

# Impacts of laurel wilt disease on arthropod herbivores of North American Lauraceae

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**Abstract** For approximately 15 years, *Raffaelea lauricola* and its vector, *Xyleborus glabratus* (redbay ambrosia beetle), have been causing extensive mortality of North American plants in the Lauraceae. All species of Lauraceae native to the USA that have been tested thus far are susceptible to the pathogen. Ecological impacts will likely continue to radiate outwards through ecosystems, yet there is no database of at-risk arthropod species that could be affected by this ecological disturbance. Endangerment risks

remain unquantified, even for known obligate specialists of laurel wilt susceptible hosts, such as the palamedes swallowtail (*Papilio palamedes* Drury). We used exhaustive literature searches and expert-based quality control measures to catalogue native arthropod herbivores of Lauraceae species. Arthropods were assigned an endangerment risk rating based on the extent of their specialization on susceptible hosts. Overall, 178 native arthropod species from 7 orders were catalogued as herbivores that could be impacted by declines of their Lauraceous host plants. Twenty-four insect species were identified as obligate specialists of Lauraceae. A further four species were categorized moderate risk of endangerment because they have one host that is not affected by laurel wilt. As a case study, we also quantified the impacts of laurel wilt on palamedes swallowtail populations. The mean number of palamedes swallowtails encountered in transects through laurel wilt infested stands was nearly sixfold less than in uninfested stands. This suggests dire consequences for the palamedes swallowtail, and warrants concern for the other 24 native species that are obligate specialists of laurel wilt susceptible host plants.

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## Introduction

It is well established that human-induced changes to ecosystems have resulted in declines of biodiversity that are unprecedented in the modern era (Vitousek 1994; Pimm et al. 1995; Sala et al. 2000). Evidence continues to mount that one of humanity's most destructive influences is the facilitation of exotic species invasions (Vitousek et al. 1997; Lovett et al. 2006). A recent global meta-analysis found that only 30 invasive mammal species were responsible for the endangerment or extinction of 738 vertebrate species [an average of 25 species threatened per invasive species (Doherty et al. 2016)]. Additionally, Bellard et al. (2016) reported that invasive species are the second leading cause of native species endangerment, and have been involved in half of all documented extinctions since 1500 AD. In the forested habitats of North America, for example, other authors have reported from 44 (Gandhi and Herms 2010) up to 98 (Wagner and Todd 2016) herbivorous arthropods that are now at high risk of endangerment because of the continued mortality of ash populations (*Fraxinus* spp.) resulting from the introduction of a single insect species, the emerald ash borer (*Agrilus planipennis*). Such targeting of dominant groups of tree species by exotic pests and pathogens may be among the most menacing threats to the biodiversity, ecosystem functions, and ecosystem services of forest biomes.

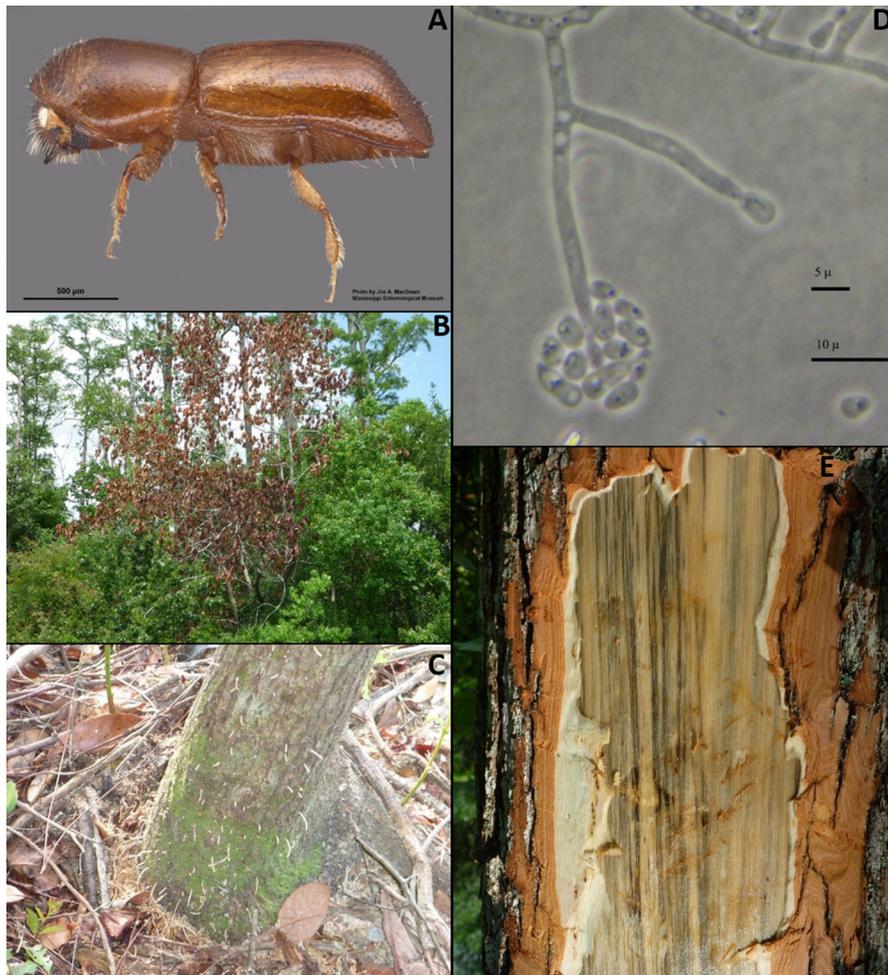
Despite the prevalence of exotic forest insect and pathogen introductions, most of the impacts caused by past and present invasions have not been quantified. In North America, chestnut blight is perhaps the most well-known case in which an exotic fungal pathogen (*Cryphonectria parasitica*), first detected in 1904, killed an estimated four billion American chestnut trees (*Castanea dentata*) over the next several decades (Anagnostakis 1987). With limited baseline data regarding the biodiversity of pre-blight chestnut ecosystems, it is difficult to determine what biodiversity may have been lost (but see Opler 1978). More recent invasive species, like the aforementioned emerald ash borer (first detected in 2002), have given researchers the opportunity to better understand the impact of such invasions on biodiversity (Ulyshen et al. 2011; Gandhi et al. 2014; Jennings et al. 2017).

