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Trap captures of invasive ambrosia beetles (Coleoptera: Curculionidae) as influenced by ethanol release rate

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Abstract

1. Infestations of ambrosia beetles in the tribe Xyleborini (Coleoptera: Scolytinae) are associated with economic losses to horticultural trees due to branch die-back and tree death. Ethanol is a key attractant used for monitoring flight activity.
2. Trapping experiments were conducted in woodlots in Ohio, USA, and Veneto, Italy, to characterize the effect of ethanol release rate on captures of *Anisandrus maiche*, *Xyleborinus saxesenii*, *Xylosandrus crassiusculus* and *Xylosandrus germanus*. In Ohio (2019, 2020 and 2021) and Italy (2021), traps were baited with centrifuge tubes that were modified to achieve ethanol release rates of 0.1–13.2 g/day. In Ohio (2022), traps were baited with varying quantities of manufactured lures to achieve release rates of 0.02–1.4 g/day.
3. There was no consistent relationship between ethanol release rate and trap captures for the modified centrifuge tubes. In nine of sixteen analyses, traps baited with the centrifuge tubes releasing ethanol at 1.1 g/day or higher collected more *A. maiche*, *X. saxesenii*, *X. crassiusculus* and *X. germanus* than traps baited with centrifuge tubes releasing 0.1 g/day. In contrast, the manufactured lures releasing 0.1–1.4 g/day attracted more *A. maiche*, *X. saxesenii*, *X. crassiusculus* and *X. germanus* than lures releasing 0.02–0.05 g/day.
4. This comprehensive study provides important insights into monitoring tactics for ambrosia beetles along with implications for optimizing ethanol-baited traps as part of a 'push-pull' strategy whereby repellents are used to 'push' beetles away from vulnerable trees and attractants are used to 'pull' them into annihilative traps.

KEYWORDS
ambrosia beetle, ethanol, Scolytinae

INTRODUCTION

Ambrosia beetles (Curculionidae: Scolytinae) in the tribe Xyleborini are destructive wood-boring insects of trees grown in ornamental nurseries and tree fruit orchards (Agnello et al., 2014, 2021; Gugliuzzo et al., 2021; Ranger et al., 2016). The invasive species *Anisandrus maiche* (Stark), *Xyleborinus saxesenii* (Ratzeburg), *Xylosandrus crassiusculus* (Motschulsky) and *Xylosandrus germanus* (Blandford) are native to Asia (*X. saxesenii* also being native to Europe) and are among the most problematic species in the United States (Agnello et al., 2014; Ranger et al., 2016; Tobin & Ginzel, 2023) causing wilting, die-back and tree death (Ranger et al., 2016). Female beetles disperse from their natal galleries and then bore and rear offspring within the xylem of the new hosts (Reding et al., 2015; Werle et al., 2015). They do not consume the wood but use the excavated galleries to cultivate their fungal mutualist, which serves as the sole source of nutrition for the larvae and adults (Biedermann et al., 2019; Hulcr & Stelinski, 2017).

These species of ambrosia beetles selectively infest trees weakened by abiotic and biotic stressors, particularly flood stress and low-temperature stress (Ranger et al., 2021). Physiological stressors of trees can induce a shift to anaerobic metabolism, producing ethanol as a byproduct (Kelsey & Westlind, 2017; Ranger et al., 2021). When ethanol is released from tree tissues, it acts as a kairomone that attracts a variety of ambrosia beetles (Ranger et al., 2021). Ethanol also enhances the growth of ambrosia beetle fungal symbionts and improves the colonization success of beetles (Cavaletto et al., 2023; Lehenberger et al., 2021; Ranger et al., 2018). For these reasons, ethanol-baited traps are commonly used for monitoring the flight activity of ambrosia beetles (Dodds et al., 2024; Gugliuzzo et al., 2021; Rabaglia et al., 2019), citizen science programmes aimed at early detection of new invaders (Colombari & Battisti, 2023), and ecological studies investigating distribution and density of ambrosia beetles in their native and invaded ranges (Rassati et al., 2016; Tarno et al., 2021).

Previous studies have demonstrated that ambrosia beetles disperse from woodlots into adjacent ornamental nurseries in search of host trees (Reding et al., 2015; Werle et al., 2015).

Ethanol-baited traps positioned at the interface between woodlots and plots of horticultural trees could be useful for intercepting dispersing beetles and, when combined with repellents as part of a 'push-pull' management strategy, could reduce insecticide treatments (Addesso et al., 2019; Rivera et al., 2020; Werle et al., 2019). Following multistate 'push-pull' trials, Werle et al. (2019) reported that the 'pull' effect of ethanol-baited traps was inconsistently effective at reducing ambrosia beetle attacks on vulnerable trees. 'Low-release' manufactured lures (16 mg/day at 20°C) were tested by Werle et al. (2019), and the authors proposed that increasing the release rate of ethanol could improve the interception 'pull' component and reduce tree attacks by ambrosia beetles.

Klimetzek et al. (1986) demonstrated that captures of *X. germanus*, *X. saxesenii* and *Anisandrus dispar* (Fabricius) increased almost linearly with every tenfold step up of ethanol release rate ranging from 0.0024 to 24 mg/day and 0.012 to 6 g/day during two field experiments. Similarly, manufactured pouch lures emitting 390 mg/day of ethanol at 20°C attracted more *X. germanus* to baited traps than 'low release' lures releasing 27 mg/day (Ranger et al., 2011). A recent study by Tobin and Ginzel (2023) also showed that ethanol release rates of 3, 3.5 and 5 g/day trapped more *A. maiche* than blank traps and that release rates of 0.1 and 0.5 g/day were not different from blank traps. In an experiment with ethanol-injected trees, high-dose ethanol-injected trees sustained more attacks than low-dose trees (Addesso et al., 2019). However, an earlier study by Montgomery and Wargo (1983) showed that traps releasing 2 g/day of ethanol caught more bark and ambrosia beetles than higher release rates.

We conducted a series of field trapping experiments to characterize the effect of ethanol release rate on attracting ambrosia beetles. Varying release rates of ethanol were achieved using modified centrifuge tube lures and manufactured lures. We hypothesized that interspecific variability would be documented in ambrosia beetle trap captures in response to ethanol release rates, whereby optimal release rates would vary among species of ambrosia beetles. Results from our current study could aid in optimizing ethanol-baited trap efficiency, resulting in enhanced monitoring of native and invasive species, or be used in future 'push-pull' management strategies.

