The Effect of an Introduced Ambrosia Beetle (*Xyleborus glabratus*) on Red Bay (*Persea borbonia*) Mortality in Maritime Forest Communities of St. Catherine’s Island, GA

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Abstract

Over the past three years, red bay (*Persea borbonia*, Lauraceae) populations along the Georgia coast have experienced high levels of mortality due to an introduced fungal pathogen (*Ophiostoma* sp.) being spread by outbreaks of a recently introduced, Asian ambrosia beetle, *Xyleborus glabratus*. The beetle carrying the fungus was believed to have arrived in this country on shipping pallets and was first identified in the port of Savannah, Georgia in 2002. Red bay is an abundant and ecologically important tree species found in the coastal plain of the southeastern United States. This study represents the first assessment of red bay decline, which as a casualty of an introduced pathogen, may be following the same fate as American chestnut, American elm and flowering dogwood in the forests of the eastern U.S. Five 5000m² plots were established on St. Catherine’s Island, a barrier island south of Savannah. The status of red bay populations in these plots was assessed in 2004, 2005 and 2006 for leaf wilt, diameter at breast height (DBH), and the presence of basal sprouts. It was determined from that red bay is a common species represented in many size classes. Across the five study sites, the proportion of fully wilted red bays increased from 0.06 in 2004 to 0.89 in 2006. A fitted logistic regression model for binary response variables suggested that DBH was not a significant predictor of probability of infection (p>0.05), while site and year were significant (p<0.05). The odds of basal sprouting on a dead tree in 2006 were 7.09 times higher than the odds of sprouting on a live tree. However, potential regeneration by basal sprouts was severely limited by deer browse. A comparison with Dutch Elm Disease (DED) and other significant tree losses suggest that red bay will likely meet the same fate. This will have serious consequences for the already degraded maritime forest ecosystem in terms of species composition, structure and function.
**Introduction**

Introduced species can cause dramatic changes in forest ecosystem dynamics, especially in terms of species composition, structure and function (Steffen *et al.*, 1996 and Hiers and Evans, 1997). In some invasions, an introduced pathogen or pest will almost exterminate one or several species. This is what happened in the Dutch elm disease (DED, *Ophiostoma ulmi*, *O. novo-ulmi* and *O. himal-ulmi*), a beetle-transmitted fungus that affects the popular urban shade tree, *Ulmus americana* and killed an estimated 50 million to 100 million trees (Harrington *et al.*, 2001 and Cheng *et al.*, 1997); the chestnut blight (*Cryphonectria parasitica*), a fungus that affects *Castanea dentata* and eliminated one of the largest and most common trees east of the Mississippi (Milgroom, 2004 and Woods and Shanks, 1959); dogwood anthracnose (*Discula destructiva*), a fungus that has had significant effects on *Cornus florida* and its ecosystem (Hiers and Evans, 1997); and the current hemlock wooly adelgid (HWA, *Adelges tsugae*), an aphid-like insect that is eliminating stands of *Tsuga candensis* and spreading quickly (Orwig and Foster, 1998).

The loss of a species from a community can have strong effects on the future composition of the remaining community (Steffen *et al.*, 1996). Removal of a species opens up a space both physically and in terms of niches that can be occupied by other species (Hiers and Evans, 1997, McCormick and Platt, 1980, Orwig and Foster, 1998 Steffen *et al.*, 1996 and Woods and Shanks, 1959). The resulting change in composition and structure will depend on how abundant that species was. Consider the chestnut blight, which removed one of the most dominant tree species in its range (McCormick and Platt, 1980 and Woods and Shanks, 1959). This resulted in a new structural opening in the forest that allowed light to reach the floor. Previously the long-lived chestnut had shaded
that forest floor. Different species took advantage of this resource and soon the forest was transformed into a community dominated by oaks, hickories and maples (McCormick and Platt, 1980 and Woods and Shanks, 1959).

Species that alter physical conditions, create ecologically useful structure and provide resources are called structural species (Huston, 1994). The replacement of such species by other species can have effects on important aspects of the forest by changing microclimates, which provide specific habitats that serve as ecological niches for other species (Orwig and Foster, 1998). This is occurring with the loss of hemlock (*Tsuga canadensis*) from eastern forests. The hemlock grows in dense stands that provide a shaded, moist environment for species such as the redback salamander (*Plethodon cinereus*, Brooks, 2001). Following infection by HWA and subsequent removal of hemlock from the overstory, there is a change in this environment marked by a greater amount of light and an increase in soil temperature. Redback salamander populations declined after this change, suggesting that the new environment was not a suitable habitat for that species.

