Plant Ecology & Diversity
Vol. 2, No. 1, February 2009, 77–83

Taylor & Francis
Taylor & Francis Group

SHORT COMMUNICATION

A comparison of arborescent vegetation pre- (1983) and post- (2008) outbreak of the invasive species the Asian ambrosia beetle *Xyleborus glabratus* in a Florida maritime hammock

Nisse Goldberg* and John Heine

Department of Biology and Marine Science, Jacksonville University, Jacksonville, FL, United States of America

(*Received 29 November 2008; final version received 18 February 2009*)

Background: An outbreak of the invasive species the Asian ambrosia beetle (*Xyleborus glabratus*) has been devastating populations of *Persea borbonia* in the southeastern USA. This is the first study to compare pre- and post-outbreak plant diversities in coastal hammock communities.
Aims: We compared present-day patterns to those reported before the beetle outbreak.
Methods: Vegetation was surveyed in the maritime hammock forest at Little Talbot Island, northeastern Florida, in June 2008. Fifteen 100 m^2 quadrats were sampled for density, frequency, and diameter at breast height of arborescent vegetation. Nested within each of the 100 m^2 quadrats, an 8 m^2 quadrat was sampled for densities of understory taxa.
Results: *Quercus virginiana* remained the most common canopy species when compared with the 1984 data. *Juniperus virginiana* var. *silicicola* replaced *P. borbonia* as the third most common species. Thirty-two percent of adult *P. borbonia* were dead in 2008. In the understory assemblage, *Quercus* spp., *Sabal palmetto*, *P. borbonia*, *Ilex opaca*, and *I. vomitoria* were more abundant in June 2008 than reported in 1984.
Conclusions: Changes in structure may be a consequence of the demise of *P. borbonia* populations. Long-term monitoring of native communities provides a means to understand the effects of exotic pathogens on plant diversity and community structure.

Keywords: ambrosia beetle; Florida; invasive species; laurel wilt disease; maritime hammock; *Persea borbonia*; *Quercus virginiana*

Introduction

Maritime or coastal hammock is a hardwood-forest habitat found on coastal dunes throughout the world (Oosting 1954). In the USA, maritime hammocks occur from southern New England to Florida and along the Gulf Coast (Oosting 1954; Florida Natural Areas Inventory (FNAI 1990). Maritime hammock is a live oak (*Quercus virginiana*; Table 1) association found in a narrow band of less than 1 km along the coast of the mainland and off-shore barrier islands of the eastern USA (Oosting 1954; Greller 2003). The maritime forest occurs inland of the rear dune where vegetation can be protected from wind and salt spray (Oosting 1954).

Dominant trees are typified by *Quercus virginiana*, *Sabal palmetto*, *Persea borbonia*, *Ilex opaca*, *Liquidambar styraciflua* L., *Magnolia grandiflora*, *Pinus elliottii* var. *elliottii*, and *Juniperus virginiana* var. *silicicola* (Greller 2003; Table 1). The zonation of arborescent taxa is influenced by specific tolerances to saltwater inundation, fire disturbance, salt spray, and wind energy from hurricanes (Williams et al. 1998). This community is relatively fire resistant due to moisture retention in the humus layer, oak leaf litter, and the temperature moderating influence of the closed *Q. virginiana* and *S. palmetto* canopy (Bratton and Davison 1987; FNAI 1990). Greater diversity of arborescent taxa is associated with higher elevation that is less susceptible to flooding and includes *S. palmetto*, *J. virginiana*, and *Q. virginiana* (Williams et al. 1998). Bratton and Miller (1994) observed a positive correlation between the dominance of *Q. virginiana*, *S. palmetto* and *Pinus* spp., and soil moisture on a barrier island in Georgia, USA. Mesic habitats along the eastern coast of the USA have been either destroyed or fragmented by logging, urbanisation, and recreational activities (FNAI 1990).

Of the trees typically found in maritime hammocks, *Persea borbonia* suffers from substantial mortality in the coastal counties of Georgia, southeastern South Carolina, and northeastern Florida (Fraedrich et al. 2008). The range of *P. borbonia* extends southward from southern Delaware to the Florida Keys and extends westward to southern Texas and southwest Arkansas (Bonner 2008). The exotic Asian ambrosia beetle (*Xyleborus glabratus* Eichoff) carries the fungal symbiont *Raffaelea* sp. which attacks the vascular tissue of *P. borbonia* and causes death within weeks to months (Mayfield III et al. 2008). *Xyleborus glabratus* is native to India, Japan, Bangladesh, Myanmar, and Taiwan (Mayfield III et al. 2008). The exotic beetle was first reported at Port Wentworth, Georgia in 2002 (Rabaglia et al. 2006). *Persea borbonia* mortality, or 'laurel wilt' disease because it targets members of the family Lauraceae (sensu Fraedrich et al. 2008), was first reported in Savannah, Georgia, in 2003. Its rate of spread is estimated to be 30–100 km per year with diseased trees

