Ethanol and (−)-α-Pinene: Attractant Kairomones for Bark and Ambrosia Beetles in the Southeastern US

Daniel R. Miller · Robert J. Rabaglia

Abstract In 2002–2004, we examined the flight responses of 49 species of native and exotic bark and ambrosia beetles (Coleoptera: Scolytidae and Platypodidae) to traps baited with ethanol and/or (−)-α-pinene in the southeastern US. Eight field trials were conducted in mature pine stands in Alabama, Florida, Georgia, North Carolina, and South Carolina. Funnel traps baited with ethanol lures (release rate, about 0.6 g/day at 25–28°C) were attractive to ten species of ambrosia beetles (*Ambrosiodmus tachygraphus*, *Anisandrus sayi*, *Dryoxylon onoharaensum*, *Monarthrum mali*, *Xyleborinus saxesenii*, *Xyleborus affinis*, *Xyleborus ferrugineus*, *Xylosandrus compactus*, *Xylosandrus crassiusculus*, and *Xylosandrus germanus*) and two species of bark beetles (*Cryptocarenus heveae* and *Hypothenemus* sp.). Traps baited with (−)-α-pinene lures (release rate, 2–6 g/day at 25–28°C) were attractive to five bark beetle species (*Dendroctonus terebrans*, *Hylastes porculus*, *Hylastes salebrosus*, *Hylastes tenuis*, and *Ips grandicollis*) and one platypodid ambrosia beetle species (*Myoplatypus flavicornis*). Ethanol enhanced responses of some species (*Xyleborus pubescens*, *H. porculus*, *H. salebrosus*, *H. tenuis*, and *Pityophthorus cariniceps*) to traps baited with (−)-α-pinene in some locations. (−)-α-Pinene interrupted the response of some ambrosia beetle species to traps baited with ethanol, but only the response of *D. onoharaensum* was interrupted consistently at most locations. Of 23 species of ambrosia beetles captured in our field trials, nine were exotic and accounted for 70–97% of total catches of ambrosia beetles. Our results provide support for the continued use of separate traps baited with ethanol alone and ethanol with (−)-α-pinene to detect and monitor common bark and ambrosia beetles from the southeastern region of the US.

Keywords *Dendroctonus* · Ethanol · Exotic species · Host attractant · *Hylastes* · *Hypothenemus* · *Ips* · Kairomone · *Myoplatypus* · α-Pinene · Platypodidae · Scolytidae · *Xyleborinus* · *Xyleborus* · *Xylosandrus*

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Introduction

Non-native bark and ambrosia beetles (Coleoptera: Scolytidae) are regularly introduced into countries via the movement of solid wood packing materials (pallets, crating, and dunnage) used in international shipments. In New Zealand, >73% of 1,505 interception records of 103 species of bark and ambrosia beetles during 1950–2000 were associated with solid wood packing material (Brockerhoff et al. 2006). Allen and Humble (2002) reared 1,549 beetles from 29 spruce bolts (*Picea abies* L.) used as dunnage to ship granite from Norway to Canada in 1998; 95% were Scolytidae. In the US, 73% of scolytid interceptions at ports of entry from 1985 to 2000 were associated with solid wood packing material (Haack 2001).

Detection and eradication of invading species are one of three strategies that are essential in countering impacts of invasive species in the forests of the US (Chornesky et al. 2005). Direct examination of shipments for the presence of bark and ambrosia beetles is problematic, as adult and larval beetles generally are hidden within bark or wood

tissues (Allen and Humble 2002). Early detection of species that have been missed by such examinations and have attempted to escape to neighboring forest habitats is essential to successful management or eradication (Chornesky et al. 2005). One common tactic used to detect bark and wood-boring beetles employs flight traps baited with lures releasing various semiochemicals, particularly ethanol and α-pinene (Haack 2006; Liu and Dai 2006; Lee et al. 2007). In the US, national programs such as the Cooperative Agricultural Pest Survey (CAPS) and the Early Detection and Rapid Response program (EDRR) employ funnel traps baited with lures releasing ethanol or ethanol and (−)-α-pinene to capture a broad array of subcortical beetles (USDA APHIS 2007; Rabaglia et al. 2008).

In Europe, ethanol is attractive to many species of bark and ambrosia beetles such as *Anisandrus* (*Xyleborus*) *dispar* (Fabricius), *Hylastes cunicularius* Erichson, *Hylastes brunneus* Erichson, *Hylastes opacus* Erichson, *Hylurgops palliatus* (Gyllenhal), *Hylesinus* (*Leperisinus) varius* (Fabricius), *Tomicus piniperda* L., and *Trypodendron lineatum* (Olivier) (Bauer and Vité 1975; Kohnle 1985; Schroeder 1988; Schroeder and Lindelöw 1989). In British Columbia, ethanol is attractive to *T. lineatum* (Moeck 1970) and acts in synergy with the pheromone of two other species of ambrosia beetles, *Gnathotrichus sulcatus* (LeConte) and *Gnathotrichus retusus* (LeConte) (Borden et al. 1980). Kelsey and Joseph (2001) found that the bark beetle *Scolytus unispinosus* LeConte was attracted to ethanol produced by stressed branches of Douglas fir, *Pseudotsuga menziesii* (Mirb.). In the US, ethanol is attractive to *A. dispar*, *Monarthrum mali* (Fitch), *Pseudopityophthorus minutissimus* (Zimmermann), and *Xyleborinus saxesenii* (Ratzeburg) (Montgomery and Wargo 1983; Dunn and Potter 1991).

Similarly, α-pinene, a monoterpene commonly found in pine trees (Mirov 1961; Smith 2000), is attractive to various species of bark beetles such as *Hylastes nigrinus* (Mannerheim), *Ips grandicollis* (Eichhoff), *Ips typographus* L., and *T. piniperda* (Rudinsky et al. 1971; Schroeder and Eidmann 1987; Witcosky et al. 1987; Schroeder 1988; Erbilgin and Raffa 2000). The combination of ethanol and α-pinene is attractive to bark and ambrosia beetles such as *Dendroctonus valens* LeConte, *Dryocoetes autographus* (Ratzeburg), *G. retusus*, *G. sulcatus*, *H. palliatus* (Gyll.), *Hylastes porculus* Erichson, *T. lineatum*, and *T. piniperda* (Borden et al. 1981; Schroeder 1988; Chénier and Philogène 1989; Schroeder and Lindelöw 1989; Erbilgin et al. 2001).

However, data on the attractiveness of such lures to bark and ambrosia beetles are limited to a small portion of known species (<1% of nearly 6,000 species; Seybold et al. 2006). Specifically lacking are response data for species common to the southeastern US. Attraction of *I. grandicollis* to small loblolly pine logs in the southeastern US was enhanced with the application of pinenes and turpentine directly onto the bark (Anderson 1977). In the northern portion of its range (Wisconsin and southern Ontario), monoterpenes including α-pinene affected trap captures of *I. grandicollis* (Chénier and Philogène 1989; Erbilgin and Raffa 2000). In Florida, the combination of ethanol and turpentine was attractive to *Dendroctonus terebrans* (Olivier), *Hylastes salebrosus* Eichhoff, and *Xyleborus pubescens* Zimmermann, whereas *Xyleborus affinis* Wood was attracted to ethanol but not turpentine (Fatzinger 1985; Fatzinger et al. 1987; Phillips et al. 1988; Phillips 1990). The use of turpentine in these studies is a concern, as the monoterpene composition of turpentine can vary widely depending on species and location of conifers used in production (Mirov 1961; Smith 2000). The main constituent of the turpentine used in at least one of the Florida studies was α-pinene (Phillips et al. 1988).

