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Multi-colored traps can enhance monitoring programs for native and non-native longhorn beetles in forest ecosystems

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ABSTRACT

Longhorn beetles (Coleoptera: Cerambycidae) are one of the most diverse families of beetles worldwide and they play critical roles in forest environments. Monitoring longhorn beetles is essential for both conservation and pest management, and baited traps are widely used for this purpose. Longhorn beetle species vary in their visual ecology and are attracted to different trap colors. A way to optimize trapping efficiency could be to combine multiple colors on a single trap, so to create a trap that captures multiple species at once. To test this approach, we carried out seven trapping experiments in Europe and North America, comparing the effectiveness of a multi-colored trap against single-colored black, red, white, and yellow traps at whole family, subfamily, and species level. At most sites, multi-colored traps captured significantly more species and individuals than black, red, and/or yellow traps. At the subfamily level, at most sites, multi-colored traps were equally or more effective than single-colored traps for Cerambycinae and Lamiinae. For Lepturinae, multi-colored traps were generally significantly more effective than black or red traps, but significantly less effective than white traps. Responses varied among species. Overall, our study suggests that the use of multi-colored traps can improve monitoring programs for longhorn beetles, supporting both faunistic surveys and early detection efforts targeting non-native species.

1. Introduction

Longhorn beetles (Coleoptera: Cerambycidae) are one of the most diverse families of beetles worldwide, including over 35,000 species (Švácha and Lawrence, 2014). With very few exceptions, larvae feed on the living, stressed, or dead tissues of woody and herbaceous plants, and adults mostly feed on flowers, twigs and leaves, or do not feed at all (Hanks, 1999). Together with other saproxylic taxa, longhorn beetles play a key role in forest ecosystems by degrading and recycling dead wood, re-shaping the forest structure, and creating micro-habitats for other organisms (Buse et al., 2008; Casula et al., 2021). Several longhorn beetle species are of special interest for biological studies because of their importance as umbrella species (Foit et al., 2016), their endangered status (Campanaro et al., 2017; Redolfi De Zan et al., 2017), or

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their usefulness as ecological indicators of habitat suitability for other saproxylic taxa (Karpiński et al., 2021). Some members of this family are also among the most economically significant pests in forest environments, as they can kill trees via mechanical damage to the trunk or by vectoring pathogens (Haack, 2017; Wang, 2017). Their importance as pests also stems from their high invasive potential, as they can be easily transported between continents on or within live plants, wood, and wood-packaging material for trade (Eyre and Haack, 2017).

Baited traps represent one of the most common tools for detecting and monitoring both native and non-native longhorn beetle species (Brockerhoff et al., 2006, 2023; Rassati et al., 2015a,b; Eyre and Haack, 2017). Baited trap efficacy has been greatly enhanced in recent decades due to advances in longhorn beetle chemical ecology across continents. Previous studies have assessed and tested the attractive effects of sex-aggregation pheromones for hundreds of longhorn beetle species (Allison et al., 2004; Hanks and Millar, 2016; Millar and Hanks, 2017; Millar et al., 2019). Following these results, more recent studies have developed and used multi-lure blends combining pheromones and host volatiles as generic tools to attract several species simultaneously (Fan et al., 2019; Rassati et al., 2019; Rice et al., 2020, 2025; Roques et al., 2023; Santoiemma et al., 2024a, 2025). However, such blends have limited efficacy for some cerambycid subfamilies (e.g., Lepturinae) that have few identified pheromones (but see Ray et al., 2011, 2012, 2014). So, these taxa may not be attracted to commonly employed blends (Roques et al., 2023).

An increasing number of studies have started to highlight the importance of trap color in determining a trap's attractiveness to certain species (Cavaletto et al., 2021; Jaworski et al., 2022; Sukovata et al., 2022; Besana et al., 2025; Puker et al., 2025; Sweeney et al., 2025), as partially summarized in Dodds et al. (2024). Whereas black traps resembling the silhouette and typical dark color of host trees are preferred over traps of other colors by some longhorn beetle species (de Groot and Nott, 2001; Campbell and Borden, 2009; Skvarla and Dowling, 2017; Kerr et al., 2017; Cavaletto et al., 2021; Miller, 2025), they were shown to be less effective for other species. Flower-visitors in the subfamily Lepturinae and Cerambycinae, for example, showed preferences for typical flower colors such as blue, white, or yellow (Imrei et al., 2014; Toshova et al., 2016; Cavaletto et al., 2021; Besana et al., 2025). Similarly, some longhorn beetle species that display aposematic color patterns are more attracted by traps of a similar color as their elytral stripes (e.g., yellow) than by black traps (Besana et al., 2025). This evidence suggests that monitoring or surveillance programs targeting longhorn beetles should not rely on a single trap color but should instead incorporate the use of multiple traps of different colors at the same location. However, this strategy clashes with practical considerations related to the costs and effort that would arise from having to use additional traps. Combining multiple colors on the same trap might help to overcome this issue.

Here, we present a trapping experiment carried out at seven sites, located in five countries across Europe and North America, where we compared the species richness and abundance of longhorn beetles captured in traps characterized by panels of a single color (i.e., black, red, white, or yellow) with those characterized by panels of multiple colors (i.e., all four colors combined). The effectiveness of these different traps was evaluated at three different taxonomic levels: whole family, subfamily, and species level. This approach was adopted with the primary objective of advising practitioners on whether multi-colored traps can be applied irrespective of the targeted taxon or should be restricted to specific taxa.

2. Materials and methods

2.1. Study sites and experimental scheme

The same trapping experiment was conducted in 2024 at seven sites on two continents: Europe (i.e., Poland, France and Italy – Sicily and Veneto) and North America (i.e., USA – Ohio and Massachusetts, and Canada – New Brunswick) (Table S1). At each site, five different trap types were replicated 5–8 times in a complete randomized block design (Table S1). At most sites, most blocks were spaced 100 m to a few kilometers apart. In France, in an effort to sample a greater diversity of longhorn beetle species, blocks were located a few hundred kilometers apart in different parts of the country. A distance of about 10 m was kept between traps within the same block. Traps were hung between 4 and 12 m above the ground to collect both species that live in the tree canopy and species that fly closer to the ground (Sheehan et al., 2019). At each site, traps were rotated at each trap check to eliminate a possible position effect, so that each color occupied every possible position within each block over the course of the experiment. All longhorn beetles were identified to species level by observing specific morphological traits using keys (e.g., Bense, 1995; Lingafelter, 2007; Wallin et al., 2009). Voucher specimens were deposited at the Entomology Lab, Department of Agronomy, Food, Natural Resources, Animals and Environment (DAFNAE), University of Padua, Italy; Unité de Recherches de Zoologie Forestière, INRAE, Orléans, France; Atlantic Forestry Centre, Fredericton, Canada; Pennsylvania Department of Agriculture, Harrisburg, Pennsylvania; and Xavier University, Cincinnati, Ohio.