*Corresponding author. Email: ngoldbe@ju.edu

ISSN 1755-0874 print/ISSN 1755-1668 online
© 2009 Botanical Society of Scotland and Taylor & Francis
DOI: 10.1080/17550870902852775
http://www.informaworld.com

Table 1. List of representative species associated with xeric-mesic coastal hammocks along the eastern coast of the USA (Oosting 1954; Greller 2003) and their relative abundances from the coastal hammock area at Little Talbot Island (LTI) (Easley and Judd 1993). Presence of these species in the current study is also included.

Growth form	Species	Common name	Abundance at LTI	Presence in 2008
Tree	*Juniperus virginiana* (L.) var. *silicicola* (Small) Silba	Southern red cedar	A	x
Tree	*Magnolia grandiflora* L.	Southern magnolia	F	
Tree	*Persea borbonia* (L.) Sprengel	Redbay	F	x
Tree	*Pinus elliottii* Engelm. var. *elliottii*	Slash pine	A	x
Tree	*Quercus geminata* Small	Sand live oak	F	
Tree	*Q. virginiana* Miller	Live oak	A	x
Tree	*Sabal palmetto* Lodd ex. J.S. and J.H. Shult.	Cabbage palm	A	x
Shrub	*Bumelia tenax* (L.) Willd.	Tough buckthorn	F	
Shrub	*Ilex opaca* Aiton	American holly	F	x
Shrub	*I. vomitoria* Aiton	Yaupon	A	x
Shrub	*Myrica cerifera* L.	Wax myrtle	F	
Shrub	*Osmanthus americanus* (L.) Benth. and Hook. F. ex A. Gray	Wild olive	F	
Shrub	*Prunus serotina* Ehrh.	Black cherry	F	
Shrub	*P. umbellata* Elliott	Hog plum	F	
Shrub	*Quercus myrtifolia* Willd.	Myrtle oak	F	
Shrub	*Serenoa repens* (Bartram) Small	Saw palmetto	A	x
Shrub	*Vaccinium arboreum* Marsh.	Sparkleberry	F	x
Liana	*Parthenocissus quinquefolia* (L.) Planchon	Virginia creeper	F	x
Liana	*Smilax auriculata* Walter	Greenbrier	A	
Liana	*S. bona-nox* L.	Catbrier	F	x
Liana	*Toxicodendron radicans* subsp. *radicans* (L.) Kuntze	Poison ivy	A	x
Liana	*Vitis aestivalis* Michaux	Summer grape	F	x
Liana	*V. rotundifolia* Michaux	Muscadine	A	x

Note: A, abundant; F, frequent; O, occasional (Easley and Judd 1993).

observed in urban, residential, and native habitats (Fraedrich et al. 2008; Koch and Smith 2008). Infected trees have been reported within 110 km from the coast, from Charleston, South Carolina, to south of Jacksonville, Florida (Hanula et al. 2008). Mortality of *P. borbonia* is positively associated with increasing diameter at breast height (DBH) (Fraedrich et al. 2008). In an 18-month investigation of *P. borbonia* mortality at Fort George Island, Florida, a site near Little Talbot Island State Park, mortality reached 100% for trees with DBH from 10.3 cm to greater than 20.3 cm and approximately 70% of trees with a DBH 2.5–5.1 cm died by the end of the study period (Fraedrich et al. 2008).

The demise of *Persea borbonia* will have direct consequences for the survivorship of the Lauraceae-specialist Palamedes swallowtail butterfly (*Papilio palamedes* Drury). Lederhouse et al. (1992) tested host preference of *P. palamedes* to native species of Lauraceae. Given the choice of *Sassafrass albidum* (Nutt.) Nees and *P. borbonia*, females of *P. palamedes* laid 87% of their eggs on *P. borbonia*. By comparison, 80% of larvae survived on *P. borbonia*, as compared to 43% on *S. albidum* (Lederhouse et al. 1992). The survival of *P. palamedes* appears therefore seriously threatened without its host plant *P. borbonia*.