A second concern is that α-pinene may interrupt attraction of some ambrosia beetles to ethanol. In southwestern British Columbia (Canada), α-pinene seems to interrupt catches of *A. dispar*, *X. saxesenii*, *Xyleborinus alni* (Niisima), *Xyleborus pfeili* (Ratzeburg), and *Xylosandrus germanus* (Blandford) (L. Humble, unpublished data). Schroeder and Lindelöw (1989) found that α-pinene interrupted catches of *A. dispar* to ethanol-baited traps in Sweden. In Europe, Lindelöw et al. (1993) found that α-pinene interrupted the attraction of *H. cunicularius*, *H. opacus*, and *D. autographus* to a blend of ethanol and turpentine. For this reason, most operational detection programs for ambrosia beetles use traps baited solely with ethanol in addition to traps baited with ethanol and α-pinene or α-pinene alone to avoid the risk of species evading detection.

Our objective was to assess the attraction of bark and ambrosia beetles (common to pine forests of the southeastern US) to standard commercially available ethanol and (−)-α-pinene lures used with funnel traps. We wanted to determine: (1) the species that are attracted to traps baited with these compounds in southern pine forests and (2) if traps baited with the combination of the two lures were as effective as, if not better than, traps baited solely with one lure. We monitored the responses of 49 species of common bark and ambrosia beetles to traps baited with ethanol and/or (−)-α-pinene in southeastern US (Tables 1 and 2). Our data on Buprestidae, Cerambycidae, Curculionidae, and Elateridae were published previously (Miller 2006). Our goal is to provide operational guidelines for the use of semiochemical-based trapping systems in monitoring populations of beetles in the southeastern US, as well as in suppression and detection programs in countries where these species may not be native.

Methods and Materials

Experimental Design Methods and materials were reported previously in Miller (2006). The same experimental design

Table 1 National forest (NF) and experimental forest (EF) locations, forest types, and trapping dates for experiments (2002–2004) in the southeastern US

Expt.	Location	Tree species	Trapping dates
1	Ocala NF near Salt Springs, FL	*P. palustris* Miller	26 February–26 May 2002
2	Osceola NF near Lake City, FL	*P. palustris* and *P. elliottii* Engelmann	25 February–25 May 2002
3	Oconee NF near Juliette, GA	*P. taeda* L.	12 June–8 August 2002
4	Blue Valley EF near Highlands, NC	*P. strobus* L.	20 June–20 August 2002
5	Bankhead NF near Grayson, AL	*P. taeda* and *T. canadensis* (L.)	28 April–10 July 2003
6	Nantahala NF near Murphy, NC	*P. strobus* and *P. echinata* Miller	1 May–14 August 2003
7	Sumter NF near Union, SC	*P. taeda*	15 April–16 July 2003
8	Apalachicola NF near Tallahassee, FL	*P. palustris* and *P. elliottii*	30 March–16 June 2004

was employed in mature pine stands on each of seven National Forests (NF) and one Experimental Forest (EF) in the southeastern US, resulting in eight experiments (Table 1). In each experiment, four treatments were randomly assigned to four eight-unit funnel traps [Phero Tech (now Contech) Inc., Delta, British Columbia, Canada] within each of eight replicate blocks ($N=8$) as follows: (1) unbaited control; (2) ethanol alone; (3) α-pinene alone; and (4) ethanol (+)-α-pinene. Traps were spaced 10–15 m apart within blocks; replicate blocks were spaced 15–500 m apart. Phero Tech Inc. supplied sealed ultra-high-release (UHR) plastic pouches containing either ethanol (150 ml) or α-pinene (200 ml; chemical purities >95%). The enantiomeric purity of α-pinene was >95%-(−). The release rate of ethanol from its UHR pouch was 0.6 g/day at 25–28°C (determined by weight loss). (−)-α-Pinene was released at 2–6 g/day from its UHR pouch at 25–28°C (determined by weight loss). Each trap was suspended between trees by rope such that the bottom of the 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, USA) as a killing and preservation agent. Voucher specimens were deposited in the Entomology Collection, Museum of Natural History, University of Georgia (Athens, GA, USA).

Statistical Analyses Trap catch data were analyzed with the SYSTAT (ver. 11.00.01) and the SigmaStat (ver. 3.01) statistical packages (SYSTAT Software Inc., Point Richmond, CA, USA) for locations where sufficient numbers ($N\geq50$) were captured for individual species. Trap catch data were transformed by $\ln(Y+1)$ to remove heteroscedasticity (Pepper et al. 1997). In each experiment, trap catch data were subjected to analysis of variance (ANOVA) by using the following model components: (1) replicate; (2) ethanol; (3) α-pinene; and (4) ethanol × α-pinene. In cases with one treatment lacking variation (due to lack of any beetle captures), the data were subjected to ANOVA by using the

following model components: (1) replicate and (2) treatment. In all experiments with three to four non-zero treatment means, the Holm–Sidak multiple-comparison procedure (Glantz 2005) was used to compare means within a location for each species when there was a significant treatment effect ($\alpha=0.05$). In cases with two treatments lacking variation (due to lack of any beetle captures), the means of catches associated with the two remaining treatments were analyzed by two-tailed *t* tests.

Results

Ambrosia Beetles A total of 28,521 ambrosia beetles were captured from all eight locations in 2002–2004, ranging from 972 to 10,683 per location (Table 2). Of 23 species captured in our trapping studies, nine are established non-native exotic species and accounted for 69.7–96.6% of total ambrosia beetle catches. The most common non-native species were *X. saxesenii*, *Xylosandrus crassiusculus* (Motschulsky), and *Dryoxylon onoharaensum* (Murayama), whereas the most common native species were *X. affinis*, *Xyleborus ferrugineus* (Fabricius), and *X. pubescens*. Generally, ethanol had an attractive effect on most ambrosia beetles with (−)-α-pinene playing a minor role (Table 3).

The exotic ambrosia beetle *X. saxesenii* was captured at all eight locations with a total catch of 13,671 (accounting for 48% of total ambrosia beetle catches; Fig. 1). Ethanol had a significant effect on trap catches of *X. saxesenii* (Table 3). At all locations, traps baited with ethanol [with or without the addition of (−)-α-pinene] caught more *X. saxesenii* than unbaited control traps. At most locations, (−)-α-pinene had no effect on catches of *X. saxesenii* (Table 3). However, catches of *X. saxesenii* in traps baited with ethanol were interrupted by (−)-α-pinene in Florida (Ocala NF) and North Carolina (Nantahala NF; Fig. 1e, f).

Catches of the exotic ambrosia beetles *Xylosandrus compactus* (Eichhoff), *X. crassiusculus*, and *X. germanus*

Table 2 Total catches of ambrosia and bark beetles at eight experimental sites in the southeastern US