MATERIALS AND METHODS

Trapping experiments using modified centrifuge tubes

Trapping experiments using modified centrifuge tubes as ethanol dispensers for baiting ambrosia beetle traps were conducted in Ohio, USA, in 2019, 2020 and 2021, and in the Veneto region of Italy in 2021. Holes were drilled into 50 mL centrifuge tubes (Falcon™, Corning Inc., Corning, New York, USA) consisting of (1) one 1.59 mm hole, (2) three 1.59 mm holes, (3) four 6.35 mm holes, (4) twelve 6.35 mm holes and (5) twenty 6.35 mm holes per tube to achieve five different release rates (Table 1 and Figure 1a). Holes were drilled near the 45 mL mark on the centrifuge tubes (Figure 1a). On the day of trap deployment, the centrifuge tube lures were filled with 20 mL of 95% ethanol (0.805 g/mL; Decon Labs, Inc., King of Prussia, Pennsylvania, USA), which was replenished to the 20 mL mark every 2–3 days.

In the Ohio experiments, individual centrifuge tubes containing ethanol were suspended within bottle traps as described by Ranger

TABLE 1 Ethanol release rates from modified centrifuge tubes and manufactured lures under laboratory conditions.

Lure type	Mean (±SE) weight change g/day[a] at 21°C
Modified centrifuge tube—one 1.59 mm hole	0.12 (±0.02A)
Modified centrifuge tube—three 1.59 mm holes	1.06 (±0.04B)
Modified centrifuge tube—four 6.35 mm holes	2.46 (±0.24C)
Modified centrifuge tube—twelve 6.35 mm holes	7.86 (±0.44D)
Modified centrifuge tube—twenty 6.35 mm holes	13.18 (±0.36E)
Manufactured 'low release' pouch	0.02 (±0.01a)
Manufactured 'high release' squeeze tube	0.71 (±0.05b)

[a]Change in weight was measured daily for 5 days and then averaged for analysis. Upper case letters indicate significant differences among the modified centrifuge tube lures ($F_{4,92} = 666.19$; $p < 0.0001$) and lower case letters indicate significant differences between the manufactured lures ($F_{1,26} = 99.39$; $p < 0.0001$) using generalized linear mixed effects models and least square means. For the modified centrifuge tubes, there were four replicates of each tube type. For the manufactured lures, there were three replicates of each lure type. Release rates reported by the manufacturer were 16 mg/day at 20°C for the 'low release' lure and 1000 mg/day at 20°C for the 'high release' lure (ChemTica Internacional).

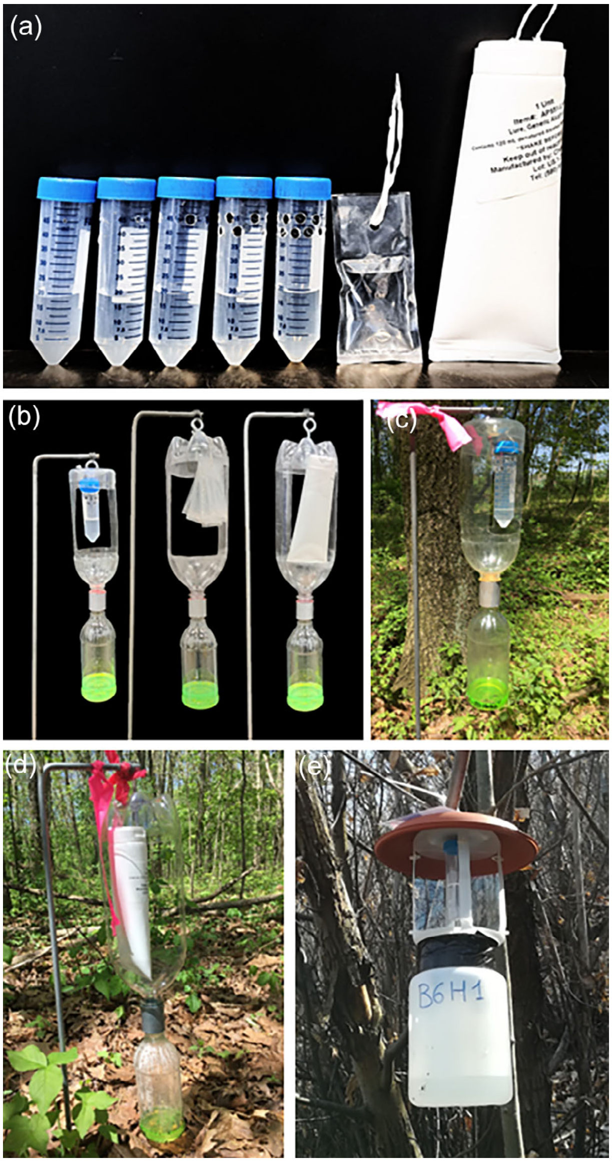

FIGURE 1 (a) Modified centrifuge tubes and manufactured 'low release' and 'high release' ethanol lures (ChemTica Int.) tested during field trapping studies for ambrosia beetles. Varying diameters and quantities of holes were drilled into the centrifuge tubes to achieve a range of ethanol release rates. (b) Bottle traps used to test the modified falcon tubes (left) and manufactured lures (centre and right) during trapping studies conducted in the USA. (c, d) Representative traps deployed under field conditions in the USA. (e) Representative trap used to test the modified centrifuge tubes in Italy.

et al. (2010) (Figure 1b,c). In short, bottle traps were prepared using a Tornado Tube® (Steve Spangler Science, Englewood, Colorado) to connect a 1 L plastic bottle to a 0.5 L plastic bottle (Figure 1b–d). Two rectangular openings (length, 11 cm; width, 7 cm) were cut into the 1-L bottle to allow the entrance of ambrosia beetles. Traps were baited with one of the five types of modified centrifuge tubes or no bait (control) and were suspended vertically 1 m above ground level by attaching the inverted end of the 1-L bottle to a metal rod (Figure 1b–d). An aqueous solution of propylene glycol (1:1 v:v; Sierra Antifreeze/Coolant [ethanol-free]; Old World Industries, Inc., Northbrook, Illinois, USA) was added to the 0.5-L collecting bottle as a killing agent (approximately 50 mL). The ethanol-baited bottle traps were deployed within a deciduous woodlot (40°45′43″ N; 81°51′14″ W) from 7 May 2019 to 11 June 2019, 8 July 2020 to 5 August 2020 and 20 May 2021 to 15 June 2021. The woodland was unmanaged and dominated by *Fagus grandifolia* (American beech), *Quercus alba* (white oak), *Quercus rubra* (red oak), *Acer saccharum* (sugar maple) and *Acer rubrum* (red maple). All traps were arranged linearly along the edge of the woodlot, and each block contained one trap of each possible release rate, plus a blank control trap. The order of the traps within a block was randomized. We had eight such blocks and spaced traps 10 m apart within a block, as this is a common spacing used for studies of ethanol-baited beetle traps (Lindgren et al., 2012; Miller, 2006, 2020; Schroeder & Lindelöw, 1989; Tobin & Ginzel, 2023). We spaced blocks at least 20 m apart from each other. Captured ambrosia beetles were collected weekly from the antifreeze in the bottle traps and stored in 70% ethanol until being identified to species level using a stereomicroscope under laboratory conditions and available keys (Rabaglia et al., 2006; Rabaglia et al., 2009).

