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Review

Laurel Wilt: Current and Potential Impacts and Possibilities for Prevention and Management

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Abstract: In recent years, outbreaks of nonnative invasive insects and pathogens have caused significant levels of tree mortality and disturbance in various forest ecosystems throughout the United States. Laurel wilt, caused by the pathogen *Raffaelea lauricola* (T.C. Harr., Fraedrich and Aghayeva) and the primary vector, the redbay ambrosia beetle (*Xyleborus glabratus* Eichhoff), is a nonnative pest-disease complex first reported in the southeastern United States in 2002. Since then, it has spread across eleven southeastern states to date, killing hundreds of millions of trees in the plant family Lauraceae. Here, we examine the impacts of laurel wilt on selected vulnerable Lauraceae in the United States and discuss management methods for limiting geographic expansion and reducing impact. Although about 13 species belonging to the Lauraceae are indigenous to the United States, the highly susceptible members of the family to laurel wilt are the large tree species including redbay (*Persea borbonia* (L.) Spreng) and sassafras (*Sassafras albidum* (Nutt.) Nees), with a significant economic impact on the commercial production of avocado (*Persea americana* Mill.), an important species native to Central America grown in the United States. Preventing new introductions and mitigating the impact of previously introduced nonnative species are critically important to decelerate losses of forest habitat, genetic diversity, and overall ecosystem value.

Keywords: disease; pathogen; insect; invasive; nonnative

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1. Introduction

Hundreds of nonnative insects and plant pathogens have become established in North American forests since the mid-nineteenth century [1]. In the United States (US), substantial levels of tree mortality and associated forest disturbance have been caused by exotic species including the emerald ash borer (*Agrilus planipennis* Fairmaire), European gypsy moth (*Lymantria dispar* Linnaeus), hemlock woolly adelgid (*Adelges tsugae* Annand), the chestnut blight fungus (*Cryphonectria parasitica* (Murr.) Barr.), and the Dutch elm disease pathogens (*Ophiostoma ulmi* (Buisman) Nannf. and *Ophiostoma novo-ulmi* Brasier) [2]. The establishment of many nonnative species is an unintended consequence of the expanding volume of global trade and the subsequent increases in the propagule pressure of exotic, potentially invasive species [3]. However, the size and scope of outbreaks are regulated by numerous biotic and abiotic factors, including climatic conditions and weather patterns, genetic variability, host diversity, and human activities. These factors can have direct or indirect effects on insect physiology, regulating developmental thresholds, the rate of multiple life stages (generations), adult longevity, adult emergence, and insect flight [4]. Similarly, these same factors are also equally critical to the establishment, development, and spread of diseases caused by introduced pathogens [5].

The deliberate or accidental introduction and establishment of a nonnative species into a new habitat can be characterized as a series of stages, including the arrival and colonization (introduction), dispersal and limited spread (establishment), attaining a pervasive and growing population (invasion proliferation), and attaining a widespread and stable population (invasion impact) [6]. The ecological impacts, potential management options, and mitigation costs can vary greatly with the different stages of a pest outbreak, and policies and responsibilities may shift accordingly among federal and state governments, local municipalities, and landowners as the outbreak progresses [3,7–9]. As an invasion progresses, the likelihood of eradication or effective control decreases, and the level of impact on the ecosystem, costs associated with management, and potential environmental risks increase [8,10,11] (Figure 1).

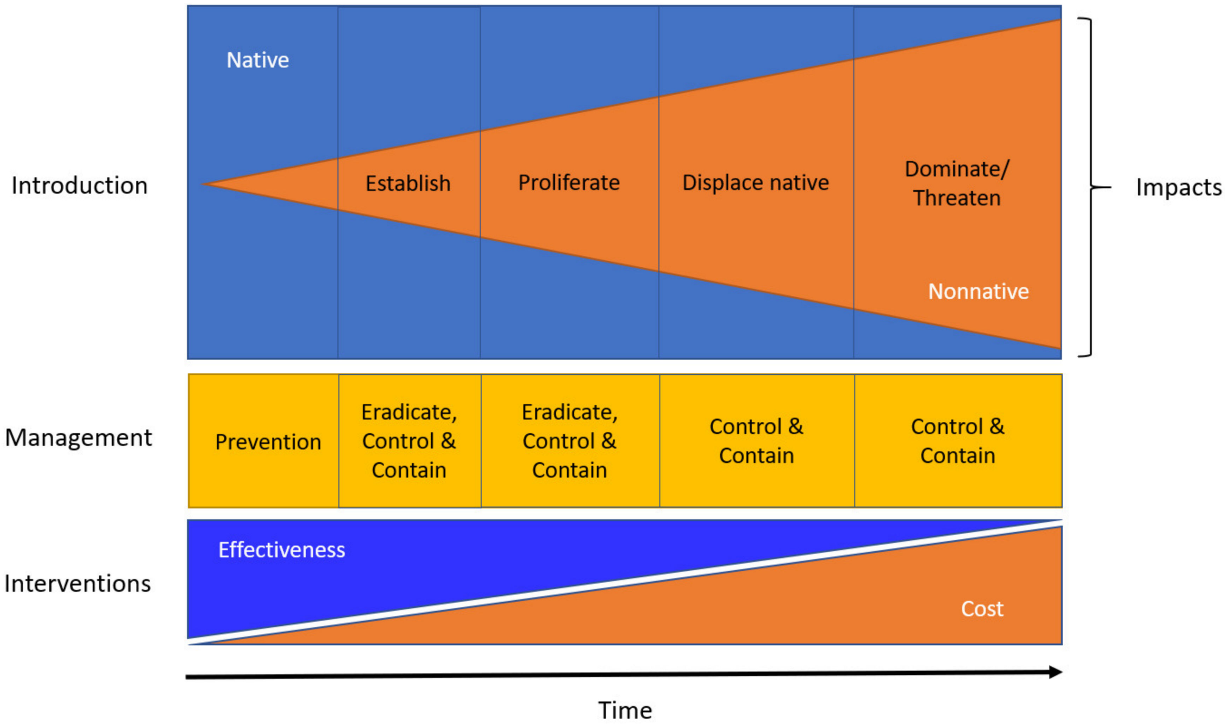

Figure 1. Management and cost/benefit of interventions as an invasive species impacts a new ecosystem starting with species introduction.

One of the most recent forest disease epidemics to occur in the US is laurel wilt, a disease that affects members of the plant family Lauraceae that are native to North America. Laurel wilt is similar to Dutch elm disease in that it is a systemic, vascular wilt caused by an ophiostomatoid fungal pathogen associated with a beetle vector. The disease has caused substantial losses of redbay (*Persea borbonia* (L.) Spreng) [12] and sassafras (*Sassafras albidum* (Nutt.) Nees) [13] trees throughout the southeastern US and impacted production of avocado (*Persea americana* Mill.) in Florida [14]. Although currently limited to the southeastern US, laurel wilt represents a potential threat to lauraceous species in other regions of the US as well as other areas of the world.

