The Canadian Entomologist (2023), **155**, e5, 1–15
doi:10.4039/tce.2022.44

Published on behalf of the Entomological Society of Canada

ARTICLE

Coleopteran predators of bark and woodboring beetles attracted to traps baited with ethanol and α-pinene in pine (Pinaceae) forests of the southern United States of America

Daniel R. Miller*

United States Department of Agriculture, Forest Service, Southern Research Station, 320 Green Street, Athens, Georgia, 30602, United States of America
*Corresponding author. Email: Daniel.Miller1@usda.gov

(Received 31 July 2022; accepted 19 October 2022)

Abstract

The effects of ethanol and α-pinene lures on trap catches of forest coleopteran predators and fungivores were evaluated in studies conducted in 2002–2004 to evaluate trap responses of bark and woodboring beetles in the southern United States of America. Traps baited with ethanol, α-pinene, or a combination of the two attracted predator species in six families of Coleoptera. The most abundant species were *Coptodera aerata* Dejean (Carabidae), *Thanasimus dubius* Fabricius (Cleridae), *Temnoscheila virescens* (Fabricius) (Trogossitidae), and *Lasconotus* spp. (Zopheridae). Most species were attracted by both ethanol and α-pinene lures; traps baited with both compounds generally caught the greatest numbers for most species. There was some evidence of geographic variation in responses to ethanol and α-pinene. For example, catches of *C. aerata* in ethanol-baited traps were enhanced by the addition of α-pinene in North Carolina but not in Alabama or South Carolina. Catches of *Lasconotus* spp. in traps baited with α-pinene were enhanced with ethanol in Florida but not in North and South Carolina. The fungivore *Pycnomerus sulcicollis* LeConte (Zopheridae) was captured in significant numbers in traps baited with α-pinene. Responses of predators to ethanol and α-pinene mirrored those of bark and woodboring beetles captured in these same experiments.

Introduction

Dead, dying, or downed trees, branches, and shrubs are ephemeral habitats for bark and woodboring beetles because most qualities of those habitats degrade quickly over time. Competition for those habitats can be strong, providing a basis for selection favouring those individuals that take advantage of chemical cues as kairomones associated with preferred habitats. Volatile monoterpenes such as α-pinene are abundant in the phloem tissues of pine (Pinaceae) trees (Mirov 1961; Smith 2000). Resin containing these monoterpenes is released from trees following events such as fire, physical injury, drought stress, or attacks by pest species such as *Ips* spp. (Coleoptera: Curculionidae) (Wood 1982; Sjödin *et al.* 1989; Fletchmann *et al.* 1999; Fettig *et al.* 2006; Jaakkola *et al.* 2022). Ethanol is released from stressed trees or as a fermentation product of dead, damaged, or dying trees (Kelsey 1994, 2001; Ranger *et al.* 2016; Kelsey and Westlind 2017).

Monoterpenes and ethanol may also be important as kairomones for predators because bark beetle–infested habitats are ephemeral for predators due to limited opportunities for their larvae to

---

Subject Editor: Therese Poland

attack and feed on the larvae of bark and woodboring beetles. In Europe, for example, the predator *Thanasimus formicarius* (Linnaeus) (Coleoptera: Cleridae) and the bark beetles *Tomicus piniperda* (Linnaeus) and *Hylurgops palliatus* (Gyllenhal) (Coleoptera: Curculionidae) were all attracted to traps baited with ethanol and α-pinene and have similar flight periods in stands of *Pinus sylvestris* (Linnaeus) and *Picea abies* (Linnaeus) Karsten (Pinaceae) (Schroeder and Lindelöw 1989; Schroeder 2003). In eastern Canada, traps baited with a blend of monoterpenes and ethanol were attractive to *Thanasimus* spp. and the bark beetle *Dryocoetes autographus* (Ratzeburg) in a mixed conifer stand (Chénier and Philogène 1989).

Fungi play a vital role in the breakdown of woody material, with numerous species of insects influencing the role of fungi by their feeding activities and ability to transport spores to new hosts (Ulyshen 2016; Marcot 2017). Assessments of forest communities in biodiversity studies often identify fungivores as an important guild in forest health (Vanderwel *et al.* 2006; Jacobs and Work 2012; Schowalter 2017; Ulyshen and Šobotnik 2018). Grazing by fungivores can influence fungal growth and community structure, thereby affecting rates of wood decay (Birkemoe *et al.* 2018). Species of Silvanidae and Zopheridae (Coleoptera) are often found under the bark of dead, dying, or decayed trees, although little is known about the biology of most species of fungivores (Gimmel and Ferro 2018). Therefore, host kairomones may be important to subcortical fungivorous beetles in finding suitable hosts. Volatiles such as ethanol and α-pinene could provide information to fungivores in search of specific fungi that are possibly associated with bark and ambrosia beetles. Fungivores may also be potential prey for predators that respond to the same compounds.

Studying the ecology of bark and woodboring beetles, and their associated species of predators and fungivores, is challenging because much of their lives is spent under the bark and hidden from view. Clarifying the relative roles of semiochemicals, such as those released from host pines, on prey and predators should provide insights into the ecological interactions between bark and woodboring beetles and their associated predators in pine forests. Assessments of behavioural responses of predators to semiochemicals may provide tools in the future for managing pest species. It is possible that lures could be used to direct predators to specific sites early in bark beetle infestations. Monitoring the ratio of predators to their prey in baited traps could provide estimates of infestation progression of pest species, such as the estimates currently used for the southern pine beetle, *Dendroctonus frontalis* Zimmermann (Coleoptera: Curculionidae), in southern pine forests of the United States of America (Billings 2017; Clarke and Hartshorn 2021).

In 2002–2004, eight trapping experiments were conducted in the southern United States of America to assess the effects of ethanol and α-pinene lures on trap catches of bark and woodboring beetles and their associated predators and fungivores. The responses of bark and woodboring beetles in these experiments have been published in Miller (2006) and Miller and Rabaglia (2009). Herein, I report on the responses of forest predatory and fungivorous species to traps baited solely with ethanol, α-pinene, or both in those eight studies.

Methods

Eight trapping experiments were conducted in mature pine forests in Alabama, Florida, Georgia, South Carolina, and North Carolina in the southern United States of America (Table 1). The methods have been published previously in Miller (2006) and Miller and Rabaglia (2009). Standard eight-unit black multiple-funnel traps with wet cups were used in all eight experiments. Traps, black ethanol pouch lures, and blue α-pinene pouch lures were obtained from Phero Tech Inc. (Delta, British Columbia, Canada). Release rates (determined by the manufacturer at 20–23 °C) from ethanol and α-pinene lures were approximately 0.5 and 1–5 g/day, respectively.