In the Italy experiments, hand-made cross-vane panel traps were baited with the same treatments used in Ohio. The panel traps consisted of two small transparent plexiglass panels (Leroy Merlin, Marghera, Italy; 20 × 15 cm, height × width) in a cross-vane configuration located above a collector cup and covered by a plastic plate (25 cm diameter) to prevent rain entry into the trap (Figure 1e). A rectangular opening was cut at the crossing point of the two plexiglass panels to suspend a modified centrifuge tube. Traps were suspended from the lower branches of available trees at 1–2 m above the ground. The collector cup held an aqueous solution of propylene glycol. Non-baited control traps were not used in the experiments in Italy. The ethanol-baited panel traps were deployed in a deciduous forest (45°17′14″N; 11°41′9″ E) in the Euganean Hills area, Veneto region, north-eastern Italy. The forest was dominated by *Ostrya carpinifolia* Scop. (hop hornbeam) and *Quercus pubescens* Willd. (downy oak), with lesser amounts of *Castanea sativa* Mill. (sweet chestnut), *Fraxinus ornus* L. (flowering ash), and *Robinia pseudoacacia* L. (black locust). The same experimental design described above was used, with 12 blocks instead of eight. Traps were set up in the field from 24 March 2021 to 10 April 2021, 17 April 2021 to 14 May 2021 and 22 June 2021 to 20 July 2021. Traps were emptied, and contents were collected every 2–3 days.

Trapping experiments using manufactured lures

This study was carried out only in Ohio in 2022. Two types of manufactured lures were assessed to characterize further the effect of ethanol release rate on attracting ambrosia beetles (Figure 1a,b,d). The lure types were 'low release' consisting of a heat-sealed, permeable membrane pouch containing 15 mL of 95% ethanol and a release rate of 16 mg/day at 20°C and >120 days estimated field life according to the manufacturer (Manufacturer: ChemTica

Internacional, S.A., San Jose, Costa Rica; Distributor: AgBio Inc., Westminster, Colorado, USA) (Figure 1a,b). The 'high release' lure consisted of a collapsible soft plastic squeeze tube containing a gel matrix infused with 120 mL of 95% ethanol and a 1 cm (diam.) opening for releasing ethanol at 1000 mg/day at 20°C with a >60 days estimated field life per the manufacturer (ChemTica Internacional) (Figure 1a,b,d). A range of release rates was achieved by varying quantities of manufactured lures within traps. Specifically, treatments included one, three, or eight 'low release' pouches, or one or two 'high release' plastic tubes per trap (Figure 1b,d). The manufactured lures were suspended within bottle traps made with 2 L bottles instead of 1 L to accommodate the selected lure combinations (Figure 1b,d). Traps were deployed from 20 April 2022 to 1 June 2022 in the previously described deciduous woodlot in a randomized complete block design with six complete blocks consisting of 10 m between adjacent traps within a block and 20 m between adjacent blocks. Ambrosia beetle specimens were collected weekly throughout the course of the experiment and identified to species level as previously described.

Ethanol release rates

Release rates of ethanol from the five types of modified centrifuge tubes and the manufactured lures were measured by placing the lures upright within a laboratory fume hood under constant airflow (21°C; airflow of 1.7 m^3/min (60 cfm); Venturi V05; Kewaunee Scientific Corporation, Statesville, North Carolina, USA). The lures were weighed every day over 5 days to determine the change in weight as a measure of ethanol release rate (Table 1). Four replicates of the modified centrifuge tube lures and three replicates of the manufactured lures were tested.

Statistical analysis

Trap captures

We used a generalized linear mixed effects model (PROC GLIMMIX) to determine the effect of ethanol release rate on cumulative trap captures of selected ambrosia beetle species within each year (SAS Institute, 2018). The cumulative number of beetles per trap for a given species was our response variable, and the ethanol release rate was our categorical explanatory variable. Block was designated as a random effect. Due to non-normality, data were initially modelled using a Poisson distribution, with the goodness of fit for the model being assessed using the scaled deviance (G^2/df) parameter. When overdispersion was detected (G^2/df >1.0), then a negative binomial distribution and log link function were used to fit the model and achieve a G^2/df close to 1.0. Differences of least square means were used for pairwise comparisons on treatment effects with significant *F*-test values from analysis of variance ($\alpha = 0.05$), and we used a *t*-test to assess significance.

Ethanol lure release rate estimates

We created two generalized linear mixed effects models to analyse ethanol lure release rates in the fume hood (PROC GLIMMIX; SAS Institute, 2018). For the first model, the amount of ethanol released per day was our response variable, and the type of modified centrifuge tube lure (one 1.59 mm, three 1.59 mm, four 6.35 mm, twelve 6.35 mm or twenty 6.35 mm holes) was our categorical explanatory variable. We included block as a random effect and used a Gaussian distribution. We then conducted pairwise comparisons of the difference of least square means for ethanol release rate following significant *F*-test values from analysis of variance ($\alpha = 0.05$). For our second model, the amount of ethanol released per day was our response variable, and manufactured lure type (either low or high release) was our categorical explanatory variable. We included block as a random effect and used a Gaussian distribution. We then conducted pairwise comparisons of the difference of least square means for ethanol release rate following significant *F*-test values from analysis of variance ($\alpha = 0.05$) and used a *t*-test to assess significance.

RESULTS

Overall trap captures

A total of 47,276 bark and ambrosia beetles representing 28 species were captured in this study using ethanol-baited traps (Tables 2 and 3). The dominant species varied among years and locations. *X. saxesenii* was the dominant species captured in Ohio, USA, in 2019 (61.7% of trap captures), while *A. maiche* was the dominant species collected in Ohio in 2020 (61.9%) (Table 2). *X. germanus* dominated trap captures in Ohio in 2021 (39.9%) and 2022 (88.8%) (Table 2). *X. saxesenii* (48.9%) dominated trap captures in Italy in 2021 (Table 3).

Effect of ethanol release rate on *X. germanus*

X. germanus showed little specificity among ethanol release rates during the modified centrifuge tube experiments, except for 2020 when there was a preference for high ethanol release rates (2.5–13.2 g/day). Beetles preferred rates of 0.1 g/day and higher for the manufactured lures.