Laurel wilt is caused by *Raffaelea lauricola* T.C. Harr., Fraedrich and Aghayeva, a fungal symbiont of the redbay ambrosia beetle (*Xyleborus glabratus* Eichhoff). *Xyleborus glabratus* was first detected in a survey trap at Port Wentworth, Georgia in 2002 [15], and over the next few years, *X. glabratus* and *R. lauricola* were associated with dead and dying redbay and sassafras trees in coastal areas of Georgia, South Carolina, and Florida [12]. The disease has since spread across eleven southeastern states, affecting trees in more than 100 counties and parishes in an area that ranges from North Carolina, south through Florida, west to eastern Texas and as far northward as Kentucky (Figure 2). Coastal forests with hundreds of redbay trees per acre and a warm, humid climate have been an optimal habitat for rapid buildup of *X. glabratus* populations and tree mortality [16].

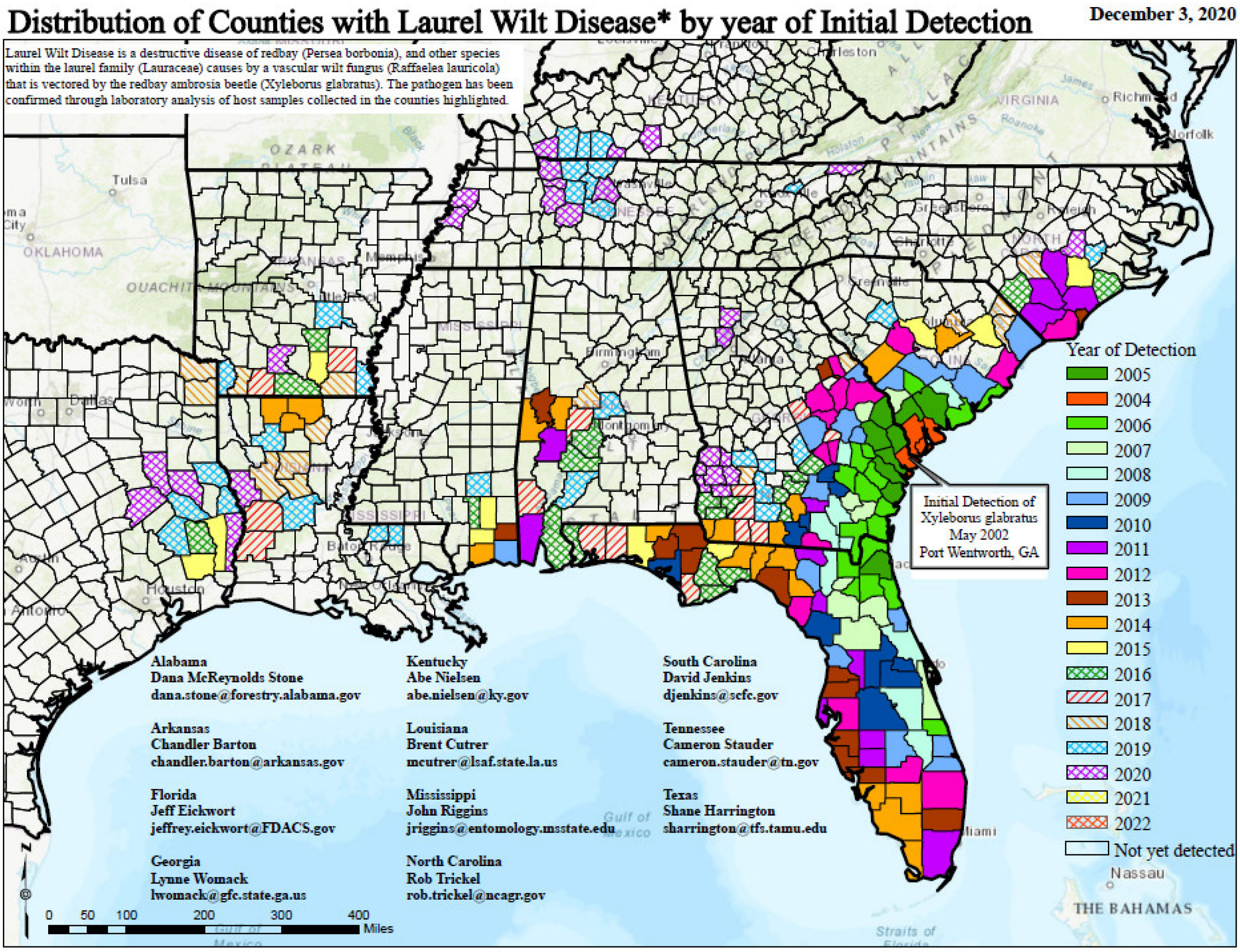

Figure 2. Distribution of counties with laurel wilt by year of initial detection updated 3 December 2020. (Available online: https://www.fs.usda.gov/main/r8/forest-grasslandhealth accessed on 29 January 2021).

Symptoms of laurel wilt include black discoloration of sapwood that typically begins as isolated streaks and later develops extensively throughout host xylem tissues (Figure 3). In redbay, infection subsequently results in wilting of branch tips and leaves, dieback of individual branches, and reddish to purplish brown coloration of dying leaves that may persist on trees for over a year after death [12]. Death of trees occurs within a few weeks to several months following infection.

In this article, we discuss the effects of laurel wilt on susceptible hosts, natural ecosystems and economic impacts in the southeastern US and efforts that have been made to learn about the vector and pathogen and their control. Information is synthesized from various studies that examine the impacts of the disease on forest ecosystems in the southeastern US and the potential impacts of this beetle and pathogen on other lauraceous species and ecosystems worldwide.

Figure 3. (**a**) An infected sassafras tree showing dead branches with symptoms of laurel wilt; (**b**) black streaks of xylem discoloration typical of laurel wilt on the infected tree; (**c**) a female redbay ambrosia beetle *Xyleborus glabratus* extracted from the bark of an infested sassafras tree; (**d**) an isolate of *Raffaelea lauricola* from an infected swampbay tree; and (**e**) microscopic oblong and ovoid conidia of *R. lauricola* observed under the microscope.

Xyleborus glabratus and Its Fungal Associates

Xyleborus glabratus and *R. lauricola* originated in Southeast Asia [17–19], and at this time, the beetle and its fungal symbiont are known to occur only in countries of Southeast Asia (e.g., India, China, Vietnam, Japan, Taiwan, and others) and the southeastern USA. In Asia, *X. glabratus* is primarily associated with members of the Lauraceae, although it has also been reported from members of other families such as the Dipterocarpaceae, Fagaceae, Theacae, Pinaceae, and Fabaceae [15,19–22]. In North America, *X. glabratus* has, thus far, only been associated with species in the Lauraceae.

