



Chemical Ecology

Predators attracted to combination of bark beetle pheromones and host kairomones in pine forests of southeastern United States

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In 2006, we evaluated the effects of combining lures releasing pine host kairomones (ethanol + α -pinene) with lures releasing bark beetle pheromones (ipsenol + ipsdienol) on trap catches of predators associated with bark and woodboring beetles in Florida, Georgia, Louisiana, and Virginia. Catches in traps baited with all 4 compounds were greater than those in traps baited with either binary blend for the common predators *Thanasimus dubius* (F.) (Coleoptera: Cleridae), *Temnoscheila virescens* (F.) (Coleoptera: Trogossitidae), *Aulonium tuberculatum* LeConte (Coleoptera: Zopheridae), and *Lasconotus* spp. (Coleoptera: Zopheridae). The same was true for: *Enoclerus nigripes* (Say) (Coleoptera: Cleridae) at 2 of 3 locations; *Platysoma cylindricum* (Paykull) (Coleoptera: Histeridae) at 3 of 4 locations; and *Corticus* spp. (Coleoptera: Tenebrionidae) at 2 of 6 locations. In contrast, the addition of ethanol + α -pinene to traps baited with ipsenol + ipsdienol reduced catches of *Platysoma attenuatum* LeConte (Coleoptera: Histeridae) at 2 of 4 locations.

Key words: kairomone, ethanol, ipsenol, ipsdienol, α -pinene

Eastern forests of the United States have a diverse fauna of bark and woodboring beetles in various families of Coleoptera (USDA 1985). Bark and woodboring beetles break down dead, dying, and downed woody material, facilitating the critical process of nutrient cycling associated with healthy forests (Ulyshen 2016). By reducing the amount of woody material on the forest floor, beetle activities help to reduce the risks of fire and erosion as well as encourage wildlife habitat in the understory. Helping to stabilize populations of bark and woodboring beetles are numerous species of predators and parasitoids (USDA 1985).

Traps baited with semiochemicals can be used to assess forest health by monitoring the diversity and abundance of bark and woodboring beetles and associated predators within forests (Dodds et al. 2015). They can also be used to monitor pest species. For example, traps baited with semiochemicals (frontalin, *endo*-brevicommin, and an α -pinene blend) are used to monitor populations of the southern pine beetle *Dendroctonus frontalis* Zimmermann (Coleoptera: Curculionidae) and its predator *Thanasimus dubius* (F.) (Coleoptera: Cleridae) in the southern United States (Sullivan 2016, Billings 2017). Numbers of *D. frontalis* and ratios of

D. frontalis to *Th. dubius* in trap catches help to determine the status of infestations of *D. frontalis* as increasing, static, or decreasing. The trapping program helps to guide management actions directed at *D. frontalis* at a stand level. Such tools may be needed for emerging pests arising due to climate change or invasions of nonnative species. If so, then a broad knowledge of the chemical ecology of native bark and woodboring beetles, and their associated predators, is required to address these potential future issues. Data on predators can also be used to determine the likelihood of establishment for nonnative invasive species.

Predators of bark and woodboring beetles function within a tritrophic context by responding to host cues used by prey to find their foraging habitats and eavesdropping on pheromones used by their prey to communicate with conspecifics (Vet and Dicke 1992, Hulcr et al. 2006). In southeastern United States, the combination of the host volatiles (kairomones) ethanol and α -pinene is attractive to numerous species of pine bark and woodboring beetles (Miller 2006, Miller and Rabaglia 2009, Miller et al. 2013, 2015). Predators such as *Th. dubius*, *Temnoscheila virescens* (F.) (Coleoptera: Trogossitidae) and

Lasconotus spp. (Coleoptera: Zopheridae) are also attracted to ethanol and α -pinene (Miller 2023). Ipsenol and ipsdienol are pheromones produced by several species of pine bark beetles, including those in the genus *Ips* (El-Sayed 2019). In eastern United States, the combination of ipsenol and ipsdienol is attractive to numerous species of pine bark and woodboring beetles (Billings and Cameron 1984, Miller and Asaro 2005, Allison et al. 2012, Miller et al. 2013, 2015). Predators such as *Enoclerus nigripes* (Say) (Coleoptera: Cleridae) *Th. dubius*, *Te. virescens* and *Platysoma attenuatum* LeConte (Coleoptera: Histeridae) are also attracted to the combination of ipsenol and ipsdienol (Billings and Cameron 1984, Allison et al. 2013).

