Variation in Effects of Conophthorin on Catches of Ambrosia Beetles (Coleoptera: Curculionidae: Scolytinae) in Ethanol-Baited Traps in the United States

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ABSTRACT In 2013, we examined the effects of conophthorin on flight responses of ambrosia beetles (Coleoptera: Curculionidae: Scolytinae) to multiple-funnel traps baited with ethanol in Georgia, Michigan, New Hampshire, and Oregon. Adventive species (=exotic, nonnative, immigrant, introduced) accounted for 91.4% of total catches of ambrosia beetles. Conophthorin increased catches of *Xyleborinus saxesenii* (Ratzeburg) in Georgia, New Hampshire, and Oregon. Catches of *Cyclorhipidion pelliculosum* (Eichhoff) were increased by conophthorin in New Hampshire but not in Michigan. In Oregon, conophthorin decreased catches of *Xylosandrus germanus* (Blandford) to ethanol-baited traps but not in Michigan and New Hampshire. In Georgia, conophthorin increased catches of *Gnathotrichus materiarius* (Fitch), *Xyleborus* spp., and *Xylosandrus crassiusculus* (Motschulsky) but decreased catches of *Cnestus mutilatus* (Blandford), *Dryoxylon onoharaensum* (Murayama), and *Cyclorhipidion bodoanum* (Reitter). Conophthorin had no effect on catches of *Ambrosiophilus atratus* (Eichhoff), *Anisandrus dispar* (F.), *Anisandrus sayi* (Hopkins), *Gnathotrichus sulcatus* (Leconte), *Monarthrum fasciatum* (Say), *Monarthrum mali* (Fitch), and *Xylosandrus compactus* (Eichhoff). Attraction of the bark beetle, *Hypothenemus rotundicollis* (Eichhoff), was interrupted by conophthorin in Georgia. Our results suggest that adding conophthorin lures to traps baited with ethanol may have utility in detection programs in North America and overseas. However, traps baited with ethanol alone should also be used due to interruption in attraction for some species of ambrosia beetles.

KEY WORDS Xyleborini, conophthorin, semiochemical, exotic, adventive

Introduction

Ecosystems and economies throughout the world are under threat of negative impacts from adventive (=exotic, nonnative, immigrant, introduced) insect species (Holmes et al. 2009, Wheeler and Hoebeke 2009, Aukema et al. 2011). Adventive species of ambrosia beetles such as *Xylosandrus germanus* (Blandford) and the granulate ambrosia beetle, *Xylosandrus crassiusculus* (Motschulsky) (Coleoptera: Curculionidae: Scolytinae) are economically important pests of numerous plant species in horticultural orchards and nurseries of eastern North America and have become naturalized in forests of several regions (Weber and McPherson 1984, Mizell et al. 1994, Oliver and Mannion 2001, Künholz et al. 2003, Kirkendall and Ødegaard 2007, Ranger et al. 2010, Reding et al. 2011). In Asia, the native species *Euwallacea fornicatus* (Eichhoff) is a major pest in plantations of tea, *Camellia sinensis* (L.) Kuntze, and orchards of longan, *Dimocarpus longan* Loureiro (Sittichaya et al. 2012). As an adventive species, *E. fornicatus* threatens commercial plantations of avocado in California and Israel (Mendel et al. 2012). Another species native to Asia, the black twig borer, *Xylosandrus compactus* (Blandford) is a serious pest in coffee plantations in Hawaii (Burbano et al. 2012).

Originating from Asia, the redbay ambrosia beetle, *Xyleborus glabratus* Eichhoff, presented a new concern about adventive species by vectoring a wilt disease that causes significant mortality of redbay, *Persea borbonia* (L.), and swampbay trees, *Persea palustris* (Rafinesque), in the southeastern United States (Fraedrich et al. 2008, Haack and Rabaglia 2013). Commercial orchards of avocado, *Persea americana* Miller, in Florida are threatened by *X. glabratus* and the wilt disease that it carries (Mayfield et al. 2008, Carrillo et al. 2012). Many other species of ambrosia beetles such as *X. crassiusculus*, *X. compactus*, and *Xyleborinus saxesenii* (Ratzeburg) are often associated with *X. glabratus* in host material and may further vector the wilt disease (Crane et al. 2008, Carrillo et al. 2012, Mayfield and Hanula 2012).