In many ways, *X. glabratus* is different from many ambrosia beetles in that it tends to attack healthy trees and is not strongly attracted to ethanol. Many ambrosia beetles are attracted to ethanol [23], a chemical which is produced by plants under stress, but early attempts in the US to trap *X. glabratus* using ethanol lures were largely ineffective [24]. Instead, *X. glabratus* is attracted to host volatiles such as α-copaene and calamenene that are normally found in redbay and other members of the Lauraceae [25]. Essential oils such as phoebe oil, extracted from *Ocotea porosa* (Nees and Martius) Barroso, and cubeb oil from *Piper cubeba* Linn., have high levels of α-copaene and have proved to be effective for attracting and trapping *X. glabratus* [25], [26]. Kendra et al. [27] demonstrated that a lure enriched to contain 50% (-)-α-copaene was more attractive than cubeb oil and copaiba oil lures.

In addition to olfactory cues, *X. glabratus* also uses visual information to find suitable hosts for colonization and reproduction [28]. Although laurel wilt and attacks by *X. glabratus* are observed on stems of smaller diameter [12,16,29], the beetle is primarily attracted to stems of larger diameter, and the probability of attack by the beetle decreases with decreasing stem diameter [28].

The redbay ambrosia beetle adult female carries spores of *R. lauricola* in mycangia located in the head region behind the mandibles [12,30] and transmits the pathogen as it bores into the xylem of healthy trees. In addition to *R. lauricola*, at least nine other *Raffaelea* spp are known to be carried by *X. glabratus*, although *R. lauricola* is the dominant species and is present in most beetles [19,31–33]. *Raffaelea lauricola* is the only known pathogen among the fungal symbionts carried by *X. glabratus* [34], and the reasons why the beetle carries numerous *Raffaelea* spp. and the possible role of each in the biology of the beetle are not clear.

Most ambrosia beetles tend to colonize stressed, weakened, dying, and dead trees [35], and it remains uncertain why *X. glabratus* initiates attacks on healthy trees. Nonetheless, these attacks inoculate trees with *R. lauricola*, and laurel wilt develops within weeks following infection. Once in the xylem, the conidia of *R. lauricola* move passively in the xylem (and presumably germinate), and the host subsequently responds by producing gum and tyloses to restrict fungal movement. These host reactions are inadequate to prevent the movement of the fungus but restrict water transport, ultimately causing trees to wilt [36,37]. As trees succumb to the disease and die, they are attacked in larger numbers by *X. glabratus* females, which establish galleries in the xylem and produce brood. Redbay ambrosia beetle females can reproduce via partial parthenogenesis; unmated females lay haploid eggs that develop into males. However, it is important to note that females most likely emerge from their brood tree already mated, by mating with siblings or progeny, and this allows emerging females the ability to quickly establish new infestations. Therefore, a single female can initiate a new population wherever suitable host material is available.

Populations of the redbay ambrosia beetle increase very rapidly in coastal forests of the southeastern US, where redbays are common and of sufficient size to serve as brood (Figure 4; [38]). Likewise, populations decrease rapidly within a couple of years after tree death, because as trees are colonized by secondary fungi and begin to decay, they become increasingly unusable by the beetle. Nonetheless, the redbay ambrosia beetle can persist at low population levels for many years following laurel wilt epidemics, despite the lack of large-diameter trees [38]. It is believed that some beetles are able to colonize and reproduce in smaller diameter redbay trees, although this does not appear to be common based on the widespread survival of small diameter seedlings, saplings, and small-diameter trees on sites affected by laurel wilt [12,16,39].

The widespread mortality of redbay and other lauraceous spp. in the US is thought to be due to a single introduction of *R. lauricola* and presumably *X. glabratus*. Although the redbay ambrosia beetle and *R. lauricola* have been reported on diverse host species in the family Lauraceae in the southeastern US, the population of *R. lauricola* is mostly genetically uniform and comprised of a single mating type, thus supporting the single introduction hypothesis [40,41]. An introduction of a second mating type into the US could result in genetic recombination and genetic variation in *R. lauricola*, which may lead to a more aggressive pathogen or one that could become adapted to a wider range of environmental conditions killing redbay and sassafras faster or could be more aggressive on a wider variety of avocado cultivars where some resistance may exist.

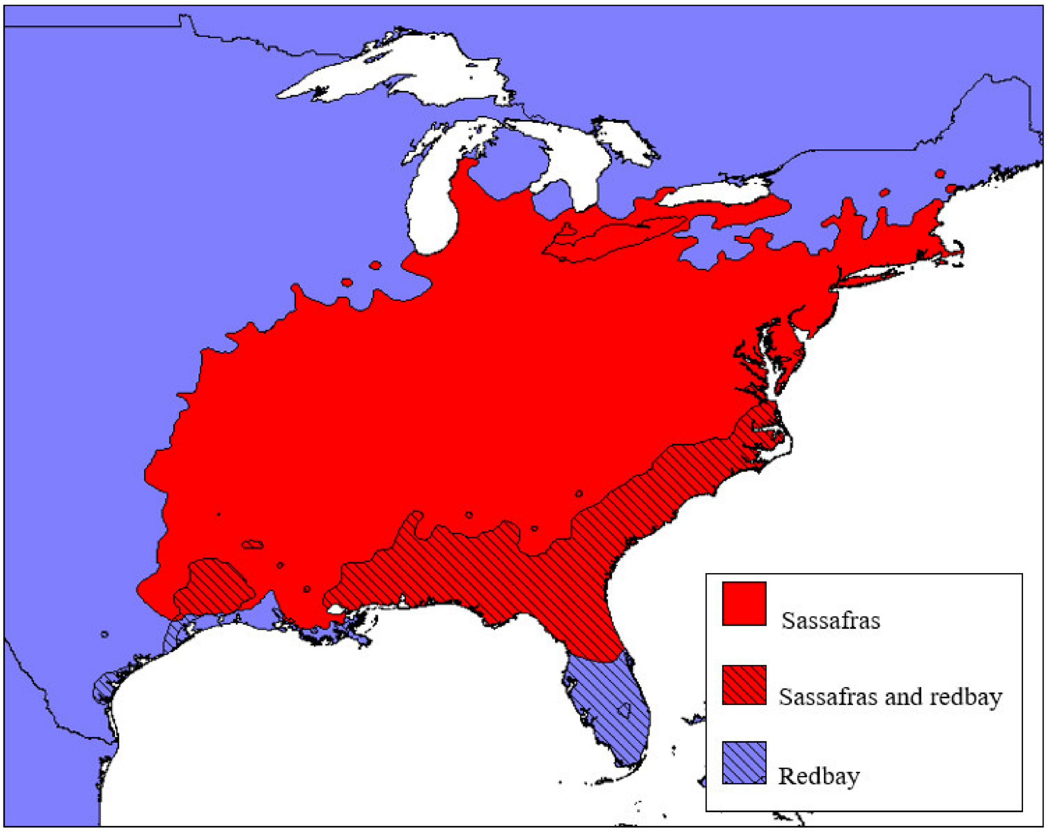

Figure 4. The geographic distribution maps of redbay (*Persea borbonia*) and sassafras (*Sassafras albidum*) in the United States, including possible overlaps between the two species.

