Environmental Entomology, 54(3), 2025, 467–479
https://doi.org/10.1093/ee/nvaf032
Advance Access Publication Date: 10 April 2025
Research

ENTOMOLOGICAL SOCIETY OF AMERICA
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Chemical Ecology

Ethanol: dose-dependent flight responses of bark and woodboring beetles, and associated species of Coleoptera

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Subject Editor: Dong H. Cha

Received on 26 November 2024; revised on 30 January 2025; accepted on 3 March 2025

In 2007 to 2008, I assessed the effects of ethanol release rate (dose) on trap catches of bark and woodboring beetles, and associated species of predators, in 6 experiments in north-central Georgia. Multiple-funnel traps were baited with ethanol alone or co-baited with α-pinene (with or without the bark beetle pheromones ipsenol and ipsdienol). The following species of bark and ambrosia beetles exhibited a positive dose-dependent response to ethanol, regardless of co-baits: *Corthylus columbianus* Hopkins, *Dryoxylon onoharaense* (Murayama), *Hylastes porculus* Erichson, *Hylastes salebrosus* Eichhoff, *Hylobius pales* (Herbst), *Monarthrum fasciatum* (Say), *Orthotomicus caelatus* (Eichhoff), *Xyleborinus saxesenii* (Ratzeburg), *Xyleborus* species, and *Xylosandrus crassiusculus* (Motschulsky) (Coleoptera: Curculionidae). *Hylastes tenuis* Eichhoff (Coleoptera: Curculionidae) exhibited a positive dose-dependent response to ethanol alone but not when traps were co-baited with α-pinene, or α-pinene and bark beetle pheromones. A consistent negative dose-dependent response was exhibited by *Ips grandicollis* (Eichhoff) whereas results with *Ips avulsus* (Eichhoff) and *Dendroctonus terebrans* (Olivier) (Coleoptera: Curculionidae) were variable. Longhorn beetles were unaffected by ethanol dose except for *Curius dentatus* Newman (Coleoptera: Cerambycidae), which exhibited a positive dose-dependent response to ethanol. Three species of predators exhibited positive dose-dependent responses to ethanol: *Temnoscheila virescens* (F.) (Coleoptera: Trogossitidae), *Platysoma parallelum* (Say) (Coleoptera: Histeridae), and *Lasconotus* species (Coleoptera: Zopheridae). Ethanol is a key kairomone for many species of bark and woodboring beetles.

Keywords: ethanol, host selection, kairomone, ambrosia beetle, bark beetle

Introduction

Nutrient cycling in a healthy forest depends heavily on the activities of a broad diversity of saproxylic and arboreal insects in several guilds: bark beetles, wood borers, fungivores, and predators (Ulyshen and Šobotník 2018, Dodds et al. 2023, Hébert 2023). Tunnelling and feeding activities by beetles allow entry of bacteria and fungi thereby facilitating the degradation of woody material. As an indicator of forest health, biodiversity across these guilds can be assessed with traps baited with various blends of semiochemicals (Dodds et al. 2015, 2024).

Additionally, species-specific monitoring lures may be needed to detect invasive species of arboreal beetles as part of integrated pest management programs to mitigate damage to forests and rangelands (Poland and Rassati 2019, Brockerhoff et al. 2023). To date, considerable damage to forest ecosystems in North America has been caused by non-native invasive species such as *Agrilus planipennis* Fairmaire (Coleoptera: Buprestidae) (Herms and McCullough 2014, Sun et al. 2024), *Anoplophora glabripennis* Motschulsky (Coleoptera: Cerambycidae) (Haack et al. 2010, Wang et al. 2023), and *Xyleborus glabratus* (Coleoptera: Curculionidae) (Fraedrich et al. 2008, Olatinwo et al. 2021). Rapid detection programs to locate non-native invasive species are required to prevent the establishment of future invasive species. Ethanol lures are commonly used in nationwide detection programs such as the USDA Forest Service Early Detection and Rapid Response program of surveillance for non-native bark and ambrosia beetles (Rabaglia et al. 2019).

In trees and woody shrubs, ethanol production is associated with stress, decay, and decomposition of woody tissues, likely due to anaerobic respiration or microbial fermentation of sugars

(Linsley 1959, Rudinsky 1962, Graham 1968, Cade et al. 1970, Kelsey 1994a, 1994b, 2001, Kelsey et al. 2014, Kelsey and Westlind 2017). For example, ethanol is released from lodgepole pines, *Pinus contorta* Douglas (Pinaceae) in Oregon infected with heartwood decay fungi (Gara et al. 1993). Douglas firs, *Pseudotsuga menziesii* (Mirbel) Franco and ponderosa pines, *Pinus ponderosa* Douglas ex Lawson, with root diseases have higher concentrations of ethanol in sapwood around the root collar than unaffected trees (Kelsey and Joseph 1998, Kelsey et al. 1998). Attacks by the Mediterranean pine shoot beetle, *Tomicus destruens* (Wollaston) (Coleoptera: Curculionidae), on drought-stressed Aleppo pines, *Pinus halepensis* Miller in Spain were associated with increased tissue levels of ethanol, a known attractant for *To. destruens* (Kelsey et al. 2014). In the United States, ethanol concentrations in phloem and sapwood tissues were higher in ponderosa pines with bark scorching from fire than in unaffected trees, decreasing when trees recovered, whereas ethanol concentrations in dead trees continued to increase (Kelsey and Joseph 2003). Ponderosa pines scorched by fire are attacked by the red turpentine beetle, *Dendroctonus valens* LeConte (Coleoptera: Curculionidae) in association with higher ethanol levels surrounding attack sites (Kelsey and Westlind 2017).

Traps with lures releasing ethanol are attractive to numerous species of bark and woodboring beetles (Coleoptera: Curculionidae, Cerambycidae, Buprestidae) (Moeck 1970, Roling and Kearby 1975, Montgomery and Wargo 1983, Chénier and Philogène 1989, Markalas and Kalapanida 1997, Joseph et al. 2001, Coyle et al. 2005, 2015, Miller 2006, 2020, Bouget et al. 2009, Miller and Rabaglia 2009, Gandhi et al. 2010, Reding et al. 2011, Ranger et al. 2016, Klingeman et al. 2017, Rabaglia et al. 2019, Fiala et al. 2023). In addition, ethanol can enhance the attraction of bark and woodboring beetles to traps baited with other host kairomones such as α-pinene (Fatzinger et al. 1987, Phillips et al. 1988, Chénier and Philogène 1989, Schroeder and Lindelöw 1989, Allison et al. 2004, Miller 2006, 2020, Miller and Rabaglia 2009, Kelsey and Westlind 2018) and to traps baited with various pheromones used by bark and woodboring beetles (Pitman et al. 1975, Phillips 1990, Allison et al. 2004, Sweeney et al. 2010, 2016, Noseworthy et al. 2012, Miller et al. 2015a, 2015b, Millar and Hanks 2016, Rice et al. 2024). Ethanol can enhance attraction of some species of predators and fungivores (Coleoptera: Cleridae, Histeridae, Trogossitidae, Zopheridae) to traps baited with kairomones and/or pheromones used by bark and woodboring beetles (Chénier and Philogène 1989, Schroeder 2003, Miller 2023, Miller and Asaro 2023, Miller et al. 2023).

Several species of Scolytinae (Coleoptera: Curculionidae) exhibit dose-dependent increases in responses to ethanol in traps in Sweden and Germany (Klimetzek et al. 1986, Schroeder 1988, Schroeder and Lindelöw 1989, Byers 1992). We should expect that similar ethanol dose-dependent responses should exist for bark and ambrosia species that breed in pine forests of the southern United States. It is possible that similar responses could be exhibited by associated species of woodborers, fungivores, and predators. Such data could provide insights into favored hosts for these species and considerations in lure selections for use in detection programs.

