygonaceae	*Polygonum pinicola*	1.00	0.06	0.25	0.011
	Lamiaceae	*Pycnanthemum floridanum*	1.00	0.06	0.25	0.016
	Fabaceae	*Rhynchosia difformis*	1.00	0.06	0.25	0.017
	Cyperaceae	*Rhynchospora divergens*	1.00	0.06	0.25	0.011
	Gentianaceae	*Sabatia macrophylla*	1.00	0.06	0.25	0.017
	Sarraceniaceae	*Sarracenia rubra*	1.00	0.06	0.25	0.015
	Poaceae	*Schizachyrium maritimum*	1.00	0.06	0.25	0.009
	Cyperaceae	*Scleria baldwinii*	1.00	0.06	0.25	0.015
	Cyperaceae	*Scleria verticillata*	1.00	0.06	0.25	0.017
	Plantaginaceae	*Sophronanthe pilosa*	1.00	0.06	0.25	0.013

Appendix A.2. Continued

Cluster	Family	Species	A	B	Indicator Value	*P* -value
5	Poaceae	*Sporobolus teretifolius*	1.00	0.06	0.25	0.009
	Asteraceae	*Symphyotrichum adnatum*	1.00	0.06	0.25	0.018
	Fabaceae	*Tephrosia chrysophylla*	1.00	0.06	0.25	0.006
	Verbenaceae	*Verbena carnea*	1.00	0.06	0.25	0.009
	Juncaceae	*Juncus roemerianus*	0.66	0.10	0.25	0.012
	Cyperaceae	*Cyperus haspan*	0.92	0.06	0.24	0.019
	Commelinaceae	*Commelina erecta*	0.87	0.06	0.24	0.023
	Orchidaceae	*Platanthera cristata*	0.87	0.06	0.24	0.031
	Poaceae	*Dichanthelium ravenelii*	0.85	0.06	0.23	0.027
	Cyperaceae	*Rhynchospora colorata*	0.85	0.06	0.23	0.021
	Rosaceae	*Agrimonia rostellata*	0.82	0.06	0.23	0.029
	Hypoxidaceae	*Hypoxis wrightii*	0.82	0.06	0.23	0.029
	Asteraceae	*Melanthera nivea*	0.82	0.06	0.23	0.03
	Adoxaceae	*Viburnum obovatum*	0.82	0.06	0.23	0.021
	Verbenaceae	*Phyla nodiflora*	0.82	0.06	0.23	0.022
	Apocynaceae	*Asclepias longifolia*	0.75	0.06	0.22	0.041
	Hypericaceae	*Hypericum setosum*	0.75	0.06	0.22	0.038
	Juncaceae	*Juncus biflorus*	0.75	0.06	0.22	0.046
	Asteraceae	*Conyza canadensis*	0.71	0.06	0.21	0.05
	Ericaceae	*Lyonia ferruginea*	0.69	0.06	0.21	0.042
6	Cupressaceae	*Taxodium ascendens*	0.78	0.85	0.81	0.001
	Poaceae	*Hymenachne hemitomon*	0.92	0.63	0.76	0.001
	Blechnaceae	*Anchistea virginica*	0.57	0.89	0.71	0.001
	Iridaceae	*Iris tridentata*	0.98	0.48	0.69	0.001
	Polygalaceae	*Polygala cymosa*	1.00	0.44	0.67	0.001
	Cyperaceae	*Rhynchospora filifolia*	0.95	0.44	0.65	0.001
	Apiaceae	*Centella asiatica*	0.65	0.56	0.60	0.001
	Poaceae	*Erianthus brevibarbis*	1.00	0.33	0.58	0.001
	Cyperaceae	*Rhynchospora cephalantha*	0.85	0.37	0.56	0.001
	Cyperaceae	*Carex striata*	0.65	0.48	0.56	0.001
	Melastomataceae	*Rhexia aristosa*	1.00	0.30	0.54	0.001
	Cyperaceae	*Carex glaucescens*	0.68	0.41	0.53	0.001
	Melastomataceae	*Rhexia nashii*	0.65	0.41	0.51	0.001
	Orobanchaceae	*Agalinis linifolia*	1.00	0.26	0.51	0.001
	Haloragaceae	*Proserpinaca pectinata*	0.87	0.30	0.51	0.001
	Gentianaceae	*Sabatia difformis*	0.84	0.30	0.50	0.001
	Xyridaceae	*Xyris fimbriata*	0.87	0.26	0.48	0.001
	Eriocaulaceae	*Eriocaulon compressum*	0.76	0.26	0.45	0.001
	Poaceae	*Dichanthelium wrightianum*	1.00	0.19	0.43	0.001
	Poaceae	*Dichanthelium erectifolium*	0.79	0.22	0.42	0.001
	Hypericaceae	*Hypericum virginicum*	0.67	0.22	0.39	0.002
	Orchidaceae	*Spiranthes laciniata*	1.00	0.15	0.39	0.001
	Poaceae	*Coleataenia tenera*	1.00	0.15	0.39	0.001
	Campanulaceae	*Lobelia canbyi*	1.00	0.11	0.33	0.001
	Cyperaceae	*Rhynchospora inundata*	1.00	0.11	0.33	0.001
	Lauraceae	*Litsea aestivalis*	0.73	0.15	0.33	0.001
	Poaceae	*Mnesithea rugosa*	0.93	0.11	0.32	0.001