2. Host Species Susceptibility

Members of the Lauraceae are primarily woody trees and shrubs that are found in tropical and subtropical regions of the world. The family contains between 2500 and 3000 species in approximately 50 genera [42]. The greatest concentrations and diversity of lauraceous species are in Southeast Asia and Central and South America. At this time, laurel wilt is only known to the southeastern portion of the US and only affects species belonging to the plant family Lauraceae that are indigenous to North America, as well as several species that originated in other parts of the world and have been planted for landscape use or commercial production in the US.

2.1. Impacts on Species in the United States

There are approximately 13 species representing eight genera in the Lauraceae that are native to the United States, but this number can vary with different taxonomic evaluations that have been conducted and reported [43,44]. With a few exceptions, members of the Lauraceae indigenous to the US are highly susceptible to laurel wilt: however, the species that have been most impacted by the disease are the larger tree species such as redbay and sassafras. In addition, avocado, which is native to Central America but cultivated in the US as a food crop, has also been affected by the disease, and some areas where this species is grown have been economically impacted.

2.1.1. Redbay (*Persea borbonia*)

A small to medium-sized understory tree growing up to 70 ft in height, redbay is found throughout the Atlantic and Gulf Coastal Plain of the southeastern US [45,46] (Figure 4).

The species is often retained or planted as a shade tree in residential neighborhoods, parks, and recreational areas. Redbay does not have high economic value in the forest products sector, although its wood materials have been used for trim in boats and cabinet construction [47] and is valued by woodturners. However, the species does have important biological, cultural, and aesthetic value. Within forest ecosystems, redbay is known for producing berry-like drupes that serve as a food source for various animals including songbirds, wild turkeys, quail, rodents, deer, and black bear [45,47]. Redbay foliage also serves as the primary food source for larvae of the Palamedes swallowtail butterfly (*Papilio palamedes* Drury) [48], the primary pollinator of yellow-fringed orchid [49]. Furthermore, redbays have provided cultural uses ranging from flavorings for teas and gumbos to medicinal uses by Native Americans [47].

The losses to populations of mature redbay trees caused by laurel wilt have been rapid and dramatic. In northern Florida, mortality increased during a 15-month period from just 10% to 92% in trees with diameters at breast height (dbh) of 10 cm or greater; however, the impact on redbay seedlings was minimal [12]. Similarly, Shields et al. [50] found that laurel wilt killed virtually all redbay trees over 10 cm dbh over a two-year period, but only 30% of saplings and 2% of seedlings died from the disease. In Georgia, the incidence of laurel wilt in redbay trees larger than 3 cm dbh was extremely high, with mortality rates ranging from 75% to 97% in different areas [51]. Thus, redbay continues to survive as an understory plant throughout much of the southeastern US, although most of these trees are under 10 cm in diameter and the species no longer functions as a canopy tree in forest ecosystems.

Two other taxa, swampbay (*Persea borbonia* var. *pubescens* or *Persea palustris* (Raf.) Sarg.) and silkbay (*Persea borbonia* var. *humilis* or *Persea humilis* Nash), are closely related and similar in appearance to *P. borbonia*, and frequently, the three taxa have been considered to be "redbays" in the broad sense [43,45,52,53]. All "redbays" appear to be highly susceptible to laurel wilt in controlled inoculation studies [12,54,55], and in the field, widespread mortality from laurel wilt has been observed in swampbay populations [56,57]. However, silkbay is thought to be restricted to the sandhills areas of central Florida and has not been as affected by the wilt as have other native *Persea* taxa [58]. One reason for this may be the overall smaller average diameter of silkbay compared to other *Persea* taxa and therefore it is less attractive to *X. glabratus* and less likely to be attacked by the beetle, which tends to preferentially attack larger diameter hosts [12,28,58].

2.1.2. *Sassafras albidum*

An ecologically important tree species, sassafras serves as a browse plant for wildlife such as deer, which use twigs as a food source in winter, while they use leaves and succulent growth during spring and summer. Sassafras has local economic importance in some areas of the US. The wood of sassafras is durable and attractive and used for paneling and millwork [59]. Griggs [60] described sassafras wood as brittle, light, and soft with limited commercial value; however, the wood is durable for making buckets, cabinets, cooperage, fenceposts, furniture, interior finish, and rails [60–62] and is rated as good for firewood [63]. Sassafras is widely distributed throughout the eastern US [46,60], often found on abandoned fields, dry ridges, and upper slopes as pioneer species following fire [60] (Figure 4).

There are approximately 1.9 billion live sassafras trees and saplings across 28 states, 53 ecoregion sections, and 69 forest types in the eastern US [64]. The species is also valued as an ornamental landscape tree [65]. As of 2013–2014, fewer than 2% of sassafras trees $\geq$2.5 cm (dbh) occurred in counties with laurel wilt, and an additional 2.8% occurred in neighboring counties [64]. However, the distribution of laurel wilt on sassafras has expanded in recent years [13,66–68], including many "jumps" in the disease distribution to disjunct areas where sassafras occurs in isolation from other hosts such as redbay. Therefore, landowners and forest managers within the range of sassafras may expect changes in local forest composition if the laurel wilt becomes established [64]. The laurel wilt pathogen is believed to spread readily from tree to tree through roots once established in a stand due to the clonal nature of sassafras and possibility of root grafts [69,70].

Even though sassafras occurs in isolated populations and is not as common as redbay in the southeastern Coastal Plain, laurel wilt's impacts on sassafras populations appear similar to those observed in redbay populations [70]. In areas where sassafras was locally common, laurel wilt killed approximately 80% of the trees, compared to 87% losses in redbay populations, and for both species, the larger diameter trees were most susceptible to the disease [70]. As in redbay populations, larger-diameter sassafras trees are disproportionally affected compared to smaller diameter class, presumably because they have a lower probability of attack by the beetle. In a recent targeted search for surviving sassafras trees in areas of coastal Georgia where laurel wilt has been present for ten years or more, sassafras stems > 4 cm dbh were extremely rare (Mayfield, personal observation).

2.1.3. Avocado (*Persea americana*)

A tropical, evergreen tree that is cultivated worldwide for fruit production, avocado is native to Central America and the Caribbean and is comprised of three distinct races (i.e., Guatemalan, Mexican, and West Indian) from which various cultivars have been produced [71,72]. In the US, about 10% of the avocado production is located in southernmost Florida and most of the remaining production is in southern California. Avocado orchards have been affected by laurel wilt in southern Florida as well as avocado trees planted in residential areas throughout the state. The impact of the disease on avocado, however, has not been as devastating as it has been on redbay. Although avocados can be highly susceptible to laurel wilt, there appears to be considerable variation in susceptibility between the various cultivars. For instance, West Indian cultivars such as the "Simmonds", which makes up about 35% of the south Florida commercial production, are among the most susceptible to the disease [73]. Conversely, the "Hass" cultivar, which is a Guatemalan × Mexican hybrid, is among the most resistant and comprises 95% of the California production [72,74,75]. Furthermore, *X. glabratus* does not appear to be an important vector for the disease in avocado orchards in south Florida. Although *X. glabratus* is somewhat attracted to avocado stems and can infect avocado with *R. lauricola* [71,76–78]; avocado is a poor reproductive host for *X. glabratus*, and the beetle is rarely trapped within avocado orchards [75,79]. Raffaelea lauricola has been associated with other Xyleborus spp. such as Xyleborus bispinatus Eichhoff, Xyleborus ferrugineus Fabricius, and Xyleborus volvulus Fabricius and these beetle species are suspected of serving as vectors for the pathogens [75,80]. Once laurel wilt is established in an orchard, *R. lauricola* can spread readily among trees through root grafts [74,75], creating disease foci that can have a serious economic impact on orchards if the disease is not managed.

