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ORIGINAL CONTRIBUTION

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4-allylanisole as a lure adjuvant for *Dendroctonus frontalis* (Coleoptera: Curculionidae: Scolytinae) and two associated beetles

Brian T. Sullivan[1] | **Holly L. Munro**[2] | **William P. Shepherd**[1] | **Kamal J. K. Gandhi**[2]

[1]USDA Forest Service, Southern Research Station, Pineville, Louisiana, USA

[2]D.B. Warnell School of Forestry and Natural Resources, University of Georgia, Athens, Georgia, USA

Correspondence
Brian T. Sullivan, USDA Forest Service Southern Research Station, 2500 Shreveport Hwy, Pineville, LA 71360, USA.
Email: Brian.sullivan2@usda.gov

Abstract

The southern pine beetle, *Dendroctonus frontalis* Zimmermann (Coleoptera: Curculionidae: Scolytinae), is a major pine tree killer in North and Central America. In the southeastern USA, responses by *D. frontalis* to its aggregation pheromone can be substantially increased by at least three host odours: the monoterpenes *alpha*- and *beta*-pinene, and the phenylpropanoid 4-allylanisole. We executed three trapping experiments to assess the influence of 4-allylanisole release rate on aggregation behaviour of *D. frontalis* and to evaluate the compound as an adjuvant for the operational monitoring lure for *D. frontalis*. Addition of devices releasing 4-allylanisole at any of three rates (4.8, 48, and 500 mg/day measured at mean 21°C) increased *D. frontalis* attraction to a pheromone lure, both in the presence and in the absence of an *alpha*-pinene lure. The increase was 5- to 50-fold with a positive dose response up to the highest tested release rate of 4-allylanisole. Attraction of an associate, the black turpentine beetle, *Dendroctonus terebrans* (Olivier), and a major *D. frontalis* predator, *Thanasimus dubius* (F.) (Coleoptera: Cleridae), was also significantly increased by 4-allylanisole. A device releasing 4-allylanisole at 0.05 g/day (at mean 23°C) increased attraction of *D. frontalis* to the current operational monitoring lure (which uses *alpha*- and *beta*-pinene as the host odour component) approximately 4-fold, but it did not increase attraction to a lure with turpentine as the host odour component (used in a former operational monitoring lure). Additionally, we observed none of the attraction-inhibiting effects that were previously reported for 4-allylanisole with *D. frontalis*. It is possible that the addition of 4-allylanisole to the *D. frontalis* lure might allow detection of beetles at lower population densities and, if so, aid in earlier detection of populations invading the northeastern USA in response to climate change. This possibility should receive further investigation.

KEYWORDS
Cleridae, monitoring, pest, *Pinus*, Scolytinae, semiochemicals

1 | INTRODUCTION

Bark beetles (Coleoptera: Curculionidae: Scolytinae) in the genus *Dendroctonus* are prominent natural disturbance agents and economic pests of conifer forests in the Northern Hemisphere (Six & Bracewell, 2015). They spend most of their life cycle within the phloem tissue of the host bole where they feed and reproduce (Six & Bracewell, 2015; Wood, 1963). *Dendroctonus* spp. generally attack weakened or dying trees, but outbreaks of aggressive species can result in widespread, catastrophic tree mortality (Grégoire et al., 2015; Wood, 1963). During outbreaks, beetles attack healthy trees in numbers sufficient to overcome constitutive resin defences and thereby render the phloem suitable for colonization (Raffa & Berrymann, 1983). These mass attacks are mediated by an aggregation pheromone released by colonizing beetles that concentrates further attacks on a host tree (Borden, 1982). In many species, the aggregation pheromone is synergized by host odours, particularly those in the host's defensive oleoresin (Billings, 1985; Borden et al., 2008). Volatilized oleoresin constituents influence the host-seeking behaviour of many bark beetles (Seybold et al., 2006), and they may function as indicators of host taxon, condition, and location (Pureswaran & Borden, 2005; Raffa, 2014). Combinations of aggregation pheromones and host odours have been integrated into management practices for pest species of *Dendroctonus*, particularly in trap lures for monitoring and detecting beetle populations and in trap-tree methods that can remove individuals from the local population (Borden, 1989; Seybold et al., 2018).

Southern pine beetle, *Dendroctonus frontalis* Zimmermann, occupies the eastern and southwestern USA, Mexico, and much of Central America (Clarke & Nowak, 2010). Historically, it is among the most significant economic pests and biotic disturbance agents of pine (*Pinus* L. spp.) forests in the southeastern USA (Clarke et al., 2016; Pye et al., 2011). Its range is expanding northward along the east coast of North America in an apparent response to climate change (Dodds et al., 2018; Lesk et al., 2017), and it is having catastrophic impacts on the ecologically sensitive coastal pine barrens forests (Heuss et al., 2019). The aggregation pheromone of *D. frontalis* consists of two bicyclic ketals, frontalin and *endo*-brevicomin (Sullivan, 2016). Host odours in turpentine distilled from resin of host species for *D. frontalis* can increase attraction by one to two orders of magnitude (Billings, 1985; Sullivan, 2016). The olfactory apparatus of *D. frontalis* is sensitive to numerous volatile compounds present in host resin (Munro et al., 2020; Payne, 1975); however, only three are known to enhance *D. frontalis* attraction to its aggregation pheromone (Munro et al., 2020; Staeben et al., 2015). These include the monoterpenes *alpha*- and *beta*-pinene and the phenylpropanoid 4-allylanisole (other trivial names: estragole and methyl chavicol). Host odours alone are not attractive to *D. frontalis* (Sullivan, 2016).