Materials and Methods

In 2007 to 2008, I conducted 6 experiments to determine the effects of ethanol, released at different rates (dose) from lures, on the attraction of bark and woodboring beetles (and associated beetle species) in north-central Georgia to multiple funnel traps baited with and without the host kairomone (α-pinene) and bark beetle pheromones (ipsenol and ipsdienol). Ethanol, (–)-α-pinene, ipsenol, and ipsdienol are broadly attractive to numerous species of saproxylic beetles and predators in the southeastern United States (Miller 2006, 2020, 2023, Miller and Rabaglia 2009, Miller et al. 2011, 2013, 2015a, Miller and Asaro 2023). My goal was to evaluate dose-dependent responses of various beetle species under various background contexts of semiochemicals commonly associated with species that inhabit pine forests.

Ethanol, α-pinene, and ipsenol lures were obtained from Contech Inc. (Delta, BC) whereas Synergy Semiochemical Corporation (Burnaby, BC) supplied ipsdienol lures (Table 1). Randomized complete block designs were used for each experiment with 3 to 4 treatments per experiment (Table 2). In each experiment, 8-unit multiple-funnel traps (Contech Inc.) were hung on ropes strung between trees such that collection cups were 0.5 to 1.0 m above ground. Traps were spaced 5 to 15 m apart and ≥ 2 m from any tree. Lures were hung outside the funnels, roughly in the middle (vertically) of the traps. Collection cups contained 100 to 150 ml of polypropylene and water mixture (SPLASH RV & Marine Antifreeze, SPLASH Products Inc., St. Paul, MN), replenished after each 2-wk collection. Vouchers were deposited in the University of Georgia Collection of Arthropods, Athens, GA.

Experiment 1 was conducted at the State Botanical Garden of Georgia, Athens, GA (33.900 N, 83.388 W) whereas experiment 3 was conducted at the University of Georgia Whitehall Forest, Athens, GA (33.896° N, 83.361° W) (Table 2). Experiments 2, 4, 5, and 6 were conducted consecutively at one site in the Oconee National Forest, Putnam County, GA (33.411° N, 83.412° W). The stand used in experiment 1 consisted primarily of *Acer negundo* L. and *Ligustrum sinense* de Loureiro, whereas a mature stand of *Pinus taeda* (L.) was used for experiment 3. The site for the remaining experiments consisted primarily of *Pinus taeda* with *Pinus echinata* Miller, *Liquidambar styraciflua* L., *Quercus falcata* Michaux, and *Carya tomentosa* Sargent also present.

Data were analyzed with the SYSTAT (ver. 13.1) and SigmaStat (ver. 3.01) statistical packages (SYSTAT Software Inc., Point Richmond, CA) for species with a total number of captured individuals ≥ 30 in an experiment. I used mixed-model ANOVA with treatment as the fixed factor for all datasets. Trap catch data were transformed by ln (y + 1) as needed to ensure normality and

Table 1. Description of lures used in the study. Manufacturers noted in text.

Code	Semiochemical lure [a]	Release rate [b]
Id	Ipsdienol (+ 50/-50) white 100 mg bubble-cap	0.1–0.2 mg/d
E1	White ethanol 40 cm sleeve	45 mg/d
E2	Black ethanol UHR pouch, 150 ml	0.5 g/d
Is	Ipsenol (+ 50/-50) white 40 mg bubble-cap	0.1–0.2 mg/d
αP	α-Pinene (+ 05/-95) blue UHR pouch, 200 ml	2–6 g/d

[a]Chemical purity > 95%.
[b]Determined by the manufacturers at 20–23°C.

homoscedasticity (Pepper et al. 1997), verified with the Shapiro-Wilk and Equal Variance tests, respectively. Analyses were followed by the Holm-Sidak multiple-comparison procedure when treatment effects were significant ($\alpha = 0.05$); the Holm-Sidak procedure controls the experiment-wise error rate at 0.05 (Glantz 2005).

Results

Ambrosia Beetles (Coleoptera: Curculionidae)

Ethanol lure treatments significantly increased trap captures of 4 xyleborine species of ambrosia beetles in all 6 experiments (Table 3). In experiments 1 to 2, catches of *Xyleborinus saxesenii* (Ratzeburg) were greater in traps baited with ethanol than in traps not baited with ethanol; catches were greatest in traps baited with the highest release rate of ethanol (Fig. 1A–B). The same pattern was noted for *Xyleborinus saxesenii* in experiments 3 to 4 with traps co-baited with α-pinene (Fig. 1C–D); the greatest catches were in traps baited with ethanol released at rates of 1–2 g/d. Catches of *Xyleborinus saxesenii* in traps with lures releasing ethanol at the 2 highest rates were greater than in traps baited solely with α-pinene + ipsenol in experiment 5 (Fig. 1E) and traps baited solely with α-pinene + ipsenol + ipsdienol in experiment 6 (Fig. 1F). In

Table 2. Trapping dates, number of replicate blocks (n), lure treatments, and ethanol release rates (RR) for 6 experiments on flight responses of bark and wood boring beetles in northcentral Georgia. Lures were E1 (ethanol, release rate = 45 mg/d), E2 (ethanol, release rate = 0.5 g/d), αP (α-pinene), Is (ipsenol), and Id (ipsdienol).

exp	Trapping dates	*n*	Lure treatments	Ethanol RR (g/d)
1	29 March–15 June 2007	5	a. Blank	0
			b. One E2	0.5
			c. Three E2	1.5
2	16 April–14 May 2008	10	a. Blank	0
			b. Two E1	0.1
			c. One E2	0.5
			d. Three E2	1.5
3	16 May–28 June 2007	8	a. αP	0
			b. αP + one E2	0.5
			c. αP + two E2	1.0
			d. αP + four E2	2.0
4	14 May–18 June 2008	10	a. αP	0
			b. αP + two E1	0.1
			c. αP + one E2	0.5
			d. αP + three E2	1.5
5	18 June–7 July 2008	9	a. αP + Is	0
			b. αP + Is + two E1	0.1
			c. αP + Is + one E2	0.5
			d. αP + Is + three E2	1.5
6	7 July–19 August 2008	10	a. αP + Is + Id	0
			b. αP + Is + Id + two E1	0.1
			c. αP + Is + Id + one E2	0.5
			d. αP + Is + Id + three E2	1.5

Table 3. Total beetle numbers (N) and ANOVA results for treatment effects on trap catches ambrosia beetles (Coleoptera: Curculionidae) in experiments (Exp) 1–6.

