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Efficacy of unbaited and baited green multi-funnel traps for detection of *Agrilus* species and other wood-boring beetle taxa

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Abstract
Semiochemical-baited traps are a key component of post-border surveillance for detection of non-native and potentially invasive bark and wood-boring beetles (Buprestidae, Cerambycidae, Curculionidae: Scolytinae) at risk of introduction in untreated woody materials used in global trade. Because the particular species that may arrive with imported goods is unknown, plant protection agencies need trapping protocols that effectively survey all three taxa. Baiting traps with host volatiles and aggregation/sex pheromones of longhorn beetles increases efficacy of detecting Cerambycidae and Scolytinae, but its effect on detection of *Agrilus* species and other jewel beetles is unknown. In this multi-country trapping study we found that the addition of ethanol and common aggregation/sex pheromones of longhorn beetles to green multi-funnel traps placed in the mid-upper forest canopy had negative effects on abundance of *Agrilus* species and other jewel beetles collected but no effect on their species richness, and significant positive effects on species richness and abundance of Cerambycidae and Scolytinae. Baiting green canopy traps with longhorn beetle pheromones increased the efficacy of traps for detecting total target taxa of bark and wood-boring beetles at risk of international movement in untreated woody materials. This information is beneficial for the design of multi-taxa surveys, potentially saving money and resources without decreasing trapping efficacy.

Keywords Buprestidae · Cerambycidae · Scolytinae · Surveillance · Trapping

Introduction

The genus *Agrilus* (Coleoptera: Buprestidae) includes more than 3,300 species worldwide (Jendek 2016; Kelnarova et al. 2019; Jendek and Grebennikov 2023), many of which feed during the larval stage in the phloem and wood of tree genera common to urban and natural forests in North America, Europe and Asia. While phytosanitary measures like ISPM 15 (Haack et al. 2014) are largely effective, the tremendous volume of globally traded goods and the wood used to package them ensures that live wood borers will continue to arrive in new continents and habitats (Meurisse et al. 2019; Ruzzier et al. 2023). Some of these arrivals, especially *Agrilus* species that colonize economically important hardwood trees, may establish and become invasive forest pests like the emerald ash borer, *Agrilus planipennis* Fairmaire, which has caused massive ecological and economic damage in North America (Kovacs et al. 2010; Klooster et al. 2018). For these reasons, several tools (e.g., Poland and Rassati 2019; Kyei-Poku et al. 2020; Peterson et al. 2023a, b) have been developed for the early-detection of *Agrilus* species at entry points, among which traps have been adopted by several phytosanitary agencies worldwide.

Among the numerous trap types developed for *Agrilus* monitoring programs (e.g., Poland et al. 2019; Imrei et al. 2020a; Kuhn et al. 2024), host volatile-baited or unbaited green glue-coated prism traps and green Fluon®-coated multi-funnel traps set up in the canopy are the most adopted and recommended types (Grant et al. 2010, 2011; Silk et al. 2011, 2020; Evans et al. 2020; Santoiemma et al. 2024a, b). The adoption of the green version of these trap types stems from a number of both lab and field studies. Lab studies, mostly focused on *A. planipennis*, showed that the eyes of

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Extended author information available on the last page of the article adults of both sexes are sensitive to green, blue, red and ultraviolet specific wavelengths (Crook et al. 2009), and that specific shades of green (i.e., wavelength range 525–540 nm, and reflectance in the 49–67% range) are attractive to males (Francese et al. 2010; Domingue et al. 2012, 2013; Poland et al. 2019; Parker et al. 2020). Field studies further confirmed that green traps catch *A. planipennis* as well as many other *Agrilus* species (Crook et al. 2009; Francese et al. 2010, 2011, 2013; Poland and McCullough 2014; Petrice and Haack 2015; Kim et al. 2016; Rhainds et al. 2017; Skvarla and Dowling 2017; Rassati et al. 2019; Cavaletto et al. 2020; Santoiemma et al. 2024a, b), even though other trap colors, such as purple or fluorescent yellow, can be more attractive than green for certain species (Imrei et al. 2020b; Kuhn et al. 2024).

Like *Agrilus* species, longhorn beetles (Cerambycidae) and bark and ambrosia beetles (Curculionidae: Scolytinae) are also commonly moved in wood packaging used in trade (Brockerhoff et al. 2006; Eyre and Haack 2017; Wu et al. 2017) and are monitored at entry points using baited traps (e.g., Rassati et al. 2015a, b; Hoch et al. 2020; Mas et al. 2023). For example, black multi-funnel or intercept-panel traps set up in the understory and baited with only ethanol and/or alpha-pinene, or with these host volatiles plus blends of longhorn beetle pheromones, are commonly used for generic surveillance of bark and ambrosia beetles and longhorn beetles, respectively (e.g., Fan et al. 2019; Rabaglia et al. 2019; Roques et al. 2023; Dodds et al. 2024). Considering that surveillance activities can be expensive, and budgets are often limited, recent efforts have been made to develop trapping protocols that can be used to target multiple taxa simultaneously (Chase et al. 2018; Rassati et al. 2019; Marchioro et al. 2020). When primarily targeting *Agrilus* species, an option for simultaneously surveying longhorn beetle and bark and ambrosia beetle communities could be to bait green-canopy multi-funnel traps with ethanol and longhorn beetle pheromones (Rassati et al. 2019; Marchioro et al. 2020; Cavaletto et al. 2020, 2021; Santoiemma et al. 2024a). This approach would improve detection of those species of bark and ambrosia beetles and longhorn beetles active in the upper forest strata (e.g., Ulyshen and Hanula 2007; Maguire et al. 2014; Rassati et al. 2019). However, the adoption of this protocol requires verification that these baits do not negatively affect catches of *Agrilus* jewel beetles. Adding a blend of longhorn beetle pheromones to ethanol-baited traps reduced the species richness of jewel beetles detected in green multi-funnel traps, though not significantly (Rassati et al. 2019).

The primary objective of this multi-country trapping study was to test whether catches of *Agrilus* species and other buprestids in green-canopy multi-funnel traps were negatively affected by the addition of either host volatiles or blends of host volatiles and longhorn beetle pheromones. We compared species richness and abundance of *Agrilus* species and other buprestids in unbaited green-canopy multi-funnel traps vs. the same traps baited with (i) ethanol; (ii) ethanol plus a blend of longhorn beetle pheromones known to be attractive primarily for species in the subfamily Lamiinae; (iii) ethanol plus a blend of longhorn beetle pheromones known to be attractive primarily for species in the subfamily Cerambycinae. As a secondary objective, we determined the effects of lure treatments on catches of longhorn beetles as well as bark and ambrosia beetles to confirm their efficacy for generic surveillance of bark and wood-boring beetles.

