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The capacity of conophthorin to enhance the attraction of two *Xylosandrus* species (Coleoptera: Curculionidae: Scolytinae) to ethanol and the efficacy of verbenone as a deterrent

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Abstract

1 Exotic invasive ambrosia beetles are among the most economically important pests of nursery stock and forest systems in the U.S.A.

2 Conophthorin, a common bark volatile of deciduous trees, acts as an attractant for the exotic black stem borer, *Xylosandrus germanus* (Coleoptera: Curculionidae: Scolytinae). Nevertheless, the extent to which a congener, *Xylosandrus crassiusculus* and other ambrosia beetles are attracted to conophthorin remains unclear. It is also unknown whether conophthorin enhances the attraction of these *Xylosandrus* beetles to traps baited with ethanol.

3 In the present study, we evaluated the extent to which conophthorin enhances the attraction of *X. crassiusculus* and *X. germanus* to ethanol-baited traps. We also tested the capacity of verbenone, an anti-aggregation pheromone component of several coniferophagous bark beetles, to deter both species.

4 More *X. crassiusculus* were captured in traps baited with both conophthorin and ethanol than in those containing either compound alone, suggesting that conophthorin enhances the response of *X. crassiusculus* to ethanol. This combination was also attractive to the checkered beetles *Madoniella dislocatus* and *Pyticeroides laticornis* (Coleoptera: Cleridae).

5 Verbenone deterred both *X. germanus* and *X. crassiusculus*, suggesting that the use of conophthorin and ethanol as an attractant and verbenone as a deterrent can be incorporated into an effective integrated pest management programme.

Keywords Conophthorin, ethanol, verbenone, *Xylosandrus crassiusculus*, *Xylosandrus germanus*.

Introduction

Exotic ambrosia beetles are serious wood-boring pests of landscape, nursery, orchard and forest trees (Oliver & Mannion, 2001; Adkins *et al.*, 2010) and among the most commonly intercepted insects at ports-of-entry in the U.S.A. (Haack, 2001; Kühnholz *et al.*, 2001; Rabaglia *et al.*, 2008; Marini *et al.*, 2011). As international trade and travel increases, the number of introductions of exotic ambrosia beetles continues to rise at an alarming rate (Haack, 2001). These pests cause substantial environmental damage and economic loss (CABI, 2012). Xyleborine beetles also have a symbiotic relationship with ambrosia fungi and, as a result of their haplodiploid lifecycle, only a few individuals are necessary to establish a growing population (Kirkendall & Ødegaard, 2007; Biedermann *et al.*, 2009). Currently, practical and technological limitations hamper the detection and subsequent management of small, newly-founded populations of exotic beetles (Mehta *et al.*, 2007; Bogich *et al.*, 2008). Once established, ambrosia beetles are difficult to control because the majority of their lifecycle is spent beneath the bark of trees, where they are physically protected from sprayed insecticides (Reding *et al.*, 2010). Indeed, conventional contact insecticides provide control only if applied soon before the adult flight period and may not kill all colonizing adults (Mizell & Riddle, 2004; Frank & Sadof, 2011).

Xylosandrus germanus (Blandford) and *Xylosandrus crassiusculus* (Motschulsky) (Coleoptera: Curculionidae: Scolytinae), two exotic ambrosia beetles of Asian origin, were first

