# Chapter 7. Emerging Forest Pest Threat: Redbay Ambrosia Beetle and Laurel Wilt

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## Introduction

Accidentally introduced from Asia, the redbay ambrosia beetle (*Xyleborus glabratus*) carries a symbiotic fungus (*Raffaelea lauricola*) that has been linked to mortality of trees and shrubs from the Lauraceae family (Fraedrich and others 2007, Harrington and others 2008). The disease caused by the fungus, subsequently named laurel wilt, has severely impacted redbay (*Persea borbonia*) in coastal areas of Florida, Georgia, and South Carolina and has also been linked to mortality of sassafras (*Sassafras albidum*) in this region. As a recently discovered invader, little is known about the biology and behavior of the beetle or its associated fungus. A number of studies are ongoing, including research in Florida related to potential control via fungicides (Mayfield 2007). To provide a basic foundation for additional research or management decisionmaking, the objectives of this chapter are to (1) provide information on the current range of the redbay ambrosia beetle and laurel wilt in the United States, (2) describe the relative distributions of known and potential host species, and (3) employ spatial models to assess climatic factors affecting the beetle's range expansion and to examine the spatial pattern of spread. Further details regarding interpolated host maps as well as the climate and spread analyses are provided in Koch and Smith (2008).

## History of the Problem

In 2003, redbay trees in the Hilton Head Island, SC, area began exhibiting high levels of mortality. By the following year, an estimated 75 to 80 percent of redbay trees on the island had been killed, with the exact cause or causes unknown at the time (Fraedrich and others 2007). The species was not known to have any significant pests (Coder 2006b), although insects and precipitation trends during the previous several years, i.e., periods of drought followed by elevated precipitation, or the interaction of the two, were suggested as possible explanations (Fraedrich and others 2007). The mortality on Hilton Head was ultimately linked to the recently introduced redbay ambrosia beetle, which had first been detected in 2002 using a U.S. Department of Agriculture early detection and monitoring trap in Port Wentworth, GA (Fraedrich and others 2007, Rabaglia 2003). More specifically, the redbay trees were killed by the laurel wilt fungus associated with the beetle (Fraedrich and others 2007). During the past few years, redbay mortality attributed to the beetle and its associated fungus has been reported extensively in coastal areas of Georgia, South Carolina, and Florida. Anecdotal estimates of the rate of spread of the beetle have been reported to range from 15 to 17.5 miles per year in Georgia.[1] However, natural spread appears to be compounded by accidental human transport, as suggested by detection of the beetle in Indian River County, FL, in 2006, more than 130 miles from the closest other county known to be infested at the time. Human-aided transport, possibly via wood chips and firewood, may also have occurred in at least two Georgia counties (see footnote 1), albeit at shorter distances than the apparent jump in Florida.

The redbay ambrosia beetle is one of 10 ambrosia beetle species first detected in the United States between 1985 and 2005 (Haack 2006). Like many other wood-boring beetles, the redbay ambrosia beetle was likely introduced to the country via solid wood packing materials (Fraedrich and others 2007, Haack 2006). Most ambrosia beetles, including the redbay ambrosia beetle, are members of the tribe Xyleborina; species in this tribe are typically difficult to detect, infest a broad suite of host species, and exhibit polygamous, sib-mating behavior, facilitating their establishment in newly invaded areas (Rabaglia and others 2006). The term ambrosia generally refers to symbiotic fungi typically carried by female ambrosia beetles in specialized storage structures (mycangia). These fungi are introduced into host trees or shrubs when the beetles bore galleries into the xylem of the hosts (Furniss and Carolin 1977). Both adult ambrosia beetles and larvae feed on the introduced fungi, rather than on the wood of the trees they infest (Mayfield and Thomas 2006). The laurel wilt fungus was probably introduced from Asia along with the redbay ambrosia beetle, and so far the beetle is the only known vector (Fraedrich and others 2007).

The redbay ambrosia beetle has been documented in India (the States of Assam and West Bengal), Bangladesh, Myanmar, Taiwan, and southern Japan, including the Bonin Islands (Holistic Insect Systematics Laboratory 2005, Rabaglia and others 2006). In its native range, the beetle is typically associated with host plant species from the Lauraceae family, such as Asian spicebush (*Lindera latifolia*) and yellow litsea (*Litsea elongata*) (Rabaglia and others 2006). The beetle is considered of minor importance in Asia, primarily infesting weakened trees as part of a complex of insects (Rabaglia 2003). Nonetheless, it seems to follow the pattern of several other

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[1] Cameron, R.S.; Bates, C.; Johnson, J. 2008. Distribution and spread of laurel wilt disease in Georgia: 2006–2008 survey and field observations. 29 p. Unpublished report. Georgia Forestry Commission. [Location unknown]. http://www.fs.fed.us/r8/foresthealth/laurelwilt/resources/pubs/georgia_laurel_wilt_report_2006-08.pdf. [Date accessed: October 3, 2008.]

nonnative ambrosia beetle species that, upon introduction in the United States, have begun to attack ostensibly healthy hosts (Mayfield and Thomas 2006). In addition to its documented impact on redbay and sassafras, the laurel wilt fungus has been found on two imperiled shrub species from the Lauraceae family: pondberry (*Lindera melissifolia*), which is on the Federal endangered species list, and pondspice (*Litsea aestivalis*), which is listed as endangered in Florida and Maryland and threatened in Georgia (Fraedrich 2007; U.S. Department of Agriculture, Natural Resources Conservation Service 2007). Laboratory tests of pathogenicity are underway for a number of tree and shrub species; Lauraceae species such as swamp bay (*Persea palustris*), northern spicebush (*Lindera benzoin*), and California laurel (*Umbellularia californica*) have proven to be susceptible to the fungus (Fraedrich 2007, Forest Service, U.S. Department of Agriculture, 2007). The only commercially important Lauraceae species growing in the United States is the avocado (*Persea americana*), which appears to be susceptible to laurel wilt but may be more resistant than other species (Forest Service, U.S. Department of Agriculture, 2007). Redbay and sassafras, while not commercially important, serve as key food sources for wildlife (Coder 2006a, Griggs 1990), and redbay is often an understory dominant in barrier island forests of the Southeast (Helm and others 1991).

## Methods

**Current Beetle/Wilt Distribution—**Forest health specialists in Florida, Georgia, and South Carolina provided data, from 2004 to 2007, indicating which counties in each State contain redbay trees with symptoms of laurel wilt and/or confirmed occurrence of the redbay ambrosia beetle. In the resulting map (fig. 7.1), affected counties have been labeled according to the year of first-confirmed detection. Additionally, in 2006–07, the Georgia and South Carolina Forestry Commissions completed surveys of redbay mortality in their coastal counties. The States followed similar protocols in their surveys, with 1/10-acre linear plots placed according to a systematic grid. In South Carolina, survey plots were established on a 10-minute longitude by 10-minute latitude grid across the range of redbay. This plot network was intensified to 5-minute longitude by 5-minute latitude in areas around the perceived edge of the infested zone.[2] In Georgia, survey plots were established on a 16.1 km by 16.1 km (10-mile by 10-mile) grid for most areas, including counties where the beetle and wilt had not been detected at the time, and on an 8-km by 8-km (5-mile by 5-mile) grid for areas with