2.2. Other Lauraceous Species in the USA

Many other lauraceous species native to the US are susceptible to laurel wilt but have not yet been severely impacted by the disease. Pondspice (*Litsea aestivalis* (L.) Fern) occurs as a shrub or small tree in isolated pockets in coastal areas of the southeastern US and is considered a species of concern by the US Fish and Wildlife Service [81]. Although laurel wilt has been found in pondspice in several states, the impact to this species does not appear to be severe, perhaps due to the relatively small diameter of the stems (making them less visually attractive to *X. glabratus*) and the very dispersed nature of the populations [29,82,83].

Three species of *Lindera* are native to eastern North America. Pondberry (*Lindera melissifolia* (Walt.) Blume) is federally listed as endangered in the southeastern US [84]. It is highly susceptible to the laurel wilt pathogen [29], but the disease appears to be rare in pondberry, presumably because of its small size; diameters rarely exceed 1.5 cm in this shrub species [85]. Spicebush (*Lindera benzoin* (L.) Blume) is a common understory shrub throughout the eastern US and into southern Canada and can reach several meters in height in the absence of disturbance [86]. Spicebush is susceptible to the laurel wilt pathogen [12], and the disease has been observed naturally in this species in a botanical garden adjacent to a forest containing infested redbay trees [87]. Compared to other North American Lauraceae, however, spicebush stems have lower quantities of α-copaene, the primary host volatile attractant of the redbay ambrosia beetle [88]. Consistent with this finding, redbay ambrosia beetles are not strongly attracted to spicebush wood and are less likely to bore into them compared to wood of other lauraceous hosts [88,89]. For these reasons, laurel wilt's impacts on spicebush may be limited, although plants might still be vulnerable to the disease in areas where populations of the redbay ambrosia beetle are able to proliferate in nearby hosts like sassafras or redbay. Laurel wilt has not yet been reported in bog spicebush (*Lindera subcoriacea* B.E. Wofford), a rare shrub species inhabiting wet, acidic sites in the southeastern Gulf and Atlantic Coastal Plain and adjacent Piedmont [86].

Two species, pepperleaf sweetwood (*Licaria trianda* (Sw.) Kosterm.) and lancewood (*Ocotea coriacea* (Sw.) Britton) are found in the tropical areas of southern Florida, and neither species appears to be highly susceptible to laurel wilt in pathogenicity tests, nor affected by the disease in their natural ranges. Pepperleaf sweetwood is a rare, evergreen tree that is considered endangered in Florida [90]. In controlled, greenhouse evaluations, xylem discoloration as well as leaf chlorosis and abscission were observed following inoculation with *R. lauricola*, but seedlings failed to die from the disease [91]. Similarly, lancewood is a small, evergreen tree that is found in scattered locations in south and central Florida. The disease has not been reported naturally in this species, and inoculations of potted plants with *R. lauricola* resulted only in light discoloration in the xylem and dieback in only a small percentage of plants (Fraedrich, unpublished). Another species, love-vine (*Cassytha filiformis* L.), is an herbaceous vine native to tropical areas of Florida and is not likely to be attacked by *X. glabratus* and therefore not expected to be affected by the disease.

California laurel (*Umbellularia californica* (Hook and Arn.) Nutt.) is the only member of the Lauraceae that is native to the western US. This species is found in coastal forests of California and Oregon, as well as the interior forests of the Sierra Nevada in California [92]. Pathogenicity tests on California laurel seedlings have found that this species is susceptible to laurel wilt [93]. Furthermore, bolts from California laurel trees are suitable brood material for *X. glabratus* [89] and are as attractive to flying *X. glabratus* as sassafras, a known brood host in the eastern US. Thus, it is reasonable to conclude that laurel wilt poses a considerable threat to California laurel in western US forests, and *X. glabratus* and *R. lauricola* should be introduced to this region.

2.3. Potential Impacts on Lauraceae Outside of the US

Over 750 lauraceous species in 26 genera are indigenous to Central and South America, and there are approximately 80 neotropical *Persea* spp. that occur throughout the region [94], but with the exception of avocado, little is known about their susceptibility to laurel wilt. This region of the world contains numerous lauraceous species that are commercially important including Greenheart (*Chlorocardium rodiei* (R.H.Schomb.) Rohwer, H.G.Richt. and van der Werff) and Lingue (*Persea lingue* Lingue, Litchi) [95], which are harvested for timber, and others such as Rosewood (*Aniba rosaeodora* Ducke) [96] and Ishpink (*Ocotea quixos* (Lam.) Kosterm.), which are valued for their essential oils.

Members of the Lauraceae are also abundant, highly diversified, and widely distributed throughout tropical and subtropical areas of southern and southeast Asia. Numerous species and genera are native to countries throughout these regions, with China alone having over 440 species in 25 genera (http://www.efloras.org/florataxon.aspx?flora_id=2&taxon_id=10479). The region contains many valuable species such as *Cinnamomum zeylanicum* Blume and *Cinnamomum cassia* Blume, which are sources of a spice (cinnamon) and numerous essential oils [97], and ironwood (*Eusideroxylon zwageri* Teijsm and Binn), an important timber species in parts of Asia [98]. Laurel wilt has not been reported in Asia among lauraceous species, and because species in Asia have coevolved with *X. glabratus* and *R. lauricola*, they are generally thought to be resistant [17,99]. Controlled inoculations and observations of Asian Lauraceae including camphortree (*Cinnamomum camphora* (L.) J. Presl.), a lauraceous tree species native to Asia that has been cultivated and has subsequently become naturalized in areas of the southeastern US, lends support to the hypothesis of natural resistance in Asian Lauraceae. Camphortree has been largely unaffected by laurel wilt in the southeastern US, and the species has continued to thrive in the same forests where redbay trees have been decimated by the disease and high populations of *X. glabratus* have occurred [13]. Furthermore, controlled inoculation studies on camphortree and other Asian species such as *Cinnamomum jensenianum* Hand.-Mazz. and *Cinnamomum osmophloeum* Kaneh. have confirmed their resistance to the disease [13,99].