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detected in the U.S.A. via infested material in 1932 and 1974, respectively (Felt, 1932; Hoffman, 1941; Wood, 1982; Weber & McPherson, 1984; Cote, 2008; CABI, 2012). Both species are considered high-risk, invasive pests and are now established in much of the eastern U.S.A. (CABI, 2012). These beetles have a broad host range of over 200 species, including valuable hardwoods, and can proliferate rapidly in agricultural and forested areas (Wood, 1982; Weber & McPherson, 1984; Oliver & Mannion, 2001; Adkins *et al.*, 2010; Reding *et al.*, 2010). *Xylosandrus crassiusculus* exclusively attacks deciduous trees, whereas *X. germanus* also attacks some *Abies*, *Picea* and *Pinus* spp. (Cote, 2008; CABI, 2012). Both species overwinter as adults and emerge in high densities in the spring. These species have two adult flight periods per year in Indiana. Overwintering adults emerge in the spring and the peak flight period of the subsequent generation occurs in late summer, although all life stages can be found within galleries during the growing season (Cote, 2008). Males are flightless and spend their entire lifecycle within the host tree (Peer & Taborsky, 2005), whereas dispersing females travel 100 m or more to locate a suitable host (Peer & Taborsky, 2005). Colonizing females vector pathogenic fungi that disrupt the flow of water and nutrients within the xylem, potentially killing the host tree (Cote, 2008; Adkins *et al.*, 2010). Both adults and larvae feed on the fungal mycelium and not the host tree (Cote, 2008; Adkins *et al.*, 2010). These fungi are of concern to growers of lumber and veneer because they can spread throughout the tree, stain the wood blue and make it less marketable (Cote, 2008). No aggregation or sex pheromone has been identified for any xyleborine species and little is known of their chemical ecology (Hulcr & Cognato, 2010). In fact, ethanol is the only semiochemical lure currently used by United States Department of Agriculture (USDA) Animal and Plant Health Inspection Service (APHIS)-Plant Protection and Quarantine (PPQ) and the U.S. Forest Service for the early detection of these and other invasive ambrosia beetles at ports-of-entry (Rabaglia *et al.*, 2008).

Ethanol, a common indicator of plant stress (Kimmerer & Kozlowski, 1982; Miller & Rabaglia, 2009; Ranger *et al.*, 2010), is a general attractant for many ambrosia beetles (Montgomery & Wargo, 1982; Miller & Rabaglia, 2009) and is commonly used to enhance the attraction of woodborers to semiochemical lures and trap trees (Montgomery & Wargo, 1982; Miller & Rabaglia, 2009; Ranger *et al.* 2013a). Ethanol enhances the attraction of both sexes of the ambrosia beetle *Gnathotrichus retusus* (Lec.) to traps baited with the aggregation pheromone, (*S*)-(+)-sulcatol (Borden *et al.*, 1980). The combination of ethanol and turpentine increases the response of the ambrosia beetle *Xyleborus pubescens* Zimmerman compared with the individual lures alone (Phillips *et al.*, 1988). Additionally, ethanol enhances the attraction of other scolytids, nitidulids and clerid beetles to traps baited with α-pinene (Phillips *et al.*, 1988; Schroeder & Lindelöw, 1988; Ranger *et al.*, 2011).

Other semiochemicals may hold promise as management tools for *Xylosandrus* beetles. For example, verbenone, an anti-aggregation pheromone component of several *Dendroctonus* bark beetles (Borden, 1985; Lindgren & Miller, 2002), inhibits the attraction of *X. germanus* to artificially damaged red pine (*Pinus resinosa* Aiton) trap trees and baited traps (Dodds & Miller, 2010). When combined with ethanol, verbenone also decreases trap catches of *X. crassiusculus*, *Xylosandrus compactus* (Eichhoff) and *Xyleborinus saxesenii* (Ratzeburg) in koa (*Acacia koa* A. Gray) stands (Burbano *et al.*, 2012); however, the bioactivity of verbenone alone has yet to be assessed.

Furthermore, *X. germanus* appears to be attracted to trap trees baited with conophthorin (Dodds & Miller, 2010), a bark volatile produced by several deciduous trees (Byers *et al.*, 1998; Huber *et al.*, 1999). Conophthorin is also a pheromone component of some bark beetles within the genera *Conophthorus*, *Leperisinus* and *Pityophthorus* (Francke *et al.*, 1979; Dallara *et al.*, 1995; Birgersson *et al.*, 1995). The addition of conophthorin to flight intercept traps baited with ethanol and Linoprax® (a synthetic pheromone lure for coniferophagous bark beetles) reduced the number of *X. germanus* captured (Kohnle *et al.*, 1992). Nevertheless, the influence of ethanol on the attraction of *Xylosandrus* beetles to conophthorin has yet to be empirically tested.