In Ohio, USA, in 2019, traps baited with modified centrifuge tubes releasing 1.1 g/day of ethanol attracted significantly more *X. germanus* than the blank control trap and higher (7.9 and 13.2 g/day) rates of ethanol (Figure 2a–e). In Ohio in 2020, traps baited with the modified tubes releasing 7.9 g/day captured more *X. germanus* than the lower release rates ranging from 0.0 to 1.1 g/day (Figure 2a–e). In the Veneto region of Italy in 2021, there were no significant differences in captures of *X. germanus* among traps baited with the modified centrifuge tubes (Figure 2a–e). In Ohio in 2021, there was no difference in the captures of *X. germanus* in traps baited with the

TABLE 2 Trap captures of Scolytinae throughout the four trapping periods in the USA.

Species	Origin[b]	Total trap Captures[a]				Percent of total trap captures			
		2019	2020	2021	2022	2019	2020	2021	2022
Ambrosiodmus rubricollis (Eich.)	Exotic	-	-	-	2	-	-	-	<1.0
Ambrosiophilus atratus (Eich.)	Exotic	66	1	7	266	1.7	<1.0	<1.0	1.0
Anisandrus maiche (Strk.)	Exotic	685	3569	396	581	17.2	61.9	31.6	2.1
Anisandrus obesus LeC.	Native	-	-	-	1	-	-	-	<1.0
Anisandrus sayi (Hop.)	Native	19	8	12	52	<1.0	<1.0	1.0	<1.0
Cnesinus strigicollis LeC.	Native	-	-	-	2	-	-	-	<1.0
Cnestus mutilatus (Blnd.)	Exotic	-	-	-	4	-	-	-	<1.0
Corthylus punctatissimus (Zimm.)	Native	2	15	8	2	<1.0	<1.0	<1.0	<1.0
Cyclorhipidion pelliculosum (Eich.)	Exotic	4	-	5	86	<1.0	-	<1.0	<1.0
Euwallacea validus (Eich.)	Exotic	52	18	9	395	1.3	<1.0	19.0	2.0
Gnathotrichus materiarius (Fitc.)	Native	8	-	-	-	<1.0	-	-	-
Hylocurus rudis (LeC.)	Native	-	-	1	1	-	-	<1.0	<1.0
Micracis swainei Blkmn.	Native	-	-	-	3	-	-	-	<1.0
Monarthrum fasciatum (S.)	Native	28	3	-	4	<1.0	<1.0	-	<1.0
Monarthrum mali (Fitc.)	Native	36	6	73	196	1.0	<1.0	5.8	11.0
Pityophthorus lautus (Eich.)	Native	-	-	-	14	-	-	-	<1.0
Pityophthorus spp.		1	-	-	-	<1.0	-	-	-
Pseudopityophthorus minutissimus (Zimm.)	Native	-	-	-	8	-	-	-	<1.0
Xyleborinus saxesenii (Ratz.)	Exotic	2453	33	194	474	61.7	<1.0	15.5	1.7
Xyleborus pubescens (Zimm.)	Native	3	-	1	6	<1.0	-	<1.0	<1.0
Xylosandrus crassiusculus (Mot.)	Exotic	4	81	46	939	<1.0	1.4	3.7	3.3
Xylosandrus germanus (Blnd.)	Exotic	22,602	22,032	22,500	24,498	15.1	35.2	39.9	88.8
Xyloterinus politus (S.)	Native	15	-	-	54	<1.0	-	-	<1.0

[a]Traps were deployed for the following durations: 7 May 2019 to 11 June 2019, 8 July 2020 to 5 August 2020, 20 May 2021 to 15 June 2021 and 20 April 2022 to 1 June 2022.
[b]Origin designated as exotic or native to N. America.

TABLE 3 Summarized trap captures of ambrosia beetles in 2021 in Italy.

Species	Origin	Total trap captures	Percent of total
Xyleborinus saxesenii	Native	4247	48.86
Xylosandrus crassiusculus	Exotic	2078	23.9
Xylosandrus germanus	Exotic	1368	15.74
Anisandrus dispar	Native	730	8.4
Anisandrus maiche	Exotic	114	1.31
Ambrosiophilus atratus	Exotic	82	<1.0
Xyleborus dryographus	Native	60	<1.0
Xyleborus monographus	Native	60	<1.0
Cyclorhipidion bodoanum	Exotic	1	<1.0
Dryoxylon onoharaensis	Exotic	1	<1.0

modified centrifuge tubes releasing 0.1 to 7.9 g/day, but the 7.9 g/day release rate attracted significantly more *X. germanus* than the 13.2 g/day release rates and blank traps (Figure 2a–e).

In Ohio in 2022, traps baited with the manufactured lures releasing 0.1, 0.7 and 1.4 g/day caught significantly more *X. germanus* than traps baited with lures releasing 0.02 and 0.05 g/day (Figure 2a–e). All treatments baited with ethanol captured more beetles than the blank control traps. More *X. germanus* were captured with the manufactured lures in 2022 (24,498 individuals) than in 2021 (500 individuals) using the modified centrifuge tube lures.