Materials and methods

Study sites and general experimental methods

Trapping experiments were carried out in 2021 at seven sites located in six different countries in Europe, North America and Asia, namely Canada (New Brunswick), China (Jilin), Italy (Friuli-Venezia Giulia), Poland (Podlaskie Voivodeship), United Kingdom (UK, England) and United States of America (USA) (Table S1; Fig. S1). In the USA, trials were conducted in Massachusetts (MA) and Kentucky (KY). Traps were always set up in a complete randomized block design within an oak-dominated forest using a minimum of 6 to a maximum of 8 blocks per site (Table S1). Within each block, treatments were spaced 20–30 m from each other and were set up following a linear transect (Fig. S1). Blocks were spaced 30–60 m from each other. In addition, traps were always suspended from a branch in the mid to upper canopy (i.e., 10–30 m above the ground) using a BigShot® throw weight launcher (SherillTree, Greensboro, NC, USA) (Hughes et al. 2014) or a hand-thrown weight, or by using a carbon-fiber telescopic pole (Telsys Ltd., Liverpool, UK) (Williams and Jonusas 2019), because traps in the forest canopy catch more *Agrilus* species and individuals than traps in the understory (e.g., Francese et al. 2008; Crook et al. 2008, 2009; Ryall et al. 2012; Rassati et al. 2019; Sallé et al. 2020). For the same reason, traps were placed in open sunny spots corresponding to canopy gaps rather than shaded ones; these spots were identified visually while setting up traps (e.g., Francese et al. 2008; Lyons et al. 2009). Traps operated for 8–13 weeks corresponding to the activity period of most *Agrilus* spp. and were emptied every 2–3 weeks. The dates of trap set-up and removal for each site were: Canada, 4 June–14 August; China, 5 June–4 September; Italy, 26 May–11 August; Massachusetts, 27 May–17 August; Kentucky, 18 May–23 August; Poland, 24 May–19 July; and UK, 24 May–20 August.

Trap type and lures

The green multi-funnel traps used in Canada, China, Italy, and Poland were sourced from Synergy Semiochemicals (Surrey, British Columbia, Canada; 525 nm, 55% reflectance) and were treated with Fluon® (active ingredient polytetrafluoroethylene; Synergy's EZ Fluon kit #5001) at 12% concentration in water, as suggested by the supplier. The traps used in the USA and United Kingdom were sourced from ChemTica Internacional (Santo Domingo, Costa Rica; 530 nm, 57% reflectance), and came pre-treated with a 30% concentration of Fluon. Fluon treatment reduces friction on the trap surface and increases trap catches of wood-boring beetles (Graham and Poland 2012; Allison et al. 2016). Trap-collecting cups (height: 11.5 cm; diameter: 9.5 cm) were filled with 150–200 ml of either a 50% propylene glycol solution in water or as a pre-mixed marine/RV antifreeze solution (USA, Italy, UK), 50% ethylene glycol in water (Poland), or a saturated solution of table salt in water (Canada, China) with a drop or two of liquid dish detergent to reduce surface tension. Trapping solutions were replaced or replenished as required at each trap check.

There were three experimental lure treatments in addition to the unbaited control: (i) ultra-high release rate (UHR) ethanol, (ii) *E/Z*-fuscumol lure + *E/Z*-fuscumol acetate lure + UHR ethanol lure (hereafter referred to as FUSC blend); and (iii) racemic 3-hydroxyhexan-2-one lure + 3-hydroxyoctan-2-one lure + *syn*-2,3-hexanediols lure + UHR ethanol lure (hereafter referred to as KET blend) (see Table S2 for details on sources and release rates of lures). UHR ethanol was selected as it is one of the most adopted host volatile trap lures when targeting bark and ambrosia beetles (e.g., Miller and Rabaglia 2009; Rabaglia et al. 2019; Fiala et al. 2023) and enhances attraction of many cerambycids to their aggregation/sex pheromones (e.g., Hanks et al. 2012, 2018; Miller et al. 2015, 2017; Rice et al. 2024). The FUSC blend was selected because its components attract multiple species of longhorn beetles in the subfamilies Lamiinae (Fonseca et al. 2010; Mitchell et al. 2011; Hanks et al. 2018; Millar et al. 2018; Meier et al. 2020) and Spondylidinae (e.g., Silk et al. 2007; Sweeney et al. 2010; Halloran et al. 2018; Žunič-Kosi et al. 2019; Kerr et al. 2024). The KET blend was selected because its components attract multiple species of longhorn beetles in the subfamily Cerambycinae (e.g., Fettköther et al. 1995; Lacey et al. 2007; Hanks and Millar 2013, 2016; Miller et al. 2015; Hanks et al. 2018, 2019; Millar et al. 2018; Flaherty et al. 2019; Rassati et al. 2021).

Statistical analyses

Generalized linear mixed models were used for all the analyses. Separate models were built for each response variable across all sites (global models), as well as for each site and response variable (local models). Data collected from each trap and pooled over the entire sampling period were treated as a distinct statistical unit. The response variables were the species richness (i.e., total number of species) and the total abundance (i.e., number of individuals pooled over all the species) of genus *Agrilus*, Buprestidae (excluding *Agrilus* species), Cerambycidae, and the subfamilies Cerambycinae, Lamiinae and Lepturinae, and Scolytinae (Curculionidae), and the abundance (i.e., number of individuals) of individual species. When testing the effect of trap treatments on the abundance of single species, only species represented by at least 50 individuals were considered. For all models, the categorical explanatory variable was the treatment (four levels: unbaited control, UHR ethanol, FUSC blend, and KET blend). The site identity and the block identity within each site were included in global models as nested random factors. The block identity was included in local models as a random factor. Models were fitted using a Poisson distribution with a natural logarithm (ln) link function for species richness, and negative binomial distribution with a ln link function for abundance. The ln-transformed number of exposure days for the traps (from set-up to removal), varying by site, was included in global models as an offset. The unbaited control was used as a baseline for comparison with the other three baited traps. All the analyses were carried out in R (R Core Team 2021). Models were fitted using the 'glmmTMB' package (Brooks et al. 2017) and were checked for overdispersion and residual distribution using the 'DHARMa' package (Hartig 2021).

Results

General results

A total of 33,540 individuals from 353 species were caught (Table S3). Buprestidae were represented by 12,607 individuals and 85 species (Table S3). Among them, 7690 individuals (50 species) belonged to the genus *Agrilus*. The European species, *Agrilus sulcicollis* Lacordaire, was the most abundant *Agrilus* species with 1845 individuals, followed by *Agrilus laticornis* (Illiger) (1060 individuals), and *Agrilus angustulus* (Illiger) (564 individuals). By contrast, 20 *Agrilus* species were represented by less than 10 individuals. Ten of the species collected in China were new species records for Jilin province: *Agrilus fareastensis* Jendek, *Agrilus fissus* Obenberger, *Agrilus rudicollis* Alexeev, *Agrilus soudeki* Obenberger, *Agrilus truncatus* Jendek, *Meliboeus ohbayashii* Kurosawa, *Anthaxia constricticollis* Bílý, *Anthaxia ungulata* Bílý, *Chrysobothris pulchripes* Fairmaire, and *Lamprodila virgata* (Motschulsky) (Table S3). Among the other Buprestidae, *L. virgata* was the most abundant species with 4035 individuals. Cerambycidae were represented by 7860 individuals from 199 species (Table S3). Cerambycinae, Lamiinae and Lepturinae were the most represented subfamilies with 5092 individuals from 65 species, 1733 individuals from 74 species, and 1026 individuals from 56 species, respectively. *Xylotrechus antilope* (Schönherr) was the most abundant species with 1368 individuals, followed by *Plagionotus detritus* (Linnaeus) (1047 individuals), and *Anelaphus villosus* (Fabricius) (410 individuals). By contrast, 123 longhorn beetle species were represented by less than 10 individuals. The lone specimen of *Arhopalus rusticus* (Linnaeus) collected in Massachusetts is the first documented record of that species for the state. Scolytinae were represented by 13,073 individuals from 69 species (Table S3). *Anisandrus maiche* Kurentsov was the most abundant species with 4893 individuals, followed by *Xyleborinus saxesenii* (Ratzeburg) (2453 individuals), and *Xylosandrus crassiusculus* (Motschulsky) (2301 individuals). By contrast, 44 Scolytinae species were represented by less than 10 individuals. Twelve species were collected in countries in which they were not native: one buprestid [*A. planipennis* (USA)], four cerambycids [*A. rusticus* (USA), *Neoclytus acuminatus* (Fabricius) (Italy), *Phymatodes testaceus* (Linnaeus) (USA, Canada), and *Xylotrechus stebbingi* Gahan (Italy)], and seven scolytines [*A. maiche* (USA), *Cnestus mutilatus* (Blandford) (USA), *Scolytus multistriatus* (Marsham) (USA), *Xyleborinus attenuatus* (Blandford) (Canada), *X. saxesenii* (USA, Canada), *X. crassiusculus* (USA, Italy), and *Xylosandrus germanus* (Blandford) (USA, Italy)] (Table S3) (Craighead 1950; Sama 2002; Schiefer and Bright 2004; Bousquet et al. 2013; Gomez et al. 2018; Jendek and Grebennikov 2023).