In the present study, we tested the hypothesis that conophthorin serves as an attractant to the exotic ambrosia beetles *X. germanus* and *X. crassiusculus* and also acts to enhance their attraction to ethonal-baited traps. Additionally, we tested the efficacy of verbenone alone to deter these beetles. The rationale for such an investigation is that an improved lure for exotic ambrosia beetles may lead to early detection of these pests and trigger timely management responses to reduce the extent of damage and prevent losses.

Materials and methods

We conducted a field experiment aiming to evaluate the attraction of *X. germanus* and *X. crassiusculus* to conophthorin and ethanol alone and determine the extent to which conophthorin enhances the response of these beetles to ethanol-baited traps. We also determined the extent to which these beetles were inhibited by verbenone. The experiment was conducted during the flight periods of both species in the summer of 2011 and 2012 and during the spring in 2012 (for dates and locations, see Table 1). During each flight period, three transects comprised of five traps (spaced 10 m apart) were positioned perpendicular to the direction of prevailing winds at one or two locations in Indiana with an active ambrosia beetle population (Table 1): Martell Forest (approximately 172 ha) and the Purdue Wildlife Area (approximately 64 ha) both located in Tippecanoe Co.; and Black Rock Barrens (NICHES Land Trust; approximately 40 ha) located in Warren Co. Each transect was considered a replicate; thus, there were nine replicates of each treatment. All sites were dominated by oak, hickory and maple, although Martell Forest and the Purdue Wildlife Area also had an abundance of black cherry. These hardwood species are common hosts for both *X. germanus* and *X. crassiusculus*.

Traps were constructed from modified inverted plastic soda bottles (Reding *et al.*, 2010) and Fluon® (Northern Products, Inc., Woonsocket, Rhode Island) was applied to the inside of the top bottle to prevent captured insects from escaping (Graham *et al.*, 2010). Traps were suspended from stands constructed of polyvinyl chloride pipe (D-2241, North

Table 1 Dates of experiments and locations and coordinates of trap transects

Date	Location	Coordinates of each transect
15 June to 8 August 2011	Martell Forest	40°25′53.44″N, 87°1′58.36″W
		40°26′7.34″N, 87°2′6.08″W
	Purdue Wildlife Area	40°26′51.17″N, 87°3′17.37″W
29 March to 15 April 2012	Martell Forest	40°25′53.44″N, 87°1′58.36″W
		40°26′18.06″N, 87°1′48.82″W
		40°26′14.52″N, 87°1′59.50″W
25 May to 13 August 2012	Martell Forest	40°25′53.44″N, 87°1′58.36″W
		40°26′14.52″N, 87°1′59.50″W
	Black Rock Barrens	40°21′23.85″N, 87°6′54.23″W

American Pipe Corporation, Houston, Texas; Graham *et al.*, 2010) and collection bottles were filled with 0.1 L of a highly concentrated sodium chloride solution. Traps were baited with individual lures consisting of either:

1 (−)-verbenone pouch (30000381, Contech Inc., Canada) with a release rate of 32 mg/day at 30 °C;
2 one millilitre of 95% ethanol solution in a polyethylene sample bag (Fisherbrand "Zipper" Seal Sample Bags, cat. no. 01-816-1A, 5.1 × 7.6 cm, Thermo Fisher Scientific Inc., Waltham, Massachusetts) with a release rate of ~100 mg/day at 30 °C;
3 (*E*)-(±)-conophthorin in microcentrifuge tubes (30000492, Contech Inc.) with a release rate of 5 mg/day at 30 °C;
4 both a conophthorin and an ethanol lure (as described above); and
5 an unbaited trap (control).

