Bark Beetle Pheromones and Pine Volatiles: Attractant Kairomone Lure Blend for Longhorn Beetles (Cerambycidae) in Pine Stands of the Southeastern United States

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ABSTRACT In 2006, we examined the flight responses of 43 species of longhorn beetles (Coleoptera: Cerambycidae) to multiple-funnel traps baited with binary lure blends of 1) ipsenol + ipsdienol, 2) ethanol + α-pinene, and a quaternary lure blend of 3) ipsenol + ipsdienol + ethanol + α-pinene in the southeastern United States. In addition, we monitored responses of Buprestidae, Elateridae, and Curculionidae commonly associated with pine longhorn beetles. Field trials were conducted in mature pine (*Pinus* pp.) stands in Florida, Georgia, Louisiana, and Virginia. The following species preferred traps baited with the quaternary blend over those baited with ethanol + α-pinene: *Acanthocinus nodosus* (F.), *Acanthocinus obsoletus* (Olivier), *Astylopsis arcuata* (LeConte), *Astylopsis sexguttata* (Say), *Monochamus scutellatus* (Say), *Monochamus titillator* (F.) complex, *Rhagium inquisitor* (L.) (Cerambycidae), *Buprestis consularis* Gory, *Buprestis lineata* F. (Buprestidae), *Ips avulsus* (Eichhoff), *Ips calligraphus* (Germar), *Ips grandicollis* (Eichhoff), *Orthotomicus caelatus* (Eichhoff), and *Gnathotrichus materiarus* (Fitch) (Curculionidae). The addition of ipsenol and ipsdienol had no effect on catches of 17 other species of bark and wood boring beetles in traps baited with ethanol and α-pinene. Ethanol + α-pinene interrupted the attraction of *Ips avulsus*, *I. grandicollis*, and *Pityophthorus* Eichhoff spp. (but not *I. calligraphus*) (Curculionidae) to traps baited with ipsenol + ipsdienol. Our results support the use of traps baited with a quaternary blend of ipsenol + ipsdienol + ethanol + α-pinene for common saproxylic beetles in pine forests of the southeastern United States.

KEY WORDS ethanol, α-pinene, ipsenol, ipsdienol, *Monochamus titillator*

Longhorn beetles (Coleoptera: Cerambycidae) can cause significant economic losses, directly from larval feeding as wood borers or indirectly from transmission of pinewood nematode (Allison et al. 2004). Larval mining can produce large-diameter holes and tunnels in wood, resulting in significant levels of degrade losses to wood products (Safranyik and Raske 1970; Cerezke 1975, 1977). Attacks by adults can result in extensive tree mortality [e.g., Asian longhorned beetle, *Anoplophora glabripennis* (Motschulsky) attacks on urban trees in Illinois, Massachusetts, and New York, as well as trees within its native range in China; Hu et al. 2009, Haack et al. 2010]. Adults also can vector pathogens. In Japan and China, the pine wilt nematode, *Bursaphelencus xylophilus* (Steiner and Buhrer) Nickle (Nematoda: Aphenlenchoididae), vectored by *Monochamus alternatus* Hope has resulted in widespread pine (*Pinus* pp.) mortality (Fan et al. 2007).

Early detection of invading species is a critical tactic in countering the possible impacts of invasive species (Chornesky et al. 2005). In an ideal world, all shipments would be fully examined before leaving ports-of-departure and certified free-of-contamination by insects and diseases. However, direct examination of all shipments and packing materials is economically unrealistic and logistically impossible. This is particularly true for woodborers as adult and larval beetles are generally hidden within bark or wood tissues, thereby necessitating the need for traps to detect incursions by exotic species (Allen and Humble 2002, Allison et al. 2004). In the United States, national programs by the U.S. Department of Agriculture such as the Animal and Plant Health Inspection Services–Cooperative Agricultural Pest Survey (CAPS) and the Forest Service–Early Detection and Rapid Response program (EDRR) use multiple-funnel traps baited with various lures to capture a broad array of insects associated with trees and wood products (Rabaglia et al. 2008, Jackson et al. 2010).

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Table 1. National forest (NF), state forest (SF), and industrial forest (IF) locations, forest types, and dates for six trapping experiments in the southeastern United States

Expt.	Location	Tree species	Trapping dates
1	Apalachicola NF near Tallahassee, FL	*Pinus palustris* Miller and *Pinus elliottii* Engelmann	4 April–6 June 2006
2	Oconee NF near Eatonton, GA	*Pinus taeda* L.	11 April–13 June 2006
3	Plum Creek IF near Madison, GA	*P. taeda*	23 Aug.–4 Oct. 2006
4	Kisatchie NF near Winnfield, LA	*P. taeda* and *P. palustris*	4 April–31 May 2006
5	Kisatchie NF near Packton, LA	*P. taeda*	6 Sept. 2006–5 Jan. 2007
6	Appomattox-Buckingham SF near Appomattox, VA	*P. taeda*	25 May–27 July 2006

Lures releasing host volatiles are popular in trapping programs targeting woodborers as many species of bark and wood boring beetles are attracted to volatiles produced by host trees (Allison et al. 2004, Haack 2006). In North America, traps baited with ethanol and α-pinene are attractive to the following species of pine woodborers: *Acanthocinus nodosus* (F.), *Acanthocinus obliquus* (LeConte), *Acanthocinus obsoletus* (Olivier), *Acanthocinus spectabilis* (LeConte), *Acmaeops proteus* (Kirby), *Arhopalus rusticus* (L.), *Asemum striatum* (L.), *Monochamus clamator* (LeConte), *Monochamus notatus* (Drury), *Monochamus scutellatus* (Say), *Monochamus titillator* (F.), *Prionus pocularis* Dalman, *Xylotrechus integer* (Haldeman), *Xylotrechus longitarsis* Casey, *Xylotrechus sagittatus* (Germar), and *Xylotrechus undulatus* (Say) (Chénier and Philogène 1989, Allison et al. 2001, Miller 2006, Costello et al. 2008).

Pheromones produced by bark beetles are also attractive to some pine cerambycids. In Texas, *M. titillator* was attracted to traps baited with ipsenol, ipsdienol and *cis*-verbenol (Billings and Cameron 1984). In British Columbia, Canada, a blend of four bark beetle pheromones that included ipsenol and ipsdienol was attractive to *M. scutellatus* and *M. clamator* (Allison et al. 2001). *M. scutellatus* was attracted to traps baited with ipsenol in Ontario, Canada (de Groot and Nott 2004). Ipsenol and ipsdienol were attractive to *M. titillator* and *A. obsoletus* in Florida, Louisiana, Georgia, and North Carolina (Miller and Asaro 2005). In Europe, *Monochamus galloprovincialis* (Olivier) was attracted to traps baited with ipsenol (Pajares et al. 2004).

