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Ecological dynamics of ambrosia beetle species in laurel wilt infected trees

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Abstract The redbay ambrosia *Xyleborus glabratus* beetle has emerged as a significant pest of Laurel trees, *Persea* spp. [Laurales: Lauraceae], in the southeastern USA due to its symbiotic association with the pathogenic fungus *Harringtonia lauricola*, the causal agent of the laurel wilt disease. We evaluated the interaction of different species of ambrosia beetles with redbay trees *Persea barbonia* infected by *H. lauricola.* We measured the landing and emergence rates of different ambrosia beetle species throughout the wilting process at different heights. We assessed landing height passively in two redbay stands by placing staggered, unbaited white sticky traps at three height levels (low: 0–1 m; middle: 1–1.5 m; high: 1.5–2 m). We collected nine other Scolytinae species including *Xyleborus volvulus*, *Xyleborinus saxesenii*, *Euplatypus compositus*, *Xyleborus bispinatus*, and *Xyleborus affinis*. In the three experiments and both locations, the primary vector of *H. lauricola, X. glabratu*s, was the most frequently collected species both in the landing captures and in the emergence rate, independently of the wilting status of the host. However, the numbers and diversity of ambrosia beetles landing on trees and emerging from logs increased when trees were in an advanced stage of wilting. Our results indicate that other ambrosia beetles benefit marginally from laurel wilt and that the contribution of secondary ambrosia beetle vectors in the spread of *H. lauricola* through lateral infection in the redbay system is most likely minimal as compared to the contribution of *X. glabratu*s.

Keywords Laurel wilt · *Xyleborus glabratus* · *Harringtonia lauricola* · Ambrosia beetles · Bark beetles

Introduction

Invasive pest species transmitting disease have devastated native forests worldwide, disturbing food webs and leading to rapid environmental degradation in some cases (Cobb et al. 2012; Hughes et al. 2017). Ambrosia beetles (Coleoptera: Curculionidae: Scolytinae and Platypodinae) can be highly invasive and have emerged as major pests of trees in nurseries and forest systems. Within their native ranges, ambrosia beetles attack stressed or dying trees instead of healthy trees and, along with their symbiotic fungi, contribute to nutrient cycling by breaking down the tree tissue. The recent incursion of exotic ambrosia beetle species and their pathogenic fungal symbionts into the United States, and the fact that these introduced species attack healthy trees, has raised the status of some ambrosia beetles

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to that of economically important forest and agricultural pests (Hulcr and Dunn 2011).

The redbay ambrosia beetle has had a devastating impact on the genus *Persea.* [Laurales: Lauraceae] in North America due to their association with the pathogenic fungal symbionts, *Harringtonia lauricola* T.C. Harr., Fraedrich & Aghayeva (Ophiostomatales: Ophiostomataceae), the causal agent of the laurel wilt (LW) disease. *Harringtonia lauricola* is an ascomycete fungus that colonizes the vascular xylem of trees in the Lauraceae family and can lead to rapid death in a susceptible host (Hulcr and Dunn. 2011; Rabaglia et al. 2019; Ploetz et al. 2017a; Hughes et al. 2015). The redbay ambrosia beetle *Xyleborus glabratus*, (Coleoptera: Curculionidae) Eichhoff, is the primary vector of LW in natural ecosystems in the southeastern USA (Fraedrich et al. 2008; Hughes et al. 2015; Hanula et al. 2008). Bark beetles in the tribe *Xyleborini* are particularly successful invaders of new ecosystems because of their wide range of host species (Hulcr et al. 2007). From 2004 until recently, LW has caused massive tree mortality in the southeastern USA and infects both native and cultivated species in the Lauraceae, including redbay (*P. borbonia*), swamp bay (*Persea palustris*), silk bay (*Persea humilis*), sassafras (*Sassafras albidum*), and avocado (*Persea americana*) (Ploetz et al. 2017a). Laurel wilt spread rapidly throughout most of the southeastern USA and caused substantial tree death, killing 95% of any localized redbay population in 18–24 months once established in an area (Carrillo et al. 2012). Scientists estimate that over one-third of redbay in the USA, approximately 300 million trees, have succumbed to the disease (Hughes et al. 2017).