Species	Experiment and state							
	1 FL	2 FL	3 GA	4 NC	5 AL	6 NC	7 SC	8 FL
Ambrosia beetles								
Ambrosiodmus lecontei Hopkins	7	11						18
Ambrosiodmus obliquus (LeConte)	28	44	2		17	13	12	25
Ambrosiodmus rubricollis (Eichhoff)[a]		1	9		9		13	2
Ambrosiodmus tachygraphus Zimmermann				1	1	57		
Anisandrus (Xyleborus) sayi (Hopkins)				26	9	103		
Corthylus columbianus Hopkins		4						1
Corthylus papulans Eichhoff	2	14						
Dryoxylon onoharaensum (Murayama)[a]	199	1,883	208	48	32	167	528	3,506
Euplatypus compositus (Say)	4	1						
Euwallacea validus (Eichhoff)[a]			30		10			
Gnathotrichus materiarus (Fitch)	2		2	14		70	12	
Monarthrum fasciatum (Say)	76	12	2			2		
Monarthrum mali (Fitch)	36	9	15	50	10	15	2	2
Myoplatypus flavicornis (Fabricius)	2	5			28	20	65	
Premnobius cavipennis Eichhoff[a]	1							
Xyleborinus saxesenii (Ratzeburg)[a]	1,020	3,297	328	2,492	417	994	889	4,234
Xyleborus affinis Eichhoff	57	359	15	3			6	187
Xyleborus atratus Eichhoff[a]		3	3	15	16	34	2	14
Xyleborus ferrugineus (Fabricius)	17	110	52	93	122	9	12	135
Xyleborus pubescens Zimmermann	178	645	3	4	24	333	187	
Xylosandrus compactus (Eichhoff)[a]	4	5	4		43	1		344
Xylosandrus crassiusculus (Motschulsky)[a]	7	125	298		1,286	212	7	2,215
Xylosandrus germanus (Blandford)[a]			1	149	3	21		
Total	1,640	6,528	972	2,895	2,017	2,051	1,735	10,683
Bark beetles								
Carphoborus bicornis Wood	1				1			
Cnesinus strigicollis LeConte	2	2	26	3		2		5
Conophthorus coniperda (Schwarz)				1				
Cryptocarenus heveae (Hagedorn)	282		1					
Crypturgus alutaceus Schwarz	1						1	
Dendroctonus frontalis Zimmermann	2				4		4	
Dendroctonus terebrans (Olivier)	730	757	389	30	2	131	153	424
Hylastes porculus Erichson			225	453	185	399	157	
Hylastes salebrosus Eichhoff	196	194	71	28	208	43	907	326
Hylastes tenuis Eichhoff	4	38	274	233	75	805	773	84
Hylurgops rugipennis pinifex (Fitch)						1		
Hypothenemus Westwood sp.	16	36	23	3	81	16	9	20
Ips avulsus (Eichhoff)	4	23				1		
Ips calligraphus (Germar)							4	
Ips grandicollis (Eichhoff)	1,033	1,846	444	282	151	234	425	1,418
Micracisella nanula (LeConte)		1	1					
Orthotomicus caelatus (Eichhoff)	21	13	5	6	2	12	40	10
Phloeosinus taxodii taxodii Blackman							2	
Phloeotribus liminaris (Harris)					4			
Pityophthorus cariniceps LeConte				50				

Table 2 (continued)

Species	Experiment and state							
	1 FL	2 FL	3 GA	4 NC	5 AL	6 NC	7 SC	8 FL
Pityophthorus confusus bellus Blackman						5	4	
Pityophthorus consimilis LeConte						2		
Pityophthorus lautus Eichhoff			2			6		
Pityophthorus pulicarius (Zimmermann)	4	1						
Pseudopityophthorus pruinosus (Eichhoff)		3						
Scolytus multistriatus (Marsham)[a]			6					
Total	2,296	2,914	1,467	1,089	713	1,657	2,479	2,287
Grand total	3,936	9,442	2,439	3,984	2,730	3,708	4,214	12,970

All species are Scolytidae (Coleoptera) except *Euplatypus compositus* and *M. flavicornis*, which are in the Platypodidae

[a] Exotic species

totaled 4,725 beetles (17% of total ambrosia beetle catches) with *X. crassiusculus* being the most common (Fig. 2). Ethanol had a significant effect on trap catches of all three species (Table 3). In five locations, catches of *X. crassiusculus* in traps baited with ethanol [with or without the addition of (−)-α-pinene] were greater than those in unbaited control traps (Fig. 2a–e). The same was true for *X. compactus* in Florida (Apalachicola NF; Fig. 2f) and *X. germanus* in North Carolina (Blue Valley EF; Fig. 2g). There was no effect of (−)-α-pinene on any of these three species (Table 3, Fig. 2).

An interruptive effect of (−)-α-pinene on the attraction of ambrosia beetles to ethanol-baited traps was apparent with two native species, *Ambrosiodmus tachygraphus* Zimmermann, *Anisandrus* (*Xyleborus*) *sayi* (Hopkins), and an exotic species, *D. onoharaensum* (Table 3, Fig. 3). All three species were attracted to traps baited with ethanol. In North Carolina (Nantahala NF), catches of *A. tachygraphus* in traps baited with ethanol alone were significantly greater than those in unbaited controls, whereas catches in traps baited with ethanol and (−)-α-pinene were not different from those in control traps (Fig. 3a). No beetles were captured in traps baited solely with (−)-α-pinene. In North Carolina (Nantahala NF), catches of *A. sayi* in traps baited with ethanol and (−)-α-pinene were significantly less than those in traps baited solely with ethanol (Fig. 3b). No beetles were caught in control traps or traps baited solely with (−)-α-pinene. In five of six locations, catches of *D. onoharaensum* in traps baited with ethanol and (−)-α-pinene were significantly less than those in traps baited solely with ethanol (Fig. 3c, e–h). We caught a total of 6,571 *D. onoharaensum* across the six locations (23% of total ambrosia beetle catches; Fig. 3c–h).

Lastly, ethanol and (−)-α-pinene significantly affected catches of five common native species of ambrosia beetles (Table 3, Figs. 4 and 5), although results were inconsistent between locations. Catches of *X. affinis*, *X. pubescens*, and *X. ferrugineus* totaled 2,458 beetles (9% of total ambrosia beetle catches). Traps baited with ethanol were attractive to *X. affinis* and *X. ferrugineus* in three and five locations, respectively (Figs. 4a–c and 5a–e), whereas *X. pubescens* were attracted to ethanol-baited traps in only one of four locations (Fig. 4g). Traps baited with (−)-α-pinene alone were attractive to *X. pubescens* in Florida (Osceola NF) with (−)-α-pinene enhancing catches of beetles in ethanol-baited traps (Fig. 4f). *X. ferrugineus* were attracted to traps baited with (−)-α-pinene in two locations in Florida (Fig. 5b, c) but interrupted by (−)-α-pinene in Alabama (Fig. 5a). (−)-α-Pinene had no effect on *X. affinis* at four locations (Fig. 4a–c). *M. mali* was attracted to traps baited with ethanol (Fig. 5f), whereas the platypodid *Myoplatypus flavicornis* (Fabricius) was attracted to traps baited with (−)-α-pinene (Fig. 5g). As with the other species for which numbers were too low for analyses ($N<50$) at some locations (Table 2), the low numbers of *M. mali* or *M. flavicornis* in traps at the other locations may have been a consequence of low population numbers or a lack of attraction at these localities.

Bark Beetles A total of 14,902 bark beetles were captured from all eight locations in 2002–2004, ranging from 713 to 2,914 per location (Table 2). Of 26 species captured in our trapping studies, only *Scolytus multistriatus* (Marsham) is a non-native species. The most common bark beetles were *D. terebrans*, *H. porculus*, *H. salebrosus*, *Hylastes tenuis* Eichhoff, and *I. grandicollis*. In contrast to ambrosia beetles, (−)-α-pinene had an effect on most bark beetle species with ethanol playing a minor role (Table 4). *Cryptocarenus heveae* (Hagedorn) and a *Hypothenemus* Westwood sp. were the only two species of bark beetles that

Table 3 Significance levels for ANOVAs on effects of ethanol and (−)-α-pinene on ambrosia beetle trap catches in the southeastern US