Combining host volatiles with bark beetle pheromones can enhance attraction of *Monochamus* species, probably indicating optimal conditions associated with an ephemeral habitat (Allison et al. 2004). Catches of *M. titillator* in Texas were higher in traps baited with turpentine and *cis*-verbenol, ipsenol, and ipsdienol than in traps baited solely with turpentine or the *Ips* pheromones (Billings 1985). In British Columbia, Canada, ipsenol and ipsdienol increased the responses of *M. scutellatus* and *M. clamator* to traps baited with ethanol and α-pinene (Allison et al. 2003). Allison et al. (2001) found that attraction of *M. notatus* and *Monochamus obtusus* Casey to traps baited with a blend of monoterpenes was enhanced with a blend of four bark beetle pheromones that included ipsenol and ipsdienol. Similarly, catches of *M. clamator* in traps baited with ethanol and α-pinene were enhanced by the addition of ipsenol or ipsdienol (Allison et al. 2003, Costello et al. 2008). In Canada, ipsenol and ipsdienol increased catches of *M. scutellatus* to traps baited with (−)-α-pinene or ethanol and α-pinene (Allison et al. 2003, de Groot and Nott 2004). In Spain, catches of *M. galloprovincialis* in traps baited with α-pinene or ethanol and α-pinene were enhanced with the addition of ipsenol or blends that included ipsenol, ipsdienol, or both (Pajares et al. 2004, Ibeas et al. 2006).

M. titillator and *A. obsoletus* are attracted to traps baited with ethanol and α-pinene as well as to traps baited with ipsenol, ipsdienol, or both (Miller and Asaro 2005, Miller 2006). Our objective was to determine the additive effects of the pine volatile blend of ethanol and α-pinene and the bark beetle pheromone blend of ipsenol and ipsdienol on catches of *M. titillator*, *A. obsoletus*, and associated species in baited traps in the southeastern United States. Specifically, we determined the responses of common bark and word boring beetles to traps baited with 1) ethanol + α-pinene, 2) ipsenol + ipsdienol, and 3) all four compounds. We monitored the responses of 43 species of common longhorn beetles as well as the responses of bark and ambrosia beetles, root-feeding weevils (Curculionidae), flatheaded woodborers (Buprestidae), and wood-boring click beetles (Elateridae).

Methods and Materials

We used the same behavioral choice type of experimental design in separate stands of mature pine at each of six locations in the southeastern United States, resulting in six separate experiments (Table 1). At each location, we deployed 30 eight-unit multiple-funnel traps (Phero Tech Inc., Delta, BC, Canada; now Contech Enterprises Inc., Victoria, BC, Canada) set in 10 replicate blocks ($n = 10$) of three traps per block. Traps were spaced 10–15 m apart within blocks, with replicate blocks spaced 15–20 m apart. Each trap was suspended between trees by rope such that each trap was >2 m from any tree and the bottom of each trap was 0.2–0.5 m above ground level. Collection cups contained 150–200 ml of pink propylene glycol solution (Peak RV and Marine Antifreeze, Old World Industries Inc., Northbrook, IL) as a killing and preservation agent (Miller and Duerr 2008).

Contech Enterprises Inc. supplied sealed ultrahigh-release (UHR) plastic pouches containing either ethanol (150 ml) or α-pinene (200 ml), as well as bubble cap lures containing either racemic ipsenol or racemic ipsdienol [chemical purities >95%, enantiomeric composition 50:50 (+)/(−)]. The enantiomeric purity of α-pinene was >95% (−). The release rate of ethanol from ethanol UHR pouches was 0.6 g/d at 25–28°C, whereas α-pinene was released at 2–6 g/d from α-pinene UHR pouches at 25–28°C (determined by weight loss). Ipsenol and ipsdienol were released from bubble caps at 0.1–0.2 μg/d at 22–25°C (Contech Enterprises Inc.).

One of the following three treatments was allocated to each of the three traps within each block: 1) ethanol + α-pinene; 2) ipsenol + ipsdienol; and 3) ethanol + α-pinene + ipsenol + ipsdienol. As the attractiveness of both binary lure blends to Cerambycidae and associated species has been documented previously (Miller and Asaro 2005, Miller et al. 2005, Miller 2006, Miller and Rabaglia 2009), blank control traps were not employed in the design to minimize the risk of zero trap variances arising from zero total catches (Reeve and Strom 2004).

Trap catch data were analyzed with the SigmaStat version 3.01 statistical package (SYSTAT Software Inc., Point Richmond, CA) for locations where sufficient numbers ($N \geq 50$) were captured for individual species. Trap catch data were transformed by ln(Y+1) to remove heteroscedasticity (Pepper et al. 1997). When possible, trap catch data were subjected to analysis of variance (ANOVA) by using the following model components: 1) replicate and 2) treatment. Normality and homoscedasticity were verified before using the Holm–Sidak multiple comparison procedure (Glantz 2005) to compare means within a location for each species exhibiting a significant treatment effect ($\alpha = 0.05$). In cases with one treatment lacking variation (due to lack of any beetle captures), the means of catches associated with the two remaining treatments were analyzed by *t*-test.

Species identifications, taxonomic names, and authors were determined using Lingafelter (2007) and ITIS (2009). In placing *Monochamus carolinensis* (Olivier) as a synonym of *M. titillator*, Hopping (1921) noted that "In long series every variation in size, maculation and reduction of the spine into a blunt form may be found". Similarly, we found separation of *M. carolinensis* from *M. titillator* to be difficult and inconsistent using characters noted by Lindsey and Chemsak (1984) and Lingafelter (2007). Therefore, we designated *M. titillator*, *M. carolinensis* and any possible hybrids, as *M. titillator* complex. The two species are broadly sympatric in pine stands throughout eastern North America (Lindsey and Chemsak 1984). Voucher specimens of all species were deposited in the Entomology Collection, Museum of Natural History, University of Georgia (Athens, GA). Large series of *M. titillator* complex (both pinned and preserved in 95% ethanol) were deposited in our collection at the USDA Forest Service (Athens, GA) for future review of the species group.

Results

Longhorn Beetles. In total, 9,994 Cerambycidae were captured across all six locations, ranging from 1,324–2,462 per location (Table 2). We collected individuals of 43 species with diversity ranging from seven to 26 species per location. The most common species were *A. nodosus*, *A. obsoletus*, *Astylopsis arcuata* (LeConte), *Acanthocinus sexguttata* (Say), *M. scutellatus*, *M. titillator* complex, *Rhagium inquisitor* (L.), and *X. sagittatus.* Catches of most species were highest in traps baited with the quaternary blend of ethanol, α-pinene, ipsenol, and ipsdienol.

The most common longhorn beetle was *M. titillator* complex captured at all six locations with a total catch of 5,419 (accounting for 54.2% of total catches of Cerambycidae; Table 2). At all locations, traps baited with the quaternary blend caught the most beetles (Fig. 1A–F). At five of the six locations, catches of *M. titillator* complex were greater in traps baited with ipsenol + ipsdienol than in traps baited with ethanol + α-pinene (Fig. 1A–C, E, F). Similarly, catches of the whitespotted sawyer, *M. scutellatus* in Virginia were greatest in traps baited with the quaternary blend (Fig. 1G).