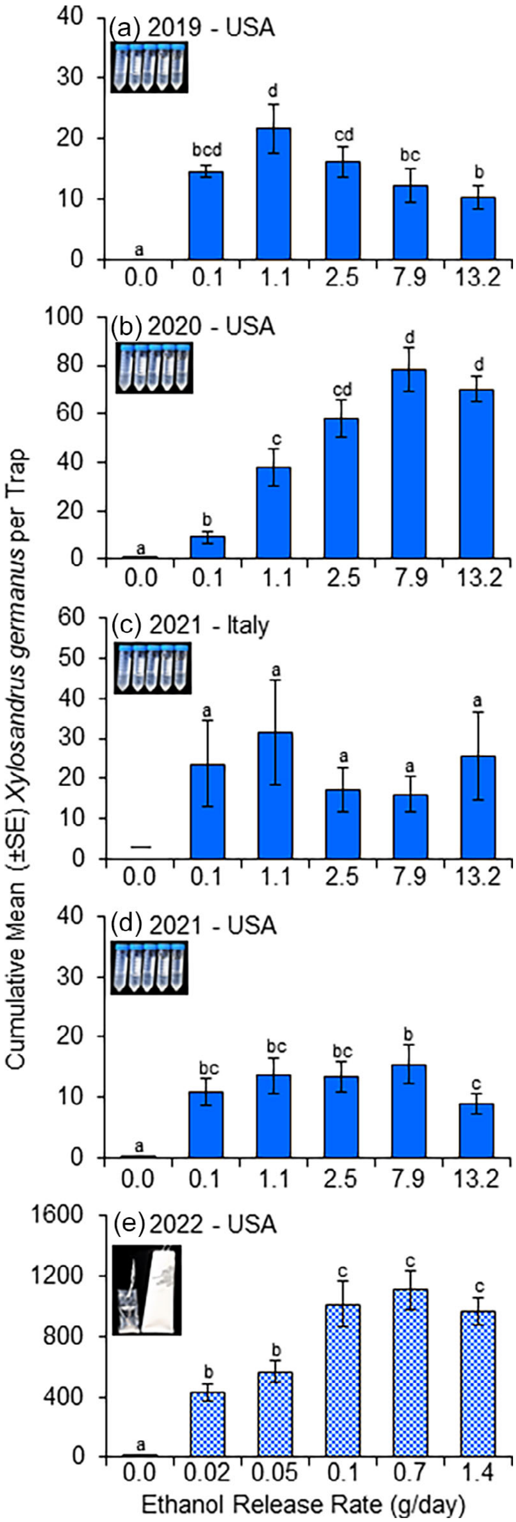

FIGURE 2 Captures of *Xylosandrus germanus* using traps baited with (a–d) modified centrifuge tubes and (e) manufactured lures to achieve varying release rates of ethanol. Blank traps were not used in Italy in 2021. Different letters within a graph represent significantly different means using generalized linear models and least square means: (a) $F_{5,35} = 13.0$; $p < 0.001$; (b) $F_{5,35} = 27.3$; $p < 0.001$ (c) $F_{4,44} = 1.52$; $p = 0.21$; (d) $F_{5,35} = 7.6$; $p < 0.001$; (e) $F_{5,25} = 20.0$; $p < 0.001$.

Effect of ethanol release rate on *A. maiche*

A. maiche preferred intermediate or low ethanol release rates during the modified centrifuge tube experiments. Beetles preferred rates of 0.1 g/day and higher for manufactured lures.

In Ohio in 2019, traps baited with the modified centrifuge tubes releasing 1.1–7.9 g/day captured significantly more *A. maiche* than the 0.0, 0.1 or 13.2 g/day release rates (Figure 3a–e). In Ohio in 2020, the modified centrifuge tubes releasing 0.1 and 1.1 g/day of ethanol attracted significantly more *A. maiche* than tubes releasing 0.0, 2.5, 7.9 and 13.2 g/day (Figure 3a–e). In Italy in 2021, traps baited with the modified centrifuge tubes releasing 2.5 g/day caught significantly more *A. maiche* than traps baited with tubes releasing lower (0.0 and 0.1 g/day) and higher (7.9 and 13.2 g/day) rates of ethanol. The 2.5 g/day release rate did not catch significantly more beetles than 1.1 g/day (Figure 3a–e). In Ohio in 2021, traps baited with centrifuge tubes releasing 1.1–13.2 g/day caught significantly more *A. maiche* than traps baited with lures releasing 0.0 and 0.1 g/day (Figure 3a–e).

In Ohio in 2022, traps baited with the manufactured lures releasing 0.1, 0.7 and 1.4 g/day captured significantly more *A. maiche* than traps baited with lures releasing 0.0, 0.02 and 0.05 g/day of ethanol (Figure 3a–e).

Effect of ethanol release rate on *X. saxesenii*

X. saxesenii preferred higher ethanol release rates during the modified centrifuge tube experiments. Beetles also preferred the highest ethanol release rate associated with the manufactured lures.

In Ohio in 2019, traps baited with the modified centrifuge tube lures releasing 7.9 g/day treatment captured significantly more *X. saxesenii* than the lower (0.0, 0.1, 1.1 and 2.5 g/day) and higher (13.2 g/day) release rates (Figure 4a–e). The tube lures releasing 2.5 and 13.2 g/day of ethanol also attracted significantly more *X. saxesenii* than the 0.0, 0.1 and 1.1 g/day release rates, and 0.1 and 1.1 g/day baited traps captured more beetles than the blank trap controls (Figure 4a–e). In Ohio in 2020, there were no significant differences in captures of *X. saxesenii* among traps baited with the modified centrifuge tubes (Figure 4a–e). In Italy in 2021, the centrifuge tubes releasing 13.2 g/day attracted significantly more *X. saxesenii* than all other release rates (Figure 4a–e). Furthermore, centrifuge tubes releasing 1.1, 2.5 and 7.9 g/day caught significantly more *X. saxesenii* than tubes releasing 0.1 g/day. In Ohio in 2021, traps baited with centrifuge tubes releasing 7.9 g/day attracted significantly more *X. saxesenii* than traps baited with tubes releasing 0.0, 0.1 and 1.1 g/day (Figure 4a–e). Traps baited with lures releasing 2.5 and 13.2 g/day also attracted more *X. saxesenii* than traps baited with 0.0 and 0.1 g/day.

In Ohio in 2022, traps baited with the manufactured lures releasing 1.4 g/day captured more *X. saxesenii* than all other treatments (Figure 4a–e). Traps baited with the manufactured lures releasing 0.7 g/day also captured significantly more *X. saxesenii* than all lower