Species	exp	*N*	*F*	df	*P*
Corthylus columbianus	1	40	13.282	2, 8	0.003
Dryoxylon onoharaense	2	1,271	179.00	3, 27	<0.001
	4	51	12.21	3,27	<0.001
	6	149	23.44	3, 27	<0.001
Monarthrum fasciatum	2	38	7.37	3, 27	<0.001
Xyleborinus saxesenii	1	1,081	86.51	2, 8	<0.001
	2	2,663	271.12	3, 27	<0.001
	3	325	34.71	3, 21	<0.001
	4	361	88.32	3, 27	<0.001
	5	75	6.86	3, 24	0.002
	6	226	11.14	3, 27	<0.001
Xyleborus species	2	70	20.60	3, 27	<0.001
	4	60	2.75	3,27	0.062
	6	30	3.20	3, 27	0.039
Xylosandrus crassiusculus	1	196	70.59	2, 8	<0.001
	2	399	33.03	3, 27	<0.001
	3	54	15.91	3, 21	<0.001
	4	112	25.58	3, 27	<0.001

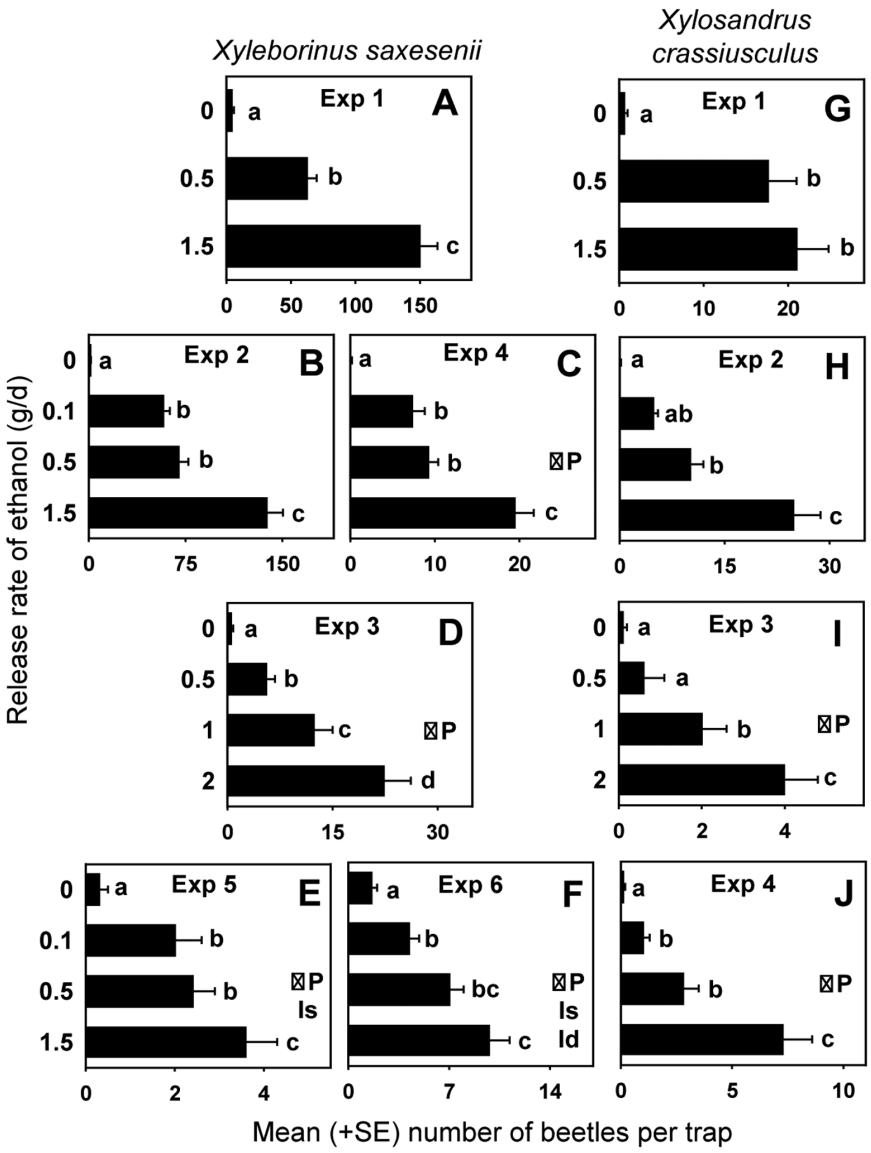

Fig. 1. Mean (+ SE) total catches of the ambrosia beetles *Xyleborinus saxesenii* (A–F) and *Xylosandrus crassiusculus* (G–J) (Curculionidae) in traps baited with ethanol (released at different rates). For each species, means followed by the same letter are not significantly different at $\alpha = 0.05$ (Holm-Sidak test). Co-baits in each experiment (Exp) when present: α-pinene (αP), ipsenol (Is), and ipsdienol (Id).

experiment 1, catches of *Xylosandrus crassiusculus* (Motschulsky) were greater in traps baited with ethanol (regardless of release rate) than in those not baited with ethanol (Fig. 1G). In experiments 2 to 4, catches of *Xylosandrus crassiusculus* were greatest in traps baited with ethanol released at the highest rate and lowest in those not baited with ethanol; catches in traps releasing ethanol at the second highest rate were intermediate (Fig. 2H–J).

Catches of *Dryoxylon onoharaense* (Murayama) in experiments 2, 4, and 6 were greater in all traps baited with ethanol than in those not baited with ethanol (Fig. 2A–C). In experiment 2, catches were greatest in traps baited with ethanol released at the highest rate (Fig. 2A) whereas catches in experiment 6 were greatest in traps baited with ethanol released at the 2 highest rates (Fig. 2C). In contrast, ethanol release rate had no effect on catches of *Dryoxylon onoharaense* in experiment 4 (Fig. 2B). In experiment 2, catches of *Xyleborus* species were greater in traps baited with ethanol released at the highest rate than in control traps with catches intermediate in traps baited with the 2 lower release rates of ethanol (Fig. 2D). In experiment 6, catches of *Xyleborus* species were greater in traps baited with ethanol released at a rate of 0.5g/d then in traps without ethanol (Fig. 2E). There was no treatment effect on catches of *Xyleborus* species in experiment 4 (Table 3); mean (± SE) trap catch = 1.5 ± 0.3.

Ethanol dose had a significant effect on catches of 2 corthyline species of ambrosia beetles (Table 3). Catches of *Corthylus columbianus* Hopkins were greatest in traps baited with ethanol released at the highest rate in Experiment 1 (Fig. 2F). In experiment 2, catches of *Monarthrum fasciatum* (Say) were greatest in traps baited with ethanol released at the highest rates and lowest in those not baited with ethanol or releasing ethanol at the lowest rate (Fig. 2G).

Bark Beetles and Snout Weevils (Coleoptera: Curculionidae)

Ethanol lure treatments affected trap catches of 8 species of bark beetles, although results were inconsistent for a few species (Table 4). There were no treatment effects on catches of *Dendroctonus*

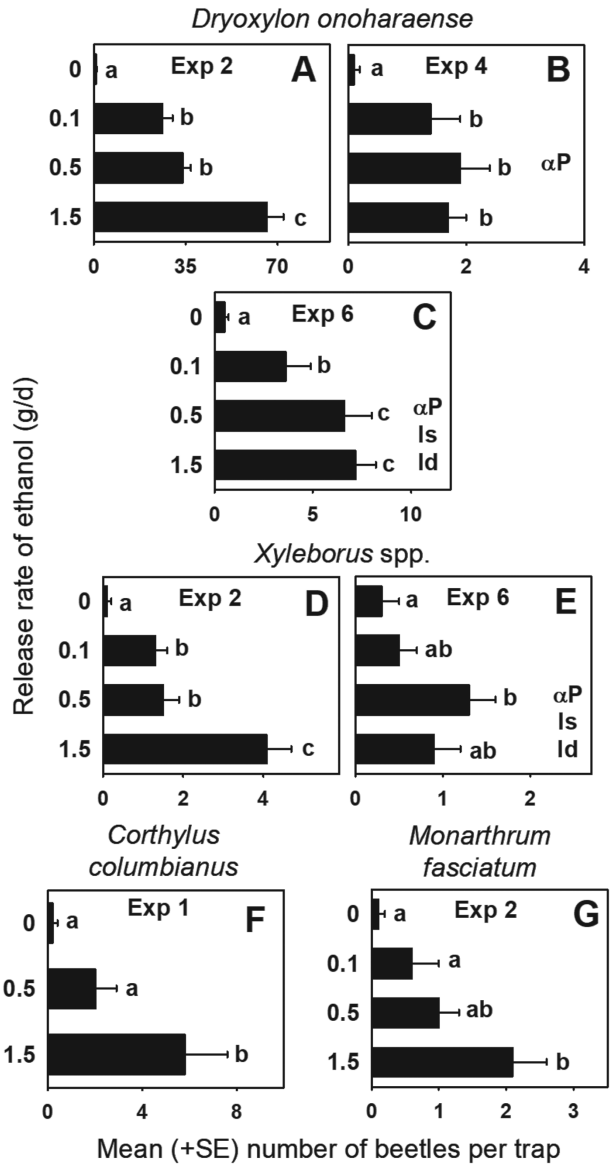

Fig. 2. Mean (+ SE) total catches of the ambrosia beetles *Dryoxylon onoharaense* (A–C), *Xyleborus* species (D–E), *Corthylus columbianus* (F), and *Monarthrum fasciatum* (G) (Curculionidae) in traps baited with ethanol (released at different rates). For each species, means followed by the same letter are not significantly different at $\alpha = 0.05$ (Holm-Sidak test). Co-baits in each experiment (Exp) when present: α-pinene (αP), ipsenol (ls), and ipsdienol (ld).

