SUBCORTICAL BEETLE COMMUNITIES OF GEORGIA

by

KAYLA AMBER BROWNELL

(Under the Direction of Kamal JK Gandhi)

ABSTRACT

I studied the population and community ecology of bark and woodboring beetles (Coleoptera: Buprestidae, Cerambycidae, and Curculionidae) and their predators (Coleoptera: Cleridae and Trogossitidae) in the Piedmont region of Georgia. Specifically, I assessed the responses of these beetle taxa to prescribed burning, their seasonal phenology, responses to semiochemicals, and species composition in forested and urban areas. A total of 112,949 *Ips* spp. and 6,200 predatory beetles were trapped over a year. The effects of immediate or short-term prescribed burning on these beetle populations were negligible indicating resilience to low-intensity disturbances. Around nurseries and warehouses, 4,093 adults representing 103 species of bark and woodboring beetles were trapped. Exotic species dominated these sites (comprising 60% of catches and 13% of species richness). Greater numbers and species of bark beetles were trapped at nurseries than warehouses, and their communities were distinct. Responses of beetles to semiochemical lures and their phenology patterns were highly species-specific.

INDEX WORDS: bark beetles, ecology, exotic, fire, *Ips* engraver, semiochemical, woodborer beetles

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DEDICATION

I dedicate this work to my grandmother, Mary Deyter. Thank you for all your love and support, Grandma.

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TABLE OF CONTENTS

Page

ACKNOWLEDGEMENTS v

LIST OF TABLES viii

LIST OF FIGURES ix

CHAPTER

1 INTRODUCTION AND LITERATURE REVIEW 1

INTRODUCTION 1

REFERENCES 12

2 *IPS* PINE ENGRAVER GUILD: RESPONSES TO PRESCRIBED BURNING AND LURE COMBINATIONS, AND SEASONAL ACTIVITY IN THE SOUTHEASTERN UNITED STATES 19

ABSTRACT 19

INTRODUCTION 21

METHODS 23

RESULTS 26

DISCUSSION 29

ACKNOWLEDGEMENTS 32

REFERENCES 33

TABLES 41

FIGURE LEGEND 42

FIGURES 44

3 SUBCORTICAL BEETLE COMMUNITIES AROUND WAREHOUSES AND NURSERIES IN GEORGIA 49

ABSTRACT 49

INTRODUCTION 50

METHODS 53

RESULTS 57

DISCUSSION 61

CONCLUSIONS 65

ACKNOWLEDGEMENTS 66

REFERENCES 67

TABLES 80

FIGURE LEGEND 84

FIGURES 86

4 CONCLUSIONS 94

THESIS CONCLUSIONS 94

REFERENCRES...98

LIST OF TABLES

Page

Table 2.1: List of individual semiochemical lures used to survey the *Ips* engraver beetle guild during November 2009 – 2010 in Whitehall Forest, Athens, Georgia.........41

Table 3.1: List of semiochemical lures used to survey the subcortical beetle community around warehouses and nurseries in 2010 in Georgia. 80

Table 3.2: Total number of all subcortical beetles (Buprestidae, Cerambycidae, and Scolytinae) caught in funnel traps in 2010 around warehouses and nurseries in Georgia...82

LIST OF FIGURES

Page

Figure 2.1: Mean (±SE) number of beetles caught in pre-burn and post-burn stands: *Ips grandicollis* trapped in stands originally burned in 2007 (A) and 2009 (B); and *Temnochila virescens* in 2007 (C), 2008 (D), and 2009 (E) at the Whitehall Forest in Athens, Georgia. Plots were burned during trapping, and beetle numbers were compared two months before (Pre-burn) and after the burn (Post-burn) from (12 February 2010 to 4 June 2010, with a burn on 9 April 2010)...............................44

Figure 2.2: Mean (±SE) number of *Ips avulsus* (A), *I. calligraphus* (B) and *I. grandicollis* (C) caught per two weeks in funnel traps with four semiochemical lure combinations during November 2009-2010 at Whitehall Forest in Athens, Georgia. (IAV: (+/-)-ipsenol, (+/-)-ipsdienol, and Lanierone, ICA: (+/-)-ipsdienol and *cis*-verbenol, and IGR: (+/-)-ipsenol and (-) α-pinene, and a Control trap with no lures). Means with the same letters are not significantly different from each other 45

Figure 2.3: (A) Mean (±SE) number of *Temnochila virescens* caught per two weeks in multiple funnel traps with four semiochemical lure combinations (IAV: (+/-)-ipsenol, (+/-)-ipsdienol, and Lanierone, ICA: (+/-)-ipsdienol and *cis*-verbenol, and IGR: (+/-)-ipsenol and (-) α-pinene, and a Control trap with no lures), (B) mean (±SE) number of *Thanasimus dubius* caught per 2 weeks with all four semiochemical lure combinations and (C) mean (±SE) number of *Thanasimus*

dubius caught per 2 weeks across in 2007/10, 2008 and 2009, and (D) interaction plot of the mean (±SE) number of *Enoclerus nigripes nigripes* caught per two weeks in funnel traps with all four semiochemical lure combinations in 2007/10, 2008 and 2009. Means with the same letters are not significantly different from each other. 46

Figure 2.4: Seasonal activity of *Ips avulsus* (A), *I. calligraphus* (B) and *I. grandicollis* (C) caught per two weeks in funnel traps with all four semiochemical lure combinations during November 2009-2010 at the Whitehall Forest in Athens, Georgia....................47

Figure 2.5: Seasonal activity of *Temnochila virescens* (A), *Thanasimus dubius* (B), and *Enoclerus nigripes nigripes* (C) caught per two weeks in multiple funnel traps with all four semiochemical lure combinations during November 2009-2010 at the Whitehall Forest in Athens, Georgia 48

Figure 3.1: Mean (±SE) number of scolytines and woodborers (Buprestidae and Cerambycidae) caught per 2 weeks in Lindgren funnel traps at warehouses (A) and nurseries (B) with three semiochemical lures (ethanol, ethanol plus α-pinene, and exotic *Ips* lure) during summer 2010 in Georgia. Means with the same letters are not significantly different from each other 86

Figure 3.2: Mean (± SE) number of *Xylosandrus crassiusculus*, *Hypothenemus* spp., *Xyleborus saxeseni*, *Cnestus mutilatus* and *Ips grandicollis* caught per 2 weeks in Lindgren funnel traps at warehouses and nurseries (A) and with three semiochemical lures (B) during summer 2010 in Georgia. Means with the same letters are not significantly different from each other....................87

Figure 3.3: Mean (± SE) number of native and exotic scolytine species caught per two weeks in Lindgren funnel traps at warehouses and nurseries (A) and with three semiochemical lures (B) during summer 2010 in Georgia. Means with the same letters are not significantly different from each other...88

Figure 3.4: Seasonal activity of *Xylosandrus crassiusculus* (A, E), *Hypothenemus* spp. (B, F), *Xyleborus saxeseni* (C, G), *Cnestus mutilatus* (H) and *Ips grandicollis* (D, I) caught in funnel traps with three semiochemical lures at warehouses and nurseries in 2010 in Georgia 89

Figure 3.5: Rarefaction curve estimating species richness for all beetles trapped during summer 2010 around warehouses and nurseries with three semiochemical lures, in Georgia. WE = traps at warehouses with ethanol lure; WEA = warehouses with ethanol + α-pinene lures; WI = warehouses with the exotic *Ips* lure; NE = nurseries with ethanol; NEA = nurseries with ethanol + α-pinene; NI = nurseries with the exotic *Ips* lure...90

Figure 3.6: Shannon-Weiner (H) and Simpson's (D') diversity indices for all scolytine (A) and woodboring (B) beetles caught in Lindgren funnel traps at warehouses and nurseries with three semiochemical lures during summer 2010 in Georgia. 91

Figure 3.7: Shannon-Weiner (H) and Simpson's (D') diversity indices for native (A) and exotic (B) scolytine beetles caught in Lindgren funnel traps at between warehouses and nurseries with three semiochemical lures during summer 2010 in Georgia...92

Figure 3.8: NMS plot for all scolytine beetles (A) and woodboring beetles (Buprestidae and Cerambycidae) (B) caught during entire summer 2010 trapping period around warehouses and nurseries with three semiochemical lures, in Georgia. WE = traps at warehouses with ethanol lure; WEA = warehouses with ethanol + α-pinene lures; WI = warehouses with the exotic *Ips* lure; NE = nurseries with ethanol; NEA = nurseries with ethanol + α-pinene; NI = nurseries with the exotic *Ips* lure 93

CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

INTRODUCTION

Subcortical Beetles

Subcortical beetles including bark and ambrosia beetles (Coleoptera: Scolytinae) and woodboring beetles (Buprestidae and Cerambycidae) are abundant and species-rich insect taxa in forest communities within the southeastern United States (U.S.). They play an important role in ecosystem processes as they assist with degradation of woody material through reproductive and developmental habits that can contribute to tree dieback and death (Rudinsky 1962, Evans et al. 2004). Larvae of these beetles cause most of the damage, although adults contribute initially through boring activities and sometimes inoculation of symbiotic fungal species into trees. Larvae of bark beetles are phloeophagous as they feed on the phloem of the tree and those of ambrosia beetles are fungivores as they feed on fungal cultures inoculated in the wood (Rudinsky 1962). In contrast, the larvae of woodboring beetles are phloeophagous/xylophagous as they feed both on the phloem and xylem layers of the tree (Evans et al. 2004).

The beetle order Coleoptera is the largest order of insects and includes the subfamily Scolytinae (Curculionidae) which is comprised of more than 6,000 species (Solomon 1995). Included among important native scolytines are *Ips* pine engraver beetles which typically colonize weakened or dying trees, and are considered secondary pests (Rudinsky 1962, Wood 1982). *Ips* engraver beetles colonize and breed in *Pinus* spp. and *Picea* spp. in North America (Wood 1982). All of the southeastern *Ips* species [*I. avulsus* (Eichhoff), *I. calligraphus* (Germar), and *I. grandicollis* (Eichhoff)] attack major pine species (e.g., *P. echinata* Mill. and *P. taeda* L.) grown in the region (Conner & Wilkinson 1983). In previous years, *Ips* species have caused estimated monetary losses of > $2 million in Georgia alone, and have caused major economic damage across the region in other years (Berisford & Douce 1997, Douce & Berisford 2003).

Taxonomy of *Ips* Beetles

Ips avulsus, the smallest of the three beetles, ranges in size from 2.1 to 2.8 mm and has four spines on the elytral declivity (Wood 1982). They are cylindrical, 2.6 times as long as wide, and appear dark reddish brown. Males and females are dimorphic: females have a reduced basal connection between the second and third spines. *Ips avulsus* is distributed throughout the southeastern U.S. (Wood 1982).

Ips calligraphus is the largest of the three beetles that ranging in size from 3.8 to 5.9 mm and has six spines on the elytral declivity (Wood 1982). They are cylindrical, 2.7 times as long as wide, and appear dark reddish brown. Males and females are dimorphic, with the third spine on females being slightly smaller than on males. *Ips calligraphus* is distributed throughout North and Central America, and the Caribbean (Wood 1982).

Ips grandicollis ranges from 2.9 to 4.6 mm and has five spines on the elytral declivity (Wood 1982). Adults are cylindrical, 2.7 times as long as wide, and appear dark reddish brown. Males and females are dimorphic: the third spine on females is slightly smaller and lacks the ventral hook possessed by the male. This species is distributed throughout North and Central America (Wood 1982). *Ips grandicollis* was introduced to South Australia in 1943, and is considered an important pest of pine trees planted in the Southern Hemisphere (Wood 1982, Morgan 1989).

Ecology of *Ips* Beetles

Ips species prefer to attack weakened or dying trees, and are generally considered secondary pests (Rudinsky 1962, Wood 1982). However, when stand conditions are optimal as prompted by tree stress caused by drought, forest fires, or improper management practices (overcrowding of trees, lack of sanitation after cutting, or intense prescribed burning), they have the capability of becoming primary pests of healthy pine trees (Rudinsky 1962, Wood 1982, Morgan 1989). In Georgia, 11 native species of pine trees are grown: sand pine, *Pinus clausa* (Chapman ex Engelmann) Vasey ex Sargent; shortleaf pine, *P. echinata* Miller; slash pine, *P. elliottii* Engelmann; spruce pine, *P. glabra* Walter; longleaf pine, *P. palustris* Miller; table mountain pine, *P. pungens* Lambert; pitch pine, *P. rigida* Miller; pond pine, *P. serotina* Michx.; eastern white pine, *P. strobus* L.; loblolly pine, *P. taeda* L.; and Virginia pine, *P. virginiana* Miller (Conner & Wilkinson 1983 and Johnson et al. 2011). At least one, if not all three, of the *Ips* species attacks each pine species grown in the South (Conner & Wilkinson 1983).

There appears to be a vertical partition of host trees by *Ips* beetles as based on their species and size (Paine et al. 1981, Ayres et al. 2001). For example, *I. avulsus*, which is the smallest *Ips* beetle in the southeastern U.S., is present in the top of the crown and in thinner branches. *Ips calligraphus*, which is the largest *Ips* beetle in the southeastern U.S., is present towards the base of the main tree bole. *Ips grandicollis* is generally present in the middle of the bole, and is intermediate in size. Such habitat partitioning may reduce interspecific competition and allows these beetles to use most of the phloem habitat effectively (Paine et al. 1981, Ayres et al. 2001).

Life cycle of *Ips* Beetles

Ips beetles are polygynous and are capable of producing one to several generations a year (Wood 1982). To begin a new generation of beetles, overwintering males emerge from their maturation chamber and initiate an attack of an optimal host tree by boring a hole through the bark and into the phloem. Each male creates a nuptial chamber under bark, and releases semiochemicals such as ipsenol, ipsdienol and *cis*-verbenol attracting several females with whom he will mate. Each female then excavates an egg gallery, resulting in a typically “Y” or “H” shaped gallery, depending on the species. Females chew out egg niches and deposit a single egg at regular or irregular intervals, on either side of the gallery, depending on the species. When larva eclose, they begin chewing their way through the inner bark, creating larval galleries, until sufficient feeding has occurred. They pupate at the end of their gallery, or in a “pupal chamber,” emerge, and feed on fungi before fully maturing and tunneling their way out of the tree to find a new host tree and/or a mate (Rudinsky 1962, Conner and Wilkinson 1983).

Seasonal activities or flight patterns of many bark beetles commonly found in the northern U.S. have been studied (Chapman and Kinghorn 1958, Roling and Kearby 1975). Atkinson et al. (1988) documented the flight patterns for *Ips* beetles in Florida, on slash pine. Their study differs from our bark beetle study in that they used sticky traps and window traps, and used ethanol and the slash pine (host tree) as baits to attract multiple bark beetles, not specifically targeting *Ips* species. Turnbow and Franklin (1980) showed that in Georgia, *I. avulsus* had a population peak in August (total trap catches = 8), and *I. grandicollis* had a population peak in July (total trap catches = 15), although only ethanol was used as the attractant. Clearly, more long-term studies about *Ips* spp. phenology in this region are needed. An in-depth understanding of the seasonal activity of bark beetles is critical to better deploy national surveys to help improve decision making about management, and control practices such as correct timing for thinning and application of insecticides to reduce pest numbers and economic damage.

Coleopteran Predators of *Ips* Beetles

Although many beetle predators were trapped in our study (Bothrideridae, Cleridae, Histeridae, Monotomidae, Staphylinidae, Tenebrionidae, Trogossitidae and Zopheridae), only three common *Ips* engraver predator species were considered in this thesis, as catches were high enough for statistical analysis: *Temnochila virescens* (Fabricius) (Trogossitidae), and *Thanasimus dubius* (Fabricius) (Cleridae) and *Enoclerus nigripes nigripes* (Say) (Cleridae). *Temnochila virescens* has one generation per year (Mignot & Anderson 1970, Lawson & Morgan 1992), and is generally only active in the summer months (Struble 1942a, Mignot & Anderson 1970). Eggs are laid continually when adults are active and they produce two types of larvae: some have six instars and mature by end of summer, but most have seven instars and overwinter as larvae or adults (Struble 1942a, Mignot & Anderson 1970). Previous studies have verified that adult *T. virescens* will prey on *Ips* beetles as larvae (Struble 1942a, b, Mignot & Anderson 1970, Riley & Goyer 1986) and adults (Mignot & Anderson 1970, Billings & Cameron 1984, Lawson & Morgan 1992, 1993). Adult feeding behaviors of *T. virescens* are most likely mediated by kairomonal responses to prey pheromones and tree volatiles (Billings & Cameron 1984, Lawson & Morgan 1993, Raffa et al. 2007, Allison et al. 2013). It has been found that *T. virescens* is attracted to *Ips* engraver pheromone components like ipsenol, ipsdienol and *cis*-verbenol (Billings & Cameron 1984, Allison et al. 2013).

Thanasimus dubius may have 2-4 generations per year (Thatcher & Pickard 1966), and are generally active only in the cooler spring and autumn months (Mignot & Anderson 1969). Eggs are laid in the cooler months and not the hotter mid-summer months (Mignot & Anderson 1969). Larvae have four instar stages. Adult feeding behaviors of *T. dubius* are also most likely mediated by kairomonal responses to prey pheromones and tree volatiles (Billings & Cameron 1984, Payne et al. 1984, Allison et al. 2013). *Thanasimus dubius* seems to be more of a generalist feeder than *T. virescens* (Kohnle & Vité 1984), which prefers feeding on *Ips* beetles to the southern pine beetle, *Dendroctonus frontalis* Zimmerman. It further prefers *I. grandicollis* over other *Ips* spp. (Mignot & Anderson 1969, 1970, Billings & Cameron 1984) although it is attracted to all three species (Rose et al. 1981). In another study, it was found that when offered a choice between SPB and *I. avulsus*, the clerid preferred *I. avulsus* (Mizell & Nebeker 1982). Interestingly, *T. dubius* is preyed upon by *T. virescens* (Thatcher & Pickard 1966). It has been found that *T. dubius* is attracted to *Ips* engraver pheromone components like ipsenol and ipsdienol, and the tree volatile α-pinene (Mizell et al. 1984) and other monoterpene blends (Chénier & Philogène 1989).

There is considerably less information available on *E. n. nigripes* in the southeastern U.S. Although little is known about *E. n. nigripes*, other studies have looked at another *E. nigripes* subspecies (Chénier & Philogène 1989), or have looked at other *Enoclerus* spp. in different pine species ecosystems, or looked at *Enoclerus* species regarded as predators of other *Ips* species not found in the southeastern U.S. (Mawdsley 2001, Erbilgin & Raffa 2002, Aukema et al. 2004, Ryall & Fahrig 2005, Raffa et al. 2007). However, *E. nigripes sensu lato* has been documented as a predator of *Ips* beetles in the southeastern U.S. (Berisford 1974, Allison et al. 2013). Assuming that *E. n. nigripes* has a similar biology to the other clerid beetle, *T. dubius*, it would also be expected to cue in on prey kairomones and host tree volatiles.

Both *T. virescens* and *T. dubius* are known to prey specifically on *I. grandicollis* in Australia, where *I. grandicollis* has been introduced (Neumann 1987, Morgan 1989, Lawson & Morgan 1992, 1993). *Ips grandicollis* is a secondary pest in these exotic pine plantations. Using these predators as a biological control, especially for southern pine beetle has also been utilized previously with varying success-levels (Struble 1942a, Thatcher & Pickard 1966).