The ethanol and conophthorin lures lasted for 20 days and verbenone lasted 120 days in the field. Captured insects were collected twice a week, at which time the position of the treatments was rotated one position within each transect to control for location effects and lures were replaced if necessary. Throughout the course of the study, each trap occupied each position in a transect for the same amount of time. Captured beetles were preserved in 70% ethanol until identified to species. Voucher specimens were deposited in the Purdue Entomology Research Collection, West Lafayette, Indiana. The number of beetles captured at each semi-weekly collection period was transformed using $\log_{10}(y+1)$ and one-way analysis of variance was used to examine variation in response of beetles to treatments. Data from each collection period were pooled prior to analysis. If there was a significant difference between treatments, post-hoc comparisons were made using Tukey's honestly significant difference means separation test ($\alpha = 0.05$; JMP®; SAS Institute Inc., 2007).

Results

Throughout the present study, we captured a total of 5973 exotic invasive ambrosia beetles, from three genera, including: 4177 *X. crassiusculus*; 1607 *X. germanus*; 143 *Corthylus columbianus* Hopkins; and 46 *Ambrosiophilus atratus* (Eichhoff). No native ambrosia beetles were captured. Traps baited with the combination of conophthorin and ethanol captured more *X. crassiusculus* than all other treatments ($F_{4,640} = 44.78$, $P < 0.001$; Fig. 1A), supporting the hypothesis that conophthorin enhances the attraction of this exotic ambrosia beetle to traps baited with ethanol. There were fewer *X. crassiusculus* (Fig. 1A) and *X. germanus* ($F_{4,640} = 25.44$,

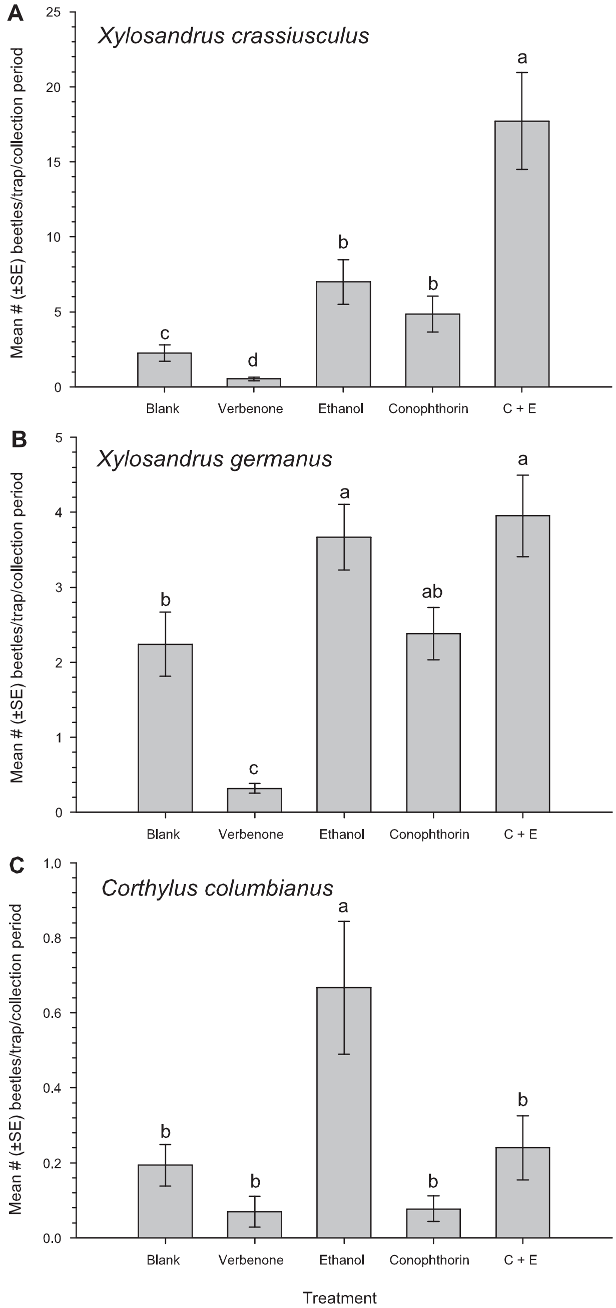

Figure 1 Mean ± SE number of the ambrosia beetles (A) *Xylosandrus crassiusculus*, (B) *Xylosandrus germanus* and (C) *Corthylus columbianus* collected (per trap per semiweekly collection period). C + E denotes conophthorin and ethanol lure together. Means with different letters within species are significantly different (one-way analysis of variance; $P < 0.05$).