The attractive influence of 4-allylanisole on *D. frontalis* was discovered only recently (Munro et al., 2020) and has received little investigation. Unlike *alpha*- and *beta*-pinene, 4-allylanisole is a minor constituent (typically <5%) of resin of hosts for *D. frontalis* (Bookwalter et al., 2019; Munro et al., 2020; Strom et al., 2002). *Dendroctonus frontalis* has higher olfactory sensitivity to 4-allylanisole than other components in host oleoresin (Munro et al., 2020), suggesting the compound has unique ecological significance. However, in contrast to the attraction increase caused by 4-allylanisole in Munro et al. (2021), earlier studies showed it reduced *D. frontalis* responses to components of its aggregation attractant (Hayes et al., 1994; Strom et al., 1999).

Populations of *D. frontalis* are currently monitored across the southeastern USA with uniformly-baited Lindgren-type funnel traps (Lindgren, 1983) deployed each spring (Billings & Upton, 2010; Sullivan et al., 2021). Catches of both *D. frontalis* and its predator *Thanasimus dubius* (Fabricius) (Coleoptera: Cleridae) are used along with other data to forecast the numbers of *D. frontalis* infestations during the forthcoming summer at the spatial scale of individual counties (https://www.spbpredict.com). The lure used operationally for *D. frontalis* monitoring is the aggregation pheromone of *D. frontalis* (i.e. frontalin and *endo*-brevicomin) with a 7:3 mixture of *alpha*- and *beta*-pinene (Sullivan et al., 2021). To maintain trap captures at manageable numbers for sample processing, the lure is formulated to limit its attractiveness. However, a more potent lure might improve detection of incipient, cryptic populations of *D. frontalis* in areas of current or anticipated range expansion (Dodds et al., 2018).

The black turpentine beetle, *Dendroctonus terebrans* (Olivier), is a pine-infesting associate of *D. frontalis* that shares some pheromone components (Payne et al., 1987; Phillips et al., 1989), and these species often colonize the same trees (Nebeker, 2011). However, *D. terebrans* is infrequently a primary tree killer and does not mass-attack (Munro et al., 2019). These sympatric species may play mutually supportive roles in locating suitable hosts and overcoming host resistance (Sullivan, 2016), and joint attacks and other interactions may be mediated by their respective responses to pheromone components and host-associated semiochemicals. Like *D. frontalis*, *D. terebrans* responds more strongly to its attractive pheromone components when released with 4-allylanisole (Munro et al., 2020).

We performed three trapping experiments to assess the capacity of 4-allylanisole to alter responses by *D. frontalis*, *D. terebrans* and *T. dubius* to lure formulations. Specifically, we examined the effects of (1) 4-allylanisole release rate on lure attractiveness; and (2) the addition of this semiochemical to the current and a previous monitoring lure formulation for *D. frontalis*. We hypothesized that *D. frontalis* might have a biphasic dose response to 4-allylanisole (i.e. attracted at low, but inhibited at high release rates) and that this might explain the contrast between studies that indicate attraction enhancement (Munro et al., 2020) or reduction (Hayes, Strom, et al., 1994; Strom et al., 1999) by 4-allylanisole. If so, 4-allylanisole would have a specific, maximally attractive dose for use as a lure adjuvant. We also assessed how catches of both *D. frontalis* and *T. dubius* (data that are informative for predicting *D. frontalis* population trends; Billings & Upton, 2010) by the current, operational monitoring lure might be affected by amendment with 4-allylanisole.

TABLE 1 Composition, construction, and release rates of lures used in trapping study

Compound	Source[a]	Purity (%)[b]	Release device	Device load	Total release rate[c]
4-Allylanisole (Experiments 1 and 2)	Sigma-Aldrich	98%	Capped polyethylene microcentrifuge tube (×4)	275 mg	4.8 mg/day (21°C)
			Sealed polyethylene transfer pipette (×2)	2.9 g	48 mg/day (21°C)
			120-ml brown glass bottle with 9.5 mm diam. dental wick protruding through cap	85 g	500 mg/day (21°C)
4-Allylanisole (Experiment 3)	Sigma-Aldrich	98%	20-ml capped polyethylene bottle	10 ml	53 mg/day (23°C)
(±)-*endo*-Brevicomin	Synergy Semiochemicals		Flexlure (polymer matrix)	11 mg	0.12 mg/day (21°C)
(±)-*exo*-Brevicomin	Synergy Semiochemicals		Flexlure (polymer matrix)	11 mg	0.12 mg/day (21°C)
(±)-Frontalin	Synergy Semiochemicals		Capped polyethylene microcentrifuge tube (×2)	300 µl	12 mg/day (24°C)
(±)-*alpha*-Pinene	Sigma-Aldrich	≥97%	120 ml brown glass bottle with 9.5 mm diam. dental wick protruding through cap	85 g	4 g/day (21°C)
Turpentine	Synergy Semiochemicals		Plastic sachet	200 ml	3 g/day (23°C)
Pinene (7:3 blend of [3+:1−]-*alpha*-pinene:[−]-*beta*-pinene)	Synergy Semiochemicals		Plastic sachet	200 ml	3 g/day (23°C)

[a] Sigma-Aldrich Corporation (source of raw chemicals), and Synergy Semiochemicals (source of finished lures).

[b] As indicated by the manufacturer.

[c] Measured gravimetrically. Devices held in a fume hood at the indicated temperature.