While there is limited quantitative information about the epidemiology of LW in forest ecosystems, the primary spread depends on *X. glabratus* finding a suitable host through olfactory and visual cues (Mayfield and Brownie 2013; Ploetz et al. 2017a). *Xyleborus glabratus* is mainly attracted to the sesquiterpenes found within the cambium of their lauraceous hosts (Niogret et al. 2011), predominantly α-copaene, as well as to α-cubebene, α-humulene, and calamenene (Hanula and Sullivan 2008; Kendra et al. 2012, 2014; Niogret et al. 2011), while leaf and fungal symbiont volatiles have minor roles in the attraction of *X. glabratus* (Hulcr et al. 2011; Martini et al. 2015; Kuhns et al. 2014).

In recent years, several species of ambrosia beetles other than *X. glabratus* were identified carrying *H. lauricola* spores obtained via lateral transfer (Carrillo et al. 2014; Ploetz et al. 2017b). Lateral transfer of a pathogen occurs among bark beetles when secondary vector species comes into contact with the pathogen via a shared host; lateral movement of phytopathogenic symbionts is known to occur in the related bark beetles (Gibbs 1978; Massoumi Alamouti et al. 2009). Carillo and Pena (2012) showed that *X. glabratus* was not successful in reproducing in avocados, indicating that only this lateral fungal transfer contributed to outbreaks of LW in the avocado industry of south Florida (Carrillo et al. 2014; Ploetz et al. 2017b). Despite the presence of multiple species of ambrosia beetles that can transmit *H. lauricola* in Florida forests, it is not clear if other ambrosia beetle species benefit from LW by breeding successfully in infected trees and therefore contribute to the spread of the fungal pathogen.

In this study, we evaluate the interaction of ambrosia beetles with redbay trees by documenting their landing height, landing periodicity, and emergence during the infection and wilting process of redbay in northern Florida forests. In addition, we intend to examine interspecies interactions of native and non-native ambrosia beetles within redbay systems undergoing an LW outbreak. The first experiment evaluates the emergence dynamics of ambrosia beetle species from trees infected with *H. lauricola*. Redbay trees with LW symptoms were monitored in forests and harvested at different stages of wilt infection. The second experiment examines the landing distribution of various ambrosia beetles along the vertical axis of the trunk of a redbay tree. Finally, the third experiment analyzes landing rates of ambrosia beetles on LW trees during the early stage of the disease. Our initial hypotheses for these experiments were that *X. glabratus* will be the dominant species in the early stages of tree invasion, and that alternative species will increase in abundance as the wilting process progresses.

Materials and methods

All three experiments were conducted in two forests, 32 km apart, and located in the North Florida panhandle: Edward Ball Wakulla Springs State

Park (Wakulla Springs, Florida – 30°14′0.60″ N; −84°18′11.40″W), and Lake Talquin State Forest (Quincy, Florida – 30° 27′8.524″ N; −84° 32′57.401″ W), from 2018 to 2019. Both locations comprise four habitats: old-growth wood plain, upland hardwood, longleaf pine forests, and mixed pine-hardwood forests. These habitats are dominated by slash pine (*Pinus elliottii)*, live oak (*Quercus virginiana* Mill.), cabbage palm (Sabal palmetto [Walter] Lodd. Ex Schult. And Schult. f.), southern magnolia (*Magnolia grandiflora* L.) laurel oak (*Quercus laurifolia* Michx.), scrub hickory (*Carya floridana* Sarg.), southern sugar maple (*Acer floridanum* [Chapm.] Pax) and redbay. In addition, both sites have a humid subtropical climate regime.