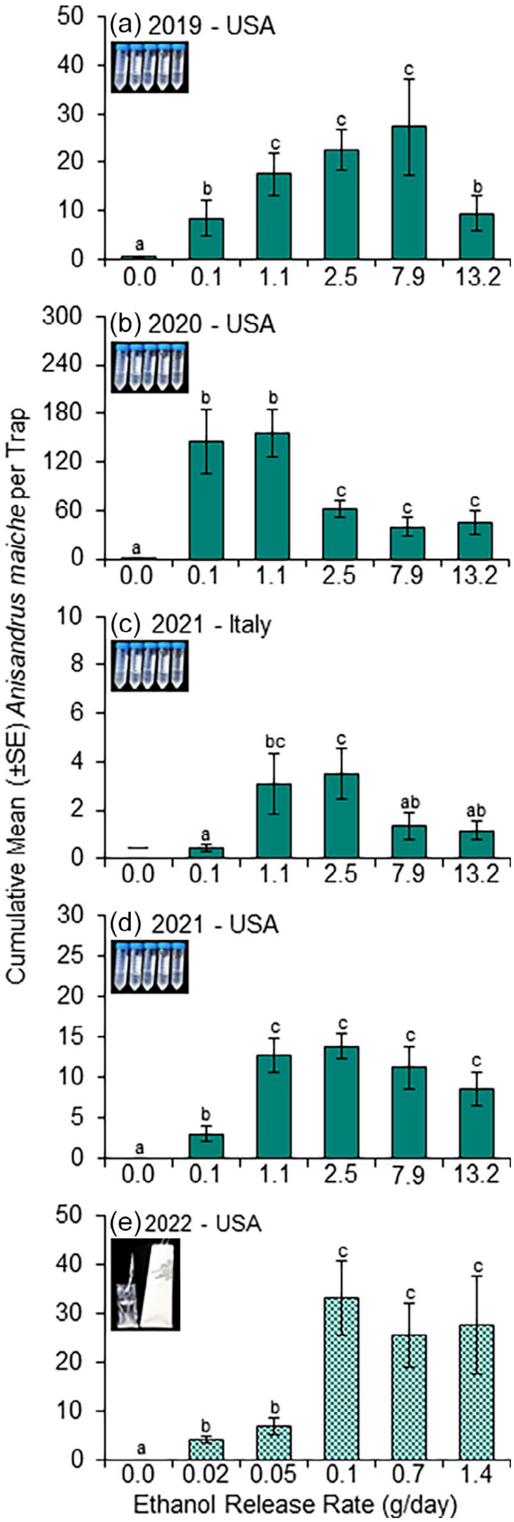

FIGURE 3 Captures of *Anisandrus maiche* using traps baited with (a–d) modified centrifuge tubes and (e) manufactured lures to achieve varying release rates of ethanol. Blank traps were not used in Italy in 2021. Different letters within a graph represent significantly different means using generalized linear models and least square means: (a) $F_{5,35} = 6.09$; $p < 0.001$; (b) $F_{5,35} = 8.12$; $p < 0.001$; (c) $F_{4,44} = 3.74$; $p = 0.011$; (d) $F_{5,35} = 10.1$; $p < 0.001$; (e) $F_{5,23} = 5.95$; $p < 0.001$.

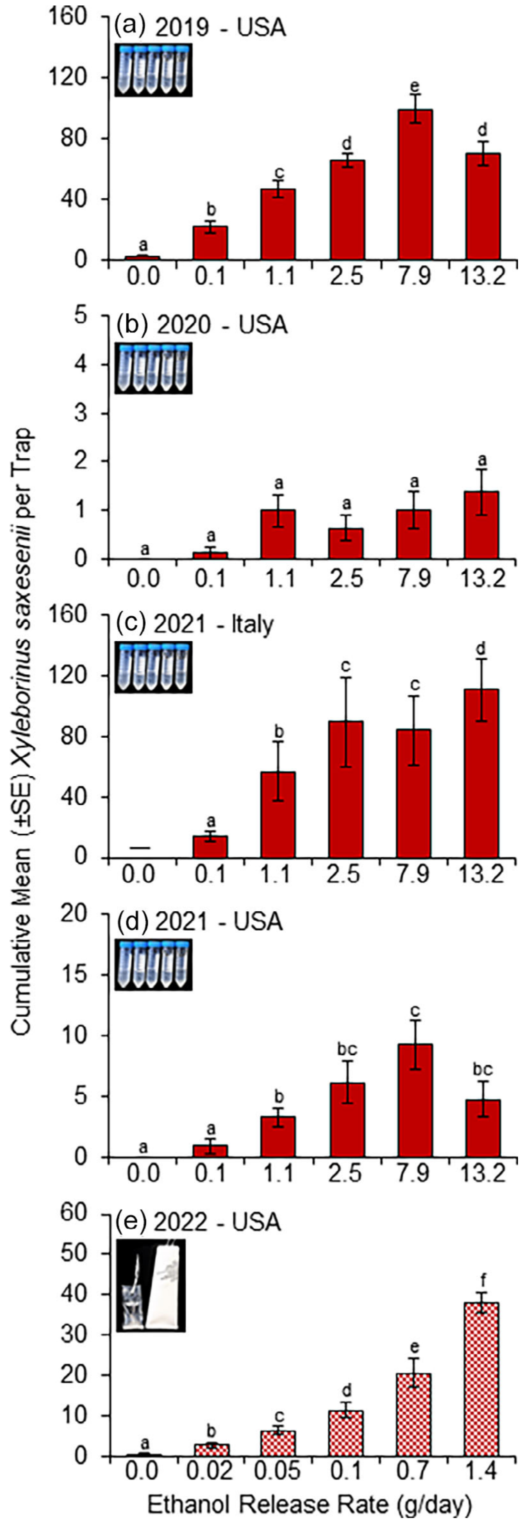

FIGURE 4 Captures of *Xyleborinus saxesenii* using traps baited with (a–d) modified centrifuge tubes and (e) manufactured lures to achieve varying release rates of ethanol. Blank traps were not used in Italy in 2021. Different letters within a graph represent significantly different means using generalized linear models and least square means: (a) $F_{5,35} = 38.3$; $p < 0.0001$; (b) $F_{5,35} = 3.48$; $p = 0.012$; (c) $F_{4,44} = 8.47$; $p < 0.0001$; (d) $F_{5,35} = 7.42$; $p < 0.001$; (e) $F_{5,23} = 49.6$; $p < 0.001$.

release rates, and traps baited with 0.1 g/day lures captured more than those baited with 0.0 and 0.02 g/day.

Effect of ethanol release rate on *X. crassiusculus*

X. crassiusculus showed no preference in ethanol release rates during the modified centrifuge tube experiments, except for 2020 when 2.5 g/day was the optimum rate. Beetles preferred release rates above 0.1 g/day during the experiment with manufactured lures.

In Ohio in 2019, captures of *X. crassiusculus* were low, and no treatments differed (Figure 5a–e). In Ohio in 2020, traps baited with centrifuge tubes releasing 2.5 g/day of ethanol collected significantly more *X. crassiusculus* than traps baited with lures releasing 0.0, 0.1 g/day, and 13.2 g/day (Figure 5a–e). Centrifuge tubes releasing 1.1 and 7.9 g/day attracted more *X. crassiusculus* than tubes releasing 0.0 and 0.1 g/day. In Italy in 2021, traps baited with centrifuge tubes releasing 1.1, 2.5, 7.9 and 13.2 g/day captured significantly more *X. crassiusculus* than traps baited with tubes releasing 0.1 g/day (Figure 5a–e). In Ohio in 2021, there were no significant differences in captures of *X. crassiusculus* among treatments (Figure 5a–e).

In Ohio in 2022, traps baited with the manufactured lures releasing 0.1, 0.7 and 1.4 g/day caught significantly more *X. crassiusculus* than traps baited with lures releasing 0.0, 0.02 and 0.05 g/day of ethanol (Figure 5a–e). Furthermore, traps baited with lures releasing 0.05 g/day collected more *X. crassiusculus* than those baited with 0.0 and 0.02 g/day.

Ethanol release rate

The five different centrifuge tube configurations had significantly different release rates from each other (Table 1). Ethanol release rates from the 'low-release' manufactured lures were significantly lower than those of the 'high-release' lures (Table 1).