In comparison to South America and Asia, the members of the Lauraceae are more modestly represented among the flora of Australia and Africa [98,100]. In Australia, there are approximately 125 native lauraceous species represented in eight genera, including *Beilschmiedia*, *Cryptocarya*, *Lindera*, and *Litsea*. However, many of the genera consist primarily of tree species, many of which are valued for their timber. The Lauraceae are thought to be poorly represented on mainland Africa, although Madagascar is considered to be relatively rich in species with about as many species occurring on this island as occur on the African continent [98,101]. Approximately 135 lauraceous species occur in Madagascar in six genera that include *Ocotea, Beilschmiedia*, and *Cryptocarya* [101]. Species in some of the same genera also occur on mainland Africa and include some important commercial and cultural species such as black stinkwood (*Ocotea bullata* (Burch.) Baill.), which is prized for its high valued wood that is used for furniture and paneling [98] and for its medicinal properties [102]. Currently, no information is available on the potential susceptibility to laurel wilt of lauraceous species that are indigenous to Africa and Australia or utilization of species on these continents for brood production by *X. glabratus*.

In mainland Europe, bay laurel (*Laurus nobilis* L.), a small aromatic tree or shrub, is the only native lauraceous species, and its distribution is primarily restricted to the Mediterranean regions [103,104]. Bay laurel is planted in the US as an ornamental and the species is also widely cultivated for its leaves, which have been highly valued as a spice for many centuries. Laurel wilt has been observed in landscape plants of this species in the southeastern US [55], and the susceptibility of bay laurel to the disease has been confirmed in controlled, pathogenicity tests [105]. Furthermore, *X. glabratus* was found to reproduce in bay laurel, and therefore, the disease could pose a threat to natural and cultivated populations of this species in Europe. However, because of the small size of bay laurel, the discontinuous distribution of the species in Europe [103], and the lack of other lauraceous host species, the probability is low that *X. glabratus* could become sufficiently established to cause a widespread epidemic.

A greater threat of laurel wilt may exist for the Laurasilva forests that occur in the Macaronesian Islands off the coasts of Europe and Africa. Here, the forests of the Azores, Canary Islands, and Madeira are thought to provide an example of laurel forests that were once common throughout southern Europe, although recent research suggests otherwise [106,107]. Nonetheless, the Laurasilva forests of Madeira have been designated as a UNESCO World Heritage Site (https://whc.unesco.org/en/list/934/), and these subtropical forests are made up of a unique mix of lauraceous tree species in the genera *Laurus, Persea, Apollonias*, and *Ocotea*. One species, Viñatigo (*Persea indica* (L.) Spreng.), has been found to be highly susceptible to laurel wilt in both field and greenhouse tests [108], and bolts from trees of this species are readily colonized by *X. glabratus* [78]. Furthermore, the canary laurel (*Laurus novocanariensis* Rivas Mart., Lousã, Fern.Prieto, E.Días, J.C.Costa and C.Aguiar) is closely related to the highly susceptible bay laurel, which is found in mainland Europe.

3. Economic Impacts

Although sassafras and redbay have interesting wood properties that are desirable for uses such as paneling and furniture, the wood of these species is not readily available, and thus, they have minor commercial value and are primarily used locally in some areas of the US [59,109]. It would be difficult to estimate the economic impact for the losses of these species. Other forest species affected by the laurel wilt such as *L. aestivalis* and *L. melissifolia* have no commercial value, and interest in these species is primarily because of their ecological and cultural importance. However, homeowners may incur costs for removing the affected trees, and perhaps depreciation in property values associated with loss of landscape trees.

Laurel wilt poses a significant economic threat to the avocado industry in Florida [75]. Estimates for the economic impacts of the disease on the Florida avocado industry have ranged between $356 million (if nothing was done) to approximately $183 million (if control measures were 50% effective) [110]. Approximately 98% of Florida commercial avocados, worth nearly $54 million per year, are produced in Miami-Dade County [14]. In 2017, it was estimated that approximately 2% of the avocados grown in the commercial production areas had been lost to the disease [75], and additional losses have occurred in residential areas. In addition to losses in production, orchard managers have to incur the cost of tree removal and treatments to protect residual trees, which is estimated to cost as much as USD 1000/acre in orchards [111].

4. Ecological Impacts

The rapid spread of laurel wilt throughout the southeastern US has caused abrupt changes in ecosystems, the long-term impact of which is poorly understood. In the Georgia coastal plains, the loss of redbay as a midstory species is causing shifts in the size structure and changes in the community composition of forests with increasing dominance of sweetbay (*Magnolia virginiana* L.) and loblolly bay (*Gordonia lasianthus* (L.) J. Ellis) [51]. In deciduous forests of North Florida, the loss of redbay to laurel wilt was found to have no short-term effects on live oak (*Quercus virginiana* Mill.) the dominant overstory species, but among subcanopy species, coastal red cedar (*Juniperus virginiana* L. *var. silicicola)* replaced *P. borbonia* as the third most common species [112]. Although redbay was lost as an overstory species, densities of redbay seedlings and saplings increased greatly in the understory following a disease outbreak, likely due to their small diameter and lack of attractiveness to *X. glabratus* beetles.

In some maritime forest communities, widespread mortality of redbay trees as well as regeneration has been observed in areas affected by laurel wilt, but the loss of sprouts and seedlings may have been due to heavy browsing by deer, particularly in areas where hunting has been restricted and deer populations are exceptionally high [57,113]. In southern Florida, the expansion of laurel wilt in the Everglades has caused concerns that the rapid loss of swampbay could result in ecosystem-level instability [56]. Swampbay is one of the major overstory tree species on some tree islands, and its loss creates openings in the canopy that can facilitate the establishment of invasive species such as Brazilian pepper (*Schinus terebinthifolius* Raddi.) or *Melaleuca quinquenervia* (Cav.) S.T.Blake [56,57,114].

Although redbay continues to survive as understory seedlings, sapling and small trees in forests affected by laurel wilt, questions remain about whether redbay will function as an integral part of these ecosystems in the future [113]. Much is still unknown about the exact roles of redbays in ecosystems, but it is apparent that the disease-related changes are affecting insect communities. Riggins et al. [115] found a significant reduction in populations of the Palamedes swallowtail butterfly in stands affected by laurel wilt and documented another 24 native arthropod species, all obligate specialists on lauraceous plants, that could be negatively affected by the disease.

As laurel wilt spreads to the north in the US beyond the Coastal Plain to more upland regions where sassafras is more common, forest characteristics and ecological interactions associated with sassafras mortality are also likely to be affected. Simulation models have found that in ecosystems where sassafras occurs, declines in sassafras basal area caused by laurel wilt would subsequently result in long-term increases in basal area of red maple (*Acer rubrum* L.) and yellow poplar (*Liriodendron tulipifera* L.) [116].

5. Climatic Conditions

The geographic range of a recently introduced nonnative insect species depends on many factors including its adaptive capability, ability to compete within the new habitat, how well it utilizes the available resources, the distribution and diversity of available host species, and how it responds to prevailing ecosystem disturbance regimes, among other factors [117]. Specifically, favorable climatic conditions may enable the rapid establishment of nonnative species [118,119], increase the frequency and severity of forest diseases, and facilitate range expansion into new niches [120,121].