Table 1. Locations of national forests (NF) and experimental forest (EF) in the southern United States of America used in experiments 1–8 along with coordinates, primary tree species, and trapping dates.

Exp	Location	Coordinates	Tree species	Trapping dates
1	Ocala NF, Florida	29.244° N, 81.841° W	*Pinus palustris* Miller	26 Feb–26 May 2002
2	Osceola NF, Florida	30.305° N, 82.432° W	*P. palustris* and *P. elliottii* Engelmann	25 Feb–25 May 2002
3	Oconee NF, Georgia	33.056°N, 83.682° W	*P. taeda* Linnaeus	12 Jun–8 Aug 2002
4	Blue Valley EF, North Carolina	35.011° N, 83.237° W	*P. strobus* Linnaeus	20 Jun–20 Aug 2002
5	Bankhead NF, Alabama	34.300° N, 87.267° W	*P. taeda* and *Tsuga canadensis* (Linnaeus)	28 Apr–10 Jul 2003
6	Nantahala NF, North Carolina	35.074° N, 84.116° W	*P. strobus* and *P. echinata* Miller	1 May–14 Aug 2003
7	Sumter NF, South Carolina	34.590° N, 81.645° W	*P. taeda*	15 Apr–16 Jul 2003
8	Apalachicola NF, Florida	30.405° N, 84.455° W	*P. palustris* and *P. elliottii*	30 Mar–16 Jun 2004

In each experiment, traps were set in a randomised complete block design, with each of the following four lure treatments applied randomly to traps within each of eight blocks per experiment: (1) blank; (2) ethanol; (3) α-pinene; and (4) ethanol + α-pinene. Lures were replaced once after 7–8 weeks. Traps were spaced 10–15 m apart within each block; blocks were spaced 15–500 m apart. Each trap was hung on twine tied between trees, such that collection cups were 0.2–0.5 m above ground level and all traps were more than two metres from any trees. Collection cups contained approximately 200 mL of a pink aqueous propylene glycol (ethanol-free) solution (Peak RV & Marine Antifreeze, Old World Industries Inc., Northbrook, Illinois, United States of America) to kill and preserve beetles (Miller and Duerr 2008). Voucher specimens were deposited in the University of Georgia Collection of Arthropods, Athens, Georgia, United States of America.

Statistical analyses were conducted with the SYSTAT, version 13, and SigmaStat, version 3.01, statistical packages (SYSTAT Software Inc., Point Richmond, California, United States of America) for species caught in sufficient numbers ($N \geq 30$). As needed, data were transformed by ln $(Y + 1)$ to attain normality and homoscedasticity, verified by the Shapiro–Wilk and equal variance tests, respectively. Treatments with zero total catches in an experiment were omitted from analyses because of the issue of heteroscedasticity (Reeve and Strom 2004). In all experiments, data were analysed by mixed-model analysis of variance, with treatment as the fixed factor, followed by the Holm–Sidak multiple comparison test for species showing effects of treatments ($\alpha = 0.05$; Glantz 2005). For species affected by treatments (with no treatments having zero catches), data were further analysed by a mixed-model analysis of variance using the following model factors: (1) ethanol (Et); (2) α-pinene (aP); and (3) ethanol × α-pinene (Et × aP).

Results

A total of 10 567 predatory and fungivore beetles was captured in the eight experiments, representing at least 12 species across eight families of Coleoptera (Table 2). The most abundant species were *Lasconotus* spp. (Zopheridae), *Pycnomerus sulcicollis* LeConte (Zopheridae), *Temnoscheila virescens* Fabricius (Trogossitidae), *Coptodera aerata* Dejean (Carabidae), and *Thanasimus dubius* (Fabricius) (Cleridae), accounting for 49%, 14%, 11%, 6%, and 6% of the total beetle catches, respectively.

Predators

Coptodera aerata were caught in sufficient numbers for analysis at all five locations where they were detected (Table 2). Trap catches of *C. aerata* were affected by ethanol but not α-pinene in Alabama and South Carolina (Table 3), with catches in traps baited with ethanol (with or without α-pinene) greater than those not baited with ethanol (Fig. 1A, B). In North Carolina (Nantahala National Forest), catches were affected by ethanol, α-pinene, and the interaction between the two treatments (Table 3). Additionally, treatments affected catches of *C. aerata* at the other location in North Carolina (Blue Valley Experimental Forest; $F_{2,14} = 9.020$, $P = 0.002$). At both North Carolina locations, catches in traps baited with ethanol were enhanced by the addition of α-pinene, although α-pinene by itself was not attractive to *C. aerata* (Fig. 1C, D). In Georgia, *C. aerata* were only caught in traps baited with ethanol or with ethanol + α-pinene (Fig. 1E), with no treatment effect between the two ($F_{1,7} = 3.512$, $P = 0.103$).

Thanasimus dubius was caught at six locations, but only one location had sufficient numbers for analyses (Table 2). Both ethanol and α-pinene affected catches of *Th. dubius* in South Carolina; no interaction was observed between the two treatments (Table 3). Catches were greatest in traps baited with ethanol + α-pinene and lowest in those not baited with α-pinene (Fig. 1F). *Enoclerus nigripes* (Say) (Cleridae) were detected at four locations, but the numbers were too low for analyses

Table 2. Numbers of predatory and fungivore Coleoptera captured in eight trapping experiments conducted in the southern United States of America (2002–2004). AL, Alabama; FL, Florida; GA, Georgia; NC, North Carolina; SC, South Carolina; Exp, experiment.

	AL	FL			GA	NC		SC	
Family **s**pecies	Exp 5	Exp 1	Exp 2	Exp 8	Exp 3	Exp 4	Exp 6	Exp 7	Total
Carabidae									
Coptodera aerata Dejean	217	–	–	–	55	51	178	86	587
Cleridae									
Enoclerus nigripes (Say)	1	–	–	–	–	2	23	6	32
Thanasimus dubius (Fabricius)	5	3	–	–	22	2	19	532	583
Histeridae									
Platysoma spp.	42	8	–	–	18	–	17	25	110
Passandridae									
Catogenus rufus (Fabricius)	–	2	106	–	23	–	–	14	145
Silvanidae									
Silvanus bidentatus (Fabricius)	41	23	54	46	54	10	–	120	348
Tenebrionidae									
Corticeus spp.	29	11	12	12	5	14	138	294	515
Trogossitidae									
Temnoscheila virescens (Fabricius)	16	93	363	4	2	–	626	28	1,132
Tenebroides spp.	8	2	46	25	14	–	3	310	408
Zopheridae									
Lasconotus spp.	7	206	318	259	25	114	116	4,090	5,135
Namunaria guttulata (LeConte)	–	–	–	–	107	–	–	19	126
Pycnomerus sulcicollis LeConte	180	–	–	–	664	13	11	578	1,446
Total	546	348	899	346	989	206	1,131	6,102	10 567