Effect of lure treatments on *Agrilus* species and other Buprestidae

Unbaited traps, traps baited with UHR ethanol, FUSC blend, and KET blend collected 43, 38, 40, and 41 *Agrilus* species, respectively (Table S4). Lure treatment did not affect richness of *Agrilus* species neither globally nor at site level (Tables 1, S5, Fig. 1A–H), whereas significant differences between unbaited control traps and other lure treatments were observed for abundance globally, and in USA (MA) and China (Table S6, Fig. 1I, J, P). Globally, traps baited with KET blend collected significantly fewer individuals than the unbaited control (Fig. 1I, Table S6). Traps baited with KET blend and UHR ethanol collected significantly fewer individuals than the unbaited control in USA (MA) and China, respectively (Fig. 1J, P, Table S6). At the species level, lure treatment affected abundance of 5 of 21 analyzed *Agrilus* species (Tables 2, S7). Traps baited with FUSC blend collected significantly more individuals of *Agrilus arcuatus* (Say) than did the unbaited control in USA (KY), whereas traps baited with the same lure collected significantly fewer *Agrilus hastulifer* (Ratzeburg) individuals than did the unbaited control in Poland (Tables 2, S7). In China, unbaited traps collected significantly more individuals of: (1) *Agrilus alutaceicollis* Obenberger than did traps baited with UHR ethanol; (2) *Agrilus asiaticus* Kerremans than did traps baited with KET blend; and (3) *A. fissus* than did traps baited with either UHR ethanol or KET blend (Tables 2, S7).

Unbaited traps, traps baited with UHR ethanol, with FUSC blend, and with KET blend collected 24, 21, 17, and 17 non-*Agrilus* species, respectively (Table S4). Lure treatment did not affect non-*Agrilus* species richness neither globally nor at site level (Tables 1, S5), whereas significant differences between unbaited control traps and other lure treatments were observed for abundance globally and in China, where traps baited with FUSC, KET or UHR ethanol collected significantly fewer individuals than unbaited traps (Table S6). At the species level, lure treatment significantly affected abundance of two of the six analyzed species of non-*Agrilus* Buprestidae (Tables 2, S7). Unbaited traps collected significantly more individuals of *Anthaxia constricticollis* Bílý than did traps baited with FUSC or KET, and significantly more individuals of *L. virgata* than did traps baited with any other lure treatment (Tables 2, S7).

Effect of lure treatments on Cerambycidae at family and subfamily level

Unbaited traps, traps baited with UHR ethanol, FUSC blend, and KET blend collected 107, 128, 114, and 141 cerambycid species, respectively (Table S4). At the family level, significant differences between unbaited control traps and other lure treatments were observed for species richness globally and at all sites except UK, Italy and Poland (Tables 1, S5, Fig. 2A–H), and at all sites except UK for total abundance (Tables 1, S6, Fig. 2I–P). Baited traps, especially with KET blend, collected significantly more species (Fig. 2A–D, H) and individuals (Fig. 2I–L, N–P) than did unbaited traps.

At the subfamily level, the same trend described above was observed for species richness and abundance of Cerambycinae globally and at all sites, except for species richness in UK (Tables 1, S5, S6). For the subfamily Lamiinae, however, traps baited with the FUSC blend collected significantly more species than did unbaited traps globally, in USA (KY) and Italy (Tables 1, S5), and significantly more individuals globally, in USA (MA and KY), Canada, Italy and China (Tables 1, S6). The subfamily Lepturinae was affected by lure treatment globally and in USA (MA and KY), where traps baited with UHR ethanol or KET collected significantly more individuals than did unbaited traps (Tables 1, S6). At the species level, the effect of lure treatment on mean catch was significant for 20 of 27 analyzed species (Tables 2, S7). Mean catch of 14 Cerambycinae species was greater in

Table 1 Analysis of deviance table from the generalized linear mixed models testing the effect of different treatments on species richness (Poisson distribution; ln link function) and abundance (negative binomial distribution; ln link function) of *Agrilus*, other Buprestidae, Cerambycidae (including subfamilies Cerambycinae, Lamiinae and Lepturinae), and Scolytinae (Curculionidae) globally and at each site. Type II Wald chi-square tests with 3 degrees of freedom (χ^2_3) and *p* values (bolded if $p < 0.05$) are provided for all models. – = taxon not collected in the site

Species richness		Global	USA (MA)	USA (KY)	Canada	UK	Italy	Poland	China
Agrilus	χ^2_3	0.799	2.433	0.263	0.190	0.229	0.143	0.133	2.695
	p value	0.850	0.487	0.967	0.979	0.973	0.986	0.988	0.441
Other Buprestidae	χ^2_3	1.161	0.908	0.597	1.184	–	1.538	0.153	2.704
	p value	0.824	0.824	0.897	0.757	–	0.674	0.985	0.440
Cerambycidae	χ^2_3	72.330	17.935	20.097	49.786	3.946	2.630	4.547	6.443
	p value	**< 0.001**	**< 0.001**	**< 0.001**	**< 0.001**	0.267	0.452	0.208	0.092
Cerambycinae	χ^2_3	160.010	46.626	22.168	43.996	6.128	38.879	5.737	13.385
	p value	**< 0.001**	**< 0.001**	**< 0.001**	**< 0.001**	0.106	**< 0.001**	0.125	**0.004**
Lamiinae	χ^2_3	17.066	5.799	6.859	10.902	2.290	6.523	1.156	5.111
	p value	**< 0.001**	0.122	0.077	**0.012**	0.515	0.089	0.764	0.164
Lepturinae	χ^2_3	2.917	5.073	3.793	3.312	0.154	2.164	0.522	0.399
	p value	0.405	0.167	0.285	0.346	0.985	0.539	0.914	0.941
Scolytinae	χ^2_3	48.946	24.422	6.987	9.572	11.709	4.231	1.039	7.707
	p value	**< 0.001**	**< 0.001**	0.072	**0.023**	**0.008**	0.238	0.792	0.052
Abundance									
Agrilus	χ^2_3	6.361	9.281	0.652	0.325	1.886	0.716	1.293	5.035
	p value	0.095	**0.026**	0.884	0.955	0.596	0.869	0.731	0.169
Other Buprestidae	χ^2_3	6.485	3.464	1.854	2.306	–	3.047	0.494	8.675
	p value	0.090	0.326	0.603	0.511	–	0.384	0.920	**0.034**
Cerambycidae	χ^2_3	173.880	67.572	74.026	84.238	3.034	30.974	41.325	37.208
	p value	**< 0.001**	**< 0.001**	**< 0.001**	**< 0.001**	0.386	**< 0.001**	**< 0.001**	**< 0.001**
Cerambycinae	χ^2_3	413.380	203.240	143.710	79.862	13.977	118.390	46.857	71.451
	p value	**< 0.001**	**< 0.001**	**< 0.001**	**< 0.001**	**0.003**	**< 0.001**	**< 0.001**	**< 0.001**
Lamiinae	χ^2_3	44.736	17.213	7.701	32.403	8.161	12.825	1.548	21.446
	p value	**< 0.001**	**< 0.001**	0.053	**< 0.001**	**0.043**	**0.005**	0.671	**< 0.001**
Lepturinae	χ^2_3	7.875	6.283	12.825	3.673	0.838	4.662	3.254	2.590
	p value	**0.049**	0.099	**0.005**	0.299	0.840	0.198	0.354	0.459
Scolytinae	χ^2_3	160.240	23.915	16.300	38.875	95.322	95.325	2.969	265.760
	p value	**< 0.001**	**< 0.001**	**< 0.001**	**< 0.001**	**< 0.001**	**< 0.001**	0.396	**< 0.001**