Appendix A.2. Continued

Cluster	Family	Species	A	B	Indicator Value	*P* -value
6	Asteraceae	*Coreopsis falcata*	0.85	0.11	0.31	0.001
	Lauraceae	*Lindera melissifolia*	0.84	0.11	0.31	0.003
	Onagraceae	*Ludwigia pilosa*	1.00	0.07	0.27	0.004
	Cyperaceae	*Rhynchospora careyana*	1.00	0.07	0.27	0.002
	Cyperaceae	*Scleria georgiana*	1.00	0.07	0.27	0.009
	Poaceae	*Dichanthelium leucothrix*	0.66	0.11	0.27	0.005
	Poaceae	*Erianthus giganteus*	0.59	0.11	0.26	0.018
	Poaceae	*Coleataenia longifolia*	0.78	0.07	0.24	0.011
	Cyperaceae	*Rhynchospora tracyi*	0.78	0.07	0.24	0.019
	Lentibulariaceae	*Utricularia purpurea*	0.68	0.07	0.23	0.014
	Droseraceae	*Drosera intermedia*	0.68	0.07	0.22	0.034
7	Cupressaceae	*Taxodium distichum*	0.83	0.56	0.68	0.001
	Saururaceae	*Saururus cernuus*	0.70	0.65	0.67	0.001
	Osmundaceae	*Osmunda spectabilis*	0.59	0.73	0.66	0.001
	Araceae	*Peltandra virginica*	0.88	0.46	0.64	0.001
	Hypericaceae	*Hypericum walteri*	0.78	0.44	0.59	0.001
	Oleaceae	*Fraxinus caroliniana*	0.91	0.32	0.54	0.001
	Rosaceae	*Rosa palustris*	0.78	0.37	0.53	0.001
	Oleaceae	*Fraxinus pennsylvanica*	0.80	0.31	0.50	0.001
	Apiaceae	*Cicuta maculata*	0.73	0.31	0.48	0.001
	Nyssaceae	*Nyssa aquatica*	0.97	0.21	0.45	0.001
	Betulaceae	*Alnus serrulata*	0.76	0.23	0.41	0.002
	Aquifoliaceae	*Ilex verticillata*	0.72	0.23	0.40	0.001
	Araliaceae	*Hydrocotyle verticillata*	1.00	0.15	0.39	0.001
	Commelinaceae	*Murdannia keisak*	0.97	0.15	0.39	0.001
	Oleaceae	*Fraxinus profunda*	0.96	0.15	0.39	0.001
	Rubiaceae	*Galium tinctorium*	0.70	0.20	0.37	0.001
	Onagraceae	*Ludwigia palustris*	0.82	0.14	0.34	0.002
	Polygonaceae	*Persicaria sagittata*	1.00	0.11	0.34	0.001
	Ranunculaceae	*Clematis crispa*	0.72	0.15	0.33	0.001
	Viscaceae	*Phoradendron leucarpum*	0.71	0.15	0.33	0.001
	Cyperaceae	*Carex radiata*	0.78	0.13	0.32	0.003
	Acanthaceae	*Justicia ovata*	1.00	0.10	0.31	0.001
	Polygonaceae	*Persicaria arifolia*	1.00	0.10	0.31	0.002
	Orchidaceae	*Platanthera clavellata*	0.77	0.13	0.31	0.004
	Cyperaceae	*Carex lonchocarpa*	0.76	0.13	0.31	0.003
	Lamiaceae	*Lycopus virginicus*	0.72	0.13	0.30	0.004
	Cyperaceae	*Carex leptalea*	0.92	0.10	0.30	0.003
	Polygonaceae	*Persicaria hydropiper*	0.68	0.13	0.29	0.005
	Poaceae	*Arundinaria gigantea*	0.61	0.14	0.29	0.006
	Gentianaceae	*Sabatia calycina*	0.86	0.10	0.29	0.003
	Balsaminaceae	*Impatiens capensis*	0.75	0.11	0.29	0.003
	Apiaceae	*Sium suave*	1.00	0.08	0.29	0.001
	Lamiaceae	*Scutellaria lateriflora*	0.85	0.10	0.29	0.004