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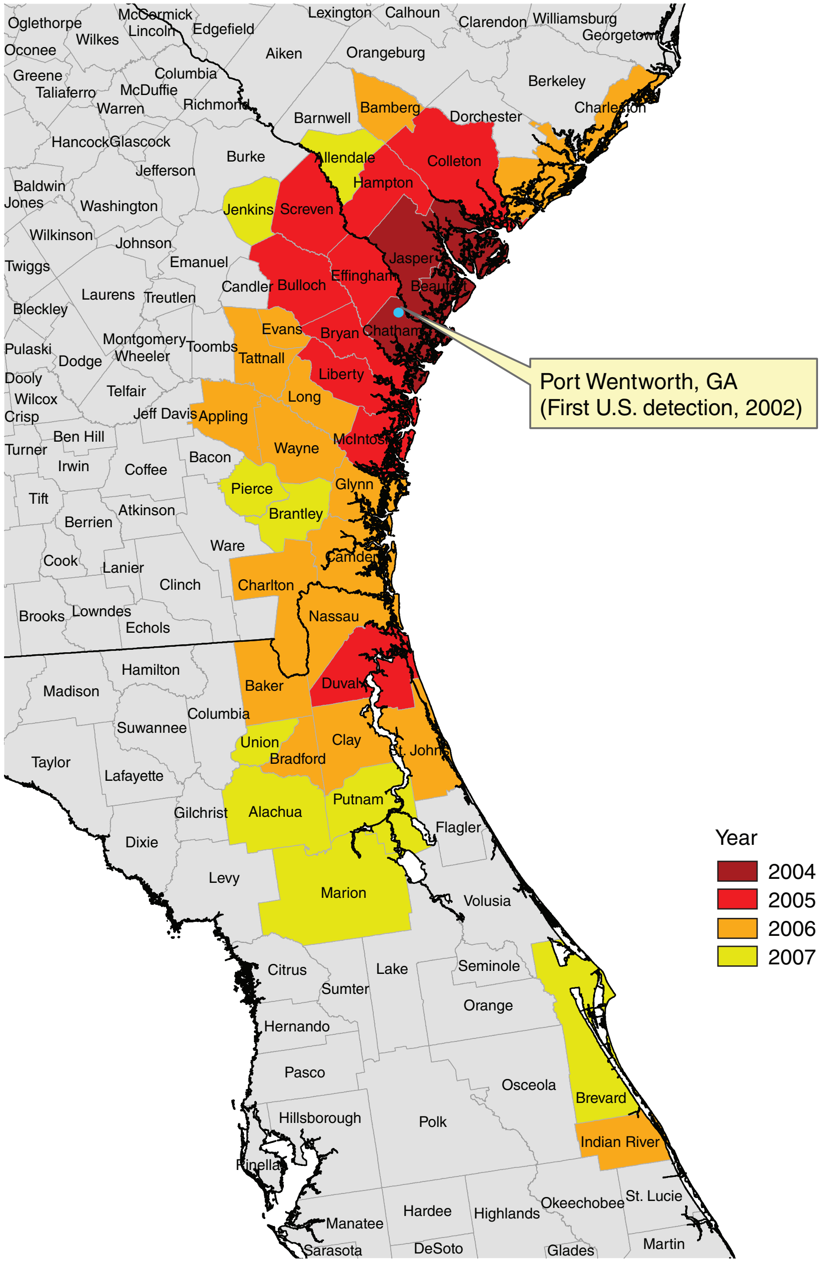
[2] Boone, A.J. 2007. A survey of redbay mortality in South Carolina. 17 p. Unpublished report to the South Carolina Forestry Commission. On file with: U.S. Forest Service National Forest Health Monitoring Research Team, 3041 Cornwallis Road, Research Triangle Park, NC 27709.



Port Wentworth, GA
(First U.S. detection, 2002)

*Figure 7.1—County-level distribution of redbay* (Persea borbonia) *mortality associated with laurel wilt* (Raffaelea lauricola) *and the redbay ambrosia beetle* (Xyleborus glabratus), *by year of first detection. (Detection data sources: James Johnson, Georgia Forestry Commission; Bud Mayfield, U.S Forest Service, formerly Florida Department of Agriculture and Consumer Services, Division of Forestry; Laurie Reid, South Carolina Forestry Commission)*

localized infestations.[3] All redbay trees in each plot were examined to derive total percent mortality, percent flagging, and percent healthy estimates for the plot (see footnotes 3 and 2). When laurel wilt was suspected to be present on a plot outside the confirmed infestation zone, affected trees were inspected for characteristic black staining of the xylem tissue, or instead, tissue samples were sent to Forest Service pathologists for verification (see footnotes 3 and 2). The approximate plot locations in both States, labeled according to each plot's percent redbay mortality estimate, were combined into a single map (fig. 7.2) in order to depict the current spatial pattern and extent of infestation. Field personnel in both States also attempted to record sassafras mortality but noted the difficulty of doing so during the dormant season when the surveys were performed, so these data were not included in the map analysis.

**Host Species Distributions—**Because it has been shown that the redbay ambrosia beetle will attack several different species from the Lauraceae family, county-level distributions of all Lauraceae species found in the conterminous United States (table 7.1), whether native or nonnative, were mapped using the Floristic Synthesis of North America and PLANTS phytogeographic databases (Kartesz 2003; U.S. Department of Agriculture, Natural Resources Conservation Service 2007). The species distribution data in these databases are based on voucher specimens, published reports, or other documentation of species occurrence. National distribution maps for each unique Lauraceae species or variety were combined into a single map depicting the diversity of potential host species per county (fig. 7.3). All Lauraceae species found in the United States are associated with forested ecosystems, so a map of forest cover developed from MODIS satellite imagery by the Forest Service Remote Sensing Applications Center was used to mask nonforest areas from the county-level map.

Maps of trees per acre for the two most prominent host species, redbay and sassafras, were generated through ordinary kriging (see appendix 7.1) of Forest Service FIA phase 2 plot data. For both species, separate interpolations were performed for each U.S. ecoregion section (Cleland and others 2007) containing plots in which the species occurred. Interpolated values for unknown locations were based on the 30 closest neighboring plots or, if the

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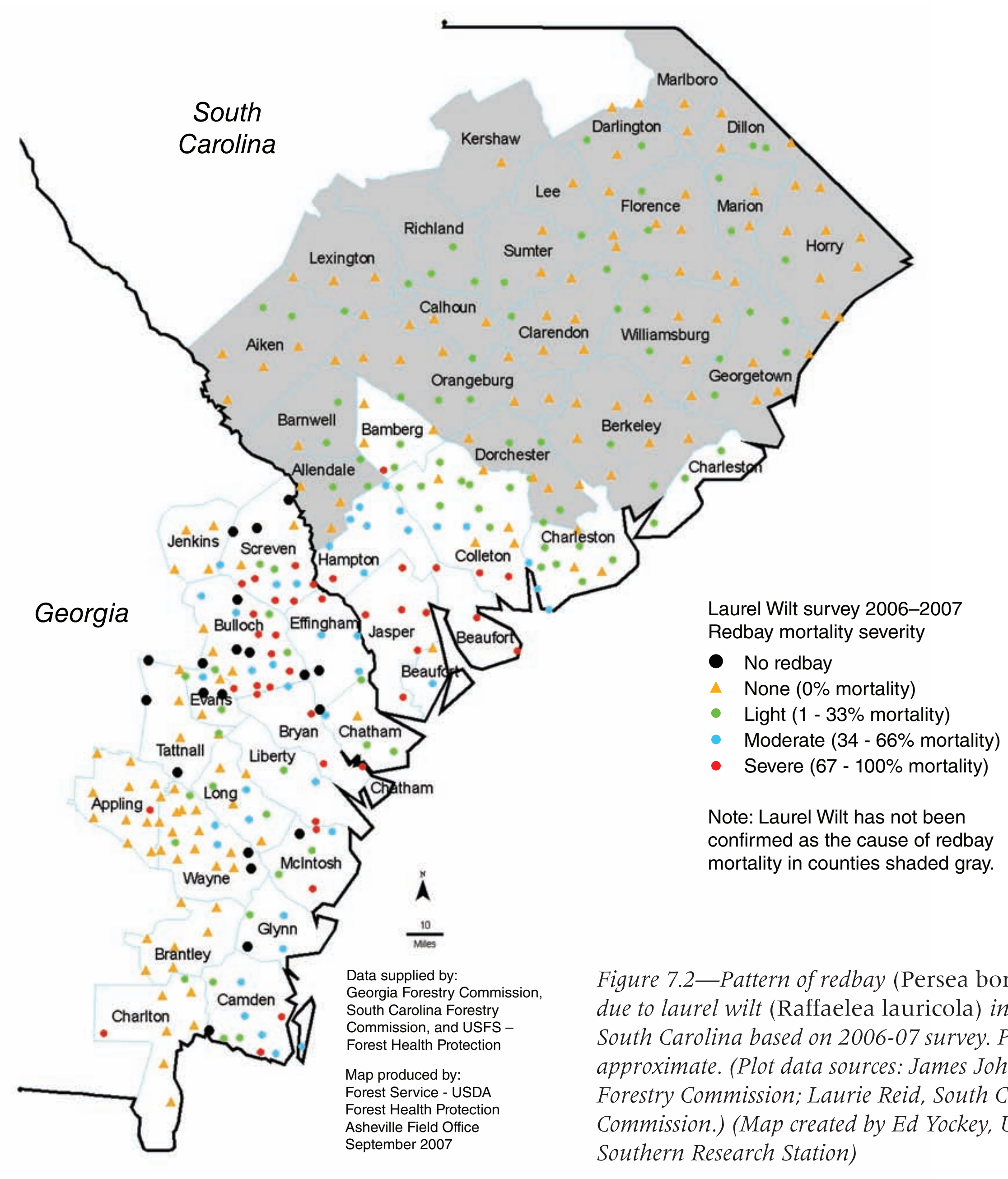
[3] Beck, M.J. 2007. Georgia redbay survey summary. 3 p. Unpublished report to the Georgia Forestry Commission. On file with: U.S. Forest Service National Forest Health Monitoring Research Team, 3041 Cornwallis Road, Research Triangle Park, NC 27709.