In the southeastern United States, a biodiversity hotspot for many taxa (Jenkins et al. 2015), laurel wilt disease is causing widespread mortality of tree species

within the Lauraceae (Hughes et al. 2017). The pathogen (*Raffaelea lauricola* T.C. Harr., Fraedrich and Aghayeva; Harrington et al. 2008) is a fungal symbiont of *Xyleborus glabratus* Eichoff, the redbay ambrosia beetle (Fig. 1a, b, respectively). The redbay ambrosia beetle was first collected in a survey trap near Port Wentworth, GA in 2002 (Rabaglia et al. 2006; Fraedrich et al. 2008). In 2004, the redbay ambrosia beetle and one of its fungal symbionts (*R. lauricola*), were implicated in a major die-off of redbay trees (*Persea borbonia* (L.) Spreng.) near Hilton Head, South Carolina (Fraedrich et al. 2008).

In addition to redbay, subsequent pathogenicity tests have indicated that all North American species within the Lauraceae that have been tested to date (11 in total, 5 only in laboratory settings thus far) are susceptible to *R. lauricola* (Kendra et al. 2013; Hughes et al. 2017). These species include swampbay (*Persea palustris*), sassafras (*Sassafras albidum*), avocado (*Persea americana*), northern spicebush (*Lindera benzoin*), the already federally-listed as endangered pondberry (*Lindera melissifolia*), and pondspice (*Lisea aestivalis*), which is a listed threatened species in two states (Fraedrich et al. 2008; Mayfield et al. 2008b; Fraedrich et al. 2011). *Raffaelea lauricola* is transported within the mycangia of female *X. glabratus* to the xylem tissue of host trees (Fraedrich et al. 2008), where as few as 100 conidiospores can induce a systemic hypersensitive host response in redbay, in which tyloses are formed and disrupt vascular tissues (Hughes et al. 2015a). Signs and symptoms of infection are similar to those of other vascular wilt diseases and ambrosia beetle infestations (Fig. 1c–e). Afflicted trees can die within a few weeks of infection (Cameron et al. 2015).

Laurel wilt disease has rapidly spread throughout the southeastern USA, and has been confirmed in nine southeastern states, from North Carolina to Arkansas and Texas (Fig. 2). A single introduction event is likely, given that both the fungus and the beetle are clonal throughout their introduced range in the USA. (Hughes et al. 2017). Considering this single introduction and greater than anticipated rate of spatio-temporal spread (Koch and Smith 2008), human aided domestic movement may be playing a large role in disseminating *X. glabratus*. Given that *R. lauricola* and the facultatively parthenogenic *X. glabratus* are clonal in North America, it is possible that the ecological impacts caused by laurel wilt are the result



**Fig. 1** **a** Adult female redbay ambrosia beetle collected from Jackson county, Mississippi in 2009 (photo credit Joe A. MacGown, Mississippi Entomological Museum, 2017); **b** wilting and discolored foliage on symptomatic redbay in southern Mississippi; **c** ambrosia beetle frass “toothpicks” on infested

redbay stem; **d** conidiophores of *Raffaella lauricola*, causative agent of laurel wilt disease (courtesy of Stephen Fraedrich, USDA Forest Service); and **e** vascular staining are characteristic signs and symptoms of laurel wilt disease

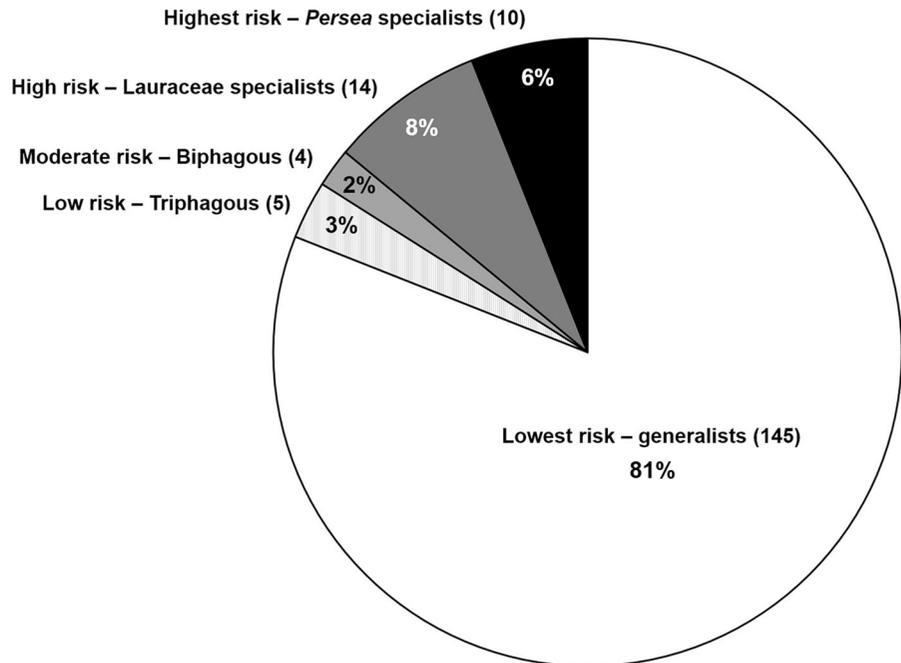
of the introduction of a single founder female beetle and her fungal mélange.