Appendix A.2. Continued

Cluster	Family	Species	A	B	Indicator Value	*P* -value
7	Asteraceae	*Solidago sempervirens*	0.94	0.08	0.28	0.003
	Amaranthaceae	*Alternanthera philoxeroides*	0.93	0.08	0.28	0.003
	Campanulaceae	*Lobelia cardinalis*	0.80	0.10	0.28	0.006
	Apiaceae	*Ptilimnium capillaceum*	0.92	0.08	0.28	0.004
	Hypoxidaceae	*Hypoxis curtissii*	0.92	0.08	0.28	0.004
	Cyperaceae	*Carex lurida*	0.90	0.08	0.28	0.005
	Rubiaceae	*Galium obtusum*	0.89	0.08	0.27	0.006
	Poaceae	*Glyceria septentrionalis*	1.00	0.07	0.27	0.008
	Asteraceae	*Pluchea camphorata*	1.00	0.07	0.27	0.007
	Malvaceae	*Kosteletzkya pentacarpos*	0.95	0.07	0.26	0.014
	Polygonaceae	*Persicaria punctata*	0.78	0.08	0.26	0.014
	Asteraceae	*Eupatorium serotinum*	0.90	0.07	0.25	0.006
	Fabaceae	*Apios americana*	1.00	0.06	0.24	0.005
	Orchidaceae	*Habenaria repens*	1.00	0.06	0.24	0.009
	Cyperaceae	*Carex lupulina*	0.80	0.07	0.24	0.017
	Cyperaceae	*Carex alata*	0.91	0.06	0.23	0.021
	Poaceae	*Leersia oryzoides*	0.71	0.07	0.22	0.03
	Commelinaceae	*Commelina virginica*	0.81	0.06	0.21	0.034
	Cyperaceae	*Carex comosa*	0.78	0.06	0.21	0.044
	Cyperaceae	*Carex festucacea*	1.00	0.04	0.21	0.043
	Poaceae	*Elymus virginicus*	1.00	0.04	0.21	0.048
	Malvaceae	*Hibiscus moscheutos*	1.00	0.04	0.21	0.043
	Araliaceae	*Hydrocotyle prolifera*	1.00	0.04	0.21	0.032
	Juncaceae	*Juncus pylaei*	1.00	0.04	0.21	0.044
	Lamiaceae	*Lycopus rubellus*	1.00	0.04	0.21	0.034
	Polygonaceae	*Persicaria maculosa*	1.00	0.04	0.21	0.047
	Apiaceae	*Ptilimnium ahlesii*	1.00	0.04	0.21	0.046
	Cyperaceae	*Schoenoplectus pungens*	1.00	0.04	0.21	0.031
	Poaceae	*Sphenopholis pensylvanica*	1.00	0.04	0.21	0.035
	Amaranthaceae	*Amaranthus cannabinus*	1.00	0.04	0.21	0.049
	Betulaceae	*Betula nigra*	1.00	0.04	0.21	0.042
1+2	Smilacaceae	*Smilax bona-nox*	0.77	0.80	0.78	0.001
	Cornaceae	*Cornus florida*	0.90	0.53	0.69	0.001
	Juglandaceae	*Carya glabra*	0.99	0.43	0.65	0.001
	Betulaceae	*Carpinus caroliniana*	0.83	0.44	0.61	0.001
	Apiaceae	*Sanicula canadensis*	0.91	0.26	0.49	0.001
	Passifloraceae	*Passiflora lutea*	1.00	0.24	0.49	0.001
	Rubiaceae	*Galium bermudense*	1.00	0.23	0.48	0.001
	Caprifoliaceae	*Lonicera sempervirens*	0.88	0.25	0.47	0.001
	Magnoliaceae	*Magnolia grandiflora*	0.91	0.24	0.47	0.001
	Aspleniaceae	*Asplenium platyneuron*	0.75	0.26	0.44	0.001
	Poaceae	*Chasmanthium sessiliflorum*	0.89	0.20	0.42	0.001
	Malvaceae	*Tilia americana*	1.00	0.17	0.41	0.001
	Araliaceae	*Aralia spinosa*	0.92	0.18	0.41	0.001
	Sapindaceae	*Aesculus pavia*	0.92	0.15	0.37	0.001

