

Impacts of laurel wilt disease on redbay (*Persea borbonia* (L.) Spreng.) population structure and forest communities in the coastal plain of Georgia, USA

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Abstract Laurel wilt disease (LWD), a fungal disease vectored by the non-native redbay ambrosia beetle (*Xyleborus glabratus* Eichhoff), has caused mortality of redbay (*Persea borbonia* (L.) Spreng.) in the coastal plain of Georgia since 2003. Despite its rapid spread, little research has evaluated its impacts on redbay population structure and forest communities. Diseased populations of redbay in five sites (2–4 years post infestation) were compared to healthy populations in three uninfested sites in five counties in Georgia. The results showed high redbay mortality, shifts in size structure, and changes in community composition. An average of 90 % of redbay trees ≥ 3 cm diameter at breast height (DBH) were dead in infested sites, compared to 0–35 % in control sites. Mortality was seen in individuals of the smallest stem diameter category (<1.00 cm diameter at ground height). DBH of live redbay trees in control sites was twice that of those in infested sites. Photosynthetically active radiation was 4.8 times greater at infested sites than control sites due to loss of redbay canopy. Community structure measurements showed redbay trees had the greatest mean importance value

(IV) at control sites compared to the 8th mean IV at infested sites for live stems. Two species co-dominant to redbay, sweetbay (*Magnolia virginiana* L.) and loblolly bay (*Gordonia lasianthus* (L.) J. Ellis), were of higher importance at infested than control sites, suggesting they are increasing in dominance following the mortality of redbay. This study shows LWD has impacted redbay populations and altered associated forest communities in Georgia.

Keywords *Persea borbonia* · Redbay · Laurel wilt disease · *Xyleborus glabratus* · Redbay ambrosia beetle · Population structure

Introduction

Of the 50,000 non-indigenous species introduced to the United States, it is conservatively estimated that 4,500 of these have proliferated and spread rapidly outside their range of introduction and become invaders that have caused major environmental damage, economic losses and loss of biodiversity (OTA 1993; Pimentel et al. 2000; Ruesink et al. 1995; Wilcove et al. 1998). Two particularly detrimental groups of invasive organisms are forest insects and pathogens which have caused widespread forest disturbance, destruction, and disruption of ecosystem processes, as well as socioeconomic impacts (Gandhi and Herms 2010; Haack and Byler 1993; Hulcr and Dunn 2011; Liebhold et al. 1995). Approximately 455

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non-indigenous forest insect pests are now established in the continental United States and 16 introduced pathogens are known to attack forest trees in the U.S. (Aukema et al. 2010). Many of these introduced insects and diseases have become serious forest pests such as the hemlock woolly adelgid (*Adelges tsugae* Annand) which kills eastern hemlock (*Tsuga canadensis* (L.) Carrière) and the chestnut blight fungus which caused the elimination of American chestnut (*Castanea dentata* (Marsh.) Borkh) from eastern forests. Some invasive fungal diseases are facilitated or introduced by an invasive insect. For example, beech bark disease facilitated by the beech scale insect (*Cryptococcus fagisuga* (Lind.) (*C. fagi* (Baer.))), kills American beech (*Fagus grandifolia* Ehrh.), and Dutch elm disease, introduced by the European elm bark beetle (*Scolytus multistriatus* Marsham), causes mortality of elm (*Ulmus americana* L. and *U. rubra* Muhl.) (Cox 1999). These species and diseases have been widely studied showing severe effects on forests of North America. More recently introduced destructive forest pests are the Asian longhorned beetle (*Anoplophora glabripennis* (Motschulsky)), the emerald ash borer (*Agrilus planipennis* Fairmaire) (Cappaert et al. 2005; Haack et al. 1997), and sudden oak death caused by the oomycete *Phytophthora ramorum* Werres, de Cock & Man in't Veld (Rizzo and Garbelotto 2003).

Beetles in the family Scolytidae, the bark and ambrosia beetles, are among the most damaging insects to forests worldwide (Haack 2001). They breed under bark or inside wood and are among the most commonly intercepted families of insects on wood packing materials at U.S. ports of entry, representing 93–94 % of all insects (Haack and Cavey 1997). The recently introduced redbay ambrosia beetle (*Xyleborus glabratus* Eichhoff) is the vector of a fungal symbiont (*Raffaelea lauricola* T.C. Harr., Fraedrich & Aghayeva) that causes laurel wilt disease (LWD) in redbay (*Persea borbonia* (L.) Spreng.) and other woody members of the plant family Lauraceae (Fraedrich et al. 2008; Harrington et al. 2008). It was first discovered in the United States in a funnel trap at Port Wentworth, Georgia in 2002 (Rabaglia et al. 2006) and it was most likely introduced via international transport of wood products containing beetles (Rabaglia 2003).

The redbay ambrosia beetle is native to Asia and has been recorded from India, Bangladesh, Japan, Myanmar, and Taiwan (Wood and Bright 1992). The

redbay ambrosia beetle has since spread LWD into almost 100 counties in the coastal plain of Georgia, Florida, Alabama, Mississippi, South Carolina, and North Carolina (Fig. 1). It has steadily expanded its range since its introduction at a calculated rate of 55 km/year based on 2004–2006 data (Koch and Smith 2008). Rates of spread are due to natural beetle dispersal and movement of infested wood by humans, particularly firewood (FDACS-DPI 2010). Considering these factors, LWD could potentially spread throughout the rest of redbay's range in the southeastern United States, which also includes eastern Texas, parts of Louisiana, and Virginia. Members of the genus *Xyleborus* attack weak, dead, or dying host trees, and there is no evidence of *X. glabratus* as an important pest in its native range (Rabaglia 2003; Wood and Bright 1992). In its introduced range it causes mortality of healthy redbay trees within a matter of weeks to a few months (Mayfield 2008). Symptoms of this disease are wilted foliage with a reddish or purplish discoloration and black stained sapwood. It only takes one redbay ambrosia beetle to infect and kill a tree (Hanula et al. 2008). The rapid death caused by this disease is likely to cause serious forest disturbance where redbay was once abundant.

Biological disturbances such as those due to exotic pathogens and insects can result in selective loss and replacement of a tree species, causing significant changes to ecosystem composition and processes (Castello et al. 1995; Liebhold et al. 1995). Exotic insects and pathogens can produce short-term (weeks to years after attack) disturbance effects on individuals which include tree defoliation, loss of vigor, or death (Lovett et al. 2006). Short-term disturbance effects may also be seen at the ecosystem level, and may include increased nutrient circulation or leaching and activation of decomposition and changes in microclimatic and light regimes in the forest due to canopy gaps (Grace 1986; Jenkins et al. 1999; Latty 2005; Lovett et al. 2002; McNulty and Masters 2005; Orwig and Foster 1998; Webb et al. 1995). Long-term (decades to centuries after attack) disturbance effects may also be seen on forests and include changes in tree species composition, which then affect ecosystem characteristics such as forest structure, productivity, nutrient cycling, soil organic matter production and turnover, hydrology, and the food web (Lovett et al. 2006). Examples of disturbance effects have been well documented for several species affected by invasive

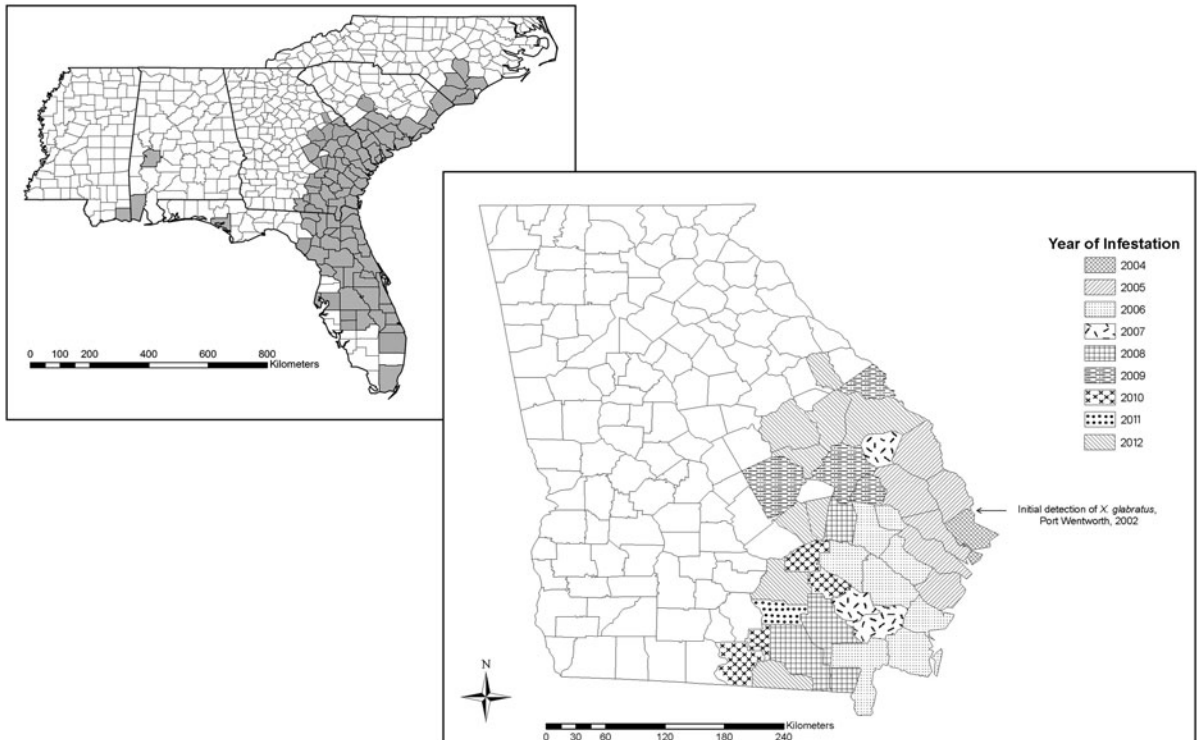


Fig. 1 Range of laurel wilt disease in the southeastern US as of August 2012 (*left*), and spread of laurel wilt disease by county from 2004–2012 in Georgia (*right*). Data provided by http://www.fs.fed.us/r8/foresthealth/laurelwilt/dist_map.shtml