The absence of a species from a forest may have consequences in cycling of certain nutrients (Hiers and Evans, 1997). This is especially prominent when the species is abundant in its community (Hanski, 1982). Certain species such as dogwood may be responsible for the cycling of certain nutrients that are necessary for healthy, functioning ecosystem. Its removal will therefore slow the cycling process and could result in the loss of those nutrients via leaching from the soil unless another species assumes that role. Dogwood is a deciduous tree that has a high calcium content in its leaves (Hiers and Evans, 1997). Because this tree drops its leaves every year, it returns the calcium to the
soil. The loss of large numbers of this species to dogwood anthracnose will therefore probably have significant effects on this cycle.

This study examines another introduced species having a significant effect on a forest species. The introduction of an Asian ambrosia beetle into Southeastern US maritime forests has caused a recent decline in red bay trees (*Persea borbonia*, Lauraceae), an ecologically important tree in the Southeastern coastal plain (Brendemuehl, 1990). This invasion and loss will inevitably have an effect on species richness and diversity of a very specialized, increasingly rare ecosystem.

Red bay is a common, medium-sized, evergreen hardwood found throughout the coastal plain of the southeastern United States (Brendemuehl, 1990). In most of the maritime forest on the Atlantic shore, it is found to be the top two or three most common tree species in terms of number and percent cover (Bourdeau and Oosting, 1959, Bratton and Davison, 1987 and Bratton and Miller, 1994). This aesthetically pleasing tree is sometimes used as an ornamental and plays an important role in native ecosystems. The small, blue-black fruits are volumetrically the 15\textsuperscript{th} most important part of the diets of several types of wildlife, including songbirds, bobwhite, wild turkey and black bear (Brendemuehl, 1990). Deer also browse the foliage, especially in fall and winter months. The tree is also the sole host for palamedes swallowtail butterfly (*Papilio palamedes*, Papilionidae) larvae (Scriber and Margraf, 2000).

The loss of the red bay tree (*Persea borbonia*, Lauraceae) due to an infestation of the ambrosia beetle *Xyleborus glabratus* (Scolitidae) has been observed for the past five years (Thomas, 2005, Figure 1). *X. glabratus* is an Asian ambrosia beetle that was discovered in the port of Savannah, Georgia in 2002 (Rabaglia, 2003). Since this time it
has spread as far north as Bamberg county, South Carolina and as far south as Putnam county, Florida, with an outlier county much further south (Figure 2). The epidemic appears to affect trees in a variety of habitats including swamps, flat and upland forests and residential areas. It is believed that the beetles arrived from Asia in wooden shipping pallets. This is the twelfth species of Asian ambrosia beetle introduced to North America. In its native range, the beetle is not common and very host specific. In general, it prefers to inhabit aromatic species.

The beetle transmits an Ascomycete fungus of the *Ophiostoma* clade by burrowing into the wood of the tree and cultivating the fungus for food (Mayfield, 2005). Ascomycete fungi commonly associate themselves with insects for dispersal and *Ophiostoma* is the largest clade of Ascomycetes that do this (Harrington *et al*, 2001). Other fungi of the same genus, *O. ulmi*, *O. novo-ulmi*, and *O. himal-ulmi*, all carried by beetles as well, are the cause of the Dutch elm disease. While the behavioral ecology of the beetle as it relates to red bays is not yet fully understood, it is recognized as the harbinger of death and the fungus is the ultimate killer of the tree.

This study quantified the severity of the *Ophiostoma* infection on a barrier island on the coast of Georgia. St. Catherine’s Island is a privately owned island about 30 miles south of Savannah with little development (Figure 3). The terrain is mostly second-growth maritime forest and long leaf pine stands. Four hypotheses were tested: First, we hypothesized that we would be able to see an increase in the severity of the epidemic on the island across two years. Second, we hypothesized that the beetle does not discriminate between trees based on size and therefore that this is not associated with red bay mortality. Third, we hypothesized that we would be able to detect differences among
sites. In particular, we predict that we will see a north to south gradient in the severity of the epidemic because the beetle is traveling south from Savannah. And fourth we hypothesized that infected trees will try to regenerate by sprouting. Therefore we predict a higher occurrence of basal sprouting in infected trees.