Appendix A.2. Continued

Cluster	Family	Species	A	B	Indicator Value	*P* -value
1+2	Cannabaceae	*Celtis laevigata*	0.90	0.15	0.36	0.002
	Poaceae	*Oplismenus setarius*	0.95	0.12	0.34	0.001
	Sapindaceae	*Acer floridanum*	1.00	0.11	0.34	0.001
	Apocynaceae	*Gonolobus suberosus*	1.00	0.10	0.31	0.004
	Asteraceae	*Elephantopus carolinianus*	0.90	0.11	0.31	0.002
	Fabaceae	*Amphicarpaea bracteata*	0.96	0.10	0.31	0.003
	Menispermaceae	*Cocculus carolinus*	1.00	0.07	0.27	0.008
	Poaceae	*Melica mutica*	1.00	0.07	0.26	0.014
	Adoxaceae	*Sambucus canadensis*	0.94	0.06	0.23	0.036
	Ranunculaceae	*Clematis catesbyana*	1.00	0.05	0.22	0.02
1+5	Smilacaceae	*Smilax auriculata*	0.86	0.36	0.56	0.001
	Rubiaceae	*Galium pilosum*	0.89	0.17	0.39	0.002
	Fabaceae	*Erythrina herbacea*	0.79	0.14	0.33	0.003
	Smilacaceae	*Smilax pumila*	0.68	0.15	0.32	0.004
2+3	Nyssaceae	*Nyssa sylvatica*	0.67	0.51	0.58	0.001
	Fagaceae	*Quercus nigra*	0.59	0.57	0.58	0.001
	Lauraceae	*Sassafras albidum*	0.71	0.38	0.51	0.001
	Fagaceae	*Quercus stellata*	0.85	0.08	0.27	0.021
2+4	Magnoliaceae	*Liriodendron tulipifera*	0.87	0.31	0.52	0.001
	Annonaceae	*Asimina triloba*	0.95	0.07	0.25	0.029
2+5	Poaceae	*Dichanthelium laxiflorum*	0.88	0.14	0.36	0.001
	Fagaceae	*Castanea pumila*	0.95	0.13	0.34	0.002
	Acanthaceae	*Ruellia caroliniensis*	0.86	0.12	0.32	0.002
	Ulmaceae	*Ulmus alata*	0.78	0.09	0.26	0.048
	Poaceae	*Piptochaetium avenaceum*	0.80	0.08	0.25	0.02
	Rosaceae	*Crataegus uniflora*	1.00	0.06	0.24	0.015
2+6	Asteraceae	*Solidago rugosa*	0.93	0.07	0.26	0.01
2+7	Hydrangeaceae	*Decumaria barbara*	0.83	0.40	0.58	0.001
	Ulmaceae	*Ulmus americana*	0.96	0.33	0.57	0.001
	Fagaceae	*Quercus laurifolia*	0.76	0.40	0.55	0.001
	Urticaceae	*Boehmeria cylindrica*	0.83	0.35	0.54	0.001
	Bignoniaceae	*Campsis radicans*	0.87	0.30	0.51	0.001
	Fagaceae	*Quercus michauxii*	0.99	0.23	0.48	0.001
	Thelypteridaceae	*Thelypteris palustris*	1.00	0.16	0.40	0.001
	Juncaceae	*Juncus coriaceus*	1.00	0.13	0.36	0.001
	Cyperaceae	*Rhynchospora miliacea*	1.00	0.12	0.34	0.002
	Polygonaceae	*Persicaria setacea*	1.00	0.10	0.32	0.001
	Cyperaceae	*Carex debilis*	0.85	0.10	0.30	0.007
	Ulmaceae	*Ulmus rubra*	0.97	0.09	0.30	0.005
	Cyperaceae	*Carex bromoides*	1.00	0.08	0.29	0.002
	Samolaceae	*Samolus parviflorus*	1.00	0.08	0.29	0.004
	Cyperaceae	*Carex stipata*	1.00	0.06	0.25	0.014
	Poaceae	*Leersia virginica*	1.00	0.06	0.25	0.012
	Hydrocharitaceae	*Limnobium spongia*	0.93	0.06	0.24	0.035
	Poaceae	*Festuca subverticillata*	1.00	0.06	0.24	0.037
	Adoxaceae	*Viburnum prunifolium*	1.00	0.05	0.22	0.045