(Table 2). At only one of five locations were *Platysoma* spp. (Histeridae) caught in sufficient numbers (Table 2). Ethanol, α-pinene, and the interaction between the two had significant effects on catches of *Platysoma* spp. in Alabama (Table 3), with traps baited with ethanol + α-pinene catching the most *Platysoma* spp. (Fig. 1G). *Catogenus rufus* (Fabricius) (Passandridae) was detected at four locations but in sufficient numbers at only one location (Table 2). Lure treatments had no effect on trap catches of *C. rufus* in Florida (Osceola National Forest; $F_{3,21} = 0.542$, $P = 0.659$); the mean (± standard error) trap catch was 3.3 ± 0.6.

Corticeus spp. (Tenebrionidae) were detected at all eight locations but in sufficient numbers at only two locations (Table 2). Lure treatments affected catches of *Corticeus* spp. in North Carolina (Nantahala National Forest; $F_{2,14} = 5.556$, $P = 0.030$) and in South Carolina (Table 3). At both locations, traps baited with α-pinene caught more beetles than those not baited with α-pinene did (regardless of the presence or absence of ethanol; Fig. 2A, B).

Detected at seven locations, *Te. virescens* were caught in sufficient numbers for analyses at three locations (Table 2). Treatments affected catches of *Te. virescens* in Florida (Ocala National Forest; $F_{2,14} = 9.193$, $P = 0.003$), with catches in traps baited with ethanol + α-pinene greater than those in traps baited with only one compound (Fig. 2C). Catches in Florida (Osceola National Forest) and North Carolina (Nantahala National Forest) were affected by ethanol, α-pinene, and the

Table 3. Analysis of variance results for the effects of ethanol (Et), α-pinene (aP), and the interaction of ethanol and α-pinene (Et × aP) on catches of predatory and fungivore beetles in 8-unit multiple-funnel traps, experiments (Exp) 1–8. *P*-values in bold are significant.

		Et		aP		Et × aP	
Family species	Exp	$F_{1,21}$	*P*	$F_{1,21}$	*P*	$F_{1,21}$	*P*
Carabidae							
Coptodera aerata	5	47.92	< **0.001**	0.031	0.863	0.221	0.643
	6	36.934	< **0.001**	5.838	**0.025**	5.838	**0.025**
	7	66.82	< **0.001**	0.760	0.393	0.760	0.393
Cleridae							
Thanasimus dubius	7	14.96	**0.001**	29.70	< **0.001**	0.007	0.935
Histeridae							
Platysoma spp.	5	9.993	**0.005**	21.79	< **0.001**	8.222	**0.009**
Silvanidae							
Silvanus bidentatus	3	27.61	< **0.001**	36.48	< **0.001**	8.287	**0.009**
	5	0.000	0.998	6.284	**0.020**	0.029	0.867
	7	2.299	0.144	19.86	< **0.001**	4.510	**0.046**
Tenebrionidae							
Corticeus spp.	7	0.100	0.755	116.4	< **0.001**	0.515	0.481
Trogossitidae							
Temnoscheila virescens	2	38.74	< **0.001**	102.7	< **0.001**	21.62	< **0.001**
	6	5.221	**0.033**	32.63	< **0.001**	4.780	**0.040**
Tenebroides spp.	7	11.19	**0.003**	133.2	< **0.001**	0.498	0.488
Zopheridae							
Lasconotus spp.	1	11.63	**0.003**	89.51	< **0.001**	17.37	< **0.001**
	2	15.81	**0.001**	81.95	< **0.001**	5.806	**0.025**
	4	0.540	0.470	13.84	**0.001**	0.759	0.393
	6	0.187	0.670	11.37	**0.003**	0.030	0.864
	7	0.138	0.714	150.2	< **0.001**	0.781	0.387
	8	27.75	< **0.001**	110.9	< **0.001**	27.75	< **0.001**
Pycnomerus sulcicollis	3	0.034	0.855	166.0	< **0.001**	0.001	0.980
	7	0.059	0.811	26.11	< **0.001**	0.106	0.748

interaction between the two compounds (Table 3). At both locations, α-pinene by itself was attractive to *Te. virescens*, whereas ethanol by itself was not; however, the combination of ethanol and alpha-pinene appeared to synergise attraction (Fig. 2D, E). *Tenebroides* spp. (Trogossitidae) were detected at seven locations and in sufficient numbers at two locations (Table 2). Catches were affected by treatments in Florida (Osceola National Forest; $F_{2,14} = 21.45$, $P < 0.001$) and South Carolina (Table 3). Catches of *Tenebroides* spp. were significantly increased by baiting traps with α-pinene alone but were higher still when baited with both alpha-pinene and ethanol; ethanol by itself did not increase catches compared to unbaited traps (Fig. 2F, G).