No census of dead *Persea borbonia* individuals has been conducted at the Little Talbot Island State Park. Little Talbot Island State Park, located in northeastern Florida, is a north–south barrier island approximately 7.1 km long with a width of 1 km (Easley and Judd 1993). The northern end of the island, where the study took place, consists of coastal hammock, dunes, and salt marsh habitats (Easley and Judd 1993). Climatic conditions along the northeastern coast of Florida consist of mean temperatures ranging between a low of 16°C and high of 25°C, and an annual mean precipitation of 1270 mm (National Oceanic and Atmospheric Administration [NOAA] 2009).

Stalter and Dial (1984) surveyed the coastal forest at Little Talbot Island State Park, targeting an area where *Quercus virginiana* with DBH ≥30 cm was abundant. They described the arborescent assemblage as dominated by *Q. virginiana* in the upper canopy and *Persea borbonia* in the subcanopy. In addition, Easley and Judd (1993) published habitat descriptions, relative frequency of occurrence per species, and an annotated species list at Little Talbot Island from vascular plant collections made between 1990 and 1992. They described xeric-mesic coastal hammocks as dominated by *Q. virginiana* and *Sabal palmetto* (Easley and Judd 1993). They also reported 'high pine islands' of *Pinus elliottii*, located within the western portion of the island. These islands consisted of a carpet of pine needles and an abundance of *Bumelia tenax*, *Ilex vomitoria*, *Juniperus virginiana*, *P. borbonia*, and *S. palmetto* (Easley and Judd 1993; Table 1).

The aim of our investigation was to compare present-day assemblage structure of the coastal hammock forest at Little Talbot Island State Park to that reported by Stalter and Dial (1984). We followed the survey protocol of Stalter and Dial (1984), sampling for densities and frequencies of arborescent vegetation and recording the number of dead *Persea borbonia*. We hypothesised that *P. borbonia* would be replaced by another subcanopy species due to its mortality caused by the fungal pathogen.

Materials and methods

Vegetation was surveyed in the coastal hammock forest at Little Talbot Island State Park, Florida, USA (30°25′ N, 81°25′ W) in June 2008. We accessed the forest via a hiking trail that is parallel to and approximately 0.5 km from the beach. Stalter and Dial (1984) targeted an area of the coastal hammock where *Quercus virginiana* had a trunk DBH of 30 cm and greater in June 1983 (R. Stalter, pers. comm.). We re-sampled the area where these large *Q. virginiana* trees occurred.

We followed the sampling design described in Stalter and Dial (1984) to allow a direct comparison in the diversity of arborescent taxa with DBH >7.6 cm. We purposely sampled in a homogeneous habitat that was further than approximately 10 m from the trail edge to avoid areas disturbed by trampling. Quadrats were separated by a minimum of 15 m. We entered the hammock community from the trail, tied off a transect tape to a plant, and set off 10 m away from the trail. The next side of the quadrat was determined randomly and then we paced off another 10 m. We laid out the transect tape to complete the final two sides of the quadrat. After sampling within the 100 m^2 quadrat and the nested 8 m^2 quadrat, we returned to the trail and walked approximately 15 m. We then re-entered the hammock vegetation and demarcated another quadrat with the transect tape.

In order to sample for woody vegetation with DBH >7.6 cm, species richness and species density per 100 m^2 were recorded for trees, shrubs, and lianas from 15 10 × 10 m quadrats. Density and DBH of *Persea borbonia* were noted for live individuals (which included healthy individuals and those with a number of dead leaves hanging from branches), and for dead ones separately. Litter composition and canopy cover were also observed. Mean frequency, density, and DBH >7.6 cm of arborescent taxa per 100 m^2 were compared to values reported by Stalter and Dial (1984).

To describe woody plants in the understory, we sampled a 2 × 4 m quadrat that was nested within each of the 15 100 m^2 quadrats. Woody plants in the understory were defined as saplings, shrubs, and seedlings with DBH ≤7.6 cm. Densities of arborescent taxa were recorded in each quadrat and then compared with the results of Stalter and Dial (1984).

Chi-square contingency tests were used to statistically evaluate whether the relative abundances and frequencies of each taxon were similar between those reported in Stalter and Dial (1984) and the present study. Tests were conducted separately for frequencies and densities per 100 m^2 of arborescent taxa with DBH >7.6 cm, and for densities per m^2 of understory arborescent taxa. In addition, species-accumulation curves were used to confirm that 15 quadrats were sufficient to estimate plant diversity in the maritime hammock. We also compared our species list with that of Easley and Judd (1993); however, as these authors had not collected frequency and density estimates, we did not include their study in our contingency tests.