**Methods**

The study was conducted across three years on St. Catherine’s Island, a barrier island on the coast of Georgia about 30 miles south of Savannah (Figure 3). The terrain includes marsh, longleaf pine, pasture, and second-growth and old growth maritime forest. Development on this privately owned island is limited. This island represents an excellent example of a healthy maritime forest. The island is within the range of the red bay (*Persea borbonia*) (Brendemuehl, 1990), and the tree is common. The sample sites visited in this study are representative of typical barrier island forest ecology with red bay as a core species (Hanski, 1982).

Five 5,000m$^2$ sample plots were established non-randomly in early July of 2004 at sites known to have red bay populations (Figure 3). In early July of 2005 and 2006 the sites were revisited and sample plots were reestablished in the approximate area of the original plots using GPS coordinates. Over two or three days, a walking census of red bays was conducted within each plot. Measurements were recorded for the diameter at breast height (DBH), presence of sprouts and amount of foliage wilt. Because the tree keeps its foliage with wilting, we were able to identify red bays post mortem (Mayfield, 2005, Figure 1).
Red bay wilt was recorded in four classes, based on an estimation of percent foliage death. Since then it has come to our attention that another beetle, *Xylosandrus compactus* that can cause partial, non-lethal wilting in red bays (Dixon, Woodruff and Foltz, 2003). These beetles burrow into small, peripheral twigs and are less host-specific than *Xyleborus glabratus*, the target beetle of this study. In order to assure that the tree is hosting the *X. glabratus* and death is immanent, we only classified trees with 100% leaf wilt as being infected.

In order to predict the probability of infection for individual trees as it relates to time, location and size, and because of the binary nature of the classification of infected and non-infected trees, logistic regression for binary response variables was used to analyze the relationship between probability of tree infection and year, site and DBH (Ramsey and Schafer, 1997). The backward elimination method of model selection was used to examine the significance of association between probability of 100% leaf wilt and the explanatory variables year and DBH and the indicator variable, site. The reference variable for the site indicator variable was *site1*, which refers to site 1 one of the plots established on the island (Figure 3). The full model that was considered, in which $\logit(\pi)$ is the log of the odds of 100% leaf mortality, is shown below.

$$\logit(\pi) = \beta_0 + \beta_1 \text{year}^2 + \beta_2 \text{site}_2 + \beta_3 \text{site}_3 + \beta_4 \text{site}_4 + \beta_5 \text{site}_5 + \beta_6 \text{DBH}$$

A drop in deviance chi-square test was used to determine whether the reduced model was sufficient for explaining the response variable when compared to the full model. The drop in deviance from the full model to the fitted model was compared to the chi-squared distribution. A small p-value would suggest that the reduced model is inadequate (alpha = 0.05).
The sprouting hypothesis was analyzed using a Mantel-Haenszel chi-square test with Yates’ continuity correction at the alpha = 0.05 level, with year used as the stratifying variable to account for changes across time. The odds ratio was calculated to compare the probabilities of sprouting in live versus dead red bays.

Results

Red bay was found to be a common tree on the island. The average tree density across the five sample sites was 1.3 trees per 100m² in 2004. The tree was also represented in a variety of size classes (Table 1). The percent of fully infected red bays increased from 6% in 2004 to 89% in 2006. This trend was evident in every site and was also evident in every DBH size class (Figure 4, Table 1).

Effect of Size on Infection

We developed an equation based on a model that allowed us to predict the probability of infection of an individual tree based on location, time and size. Following explanatory analysis of data and backward elimination of model parameters using the drop in deviance chi-square test, the following model was developed:

\[
\text{logit}(\pi) = -4.11 + 0.76year^2 + 0.72site_2 - 0.62site_3 - 0.17site_4 - 0.62site_5
\]

In the full model, which included year, site and DBH, DBH was an insignificant variable in red bay mortality (p>0.05) and was consequently removed from the model. This means that DBH has very little predictive value in determining the probability of a tree being infected. In terms of this study, it means that trees of every size class are being infected evenly on a year-to-year basis. Even so, when split into size classes, DBH was suggestive of a pattern in which larger trees are infected more quickly than smaller trees (Table 1).
Effect of Time on infection

Time was a significant predictor of the probability of infection (p<0.05, figure 4). Over the course of the three years there was an increase in probability of infection in every site. By the third year of the study, most sites were at or near a 90% probability of infection for individual trees. This is indicated by both our findings of the proportion of trees infected at each stand as well as the probability of death for individual trees during each year suggested by the model.