KET blend-baited traps than unbaited traps (Tables 2, S7). Mean catch of six Lamiinae species was greater in FUSC blend-baited traps than unbaited traps, but two of these species [*Hyperplatys maculata* Haldeman and *Mesosa myops* (Dalman)] also had greater mean catches in traps baited with KET blend or UHR ethanol than in unbaited traps, suggesting they were attracted by ethanol rather than *E/Z*-fuscumol or *E/Z*-fuscumol acetate (Tables 2, S7).

Effect of lure treatments on Scolytinae (Curculionidae)

Unbaited traps, traps baited with UHR ethanol, FUSC blend, and KET blend collected 31, 48, 47, and 47 species, respectively (Table S4). Lure treatment significantly affected either species richness or total abundance at all sites except for Poland (Table 1, Fig. 3, Tables S5, S6). Globally and at most sites, traps baited with any of the lure treatments collected significantly more species (Fig. 3A–E, H) and individuals (Fig. 3I–N, P) than did unbaited traps. Lure treatment affected trap catch of 11 of 13 analyzed species, and for most species, mean catch for all three lure treatments differed significantly from that in unbaited trap, suggesting UHR ethanol was the common attractant (Tables 2, S7). However, there were two Scolytinae species for which mean catch in unbaited traps differed from traps baited with UHR ethanol plus cerambycid pheromones but not from traps baited with UHR ethanol alone. Mean catch of *S. multistriatus* in

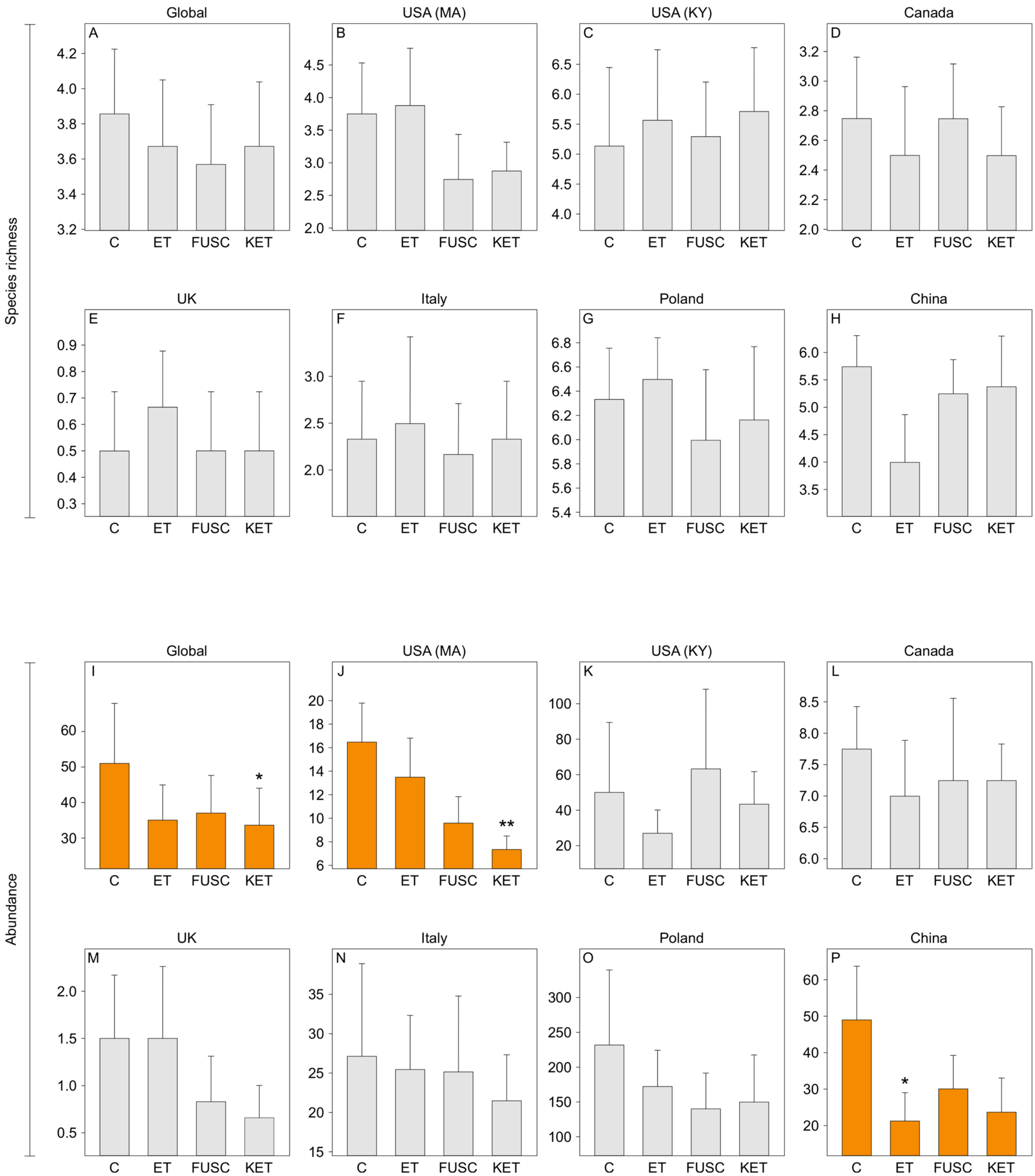

Fig. 1 Mean species richness and abundance of *Agrilus* for each treatment globally (**A**, **I**) and at each site (**B**–**H**, **J**–**P**). Error bars indicate the positive standard error. Asterisks over the bars indicate the statistical difference with the unbaited control from the generalized linear mixed models. *P* values: *0.01–0.05; **0.001–0.01; ***< 0.001. Grey plots = no statistical difference with the unbaited control. Orange plots = significant difference of at least one lure treatment with the unbaited control. C = unbaited control; ET = UHR ethanol; FUSC = *E/Z*-fuscumol + *E/Z*-fuscumol acetate + UHR ethanol (FUSC blend); KET = racemic 3-hydroxyhexan-2-one + 3-hydroxyoctan-2-one + *syn*-2,3-hexanediols + UHR ethanol (KET blend). Model details are provided in Tables 1, S5, S6