Results

Present-day diversity

In the coastal hammock forest of Little Talbot Island State Park, the assemblage was typical of a coastal hardwood forest (Table 1) with an upper canopy of *Quercus virginiana*, *Sabal palmetto*, *Pinus elliottii*, and *Juniperus virginiana* that provided full to partial cover. The subcanopy consisted of *Persea borbonia*, an occasional mulberry (*Morus rubra* L.) and *Quercus laurifolia* Michx. Common shrubs included *Ilex opaca*, *I. vomitoria*, *Vaccinium arboreum*, and *Vaccinium* sp. Understory taxa included the lianas *Smilax bona-nox*, *Vitis rotundifolia*, *Ampelopsis arborea* (L.) Koehne, *Rubus trivialis* Michx., and *Parthenocissus quinquefolia* (Table 1). Herbaceous plants *Cnidoscolus stimulosus* (Michx.) Engelm and A. Gray, and an unidentified *Sporobolus* species were each present in two of the 15 quadrats sampled. Litter cover was typically 100%, consisting of *Quercus* and *P. borbonia* leaves, *P. elliottii* and *J. virginiana* needles, and *S. palmetto* fronds.

Species richness was well described with 15 quadrats. Species-accumulation curves levelled off at eight species per 100 m^2 with eight replicate quadrats for arborescent taxa with DBH >7.6 cm. The species-accumulation curve levelled off at 15 species with 12 replicate 8 m^2 quadrats for understory arborescent taxa.

Quercus virginiana, *Juniperus virginiana*, and *Persea borbonia* were the most abundant species with DBH >7.6 cm (Figure 1). By comparison, the three most frequently encountered species were *Q. virginiana*, *Sabal palmetto*, and *J. virginiana* (Figure 2). Mean DBH ± 1 SE of *Q. virginiana* was 46.5 ± 6.1 cm for the 26 individuals present in the 15 quadrats. Species present in fewer than five quadrats were *Pinus elliottii*, *Ilex opaca*, *I. vomitoria*, *Quercus*

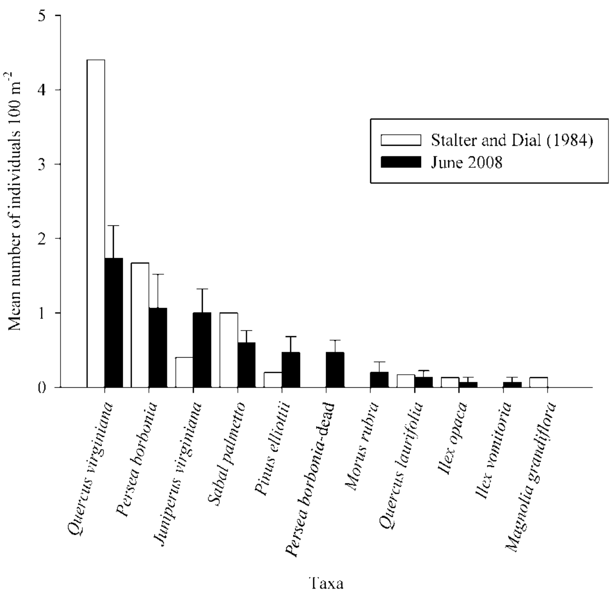

Figure 1. Comparison of mean density (±1 SE) of trees and shrubs with diameter at breast height >7.6 cm per 100 m^2 between the present study and Stalter and Dial (1984); n = 15 quadrats.

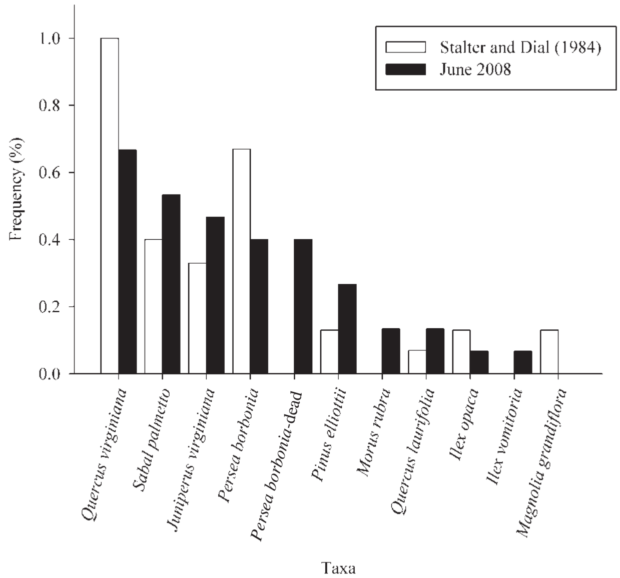

Figure 2. Comparison of frequency of trees and shrubs with diameter at breast height >7.6 cm per 100 m^2 between the present study and Stalter and Dial (1984); n = 15 quadrats.

laurifolia, and *Morus rubra* (Figure 2) with mean densities less than 0.5 individual per 100 m^2 (Figure 1).