Site and infection

This model indicates a strong association of probability of infection and site (p<0.05). For each site, the individual predicted probabilities of tree infection were very close to the actual observed proportions of infected trees in the sampled populations (Figure 4). A general trend was observed based on site: Populations on the northern end of the island and closer to the shore were affected sooner and more severely than more southerly, centrally situated sites (Figure 4).

Sprouts and infection

The final variable of interest, sprouting, was observed on a number of trees, most of which were infected. Our unsystematic field observations were confirmed by analysis of our systematically collected data. The Mantel-Haenszel chi-square test with Yates’ continuity correction was highly significant, suggesting a greater amount of sprouting among trees with 100% leaf wilt (p<0.05, Table 2). This trend was consistent over the three years. The odds of sprouting in fully wilted red bay was 2.83 times greater than sprouting in a tree with less than 100% infection in 2004, 5.91 times greater in 2005 and 7.09 times greater in 2006.
Discussion

The hypothesis that the proportion of infected *Persea borbonia* (red bay) on the island is increasing was supported by the fact that time was a significant predicting variable in our reduced model. The predictions based on this model are very close to the actual observed proportions at each site every year (Figure 4). This means that our model is an accurate predictor of the probability of death for trees in those populations at that time. The increase in the odds of becoming infected implies that the tree infection is an epidemic and is spreading locally.

The other significant predicting variable in the reduced model was site. This means that the probability of red bay infection varies as a result of the location of the population. The observed trend was that trees in the north and closer to island edges had a greater probability of infection. This confirms our hypothesis that, based on the fact that the beetle was first found north of the island in Savannah (Rabaglia, 2003), we could see a local north to south gradient because the beetle arrived on the island from the north. This gradient also suggests that the beetle is spreading southward through the red bay populations. This is consistent with other observations (Figure 3). It is known to travel up to 3 km actively searching for red bays to be colonized (Rabaglia, 2003).

Although this is promising and fitting data, there are other variables that could influence site and the north-south gradient. The first is that because the three northernmost sites are located near island edges, they are subject to edge effects such as salt spray that could weaken trees (Wells and Shunk, 1938), making them more susceptible to death of any type. It is not uncommon for an entire forest to succumb to
beach erosion and die. The two populations sampled in the south were located in the interior of the island where they were not exposed to such harsh conditions.

The data support our hypothesis that infected red bays sprout more often than non-infected red bays (Table 2). The odds of an infected red bay sprouting was always greater than twice the odds of a non-infected red bay, reaching a high of seven times in our most recent data. This trend of increasing odds ratios by year is probably due to the increase in number of trees that are beginning to be infected. It must be remembered that we used a 100% wilt cutoff for infection, therefore trees that were just beginning to be infected were counted as non-infected. They may also have begun sprouting. The reason sprouting is important is that it echoes what is seen as a response to the chestnut blight (Stephenson, Adams and Lipford, 1991). Chestnut sprouts are actually still a significant understory plant in terms of composition in Appalachia, and it is predicted that they will be for years to come (McCormick and Platt, 1980). Unfortunately, sprouts usually become infected by the fungus and die before they are old enough to flower. We are not sure if this scenario will be duplicated, but the fact that they are sprouting suggests this course. A second destructive force for sprouts are white-tailed deer, which have been increasing in numbers sharply over the last few decades and feed on red bay vegetation (Cote et al., 2004).

Although no significance was found for any association between probability of infection and DBH, the data were suggestive of a pattern in which the older trees were infected before the younger trees (Table 1). This may be a result of a larger tree’s greater capacity to release aromatic chemicals. These chemicals have been implicated in both attracting and repelling certain insects (Frankfater and Scriber, 1999 and Scriber and
The beetle in its native habitat is attracted to several aromatic species (Rabaglia, 2003). Further research is needed in determining what attracts the beetle to red bays.