fungal diseases in the U.S. such as American elm, American beech, and American chestnut. In these species shifts in population structure have occurred (Barnes 1976; Forrester et al. 2003; Karnosky 1979; Van Leaven and Evans 2005), followed by forest composition shifts (Augenbaugh 1935; Boggess and Bailey 1964; Boggess and Geis 1966; Good 1968; Keever 1953; Korstian and Stickel 1927; Nelson 1955). Ecosystem level disturbances such as increased light levels due to tree mortality have been associated with increased vegetation cover, species richness, and occurrence of invasive plant species (Eschtruth et al. 2006; Jenkins et al. 1999; McNulty and Masters 2005; Orwig and Foster 1998; Small et al. 2005).

Mortality of redbay as a result of LWD may significantly impact redbay population structure, create canopy gaps, and induce similar disturbances and forest community composition shifts as seen with other tree diseases in the U.S. Redbay is fairly common, but rarely abundant, throughout the southeastern United States (Brendemuehl 1990). It is generally considered a midstory tree or understory

shrub (Harrar and Harrar 1946), but has the potential to reach the canopy and is a co-dominant species in certain habitat types. In smaller canopy gaps, adjacent dominant and co-dominant trees may respond by closing in the gaps left by redbay mortality. In larger canopy gaps, rapid growth of shrubs and seedlings may occur, as well as colonization by species adapted to higher light environments. In the forest types in which redbay is a co-dominant tree, species composition shifts are especially likely to occur. Shields et al. (2011) showed 100 % mortality of redbay >10 cm DBH in a mixed-evergreen deciduous forest in northern Florida and declines in redbay importance values in the overstory from 12th highest to not existent. Goldberg and Heine (2009) compared arborescent vegetation in maritime hammock communities in Florida pre- (1983) and post- (2008) redbay mortality due to LWD and found changes in forest structure. These studies provide evidence as to the effects of LWD on forests; however, no research has been published on changes to forest communities as a result of LWD in the coastal plain of Georgia.

The goals of this research were to determine the changes in redbay population structure and the short-term changes in forest communities that have occurred as a result of redbay mortality. The specific objectives of this study were: (1) to compare the size structure of redbay populations in infested and uninfested sites; (2) to examine the effects of redbay mortality on forest composition and community structure; and (3) to examine the effects of redbay mortality on abiotic factors such as light level (canopy cover) and litter depth.

Materials and methods

Study species

Redbay is an aromatic evergreen tree native to the Atlantic and Gulf coastal plain forests of the southeastern U.S. (Brendemuehl 1990). It is also found in the Bahamas (Duncan and Duncan 1988). Some taxonomists recognize a second species of *Persea*, swampbay (*P. palustris* (Raf.) Sarg.) (Duncan and Duncan 1988; Sargent 1922) or consider it to be a variety of redbay (*P. borbonia* var. *pubescens* (Pursh) Little) (Coker and Totten 1945; Little 1979). A third species of *Persea*, silk bay (*P. humilis* Nash), is found in Florida (Wofford 1997). In the research presented here, we followed the same protocol as the Georgia Forestry Commission and USDA Forest Service and did not attempt to differentiate between species or varieties, and referred to redbay as *P. borbonia* sensu lato (Cameron et al. 2008; Fraedrich et al. 2008).

Redbay thrives in a variety of conditions ranging from wet to well-drained (Coder 2007). It can be found in hammocks, mixed hardwoods, low pinewoods, coastal dunes, maritime forests (Wofford 1997) and evergreen hardwood forests known as bayheads or bay swamps where fresh water flows out of a spring or seep (Coder 2007). Redbay is tolerant of shade but is also found growing well in open sunlight, in both young and old forest stands (Brendemuehl 1990). Coastal forests of Georgia and South Carolina support an average density of 200–400 redbay trees (≥ 2.5 cm diameter) per hectare (Hanula et al. 2008).

Most redbay are midstory trees or understory shrubs, but mature redbay trees can grow 18–21 m in height with diameters of 60–90 cm (Harrar and Harrar 1946).

Redbay flowers are perfect, yellow, about 6 cm long, found in axillary panicles and appear May through June (Brown and Kirkman 1990). They are primarily pollinated by insects, mostly by bees, but may also be wind pollinated (Brendemuehl 1990). The fruit is a small dark blue drupe about 13 mm long that matures in the fall from September to October (Brown and Kirkman 1990). Fruit are produced annually and are eaten and seeds are dispersed by songbirds, white-tailed deer, bobwhite, wild turkey, and black bear (Brendemuehl 1990). Redbay fruit were in 15th place in a list of 63 food items in order of volumetric importance to wildlife (Goodrum 1977). The leaves are eaten by deer and black bear (Goodrum 1977). Redbay and other varieties of *Persea* and sassafras (*Sassafras albidum* (Nutt.) Nees) are the primary food plants of the Palamedes swallowtail (*Papilio palamedes* Drury) caterpillar (Minno et al. 2005).

Study sites

Eight sites were sampled in the coastal plain of Georgia; five sites where laurel wilt disease was present for 2–4 years (hereafter infested) and three sites where it had not yet invaded (hereafter control) (Figs. 1, 2, Table 1). Control sites were determined according to observational lack of LWD in redbay (i.e. no wilted leaves) and confirmed by data provided by the Georgia Forestry Commission (Bates et al. 2012). The control sites remain uninvaded as of April 2012 (Cameron et al. 2012). Sites were located in wet areas in bayheads (3) or mixed hardwood forests (4) and Carolina bays (1) (Table 1). Bayheads are evergreen hardwood swamps composed primarily of loblolly bay (*Gordonia lasianthus* (L.) J. Ellis), sweetbay (*Magnolia virginiana* L.), and redbay (Davis 1943). The hardwood forests varied in their composition from one site to the next and included previously mentioned evergreen species, pines (*Pinus* spp.), and deciduous species such as sweet gum (*Liquidambar styraciflua* L.), tulip poplar (*Liriodendron tulipifera* L.), red maple (*Acer rubrum* L.), oaks (*Quercus* spp.), and *Nyssa* spp. Carolina bays are elliptical shaped, isolated shallow depressions largely fed by rain and shallow groundwater found in the coastal plain (SREL 2007). Typical woody plants in a Carolina Bay are black gum (*Nyssa sylvatica* Marshall), sweet gum, sweetbay, bald cypress (*Taxodium distichum* (L.) Rich), red maple, gallberry (*Ilex coriacea* (Pursh) Chapm.), and redbay

(SREL 2007). See Table 1 for study site information. The sites sampled were in different habitat types and differed in their community composition, but attempts were made to standardize them as much as possible. All sites had a slope of 0–2 % and poorly or very poorly drained soils (Table 2) with redbay as a dominant or co-dominant canopy species (or previously so before LWD).

Only 3 control sites were used because redbay population structure was less variable in control sites, whereas the infested sites were in various stages of decline and thus the population structure was more varied.

Experimental design

Four to seven transects >10 m apart were run through each study location, with up to 2 points along each transect randomly selected for plot location (Table 1).

The length of transects varied based on the size and shape of the forest area containing redbay. Site C3 was too small for transects, but instead a compass was used to line up roughly parallel plots to the highway in a triangular section of forest. Species area curves were used to determine the number of plots to sample for tree, shrub, and herb layers separately. The point at which there was no increase in the number of species in the sample was determined as a sufficient sample size.

A 10 × 10 m plot was set up to measure redbay at the tree layer at each random point selected along the transect, for a total of 8–10 plots per site. The 10 × 10 m plot was sectioned into 25 2 × 2 m subplots, and 4–5 were randomly selected to sample the redbay shrub layer for a total of 32–50 plots per site (Table 1). Within each of the 2 × 2 m subplots, a nested 1 × 1 m plot was set up to sample redbay seedlings at the herb layer.