A. obsoletus was captured at all six locations with a total catch of 1,484 (14.8% of total catches; Table 2). As with *M. titillator* complex, the preferred treatment for *A. obsoletus* at all six locations was the quaternary blend (Fig. 1H—M). At four locations, catches of *A. obsoletus* were greater in traps baited with ipsenol + ipsdienol than in traps baited with ethanol + α-pinene (Fig. 1H and J–L). In Florida, catches of *A. nodosus* in traps baited with the quaternary blend were no different than those in traps baited with ethanol + α-pinene (Fig. 1N), whereas in Louisiana, the preferred treatment for *A. nodosus* was the quaternary blend (Fig. 1O).

A similar preference for the quaternary blend was demonstrated by four less common species of Cerambycidae. In Georgia, Louisiana, and Virginia, catches of *R. inquisitor* were greater in traps baited with the quaternary blend than in traps baited with either binary blend (Fig. 2A–C). At all three locations, catches of *R. inquisitor* in traps baited with ipsenol + ipsdienol were not different from those in traps baited with ethanol + α-pinene. In Georgia, catches of *A. arcuata* and *A. sexguttata* were greater in traps baited with the quaternary blend than those in traps baited with either binary blend (Fig. 3D and E). Traps baited with ipsenol + ipsdienol caught more *A. sexguttata* but not more *A. arcuata* than traps baited with ethanol + α-pinene.

X. sagittatus was the second most common cerambycid, captured at all six locations with a total catch of 1,828 (18.3% of total Cerambycidae). In contrast to all of the above-mentioned species, *X. sagittatus* did not demonstrate a preference for traps baited with the quaternary blend (Fig. 2F–K). At five of six locations, catches of beetles in traps baited with the quaternary blend were not different from those in traps baited with ethanol + α-pinene (Fig. 2F and H–K). At one location in Georgia, traps baited with ethanol +

Table 2. Total catches of Cerambycidae (Coleoptera) at six experimental sites in southeastern United States

Species	Exp and state						Total
	1	2	3	4	5	6	
	FL	GA	GA	LA	LA	VA	
Acanthocinus nodosus (F.)	68	15	3	68	10	10	174
A. obsoletus (Olivier)	261	75	155	605	344	44	1,484
Acmaeops discoideus (Haldeman)		18	1			2	21
Ancylocera bicolor (Olivier)	1						1
Anelaphus paralellus (Newman)	1	1		5		16	23
A. pumilus (Newman)				1			1
A. villosus (F.)				1		1	2
Arhopalus rusticus (LeConte)						32	32
Asemum striatum (L.)		5		5		114	124
Astylopsis arcuata (LeConte)	6	12	173	10	1	5	207
A. sexguttata (Say)	16	3	70	2	13	1	105
Ataxia crypta (Say)		2		2	1	2	7
A. falli Breuning				2			2
Curius dentatus Newman	1		2	1			4
Cyrtophorus verrucosus (Olivier)		13		6		8	27
Elaphidion mucronatum (Say)	1	5		9		1	16
Euderces picipes (F.)						1	1
E. pini (Olivier)		5		1			6
Gaurotes cyanipennis (Say)		1					1
Judolia cordifera (Olivier)						3	3
Knulliana cincta (Drury)						3	3
Lypsimena fuscata Haldeman				1			1
Monochamus scutellatus (Say)						191	191
M. titillator (F.) complex	1283	1080	448	1310	637	661	5,419
Neandra brunnea (F.)			1				1
Neoclytus acuminatus (F.)				1		3	4
N. mucronatus (F.)				1			1
Obrium maculatum (Olivier)				15			15
Orthosoma brunneum (Forster)			1	1	1		3
Prionus pocularis Dalman			4				4
Rhagium inquisitor (Linnaeus)	2	74		37		101	214
Saperda lateralis F.						1	1
Smodicum cucujiforme (Say)		1					1
Stenelytrana emarginata (F.)						1	1
Strangalepta abbreviata (Germar)						1	1
Strangalia famelica Newman				1			1
Styloleptus biustus (LeConte)	1						1
Tragidion coquus (L.)				1			1
Typocerus lunulatus (Swederus)				1			1
T. velutinus (Olivier)		1				1	2
T. zebra (Olivier)	2	12		18		7	39
Xylotrechus colonus (F.)		2		17		9	28
X. sagittatus (Germar)	97	110	473	340	699	109	1,828
Total	1,740	1,435	1,324	2,462	1,706	1,327	9,994

α-pinene caught more *X. sagittatus* than traps baited with the quaternary blend ($t_{18} = 2.296$, $P = 0.034$, Fig. 2G). Similarly in Virginia, catches of *A. striatum* were highest in traps baited with the quaternary blend or ethanol + α-pinene and lowest in traps baited with ipsenol + ipsdienol (Fig. 2L).

Flatheaded Wood Borers. Three species of flatheaded wood borers (Buprestidae) were captured in our study. Catches of *Buprestis consularis* Gory in Louisiana were lowest in traps baited with ethanol + α-pinene, with no difference between the remaining two treatments (Fig. 2M). In Georgia and Louisiana, catches of *Buprestis lineata* F. were higher in traps baited with the quaternary blend than in those baited with ipsenol + ipsdienol (Fig. 2N and O). Catches of *B. lineata* were higher in traps baited with ethanol + α-pinene than in traps with ipsdienol + ipsenol in Georgia, but not in Louisiana where the reverse was true. We caught 166 *Chalcophora virginiensis* (Drury) in Louisiana with no significant treatment effect ($F_{2,18} = 0.577$; $P = 0.571$) and a mean ± SE trap catch of 5.5 ± 0.8 beetles.

Ambrosia Beetles. The most common ambrosia beetles were *Xyleborinus saxesenii* (Ratzeburg) and *Xylosandrus crassiusculus* (Motschulsky), with total catches of 10,805 and 1,908, respectively (Fig. 3A–F, I–N). *X. saxesenii, Xyleborus pubescens* Zimmermann, *Xylosandrus compactus* (Eichhoff), *X. crassiusculus,* and *Dryoxylon onoharaensis* (Murayama) were largely unaffected by ipsenol + ipsdienol. Irrespective of location, catches of all five species were highest in traps baited with ethanol + α-pinene or the quaternary blend, with no significant differences between them (Fig. 3A–N). The lowest catches of all species were in traps baited with ipsenol + ipsdienol. Catches of *X. crassiusculus* in traps baited with the quaternary blend were no different from those baited with ethanol + α-pinene in Virginia ($t_{18} = 0.076$, $P = 0.940$; Fig. 3K) and one location in Louisiana ($t_{18} = 1.899$, $P = 0.074$; Fig. 3L). The same was true for *X. compactus* at one