Data supplied by:
Georgia Forestry Commission,
South Carolina Forestry
Commission, and USFS –
Forest Health Protection

Map produced by:
Forest Service - USDA
Forest Health Protection
Asheville Field Office
September 2007

*Figure 7.2—Pattern of redbay* (Persea borbonia) *mortality due to laurel wilt* (Raffaelea lauricola) *in Georgia and South Carolina based on 2006-07 survey. Plot locations are approximate. (Plot data sources: James Johnson, Georgia Forestry Commission; Laurie Reid, South Carolina Forestry Commission.) (Map created by Ed Yockey, U.S. Forest Service, Southern Research Station)*

**Table 7.1—Plant species from the Lauraceae family found within the conterminous United States**

| Species | Common name(s) | Growth form | Native? | Distribution |
|---|---|---|---|---|
| *Cassytha filiformis* | Love vine | Vine | Yes | FL, TX |
| *Cinnamomum camphora* | Camphor tree | Tree | No | CA and Southeastern United States |
| *Laurus nobilis* | Bay laurel; sweet bay | Tree | No | CA |
| *Licaria triandra* | Pepperleaf sweetwood | Tree | Yes | Rare; limited to one FL county |
| *Lindera benzoin* | Northern spicebush | Shrub; tree | Yes | Common throughout Eastern United States |
| *Lindera melissifolia* | Southern spicebush; pondberry | Shrub; tree | Yes | Rare; endangered (five Southeastern States) |
| *Lindera subcoriacea* | Bog spicebush | Shrub; tree | Yes | Rare; endangered (FL, NC) |
| *Litsea aestivalis* | Pondspice | Shrub | Yes | Rare; endangered (FL, MD) / threatened (GA) |
| *Nectandra coriacea* | Lancewood | Shrub; tree | Yes | FL |
| *Persea americana* | Avocado | Tree | No | FL (commercially grown in southern part of state and in CA) |
| *Persea borbonia* | Redbay | Shrub; tree | Yes | Southeastern United States |
| *Persea humilis* | Silk bay | Shrub; tree | Yes | Rare; endemic to FL |
| *Persea palustris* | Swamp bay | Shrub; tree | Yes | Southeastern United States, distribution similar to redbay |
| *Sassafras albidum* | Sassafras | Shrub; tree | Yes | Common throughout Eastern United States |
| *Umbellularia californica*<br>var. *californica*<br>var. *fresnensis* | California bay laurel | Shrub; tree | Yes | var. *californica*: CA, OR, WA; var. *fresnensis*: limited to Fresno County, CA |

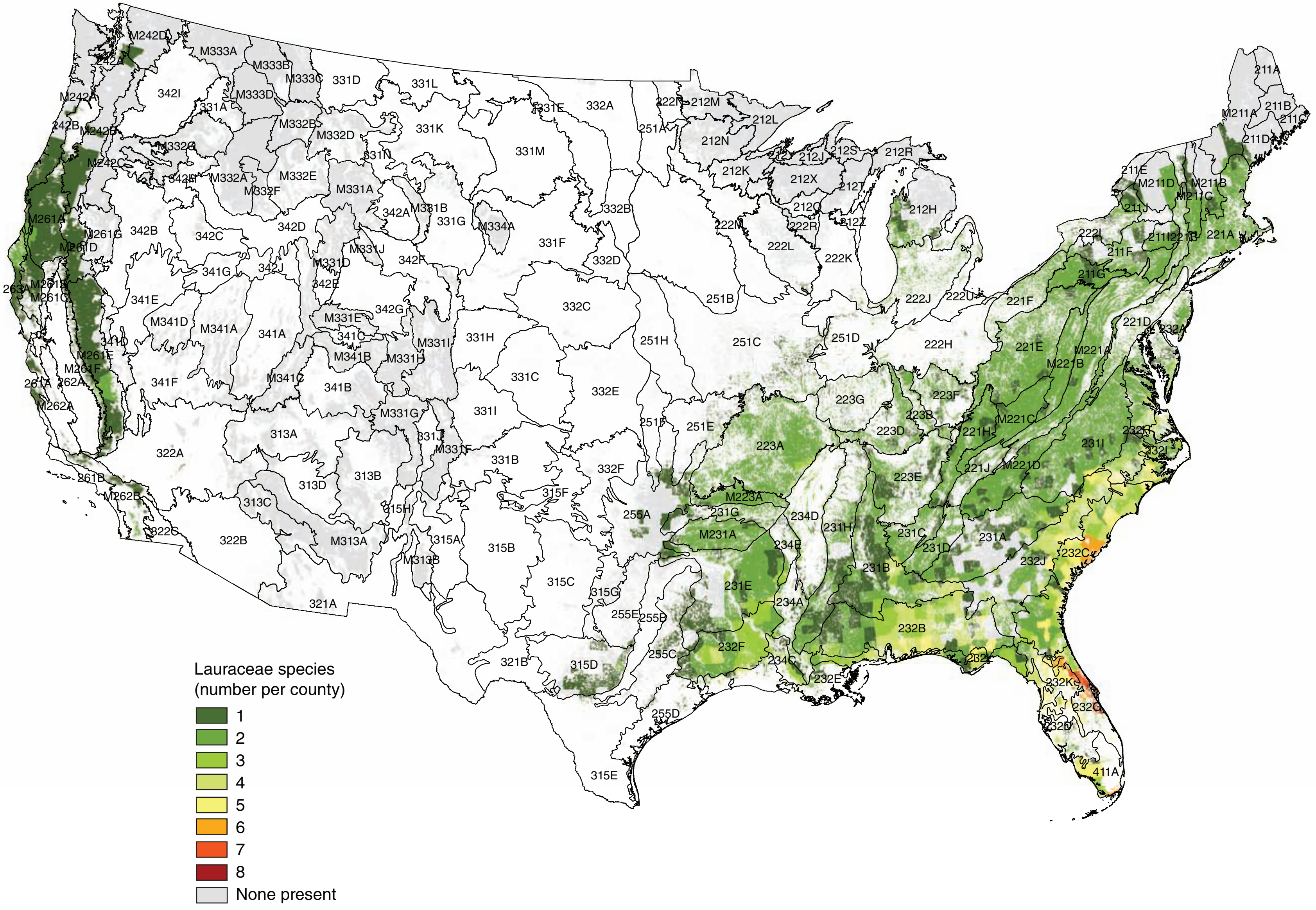


*Figure 7.3—Number of species from the Lauraceae family occurring in U.S. counties. Distribution data: Synthesis of the North American Flora (Kartesz 2003); U.S. Department of Agriculture PLANTS Database (U.S. Department of Agriculture, Natural Resources Conservation Service 2007). Ecoregion section boundaries (Cleland and others 2007) are shown for reference. The source for background forest cover, used as a mask, was the U.S. Forest Service, Remote Sensing Applications Center.*

number of plots within a 60-km radius of an unknown location was < 30, then all plots within this distance threshold were used. The resulting kriged surfaces for each section, with a 1-$km^2$ spatial resolution, were merged into comprehensive trees-per-acre maps for each species (figs. 7.4 and 7.5), which were masked using the MODIS forest-cover map developed by the Remote Sensing Applications Center.

**Climate Matching—**A comparison of climatic conditions between the conterminous United States and the other countries where the redbay ambrosia beetle is known to occur was performed using NCSU/APHIS Plant Pest Forecast (NAPPFAST), a Web-based software application for modeling the potential distributions of pest species (Magarey and others 2007; U.S. Department of Agriculture, Animal and Plant Health Inspection Service 2007). NAPPFAST employs global datasets for a large suite of climatic and environmental variables and includes a module for performing broad-scale climate matching. Based on a user-selected subset of input variables and a set of defined locations representing a pest's known geographic range, NAPPFAST generates gridded maps (approximately 10-$km^2$ spatial resolution) of all areas on the globe with conditions matching those in the defined range. The matching process follows a simple bioclimatic envelope approach. For each input variable, minimum and maximum possible values are defined according to the values found in the pest's known geographic range. Then, for a new region of interest, e.g., the conterminous United States, geographic areas are identified that fall between these minimum and maximum values. A set of geographic areas is defined for each input variable in this manner, and in a subsequent overlay process, only those areas indicated as suitable, i.e., between the minimum and maximum values, for all variables are retained in the final climate match for the region of interest.