2.2. Trap type

At each site, we used intercept-panel traps (WitaPrall cross-vane panel trap, Witasek, Austria) which were customized by replacing the standard black panels either with 30 × 80 cm single colored, i.e., black, red, white, or yellow, polypropylene panels (Eurmoma, Rome, Italy), or with hand-made multi-colored panels made by gluing smaller pieces (15 × 40 cm) of the four colors to a black panel (Fig. 1). Consequently, when viewing the visible surface of the trap created by the intersection of the two panels, an insect would perceive all four colors simultaneously. Although following these procedures resulted in traps that were to some extent all multi-colored (Fig. 1), we chose to modify only the color of the two intersecting panels, while keeping the upper cap, bottom funnel, and collector cup in their original color. This decision was made to ensure that the traps could eventually be produced and commercialized on a large scale. The only practical way to achieve this is to use the most commonly available black panel traps and replace the black panels with panels of different colors. While it is theoretically possible to also manufacture colored or multi-colored upper caps and bottom funnels, doing so would considerably increase production costs due to the complex shapes of these components. Despite all traps having black upper caps and bottom funnels as well as white collector cups, for

Fig. 1. Picture of the multi-colored and single-colored traps employed in this study.

simplicity, traps with multi-colored, black, red, white, and yellow panels are hereafter referred to as "multi-colored", "black", "red", "white", and "yellow" traps, respectively. Reflectance spectra of the four trap colors were measured on small pieces of the polypropylene panels (square with side length 10 μm) using a microspectrophotometer (Vukusic and Stavenga, 2009; Sosa Espinosa et al., 2024) (Fig. S1). The four colors that we used in this study were selected based on the results obtained in previous studies testing the effect of different trap colors on longhorn beetles. Black and red were found to be attractive for a number of species in the subfamily Cerambycinae, Lamiinae, and Spondylidinae (Kerr et al., 2017; Skvarla and Dowling, 2017; Cavaletto et al., 2021), whereas white and yellow are known to be attractive for a number of species in the subfamilies Cerambycinae and Lepturinae (Imrei et al., 2014; Toshova et al., 2016; Cavaletto et al., 2021; Westerberg et al., 2021; Besana et al., 2025). All panels were coated with a 10 % Fluon solution (Insect-A-Stop, Springwood, Queensland, Australia) diluted in water. Fluon was used to improve trapping efficacy by making the surface more slippery, without affecting the reflectance spectrum (Graham and Poland, 2012; Allison et al., 2016; Fig. S1). The reflectance spectra (Fig S1) show that the Fluon coating does not affect the modulation of the reflected light, i.e. the perceived color (van der Kooi et al., 2016). A 50 % solution of propylene glycol was used to preserve captured insects at all sites but France. In France, a section of mesh impregnated with α-cypermethrin insecticide (Storanet, BASF Pflanzenschutz Deutschland, Germany) was placed inside the collector cups, with the cups' bottoms replaced with a wire mesh to allow drainage and to keep specimens dry. Traps were checked weekly (in Ohio), or every three weeks (in all other sites). Start and end dates of the experiment for each site are provided in Table S1.

2.3. Attractive lures

In Canada and Europe, traps were baited with a blend (hereafter referred to as "blend 1") containing the primary pheromone components of species in the subfamily Cerambycinae, Lamiinae, Prioninae and Spondylidinae. The blend (release rate at 20°C estimated as 0.0263 ± 0.002 g/d, Fan et al., 2019) included: (i) fuscumol (mass: 50 mg); (ii) fuscumol acetate (50 mg); (iii) geranyl acetone (25 mg); (iv) racemic 3-hydroxyhexan-2-one (50 mg); (v) prionic acid (1 mg); (vi) 2-methylbutan-1-ol (50 mg); (vii) anti-2,3-hexanediol (50 mg); and (viii) monochamol (50 mg), dissolved in isopropanol as a carrier to a total volume of 1 ml per lure. All these compounds were purchased from ChemTica Internacional, S.A. (Heredia, Costa Rica). Dispensers consisted of a cotton dental wick placed into a ziplock polyethylene sachet (Minigrip, 4 cm × 6 cm × 60 μm; Dutscher, Brumath, France) and dosed with 1 ml of the blend solution. The efficacy of this and similar blends were shown in previous studies carried out in various ecosystems and countries (e.g., Hanks et al., 2012; Fan et al., 2019; Hoch et al., 2020; Millar et al., 2021; Roques et al., 2023; Santoiemma et al., 2024a, 2025). The blend was also complemented with UHR (ultra-high release rate) ethanol (100 ml dose, 96 % purity, release rate 2 g/day at 20°C; Econex, Spain), as it is known to increase the attractive effect of cerambycid pheromones for several species (e.g., Allison et al., 2012; Collignon et al., 2016; Miller et al., 2017).

In USA (Ohio and Massachusetts), the attractant lure blend (hereafter referred to as "blend 2") consisted of individual component sachets loaded by the manufacturers and included: i) anti-2,3-hexanediol (medium release), ii) 3-hydroxyhexan-2-hexanone (medium release), iii) fuscumol acetate (medium release), purchased from ChemTica International S.A. (Heredia, Costa Rica); iv) monochamol; v) trichoferone, purchased from AlphaScents (Canby, Oregon, USA) (medium release); vi) S-fuscumol (50 mg), purchased from Sylvar Technologies Inc (Fredericton, New Brunswick, Canada) (medium release). The blend was also complemented with UHR ethanol (0.5–0.8 g/day release rate, AlphaScents). UHR ethanol was replaced after about two months according to its expected field life, whereas the blend was replaced every three weeks.

2.4. Statistical analysis

Generalized linear mixed models were used for all the analyses. The response variables were species richness (total number of species) and abundance (number of individuals across all species) of the family Cerambycidae, species richness and abundance of the subfamilies Cerambycinae, Lamiinae, and Lepturinae, and the abundance of each individual species. For both family and subfamily levels, separate models were built for each site. In contrast, models for individual species were generally built across all sites where the species was collected, except when the species was found at only a single site. For models built across multiple sites, we consistently maintained a separation between sites where blend 1 was used and sites where blend 2 was used. Data collected from each trap at each sampling round (i.e., the sampling unit) were pooled over the entire sampling period into a single data point per trap, and then treated as a distinct statistical unit for analysis. For models targeting species richness or abundance at family or subfamily level, only sites with ≥ 3 species and ≥ 50 individuals were included. For models targeting single species, only species with ≥ 50 individuals were included. These thresholds were used to ensure statistical robustness. Species richness was divided by the number of exposure days (from setup to removal of each trap) and modeled using a Gaussian distribution. Abundance was modeled using a negative binomial distribution with a ln link function, including the number of exposure days as a ln-transformed offset. For all models, the categorical explanatory variable was the color of the trap panels (five levels: multi-color, black, red, white, and yellow). The multi-colored trap was used as a baseline for comparison with the other traps. Block identity was included as a random factor in models based on data from single sites. Site and block identity within each site were included as nested random factors in single-species models based on data from multiple sites. Blocks in which zero catches were recorded in all traps over the entire sampling period were omitted from the analysis. All the analyses were carried out in R (R Core Team, 2025). Models were fitted using the 'glmmTMB' package (Brooks et al., 2017). Models were checked for overdispersion and residual distribution using the 'DHARMa' package (Hartig, 2024). Barplots and circular bar plots were plotted using the package 'ggplot2' (Wickham, 2016), with bar height proportional to the average number of individuals caught in each trap across the entire season.