During the summer of 2002, the entire state of South Carolina was under severe drought conditions, and Hilton Head Island, SC (where laurel wilt was initially reported) was under extreme drought for a considerable period. According to local accounts, the drought was followed by heavy rains during 2003/2004. Although droughts induce significant abiotic stress that can often predispose host trees to insect attacks and diseases, the history of the laurel wilt epidemic over the last 15 years does not suggest that abiotic stress is required for trees to become vulnerable to beetle attack or infection by the pathogen. Nonetheless, how factors such as rainfall, drought, and temperatures regulate the development and activity of *X. glabratus*, as well as disease development within trees, remains largely unknown.

The climatic conditions in the parts of the US where *X. glabratus* and laurel wilt presently occurs range from tropical to humid subtropical. The average annual rainfall within the range of sassafras habitat varies from 760 to 1400 mm, and the average frost-free period ranges from 160 to 300 days, with average temperatures in January ranging between −7 °C in the north and 13 °C in the South and the average July temperatures from 21 to 27 °C [60]. In contrast, the average annual rainfall within the redbay habitat varies from 1020 to 1630 mm. The average frost-free period ranges from 200 to 365 days, with average temperatures in January ranging between 3 °C in the northern part of the species range and 13 °C in the southern-most part, and average July temperatures from 26 to 28 °C. Temperature extremes in this region can reach above 38 °C in summers and seldom go below −12 °C in winters over most of the redbay range [45]. The areas of overlap in suitable climatic conditions between the two species stretches from Georgia to Texas with some isolated sassafras-dominated areas in between. Sassafras has a large geographic distribution range that extends over much of the eastern half of the US from northern Florida to central Michigan, while the range of the redbay is primarily restricted to the coastal plains of the southeastern US and extends from southern Florida, but mostly restricted to the southeastern US, with habitat overlaps with sassafras in this region (Figure 4).

Cold temperature may be an important limiting factor to the establishment of *X. glabratus* in northern populations of sassafras. The beetle is freeze-intolerant and susceptible to chill, with a lower lethal temperature of −10.0 °C, suggesting that about 0.1% of the current US sassafras spatial extent experiences winters cold enough to prevent *X. glabratus* establishment [122,123]. However, approximately 52% of the current spatial extent of sassafras may experience cold winter temperatures sufficient to cause significant beetle mortality [123]. Climatic conditions in approximately 91% of the current sassafras geographic range in the eastern USA will not likely cause any mortality to *X. glabratus* under a modest climate change scenario of 1.4 °C increase in the winter minimum temperatures by 2050 [122].

Future climate projections [124] indicate that by 2080, the average temperatures in the South will rise by 2.5 °C (under conservative carbon dioxide (CO_2) and other greenhouse gas emissions projections) to 5.0 °C (under more aggressive emissions projections). Average temperatures may increase approximately 5.8 °C in summer, when the frequency, duration, and intensity of droughts will most likely increase because of higher temperatures, more evaporation from soils, and more water loss from plants (increased stress). In states bordering the Gulf of Mexico, less rainfall is projected in the winter and spring compared to states that are farther north [124]. Based on *R. lauricola* thermal requirements and host precipitation requirements, future climatic changes could have significant effects on ecosystems and the spread of laurel wilt in the Southeastern US. An investigation of the impacts of temperature on the population dynamics of the southern pine beetle (*Dendroctonus frontalis* Zimmermann) at the northern edge of its range found that the general rise in minimum air temperatures of 3.3 °C from 1960 to 2004 could account for the expansion of SPB outbreaks into more northern forests [125]. The rising temperatures and milder winters could also facilitate the northward movement of *X. glabratus* and more widespread disease incidence in sassafras, especially in areas, where redbay is absent [5,45,60,122,126]. Overall, conditions would remain suitable for redbay in the South and sassafras to the North [5].

6. Management

Management options to control laurel wilt are unfortunately very limited, with no single strategy effective in preventing disease spread or reducing its impacts. Although the beetle can spread naturally by flight, restricting long-distance movement of wood infested with ambrosia beetles is perhaps the best short-term option presently available for slowing the spread and limiting the impacts of the disease. Many states prohibit or discourage the long-distance movement of firewood or other untreated wood products without a permit [127], but enforcement of such regulations can be difficult, particularly for species like redbay and sassafras that have low commercial value.

An integrated management approach that addresses human-aided movement of infected plant material, along with various components of an integrated pest management (IPM) system is likely needed to maximize control of the disease. Components of an IPM approach for laurel wilt could include development and deployment of resistance hosts, the use of silviculture practices such as sanitation where necessary, targeted application of preventive chemical treatments for protecting high-value trees, and severing root grafts in a situation where the pathogen is likely to spread underground (avocado orchards, sassafras clones). However, the success of such an approach is likely dependent on sustained funding and a commitment to long-term area-wide implementation, requiring public support and civic coordination. In this section, some of the important factors to be considered in the management of laurel wilt are examined.

6.1. Sanitation

The rapid spread of laurel wilt in the southeastern US likely resulted from a combination of factors, including a highly virulent pathogen, an efficient insect vector that can initiate new populations without mating (along with mated females emerging from their brood tree, which allows the ability to quickly establish new infestations), high densities of highly susceptible hosts, a hospitable climate for both pathogen and vector, accidental spread by humans via movement of infested wood, delayed recognition of the cause of the disease, and a lack of feasible control options. In the US, there was at least a 3-year delay (2002–2005) between the first occurrence of *X. glabratus* and a conclusive understanding of the cause of laurel wilt. These factors, along with the low economic value of the native host trees species in the US, have severely constrained management of laurel wilt in forest ecosystems [75]. In the case of avocado, firewood is generally not transported into avocado production areas, but a lack of host resistance and management options have resulted in impacts in these agricultural systems. Furthermore, in Florida, avocado plantations are sometimes located adjacent to natural areas containing redbay and swampbay trees, from which *X. glabratus* and other potential ambrosia beetle vectors likely disperse into the orchards.

Raffaelea lauricola can persist in dead, standing redbay trees for up to 14 months. However, Spence et al. [128] failed to recover *R. lauricola* from redbay wood chips two days post-chipping, suggesting the pathogen may not survive for long in wood chips. Sanitation through wood chipping could be a management tool that would reduce the amount of *R. lauricola* in the local environment as well as the number of surviving *X. glabratus* [128]. Individual beetles may survive a standard wood chipping process due to their small size, but chipping might sufficiently dry out the wood to prevent ambrosia beetle survival, development, and subsequent dispersal. These factors suggest that localized sanitation treatments including cutting and burning, burying, chipping, or tightly covering wood might limit the disease to a local area when pursued early and diligently [129].