DISCUSSION

Our four-year study provides an in-depth assessment of ambrosia beetle trap captures using a wide range of ethanol release rates. We found inter-year variation in optimal release rate for most species using the modified centrifuge tube lures, which made it difficult to characterize general trends. In contrast, individual 'high-release' manufactured lures caught more *A. maiche*, *X. saxesenii*, *X. crassiusculus* and *X. germanus* than individual 'low-release' lures. Characterizing the impact of ethanol release rate on trap captures of invasive ambrosia beetles can benefit monitoring programmes and semiochemical-based 'push-pull' management strategies.

With over 47,000 individuals caught belonging to 28 species, our study further demonstrates that ethanol-baited traps represent an efficient tool for monitoring native and invasive ambrosia beetles

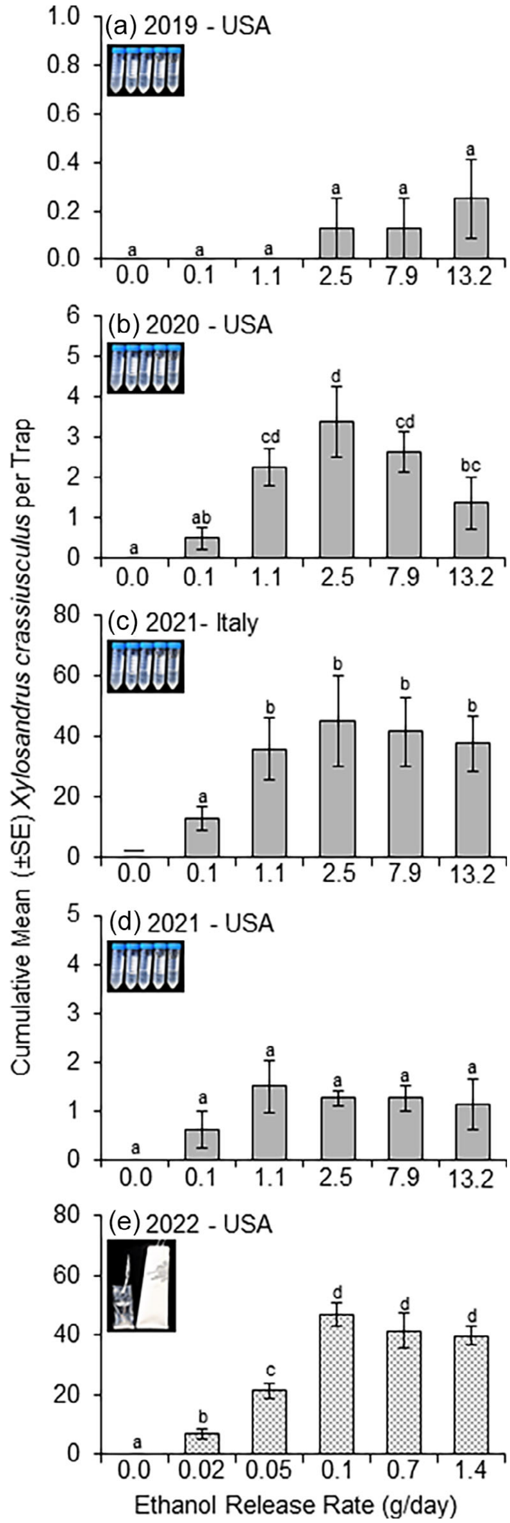

FIGURE 5 Captures of *Xylosandrus crassiusculus* using traps baited with (a–d) modified centrifuge tubes and (e) manufactured lures to achieve varying release rates of ethanol. Blank traps were not used in Italy in 2021. Different letters within a graph represent significantly different means using generalized linear models and least square means: (a) $F_{5,35} = 1.1$; $p = 0.375$; (b) $F_{5,35} = 6.56$; $p = 0.0002$; (c) $F_{4,44} = 3.55$; $p = 0.014$; (d) $F_{5,35} = 2.34$; $p = 0.062$; (e) $F_{5,23} = 45.6$; $p < 0.001$.

(Galko et al., 2014; Gugliuzzo et al., 2021; Reding et al., 2011; Reding et al., 2015) and for surveillance activities aimed at intercepting new invaders (Colombari & Battisti, 2023; Holusa et al., 2023; Ruzzier et al., 2023). Catches of *D. onhoharense* and *A. maiche* in Italy in 2021, for example, represent the first records of those species in Europe and Italy, respectively (Ruzzier et al., 2022). Furthermore, 98.5% of beetles captured in Ohio were invasive species.

For the modified centrifuge tube lures used from 2019 to 2021, we found that in absolute numbers, tubes releasing 0.1 g/day had the lowest cumulative mean captures for *A. maiche*, *X. saxesenii*, *X. crassiusculus* and *X. germanus* compared with 1.1 g/day or higher release rates in 11 of 16 analyses. Release rates of ethanol from the centrifuge tube lures higher than 1.1 g/day also tended to attract more *X. saxesenii*. However, variability across years in trap captures of *X. germanus*, *A. maiche*, *X. crassiusculus* and *X. saxesenii* was observed using the modified centrifuge tube lures. This variability could be attributed to inconsistent release rates from the modified centrifuge tube lures due to varying climatic conditions.

A recent study using the same configuration of modified centrifuge tubes as in our study found that captures of *A. maiche* increased markedly between 0.0 and 0.1 g/day, and between 0.1 and 0.5 g/day, but then increased only slightly with higher release rates (i.e., an asymptotic function) (Tobin & Ginzel, 2023). While ethanol release rates of 3.0, 3.5 and 5.0 g/day captured about twice as many *A. maiche* as the lowest release rate (0.1 g/day), this difference was reported as not statistically different, and the highest three release rates were similar to each other (Tobin & Ginzel, 2023). Our 3 years of combined data did not find a clear relationship between ethanol rate from the modified centrifuge tubes and capture of *A. maiche*. The variability of trap captures in relation to ethanol release rate between our two studies could be due to temperature, wind speed and site conditions. Although our study and that of Tobin and Ginzel (2023) used the same modified centrifuge tube configuration, different release rate estimates were documented between the two studies. Notably, Tobin and Ginzel (2023) measured release rates under ambient, outdoor environments, while our measurements were conducted in a laboratory fume hood. Using manufactured lures in future studies could help to reduce variability through more consistent ethanol release rates.