Appendix A.2. Continued

Cluster	Family	Species	A	B	Indicator Value	*P* -value
3+4	Ericaceae	*Kalmia carolina*	1.00	0.07	0.27	0.004
	Pinaceae	*Pinus palustris*	0.88	0.82	0.85	0.001
	Ericaceae	*Gaylussacia dumosa*	0.96	0.63	0.78	0.001
	Dennstaedtiaceae	*Pteridium latiusculum*	0.79	0.58	0.68	0.001
	Xyridaceae	*Xyris caroliniana*	1.00	0.45	0.67	0.001
	Melastomataceae	*Rhexia alifanus*	0.96	0.44	0.65	0.001
	Asteraceae	*Pityopsis graminifolia*	0.93	0.44	0.64	0.001
	Anacardiaceae	*Rhus copallinum*	0.82	0.47	0.62	0.001
	Asteraceae	*Sericocarpus tortifolius*	1.00	0.32	0.57	0.001
	Asteraceae	*Trilisa paniculata*	1.00	0.28	0.53	0.001
	Poaceae	*Dichanthelium tenue*	0.91	0.27	0.50	0.001
	Asteraceae	*Solidago odora*	0.90	0.27	0.49	0.001
	Polygalaceae	*Polygala lutea*	0.86	0.27	0.48	0.001
	Asteraceae	*Eupatorium pilosum*	0.90	0.26	0.48	0.001
	Asteraceae	*Pterocaulon pycnostachyum*	0.93	0.23	0.46	0.001
	Fagaceae	*Quercus laevis*	0.93	0.23	0.46	0.001
	Hypericaceae	*Hypericum tenuifolium*	1.00	0.21	0.45	0.001
	Fagaceae	*Quercus geminata*	0.94	0.22	0.45	0.001
	Fagaceae	*Quercus incana*	0.93	0.22	0.45	0.001
	Ericaceae	*Vaccinium stamineum*	0.68	0.27	0.43	0.001
	Asteraceae	*Trilisa odoratissima*	1.00	0.18	0.42	0.001
	Asteraceae	*Coreopsis linifolia*	0.96	0.17	0.40	0.001
	Fagaceae	*Quercus margarettae*	0.90	0.17	0.39	0.001
	Cyperaceae	*Rhynchospora plumosa*	0.87	0.15	0.37	0.001
3+5	Euphorbiaceae	*Tragia urens*	0.97	0.13	0.35	0.001
	Fabaceae	*Tephrosia hispidula*	1.00	0.12	0.34	0.001
	Poaceae	*Sporobolus pinetorum*	1.00	0.10	0.32	0.002
	Fabaceae	*Lespedeza capitata*	1.00	0.09	0.30	0.001
	Lamiaceae	*Pycnanthemum flexuosum*	1.00	0.09	0.30	0.005
	Orobanchaceae	*Seymeria cassioides*	1.00	0.09	0.30	0.001
	Euphorbiaceae	*Cnidoscolus stimulosus*	0.70	0.12	0.29	0.009
	Droseraceae	*Dionaea muscipula*	1.00	0.08	0.28	0.006
	Asteraceae	*Eurybia paludosa*	1.00	0.08	0.28	0.008
	Fabaceae	*Stylosanthes biflora*	1.00	0.08	0.28	0.005
	Nartheciaceae	*Aletris farinosa*	1.00	0.06	0.25	0.011
	Fabaceae	*Crotalaria purshii*	1.00	0.06	0.25	0.007
	Asteraceae	*Eupatorium rotundifolium*	1.00	0.06	0.25	0.01
	Cyperaceae	*Fimbristylis puberula*	1.00	0.06	0.25	0.005
	Tofieldiaceae	*Pleea tenuifolia*	1.00	0.06	0.25	0.01
	Iridaceae	*Sisyrinchium capillare*	1.00	0.06	0.25	0.014
	Asteraceae	*Solidago pulchra*	1.00	0.06	0.25	0.009
	Asteraceae	*Coreopsis major*	0.94	0.06	0.25	0.019
	Poaceae	*Andropogon gyrans*	1.00	0.05	0.23	0.024
	Fabaceae	*Baptisia cinerea*	1.00	0.05	0.23	0.028
	Fabaceae	*Desmodium tenuifolium*	1.00	0.05	0.23	0.04
	Poaceae	*Gymnopogon brevifolius*	1.00	0.05	0.23	0.036
	Asteraceae	*Silphium compositum*	1.00	0.05	0.23	0.028
	Fabaceae	*Lespedeza stuevei*	0.91	0.05	0.22	0.049