A climate-matching surface for the redbay ambrosia beetle was generated by first delineating the countries of the beetle's native range. Only the States of Assam and Bengal were included from India, and northern Japan was excluded because none of the beetle's known host species grows in that portion of the country. Species distributions are seldom defined by a single variable; temperature is often the most important limiting factor, but moisture affects both insect and host life cycles (Baker and others 2000, Peacock and others 2006). Hence, a climate model was applied that included three annual variables (growing degree days,

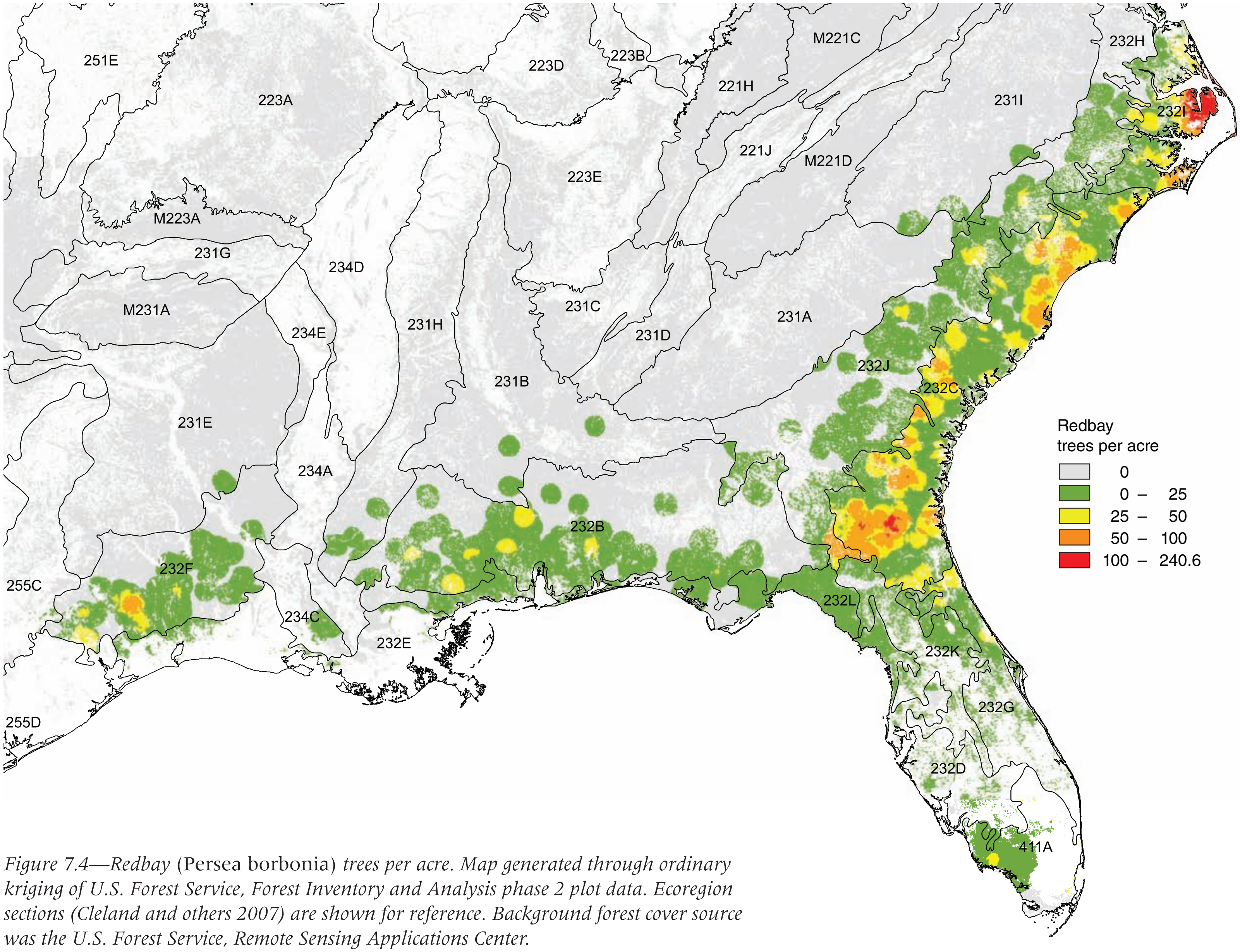


*Figure 7.4—Redbay* (Persea borbonia) *trees per acre. Map generated through ordinary kriging of U.S. Forest Service, Forest Inventory and Analysis phase 2 plot data. Ecoregion sections (Cleland and others 2007) are shown for reference. Background forest cover source was the U.S. Forest Service, Remote Sensing Applications Center.*

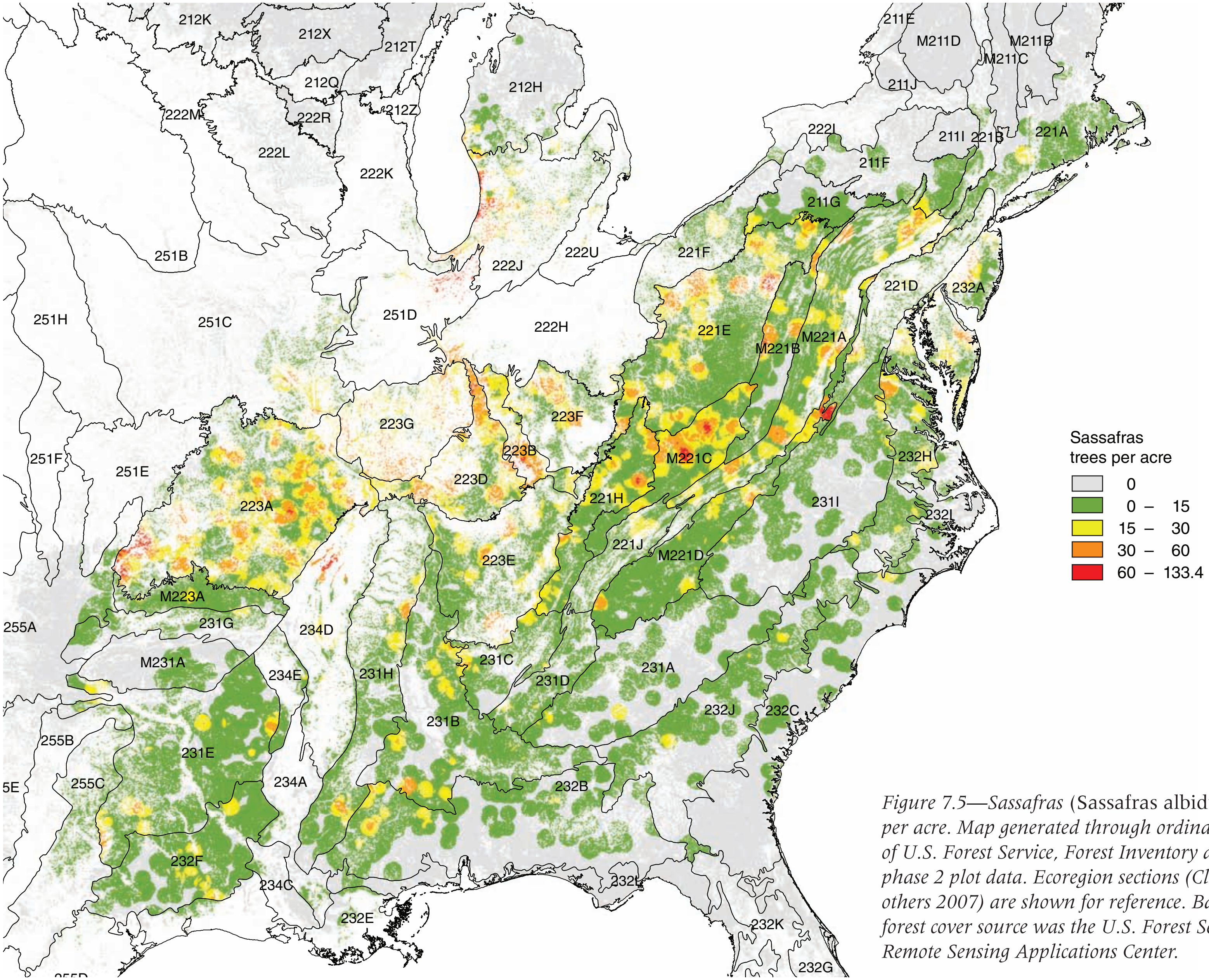


*Figure 7.5—Sassafras* (Sassafras albidum) *trees per acre. Map generated through ordinary kriging of U.S. Forest Service, Forest Inventory and Analysis phase 2 plot data. Ecoregion sections (Cleland and others 2007) are shown for reference. Background forest cover source was the U.S. Forest Service, Remote Sensing Applications Center.*

growing season moisture percentage, and 10-year extreme minimum temperature) to describe general climatic conditions. In addition, the model included variables representing seasonal effects, i.e., the amount of rainfall in each month of the approximate growing season, April through October (table 7.2). For the purpose of comparison, the model results were overlaid on the distributions of redbay and sassafras as mapped from FIA data (fig. 7.6).