6.2. Public Awareness

Awareness and participation by the public could help limit the spread of the redbay ambrosia beetle and laurel wilt in neighborhoods, parks, roadsides, and other public places. Movement of infested wood materials by private citizens and by industry likely plays a significant role in the spread of the laurel wilt pathogen and *X. glabratus* over short as well as long distances. Numerous instances have occurred where the disease has been found hundreds of kilometers from previously known disease fronts, and movement of infected wood has long been suspected as the cause [13,68,130–132]. During the early stages of the laurel wilt epidemic, new spots of infected trees were commonly located many miles from sites with disease along major roads and train tracks where logs and other unprocessed woody materials were transported. In addition, cases have been documented where infested wood for firewood and wood-working projects were moved by homeowners, woodworkers, woodturners, and campers [16,39]. Public awareness campaigns that discourage transportation of infested wood materials from infested to noninfested areas may help slow the spread of the disease.

6.3. Chemical Control

Propiconazole is a demethylation-inhibiting fungicide (DMI), and macro-injection with this fungicide has been shown to be effective for preventing laurel wilt in redbay trees experimentally inoculated with the laurel wilt pathogen [133]. However, its slow rate of uptake and short residual efficacy may limit its usefulness. Propiconazole was retained in redbay stem xylem for at least 7.5 months after injection but was more frequently detected in samples from trees injected 4.5 months earlier and was not well detected in small-diameter branches [133]. Moreover, the treatment has not yet been evaluated under varying levels of disease pressure, nor in other native hosts like sassafras. Still, it may have value in providing short term protection of high-value trees.

In greenhouse studies, Ploetz et al. [73] found that soil drench applications of DMIs and thiabendazole provided significant control of laurel wilt in avocado saplings and observed that topical branch or trunk applications of propiconazole and triadimenol in 2% Pentrabark, a bark-penetrating surfactant, were effective at lower rates than were used in soil drench applications. Although, topical fungicide applications in bark-penetrating surfactants could be a less expensive practice than macro-infusion, moving sufficient concentrations of propiconazole or other fungicides into host xylem for disease control would be difficult in large trees and is not practical at present [73]. Although triazole and DMI fungicides could possibly protect avocado trees from laurel wilt by macro-infusion, they would not be cost-effective measures in orchards [134] but might be effective for landscape trees. Furthermore, bark applications of propiconazole with Pentrabark have not been successful on redbay trees under field conditions (Bates, Georgia Forestry Commission, personal communication, B. Fraedrich, Bartlett Tree Company, personal communication). The lack of success for propiconazole with Pentrabark to protect redbay may have been due to the inability for sufficient amounts of fungicide to penetrate the thicker bark of the mature trees and reach the xylem, where it could move systemically through trees. In addition, applications of azoxystrobin, pyraclostrobin, fluazinam, and phosphorus acid salt were ineffective for control of laurel wilt [134]. Likewise, contact insecticides have been found to be ineffective against ambrosia beetles once adult beetles have bored into the trees [135].

6.4. Biological Control and Genetic Resistance

Various biocontrol agents have been examined for use against *X. glabratus* or *R. lauricola*, and although some have shown promise, none are viable options for control of laurel wilt at this time. Endophytic fungi isolated from the xylem of avocado were found to have significant in vitro antagonistic activities against the laurel wilt pathogen, but they did not prevent the development of laurel wilt in plants [136]. *Raffaelea lauricola* successfully colonized plants rapidly and systemically, but the endophytes generally did not colonize xylem more than 2 cm above the point at which plants were inoculated. Olatinwo and Fraedrich [137] reported the efficacy and inhibition of *R. lauricola* with a crude extract of *Acaromyces ingoldii* Boekhout, Scorzetti, Gerson and Sztejnb. secondary metabolites in greenhouse and in vitro experiments. *Acaromyces ingoldii* is an anamorphic mite-associated fungus belonging to the Ustilaginomycetes [138]. Some entomopathogenic fungi including *Beauveria bassiana* (Balsamo) Vuillemin have demonstrated potential biological control abilities against the redbay ambrosia beetle [80]. *Paenibacillus* species and *Bacillus* species have also shown active antagonistic activities against the laurel wilt pathogen of avocado, *R. lauricola* [139]. Whether any of these potential biological control agents can be applied to reduce field populations of the laurel wilt causal agents or to reduce disease impact on lauraceous plant populations, remains to be demonstrated.

Tree species in the native range of redbay ambrosia beetle in Asia may have genetically based resistance to the causal pathogen *R. lauricola* [140], and such plants could serve as a source for understanding host resistance mechanisms, identifying genes for resistance, or breeding resistant hybrids. This would complement previous efforts to identify host resistance in redbays [141] and avocado cultivars [74].

6.5. Survey and Detection

Other potential management options explored in recent years include the application of visible-near infrared reflectance spectra on avocado leaves as a non-destructive sensing tool for detection of laurel wilt [142], and detection of laurel wilt in avocado using low-altitude aerial imaging for rapid detection, which could be a potentially valuable tool in mitigating laurel wilt threat in commercial avocado production [143]. Other survey and detection methods include the use of detector dogs [144] and the use of multi-spectral sensors for aerial detection of rapid death caused by tree diseases such as wilts [145]. As scientists explore the genetics of host resistance, development of early detection tools and other emerging technologies, additional management options may become available to help address the expanding threats of nonnative species.

6.6. Disrupting Pest Introduction Pathway

Arrivals and influx of new invasive pests together with the spread of already established nonnative species will continue to pose a significant risk to US forests and urban and suburban landscapes [3]. The threat of invasive nonnative pests such as *X. glabratus* and the associated laurel wilt pathogen is a global problem that requires international cooperation and commitment, strict enforcement of effective phytosanitary standards, and adequate deterrents for non-compliance to achieve real success. Lovett et al. [3] observed that although several policy options have been implemented to reduce pest invasions, these options must be strengthened in some cases or expanded in other cases for them to be more effective. Therefore, management and mitigation policies must include pre-importation measures that limit the arrival of new pests through inspections, or post-entry quarantine and exploratory surveillance measures that prevent the escape of new species beyond the port of entry.

7. Conclusions

In anticipation of changing climatic conditions, continued expansion of global commerce, and increasing global trade volume, the frequency of new introductions and the expansion of previously introduced nonnative insects and pathogens (such as *X. glabratus* and *R. lauricola*) is expected to increase in the US. Range expansion of the laurel wilt vector and pathogen could threaten additional susceptible hosts, including members of Lauraceae that are highly diversified and widely distributed elsewhere in the Americas and on other continents. Prevention of new introductions is extremely important because the likelihood of effectively eradicating nonnative species decreases once they become established. Nearly 20 years after the introduction of the laurel wilt causal agents, few effective management options are currently available for this disease. Thus, the current laurel wilt epidemic in the US illustrates the importance of preventing new invasive species from arriving. Preventative measures and mitigation efforts must anticipate and target the pathways of new introductions otherwise, the threat and the impact of nonnative species on forest ecosystems will continue to grow. Monitoring the flow of global trade, changing climatic conditions, and trends in human recreational and social activities could help inform efforts to detect, quarantine, and eradicate new invasive species.

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