In 2006, we conducted a trapping study at 6 locations in south-eastern United States to determine the effects of combining the binary blend of ethanol + α -pinene lures with the binary blend of ipsenol + ipsdienol lures on trap catches of bark and woodboring beetles, and associated predators. Catches of 7 species of long-horn beetles (Coleoptera: Cerambycidae), 2 species of flatheaded woodborers (Coleoptera: Buprestidae), 4 species of bark beetles, and 1 species of ambrosia beetles (Coleoptera: Curculionidae) were greatest in traps baited with all 4 compounds (Miller et al. 2011). Herein, we report the responses of predators in this same study.

Materials and Methods

Six trapping experiments were conducted within mature pine forests in Florida, Georgia, Louisiana, and Virginia (Table 1). Experiments 1 and 2 were conducted on the Apalachicola and Oconee National Forests, respectively, whereas Experiments 4–5 were conducted on the Kisatchie National Forest. Experiment 3 was conducted on a Plum Creek industrial forest, whereas the Appomattox-Buckingham State Forest was used in Experiment 6. The trapping protocols for the 6 experiments have been published previously (Miller et al. 2011). In each experiment, we deployed 10 replicate blocks of 3 8-unit black multiple-funnel traps (Phero Tech Inc., Delta, BC, Canada) per block. Traps were spaced 10–20 m apart (within and between blocks) and hung on twine strung between trees. Each collection cup contained an aqueous solution of propylene glycol (Peak RV and Marine Antifreeze, Old World Industries Inc., Northbrook, IL) to kill and preserve beetles (Miller and Duerr 2008).

Traps within a block randomly received one of the following treatments: (i) ethanol and α -pinene lures; (ii) ipsenol and ipsdienol lures; and (iii) all 4 lures. All lures were purchased from Contech Enterprises Inc. (Victoria, BC, Canada) and hung on the outside of the middle funnels. The ethanol lures consisted of sealed black plastic tubes, each containing 150 ml of ethanol, whereas the α -pinene lures consisted of sealed blue plastic tubes, each containing 200 ml of α -pinene [$>95\%$ (-)]. Release rates from

the ethanol and α -pinene lures were 0.6 g/day and 2–6 g/day, respectively, at 25–28 °C. Racemic ipsenol and racemic ipsdienol were each released from white plastic bubble-cap lures at rates of 0.1–0.2 mg/day at 22–25 °C. All release rates were determined by the manufacturer.

We used the SYSTAT (ver. 13) and SigmaStat (ver. 3.01) statistical packages (SYSTAT Software Inc., Point Richmond, CA) to analyze trap catch data for species caught in sufficient numbers ($N \geq 30$) in an experiment. Data were transformed by $\ln(y + 1)$ (Pepper et al. 1997) as needed to meet the assumptions of normality and homoscedasticity (verified by the Shapiro–Wilk and Equal Variance tests, respectively). In each experiment, data were subjected to mixed-model ANOVA with lure treatment as the fixed factor. We compared treatment means with the Holm–Sidak multiple-comparison test (Glantz 2005) when $P \leq 0.05$. The paired t -test was used to compare 2 treatment means for a species when beetles were not caught in the third treatment.

Results

More than 29,000 predatory beetles from 5 families were collected across the 6 experiments (Table 2). The most common species were *Lasconotus* spp., *Te. virescens*, and *Th. dubius*, accounting for 59, 13, and 7% of total catch, respectively.

Lure treatments had significant effects on catches of *Th. dubius* in Georgia, Louisiana, and Virginia, and on catches of *E. nigripes* in Georgia and Virginia (Table 3). At all locations, the greatest catches of *Th. dubius* were in traps baited with all 4 lures (Fig. 1A–E). The same was true for catches of *E. nigripes* in Georgia and Virginia (Fig. 1F and H). In Louisiana, *E. nigripes* were not caught in traps baited solely with ethanol + α -pinene; catches in traps baited with ipsenol + ipsdienol were not different to those baited with all 4 lures ($t_9 = 1.057$, $P = 0.318$; Fig. 1G). In Virginia and 1 location in Georgia, more *Th. dubius* were caught in traps baited with ethanol + α -pinene than in traps baited with ipsenol + ipsdienol (Fig. 1A and E) whereas more *E. nigripes* were caught in traps baited with ipsenol + ipsdienol than in traps baited with ethanol + α -pinene at all 3 locations (Fig. 1F–H).