2 | MATERIALS AND METHODS

2.1 | Effects of 4-allylanisole release rate on beetle attraction

Experiments 1 and 2 tested the effect of three different release rates of 4-allylanisole on beetle response to attractive semiochemicals. Both experiments followed the design in Munro et al. (2020). Trials occurred at four sites in the Oconee Ranger District, Chattahoochee National Forest, Greene County, Georgia, USA (all within 5 km of 33.68° N, −83.35° W). *Dendroctonus frontalis* populations were not in outbreak status, defined as one or more multiple-tree infestations per 405 ha of susceptible host type (Clarke & Nowak, 2010). Sites were in mixed hardwood/pine stands with the dominant host species being mature loblolly (*P. taeda* L.) and shortleaf (*P. echinata* Mill.) pines.

Lures were deployed from black cross-vane panel traps (IPM Technologies) positioned ~1.5 m above the ground and >10 m from the nearest pine. Trap collection cups were partially filled with dilute propylene glycol (Prestone® Low Tox® Antifreeze/Coolant, Prestone Products Corporation) to retain and preserve captured insects. A multiple Latin squares-type design was used with sites as squares; traps and successive collections represented columns and rows, respectively, of each square. Within each site, four traps were established >200 m apart (to reduce potential interactions among lures of different traps) roughly parallel to a road, and one of four treatments was assigned randomly to each trap. Traps were >50 m from the road. At each collection of catches (every 2 days), treatments were re-randomized without replacement among traps within sites until every treatment had been at a trap once. Panel traps in both experiments were consistently baited with a ternary combination of frontalin, and both *endo*- and *exo*-brevicomin, all attached at trap centre (Table 1). This combination was used to attract all three beetle species of interest. Frontalin is the major attractive pheromone component for *D. frontalis* and *D. terebrans* and an attractive kairomone for *T. dubius*, and both *endo*- and *exo*-brevicomin are pheromone components for *D. frontalis* and *D. terebrans*, respectively, that can be attraction enhancers for both species (Munro et al., 2019; Sullivan, 2016).

In both experiments (experiment 1 on 18–26 May 2018 and experiment 2 on 8–16 April 2019, dates within the spring dispersal flight of *D. frontalis*), the variable treatment was the release rate of 4-allylsanisole. These treatments included the following: (1) 0 = control; (2) 4.8 mg/day = low; (3) 48 mg/day = intermediate; and (4) 500 mg/day = high release rates of 4-allylsanisole when measured at 21°C (Table 1). In experiment 1, the invariable portion of the lure also included *alpha*-pinene (4 g/day at 21°C). *alpha*-Pinene is an attractant or attractant synergist for all three beetle species (Miller & Rabaglia, 2009; Staeben et al., 2015), and it was included to test whether and at what release rate 4-allylanisole might be capable of enhancing response to lures already releasing a high rate of a synergistic host odour. Experiment 2 was identical to 1 except that *alpha*-pinene was absent. Both the 4-allylanisole and the *alpha*-pinene devices were attached at the centre of the trap.

2.2 | Potential for 4-allylanisole to enhance *Dendroctonus frontalis* monitoring lures

Experiment 3 assessed whether 4-allylanisole, when released at a rate found synergistic in experiments 1 and 2 and in a previous study (Munro et al., 2020), could enhance attractiveness of the *D. frontalis* monitoring lure either in its current formulation or with an earlier host odour component. The current, operational lure consists of frontalin, *endo*-brevicomin, and a blend of *alpha*- and *beta*-pinene (hereafter 'pinene lure') (Sullivan et al., 2021). A prior monitoring lure used turpentine from a host species for *D. frontalis* instead of *alpha/beta*-pinene as the host odour component, and the turpentine was released from a wick-and-reservoir device (Billings & Upton, 2010). The earlier monitoring lure also lacked *endo*-brevicomin. In this study, both pinene and turpentine were released from an identical plastic sachet device at a similar release rate (3 mg/day at 23°C; Table 1) to permit a valid comparison of attractant composition alone.

Six 12-unit Lindgren funnel traps were established along each of three lines along roads in the Homochitto National Forest, Adams County, Mississippi, USA (within 5 km of 31.42° N, 91.20° W) with >200 m between lines and traps within lines. The location was in non-outbreak status; however, a major *D. frontalis* outbreak had collapsed in the previous two years. Traps were in stands of mixed pine/hardwood, >20 m from roads, >20 m from the nearest pine, and 1–1.5 m above the ground. Trap cups were partially filled with propylene glycol and water (1:3). The experimental design was identical to that of experiments 1 and 2 with each trap line yielding a single Latin square. Trap catch collections and treatment re-randomizations among traps within lines occurred at 6–8 day intervals. All traps were baited with frontalin (centre of trap) and *endo*-brevicomin (4–6 m away from trap) devices according to standard protocol for the *D. frontalis* monitoring lure (Sullivan et al., 2021). The *endo*-brevicomin device was attached to the top of a 1.5-m plastic pole inserted in the ground, and the host odour lure was attached below the top of the trap. Treatments included: (1) no host odours; or addition of (2) 4-allylanisole lure; (3) pinene lure (as used in current *D. frontalis* monitoring lure); (4) pinene and 4-allylanisole lures; (5) turpentine lure; and (6) turpentine and 4-allylanisole lures (Table 1). The test was conducted from 15 May to 26 June 2019.