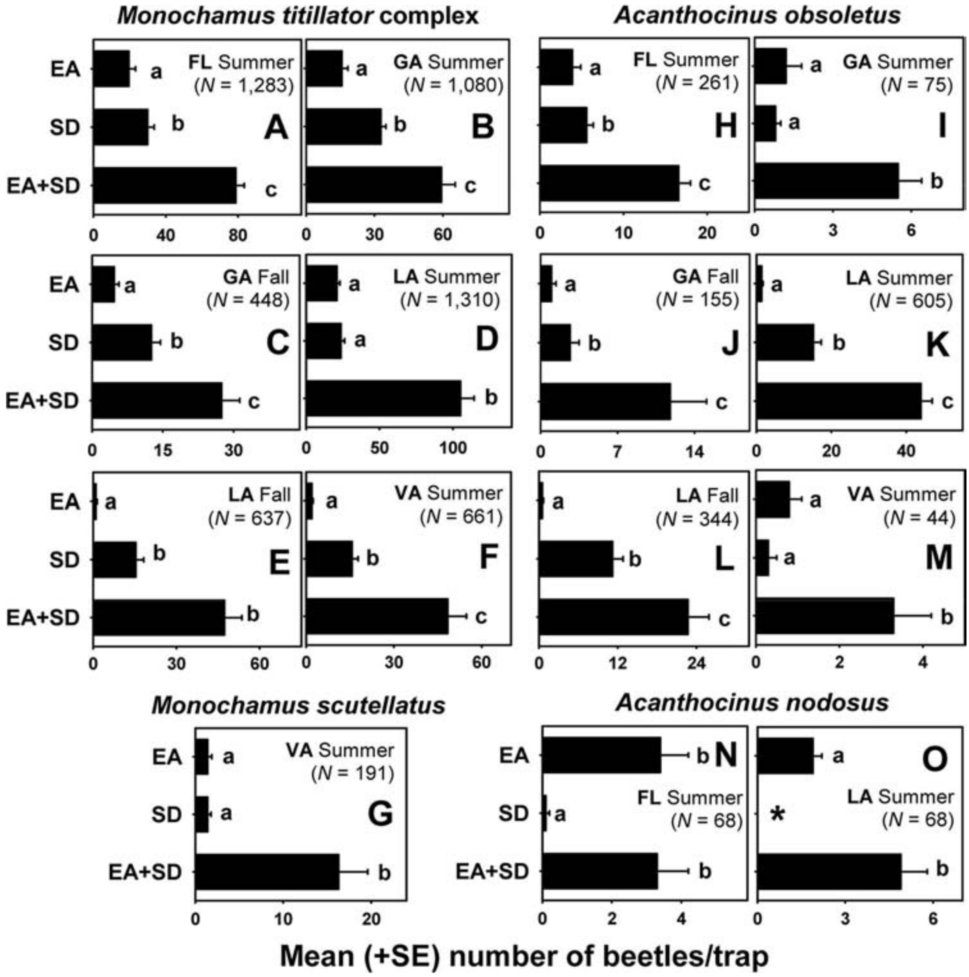

Fig. 1. Effects of ethanol + α-pinene (EA), ipsenol + ipsdienol (SD), and all four compounds (EA + SD) on trap catches of *M. titillator* (A–F), *M. scutellatus* (G), *A. obsoletus* (H–M), and *A. nodosus* (N,O) in the southeastern United States. Means followed by the same letter are not significantly different at $P = 0.05$ (Holm–Sidak test [A–N] or *t*-test [O], see text). Treatment with an asterisk had zero catches.

location in Louisiana ($t_{18} = 0.196$; $P = 0.847$; Fig. 3M). Traps baited with ipsenol + ipsdienol caught no *X. crassiusculus* in Virginia (Fig. 3L) and at one location in Louisiana (Fig. 3K), and no *X. compactus* in Louisiana (Fig. 3M).

The highest catches of *Gnathotrichus materiarus* (Fitch) were obtained in traps baited with the quaternary blend in Louisiana and Virginia (Fig. 3O and P). In both locations, catches of *G. materiarus* in traps baited with the quaternary blend was greater than those in traps baited with ipsenol + ipsdienol. In Virginia but not Louisiana, catches in traps baited with the quaternary blend was greater than those in traps baited with ethanol + α-pinene. At both locations, catches in traps baited with ethanol + α-pinene were not different from those baited with ipsenol and ipsdienol.

Bark Beetles. Only one of ten common bark beetle species captured in our study exhibited a preference for the quaternary blend. In Florida and Louisiana, catches of *Orthotomicus caelatus* (Eichhoff) in traps baited with the quaternary blend were greater than those in traps baited with either binary blend (Fig. 4A and B). Traps baited with ipsenol + ipsdienol were the least preferred by *O. caelatus.* The two most common species of bark beetles were *Ips grandicollis* (Eichhoff) and *Ips avulsus* (Eichhoff), captured at all six locations with total catches of 66,741 and 92,535, respectively (Fig. 4C–H, K–P). At all six locations, both species preferred traps baited with ipsenol + ipsdienol than traps baited with the quaternary blend or ethanol + α-pinene. In contrast, catches of *Ips calligraphus* (Germar) in traps baited with the quaternary blend at two locations in Louisiana were not different from those in traps baited with ipsenol + ipsdienol (Fig. 4I and J). Catches of all three species in traps baited with the quaternary blend were greater than those in traps baited with ethanol + α-pinene (Fig. 4C–P). Catches of *I. avulsus* in Virginia were greater in traps baited with ipsenol + ipsdienol than in traps baited with the