Table 2 Mean (±standard error) number of individuals collected per trap by treatment at each site, over the entire sampling period. Only species with catches that significantly differed from the unbaited control (based on generalized linear mixed models) are reported. Bold values indicate a significant difference from the unbaited control (p value < 0.05). C = unbaited control; ET = UHR ethanol; FUSC = *E/Z*-fuscumol + *E/Z*-fuscumol acetate + UHR ethanol (FUSC blend); KET = racemic 3-hydroxyhexan-2-one + 3-hydroxyoctan-2-one + *syn*-2,3-hexanediols + UHR ethanol (KET blend). Species within each family and subfamily are listed in alphabetical order. Statistical significance levels are reported in Table S7

Buprestidae	C	ET	FUSC	KET	Country
Agrilinae					
Agrilus alutaceicollis	3.88 ± 1.98	**0.25 ± 0.16**	1.38 ± 1.30	1.25 ± 1.17	China
Agrilus arcuatus	2.00 ± 0.82	3.86 ± 1.52	**12.71 ± 7.78**	6.43 ± 3.21	USA (KY)
Agrilus asiaticus	3.25 ± 1.18	2.13 ± 1.23	1.50 ± 0.54	**0.88 ± 0.58**	China
Agrilus fissus	7.13 ± 2.66	**2.13 ± 1.43**	2.75 ± 1.53	**2.00 ± 0.57**	China
Agrilus hastulifer	8.33 ± 7.74	1.17 ± 0.75	**0.17 ± 0.17**	4.17 ± 3.58	Poland
Buprestinae					
Anthaxia constricticollis	5.25 ± 1.46	4.00 ± 2.80	**0.75 ± 0.25**	**1.13 ± 0.55**	China
Chrysochroinae					
Lamprodila virgata	248.38 ± 57.01	**87.75 ± 33.04**	**78.25 ± 32.05**	**90.00 ± 26.49**	China
Cerambycidae					
Cerambycinae					
Anelaphus pumilus	0.71 ± 0.36	**3.14 ± 0.86**	1.71 ± 0.64	**46.57 ± 16.68**	USA (KY)
Anelaphus villosus	0.88 ± 0.35	**7.75 ± 2.58**	**4.00 ± 1.10**	**30.38 ± 3.46**	USA (MA)
	0.43 ± 0.30	**3.14 ± 0.67**	1.14 ± 0.51	**2.86 ± 0.96**	USA (KY)
Clytus tropicus	2.83 ± 0.87	3.17 ± 0.87	2.00 ± 0.52	**11.50 ± 2.29**	Poland
Neoclytus acuminatus	0.00 ± 0.00	0.13 ± 0.13	0.13 ± 0.13	**10.38 ± 2.15**	USA (MA)
Neoclytus mucronatus	0.14 ± 0.14	0.00 ± 0.00	0.71 ± 0.29	**23.71 ± 4.62**	USA (KY)
Phymatodes aereus	0.00 ± 0.00	0.00 ± 0.00	0.13 ± 0.13	**8.25 ± 2.57**	USA (MA)
Phymatodes alni	2.00 ± 0.82	2.67 ± 1.09	**5.17 ± 2.11**	**10.33 ± 4.22**	Poland
Phymatodes testaceus	0.83 ± 0.83	1.67 ± 0.76	0.50 ± 0.34	**27.00 ± 5.72**	Poland
Plagionotus detritus	3.17 ± 2.06	5.33 ± 1.94	1.83 ± 0.60	**162.00 ± 7.90**	Poland
Plagionotus pulcher	0.13 ± 0.13	0.75 ± 0.62	0.63 ± 0.18	**29.50 ± 4.75**	China
Rhaphuma gracilipes	1.38 ± 0.32	0.88 ± 0.48	2.00 ± 0.68	**3.63 ± 1.10**	China
Xylotrechus antilope	42.17 ± 39.59	41.33 ± 27.77	7.00 ± 4.04	**134.67 ± 52.85**	Poland
Xylotrechus colonus	0.00 ± 0.00	0.57 ± 0.43	0.00 ± 0.00	**8.00 ± 2.39**	USA (KY)
Xylotrechus stebbingi	0.17 ± 0.17	0.50 ± 0.22	0.83 ± 0.31	**13.00 ± 1.61**	Italy
Lamiinae					
Ecyrus dasycerus	1.00 ± 0.50	1.50 ± 0.46	**5.63 ± 1.94**	**5.25 ± 1.13**	USA (MA)
Graphisurus fasciatus	3.50 ± 1.04	2.75 ± 0.82	**12.25 ± 6.43**	3.63 ± 0.93	USA (MA)
	0.71 ± 0.36	1.43 ± 0.97	**4.29 ± 2.15**	1.14 ± 0.63	USA (KY)
Hyperplatys maculata	0.00 ± 0.00	**2.75 ± 0.45**	**1.25 ± 0.45**	**3.38 ± 0.26**	Canada
Mesosa myops	1.75 ± 0.53	**7.00 ± 1.04**	**4.75 ± 0.98**	**3.75 ± 0.62**	China
Neacanista tuberculipennis	0.38 ± 0.13	**4.88 ± 1.72**	0.88 ± 0.31	**1.88 ± 0.66**	China
Sternidius alpha	1.00 ± 0.38	1.38 ± 0.42	**3.88 ± 1.47**	0.75 ± 0.25	USA (MA)
Curculionidae					
Scolytinae					
Anisandrus dispar	0.00 ± 0.00	**5.33 ± 2.06**	**4.50 ± 0.99**	**3.50 ± 1.20**	UK
	1.33 ± 0.62	**10.17 ± 3.57**	**14.17 ± 2.93**	**13.17 ± 4.77**	Italy
Anisandrus maiche	0.14 ± 0.14	**5.57 ± 1.38**	**3.29 ± 1.57**	**7.00 ± 2.48**	USA (KY)
	14.75 ± 2.01	**188.88 ± 35.51**	**121.63 ± 22.67**	**272.38 ± 41.11**	China
Anisandrus sayi	0.13 ± 0.13	**6.63 ± 3.34**	**5.25 ± 1.03**	**4.00 ± 1.64**	USA (MA)
	0.00 ± 0.00	**2.88 ± 0.35**	**3.75 ± 0.31**	**3.75 ± 0.25**	Canada
Hypothenemus eruditus	4.83 ± 1.20	**14.17 ± 3.06**	**30.33 ± 15.47**	4.83 ± 2.09	Italy
Pseudopityophthorus minutissimus	1.00 ± 0.27	**3.13 ± 0.52**	**3.13 ± 0.35**	**3.88 ± 0.30**	Canada
Pityogenes chalcographus	0.00 ± 0.00	0.83 ± 0.40	**5.17 ± 3.98**	**4.83 ± 2.02**	Poland

Table 2 (continued)

Buprestidae	C	ET	FUSC	KET	Country
Scolytus multistriatus	5.83 ± 2.07	26.50 ± 14.93	**121.00 ± 113.28**	4.83 ± 2.01	Italy
Trypodendron domesticum	0.00 ± 0.00	**4.67 ± 0.84**	**4.50 ± 1.73**	**2.50 ± 0.92**	UK
Xyleborinus saxesenii	0.17 ± 0.17	**46.50 ± 9.20**	**38.67 ± 4.78**	**26.00 ± 4.28**	UK
	3.33 ± 0.49	**101.17 ± 7.60**	**110.67 ± 24.96**	**52.00 ± 13.01**	Italy
	0.13 ± 0.13	**3.13 ± 1.19**	**2.88 ± 0.77**	**2.25 ± 0.59**	China
Xylosandrus crassiusculus	34.71 ± 5.32	**110.29 ± 15.01**	**83.86 ± 15.17**	**91.86 ± 25.34**	USA (KY)
Xylosandrus germanus	1.71 ± 0.99	**8.71 ± 2.59**	3.71 ± 1.86	**12.29 ± 6.23**	USA (KY)

Italy was greater in FUSC-baited traps than unbaited traps, and mean catch of *Pityogenes chalcographus* (Linnaeus) in Poland was greater in both FUSC- and KET-baited traps than unbaited traps (Tables 2, S7).