terebrans (Olivier) in experiments 3 to 5 (Table 4). In experiment 6 with co-baits of α-pinene + ipsenol + ipsdienol, catches of *De. terebrans* were greatest in traps baited with ethanol released at the highest rate and lowest in traps not baited with ethanol or baited with ethanol released at the lowest rate (Fig. 3A). Lure treatments had significant effects on trap catches of *Hylastes porculus* Erichson and *Hylastes salebrosus* Eichhoff in experiments 3 to 6 (Table 4). In experiments 3 to 5, catches of *Hylastes porculus* in traps not baited with ethanol were lower than those in traps baited with ethanol released at the 2 highest rates (Fig. 3B–D), and lower than those in traps baited with ethanol released at the highest rates in experiment 6 (Fig. 3E). In experiment 3, catches of *Hylastes salebrosus* were lowest in traps not baited with ethanol lures and greatest in traps baited with ethanol released at the highest rate (Fig. 4A). In experiments 4 to 6, catches were greatest in traps baited with ethanol released at the 2 highest rates (Fig. 4B–D). Ethanol dose affected catches of *Hylastes tenuis* Eichhoff in only one experiment (Table 4). In experiment 2, catches were lower in traps not baited with ethanol than in traps releasing ethanol at the highest rate (Fig. 4E).

In experiment 2, all traps baited with ethanol caught more *Hypothenemus* species than those not baited with ethanol with no differences based on the release rate of ethanol (Fig. 5A). In experiment 6, catches of *Orthotomicus caelatus* (Eichhoff) were lowest in traps not baited with ethanol and greatest in traps baited with ethanol released at the highest rate (Fig. 5B). In experiment 5, catches of *Ips avulsus* (Eichhoff) (were greatest in traps releasing ethanol at the highest rates and lowest in traps not baited with ethanol (Fig. 5C). In contrast, catches of *I. avulsus* in experiment 6 were greatest in traps not baited with ethanol and in traps baited with ethanol released at the highest rate (Fig. 5D). In experiments 3 and 5, catches of *Ips grandicollis* (Eichhoff) were greater in traps not baited with ethanol than in those baited with ethanol (Fig. 5E–F). Catches in experiment 6 were lowest in traps baited with ethanol released at the highest rate (Fig. 5G). Ethanol treatments had no effect on catches of *I. grandicollis* in experiment 4 (Table 4).

Ethanol lure treatments affected catches of the snout weevils *Cossonus corticola* Say, *Hylobius pales* (Herbst), *Pachylobius picivorus* (Germar) (Table 5). In experiments 4 to 6, more *Hylobius pales* were caught in traps baited with ethanol released at the 2 highest rates than in traps not baited with ethanol (Fig. 6A–C). Catches of *Pa. picivorus* were affected by treatments in 2 of 4 experiments (Table 5). In experiment 4, weevil catches in traps baited with ethanol released at the 2 highest rates were greater than those in traps not baited with ethanol (Fig. 5DE). In experiment 6, catches of *Pa. picivorus* in traps baited with ethanol released at the 2 lowest rates were greater than those in traps not baited with ethanol (Fig. 5E). Lures releasing ethanol at the highest rate significantly reduced catches of *Cossonus corticola* in traps in experiment 6 (Fig. 5F). Trap catches of *Stenoscelis brevis* (Boheman) and *Dryophthorus americanus* Bedel were unaffected by ethanol treatments (Table 5).

Woodborers

Ethanol treatments had no significant effect on catches of *Buprestis* species and *Chalcophora virginiensis* (Drury) (Coleoptera: Buprestidae), *Acanthocinus nodosus* (F.) and *Astylopsis arcuata* (LeConte) (Coleoptera: Cerambycidae) (Table 6). However, lure treatments did affect trap catches of *Acanthocinus obsoletus* (LeConte), *Curius dentatus* Newman, *Monochamus titillator* (F.), and *Xylotrechus sagittatus* (Germar) (Coleoptera: Cerambycidae), although effects were variable for some species (Table 6). In experiments 5 to 6, catches of *Ac. obsoletus* were greater in traps baited with ethanol released at the 2 lowest rates than in traps baited with ethanol released at the highest rate (Fig. 7A–B). Similarly, catches of *Monochamus titillator* in experiment 6 were greater in traps baited with ethanol released at the lowest rate than in traps baited with ethanol released at the highest rate (Fig. 7C). Lure treatments had no effect on catches of *Monochamus titillator* in experiments 4–5 (Table 6). In contrast, catches of *Curius dentatus* in experiment 6 were greater in traps baited with ethanol released at the highest rate than in those baited with the 3 other treatments (Fig. 7D). Catches of *Xylotrechus sagittatus* in traps baited with ethanol released at the lowest rate in experiments 4 and 6, and catches in traps baited with ethanol at the second highest release rate in experiment 5, were greater than those in traps not baited with ethanol

Table 4. Total beetle numbers (*N*) and ANOVA results for treatment effects on trap catches of bark beetles (Coleoptera: Curculionidae) in experiments 2–6 with mean (± SE) catches for those species unaffected by ethanol lure treatments.

Species	exp	*N*	*F*	df	*P*	Mean (± SE) trap catch
Dendroctonus terebrans	3	137	2.68	3, 21	0.073	4.3 ± 0.6
	4	262	2.67	3, 27	0.068	6.6 ± 0.7
	5	272	1.18	3, 24	0.339	7.6 ± 0.9
	6	1,311	5.31	3, 27	0.005	–
Hylastes porculus	3	66	5.54	3, 21	0.006	–
	4	166	9.56	3, 27	<0.001	–
	5	156	4.57	3, 24	0.011	–
	6	342	7.44	3, 27	<0.001	–
Hylastes salebrosus	3	95	13.04	3, 21	<0.001	–
	4	839	39.42	3, 27	<0.001	–
	5	315	7.88	3, 24	<0.001	–
	6	643	45.43	3, 27	<0.001	–
Hylastes tenuis	2	52	5.18	3, 27	0.006	–
	3	251	1.49	3, 21	0.246	7.8 ± 1.1
	4	351	1.20	3, 27	0.330	8.8 ± 0.9
	5	289	1.51	3, 24	0.237	8.0 ± 0.7
	6	1,097	1.18	3, 27	0.335	27.4 ± 1.7
Hypothenemus species	2	194	22.48	3, 27	<0.001	–
Ips avulsus	5	218	16.48	3, 24	<0.001	–
	6	1,752	4.76	3, 27	0.009	–
Ips grandicollis	3	240	3.87	3, 21	0.024	–
	4	362	0.36	3, 27	0.780	9.1 ± 0.7
	5	899	5.95	3, 24	0.004	–
	6	1,558	6.96	3, 27	0.001	–
Orthotomicus caelatus	6	245	68.57	3, 27	<0.001	–