Species	Location	Rep	Ethanol (E)	α-Pinene (A)	E×A
Dryoxylon onoharaensum	FL—Apalachicola NF	0.033	<0.001	0.001	0.070
	FL—Ocala NF	0.990	<0.001	0.012	0.023
	FL—Osceola NF	0.033	<0.001	0.106	0.063
	GA—Oconee NF	0.277	<0.001	0.171	0.171
	NC—Nantahala NF	0.093	<0.001	0.006	0.015
	SC—Sumter NF	0.984	<0.001	0.002	0.110
Gnathotrichus materiarus	NC—Nantahala NF	<0.001	0.852	0.078	0.993
Monarthrum fasciatum	FL—Ocala NF	0.115	0.384	0.384	0.354
Myoplatypus flavicornis	SC—Sumter NF	0.315	0.660	<0.001	0.233
Xyleborinus saxesenii	AL—Bankhead NF	0.021	<0.001	0.413	0.366
	FL—Apalachicola NF	0.009	<0.001	<0.001	0.006
	FL—Ocala NF	0.179	<0.001	0.299	0.002
	FL—Osceola NF	0.435	<0.001	0.528	0.291
	GA—Oconee NF	0.051	<0.001	0.171	0.287
	NC—Blue Valley EF	0.306	<0.001	0.517	0.668
	NC—Nantahala NF	0.051	<0.001	0.140	0.027
	SC—Sumter NF	0.322	<0.001	0.247	0.356
Xyleborus affinis	FL—Apalachicola NF	0.423	<0.001	0.002	0.527
	FL—Ocala NF	0.531	<0.001	0.723	0.822
	FL—Osceola NF	0.307	<0.001	0.955	0.119
Xyleborus ferrugineus	AL—Bankhead NF	0.019	<0.001	<0.001	0.554
	FL—Apalachicola NF	0.253	<0.001	0.517	0.004
	FL—Osceola NF	0.079	0.166	<0.001	0.008
	GA—Oconee NF	0.060	<0.001	0.761	0.853
	NC—Blue Valley EF	0.381	<0.001	0.177	0.310
Xyleborus pubescens	FL—Ocala NF	0.230	0.282	0.002	0.144
	FL—Osceola NF	0.083	0.005	<0.001	0.278
	NC—Nantahala NF	0.001	0.102	0.968	0.070
	SC—Sumter NF	0.064	<0.001	0.053	0.933
Xylosandrus compactus	FL—Apalachicola NF	0.901	<0.001	0.317	0.317
Xylosandrus crassiusculus	AL—Bankhead NF	0.005	<0.001	0.557	0.286
	FL—Apalachicola NF	0.354	<0.001	0.488	0.590
	FL—Osceola NF	0.034	<0.001	0.532	0.532
	GA—Oconee NF	0.659	<0.001	0.744	0.637
	NC—Nantahala NF	0.519	<0.001	0.548	0.309
Xylosandrus germanus	NC—Blue Valley EF	<0.001	<0.001	0.236	0.125

were attracted to ethanol-baited traps with no effect from (−)-α-pinene (Fig. 6a, b).

A total of 2,616 black turpentine beetles *D. terebrans* were captured across six locations (18% of total bark beetle catches; Fig. 6c–h). Catches of *D. terebrans* were significantly affected by (−)-α-pinene with little, if any, effect of ethanol (Table 4). At all locations, traps baited with (−)-α-pinene (with or without the addition of ethanol) caught more *D. terebrans* than unbaited control traps. However, in Florida (Ocala NF), catches of *D. terebrans* in traps baited with (−)-α-pinene were enhanced by the addition of ethanol (Fig. 6e); there was no effect of ethanol at the other locations (Fig. 6a–d, f).

The eastern five-spined ips, *I. grandicollis*, was captured at all eight locations with a total catch of 5,833 beetles (39% of total bark beetle catches; Fig. 7). As with *D. terebrans*, catches of *I. grandicollis* were significantly affected by (−)-α-pinene at all locations with inconsistent effects of ethanol among locations (Table 4). At all locations, traps baited with (−)-α-pinene (with or without the addition of ethanol) caught more *I. grandicollis* than blank control traps. The addition of ethanol to traps baited with (−)-α-pinene enhanced catches of *I. grandicollis* in Alabama (Fig. 7a) but interrupted catches in Florida (Ocala NF; Fig. 7e). There was no effect of ethanol at the other locations (Fig. 7b–d, f, g).
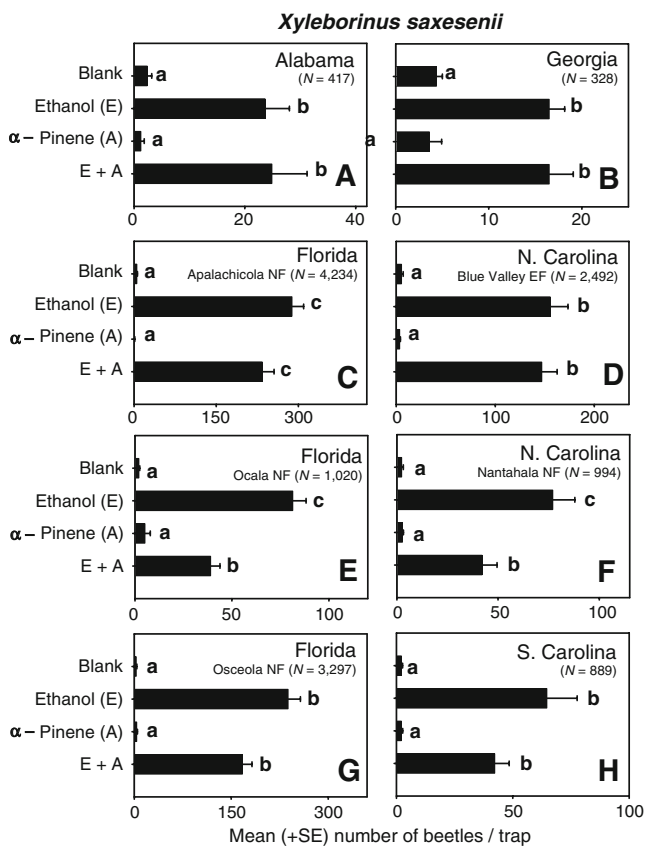
Fig. 1 a–h Effects of ethanol and (−)-α-pinene on trap catches of *X. saxesenii* (Scolytidae) in the southeastern US. Means followed by the same *letter* are not significantly different (α=0.05, Holm–Sidak multiple comparison)

(Fig. 10a–c, f). In South Carolina, traps baited with ethanol were more attractive than control traps (Fig. 10f). Similarly, catches of *Pityophthorus cariniceps* LeConte were highest in traps baited with ethanol and (−)-α-pinene (Fig. 10g).

Discussion

In addressing our first objective, we found that traps baited with ethanol and/or (−)-α-pinene were attractive to 20 species of common bark and ambrosia beetles in the southeastern US, including five exotic species of ambrosia beetles. In southern pine forests, traps baited with (−)-α-pinene were attractive to the bark beetles, *D. terebrans*, *I. grandicollis*, *H. tenuis*, *H. porculus*, and *H. salebrosus* (Figs. 6, 7, 8, 9, and 10) and the platypodid ambrosia beetle *M. flavicornis* (Fig. 5g). In some locations, traps baited with (−)-α-pinene were attractive to the ambrosia beetles, *X. ferrugineus* (Fig. 5b, c) and *X. pubescens* (Fig. 4f).

Our results with *D. terebrans* are consistent with previous tests that employed turpentine (Fatzinger et al.

Catches of *H. porculus*, *H. salebrosus*, and *H. tenuis* totaled 5,678 (38% of total bark beetle catches) with *H. tenuis* the most common (Figs. 8, 9, and 10a–f). (−)-α-Pinene had a significant effect on all three species (Table 4). At all locations, traps baited with (−)-α-pinene (with or without the addition of ethanol) caught more *H. porculus* and *H. tenuis* than blank control traps (Figs. 8 and 9). The effect of ethanol on catches of *H. porculus* and *H. tenuis* was inconsistent among locations (Table 4). Ethanol enhanced catches of *H. tenuis* to traps baited with (−)-α-pinene in Florida (Apalachicola NF; Fig. 8c) but not at the other five locations (Fig. 8a, b, d–f). Similarly, catches of *H. porculus* in traps baited with (−)-α-pinene were enhanced by the addition of ethanol in Georgia and North Carolina (Blue Valley EF; Fig. 9c, e) but not at the other three locations (Fig. 9a, b, d).