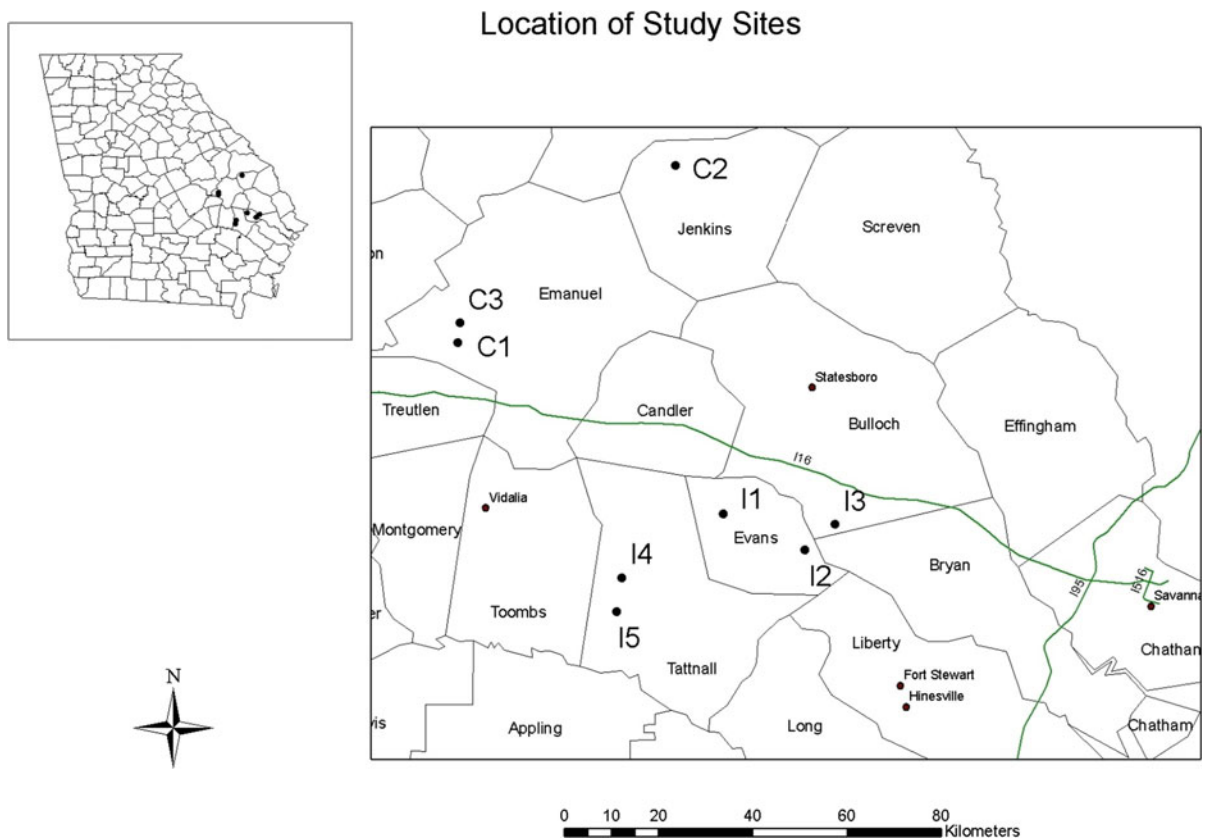


Fig. 2 Location of study sites. C1–C3 are control sites in Emanuel and Jenkins counties, I1–I5 are infested sites in Bulloch, Evans, and Tattnall counties

Table 1 Study site information, for site codes: I = infested and C = control

Site	County	Year of infestation in county/year sampled	Site description	Community type	Area ^a (m ²)	Latitude (N)	Longitude (W)	N Transects	N (10 m ² plots)	N (2 and 1 m ² plots)
I1	Evans	2006/2008	Private property off GA 169	Bay swamp	50,000	32°12'06"	81°56'54"	7	8	32
I2	Evans	2006/2008	Evans County Public Fishing Area	Mixed hardwood forest	10,000	32°07'56"	81°47'28"	6	10	50
I3	Bulloch	2005/2009	Bulloch Bay, private property	Bay swamp	16,000	32°10'52"	81°44'02"	4	8	40
I4	Tattall	2006/2009	Private property off GA 56	Mixed hardwood forest	12,000	32°04'44"	82°08'33"	5	8	40
I5	Tattall	2006/2009	Private property off GA 147	Mixed hardwood forest	12,000	32°00'54"	82°09'10"	4	8	40
C1	Emanuel	–/2008 ^b	Ohoopsee Dunes Natural Area, Halls Bridge Tract	Mixed hardwood forest	15,000	32°31'42"	82°27'18"	6	8	32
C2	Jenkins	–/2009 ^c	Big Dukes Pond Natural Area	Carolina bay	17,000	32°52'03"	82°02'24"	4	8	32
C3	Emanuel	–/2009 ^b	Private property off Highway 80	Bay swamp	12,000	32°33'56"	82°27'03"	–	8	32

^a The area selected for transect locations, and not necessarily the entire habitat containing redbay

^b LWD was found in southeastern Emanuel County in 2009 but has not yet been found in the western part of the county where the study site is located as of April 2012 (Cameron et al. 2012)

^c LWD was noted in eastern Jenkins County in 2007, but was not found in the northwestern part of the county in the control site during sampling and as of April 2012 was still not found at this location (Cameron et al. 2012)

Table 2 Soil data for study sites: I = infested and C = control

Site	Soil type	Land form	Slope (%)	Drainage class	Depth to water table (cm)	Flooding frequency	Typical profile (cm)
I1	Ru: Rutledge sand	Bays, depressions	0–2	Very poorly drained	0–15	None	0–178: sand
I2	OS: Osier soils	Floodplains	0–2	Poorly drained	0–30	Frequent	0–15: loamy fine sand 15–167: sand
I3	RkA: Rutledge sand	Bays, depressions, drainageways	0–2	Very poorly drained	0	Frequent	0–69: loamy fine sand 69–183: sandy clay loam
I4	OS: Osier soils	Floodplains	0–2	Poorly drained	0–30	Frequent	0–15: loamy fine sand 15–168: sand
I5	Ru: Rutledge sand	Bays, depressions	0–2	Very poorly drained	0–15	None	0–178: sand
C1	Me: Meggett loam	Floodplains	0–2	Poorly drained	0–30	Frequent	0–10: loam 10–66: sandy clay 66–132: clay 132–160: sandy clay loam
C2	PeA: Plummer sand	Flats, stream terraces, shallow depressions	0–2	Poorly drained	0–30	None	0–127: sand 127–183: sandy clay loam
C3	KFA: Kinston and Bibb soils	Floodplains	0–2	Poorly drained	0–30	Frequent	0–15: loam 15–160: sandy clay loam

Data from Web Soil Survey (2010) Natural Resources Conservation Service (<http://websoilsurvey.nrcs.usda.gov/app>)

Measurements

Redbay population structure measurements

Measurements of redbay population size structure were conducted once per site and took place May–September 2008 and May–October 2009.

Tree layer: The diameter at breast height (DBH, 1.3 m above ground surface), diameter at ground height (DGH), number of live and dead stump sprouts, and tree status (live or dead primary stem) were recorded for all redbay trees ≥ 3 cm DBH, both live and dead and including fallen trees in the 10×10 m plots in control and infested sites. A total of 352 trees were sampled, 186 in infested sites and 166 in control sites. It was not always possible to obtain a DBH measurement if the tree broke below breast height (12 trees) or to obtain a DGH if the tree was too rotted (7 trees). DBH was obtained for fallen trees by measuring them on the ground 1.3 m from ground level, including the stump. Primary redbay stems were defined as the largest stem of an individual tree. Dead stems were identified to species either by the presence of live stump sprouts, wilted leaves that persisted on branches, or by its characteristic bark texture: grayish to reddish brown, with deep irregular fissures that turn into scaly ridges on older trees. Stump sprouts were defined as such by their close proximity to a larger diameter redbay, and were attached to the base of it or to its root system.

Shrub Layer: The height and DGH of all live and dead redbay stems including shrubs, saplings, and tree stump/root sprouts < 3 cm DGH and ≥ 50 cm tall were measured. Stem diameters were taken with a digital caliper. Any presence of laurel wilt or stem dieback was noted.

Herb Layer: The height and stem diameter of all redbay < 50 cm tall were measured at the herb layer with a digital caliper.