Laurel wilt, though a recent outbreak, has already affected the distribution of *Persea borbonia* in Little Talbot Island State Park. Thirty-two percent of adult *P. borbonia* from the sampled population were dead (Figure 1). The DBH of living *P. borbonia* was greater than that of dead individuals, 16.6 ± 2.0 cm and 11.9 ± 1.6 cm, respectively. Of those individuals that were alive, the majority showed evidence of disease with dead and hanging leaves and the presence of beetle entrance holes.

Quercus spp., *Sabal palmetto*, *Persea borbonia*, and the shrub *Ilex vomitoria* were the most common (mean frequency >85%) and abundant (>5 individuals per 8 m^2) understory taxa (Table 2). Densities of *Quercus* spp. ranged from none present to 150 individuals per 8 m^2. By comparison, a maximum number of 158 individuals was recorded for *I. vomitoria*, 13 for *S. palmetto*, and 11 for *P. borbonia*. *Ilex opaca* was less abundant than *I. vomitoria* (Table 2). Other taxa included the lianas *Smilax bona-nox*, *Parthenocissus quinquefolia*, and *Vitis rotundifolia* with mean densities of <2 individuals per 8 m^2. *Vaccinium* sp., *Cnidoscolus stimulosus*, *Rubus trivialis*, an unidentified *Sporobolus*, and *Ampelopsis arborea* were each present in one to four quadrats with mean densities <1 individual per 8 m^2.

Table 2. Frequency (%) and density (mean number ± 1 SE) of understory individuals per 8 m^2 at Little Talbot Island State Park, Florida; n = 15 quadrats.

Species	Frequency	Density
Sabal palmetto	93%	6.8 ± 1.0
Ilex vomitoria	87%	34.2 ± 10.8
Persea borbonia	80%	5.4 ± 1.0
Quercus spp.	73%	17.7 ± 9.9
Smilax bona-nox	60%	1.2 ± 0.3
Ilex opaca	47%	3.1 ± 1.0
Vitis rotundifolia	33%	1.1 ± 0.6
Vaccinium arboreum	20%	1.0 ± 0.9

Comparison of past and present diversity

Climatological data over the period of 1980–2007 show that mean annual temperatures have increased by 0.4°C since 1997 (NOAA 2009). Annual precipitation was highly variable, ranging from 775 mm to a high of 2101 mm. Wet years (defined as years with >20% above average rainfall) occurred in 1983, 1991, 1992, 1994, and 1995. Dry years (defined as years with <20% below average rainfall) occurred in 1980, 1981, 1990, 1999, and 2006 (NOAA 2009).

The structure of the hammock vegetation at Little Talbot Island State Park has changed between the June 1983 survey (Stalter and Dial 1984) and the present study. The relative frequencies and densities of the different taxa were significantly different between the two surveys (Chi-square for frequency data = 218000; df = 9, P < 0.001; Chi-square for density data = 47.8; df = 9, P < 0.001). An apparent shift in the dominant members of the arborescent community is evidenced by the numbers of adult *Juniperus virginiana*, which were more than double in 2008 as compared with 1984 (Figure 1). *Juniperus virginiana* has now replaced *Sabal palmetto* as one of the top three abundant species, and has replaced *Persea borbonia* as the third most frequently encountered species (Figures 1 and 2). By comparison, numbers of adult *Quercus virginiana* were much less than reported in 1984 (Stalter and Dial 1984). The lower numbers of *S. palmetto* in our study were offset by their relatively higher frequency of occurrence in our quadrats (0.53 in 2008, and 0.40 in 1984).

In the understory assemblage, many more individuals of *Quercus* spp., *Sabal palmetto*, *Persea borbonia*, *Ilex opaca*, and *I. vomitoria* were recorded in the present study as compared to Stalter and Dial (1984) (Table 3). Distributions of abundances were statistically different (Chi-square = 14700; df = 9, P < 0.001; Table 3). In the present study, *I. vomitoria* was the most abundant with 64 individuals per m^2. Densities of juvenile *P. borbonia* were much greater in 2008 (10 individuals per m^2) relative to 0.2 individuals per m^2 reported from 1983 (Stalter and Dial 1984). *Juniperus virginiana* and the lianas *Smilax bona-nox* and *Vitis rotundifolia* were present in both studies, albeit in small numbers (Table 3). *Vaccinium arboreum*, *Rubus trivialis*, *Parethenocissus quinquefolia*, *Cnidoscolus stimulosus*, and *Ampelopsis arborea* were also present but had not been reported in Stalter and Dial (1984). No seedlings or saplings of *Pinus elliottii* or *Callicarpa americana* were observed (Table 3).