Trap catches of *P. attenuatum* and *Platysoma cylindricum* (Paykull) (Coleoptera: Histeridae) were affected by lure treatments in Georgia, Louisiana, and Virginia (Table 3). For both species, catches were greater in traps baited with ipsenol + ipsdienol than in those baited with ethanol + α -pinene (Fig. 2A–H). The addition of ethanol + α -pinene to traps baited with ipsenol + ipsdienol significantly reduced catches of *P. attenuatum* at 2 locations (Fig. 2A and C). In contrast, the addition of ethanol + α -pinene to traps baited with ipsenol + ipsdienol increased catches of *P. cylindricum* (Fig. 2E, G–H). At 1 location in Georgia, catches of *P. cylindricum* in traps baited with ipsenol + ipsdienol were not different to those in traps baited with all 4 lures ($t_9 = 0.452$, $P = 0.662$); no beetles were caught in traps baited solely with ethanol + α -pinene (Fig. 2F).

Table 1. Locations, forest compositions, and trapping dates for 6 experiments conducted in Florida, Georgia, Louisiana and Virginia

| Exp | State | County | Coordinates | Tree species | Trapping dates |
|-----|-------|------------|------------------|--|---------------------------------|
| 1 | FL | Leon | 30.424N, 84.463W | <i>Pinus palustris</i> Miller, <i>Pinus elliottii</i> Engelm | 4 April–6 June 2006 |
| 2 | GA | Putnam | 33.342N, 83.488W | <i>Pinus taeda</i> L. | 11 April–13 June 2006 |
| 3 | GA | Oconee | 33.729N, 83.432W | <i>P. taeda</i> | 23 August–4 October 2006 |
| 4 | LA | Winn | 31.899N, 92.791W | <i>P. taeda</i> , <i>P. palustris</i> | 4 April–31 May 2006 |
| 5 | LA | Winn | 31.818N, 92.546W | <i>P. taeda</i> | 6 September 2006–5 January 2007 |
| 6 | VA | Buckingham | 37.457N, 78.658W | <i>P. taeda</i> | 25 May–27 July 2006 |

Table 2. Total catches of predators in 6 trapping experiments conducted in Florida, Georgia, Louisiana, and Virginia in 2006

| Family, Species | Experiment—State | | | | | |
|-------------------------------|------------------|-------|-------|--------|-------|-------|
| | 1—FL | 2—GA | 3—GA | 4—LA | 5—LA | 6—VA |
| Cleridae | | | | | | |
| <i>Chariessa pilosa</i> | — | — | — | 23 | — | — |
| <i>Enoclerus nigripes</i> | — | 514 | — | 59 | — | 1,359 |
| <i>Thanasimus dubius</i> | 7 | 412 | 549 | 246 | 316 | 625 |
| HISTERIDAE | | | | | | |
| <i>Platysoma attenuatum</i> | — | 63 | 61 | 558 | — | 132 |
| <i>Platysoma cylindricum</i> | — | 140 | 36 | 789 | — | 717 |
| Tenebrionidae | | | | | | |
| <i>Corticeus</i> spp. | 70 | 106 | 40 | 74 | 269 | 576 |
| TROGOSSITIDAE | | | | | | |
| <i>Temnoscheila virescens</i> | — | 1,194 | 294 | — | — | 2,266 |
| Zopheridae | | | | | | |
| <i>Aulonium tuberculatum</i> | 176 | — | — | 192 | 43 | — |
| <i>Lasconotus</i> spp. | 2,084 | 276 | 2,260 | 9,634 | 2,859 | 107 |
| Total | 2,337 | 2,705 | 3,240 | 11,575 | 3,487 | 5,782 |

Table 3. ANOVA results on the effects of combining ethanol + α -pinene lures with ipsenol + ipsdienol lures on mean catches of beetle predators in multiple-funnel traps deployed in 6 experiments (Exp) in Florida, Georgia, Louisiana, and Virginia in 2006