Chemical Ecology of *Ips* Beetles

Previous studies have been conducted on the attractiveness of lures, both alone and in combination with others, in attracting bark beetles (Miller et al. 1997, Aukema et al. 2004, Dahlsten et al. 2004). Semiochemical attractants, which include enantiomeric ratios [ratio of the percentage of one enantiomer to another, (+) : (-), in a mixture] of ipsenol, ipsdienol, and lanierone, have been used in several studies.

Ips avulsus has been found to be attracted to the aggregation pheromones composed of ipsdienol (Renwick and Vité 1972), more specifically (*R*)-(-)-ipsdienol (2-

methyl-6-methylene-2,7-octadien-4-ol) (Vité et al. 1978); (*S*)-(-)-ipsenol (2-methyl-6-methylene-7-octen-4-ol) (Hedden et al. 1976); 2-methyl-3-buten-2-ol; and lanierone (2-hydroxy-4,4,6-trimethyl-2,5-cyclohexadien-1-one) (Smith et al. 1993, Skillen et al. 1997). Miller et al. (2005) reported that *I. avulsus* was most attracted to lanierone with (+/-)-ipsdienol, and lanierone with (+/-)-ipsenol and (+/-)-ipsdienol, in Georgia. However, aggregation of *I. avulsus* was interrupted by the presence of (*S*)-(+)-ipsdienol (Skillen et al. 1997).

Ips calligraphus are attracted to the aggregation pheromones composed of (*R*)-(-)-ipsdienol (2-methyl-6-methylene-2,7-octadien-4-ol) (Vité et al. 1978); (*S*)-*cis*-verbenol [*cis*-4,6,6-trimethylbicyclo (3.1.1) hept-3-en-2-ol]; and *trans*-verbenol [trans-4,6,6-trimethylbicyclo (3.1.1) hept-3-en-2-ol] (Vité et al. 1978 & Skillen et al. 1997). A combination of ipsdienol plus *cis*-verbenol was more effective in trapping beetles than was ipsdienol plus *trans*-verbenol (Renwick and Vité 1972). Mass aggregation is prompted by a combination of (*R*)-(-)-ipsdienol, (*S*)-*cis*-verbenol, and host volatiles (Smith et al. 1993). Miller et al. (2005) reported that *I. calligraphus* was most attracted to (+/-)-ipsdienol alone, lanierone with (+/-)-ipsdienol, (+/-)-ipsenol with (+/-)-ipsdienol, and lanierone with (+/-)-ipsenol plus (+/-)-ipsdienol, in Georgia. However, aggregation is interrupted by the presence of (*S*)-(+)-ipsdienol (2-methyl-6-methylene-7-octen-4-ol) and (*R*)-*cis*-verbenol [*cis*-4,6,6-trimethylbicyclo (3.1.1) hept-3-en-2-ol] (Skillen et al. 1997).

Ips grandicollis are attracted to the aggregation pheromones composed of (*S*)-(-)-ipsenol (2-methyl-6-methylene-7-octen-4-ol) (Hedden et al. 1976); *cis*-verbenol [*cis*-4,6,6-trimethylbicyclo (3.1.1) hept-3-en-2-ol]; and E-myrcenol (trans-2-methyl-6-methylene-7-octen-2-ol) (Skillen et al. 1997). Miller et al. (2005) showed that statistically, *I. grandicollis* was equally attracted to (+/-)-ipsenol alone, lanierone with (+/-)-ipsenol, (+/-)-ipsenol with (+/-)-ipsdienol, and lanierone with (+/-)-ipsenol and (+/-)-ipsdienol, in Georgia. However, aggregation is interrupted by the presence of (*R*)-(+)-ipsenol (2-methyl-6-methylene-7-octen-4-ol) (Skillen et al 1997).

Forest Disturbances and *Ips* Beetles

Piedmont forests are subject to several types of disturbances by both biotic (e.g., insects and pathogens) and abiotic (e.g., fire, drought, frost, and soil types) agents in the southeastern U.S. (Moore et al. 2002, Thomas et al. 2002). Wildfires historically dominated southern pine forests, but have been largely replaced by prescribed fires to promote ecosystem health (Wade et al. 1989, Brennan & Hermann 1994, Stanturf & Goodrick 2011). Fire plays a major role in forest ecology, affecting the insects not only on the forest floor, but also under the bark of trees. Prescribed burning has been used as a technique for management of pine stands for many years, especially in the Southeast where a fire frequency of 1-3 years promotes a healthy longleaf pine stand (Glitzenstein et al. 2003). Prescribed fire reduces hazardous forest fuels like coarse woody debris, creates new wildlife habitats, and enhances nutrient cycling (Georgia Forestry Commission 2008). The intensity of fires plays a role in forest dynamics. For example, the heat from low intensity flames can kill insect pests underneath the bark, while doing little damage to the tree, allowing it to recover. One drawback to prescribed burning is that if the fire is too intense, it could damage trees making them more susceptible to beetle attack.

Several studies have looked at interactions between prescribed fire and *Ips* beetles in the western U.S. (Miller & Patterson 1927, McHugh et al. 2003, McCullough et al. 1998). Most studies seem to be concerned with tree mortality due to beetle attacks after fire or tree mortality due to fire because of beetle attacks on the tree before the fire. One study suggests that *Ips* species colonize fire-damaged ponderosa pines (*P. ponderosa* Douglas ex Lawson) in northern Arizona (McHugh et al. 2003). It is currently not well known how prescribed burning may affect the seasonal activity of *Ips* beetles and their predators in the southeastern region. A study by Campbell et al. (2008) documented the effects of prescribed fire on bark beetles in Alabama, and although some scolytines were found [*Dendroctonus terebrans* (Olivier), *Xyleborinus saxeseni* (Ratzeburg), *Xyleborus* species, and *Hylastes tenuis* (Eichhoff)], no *Ips* species were trapped. This study also found that the clerid beetle abundance was greater on burned than in control plots (with no burning). This study will not look at tree mortality *per se*, but rather population-level changes of *Ips* species and their predators after a prescribed fire in the Piedmont region of Georgia.

Another major forest disturbance during the last two centuries has been the invasion of novel habitats by many exotic insects and diseases (Liebhold et al. 1995, Gandhi & Herms 2010). These invasions have occurred due to greater amounts of cargo and human traffic around the world, and especially into North America. In particular, subcortical beetles have been intercepted frequently at ports-of-entry in wood packing materials (termed as “solid wood packing material”) used for shipment (Dobbs & Brodel 2004, Work et al. 2005, Brockeroff et al. 2006, Price et al. 2011) and in live plant material (Humble & Allen 2004, Poland & McCullough 2006, Aukema et al. 2010, Liebhold et al. 2012). There have been major consequences in terms of alteration of ecological processes, reduction in forest health, and economic impacts in urban and forest areas due to tree dieback and mortality caused by exotic pests (Lovett et al. 2006, Gandhi & Herms 2010). As the numbers of exotic pests are increasing over time and the species accumulation curves indicate exponential growth, we expect such ecological and economic impacts to be magnified over larger areas and time frames (Aukema et al. 2010).

Research Objectives

My two-year study focused on the ecology of native and exotic bark and woodboring beetles, and their associates under forest disturbance regimes and urbanization in Georgia. I had four major research objectives as follows: 1) to determine the seasonal activity of *Ips* spp. and their coleopteran predators over 12 months in loblolly and shortleaf pine stands in the southeastern U.S.; 2) to assess if fire disturbance through prescribed burning, has either short- or long-term effects on the activity of *Ips* beetles and their coleopteran predators; 3) to determine differences in subcortical beetle communities between two major types of ports-of-entry for exotic species: warehouses and nurseries; and 4) to assess the responses of subcortical beetles to lures (e.g., α-pinene, ethanol, and exotic *Ips* lure) commonly used in national surveys for exotic pest detection.

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CHAPTER 2

IPS PINE ENGRAVERS: RESPONSES TO PRESCRIBED BURNING AND LURE COMBINATIONS, AND SEASONAL ACTIVITY IN THE SOUTHEASTERN UNITED STATES

ABSTRACT

Bark beetles (Coleoptera: Curculionidae: Scolytinae) and their predators (Coleoptera: Cleridae and Trogossitidae) are economically and ecologically important insects in southeastern U.S. forests. We studied the immediate (two months before and after fire) and short-term (1-3 years after fire) effects of prescribed burning on *Ips* spp. and their most common predators in endemic southern pine (*Pinus* spp.) forests. Further, we determined their responses to commonly used semiochemical lures and their seasonal activity over 12 months (November 2009-2010). A fire chronology was established where pine stands previously burned in 2007, 2008, and 2009 were chosen for the study. The stands that were burned in 2007 were also burned in April 2010, allowing us to assess immediate responses of beetles to burning. Multiple funnel traps were used to trap beetles, and were baited with one of the following lure combinations: 1) (+/-)-ipsenol, (+/-)-ipsdienol and lanierone; 2) (+/-)-ipsdienol and *cis*-verbenol; 3) (+/-)-ipsenol and (-) α-pinene; and 4) a control trap with no lures.

A total of 112,949 *Ips* engraver beetles [*I. avulsus* (Eichhoff), *I. calligraphus* (Germar) and *I. grandicollis* (Eichhoff)] and 6,200 predator beetles [*Temnochila* *virescens* (F.), *Thanasimus dubius* (F.) and *Enoclerus nigripes nigripes* (Say)] were trapped over a year. Greater numbers of *I. grandicollis* and *T. virescens* were trapped immediately after the burning in 2010, although the same trend was evident during those months in stands that remained unburned that year. There was no difference in beetle catches among stands that were burned in 2007-2009. These trends indicate that the effects of immediate or short-term prescribed burning on these beetle populations were negligible.

Ips avulsus and *I. calligraphus* were more responsive in terms of greater catches to their target lure combinations [(+/-)-ipsenol + (+/-)-ipsdienol + lanierone and (+/-)-ipsdienol + *cis*-verbenol, respectively]. However, *I. grandicollis* was the most responsive (>2 times) to the *I. avulsus* lure combination, followed by its target combination [(+/-)-ipsenol + (-) α-pinene]. Greater numbers of *T. virescens* were trapped with lures for *I. calligraphus* and *I. grandicollis*, and *T. dubius* with the *I. grandicollis* lure. *Enoclerus n. nigripes* appeared to respond in greater numbers to the *I. avulsus* lure in stands burned in 2007 than in the stands burned in 2008-2009.

Trapping for a year indicated that there are perhaps 4-6 generations of *Ips* spp., with *I. calligraphus* having the earliest activity in the season. About 3-4 annual peaks were also observed for the three predator beetles with the longest activity shown by *T. virescens*. Overall, this study provides results relevant to optimal sampling times and use of specific lures to maximize catches of subcortical beetle species in southeastern pine forests.

Index Words: bark beetles, *Ips* spp., pine, predators, prescribed fire, southeastern U.S.

INTRODUCTION

Bark beetles (Coleoptera: Curculionidae: Scolytinae) are economically and ecologically important pests of southeastern forests. Included among important scolytines are *Ips* pine engraver beetles which typically colonize weakened or dying trees, and are considered secondary pests (Rudinsky 1962, Wood 1982). However, when stand conditions are optimal (prompted by tree stress caused by drought, forest fires, overcrowding of trees, or improper thinning procedures), *Ips* beetles can become primary pests of living, healthy trees (Rudinsky 1962, Wood 1982, Morgan 1989). *Ips* engraver beetles attack and breed in *Pinus* spp. and *Picea* spp. in North America (Wood 1982). At least one, if not all three, of the southeastern United States (U.S.) *Ips* species [*I. avulsus* (Eichhoff), *I. calligraphus* (Germar), and *I. grandicollis* (Eichhoff)] attacks major pine species grown in the South (Conner & Wilkinson 1983). *Ips* beetles cause damage to trees through the creation of entrance/exit holes on bark and by tunneling into the phloem, resulting in growth loss, girdling, and tree death. In previous years, *Ips* species have caused estimated monetary losses of > $2 million in Georgia alone (Berisford & Douce 1997, Douce & Berisford 2003).

In the southeastern U.S., Piedmont forests are subject to several types of disturbances by both biotic (e.g., insects and pathogens) and abiotic (e.g., fire, drought, frost, and soil types) agents (Moore et al. 2002, Thomas et al. 2002). Fire (both natural and prescribed) is the major disturbance agent, and it occurs frequently (1-5 years) in the region (Garren 1943, Waldrop et al. 1992, Glitzenstein et al.1995, 2003). Wildfires historically dominated the pine forests, but in recent years, they have been largely replaced by prescribed fires to promote ecosystem health (Wade et al. 1989, Brennan &

Hermann 1994, Stanturf & Goodrick 2011). Prescribed fires improve wildlife habitat and biodiversity, control diseases and control competing plant species, promote the growth of fire-dependent species, and aid in nutrient cycling (Grano 1970, McKevin & McKee 1986, Wade et al. 1989).

Interactions between bark beetles and fire have been well studied primarily in the northern and western forests (McCullough et al. 1998, Ayres et al. 1999, Breece et al. 2008). These studies have focused on how the host tree becomes more susceptible to damage or death by bark beetles under fire regimes (Schwilk et al. 2006), and considers other factors (e.g. tree physiology like resin flow, fungi introduction, and stand management practices) affecting tree susceptibility to attack or death (Goheen & Hansen 1993, Campbell et al. 2008a, Davis et al. 2012). In contrast, little work has been conducted on effects of prescribed burning on bark beetle communities in the southeastern U.S. Not all three species of the *Ips* engraver beetle guild are represented or considered in these studies [only *I. grandicollis* is mentioned in Campbell et al. (2008b)], and sometimes the beetles inhabit different pines [e.g., Menges & Deyrup (2001) focused on such effects in slash pine (*P. elliottii* Engelm var. *densa* Little & Dorman) stands]. However, we do know that fire can either increase beetle numbers by attracting more beetles to fire-damaged trees or reduce beetle numbers by killing them directly (Ayres et al. 1999, Kelsey & Joseph 2003). It is unknown whether prescribed fire may generally increase or decrease *Ips* bark beetle numbers in southeastern U.S. pine stands. However, in Louisiana, it was found that prescribed burns implemented during both the dormant and growing seasons did not affect the numbers of bark beetles, and the catches were not significantly different between seasons (Bauman 2003).

Attraction of *Ips* beetles to conspecifics and to fire-damaged trees includes responsiveness to semiochemicals (pheromones and host-attractants). It is known that *I. avulsus* is attracted to *R*-(-)-ipsdienol and lanierone (Skillen 1997). *Ips calligraphus* is attracted to *R*-(-)-ipsdienol and *S*-*cis*-verbenol (Skillen 1997). We expect that *I. avulsus* and *I. calligraphus* will be attracted to the same semiochemicals, because several studies report that *I. avulsus* was attracted to bolts infested with *I. calligraphus* in addition to its conspecifics (Vité et al. 1964, Renwick & Vité 1972, Birch et al. 1980, Svhira et al. 1980, Svhira 1982, Smith et al. 1993). *Ips grandicollis* is attracted to *S*-(-)-ipsenol and *cis*-verbenol (Skillen 1997), and α-pinene (Miller & Rabaglia 2009), and, as indicated in a previous study, we do not expect it to have any inter-species attraction to the other pheromones (Vité and Renwick 1971).

Our primary research objective was to determine if fire disturbance through prescribed burning has an effect on the populations of *Ips* beetles and associated coleopteran predators (Cleridae and Trogossitidae) in loblolly (*P. taeda* L.) and shortleaf pine (*P. echinata* Mill.) stands in the southeastern U.S. Our secondary objective was to assess the responses to these beetles to commonly used lures, and to determine the seasonality of these beetle species to find effective times to monitor their populations in forested areas.

METHODS

Study Sites

The study was conducted at the Warnell School of Forestry and Natural Resources Whitehall Forest, University of Georgia in Athens, Georgia (33°53.8’N, 83°21.7’W). Forest overstory was dominated by loblolly and shortleaf pines (27-45 years old) intermixed with red oak (*Quercus rubra* L.). The understory contained primarily sweetgum (*Liquidambar styraciflua* L.), water oak (*Q. nigra* L.), yellow poplar (*Liriodendron tulipifera* L.), winged elm (*Ulmus alata* Michx.), and dogwood (*Cornus florida* L.) trees. Soil is of the Piedmont-type (Coder 1996) but more specifically, includes Cecil sandy clay loam, Davidson clay loam, Madison sandy loam, and Pacolet sandy clay loam (http://websoils urvey.nrcs.usda.gov). Average soil temperatures near the experiment site were 9.62 °C at 10 cm during 5 November, 2009 - 31 December, 2009 and 20.31 °C during 1 January, 2010 - 5 November, 2010 (www.GeorgiaWeather.net). Total annual precipitation was 160.81 cm with 91 rainy days, though there was a water balance deficit i.e., the site was under drought.

Nine replicate pine stands were established including three stands representing each of the three burn years (2007, 2008, and 2009). The stands burned in 2007 were burned again on 9 April, 2010 because of the three-year controlled burn cycle implemented at the Whitehall Forest. This burning cycle additionally allowed us to assess the immediate effects of prescribed burning on subcortical beetles.

Beetle Sampling

Four wet-cup 12-unit Lindgren funnel traps were placed in each stand, for a total of 36 traps for the study (Lindgren 1983). Traps were assigned randomly with one of the following four lure combinations: 1) (+/-)-ipsenol, (+/-)-ipsdienol, and lanierone for *Ips avulsus* (thereafter referred to as IAV); 2) (+/-)-ipsdienol and *cis*-verbenol for *Ips calligraphus* (ICA); 3) (+/-)-ipsenol and (-) α-pinene for *Ips grandicollis* (IGR); and 4) control trap with no lures (Table 2.1). These lures are established as effective attractants for the three species of *Ips* beetles in the Southeast (Miller & Rabaglia 2009, Miller et al. 2011, Allison et al. 2012, Miller et al. 2013). A 3-4 cm solution of propylene glycol (Peak® RV & Marine Antifreeze without ethanol) was used in the collection cups as a preservative and killing agent for trapped insects. Each funnel trap was hung between two trees so that no trap was within 2 m of a tree. Individual traps were placed 10-15 m apart along a transect, and each replicate stand was >250 m apart to reduce interactions between transects.

Traps were deployed from mid-October 2009 to early November 2010, and were emptied approximately every 15 days, for a total of 26 collections over a one-year period. Lures were replaced approximately every 60 days, with changes more frequent in warmer months (20 October, 2009; 15 January, 2010; 9 April, 2010; 4 June, 2010; 16 July, 2010; and 10 September, 2010). All *Ips* engraver beetles and their common beetle predators (Trogossitidae and Cleridae) were identified to the species-level using taxonomic keys (Wood 1982, Arnett & Thomas 2005a, b). Voucher collections will be deposited in the University of Georgia Collection of Arthropods (UGCA) at the Georgia Museum of Natural History, Athens, GA.

Statistical Analyses

To assess the effects of prescribed burning on beetles, analysis of variance (ANOVA) tests were performed on trap catch data standardized to beetle catches per two weeks (SAS Institute 2002-2003). Each individual stand was a unit of replication ($N = 3$). Data were pooled for all lure-types within a stand, and were first checked for normality and constant variance across treatments. Only trap catches from approximately two months before (12 February, 2010) and after (4 June, 2010) the burn (on 9 June, 2010) were used for these analyses since comparison of other months pre- and post-burn are likely confounded by seasonal variation in catches. Analyses were performed separately for each beetle species and year of sampling.