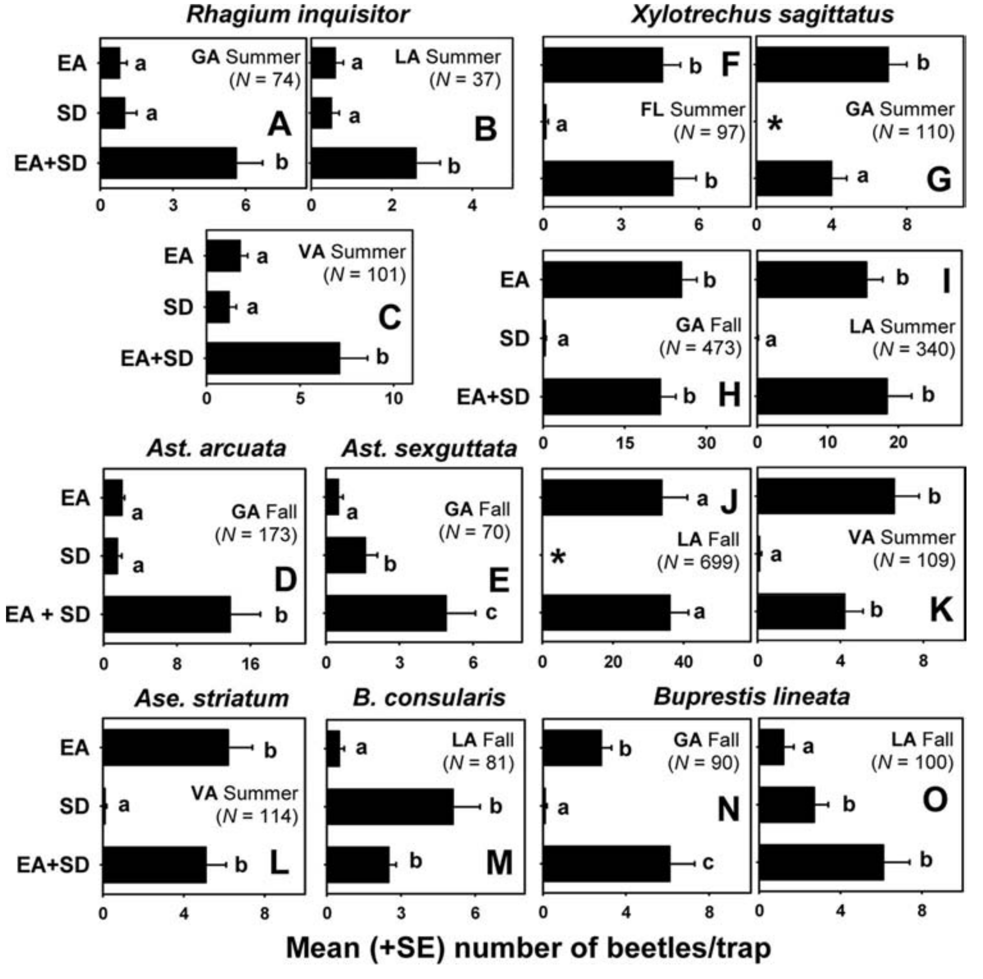

Fig. 2. Effects of ethanol + α-pinene (EA), ipsenol + ipsdienol (SD), and all four compounds (EA + SD) on trap catches of *R. inquisitor* (A–C), *A. arcuata* (D), *A. sexguttata* (E), *X. sagittatus* (F–K), *A. striatum* (L), *B. consularis* (M), and *B. lineata* (N and O) in the southeastern United States Means followed by the same letter are not significantly different at $P = 0.05$ (Holm–Sidak test [A–F, H, I, K–O] or *t*-test [G and J]; see text). Treatments with an asterisk had zero catches.

quaternary blend ($t_{18} = 2.760$, $P = 0.013$); no beetles were captured in traps baited with ethanol + α-pinene (Fig. 4P).

Three common *Hylastes* species were largely unaffected by the addition of ipsenol + ipsdienol to traps baited with ethanol + α-pinene. *Hylastes salebrosus* Eichhoff and *Hylastes tenuis* Eichhoff were captured at all six locations, with total catches of 2,067 and 1,655, respectively whereas *Hylastes porculus* Erichson was captured at three locations, with a total catch of 845. Catches of all three species were highest in traps baited with ethanol + α-pinene or the quaternary blend and lowest in traps baited with ipsenol + ipsdienol (Fig. 5). For all three species, there were generally no differences in catches in traps baited with the quaternary blend compared with those baited with ethanol + α-pinene (Fig. 5). The only exceptions were for *H. salebrosus* at one location in Louisiana and *H. tenuis* at one location in Georgia where catches were lower in traps baited with the quaternary blend than those in traps baited with ethanol + α-pinene (Fig. 5D and H).

The black turpentine beetle, *Dendroctonus terebrans* (Olivier) was present at all six locations with a total catch of 2,674 (Fig. 6A–F). Catches of *D. terebrans* were highest in traps baited with ethanol + α-pinene or the quaternary blend, and lowest in traps baited with ipsenol + ipsdienol. With two exceptions, there were no differences in catches in traps baited with the quaternary blend compared with those baited with ethanol + α-pinene (Fig. 6). The exceptions were one location in Louisiana where catches were lower in traps baited with the quaternary blend than those in traps baited with ethanol + α-pinene (Fig. 6D) and at one location in Virginia where the converse was true and catches were higher with the quaternary blend than those in traps baited with ethanol + α-pinene (Fig. 6F).

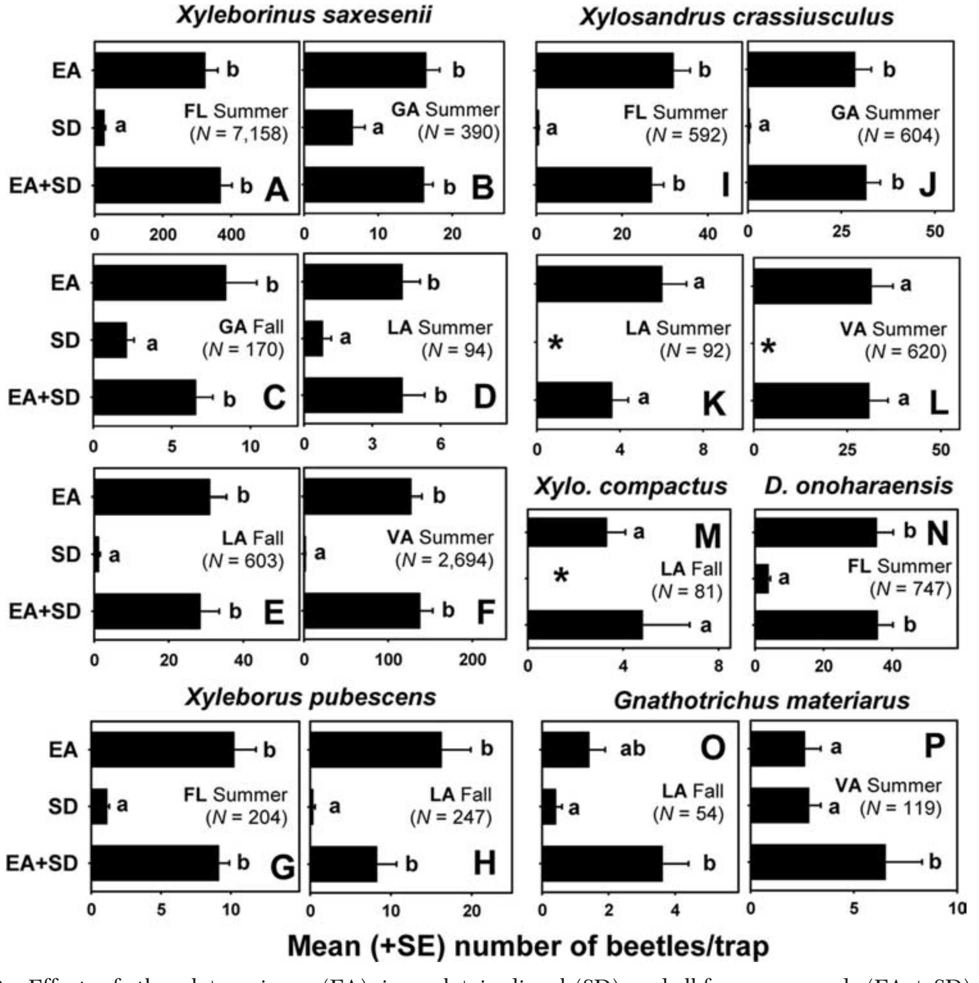

Fig. 3. Effects of ethanol + α-pinene (EA), ipsenol + ipsdienol (SD), and all four compounds (EA + SD) on trap catches of *X. saxesenii* (A–F), *X. pubescens* (G and H), *X. crassiusculus* (I–L), *X. compactus* (M), *D. onoharaensis* (N), and *G. materiarus* (N and O) in the southeastern United States. Means followed by the same letter are not significantly different at $P = 0.05$ (Holm–Sidak test [A–F, J, K, L–O] or *t*-test [I, L, M]; see text). Treatments with an asterisk had zero catches.