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Early detection of adventive species is critical for countering their potential impacts on native trees and forests (Chornesky et al. 2005, Wheeler and Hoebeke 2009, Klepzig et al. 2010, Liebhold 2012, Rassati et al. 2014). The cryptic nature of bark and wood boring beetles that hide in wood products, wooden packing material, and nursery stock, can pose significant challenges for detection programs (Allen and Humble 2002, Liebhold et al. 2012, Haack and Rabaglia 2013). In the United States, national programs administered by the U.S. Department of Agriculture, such as the Animal and Plant Health Inspection Service–Cooperative Agricultural Pest Survey and the Forest Service–Early Detection and Rapid Response program, focus on flying adults by using multiple-funnel traps baited with ethanol to detect and monitor adventive species of ambrosia beetles (Rabaglia et al. 2008, Jackson et al. 2010).

Ethanol is broadly attractive to ambrosia beetles including many adventive species of Xyleborini (Coyle et al. 2005, Miller and Rabaglia 2009, Reding et al. 2011, Kelsey et al. 2013, Ranger et al. 2010, 2011, 2014). For some species, catches in ethanol-baited traps can be enhanced by addition of host compounds (Miller and Rabaglia 2009, Gandhi et al. 2010, Kendra et al. 2014, Ranger et al. 2014). Recently, Dodds and Miller (2010) noted that racemic (*E*)-conophthorin (7-methyl-1,6-dioxaspirol[4.5]decane) enhanced catches of *X. germanus* in nonbaited traps adjacent to trap trees in New York.

Conophthorin is found in the bark of several genera of angiosperms (Huber et al. 1999, Zhang et al. 2001). Additionally, various stereoisomers of conophthorin are utilized as pheromones (attractive or repellent) for several species of twig beetles *Pityophthorus* spp. (Dallara et al. 2000, de Groot and DeBarr 2000), the bark beetles *Hylesinus* (=*Leperisinus*) *varius* (F.) and *Cryphalus piceae* (Ratzeburg) (Francke et al. 1979, Kohnle et al. 1992), and several species of pine cone beetles, *Conophthorus* spp. (Birgersson et al. 1995, Pierce et al. 1995, de Groot and DeBarr 2000, Miller et al. 2000).

Conophthorin enhanced catches of *X. germanus*, *Euwallacea validus* (Eichhoff), and *Cyclorhipidion pelliculosum* (Eichhoff) in ethanol-baited traps in Ohio (Ranger et al. 2014). In Indiana, catches of *X. germanus* in ethanol-baited traps were unaffected by conophthorin whereas conophthorin enhanced catches of *X. crassiusculus* by approximately 145% (VanDerLaan and Ginzel 2013). In Germany, attraction of *X. germanus* to ethanol was interrupted by conophthorin (Kohnle et al. 1992). Our objective was to evaluate the effects of conophthorin on trap catches of various species of ambrosia beetles in ethanol-baited traps over a broad geographic range in the United States, using the same lures at all sites in an attempt to clarify the disparity in results by Kohnle et al. (1992), Dodds and Miller (2010), VanDerLaan and Ginzel (2013), and Ranger et al. (2014).

Materials and Methods

In 2013, we conducted four trapping experiments across the United States to determine the effect of conophthorin on catches of ambrosia beetles in ethanol-baited traps (Table 1). Contech Enterprises Inc. (Victoria, BC) supplied ethanol pouches that release ethanol at a rate of approximately 0.5 g/d at 25°C. Low (C1) and medium release-rate (C2) conophthorin lures, consisting of racemic *E*-conophthorin in closed, polyethylene microcentrifuge tubes were obtained from Synergy Semiochemicals Corp. (Burnaby, BC; 400 µl polyethylene microcentrifuge tube) and Contech Enterprises Inc. (250 µl polyethylene microcentrifuge tube), respectively. The release rates were approximately 0.25 and 0.50 mg/d at 20°C, respectively. All release rates of lures mentioned in the text were determined by the respective manufacturers.

We had hoped to use the high release-rate conophthorin lure (400 µl polyethylene microcentrifuge tube; 1 mg/d at 20°C) used by VanDerLaan and Ginzel (2013) in order to make direct comparisons to their results. Unfortunately, the high release-rate device from Contech was unavailable at the time of our study. Instead, we purchased conophthorin lures (400 µl microcentrifuge tube) from Synergy. Our expectation was that the 400-µl conophthorin lures from the two companies would have comparable release rates. Determination of the release rate for the 400 µl lure produced by Synergy (conducted by the manufacturer after the conclusion of our studies) revealed a release rate of 0.25 mg/d at 20°C, considerably lower than the expected rate of 1 mg/d at 20°C. Therefore, high release-rate conophthorin lures were not used in our experiments.