3. Results

3.1. Longhorn beetle diversity and abundance

A total of 15,627 individuals from 194 species were collected (Table S2). The most species-rich subfamily was Cerambycinae (76 species), followed by Lepturinae (54 species), Lamiinae (53 species), Spondylidinae (8 species), Prioninae (2 species), and Necydalinae (1 species). Abundance showed a similar trend, with the highest number of individuals belonging to Cerambycinae (11,157 individuals), followed by Lamiinae (2709 individuals), Lepturinae (884 individuals), Prioninae (794 individuals), Spondylidinae (79 individuals), and Necydalinae (4 individuals).

In all four European sites, *Phymatodes testaceus* (Linnaeus) was the most abundant species (3591 individuals in total), with *Phymatodes alni* (Linnaeus) (898 individuals), *Prionus coriarius* (Linnaeus) (787

individuals), and the exotic *Xylotrechus stebbingi* Gahan (578 individuals) constituting a considerable proportion of the catches. By contrast, in North America the captures were dominated by different species for each location: in Massachusetts (USA) the most abundant species was *Phymatodes varius* (Fabricius) (776 individuals), in Ohio (USA) *Neoclytus mucronatus* (Fabricius) (464 individuals), and in Canada *Sarosesthes fulminans* (Fabricius) (296 individuals).

3.2. Efficacy of multi-colored traps vs. single-colored traps at family level

Species richness and abundance in different trap colors showed a consistent response at family level (Table 1). Multi-colored traps collected significantly more species than at least one of the other tested colors at four of the seven sites. Specifically, a higher number of species was captured in multi-colored traps compared to black traps in Veneto (Italy) (Fig. 2D), to both black and red traps in Canada (Fig. 2A), to black, red, and yellow traps in Massachusetts (USA) (Fig. 2E), and to yellow traps in Sicily (Italy) (Fig. 2C). At two sites (i.e., Veneto (Italy) and Poland), multi-colored traps were outperformed by white traps (Fig. 2D, G), whereas no significant differences between the tested traps were observed in France and Ohio (USA) (Fig. 2B, F).

For abundance, multi-colored traps collected significantly more individuals than yellow traps at five of the seven sites, namely Canada (Fig. 3A), Veneto and Sicily (Italy) (Fig. 3C, D), Massachusetts (Fig. 3E) and Poland (Fig. 3G). Multi-colored traps also collected significantly more individuals than black traps in Massachusetts, Ohio (Fig. 3F), and Poland, and more than red traps in Massachusetts. No significant differences among trap colors were observed in France (Fig. 3B).

Table 1
Analysis of deviance table from the generalized linear mixed models testing the effect of different trap panel colors on species richness and abundance of the family Cerambycidae, and the subfamilies Cerambycinae, Lamiinae, and Lepturinae (at each site). Only sites represented by at least 3 species and 50 individuals were analyzed and included in the table. Type II Wald chi-square tests with 4 degrees of freedom (χ^2_4) and *p*-values (bolded if $P < 0.05$) are provided for all models.

	Species richness		Abundance	
	χ^2_4	*p*-value	χ^2_4	*p*-value
Cerambycidae				
Canada	40.082	**< 0.001**	9.316	0.054
France	8.415	0.078	4.006	0.405
Italy (Sicily)	14.194	**0.007**	14.522	**0.006**
Italy (Veneto)	28.131	**< 0.001**	10.914	**0.028**
USA (Massachusetts)	18.349	**0.001**	24.393	**< 0.001**
USA (Ohio)	6.516	0.164	5.291	0.259
Poland	16.017	**0.003**	22.041	**< 0.001**
Cerambycinae				
Canada	4.987	0.289	7.112	0.130
France	4.903	0.297	5.458	0.244
Italy (Sicily)	15.556	**0.004**	20.131	**< 0.001**
Italy (Veneto)	4.396	0.355	8.117	0.087
USA (Massachusetts)	17.200	**0.002**	15.502	**0.004**
USA (Ohio)	5.214	0.266	6.878	0.143
Poland	11.437	**0.022**	29.544	**< 0.001**
Lamiinae				
Canada	3.470	0.482	5.460	0.243
France	1.979	0.740	5.652	0.227
Italy (Veneto)	3.904	0.419	11.637	**0.020**
USA (Massachusetts)	9.679	**0.046**	11.689	**0.020**
USA (Ohio)	5.617	0.230	2.938	0.568
Poland	3.394	0.494	8.143	0.086
Lepturinae				
France	19.287	**< 0.001**	36.959	**< 0.001**
Italy (Veneto)	65.575	**< 0.001**	114.730	**< 0.001**
USA (Massachusetts)	18.122	**0.001**	23.987	**< 0.001**
Poland	69.743	**< 0.001**	30.383	**< 0.001**

3.3. Efficacy of multi-colored traps vs. single-colored traps at subfamily level

Species richness and abundance in different trap colors showed a consistent response for each subfamily (Table 1). For Cerambycinae, multi-colored traps collected an equal or higher number of species than single-colored traps at all sites except in Massachusetts, where white traps outperformed multi-colored traps (Fig. 4E). In France, Italy (Veneto), and Ohio, no difference was found among the multi-colored traps and single-colored traps (Fig. 4 B, D, F), whereas in Canada, Italy (Sicily), and Poland, multi-colored traps captured significantly more species than black (Fig. 4A), yellow (Fig. 4C), and black, red and yellow traps (Fig. 4G), respectively. A similar trend was observed for abundance, with multi-colored traps capturing either an equal number of Cerambycinae individuals as the other trap colors (in Canada and France) (Fig. 5 A, B) or more individuals than yellow (Fig. 5D), black and yellow (Fig. 5F, H), and black, red, and yellow traps (Fig. 5E). The only exception was in Sicily (Italy), where the red traps captured more Cerambycinae individuals than the multi-colored ones (Fig. 5C).