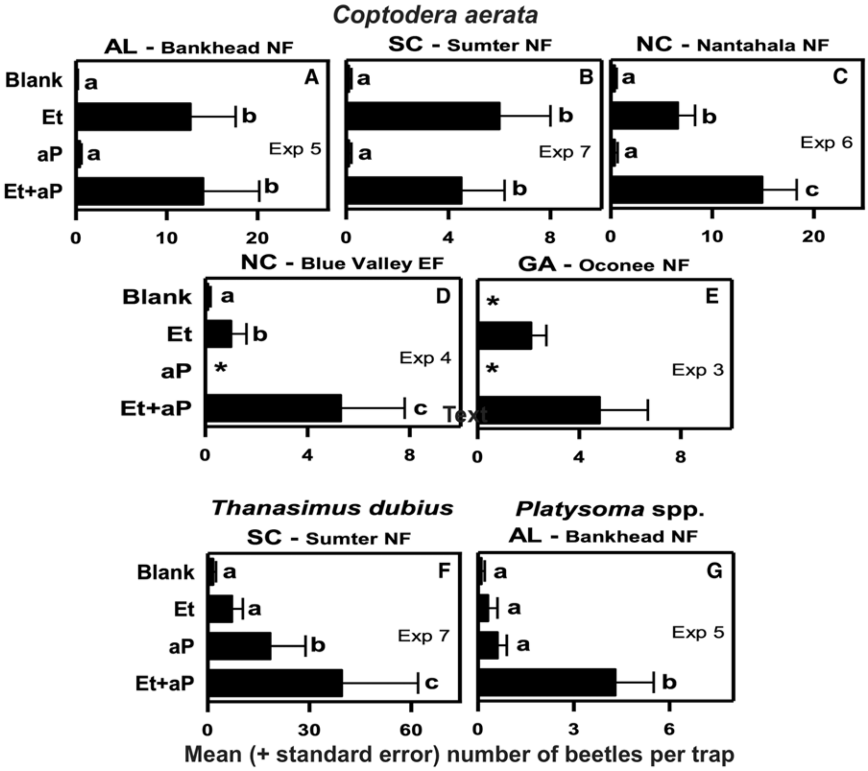

Fig. 1. Effects of ethanol (Et) and α-pinene (aP) on mean (± standard error) trap catches of **A–E**, *Coptodera aerata* (Carabidae) in experiments 3–7; **F**, *Thanasimus dubius* (Cleridae) in experiment 7; and **G**, *Platysoma* spp. (Histeridae) in experiment 5. Means within an experiment followed by the same letter are not significantly different at $P = 0.05$ (Holm–Sidak test). Treatments with an asterisk (*) had zero catches. AL, Alabama; GA, Georgia; NC, North Carolina; SC, South Carolina; NF, National Forest; EF, Experimental Forest.

Lasconotus spp. were detected at all eight locations, with sufficient numbers caught at six locations for analyses (Table 2). Ethanol, α-pinene, and the interaction between the two affected catches of *Lasconotus* spp. at all three Florida locations (Ocala, Osceola, and Apalachicola National Forests; Table 3). Catches were highest in traps baited with ethanol + α-pinene and lowest in traps not baited with ethanol (Fig. 3A–C). Only α-pinene affected catches of *Lasconotus* spp. in South Carolina and the two locations in North Carolina (Blue Valley Experimental Forest and Nantahala National Forest; Table 3). In South Carolina, catches in traps baited with α-pinene (with or without ethanol) caught more beetles than did those not baited with α-pinene (with or without ethanol; Fig. 3D). The Holm–Sidak test was unable to separate treatment means for beetles caught in North Carolina (Nantahala National Forest; Fig. 3E). In North Carolina (Blue Valley Experimental Forest), catches of *Lasconotus* spp. were greater in traps baited with ethanol + α-pinene than in those not baited with α-pinene (Fig. 4F).

Fungivores

Silvanus bidentatus (Fabricius) (Silvanidae) was detected at seven locations, with sufficient numbers obtained at five locations (Table 2). Lure treatments had a significant effect on catches of *S. bidentatus* in Florida at two locations: Osceola National Forest ($F_{2,14} = 11.12$, $P = 0.001$) and Apalachicola National Forest ($F_{2,14} = 20.35$, $P < 0.001$). No *S. bidentatus* was

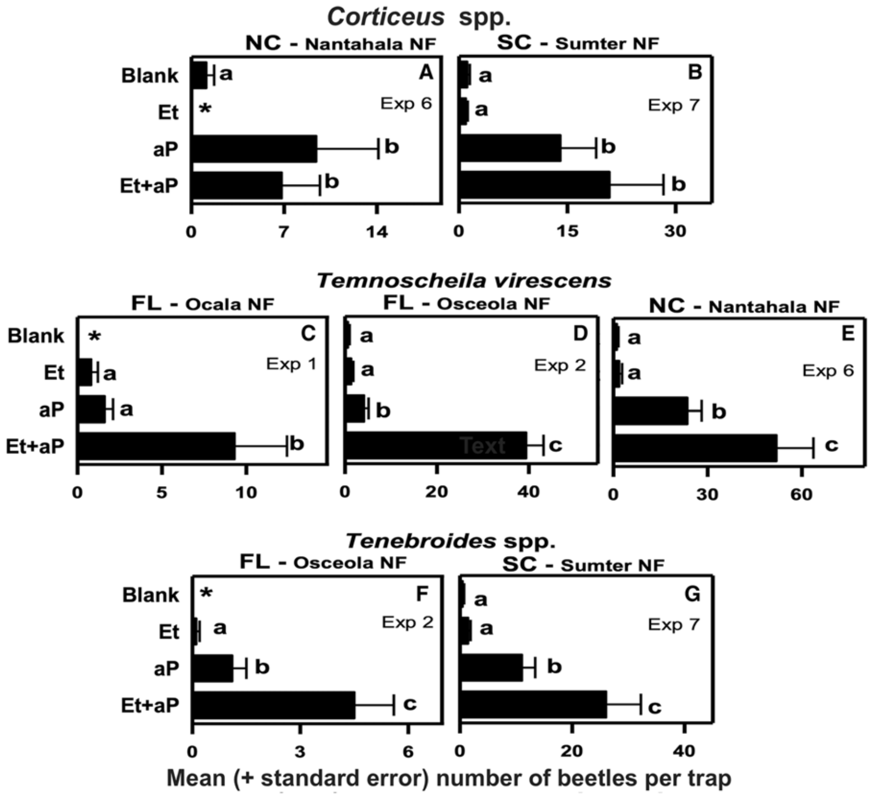

Fig. 2. Effects of ethanol (Et) and α-pinene (aP) on mean (± standard error) trap catches of **A–B**, *Corticeus* spp. (Tenebrionidae) in experiments 6–7; **C–E**, *Temnoscheila virescens* (Trogossitidae) in experiments 1, 2, and 6; and **F–G**, *Tenebroides* spp. (Trogossitidae) in experiments 2 and 7. Means for a species within an experiment followed by the same letter are not significantly different at $P = 0.05$ (Holm–Sidak test). Treatments with an asterisk (*) had zero catches. FL, Florida; NC, North Carolina; SC, South Carolina; NF, National Forest; EF, Experimental Forest.

caught in blank traps at either locations (Fig. 4A, C). Catches in Georgia were affected by both treatments, as well as by the interaction between the two treatments (Table 3). At both Florida locations and in Georgia, catches of *S. bidentatus* in traps baited with both compounds were greater than were those in traps baited with only one compound (Fig. 4A–C). In South Carolina, catches of *S. bidentatus* were affected by α-pinene and the interaction between ethanol and α-pinene (Table 3), with catches in traps baited with both compounds greater than those in traps baited with ethanol alone (Fig. 4D). In Florida (Apalachicola National Forest) and South Carolina, catches in traps baited with α-pinene were greater than those in traps baited with ethanol alone (Fig. 4C, D). In Alabama, catches of *S. bidentatus* were affected by α-pinene (Table 3), but treatment means could not be separated by the Holm–Sidak test (Fig. 4E).