Once a beetle has been attracted to a site, it spreads very quickly (Figure 4). This means that the beetle infects all trees, even smaller ones, quickly. So even if larger trees are infected first, because we had a one-year lapse between measures, we were probably not able to pick up on any trends in the order of infection for different size classes. This would account for the lack of predictive power of DBH in our reduced model. If small trees are infected after larger ones, but both become infected over the course of a year, our measures would not have been sensitive enough to detect this. Although this is highly speculative, it exposes avenues for new research that may find a pattern of infestation in a population that is mediated by DBH.

Our interpretation of the data suggests that Red bay is in serious danger of becoming ecologically extinct. All of our hypotheses were supported by our findings. Most sites are approaching a state in which 100% of trees are wilted, if they are not there already (Figure 4). Site is an important factor in probability of death, and the trend suggests that the probability of death is higher near the edges of the island and in the northern parts. Sprouting is much more likely in a dead tree than in a living tree. Diameter at breast height (DBH) is an insignificant factor, making this disease similar to other extremely harmful pathogens and pests.

Comparison with other pathogen and pest-caused tree declines

Red bay is quickly becoming ecologically extinct throughout its range. A certain population size and density are required to maintain ecological effectiveness in
interactive species (Soule et al, 2005). In contrast, if this is not maintained then ecological effectiveness will decline. Coupled with our results, this suggests that the population of red bay will eventually become so low that it will no longer have a significant role in the ecosystem. The infestation and subsequent death of \textit{P. borbonia} by \textit{Xyleborus glabratus} shares many common features of other ecosystem-altering invasive pathogens. It can be compared to other large-scale pest and pathogen problems such as the hemlock wooly adelgid (HWA), the chestnut blight, Dutch elm disease (DED) and dogwood anthracnose.

The method by which the individual trees are killed in these five epidemics have one basic underlying theme: strangulation. Each one of the infestations discussed in relation to red bay kill their host by eventually cutting off the flow between the leaves and the roots. The main stem of the chestnut and the dogwood are both eventually girdled by a growth caused by a fungus (Carr and Banas, 2000, Milgroom 2004 and Woods and Shanks, 1959). The hemlock wooly adelgid is a small aphid that feeds with a stylet on ray parynchyma cells in young twigs (Orwig and Foster, 1998). Within four years it kills the leaves, buds, branches and the entire tree.

The elm has a very similar story to the red bay. Like the in the case of the red bay, a non-native beetle transports a fungal pathogen to the tree, which eventually kills it (Harrington et al, 2001 and Cheng et al, 1997). The use of beetles as a dispersal mechanism probably increases the rate at which the epidemic spreads. In the case of red bay, the beetle can fly for up to 3 kilometers actively seeking out trees. (Rabaglia, 2003). Other dispersal mechanisms for these diseases include deer, wind, birds and human activity such as logging (Orwig and Foster, 1998).
These five pathogens also share characteristics commonly found in successful invasive species in general. None of them have any natural enemies to act as a population control. All of them have a high rate of reproduction, as most fungi and insects do. The hemlock wooly adelgid reproduces twice every year (Orwig and Foster, 1998). These two traits in combination with the ability to disperse are why these pathogens’ and pests’ abilities to wipe out entire populations were limited only by the range and number of surviving hosts.

The lack of size discrimination is a shared trait between the four blights and this current infestation, as suggested by our data analysis. The infestation eventually occurs in both small and large trees; in this respect it does not matter which comes first. This has serious negative consequences on the fecundity of the species as it kills both reproductively mature and possibly immature trees, eliminating both juveniles and their source. This is another sign that the species is likely to become ecologically extinct if it has not done so already.

The lack of size discrimination also has an effect on sprouting. St. Catherine’s island has a well-defined deer browse line below which there is very little edible vegetation. Red bay is a food source for deer (Brendemuehl, 1990), therefore sprouts below this line will likely succumb to deer browse. This is applicable to the entire range of red bay, considering the increase in deer populations in the Southeastern U.S. (Cote et al, 2004). Any sprouts that mature above the deer browse line may be infected by the beetle, just as any other branch would. This same phenomenon can be observed in resprouting chestnuts (Castanea dentata): once their sprouts reach a certain age, they are infected and killed by the fungus that caused the blight (Stephenson, Adams and Lipford,
It is not yet known if the beetle affects sprouts or trees with a very small DBH, but the concept is supported by our data.