Species that had not been observed by Easley and Judd (1993) were *Ampelopsis arborea*, *Rubus trivialis*, *Cnidoscolus stimulosus*, and an unidentified *Sporobolus* species. These species contributed to diversity, though present in less than 25% of the quadrats sampled. *C. stimulosus* was especially common along the hiking trail. The Palamedes

Table 3. Comparison of total number of understory individuals per m^2.

Taxa	Present study	Stalter and Dial (1984)
Quercus spp.	33.1	0.3
Pinus elliottii	0	0.02
Juniperus virginiana	0.1	0.01
Sabal palmetto	12.7	0.08
Persea borbonia	10.1	0.2
Ilex opaca	5.7	0.07
Ilex vomitoria	64.1	0.5
Smilax bona-nox	2.2	0.6
Vitis rotundifolia	2.0	0.03
Callicarpa americana	0	0.05

Note: Values were scaled from 8 m^2 areas to 1 m^2 areas to allow for comparisons with values reported in Stalter and Dial (1984). Values reflect total densities from the 15 quadrats that were sampled.

Swallowtail butterfly was observed feeding on the flowers of *C. stimulosus*, suggesting that the butterfly was still present at the park despite the number of dead *Persea borbonia*. No invasive plant species were observed from the maritime hammock habitat in the present study, by Easley and Judd (1993), or by Stalter and Dial (1984).

Discussion

In a comparison of present-day plant diversity with that reported by Stalter and Dial (1984) in a maritime hammock at Little Talbot Island State Park, Florida, evidence of laurel wilt disease was observed, relative abundances of canopy species have changed, and the relative numbers of individuals in the understory were significantly greater than observed previously. However, overall species composition of trees, shrubs, and lianas remains typical of a maritime hammock that has not been exposed to disturbances from fire or saltwater inundation. As laurel wilt spreads, relative abundances of subcanopy taxa will most likely change.

Mortality of *Persea borbonia* was likely to have been caused by the exotic Asian ambrosia beetle as evidenced by the beetle entrance holes and hanging dead leaves. Densities of adult *P. borbonia* were less than that recorded by Stalter and Dial (1984) despite a greater number of individuals in the understory. A similar pattern was observed for American elm (*Ulmus americana* L.) populations in Indiana, USA (Castello et al. 1995). Densities of juvenile *U. americana* increased with the death of adults by the Dutch elm disease and/or elm yellows (Castello et al. 1995). Compared to monitoring of *P. borbonia* populations at the nearby Fort George Island (Fraedrich et al. 2008), adults with DBH >20 cm have not been completely decimated and may continue to provide viable offspring.

Although laurel wilt is devastating *Persea borbonia* in the southeastern USA, the future of the Asian ambrosia beetle may be in jeopardy (Hanula et al. 2008). Populations of the beetle have been reported to decline precipitously in seriously affected areas, indicating that it may not breed successfully on other arborescent taxa (Hanula et al. 2008). Beetle densities were four to seven individuals per trap per day where *P. borbonia* was attacked as compared to <1 beetle per trap per day in areas where populations of *P. borbonia* were decimated. Hanula et al. (2008) suggest that *P. borbonia* may recover from seedlings and sprouts following eradication of the beetle via traps and insecticide treatments.

The persistent abundances of *Quercus virginiana* and *Juniperus virginiana* at Little Talbot Island suggest that the coastal hammock had not been exposed to excessive saltwater inundations. Williams et al. (1998) observed that *J. virginiana* is less tolerant to soil salinity than *Sabal palmetto*. Although *Q. virginiana* was the least tolerant of the three species to increasing soil salinity, seedlings were able to resprout (Willams et al. 1998). In the rare instances of exposure to tidal inundations, the seedlings of the three common canopy species *Q. virginiana*, *J. virginiana*, and *S. palmetto* would not be severely impacted given their tolerance to increased soil salinity.

A lack of severe disturbance, such as caused by fire, may have contributed to the decrease in *Pinus elliottii* densities since 1983. Bratton and Davison (1987) noted similar changes in *Pinus* abundances between 1937 and 1984 from their studies of a maritime forest located on a barrier island of North Carolina, USA. Pine seedlings were less abundant relative to hardwood seedlings and sprouts in 1984 (Bratton and Davison 1987). No evidence of recent fire was observed in the coastal hammock at Little Talbot Island, which may explain the continued dominance of *Quercus virginiana* and the absence of *P. elliottii* in the understory.