Appendix A.2. Continued

Cluster	Family	Species	A	B	Indicator Value	*P* -value
3+6	Asteraceae	*Eupatorium album*	0.85	0.08	0.26	0.01
4+5	Theaceae	*Gordonia lasianthus*	0.91	0.27	0.49	0.001
	Anacardiaceae	*Toxicodendron vernix*	0.81	0.13	0.32	0.004
4+6	Ericaceae	*Zenobia pulverulenta*	0.89	0.13	0.34	0.001
4+7	Iteaceae	*Itea virginica*	0.83	0.44	0.61	0.001
5+6	Poaceae	*Andropogon capillipes*	0.94	0.48	0.67	0.001
	Eriocaulaceae	*Eriocaulon decangulare*	0.99	0.43	0.65	0.001
	Haemodoraceae	*Lachnanthes caroliniana*	0.94	0.36	0.58	0.001
	Poaceae	*Panicum verrucosum*	0.94	0.33	0.55	0.001
	Poaceae	*Aristida palustris*	1.00	0.21	0.46	0.001
	Asteraceae	*Eupatorium leucolepis*	0.88	0.22	0.44	0.001
	Lycopodiaceae	*Lycopodiella alopecuroides*	0.93	0.21	0.44	0.001
	Melastomataceae	*Rhexia mariana*	0.88	0.21	0.43	0.001
	Asteraceae	*Pluchea baccharis*	0.95	0.19	0.43	0.001
	Asteraceae	*Euthamia caroliniana*	0.87	0.21	0.42	0.001
	Poaceae	*Panicum virgatum*	0.85	0.21	0.42	0.001
	Sarraceniaceae	*Sarracenia flava*	0.83	0.21	0.41	0.001
	Aquifoliaceae	*Ilex myrtifolia*	0.83	0.19	0.40	0.001
	Poaceae	*Paspalum praecox*	1.00	0.16	0.39	0.001
	Poaceae	*Andropogon perangustatus*	0.95	0.16	0.38	0.001
	Cyperaceae	*Rhynchospora gracilenta*	1.00	0.14	0.37	0.001
	Poaceae	*Dichanthelium scabriusculum*	0.91	0.10	0.31	0.003
	Aquifoliaceae	*Ilex cassine*	0.65	0.14	0.30	0.007
	Poaceae	*Eragrostis refracta*	1.00	0.09	0.29	0.003
	Asteraceae	*Helenium pinnatifidum*	1.00	0.09	0.29	0.002
	Cyperaceae	*Rhynchospora microcephala*	1.00	0.09	0.29	0.003
	Lentibulariaceae	*Utricularia subulata*	1.00	0.09	0.29	0.003
	Apiaceae	*Tiedemannia filiformis*	1.00	0.07	0.26	0.004
	Cyperaceae	*Rhynchospora rariflora*	1.00	0.07	0.26	0.005
	Asteraceae	*Ambrosia artemisiifolia*	0.95	0.07	0.26	0.009
	Apocynaceae	*Asclepias lanceolata*	0.94	0.07	0.26	0.007
	Juncaceae	*Juncus marginatus*	1.00	0.05	0.23	0.029
	Loganiaceae	*Mitreola petiolata*	1.00	0.05	0.23	0.029
	Cyperaceae	*Rhynchospora wrightiana*	1.00	0.05	0.23	0.031
	Xyridaceae	*Xyris brevifolia*	1.00	0.05	0.23	0.029
	Asteraceae	*Eupatorium mohrii*	1.00	0.05	0.23	0.035
	Asteraceae	*Eupatorium leptophyllum*	1.00	0.03	0.19	0.05