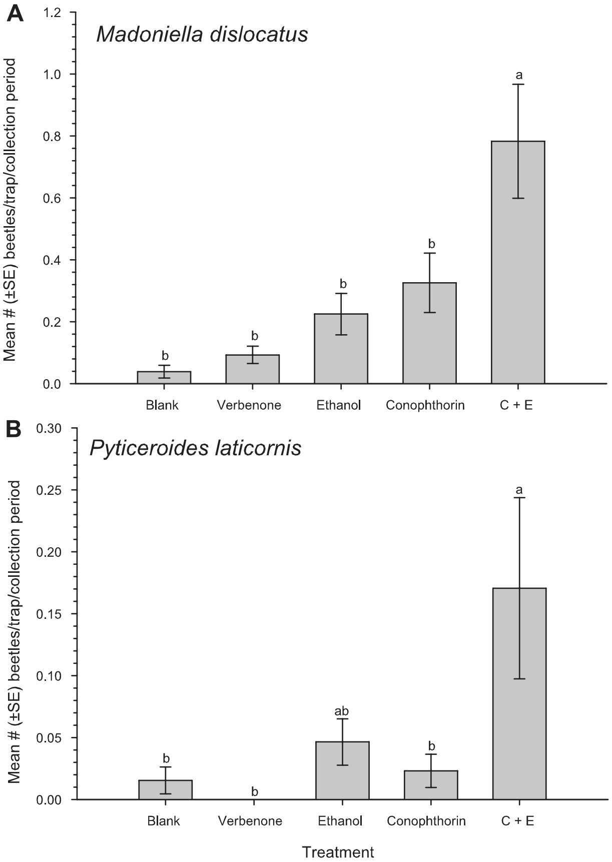

Figure 2 Mean ± SE number of the clerid beetles (A) *Madoniella dislocatus* and (B) *Pyticeroides laticornis* collected (per trap per semiweekly collection period). C + E denotes conophthorin and ethanol lure together. Means with different letters are significantly different (one-way analysis of variance; $P < 0.05$).

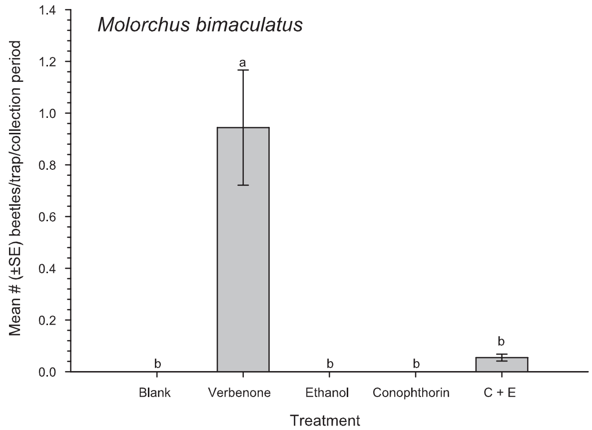

Figure 3 Mean ± SE number of the cerambycid beetle *Molorchus bimaculatus* beetles collected during spring 2012 (per trap per semiweekly collection period). C + E denotes conophthorin and ethanol lure together. Means with different letters are significantly different (one-way analysis of variance; $P < 0.05$).

$P < 0.001$; Fig. 1B) captured in verbenone-baited traps than unbaited control traps. The capture of ambrosia beetles in unbaited control traps accounted for 7% and 18% of the total trap catch for *X. crassiusculus* and *X. germanus*, respectively, and this is likely the result of incidental capture. Conophthorin did not enhance the attraction of *X. germanus* to ethanol-baited traps, whereas *Corthylus columbianus* was only attracted to ethanol-baited traps ($F_{4,640} = 7.68$, $P < 0.001$; Fig. 1C).