2.3 | Statistical analyses

Dendroctonus frontalis, *D. terebrans* and *T. dubius* were identified to species and counted, and *D. frontalis* were sexed for experiment 3. For experiments 1 and 2, the main treatment effects on insect trap catches (i.e. dependent variable) were determined using fixed-effects negative binomial generalized linear models (GLM), controlling for collection date, site, and trap location ($\alpha = 0.05$). For collection date, site, and trap location, comparisons were made for the grand mean for each parameter (sum-to-zero contrasts), as opposed to controlling for a single collection date, site, and trap. Trap and interactions among the parameters were found to be non-significant and were removed from the final model. Hence, the final models were additive with the main treatment effect and covariates site and collection date (Equation 1).

$$\mu_{ijk} = \exp(\alpha + \tau_i + \delta_j + \gamma_k) \tag{1}$$

Where μ is the expected mean of trap catches, α is the intercept, τ is the i^{th} treatment, δ is the j^{th} site, and γ is the k^{th} collection date. Post hoc Dunn's tests (i.e. non-parametric pairwise multiple comparisons) with a Holm stepwise adjustment were performed to detect significant differences between lure treatments. For experiment 3, linear models with logarithmic transformations of the dependent variables were used to assess the main effect of treatment on trap catches of *D. frontalis* and *T. dubius*. The model controlled for collection date, trap line, and trap, as well as sex for *D. frontalis*. For collection date, trap line, and trap location, we contrasted differences from the grand mean for each parameter (sum-to-zero contrasts), as opposed to controlling for each individual collection date, trap line, and trap. Sex (for *D. frontalis*) and all interactions between parameters were found to be insignificant and were removed from the final model; thus, the final model was additive with the main treatment effect and the covariates of trap line, collection date and trap location (Equation 2).

$$\log(Y_{ijkm}) = \alpha + \tau_i + \delta_j + \gamma_k + \rho_m \tag{2}$$

Where α is the intercept, τ is the i^{th} treatment, δ is the j^{th} trap line, γ is the k^{th} collection date, and ρ is the m^{th} trap location. Post hoc Tukey's Honest Significant Difference tests with a Holm stepwise adjustment were performed to detect significant differences between treatments. All analyses and visualizations were completed with R statistical software version 3.6.2 (R Core Team, 2019) and RStudio (RStudio Team, 2016) using the packages dplyr (Wickham et al., 2021), FSA (Ogle et al., 2019), ggplot2 (Wickham, 2016), lattice (Sarkar, 2008), MASS (Venables & Ripley, 2002), multcomp (Hothorn et al., 2008), and rcompanion (Mangiafico, 2018).

3 | RESULTS

3.1 | Effects of 4-allylanisole release rate on beetle attraction to baited panel traps. Experiment 1: *alpha*-pinene present

Dendroctonus frontalis were over six times more abundant in catches (12,362) than the other species captured, followed by *D. terebrans* (1243) *and T. dubius* (743) (Munro et al., 2021). All three release rates of 4-allylanisole increased trap catches of *D. frontalis* when paired with pheromone components and *alpha*-pinene (Figure 1). *Dendroctonus frontalis* catches increased with release rate, and there