For Lamiinae, multi-colored traps collected a number of species comparable to the other trap colors at all sites but one. Only in Massachusetts multi-colored traps performed significantly better than yellow traps (Fig. 4K). For abundance, the number of individuals collected was comparable between multi-colored and single-colored traps in Canada and Ohio (Fig. 5H, L). However, multi-colored traps captured more individuals than black, red, and yellow traps in Italy (Veneto) (Fig. 5J) and more than yellow traps in Massachusetts (Fig. 5K). In contrast, in France, abundance was higher in red traps than in the multi-colored traps (Fig. 5I).

For Lepturinae, species richness was significantly higher in white traps than in multi-colored traps at two of the four sites (Veneto (Italy) and Poland) (Fig. 4O, Q). However, multi-colored traps generally outperformed black and/or red traps in most cases (Fig. 4N–P). Abundance was also significantly higher in white traps than in multi-colored traps in France, Veneto (Italy), and Poland (Fig. 5N, O, Q). Moreover, in Veneto (Italy), multi-colored traps captured significantly more individuals than black and red traps, but fewer individuals than yellow traps (Fig. 5O); in Massachusetts, multi-colored traps outperformed black, red and yellow traps (Fig. 5P).

No analysis was made on the remaining subfamilies, as they were either represented by only one or two species (*Necydalis major* Linnaeus for Necydalinae; *Aegosoma scabricorne* (Scopoli) and *Prionus coriarius* (Linnaeus) for Prioninae), or more than 50 % of individuals belonged to just two species (*Asemum striatium* (Linnaeus) and *Tetropium schwarzianum* (Casey) for Spondylidinae).

3.4. Efficacy of multi-colored traps vs. single-colored traps at species level

Out of 195 species collected, 39 had at least 50 individuals and were thus analyzed (Table 2). Five of them had more than 50 individuals across both Canadian/European sites, where the blend 1 was used, and USA sites, where blend 2 was used., and were thus analyzed separately (Table 2). For two species (i.e., *Cyrtophorus verrucosus* (Olivier) and *Molorchus minor* (Linnaeus)), multi-colored traps caught significantly more individuals than all single-colored traps (Fig. 6A, B). In contrast, for five species, single-colored traps captured significantly more individuals than multi-colored traps. The most effective single-colored trap varied by species: *Anaglyptus gibbosus* (Fabricius) preferred yellow traps (Fig. 6C); *Pachytodes erraticus* (Dalman) and *Rutpela maculata* (Poda von Neuhaus) preferred white traps (Fig. 6F, G); *Monochamus sartor* (Fabricius) preferred black traps (Fig. 6D), while *M. scutellatus* (Say) in Canada preferred red traps (Fig. 6E). For 13 species, one or more single-colored traps captured significantly fewer individuals than multi-colored traps (Fig. 6H–T). The specific color(s) that underperformed varied by species. Finally, no significant difference was detected between multi-colored traps and single-colored traps for the remaining 24

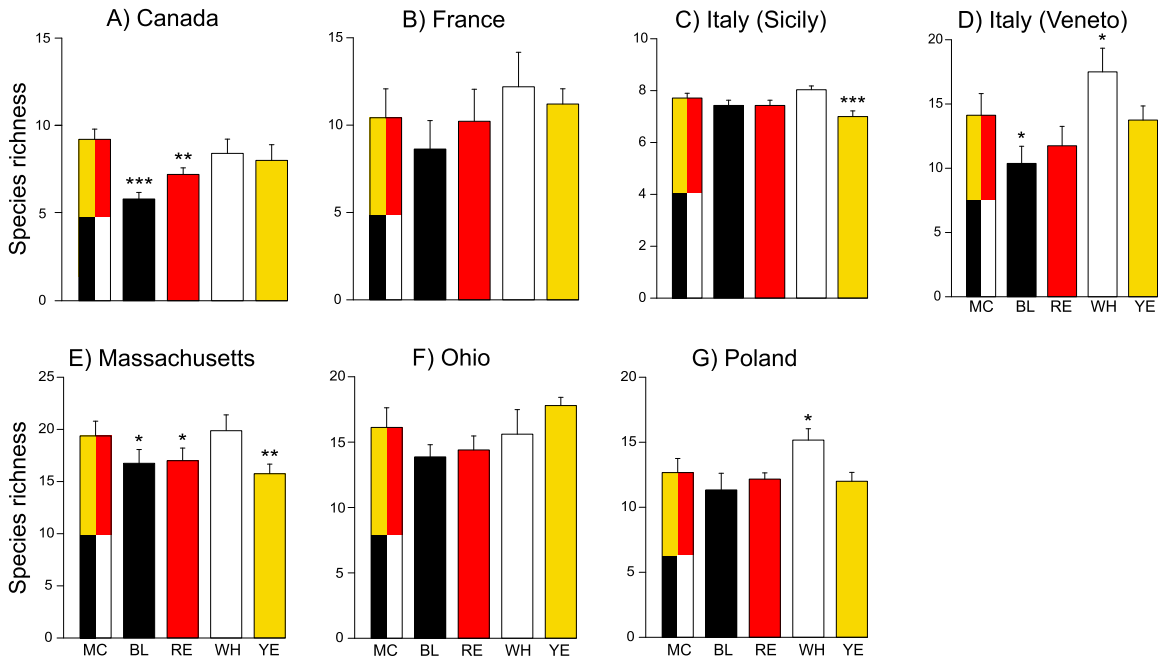

Fig. 2. Mean number of longhorn beetle species (i.e., species richness) collected in multi-colored vs. single-colored traps at the different study sites (A–G). MC = multi-color; BL = black; RE = red; WH = white; YE = yellow. Error bars indicate the positive standard error. Within each panel, single-colored traps that attracted a significantly different mean number of species than multi-colored traps are indicated with asterisk/s depending on the *p*-value: *** = $P < 0.001$; ** = $0.001 < P < 0.01$; * = $0.01 < P < 0.05$.