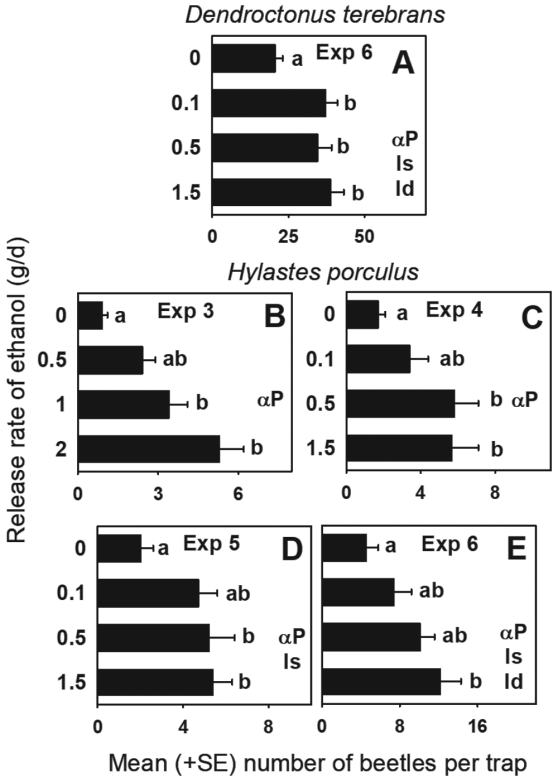

Fig. 3. Mean (+ SE) total catches of the bark beetles *Dendroctonus terebrans* (A) and *Hylastes porculus* (B–E) (Curculionidae) in traps baited with ethanol (released at different rates). For each species, means followed by the same letter are not significantly different at $\alpha = 0.05$ (Holm-Sidak test). Co-baits in each experiment (Exp) when present: α-pinene (αP), ipsenol (Is), and ipsdienol (Id).

(Fig. 7E–G). Lure treatments had no effect on catches of *Xylotrechus sagittatus* in experiment 3 (Table 6).

Predators

Ethanol lure treatments had no effect on trap catches of *Thanasimus dubius* (F.) (Coleoptera: Cleridae), *Catogenus rufus* (F.) (Coleoptera: Passandridae), *Corticeus* species (Coleoptera: Tenebrionidae), *Tenebroides* species (Coleoptera: Trogossitidae), and *Pycnomerus sulcicollis* LeConte (Coleoptera: Zopheridae) (Table 7). Lure treatments did affect catches of *Alaus myops* (F.) (Coleoptera: Elateridae), *Platysoma parallelum* (Say) (Coleoptera: Histeridae), *Temnoscheila virescens* (F). (Coleoptera: Trogossitidae), and *Lasconotus* species (Coleoptera: Zopheridae) (Table 7).

In experiment 6, catches of *Pl. parallelum* were greatest in traps baited with ethanol released at the highest rate (Fig. 8A). Traps baited with ethanol released at the 2 highest rates caught the most *Lasconotus* species in experiment 5 (Fig. 8B); *Lasconotus* species were unaffected by lures in experiment 6 (Table 7). In experiment 3, catches of *Te. virescens* in traps baited with the highest and lowest release rates of ethanol were greater than those in control traps (Fig. 8C). Catches of *Te. virescens* were greatest in traps baited with ethanol released at the 2 highest rates in experiments 4 and 6 (Fig. 8D, F), and traps baited with ethanol released at the highest rate in experiment 5 (Fig. 8E),

Discussion

The diversity of bark and woodboring beetles is high in the southeastern United States (USDA 1985). Ecological niches for beetles vary by species of host trees and shrubs, parts of trees and shrubs, and condition of host material. Time is an important variable in defining the condition of downed woody material and utilization

by bark and woodboring beetles as host resistance declines and the nutritional composition of woody material changes over time, providing optimal niches for different species (Linsley 1959, Rudinsky 1962, Ulyshen and Šobotník 2018, Dodds et al. 2023). In addition to aggregation and anti-aggregation pheromones used by beetles, and host volatiles such as α-pinene that help define host species, fermentation products such as ethanol are important elements in determining host availability and suitability for bark and woodboring beetles (Byers 2007).

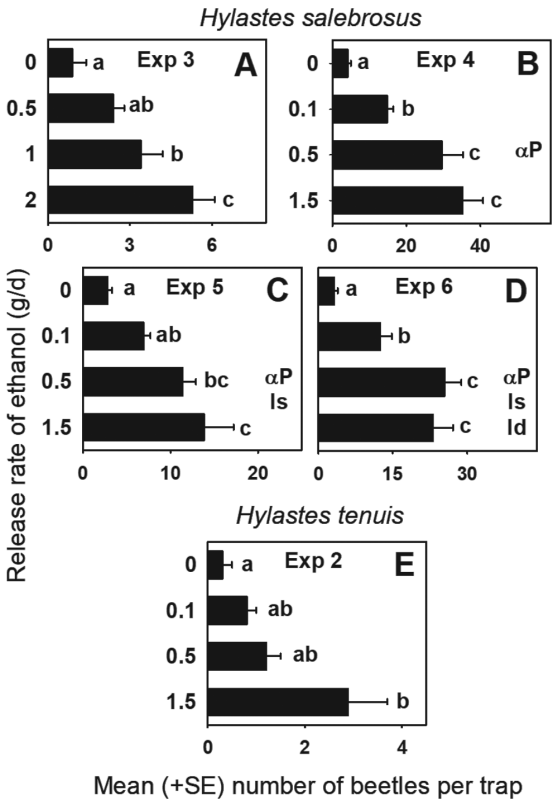

Fig. 4. Mean (+ SE) total catches of the bark beetles *Hylastes salebrosus* (A–D) and *Hylastes tenuis* (E) (Curculionidae) in traps baited with ethanol (released at different rates). For each species, means followed by the same letter are not significantly different at $\alpha = 0.05$ (Holm-Sidak test). Co-baits in each experiment (Exp) when present: α-pinene (αP), ipsenol (Is), and ipsdienol (Id).