Experiment 1: Emergence dynamics of infected redbay logs at different heights

The first experiment evaluated the emergence dynamics of different ambrosia beetle species that make galleries in laurel trees infected with *H. lauricola*. Trees were collected from September 13, 2018, to April 30, 2019, in Wakulla (n = 7) and Lake Talquin (n = 11). Mature redbay trees with LW symptoms (diameter at breast height (dbh) greater than 7 cm) were monitored in forests and harvested at different stages of wilt infection. The wilting stage was evaluated as "early" (foliage partially wilted (25–75%), n = 9) and "late" foliage completely wilted, n = 9). Segments of the 23 tree trunks were cut into 40 cm logs. Logs were taken from either in the first 2 m (n = 10) or between 2 and 4 m (n = 8) from the ground. Because mature redbay trees have severely declined in our area due to LW, we did not include uninfected control redbay trees in our treatments. These logs were marked, diameter measured and placed in containers in the laboratory. The logs were separated into different containers by height and wilting stage. Each container was modified with a 6 cm hole at the bottom where a collection jar was placed. On top of the containers was a fine mesh covered 10 cm square opening to allow ventilation and evaporation. Containers were placed on shelves in a growth room maintained at 24 °C with 34% humidity and a 12 h photoperiod. Emerging adult female ambrosia beetles were collected from collection jars attached to the containers with the infested logs. Ambrosia beetles collected were placed under a stereomicroscope and identified according to the key from Gomez et al. (2018).

Experiment 2: Vertical distribution of ambrosia beetles landing rate in redbay depending on laurel wilt status

The second experiment examined the distribution of ambrosia beetles landing along the vertical axis of the trunk of a redbay tree. The experiment was conducted only in Wakulla Springs State Park from November 2018 to January 2019. Uninfected (n = 5) and LW trees (n = 4) were monitored for ambrosia beetle activity. White sticky card traps (22 cm × 30 cm) were placed on one side of the trunk of uninfected of completely wilted redbay trees using a staple gun. Traps were set at 0.5, 1, and 1.5 m from the ground on the redbay tree. Ambrosia beetles were collected biweekly off the stick trap with and dissecting probe and then placed in a vial filled with ethanol and identified under a stereomicroscope using the identification key from Gomez et al. (2018).

Experiment 3: Overtime distribution of ambrosia beetles' landing rate in redbay depending on laurel wilt status

In the second experiment, the trees selected were already wilted; therefore, the infection date was unknown. To address this issue, we conducted a third experiment where the landing by ambrosia beetles during the infection process was analyzed. Fifteen asymptomatic redbay trees in in Wakulla Springs State Park (n = 7) and in Lake Talquin State Forest (n = 8), were monitored from 2018 to 2019 for ambrosia beetle activity. White sticky card traps were placed on non-symptomatic redbay trees 1.5 m from the ground. Ambrosia beetles were collected biweekly and identified before and during the wilting process. The initiation of LW infestation was determined by the visual observation of the first wilting symptoms, which was designated as day one of the wilt symptoms. Collected ambrosia beetles were identified based on the key from Gomez et al. (2018).

Statistical analysis

Data analysis was conducted using statistical software R version 4.03 (R core team, Vienna, Austria). Data from experiment 1and 2 were analyzed using a generalized linear model (GLM) with height, location, and wilt status as fixed factors. After a log transformation, the normality of the data was assessed with a Shapiro-Wilk test for normality ($P > 0.050$), and Gaussian, Poisson or quasi-Poisson distributions were applied, as appropriate, depending on the distribution of the data. For both studies, the dependent variables were the number of adult beetles for the specific species.

Results

Experiment 1: Emergence dynamics of infected redbay logs at different heights

Most emerging ambrosia beetle females were *X. glabratus* (5520 individuals), *Xyleborus affinis* (103), and *Xylosandrus crassiusculus* (628), which emerged from both early and late stage wilted trees in Wakulla and Lake Talquin. Other species found in small numbers included *Xyleborus horridus* (5), *Xyleborus ferrugineus* (10), *Euwallacea perbrevis* (10), and *Euplatypus compositus* (20). Though *X. glabratus* emerged at a similar rate across different heights, more adult females emerged from late-stage wilted trees than early-stage (Table 1). While different heights did not affect beetle emergence except for *X. crassiusculus*, the wilt stage increased the number of *X. glabratus, X. crassisculus*, and *X. affinis* adult beetles emerging. (Fig. 1; Table 1).