To determine the efficacy of lure-type and difference in catches over three years, both non-parametric and parametric tests were performed. Analyses were performed separately for each beetle species. Catches were summed across all collection dates, and standardized to two weeks. For *Ips* beetles, data were not normal, and transformations did not improve normality, so non-parametric analyses (Kruskal-Wallis tests) were conducted (SAS Institute 2002-2003). As such, we could not assess interactions between lure-type and year for *Ips* beetles under non-parametric tests. For predators, data were not normal, and they were transformed to log-scale (ln + 1) to achieve normality before analyses. A two-way factorial design was used with lure-type and year as the major factors for each predator beetle species (SAS Institute 2002-2003). When the main model was significant, Tukey tests were used as posthoc analyses to assess differences in pairwise comparison among lures and years. Data for phenology graphs were summed across all lures and plots for each beetle species. Data for seasonal phenology were standardized to catches per trap per week.

RESULTS

In total, 112,949 *Ips* engraver beetles were trapped in 12 months with greatest catches of *I. avulsus* (number of beetles = 84,600) followed by *I. grandicollis* (26,828) and *I. calligraphus* (1,521). Further, a total of 6,200 predator beetles were trapped: *Temnochila virescens* (F.) (4,204), *Thanasimus dubius* (F.) (1,337), and *Enoclerus nigripes nigripes* (Say) (659) in the study.

Trap catches of beetles were compared two months before and after the prescribed burning in 2010. There was no difference in beetle numbers before and after burning for *I. avulsus* and *I. calligraphus* for all burn years ($P > 0.092$). There was no difference in pre/post burn catches for *I. grandicollis* in the burn year 2008 ($P = 0.459$), although there was a difference in sites previously burned in 2007 ($F_{1,5} = 10.83$; $P = 0.030$) and 2009 ($F_{1,5} = 9.50$; $P = 0.037$), with more trapped post-burn for both years (Fig. 2.1 A, B). Among predator species, there was a difference in beetle populations before and after the burning for *T. virescens* for each burn year group: 2007 ($F_{1,5} = 131.57$; $P = 0.003$), 2008 ($F_{1,5} = 17.34$; $P = 0.014$), and 2009 ($F_{1,5} = 67.61$; $P = 0.001$), with more beetles trapped post-burn for all three years (Fig. 2.1 C-E). There was no difference in catches for any burn year group for *T. dubius* ($P > 0.157$) or *E. n. nigripes* ($P > 0.071$).

In terms of lure-types, greater numbers of *I. avulsus* ($\chi^2_3 = 30.419$; $P < 0.001$) and *I. calligraphus* ($\chi^2_3 = 28.777$; $P < 0.001$) were trapped with the IAV and ICA lure combination, respectively (Fig. 2.2 A, B). Greater numbers of *I. grandicollis* ($\chi^2_3 = 30.366$; $P < 0.001$) were trapped with the IAV lure combination instead of the expected IGR lure combination, although catches in these lures were greater than ICA (Fig. 2.2 C). There was no difference in catches of *I. avulsus* ($P = 0.953$), *I. calligraphus* ($P = 0.947$) or *I. grandicollis* ($P = 0.664$) among all the three burn years. Similarly, there was no interaction between lure-type and burn year for any species.

For predator beetles, greater numbers of *T. virescens* ($F_{35,3}$ = 72.85; $P < 0.001$) and *T. dubius* ($F_{35,3}$ = 54.79; $P < 0.001$) were trapped with the ICA and IGR, and IGR lure combination, respectively (Fig. 2.3 A, B) (IAV: (+/-)-ipsenol, (+/-)-ipsdienol, and lanierone; ICA: (+/-)-ipsdienol and *cis*-verbenol; IGR: (+/-)-ipsenol and (-) α-pinene) (Table 2.1). Trap catches were not different for *T. virescens* among three burn years (P = 0.233). However, greater numbers of *T. dubius* ($F_{35, 2}$ = 3.92; P = 0.034) were trapped in plots burned in 2009 (Fig. 2.3 C). There was no interaction between lures and burn years for *T. virescens* (P = 0.725) or *T. dubius* (P = 0.381). However there was a significant interaction for *E. n. nigripes* that responded in greater numbers to the IAV lure-type in 2007 than in the other two years ($F_{35, 6}$ = 4.50; P = 0.003) (Fig. 2.3 D).

Seasonal phenology graphs indicated that *I. avulsus* was active throughout November 2009, but had no activity, until the beginning of March 2010, when numbers began to rise, with peak numbers trapped at the end of March/beginning of April 2010 (Fig. 2.4 A). The second greatest peak in catches was in the middle of August 2010. *Ips avulsus* remained active until trapping was concluded in November 2010. There were 5-6 activity peaks, indicating generations per year for this species. *Ips calligraphus* was active in November 2009 when trapping began, but dropped to zero until the end of January 2010, where we observed a small peak, then a decrease to zero again. Numbers of *I. calligraphus* then increased in February with another high peak in April. There were four more peaks indicating that this species may have at least six generations per year (Fig. 2.4 B). *Ips grandicollis* activity varied less dramatically than the other two *Ips* spp., with only three peaks, or possibly three generations per year. The highest numbers were trapped at the end of March 2010. Numbers of *I. grandicollis* dropped in April, but increased again in May 2010, where numbers slowly tapered until the end of July where we observed a small dip, and then an increase in August 2010. Numbers were nearly zero by October 2010, which was earlier than the other two *Ips* species (Fig. 2.4 C).

Temnochila virescens was active only from the latter half of April 2010 to the end of September 2010, with a total of four peaks. Highest numbers were trapped in June 2010 (Fig. 2.5 A). *Thanasimus dubius* was active when trapping began in November 2009, but numbers dropped until the end of January with numbers increasing again in March 2010. There were about five peaks with the highest numbers trapped in March 2010. Fewer *T. dubius* were trapped after April 2010, although there was a small peak in November 2010, with catches still observed until trapping was concluded (Fig. 2.5 B). *Enoclerus nigripes nigripes* had only one major peak from mid-March to April 2010. There were two much smaller peaks in mid-May and mid-July. This was the last species to fly in the beginning of the year and the first one to stop flying at the end of the trapping period (Fig. 2.5 C).

DISCUSSION

Overall, there was no significant difference in populations of five beetle species among forest stands burned in 2007, 2008, and 2009. Further, such differences were absent for most beetle species immediately before and after prescribed burning in 2010 of stands previously burned in 2007. Catches were significantly different only for *I. grandicollis* in stands burned in 2007/2010 and 2009, and for *T. virescens* in 2007/2010, 2008, and 2009 burned stands; this trend suggests that increases in catches post-burn period may be an artifact of sampling time. Prescribed burns were implemented when temperatures were still cool in early spring, and beetle activity is typically low (Taylor 1963, Raffa et al. 2008). Perhaps, a greater impact of fires on beetles would have been in mid-summer when populations are typically the highest (Schwilk et al. 2006). Further, surface-fires with little or no canopy burning were used at Whitehall Forest which likely led to minimal impact on trees and release of oleoresin, which contain host terpenes that attract beetles (Fatzinger 1985, Phillips et al. 1988). Our results clearly indicate that these beetle species are resilient and perhaps adapted to low-intensity prescribed-burning conducted in early spring in the Piedmont region.

As expected, greater numbers of *I. avulsus* and *I. calligraphus* were trapped with the IAV and ICA lure combination, respectively, as it has been observed in other studies (Miller et al. 2005 and Renwick & Vité 1972, respectively). Unexpectedly, much greater numbers of *I. grandicollis* were trapped with the IAV lure combination rather than the IGR lure combination. The IAV lure consisted of (+/-)-ipsenol, (+/-)-ipsdienol, and lanierone, whereas the IGR lure consisted of (+/-)-ipsenol and (-) α-pinene. Among the three *Ips* species, *I. grandicollis* is the most widely distributed species, and has been reported to respond to (+/-)-ipsenol and (+/-)-ipsdienol in Georgia, ethanol + α-pinene in Minnesota, and ipsenol alone in Wisconsin (Miller et al. 2005, Ayres et al. 2001, Pfammatter et al. 2011). The host monoterpene, α-pinene, typically acts as a synergist to the *I. grandicollis* lure (Erbilgin & Raffa 2000, Miller & Rabaglia 2009), but it seems that either ipsdienol or lanierone may be enhancing catches in the southeastern pine forests, although such results have not been reported elsewhere.

Trapping for a year revealed that *I. avulsus* and *I. calligraphus* showed five peak activity periods indicating that beetles may have up to five generations per year. *Ips* *grandicollis* showed three peaks, suggesting that this population can produce at least three generations per year. This agrees with previous studies in the Southeast, where 8-10 generations of beetles have been documented (Dixon 1984, Eickwort et al. 2006) with one generation requiring only 21 to 40 days to complete in warm weather (Connor & Wilkinson 1983). *Ips calligraphus* was the first beetle to become active in the beginning of the year, and reports indicate that *I. calligraphus* is the first species to attack trees especially under drought conditions (Conner & Wilkinson 1983).

Seasonal phenologies of predators of bark beetles have generally been not well documented. We found that *T. virescens* and *T. dubius* had 3-4 peak activity periods, whereas *E. n. nigripes* had only one major peak. It appears that the first peak of *T. dubius* coincides with that of *I. grandicollis* and *I. avulsus*, whereas the second peak of *T. virescens* coincides with those of *I. calligraphus* and *I. avulsus*. Further, both of these predator beetles were caught in greatest numbers in lures for the respective *Ips* species leading support to the hypothesis that they may be preying mostly on these two beetle species (Fig. 2.3).

To conclude, this one-year trapping study of bark beetles and their major predators revealed a number of ecological trends related to their populations, activity period, and response to semiochemicals. The beetles in this region appear to be unaffected by high frequency (1-3 years) and low intensity prescribed burning. While *I. avulsus* and *I. calligraphus* responded to their respective lures, *I. grandicollis* responded most strongly to the lure for *I. avulsus*. *Temnochila virescens* responded the most to *I. calligraphus* and *I. grandicollis* lures, *T. dubius* to *I. grandicollis* lure, and *E. n. nigripes* to the *I. avulsus* lure. There may be 4-5 generations per year for each *Ips* species, with *I.*

calligraphus showing the earliest activity in the season. About 1-4 peak activity periods were observed for the predatory beetles with some peaks coinciding with those of particular *Ips* species. Considering that we caught a high number of beetles (>100,000) in this study, these trends have relevance to the management of bark beetles under disturbance regimes in pine-dominated landscapes in our region.

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Table 2.1 List of individual semiochemical lures used to survey the *Ips* engraver beetle guild during November 2009 – 2010 in Whitehall Forest, Athens, Georgia.

Semiochemical	Device Type	Enantiomeric composition	Amount in device	Release rate/day	Chemical purity
Ipsenol	BCD[a]	50:50 (+)/(-)	40 mg	0.2 mg/d	>98%
Ipsdienol	BCD[a]	50:50 (+)/(-)	40 mg	0.2 mg/d	>95%
Lanierone	BCD	>98%	40 mg	0.02 mg/d	>98%
cis-verbenol	BCD[a]	17:83 (+)/(-)	0.6 g	150 mg	UA[c]
α-pinene	UHR[b]	>95%	200 mL	2-6 g	>95%(-)

[a] Bubble cap device

[b] Ultra High Release plastic pouch

[c] Unavailable

FIGURE LEGEND

Fig. 2.1 Mean (±SE) number of beetles caught in pre-burn and post-burn stands: *Ips grandicollis* trapped in stands originally burned in 2007 (A) and 2009 (B); and *Temnochila virescens* in 2007 (C), 2008 (D), and 2009 (E) at the Whitehall Forest in Athens, Georgia. Plots were burned during trapping, and beetle numbers were compared two months before (Pre-burn) and after the burn (Post-burn) from (12 February 2010 to 4 June 2010, with a burn on 9 April 2010).

Fig. 2.2 Mean (±SE) number of *Ips avulsus* (A), *I. calligraphus* (B) and *I. grandicollis* (C) caught per two weeks in funnel traps with four semiochemical lure combinations during November 2009-2010 at Whitehall Forest in Athens, Georgia. (IAV: (+/-)-ipsenol, (+/-)-ipsdienol, and Lanierone, ICA: (+/-)-ipsdienol and *cis*-verbenol, and IGR: (+/-)-ipsenol and (-) α-pinene, and a Control trap with no lures). Means with the same letters are not significantly different from each other.

Fig. 2.3 (A) Mean (±SE) number of *Temnochila virescens* caught per two weeks in multiple funnel traps with four semiochemical lure combinations (IAV: (+/-)-ipsenol, (+/-)-ipsdienol, and Lanierone, ICA: (+/-)-ipsdienol and *cis*-verbenol, and IGR: (+/-)-ipsenol and (-) α-pinene, and a Control trap with no lures), (B) mean (±SE) number of *Thanasimus dubius* caught per 2 weeks with all four semiochemical lure combinations and (C) mean (±SE) number of *Thanasimus dubius* caught per 2 weeks across in 2007/10, 2008 and 2009, and (D) interaction plot of the mean (±SE) number of *Enoclerus nigripes*

nigripes caught per two weeks in funnel traps with all four semiochemical lure combinations in 2007/10, 2008 and 2009. Means with the same letters are not significantly different from each other.

Fig. 2.4 Seasonal activity of *Ips avulsus* (A), *I. calligraphus* (B) and *I. grandicollis* (C) caught per two weeks in funnel traps with all four semiochemical lure combinations during November 2009-2010 at the Whitehall Forest in Athens, Georgia.

Fig. 2.5 Seasonal activity of *Temnochila virescens* (A), *Thanasimus dubius* (B), and *Enoclerus nigripes nigripes* (C) caught per two weeks in multiple funnel traps with all four semiochemical lure combinations during November 2009-2010 at the Whitehall Forest in Athens, Georgia.

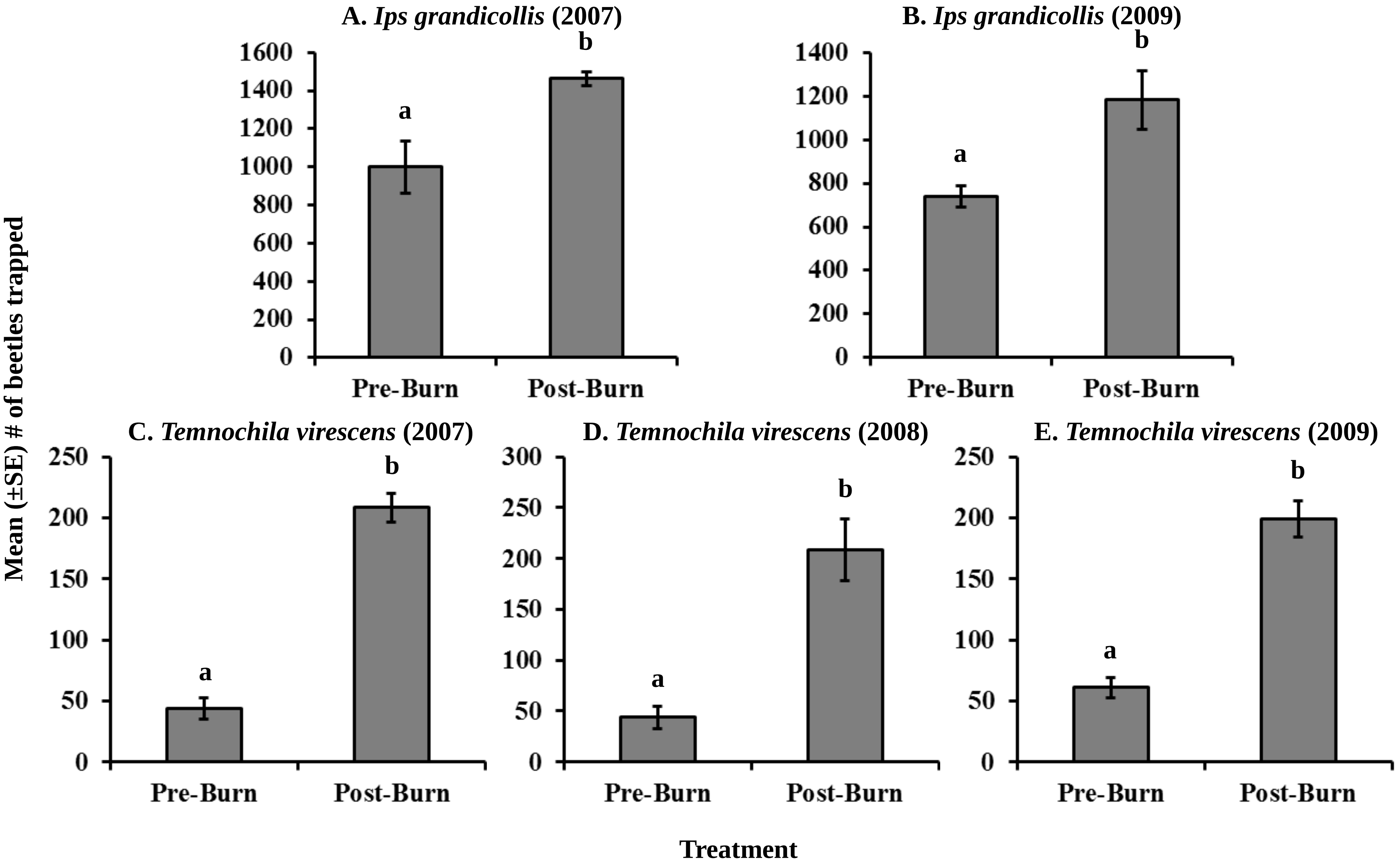
A. Ips grandicollis (2007)
B. Ips grandicollis (2009)
C. Temnochila virescens (2007)
D. Temnochila virescens (2008)
E. Temnochila virescens (2009)
Mean (±SE) # of beetles trapped
Treatment
Pre-Burn
Post-Burn
a
b
1600
1400
1200
1000
800
600
400
200
0
300
250
200
150
100
50