**Spread Modeling**—A simple estimate of the rate of spread for the redbay ambrosia beetle and its associated fungus, assuming radial dispersion with exponential population growth, was developed from the county-level distribution data. In general, a spread rate estimated from such coarse-scale spatial data will not differ substantially from the rate that might be estimated with a more intensive, but costly, network of monitoring plots (Tobin and others 2007). Following procedures outlined by Banks (1994), the velocity of the expanding invasion front, i.e., the annual rate of spread, was calculated based on the infestation extents in 2004 through 2007, which were estimated as the total area (in km$^2$) of the counties infested as of

**Table 7.2—Variables used in the NAPPFAST climate-matching model (Magarey and others 2007), and the minimum and maximum values for those variables found within the estimated native geographic range of the redbay ambrosia beetle**

| Variable | Minimum value | Maximum value |
|---|---|---|
| 10-year mean extreme minimum cold temperature (°F) | -16 | 60 |
| 30-year mean growing degree days (baseline temperature 50 °F)[a] | 1,645 | 13,036 |
| 30-year mean growing season moisture (percent)[b] | 61 | 482 |
| 30-year mean April precipitation (inches) | 0.08 | 11.87 |
| 30-year mean May precipitation (inches) | 1.75 | 24.89 |
| 30-year mean June precipitation (inches) | 3.15 | 37.38 |
| 30-year mean July precipitation (inches) | 5.49 | 36.15 |
| 30-year mean August precipitation (inches) | 4.15 | 36.07 |
| 30-year mean September precipitation (inches) | 3.76 | 22.8 |
| 30-year mean October precipitation (inches) | 1.83 | 11.83 |

NAPPFAST = NCSU/APHIS Plant Pest Forecast.

[a] Measure of accumulated warmth supporting the growth of organisms. For any given day in a year, its contribution to the accumulated annual growing degree days is based on the difference between the mean of the minimum and maximum daily temperature values and the baseline temperature.

[b] Ratio of precipitation to potential evapotranspiration.

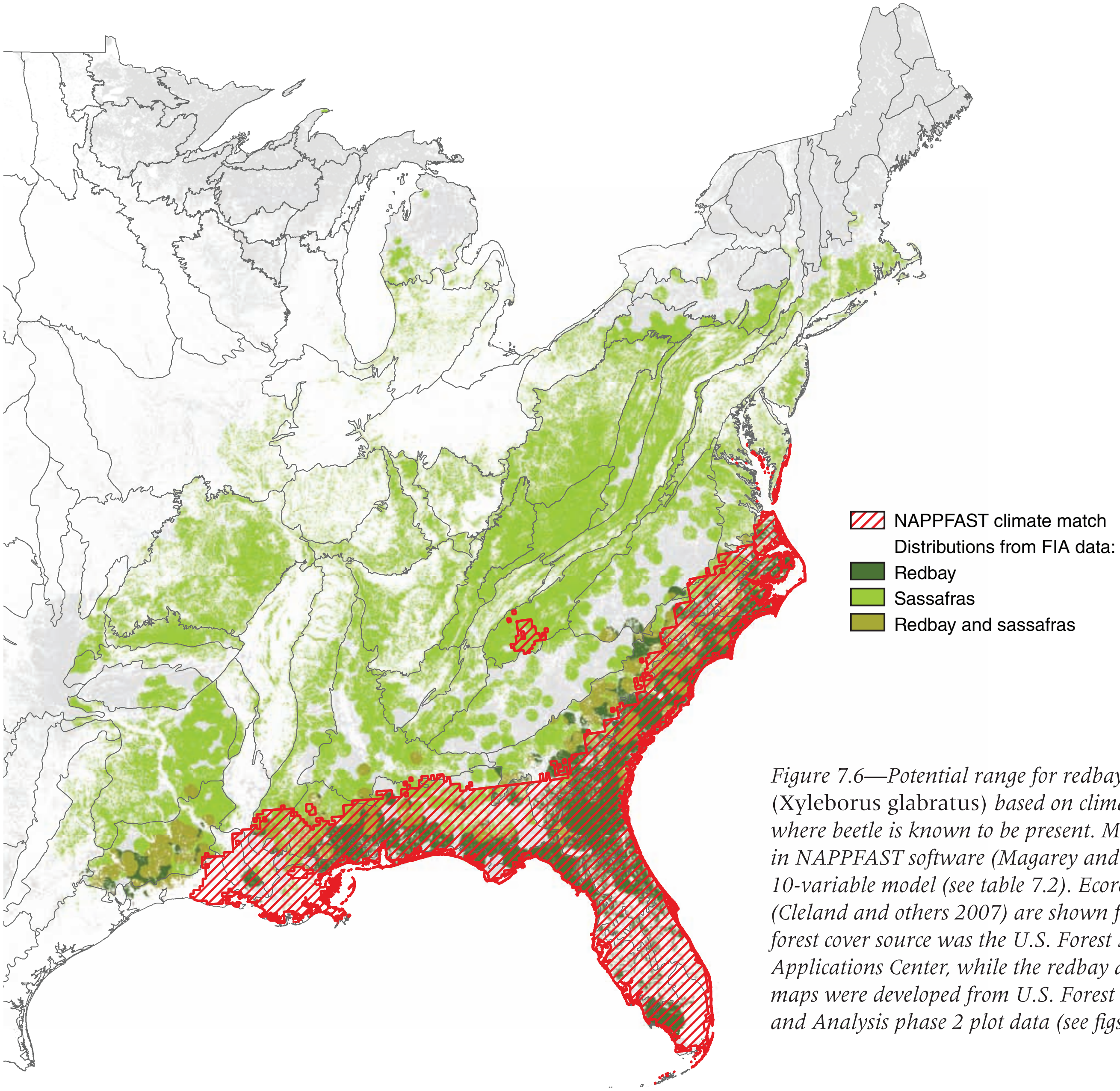


*Figure 7.6—Potential range for redbay ambrosia beetle* (Xyleborus glabratus) *based on climate match with countries where beetle is known to be present. Matching performed in NAPPFAST software (Magarey and others 2007) using a 10-variable model (see table 7.2). Ecoregion section boundaries (Cleland and others 2007) are shown for reference. Background forest cover source was the U.S. Forest Service, Remote Sensing Applications Center, while the redbay and sassafras distribution maps were developed from U.S. Forest Service, Forest Inventory and Analysis phase 2 plot data (see figs. 7.4 and 7.5).*

the year in question (table 7.3). If the dispersion geometry is assumed to be semicircular, i.e., in cases where dispersion is partially prohibited by a lengthy geographic barrier such as a coastline, the infestation extent $A$ at time $t$ may be approximated as

$$A = \frac{\pi R^2}{2} = 2\pi a D t^2$$

where

$R$ = the radius of the semicircular invasion extent

$a$ = the net growth rate

$D$ = the dispersion coefficient

This equation may be simplified for $t$ by taking the square root of both sides:

$$\sqrt{A} = \sqrt{2\pi a D}t$$

In short, the square root of the infested area is directly proportional to time $t$. The data from table 7.3 were applied in a least squares regression of $\sqrt{A}$ on year ($t$) to derive an estimate of $\sqrt{2\pi a D}$. Using this parameter estimate, the velocity of the expanding invasion front was subsequently calculated as

$$v = \frac{\delta R}{\delta t} = 2\sqrt{aD}$$

where

$v$ = the velocity of expansion, or annual rate of spread, in km per year (Banks 1994).