Table 1 Generalized linear models for ambrosia beetle emergence at different heights depending on wilting status

Model	Df	F value	*P* value
X. glabratus – Gaussian[a]			
Wilting stage	1	17.88	< 0.001
Height	1	0.014	0.875
Location	1	3.02	0.033
Height x Location	1	2.19	0.064
X. affinis - Quasipoisson			
Wilting stage	1	20.65	< 0.001
Height	1	0.02	0.884
Location	1	11.49	0.004
X. crassiusculus - Quasipoisson			
Wilting stage	1	9.50	0.008
Height	1	5.52	0.034
Location	1	4.99	0.042

[a] Data were log transformed in order to obtain a normal distribution

For each species, the distribution and the factors used in the model are indicated. The final model was determined after stepwise deletion: interactions that were not significant (> 0.10) were removed from the model

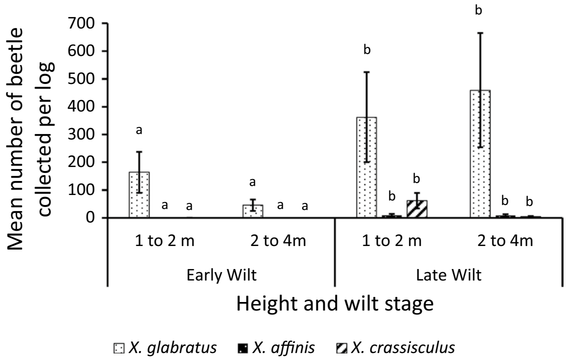

Fig. 1 Mean (± SE) number of ambrosia beetle species emerging from wilted redbay trees from 2018–2019 in the two locations. Logs were harvested from different heights along the vertical axis of the trees at either early-stage wilt or late-stage wilt. Different letters indicate significant difference ($P < 0.05$) among laurel wilt treatments

Experiment 2: Vertical distribution of ambrosia beetles' landing rate in redbay depending on laurel wilt status

There was no significant pattern in the distribution of *X. glabratus* along the vertical axis of the trees through the experiment, whereas the number of *X. glabratus* captured on LW trees was higher compared to uninfected trees in the November samplings (Fig. 2; Table 2). Other ambrosia beetle species were lower in number than *X. glabratus* and only found on wilted trees except for two *Xa. crassiusculus* (out of 143 beetles collected). In addition, some of these beetles showed a difference in the capture distribution along the vertical trunk axis (Table 3): *Xi. saxesenii* were captured significantly more at 1.5 m, and *Euplatypus compositus* were captured significantly more at 1 m (Table 3).

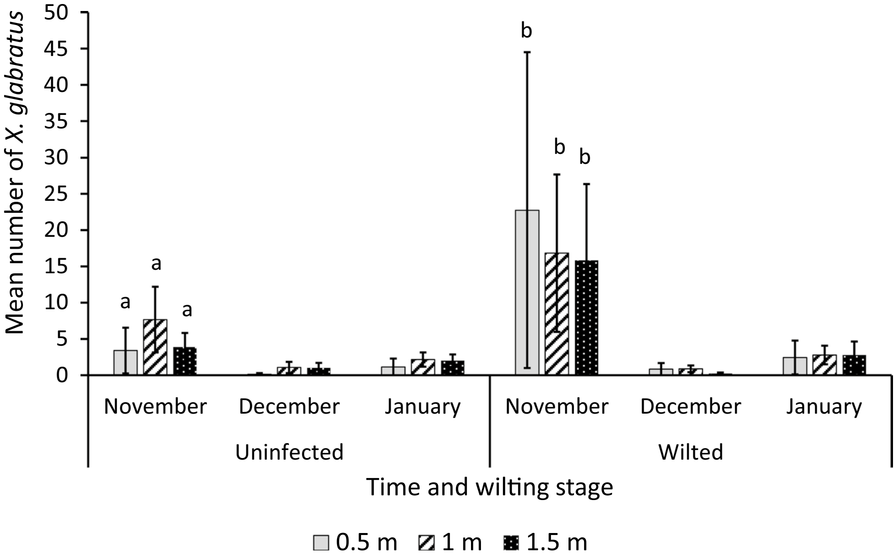

Fig. 2 Mean (±SE) number of *X. glabratus* landing on uninfected and wilted redbay trees from November 2019 through January 2020 in Wakulla Spring State Park, depending on the height of the trap along the vertical axis of the trees and the infection status of the tree. Different letters indicate significant difference ($P < 0.05$) among laurel wilt treatments for the November samplings