| Species | Exp | State | F | P | |
|-------------------------------|------------------------------|-------|--------|--------|--------|
| Cleridae | | | | | |
| <i>Enoclerus nigripes</i> | 2 | GA | 88.17 | <0.001 | |
| | 6 | VA | 119.75 | <0.001 | |
| | <i>Thanasimus dubius</i> | 2 | GA | 60.84 | <0.001 |
| | | 3 | GA | 55.45 | <0.001 |
| | | 4 | LA | 80.20 | <0.001 |
| | | 5 | LA | 58.53 | <0.001 |
| 6 | VA | 16.11 | <0.001 | | |
| Histeridae | | | | | |
| <i>Platysoma attenuatum</i> | 2 | GA | 11.30 | <0.001 | |
| | 3 | GA | 4.03 | 0.036 | |
| | 4 | LA | 311.35 | <0.001 | |
| | 6 | VA | 7.65 | 0.004 | |
| | <i>Platysoma cylindricum</i> | 2 | GA | 45.53 | <0.001 |
| | | 4 | LA | 205.35 | <0.001 |
| 6 | | VA | 78.59 | <0.001 | |
| 6 | | VA | 2.87 | 0.084 | |
| Tenebrionidae | | | | | |
| <i>Corticeus</i> spp. | 1 | FL | 9.88 | 0.001 | |
| | 2 | GA | 22.06 | <0.001 | |
| | 3 | GA | 14.29 | <0.001 | |
| | 4 | LA | 10.23 | 0.001 | |
| | 5 | LA | 23.52 | <0.001 | |
| | 6 | VA | 26.47 | <0.001 | |
| Trogossitidae | | | | | |
| <i>Temnoscheila virescens</i> | 2 | GA | 69.40 | <0.001 | |
| | 3 | GA | 33.36 | <0.001 | |
| | 6 | VA | 62.23 | <0.001 | |
| Zopheridae | | | | | |
| <i>Aulonium tuberculatum</i> | 4 | LA | 47.02 | <0.001 | |
| | 5 | LA | 3.97 | 0.037 | |
| <i>Lasconotus</i> spp. | 1 | FL | 99.82 | <0.001 | |
| | 2 | GA | 24.44 | <0.001 | |
| | 3 | GA | 13.77 | <0.001 | |
| | 4 | LA | 9.57 | <0.001 | |
| | 5 | LA | 69.76 | <0.001 | |
| | 6 | VA | 21.94 | <0.001 | |

Lure treatments significantly affected trap catches of *Aulonium tuberculatum* LeConte (Coleoptera: Zopheridae) and *Lasconotus* spp. (Table 3). Catches of *Au. tuberculatum* and *Lasconotus* spp. were greatest in traps baited with all 4 lures (Fig. 3A–I). The lowest catches of *Au. tuberculatum* were in traps baited with ethanol + α -pinene (Fig. 3A–C) whereas the lowest catches of *Lasconotus* spp. at 4 locations were in traps baited with ipsenol + ipsdienol (Fig. 3D–G). At the other 2 locations, the lowest catches were in traps baited with either binary blend equally (Fig. 3H–I).

Catches of *Te. virescens* and *Corticeus* spp. (Coleoptera: Tenebrionidae) were affected by lure treatments (Table 3). In Virginia and 2 locations in Georgia, catches of *Te. virescens* were lowest in traps baited with ipsenol + ipsdienol and highest in traps baited with all 4 lures (Fig. 4A–C). Similarly, catches of *Corticeus* spp. were lowest in traps baited with ipsenol + ipsdienol (Fig. 4D–I). At 1 location in Georgia and 1 location in Louisiana (both conducted in the fall), catches of *Corticeus* spp. were highest in traps baited with all 4 lures (Fig. 4F and H). The addition of ipsenol + ipsdienol had no effect on catches of *Corticeus* spp. in traps baited with ethanol + α -pinene at the other 4 locations (Fig. 4D, E, G, and I).

Discussion

Understanding the chemical ecology of bark and woodboring beetles, and their predators, can provide insights into their ecological interactions (Vet and Dicke 1992, Hulcr et al. 2006). Simply stated, species that are attracted to the same semiochemicals at the same time are likely to have some sort of relationship or interaction. Bark and woodboring beetles that respond to the same semiochemicals may share the same resource, partitioning the resource over time or space (Brin and Bouget 2018). Predators responding to kairomones released by pines should place them in the same habitat as their prey (Miller 2023). Eavesdropping on bark beetle pheromones should further enhance the likelihood of predators finding prey, especially for those species that need to find larvae of bark and woodboring beetles in a timely manner for their larvae to have larval prey (Miller et al. 2023).

In the southern United States, the clerid *Th. dubius* is a common predator of the southern pine beetle *D. frontalis* (Franklin and Green 1965, Thatcher and Pickard 1966, Mignot and Anderson 1969,