Mortality estimates do not exist for most host species, but more than 300 million redbays, or 1/3 of the pre-introduction population, are estimated to have died (Hughes et al. 2017). Extensive host mortality due to laurel wilt disease will likely not be limited to coastal forest habitats in the southeastern USA, because it is occurring in inland populations of sassafras (Fraedrich et al. 2008, 2015; Smith et al. 2009; Riggins et al. 2011; Bates et al. 2013; Olatinwo et al. 2016). It is uncertain whether laurel wilt will continue to spread north of its current distribution, but

the relatively robust cold tolerance of *X. glabratus* suggests that the vector can survive in more northern latitudes (Formby et al. 2013, 2017).

Several important vertebrate herbivores, including turkey, quail, white-tailed deer, and black bears use redbay and swampbay fruits as an important food source (Coder 2007), however the associations are likely even more specialized and numerous within invertebrate herbivores that depend on members of the Lauraceae. Certain well-known redbay specialist insect herbivores, such as the palamedes swallowtail (*Papilio palamedes* Drury; Lederhouse 1992) have already been speculated to be at risk of population

**Fig. 2** Percentage and number (parentheses) of North American herbivorous arthropod species rated by risk of endangerment from laurel wilt-induced mortality of host plants



decline due to laurel wilt (Chupp and Battaglia 2014). However, no scientific attempts have been made to observe the effects of laurel wilt on *P. palamedes* in the wild, nor have other potentially impacted insect herbivores been catalogued. Even limited to one trophic level, it is likely that many species of organisms will be affected via the mortality of their host plants. Across all trophic levels potentially affected by the one-time introduction of one or a few apparently innocuous female beetle(s) from Asia, the implications are hard to conceptualize.

Our objectives in this study were to: (1) catalog and assess risk for arthropod herbivores of North American host plants impacted by laurel wilt disease, and (2) quantify the impacts of laurel wilt disease on the palamedes swallowtail, a well-known specialist herbivore of redbay trees.

## Methods

### Database of insect herbivores of Lauraceae

Exhaustive searches of literature databases (e.g., AGRICOLA, Web of Science, JSTOR, Google Scholar) were conducted to catalog and record insects associated with members of North American

Lauraceae that are susceptible to laurel wilt. Sources examined included refereed journal articles, books, conference proceedings, extension publications, and reliable internet sources. References inspected during this process are available as Electronic Supplementary Material 2. The eleven host species from the Lauraceae for which insect associates were catalogued included the following: *Persea borbonia* (redbay), *Persea palustris* (swampbay), *Persea borbonia* var. *humulis* (silkbay), *Sassafras albidum* (sassafras), *Lindera melissifolia* (pondberry), *Lindera benzoin* (northern spicebush), *Umbellularia californica* (California laurel), *Litsea aestivalis* (pondspice), *Ocotea coriacea* (lancewood), *Persea americana* (avocado), and the introduced *Cinnamomum camphora* (camphor tree).

We used a two-tiered approach, whereby all literature mentions of arthropods utilizing or being associated with the laurel species of interest were initially recorded, and then each record was vetted (either through expertise or specific literature searches on the natural history of dubious entries) by one or more of the co-authors, who were chosen based on expertise with main insect groups likely to be encountered in the literature (e.g., RLB and ADC for Lepidopterans; JJR, JPF, and HMB for Coleopterans). For example, a report of a primarily predaceous species such as *Cicindela repanda* Dejean (a tiger

beetle) feeding on sassafras fruits (Hill and Knisley 1992), and other such entries, were assumed to be incidental encounters and coded as “dubious” records that were in need of further literature- or expert-based investigation. In most cases, further literature searches on dubious records would clear up any concerns, but if required, another expert in that specific group was contacted to help. Illogical or unlikely reports were discarded by the appropriate expert, and only arthropods that appropriate experts deemed legitimate were retained in the database. The resulting database (Electronic Supplementary Material 1) is not intended as an all-encompassing list: no doubt there are other species that should be included, and possibly some currently included that shouldn't be. However, this is an important first step in the conservation of native arthropods that may be impacted by laurel wilt disease. Additionally, we mostly omitted records for species that only occur south of the USA in Mexico, but a few well-studied agronomically-important insects from Mexico were included in the appendix.

A risk rating of one (highest risk) through five (lowest risk) was assigned to each insect species based on the number of non-lauraceous hosts they use, and degree of specialization to laurel wilt-susceptible host species. The host and geographic ranges, along with basic taxonomic and relevant biological information (such as feeding guild) was recorded for each arthropod species reported in the literature as using a susceptible lauraceous host. A risk rating of one (highest) was assigned to specialists on *P. borbonia* and/or *P. palustris* because of their limited range and high degree of susceptibility to laurel wilt. A risk rating of two (high) was assigned to arthropods reported to feed only on susceptible lauraceous host species. A risk rating of three (moderate) was assigned to arthropods reported to feed on only one non-lauraceous host species in addition to one or more susceptible lauraceous hosts. A risk rating of four (low) was assigned to arthropods reported to feed on two non-lauraceous host species in addition to one or more susceptible lauraceous host. Lastly, a risk rating of five (lowest) was assigned to generalist arthropods, capable of feeding on three or more non-lauraceous host species in addition to one or more susceptible lauraceous hosts. A risk rating of five was also assigned to arthropods that are specialists on non-lauraceous hosts or *C. camphora*. Both lauraceous and non-lauraceous hosts were recorded for each insect

species, along with the number (0, 1, 2, 3, or 3+) of non-lauraceous hosts. Additionally, each insect species was categorized into the following modes of interaction: leaf feeding, wood boring, phloem feeding, fruit and seed feeding, gall forming, and flower feeding.