Ecological Implications

Red bay is one of the most common trees in maritime forests along the entire southeastern, Atlantic coast of the United States. (Bourdeau and Oosting, 1959, Bratton and Davison, 1987 and Bratton and Miller, 1994). This is especially true on barrier islands like St. Catherine’s. Bratton and Miller’s (1994) dominance assessment of maritime forest communities suggested that red bay is the most dominant understory tree species in old-growth maritime forest and the second most dominant understory tree in old field sites, behind palmetto. In the canopy, Bratton and Miller (1994) found to be the second most dominant tree species behind live oak (*Quercus virginiana*) in several sites. On a North Carolina barrier island, red bay was found to comprise 8.5% of the total basal area for all plants, which was once again second only to live oak.

Therefore the loss of red bay from this ecosystem is the loss of an abundant species; its decline is causing the loss of an enormous number of trees from maritime forest communities. Its loss alone will probably have a significant impact on the ecosystem, similar to what has happened in hemlock stands damaged by the wooly adelgid. Hemlock has marginal functional importance in its ecosystem, but completely dominate it. The effects of its decline on that ecosystem have been compared to the impacts of logging (Brooks, 2001). It has been associated with increased soil temperature as well as a greater amount of available light. Removing red bay from maritime ecosystems will probably have a similar result. It also means the loss of a structural
species that provides resources and a structural ecological niche for some environmentally specific species that depend on this tree.

The loss of the red bay will also affect specific species that depend on it for food during development. The palamedes swallowtail butterfly (*Papilio palamedes*) lays its eggs solely on red bay leaves (Scriber and Margraf, 2000). When placed leaves of other similar species, the first instar larvae did not feed and died. The extermination of the red bay will cause *P. palamedes* to either go extinct or force it to adapt to lay its eggs on another plant. But even adapting may lead to extinction. The tiger swallowtail butterfly (*P. glaucus*) is chemically deterred from oviposition on red bay leaves (Frankfater and Scriber, 1999). So oviposition on a red bay leaf is an ecological niche occupied by *P. palamedes*. Competition between *P. palamedes* and *P. glaucus* could continue or end when one outcompetes the other (Crowell and Pimm, 1976). To summarize this point: the loss of the red bay will likely lead to the loss of its dependent species.

Although it has yet to be scientifically confirmed, field reports and preliminary studies suggest that the beetle also affects other species and even genera in the Lauraceae family (Mayfield, 2005). Inoculation of sassafras (*Sassafras albidum*), another tree in the family Lauraceae, with the *Ophiostoma* fungus has caused wilt (Mayfield, 2005). Sassafras wilt has also been observed in the wild in association with red bay infection. If the infection of *S. albidum* reaches a proportion similar to that of *P. borbonia* then it could mean the loss of another prominent tree species across all of North America’s forest. If the affects *P. americana* (avocado), a closely related species to *P. borbonia*, in a way similar to the red bay epidemic, it could have severe consequences on southern

The destruction of maritime forests, one of red bay’s habitats (Brendemuehl, 1990) for coastal living by humans has increased sharply over the last century. Between 1970 and 1980 almost 50% of structures built in the United States were on the coast (Dean, 1999). This ecosystem is currently very patchy and probably unhealthy because of the intense edge effects caused by the harsh, coastal environment in which the forest is found (Wells and Shunk, 1938). The loss of the abundant red bay tree will change the entire dynamic of this ecosystem. In addition, if the loss of the tree means the subsequent loss of other species, it could create a cascade effect that ripples throughout the entire ecosystem (Steffen *et al.*, 1996). Because this ecosystem is already being negatively affected by humans and edge effects, this additional problem should raise great concern; an ecosystem can only take so much before it collapses (Walker, 1992).

*Implications for Management*

Although the ecological extinction of the red bay seems imminent, there are a few things that could be done to slow the process. Many lessons can be learned from attempts to control other plant diseases. The red bay wilt epidemic’s similarities to the chestnut blight, Dutch elm disease (DED) and dogwood anthracnose provide an avenue by which possible solutions can be formed.

In particular, the work being done with elms to produce DED resistant trees may shine light on a possible solution to the red by decline. By finding several DED resistant trees and isolating a gene that aids in this resistance, other DED resistant elms can be
created and the tree can be reintroduced (Cheng et al, 1997). While no gene has yet been isolated and therefore no DED resistant elm created, DED resistant elms do exist and the search for the gene continues.