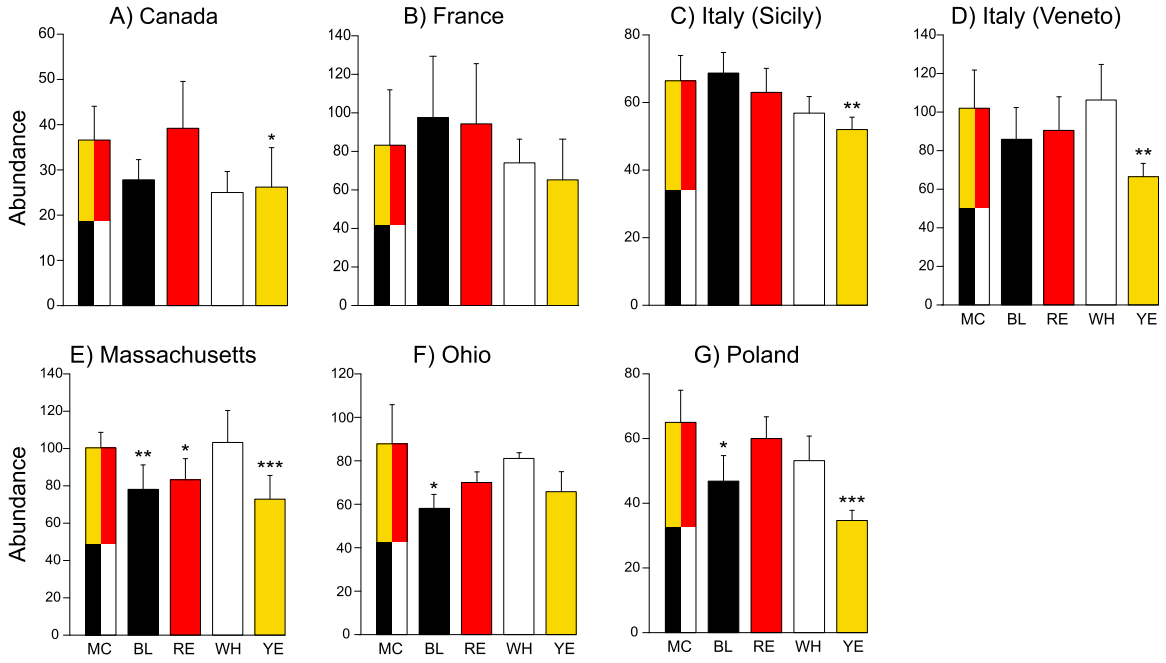

Fig. 3. Mean number of longhorn beetle species individuals (i.e., abundance) collected in multi-colored vs. single-colored traps at the different study sites (A–G). MC = multi-color; BL = black; RE = red; WH = white; YE = yellow. Error bars indicate the positive standard error. Within each panel, single-colored traps that attracted a significantly different mean number of individuals than multi-colored traps are indicated with asterisk/s depending on the *p*-value: *** = $P < 0.001$; ** = $0.001 < P < 0.01$; * = $0.01 < P < 0.05$.

species (Fig. 7A–X).

4. Discussion

There are several advantages to using multi-colored traps, most notably in terms of abundance and species richness across the entire Cerambycidae family. Multi-colored traps collected significantly more individuals compared to one or more of the single-colored traps at most trapping sites. Multi-colored traps also outperformed black, red, and yellow traps at multiple sites in terms of species richness, although they caught fewer species than white traps at two sites. Increased catches resulting from the use of multi-colored traps have been reported in

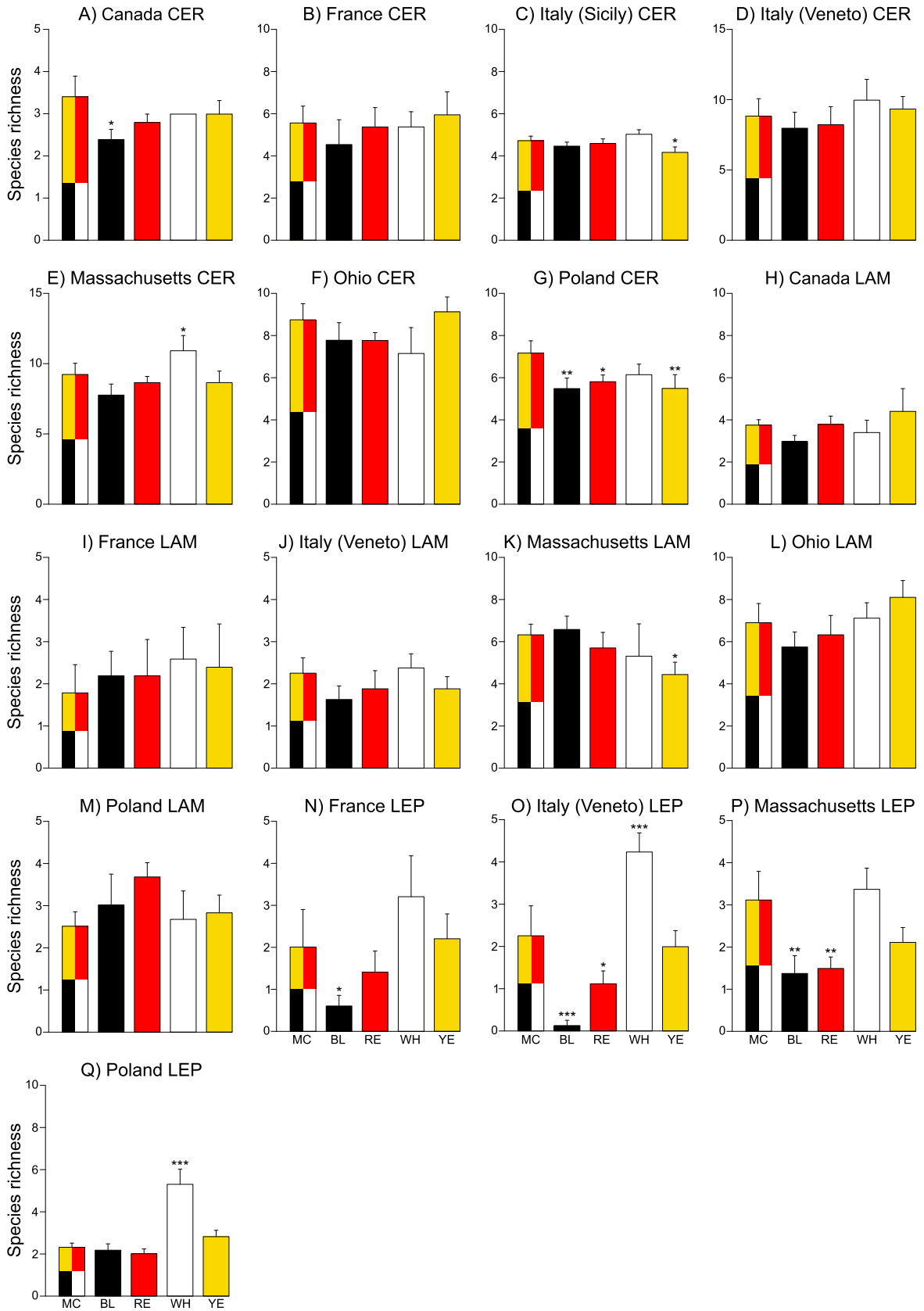

Fig. 4. Mean number of longhorn beetle species (i.e., species richness) collected in multi-colored vs. single-colored traps at the different study sites for Cerambycinae (A–G), Lamiinae (H–M), and Lepturinae (N–Q). MC = multi-color; BL = black; RE = red; WH = white; YE = yellow. Error bars indicate the positive standard error. Within each panel, single-colored traps that attracted a significantly different mean number of species than multi-colored traps are indicated with asterisk/s depending on the *p*-value: *** = $P < 0.001$; ** = $0.001 < P < 0.01$; * = $0.01 < P < 0.05$.