#### Case study: effects of laurel wilt on palamedes swallowtail abundance

To determine if laurel wilt-induced mortality of redbay has an effect on palamedes swallowtail abundance, three permanent 404 m (1/4 mile) transects were established adjacent to laurel wilt infested and uninfested redbay stands, for a total of 6 transects in Mississippi and 6 in North Carolina. Transects were repeatedly sampled during June, July, and August during each year of the study (2012–2015). All 6 transects were visited in a random order on each sampling day, within a 4 h window. Sampling days were spread out throughout the months of June–August. Stands designated as ‘infested’ had laurel wilt for at least 3 years prior to the first survey year. Uninfested stands were inspected before project start and again each spring, and contained no symptomatic trees.

During data collection events at each transect, *P. palamedes* within 15 m to the front and on each side of the observer were tallied from the outbound walk only (modified from Pollard 1977). Extreme care was taken to not count the same palamedes swallowtail more than once during one transect. It is possible, with some practice, to reliably differentiate *P. palamedes* from other similar swallowtails out to at least 15 m based on color patterns of the dorsal and ventral surfaces of the hind wings. Transects were located along an open area (either a road or utility right-of-way) with adjacent mixed pine-hardwood maritime forests containing redbay. Weather conditions (wind speed, temperature, % cloud cover, and relative humidity) were recorded at the beginning of each transect, and no surveys were conducted on days with more than 70% cloud cover, wind speeds greater than 10 kph, or precipitation.

#### Statistical analyses

Palamedes abundance (butterflies/transect/day) was compared separately within location-year combinations, as well as pooled across locations and years,

using matched pairs analysis and a Wilcoxon Sign-Rank test (for data that did not fit a normal distribution) in JMP 8.0 (© 2008 SAS Institute, Inc.). The Wilcoxon Sign-Rank does not assume normal distribution, and was therefore used to offset the left-skewness of the data (all individual site and location combinations best fit a Gamma-Poisson distribution, as did the data when pooled across years and locations).

## Results

### Database of insect herbivores of Lauraceae

We catalogued 178 native arthropod species (from 7 orders) that are herbivores of North American laurel-wilt susceptible host species. The most commonly represented taxa were Coleoptera (78 species), followed by Lepidoptera (74), Hemiptera (18), Thysanoptera (3), Hymenoptera (2), Trombidiformes (2), and Diptera (1) (Table 1).

Ten species (6%) were included in category 1 (highest risk of endangerment, *Persea* specialists). Of these 10 species, 1 was *Trioza magnoliae* (Ashmead), the red bay psyllid (Hemiptera: Triozidae); 3 are moths (order Lepidoptera) within the Tortricidae (*Cryptaspasma bipenicilla* Brown & Brown, *Cryptaspasma perseana* Gilligan & Brown, and *Riculorampha ancyloides* Rota & Brown); 2 are moths within Gracillariidae (*Phyllocnistis longipalpa* Davis & Wagner, and *Phyllocnistis subpersea* Davis & Wagner); and 4 are weevils within Curculionidae (*Conotrachelus perseae* Barber, *Copturus aguacatae* Kissinger, *Heilipus albopictis* Champion, and *Heilipus lauri* Boheman). Fourteen species (8%) were

category 2 (high risk, monophagous on laurel wilt susceptible hosts), 4 species (2%) were category 3 (moderate risk, biphagous, feeding on one non-susceptible host), 5 species (3%) were category 4 (low risk, triphagous, feeds on 2 other non-susceptible hosts), and 145 species (81%) were category 5 (lowest risk, generalists that can use laurels) (Fig. 2, Electronic Supplementary Material 1).

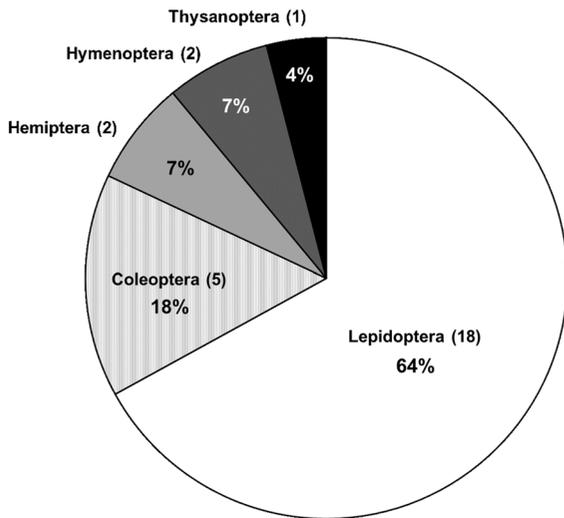
Orders with the highest numbers of moderate to very high risk of endangerment (categories 1–3) were Lepidoptera (18 species), Coleoptera (5), Hemiptera (2), Hymenoptera (2), and Thysanoptera (1) (Fig. 3). Overall, the majority of arthropod species recorded to use laurel wilt-susceptible host plants in North America are leaf feeding or wood boring (Fig. 4). However, among species with moderate to very high endangerment risk, richness was greatest for leaf feeders (18 species), followed by fruit/seed feeders (7), gall formers (2), and wood borers (1) (Fig. 5). High and very high risk of endangerment categories (1 and 2) made up a substantial proportion of catalogued species in Hymenoptera (100%), Thysanoptera (33%), Lepidoptera (19%), and Hemiptera (11%) (Table 1). Despite having the highest overall species richness, coleopteran herbivores of laurels were more likely to be generalists, with only 6% categorized as laurel specialists (risk of endangerment categories 1 and 2).