One hindrance to the process is funding. Public awareness of DED is decreasing because it is considered a phenomenon of the past. If interest in saving one of North America’s most grandiose shade trees is declining, then appropriating funds for saving a medium sized, anthropogenicly useless tree in a rare forest ecosystem will be almost impossible.

The method of infection for chestnuts is slightly different from that of red bay and elm, but research in controlling the responsible disease has implications in red bay conservation as well. The most successful form of control has been by the use of hypovirulence (Milgroom, 2004). Hypovirulence is the introduction of a virus into the cavities formed by Cryphonectria parasitica, the fungus that attacks chestnuts (Milgroom, 2004). The virus reduces the effects of the fungus on the chestnut and prevents the cavity from surrounding the stem. Unfortunately this is only successful when the virus is directly applied to an infected chestnut. Introductions of the virus into natural chestnut populations throughout Europe and North America have been met with little success (Milgroom, 2004). In order to effectively eliminate or even have a noticeable effect on a large population of chestnuts, the virus needs to spread faster than the fungus can reproduce, and this is apparently not the case (Milgroom 2004). Intense management is therefore required for this method of control to significantly decrease mortality.

If a virus that affects the fungus responsible for the red bay decline can be found, then there may be hope for both P. borbonia as well as U. americana. But because P.
borbonia is not a major timber crop, large timber industries will not be willing to invest time and money into its survival. Therefore intense management of the species is not likely a feasible solution. A virus capable of naturally reproducing faster than a beetle-dispersed fungus can spread is also unlikely, considering there has been no success with controlling the non-beetle dispersed C. parasitica.

A final proposition is to eradicate red bays in a 4 or 5 km thick belt surrounding the population. Because the beetle is only known to fly up to 3 km (Rabaglia, 2003), this could successfully hinder its spread. Although that would be a large number of trees removed, they are trees that would succumb to the beetle anyway. Because this phenomenon is an unnatural, destructive result of an invasive species, drastic controlling measures are justified. Unfortunately, this would be very difficult and costly to do and may not even work in the first place.

The red bay’s utilitarian lack of importance is reason why there may be hesitation to attribute large funds to its preservation. Approaching this problem from an angle that incorporates the consequences of losing S. albidum and P. americana may be essential for raising red bay awareness among the greater scientific community and public media. Also, associating it with the rich local culture will assign it further anthropogenic, sentimental value.

Currently the only steps taken to prevent the spread of the beetle have been issuances of public advice to cut down infected red bays and report them to the USDA. This probably does very little to prevent the spread of the beetle. Rabaglia (2003) suggests that methods of eliminating X. glabratus are “unknown, infeasible or expected to be ineffective” (Rabaglia, 2003).
The results of this study suggest that the red bay tree will eventually become ecologically extinct throughout its entire range as a result of the beetle infestation, unless naturally resistant genotypes already exist. This decline in red bays is likely to cause significant changes in forest dynamics because it is both a core and a structural species (Hanski, 1982, Hiers and Evans, 1997, Huston, 1994, Orwig and Foster, 1998, Steffen et al, 1996). The beetle has also been tied to indirect and direct loss in other species (Mayfield, 2005 and Scriber and Margraf, 2000). Because southeastern maritime forests are already being lost to anthropogenic causes (Dean, 1999), this major loss could result in chain reactions that affect multiple other species and lead to the loss of an entire ecosystem.
Literature Cited


McCormick, J. F. and R. B. Platt. 1980. Recovery of an Appalachian forest following the chestnut blight or Catherine Keever you were right!. American Midland Naturalist, 104: 264 – 273.

taxonomy of the *Ophiostoma piceae* complex and the Dutch elm disease fungi.
Mycologia. **93**:111 – 136

Rabaglia, R. 2003. Exotic forest pest information system for north America. created:
05/09/03, modified: same
http://spfnic.fs.fed.us/exfor/data/pestreports.cfm?pidval=148&langdisplay=english

data analysis. Wadsworth Publishing Company, Belmont, CA.

for *Papilio palamedes* and *P. glaucus* (Papilionidae). Journal of the
Lepidopterists’ Society, **54**: 131 – 136.

incorporated transient changes to structure and composition. Journal of Vegetative
Science, **7**: 321 – 328

Stephenson, S. L., H. S. Adams and M. L. Lipford. 1991. The present distribution of
chestnut in the upland forest communities of Virginia. Bulletin of the Torrey
Botanical Club, **118**: 24 – 32.

http://www.extento.hawaii.edu/kbase/crop/Type/xylosand.htm

Thomas, M. C. 2005. Pest alert: another asian ambrosia beetle, *Xyleborus glabratus*
Eichhof (Scolytinae: Curculionidae). Accessed: 5/02/06
www.doacs.state.fl.us/pi/enpp/ento/x.glabratus.html

18 – 23.