Discussion

Semiochemical-baited traps are a key component of post-border surveillance for invasive bark and wood-boring beetles (Dodds et al. 2024). Budget limitations require plant protection agencies to use trapping protocols that survey for multiple target taxa both effectively and efficiently. The goal of these surveys is to detect the presence of non-native, potentially invasive species of bark and wood-boring beetles as early as possible, because the smaller the area of infestation, the easier it is to contain or eradicate (Brockerhoff et al. 2010; Liebhold et al. 2016). Trapping protocols that increase the species richness of target taxa collected are more likely to detect the presence of non-native species in the same taxa (Dodds et al. 2024). In this multi-country study, we have shown that species richness of *Agrilus* spp. and other jewel beetles detected in green-canopy multi-funnel traps was not affected by baiting traps with ethanol and longhorn beetle aggregation/sex pheromones. At the same time, our results confirmed the positive effects of these semiochemical lures on the species richness of Cerambycidae and Scolytinae detected in traps. This information is beneficial for the design of multi-taxa surveys, potentially saving money and resources without decreasing trapping efficacy.

There were, however, some negative effects of lure treatments on the abundance of some *Agrilus* species and non-*Agrilus* buprestids collected in traps. When data were pooled across all sites, green canopy traps baited with ethanol plus the KET blend captured significantly fewer specimens of *Agrilus* and other buprestids than did unbaited traps, suggesting that this trap-blend combination may be relatively less effective at detecting jewel beetles present at low population densities. There is evidence that the probability of detecting non-native species of longhorn beetles in traps is greater for species captured in high abundance in the same kinds of trap in their native range (Roques et al. 2023). Thus, if the objective of trapping surveys in a particular year or site was exclusively the detection of *Agrilus* species, then our data suggest that unbaited traps should be preferred to traps baited with the semiochemical treatments evaluated in this study, both for greater efficacy and lower costs. However, most trapping surveys at ports of entry target non-native cerambycids and scolytines in addition to buprestids (Rassati et al. 2014, 2015a, b; Rabaglia et al. 2019; Thurston et al. 2022). Our results show that baiting traps with ethanol and longhorn beetle pheromones increased the abundance of some Scolytinae and Cerambycidae in traps without reducing the numbers of species of jewel beetles detected, and thus had an overall positive effect on the efficacy of traps for detecting non-native species of beetles at risk of international transport in wood packaging.

Compared to Scolytinae and Cerambycidae, little is known about the chemical ecology of jewel beetles, but there is evidence that adults of some species of *Agrilus* and *Coraebus* respond to volatiles emitted from host foliage and cortical tissues when foraging for food and suitable brood hosts (Dunn et al. 1986; Rodriguez-Saona et al. 2006; de Groot et al. 2008; Crook and Mastro 2010; Fürstenau et al. 2012; Coleman et al. 2014; Silk and Ryall 2015; Vuts et al. 2016). Attraction to stressed host trees or to blends of volatiles emitted from stressed host trees has been observed in *Agrilus bilineatus* (Weber) (Dunn et al. 1986), *A. planipennis* (Crook et al. 2008; Grant et al. 2010; McCullough et al. 2009a, b), and *A. anxius* Gory (Silk et al. 2019). The common green leaf volatile, *Z*-3-hexenol, increased trap catches of *A. planipennis* (de Groot et al. 2008; Grant et al. 2010, 2011; Ryall et al. 2012), *A. auroguttatus* Schäffer (Coleman et al. 2014), and *A. sulcicollis* (Domingue et al. 2013), but had no effect on trap catches of *Agrilus anxius* (Silk et al. 2019), *Agrilus angustulus* (Illiger), *Agrilus graminis* Keisenwetter, *Agrilus laticornis, Agrilus obscuricollis* Keisenwetter (Domingue et al. 2013) or more than 20 other *Agrilus* species (Santoiemma et al. 2024b). Unlike many species of bark and ambrosia beetles (Miller and Rabaglia 2009), jewel beetles do not appear to be attracted to ethanol (Montgomery and Wargo 1983; Dunn et al. 1986; Chénier and Philogène