Catches of *Hypothenemus* Westwood spp. were highest in traps baited with the quaternary blend or ethanol + α-pinene in Georgia and Louisiana, with no differences between the two treatments (Fig. 6G and H). At both locations, catches of *Hypothenemus* spp. in traps baited with ipsenol + ipsdienol were less than those in traps baited with the quaternary blend. In Georgia, *Pityophthorus* Eichhoff spp. preferred traps baited with ipsenol + ipsdienol over those baited with ethanol + α-pinene or the quaternary blend (Fig. 6J). There was no difference in catches of *Pityophthorus* spp. in traps baited with ethanol + α-pinene and the quaternary blend.

Weevils. Three species of root-or stem feeding weevils were captured in our study. *Pissodes* Germar spp. were captured in sufficient numbers only at one location (Fig. 6K), whereas *Hylobius pales* Herbst and *Pachylobius picivorus* LeConte were captured at four of the six locations, with total catches of 3,829 and 1,371 beetles, respectively (Fig. 7A–K). The catches of each species were highest in traps baited with ethanol + α-pinene or the quaternary blend and lowest in traps baited with ipsenol and ipsdienol with no difference in catches between traps baited with ethanol + α-pinene or traps baited with the quaternary blend for all three species at any location. (Figs. 6J and 7A–K).

Click Beetles. *Alaus myops* (F.) (Elateridae) was captured in sufficient numbers at four of six locations, with a total catch of 609 (Fig. 7L–O). At each location, the lowest catches of *A. myops* were obtained in traps baited with ipsenol + ipsdienol. At three locations, catches of *A. myops* in traps baited with the quaternary blend were not different from those in traps baited with ethanol + α-pinene (Fig. 7L, M, and O). In Louisiana, catches of *A. myops* were lower in traps baited with the quaternary

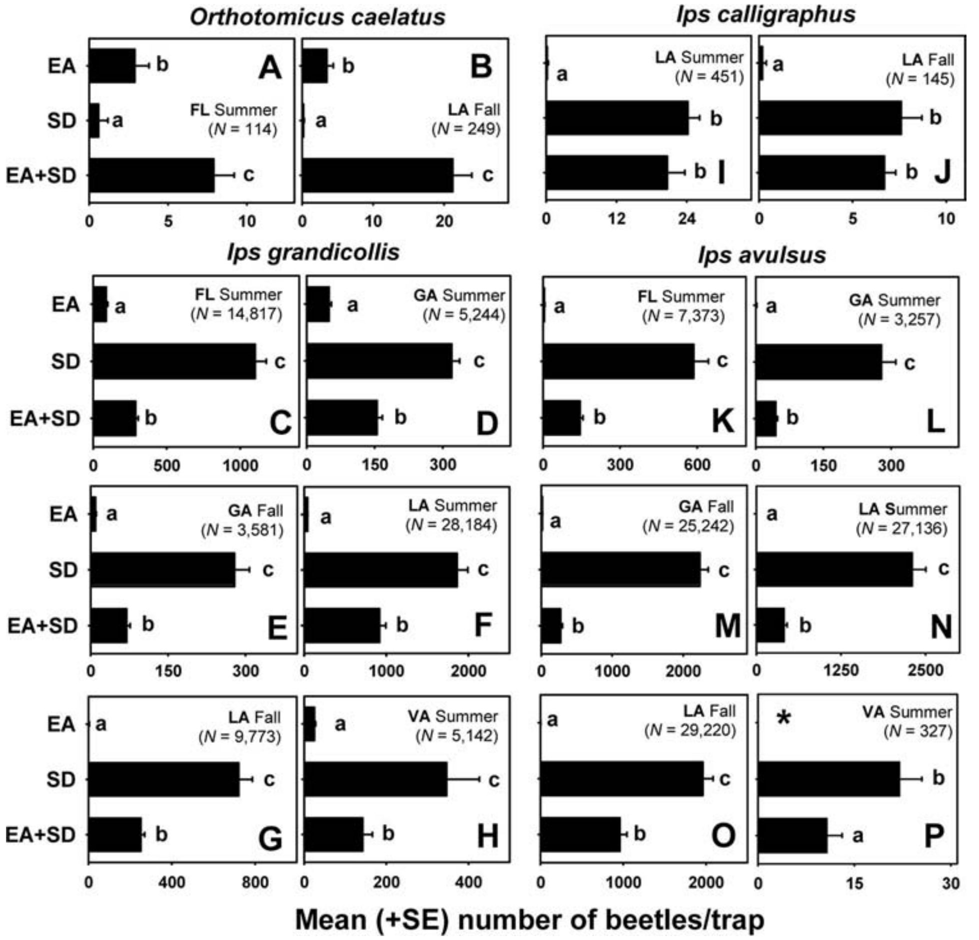

Fig. 4. Effects of ethanol + α-pinene (EA), ipsenol + ipsdienol (SD), and all four compounds (EA + SD) on trap catches of *O. caelatus* (A and B) *I. grandicollis* (C–H), *I. calligraphus* (I and J), and *I. avulsus* (K–P) in the southeastern United States. Means followed by the same letter are not significantly different at $P = 0.05$ (Holm–Sidak test [A–M, O, P] or *t*-test [N]; see text). Treatment with an asterisk had zero catches.

blend than in traps baited with ethanol + α-pinene (Fig. 7N).

Discussion

At all six locations in the southeastern United States, the quaternary combination of ethanol, α-pinene, ipsenol, and ipsdienol was more attractive to *M. titillator* complex than either of the two binary combinations (ethanol + α-pinene or ipsenol + ipsdienol' Fig. 1A–F). All four of these compounds occur naturally in pine stands and are probably associated with host quality conditions favorable to oviposition by *M. titillator* complex. Because phloem tissues are ephemeral, selection should favor individuals that take advantage of any information that could lead them to oviposition sites in a timely manner. α-Pinene is a major constituent of the resin of southern pines (Mirov 1961, Smith 2000). The release of α-pinene is consistent with recent physical damage to potential hosts. Attraction of sawyer beetles to felled trees is usually delayed by a short time interval, possibly to minimize detrimental effects of resin pressure by allowing resin pressure to drop before ovipositing on new hosts (Dyer and Seabrook 1978). The attraction of beetles to ethanol along with host terpenes is consistent with a delay for initial oviposition on felled trees as there may be a delay in initial ethanol production after damage to a tree.