In each experiment, we used a randomized block design with multiple-funnel traps (Contech Enterprises in Georgia, Michigan, and Oregon, and Synergy Semiochemicals in New Hampshire) spaced 10–25 m within blocks and ≥15 m between blocks. Traps were suspended between trees by rope such that the bottom of each trap was 0.5–1.0 m above ground level and each trap was >2 m from any tree to avoid any influence from trees. Eight-unit traps were used in Oregon whereas 12-unit traps were used in Michigan and New Hampshire. In Georgia, we used 10-unit traps that were modified by increasing the center hole of each funnel from 5 cm to 12 cm thereby allowing placement of lures within the funnels (Miller et al. 2013).

Each collection cup contained 150–200 ml of antifreeze solution as a killing and preservation agent (Miller and Duerr 2008). We used four different brands of commercial antifreeze solutions (Table 1), with concentrations of propylene glycol ranging from 10–40%. Each solution contained either a red or green dye but no ethanol (verified by examination of product labels and associated MSDS sheets). Catches were collected every 2–3 wks with new antifreeze solution added on each occasion. Voucher specimens of all species were deposited in the University of Georgia Collection of Arthropods, Georgia Museum of Natural History, University of Georgia (Athens, GA).

The objective of Experiment 1 was to compare the effects of conophthorin lures released at two different rates. We deployed 30 multiple-funnel traps in a mixed species forest on the Oconee National Forest (Table 1). The stand consisted of *Pinus taeda* L., *Pinus echinata*

Table 1. Locations, coordinates, brands of antifreeze, and trapping dates for each of four experiments on the flight responses of ambrosia beetles to multiple-funnel traps baited with ethanol or ethanol and conophthorin in 2013

Exp	Location	Coordinates	Brand of RV antifreeze	Trapping dates
1	Putnam Co., GA	33.233N, 83.520W	Splash[a]	13 March–9 May
2	Strafford Co., NH	Sites 1 & 2—43.114N, 70.949W	Prestone LT[b]	3 May–26 June
3	Kalamazoo Co., MI	Site 1—42.372N, 85.356W Site 2—42.358N, 85.337W	Prestone RV[c]	8 May–1 July
4	Multnomah Co., OR Clackamas Co., OR	Site 1—45.572N, 122.731W Site 2—45.422N, 122.250W	MotoTech[d]	16 May–11 July

[a] Splash RV & Marine Antifreeze, Fox Packaging Inc., St. Paul, MN.
[b] Prestone Low Tox Antifreeze, Prestone Products Corp., Danbury, CT.
[c] Prestone RV Waterline Antifreeze, Prestone Products Corp., Danbury, CT.
[d] MotoTech RV Antifreeze, Kroger Co. of Michigan, Livonia, MI.

Miller, *Quercus alba* L., and *Quercus falcata* Michaux with mean diameters of approximately 27.6, 40.2, 41.8, and 38.5 cm, respectively, at breast height (dbh). Traps were set in 10 replicate blocks ($n = 10$) of three traps per block. One of the following three treatments was allocated to each of the three traps within each block: 1) ethanol lure alone; 2) ethanol lure+low release-rate conophthorin lure (C1); and 3) ethanol lure+medium release-rate conophthorin lure (C2).

The objective of Experiments 2–4 was to evaluate the effect of conophthorin released from one type of lure (provided by one supplier) across a broad geographic range with each experiment having the same experimental design. Traps were set in 10 replicate blocks ($n = 10$) of two traps per block with five blocks at each of two sites at each location. The distance between sites ranged from 100 m in New Hampshire to over 2 km in Oregon (Table 1). In New Hampshire, both sites were dominated by *Pinus strobus* L. (mean dbh, 47.4 cm) whereas the sites in Michigan were dominated by *Pinus resinosa* Aiton (mean dbh, 20.5 cm). The sites in New Hampshire had experienced recent logging. In Oregon, site 1 consisted primarily of *Pinus ponderosa* P. Lawson ex. C. Lawson (mean dbh, 22.1 cm) with minor components of *Pinus sylvestris* L., *Quercus garryana* Douglas, *Acer macrophyllum* Pursch, *Fraxinus latifolia* Bentham, and *Sequoia sempervirens* D. Don whereas site 2 consisted primarily of *Pseudotsuga menziesii* (Mirbel) Franco (mean dbh, 16.9 cm) with *Alnus rubra* Bongard as the secondary species. In each experiment, one of the following two treatments was allocated to each of the two traps within each block: 1) ethanol lure alone; and 2) ethanol lure + low release-rate conophthorin lure (C1).