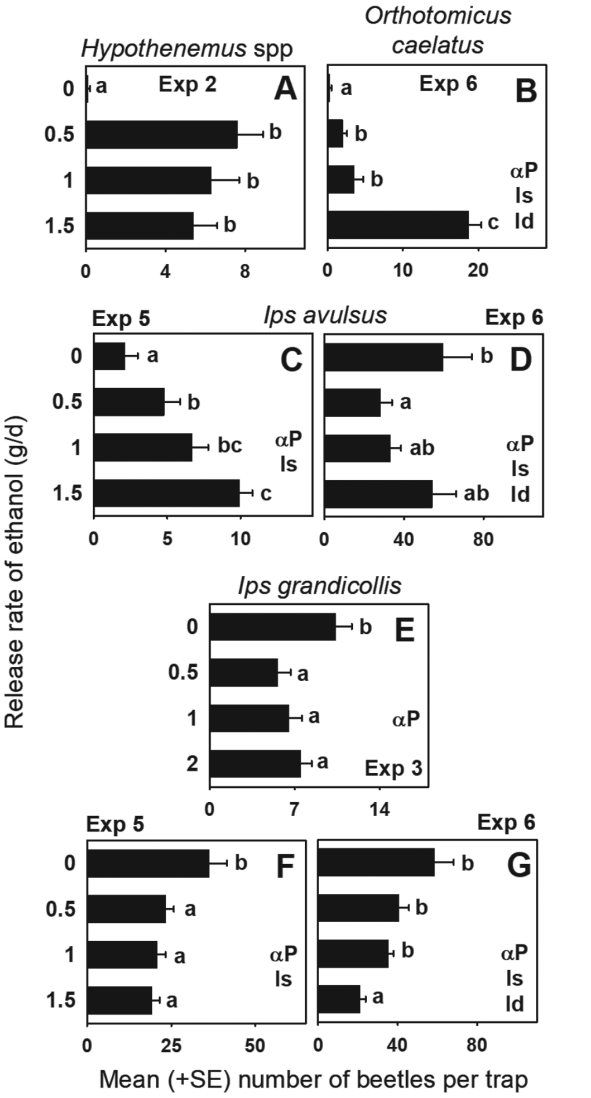

Fig. 5. Mean (+ SE) total catches of the bark beetles *Hypothenemus* species (A), *Orthotomicus caelatus* (B), *Ips avulsus* (C–D), and *Ips grandicollis* (E–G) (Curculionidae) in traps baited with ethanol (released at different rates). For each species, means followed by the same letter are not significantly different at $\alpha = 0.05$ (Holm-Sidak test). Co-baits in each experiment (Exp) when present: α-pinene (αP), ipsenol (Is), and ipsdienol (Id).

Table 5. Total beetle numbers (*N*) and ANOVA results for treatment effects on trap catches of snout weevils (Coleoptera: Curculionidae) in experiments 1–6 with mean (± SE) catches for those species not affected by ethanol lure treatments.

Species	exp	*N*	*F*	df	P	Mean (± SE) trap catch
Cossonus corticola	6	96	4.06	3, 27	0.017	–
Dryophthorus americanus	1	246	0.91	2, 8	0.440	16.4 ± 4.0
Hylobius pales	4	116	7.34	3, 27	<0.001	–
	5	84	7.56	3, 24	<0.001	–
	6	409	25.71	3, 27	<0.001	–
Pachylobius picivorus	3	69	1.93	3, 21	0.155	2.2 ± 0.4
	4	189	8.50	3, 27	<0.001	–
	5	102	1.44	3, 24	0.256	2.8 ± 0.4
	6	493	8.42	3, 27	<0.001	–
Stenoscelis brevis	1	265	2.19	2, 8	0.175	17.0 ± 2.1
	2	31	1.33	3, 27	0.286	0.8 ± 0.1
	4	109	0.69	3, 27	0.569	2.7 ± 0.5

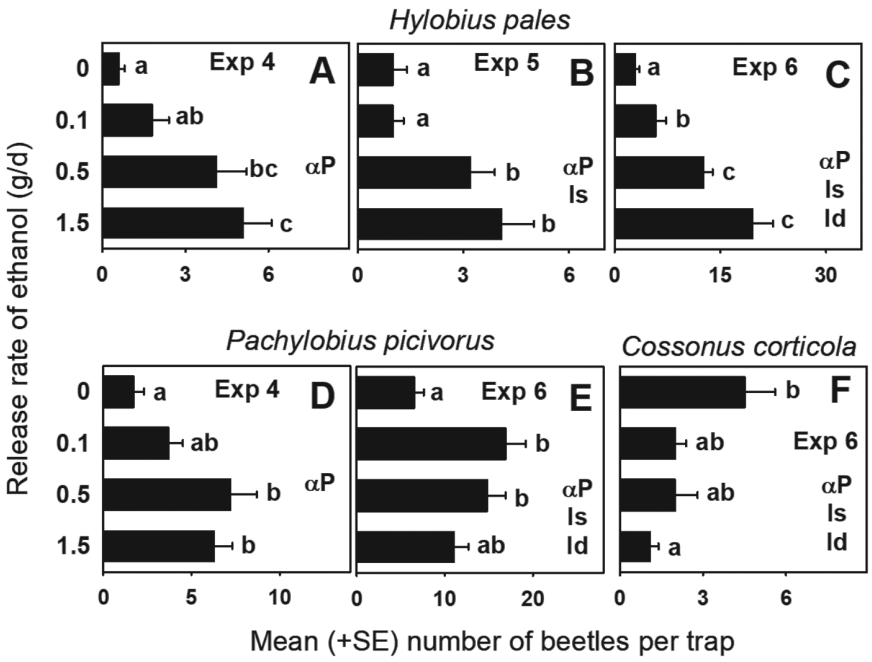

Fig. 6. Mean (+ SE) total catches of the weevils *Hylobius pales* (A–C), *Pachylobius picivorus* (D–E), and *Cossonus corticola* (F) (Curculionidae) in traps baited with ethanol (released at different rates). For each species, means followed by the same letter are not significantly different at $\alpha = 0.05$ (Holm-Sidak test). Co-baits in each experiment (Exp) when present: α-pinene (αP), ipsenol (Is), and ipsdienol (Id).

Table 6. Total beetle numbers (N) and ANOVA results for treatment effects on trap catches of woodborers (Coleoptera) in experiments 2–6 with mean (± SE) catches for those species not affected by ethanol lure treatments.

Family, Species	exp	*N*	*F*	df	*P*	Mean (± SE) trap catch
Buprestidae						
Buprestis species	4	72	2.57	3, 27	0.075	1.8 ± 0.4
	5	154	0.95	3, 24	0.433	4.3 ± 0.6
	6	248	2.57	3, 27	0.075	6.2 ± 0.6
Chalcophora virginiensis	2	37	0.14	3, 27	0.938	0.9 ± 0.2
	6	39	1.16	3, 27	0.344	1.0 ± 0.2
Cerambycidae						
Acanthocinus nodosus	4	37	0.63	3, 27	0.602	0.9 ± 0.2
	5	43	0.40	3, 24	0.756	1.2 ± 0.3
	6	44	1.90	3, 27	0.154	1.1 ± 0.2
Acanthocinus obsoletus	5	60	6.85	3, 24	0.002	–
	6	124	3.00	3, 27	0.048	–
Astylopsis arcuata	5	35	0.36	3, 24	0.782	1.0 ± 0.2
	6	48	2.32	3, 27	0.097	1.2 ± 0.3
Curius dentatus	6	67	19.06	3, 27	<0.001	–
Monochamus titillator	4	46	2.58	3, 27	0.075	1.2 ± 0.2
	5	589	2.06	3, 24	0.132	16.4 ± 2.0
	6	775	3.64	3, 27	0.025	–
Xylotrechus sagittatus	3	141	0.56	3, 21	0.649	4.4 ± 0.5
	4	177	4.16	3, 27	0.015	–
	5	82	3.47	3, 24	0.032	–
	6	98	3.04	3, 27	0.046	–

Rudinsky (1962) categorized primary species of bark beetles (such as some species of *Dendroctonus*) as those species that attack living trees with no deterioration of phloem and cambium tissues. He specified that secondary species of bark beetles (such as *Ips* species) attack trees weakened by such factors as drought or age, as well as fresh logs and windthrow. Starch and protein contents are still high in the breeding material but resistance mechanisms have decreased significantly. Saprophagous species are defined as those that colonize hosts with low starch and protein content but high levels of fermented products such as ethanol. The same species-specific phenology pattern of host utilization is also apparent with Cerambycidae (Dodds et al. 2023). Some species breed in living parts of trees and others in dead parts of trees or logs (Linsley 1959). Other species prefer wood that has been seasoned over time.