Spatial spread of the redbay ambrosia beetle and laurel wilt through time (fig. 7.7) was modeled in a gridded environment using a cost-weighted distance function. Rather than calculating the shortest Euclidean distance between a pixel in a map grid and the nearest origin or source location, this function weights the distance vector according to an underlying cost grid. Cost grid values > 1 increase the cost of moving along the vector, while values < 1 decrease the cost of moving along the vector. The result is an accumulated cost, in distance units, of traveling along the vector; this accumulated cost may be more or less than the vector's actual Euclidean length.

**Table 7.3—Infestation extents calculated from the combined areas of all counties confirmed as infested by the year in question**

| Year | Infestation extent |
|---|---|
| | *km*$^2$ |
| 2004 | 4 398 |
| 2005 | 18 965 |
| 2006 | 41 480 |
| 2007 | 57 723 |

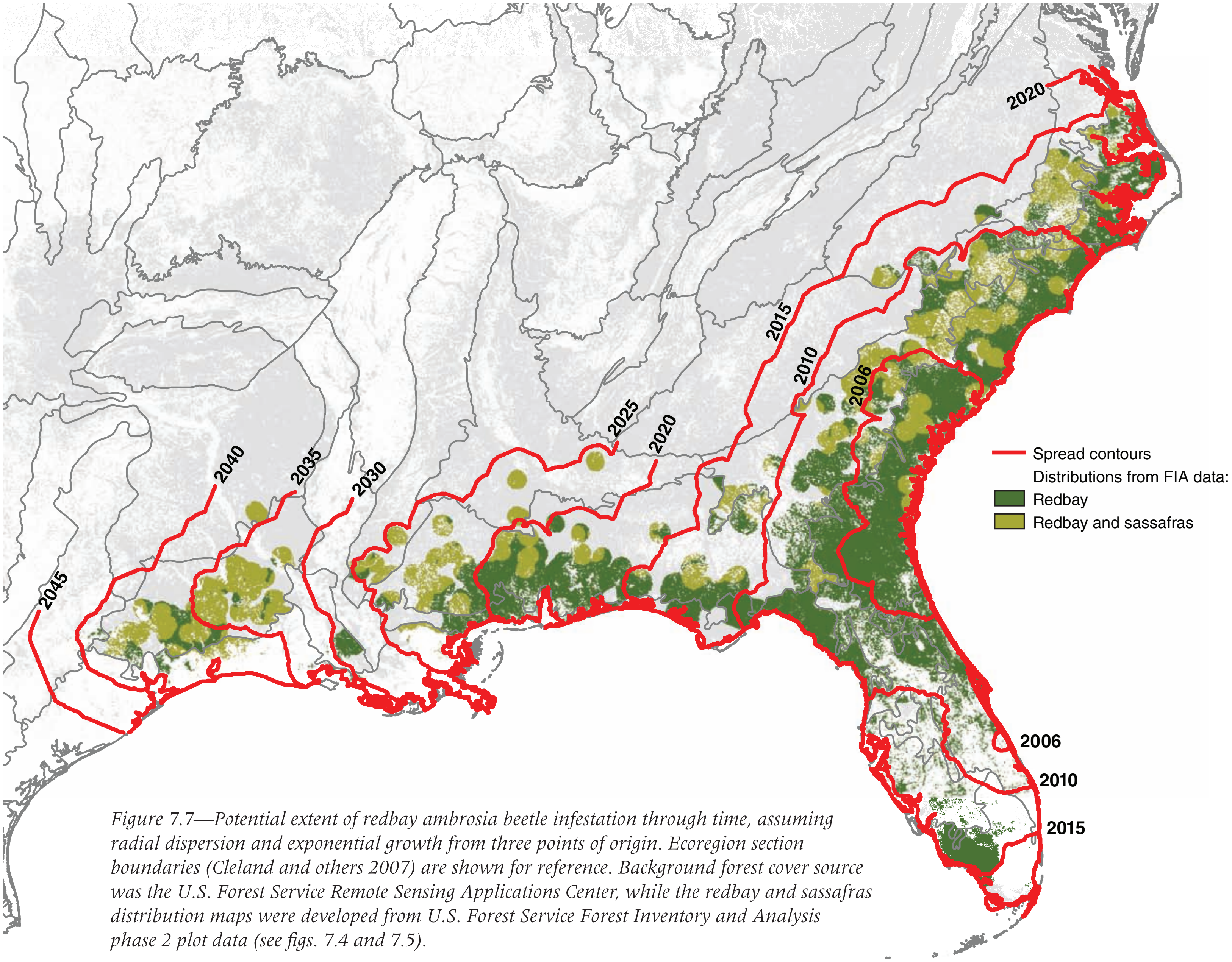


*Figure 7.7—Potential extent of redbay ambrosia beetle infestation through time, assuming radial dispersion and exponential growth from three points of origin. Ecoregion section boundaries (Cleland and others 2007) are shown for reference. Background forest cover source was the U.S. Forest Service Remote Sensing Applications Center, while the redbay and sassafras distribution maps were developed from U.S. Forest Service Forest Inventory and Analysis phase 2 plot data (see figs. 7.4 and 7.5).*

A nationwide cost grid was developed primarily from the interpolated map of redbay trees per acre, under the assumption that high host densities would decrease the travel cost for dispersing redbay ambrosia beetles, while a lack of hosts would greatly increase the travel cost, i.e., travel cost is inversely related to host availability. Although the beetle does attack sassafras, these attacks have so far occurred only in areas where redbay is common, so it is unclear whether the beetle is attracted to and will infest sassafras when redbay is absent. Therefore, we only added sassafras trees per acre to the total value for grid cells where the redbay trees per acre value was also greater than zero. Typically, the addition of sassafras resulted in a negligible increase in the total trees per acre value. A series of simple step functions, relating trees per acre ($x$) to cost ($y$), was developed by varying minimum and maximum possible cost values, as well as the threshold values between steps. The step functions were applied to the total trees per acre grid in order to make preliminary cost-weighted spread maps, which were then compared to the county-level infestation data. The step function that yielded the best approximation of the infestation pattern through time had a maximum cost value of 3 when no host was present and a minimum cost value of 0.25 at a host density of 240 trees per acre. Subsequently, a continuous function was estimated by fitting the selected step function with the complemented Weibull equation (Haefner 2005):

$$y = a * \exp\left( - \left[ \frac{x}{b} \right]^{c} \right)$$

where

$x$ = the trees per acre value

$y$ = the cost value

$a$ = a parameter that scales the maximum value

$b$ = a parameter that controls the point on the x-axis at which the function is approximately zero

$c$ = a parameter specifying whether the function is convex or concave

Parameters *a*, *b*, and *c* were estimated using the NLIN procedure for fitting nonlinear models in SAS (SAS Institute 2004); the parameterized function, as well as the step function to which it was fitted, is shown in figure 7.8. The function was applied to the total trees per acre map to create the cost grid, which was then used to create a map of cost-weighted distance from points of origin in Beaufort County, SC, as well as Duval and Indian River Counties in Florida.

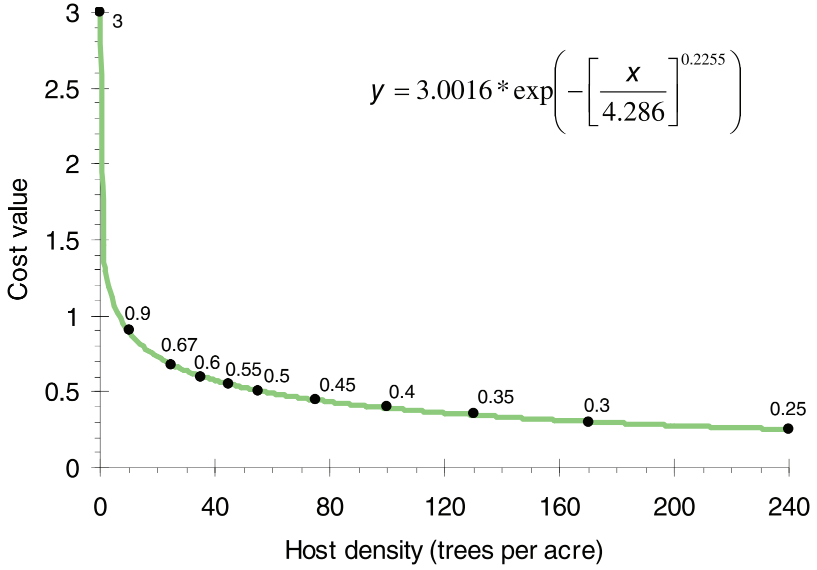


*Figure 7.8—Complemented Weibull function used to relate host density in trees per acre to cost for the cost-weighted spread model. Black circles indicate point values that describe the step function to which this continuous function was fitted. See text for additional explanation. Residuals between step function values and predicted cost values were all within +/- 0.01.*

The latter two points of origin were assumed to represent initially isolated infestations that had been caused by accidental long-distance transport of the redbay ambrosia beetle from locations to the north. All three originating infestations were assumed to have started 1 year prior to the confirmed presence of the beetle and/or fungus at each location. The cost-weighted distance map was reclassified into an increasing series of equal intervals based on the previously calculated invasion front velocity, such that each interval represented the amount of area added to the infestation extent with one additional year of infestation.