Another introduced Asian beetle whose distribution in the US overlaps that of *X. glabratus*, the brown twig borer (*Xylosandrus compactus* (Eichhoff)), also attacks redbay and damage from this insect can be confused with that of laurel wilt disease. Wilt and twig dieback of redbay caused by *X. compactus* appears like a very early stage of LWD, but unlike trees with LWD, these trees will still be alive weeks later with no noticeable progression of disease-like symptoms (Dixon and Woodruff 1982). Diagnosis of laurel wilt disease was

therefore problematic on smaller redbay at the shrub and herb layers. We are confident about diagnosis of laurel wilt disease with full mortality of individuals at the tree layer. It was not possible to check all stems for black staining of sapwood that would be indicative of laurel wilt disease, and we concede that death and dieback in smaller individuals at the shrub and herb layers could have been a result of *X. compactus*. Yet in the majority of these small stems there was an absence of any beetle holes, which leads to the possibility they were root sprouts that could become re-infected with LWD spread from the root system (S. Fraedrich, personal communication). Small redbay may have been confused as individual seedlings or saplings when they were actually connected to an underground root system if the larger parent stem had fallen and decomposed.

A survey conducted by the Georgia Forestry Commission showed that in infested areas, large redbay trees were found dead, but trees from 2.5 to 10 cm DBH were observed with live primary stems (Cameron et al. 2008). To determine redbay mortality by stem size for this study, all redbay measured were sorted into size classes based on DGH for comparison between control and infested sites. The larger individuals (> 5 cm DGH) were categorized into broader scale size classes because they were more noticeably affected by LWD. Smaller individuals (< 5 cm DGH) were categorized into finer scale size classes because they were less noticeably affected. The finer scale size classes aided in determination of the size at which redbay began to succumb to the disease. Note that Georgia Forestry Commission used DBH because they only observed trees and we used DGH for analyses because we measured individuals at all life stages from seedlings to trees. The mean proportion live redbay by size class were compared in two ways. For one analysis, live redbay and redbay with symptoms of LWD (wilted leaves) or stem dieback (not yet dead) were combined to determine mean proportion live redbay by size class. For a separate analysis, only live redbay not symptomatic of LWD or without stem dieback were used to determine mean proportion live redbay by size class. Considering that the majority of redbay observed with LWD symptoms eventually die and no resistant trees have yet been found (K. Spiegel personal observation), calculations with live, asymptomatic redbay only most accurately depicted the proportion of live redbay. Stump sprouts were included in these calculations.

Forest community structure measurements

The same study sites, study design, and plots were used for this portion of the research as in evaluating redbay population structure. Measurements of forest communities were conducted once per site from May–September 2008 and May–October 2009 (simultaneous with redbay population structure measurements).

Tree layer: The diameter at breast height (DBH) and status (live or dead) were recorded for all stems of all species ≥ 3 cm DBH at the 10×10 m plots in three control sites and five infested sites. For trees with multiple stems, each was counted separately because comparisons were of stems and not genotypes. Frequency (# live trees/# plots) and density (# live trees/plot size) of all live trees were calculated as well as basal area of all live trees using the formula:

$$\text{Basal Area} = \pi(\text{DBH}/2)^2$$

Shrub layer: The crown area and height of all live stems < 3 cm DBH and ≥ 50 cm tall were measured. Crown area was determined by measuring the width of the crown at its widest part (W_1), then measuring a second width of the crown perpendicular to the first (W_2), and these values were used in the formula for the area of an ellipse:

$$\text{Crown Area} = \pi(W_1/2)(W_2/2)$$

Frequency of all live shrubs was also calculated.

Herb layer: Ocular estimates were made of the percent cover of each species, litter, and woody debris and standardized with a 10×10 cm square covering 1 % of the 1×1 m plot. Any percent cover of a species < 1 % was rounded up to 1 %. The frequency of each species was calculated.

Importance values (IV) were calculated for each species at tree, shrub, and herb layers for each site. Relative frequency, relative density, and relative dominance using basal area of all live stems ≥ 3 cm DBH were summed to determine importance value of a species at the tree layer. The same values were also calculated for live and dead stems ≥ 3 cm DBH combined to compare importance values of redbay before and after the occurrence of laurel wilt disease. The relative frequency, relative density, and relative dominance using crown area of all live shrubs < 3 cm DGH and ≥ 50 cm tall were summed to determine the importance value of a species at the shrub layer. Relative frequency and relative dominance using

percent cover were calculated for all live stems < 50 cm tall, and summed to determine importance values of each at the herb layer.

The following formulas were used to calculate relative frequency, density, and dominance:

$$\text{Relative frequency} = (\text{Absolute frequency of species } i / \sum \text{ of freq. for all species}) \times 100$$

$$\text{Relative density} = (\text{Absolute density for species } i / \sum \text{ of density for all species}) \times 100$$

$$\text{Relative dominance} = (\text{Absolute dominance for species } i / \sum \text{ of dom. for all species}) \times 100$$

The importance value for tree and shrub layer was calculated as (max. = 300):

$$\text{IV} = \text{Relative frequency} + \text{Relative density} + \text{Relative dominance}$$

The importance value for herb layer was calculated as (max. = 200):

$$\text{IV} = \text{Relative frequency} + \text{Relative dominance}$$

Species richness was determined at all sites for tree, shrub, and herb layers separately as the number of species per plot or subplot averaged by site. Plot size was 10×10 m for tree layer, 2×2 m for shrub layer, and 1×1 m for herb layer.

Abiotic factors

To determine light availability below the canopy in control and infested sites, photosynthetically active radiation (PAR) measurements were taken with a Model PAR-80 AccuPAR ceptometer (Decagon Devices, Inc., Pullman, WA). The AccuPAR ceptometer has a linear array of 80 adjacent 1 cm^2 PAR sensors along a 1 m long bar for more accurate measurements in variable light environments. Measurements were taken between August 8, 2009 and September 4, 2009 during the time of day when the sun was most directly overhead, 11 AM–1:30 PM, with clear skies. If clouds passed overhead, we waited until they were clear of the sun before continuing measurements. Measurements were taken in all 2×2 m subplots along two perpendicular axes approximately 1 m above ground level. Three measurements were taken at each axis and all measurements at each subplot were averaged.

Litter depth was haphazardly measured in one location in each 2×2 m subplot as the depth of leaf litter above the organic matter layer.

Data analysis

Redbay population structure analyses

This study was designed as a nested ANOVA, with treatment and sites nested within treatment (control vs. infested) as effects. However, data were not normally distributed, therefore data were averaged by site and the site averages were used in a one-way ANOVA to determine differences in control and infested sites. All data were tested for the assumptions of normality with the Shapiro–Wilk test and equal variance with the Levene test. For averaged data that met the assumptions, a one-way ANOVA was used to analyze differences in control and infested sites for the following factors: mean percent live redbay by layer, mean tree DBH, mean shrub DGH, mean DGH of all stems, mean proportion live redbay by size class, and mean number of stump sprouts per tree. When one of the assumptions was not met, a non-parametric Mann–Whitney U test was used. In all non-parametric tests sample size was <20 ($N_C = 3$, $N_I = 5$), so a table of critical upper and lower limit values was used to determine significance of the U statistic at $p \leq .05$ (Rohlf and Sokal 1994). This test was used to analyze differences in mean percent live redbay by layer, mean

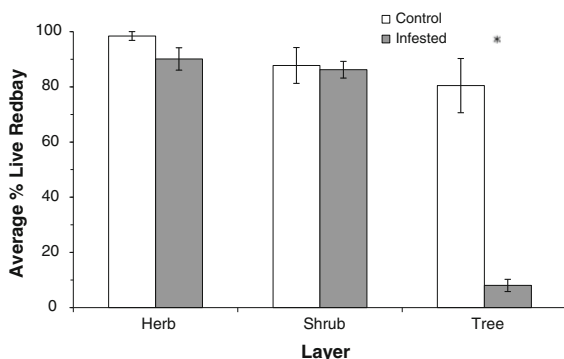


Fig. 3 Mean percent live redbay stems \pm SE by layer. Five infested sites were compared to three control sites. *Show a significant difference in control and infested sites at $p \leq .05$. Herb layer = individuals <50 cm tall, shrub layer = individuals ≥ 50 cm tall but <3 cm DBH, tree layer = individuals ≥ 3 cm DBH

proportion live redbay by size class, and mean number of stump sprouts per tree.

Linear regression was used to determine the relationship between DBH and the number of stump sprouts per tree at dead trees in control and infested sites. All statistical analyses were conducted using JMP 8.0 (SAS Institute Inc., Cary, NC, 2008).