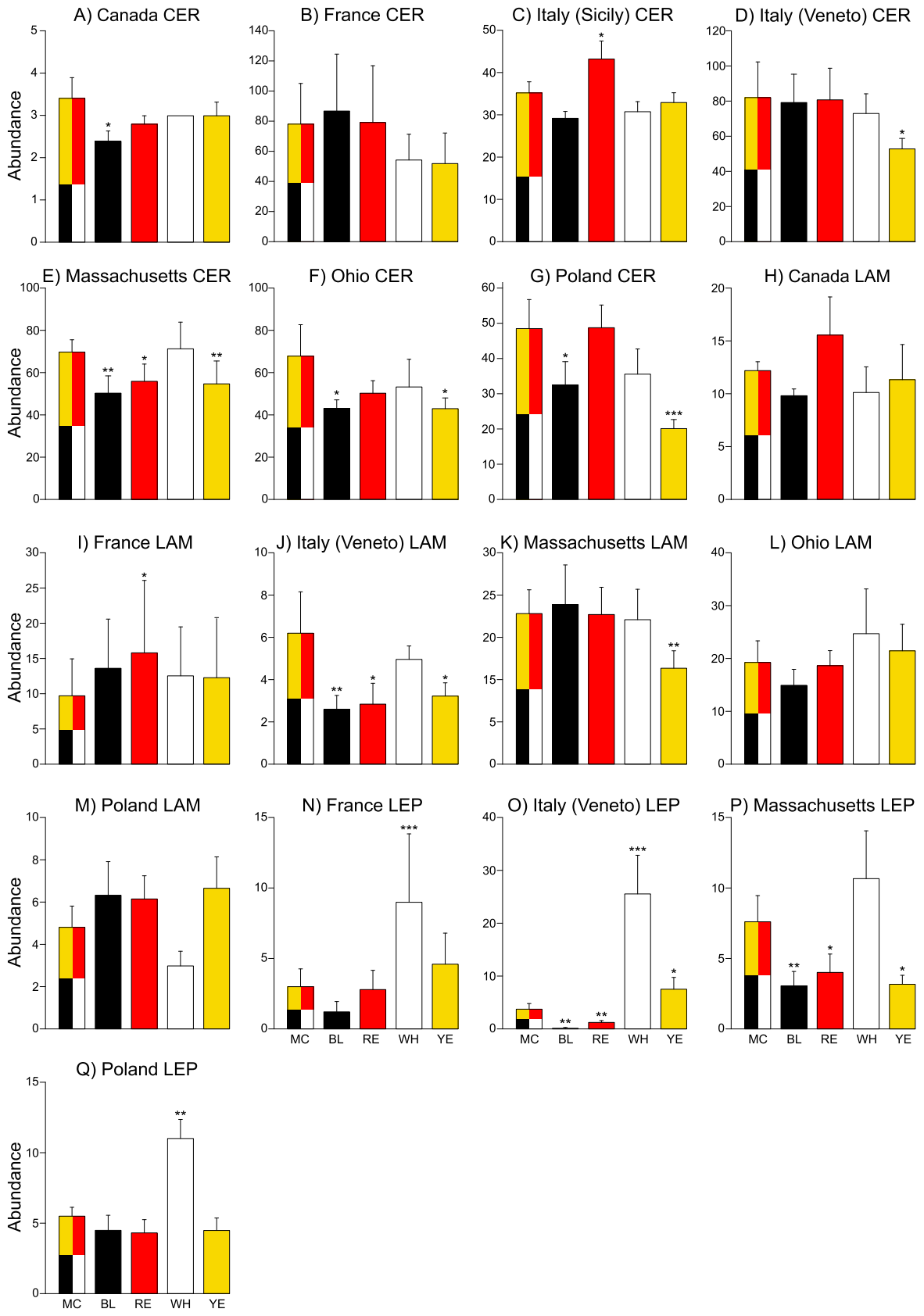

Fig. 5. Mean number of longhorn beetle individuals (i.e., abundance) collected in multi-colored traps vs. single-colored traps at the different study sites for Cerambycinae (A–G), Lamiinae (H–M), and Lepturinae (N–Q). MC = multi-color; BL = black; RE = red; WH = white; YE = yellow. Error bars indicate the positive standard error. Within each panel, single-colored traps that attracted a significantly different mean number of individuals than multi-colored traps are indicated with asterisk/s depending on the *p*-value: *** = $P < 0.001$; ** = $0.001 < P < 0.01$; * = $0.01 < P < 0.05$.

Table 2
Mean (± standard error) number of individuals collected per trap over the entire sampling period using multi-colored vs. single-colored traps. Only species represented by at least 50 individuals across Canadian/European sites (which used blend 1) or USA sites (which used blend 2) were analyzed and included in the table. Bold values indicate a significant difference from the multi-colored trap ($P < 0.05$); values with an asterisk were greater than those for the multi-colored trap. MC = multi-colored; BL = black; RE = red; WH = white; YE = yellow. Species within each subfamily are listed in alphabetical order.