Appendix A.2. Continued

Cluster	Family	Species	A	B	Indicator Value	*P* -value
5+7	Asteraceae	*Mikania scandens*	0.77	0.31	0.49	0.001
	Asteraceae	*Baccharis halimifolia*	0.89	0.25	0.48	0.001
	Poaceae	*Dichanthelium dichotomum*	0.75	0.18	0.36	0.002
6+7	Smilacaceae	*Smilax walteri*	0.69	0.40	0.53	0.001
	Iridaceae	*Iris virginica*	0.90	0.23	0.46	0.001
	Pontederiaceae	*Pontederia cordata*	1.00	0.12	0.35	0.001
1+2+3	Poaceae	*Chasmanthium laxum*	0.75	0.24	0.42	0.001
1+2+5	Lamiaceae	*Callicarpa americana*	0.97	0.38	0.60	0.001
	Poaceae	*Dichanthelium commutatum*	0.81	0.34	0.53	0.001
	Ericaceae	*Vaccinium arboreum*	0.88	0.29	0.50	0.001
	Aristolochiaceae	*Endodeca serpentaria*	1.00	0.21	0.46	0.001
	Vitaceae	*Vitis aestivalis*	0.93	0.20	0.43	0.001
	Smilacaceae	*Smilax smallii*	0.94	0.15	0.37	0.001
	Asteraceae	*Elephantopus tomentosus*	0.90	0.08	0.26	0.017
1+2+7	Vitaceae	*Parthenocissus quinquefolia*	0.82	0.80	0.81	0.001
	Rubiaceae	*Mitchella repens*	0.86	0.64	0.74	0.001
	Bignoniaceae	*Bignonia capreolata*	0.91	0.44	0.63	0.001
	Arecaceae	*Sabal minor*	1.00	0.26	0.51	0.001
	Rhamnaceae	*Berchemia scandens*	0.79	0.30	0.49	0.001
	Polypodiaceae	*Pleopeltis michauxiana*	0.83	0.27	0.48	0.001
	Vitaceae	*Nekemias arborea*	1.00	0.16	0.40	0.001
1+3+5	Fabaceae	*Clitoria mariana*	0.93	0.10	0.31	0.005
2+3+5	Hypericaceae	*Hypericum hypericoides*	0.78	0.29	0.48	0.001
	Fagaceae	*Quercus falcata*	0.93	0.23	0.46	0.001
2+3+7	Rosaceae	*Rubus pensilvanicus*	0.80	0.16	0.36	0.003
2+4+7	Ericaceae	*Leucothoe axillaris*	1.00	0.09	0.31	0.007
2+5+7	Cornaceae	*Cornus stricta*	1.00	0.20	0.45	0.001
	Ericaceae	*Vaccinium elliottii*	0.87	0.10	0.29	0.018
	Vitaceae	*Vitis cinerea*	1.00	0.08	0.28	0.008
2+6+7	Caprifoliaceae	*Lonicera japonica*	0.80	0.24	0.44	0.001
	Juncaceae	*Juncus effusus*	0.95	0.06	0.25	0.036
	Aquifoliaceae	*Ilex decidua*	1.00	0.06	0.24	0.039
	Dryopteridaceae	*Onoclea sensibilis*	1.00	0.05	0.23	0.042
3+4+5	Aquifoliaceae	*Ilex coriacea*	0.87	0.50	0.66	0.001
	Myricaceae	*Morella caroliniensis*	0.88	0.26	0.48	0.001
3+4+6	Ericaceae	*Vaccinium formosum*	0.77	0.53	0.64	0.001
3+4+7	Ericaceae	*Eubotrys racemosus*	0.86	0.37	0.57	0.001
3+5+6	Aquifoliaceae	*Ilex glabra*	0.79	0.82	0.80	0.001
	Poaceae	*Andropogon virginicus*	0.92	0.43	0.63	0.001
	Poaceae	*Andropogon glaucopsis*	0.99	0.34	0.58	0.001
	Droseraceae	*Drosera capillaris*	1.00	0.13	0.37	0.002
	Campanulaceae	*Lobelia nuttallii*	1.00	0.10	0.32	0.001
	Cyperaceae	*Rhynchospora fascicularis*	0.90	0.08	0.26	0.012
4+5+7	Adoxaceae	*Viburnum nudum*	0.79	0.26	0.45	0.001
4+6+7	Cyperaceae	*Dulichium arundinaceum*	1.00	0.06	0.25	0.034