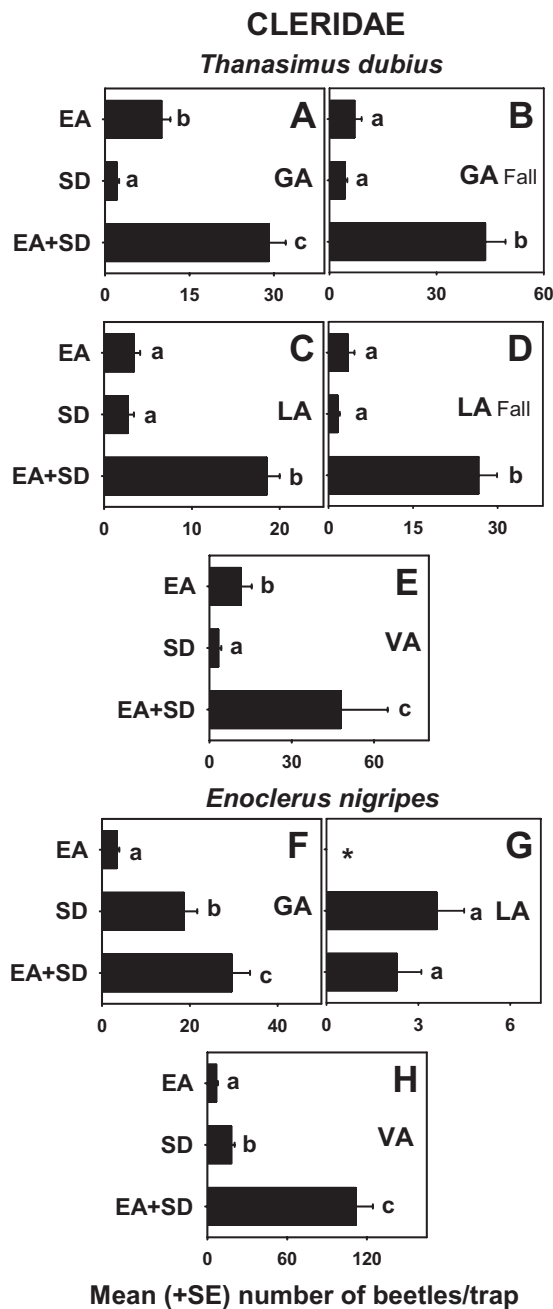


Fig. 1. Effects of combining ethanol + α -pinene (EA) and ipsenol + ipsdienol (SD) on mean (+SE) trap catches of *Thanasimus dubius* (A–E) and *Enoclerus nigripes* (F–H) in southeastern United States. For each species at each location, means followed by different letters are significantly different at $P \leq 0.05$ (Holm–Sidak multiple-comparison test [A–E, H] or paired t -test [G], see text). Treatment with an asterisk had zero catch.

Goyer et al. 1974, Mizell and Nebeker 1981, Linit and Stephen 1983, Billings and Cameron 1984, Taylor et al. 1992, Reeve 1997, 2011, Sullivan 2016). The strong ecological association between these 2 species allows for the ratio of the species caught in baited monitoring traps baited with the pheromones frontalin and endobrevicomin, and a host blend of α - and β -pinene to be used as a predictor of population trends for *D. frontalis* (Payne et al. 1984, Sullivan 2016, Billings 2017). *Lasconotus* spp. and *Te. virescens* are also common predators of *D. frontalis* (Goyer et al. 1974, Billings and Cameron 1984).