## Results and Discussion

**Current Beetle/Wilt Distribution**—In interpreting the county-level distribution map for the redbay ambrosia beetle and laurel wilt (fig. 7.1), it is important to acknowledge the coarseness of the data and the fact that difficulties in positively confirming any pest’s presence may result in a timelag in reporting. According to these data, in the 5 years since the ambrosia beetle was first detected in Port Wentworth, 18 Georgia counties, comprising the majority of the State’s Lower Coastal Plain province (Hodler and Schretter 1986), have been impacted by laurel wilt (fig. 7.1). In South Carolina, the seven counties closest to Port Wentworth have been impacted. Based on the chronology depicted by these data, it seems that the northward expansion of the beetle and fungus along the coast of South Carolina has been slower than the southward expansion in Georgia. However, the current extent of the invasion in Georgia may also have been influenced by northward movement of the beetle and fungus from locations in Florida. In northeastern Florida, the addition of four impacted counties in 2007 suggests rapid inland and westward expansion in addition to spreading south along the Atlantic coast. In addition, the recent detection of laurel wilt in Brevard County, FL, seems to indicate ongoing northward expansion from the previously isolated occurrence in Indian River County.

The Georgia and South Carolina redbay mortality survey results (fig. 7.2) provide some specific details on geographic pattern. In South Carolina, approximately 21 percent of the plots contained redbay trees affected by laurel wilt. The highest concentration of mortality was in the two coastal counties—Jasper and Beaufort—that are closest to Port Wentworth. However, Hampton, Bamberg, and Colleton Counties also had plots exhibiting severe (> 67 percent) redbay mortality. The leading edge of the infestation in the State appears to run along the border between Allendale and Hampton Counties, and then through southern Bamberg, Colleton, and southern Charleston Counties, basically mirroring the map of confirmed positive counties (fig. 7.1). Complicating the matter somewhat is light (< 33 percent) redbay mortality recorded in many plots throughout South Carolina. A lack of evidence of the laurel wilt fungus in these plots suggests the mortality was not precipitated by the redbay ambrosia beetle but instead represents a level of background mortality due to other insects, diseases, or undetermined environmental factors (see footnote 2).

The pattern of moderate (34 to 66 percent) to severe redbay mortality is more diffuse in Georgia. While there appears to be a large cluster of heavy mortality spanning Screven and Bulloch Counties, it should be noted that these two counties were intensively sampled; substantial redbay mortality was also recorded at plots in all of the less-intensively sampled counties directly along the coast, particularly Bryan County. Several plots in Camden County, just north of the Florida border, also exhibited moderate to severe mortality, supporting the notion of northward spread of the beetle and its associated fungus. Clear identification of the leading front of infestation in Georgia is more difficult than for South Carolina because relatively isolated inland plots in Charlton and Appling Counties exhibited severe redbay mortality while neighboring plots displayed no mortality. As in South Carolina, the leading front appears to mirror the furthest extent of infestation as depicted in the county-level map. The Georgia survey also noted mortality of sassafras on one plot each in MacIntosh and Glynn Counties (see footnote 3), and mortality of sassafras due to laurel wilt has since been confirmed in Beaufort County, SC[4]. As previously noted, there is no evidence that the redbay ambrosia beetle is preferentially attracted to sassafras, so it appears likely the attacks on sassafras in these locations were merely opportunistic.

**Host Species Distributions—**As with fig. 7.1, the distributions of Lauraceae species are represented coarsely, i.e., at the county level, in fig. 7.3, so the amount and connectivity of potential host habitat may be less than the map suggests. Moreover, it is important to consider the lack of evidence that any Lauraceae species besides redbay, despite their demonstrated susceptibility to the laurel wilt fungus, is an equally attractive host for the redbay ambrosia beetle. Keeping these points in mind, with the exception of the Rocky Mountain region and at northern latitudes (above roughly 45° N.), most forested areas of the conterminous United States have at least one species from the Lauraceae family. California bay laurel is a common understory species in the forests of the Pacific coast; notably, this species has played a major role in the epidemiology of *Phytophthora ramorum*, the pathogen that causes sudden oak death (Rizzo and Garbelotto 2003). Northern spicebush and sassafras are both widespread throughout the East. Nevertheless, coastal areas of the Southeastern United States exhibit the greatest diversity of Lauraceae species. As noted in table 7.1, many of these species are rare and thus only sporadically distributed. The nonnative camphor tree (*Cinnamomum camphora*) is also sporadically distributed across the Southeast and the Pacific coast, while the bay laurel (*Laurus nobilis*) is limited to a few counties in northern California. Avocado trees are grown in commercial orchards in south Florida but can be found in a few sites elsewhere in the State. The avocado industry is actually far more extensive in southern California, but occurrence of the species outside a commercial setting in the State is undocumented.

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[4] Personal communication. 2007. Laurie Reid, Forest Health Program Coordinator, South Carolina Forestry Commission, P.O. Box 21707, Columbia, SC 29212.

Redbay (fig. 7.4) is widespread across most of the ecoregion sections of the southeastern Coastal Plain at low densities (< 25 trees per acre), reaching as far south as the Everglades (section 411A). In particular, section 232C—Atlantic Coastal Flatwoods, which encompasses much of the area currently affected by redbay ambrosia beetle and laurel wilt, contains numerous redbay clusters of moderate to very high (> 100 trees per acre) density. Nonetheless, the greatest concentration of redbay by far is found on the Albemarle Peninsula of eastern North Carolina (in section 232I—Northern Atlantic Coastal Flatwoods). Along the gulf coast, there appears to be a break in the distribution of redbay at section 234A—Southern Mississippi Alluvial, which may be due in part to a lack of forested area in this section. West of this break, the species persists into the forests of eastern Texas.

Sassafras (fig. 7.5) is widely distributed at low levels (< 15 trees per acre) throughout the Southeast. Notably, the species reaches very high (> 60 trees per acre) density levels in the westernmost portions of section 223A—Ozark Highlands; this section serves as the western end of a swath of moderate to very high sassafras density extending eastward to sections 221E—Southern Unglaciated Allegheny Plateau and M221C— Northern Cumberland Mountains. Sassafras is present at low to moderate levels at least as far north as Michigan (section 212H—Northern Lower Peninsula and section 221A—Lower New England). In short, with the exception of some apparent gaps in sections 231A—Southern Appalachian Piedmont and 231I—Central Appalachian Piedmont, there appears to be a near-continuous distribution of sassafras from the upper edge of the southeastern Coastal Plain, although it is worth noting the great variation in topography and other environmental characteristics across the species' range.

**Climate Matching—**The range of values for each variable used in the climate matching is fairly large (table 7.2). This may be partially attributed to the scale at which the native geographic distribution of the redbay ambrosia beetle was defined during the modeling process. Without detailed distribution information, it was typically necessary to include entire countries or large portions of those countries in the delineated extent. More specific observational data on the beetle's occurrence would allow refinement of this distribution and probably decrease the range in variable values. Regardless, the resulting map (fig. 7.6) illustrates some points relevant to the risk of the beetle's spread in the United States. Most importantly, the climatically suitable area is largely constrained to the Coastal Plain of the

Southeastern United States, or essentially the range of redbay; with the exception of a small area in the southern portion of the Blue Ridge Mountains (ecoregion section M221D), no other part of the conterminous United States appears suitable under the model. Functionally, the model does not define meaningful upper limits for monthly rainfall since the maximum values for these variables under the model are generally far beyond the maximums found in the conterminous United States. However, the model does define minimum acceptable levels of monthly rainfall during the growing season, and these minimums, especially for August and September, exclude much of the area deemed suitable under the model, i.e., only the Southeastern United States receives adequate rainfall across all months of the growing season. The ecological importance of this seasonal effect is uncertain, but it is worth noting that the fungi associated with ambrosia beetles typically have exacting moisture requirements: if there is too much moisture, the beetles and larvae will drown in an overabundance of fungi, and if there is too little moisture, the fungi will die, leaving no food source for the beetles (Furniss and Carolin 1977). At the least, the climate matching results suggest that coastal areas of the Southeast are far more susceptible than elsewhere in the United States, and that this may limit the spread of redbay ambrosia beetle and laurel wilt into forests of the U.S. interior.