Table 2 Generalized linear mixed models for *X. glabratus* captured on sticky traps at different heights dependent on laurel wilt status

Model	DF	F	*P*-value
November – Gaussian[a]			
Height	2	0.138	0.872
Wilt	1	8.163	0.013
Height × Wilt	2	0.073	0.929
December - Poisson			
Height	2	2.031	0.131
Wilt	1	3.627	0.057
Height × Wilt	2	2.891	0.055
January – Gaussian[a]			
Height	2	0.079	0.924
Wilt	1	0.473	0.503
Height x Wilt	2	0.028	0.972

[a] Data were log transformed in order to obtain a normal distribution

For each species, the distribution and the factors used in the model are indicated

Table 3 Total ambrosia beetles other than *X. glabratus* captured between November and January 2019 at different heights (in m) on redbay trees

Species	0.5 m	1 m	1.5 m	χ	*P*-value
X. pubescens	1	0	0		
X. ferrugineus	1	0	0		
X. crassiusculus	1	7	7	4.80	0.091
X. affinis	7	10	10	0.67	0.72
X. saxesenii	0	2	7	8.67	0.013
D. onoharaense	14	9	9	1.56	0.458
Euplatypus compositus	13	35	10	19.28	<0.001

Chi-square tests were conducted to determine if the distributions of the beetles were even

Experiment 3: Overtime distribution of ambrosia beetles' landing rate in redbay depending on laurel wilt status

Redbay ambrosia beetles were recorded landing on trees as early as four weeks before symptoms appeared on the treatment redbay trees. Redbay ambrosia beetle remains the dominant invader throughout the wilting process in both locations. In Lake Talquin, *X. glabratus* landing rates peaked three times during the wilting process, at the seven, 13, and 17-week mark after symptoms began. Three weeks after wilt symptoms appeared *X. affinis*, *Xa. crassiusculus*, and *Euplatypus compositus* started landing on redbay trees (Fig. 3). In Wakulla, *X. glabratus* landing rates peaked around 2 weeks after wilting began, with two minor peaks at seven and 17 weeks. The only other species that landed on wilted redbay in Wakulla was *Xa. crassiusculus*, which only landed on the trees between 2 and 6 weeks after wilting began (Fig. 3). In both locations, *X. glabratus* landing rates gradually increased as LW symptoms developed, peaking intermittently

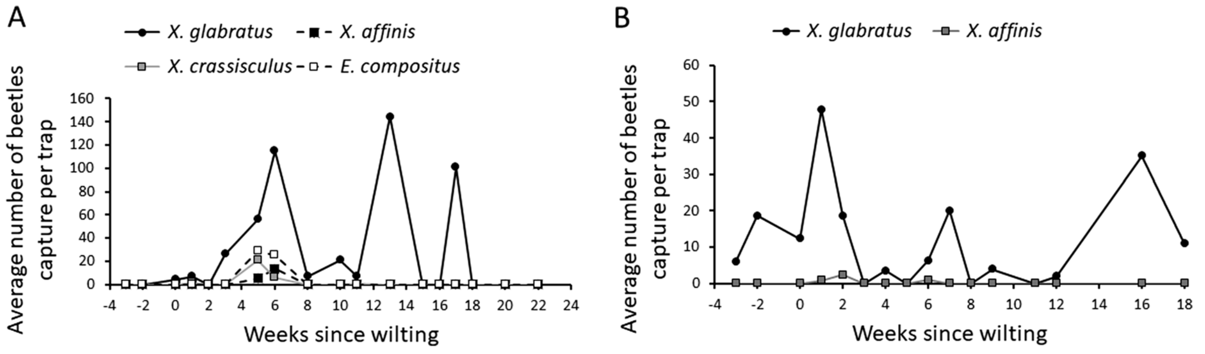

Fig. 3 Mean landing rates of the three most collected species of ambrosia beetle on redbay trees infected with *H. lauricol* in (**A**) the Lake Talquin and in (**B**) the Wakulla location. Negative numbers in weeks indicate collection dates before the first wilting symptoms were observed on the tree

between 2 and 17 weeks post symptoms, then decreasing progressively (Fig. 3).