For each species, analyses were conducted on total cumulative numbers of insects captured throughout the trapping period per trap for each experiment. Trap catch data were transformed by ln (Y + 1) to ensure homoscedasticity (Pepper et al. 1997) for species with sufficient number of captured beetles ($N \geq 25$). Normality and homoscedasticity were verified using the Kolmogorov–Smirnov and Equal Variance tests, respectively, with the SigmaStat (ver. 3.01) statistical package (SYSTAT Software Inc., Point Richmond, CA). In Experiment 1, trap catch data were subjected to ANOVA with the SigmaStat package using the following model components: 1) replicate; and 2) treatment. The Holm–Sidak multiple comparison procedure (Glantz 2005) was used to compare means for each species exhibiting a significant treatment effect ($\alpha = 0.05$). In Experiments 2–4, trap catch data were paired by block then subjected to analyses by paired *t* test for each species using the SYSTAT (ver. 11.0.01) statistical package (SYSTAT Software Inc., Point Richmond, CA).

Results

We collected 19,713 ambrosia beetles in the four experiments conducted across the United States, with xyleborine species accounting for 94.9% of all beetles captured (Table 2). Of 17 ambrosia beetle species captured from the four regions, 11 were adventive species (all Xyleborini) and accounted for 91.4% of total catches. There were significant differences in species composition across the four locations, with abundance and diversity greatest in Georgia and New Hampshire. Only *X. saxesenii* was captured at all four locations. *Xylosandrus germanus* was dominant in three locations along with *X. saxesenii* in Oregon, *Ambrosiophilus atratus* (Eichhoff) in Michigan, and *X. saxesenii* and *C. pelliculosum* in New Hampshire. In Georgia, catches were dominated by *Cyclorhipidion bodoanum* (Reitter), *Dryoxylon onoharaensum* (Murayama), and *X. saxesenii*.

In Georgia (Expt. 1), catches of seven ambrosia beetle species and one bark beetle species *Hypothenemus rotundicollis* (Eichhoff) were significantly affected by conophthorin treatments (Table 3). Traps baited with ethanol and the medium release-rate conophthorin lure (C2) caught the greatest numbers of the ambrosia beetles *Gnathotrichus materiarius* (Fitch), *Monarthrum mali* (Fitch), *X. saxesenii*, and *Xyleborus* spp. (Fig. 1A–D). Catches of the four species were unaffected by the addition of the low release-rate conophthorin lure (C1). Catches of the ambrosia beetles *A. atratus*, *Monarthrum fasciatum* (Say), *X. compactus*, and *X. crassiusculus* to ethanol-baited traps were unaffected by the addition of conophthorin lures (Fig. 1E–H). Conophthorin released at the medium rate (C2) interrupted the attraction of the ambrosia beetles *C. bodoanum*, *D. onoharaensum*, the camphor shot borer, *Cnestus mutilatus* (Blandford), and the bark beetle *H. rotundicollis* (Fig. 1I–L).

Table 2. Total catches of ambrosia beetles in multiple-funnel traps baited with ethanol or ethanol and conophthorin in four experiments conducted in 2013

Species	Georgia (Exp 1)	New Hampshire (Exp 2)	Michigan (Exp 3)	Oregon (Exp 4)
Corthylini				
Gnathotrichus materiarius	48	1	5	–
Gnathotrichus sulcatus	–	–	–	99
Monarthrum fasciatum	58	7	–	–
Monarthrum mali	385	41	5	–
Xyleborini				
Ambrosiophilus atratus[a]	612	–	117	–
Anisandrus dispar[a]	–	–	–	26
Anisandrus sayi	–	939	35	–
Cnestus mutilatus[a]	40	–	–	–
Cyclorhipidion bodoanum[a]	960	–	–	5
Cyclorhipidion pelliculosum[a]	–	4,255	40	–
Dryoxylon onoharaensum[a]	1,428	2	–	–
Euwallacea validus[a]	–	2	–	–
Xyleborinus saxesenii[a]	1,073	1,438	18	2,166
Xyleborus spp.	49	18	5	–
Xylosandrus compactus[a]	26	–	–	–
Xylosandrus crassiusculus[a]	397	–	–	–
Xylosandrus germanus[a]	–	3,591	249	1,211
Total	5,076	10,294	474	3,507
Percent adventive species	89.3	90.2	89.5	97.2

[a] Adventive (=exotic, nonnative) species.