Detected at five locations, *P. sulcicollis* were caught in sufficient numbers at three locations (Table 2). In Georgia and South Carolina, catches were affected by α-pinene but not ethanol (Table 3). Treatments had a significant effect on catches of *P. sulcicollis* in Alabama, as well ($F_{2,14} = 7.994$, $P = 0.005$). At all three locations, traps baited with α-pinene (with or without ethanol) caught more beetles than did those not baited with α-pinene (Fig. 5A–C). Catches of *Namunaria guttulata* (LeConte) (Zopheridae) in Georgia were unaffected by lure treatments ($F_{3,21} = 1.504$, $P = 0.243$); the mean (± standard error) trap catch was 3.3 ± 0.6.

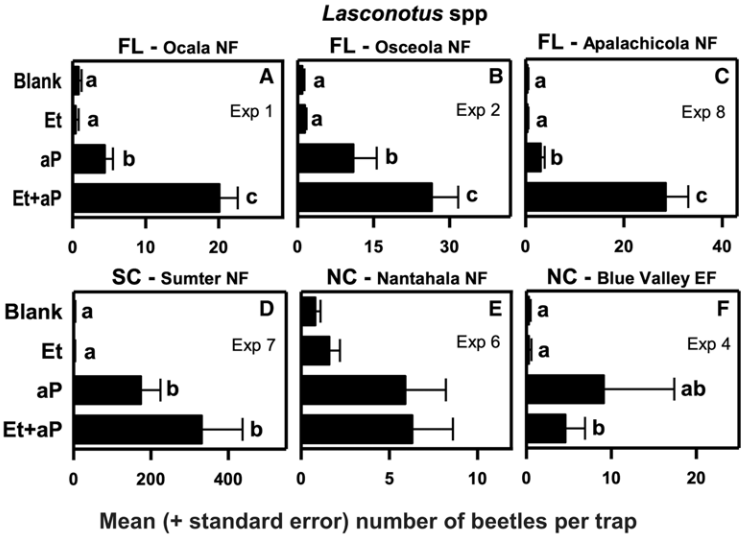

Fig. 3. Effects of ethanol (Et) and α-pinene (aP) on mean (± standard error) trap catches of **A–F**, *Lasconotus* spp. (Zopheridae) in experiments 1, 2, 4, and 6–8. Means within an experiment followed by the same letter are not significantly different at $P = 0.05$ (Holm–Sidak test). FL, Florida; NC, North Carolina; SC, South Carolina; NF, National Forest; EF, Experimental Forest.

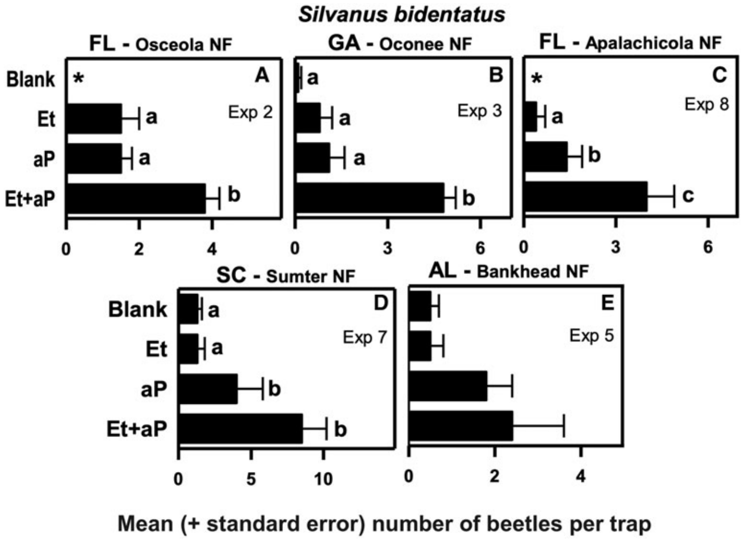

Fig. 4. Effects of ethanol (Et) and α-pinene (aP) on mean (± standard error) trap catches of *Silvanus bidentatus* (Silvanidae) in **A–E**, experiments 2, 3, 5, 7, and 8. Means for a species within an experiment followed by the same letter are not significantly different at $P = 0.05$ (Holm–Sidak test). Treatments with an asterisk (*) had zero catches. AL, Alabama; FL, Florida; GA, Georgia; SC, South Carolina; NF, National Forest; EF, Experimental Forest.

Discussion

Research on species of forest-dwelling beetles has focused largely on species that attack and kill trees. With respect to the biological control of these pest species, parasitoids have been emphasised because of their general capacity to infect many individuals over a short amount of time (Furniss

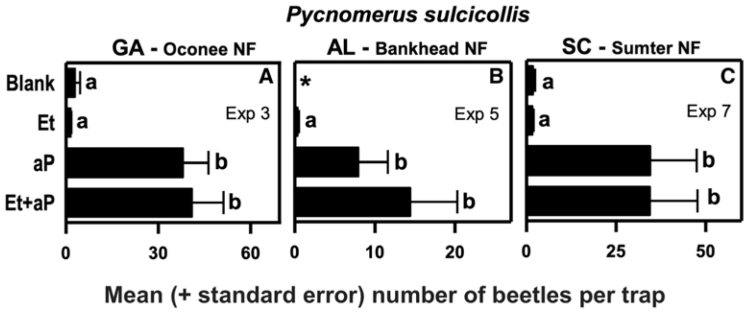

Fig. 5. Effects of ethanol (Et) and α-pinene (aP) on mean (± standard error) trap catches of *Pycnomerus sulcicollis* (Zopheridae) in **A–C**, experiments 3, 5, and 7. Means within an experiment followed by the same letter are not significantly different at $P = 0.05$ (Holm–Sidak test). Treatments with an asterisk (*) had zero catches. AL, Alabama; GA, Georgia; SC, South Carolina; NF, National Forest; EF, Experimental Forest.

and Carolin 1980; Kenis and Hilszcanski 2007; Kenis *et al.* 2007; Paine 2017). Except for some species of Cleridae, predators have not been significantly studied, particularly with respect to interactions with Buprestidae and Cerambycidae. Understanding the interactions between species and the biodiversity of forest bark and woodboring beetle communities is important because these guilds provide critical roles in the breakdown of woody material, facilitating nutrient cycling and forest regeneration. Activities by bark and woodboring beetles help to minimise the build-up of downed woody material, which impedes movement of wildlife and growth of understorey vegetation, and reduce fire hazards.