Forest community analyses

All data were tested for the assumptions of normality with the Shapiro–Wilk test and equal variance with the Levene test. Mean importance value for individual species at tree, shrub, and herb layers in infested and control sites were compared using t tests for parametric data and a Mann–Whitney U test for nonparametric data. Importance values calculated with live stems and calculated with live plus dead stems for trees were compared by treatment (control, infested) using t -tests for parametric data and a Mann–Whitney U test for nonparametric data. If sample sizes were <20 , a table of critical upper and lower limit values was used to determine significance of the U statistic at $p \leq .05$. Light level, litter depth, and percent cover of woody debris and leaf litter were log transformed to obtain a

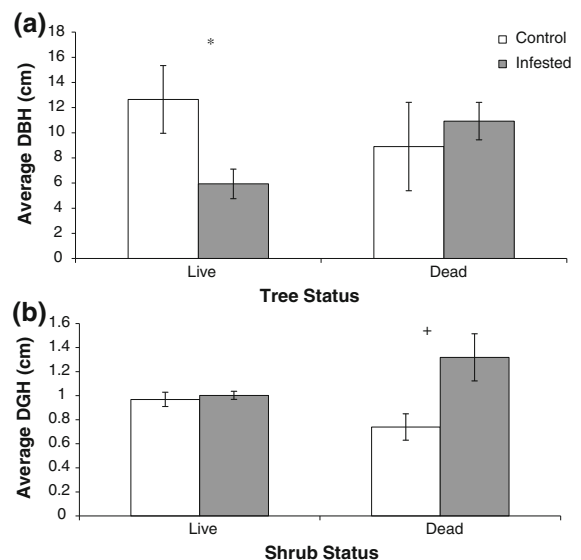


Fig. 4 Mean **a** DBH of all redbay stems (≥ 3 cm DBH) \pm SE and **b** DGH of all redbay stems (<3 cm DBH, ≥ 50 cm high) \pm SE in control and infested sites. Five infested sites were compared to three control sites. *Indicates a significant difference at $p \leq .05$, + sign indicates a trend ($p = .07$) between control and infested sites

normal distribution, then tested with a nested ANOVA. Species richness was compared for each layer with a nested ANOVA. For each nested ANOVA, treatment (control, infested) and sites nested within treatment were the effects tested. All statistical analyses were conducted using JMP 8.0 (SAS Institute Inc., Cary, NC 2008).

Results

Size structure of redbay populations

Infested and control sites differed in many of the population characters measured, suggesting that redbay population structure has been altered by laurel wilt disease in the 2–4 years since infestation. The disease has primarily killed redbay trees (≥ 3 cm DBH), while smaller individuals survived (Fig. 3). Only 8.1 ± 2.2 % of redbay trees were live in infested sites,

compared to 80.4 ± 9.8 % live at control sites, a tenfold difference (Mann–Whitney U test: $U = 21$, $N_C = 3$, $N_I = 5$, $p \leq .05$, Fig. 3). In infested sites average mortality of redbay trees was very high at 90 %, ranging from 75 to 97 % dead. In control sites, 0, 33 and 35 % of redbay trees were dead. Infested and control sites did not differ in the percentage of live redbay in the shrub and herb layers (shrub: $F(1,6) = 0.061$, $p = .81$; herb: $U = 18$, $N_C = 3$, $N_I = 5$, $p > .05$; Fig. 3).

Live redbay trees had twice the DBH in control than infested sites but the DBH of dead trees did not differ (live trees: $F(1,6) = 7.124$, $p = .04$; dead trees: $F(1,5) = 0.422$, $p = .54$; Fig. 4a). In infested sites, the mean DBH of dead trees was 1.8 times higher than live trees ($F(1,8) = 6.887$, $p = .03$) but in control sites the DBH of live versus dead trees did not differ ($F(1,3) = 0.741$, $p = .45$; Fig. 4a). These results suggest that laurel wilt disease has caused significant mortality of larger trees while smaller stems were less affected.

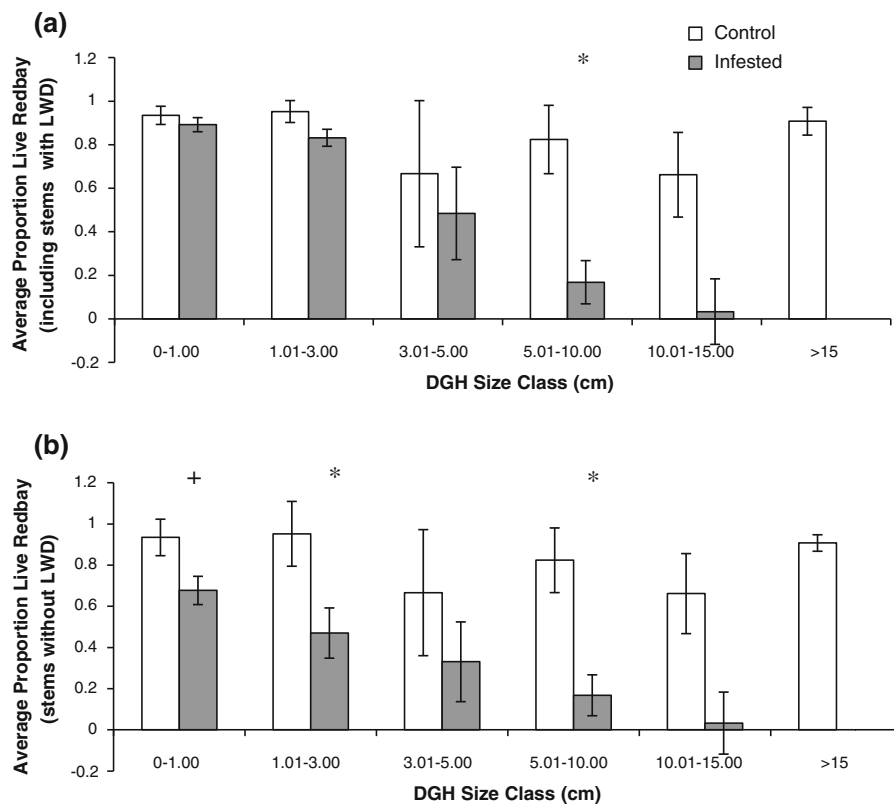


Fig. 5 Mean proportion **a** live and LWD infested redbay stems \pm SE and **b** healthy live redbay stems \pm SE by DGH size class. Five infested sites were compared to three control sites.

*Indicates a significant difference between control and infested sites at $p \leq .05$, + indicates a trend ($p = .06$)

Table 3 Statistics for mean proportion live and LWD infested redbay and mean proportion of live redbay only within each diameter size class

DGH size class (cm)	Test	F/U^\dagger	df	p
Live and LWD infested redbay				
0–1.00	ANOVA	0.657	1, 6	n.s.
1.01–3.00	ANOVA	3.584	1, 6	n.s.
3.01–5.00	Mann–Whitney U test	10 [†]		n.s.
5.01–10.00	ANOVA	12.451	1, 5	.02*
10.01–15.00	Mann–Whitney U test	18 [†]		n.s.
>15				
Live, asymptomatic redbay				
0–1.00	ANOVA	5.276	1, 6	.06 ⁺
1.01–3.00	Mann–Whitney U test	21 [†]		<.05*
3.01–5.00	ANOVA	0.860	1, 5	n.s.
5.01–10.00	ANOVA	12.451	1, 5	.02*
10.01–15.00	Mann–Whitney U test	18 [†]		n.s.
>15				

Five infested sites were compared to three control sites

* Significance at $p \leq .05$

+ Indicates a trend

[†] U is the rank sum of mean proportion redbay for the control sites, which was compared to critical values of U to determine significance, where $N_C = 3$, $N_I = 5$, $U_L = 6$, $U_U = 21$

The diameter of live or dead redbay did not differ in control and infested sites (live shrubs: $F(1, 6) = 0.159$, $p = .70$; dead shrubs: $F(1, 6) = 4.484$, $p = .08$; Fig. 4b). However, a statistical trend of larger diameter shrubs were found dead in infested sites than in control sites, suggesting LWD may have a negative impact on larger shrubs.

A finer scale analysis showed that mortality differed in the smallest size categories of redbay (Fig. 5). Mean proportion live redbay in the 5.01–10.00 cm size class was almost 5 times greater at control than infested sites when calculated (1) with only live stems with no LWD symptoms or twig dieback and (2) with live stems including those with LWD symptoms or dieback (Table 3; Fig. 5a, b). The proportion live redbay was 2 times greater in control than infested sites in the 1.01–3.00 cm size class when calculated with live, asymptomatic stems only (Table 3; Fig. 5b). Also, a trend of a higher proportion live redbay in control sites was found at the 0–1.00 cm size class when calculated with live, asymptomatic stems only (Table 3; Fig. 5b). Beetle holes were not observed in these stems, and it is

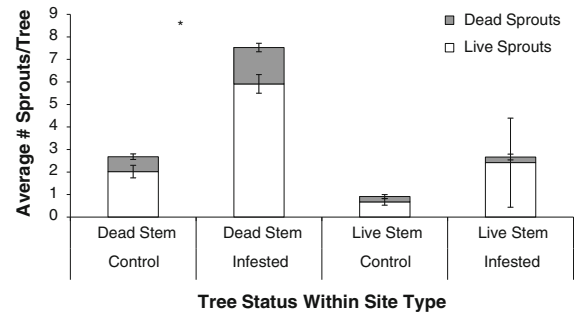


Fig. 6 The mean number of stump sprouts (live and dead) per stem \pm SE for live and dead primary stems (≥ 3 cm DBH) at control and infested sites. Five infested sites were compared to three control sites. *Indicates a significant difference in total number of sprouts at dead trees in control versus infested sites at $p \leq .05$

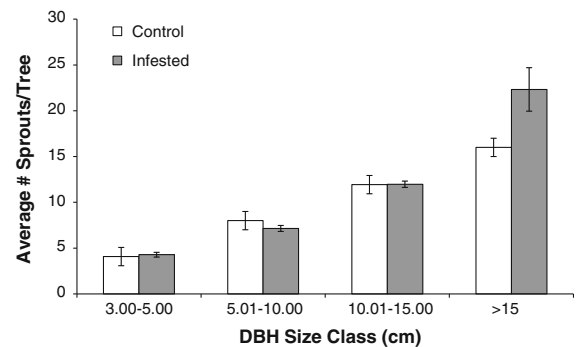


Fig. 7 Mean number of clonal stump sprouts per tree \pm SE by DBH size class for control and infested sites. Five infested sites were compared to three control sites

likely the majority of these were root sprouts infected with LWD through systemic movement of the pathogen into the roots. Importantly, no live redbay ≥ 15 cm DBH were found in infested sites.