Table 3. Results of ANOVA on trap catches on bark and ambrosia beetles in Experiment 1 conducted in Georgia

Species	Replicate (df = 918)		Treatment (df = 218)	
	F	*P*	*F*	*P*
Ambrosiophilus atratus	2.252	0.068	0.236	0.792
Cnestus mutilatus	2.295	0.064	4.161	0.033
Cyclorhipidion bodoanum	6.669	<0.001	6.893	0.006
Dryoxylon onoharaensum	1.060	0.435	9.003	0.002
Gnathotrichus materiarius	2.667	0.037	13.067	<0.001
Hypothenemus rotundicollis	2.667	0.037	13.067	<0.001
Monarthrum fasciatum	1.259	0.322	0.328	0.724
Monarthrum mali	3.818	0.008	9.381	0.002
Xyleborinus saxesenii	8.221	<0.001	6.323	0.008
Xyleborus spp.	2.650	0.037	3.883	0.040
Xylosandrus compactus	1.603	0.188	0.468	0.634
Xylosandrus crassiusculus	2.575	0.042	1.911	0.177

In New Hampshire (Expt. 2), catches of *X. saxesenii* and *C. pelliculosum* in ethanol-baited traps were enhanced by the addition of low release-rate conophthorin(C1) lures (Fig. 2). Catches of the remaining three species were unaffected by the addition of conophthorin. In Michigan (Expt. 3), catches of four species of ambrosia beetles in ethanol-baited traps were unaffected by the addition of conophthorin (Fig. 3). In Oregon, catches of *X. germanus* were reduced with the addition of conophthorin (C1) whereas those of *X. saxesenii* were enhanced (Fig. 4). Catches of *Gnathotrichus sulcatus* (LeConte) and *Anisandrus dispar* (F.) were unaffected by the addition of conophthorin.

Discussion

At present, 24 species of adventive xyleborine species are established in North America, but not necessarily widely distributed (Cognato et al. 2013, Haack and Rabaglia 2013). The risk of invasion expansions by these species to new regions within North America continues to be high, as many species are polyphagous and easily transported in wood products. Moreover, the risk of further invasions by ambrosia beetles into North America is still high, particularly in the Southeast where the climate is suitable for establishment of beetles from tropical regions and international trade is still growing (Marini et al. 2011). Tropical regions tend to have a high diversity of ambrosia beetle species, many not known for North America. Sitichaya et al. (2012) captured 64 xyleborine species in mixed-crop durian, *Drio zibethinus* Murray orchards in southern Thailand over a period of 14 months. The risk of invasions is high even in tropical areas with existing diverse populations. Kirkendall and Ødegaard (2007) noted recent invasions by *E. fornicatus*, *X. crassiusculus*, and *Xyleborinus exiguus* (Walker) into old-growth tropical forests of southern Central America.

The potential for invasions by ambrosia beetles is likely associated, in part, with their broad host range, particularly for species of Xyleborini. More than 200 host plants in more than 60 families are associated with *X. crassiusculus*, *X. compactus*, and *X. germanus* alone (Ngoan et al. 1976, Weber and McPherson 1983, Oliver and Mannion 2001). In any given forest, it is highly likely that adventive species can find suitable hosts for brood production.

Improving the efficiency of existing trapping systems is of paramount importance in minimizing the threats posed by adventive species: the more attractive a lure is for a species, the more likely it will attract rare individuals of that species. Trap catches of ambrosia beetles in ethanol-baited traps seem low when considering the emergence numbers of beetles from a single log, particularly in comparison to trap catches of the striped ambrosia beetle, *Trypodendron lineatum* (Olivier)