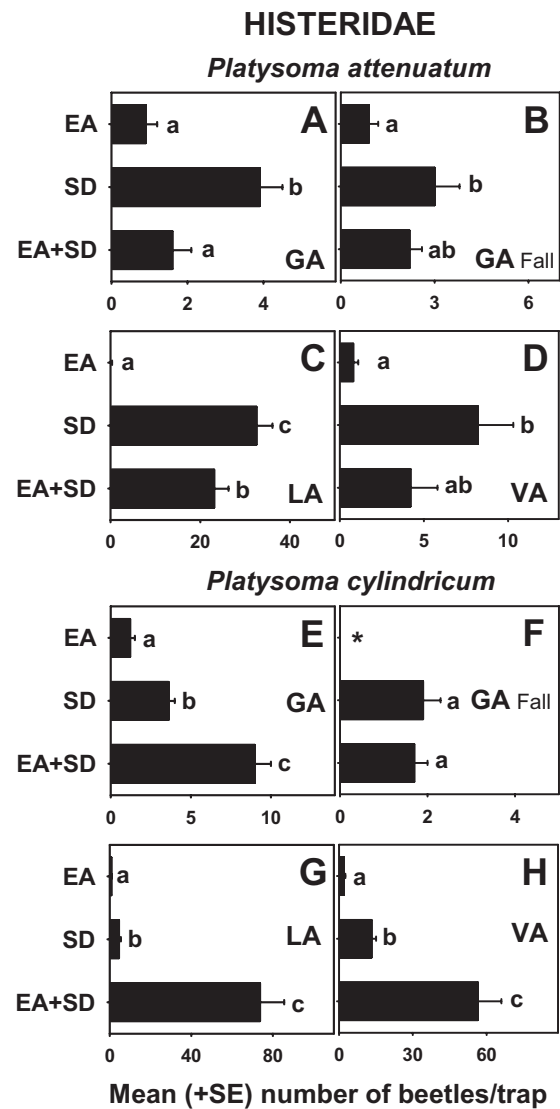


Fig. 2. Effects of combining ethanol + α -pinene (EA) and ipsenol + ipsdienol (SD) on mean (+SE) trap catches of *Platysoma attenuatum* (A–D) and *Platysoma cylindricum* (E–H) in southeastern United States. For each species at each location, means followed by different letters are significantly different at $P \leq 0.05$ (Holm–Sidak multiple-comparison test [A–E, G–H] or paired t -test [F], see text). Treatment with an asterisk had zero catch.

However, when populations of *D. frontalis* are rare or non-existent, then *Th. dubius*, *Lasconotus* spp., and *Te. virescens* need to switch to other prey species to survive (Mignot and Anderson 1970, Costa and Reeve 2011). Bark and ambrosia beetles such as *Ips avulsus* (Eichhoff) and *Myoplatypus flavicornis* (F.) (Coleoptera: Curculionidae) are among dozens of species of bark and woodboring beetles commonly associated with trees attacked by *D. frontalis*, serving as alternate prey for predators such as *Th. dubius* (Vité et al. 1964, Dixon and Payne 1979, Clarke and Menard 2006, Sullivan 2016).

The ability to switch target prey in response to prey availability is an important trait for generalist predators (Brin and Bouget 2018). A broad response profile by predators to semiochemicals associated with bark and woodboring beetles provides predators with the ability to efficiently locate alternate feeding opportunities in stands of pine trees. The host volatiles (kairomones) ethanol and α -pinene are attractive to ambrosia beetles and woodborers, likely indicating

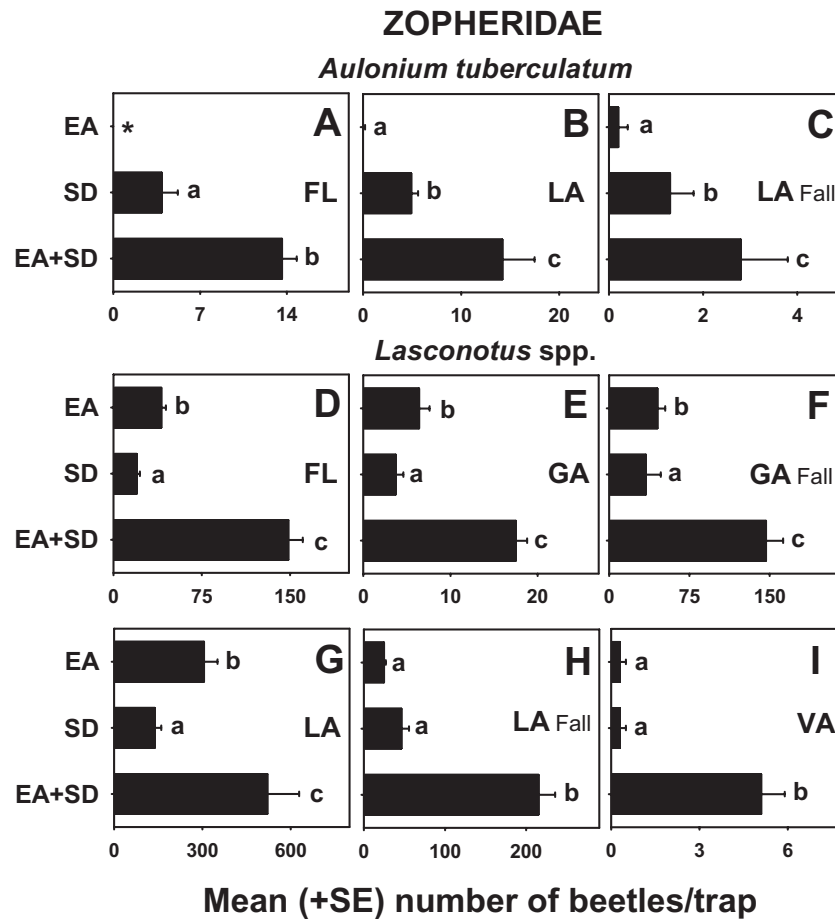


Fig. 3. Effects of combining ethanol + α -pinene (EA) and ipsenol + ipsdienol (SD) on mean (+SE) trap catches of *Aulonium tuberculatum* (A–C) and *Lasconotus* spp. (D–I) in southeastern United States. For each species at each location, means followed by different letters are significantly different at $P \leq 0.05$ (Holm–Sidak multiple-comparison test [B–K] or paired t -test [A], see text). Treatment with an asterisk had zero catch.