Sprouts were found at the base of dead and live redbay trees in both infested and control sites (Fig. 6). However, in control sites the trees classified as live with sprouts were generally injured or in infested sites showed signs of laurel wilt disease. Injuries occurred from nearby treefalls. Dead primary stems had 2.6 times more stump sprouts per tree on average in infested sites than in control sites ($F(1, 5) = 13.840$, $p = .01$) but there was no difference in the number of stump sprouts per tree at live trees between infested and control sites ($U: 14.5$, $N_C = 3$, $N_I = 5$, $p > .05$; Fig. 6). The number of sprouts per dead tree increased as DBH of the tree increased in both infested and

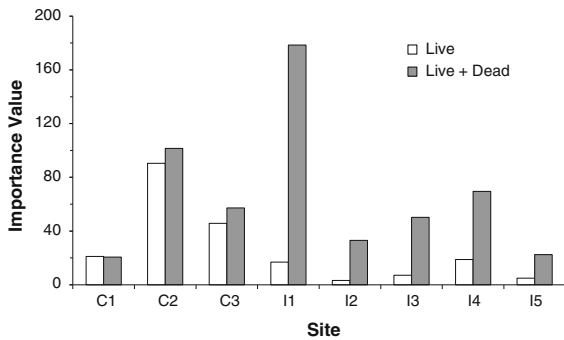


Fig. 8 Comparison of redbay importance values in 8 sites at the tree layer calculated with live redbay stems only and with live and dead redbay stems combined. IVs were calculated by summing relative frequency, relative density, and relative dominance using basal area. Maximum IV was 300. C = control, I = infested

control sites (Fig. 7: control: $R^2(1, 36) = 0.281$, $p < .001$; infested: $R^2(1, 149) = 0.039$, $p = .01$).

Effects of redbay mortality on forest composition and community structure

Mortality of redbay trees as a result of the introduction of laurel wilt disease has opened canopy gaps in only 2–4 years since infestation, which has facilitated alterations in community composition and structure. Calculated importance values of live and dead stems at the tree layer showed redbay was the most prevalent species in infested sites before laurel wilt disease ($IV = 70.8 \pm 28.1$), and after LWD (only dead stems included in calculations) redbay showed a significant decrease in IV (10.2 ± 3.2) and ranked 8th in importance (Fig. 8; Table 4). Redbay had the highest IV at control sites whether calculated with live stems only or live and dead stems. The IV of live redbay at control sites was significantly greater than that of live redbay at infested sites, showing communities have been affected by the disease (Table 4). Also, there was no difference in IV of live and dead stems combined of redbay in control and infested sites ($t(6) = 0.27$, $p = .80$). This suggests there were no preexisting differences in importance of redbay trees between control and infested sites before the onset of LWD. Redbay IVs were comparable at the shrub and herb layers between control and infested sites.

Redbay was followed as highest IV at the tree layer by *Magnolia virginiana*, *Gordonia lasianthus* and

Acer rubrum at control sites (Table 4). In the infested sites, *M. virginiana* had the highest mean IV, followed by *G. lasianthus*, *Pinus taeda* L. and *Nyssa* sp. (*N. sylvatica* or *N. biflora* Walter) (Table 4). This may suggest *M. virginiana* and *G. lasianthus* are increasing in importance at infested sites.

Species richness differed between control and infested sites only at the herb layer ($F(1, 6) = 17.339$, $p < .001$). Fifty-eight species were recorded in the herb layer in 298 1×1 m plots across all study sites. Forty-two species occurred in control sites and 45 in infested sites, however, mean species richness was 1.3 times greater in control sites at the herb layer. Fifty-two species were found in 298 2×2 m plots across all study sites at the shrub layer. Thirty-one species were present in control sites compared to 43 in the infested sites, yet species richness of shrubs did not differ statistically ($F(1, 6) = 3.187$, $p = .07$). Twenty-four species were recorded in 66 10×10 plots across all study sites at the tree layer. Eighteen species at control sites and 20 species in infested sites occurred. Species richness did not differ at the tree layer in infested and control sites ($F(1,6) = 0.249$, $p = \text{n.s.}$), but varied by site ($F(6, 58) = 7.000$, $p < .001$).

Effects of redbay mortality on abiotic factors

Among the abiotic factors measured, photosynthetically active radiation was the only factor that differed between control and infested sites ($p < .001$, Table 5). In infested sites the understory light levels were almost 5 times greater than in control sites. For example, at site I1 which was infested in 2006, significant canopy loss has occurred, where 74 % of all trees were dead, 97 % of which were redbay. PAR readings here averaged very high at $935.1 \mu\text{mol m}^{-2}\text{s}^{-1}$, for comparison the highest average PAR reading in a control site was $86.11 \mu\text{mol m}^{-2}\text{s}^{-1}$. This site was visited both in 2008 and 2009 and observed changes including an increase in opportunistic early successional species which require high light for establishment such as *Erechtites hieracifolius* (L.) Raf. ex DC. and *Phytolacca americana* L. *Phytolacca americana* was also present at study site I4.

The percent cover of woody debris and percent cover of litter did not differ between control and infested sites (Table 5). Litter depths also did not

Table 4 Mean importance values \pm standard error (SE) at the tree layer calculated with live stems only and with live and dead stems for control and infested sites

Species	Control			Infested			Control versus Infested		
	Live mean IV \pm SE	Live + Dead mean IV \pm SE	<i>t</i> -ratio/ <i>U</i> [†]	Live mean IV \pm SE	Live + Dead mean IV \pm SE	<i>t</i> -ratio/ <i>U</i> [†]	<i>t</i> -ratio/ <i>U</i> [†]	<i>t</i> -ratio/ <i>U</i> [†]	<i>t</i> -ratio/ <i>U</i> [†]
<i>Acer rubrum</i>	32.2 \pm 16.1	31.4 \pm 15.7	9.5	27.1 \pm 10.3	23.3 \pm 9.6	-0.27 [†]	-0.27 [†]	-0.27 [†]	-
<i>Cliftonia monophylla</i>	-	-	-	20.0 \pm 13.1	17.2 \pm 10.7	27	27	27	-
<i>Cyrilla racemiflora</i>	-	-	-	2.3 \pm 2.3	2.0 \pm 2.0	27	27	27	-
<i>Gordonia lasianthus</i>	38.5 \pm 19.6	37.2 \pm 18.8	9.5	59.4 \pm 35.1	34.2 \pm 16.1	-0.65 [†]	-0.65 [†]	0.52 [†]	15
<i>Ilex coriacea</i>	4.2 \pm 4.2	4.6 \pm 4.6	11	1.4 \pm 1.4	1.2 \pm 1.2	27	27	27	18
<i>Ilex opaca</i>	7.1 \pm 5.1	6.8 \pm 4.8	-0.04 [†]	0.8 \pm 0.8	0.7 \pm 0.7	27	27	27	14
<i>Liquidambar styraciflua</i>	14.9 \pm 14.9	14.1 \pm 14.1	10	3.1 \pm 2.4	2.9 \pm 2.1	26.5	26.5	26.5	-
<i>Liriodendron tulipifera</i>	18.1 \pm 13.5	17.7 \pm 13.2	9.5	-	-	-	-	-	-
<i>Lyonia lucida</i>	-	-	-	0.8 \pm 0.8	0.7 \pm 0.7	27	27	27	-
<i>Magnolia virginiana</i>	51.6 \pm 26.0	49.7 \pm 25.1	9.5	60.8 \pm 16.9	50.6 \pm 14.9	0.30 [†]	0.30 [†]	0.30 [†]	13
<i>Nyssa ogeche</i>	-	-	-	1.9 \pm 1.9	1.9 \pm 1.9	27	27	27	-
<i>Nyssa</i> sp.	18.6 \pm 9.8	17.8 \pm 9.3	9	39.3 \pm 20.0	33.9 \pm 17.2	24.5	24.5	24.5	-
<i>Osmanthus americanus</i>	3.3 \pm 1.7	3.2 \pm 1.7	-0.04 [†]	-	-	-	-	-	-
<i>Persea borbonia</i>	52.4 \pm 20.3	59.8 \pm 23.4	0.24 [†]	10.2 \pm 3.2	70.8 \pm 28.1	40*	40*	40*	21*
<i>Pinus elliotii</i>	-	-	-	11.9 \pm 9.4	1.8 \pm 1.8	24	24	24	-
<i>Pinus palustris</i>	3.1 \pm 3.1	3.0 \pm 3.0	10	-	-	-	-	-	-
<i>Pinus</i> sp.	1.5 \pm 1.5	1.5 \pm 1.5	10	-	-	-	-	-	11
<i>Pinus taeda</i>	11.9 \pm 7.1	13.0 \pm 8.3	10.5	45.0 \pm 22.2	44.2 \pm 21.5	27	27	27	-
<i>Quercus laevis</i>	1.2 \pm 1.2	1.2 \pm 1.2	10	-	-	-	-	-	-
<i>Quercus laurifolia</i>	3.0 \pm 1.7	3.0 \pm 1.7	-0.03 [†]	3.8 \pm 3.8	3.4 \pm 3.4	27	27	27	16
<i>Quercus nigra</i>	31.4 \pm 25.7	29.5 \pm 23.9	9.5	2.7 \pm 1.7	2.3 \pm 1.5	26.5	26.5	26.5	17.5
<i>Quercus</i> sp.	4.9 \pm 2.6	4.8 \pm 2.6	-0.04 [†]	3.9 \pm 2.5	3.5 \pm 2.3	27	27	27	-0.28 [†]
<i>Rhododendron</i> sp.	-	-	-	0.6 \pm 0.6	0.5 \pm 0.5	27	27	27	-
<i>Symplocos tinctoria</i>	1.8 \pm 1.8	1.7 \pm 1.7	10	0.8 \pm 0.8	0.7 \pm 0.7	27	27	27	15