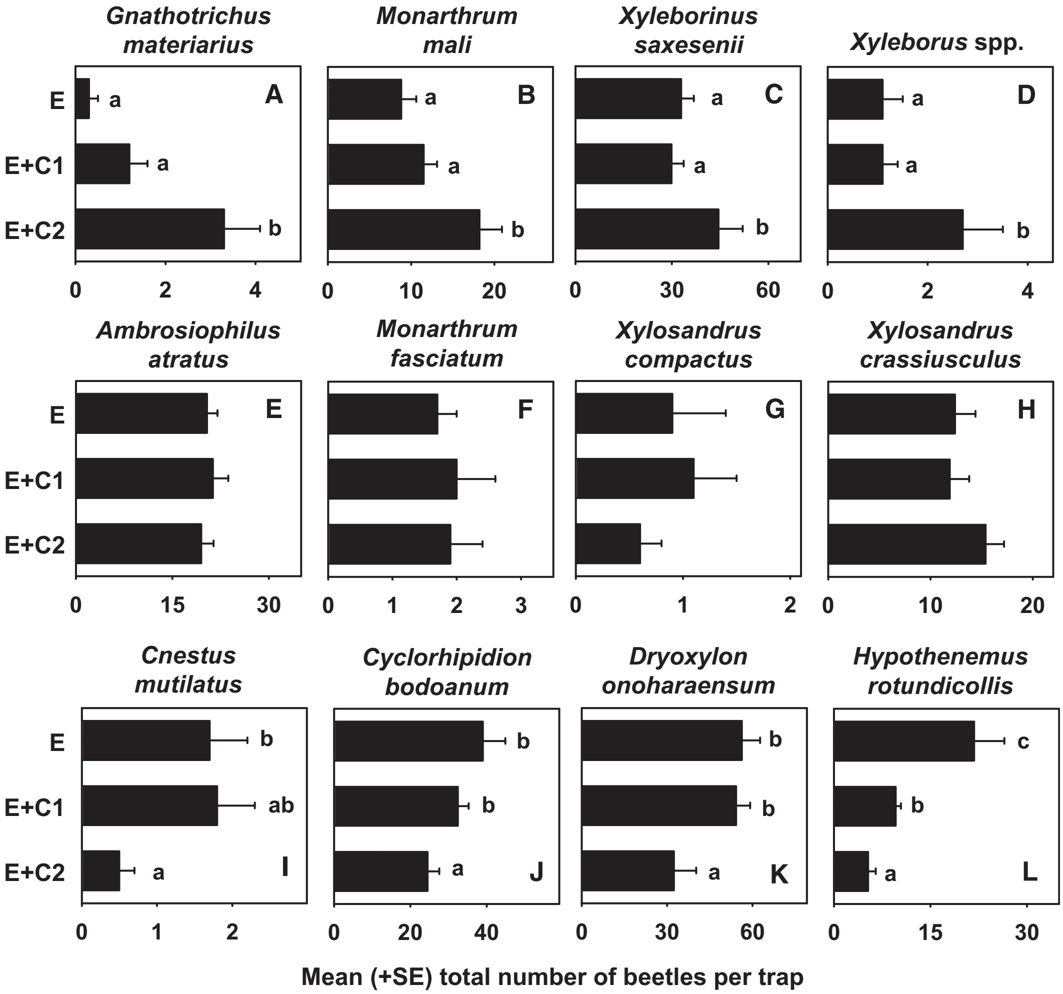

Fig. 1. Mean (+SE) total number of ambrosia (A–K) and bark beetles (L) captured in multiple-funnel traps baited with ethanol UHR lure (**E**), ethanol UHR lure and low-release rate conophthorin lure (**E + C1**), or ethanol UHR lure and medium-release rate conophthorin lure (**E + C2**) in Georgia (Experiment 1) for the period of 13 March–9 May 2013. For each species, means followed by the same letter are not significantly different at $P = 0.05$ (Holm–Sidak test).

(Xyloterini) in northwestern North America (Lindgren and Fraser 1994). Unlike xyleborine species of ambrosia beetles, *T. lineatum* is a diploid species with equal numbers of males and females, all capable of flight and dispersal. *T. lineatum* adults use lineatin as a sex pheromone that attracts both sexes in large numbers (Byrne et al. 1974; Borden et al. 1976, 1979; Vité and Bakke 1979; Salom and McLean 1988). Lures for these species are highly attractive, resulting in the capture of tens of thousands of beetles per trap in wood-processing areas in the Pacific Northwest (Lindgren and Fraser 1994).

No sex pheromones are currently known for xyleborine beetles (El-Sayed 2014), and the probability of finding any is likely low due to their breeding system. Unique among Scolytinae and Platypodinae, xyleborine species typically exhibit a haplodiploid breeding system (Kirkendall 1993, Peer and Taborsky 2005). The proportion of males in a breeding group is generally low [e.g., 5–10% for *X. germanus* (Peer and Taborsky 2004)]. Haploid males are diminutive and incapable of flight, although males can disperse to adjacent galleries by walking. Males mate with sisters within their gallery as well as females in adjacent galleries. All colonization of new breeding sites is done by fertilized females. The mating system precludes the need for long-range sex pheromones, as males cannot fly. The ability of females to invade new hosts rapidly is likely a reason for the dominance of xyleborine ambrosia beetles as adventive species, particularly as their inbreeding mating system seems to have minimal adverse effects that typically arise from inbreeding depression (Peer and Taborsky 2005, Kirkendall and Jordal 2006).

Ethanol is broadly associated with dead or dying host material of numerous taxa and correspondingly, broadly attractive to ambrosia beetles (Coyle et al. 2005; Miller and Rabaglia 2009; Reding et al. 2011; Kelsey et al. 2013; Ranger et al. 2010, 2011, 2014).