The effects of ethanol and (−)-α-pinene on catches of *H. salebrosus* were fairly consistent among six locations (Table 4). At all six locations, catches of *H. salebrosus* were highest in traps baited with both ethanol and (−)-α-pinene (Fig. 10). At four of six locations, traps baited with (−)-α-pinene caught more *H. salebrosus* than control traps

Fig. 2 Effects of ethanol and (−)-α-pinene on trap catches of *X. crassiusculus* (**a–e**), *X. compactus* (**f**), and *X. germanus* (**g**; Scolytidae) in the southeastern US. Means followed by the same *letter* are not significantly different (α=0.05, Holm–Sidak multiple comparison)
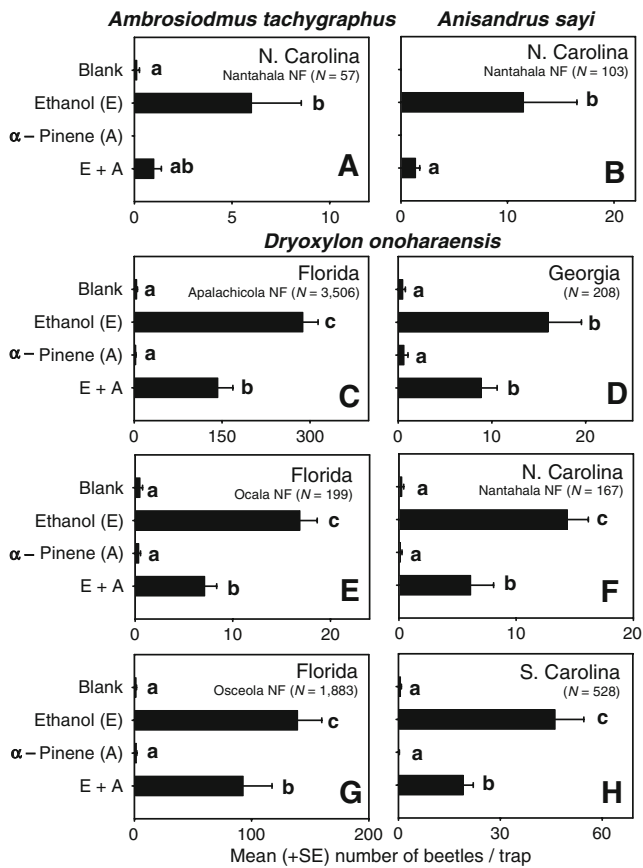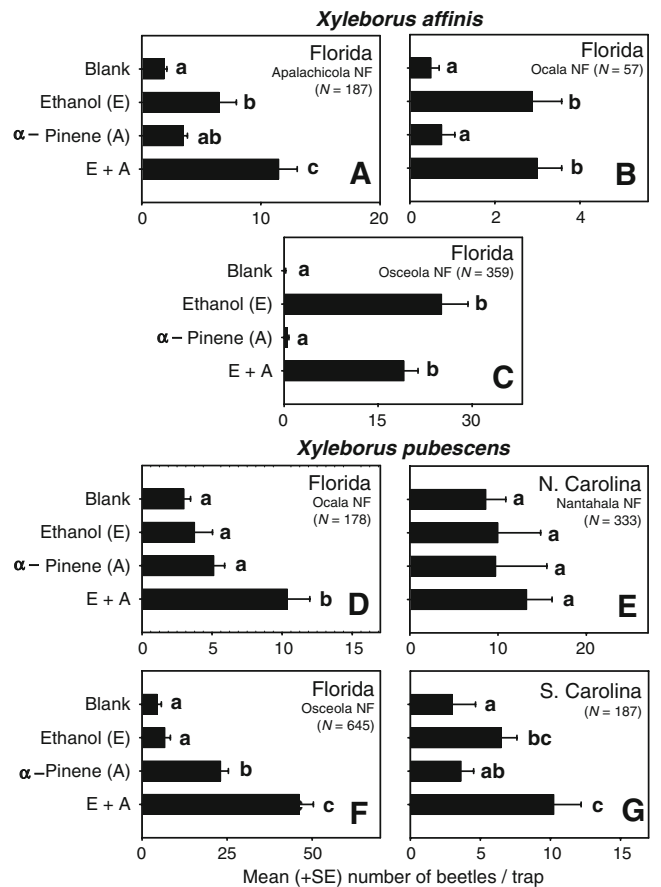
Fig. 3 Effects of ethanol and (−)-α-pinene on trap catches of *A. tachygraphus* (**a**), *A. sayi* (**b**), and *D. onoharaensum* (**c**–**h**; Scolytidae) in the southeastern US. Means followed by the same *letter* are not significantly different (α=0.05, Holm–Sidak multiple comparison) for three to four treatments (**a** and **c**–**h**) or by *t* test for two treatments (**b**). Treatments without a *letter* had zero catches

1987; Phillips et al. 1988). We specifically identify (−)-α-pinene as one of the active components for *D. terebrans*. Previously, Anderson (1977) found that α-pinene, technical pinene, and turpentine increased the attractiveness of loblolly pine logs to *I. grandicollis*. In Ontario, Chénier and Philogène (1989) captured more *I. grandicollis* in traps baited with lures that included α-pinene (total catch was only 25 beetles over six treatments). In Wisconsin, Erbilgin and Raffa (2000) found that *I. grandicollis* were attracted to traps baited with (−)-α-pinene. We know of no prior data on the specific attraction of *H. tenuis*, *H. porculus*, *H. salebrosus*, *X. ferrugineus*, and *X. pubescens* to α-pinene.

Attraction of bark beetles to monoterpenes is a fairly common phenomenon, especially in combination with pheromones (Seybold et al. 2006). Monoterpenes are common constituents of the air within forested stands, changing constantly due to various environmental and anthropogenic factors (Seybold et al. 2006). Compounds such as α-pinene are abundant in the resin of coniferous trees, particularly pine species (Smith 2000), providing

important defenses against invasion by insects and diseases (Franceschi et al. 2005; Seybold et al. 2006). Leakage of monoterpenes into the environment around trees may occur through the outer bark and foliage of healthy trees, perhaps increasingly so from physically damaged trees or from trees weakened by factors such as drought or disease, which may indicate suitable breeding opportunities for bark and ambrosia beetles (Byers 1989; Franceschi et al. 2005; Raffa et al. 2005; Seybold et al. 2006). In addition, trees under attack by bark beetles release monoterpenes through the flow of resin and from the frass produced by boring beetles, thereby providing further attractiveness to other beetles (Seybold et al. 2006).

There are hundreds of volatile compounds in tree resins, and it is likely that bark beetles are attracted to monoterpenes other than α-pinene within this "dynamic aerial sea of monoterpenes" (Seybold et al. 2006). In felled loblolly pine, α-pinene is the dominant monoterpene in tree resin with four additional monoterpenes (myrcene, camphene, limonene, and β-pinene) present at levels of >5%

Fig. 4 Effects of ethanol and (−)-α-pinene on trap catches of *X. affinis* (**a**–**c**) and *X. pubescens* (**d**–**g**; Scolytidae) in the southeastern US. Means followed by the same *letter* are not significantly different (α=0.05, Holm–Sidak multiple comparison)
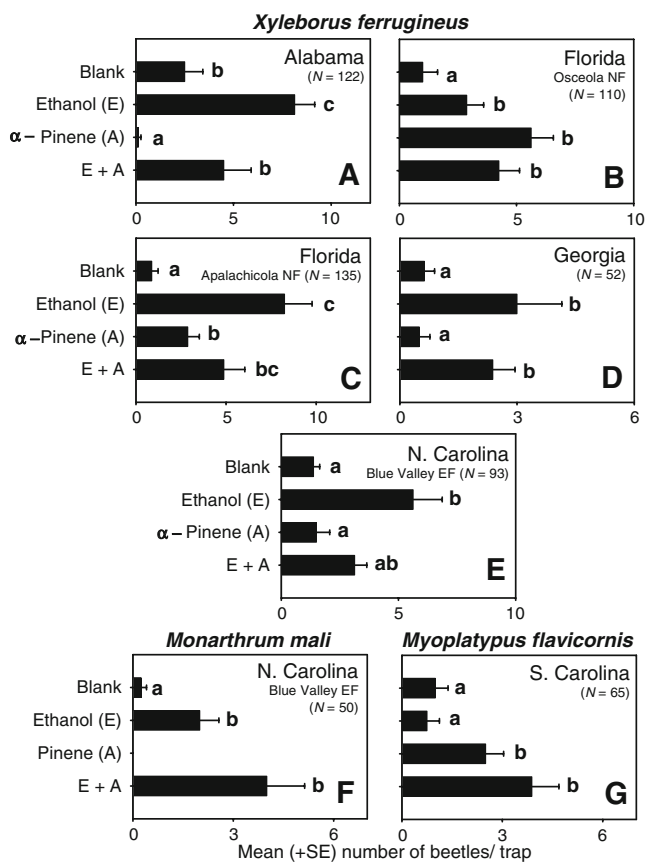
Fig. 5 Effects of ethanol and (−)-α-pinene on trap catches of *X. ferrugineus* (**a**–**e**), *M. mali* (**f**; Scolytidae), and *M. flavicornis* (**g**; Platypodidae) in the southeastern US. Means followed by the same *letter* are not significantly different (α=0.05, Holm–Sidak multiple comparison) for three to four treatments. Treatments without a *letter* had zero catches