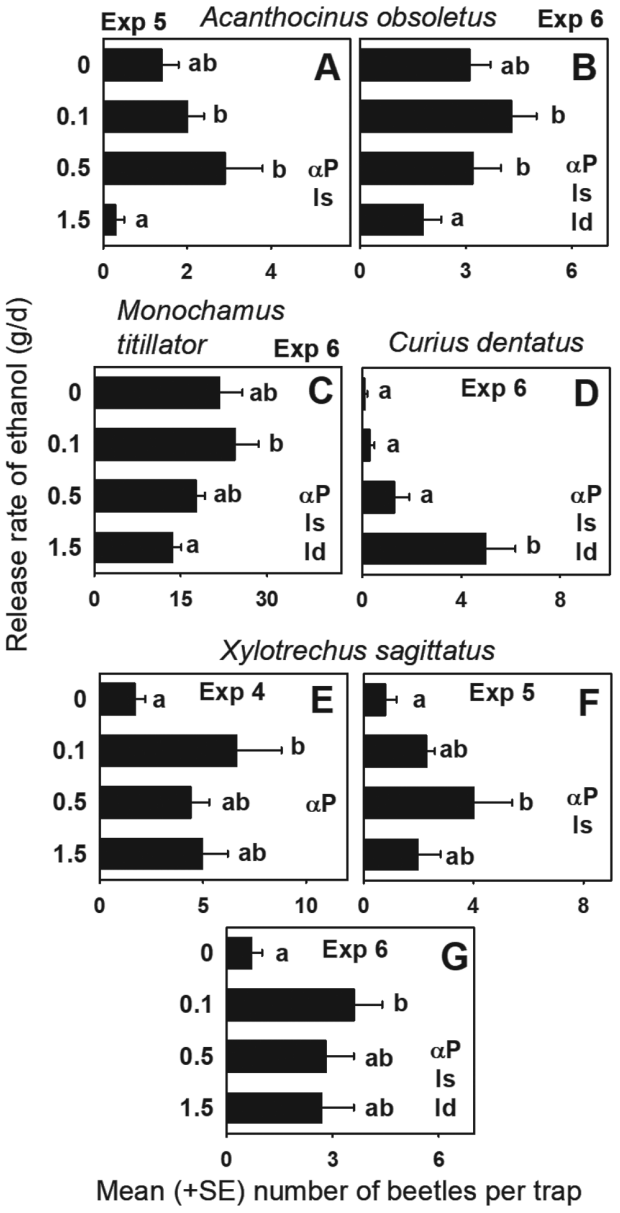

Fig. 7. Mean (+ SE) total catches of the longhorn beetles *Acanthocinus obsoletus* (A–B), *Monochamus titillator* (C), *Curius dentatus* (D), and *Xylotrechus sagittatus* (E–G) (Cerambycidae). For each species, means followed by the same letter are not significantly different at $\alpha = 0.05$ (Holm-Sidak test). Co-baits in each experiment (Exp) when present: α-pinene (αP), ipsenol (Is), and ipsdienol (Id).

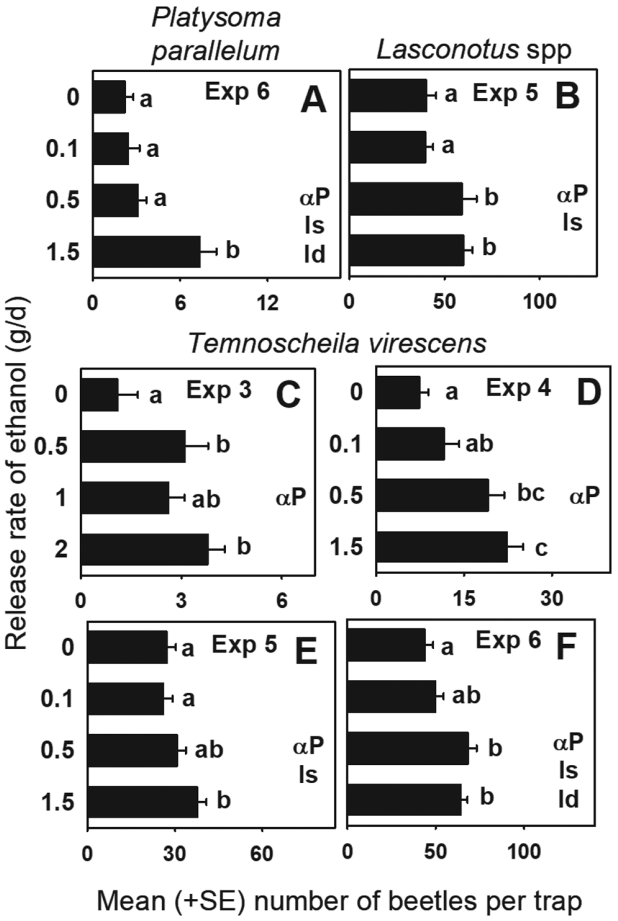

Fig. 8. Mean (+ SE) total catches of the beetle predators *Platysoma parallelum* (A) (Histeridae), *Lasconotus* species (B) (Zopheridae), and *Temnoscheila virescens* (C–F) (Trogossitidae) in traps baited with ethanol, released at different rates. For each species, means followed by the same letter are not significantly different at $P = 0.05$ (Holm-Sidak test). Co-baits in each experiment (Exp) when present: α-pinene (αP), ipsenol (Is), and ipsdienol (Id).

In Georgia, Fletchmann et al. (1999) evaluated the responses of bark and ambrosia beetles to billets (small logs) of *P. taeda* as the billets aged under field conditions. They found that bark beetles arrived soon after felling whereas ambrosia beetles arrived later (4 to 6 wk after the felling date). Monoterpene emissions decreased over the 6-wk post-felling period whereas ethanol emissions increased but then decreased after 6 wk, likely due to desiccation. Attraction of all Scolytinae ceased after 8 wk.

Species such as *I. grandicollis* typically arrive as soon as trees are felled or struck by lightning, a time when host resources are still intact, tree resistance has been reduced, and minimal ethanol is being produced. I found that the presence of ethanol (particularly at high release rates) interrupted attraction of *I. grandicollis* in 3 experiments that included α-pinene in the current study (Fig. 5 E–G). In contrast, the responses of *I. avulsus* differed among 2 experiments (Fig. 5 C–D). I am unable to speculate on the reason for such variation. A lack of response to or interruption by ethanol (Table 6) should be expected for longhorn beetles such as *Monochamus titillator* which attack trees that have been attacked by *Ips* bark beetles. Responses by some pine Cerambycidae are strongly enhanced by *Ips* pheromones such as ipsenol and ipsdienol (Allison et al. 2001, 2003, 2004, Miller et al. 2013, 2015a). The effects of ethanol dose might be different for hardwood cerambycids when combined with their pheromones. Ethanol enhances attraction of cerambycids to traps baited with cerambycid pheromones such as 2,3-*syn*-hexanediol and 3-hydroxyhexan-2-one (Miller et al. 2015b, 2017). Linsley (1959) noted that ethanol would be more important to cerambycids breeding in hardwoods than those breeding in softwoods such as pine.

In dead trees and downed woody material, ethanol concentrations should continue to increase until the tissues dry out or are fully utilized by microbes. Bark beetle species such as *Hylastes porculus*, *Hylastes salebrosus*, *Hylastes tenuis*, and *O. caelatus* typically arrive later than *Dendroctonus* or *Ips* species on downed woody material (personal observations), likely when ethanol production has started to occur, thereby providing a possible explanation for their response

Table 7. Total beetle numbers (N) and ANOVA results for treatment effects on trap catches of beetle predators (Coleoptera) in experiments 2–6 with mean (± SE) catches for those species not affected by ethanol treatments.