Table 4 continued

Species	Control		Infested		Control versus Infested	
	Live mean IV ± SE	Live + Dead mean IV ± SE	Live mean IV ± SE	Live + Dead mean IV ± SE	t-ratio/ U [†]	t-ratio/U [†] for live stems
<i>Vaccinium corymbosum</i>	-	-	4.3 ± 4.3	8.3 ± 5.1	29	-

The top 4 greatest mean IVs are bolded. Maximum mean IV was 300 for live and live + dead for each treatment

* Significance at $p \leq .05$

† T-tests used for parametric data, Mann-Whitney U test used for nonparametric data. U is the rank sum of IVs which was compared to critical values of U to determine significance, where $N_1 = 3$, $N_2 = 3$, $U_L = 5$, $U_U = 16$ for control sites and $N_1 = 5$, $N_2 = 5$, $U_L = 18$, $U_U = 37$ for infested sites

† Value represents t-ratio for parametric data. All others represent U

Table 5 Nested ANOVA for abiotic factors tested where treatment and site nested within treatment were the effects

Factor tested	df	F	p
% Cover Woody Debris			
Treatment (control, infested)	1, 6	0.056	.82
Site[Treatment]	6, 58	5.638	<.001*
% Cover litter			
Treatment (control, infested)	1, 6	0.750	.39
Site[Treatment]	6, 58	6.851	<.001*
Photosynthetically active radiation			
Treatment (control, infested)	1, 6	52.060	<.001*
Site[Treatment]	6, 58	26.431	<.001*
Litter depth			
Treatment (control, infested)	1, 6	1.375	.24
Site[Treatment]	6, 58	11.147	<.001*

* Significance at $p \leq .05$

differ between control and infested sites (Table 5). All factors varied by site (Table 5).

Discussion

Redbay is under threat due to laurel wilt disease, which causes mortality of mature trees, and attack by other beetle species such as *X. compactus* (Fraedrich et al. 2008). This study showed that regardless of cause, mortality of redbay occurs at higher rates in infested sites at even the smallest size stem classes, with the highest mortality found in the largest individuals. This supports Fraedrich et al.'s findings (2008) that redbay seedlings were less affected by laurel wilt disease compared with larger diameter trees. They observed aborted tunnels similar in size to those made by *X. glabratus* in stems and branches as small as 1 cm in diameter, however, and hypothesized that *X. glabratus* is able to infect healthy redbay with the laurel wilt fungus by tunneling even without egg laying (Fraedrich et al. 2008). The present study provides support for this hypothesis with higher small-size class mortality in infested than control sites. Stump sprouts (included in our calculations), can become infected by the laurel wilt fungus via roots and die back; therefore, it is possible that the smaller individuals affected were stump sprouts reinfected with LWd from the root system and not attacked by beetles themselves. Alternatively, higher small-size

class mortality in infested sites might be due to a potentially increasing gradient of *X. compactus* abundance from west to east, as all control sites were located at the western edge of the LWD invasion front.

This study provides evidence that the size structure of redbay has shifted to smaller individuals. Similar shifts in size structure from larger individuals to a predominance of sprouts and smaller individuals in greater densities have been shown in populations of American chestnut affected by the chestnut blight (Griffin 1989; Stephenson et al. 1991), among populations of elms (*Ulmus americana* and *U. rubra*) affected by Dutch elm disease (Barnes 1976; Johnson and Bell 1975; Karnosky 1979; Root et al. 1971), and in those of American beech (*Fagus grandifolia*) affected by beech bark disease (Forrester et al. 2003; Houston 1994; Latty 2005; Mize and Lea 1979; Van Leaven and Evans 2005). We found similar shifts in size structure with the majority of surviving individuals in small diameter classes and a prevalence of sprouts. American chestnut also produces sprouts from tree roots after primary stem mortality which eventually succumbs to the fungal disease, new sprouts form, and the process starts over (Anagnostakis 2001). This pattern may also exist in redbay. Fraedrich et al. (2008) also observed numerous sprouting of redbay at the ground line of dead trees. Most sprouts observed occurred at dead or injured trees and were found in both infested and control sites. More sprouts were found at larger trees in control and infested sites, which could mean that root systems were still intact and loss of primary stems increase the amount of water and nutrients available to put into new growth. It was sometimes difficult to determine whether an individual redbay was a root sprout or an individual plant if the original tree had rotted away completely. It appears *X. glabratus* does not reproduce well in smaller diameter stems and beetle populations dropped to very low levels once mature redbay trees in an area were killed (Hanula et al. 2008). Because stump sprouts can become infected via roots, redbay may not be able to grow to maturity to produce seed unless the beetles move out of an area and seeds in the seed bank are able to regenerate a population.

In our study, the decrease in basal area of redbay was correlated with increases in basal areas of other species, which has implications for altering forest composition where redbay has severely declined. One example is in Illinois mesic forests a 70 % decrease in

basal area of elms (*Ulmus americana* and *U. rubra*) was correlated with a 60 % increase in basal area of sugar maple (*Acer saccharum* Marsh.) due to Dutch elm disease (Boggess and Bailey 1964). Elimination of American chestnut due to chestnut blight and replacement by co-dominant tree species, especially oaks, has been well studied (Augenbaugh 1935; Good 1968; Keever 1953; Korstian and Stickel 1927; Nelson 1955). Mortality of larger elms left canopy gaps in which elm saplings were out-competed and replaced by faster growing sugar maple (Boggess and Geis 1966). Ecosystem level disturbance such as increased light levels due to tree mortality have been associated with increased vegetation cover, species richness, and occurrence of invasive plant species (Eschtruth et al. 2006; Jenkins et al. 1999; McNulty and Masters 2005; Orwig and Foster 1998; Small et al. 2005). Similar effects of disturbance due to disease may occur in former redbay dominated communities, but more research is needed.

Our results suggest that in infested sites, redbay mortality has altered community composition and contributed to greater IVs of the co-dominant species *Magnolia virginiana* and *Gordonia lasianthus*. These two co-dominant tree species may respond to redbay mortality by closing in canopy gaps in time. We surveyed sites 2–4 years after LWD was first detected, which was too soon for co-dominant species to fill in the canopy gaps.

At the shrub layer, redbay had the greatest mean IV in infested sites and the second greatest mean IV at control sites. The IVs were not statistically different, but these results may suggest that some amount of regeneration of redbay has occurred in the understory in infested sites. Regeneration of redbay could have been a response to increased light from open canopy gaps left by the death of primary stems or increases in abundance of stump sprouts. Similarly, seedling regeneration and increases in clonal saplings occurred in forests affected by hemlock woolly adelgid (Jenkins et al. 1999; Small et al. 2005).