Appendix A.2. Continued

Cluster	Family	Species	A	B	Indicator Value	*P* -value
5+6+7	Cyperaceae	*Cladium jamaicense*	1.00	0.09	0.29	0.005
	Haloragaceae	*Proserpinaca palustris*	1.00	0.07	0.26	0.01
	Alismataceae	*Sagittaria lancifolia*	1.00	0.07	0.26	0.007
1+2+3+6	Ericaceae	*Vaccinium pallidum*	0.92	0.11	0.31	0.007
1+2+6+7	Bromeliaceae	*Tillandsia usneoides*	0.90	0.50	0.67	0.001
2+3+4+5	Symplocaceae	*Symplocos tinctoria*	0.95	0.22	0.45	0.001
2+3+5+6	Ebenaceae	*Diospyros virginiana*	0.87	0.34	0.55	0.001
2+4+6+7	Blechnaceae	*Lorinseria areolata*	0.93	0.48	0.67	0.001
3+4+5+6	Ericaceae	*Lyonia lucida*	0.83	0.63	0.72	0.001
	Clethraceae	*Clethra alnifolia*	0.83	0.57	0.69	0.001
	Rosaceae	*Aronia arbutifolia*	0.89	0.47	0.65	0.001
	Pinaceae	*Pinus serotina*	0.90	0.45	0.63	0.001
	Ericaceae	*Lyonia ligustrina*	0.86	0.24	0.45	0.001
3+4+5+7	Cyrillaceae	*Cyrilla racemiflora*	0.94	0.32	0.55	0.001
	Ericaceae	*Rhododendron viscosum*	1.00	0.14	0.37	0.002
4+5+6+7	Nyssaceae	*Nyssa biflora*	0.88	0.78	0.83	0.001
	Asteraceae	*Erechtites hieraciifolius*	0.95	0.09	0.30	0.018
1+2+3+4+7	Aquifoliaceae	*Ilex opaca*	0.97	0.69	0.82	0.001
1+2+3+6+7	Pinaceae	*Pinus taeda*	0.88	0.59	0.72	0.001
1+2+4+5+7	Vitaceae	*Muscadinia rotundifolia*	0.93	0.70	0.80	0.001
1+2+4+6+7	Anacardiaceae	*Toxicodendron radicans*	0.93	0.75	0.83	0.001
	Smilacaceae	*Smilax rotundifolia*	0.94	0.53	0.71	0.001
2+3+4+5+7	Poaceae	*Arundinaria tecta*	0.99	0.24	0.49	0.002
2+3+4+6+7	Altingiaceae	*Liquidambar styraciflua*	0.93	0.61	0.75	0.001
3+4+5+6+7	Smilacaceae	*Smilax laurifolia*	0.92	0.76	0.84	0.001
1+2+3+4+5+7	Gelsemiaceae	*Gelsemium sempervirens*	0.99	0.44	0.66	0.001
1+2+3+5+6+7	Myricaceae	*Morella cerifera*	0.95	0.65	0.79	0.001
2+3+4+5+6+7	Lauraceae	*Persea palustris*	0.99	0.93	0.96	0.001
	Sapindaceae	*Acer rubrum*	0.99	0.75	0.86	0.001
	Magnoliaceae	*Magnolia virginiana*	0.98	0.62	0.78	0.001
	Ericaceae	*Vaccinium fuscatum*	0.96	0.40	0.62	0.002
	Osmundaceae	*Osmundastrum cinnamomeum*	0.99	0.33	0.57	0.001