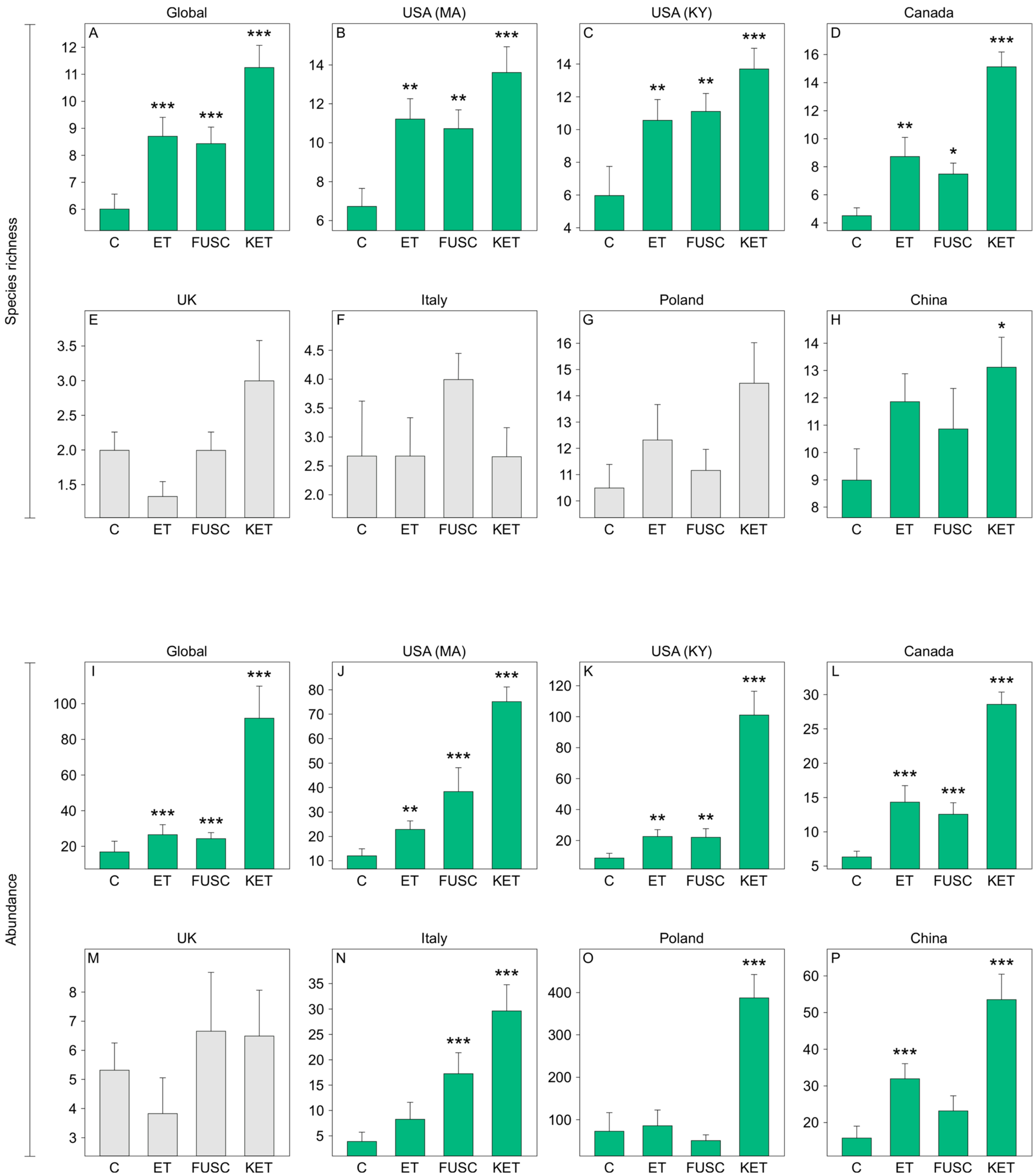

Fig. 2 Mean species richness and abundance of Cerambycidae for each treatment globally (**A**, **I**) and at each site (**B**–**H**, **J**–**P**). Error bars indicate the positive standard error. Asterisks over the bars indicate the statistical difference with the unbaited control from the generalized linear mixed models. *P* values: *0.01–0.05; **0.001–0.01; ***< 0.001. Grey plots = no statistical difference with the unbaited control. Green plots = significant difference of at least one lure treatment with the unbaited control. C = unbaited control; ET = UHR ethanol; FUSC = *E/Z*-fuscumol + *E/Z*-fuscumol acetate + UHR ethanol (FUSC blend); KET = racemic 3-hydroxyhexan-2-one + 3-hydroxyoctan-2-one + *syn*-2,3-hexanediols + UHR ethanol (KET blend). Model details are provided in Tables 1, S5, S6

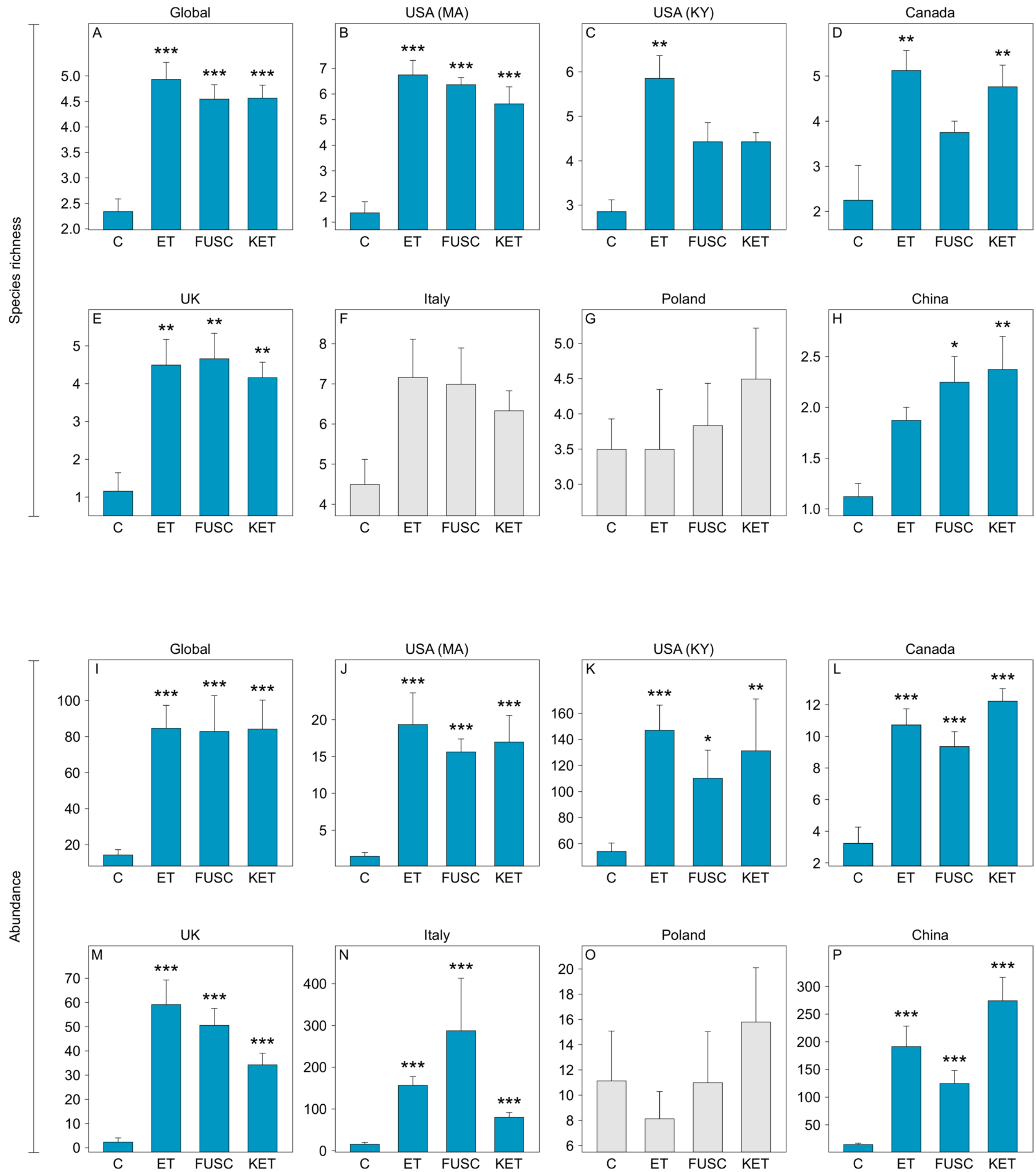

Fig. 3 Mean species richness and abundance of Scolytinae (Curculionidae) for each treatment globally (**A**, **I**) and at each site (**B**–**H**, **J**–**P**). Error bars indicate the positive standard error. Asterisks over the bars indicate the statistical difference with the unbaited control from the generalized linear mixed models. *P* values: *0.01–0.05; **0.001–0.01; ***<0.001. Grey plots = no statistical difference with the unbaited control. Blue plots = significant difference of at least one lure treatment with the unbaited control. C = unbaited control; ET = UHR ethanol; FUSC = *E/Z*-fuscumol + *E/Z*-fuscumol acetate + UHR ethanol (FUSC blend); KET = racemic 3-hydroxyhexan-2-one + 3-hydroxyoctan-2-one + *syn*-2,3-hexanediols + UHR ethanol (KET blend). Model details are provided in Tables 1, S5, S6

1989; Miller 2006, 2020). Similarly, the presence of the same longhorn beetle sex/aggregation pheromones present in the KET and FUSC blends did not significantly affect trap catches of jewel beetles (Flaherty et al. 2019; Rassati et al. 2019). The repellent effects of UHR ethanol and/or the combinations of UHR ethanol and common longhorn beetle pheromones that we observed on trap catches of *A. alutaceicollis*, *A. asiaticus*, *A. hastulifer*, *A. fissus*, *A. consticticollis*, and *L. virgata* suggest that these and some other buprestid species may avoid host trees emitting high rates of ethanol [e.g., resulting from tree stress (Kelsey and Westlind 2017)] or trees at risk of colonization by longhorn beetles, either because the substrate is not suitable for larval establishment or growth, or to avoid competition for resources. Only one species of jewel beetles, *A. arcuatus*, was captured in significantly greater numbers in baited traps than unbaited traps, with about six times the abundance in FUSC blend-baited traps than unbaited traps. It is possible this species seeks hosts of a similar type or condition as those used by a longhorn beetle species whose aggregation/sex pheromone contains fuscumol or fuscumol acetate and uses one or more of the components in the FUSC lure as kairomones. Disentangling these mechanisms would require more specific studies and a better knowledge on the chemical ecology of jewel beetles, which has been so far explored only for relatively few species (Dunn and Potter 1988; Crook and Mastro 2010; Fürstenau et al. 2012; Silk et al. 2019; López et al. 2021).