Fig. 2.1

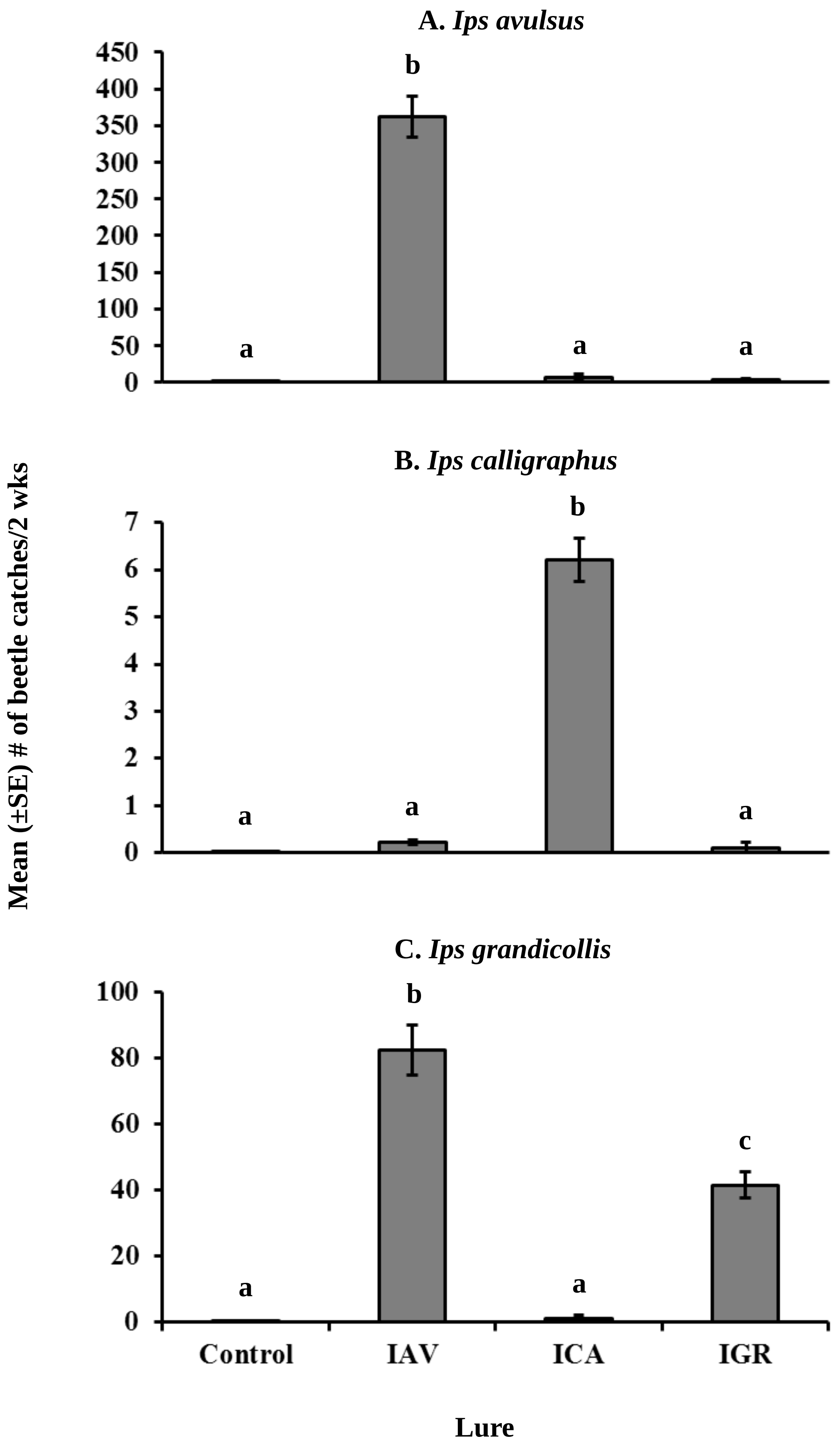
A. *Ips avulsus*
450
400
350
300
250
200
150
100
50
0
a
b
a
a
B. *Ips calligraphus*
7
6
5
4
3
2
1
0
a
a
b
a
C. *Ips grandicollis*
100
80
60
40
20
0
a
b
a
c
Control
IAV
ICA
IGR
Mean (±SE) # of beetle catches/2 wks
Lure

Fig. 2.2

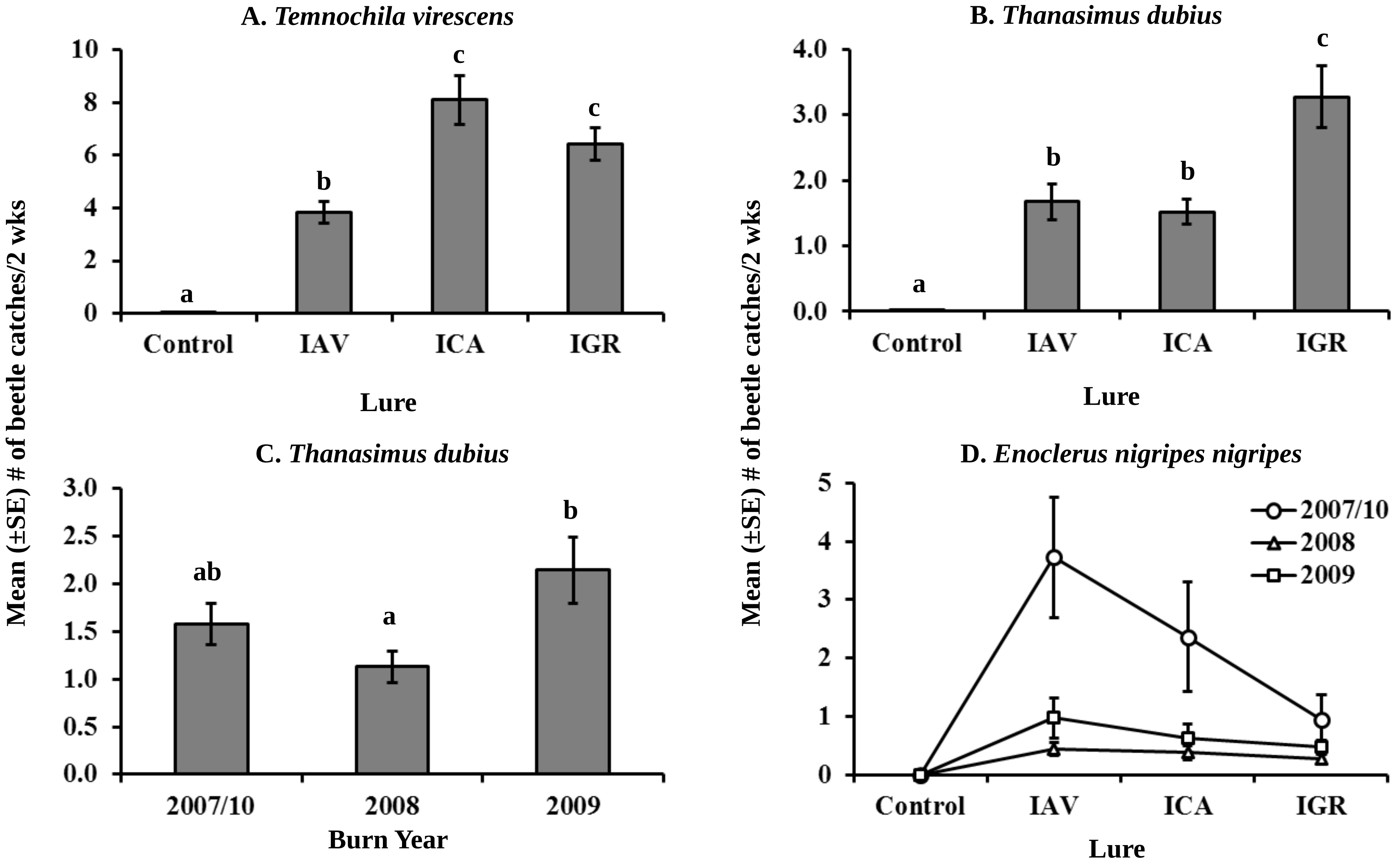
A. *Temnochila virescens*
Mean (±SE) # of beetle catches/2 wks
10
8
6
4
2
0
a
b
c
c
Control
IAV
ICA
IGR
Lure
B. *Thanasimus dubius*
4.0
3.0
2.0
1.0
0.0
a
b
b
c
Control
IAV
ICA
IGR
Lure
C. *Thanasimus dubius*
3.0
2.5
2.0
1.5
1.0
0.5
0.0
ab
a
b
2007/10
2008
2009
Burn Year
D. *Enoclerus nigripes nigripes*
Mean (±SE) # of beetle catches/2 wks
5
4
3
2
1
0
2007/10
2008
2009
Control
IAV
ICA
IGR
Lure

Fig. 2.3

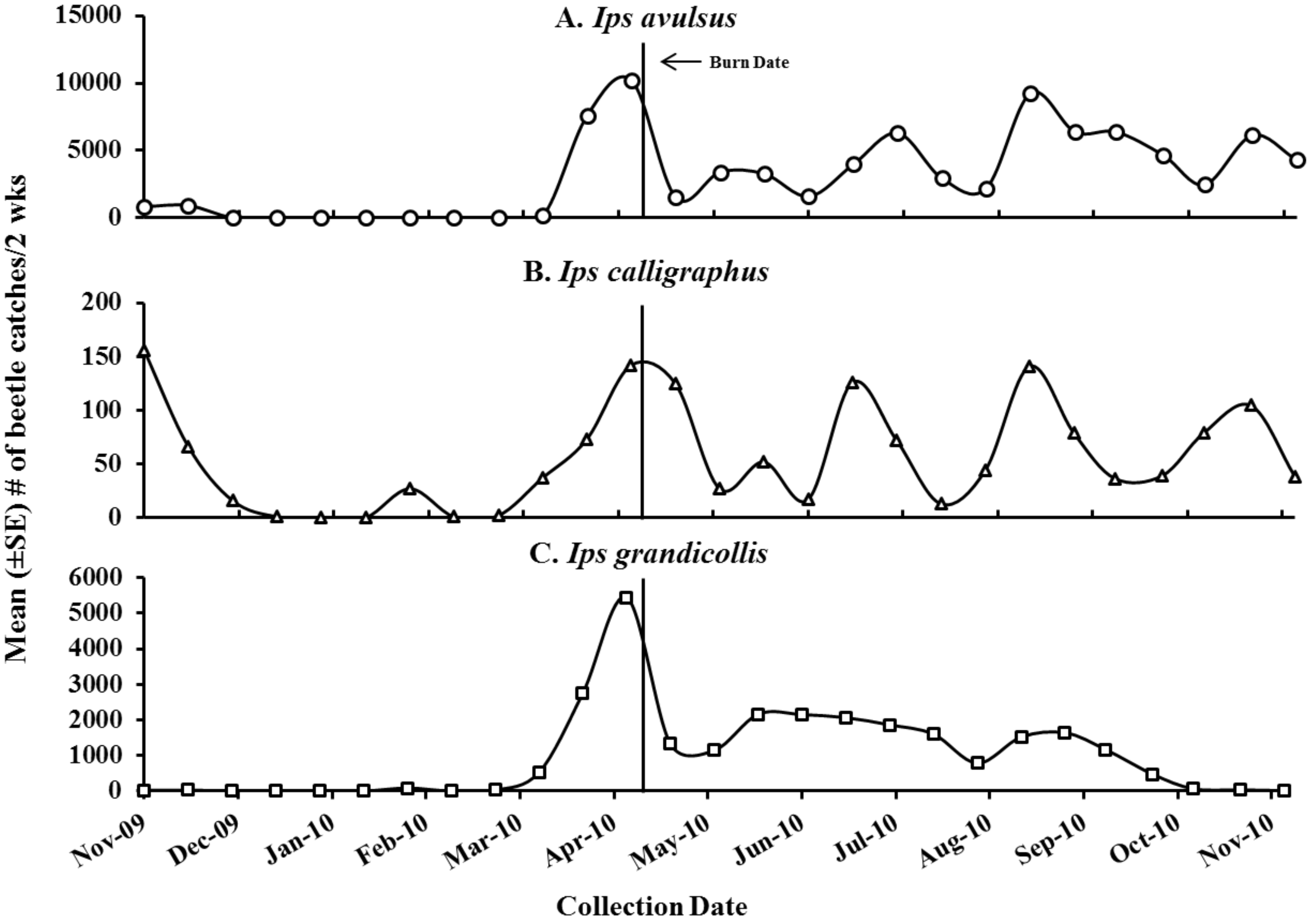
A. *Ips avulsus*
Burn Date
15000
10000
5000
0
B. *Ips calligraphus*
200
150
100
50
0
C. *Ips grandicollis*
6000
5000
4000
3000
2000
1000
0
Mean (±SE) # of beetle catches/2 wks
Nov-09
Dec-09
Jan-10
Feb-10
Mar-10
Apr-10
May-10
Jun-10
Jul-10
Aug-10
Sep-10
Oct-10
Nov-10
Collection Date

Fig. 2.4

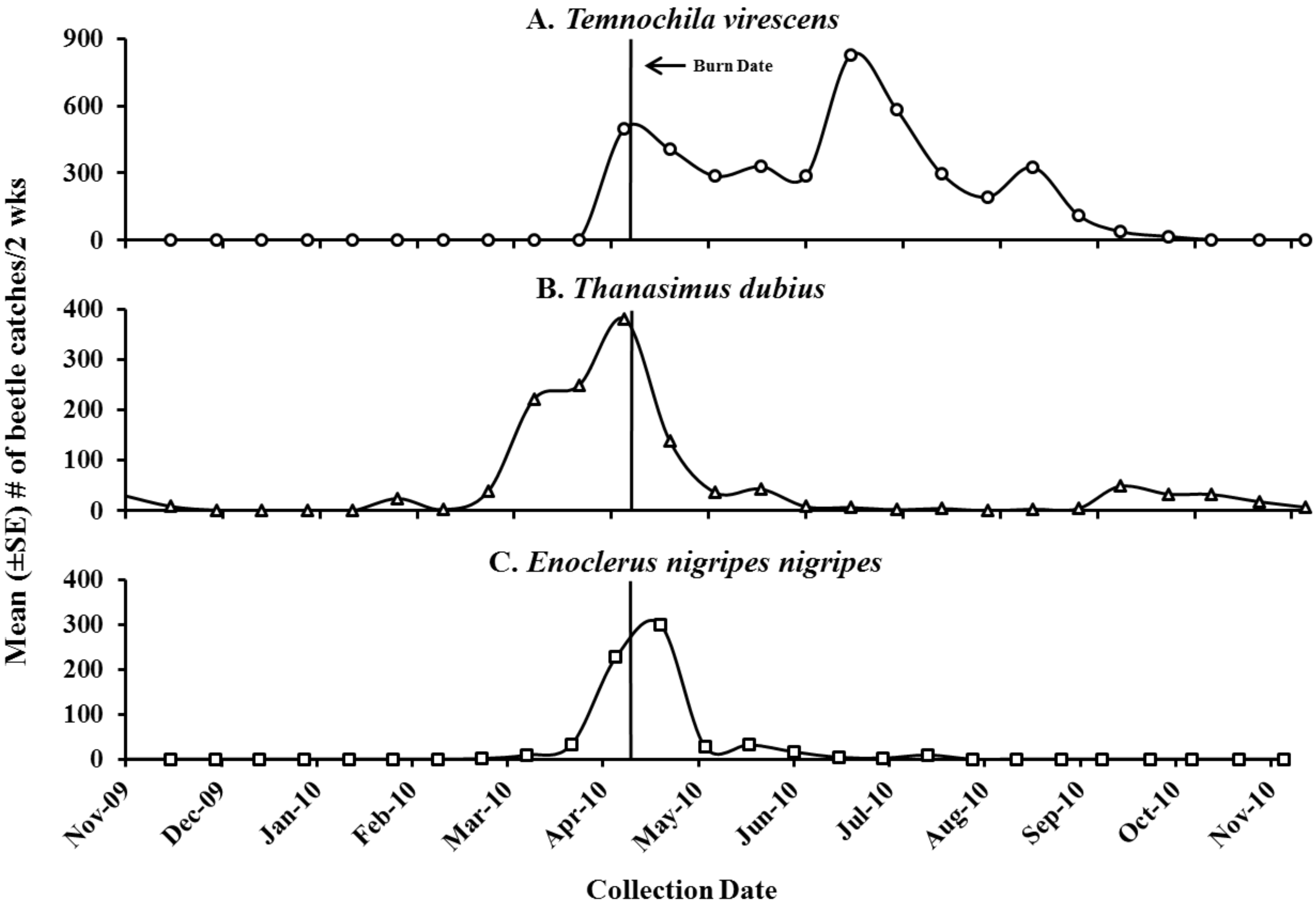
A. Temnochila virescens
900
600
300
0
Burn Date
B. Thanasimus dubius
400
300
200
100
0
C. Enoclerus nigripes nigripes
400
300
200
100
0
Mean (±SE) # of beetle catches/2 wks
Nov-09
Dec-09
Jan-10
Feb-10
Mar-10
Apr-10
May-10
Jun-10
Jul-10
Aug-10
Sep-10
Oct-10
Nov-10
Collection Date

Fig. 2.5

CHAPTER 3

A COMPARISON OF SUBCORTICAL BEETLE COMMUNITIES BETWEEN WAREHOUSES AND NURSERIES IN GEORGIA

ABSTRACT

We studied the community and population ecology of subcortical (bark and woodboring) beetles at two major types of ports-of-entry (warehouses and nurseries) under the umbrella of a national exotic species survey in 2010 in Georgia. A species-rich community of subcortical beetles was trapped including 4,093 beetles representing 64 genera and 103 species from three families: Curculionidae (Scolytinae), Buprestidae, and Cerambycidae. About 60% of total catches and 13% of total species richness of scolytine beetles were comprised of exotic species to North America. This study trapped the first specimens of the tropical ambrosia beetle, *Xyleborinus artestriatus* (Eichhoff) in North America. Greater numbers of scolytine beetles were trapped at nurseries than warehouses, but no such differences were observed for woodboring beetles. More scolytine and woodboring beetles (with species-level differences) were attracted to traps with ethanol and ethanol + α-pinene lures instead of exotic *Ips* lure. However, species diversity was higher for scolytines and lower for woodborers with only the exotic *Ips* lure, and at warehouses than nurseries. Seasonal phenology graphs indicated that *Xylosandrus crassiusculus* (Motschulsky) and *Cnestus mutilatus* (Blandford) had two, *Hypothenemus* spp. Westwood and *Ips grandicollis* (Eichhoff) had three, and *Xyleborinus* *saxeseni* (Ratzeburg) had four activity peaks per year in Georgia. Species composition analysis of scolytine beetles suggested two distinct beetle communities between warehouses and nurseries, but more similar communities of woodboring beetles in these sites. Higher variability in species composition of subcortical beetles was observed for nurseries than warehouses. Our results highlight the importance of national surveys for monitoring and documenting exotic subcortical beetles, and provide information about differences in species composition, responses to lures used in annual surveys, and seasonal phenology of the most common subcortical beetles in urban areas in Georgia.

Index Words: bark beetle, diversity, lures, nursery, phenology, warehouse

INTRODUCTION

Subcortical insects such as bark and ambrosia (Coleoptera: Scolytinae), and woodboring (Buprestidae and Cerambycidae) beetles are commonly found in forest communities and their developmental and reproductive strategies may affect tree health (Rudinsky 1962, Evans et al. 2004). Immature life stages of subcortical insects complete their life-cycle under bark, and can either cause tree damage or contribute to tree mortality. Subcortical beetles typically assist in degradation of woody material in forests as they primarily colonize dying or dead trees, although attack of healthy or stressed trees by some species (e.g., southern pine beetle, *Dendroctonus frontalis* Zimmerman) is possible (Rudinsky 1962, Allison et al. 2004, Evans et al. 2004). The larvae of bark beetles feed on the phloem of the tree and those of ambrosia beetles feed on fungal cultures inoculated in the xylem (Rudinsky 1962). In contrast, the larvae of woodboring beetles feed both on the phloem and xylem layers (Evans et al. 2004). Damage caused by the feeding habits of the larva often kill the tree, and when harvested, the timber value may be affected through inoculation of blue-stain fungi and gallery formations (Conner & Wilkinson 1983, Ballard et al. 1984, Evans et al. 2004).