Discussion

We found that *X. glabratus* was the dominant species through all the three experiments. While there were other ambrosia beetle species collected, their numbers were much less than *X. glabratus*. The introduction of *X. glabratus* and the pathogen *H. lauricola* into the eastern USA has resulted in other ambrosia beetle species transmitting LW by lateral transfer. Specifically, the following ambrosia beetles, *X. affinis*, *X. ferrugineus, X. volvulus, Xi. gracilis, Xi. saxesenii* and *Xa. crassiusculus* were identified as secondary vectors in south Florida avocado systems (Carrillo 2014). Unlike *X. glabratus*, the other beetle species in this study are non-host specific and will infest multiple genera to cultivate symbiont fungi and reproduce (Hulcr and Stelinski 2017).

We analyzed the community dynamics of ambrosia beetle species associated with LW in North Florida. Seeing how different ambrosia beetle species interact in the same system may shed light on the potential lateral transfer of pathogens. Three of our study's four most abundant beetles are globally distributed and non-native species to North America (Biedermann and Taborsky 2012; Gohli et al. 2016). In both locations, the most abundant beetle reproducing in infected redbay was *X. glabratus*, the primary vector of *H. lauricola* (Haack 2003; Mayfield and Thomas 2006; Rabaglia et al. 2019).

Like other insects, abiotic conditions such as temperature, light intensity, precipitation, and wind speed impact female dispersal and host-seeking activity (Six and Bracewell 2015; Chen and Seybold 2014; Aluja et al. 1993). Though *X. glabratus* and the other species of ambrosia beetles did not show any trend in selecting a landing height, overall, the 1–1.5 m area of the tree trunk appears to be the preferred landing height for other ambrosia beetles (Fig. 2). In prior research, ambrosia beetles' flight height was in the range of 0.5–1.5 m above the ground, which is consistent with our findings (Weber and McPherson 1991; Reding et al. 2010; Menocal et al. 2018). Ambrosia beetles may fly 1–1.5 m above the ground to avoid higher wind speeds and turbulence at higher elevations (Brar et al. 2012). Insects such as bark and ambrosia beetle species under 5 mm in length fly at speeds less than 1 m/s (Kinn et al. 1994; Williams and Robertson 2008; Evenden et al. 2014). Therefore, they can incur more interference from mild air movement than larger insects (Farrow 1986). As wind speed increases with increased altitude, it is conjectured that ambrosia beetles decrease flight activity as the distance increases from the ground (Taylor 1963; Farrow 1986). Variability in flying heights could be related to volatile concentrations that signal dispersing female beetles to infest where plant volatiles may be more concentrated and where there is less air movement closer to the base of the tree. However, the emergence of beetles was not influenced by the height of where the log sample was taken. This indicates that the beetles can rapidly colonize tree trunks between 0 and 4 m from the ground.

Throughout this study, LW had a significant impact on ambrosia beetle activity. Symptomatic trees undergoing LW disease had more *X. glabratus* and other species land on them and emerge from them. At the same time, *X. glabratus* appeared to be the dominant species in redbay systems before and during LW; secondary species of ambrosia beetles' activity only appeared once symptoms began. In addition, as the redbay tree decayed from the LW, contrary to our initial hypothesis, *X. glabratus* remained the dominant species. While our results indicate that the wilting process attracts not only *X. glabratus* but also secondary ambrosia beetle species, other ambrosia beetle species do not benefit from LW and are overcast by *X. glabratus*. Based on these data, we hypothesize that in the redbay system, the effect of secondary ambrosia beetle vectors through lateral infection is minimal compared to the importance of *X. glabratus*.

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Author contributions Conceptualization: DC, Methodology: DC, Formal analysis: XM, TP, Investigation: DC, Resources: XM, Writing - Original Draft: DC, Writing - Review & Editing: XM, TP; Supervision: XM, Project administration: XM, Funding acquisition: XM, DC.

Declarations

Conflict of interest The authors have no relevant financial or non-financial interest to disclose.

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