(Werner 1972). In addition to α-pinene, *I. grandicollis* responded to myrcene, camphene, and limonene in walking bioassays (Werner 1972).

The issue of enantiomeric composition of α-pinene may be important as well (Seybold et al. 2006). We used (−)-α-pinene in our studies. Enantiomeric composition of α-pinene in pine trees can vary widely among pine species (Mirov 1961), although the relationship between enantiomeric composition and bark beetle responses may not be clear (Seybold et al. 2006). In California, Hobson et al. (1993) found that (+)-α-pinene was attractive to *D. valens* with attraction to (+)-α-pinene interrupted by (−)-α-pinene. (+)-α-Pinene is predominant in species such as *Pinus flexilis* James, *Pinus lambertiana* Dougl., and *Pinus resinosa* Ait., whereas (−)-α-pinene is the most common enantiomer in species such as *Pinus monticola* Dougl., *Pinus coulteri* D. Don, and *Pinus contorta* Dougl. ex Loud. (Mirov 1961), all of which occur within the range of *D. valens* and can be used as host material by *D. valens* (Furniss and Carolin 1977).

In another finding relevant to our first objective, traps baited with ethanol were attractive to the ambrosia beetles, *A. tachygraphus*, *A. sayi*, *D. onoharaensum*, *M. mali*, *X. saxesenii*, *X. affinis*, *X. ferrugineus*, *X. pubescens*, *X. crassiusculus*, *X. compactus*, and *X. germanus* (Figs. 1, 2, 3, 4, and 5), and the bark beetles, *C. heveae* and *Hypothenemus* sp. (Fig. 6a, b). Previously, Klimetzek et al. (1986) found that *X. saxesenii* was attracted to ethanol released at rates >1 mg/h whereas Phillips et al. (1988) found that *X. affinis*, but not *X. pubescens*, were attracted to traps baited solely with ethanol. Montgomery and Wargo (1983) state that ethanol was attractive to *M. mali* and *X. saxesenii* in oak forests in Connecticut (USA), although data were not presented. In southern California, *X. saxesenii* is attracted to ethanol-baited traps (Flint et al. 2007).

We know of no other prior data on the ethanol-based attraction of the ambrosia beetle species caught in our study. Yet, ethanol-baited traps are commonly (and successfully) used to assess temporal and spatial patterns of ambrosia beetles as well as in detection programs like CAPS and EDRR. For example, Roling and Kearby (1975) used ethanol-baited window traps to successfully monitor the seasonal flight patterns of *A. sayi*, *M. mali*, *X. saxesenii*, and *X. ferrugineus* in stands of oak in Missouri (US). Although no data are presented, they noted that previous attempts without ethanol were unsuccessful. Similarly, Markalas and Kalapanida (1997) used ethanol-baited traps to monitor flight periods of *X. saxesenii* in an oak forest in Greece. Ethanol-baited traps are used to monitor the flight activity of ambrosia beetles such *X. saxesenii*, *X. crassiusculus*, and *X. germanus* in horticultural tree nurseries prior to initiating an insecticide control program (Oliver and Mannion 2001; Bambara et al. 2008). Coyle et al. (2005) used ethanol-baited funnel traps to monitor flight activity of 28 species of bark and ambrosia beetles in stands of cottonwoods in South Carolina. Our data simply add evidential weight to the experiences of professionals in support of ethanol-baited traps for ambrosia beetles.

The attraction of ambrosia beetles to ethanol is likely related to their preference for woody material that has aged for a sufficient period of time for anaerobic respiration to generate ethanol within the tissues (Graham 1968; Cade et al. 1970; Moeck 1970; Lindelöw et al. 1993). Kelsey (1994) found that the ambrosia beetles *G. retusus* and *T. lineatum* preferred Douglas fir logs, *P. menziesii* (Mirb.) Franco, that had been felled in November of the previous year over logs that had been felled in January or March of the current year; ethanol concentrations were highest in logs felled in November of the previous year.

Hypoxia conditions arising in stressed trees also can lead to the production of ethanol and subsequent attack by bark and ambrosia beetles. Gara et al. (1993) found that lodgepole pines infected with heartwood decay fungi

Table 4 Significance levels for ANOVAs on effects of ethanol and (−)-α-pinene on bark beetle trap catches in the southeastern US

Species	Location	Rep	Ethanol (E)	α-Pinene (A)	ExA
Cryptocarenus heveae	FL—Ocala NF	0.810	<0.001	0.567	0.455
Dendroctonus terebrans	FL—Apalachicola NF	0.993	0.826	<0.001	0.826
	FL—Ocala NF	0.362	0.027	<0.001	0.216
	FL—Osceola NF	0.896	0.131	<0.001	0.956
	GA—Oconee NF	0.806	0.596	<0.001	0.831
	SC—Sumter NF	0.437	0.402	<0.001	0.085
Hylastes porculus	AL—Bankhead NF	0.006	0.008	<0.001	0.502
	GA—Oconee NF	0.091	<0.001	<0.001	0.008
	NC—Blue Valley EF	0.589	0.006	<0.001	0.002
	NC—Nantahala NF	0.147	0.189	<0.001	0.477
	SC—Sumter NF	0.678	0.440	<0.001	0.445
Hylastes salebrosus	AL—Bankhead NF	0.004	0.014	<0.001	0.463
	FL—Apalachicola NF	0.086	<0.001	<0.001	<0.001
	FL—Ocala NF	0.523	<0.001	<0.001	0.011
	FL—Osceola NF	0.165	<0.001	<0.001	<0.001
	GA—Oconee NF	0.819	0.006	<0.001	<0.015
	SC—Sumter NF	0.788	<0.001	<0.001	0.062
Hylastes tenuis	AL—Bankhead NF	0.700	0.870	<0.001	0.589
	FL—Apalachicola NF	0.467	0.738	<0.001	0.864
	GA—Oconee NF	0.981	0.913	<0.001	0.913
	NC—Blue Valley EF	0.163	0.446	<0.001	0.637
	NC—Nantahala NF	0.001	0.831	<0.001	0.573
	SC—Sumter NF	0.635	0.013	<0.001	0.301
Hypothenemus sp.	AL—Bankhead NF	0.003	<0.001	0.474	0.961
Ips grandicollis	AL—Bankhead NF	0.457	0.040	<0.001	0.040
	FL—Apalachicola NF	0.993	0.826	<0.001	0.826
	FL—Ocala NF	0.362	0.027	<0.001	0.216
	FL—Osceola NF	0.896	0.131	<0.001	0.956
	GA—Oconee NF	0.806	0.596	<0.001	0.831
	NC—Nantahala NF	0.024	0.775	<0.001	0.775
	SC—Sumter NF	0.437	0.402	<0.001	0.085
Pityophthorus cariniceps	NC—Blue Valley EF	0.888	0.001	<0.001	<0.001

emitted ethanol at rates higher than uninfected trees. Ethanol concentrations are higher in the roots and root collars of Douglas fir and ponderosa pine infected with root disease than in healthy uninfected trees (Kelsey and Joseph 1998; Kelsey et al. 1998). Ethanol production in Douglas fir branches increases with water stress, resulting in attacks by the Douglas fir engraver, *S. unispinosus* LeConte, in Oregon (Kelsey and Joseph 2001). Ethanol production and landing preferences by bark and wood-boring beetles in ponderosa pine are correlated strongly with stress from crown scorch caused by wildfires (Kelsey and Joseph 2003).