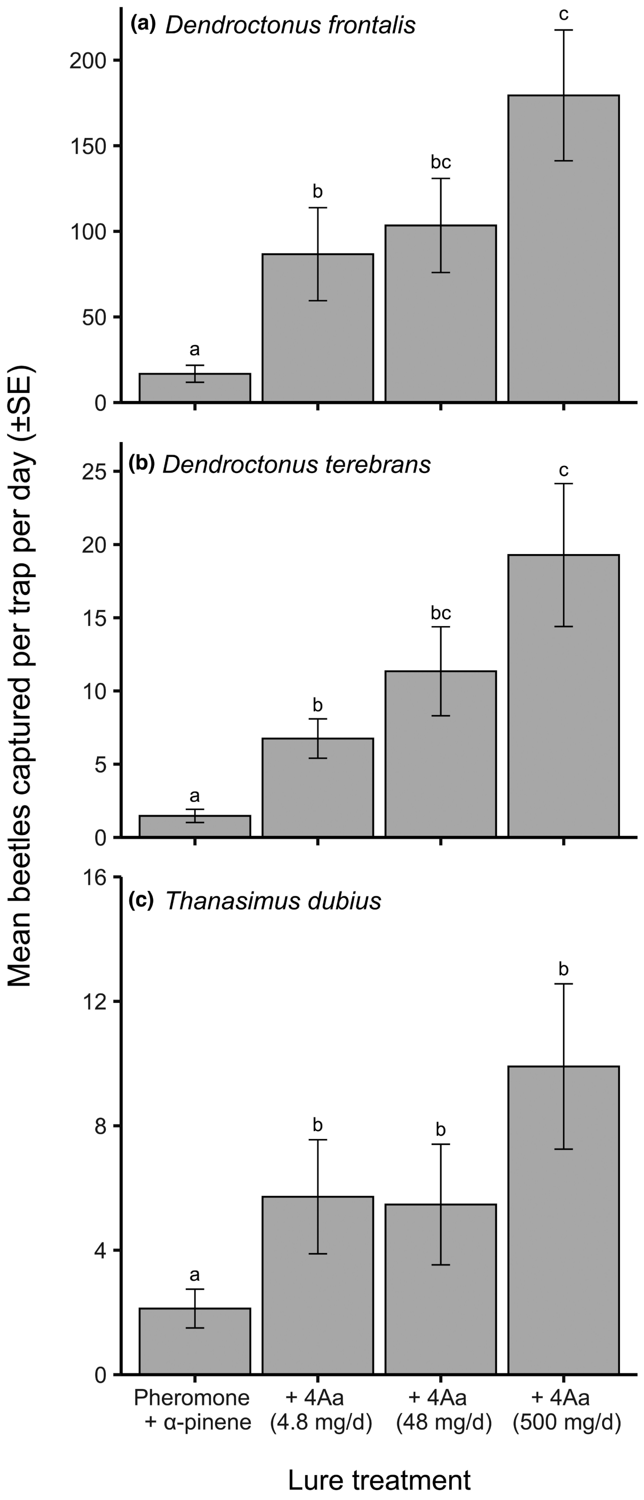

FIGURE 1 Mean (±SE) number of bark beetles *Dendroctonus frontalis* (a), *D. terebrans* (b), and predator *Thanasimus dubius* (c) trapped with bark beetle pheromone components (frontalin, *endo*-, and *exo*-brevicomin) and the host odour *alpha*-pinene, either alone or with the host odour 4-allylanisole ('4Aa') at one of three release rates from panel traps

was approximately a five-, six-, and tenfold increase in mean trap catches between the control and the low ($z = 5.54$; $p < 0.001$), intermediate ($z = 6.82$; $p < 0.001$), and high ($z = 9.29$; $p < 0.001$) release rates, respectively. Catches with the low and intermediate release rates ($p = 0.563$), and the high and intermediate rates ($p = 0.056$), respectively, did not differ, whereas catches with the low and high rates differed ($p < 0.001$). Similarly for *D. terebrans*, all three 4-allylanisole release rates enhanced trap catches with approximately five-, eight-, and thirteen-fold higher mean catches than the control for low ($z = 5.10$; $p < 0.001$), intermediate ($z = 6.22$; $p < 0.001$), and high ($z = 8.01$; $p < 0.001$) release rates, respectively. Only the high and low release rates of 4-allylanisole differed from each other in *D. terebrans* catches ($p = 0.007$). All three 4-allylanisole release rates increased catches of *T. dubius* above the control (low: $z = 3.69$, $p < 0.001$; intermediate: $z = 3.02$; $p = 0.002$; high: $z = 5.46$; $p < 0.001$), but there were no pairwise differences among the release rates.

3.2 | Effects of 4-allylanisole release rate on beetle attraction to baited panel traps. Experiment 2: *alpha*-pinene absent

Dendroctonus frontalis was the most abundant species captured (6717), followed by *T. dubius* (463) and *D. terebrans* (5) (Munro et al., 2021). All three release rates of 4-allylanisole enhanced trap catches of *D. frontalis* and produced an approximate 7-, 27-, and 50-fold increase in mean trap catches relative to the control (pheromone components alone) for the low ($z = 7.09$; $p < 0.001$), intermediate ($z = 12.4$; $p < 0.001$), and high ($z = 15.5$; $p < 0.001$) release rates, respectively (Figure 2). All contrasts between release rates were significant ($p < 0.001$). For *T. dubius*, the intermediate ($z = 3.88$; $p < 0.001$) and high ($z = 4.29$; $p < 0.001$) release rates of 4-allylanisole resulted in an approximate threefold increase in trap catches relative to the control, whereas the low release rate had no effect ($z = -0.291$; $p = 0.771$). The intermediate ($z = 4.15$; $p < 0.001$) and high ($z = 4.560$; $p < 0.001$) release rates enhanced *T. dubius* catches relative to the low release rate, whereas there was no difference between the high and intermediate rates ($z = -0.438$; $p = 0.972$). *Dendroctonus terebrans* trap catches were too low for statistical analyses.

3.3 | Experiment 3: Potential for 4-allylanisole to enhance *Dendroctonus frontalis* monitoring lures in funnel traps

Dendroctonus frontalis was over four times more abundant in traps (1274) than *T. dubius* (306); no *D. terebrans* were caught (Munro et al., 2021). All lure additions enhanced attraction of *D. frontalis* to traps with pheromone components except 4-allylanisole by itself ($t = 1.09$; $p = 0.276$) (Figure 3). Relative to catches by the pheromone-only control, the pinene lure paired with 4-allylanisole increased catches by approximately 65-fold ($t = 7.50$; $p < 0.001$), turpentine alone by 35-fold ($t = 4.65$; $p < 0.001$), turpentine with 4-allylanisole by 20-fold ($t = 5.10$; $p < 0.001$), and pinene alone by 16-fold ($t = 3.49$; $p = 0.001$). Addition of 4-allylanisole enhanced trap catches by pinene and pheromone components (i.e. the current *D. frontalis* monitoring lure; *t* = 3.91; *p* = 0.002) but not turpentine and pheromone components (*t* = 0.448; *p* = 0.998). Similar trends were seen for *T. dubius*; only 4-allylanisole (when alone) failed to enhance catches by the pheromone lure (*t* = 1.80; *p* = 0.469). Addition of 4-allylansiole increased catches by the pinene/pheromone lure (*t* = 3.43; *p* = 0.011), but not the turpentine/pheromone lure (*t* = 1.23; *p* = 0.823). No *T. dubius* were captured in the absence of host odours.