The additive effect of the bark beetle pheromones, ipsenol + ipsdienol in attracting *M. titillator* complex to sources of ethanol + α-pinene may reflect an environmental condition with a higher likelihood of suitable hosts for *M. titillator* complex. One or both of the pheromones are used by southern pine engravers (Smith et al. 1993). Pine engravers are typically the earliest invaders of prime host material such as lightning-struck trees, or recently downed live trees or limbs (USDA–FS 1985). Engravers often attack host material in large numbers, producing pheromones only for a brief time. The same material would likely be ideal for oviposition and brood development by *M.*

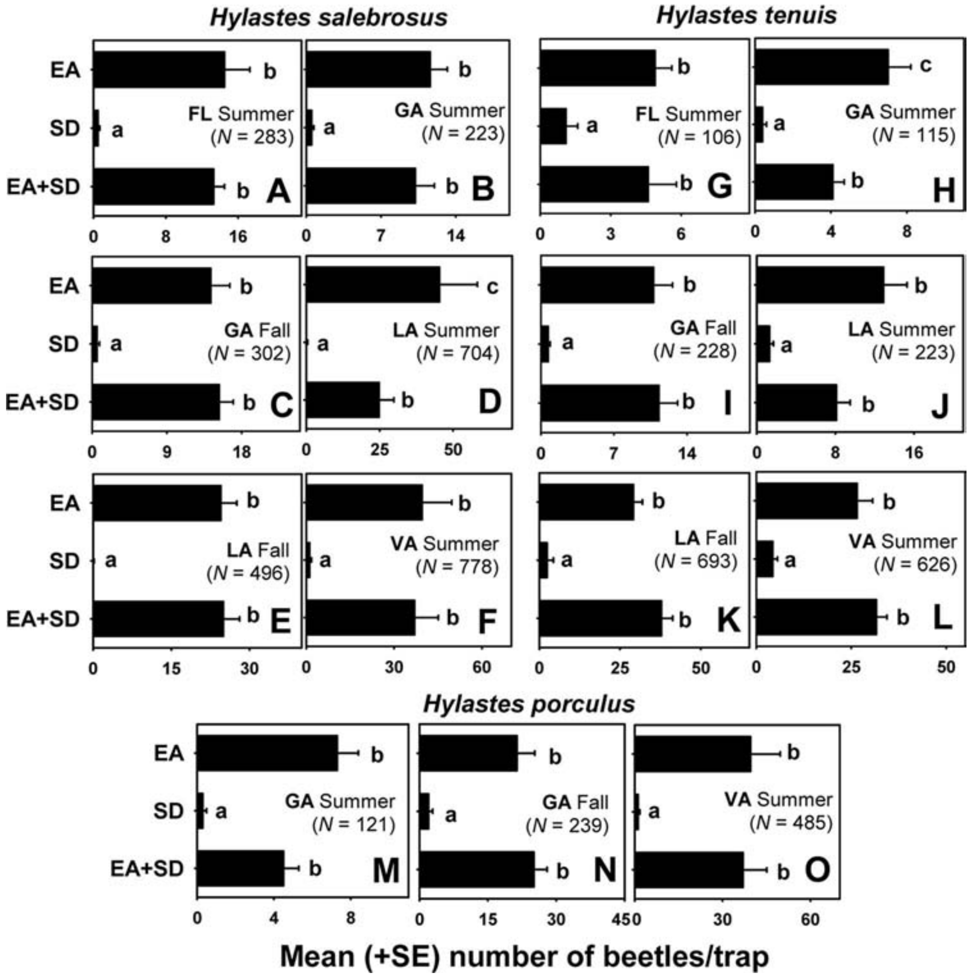

Fig. 5. Effects of ethanol + α-pinene (EA), ipsenol + ipsdienol (SD), and all four compounds (EA + SD) on trap catches of *H. salebrosus* (A–F), *H. tenuis* (G–L), and *H. porculus* (M–O) in the southeastern United States. Means followed by the same letter are not significantly different at $P = 0.05$ (Holm–Sidak test).

titillator complex, before further host deterioration. Sawyers might also benefit from breeding in material occupied by bark beetles. In a laboratory study, Dodds et al. (2001) found high mortality of larval bark beetles from attacks or ingestion by larval *M. carolinensis*, speculating that species of *Monochamus* may be facultative intraguild predators of bark beetles and associated species. Miller (1986) found that predation by larval *M. titillator* accounted for 50% of larval mortality of *I. calligraphus* in Louisiana. Similarly, foraging by larval *M. titillator* can have a significant impact on brood production by the southern pine beetle, *Dendroctonus frontalis* Zimmermann (Coulson et al. 1980).

Other pine longhorn species also exhibited a preference for the quaternary combination, probably in response to the same selection pressures as with *M. titillator* complex. We found that *M. scutellatus, A. obsoletus, R. inquisitor, A. arcuata,* and *A. sexguttata* preferred traps baited with the quaternary blend over those with either binary blend (Figs. 1G–M and 2A–E). The same was true for *A. nodosus* at one of two sites (Fig. 1O). All these species breed in pine trees (Lingafelter 2007).

Traps baited with compounds such as ethanol and α-pinene can be used to detect and monitor impacts of forest management practices and natural forest disturbances on the dynamics of a broad guild of saproxylic beetles (e.g., Hanula et al. 2002). Traps baited with ethanol are broadly attractive to many species of saproxylic beetles in pine stands in the southeastern United States (Miller 2006, Miller and Rabaglia 2009). The addition of α-pinene to traps baited with ethanol can significantly increase the diversity and abundance of saproxylic species (Miller 2006, Miller and Rabaglia 2009). A protocol with two separate trap–lure combinations is required to maximize diversity and abundance of beetles as the responses of some species to traps baited with ethanol can be interrupted by α-pinene (Miller and Rabaglia 2009).

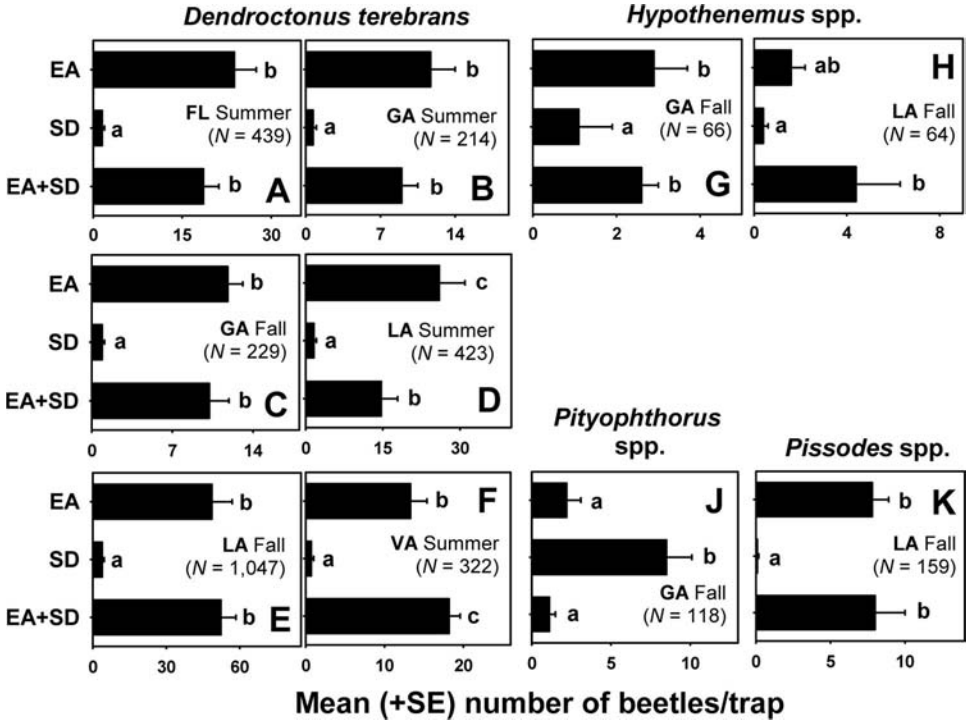

Fig. 6. Effects of ethanol + α-pinene (EA), ipsenol + ipsdienol (SD), and all four compounds (EA + SD) on trap catches of *D. terebrans* (A–F), *Hypothenemus* spp (G and H), *D. onoharaensis* (I), *Pityophthorus* spp (J), and *Pissodes* spp (K) in the southeastern United States. Means followed by the same letter are not significantly different at $P = 0.05$ (Holm–Sidak test).