During the last two centuries, high numbers of exotic insects, as aided by global trade, have invaded new countries, including the United States (U.S.) (Liebhold et al. 1995, Gandhi and Herms 2010). Subcortical beetles are typically transported within the wood packing materials (termed as “solid wood packing material” or SWPM) used for shipment (Dobbs & Brodel 2004, Work et al. 2005, Brockeroff et al. 2006, Price et al. 2011) and through live plant material (Humble & Allen 2004, Poland & McCullough 2006, Aukema et al. 2010, Liebhold et al. 2012). Both of these materials may house exotic insects from virtually any country in the world, and these insects can develop in the wood and emerge as adults shortly after arrival in a new region. Warehouses located near ports of entry receive large amounts of SWPM used for shipping from foreign ports. SWPMs are often stored at large warehouses for lengths of time, where exotic species may have a chance to emerge and start infesting native tree species. Similarly, live plant material is introduced to nurseries from which exotic species may emerge with time and establish onto surrounding vegetation (Liebhold et al. 2012). Both warehouses and nurseries may play an important role in the first and second parts of the invasion process of exotic species which includes the introduction and establishment phases (Reichard & White 2001, Liebhold et al. 2012). Some exotic plant species are intentionally imported because of the similarities between the native and exotic climates, allowing for easier cultivation (Niemelä & Mattson 1996). For example, nurseries are particularly interested in Chinese plant species due to similarities in climatic conditions between two countries (National Research Council 2002). However, a large number of introductions of exotic species have occurred through accidental transfer such as emerald ash borer (*Agrilus planipennis* Fairmaire) and Asian longhorned beetle [*Anoplophora glabripennis* (Motschulsky)] in eastern North America (Poland & McCullough 2006, Britton et al. 2010).

Between 1985 and 2000, many interceptions of exotic insects have been made at the U.S. sea ports along the Atlantic Ocean, Pacific Ocean, Gulf of Mexico, and Great Lakes region (Haack 2006). Approximately 30 species of introduced bark and ambrosia beetles and woodboring beetles were included in the list of National Pests of Concern Database (NAPIS) (USDA-APHIS 2009). Such introductions are problematic due to the high risk of economic and ecological impacts to the North American forests (Lovett et al. 2006, Gandhi & Herms 2010). For example, emerald ash borer attacks many species of ash (*Fraxinus* spp. L.), and has caused the destruction of millions of ash trees in North America (Gandhi & Herms 2010, Pureswaran & Poland 2010, Tluczek et al. 2011). Asian longhorned beetle primarily colonizes maple trees (*Acer* spp. L.) and has contributed to the death of maples in the northeastern U.S. (Haack et al. 1997, Haack et al. 2009, Hu et al. 2009)

Early detection of exotic insects is therefore, critical for minimizing cascading ecological impacts of exotic species on forested landscapes. If infestations of new exotic insect pests are caught early, then there may be a greater chance for successful eradication and control tactics. The United States Department of Agriculture– Animal and Plant Health Inspection Service (USDA-APHIS) administers the Cooperative

Agricultural Pest Survey (CAPS) to annually survey of national pests of concern. The state of Georgia is included in these annual surveys, as it was ranked third as having the highest number of wood-related insect interceptions during that period (Haack 2006). Georgia has at least two main ports of entry: Hartsfield-Jackson Atlanta International Airport (HJAIA) and Port of Savannah. HJAIA is the world's busiest airport, both with number of passengers and aircraft movements (landings and takeoffs) (Kennedy 2011). The Port of Savannah is the fastest growing seaport in the U.S., and efforts are being made to deepen the port, allowing for increased trade (Georgia Ports Authority 2010). We conducted CAPS survey for exotic bark and woodboring beetles in 2010 in Georgia, and used this opportunity to better understand the community and population ecology of subcortical beetles in urban areas. Our three research objectives were to: 1) determine differences in subcortical beetle communities between two ports-of-entry: warehouses and nurseries; 2) assess the response of subcortical beetle communities to lures commonly used in national surveys (α-pinene, ethanol, and exotic *Ips* lure); and 3) determine phenology of subcortical insects in Georgia. A better understanding subcortical species composition of these urban habitats may help assess which pests are likely to spread and establish in adjacent forest communities.

METHODS

Study Sites

Scolytine, cerambycid, and buprestid beetles were trapped between April and August 2010 at seven sites in Georgia. Three sites were located at warehouses and four were located at nurseries. Three warehouses were located near the port of Savannah in the Lower Coastal Plains of the state in Effingham and Chatham Counties. In general, warehouse sites were surrounded by mixed, uneven-aged vegetation, both conifers and deciduous species, with water sources such as a canal or retention pond on site. The major forest type in the Lower Coastal Plain is longleaf and slash pine (*Pinus palustris* Mill. and *P. elliottii* Engelm., respectively), mixed with sweetgum (*Liquidambar styraciflua* L.), beech (*Fagus* spp. L.), magnolia (*Magnolia* spp. L.), and oak (*Quercus* spp. L.) trees. Four nurseries were located around the city of Athens in Athens-Clarke, Barrow, and Oconee Counties, in the Piedmont region of Georgia. In general, nurseries were surrounded by mixed hardwood forest and by roads with either a retention pond or stream on site. The major forest type of the Piedmont region is loblolly and shortleaf pine (*P. taeda* L. and *P. echinata* Mill., respectively), mixed with oak, sweetgum, and hickory (*Carya* spp. Nutt.) (Coder 1996).

All historical climate data presented here was based on two automated weather stations located within 40 km of each site type, data were calculated only for days in which the traps were deployed, and were obtained from the Georgia Automated Environmental Monitoring Network (www.GeorgiaWeather.net). Total precipitation near warehouse locations was 14.28 cm with 23 rainy days and near nursery locations was 35.13 cm with 28 rainy days, though there was a water balance deficit, meaning that all sites were in a state of drought during our sampling period.

Beetle Sampling

Beetles were trapped using 12-unit Lindgren funnel traps with a wet collection cup (Lindgren 1983). The collection cups were filled with a killing agent and preservative

(Peak® RV & Marine Antifreeze without ethanol) to a depth of approximately 7 cm. Three traps spaced 250 m apart were installed at each site along a transect. Each trap had one of the following randomly selected three lure combinations: a) ultra-high release (UHR) ethanol; b) UHR ethanol and UHR α-pinene; or c) exotic *Ips* lure, comprised of three chemical components [50:50 (+)/(-) Ipsdienol, 17:83 (+)/(-) *cis*-verbenol and 2-methyl-3-buten-2-ol] (Contech Enterprises Inc.) (Table 3.1). Collection cups were emptied and clean fluid replaced, every 14-15 days. Lures were replaced every 30 days for six months. Trapping produced a total of 126 samples from 21 traps during the season.

All adult scolytine, buprestid, and cerambycid beetles were identified to species using available literature (e.g., Franklin & Lund 1956, Wood 1982, Rabaglia et al. 2006, Lingafelter 2007).Voucher specimens were deposited in the University of Georgia Collection of Arthropods (UGCA) at the Georgia Museum of Natural History, Athens, GA.

Statistical Analyses

All data for each trap was pooled for the entire trapping period, and catches were standardized to 14 days to account for missing data caused by trap disturbances. Total catch data were first assessed for normality and constant variance. Two-way analysis of variance tests (ANOVA) were used to assess differences between beetle catches at warehouses and nurseries, and the responses of beetle species to each lure (SAS Institute 2002-2008). For species-level, data were not normal as concluded by results from the univariate procedure in the SAS program, and transformations did not improve normality.

Non-parametric analyses, such as the NPAR1WAY procedure in the SAS program, were therefore used for species-level catches of the three families and most abundant species (>5% of total catches). None of the species of buprestid or cerambycid beetles accounted for >5% total catches, and so we focused only on scolytine beetles for species-level analyses. We also categorized beetles into native and exotic species as based on literature. We conducted a two-way analysis of variance tests (ANOVA) to assess differences between total beetle catches of native and exotic beetles separately between warehouses and nurseries, and among lure-type.

Data for seasonal phenology were standardized to catches per trap and per week. Phenology graphs were plotted for the most abundant species within each beetle family separated by site type, as traps were deployed and taken down at different times at warehouses and nurseries.

Species accumulation curves for each group was created using rarefaction (Holland 2003) to compare species diversity between site types and among lure types. Sample based rarefaction calculated the expected number of species when samples are drawn at random (without replacement) from the community pool (Magurran and McGill 2011).

Two diversity measures, Shannon-Weiner (H) and Simpson's (D) indices, were also used to assess species diversity of scolytines and woodborers (Magurran 2004). These indices were used separately for native and exotic scolytine species to determine if there was a different response to site or lure type within these two groups. A Bonferroni correction was used to determine error bar values (Miller 1981, Simes 1986).

Non-metric multidimensional scaling (NMS) was used to compare species composition of scolytine and woodboring beetle communities between site types and among lure types (McCune and Grace 2002, McCune and Mefford 2006). As the coefficient of variation was >100%, data were adjusted by first adding a constant (+1) and then by applying a power transformation. NMS was initially conducted with six axes, 50 runs of real data, stability criterion of 0.0005, 15 iterations for stability with a maximum of 250 iterations, and 0.20 steps down in dimensionality. A NMS scree plot was created to assess the final number of dimensions, and a plot of stress versus number of iterations was assessed for stability of the model. The final NMS was conducted using the same parameters as above, but with two axes, one run of real data, and no step down in dimensionality. The final stability of the model was 3.118 and the final stress for the two dimensional solutions was 0.00036. For woodborers, the coefficient of variation was 80.7%, and the data was not transformed. NMS was conducted for woodborers as described previously for scolytines. The final stability of the model was 7.492 and the final stress for the two dimensional solutions was <0.001. An ordination plot was created for both scolytines and woodboring beetles using means and standard errors of ordination points along two hypothetical axes for each lure type at both warehouses and nurseries.

RESULTS

During the summer of 2010, a total of 4,093 beetles were trapped including 103 species representing 64 genera in three families: Curculionidae (Scolytinae), Buprestidae, and Cerambycidae (Table 3.2). Scolytine beetles comprised the majority of trap catches (93.6%), with a total of 3,831 beetles, including 54 species from 29 genera. Cerambycid beetles accounted for the second highest number of trap catches (5.6%) with a total of 229 beetles including 43 species from 31 genera. Buprestids were the least common group (0.8%) with only 33 beetles comprising six species from four genera. Five species represented >5% of total beetle catches, comprising 81.33% of all catches, which included *Xylosandrus crassiusculus* (Motschulsky) (39.26%), *Hypothenemus* spp. (13.39%), *Xyleborinus saxeseni* (Ratzeburg) (11.56%), *Cnestus mutilatus* (Blandford) (8.48%) and *Ips grandicollis* (Eichhoff) (7.57%). *Xylosandrus crassiusculus*, *X. saxeseni*, and *C. mutilatus* are introduced exotic species, as were 13.27% of total species trapped in the study. We documented the first continental record in North America for the tropical ambrosia beetle, *Xyleborinus artestriatus* (Eichhoff) (Cognato et al. 2013).

For all ANOVA analyses, interaction between sites and among lures was not significant for any beetle families. For total numbers of scolytine beetles, sites ($F_{1,20}$ = 5.49; P = 0.032) and lures ($F_{2,20}$ = 3.63; P = 0.049) were significant factors. Approximately four times the number of scolytine beetles were trapped at nurseries than at warehouses (Fig. 3.2A). About 11-16 times the number of beetles were trapped with ethanol and ethanol plus α-pinene lures, respectively, than with the exotic *Ips* lure (Fig. 3.2B). For total numbers of woodboring beetles, site was not a significant factor (P = 0.919) (Fig. 3.2A). However, there was a significant difference in catches between lures ($F_{2,20}$ = 6.95; P = 0.006), where 2.5 to 4.5 times more beetles were trapped with ethanol and ethanol plus α-pinene, respectively, than with the exotic *Ips* lure (Fig. 3.2B).

Two of the most commonly trapped species showed significant differences in trap catches between warehouses and nurseries. *Hypothenemus* spp. (χ^2_1 = 6.04; P = 0.014) and *C. mutilatus* (χ^2_1 = 8.58; P = 0.003) catches were greater at nurseries (Fig. 3.2A). In terms of lure type, very few beetles were caught in the exotic *Ips* lure (ipsdienol, *cis*-verbenol and 2-metyl-3-buten-2-ol). *Ips grandicollis* catches were different among lure types (χ^2_2 = 13.587; P = 0.001), with about six times more caught with the ethanol plus α-pinene lure. *Xylosandrus crassiusculus* (χ^2_2 = 13.321; P = 0.002), *Hypothenemus* spp. (χ^2_2 = 7.281; P = 0.026), and *X. saxeseni* (χ^2_2 = 12.649; P = 0.002) catches were lower with the exotic *Ips* lure than with the other two lure-types (Fig. 3.2B).

For the total number of native scolytine beetles, there was no difference (P = 0.094) in catches between warehouses and nurseries (Fig. 3.3A). In contrast, about seven times more exotic scolytines were beetles trapped at nurseries than warehouses ($F_{1,20}$ =5.26; P = 0.035) (Fig. 3.3A). When comparing lure-types among native scolytines, there was a significant difference in beetle catches with 10 times more beetles trapped with ethanol and ethanol + α-pinene among lure type ($F_{2,20}$ = 6.73; P = 0.007) (Fig. 3.3B). Among exotic species, there was no significant difference in catches among lure type (P = 0.112) (Fig. 3.3B).

Since beetles were trapped at slightly different times in warehouses and nurseries, a synthesis of phenology patterns are presented. Seasonal phenology curves indicate that peak numbers of *X. crassiusculus* were trapped during the end of April and the beginning of June (Fig. 3.4A, E). Highest catches of *Hypothenemus* spp. were found mostly at the end of April/beginning of May, with an additional peak near the end of July (Fig. 3.4B, F). Highest numbers of *X. saxeseni* were trapped at the end of April/beginning of May, with an increase in numbers toward the end of July (Fig. 3.4C, G). The highest numbers of *C. mutilatus* were trapped at the end of April/beginning of May (Fig. 3.4H). Peak numbers of *I. grandicollis* were trapped during the middle of April and June (Fig. 3.4D, I).

A species accumulation curve was created for all beetle species trapped for each site type and lure (Fig. 3.5). Rarefaction analyses indicated that the majority of beetle assemblages were not adequately sampled over the trapping period. Beetle diversity differed among site and lure types. At the lowest sample number, diversity was highest at nurseries with the *Ips* lure, followed by warehouses with ethanol, warehouses with *Ips* lure, warehouses with ethanol + α-pinene, nurseries with ethanol + α-pinene, and nurseries with ethanol lures, respectively (Fig. 3.5).

Shannon-Weiner and Simpson's diversity indices were calculated for all scolytines and woodborers (Fig. 3.6) as well as native and exotic scolytines (Fig. 3.7). Both diversity measures inferred the same results. Scolytines communities were more diverse at warehouses than nurseries (Fig. 3.6A), whereas no such differences were present for woodborers (Fig. 3.6B). There was no difference in species diversity of native and exotic scolytines between site-types (Fig. 3.7A, B).

For the lure-types, there were no differences in scolytine and woodborer species diversity among lures at nurseries, but highest and lowest diversity was found for scolytines and woodborers, respectively, in exotic *Ips* lure at warehouses (Fig. 3.6). Shannon-Weiner index did not reveal any significant differences in diversity of native scolytine beetles among lures at both nurseries and warehouses, however greater diversity was found for ethanol and alpha-pinene and exotic *Ips* lure using Simpson's index (Fig. 3.7A). For the exotic scolytine beetle, greater species diversity was in traps with ethanol alone at both nurseries and warehouses (Fig. 3.7B).

In general, there was more variability in species composition at nurseries than at warehouse sites (Fig. 3.8). The NMS graph for scolytine beetles indicated that communities at warehouses and nurseries differed from each other, as the grouping of beetle response to lures at warehouses and nurseries was a common point (Fig. 3.8A). The NMS graph for woodborers indicated that warehouse and nursery communities were more similar to each other and less separated than those of scolytines (Fig. 3.8B).

DISCUSSION

We documented the first continental record in North America for the tropical ambrosia beetle, *X. artestriatus* (Cognato et al. 2013). This beetle is distributed throughout Asia, including Burma (Wood & Bright 1992), India (Beeson 1915, Roonwal 1954, Schedl 1969), Indonesia (Kalshoven 1958, 1959, Schedl 1935, 1942), Malaysia (Schedl 1936, 1939, Browne 1961, Bright 2000), Sri Lanka (Schedl 1959), Taiwan (Beaver & Liu 2010), Thailand (Beaver 1999) and Vietnam (Schedl 1965), and around the Australian continent including Australia, Darwin, Fiji and Queensland (Wood & Bright 1992). It is also found in the Oceania region of the Pacific Ocean in the Bismarck Islands (Browne 1966), New Guinea (Wood & Bright 1992) and Samoa (Beeson 1929). The documented hosts of *X. artestriatus* are *Eugenia jambolana* (L.) Skeels, *Ficus religiosa* L., *Heritiera fomes* Buch.-Ham., *Juglans regia* L., *Lannea grandis* (Dennst.) Engl., *Mallotus philippinensis* (Lam.) Muell.Arg., *Mangifera indica* L., *Phyllanthus emblica* L., *Semecarpus anacardium* L.f. and *Shorea robusta* Roth (Wood & Bright 1992). Several of these genera are present in Georgia (e.g., *Juglans* and *Ficus* spp.), and hence there is a likelihood that this species will become established in North America.

However, the ecological and economic impacts of this exotic species are currently unknown and it is generally considered a secondary insect pest species (Cognato et al. 2013).

Our survey of warehouses and nurseries in eastern Georgia found that these sites were numerically dominated by exotic scolytine beetles that comprised ~60% of total catches and 13% of species including Asian ambrosia beetles, *X. crassiusculus*, *X. saxeseni*, and *C. mutilatus*. Considering the high numbers of these beetles caught in our traps, it is clear that they have established populations in these urban areas. *Xylosandrus crassiusculus* was imported from Asia and introduced to Florida (Atkinson 1988, Chapin & Oliver 1986), Louisiana (Chapin & Oliver 1986), North Carolina (Wood 1982), and South Carolina (Anderson 1974). From there it has spread throughout the remaining southeastern U.S. (Rabaglia et al. 2006). *Xyleborinus saxeseni* is most likely an Asian beetle probably imported from Europe more than 100 years ago, and has spread throughout the entire U.S. (Rabaglia et al. 2006). *Cnestus mutilatus* was imported from Asia and originally introduced to Florida and Mississippi (Schiefer & Bright 2004), and has recently been reported from Georgia (Gandhi et al. 2009a).

Significantly more scolytine beetles, especially *Hypothenemus* spp. and *C. mutilatus* were trapped at nurseries than at warehouses, but such differences were not observed for woodborers. Nurseries have a constant source of new plant material, a relatively high turnover of host material, and on-site refuge piles for decaying plant material. This may lead to more available and novel hosts for subcortical beetles. Further, scolytines may be more abundant at nurseries because their small size and generation time permits them to take advantage of smaller plants and decaying material.

In contrast, most woodborers are much larger in size and have a longer life-cycle (sometimes up to 2 years), and the transfer to and storage of SWPM at warehouses may allow for their full maturation and emergence with time (LaBonte et al. 2005, Haack 2006, Shauwecker 2006).