### Case study: effects of laurel wilt on *Palamedes* swallowtail abundance

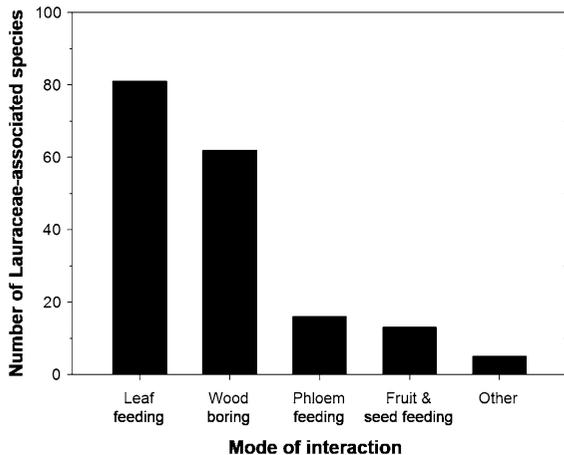
The mean abundance of *P. palamedes* recorded per transect per day in Mississippi (2012–2015) and North Carolina (2013) was significantly greater in uninfested stands than in infested stands at all location-year combinations (Table 2). More specifically, palamedes

**Table 1** Number of arthropod herbivores associated with North American Lauraceae, by Order and risk of endangerment from mortality of host plants due to laurel wilt disease

Order	Endangerment risk category					Total species
	Highest	High	Moderate	Low	Lowest	
Coleoptera	4	1	0	3	70	78
Diptera	0	0	0	0	1	1
Hemiptera	1	1	0	0	16	18
Hymenoptera	0	2	0	0	0	2
Lepidoptera	5	9	4	2	54	74
Thysanoptera	0	1	0	0	2	3
Trombidiformes	0	0	0	0	2	2
Total species	10	14	4	5	145	178

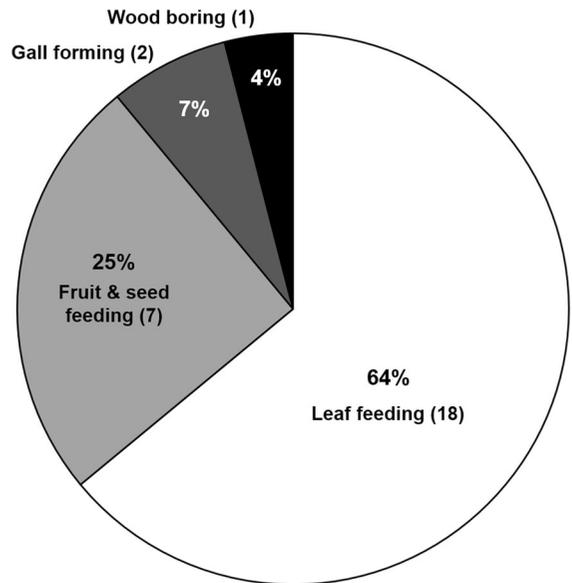


**Fig. 3** Orders of North American herbivorous arthropods at highest to moderate risk (ratings 1–3) because of host plant mortality from laurel wilt disease. Number of species is in parentheses



**Fig. 4** Number of herbivorous arthropod species per mode of interaction with laurel wilt-susceptible Lauraceae in North America. The “Other” category is represented by gall forming (2), and flower feeding (3) species; the number of species in each group is in parentheses

swallowtail abundance in Mississippi (years 2012, 2013, 2014, and 2015) and North Carolina (2013 only) was ca. 7.2, 7.0, 6.3, 8.3, and 3.9 times greater in laurel wilt uninfested forest stands vs. infested stands (respectively). Additionally, the greatest number of palamedes swallowtails encountered during observations of any one transect was 11 butterflies in an



**Fig. 5** Modes of interaction for North American herbivorous arthropod species at highest to moderate risk (categories 1–3) from host plant mortality caused by laurel wilt disease (ratings 1–3). Number of species is in parentheses

uninfested stand versus a maximum of 3 in an infested stand.

Across all four sampling years, palamedes swallowtail abundance in Mississippi was about sevenfold greater in forests not yet impacted by laurel wilt, versus infested stands (Table 2). Pooled together across both States and years (representing 234 transect observations over a four year period and in two different States), palamedes swallowtail encounters on transects adjacent to uninfested stands were significantly more frequent (ca. 5.8-fold) than in infested stands (Table 2).

**Discussion**

Since the introduction of the laurel wilt vector and pathogen into the southeastern U.S. ca. 2002, redbay trees have been rapidly dying (an estimated 300 million redbays killed as of 2017; Hughes et al. 2017), and laurel wilt continues to spread in the eastern USA. Our results quantitatively support early speculation that laurel wilt-induced mortality of redbay and swampbay could heavily impact the abundance and distribution of one of the most common butterflies of the Atlantic and Gulf Coastal Plains, the palamedes

**Table 2** Comparison of mean ( $\pm$  SE) palamedes swallowtail (*Papilio palamedes* Drury) abundance (palamedes/transect/day) on three transects adjacent to laurel wilt infested

stands and three transects adjacent to uninfested forest stands in Mississippi (2012–2015) and North Carolina (2013)

State/year	Infested mean	Uninfested mean	Obs.	Days	<i>p</i>	<i>z</i>	<i>df</i>
MS 2012	0.4 $\pm$ 0.11	2.8 $\pm$ 0.37	33	11	< 0.0001	– 208	32
MS 2013	0.06 $\pm$ 0.04	0.4 $\pm$ 0.10	33	11	0.0032	– 39	32
MS 2014	0.2 $\pm$ 0.08	1.3 $\pm$ 0.30	24	8	0.0006	– 50	23
MS 2015	0.06 $\pm$ 0.06	0.5 $\pm$ 0.02	18	6	0.0313	– 11	17
<i>MS pooled</i>	<i>0.2 <math>\pm</math> 0.04</i>	<i>1.4 <math>\pm</math> 0.17</i>	<i>108</i>	<i>36</i>	<i>&lt; 0.0001</i>	<i>– 946</i>	<i>107</i>
NC 2013	1.6 $\pm$ 0.34	6.1 $\pm$ 0.82	9	3	0.0039	– 23	8
<i>All pooled</i>	<i>0.3 <math>\pm</math> 0.06</i>	<i>1.7 <math>\pm</math> 0.20</i>	<i>117</i>	<i>72</i>	<i>&lt; 0.0001</i>	<i>– 1212</i>	<i>116</i>

Number of observations is per treatment (stand type), and number of days refers to the number of days observations were made

swallowtail. Within 3 years after laurel wilt invasion, encounters with palamedes swallowtails adjacent to infested stands were nearly six times less frequent than adjacent to uninfested stands.