dead, dying, or decomposing pine trees suitable for the establishment of broods (Miller 2006, 2023, Miller and Rabaglia 2009). The pheromones ipsenol and ipsdienol are attractive to numerous species of bark and woodboring beetles (Billings and Cameron 1984, Miller and Asaro 2005, Miller et al. 2005, 2013, 2015, Allison et al. 2013). Bark beetles such as *I. avulsus* respond to these pheromones to find conspecifics for mating or to take advantage of breeding hosts, often with host volatiles enhancing the responses of some species. Similarly, longhorn woodborers such as *Monochamus* spp. respond to these same compounds as indicators of suitable mating and breeding sites.

Therefore, in our study, it is not surprising that traps baited with all 4 compounds were consistently the most attractive to *Th. dubius* (Fig. 1A–E), *Lasconotus* spp. (Fig. 3D–I), and *Te. virescens* (Fig. 4A–C). This response profile mirrors those of several species of bark and woodboring beetles such as *Orthotomicus caelatus* (Coleoptera: Curculionidae), *Monochamus titillator* (Coleoptera: Cerambycidae), and *Buprestis lineata* (Coleoptera: Buprestidae) as previously reported in Miller et al. (2011) for this same study.

At 2 of 3 locations, the clerid *E. nigripes* exhibited the same preference profile as the zopherid *Au. tuberculatum* and the histereid *P. cylindricum* at 3 of 4 locations (Figs. 1F and H; 2E, G–H; 3A–C). In Louisiana, trap catches of *E. nigripes* were low compared to Georgia and Virginia. Similarly, catches of *P. cylindricum* were lowest in Georgia in the fall compared to the other locations. These patterns may suggest variation in prey

diversity and availability at these locations requiring a specific response by predators to ipsenol and ipsdienol (Reeve et al. 2009). Variation in forest composition and dynamics is not unusual in pine and mixed-wood forests.

The general response of predators to the 4-component blend may be linked to prey that responds to all 4 compounds, or it might represent an additive response profile by generalist predators responding to these 2 binary combinations individually as well as the 4-component blend. The emission of all 4 compounds from pine hosts would attract species that respond simply to the combination of ethanol and α -pinene with no deterrence from ipsenol or ipsdienol such as the longhorn beetles *Asemum striatum* (L.) and *Xylotrechus sagittatus* (Germar) (Coleoptera: Cerambycidae), the bark beetles *Dendroctonus terebrans* (Olivier) and *Hylastes salebrosus* Eichhoff (Coleoptera: Curculionidae), the weevils *Hylobius pales* (Herbst) and *Pachylobius picivorus* (Germar) (Coleoptera: Curculionidae), the click beetle *Alaus myops* (F.) (Coleoptera: Elateridae), the ambrosia beetles *Xyleborinus saxesenii* (Ratzeburg) and *Xylosandrus crassiusculus* (Motschulsky) (Coleoptera: Curculionidae), and various species of fungivores (Miller 2006, Miller and Rabaglia 2009, Miller et al. 2011). There would also be some attraction of several species of *Ips* bark beetles to ipsenol and ipsdienol although the numbers of *I. avulsus* and *Ips grandicollis* (Eichhoff) (Coleoptera: Curculionidae) would be reduced by the presence of ethanol and α -pinene (Billings and Cameron 1984, Miller et al. 2011, Allison et al. 2012, Miller 2020). The flexibility of predators to respond to any