Additionally, we collected a total of 232 checkered beetles (Coleoptera: Cleridae) from four different genera: 188 *Madoniella dislocatus* (Say); 33 *Pyticeroides laticornis* (Say); nine *Enoclerus nigripes* (Say); and two *Cymatodera bicolor* (Say). The checkered beetles *M. dislocatus* and *P. laticornis* were captured in greater numbers in traps baited with conophthorin and ethanol ($F_{4,640} = 11.08$, $P < 0.001$; Fig. 2A; $F_{4,640} = 5.0$, $P < 0.001$; Fig. 2B). Interestingly, verbenone-baited traps captured a total of 17 *Molorchus bimaculatus* (Say), a cerambycid beetle that mimics a wasp, during spring 2012 and only one beetle was captured in a trap baited with conophthorin and ethanol together ($F_{4,89} = 6.54$, $P < 0.001$; Fig. 3). No *M. bimaculatus* were captured during either summer, so only those data from spring 2012 were analyzed.

Discussion

Xylosandrus crassiusculus was no more attracted to conophthorin than it was to the ethanol lure, and conophthorin-baited traps captured no more *X. germanus* than control traps and those baited with ethanol. Although most work to date on the chemical ecology of *Xylosandrus* species has occurred in nurseries with high population densities (Oliver & Mannion, 2001; Ranger *et al.*, 2010, 2011; Reding *et al.*, 2010; Burbano *et al.*, 2012), we found that *X. crassiusculus* was most attracted to traps baited with both conophthorin and ethanol in hardwood forests. These findings suggest that an improved semiochemical lure containing both conophthorin and ethanol may be effective at detecting incipient populations of these beetles at ports-of-entry and other hot spots, while management is still a viable option. Early detection efforts of USDA APHIS-PPQ and the U.S. Forest Service using ethanol-baited traps have led to the discovery of two exotic bark beetles and three ambrosia beetles: *Hylurgops palliatus* (Gyllenhal), *Scolytus schevyrewi* Semenov, *Xyleborus similis* Ferrari, *Xyleborus glabratus* Eichhoff and *Xyleborus seriatus* Blandford (Rabaglia *et al.*, 2008). At the time of their detection, these exotic species were otherwise unknown within the U.S.A. However, continued delimiting surveys within the surrounding states found that all five species had been established for some time (Rabaglia *et al.*, 2008). Had these species been detected earlier, management actions and eradication may have been more feasible (Rabaglia *et al.*, 2008).

Although conophthorin has been demonstrated to both attract (Dodds & Miller, 2010) and repel (Kohnle *et al.*, 1992) *X. germanus* in the field, conophthorin alone did not appear to act as an attractant or a deterrent in our study, nor did it enhance the attraction of *X. germanus* to ethanol-baited traps. Moreover, in a mixed hardwood forest in Ohio, *X. germanus* was not attracted to conophthorin-baited traps (C. M. Ranger, personal communication). However, traps baited with the combination of conophthorin and ethanol captured more *X. germanus* than those baited with ethanol alone (C. M. Ranger, personal communication). The ability of conophthorin to enhance the response of this species to ethanol baited traps remains unclear. Nevertheless, the response of *X. crassiusculus* in the present study (and *X. germanus* in Ohio; C. M. Ranger, personal communication) to conophthorin with ethanol, suggests that this combination may provide an improved lure to monitor for these pests and possibly other exotic ambrosia beetle generalists affecting deciduous trees (Wood, 1982; Haack, 2001; CABI, 2012).