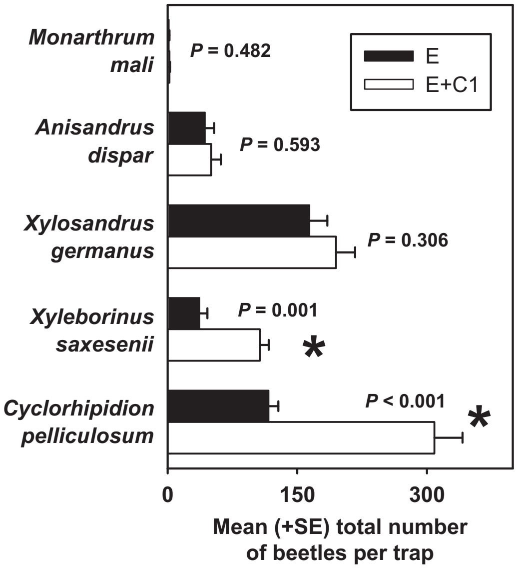

Fig. 2. Mean (+SE) total number of ambrosia beetles captured in multiple-funnel traps baited with ethanol UHR lure (**E**) or ethanol UHR lure and low-release rate conophthorin lure (**E + C1**) in New Hampshire (Experiment 2) for the period of 3 May–26 June 2013. For each species, pairs of means followed by an asterisk are significantly different at $P = 0.05$ (paired t test).

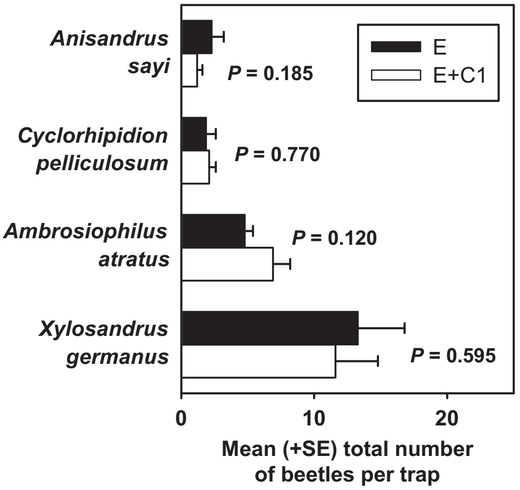

Fig. 3. Mean (+SE) total number of ambrosia beetles captured in multiple-funnel traps baited with ethanol UHR lure (**E**) or ethanol UHR lure and low-release rate conophthorin lure (**E + C1**) in Michigan (Experiment 3) for the period of 8 May–1 July 2013.

The efficacy of ethanol-baited traps may be compromised by competing natural odor sources of ethanol occurring throughout forested stands. Finding additional attractive compounds such as conophthorin could improve the efficacy of baited traps and lead to improved detection and management programs, particularly for targeted species such as *X. germanus*. Although species such as *X. crassiusculus* and *X. germanus* have a broad host range, they may have host preferences within specific locations (Frank et al. 2013, Ranger et al. 2014). Host specificity might be reflected by optimal blends of host compounds for these species (Kendra et al. 2014).

In 2013, we found that attraction of five species was enhanced by the addition of conophthorin to ethanol-baited traps (Figs. 1–4). Catches of *G. materiarius* and *M. mali* (Corthylini), and *Xyleborus* species (Xyleborini) increased by 100–145% in Georgia. The effect of conophthorin on catches of *X. saxesenii* (Xyleborini) was consistent across Georgia, New Hampshire, and Oregon, increasing trap catches by 35–188%. As in Ranger et al. (2014) in Ohio, conophthorin increased catches of *C. pelliculosum* in New Hampshire (Fig. 2). Additional attractive compounds for ambrosia beetles may yet be found in plant extracts or essential oils such as cubeb oil (Kendra et al. 2013).

For other species of ambrosia beetles, there seems to be considerable variation in responses to conophthorin between locations and/or published studies. Unlike VanDerLaan and Ginzel (2013) in Indiana, conophthorin had no effect on trap catches of *X. crassiusculus* in Georgia (Fig. 1). Conophthorin enhanced catches of *G. materiarius* in Georgia (Fig. 1) but not in New Hampshire (Dodds and Miller 2010). In contrast to Dodds and Miller (2010) and Ranger et al. (2014), conophthorin had no effect on trap catches of *X. germanus* in New Hampshire and Michigan (Figs. 2 and 3) and was interruptive in Oregon (Fig. 4). As in Ranger et al. (2014), attraction of *C. pelliculosum* was enhanced by conophthorin in New Hampshire (Fig. 2) but not in Michigan (Fig. 3).