Species in four beetle families (Cleridae, Histeridae, Trogossitidae, and Zopheridae) are known to broadly prey on bark and woodboring beetles (Stephen and Dahlsten 1976; Furniss and Carolin 1980; United States Department of Agriculture 1985; Kenis *et al.* 2007; Evans 2014; Wegensteiner *et al.* 2015). The combination of ethanol and α-pinene was attractive for the following predator species of bark and woodboring beetles commonly found in the southern United States of America (Goyer *et al.* 1980; United States Department of Agriculture 1985; Allison *et al.* 2013): *Th. dubius* (Fig. 1F), *Platysoma* spp. (Fig. 1G), *Corticeus* spp. (Fig. 2A, B), *Te. virescens* (Fig. 2C–E), and *Lasconotus* spp. (Fig. 3A–D, F). The response profiles of these predators mirror those of numerous species of bark and woodboring beetles captured in the same study (Miller 2006; Miller and Rabaglia 2009). Ten species of ambrosia beetles and two species of bark beetles were attracted to ethanol, five species of bark beetles were attracted to α-pinene, and ethanol enhanced attraction for six species (Miller and Rabaglia 2009). Eight of 10 species of woodborers were attracted to α-pinene, with ethanol enhancing responses of six species (Miller 2006).

Little is known about the biology of *C. aerata*, although it is commonly found on and under bark (Evans 2014). Other species of Carabidae are recognised as predators of bark beetles (Wegensteiner *et al.* 2015). Given its response profiles, *C. aerata* may prey on bark and woodboring beetles or associated species. Lure treatments had no effect on catches of *C. rufus*. Similarly, trap catches of *C. rufus* in Georgia were unaffected by pheromones of southern *Ips* spp. (Allison *et al.* 2013). These results are not surprising because larval *C. rufus* are larval ectoparasites of woodboring beetles (United States Department of Agriculture 1985; Thomas 1993; Evans 2014). There would be no benefit to adults arriving on habitats before prey larvae have developed to mid- or late-instar stages, generally at times when release of ethanol, α-pinene, and *Ips* pheromones is likely finished. Further work is needed to determine the cues used by ectoparasites to locate their prey.

The biology of species such as the zopherid *P. sulcicollis* and the non-native silvanid *S. bidentatus* is largely unknown (Majka 2008; Evans 2014; Lord *et al.* 2015). These species are often found in, on, or around bark of downed woody material and are considered fungivorous because they are commonly found with fungal mats, which are often associated with bark and ambrosia beetles. In a study with passive traps, Ulyshen and Hanula (2009) found that *P. sulcicollis* were more common in upland pine stands than in hardwood stands. The attraction of *P. sulcicollis* to α-pinene but not to ethanol (Fig. 5) suggests attraction of the species to freshly damaged pine boles and branches. In a separate study, trap catches of *P. sulcicollis* in traps baited with ipsenol and ipsdienol increased with the addition of α-pinene and with no effect from the addition of ethanol, further enhancing the likelihood of the species' association with bark beetles and possible associated fungi (Miller 2020). In contrast, attraction of *S. bidentatus* to the combination of α-pinene and ethanol suggests a different pine habitat association than that for *P. sulcicollis*, probably one with some decay, as suggested by the attraction to ethanol, as well as to α-pinene (Fig. 4).

The biology of zopherids and silvanids may be a more complex than simply one feeding activity. For example, some zopherids, such as *Lasconotus* spp., are predominantly predators, although some feed on fungi as early instar larvae before switching to feed on bark beetle larvae as later instars (Hackwell 1973). Species of *Silvanus* are considered to be partly fungivorous (Thomas 1993). *Silvanus bidentatus* is commonly found under the bark of trees with bark beetles in the southern United States of America (Goyer *et al.* 1980). The feeding habits of these species require more research.

Host volatiles are known to interact with bark beetle pheromones in attracting predators, again mirroring the responses of their prey. For example, in the southern United States of America, ipsenol and ipsdienol are pheromones for *Ips* spp. (Coleoptera: Curculionidae) (Miller *et al.* 2005; Allison *et al.* 2012). Both compounds also attract numerous species of beetle predators (Allison *et al.* 2013). Adding ethanol + α-pinene to traps baited with ipsenol + ipsdienol increased trap catches of several predatory species, including *Th. dubius*, *Te. virescens*, and *Lasconotus* spp. (Miller 2020). Catches of *Platysoma* spp. increased with the addition of ethanol, with attraction interrupted by the addition of α-pinene, whereas catches of *Corticeus* spp. increased with the addition of α-pinene but with no effect from the addition of ethanol (Miller 2020). Response profiles of these predators to ethanol and α-pinene in the presence of ipsenol and ipsdienol are similar to those in the current study without those pheromones.

Numerous monoterpenes other than α-pinene are commonly found in the resin of pine trees, with composition varying between species and geographic location (Mirov 1961; Gansel and Squillace 1976; Squillace and Wells 1981; Smith 2000). Many of these monoterpenes can influence the behaviours of bark beetles and their associated predators. For example, in lodgepole pine (*Pinus contorta* variant *latifolia* Engelmann) forests of British Columbia, Canada, catches of the bark beetle *Ips pini* (Say) and associated predators *Lasconotus* spp. and *Corticeus* spp. in traps baited with the pheromone ipsdienol were enhanced by the addition of monoterpenes such as 3-carene, β-pinene, and β-phellandrene (Miller and Borden 1990, 2000, 2003).

Numerous families of Coleoptera are known to have predatory species (Furniss and Carolin 1980; United States Department of Agriculture 1985; Evans 2014). The presence and diversity of predators may limit the ability of non-native species to establish in our forests. Greater diversity of predators may allow for greater resilience to impacts from pest species in forests that are altered as a result of climate change. As relative abundance of prey species changes over time, predator abundance could respond to these changes, thereby minimising the risk of one species exploding in numbers. Research on the entire community of bark and woodboring beetles and their associated species of commensals and predators is needed to support improved management of our forest resources. This is especially true in addressing the variation exhibited by some species, particularly as the variation in behavioural responses is not the same across the species reported here for predators and fungivores, and for bark and woodboring beetles in Miller (2006) and Miller and Rabaglia (2009). Although the causes of these variations are unknown, they underscore the need for such studies to be conducted over a broad geographic range so that the reliability of these lures for use in detection and control programmes can be assessed.

Acknowledgements. The author thanks Will Shepherd (United States Department of Agriculture, Forest Service) for a critical review of the manuscript, Chris Crowe (United States Department of Agriculture, Forest Service) for field assistance, and Richard Hoebeke (University of Georgia Collection of Arthropods) for verification of insect identifications. The use of trade names and the identification of firms or corporations do not constitute an official endorsement or approval by the United States government of any product or service to the exclusion of others that may be suitable. The United States Department of Agriculture is an equal opportunity provider, employer, and lender.