In previous studies, verbenone reduced the attraction of *X. germanus* and other ambrosia beetles to ethanol-baited traps, and reduced ambrosia beetle attacks on ethanol-injected trap trees (Dodds & Miller, 2010; Burbano *et al.*, 2012; Ranger *et al.*, 2013b). In the present study, verbenone alone was less attractive to both *X. crassiusculus* and *X. germanus* than the unbaited control, suggesting that verbenone may act as a general deterrent for xyleborine species. Further work is needed to evaluate the capacity of verbenone to act as a repellent and to attenuate the attraction of beetles when placed on conophthorin and ethanol baited traps. Verbenone could be used to deter unwanted infestations of already established ambrosia beetles from marketable trees in a push-pull strategy. The 'push' is typically a deterrent/repellent located within the epicentre of a nursery (Cook *et al.*, 2007). Beetles are then drawn or 'pulled' towards an attractant located outside the nursery. The attractant can be a pheromone/kairomone attached to kill traps or a tree coated with insecticides (Cook *et al.*, 2007). The push–pull strategy is effective at deterring coniferophagous bark beetles, such as *Dendroctonus ponderosae* Hopkins, *Dendroctonus frontalis* Zimmerman, *Dendroctonus pseudotsugae* Hopkins and *Ips paraconfusus* Lanier, from high-value hosts (Ross & Daterman, 1994; Borden *et al.*, 2006; Cook *et al.*, 2007). Of these four species, three were deterred from hosts by use of verbenone as the repellent (Borden *et al.*, 2006; Cook *et al.*, 2007). Nevertheless, the push–pull method has not been evaluated for control of scolytids in deciduous forests.

The only information regarding the natural enemies of ambrosia beetles is limited to those affecting conifers. In conifer systems, the clerid, *Thanasimus formicarius* (L.) is attracted to the pheromone of *Trypodendron lineatum* Olivier (Tømmerås, 1988) and *Thanasimus dubius* (Fabricius) has been observed to prey upon *Platypus flavicornis* (Fabricius) (Clarke & Menard, 2006). In the present study, we found that *M. dislocatus* and *P. laticornis* were strongly attracted to traps baited with conophthorin and ethanol, and it is possible that these predators locate prey by responding to plant volatiles as kairomones. For example, *T. dubius* (F.), *Thanasimus undatulus* (Say) and several *Zinodosis* species are attracted to feeding induced pine volatiles from *Ips pini* (Say) and *Ips grandicollis* (Eichhoff) (Erbilgin & Raffa, 2001). In laboratory experiments, *T. dubius* is attracted to α- and β-pinene in a wind tunnel (Mizell *et al.*, 1983). *Enoclerus nigripes rufiventris* (Spinola) and *Enoclerus nigrifrons gerhardi* Wolcott are attracted to monoterpenes in field assays (Mizell *et al.*, 1983; Chénier & Philogéne, 1988; Costa & Reeve, 2011). *Xylosandrus crassiusculus* and *X. germanus* are native to Asia and have no known natural enemies in the U.S.A. (CABI, 2012); however, *M. dislocatus* and *P. laticornis* may be possible predators of both ambrosia beetles. Using host volatiles as lures could increase the presence of scolytid predators in the proximity and the subsequent predation pressure on pest populations (Mizell *et al.*, 1983; Chénier & Philogéne, 1988; Erbilgin & Raffa, 2001; Kenis *et al.*, 2004; Costa & Reeve, 2011).

Aside from bark and ambrosia beetles, verbenone may be a kairomone for other wood-boring insects. Combining verbenone with pheromones of *Pinus*-infesting bark beetles attracts a number of cerambycids such as *Monochamus titillator* (Fabricius), *Monochamus clamator* (LeConte), *Monochamus notatus* (Drury), *Monochamus obtusus* Casey and *Monochamus scutellatus* (Say) (Allison *et al.*, 2001). We discovered that the longhorned beetle *M. bimaculatus* was attracted to verbenone during the spring of 2012, the first report of this species responding to a semiochemical. Larvae of *M. bimaculatus* feed within dead branches of *Acer rubrum* L., *Carya glabra* (Miller), *Vitis riparia* Michaux and other hardwoods (Gosling, 1984; Yanega, 1996), and adults feed on pollen from flowers of *Amelanchier arborea* (Michx. F) Fern., *Aronia prunifolia* (Marsh.) Rehd., *Viburnum acerifolium* L., *Spiraea* x *vanhouttei* and *Cornus* spp. (Gosling, 1984). More research is needed to understand the role of verbenone in the chemical ecology of *M. bimaculatus*.

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