Without fire, leaf litter will accumulate and can negatively impact species richness via reduced seed germination (Xiong and Nilsson 1999). Leaves of evergreen trees decompose more slowly than those of forbs and deciduous trees (Xiong and Nilsson 1999). However, we observed much greater densities of individuals in the understory as compared to Stalter and Dial (1984), suggesting that the leaf litter did not suppress seed germination of arborescent taxa. Instead, leaf litter may ameliorate physical conditions by retaining moisture and positively affecting temperature ranges (Xiong and Nilsson 1999). For example, Joy and Young (2002) reported greater survivorship and diversity of woody seedlings beneath *Juniperus virginiana* canopy on a Virginia barrier island, USA. Thus, *J. virginiana*, like *Quercus virginiana*, may provide a favourable and mesic environment to understory taxa via canopy shading and increasing litter thickness.

Demographic and ecological studies of *Persea borbonia* had not been previously conducted, making predictions of future community shifts difficult. Based on studies that followed community shifts due to the presence of an invasive pathogen such as the introduced Asian chestnut fungus (*Cryphonectria parasitica* (Murrill) Barr) that eliminated native populations of the North American chestnut (*Castanea dentata* (Marshall) Borkh.), ecological diversity can increase due to a lack of a clear dominant (Castello et al. 1995; Burdon et al. 2006). In the maritime hammock at Little Talbot Island, other subcanopy members such as *Ilex vomitoria* may increase in abundance as the exotic fungal pathogen kills adult trees of *P. borbonia* (Burdon et al. 2006). Shading by *I. vomitoria* and lianas can also inhibit the growth of tree seedlings (Smith et al. 1997). Once abundant, shrubs occupy and maintain space via the density of their stems and presence in the canopy layer (Dunn 1986; Menges et al. 1993). Smith et al. (1997) suggested that *I. vomitoria* prevented recovery of canopy taxa in a maritime hammock following disturbance by Hurricane Hugo at Bull Island, South Carolina. Future studies testing interactions between *P. borbonia* and *I. vomitoria* would help elucidate whether *I. vomitoria* will prevent the future recovery of *P. borbonia* due to interspecific competition.

Shifts in the arborescent community at Little Talbot Island may be a function of the demise of *Persea borbonia* by the fungal pathogen and the lack of major disturbances due to fire or saltwater inundation. Pathogens affect community function by influencing processes such as nutrient cycling, succession, and survivorship of specialists such as the Palamedes Swallotail butterfly that depend on the host species for laying eggs (Burdon et al. 2006). In addition, loss of food from nuts and berries contributes to a decrease in local faunal diversity (Castello et al. 1995). The toll caused by pathogenic organisms to native woody plants in the USA is staggering. Approximately 20 species of plant pathogens are non-native and account for an annual economic loss of approximately US$2.1 billion in wood products (Pimentel et al. 2005). The commercial avocado (*Persea americana* var. *americana* Mill. and *P. americana* cv. Simmonds) is also susceptible to the laurel wilt fungus. Thus, this disease may have serious consequences to the commercial avocado industry (Mayfield III et al. 2008) should sanitation and insecticide treatments fail (Hanula et al. 2008). Monitoring of native plant communities provides evidence of the deleterious effects of exotic invasions to plant diversity and community structure that may already be compromised by development and recreational activities.

Acknowledgements

We would like to thank the rangers of Little Talbot Island State Park for providing access. We thank R. Stalter for information on the previous study conducted in 1983. G. Brown provided support for this study. This paper was greatly improved from insightful comments provided by the journal's reviewers and the associate editor.

Notes on contributors

Nisse Goldberg is an assistant professor in Biology and Marine Science at Jacksonville University, Florida. She studies the ecology, biogeography, and conservation biology of terrestrial and marine flora.

John Heine is a research associate at Jacksonville University, Florida. He is a marine ecologist with interests in the coastal environment.

References

Bonner FT. 2008. *Persea borbonia* (L.) Spreng. Redbay [Internet]. [cited 2008, November 1]. Available from: http://www.nsl.fs.fed.us/wpsm/Persea.pdf

Bratton SP, Davison K. 1987. Disturbance and succession in Buxton Woods, Cape Hatteras, North Carolina. Castanea 52:166–179.

Bratton SP, Miller SG. 1994. Historic field systems and the structure of maritime oak forests, Cumberland Island National Seashore, Georgia. Bulletin of the Torrey Botanical Club 121:1–12.