In maritime hammock communities affected by LWD in Florida, Goldberg and Heine (2009) found frequency and density of canopy species had changed and densities of understory shrubs increased (Goldberg and Heine 2009). Maritime hammocks are hardwood forest habitats of live oak associations (*Quercus virginiana* Mill.) in coastal dunes <1 km from the coast (Oosting 1954). Shields et al. (2011)

studied the short-term impacts of laurel wilt on redbay and forests in one site in a mixed evergreen-deciduous forest in northern Florida and found similar results as our study of high mortality of overstory redbay and drastic reductions in redbay importance.

Species richness did not differ between treatments at the tree or shrub layer, but it was 1.3 times greater in control sites at the herb layer. Over time, greater species richness in infested sites may occur as a response to the increased light availability to the forest floor. As other studies have shown, new species may become established that survive only in higher light conditions that would not have been present under a shaded canopy. In forests affected by HWA, Eschruth et al. (2006) found increases in species richness, which was positively correlated with change in understory light availability. Others have also found increases in light availability corresponding to increases in herb richness and abundance in forests affected by HWA (Orwig and Foster 1998; Small et al. 2005).

As a result of redbay mortality, light levels were almost 5 times higher in infested sites than in control sites. These differences in light availability may have led to colonization of site I1 by two species known to be pioneer species on disturbed sites, *Phytolacca americana* and *Erechtites hieracifolius*. Orwig and Foster (1998) also found *P. americana* and *E. hieracifolius* had become established as a forest response to hemlock mortality from HWA. Both species exhibit a buried seed strategy and can rapidly increase in abundance following disturbance (Del Tredici 1977; Peterson and Pickett 1990). *Parthenocissus quinquefolia* (L.) Planch., also a higher-light demanding species (Eschruth et al. 2006), was present at the herb layer in three infested sites. Similarly, *P. quinquefolia* was found in plots after death of hemlocks from HWA (Eschruth et al. 2006).

Both Small et al. (2005) and Eschruth et al. (2006) found non-native plant species in their sites following disturbance by HWA. However, only one non-native species was observed in one plot of one study site (I4), Chinese privet (*Ligustrum sinense* Lour.), and thus was not a major factor in community composition shifts as of yet.

There was no difference in amount of woody debris or litter depth between control and infested sites. The earliest infestation was in 2005 at I3 and I1, I2, I4, and I5 were infested in 2006. There was still a great amount of standing dead biomass of redbay in infested

sites and the 2008–2009 study may be too soon for trees to have rotted and fallen to add significant amounts of debris at study sites. Also, leaves are retained for several years on trees and thus inputs of woody debris and litter would be gradual, unlike other types of disturbance such as hurricanes which produce an immediate pulse of leaf litter and biomass (Pascarella 1998). Future studies of LWD infested forests may show increases in woody debris and leaf litter as the rest of the dead biomass falls, and thus alterations in nutrient cycling.

Long-term studies of these forest communities will show what species will replace redbay in the future. Based on current importance values at infested sites, it is likely *M. virginiana* and *G. lasianthus* will continue to increase in importance. No seedlings of *M. virginiana* were observed, however, numerous seedlings of *G. lasianthus* were present, suggesting that *G. lasianthus* will become the most important tree species over time. Assuming that *X. glabratus* can reproduce in smaller diameter stems or can reproduce in another tree species, at the shrub layer it is unlikely that redbay will continue to be the most important species at infested sites as they grow and become reinfested with LWD and when all the seeds from the seed bed are exhausted. Shifts in species compositions are likely to affect nutrient cycling as well.

Broader implications

In its native range of Asia, the redbay ambrosia beetle exists between latitudes $\sim 10^\circ$ N and up to $\sim 40^\circ$ N (Wood and Bright 1992). In the United States, redbay is found $\sim 25^\circ$ N in Florida to $\sim 38^\circ$ N in Virginia (Brendemuehl 1990). It is therefore quite possible for the redbay ambrosia beetle to spread laurel wilt disease to redbay throughout its range. It may also spread to other members of its genus and other species of Lauraceae. There are 70 members in the genus *Persea* throughout the neotropics to which LWD could potentially spread if climatic conditions are favorable. Importantly, avocado (*Persea americana* Mill.) grown in Florida, California, Mexico, and tropical Americas (Morton 1987) could potentially be at risk of the disease (Mayfield et al. 2008) and subject local economies to losses of millions of dollars (Evans et al. 2010). Ploetz et al. (2012) showed significant differences in disease severity among various cultivars of avocado. They also showed disease severity

increased on the Simmonds cultivar as stem diameter increased. Other species such as sassafras (*Sassafras albidum*), which occurs throughout the entire east coast, may also be at risk of decline and more so than previously thought (Mayfield and Hanula 2012). Hanula et al. (2008) found that sassafras was not more attractive than non-host species such as live oak (*Quercus virginiana*) and sweetgum (*Liquidambar styraciflua*), however, *X. glabratus* could successfully breed in sassafras wood (Mayfield and Hanula 2012). It is possible more sassafras are being affected than currently realized, because once they are affected with LWD, their leaves drop immediately and they are harder to identify (Smith et al. 2009b). Redbay, on the other hand, retains its leaves after death for several months and is easily noticed, even from long distances (Cameron et al. 2008).

There are also potential threats from laurel wilt disease to the federally endangered pondberry (*Lindera melissifolia* (Walter) Blume) and the state-threatened pondspice (*Litsea aestivalis* (L.) Fernald), both in the Lauraceae family. The *Raffaelea lauricola* pathogen was recovered from some pondberry and pondspice plants, but their small stem diameter may prevent beetles from using these as hosts (Fraedrich et al. 2011). Hughes et al. (2011) reported several instances of laurel wilt in pondspice including recovery of both *X. glabratus* and *R. lauricola*.

Resistance to laurel wilt disease in redbay has not yet been found, but it is exhibited in a non-native Lauraceous species introduced to the U.S. The fungus that causes laurel wilt has been found in several camphor trees (*Cinnamomum camphora* (L.) J. Presl) in McIntosh and Glynn counties in Georgia and in Baker County in Florida (Smith et al. 2009a). In some camphor trees, large branches and parts of the crown were affected, in others, smaller branches were wilted or dead, and some were asymptomatic (Smith et al. 2009a). Total wilt leading to death has not been found in camphor trees (Smith et al. 2009a). Camphor trees are native to southeast Asia, and this species shows possible resistance due to coevolution of exposure to the fungus in its native range (Cameron et al. 2008). Southeast Asia and Brazil are the two major centers of diversity for Lauraceae (Kopp 1966). There is also experimental evidence that North American hosts of alien insects are more susceptible than their coevolved congeners as in beech scale and North American

beeches (Houston 1987) and hemlock woolly adelgid and eastern hemlocks (Havill et al. 2006).

Significant losses of redbay, as in site I1, may affect ecosystem processes. Redbay mortality may alter soil moisture and soil temperatures as has been shown in hemlock woolly adelgid infested forests (Cobb and Orwig 2002; Jenkins et al. 1999; Orwig et al. 2008; Small et al. 2005). Loss of biomass may decrease total transpiration in redbay forests and affect hydrology as Ford and Vose (2007) have shown in forests with severe decline of eastern hemlock. Inputs of leaf litter and woody debris from dead and dying trees might increase decomposition in the forest floor and alter nutrient cycling as has been shown in HWA infested forests (Jenkins et al. 1999; Yorks et al. 2003). Increases in nitrogen availability may runoff to streams and alter their water quality.

The effects of redbay mortality could proliferate through the food web and affect the overall community by changes in wildlife species. Declining populations of redbay might result in significant declines for the Palamedes swallowtail caterpillar (*Papilio palamedes*) (Gramling 2010), whose primary food plant is redbay (Minno et al. 2005). Also, populations of psyllid leaf gallers (*Trioza magnoliae* (Ashmead)) that feed exclusively on redbay (Leege 2006) may be altered. Loss of trees might reduce the amount of fruit production of redbay as a food source to birds and other wildlife as has reductions in beech nuts (Lovett et al. 2006) and seeds of elms (Waldron 2003). Mortality of redbay might also reduce habitat for wildlife and nesting sites for birds as declines in elms in England have shown (Osbourne 1985).

Some dramatic changes in redbay population and size structure have occurred within the introduced range of *X. glabratus* and will most likely occur wherever it spreads. Long-term monitoring of redbay populations are needed to determine further shifts in population structure that may occur, and if regenerating sprouts will have the ability to grow into mature trees. Redbay may face a similar fate as American chestnut, and may continually regenerate via stump sprouts that will never be able to mature enough to fruit and flower. Other species, such as sassafras, should also be monitored for effects of laurel wilt disease. Ecosystem processes may also be affected by redbay mortality and will be an important area of future study.

Finally, if control sites used in this study become infested with LWD, data gathered here can be useful for pre- and post-infestation community studies. We hope to follow these sites over time to determine the long-term changes in species composition and population structure.

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