For longhorn beetles, we found a clear positive effect of lure treatments on species richness and abundance at the family level and on both Cerambycinae and Lamiinae at the subfamily level. Traps baited with KET and FUSC blends collected more species and individuals of Cerambycinae and Lamiinae, respectively, than did unbaited traps. This was not surprising and agrees with numerous studies showing that the aggregation/sex pheromones in our lure treatments are highly conserved in the Cerambycidae (e.g., Hanks and Millar 2013, 2016; Sweeney et al. 2014; Rassati et al. 2019; Silva et al. 2024) and that combining these pheromones with ethanol on traps enhances catches of many cerambycid species (Hanks et al. 2012, 2018; Miller et al 2015, 2017; Rice et al. 2024). For example, (*R*)-3-hydroxyhexan-2-one, present in racemic 3-hydroxyhexan-2-one, one of the three components of the KET blend, is a known or suspected pheromone component for numerous species within at least 25 genera and 12 tribes in the Cerambycinae (Hanks and Millar 2016; Silva et al. 2024). Similarly, fuscumol and fuscumol acetate are aggregation/sex-pheromone components for many species in the subfamily Spondylidinae and Lamiinae (Mitchell et al. 2011; Hanks and Millar 2016). Most of the cerambycid species significantly attracted to the KET or FUSC blends in our study have been previously shown to be attracted to one or more of the aggregation/sex pheromones in those blends (Lacey et al. 2007, 2009; Hanks and Millar 2013; Miller et al. 2017; Millar et al. 2018; Flaherty et al. 2019; Molander et al. 2019a, b, c; Rassati et al. 2021). However, we report the first evidence that the Cerambycinae species, *Plagionotus pulcher* (Blessig), and *Rhaphuma gracilipes* (Faldermann), are attracted to one or more of the aggregation/sex pheromones in the KET blend, and the Lamiinae species, *Mesosa myops* (Dalman) and *Neacanista tuberculipennis* Gressitt are attracted to ethanol. Pheromones identified in the Lepturinae are female-produced, attract only males, and differ in structure from those used by Cerambycinae and Lamiinae (Ray et al. 2011, 2014). This likely explains why Lepturinae species richness and abundance differed little between unbaited and baited traps.

A positive effect of lure treatments on species richness and abundance was also observed for Scolytinae and was due to the presence of UHR ethanol. Ethanol is emitted by trees in response to a variety of stressors and represents an important olfactory cue for many species of bark and ambrosia beetles for locating suitable brood hosts (Montgomery and Wargo 1983; Kelsey et al. 2014; Ranger et al. 2021; Yilmaz et al. 2024). Ethanol is always included in trapping protocols targeting these taxa because it attracts many xylophagous species (e.g., Miller and Rabaglia 2009; Rassati et al. 2014, 2015a, b; Rabaglia et al. 2019; Hartshorn et al. 2021). However, traps baited with the FUSC blend caught more *Scolytus multistriatus* and fewer *Xylosandrus germanus* than did unbaited traps. Significant attraction of some species of Scolytinae to racemic 3-hydroxyhexan-2-one or racemic 3-hydroxyoctan-2-one has previously been reported, suggesting these species may use particular aggregation/sex pheromones of longhorn beetles as kairomones when searching for suitable hosts, as many species of longhorn beetles and bark and ambrosia beetles infest stressed or recently dead trees (Miller et al. 2015; Sweeney et al. 2016). The negative effects of the FUSC blend on trap catches of *X. germanus* or of racemic 3-hydroxyoctan-2-one on trap catches of *Dryoxylon onoharaense* (Murayama) (Miller et al. 2015), *Anisandrus maiche*, *Xyleborinus attenuatus*, and *Trypodendron lineatum* (Linnaeus) (Sweeney et al. 2016) suggest these species use these cerambycid pheromones as cues that signal host unsuitability, possibly due to the potential for interspecific competition. Our finding that *A. maiche* was significantly attracted to traps baited with UHR ethanol regardless of the presence of pheromones in the KET blend differs from that of Sweeney et al. (2016) who observed a significant reduction in catches of this species when racemic 3-hydroxyoctan-2-one was added to ethanol-baited traps; it is possible that the additional presence of racemic 3-hydroxyhexan-2-one and *syn*-2-3-hexanediols in the KET blend accounts for the difference. The presence of longhorn beetle pheromones on ethanol-baited traps had no effect on catches of most Scolytinae species, as observed in previous studies (Miller et al. 2015, 2022; Sweeney et al. 2016; Marchioro et al. 2020).

In conclusion, the addition of ethanol and common aggregation/sex pheromones of longhorn beetles to green multi-funnel traps placed in the mid-upper forest canopy had significant positive effects on species richness and abundance of Cerambycidae and Scolytinae, negative effects on abundance of jewel beetles, but no effects on species richness of *Agrilus* species or other jewel beetles collected. Baiting green canopy traps with longhorn beetle pheromones increased the efficacy of traps for detecting total target taxa of bark and wood-boring beetles (i.e., Cerambycidae, Buprestidae, Scolytinae) at risk of international movement in untreated wood or wood packaging. Nonetheless, as shown in this and previous studies, plant protection agencies and phytosanitary personnel must be aware that the use of certain longhorn beetle aggregation/sex pheromones and ethanol may reduce catches of certain species in each of the targeted families. One limitation of our study was the lack of traps baited with ethanol and both FUSC and KET blends, as we cannot state whether it might be possible to save further resources by baiting the same trap with all lures together without decreasing overall trapping efficacy. Similarly, future work could test the effects of more complex blends of cerambycid pheromones (e.g., Roques et al. 2023) on the efficacy of detecting jewel beetles in traps. In addition, it might be worth testing whether the same trends can be observed when using other trap colors that could be used to target other important jewel beetle species (e.g., purple or yellow).

Author contributions

DW, JAF, and JS conceived the study; DR, GS, and JS wrote the first draft of the manuscript; CH, DW, EGB, EKLF, GCa, GS, JMG, LY, MQ, RP, and SMD conducted field experiments; CK, DR, EKLF, FG, GCu, JMG, LY, MG, RP, and TM identified beetle specimens; GS analyzed the data; AMR, DR, DW, JS, JAF, MQ, and TK acquired funds. All authors reviewed and approved the manuscript.

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Availability of data and materials The datasets generated during and/or analyzed during the current study are available from the corresponding authors on reasonable request.

Code availability R codes used to analyse the data are available from the corresponding authors on reasonable request.

Declarations

Conflict of interest The authors declare no competing interests.

Ethical approval This article does not contain any studies with human participants or vertebrates performed by any of the authors.

Consent to participate Not applicable.

Consent to publish Not applicable.

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