Competing interests. The author declares none.

References

Allison, J.D., McKenney, J.L., Miller, D.R., and Gimmel, M.L. 2012. Role of ipsdienol, ipsenol, and *cis*-verbenol in chemical ecology of *Ips avulsus*, *Ips calligraphus*, and *Ips grandicollis* (Coleoptera: Curculionidae: Scolytinae). Journal on Economic Entomology, **105**: 923–929.

Allison, J.D., McKenney, J.L., Miller, D.R., and Gimmel, M.L. 2013. Kairomonal responses of natural enemies and associates of the southern *Ips* (Coleoptera: Curculionidae: Scolytinae) to ipsdienol, ipsenol and *cis*-verbenol. Journal of Insect Behavior, **26**: 321–335.

Billings, R.F. 2017. Revised protocol for predicting southern pine beetle infestation trends with pheromone traps (with use of endo-brevicomin). Texas A&M Forest Service, College Station, Texas, United States of America. 12 pp.

Birkemoe, T., Jacobsen, R.L., Sverdrup-Thygeson, A., and Biedermann, P.H.W. 2018. Insect–fungus interactions in dead wood systems. *In* Saproxylic insects: diversity, ecology and conservation. *Edited by* M.D. Ulyshen. Zoological Monographs. Volume 1. Springer Press, Cham, Switzerland. Pp. 377–427.

Chénier, J.V.R. and Philogène, B.J.R. 1989. Field responses of certain forest Coleoptera to conifer monoterpenes and ethanol. Journal of Chemical Ecology, **15**: 1729–1745.

Clarke, S.R. and Hartshorn, J. 2021. Contrasting competitor and predator responses to a short-lived southern pine beetle outbreak: a case study. Forest Science, **67**: 22–29.

Evans, A.V. 2014. Beetles of eastern North America. Princeton University Press, Princeton, New Jersey, United States of America.

Fettig, C.J., McMillin, J.D., Anhold, J.A., Hamud, S.M., Borys, R.R., Dabney, C.P., and Seybold, S.J. 2006. The effects of mechanical fuel reduction treatments on the activity of bark beetles (Coleoptera: Scolytidae) infesting ponderosa pine. Forest Ecology and Management, **230**: 55–68.

Fletchmann, C.A., Dalusky, M.J., and Berisford, C.W. 1999. Bark and ambrosia beetle (Coleoptera: Scolytidae) responses to volatiles from aging loblolly pine billets. Environmental Entomology, **28**: 638–648.

Furniss, R.L. and Carolin, V.M. 1980. Western forest insects. Miscellaneous Publication No. 1339. Pacific Northwest Forest and Range Experiment Station, Forest Service, United States Department of Agriculture, Portland, Oregon, United States of America.

Gansel, C.R. and Squillace, A.E. 1976. Geographic variation of monoterpene in cortical oleoresin of slash pine. Silvae Genetica, **25**: 150–154.

Gimmel, M.L. and Ferro, M.L. 2018. General overview of saproxylic Coleoptera. *In* Saproxylic insects: diversity, ecology and conservation. *Edited by* M.D. Ulyshen. Zoological Monographs. Volume 1. Springer Press, Cham, Switzerland. Pp. 51–128.

Glantz, S.A. 2005. Primer of biostatistics. McGraw-Hill Professional, New York, New York, United States of America.

Goyer, R.A., Lengard, G.J., Nebeker, T.E., and Garrard, L.D. 1980. Southern pine beetle handbook: how to identify common insect associates of the southern pine beetle. Agriculture Handbook 563. Combined Forest Pest Research and Development Program, United States Department of Agriculture, Washington, DC, United States of America.

Hackwell, G.A. 1973. Biology of *Lasconotus subcostulatus* (Coleoptera: Colydiidae) with special reference to feeding behavior. Annals of the Entomological Society of America, **66**: 62–65.

Jaakkola, E., Gärtner, A., Jönsson, A.M., Ljung, K., Olsson, P.-O., and Holst, T. 2022. Spruce bark beetle (*Ips typographus*) infestation cause up to 700 times higher bark BVOC emission rates from Norway spruce (*Picea abies*) [preprint]. Biogeosciences, **2022**: 125. https://doi.org/10.5194/bg-2022-125.

Jacobs, J.M. and Work, T.T. 2012. Linking deadwood-associated beetles and fungi with wood decomposition rates in managed black spruce forests. Canadian Journal of Forest Research, **42**: 1477–1490.

Kelsey, R.G. 1994. Ethanol synthesis in Douglas-fir logs felled in November, January, and March and its relationship to ambrosia beetle attack. Canadian Journal of Forest Research, **24**: 2096–2104.

Kelsey, R.G. 2001. Chemical indicators of stress in trees: their ecological significance and implications for forestry in eastern Oregon and Washington. Northwest Science, **75**: 70–76.

Kelsey, R.G. and Westlind, D.J. 2017. Physiological stress and ethanol accumulation in tree stems and woody tissues at sublethal temperatures from fire. BioScience, **67**: 443–451.

Kenis, M. and Hilszcanski, J. 2007. Natural enemies of Cerambycidae and Buprestidae infesting living trees. *In* Bark and wood boring insects in living trees in Europe: a synthesis. *Edited by* F. Lieutier, K.R. Day, A. Battisti, J.-C. Grégoire, and H.F. Evans. Springer Press, Dordrecht, The Netherlands. Pp. 475–498.

Kenis, M., Wermelinger, B., and Grégoire, J.-C. 2007. Research on parasitoids and predators: a review. *In* Bark and wood boring insects in living trees in Europe: a synthesis. *Edited by* F. Lieutier, K.R. Day, A. Battisti, J.-C. Grégoire, and H.F. Evans. Springer Press, Dordrecht, The Netherlands. Pp. 237–290.

Lord, N.P., Nearns, E.H., and Miller, K.B. 2015. Ironclad ID: tools for diagnosing ironclad and cylindrical bark beetles (Coleoptera: Zopheridae) of North America north of Mexico. Lucid Key. Available from https://cerambycids.com/ironcladid/ [accessed 7 July 2022].

Majka, C.G. 2008. The flat bark beetles (Coleoptera, Silvanidae, Cucujidae, Laemophloeidae) of Atlantic Canada. ZooKeys, **2**: 221–238.

Marcot, B.G. 2017. A review of the role of fungi in wood decay of forest ecosystems. Research Note PNW-RN-575. Pacific Northwest Forest and Range Experiment Station, Forest Service, United States Department of Agriculture, Portland, Oregon, United States of America.