Bulletin of the Torrey Botanical Club, **65**: 485 – 492

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Tables and Figures

Figure 1. A photograph of a stand of *P. borbonia* taken in July of 2006 on St. Catherine’s Island, Georgia.
Figure 2. A map of counties in Florida, Georgia and South Carolina reported to have the red bay beetle. Information provided by Laurie Reid (South Carolina Forestry Commission), Bud Mayfield (Florida Division of Forestry) and James Johnson (Georgia Forestry Commission).
Figure 3. Location of the five sample plots used in this study on St. Catherine’s Island, Georgia.

Figure 4. The probability of a tree in a sample site having 100% wilt as a function of year on St. Catherine’s Island, Georgia. Predicted values (represented by dotted lines) were calculated for each tree at the site by running variables through the fitted model. Observed odds are the proportion of trees at that site and time that have 100% leaf wilt ($n_{2004} = 333$, $n_{2005} = 369$, $n_{2006} = 377$). Year 1 corresponds to 2004; year 2 corresponds to 2005; year 3 corresponds to 2006.
<table>
<thead>
<tr>
<th>DBH (cm)</th>
<th>2004</th>
<th>2005</th>
<th>2006</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.0-5.0</td>
<td>0.00 (7)</td>
<td>0.10 (20)</td>
<td>1.00 (12)</td>
</tr>
<tr>
<td>5.1-10.0</td>
<td>0.07 (54)</td>
<td>0.27 (59)</td>
<td>0.88 (66)</td>
</tr>
<tr>
<td>10.1-20.0</td>
<td>0.03 (179)</td>
<td>0.19 (215)</td>
<td>0.88 (210)</td>
</tr>
<tr>
<td>&gt;20.0</td>
<td>0.12 (93)</td>
<td>0.48 (75)</td>
<td>0.91 (89)</td>
</tr>
</tbody>
</table>

Table 1. The proportion of *Persea borbonia* (red bay) infected trees (100% leaf wilt) found in each size class, operationalized as diameter at breast height (DBH), as a function of year on St. Catherine’s Island, Ga. The total number of trees combined (both with and without infection) appears in parentheses next to the proportion ($n_{2004} = 333$, $n_{2005} = 369$, $n_{2006} = 377$).

<table>
<thead>
<tr>
<th>Year</th>
<th>Leaf Wilt</th>
<th>Trees With Sprouts</th>
<th>Trees Without Sprouts</th>
<th>Odds of Sprouting</th>
<th>Odds Ratio</th>
</tr>
</thead>
<tbody>
<tr>
<td>2004</td>
<td>&lt;100%</td>
<td>161</td>
<td>152</td>
<td>1.06</td>
<td></td>
</tr>
<tr>
<td></td>
<td>100%</td>
<td>15</td>
<td>5</td>
<td>3.00</td>
<td>2.83</td>
</tr>
<tr>
<td>2005</td>
<td>&lt;100%</td>
<td>99</td>
<td>174</td>
<td>0.57</td>
<td></td>
</tr>
<tr>
<td></td>
<td>100%</td>
<td>74</td>
<td>22</td>
<td>3.36</td>
<td>5.91</td>
</tr>
<tr>
<td>2006</td>
<td>&lt;100%</td>
<td>15</td>
<td>26</td>
<td>0.58</td>
<td></td>
</tr>
<tr>
<td></td>
<td>100%</td>
<td>270</td>
<td>66</td>
<td>4.09</td>
<td>7.09</td>
</tr>
</tbody>
</table>

Table 2. The number of trees with and without sprouts that are infected (100% Leaf wilt) and not infected (<100% leaf wilt) as a function of time in years on St. Catherine’s Island, Ga ($n_{2004} = 333$, $n_{2005} = 369$, $n_{2006} = 377$). Odds ratios were calculated for the probability infected trees sprouting compared to non-infected trees sprouting.