In answer to our second objective, we found that the binary combination of ethanol and (−)-α-pinene was preferred by *H. salebrosus* and *P. cariniceps* (Fig. 10). Previously, Phillips (1990) found that *H. salebrosus* preferred the combination of turpentine with ethanol to turpentine alone. However, the benefit of adding ethanol to

(−)-α-pinene-baited traps was inconsistent for several other species among locations. The binary combination was preferred by *D. terebrans* at only one of six locations (Fig. 6e), *X. affinis* at one of three locations (Fig. 4a), *X. pubescens* at two of four locations (Fig. 4d, f), *I. grandicollis* at one of eight locations (Fig. 7a), *H. tenuis* at one of six locations (Fig. 8c), and *H. porculus* at two of five locations (Fig. 9c, e). Fatzinger et al. (1987) and Phillips et al. (1988) found that *D. terebrans* and *X. pubescens* in Florida preferred the binary combination of ethanol and turpentine, whereas *X. affinis* was unaffected by the addition of turpentine to ethanol-baited traps. In southern California, Flint et al. (2007) found that *H. tenuis* preferred traps baited with ethanol and (−)-α-pinene over those baited with either ethanol or (−)-α-pinene alone. We know of no other prior data on the specific attraction of these species to the combination of ethanol and (−)-α-pinene.
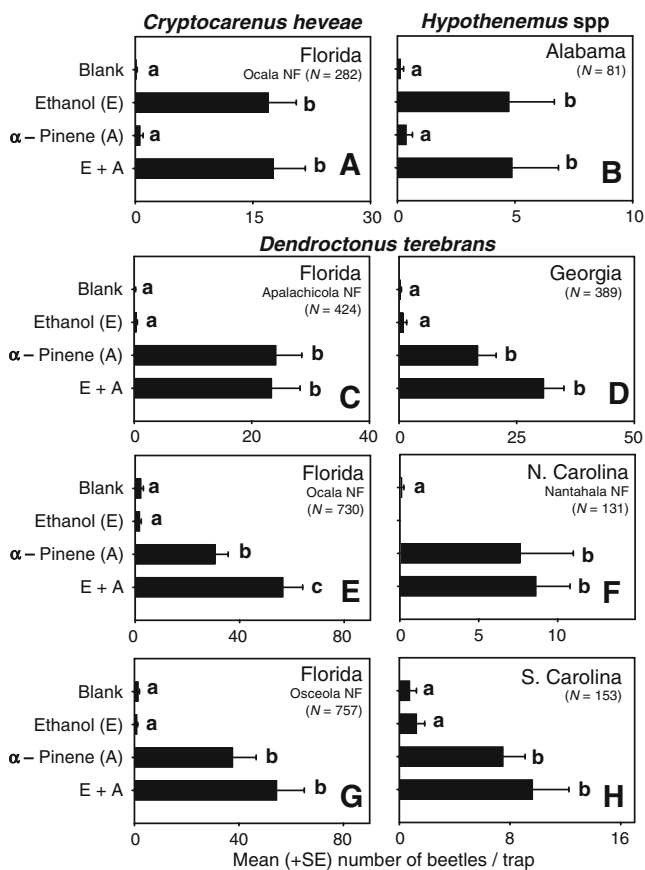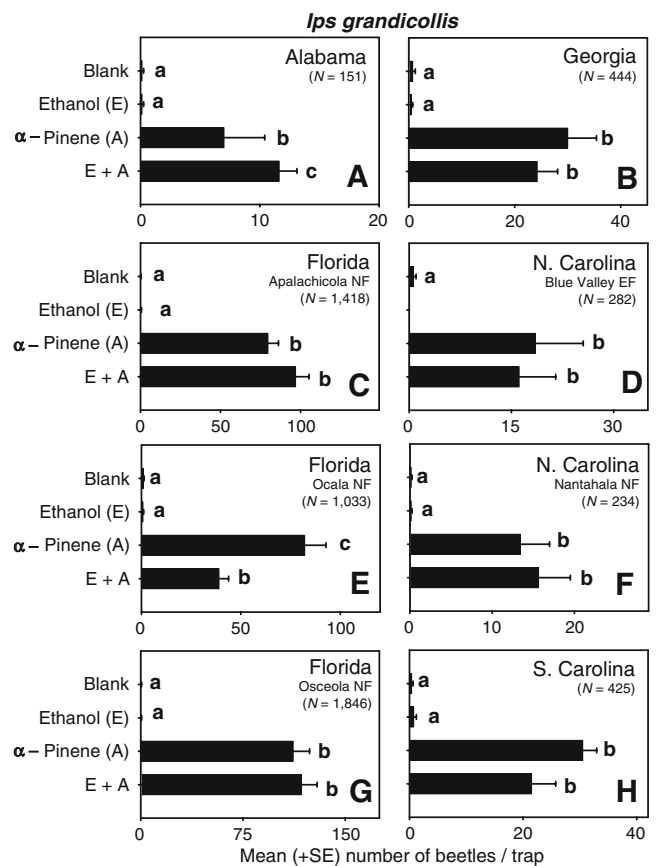
Fig. 6 Effects of ethanol and (−)-α-pinene on trap catches of *C. heveae* (**a**), *Hypothenemus* sp. (**b**), and *D. terebrans* (**c**–**h**; Scolytidae) in the southeastern US. Means followed by the same *letter* are not significantly different (α=0.05, Holm–Sidak multiple comparison)

In contrast, (−)-α-pinene had an interruptive effect on the responses of some species of ambrosia beetles to traps baited with ethanol. Catches of the ambrosia beetles *A. sayi* and *D. onoharaensum* to ethanol-baited traps were reduced by the addition of (−)-α-pinene (Fig. 3b–h). The exotic ambrosia beetle *D. onoharaensum* was one of the most common species in our trapping studies (Table 1). In two of eight locations, (−)-α-pinene had an interruptive effect on the attraction of *X. saxesenii* to ethanol (Fig. 1e–f). In British Columbia (Canada), α-pinene interrupted catches of *X. saxesenii* in ethanol-baited traps (L. Humble, unpublished data). However, Flint et al. (2007) found that (−)-α-pinene had no interruptive effect on catches of *X. saxesenii* to ethanol-baited traps in southern California, similar to our results with *X. saxesenii* in six of eight locations (Fig. 1a–d, g, h). With the exception of *I. grandicollis* at the Ocala NF (Florida; Fig. 7e), ethanol did not interrupt the response of bark beetles to traps baited with (−)-α-pinene. Catches of *I. grandicollis* at the seven other locations were not interrupted by ethanol (Fig. 7a–d, f–h).

Preferences for various combinations of ethanol and (−)-α-pinene may reflect conditions found in suitable hosts. In damaged or severed trees, the emissions of monoterpenes are likely high initially, decreasing over time with effects of desiccation and oxidation. In contrast, ethanol emissions are likely low initially, increasing over time as a consequence of anaerobic respiration (Kelsey 1994). Preferences of some species to ethanol with no apparent effect of (−)-α-pinene may relate to broad host ranges that include hardwood tree species; in fact, some ambrosia beetle species may be more common in hardwood species (Jordal et al. 2001).