Miller, D.R. 2006. Ethanol and (−)-α-pinene: attractant kairomones for some large wood-boring beetles in southeastern USA. Journal of Chemical Ecology, **32**: 779–794.

Miller, D.R. 2020. Effects of ethanol and α-pinene in a generic trap lure blend for pine bark and wood-boring beetles in southeastern United States. Journal of Entomological Science, **55**: 31–320.

Miller, D.R. and Borden, J.H. 1990. β-Phellandrene: kairomone for pine engraver, *Ips pini* (Say) (Coleoptera: Scolytidae). Journal of Chemical Ecology, **16**: 2519–2531.

Miller, D.R. and Borden, J.H. 2000. Dose-dependent and species-specific responses of pine bark beetles (Coleoptera: Scolytidae) to monoterpenes in association with pheromones. The Canadian Entomologist, **132**: 183–195. https://doi.org/10.4039/Ent132183-2.

Miller, D.R. and Borden, J.H. 2003. Responses of *Ips pini* (Say), *Pityogenes knechteli* Swaine and associated beetles (Coleoptera) to host monoterpenes in stands of lodgepole pine. Journal of Entomological Science, **38**: 602–611.

Miller, D.R. and Duerr, D. 2008. Comparison or arboreal beetle catches in wet and dry collection cups with Lindgren multiple funnel traps. Journal of Economic Entomology, **101**: 107–113.

Miller, D.R. and Rabaglia, R.J. 2009. Ethanol and (−)-α-pinene: attractant kairomones for bark and ambrosia beetles in the southeastern US. Journal of Chemical Ecology, **35**: 435–448.

Miller, D.R., Asaro, C., and Berisford, C.W. 2005. Attraction of southern pine engravers and associated bark beetles (Coleoptera: Scolytidae) to ipsenmol, ipsdienol, and lanierone in southeastern United States. Journal of Economic Entomology, **98**: 2058–2066.

Mirov, N.T. 1961. Composition of gum turpentines of pines. Technical Bulletin 1239. Pacific Southwest Forest and Range Experiment Station, Forest Service, United States Department of Agriculture, Portland, Oregon, United States of America.

Paine, T.D. 2017. Natural enemies and biological control of cerambycid pests. *In* Cerambycidae of the world: biology and pest management. *Edited by* Q. Wang. CRC Press, Taylor & Francis Group, New York, New York, United States of America. Pp. 291–303.

Ranger, C.M., Reding, M.E., Schultz, P.B., Oliver, J.B., Frank, S.D., Addesso, K.M., *et al.* 2016. Biology, ecology, and management of nonnative ambrosia beetles (Coleoptera: Curculionidae: Scolytinae) in ornamental plant nurseries. Journal of Integrated Pest Management, **7**: 1–23.

Reeve, J.D. and Strom B.L. 2004. Statistical problems encountered in trapping studies of scolytids and associated insects. Journal of Chemical Ecology, **30**: 1575–1590.

Schowalter, T. 2017. Arthropod diversity and functional importance in old-growth forests of North America. Forests, **8**: 97.

Schroeder, L.M. 2003. Differences in responses to α-pinene and ethanol, and flight periods between the bark beetle predators *Thanasimus femoralis* and *T. formicarius* (Col.: Cleridae). Forest Ecology and Management, **177**: 301–311.

Schroeder, L.M. and Lindelöw, Å. 1989. Attraction of scolytids and associated beetles by different absolute amounts and proportions of α-pinene and ethanol. Journal of Chemical Ecology, **15**: 807–817.

Sjödin, K., Schroeder, L.M., Eidmann, H.H., Norin, T., and Wold, S. 1989. Attack rates of scolytids and composition of wood constituents in healthy and mechanically weakened pine trees. Scandinavian Journal of Forest Research, **4**: 379–391.

Smith, R.H. 2000. Xylem monoterpenes of pines: distribution, variation, genetics, function. General Technical Report PSW-GTR-177. Pacific Southwest Research Station, Forest Service, United States Department of Agriculture, Albany, California, United States of America.

Squillace, A.E. and Wells, O.O. 1981. Geographic variation of monoterpenes in cortical oleoresin of loblolly pine. Silvae Genetica, **30**: 127–135.

Stephen, F.M. and Dahlsten, D.L. 1976. The arrival sequence of the arthropod complex following attack by *Dendroctonus brevicomis* (Coleoptera: Scolytidae) in ponderosa pine. The Canadian Entomologist, **108**: 283–304. https://doi.org/10.4039/Ent108283-3.

Thomas, M.C. 1993. The flat bark beetles of Florida (Coleoptera: Silvanidae, Passandridae, Laemophloeidae). Arthropods of Florida and neighboring lands. Volume 15. Contribution No 789. Florida Department of Agriculture & Consumer Services, Gainesville, Florida, United States of America.

Ulyshen, M.D. 2016. Wood decomposition as influenced by invertebrates. Biological Reviews, **91**: 70–85.

Ulyshen, M.D. and Hanula, J.L. 2009. Habitat associations of saproxylic beetles in the southeastern United States: a comparison of forest types, tree species and wood postures. Forest Ecology and Management, **257**: 653–664.

Ulyshen, M.D. and Šobotnik, J. 2018. An introduction to the diversity, ecology, and conservation of saproxylic insects. *In* Saproxylic insects. diversity, ecology and conservation. *Edited by* M.D. Ulyshen. Zoological Monographs. Volume 1. Springer Press, Cham, Switzerland. Pp. 1–47.

United States Department of Agriculture. 1985. Insects of eastern forests. Miscellaneous Publication No. 1426. Forest Service, United States Department of Agriculture, Washington, DC, United States of America.

Vanderwel, M.C., Malcolm, J.R., Smith, S.M., and Islam, N. 2006. Insect community composition and trophic guild structure in decaying logs from eastern Canadian pine-dominated forests. Forest Ecology and Management, **225**: 190–199.

Wegensteiner, R., Wermelinger, B., and Herrmann, M. 2015. Natural enemies of bark beetles: predators, parasitoids, pathogens, and nematodes. *In* Bark beetles: biology and ecology of native and invasive species. *Edited by* F.E. Vega and R.W. Hofstetter. Academic Press, Elsevier, New York, New York, United States of America.

Wood, D.L. 1982. The role of pheromones, kairomones, and allomones in the host selection and colonization behavior of bark beetles. Annual Review of Entomology, **27**: 411–446.

Cite this article: Miller, D.R. 2023. Coleopteran predators of bark and woodboring beetles attracted to traps baited with ethanol and α-pinene in pine (Pinaceae) forests of the southern United States of America. The Canadian Entomologist. https://doi.org/10.4039/tce.2022.44.