In general, more scolytine beetles (e.g., *Hypothenemus* spp., *I. grandicollis, X. saxeseni* and *X. crassiusculus*), and woodboring beetles were attracted to traps with ethanol and ethanol + α-pinene lures. Ethanol and ethanol + α-pinene are general host-attractants released by stressed trees and attract more beetles than the exotic *Ips* lure, which with specific chemical compounds, targets only a small group of exotic beetles (Mattson & Haack 1987). Similar results have been found in other studies such as Mattson & Haack (1987), Phillips et al. (1988), Allison et al. (2004), Petrice et al. (2004), Miller and Rabaglia (2009), Gandhi et al. (2010) and Miller et al. (2011).

The number of generations per year varied among the most common beetle species. The highest number of peaks was seen with *X. saxeseni*. Peaks in their flight pattern suggests emergence of at least 4-5 generations per year. Flight patterns were nearly consistent with previous studies conducted in the southeastern U.S. (Turnbow and Franklin 1980, Atkinson et al. 1988, Oliver and Mannion 2001). The flight patterns of *Hypothenemus* spp. and *Ips grandicollis* observed were similar to those reported in a study conducted by Atkinson et al. (1988). Patterns infer the emergence of at least 2-3 generations per year for *Hypothenemus* spp. and at least 3 generations per year for *I. grandicollis*. The initial flight or emergence of these beetles may have been missed in our study, as traps were not deployed early enough in the season. Peaks in the flight pattern of *X. crassiusculus* suggests emergence of at least two generations per year, which is nearly consistent with previous studies conducted in the U.S. (Coyle et al 2005, Reding et al. 2010). *Cnestus mutilatus* was trapped only at nursery sites, and appeared to have at least two generations per year. As this beetle was recently introduced to the southeastern U.S., very little literature is available for flight comparison (Gandhi et al. 2009a). However, in its native range, it is univoltine and is most active from June to August (Kajimura and Hijii 1992, Schiefer and Bright 2004).

Scolytine beetles, as a whole group, have more diverse communities at warehouses than nurseries. However, woodborer diversity was not different between site-types. Also, when scolytines were separated into native and exotic species, there was no difference in diversity between site-types. There is little research comparing bark and woodboring beetle diversity between nurseries and warehouses, or two locations at the same time (Ulyshen et al. 2004), as most studies typically focus on only one location (Hulcr et al. 2008), sometimes comparing stand types (Peltonen 1999, Sánchez-Martínez & Wagner 2002), one forest type (Safranyik et al. 2004), or after natural and anthropogenic disturbances (Gilbert et al. 2005, Gandhi et al. 2007, Gandhi et al. 2009b).

There were differences in species diversity at nurseries and warehouses as based on lure-type. At nurseries, greater numbers of scolytine species were attracted to the exotic *Ips* lure. Interestingly, native scolytine communities attracted to the exotic *Ips* lure were slightly more diverse. Several unique scolytine species were trapped only with the exotic *Ips* lure, including *Carphoborus bifurcus* Eichhoff, *Hylocurus langstoni* Blackman, *Lymantor decipiens* (LeConte), *Pityophthorus crinalis* Blackman, *Pseudopityopthorus pruinosus* (Eichhoff) and *Xyleborus xylographus* (Say). Exotic scolytine communities attracted to ethanol were the most diverse, and *X. artestriatus* and

Scolytus multistriatus (Marsham) are exotic scolytines trapped only with the ethanol lure. However the exotic scolytines, *C. mutilatus* and *Xyleborus californicus* Wood, were trapped with ethanol and the ethanol + α-pinene lure (but in fewer numbers than ethanol) meaning that ethanol is not as attractive when combined with α-pinene, nor is α-pinene a complete deterrent for these species.

The NMS plot of scolytines depicts two distinct assemblages between warehouses and nurseries whereas those of woodborers were more similar as there was a greater degree of overlap of traps in ordination space. These results may indicate differences in host plants present at warehouses and nurseries, and a degree of host specialization by scolytine and woodboring beetles where scolytines may be more specialist than woodborers (Novotny et al. 2011). However, these trends could also be due to geographic location of each site type as nurseries were located in north-central Georgia, and warehouses were located on the southeastern coast of Georgia. Perhaps there are significant differences in scolytine beetle communities as based on the latitude, but less so for the woodboring beetle communities.

CONCLUSIONS

We documented the first record for *Xyleborinus artestriatus* in continental North America (Cognato et al. 2013). Since this record was from a warehouse, these sites are potential introduction sources for exotic species. Sites were numerically dominated by exotic scolytine beetles indicating that exotic species are well established and are reproducing out of their native range. Significantly more scolytine beetles were trapped at nurseries than warehouses, and more scolytine beetles and woodboring beetles were attracted to traps baited with ethanol and ethanol + α-pinene lures. Phenology graphs show that the number of generations of scolytine beetles varied between 2-3 and 4-5 generations per year. Scolytine beetles were more diverse at warehouses and, there are two distinct beetle assemblages present in these two sites.

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Table 3.1 List of semiochemical lures used to survey the subcortical beetle community around warehouses and nurseries in 2010 in Georgia.

Semiochemical	Device Type	Enantiomeric composition	Amount in device	Release rate/day	Chemical purity
Ethanol	UHR[a]	NA[c]	150 mL	0.6 g	>95%
α-pinene	UHR[a]	>95%	200 mL	2-6 g	>95%(-)
Ipsdienol	BCD[b]	50:50 (+)/(-)	40 mg	0.1-0.2µg	>95%
cis-verbenol	BCD[b]	17:83 (+)/(-)	0.6 g	UA[d]	UA[d]
2-methyl-3-buten-2-ol	BCD[b]	NA[c]	3.3 g	UA[d]	UA[d]

[a] Ultra High Release plastic pouch

[b] Bubble cap device

[c] Not applicable

[d] Unavailable

Table 3.2 Total number of all subcortical beetles (Buprestidae, Cerambycidae, and Scolytinae) caught in funnel traps in 2010 around warehouses and nurseries in Georgia.

Family	Subfamily	Species	Warehouses w/ethanol lure	Warehouses w/ethanol & α-pinene lure	Warehouses w/the exotic *Ips* lure	Nurseries w/ethanol lure	Nurseries w/ethanol & α-pinene lures	Nurseries w/the exotic *Ips* lure	Total	% Total
Buprestidae	Buprestinae	*Buprestis lineata* Fabricius	1	0	2	0	1	2	6	0.15
		Buprestis maculipennis Gory	1	0	0	0	0	0	1	0.02
		Chrysobothris femorata Olivier	3	5	2	0	0	0	10	0.24
		Chalcophora georgiana (LeConte)	0	0	1	0	0	2	3	0.07
		Chalcophora virginiensis (Drury)	2	8	2	0	0	0	12	0.29
		Dicerca obscura (Fabricius)	0	0	0	0	0	1	1	0.02
Cerambycidae	Cerambycinae	*Ancylocera bicolor* (Olivier)	0	0	1	0	3	0	4	0.10
		Anelaphus parallelus (Newman)	0	0	0	1	0	0	1	0.02
		Anelaphus villosus (Fabricius)	0	0	0	2	3	0	5	0.12
		Clytus ruricola (Olivier)	0	0	0	0	1	0	1	0.02
		Curius dentatus Newman	0	0	0	4	1	0	5	0.12
		Cyrtophorus verrucosus (Olivier)	0	0	0	2	0	1	3	0.07
		Elaphidion mucronatum (Say)	1	0	0	1	0	0	2	0.05
		Euderces picipes (Fabricius)	0	0	0	3	2	0	5	0.12
		Euderces pini (Olivier)	0	0	0	0	1	0	1	0.02
		Molorchus bimaculatus bimaculatus Say	0	0	1	1	0	0	2	0.05
		Molorchus bimaculatus corni Haldeman	0	0	0	0	1	0	1	0.02
		Molorchus bimaculatus semiustus (Newman)	0	0	0	7	2	0	9	0.22
		Neoclytus mucronatus (Fabricius)	0	0	0	0	1	0	1	0.02
		Obrium maculatum (Olivier)	0	0	0	14	10	0	24	0.59
		Phymatodes amoenus (Say)	0	0	0	1	2	0	3	0.07
		Smodicum cucujiforme (Say)	0	0	0	1	0	0	1	0.02
		Tessaropa tenuipes (Haldeman)	0	0	0	2	2	0	4	0.10
		Tilloclytus geminatus (Haldeman)	0	0	0	1	0	0	1	0.02
		Xylotrechus colonus (Fabricius)	0	0	0	6	4	0	10	0.24
		Xylotrechus sagittatus (Germar)	12	28	0	1	33	0	74	1.81
	Lamiinae	*Acanthocinus obsoletus* (Olivier)	0	1	2	0	0	0	3	0.07
		Aegomorphus modestus (Gyllenhal)	0	0	0	1	0	0	1	0.02
		Aegomorphus quadrigibbus (Say)	0	0	0	1	0	0	1	0.02
		Astylopsis collaris (Haldeman)	0	0	1	0	0	0	1	0.02
		Astylopsis sexguttata (Say)	0	0	1	0	0	0	1	0.02
		Cyrtinus pygmaeus (Haldeman)	0	0	0	1	0	0	1	0.02
		Dorcaschema cinereum (Olivier)	0	0	0	0	0	1	1	0.02
		Ecyrus dasycerus (Say)	0	0	0	1	0	0	1	0.02
		Eupogonius subarmatus (LeConte)	0	0	0	0	0	1	1	0.02
		Eupogonius tomentosus (Haldeman)	0	1	1	0	0	0	2	0.05
		Leptostylus asperatus (Haldeman)	0	0	0	3	1	0	4	0.10

		Monochamus carolinensis (Olivier)	2	15	2	0	8	0	27	0.66
		Monochamus titillator (Fabricius)	0	1	0	0	0	0	1	0.02
		Psenocerus supernotatus (Say)	0	0	0	4	2	0	6	0.15
		Styloleptus biustus (LeConte)	0	0	0	1	0	0	1	0.02
	Lepturinae	*Acmaeops discoideus* (Haldeman)	0	0	0	0	1	0	1	0.02
		Grammoptera exigua (Newman)	0	0	0	0	0	1	1	0.02
		Strangalia luteicornis (Fabricius)	0	0	1	1	0	0	2	0.05
		Typocerus badius (Newman)	0	0	1	0	0	0	1	0.02
		Typocerus zebra (Olivier)	3	0	0	0	0	0	3	0.07
	Prioninae	*Orthosoma brunneum* (Forster)	0	0	0	0	1	0	1	0.02
	Spondylidinae	*Arhopalus rusticus* (LeConte)	0	0	0	0	1	0	1	0.02
		Asemum striatum (Linnaeus)	0	0	0	0	5	5	10	0.24
Curculionidae	Scolytinae	*Ambrosiodmus obliquus* (LeConte)	0	1	0	0	1	0	2	0.05
		Ambrosiodmus rubricollis (Eichhoff)[a]	2	0	0	2	2	0	6	0.15
		Carphoborus bifurcus Eichhoff	0	0	0	0	0	4	4	0.10
		Chramesus chapuisii LeConte	0	0	0	1	0	0	1	0.02
		Cnesinus strigicollis LeConte	0	0	0	4	1	0	5	0.12
		Cnestus mutilatus (Blandford)[a]	0	0	0	248	99	0	347	8.48
		Corthylus columbianus Hopkins	0	0	0	2	0	0	2	0.05
		Cryphalus rubentis Hopkins	0	0	0	3	0	0	3	0.07
		Dendroctonus terebrans (Olivier)	0	2	0	0	7	0	9	0.22
		Dryoxylon onoharaensum (Murayama)[a]	17	3	0	46	39	1	106	2.59
		Euwallacea validus (Eichhoff)[a]	0	0	3	3	1	1	8	0.20
		Gnathotrichus materiarius (Fitch)	0	0	0	1	14	1	16	0.39
		Hylastes porculus Erichson	0	0	0	0	10	0	10	0.24
		Hylastes salebrosus Eichhoff	0	2	0	0	6	0	8	0.20
		Hylastes tenuis Eichhoff	0	0	0	1	10	0	11	0.27
		Hylocurus flaglerensis Blackman	0	0	0	0	1	0	1	0.02
		Hylocurus langstoni Blackman	0	0	0	0	0	1	1	0.02
		Hylocurus rudis (LeConte)	0	0	0	1	0	0	1	0.02
		Hylocurus spp.	0	0	0	2	6	1	9	0.22
		Hypothenemus birmanus (Eichhoff)[a]	0	0	0	1	0	0	1	0.02
		Hypothenemus spp.	24	4	6	172	327	15	548	13.39
		Ips avulsus (Eichhoff)	0	2	0	0	1	0	3	0.07
		Ips calligraphus (Germar)	3	1	6	0	1	11	22	0.54
		Ips grandicollis (Eichhoff)	21	110	4	1	174	0	310	7.57
		Lymantor decipiens (LeConte)	0	0	1	0	0	2	3	0.07
		Micracisella opacicollis (LeConte)	0	0	0	4	2	1	7	0.17
		Monotharum fasciatum (Say)	1	0	0	2	0	1	4	0.10
		Monotharum mali (Fitch)	1	1	0	6	10	0	18	0.44
		Orthotomicus caelatus (Eichhoff)	0	1	0	0	0	0	1	0.02

	Orthotomicus spp.	1	0	0	1	1	0	3	0.07
	Phloeotribus dentifrons (Blackman)	0	0	0	1	0	0	1	0.02
	Phloeotribus frontalis (Olivier)	0	0	0	2	1	0	3	0.07
	Phloeotribus liminaris (Harris)	0	0	0	8	0	0	8	0.20
	Phloeotribus texanus Schaeffer	0	0	0	0	1	0	1	0.02
	Pityoborus hirtellus Wood	0	0	0	0	1	0	1	0.02
	Pityophthorus crinalis Blackman	0	0	0	0	0	1	1	0.02
	Pityophthorus spp.	3	2	1	10	28	6	50	1.22
	Pseudopityopthorus pruinosus (Eichhoff)	0	0	0	0	0	1	1	0.02
	Pseudothysanoes spp.	0	0	0	5	3	0	8	0.20
	Scolytus multistriatus (Marsham)[a]	0	0	0	2	0	0	2	0.05
	Scolytus muticus (Say)	0	0	0	3	0	0	3	0.07
	Xyleborinus saxeseni (Ratzeburg)[a]	52	8	3	210	194	6	473	11.56
	Xyleborinus artestriatus (Eichhoff)[a,b]	2	0	0	0	0	0	2	0.05
	Xyleborus affinis Eichhoff	0	0	0	0	1	0	1	0.02
	Xyleborus atratus Eichhoff [a]	0	0	1	3	2	1	7	0.17
	Xyleborus californicus Wood[a]	1	0	0	0	1	0	2	0.05
	Xyleborus ferrugineus (Fabricius)	9	4	1	4	8	2	28	0.68
	Xyleborus impressus Eichhoff	1	0	0	0	0	0	1	0.02
	Xyleborus pubescens Zimmermann	8	29	6	10	18	2	73	1.78
	Xyleborus xylographus (Say)	0	0	0	0	0	1	1	0.02
	Xylosandrus compactus (Eichhoff)[a]	9	2	29	3	0	1	44	1.08
	Xylosandrus crassiusculus (Motschulsky)[a]	37	29	12	515	1010	4	1607	39.26
	Xylosandrus germanus (Blandford)[a]	2	0	0	19	16	2	39	0.95
	Xyloterinus politus (Say)	0	0	0	2	0	2	4	0.10
Total number of beetles		**219**	**260**	**91**	**1358**	**2083**	**82**	**4093**	
Total number of species		**26**	**22**	**25**	**54**	**50**	**31**	**103**	

[a] Exotic beetle species.

[b] New record for North America

FIGURE LEGEND

Fig. 3.1 Mean (±SE) number of scolytines and woodborers (Buprestidae and Cerambycidae) caught per 2 weeks in Lindgren funnel traps at warehouses (A) and nurseries (B) with three semiochemical lures (ethanol, ethanol plus α-pinene, and exotic *Ips* lure) during summer 2010 in Georgia. Means with the same letters are not significantly different from each other.

Fig. 3.2 Mean (± SE) number of *Xylosandrus crassiusculus*, *Hypothenemus* spp., *Xyleborus saxeseni*, *Cnestus mutilatus* and *Ips grandicollis* caught per 2 weeks in Lindgren funnel traps at warehouses and nurseries (A) and with three semiochemical lures (B) during summer 2010 in Georgia. Means with the same letters are not significantly different from each other.

Fig. 3.3 Mean (± SE) number of native and exotic scolytine species caught per two weeks in Lindgren funnel traps at warehouses and nurseries (A) and with three semiochemical lures (B) during summer 2010 in Georgia. Means with the same letters are not significantly different from each other.

Fig. 3.4 Seasonal activity of *Xylosandrus crassiusculus* (A, E), *Hypothenemus* spp. (B, F), *Xyleborus saxeseni* (C, G), *Cnestus mutilatus* (H) and *Ips grandicollis* (D, I) caught in funnel traps with three semiochemical lures at warehouses and nurseries in 2010 in Georgia.

Fig. 3.5 Rarefaction curve estimating species richness for all beetles trapped during summer 2010 around warehouses and nurseries with three semiochemical lures, in Georgia. WE = traps at warehouses with ethanol lure; WEA = warehouses with ethanol + α-pinene lures; WI = warehouses with the exotic *Ips* lure; NE = nurseries with ethanol; NEA = nurseries with ethanol + α-pinene; NI = nurseries with the exotic *Ips* lure.

Fig. 3.6 Shannon-Weiner (H) and Simpson's (D') diversity indices for all scolytine (A) and woodboring (B) beetles caught in Lindgren funnel traps at warehouses and nurseries with three semiochemical lures during summer 2010 in Georgia.

Fig. 3.7 Shannon-Weiner (H) and Simpson's (D') diversity indices for native (A) and exotic (B) scolytine beetles caught in Lindgren funnel traps at between warehouses and nurseries with three semiochemical lures during summer 2010 in Georgia.

Fig. 3.8 NMS plot for all scolytine beetles (A) and woodboring beetles (Buprestidae and Cerambycidae) (B) caught during entire summer 2010 trapping period around warehouses and nurseries with three semiochemical lures, in Georgia. WE = traps at warehouses with ethanol lure; WEA = warehouses with ethanol + α-pinene lures; WI = warehouses with the exotic *Ips* lure; NE = nurseries with ethanol; NEA = nurseries with ethanol + α-pinene; NI = nurseries with the exotic *Ips* lure.