Family, Species	exp	*N*	*F*	df	*P*	Mean (± SE) trap catch
Cleridae						
Thanasimus dubius	5	38	0.29	3, 24	0.829	1.1 ± 0.2
Elateridae						
Alaus myops	4	87	2.00	3, 27	0.138	2.2 ± 0.3
Histeridae						
Platysoma attenuatum	6	207	0.31	3, 27	0.816	5.2 ± 0.6
Platysoma cylindricum	6	186	1.61	3, 27	0.211	4.7 ± 0.6
Platysoma parallelum	6	151	13.64	3, 27	<0.001	–
Passandridae						
Catogenus rufus	4	59	2.33	3, 27	0.097	1.5 ± 0.3
	6	42	2.33	3, 27	0.097	1.1 ± 0.2
Tenebrionidae						
Corticeus species	6	298	2.44	3, 27	0.086	7.5 ± 0.8
Trogossitidae						
Temnoscheila virescens	3	85	5.91	3, 21	0.004	–
	4	606	10.41	3, 27	<0.001	–
	5	1,093	6.46	3, 24	0.002	–
	6	2,263	8.33	3, 27	<0.001	–
Tenebroides species	2	50	0.30	3, 27	0.829	1.3 ± 0.2
	4	142	2.70	3, 27	0.065	3.6 ± 0.4
	5	51	2.00	3, 24	0.140	1.4 ± 0.3
	6	98	2.40	3, 27	0.090	2.5 ± 0.3
Zopheridae						
Lasconotus species	5	1,796	4.55	3, 24	0.012	–
	6	4,482	0.67	3, 27	0.576	112.1 ± 8.6
Pycnomerus sulcicollis	4	95	1.09	3, 27	0.370	2.4 ± 0.3
	5	173	0.65	3, 24	0.592	4.8 ± 0.7
	6	431	0.17	3, 27	0.168	10.8 ± 1.4

to ethanol release rate in the current study (Figs. 3 B–E, Fig. 4 A–E, Fig. 5B). Root weevils such as *Hylobius pales* and *Pa. picivorus* likely have similar requirements as noted by their responses to ethanol dose (Fig. 6 A–E).

Ambrosia beetles typically attack hosts later than bark beetles and at a time when ethanol production is typically high (Fletchmann et al. 1999). In the Pacific Northwest of the United States, ambrosia beetles such as *Trypodendron lineatum* L. (Coleoptera: Curculionidae) attack logs or downed conifers that have been allowed to age over a season or two (Dyer and Chapman 1965, Kelsey 1994a). The concentration of ethanol in phloem and xylem tissues of downed trees such as Douglas fir increases with time (Kelsey 1994a). My trapping results on responses of ambrosia beetles to ethanol lures releasing at different rates in north-central Georgia are consistent with those of Byers (1992), Klimetzek et al. (1986), and Schroeder and Lindelöw (1989) in Sweden and Germany.

In recent trials conducted in the United States and Italy, Yilmaz et al. (2024) found that commercial lures releasing ethanol at high rates were attractive to 4 species of ambrosia beetles: *Anisandrus maiche* (Stark) (Coleoptera: Curculionidae), *Xyleborinus saxesenii*, *Xylosandrus crassiusculus*, and *Xylosandrus germanus* (Blandford) (Coleoptera: Curculionidae). Similarly in fruit and nut orchards, and ornamental nurseries in the eastern United States, Govindaraju et al. (2025) found that trap catches of *Xylosandrus crassiusculus* and *Xylosandrus germanus* were higher in bottle traps with lures releasing ethanol at high rates. I found similar responses by ambrosia beetles in the current study (Figs. 1–2).

The positive dose-dependent responses exhibited by ambrosia beetles may be particularly important to their reproductive success. Beetles bore into the sapwood/heartwood and inoculate galleries with ambrosia fungi; larval ambrosia beetles feed exclusively on ambrosia fungi (Biedermann et al. 2009, Kirkendall et al. 2015, Hulcr and Stelinski 2017, Hulcr and Skelton 2023). Lehenberger et al. (2021) found that ethanol-rich hosts facilitated the development of ambrosia fungi, but inhibited fungi associated with bark beetles. In the eastern United States, flood-stress on nursery trees resulted in higher levels of ethanol in woody tissues, making them attractive to ambrosia beetles (Ranger et al. 2012, 2013, 2015a, 2015b, 2016, 2021). Injecting trees with ethanol can also induce attacks by ambrosia beetles such as *Xylosandrus germanus* (Ranger et al. 2010, 2013, 2021, Reding et al. 2017, Govindaraju et al. 2025). Ranger et al. (2018) found that *X. germanus* were attracted to trees baited with ethanol; foundresses were only able to establish fungal gardens and brood in trees containing ethanol.

Ambrosia fungi can both produce and detoxify ethanol, allowing them the ability to maintain ethanol levels optimal for producing gardens of *Ambrosiella* species (Ceratocystidaceae) and *Raffaelea* species (Ophiostomataceae) fungal colonies over a longer period of time, while minimizing invasions by other fungal species such as *Aspergillus* and *Penicillium* species (Aspergillaceae) which are inhibited by ethanol (Ranger et al. 2018, Lehenberger et al. 2021). Species specificity in host selection by ambrosia beetles can be related to ethanol concentration within woody tissues (Cavaletto et al. 2021, 2023).

In the southeastern United States, predators eavesdrop on the pheromones used by bark and woodboring beetles, and the kairomones that attract them (Miller 2023, Miller and Asaro 2023, Miller et al. 2023). Except for 3 species, most predators in this study did not exhibit a dose-dependent response to ethanol. *Pl. parallelum* and *Lasconotus* species exhibited a dose response under

semiochemical context associated with *Ips* bark beetles (Fig. 8 A–B), suggesting a predator-prey association between these species. Trap catches of *Te. virescens* were positively dose dependent to ethanol in all 4 experiments (Fig. 8 C–F), similar to the responses by several species of ambrosia beetles and several species of bark beetles (Figs 1–4). Further research is required to identify the importance of these predators on these species of bark and ambrosia beetles.

Dose responses to kairomones and pheromones are common among bark and woodboring beetles, raising an important issue for managers of detection programs for non-native species (Dodds et al. 2024). If we assume that traps baited with lures capturing the greatest numbers of beetle are more likely to catch the same species when their numbers are low, then lure selection should be one of several factors to consider in operational programs. Current lures manufactured for operational use are guided, in part, on the market acceptance of lure costs, especially when large programs put out request for bids (personal observation). In general, lures releasing at higher rates are likely to be more expensive. Two other important considerations include lures for other species and enough traps to ensure adequate coverage over a geographic range (Dodds et al. 2024). Managers must balance these 3 variables within their limited funding for detection programs.

Managers should also consider competing sources of attractants when dealing with traps baited with host kairomones such as ethanol and α-pinene. Downed, dead, or damaged woody material is common in most forests, and may be more attractive to new invasive species arriving in low numbers. Practices such as selective logging of dead or dying trees, prescribed burns to remove downed woody debris, and planting of site-specific trees and shrubs could enhance forest health and provide an optimal environment for detection traps.

Acknowledgments

I thank Chris Crowe for field assistance (USDA Forest Service), Rick Hoebeke (University of Georgia Collection of Arthropods) for verification of insect identifications. Rick Kelsey and Chris Asaro (USDA Forest Service) graciously provided critical review comments on the manuscript. The findings and conclusions in this publication are those of the author and should not be construed to represent any official USDA or U.S. Government determination or policy. The use of trade or firm names in this publication is for reader information only and does not imply endorsement by the USDA of any product or service. The USDA is an equal opportunity provider, employer, and lender.

Author contributions

Daniel Miller (Conceptualization [lead], Formal analysis [lead], Methodology [lead], Supervision [lead], Writing—original draft [lead], Writing—review & editing [lead])

Funding

This research was supported by the U.S. Department of Agriculture (USDA)–Forest Service.

Conflicts of interest. None declared.

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