Logically, it follows that the mortality of host plants should affect the populations of herbivores that rely on those hosts. However, it is important to quantify and monitor the cascade of trophic impacts that result from widespread host plant mortality, perhaps especially in uncertain situations like the introduction and spread of new invasive species. Studies such as this quantify the risk of endangerment to native species that results from the impacts of invasive species as they cascade through trophic levels. Additionally, they provide baseline data to inform and evaluate subsequent conservation efforts, should they be needed.

The Palamedes swallowtail is a large, showy, and historically a very commonly encountered native species, and its association with redbay and swampbay was well known prior to laurel wilt (Lederhouse et al. 1992; Scriber et al. 2000). Chupp and Battaglia (2014) clarified this association by determining that palamedes swallowtail larvae are specialist herbivores on redbay/swampbay, and feeding on other potential hosts (e.g., *C. camphora*) within the Lauraceae resulted in significant larval mortality. In addition, oviposition only occurred on redbay/swampbay foliage. Therefore, *P. palamedes* was one of the first species assumed to be at risk after the determination of laurel wilt host range in the southeastern USA. We intentionally chose this species as a case study to illustrate the potential impacts of laurel wilt on arthropod herbivores of affected species of Lauraceae.

However, no exhaustive compilation of other potentially affected organisms had been created prior to this investigation. Review of literature-reported arthropod herbivores of North American Lauraceae yielded another 24 species that specialize on laurel wilt susceptible hosts. While we cannot assume that all 24 of these Lauraceae specialists will experience population reductions similar to *P. palamedes*, they likely share a high-risk of endangerment given their degree of host specialization.

Ecosystem impacts of laurel wilt disease will continue to radiate beyond the species that we report herein, as other trophic levels are impacted. For example, in some areas, *P. palamedes* is the most abundant long-tongued butterfly and primary pollinator of *Platanthera ciliaris*, the orange-fringed orchid (Robertson and Wyatt 1990a, b; Chupp et al. 2015). Laurel wilt-induced declines of *P. palamedes* may therefore reduce fecundity and survival of *P. ciliaris* populations (Chupp et al. 2015). In other cases, vertebrate species will experience changes in food availability as laurel wilt disease results in the decline of Lauraceae fruit crops upon which they feed. In southern Mississippi, five species of overwintering birds were observed consuming large numbers of Lauraceae fruit and even showed preferences for certain species during periods of energetic stress (Chupp and Battaglia 2016). Historical accounts suggest that several other important vertebrate herbivores, including turkey, quail, white-tailed deer, and black bears use redbay and swampbay fruits as an important food source (Coder 2007).

However, literature-based approaches to compiling native arthropod herbivore-host associations and using them to derive endangerment risk has known limitations (Wagner and Todd 2016). Outdated taxonomy, field misidentifications, and transient arthropods resting on non-host plants are just a few of the disadvantages of literature-based methodologies. Like Wagner and Todd (2016), we used a hybrid between literature- and expert-based approaches, although we did not use a crowdsourced network of 80+ experts to verify literature records. The main difference in our approach is that we consulted other experts only when co-author expertise or further literature searches regarding the database record did not resolve the uncertainty.

Given that laurel wilt disease has spread throughout the southeastern USA, and that lateral transfer of the pathogen has occurred to other ambrosia beetles (Carrillo et al. 2014), there is little hope of eradication. Because of the extremely virulent nature of this disease, it may warrant considering conservation efforts, which include collection and storage of at-risk host plant germplasm, especially from rare species or putatively resistant individuals, ongoing reforestation trials using putatively resistant varieties of redbay, and/or use of systemic fungicides to protect high value host tree specimens (Mayfield et al. 2008a; Hughes et al. 2015b). Additionally, systemic fungicide injections of susceptible but uninfected host trees on a slightly larger scale might be used to create refugia for susceptible host plants and their associated herbivores, although the effects of the fungicide propiconazole on herbivores such as palamedes swallowtail and the overall ecosystem following such an endeavor are unknown.

The Lauraceae family is very diverse, and contains more than 2600 species worldwide, however, most of this diversity is clustered primarily in two diversity hotspots; southeast Asia, where the laurel wilt pathogen originated, and Central and South America (Erkens et al. 2007; Nie et al. 2007). Many Lauraceae in the Central and South American tropics are important economically for lumber, and production of ethereal oils, and Mexico is the world's largest avocado producer. Additionally, the diversity of Lauraceous species allows for the possibility of vast ecological ramifications in sub-tropical and tropical forests if many of these species prove susceptible to laurel wilt, and should it continue its invasion through

Texas, into Mexico, and eventually Central and South America.

Recent forest invaders like the emerald ash borer and laurel wilt disease have the potential to cause unprecedented landscape-scale ecological impacts in the southeastern USA. Historically, many other invasive forest insects and pathogens have impacted only one or a few host species, but have done so in a severe manner. This scenario is perhaps most classically illustrated by the introduced chestnut blight fungus (*Cryphonectria parasitica*), which caused the functional extinction of the dominant mast-producing tree of North American eastern hardwood forests (Anagnostakis 1987). Despite the vast ecological and socio-economic damage caused by chestnut blight, only one North American tree species was highly susceptible. Other invasive forest insects and pathogens have historically caused less specific and less severe impacts, as is the case with gypsy moth, which can feed on and stress numerous tree species, but has not resulted in the functional extinction of hosts in its introduced range. Even in the case of an invasion as devastating as the emerald ash borer, the introduced pest is threatening functional extirpation of five North American host tree species in only one genus (*Fraxinus*), and incidentally threatening 44 species of native arthropod herbivores. In the case of laurel wilt, a single introduction event of a clonal forest insect pest and its requisite symbiotic fungal counterpart have spread throughout the southeastern USA (Hughes et al. 2017) and threaten an entire plant family (Lauraceae) comprised of a dozen susceptible host species across 6 genera. This disease could impact 178 species of arthropod herbivores on some level, 24 of which could become highly or very highly imperiled.