Burdon JJ, Thrall PH, Ericson E. 2006. Dynamics of disease in plant communities. Annual Review of Phytopathology 44:19–39.

Castello JD, Leopold DJ, Smallidge PJ. 1995. Pathogens, patterns, and processes in forest ecosystems. BioScience 45:16–24.

Dunn, CP. 1986. Shrub layer response to death of *Ulmus americana* in southeastern Wisconsin lowland forests. Bulletin of the Torrey Botanical Club 113:142–148.

Easley MC, Judd WS. 1993. Vascular flora of Little Talbot Island, Duval County, Florida. Castanea 58:162–177.

Florida Natural Areas Inventory. 1990. Guide to the natural communities of Florida. Tallahassee, FL: Florida Natural Areas Inventory and Florida Department of Natural Resources. 111 p.

Fraedrich SW, Harrington TC, Rabaglia RJ, Ulyshen MD, Mayfield III AE, Hanula JL, Eickwort JM, Miller DR. 2008. A fungal symbiont of the redbay ambrosia beetle causes a lethal wilt in redbay and other Lauraceae in the southeastern United States. Plant Disease 92:215–224.

Greller AM. 2003. A review of the temperate broad-leaved evergreen forest zone of southeastern North America: floristic affinities and arborescent vegetation types. Botanical Review 69:269–299.

Hanula JL, Mayfield III AE, Fraedrich SW, Rabaglia RJ. 2008. Biology and host associations of redbay ambrosia beetle (Coleoptera: Curculionidae: Scolytinae), exotic vector of laurel wilt killing redbay trees in the southeastern United States. Forest Entomology 101:126–1286.

Joy DA, Young DR. 2002. Promotion of mid-successional seedling recruitment and establishment of *Juniperus virginiana* in a coastal environment. Plant Ecology 160:125–135.

Koch FH, Smith, WD. 2008. Spatio-temporal analysis of *Xyleborus glabratus* (Coleoptera: Curculionidae: Scolytinae) invasion in eastern US forests. Environmental Entomology 37: 442–452.

Lederhouse RC, Ayres MP, Nitao JK, Scriber JM. 1992. Differential use of lauraceous hosts by swallowtail butterflies, *Papilio troilus* and *P. palamedes* (Papilionidae). Oikos 63:244–252.

Mayfield III AE, Pena JE, Crane JH, Smith, JA, Brach CL, Ottoson ED, Hughes M. 2008. Ability of the redbay ambrosia beetle (Coleoptera: Curculionidae: Scolytinae) to bore into young avocado (Lauraceae) plants and transmit the laurel wilt pathogen (*Raffaelea* sp.). Florida Entomologist 91:485–487.

Menges ES, Abrahamson WG, Givens KT, Gallo NP, Layne JN. 1993. Twenty years of vegetation change in five long-unburned Florida plant communities. Journal of Vegetation Science 4:375–386.

National Oceanic and Atmospheric Administration. 2009. National climate data center [Internet]. [cited 2009, January 6]. Available from: http://www7.ncdc.noaa.gov/IPS/cd/cd.html

Oosting, HJ. 1954. Ecological processes and vegetation of the maritime strand in the southeastern United States. Botanical Review 20:226–262.

Pimentel, D, Zuniga, R, Morrison D. 2005. Update on the environmental and economic costs associated with alien-invasive species in the United States. Ecological Economics 52:273–288.

Rabaglia RJ, Dole SA, Cognato AI. 2006. Review of American *Xyleborina* (Coleoptera: Curculionidae: Scolytinae) occurring north of Mexico, with an illustrated key. Annals of the Entomological Society of America 99:1034–1056.

Smith GF, Nicholas NS, Zedaker SM. 1997. Succession dynamics in a maritime forest following Hurricane Hugo and fuel reduction burns. Forest Ecology and Management 95:275–283.

Stalter R, Dial SC. 1984. Hammock vegetation of Little Talbot Island State Park, Florida. Bulletin Torrey Botanical Club 111:494–497.

Williams K, Meads MV, Sauerbrey DA. 1998. The roles of seedling salt tolerance and resprouting in forest zonation on the west coast of Florida, USA. American Journal of Botany 85:1745–1752.

Xiong S, Nilsson C. 1999. The effects of plant litter on vegetation: a meta-analysis. Journal of Ecology 87:984–994.

Copyright of Plant Ecology & Diversity is the property of Taylor & Francis Ltd and its content may not be copied or emailed to multiple sites or posted to a listserv without the copyright holder's express written permission. However, users may print, download, or email articles for individual use.