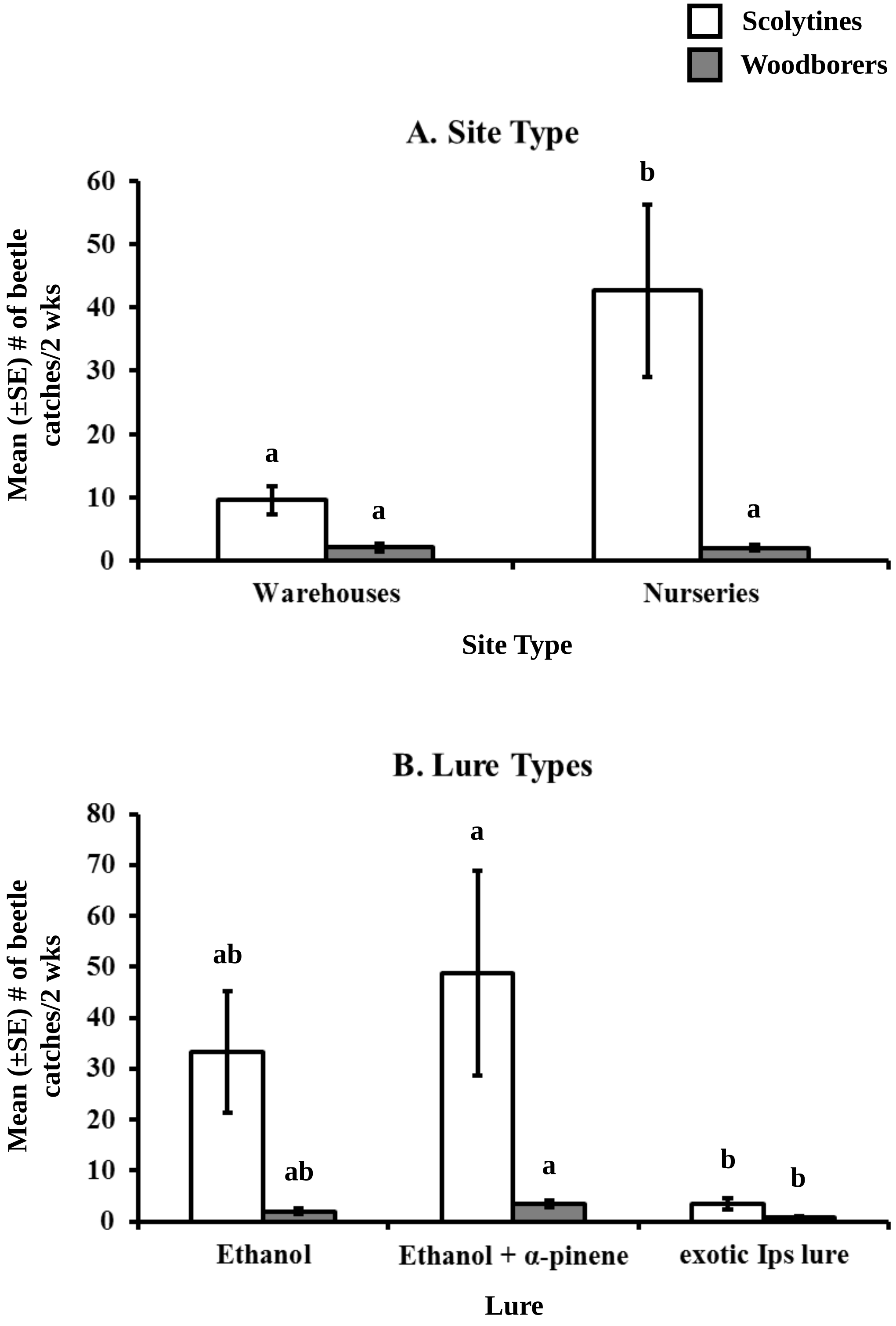

Scolytines
Woodborers
A. Site Type
Mean (±SE) # of beetle catches/2 wks
60
50
40
30
20
10
0
b
a
a
a
Warehouses
Nurseries
Site Type
B. Lure Types
Mean (±SE) # of beetle catches/2 wks
80
70
60
50
40
30
20
10
0
a
ab
ab
a
b
b
Ethanol
Ethanol + α-pinene
exotic Ips lure
Lure

Fig. 3.1

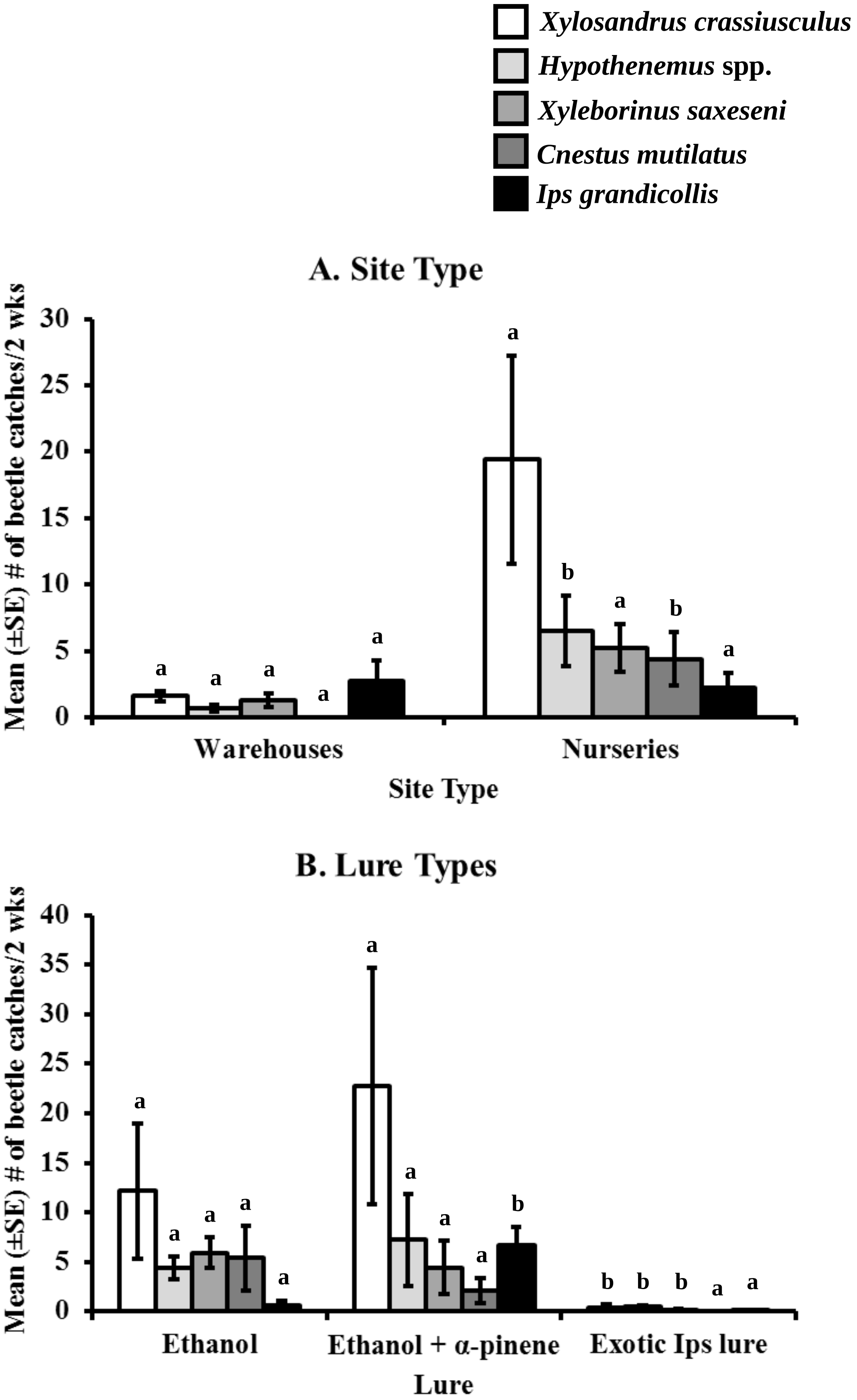

Xylosandrus crassiusculus
Hypothenemus spp.
Xyleborinus saxeseni
Cnestus mutilatus
Ips grandicollis
A. Site Type
Mean (±SE) # of beetle catches/2 wks
0
5
10
15
20
25
30
a
a
a
a
a
a
b
a
b
a
Warehouses
Nurseries
Site Type
B. Lure Types
Mean (±SE) # of beetle catches/2 wks
0
5
10
15
20
25
30
35
40
a
a
a
a
a
a
a
a
a
b
b
b
b
a
a
Ethanol
Ethanol + α-pinene
Exotic Ips lure
Lure

Fig. 3.2

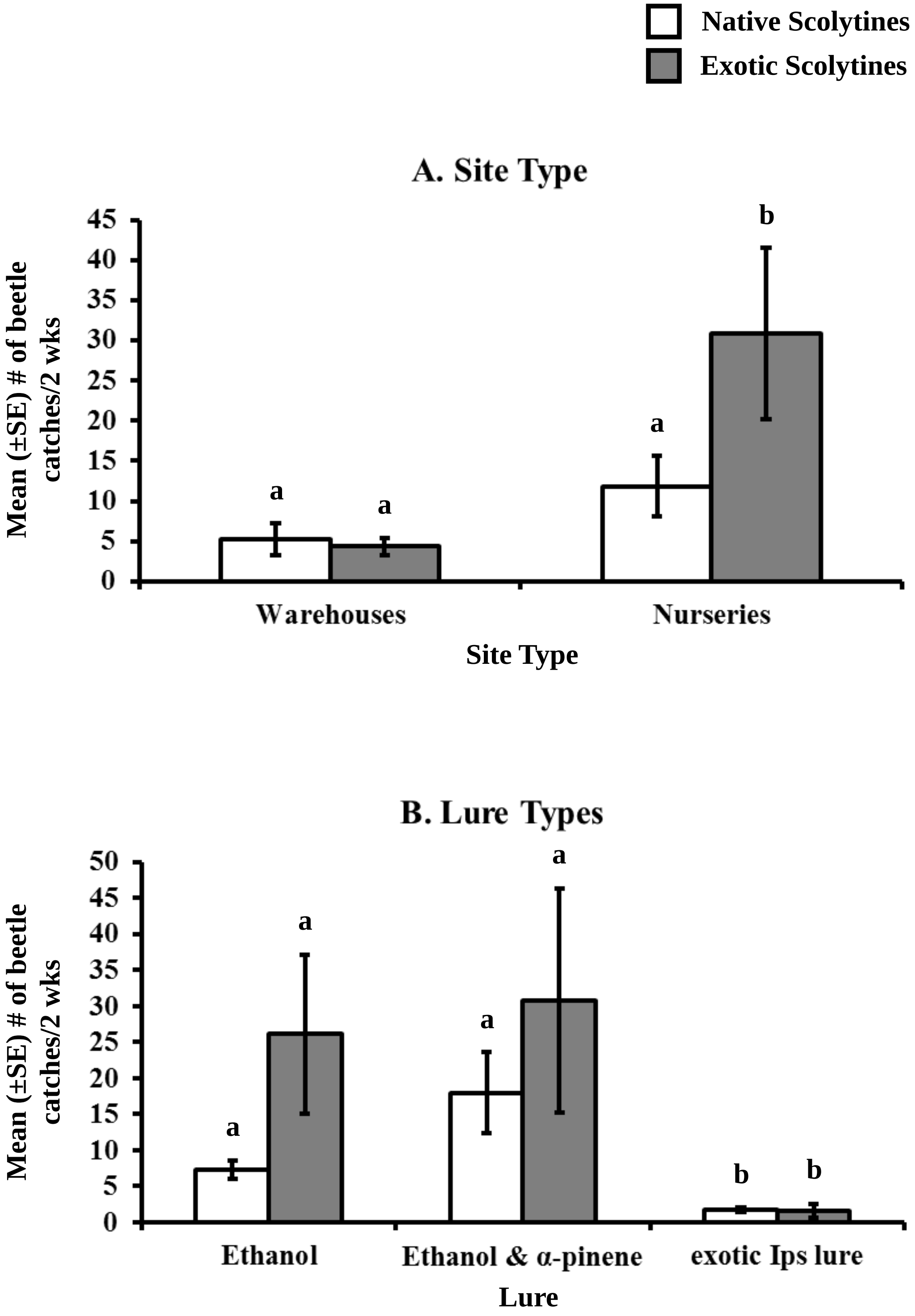
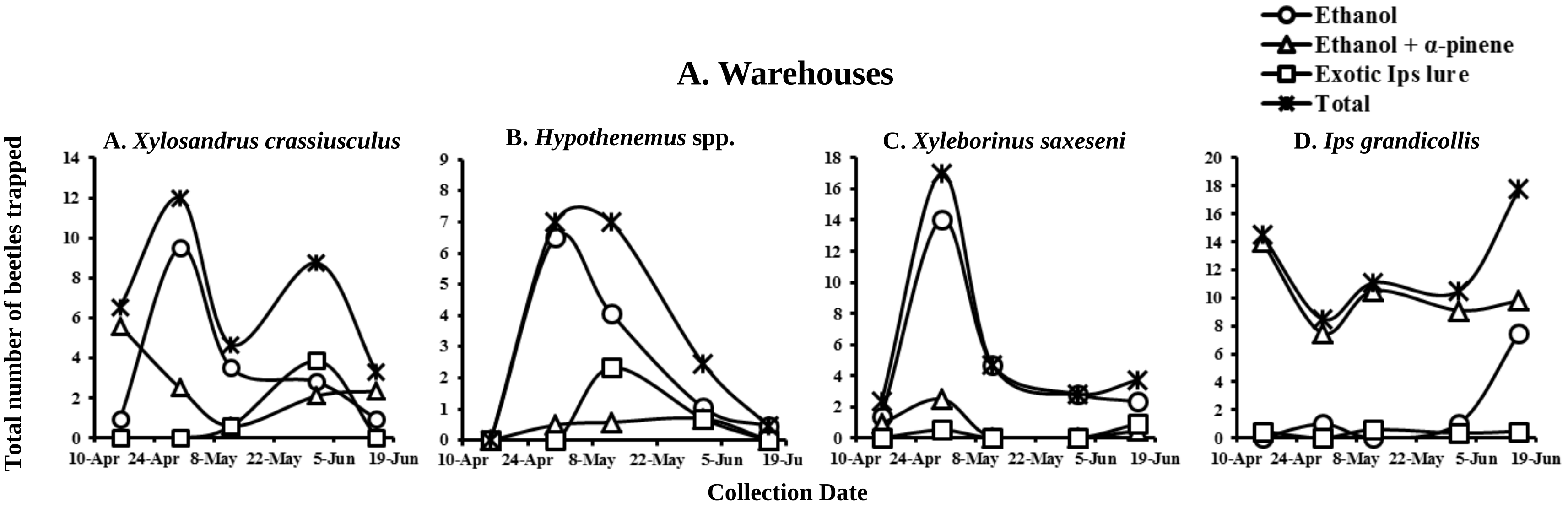

Native Scolytines
Exotic Scolytines
A. Site Type
Mean (±SE) # of beetle catches/2 wks
45
40
35
30
25
20
15
10
5
0
a
a
a
b
Warehouses
Nurseries
Site Type
B. Lure Types
Mean (±SE) # of beetle catches/2 wks
50
45
40
35
30
25
20
15
10
5
0
a
a
a
a
b
b
Ethanol
Ethanol & α-pinene
exotic Ips lure
Lure