In contrast to commercially important trees like ash (*Fraxinus* spp.), only avocado among the North American Lauraceae is commercially valuable, and their arthropod herbivores are understudied as a consequence. Therefore, the number of arthropod herbivores reported here could be undersampled and/or underreported. The fact that 2 of the 10 category 1 species (*Phyllocnistis longipalpa* Davis & Wagner, and *Phyllocnistis subpersea* Davis & Wagner), and 1 of the 14 category 2 species (*Phyllocnistis hyperpersea* Davis & Wagner) were unknown to science until 2011 (Davis and Wagner 2011) is a good case in point. More research is needed regarding the potential ecological and economic impacts of laurel wilt disease,

especially in Mexico, Central America, and South America, where it does not yet occur.

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## References

- Anagnostakis SL (1987) Chestnut blight: the classical problem of an introduced pathogen. *Mycologia* 79:23–37
- 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
- Bellard C, Cassey P, Blackburn TM (2016) Alien species as a driver of recent extinctions. *Biol Lett*. <https://doi.org/10.1098/rsbl.2015.0623>
- Cameron RS, Hanula J, Fraedrich S, Bates C (2015) Progression and impact of laurel wilt disease within redbay and sassafras populations in southeast Georgia. *Southeast Nat* 14:650–674
- Carrillo D, Duncan RE, Ploetz JN, Campbell AF, Ploetz RC, Peña JE (2014) Lateral transfer of a phytopathogenic symbiont among native and exotic ambrosia beetles. *Plant Pathol* 63:54–62
- Chupp AD, Battaglia LL (2014) Potential for host shifting in *Papilio palamedes* following invasion of laurel wilt disease. *Biol Invasions* 16:2639–2651
- Chupp AD, Battaglia LL (2016) Bird-plant interactions and vulnerability to biological invasions. *J Plant Ecol* 9:692–702
- Chupp AD, Battaglia LL, Schaubert EM, Sipes SD (2015) Orchid-pollinator interactions and potential vulnerability to biological invasion. *AOB Plants* 7:plv099
- Coder KD (2007) Taxonomy and identification: redbay (*Persea borbonia*). University of Georgia, Warnell School of Forestry and Natural Resources, Outreach Publication SFNR07-2, 10p
- Davis DR, Wagner DL (2011) Biology and systematics of the New World *Phyllocnistis Zeller leafminers* of the avocado genus *Persea* (Lepidoptera, Gracillariidae). *Zookeys* 97:39–73
- Doherty TS, Glen AS, Nimmo DG, Ritchie EG, Dickman CR (2016) Invasive predators and global biodiversity loss. *Proc Natl Acad Sci* 113:11261–11265
- Erkens RH, Chatrou LW, Maas JW, van der Niet T, Savolainen V (2007) A rapid diversification of rainforest trees (Guateria; Annonaceae) following dispersal from Central into South America. *Mol Phylogenet Evol* 44:399–411
- Formby JP, Krishnan N, Riggins JJ (2013) Supercooling in the redbay ambrosia beetle (Coleoptera: Curculionidae). *Fla Entomol* 96:1530–1540
- Formby JP, Rodgers JC III, Koch FH, Krishnan N, Duerr DA, Riggins JJ (2017) Cold tolerance and invasive potential of the redbay ambrosia beetle (*Xyleborus glabratus*) in the eastern United States. *Biol Invasions*. <https://doi.org/10.1007/s10530-017-1606-y>
- Fraedrich SW, Harrington TC, Rabaglia RJ, Ulyshen MD, Mayfield AE III, Hanula JL, Eickwort JM, Miller DR (2008) A fungal symbiont of the redbay ambrosia beetle causes a lethal wilt in redbay and other Lauraceae in the southeastern United States. *Plant Dis* 92:215–224
- Fraedrich SW, Harrington TC, Bates CA, Johnson J, Reid LS, Best GS, Leininger TD, Hawkins TS (2011) Susceptibility to laurel wilt and disease incidence in two rare plant species, pondberry and pondspice. *Plant Dis* 95:1056–1062
- Fraedrich SW, Johnson CW, Menard RD, Harrington TC, Olatinwo R, Best GS (2015) First report of *Xyleborus glabratus* (Coleoptera: Curculionidae: Scolytinae) and laurel wilt in Louisiana, USA: the disease continues westward on sassafras. *Fla Entomol* 98:1266–1268
- Gandhi KJK, Herms DA (2010) North American arthropods at risk due to widespread *Fraxinus* mortality caused by the alien emerald ash borer. *Biol Invasions* 12:1839–1846
- Gandhi KJK, Smith A, Hartzler DM, Herms DA (2014) Indirect effects of emerald ash borer-induced ash mortality and canopy gap formation on epigeic beetles. *Environ Entomol* 43:546–555
- Harrington TC, Fraedrich SW, Aghayeva DN (2008) *Raffaelea lauricola*, a new ambrosia beetle symbiont and pathogen on the Lauraceae. *Mycotaxon* 104:399–404
- Hill JM, Knisley CB (1992) Frugivory in the tiger beetle, *Cicindela repanda* (Coleoptera: Cicindelidae). *Coleopt Bull* 46:306–310
- Hughes MA, Inch SA, Ploetz RC, Er HL, Bruggen AHC, Smith JA (2015a) Responses of swamp bay, *Persea palustris*, and avocado, *Persea americana*, to various concentrations of the laurel wilt pathogen, *Raffaelea lauricola*. *For Pathol* 45:111–119
- Hughes MA, Smith JA, Ploetz RC, Kendra PE, Mayfield AB, Hanula J, Hulcr J, Stelinski LL, Cameron S, Riggins JJ, Carrillo D, Rabaglia R, Eickwort J (2015b) Recovery plan for laurel wilt on redbay and other forest species caused by *Raffaelea lauricola* and disseminated by *Xyleborus glabratus*. *Plant Health Prog* 16:174–210
- Hughes MA, Riggins JJ, Koch FH, Cognato AI, Anderson C, Formby JP, Dreaden TJ, Ploetz RC, Smith JA (2017) No rest for the laurels: symbiotic invaders cause unprecedented damage to southern USA forests. *Biol Invasions* 19:1–15
- Jenkins CN, Van Houtan KS, Pimm SL, Sexton JO (2015) US protected lands mismatch biodiversity priorities. *Proc Natl Acad Sci* 112:5081–5086
- Jennings DE, Duan JJ, Bean D, Rice KA, Williams GL, Bell SK, Shurtleff AS, Shrewsbury PM (2017) Effects of the emerald ash borer invasion on the community composition