We are unable to explain the variation among locations in responses of some species to baited traps. Although the same experimental design was employed at all locations, it is possible that the power was lower at some locations than others, particularly for species with low total catches. In some locations, sample size may have been insufficient to detect significant differences where such differences truly existed. It is possible that background or competing sources of ethanol and/or (−)-α-pinene may have differed significantly among locations. In some areas, emissions from baits
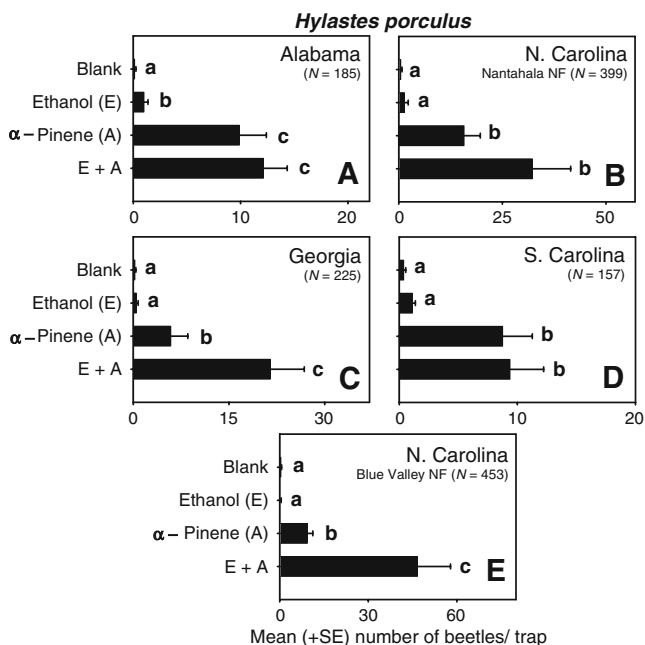

Fig. 7 a–**h** Effects of ethanol and (−)-α-pinene on trap catches of *I. grandicollis* (Scolytidae) in the southeastern US. Means followed by the same *letter* are not significantly different (α=0.05, Holm–Sidak multiple comparison)
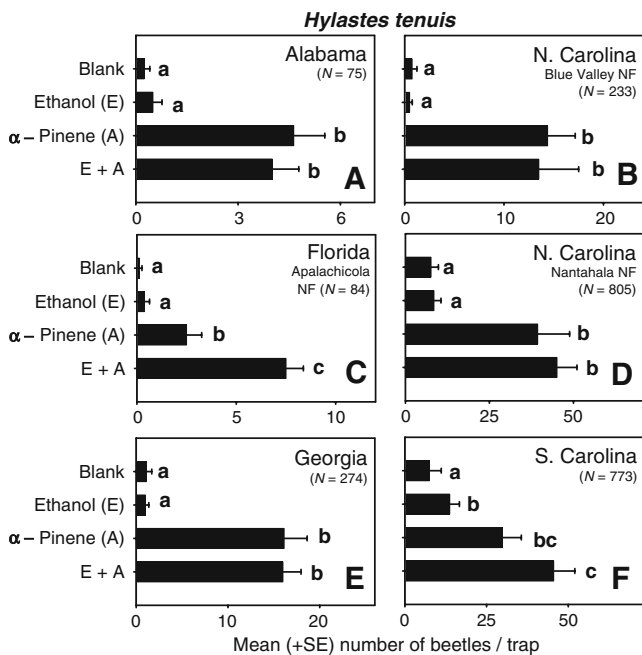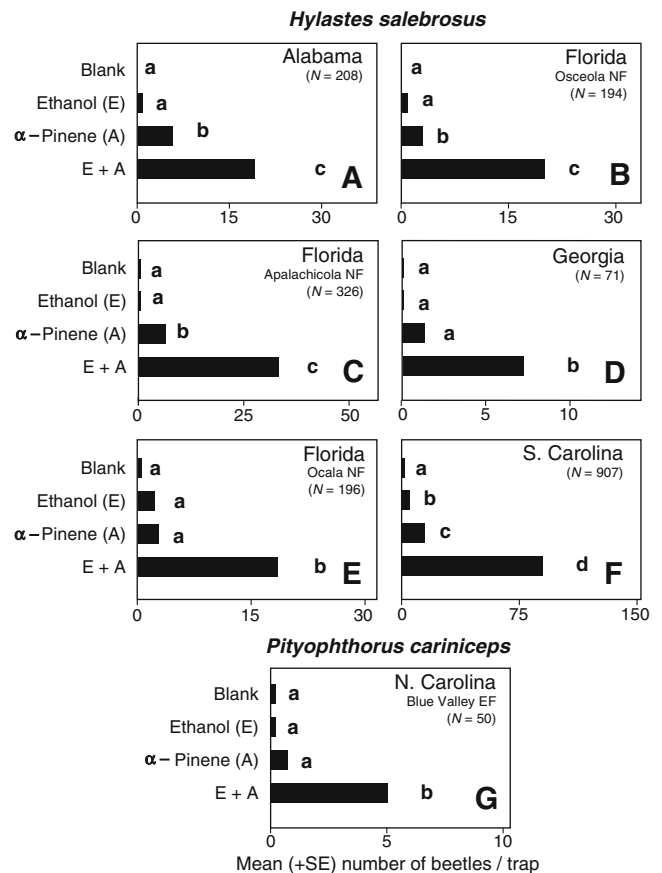
Fig. 8 **a**–**f** Effects of ethanol and (−)-α-pinene on trap catches of *H. tenuis* (Scolytidae) in the southeastern US. Means followed by the same *letter* are not significantly different (α=0.05, Holm–Sidak multiple comparison)

Fig. 10 Effects of ethanol and (−)-α-pinene on trap catches of *H. salebrosus* (**a**–**f**) and *P. cariniceps* (**g**; Scolytidae) in the southeastern US. Means followed by the same *letter* are not significantly different (α=0.05, Holm–Sidak multiple comparison)

might have been overwhelmed by background levels of ethanol and/or (−)-α-pinene. In other areas, these emissions might have been dampened directly by vegetation. In addition to variation in trapping dates and primary pine species (Table 1), the eight study sites used in our study likely differed in many aspects including host composition, damage type, understory vegetation, and climate regimes. Unfortunately, we have no detailed information over an adequate sample size of locations to evaluate or explain this type of variation. Suffice it to say that our results suggest that variation in responses can be expected in an operational program as well.

In summary, we provide evidence to support the continued use of traps baited with ethanol and/or (−)-α-pinene in detection and monitoring programs for bark and wood-boring beetles. Moreover, the interruptive effect of (−)-α-pinene does necessitate the use of a separate trap baited solely with ethanol. Serendipitous to our stated objectives, we found a significant and disturbing pattern in the relative abundance of exotic species. Exotic non-native species of ambrosia beetles were consistently dominant in total trap catches of ambrosia beetles throughout our study area, accounting for 69.7–93.4% in North Carolina, 90.6% in Georgia, 82.9% in South Carolina, 90.0% in Alabama, and 75.1–96.6% in Florida.

Fig. 9 **a**–**e** Effects of ethanol and (−)-α-pinene on trap catches of *H. porculus* (Scolytidae) in the southeastern US. Means followed by the same *letter* are not significantly different (α=0.05, Holm–Sidak multiple comparison)

The abundance of non-native ambrosia beetles in trap catches likely reflects their relative abundance in forested areas of the South. Previously in South Carolina and Tennessee, Coyle et al. (2005) and Oliver and Mannion (2001) found that the percentage of exotic beetles in ethanol-baited baited traps was 88% and 74%, respectively. Ambrosia beetles generally play an important role in initiating the decomposition cycle (Lindgren 1990). Yet, little is known of the impacts of exotic ambrosia beetles on forest ecology in southern forests, particularly with respect to decomposition of woody material and carbon sequestration. Moreover, the generalist host requirements and the incestuous nature of xyleborine ambrosia beetles suggest that new invasions and expansion of existing invasions are likely (Jordal et al. 2001; Hulcr et al. 2007), all without known consequences.

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