4 | DISCUSSION

In experiments 1 and 2, the host resin constituent 4-allylanisole strongly enhanced attraction of *D. frontalis* when combined with attractive bark beetle pheromone components, both in the presence and in the absence of *alpha*-pinene. The capacity of 4-allylanisole to increase attraction of *D. frontalis* as the sole host odour component of the lure (experiment 2) was observed in a previous study (Munro et al., 2020). However, in experiment 3, 4-allylanisole alone failed to increase *D. frontalis* responses to its aggregation pheromone despite being released at a rate that increased attraction in experiment 2. *Thanasimus dubius* displayed the same apparent inconsistency in responses between experiments 2 and 3, although the very low catches of these predators in experiment 3 likely contributed to the absence of a detectable effect for 4-allylanisole alone. There were several procedural differences between experiments 2 and 3 (e.g. composition of the pheromone component of the lure, trap construction, experiment dates, trial locations, and spatial arrangement of the release devices), but none particularly suggest themselves as a likely cause of the inconsistent effects of 4-allylanisole as sole host odour. However, 4-allylanisole consistently increased attraction when pinene (either *alpha*- alone or both *alpha*- and *beta*-) was present (experiments 1 and 3). The substantial increase in catches caused by combining the 4-allylanisole and terpene lures (experiment 3) indicates that 4-allylanisole does not duplicate the attractive effects of *alpha*- or *beta*-pinene and that the respective signals could have different ecological significance for the beetles. However, the failure of 4-allylanisole to enhance the attractiveness of the turpentine-amended lure appears inconsistent with this conclusion, as the turpentine was dominated by *alpha*-pinene (Sullivan et al., 2021). The turpentine contained additional *D. frontalis* semiochemicals that could have influenced the effects of 4-allylanisole (Sullivan et al., 2021).

Our results and those of Munro et al. (2020) indicate a strong attraction-enhancing effect of 4-allylanisole for *D. frontalis*, a finding that contrasts with earlier research that found 4-allylanisole to be an attraction inhibitor for this species (Hayes, Strom, et al., 1994; Strom et al., 1999). In these earlier studies, devices releasing 4-allylanisole reduced *D. frontalis* responses to funnel traps baited with frontalure (a 1:3 blend of frontalin and *alpha*-pinene) and deployed in active *D. frontalis* infestations. 4-Allylanisole applied to surfaces also repelled walking *D. frontalis*. These findings spurred research into use of 4-allylanisole as a tree protectant (Hayes, Ingram, et al., 1994) and led to registration by the United States Environmental Protection Agency (EPA) of a 4-allylanisole-based control product (PC Code 062150). However, subsequent research on 4-allylanisole as a tree protectant against *D. frontalis* failed to demonstrate efficacy (Strom et al., 2004), and this control technology received no further development.

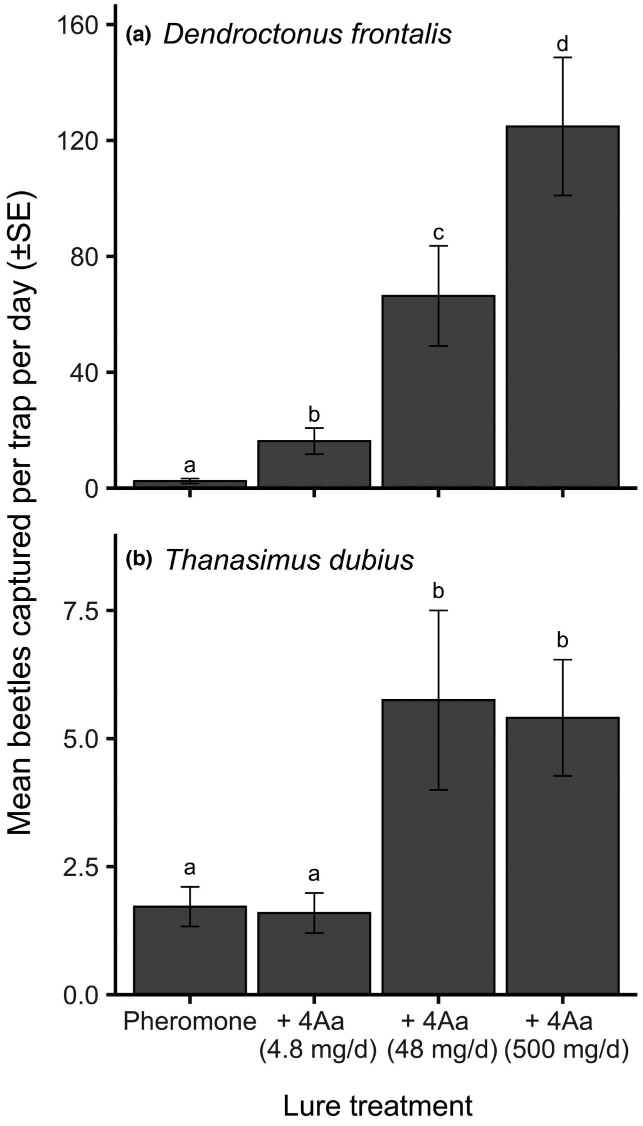

FIGURE 2 Mean (±SE) number of bark beetle *Dendroctonus frontalis* (a) and predator *Thanasimus dubius* (b) trapped with bark beetle pheromone components (frontalin, *endo*-, and *exo*-brevicomin) either alone or with the host odour 4-allylanisole ('4Aa') at one of three release rates from panel traps

Our data do not support the hypothesis that the contrasting attractive/inhibitory effects observed for 4-allylanisole with *D. frontalis* are the result of a biphasic dose response, as increasing the release of 4-allylanisole into the range of rates shown in earlier studies to be inhibitory (Hayes, Strom, et al., 1994) did not result in loss of attraction. Rather, the dose response trends for experiments 1 and 2 suggest that attractive effects were still increasing at the highest tested rate (i.e. 0.5 g/day). There are numerous plausible reasons for