**Spread Modeling—**The calculated invasion front velocity, i.e., the annual rate of spread, for the beetle and its associated fungus was 46.9 km (29.1 miles) per year, which falls in the range of anecdotal estimates. However, our assumption of simple radial diffusion does not account for potential variability in the rate of spread between geographically distinct areas; there is some evidence suggesting the actual rate of spread is much higher in Florida than in South Carolina,[5] where northward expansion has been relatively slow despite a relative abundance of redbay (see footnote 2). The rate also does not account for the possibility of long-distance dispersal events and so may be seen as a conservative estimate of the spread rate in this regard. Broadly, pest invasions may occasionally accelerate or decelerate through time, particularly in response to anthropogenic influences (Liebhold and others 1992). A more realistic model might incorporate specific population parameters or allow for long-distance dispersal beyond the main infestation front. Furthermore, it is important to consider that the rate of spread was estimated using only a few years of data and for a pest that was

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[5] Mayfield, A.E. 2007. RE: redbay wilt/ambrosia beetle. fkoch@fs.fed.us. (22 May, 2007).

only recently identified in the United States. The limited data make the estimate especially sensitive to the possibility that some of the apparently new infestations discovered in any given year are actually just late detections of infestations that had existed for some time previously. As a result, the invasion timeline may be falsely accelerated and the actual rate of spread may be overestimated. To alleviate this problem, the rate of spread estimate may be refined as additional years of data become available; indeed, the estimate presented here has decreased from a spread rate of approximately 55 km per year calculated using only the distribution data from 2004 to 2006 (Koch and Smith 2008). This decrease, based on an additional year of data, emphasizes that the estimate should only be interpreted as preliminary.

The possible timelag in detections also has bearing for the cost function and corresponding cost grid used in modeling spread, since we fitted the function to the county-level distribution data as they are currently depicted. Beyond this issue, it must also be acknowledged that the cost-weighted spread model assumes a fairly straightforward relationship between host density and the dispersal capability of the redbay ambrosia beetle. When viewed at a broad scale, i.e., at the metapopulation level, it seems reasonable that the distance the main invasion front advances in a given year depends on the availability of hosts to sustain population growth near the front. However, this approach does not account for individual beetles that may venture beyond the main front in search of hosts. Still, if nothing else, this simple model illustrates the scope of the threat represented by the beetle and its associated fungus (fig. 7.7). Assuming a mean rate of spread of approximately 47 km/year and assuming spread is influenced by the density of available hosts, the redbay ambrosia beetle could reach both the northern and southern limits of redbay by 2020, with nearly the entire range of redbay infested by 2040. Even if spread is reduced by 16 km (10 miles) per year, e.g., as a result of suppression efforts, the entire range of redbay may be infested in just over 50 years.

## Conclusions

There is little reason to doubt that the current redbay ambrosia beetle infestation, if unchecked, will expand north and south along the Atlantic coast of the United States and west along the gulf coast. Redbay is present throughout these regions along with other susceptible and potentially susceptible hosts such as sassafras that, while not necessarily attractive, may still be utilized by the beetle. There are few geographic barriers aside from the Mississippi River, and a fairly restrictive model of climatic suitability puts nearly the entire range of redbay at approximately equal risk of infestation. While the climate-matching model does seem to suggest that the western edge of the redbay range may be unsuitable, this should be viewed cautiously given the limitations of the analysis. In any case, it seems unlikely the redbay ambrosia beetle and its associated fungus will spread significantly into inland forests based on the apparent climatic and host constraints. Moreover, the Appalachians or related mountain chains may represent an additional geographic barrier to broad northward expansion. Further research is needed on both the beetle and fungus to ascertain a more certain picture of the potential risks.

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## Appendix

Kriging is a geostatistical technique for spatially interpolating values of a continuous variable at unknown points from the values of neighboring points. The underlying spatial structure, i.e., spatial dependence or autocorrelation, of a variable may be quantified using an empirical semivariogram constructed from pairs of the known points comprising a sample of the variable. For a set of points, the semivariance at a given distance $h$ is calculated as:

$$\gamma(h) = \frac{1}{2N(h)} \sum_{N(h)} (Z(x_i) - Z(x_j))^2$$

where

$x_i$ and $x_j$ = known point locations separated by distance $h$

$Z(x_i)$ and $Z(x_j)$ = variable values at the known points

$N(h)$ = the number of point pairs separated by distance $h$ (Cressie 1993)

Briefly, the semivariance at distance $h$ equals one-half the mean squared difference in variable values between all point pairs at distance $h$. When plotted, an empirical semivariogram depicts the relationship between semivariance and distance (fig. 7A.1). Generally, it is impractical to plot the semivariance values at all possible values of $h$, so the values are grouped into lag distance bins, e.g., all point pairs between 10 km and 20 km apart, for simplicity. A semivariogram has three key parameters. The nugget is the semivariance when the distance equals zero and is often equated to measurement error. The sill is the semivariance, and the range is the distance at which the plot flattens out, i.e., where the sample locations are no longer spatially autocorrelated (Environmental Systems Research Institute 2003). The partial sill is the difference between the nugget and sill values.

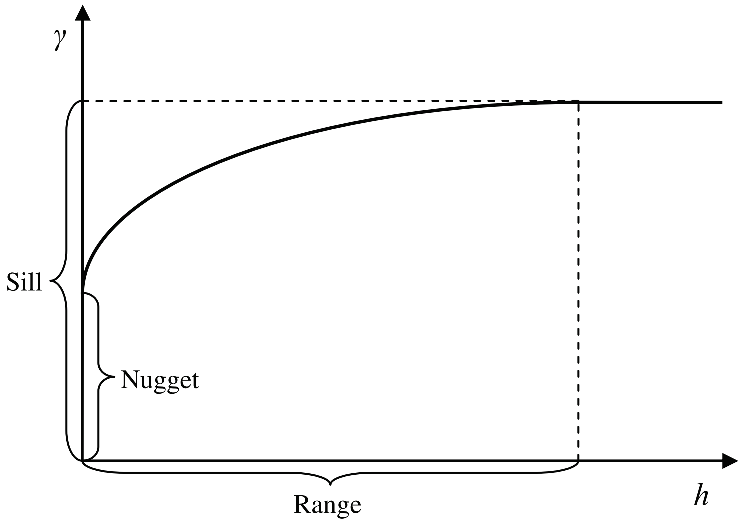

*Figure 7A.1—Conceptual rendering of a semivariogram showing the nugget, range, and sill.*

An empirical semivariogram may be estimated using one of numerous model semivariograms. For the redbay and sassafras trees-per-acre surfaces, spherical semivariogram models were fitted to empirical semivariograms constructed using all FIA plots in the ecoregion sections containing each species. For each, the lag distance was set to 30 000 m, and weighted least squares (Cressie 1993) was used to estimate the model semivariogram parameters: for redbay, range = 355,600 m, partial sill = 467.79, and nugget = 1544.7; for sassafras, range = 212,480 m, partial sill = 323.11, and nugget = 1333.5. These estimated spherical models were applied when performing the bysection interpolations for each species.

Ordinary kriging is a commonly used form of kriging that assumes a constant mean. With respect to spatial prediction, kriging is similar to inverse distance weighting and other methods that estimate values for unknown points based on a weighted average of known neighboring points. The variable value $Z$ at unknown location $s_0$ is estimated as

$$\hat{Z}(s_0) = \sum_{i=1}^{n} \lambda_i Z(s_i)$$

where

$Z(s_i)$ = the known variable value at neighboring location $s_i$

$n$ = the number of neighboring known points used to estimate the value at $s_o$

$\lambda_i$ = the kriging weight for location $s_i$, such that $\sum_{i=1}^{n} \lambda_i = 1$

The kriging weight for a given neighboring point $s_i$ is calculated using the model semivariogram, such that the weight reflects not just distance but also the degree of spatial autocorrelation indicated by the model.

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