Some of the variation among localities may be attributable to differences in release rates from lures used in the various studies. In our study, we used a low release-rate lure (0.25 mg/d) in Oregon, Michigan, and New Hampshire whereas Dodds and Miller (2010) and Ranger et al. (2014) used a medium release-rate lure (0.5 mg/d). In Georgia, we used both lures and found that several species of beetles exhibited a dose-dependent response to conophthorin with differences in trap catches evident with the medium release-rate lure (0.5 mg/d) but not with the low release-rate lure (0.25 mg/d). In contrast, VanDerLaan and Ginzel (2013) used a high release-rate conophthorin lure (1 mg/d) in their study.

There was also variation among the various studies with the lures used to release ethanol. VanDerLaan and Ginzel (2013) and Ranger et al. (2014) used a low release-rate ethanol lure (65 mg/d at 25°C) whereas we used a high release-rate ethanol lure (0.5 g/d at 25°C). Dose-dependent responses by ambrosia beetles to ethanol have been observed for *A. sayi*, *Xyleborinus alni* (Niisima), and *X. saxesenii* in Ohio (Ranger et al. 2011) and for *A. dispar*, *X. saxesenii*, *X. germanus*, and *T. lineatum* in Germany (Klimetzek et al. 1986). Clearly, additional studies are required to determine the contribution of release rate of conophthorin and ethanol on the observed variation between locations and studies in North America.

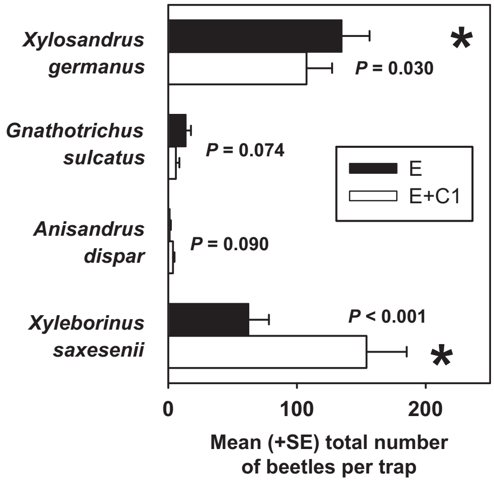

Fig. 4. Mean (+SE) total number of ambrosia beetles captured in multiple-funnel traps baited with ethanol UHR lure (**E**) or ethanol UHR lure and low-release rate conophthorin lure (**E + C1**) in Oregon (Experiment 4) for the period of 16 May–11 July 2013. For each species, means followed by an asterisk are significantly different at $P = 0.05$ (paired *t* test).

Specificity to host blends can be enhanced by interruption of attraction by compounds not associated with preferred hosts. For example, α-pinene interrupts attraction of *Ambrosiodmus tachygraphus* Zimmermann, *A. sayi*, *D. onoharaensum*, and *X. saxesenii* but enhances attraction of *Xyleborus affinis* Eichhoff, *Xyleborus pubescens* Zimmermann, and *Myoplatypus flavicornis* (F.) (Platypodinae) to ethanol-baited traps; *X. crassiusculus*, *X. germanus*, and *X. compactus* are unaffected by the presence of α-pinene (Miller and Rabaglia 2009, Ranger et al. 2011). In our study, attraction of some species of ambrosia beetles was interrupted by conophthorin, suggesting some degree of host specificity among species. In Georgia, catches of *C. mutilatus*, *C. bodoanum*, and *D. onoharaensum* (Xyleborini) and one bark beetle species, *H. rotundicollis* were reduced with the addition of conophthorin (Fig. 1). The geographic variation in response to conophthorin may reflect different optimal attractive blends arising from different assemblages of host and nonhost plants over that range.

Adventive species appear to dominate ambrosia beetle communities in forested ecosystems in eastern North America. In 1998, adventive species accounted for 78% of ambrosia beetles catches in ethanol-baited traps in a study conducted in middle Tennessee (Oliver and Mannion 2001). In studies conducted in 2002–2004 at various locations in southeastern United States, Miller and Rabaglia (2009) found that adventive species accounted for 70–97% of the total number of ambrosia beetles captured in traps baited with ethanol, α-pinene, or both, lures. The percentage of adventive species in our current study ranged from 89–90% in Georgia, Michigan, and New Hampshire to 97% in Oregon. The effect of competition among species of ambrosia beetles is unknown. Carrillo et al. (2012) reared 12–14 species of ambrosia beetles from avocado and swampbay in Florida, with 4–9 species co-occurring in the same plant and no clear evidence of dominance by any one species. At this time, it is unclear if the dominance of adventive species in trap catches reflects the elimination of native species or a general increase in the abundance and diversity of all ambrosia beetles across forested lands.

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