- of arthropods associated with ash tree boles in Maryland, USA. *Agric For Entomol* 19:122–129
- Kendra PE, Montgomery WS, Niogret J, Epsky ND (2013) An uncertain future for American Lauraceae: a lethal threat from redbay 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: Curculionidae: Scolytinae) invasion in eastern US forests. *Environ Entomol* 37:442–452
- Lederhouse RC, Ayres MP, Nitao JK, Scribner JM (1992) Differential use of lauraceous hosts by swallowtail butterflies, *Papilio troilus* and *P. palamedes* (Papilionidae). *Oikos* 63:244–252
- Lovett GM, Canham CD, Arthur MA, Weathers KC, Fitzhugh RD (2006) Forest ecosystem responses to exotic pests and pathogens in eastern North America. *Bioscience* 56:395–405
- Mayfield AE III, Barnard EL, Smith JA, Bernick SC, Eickwort JM, Dreaden TJ (2008a) Effect of propiconazole on laurel wilt disease development in redbay trees and on the pathogen in vitro. *Arboric Urban For* 34:317–324
- Mayfield AE III, Peña JE, Crane JH, Smith JA, Branch CL, Ottoson ED, Hughes M (2008b) Ability of the redbay ambrosia beetle (Coleoptera: Curculionidae: Scolytinae) to bore into young avocado (Lauraceae) plants and transmit the laurel wilt pathogen (*Raffaelea* sp.). *Fla Entomol* 91:485–487
- Nie ZL, Wen J, Sun H (2007) Phylogeny and biogeography of *Sassafras* (Lauraceae) disjunct between eastern Asia and eastern North America. *Plant Sys Evol* 267:191–203
- Olatinwo R, Barton C, Fraedrich SW, Johnson W, Hwang J (2016) First report of laurel wilt, caused by *Raffaelea lauricola*, on sassafras (*Sassafras albidum*) in Arkansas. *Plant Dis* 100:2231
- Opler PA (1978) Insects of American chestnut: possible importance and conservation concern. In: McDonald J (ed) *The American chestnut symposium*. West Virginia University Press, Morgantown
- Pimm SL, Russell GJ, Gittleman JL, Brooks TM (1995) The future of biodiversity. *Science* 269:347–350
- Pollard E (1977) A method for assessing changes in the abundance of butterflies. *Biol Conserv* 12:115–134
- 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
- Riggins JJ, Fraedrich S, Harrington T (2011) First report of laurel wilt caused by *Raffaelea lauricola* on Sassafras in Mississippi. *Plant Dis* 95:1479
- Robertson JL, Wyatt R (1990a) Evidence for pollination ecotypes in the yellow-fringed orchid, *Platanthera ciliaris*. *Evolution* 44:121–133
- Robertson JL, Wyatt R (1990b) Reproductive biology of the yellow-fringed orchid, *Platanthera ciliaris*. *Am J Bot* 77:388–398
- Sala OE, Chapin FS III, Armesto JJ, Berlow E, Bloomfield J, Dirzo R, Huber-Sanwald E, Huenneke LF, Jackson RB, Kinzig A, Leemans R, Lodge DM, Mooney HA, Oesterheld M, Poff NL, Sykes MT, Walker BH, Walker M, Wall DH (2000) Global biodiversity scenarios for the year 2100. *Science* 287:1770–1774
- Scriber JM, Margraf N, Wells T (2000) Suitability of four families of Florida” bay” species for *Papilio palamedes* and *P. glaucus* (Papilionidae). *J Lepid Soc* 54:131–136
- Smith JA, Dreaden TJ, Mayfield AE III, Boone A, Fraedrich SW, Bates C (2009) First report of laurel wilt disease caused by *Raffaelea lauricola* on Sassafras in Florida and South Carolina. *Plant Dis* 93:1079
- Ulyshen MD, Klooster WS, Barrington WT, Herms DA (2011) Impacts of emerald ash borer-induced tree mortality on leaf litter arthropods and exotic earthworms. *Pedobiologia* 54:261–265
- Vitousek PM (1994) Beyond global warming: ecology and global change. *Ecology* 75:1861–1876
- Vitousek PM, Mooney HA, Lubchenco J, Melillo JM (1997) Human domination of earth’s ecosystems. *Science* 277:94–499
- Wagner DL, Todd KJ (2016) New ecological assessment for the emerald ash borer: a cautionary tale about unvetted host-plant literature. *Am Entomol* 62:26–35