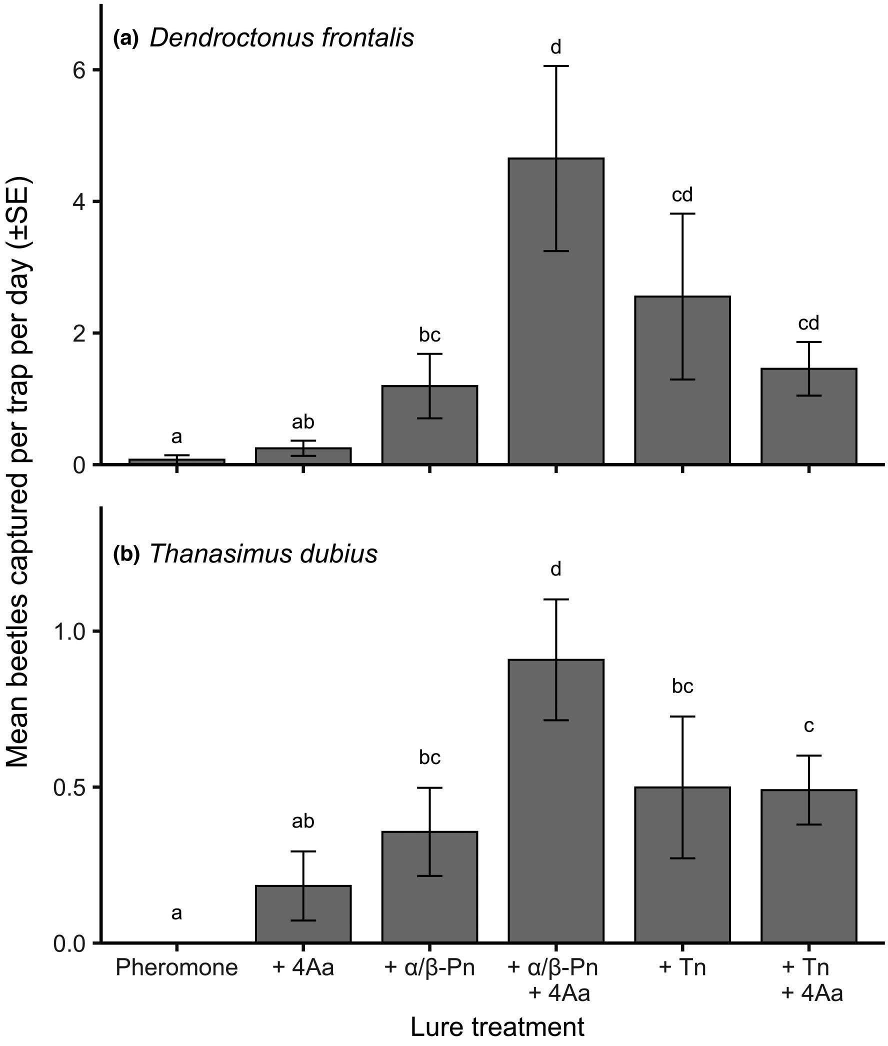

FIGURE 3 Mean (±SE) number of bark beetle *Dendroctonus frontalis* (a) and predator *Thanasimus dubius* (b) trapped with *D. frontalis* pheromone components (frontalin and *endo*-brevicomin) either alone or with different combinations of 4-allylanisole ('4Aa'), a pinene lure (7:3 ratio of *alpha*- and *beta*-pinene; 'α/β-Pn'), and turpentine ('Tn') from multiple-funnel traps

the contrasts in behavioural effects of 4-allylanisole between studies. In addition to differences in the invariable lure components and the dates and locations of the experiments, the tests of this study and Munro et al. (2020) were conducted outside of infestations whereas the earlier tests were conducted within active *D. frontalis* infestations. At a single release rate, the *D. frontalis* pheromone component *endo*-brevicomin is simultaneously an attraction inhibitor inside active *D. frontalis* infestations but an attraction enhancer outside (Sullivan et al., 2011), and evidence suggests this is due to the background of semiochemicals released from attacked trees within infestations (Sullivan & Brownie, 2021). Hence, a similar interaction between 4-allylanisole devices and semiochemical background inside infestations is possible, and we are investigating this possibility (Sullivan et al., unpublished data).

Some studies have found that 4-allylanisole concentrations in pines are negatively associated with host susceptibility to *D. frontalis* attack; hence, this semiochemical has been proposed to be a host selection cue for *D. frontalis*. A fungicide treatment (sodium-N-methyldithiocarbamate with DMSO) that renders pines susceptible to *D. frontalis* attack is associated with a significant decline in 4-allylanisole in the resin (Hayes, Ingram, et al., 1994). Furthermore, elevated levels of 4-allylanisole are associated with lower *D. frontalis*-caused mortality of *Pinus caribaea* var. *hondurensis* Barrett & Golfari in Central America (Hammer et al., 2020; Snyder & Bower, 2005). However, *P. taeda* bred from parents that had escaped predation by *D. frontalis* within infestations had lower levels of 4-allylanisole than trees in the general population (Strom et al., 2002). 4-allylanisole is directly toxic to *Dendroctonus* bark beetles (Werner, 1995), and growth of mutualistic fungal symbionts of *D. frontalis* in culture is more strongly inhibited by a saturated atmosphere of 4-allylanisole than other *P. taeda* resin constituents (Bridges, 1987). Hence, a significant amount of indirect evidence indicates there should be selective benefits to *D. frontalis* in avoiding 4-allylanisole during host selection. This inference conflicts with our observation of strong attraction enhancement by this semiochemical. It should be noted, however, that attraction of bark beetles to deleterious compounds is common. *Dendroctonus frontalis* attraction synergists *alpha*- and *beta*-pinene, like 4-allylanisole, are toxic to bark beetles (Chiu et al., 2017; Coyne & Lott, 1976) and resin flow, which involves release of these monoterpenes from host trees, is a resistance mechanism against *D. frontalis* and other bark beetles (Christiansen et al., 1987; Tisdale et al., 2003). Relationships between behavioural responses to, and ecological roles of, host resin constituents can be complex and seem counter-intuitive (Seybold et al., 2006).