	MC	BL	RE	WH	YE
Canada and Europe (blend 1)					
Cerambycinae					
Anaglyptus gibbosus (Fabricius)	2.50 ± 0.62	2.60 ± 0.92	3.50 ± 0.85	3.90 ± 1.26	**4.70 ± 1.27***
Cerambyx scopolii Fuessly	1.00 ± 0.42	1.70 ± 0.68	0.90 ± 0.41	1.60 ± 0.99	1.80 ± 0.42
Gracilia minuta (Fabricius)	8.75 ± 6.37	4.50 ± 2.53	**1.50 ± 0.96**	**2.25 ± 1.44**	**1.50 ± 0.87**
Molorchus minor (Linnaeus)	5.67 ± 1.50	**0.83 ± 0.48**	**3.50 ± 0.96**	**3.50 ± 1.26**	**2.17 ± 0.54**
Phymatodes alni (Linnaeus)	7.79 ± 1.66	8.08 ± 2.89	7.71 ± 1.63	7.13 ± 1.75	6.71 ± 1.74
Phymatodes testaceus (Linnaeus)	31.27 ± 6.51	31.77 ± 6.48	34.23 ± 6.44	23.73 ± 3.95	**17.12 ± 3.75**
Plagionotus detritus (Linnaeus)	1.79 ± 0.43	1.43 ± 0.43	1.36 ± 0.39	1.50 ± 0.37	1.07 ± 0.40
Purpuricenus kaehleri (Linnaeus)	2.00 ± 0.82	2.00 ± 1.29	3.00 ± 1.91	3.83 ± 2.06	4.33 ± 3.16
Pyrrhidium sanguineum (Linnaeus)	7.86 ± 1.78	8.14 ± 3.92	10.00 ± 3.99	**4.64 ± 1.94**	**4.50 ± 1.27**
Sarosesthes fulminans (Fabricius)	12.80 ± 4.51	12.40 ± 3.80	15.40 ± 5.32	8.60 ± 2.84	10.00 ± 4.68
Trichoferus pallidus (Olivier)	5.75 ± 2.06	4.00 ± 1.78	12.75 ± 5.76	3.25 ± 1.65	4.00 ± 2.48
Xylotrechus antilope (Schönherr)	4.00 ± 1.05	**2.53 ± 0.84**	3.47 ± 0.97	5.20 ± 1.71	**2.13 ± 0.58**
Xylotrechus arvicola (Olivier)	4.11 ± 1.43	2.67 ± 0.85	3.33 ± 1.01	2.56 ± 0.56	3.67 ± 1.09
Xylotrechus colonus (Fabricius)	4.20 ± 2.35	4.60 ± 1.17	6.40 ± 3.93	1.40 ± 0.51	2.40 ± 0.93
Xylotrechus stebbingi Gahan	6.63 ± 1.88	5.68 ± 1.67	6.79 ± 1.71	6.26 ± 1.89	5.05 ± 1.41
Lamiinae					
Aegomorphus clavipes (Schrank)	4.04 ± 1.14	2.96 ± 0.71	**1.83 ± 0.35**	**2.39 ± 0.73**	**1.87 ± 0.44**
Astylopsis macula (Say)	2.60 ± 0.98	1.80 ± 0.58	2.60 ± 0.81	1.40 ± 0.75	3.00 ± 1.30
Leiopus nebulosus (Linnaeus)	5.53 ± 1.40	4.32 ± 1.28	**2.47 ± 0.71**	**3.84 ± 1.12**	**2.74 ± 0.81**
Monochamus galloprovincialis (Olivier)	7.25 ± 7.25	9.50 ± 9.50	13.50 ± 13.17	10.00 ± 9.67	11.25 ± 10.92
Monochamus sartor (Fabricius)	1.57 ± 0.87	**3.71 ± 1.81***	1.86 ± 1.22	1.71 ± 1.23	2.00 ± 0.62
Monochamus scutellatus (Say)	6.00 ± 1.58	6.20 ± 1.32	**10.00 ± 2.59***	3.20 ± 2.03	3.60 ± 1.21
Lepturinae					
Pachytodes erraticus (Dalman)	1.25 ± 0.37	**0.00 ± 0.00**	**0.13 ± 0.13**	**14.63 ± 5.69***	**5.25 ± 2.28***
Rhagium mordax (De Geer)	3.57 ± 0.69	2.57 ± 0.78	2.71 ± 0.68	3.00 ± 0.79	**1.29 ± 0.29**
Rutpela maculata (Poda von Neuhaus)	1.08 ± 0.43	**0.00 ± 0.00**	0.42 ± 0.15	**4.08 ± 1.06***	0.75 ± 0.28
Prioninae					
Prionus coriarius (Linnaeus)	9.00 ± 2.29	9.77 ± 2.48	**5.91 ± 1.69**	6.05 ± 1.29	**5.05 ± 0.93**
USA (blend 2)					
Cerambycinae					
Anelaphus pumilus (Newman)	4.20 ± 0.58	2.24 ± 1.00	1.52 ± 0.68	1.34 ± 0.60	3.03 ± 1.36
Cyrtophorus verrucosus (Olivier)	12.67 ± 2.71	**4.67 ± 1.51**	**5.33 ± 1.50**	**7.25 ± 2.26**	**5.42 ± 1.71**
Eburia quadrigeminata (Say)	4.80 ± 1.32	**1.20 ± 0.20**	**0.80 ± 0.37**	4.40 ± 1.33	3.00 ± 1.22
Elaphidion mucronatum (Say)	2.36 ± 0.89	2.09 ± 0.84	2.27 ± 0.78	2.73 ± 1.24	2.00 ± 0.52
Neoclytus acuminatus (Fabricius)	2.57 ± 1.11	3.43 ± 1.36	2.43 ± 0.69	2.14 ± 0.67	2.29 ± 0.89
Neoclytus mucronatus (Fabricius)	12.38 ± 3.29	9.54 ± 2.21	10.54 ± 2.99	13.15 ± 3.78	7.62 ± 1.62
Phymatodes aereus (Newman)	1.25 ± 0.41	0.38 ± 0.26	1.63 ± 0.73	3.13 ± 0.83	2.00 ± 0.98
Phymatodes amoenus (Say)	1.80 ± 0.94	2.50 ± 1.67	1.80 ± 1.13	1.70 ± 0.65	1.00 ± 0.37
Phymatodes testaceus (Linnaeus)	1.63 ± 0.46	1.88 ± 0.69	2.75 ± 1.22	1.88 ± 0.58	1.63 ± 0.42
Phymatodes varius (Fabricius)	19.63 ± 2.24	13.25 ± 2.05	20.50 ± 4.02	27.00 ± 7.28	16.63 ± 1.92
Sarosesthes fulminans (Fabricius)	9.22 ± 2.28	8.11 ± 1.87	8.78 ± 2.30	9.33 ± 2.81	9.56 ± 3.18
Xylotrechus colonus (Fabricius)	14.00 ± 4.59	9.54 ± 1.61	**9.46 ± 1.96**	**6.85 ± 2.03**	**8.62 ± 1.72**
Lamiinae					
Aegomorphus modestus (Gyllenhal)	4.69 ± 0.86	5.92 ± 1.43	5.62 ± 1.28	5.31 ± 1.07	4.77 ± 0.93
Astylopsis macula (Say)	1.77 ± 0.47	1.54 ± 0.48	2.23 ± 0.64	1.92 ± 0.79	1.77 ± 0.58
Graphisurus fasciatus (DeGeer)	4.38 ± 0.90	5.08 ± 1.13	6.15 ± 1.25	6.77 ± 1.66	**2.54 ± 0.90**
Lepturges angulatus (LeConte)	4.17 ± 1.30	**0.33 ± 0.33**	1.83 ± 0.60	5.33 ± 4.14	3.17 ± 1.01
Monochamus scutellatus (Say)	5.63 ± 2.25	3.13 ± 0.67	3.00 ± 0.78	**2.88 ± 0.85**	**2.50 ± 0.76**
Sternidius alpha (Say)	1.09 ± 0.49	1.27 ± 0.56	0.45 ± 0.16	1.09 ± 0.28	0.73 ± 0.33
Lepturinae					
Gaurotes cyanipennis (Say)	2.60 ± 0.95	2.00 ± 0.88	2.70 ± 1.09	5.30 ± 2.71	1.50 ± 0.50

earlier studies across various insect taxa (e.g., Mitchell et al., 1989; Roubos and Liburd, 2008; Francese et al., 2011). This effect may be due to the combination of multiple visual stimuli that are attractive to the target species for different ecological reasons. In response to chromatic stimuli, insect species may display one of three behaviors: attraction, avoidance, or indifference (Acharya et al., 2022; Arnold et al., 2016; Hempel de Ibarra et al., 2015; Sukovata et al., 2022). By incorporating colors that attract certain taxa while remaining neutral to others, multi-colored traps can target a broader suite of species than single-colored traps composed of panels of a single color. Additionally, individuals that respond indifferently, or are mildly repelled by a particular color, may still be captured by other attractive colors or olfactory cues. This combined effect may contribute to the higher overall abundance and species richness observed in multi-colored traps.