Fig. 3.3

A. Warehouses



B. Nurseries

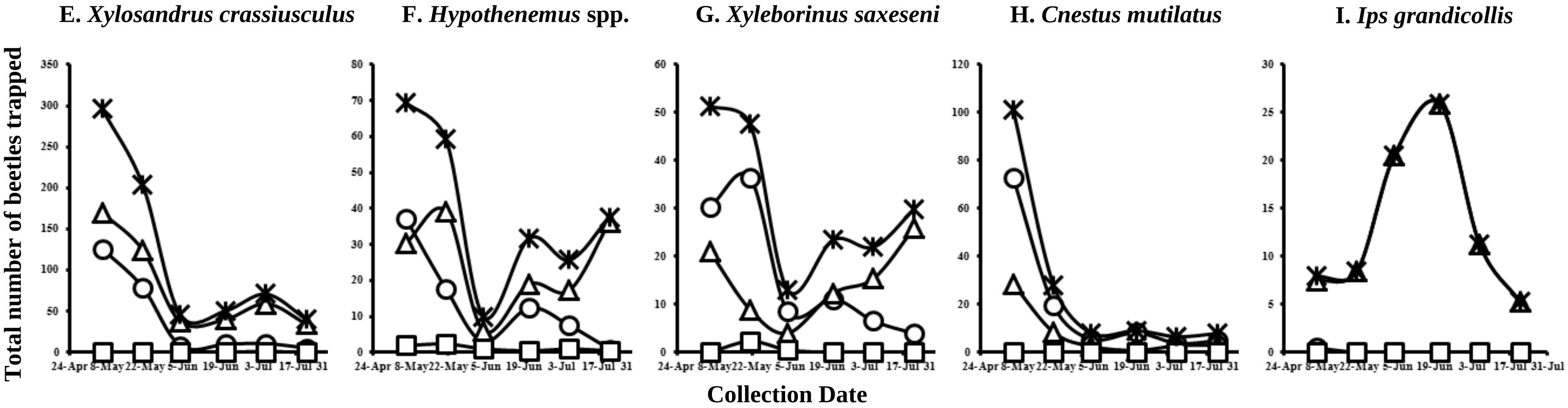


Fig. 3.4

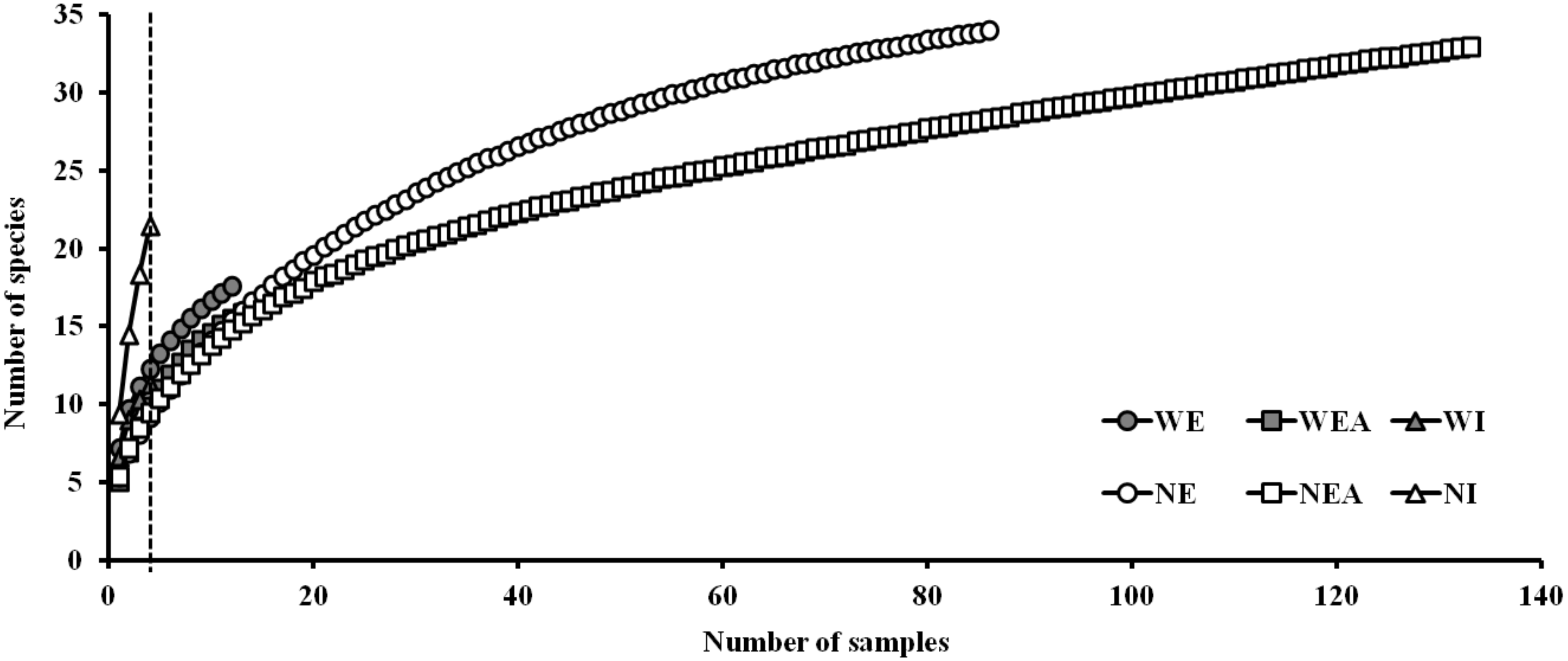
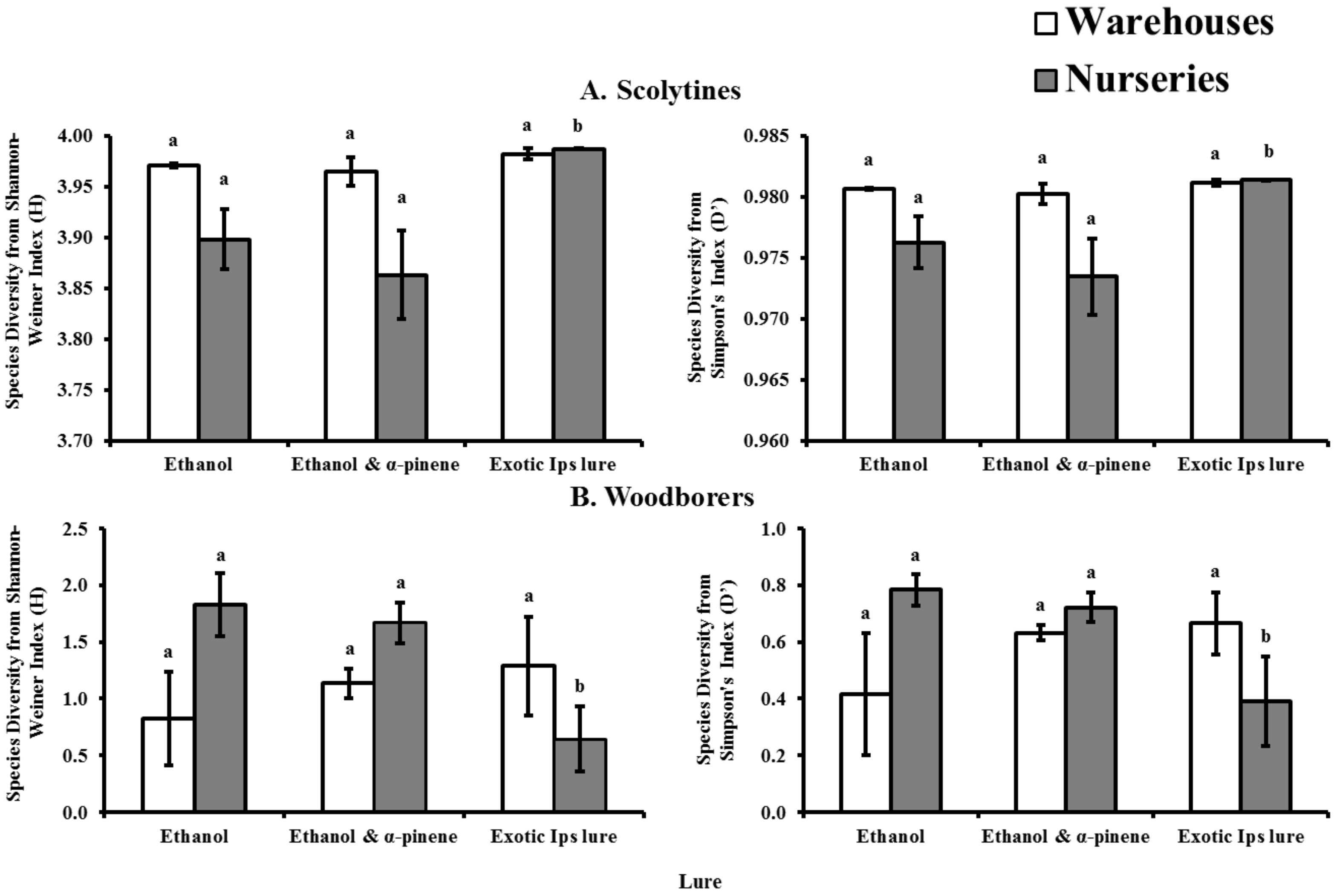

35
30
25
20
15
10
5
0
Number of species
0
20
40
60
80
100
120
140
Number of samples
WE
WEA
WI
NE
NEA
NI

Fig. 3.5



☐ Warehouses
▨ Nurseries
A. Scolytines
Species Diversity from Shannon-Weiner Index (H)
4.00
3.95
3.90
3.85
3.80
3.75
3.70
a
a
a
a
a
b
Ethanol
Ethanol & α-pinene
Exotic Ips lure
Species Diversity from Simpson's Index (D')
0.985
0.980
0.975
0.970
0.965
0.960
a
a
a
a
a
b
Ethanol
Ethanol & α-pinene
Exotic Ips lure
B. Woodborers
Species Diversity from Shannon-Weiner Index (H)
2.5
2.0
1.5
1.0
0.5
0.0
a
a
a
a
a
b
Ethanol
Ethanol & α-pinene
Exotic Ips lure
Species Diversity from Simpson's Index (D')
1.0
0.8
0.6
0.4
0.2
0.0
a
a
a
a
a
b
Ethanol
Ethanol & α-pinene
Exotic Ips lure
Lure

Fig. 3.6

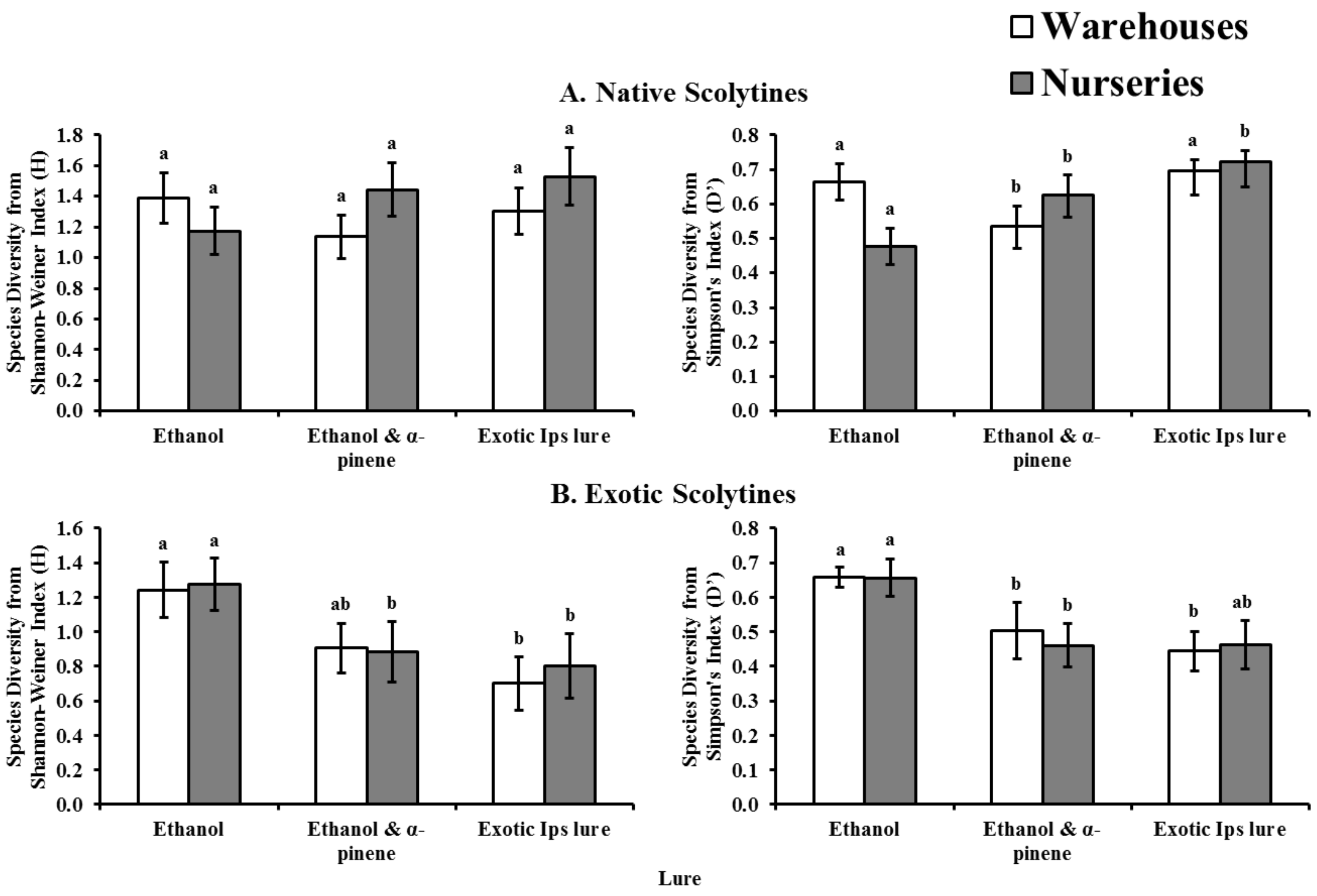
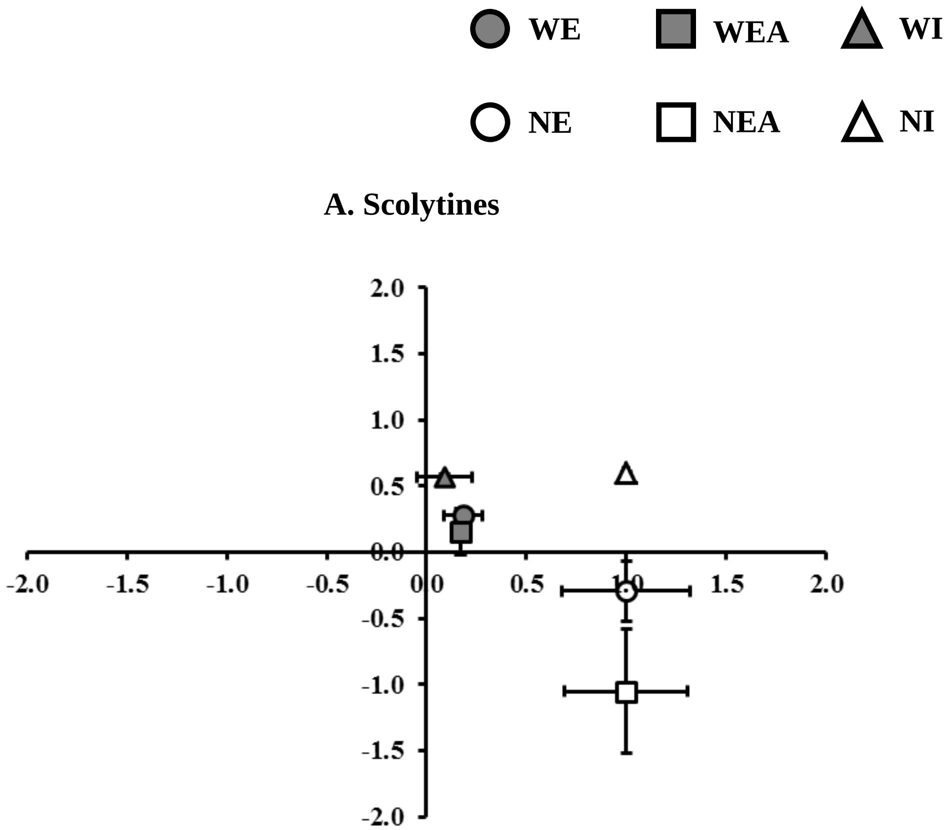

☐ Warehouses
▨ Nurseries
A. Native Scolytines
Species Diversity from Shannon-Weiner Index (H)
1.8
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
a
a
a
a
a
a
Ethanol
Ethanol & α-pinene
Exotic Ips lure
Species Diversity from Simpson's Index (D')
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
a
a
b
b
a
b
Ethanol
Ethanol & α-pinene
Exotic Ips lure
B. Exotic Scolytines
Species Diversity from Shannon-Weiner Index (H)
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
a
a
ab
b
b
b
Ethanol
Ethanol & α-pinene
Exotic Ips lure
Species Diversity from Simpson's Index (D')
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
a
a
b
b
b
ab
Ethanol
Ethanol & α-pinene
Exotic Ips lure
Lure

Fig. 3.7



A. Scolytines

B. Woodborers

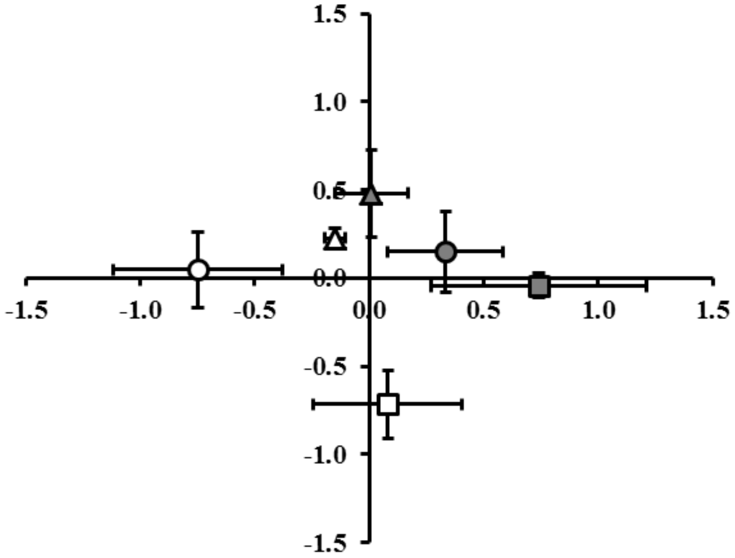


Fig. 3.8

CHAPTER 4

CONCLUSIONS

THESIS CONCLUSIONS

I studied the effects of forest disturbances (prescribed fire) and urbanization on the population and communities of native and exotic bark and woodboring beetles in Piedmont Georgia. My four major research objectives were as follows: 1) to determine the seasonal activity of *Ips* spp. and their coleopteran predators over 12 months in loblolly (*Pinus taeda* L.) and shortleaf pine (*P. echinata* Miller) stands in the southeastern U.S.; 2) to assess if fire disturbance through prescribed burning, has either immediate or short-term effects on the activity of *Ips* beetles and their coleopteran predators; 3) to determine differences in subcortical beetle communities between two major ports-of-entry (e.g. seaports and airports) for exotic species: warehouses and nurseries; and 4) to assess the responses of subcortical beetles to lures commonly used in national surveys for exotic pest detection.

Chapter 2 was focused on the *Ips* engraver beetle guild that includes *Ips avulsus* (Eichhoff), *I. calligraphus* (Germar), and *I. grandicollis* (Eichhoff), and three of their predators, *Temnochila virescens* (Fabricius) (Trogossitidae), *Thanasimus dubius* (Fabricius) (Cleridae) and *Enoclerus nigripes nigripes* (Say) (Cleridae). I determined the phenology of *Ips* beetles and their predators over 13 months, and their immediate and short-term responses to prescribed fire. In total, 112,949 *Ips* engraver beetles were trapped during the year-long study: 84,600 *I. avulsus*, 26,828 *I. grandicollis*, and 1,521 *I. calligraphus*. *Ips calligraphus* was the last species to remain active during winter 2009 and the first to become active the following spring 2010. Although the number of catches for this species was fewest, it remained active for a longer period of time than the other two *Ips* species. *Ips grandicollis* was the next species to become active in spring 2010. This species showed the least dramatic rise and fall in numbers compared to the other two *Ips* species, which showed at least five peaks in numbers throughout the study. *Ips avulsus* was trapped in the highest numbers and was the last species to become active in spring 2010. Catches of all three *Ips* species were highest just before or during the prescribed burn. It appears that the first peak of *T. dubius* coincides with that of *I. grandicollis*, whereas the second peak of *T. virescens* coincides with those of *I. calligraphus* and *I. grandicollis*. Further, both of these predator beetles were caught in greatest numbers in lures for the respective *Ips* species leading support to the hypothesis that they may be preying mostly on these two beetle species.

There was no significant difference in populations of the five beetle species among forest stands burned in 2007, 2008, and 2009, meaning there were no effects of prescribed fires on *Ips* beetles or their coleopteran predators. This implies that these beetle populations are well established, resilient and well adapted to frequent fire. Only *I. grandicollis* had lower populations in stands burned in 2007/2010 and 2009 and *T. virescens* in all three burn years. This trend suggests that increases in catches post-burn period may be an artifact of sampling time. Prescribed burns were implemented when temperatures were still cool in early spring, and beetle activity was low. Perhaps a greater impact of fires on beetles would have been observed if stands were ignited in mid-summer when the adult beetles were most active.

Chapter 3 focused on the responses of subcortical beetles to commonly used lures, and their prevalence in nurseries versus warehouses, especially for exotic species. As expected, *I. avulsus* was trapped most effectively with IAV lure combination [(+/-)-ipsenol, (+/-)-ipsdienol, and lanierone] and *I. calligraphus* with the ICA lure [(+/-)-ipsdienol and cis-verbenol]. However, more *I. grandicollis* were trapped with the IAV lure combination than with the IGR lure combination [(+/-)-ipsenol and (-) α-pinene)] Host monoterpenes, α-pinene, typically acts as a synergist to *I. grandicollis* (Erbilgin & Raffa 2000, Miller & Rabaglia 2009), but it seems that either ipsdienol or lanierone may be enhancing catches in the southeastern pine forests, although such results have not been reported elsewhere.

The study trapped the first record for *Xyleborinus artestriatus* in continental North America (Cognato et al. 2013). My study sites were numerically dominated by exotic scolytine beetles indicating that exotic species are well established and reproducing out of their native range. Significantly more scolytine beetles were trapped at nurseries than warehouses. Greater numbers of scolytine beetles and woodboring beetles were attracted to traps baited with ethanol and ethanol + α-pinene lures than other lures. Phenology graphs show that the number of generations of scolytine beetles varied between 2-3 and 4-5 generations per year. Scolytine beetles were more diverse at warehouses than at nurseries and, there are two distinct beetle assemblages present in these two sites.

Overall, results from this study could be used to refine trapping times and methods for *Ips* beetles and other exotic bark and ambrosia beetle species in the southeastern U.S. It appears that the short-interval (1-3 years) and low intensity understory prescribed burning had negligible effects on the populations of *Ips* beetles and their three common predators. The study also lends support to continued monitoring and surveying of ports-of-entry, especially nurseries and warehouses for detection of exotic species in this region.

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Erbilgin, N and Raffa, KF (2000) Opposing effects of host monoterpenes on responses by two sympatric species of bark beetles to their aggregation pheromones. Journal of Chemical Ecology 26: 2527-2548

Miller, DR and Rabaglia, RJ (2009) Ethanol and (-)-α-pinene: Attractant kairomones for bark and ambrosia beetles in the southeastern US. Journal of Chemical Ecology 35: 435-448