Dendroctonus frontalis and sympatric *D. terebrans* often share the same host trees, but they exploit different portions and likely compete minimally (Nebeker, 2011). Selection of the same trees is likely mediated in part by shared or cross-attractive pheromone components (frontalin and *endo*-brevicomin from *D. frontalis*, and frontalin and *exo*-brevicomin from *D. terebrans*) (Munro et al., 2019; Payne et al., 1987; Phillips et al., 1989; Sullivan, 2016) and host odours attractive to both species (*alpha*-pinene, *beta*-pinene and 4-allylanisole) (Munro et al., 2020). In experiment 1, responses of both *D. terebrans and D. frontalis* increased in a similar dose-dependent manner when 4-allylanisole was added to bark beetle pheromone components and *alpha*-pinene. In a previous study, attraction of *D. terebrans* was also increased when 4-allylanisole was added to a pheromone lure in the absence of other host odours (Munro et al., 2020). In the present study, however, very few *D. terebrans* were trapped by 4-allylanisole-amended lures in the absence of other host odour components, and it is not known whether the contrast between experiments 1 (with *alpha*-pinene) and 2 (without *alpha*-pinene) was due to lack of attractiveness of the lure or insufficient populations or responsiveness of *D. terebrans* in experiment 2. Unlike *D. frontalis*, *D. terebrans* is attracted to host odours in the absence of pheromone components, and it awaits to be tested whether 4-allylanisole is a primary host location cue (i.e. in the absence of pheromone) for this species.

Thanasimus dubius is a major predator for *D. frontalis*, and trap catches of this species are used with other data in forecasting *D. frontalis* outbreaks (Billings & Upton, 2010). During prey location, bark beetle predators commonly exploit both the pheromones of their prey and odours of resin constituents from damaged host trees (Payne, 1989; Raffa, 2001). In the present study, 4-allylanisole enhanced *T. dubius* responses to prey pheromone components as observed in Munro et al. (2020), and, when *alpha*-pinene was also present, *T. dubius* and *D. frontalis* exhibited a similar, positive dose response to 4-allylanisole. Parallel responses by predator and prey to the same semiochemicals should be adaptive for the predator by enhancing prey location. However, earlier research observed differing responses of *D. frontalis* and *T. dubius* to 4-allylanisole (Hayes, Strom, et al., 1994), where it reduced attraction of *D. frontalis* but had no effect on *T. dubius*.

Lures amended with 4-allylanisole could potentially detect *D. frontalis* at lower population levels than possible with the current operational monitoring lure. Such a lure would be particularly useful for earlier detection of, and timely management actions against, invasive populations of *D. frontalis* expanding their range into the northeastern USA (Dodds et al., 2018; Lesk et al., 2017). Given the restricted conditions of our experiments (e.g. the deep southern USA; locations where *D. frontalis* were abundant), additional research is necessary before operational use of 4-allylanisole as a lure adjuvant for beetle detection can be recommended. Furthermore, the conditions governing the alternately attraction-enhancing or attraction-reducing effects of 4-allylanisole are not known. It is thus possible that attempts to apply 4-allylanisole in novel contexts and uses could produce unexpected and even counterproductive outcomes. 4-Allylanisole was developed as a tree protectant against *D. frontalis* based on its ability to reduce beetle response to attractants; however, our data suggest that this semiochemical has the potential to put treated trees at greater risk by increasing their attractiveness. Our results illustrate how lack of a basic understanding of the underlying ecology of a semiochemical could undermine or forestall development of a management tool. Further research is needed to clarify the role of 4-allylanisole in *D. frontalis* ecology, and similar investigations may be advisable for other bark beetle semiochemicals being developed for tree and stand protection.

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CONFLICT OF INTEREST

The authors certify that they have no affiliations with or involvement in any organization or entity with a financial or non-financial interest in the subject matter or materials discussed in this manuscript.

AUTHOR CONTRIBUTIONS

BTS, HLM, and KJKG conceived and designed the research. HLM and WPS conducted experiments. HLM analysed data and conducted statistical analyses. BTS and HLM wrote the manuscript. KJKG and BTS secured funding. All authors read and approved the manuscript.

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DATA AVAILABILITY STATEMENT

All data for this research is freely available online: Munro et al. (2021). Bark Beetle Behavioral Response to 4-Allylanisole (Version 1) [Data set]. Zenodo. https://doi.org/10.5281/zenodo.5722591

ORCID

Brian T. Sullivan https://orcid.org/0000-0001-9832-9696
Holly L. Munro https://orcid.org/0000-0001-6026-5607
William P. Shepherd https://orcid.org/0000-0003-1041-7400
Kamal J. K. Gandhi https://orcid.org/0000-0001-6217-5859

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