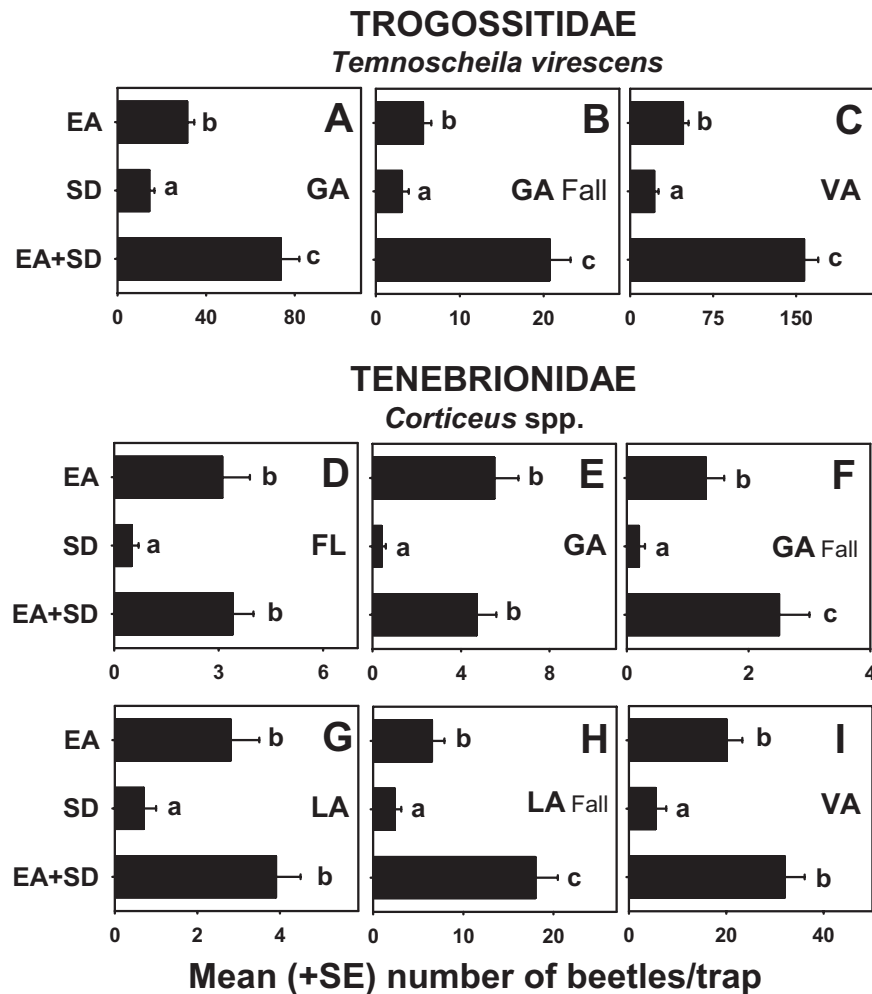


Fig. 4. Effects of combining ethanol + α -pinene (EA) and ipsenol + ipsdienol (SD) in traps on mean (+SE) catches of *Temnoscheila virescens* (A–C) and the tenebrionid *Corticeus* spp. (D–I) in southeastern United States. For each species at each location, means followed by different letters are significantly different at $P \leq 0.05$ (Holm–Sidak multiple-comparison test).

and all combinations of these 4 compounds may increase the likelihood of finding and competing for prey.

In contrast to other predators captured in this study, attraction of the histerid species *P. attenuatum* to traps baited with ipsenol and ipsdienol was interrupted by the addition of ethanol + α -pinene at 2 locations (Fig. 2A and C), similar to the response profile of *I. avulsus* and *I. grandicollis* exhibited in this study (Miller et al. 2011). It is unclear how consistent this specificity would be over time. Specialization by predators can be detrimental when specific species of prey are scarce (Brin and Bouget 2018).

The dynamics of predators and prey within pine stands appear to be complex, diverse, and constantly in flux (Brin and Bouget 2018). The ecosystems associated with saproxylic insects are highly diverse and critical in the decomposition of woody material (Ulyshen 2016). Further research and evaluation of inter-specific relationships will be needed to better understand forest insect dynamics and our opportunities to manage them. For example, different species of predators could be preying on each other, which may mediate their responses to kairomones. Changing ratios of pheromone and host volatiles over time may function as a complex signal for predators to balance prey opportunities with the risk of competition or exposure to other predators. Moreover, numerous species of fungivores as well as dipteran and hymenopteran

parasitoids are associated with bark beetle-infested pine logs (Goyer et al. 1974, Sullivan et al. 2000, Sullivan and Berisford 2004).

Our results provide some impetus for additional research to explore these possibilities in the future. Lures that attract both predators and pest bark beetles may prove important as monitoring tools as communities are altered by climate change and occurrence of invasive species (Dahlsten et al. 2004). Lures may also be used to direct predators to bark beetle infestations after bark beetles have ceased emission of pheromone (Aukema and Raffa 2005). Lure blends that can detect broad arrays of bark and woodboring species along with various predators could be used as a cost-effective method to assess biodiversity and early detection of forest health issues (Dodds et al. 2015).

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Author Contributions

Daniel Miller (Conceptualization [Lead], Formal analysis [Lead], Investigation [Equal], Methodology [Equal], Writing – original draft [Lead], Writing – review & editing [Equal]), and Christopher Asaro (Conceptualization [Supporting], Formal analysis [Supporting], Investigation [Equal], Methodology [Equal], Writing – original draft [Supporting], Writing – review & editing [Equal])

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