Our results suggest that traps baited with the quaternary combination of ipsenol, ipsdienol, ethanol, and α-pinene could be substituted for those baited with ethanol and α-pinene as a broad-spectrum lure for saproxylic beetles in the southeastern United States. Catches of seven species of longhorn beetles, two species of flatheaded wood borers, four species of bark beetles, and one species of ambrosia beetles to traps baited with ethanol + α-pinene were increased with the addition of ipsenol + ipsdienol. Ipsenol + ipsdienol did not interrupt attraction of 15 species of longhorn beetles, click beetles, root-feeding weevils, and bark and ambrosia to traps baited with ethanol + α-pinene. To maximize catches of pine engravers such as *I. avulsus*, *I. grandicollis*, and *Pityophthorus* spp., a third trap would probably be required in a guild-targeted protocol as attraction of these species to ipsenol + ipsdienol was interrupted by the addition of ethanol + α-pinene. The addition of lanierone to a trap baited with ipsenol + ipsdienol would significantly enhance catches of *I. avulsus* without interrupting catches of *I. grandicollis* (Miller et al. 2005). Moreover, the tertiary blend of ipsenol, ipsdienol, and lanierone would be effective in detecting a third engraver species, *Ips pini* (Say), common in the Appalachian Mountain region of the southeastern United States. The interruptive effect of ipsenol on catches of *I. pini* to traps baited with ipsdienol is nullified by the addition of lanierone (Miller et al. 2005). A protocol using these three trap-lure combinations would provide considerable power in assessing population disturbances of a large number of saproxylic beetles in pine stands of the southeastern United States. The same protocol should be useful in other countries in their attempts to detect exotic species arising from the southeastern United States as well.

From an operational stand point, national programs geared toward detection of nonnative species need to minimize the number of trap/lure combinations to be cost-effective. There is some evidence that the quaternary blend would be effective in national programs such as CAPS and EDRR even though our tests were conducted in the southeastern United States. The combination of ethanol and α-pinene is attractive to many of the exotic ambrosia beetles in the United States (Miller and Rabaglia 2009). Many bark beetles in Europe and China use many of the same compounds, such as ipsenol and ipsdienol, as North American species (El-Sayed 2010). Traps baited with ethanol, α-pinene, and various bark beetle pheromones, including ipsenol and ipsdienol, are attractive to various ambrosia beetles in Italy, including *X. saxesenii* and *X. crassiusculus* (Francardi et al. 2009). In Italy, Francardi et al. (2009) found that the cerambycids *Arhopalus syriarus* (L.), *Acanthocinus griseus* (F.), and *M. gal-*

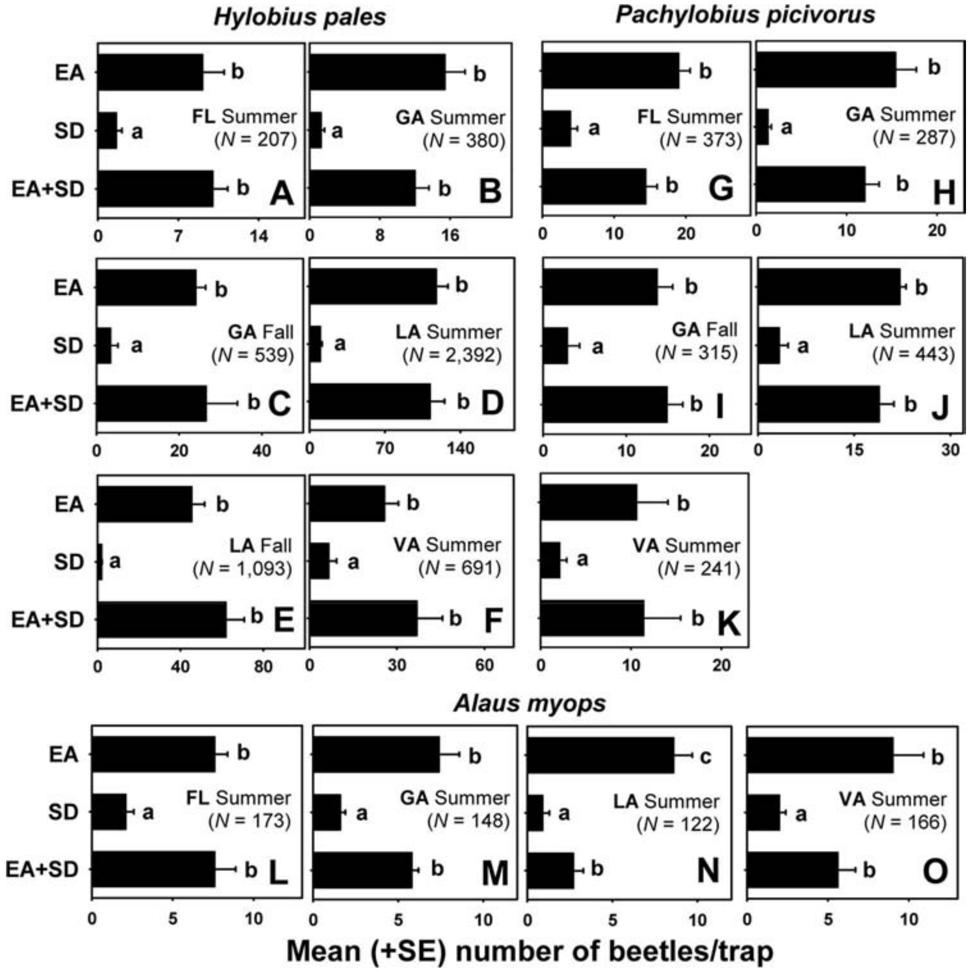

Fig. 7. Effects of ethanol + α-pinene (EA), ipsenol and ipsdienol (SD), and all four compounds (EA + SD) on trap catches of *H. pales* (A–F), *P. picivorus* (G–K). and *A. myops* (L–O) in the southeastern United States. Means followed by the same letter are not significantly different at $P = 0.05$ (Holm–Sidak test).

loprovincialis were attracted to traps baited with blends that included ipsenol and ipsdienol along with ethanol and α-pinene. Further trials are needed across North America as well as on other continents to verify that the addition of ipsenol + ipsdienol can improve the diversity and abundance of saproxylic beetles captured in traps baited with ethanol + α-pinene without interruption of targeted species.

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