For the manufactured ethanol lures, we found that traps associated with one 'high release' lure (0.7 g/day) captured more beetles than one 'low release' lure (0.02 g/day) for *X. germanus*, *A. maiche*, *X. saxesenii* and *X. crassiusculus*. Captures of *X. germanus*, *A. maiche* and *X. crassiusculus* using the manufactured lures tended to decrease in response to increasing release rates while the relationship was more linear for *X. saxesenii*. These results suggest *X. saxesenii* may prefer a higher release rate of ethanol as compared to *X. germanus*, *A. maiche* and *X. crassiusculus*. In a field experiment, Rassati et al. (2020) observed that the number of entry holes increased with higher ethanol concentration for *X. saxesenii* but decreased for *X. germanus* when using hornbeam (*Carpinus betulus*) logs soaked in ethanol-water solutions of 3%, 5%, 8%, 10% or 12.5%. Additionally, we captured nearly 50 times more *X. germanus* using the manufactured lures in 2022 than we did with the modified centrifuge tubes in 2021 (22,498 vs. 500 individuals, respectively). As the peak activity of *X. germanus* in Ohio spans late April to late May (Baniszewski et al., 2024), this discrepancy is likely due to traps being deployed in April 2022 vs. June 2021, thereby capturing the peak of *X. germanus*' flight activity in 2022 but missing the peak in 2021.

Results from our current study also indicate that an upper threshold exists in the optimal release rate of ethanol whereby attraction can turn into interruption, as our highest release rate of 13.2 g/day generally caught fewer *A. maiche*, *X. saxesenii*, *X. crassiusculus* and *X. germanus* than other release rates for most years. Montgomery and Wargo (1983) found that Scolytine species dominated by *A. dispar* were more attracted to traps releasing 2 g/day of ethanol than to those releasing 10 or 29 g/day. Studies on the attraction of ethanol-methanol mixtures to the bark beetle *Hypothenemus hampei* Ferrari found no effect of ethanol release rate under 1 g/day (Dufour & Frérot, 2008; Silva et al., 2006), but an interruption in the attraction to traps was documented at release rates of 20 g/day (Mathieu et al., 1997). Captures of the bark beetle *Tomicus piniperda* (L.) decreased with increasing ethanol release rates of 0, 0.04, 0.3, 3.1 and 51 g/day with 95% ethanol-baited flight barrier traps (Schroeder, 1988). Conversely, a range of ethanol release rates from 0.0075 to 0.48 g/day were equally unattractive to ambrosia beetles in the *Euwallacea fornicatus* spp. complex, which are known to rely on other host-derived volatiles (Byers et al., 2020).

Interspecific variability among ambrosia beetles regarding optimal ethanol rate has been suggested to result from niche-partitioning, with species being influenced differentially by their responses to ethanol concentration in host trees (Cavaletto et al., 2021, 2023). Using cored bolts of several tree species and filled with either 5% or 90% ethanol, Cavaletto et al. (2021) found substantial variation in attack rate and successful gallery establishment for *X. crassiusculus*, *A. dispar* and *X. saxesenii*. Their study found that ethanol concentration and host tree species significantly influenced the number of entry holes by species, with *A. dispar* creating more entry holes at the higher ethanol concentration, *X. crassiusculus* having more entry holes and developed galleries at the lower concentration, and *X. saxesenii* being indifferent to ethanol concentration regarding entry holes (Cavaletto et al., 2021). This suggests that ethanol concentration and host tree species influence the ecological niche of ambrosia beetle species, as different species exhibit preferences for specific ethanol concentrations, potentially as a means to reduce competition in beetles that have overlapping flight activity periods (Cavaletto et al., 2021). These results are consistent with ours, in that we also found what appear to be some species-specific differences in ethanol preference. Despite some marked intra-year variation in optimal ethanol rate within species, identifying the general characteristics of ambrosia species' niches may aid in their management.

Along with ambrosia beetle monitoring, characterizing the influence of ethanol release rate on trap captures could also benefit efforts to develop a 'push-pull' strategy for ambrosia beetles. Previous studies have shown weak or inconsistent efficacy for integrating repellents and attractants into a 'push-pull' strategy for protecting trees from ambrosia beetles (Addesso et al., 2019; Rivera et al., 2020; Werle et al., 2019). Field trials by Addesso et al. (2019) found that interception (i.e., 'pull') traps baited with manufactured lures with an ethanol release rate of 0.065 g/day failed to reduce the number of beetles reaching sentinel traps compared to traps not associated with the interception treatment. During multi-state 'push-pull' trials, Werle et al. (2019) reported that traps baited with the 'low release' lures tested in our current study provided an inconsistent but promising reduction in ambrosia beetle attacks on ornamental trees. As such, Werle et al. (2019) proposed that traps baited with manufactured lures emitting >0.02 g/day of ethanol could improve the efficacy of the 'pull' component for luring beetles into annihilative traps. In a recent study, attaching verbenone and methyl salicylate repellent dispensers to flooded *Cornus florida* L. trees and deploying interception traps baited with 'high release' ethanol lures (0.7 g/day) resulted in a reduction in attacks and beetle colonization by *X. germanus* and *X. crassiusculus* (Yilmaz, unpub. data).

Since our current study indicates that ethanol release rate is an important consideration for attracting ambrosia beetles, future studies should attempt to characterize the optimal distance between adjacent interception 'pull' traps. Our study is limited in that we did not arrange our traps in a way that allows us to analyse the effects of adjacent ethanol-baited traps on each other, as traps placed too close together could compete for captures whereas traps placed too far apart could fail to intercept dispersing beetles (Bacca et al., 2006; Jactel et al., 2019; Suckling et al., 2015). While our trap spacing of 10 m is common for studies involving ethanol-baited traps (Lindgren et al., 2012; Miller, 2006, 2020; Schroeder & Lindelöw, 1989; Tobin & Ginzel, 2023), more fully understanding trap spacing is important to evaluate a 'push-pull" strategy against ambrosia beetles. Future efforts should also consider the interaction between trap design, ethanol release rate and trap capture efficiency, as trap type can influence beetle capture (Allison & Redak, 2017) and downwind volatile dispersal patterns and concentration (Bouwer et al., 2020). Finally, our work suggests that modified centrifuge tube lures are highly variable regarding optimal ethanol rate for trap captures, but manufactured lures of 0.7–1.4 g/day represent an optimal release rate for maximum captures of *X. germanus*, *A. maiche*, *X. saxesenii* and *X. crassiusculus*.

AUTHOR CONTRIBUTIONS

Aaron R. Yilmaz: Formal analysis; validation; visualization; writing – original draft; writing – review and editing. **Christopher M. Ranger:** Conceptualization; data curation; formal analysis; funding acquisition; investigation; methodology; project administration; resources; supervision; writing – review and editing. **Michael E. Reding:** Conceptualization; data curation; formal analysis; investigation; methodology; software; validation; visualization; writing – review and editing. **Giacomo Cavaletto:** Formal analysis; visualization. **Giacomo Santoiemma:** Formal analysis; visualization. **Davide Rassati:** Formal analysis; visualization. **Jenny Barnett:** Methodology; project administration; resources; supervision.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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