The effectiveness of multi-colored traps varied across subfamilies. The benefit of using panel traps with a combination of different colors over panels of a single color was particularly evident for Cerambycinae, for which multi-colored traps captured more species and more individuals than black, red and/or yellow traps at several sites. The subfamily Cerambycinae comprises species with diverse life histories and diel activity patterns (Monné et al., 2017; Rassati et al., 2021), and some of its members use color vision for both foraging and mate location (Wang, 2002; Imrei et al., 2014; Johnson et al., 2019; Besana et al., 2025). Moreover, species in the subfamily Cerambycinae often exhibit species-specific, sometimes pronounced, color preferences (Cavaletto et al., 2021; Besana et al., 2025). Therefore, incorporating multiple colors into a single trap may increase the probability that different species will encounter their preferred color, enhancing overall trap

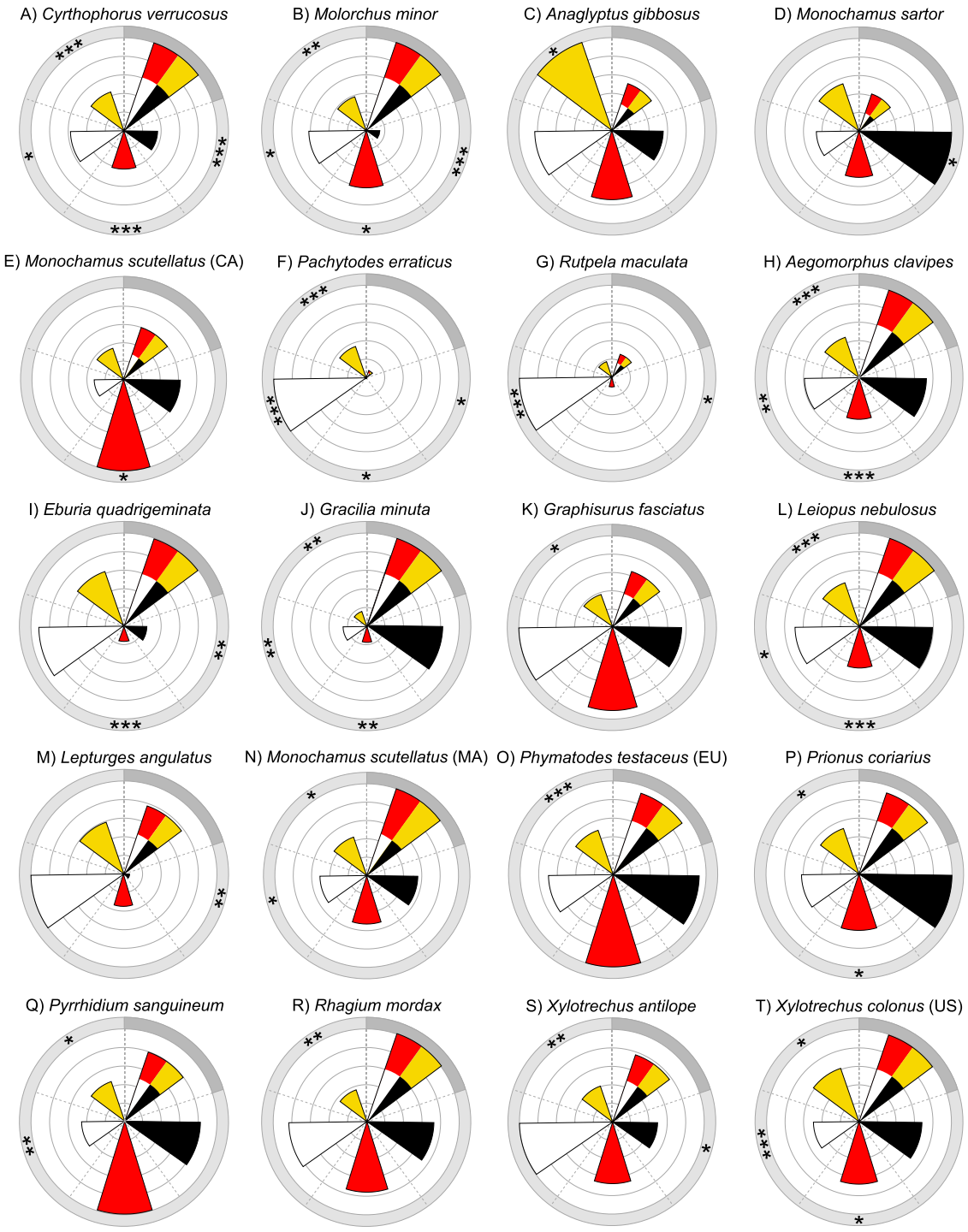

Fig. 6. Number of individuals collected in multi-colored vs. single-colored traps for longhorn beetle species for which: i) multi-colored traps captured significantly more individuals than all single-colored traps (A, B); ii) at least one single-colored trap captured significantly more individuals than the multi-colored traps (C-G); and iii) one or more single-colored traps captured significantly fewer individuals than the multi-colored traps (H–T). The length of the cone is proportional to the average number of individuals collected across the season. Within each panel, single colors that attracted a significantly different mean number of individuals compared to multi-colored traps are indicated with asterisk/s depending on the *p*-value: *** = $P < 0.001$; ** = $0.001 < P < 0.01$; * = $0.01 < P < 0.05$. Standard errors are reported in Table 2. If a species was found in multiple sites where different blends were used, the corresponding site acronyms are indicated (EU = any of the European sites, CA = Canada, MA = Massachusetts, US = Massachusetts + Ohio).

efficacy. This pattern was less pronounced for Lamiinae, as species richness was equal between multi-colored and single-colored traps in all but one case. Similarly, abundance was significantly higher in multi-colored traps than one or more single-colored traps only in two sites. Many lamiines are crepuscular or nocturnal (Monné et al., 2017), but notable exceptions exist, such as several *Monochamus* spp. (Kim et al., 2021; Sukovata et al., 2023). Although these species are expected to rely primarily on olfactory cues, some beetles in the Lamiinae have been shown to use visual signals in mate recognition (Fukaya et al., 2004, 2005; Lu et al., 2007) and to exhibit preferences for specific colors (Cavaletto et al., 2021; Sukovata et al., 2022). The presence of one of the least attractive colors for lamiines, i.e., yellow, as identified in this and

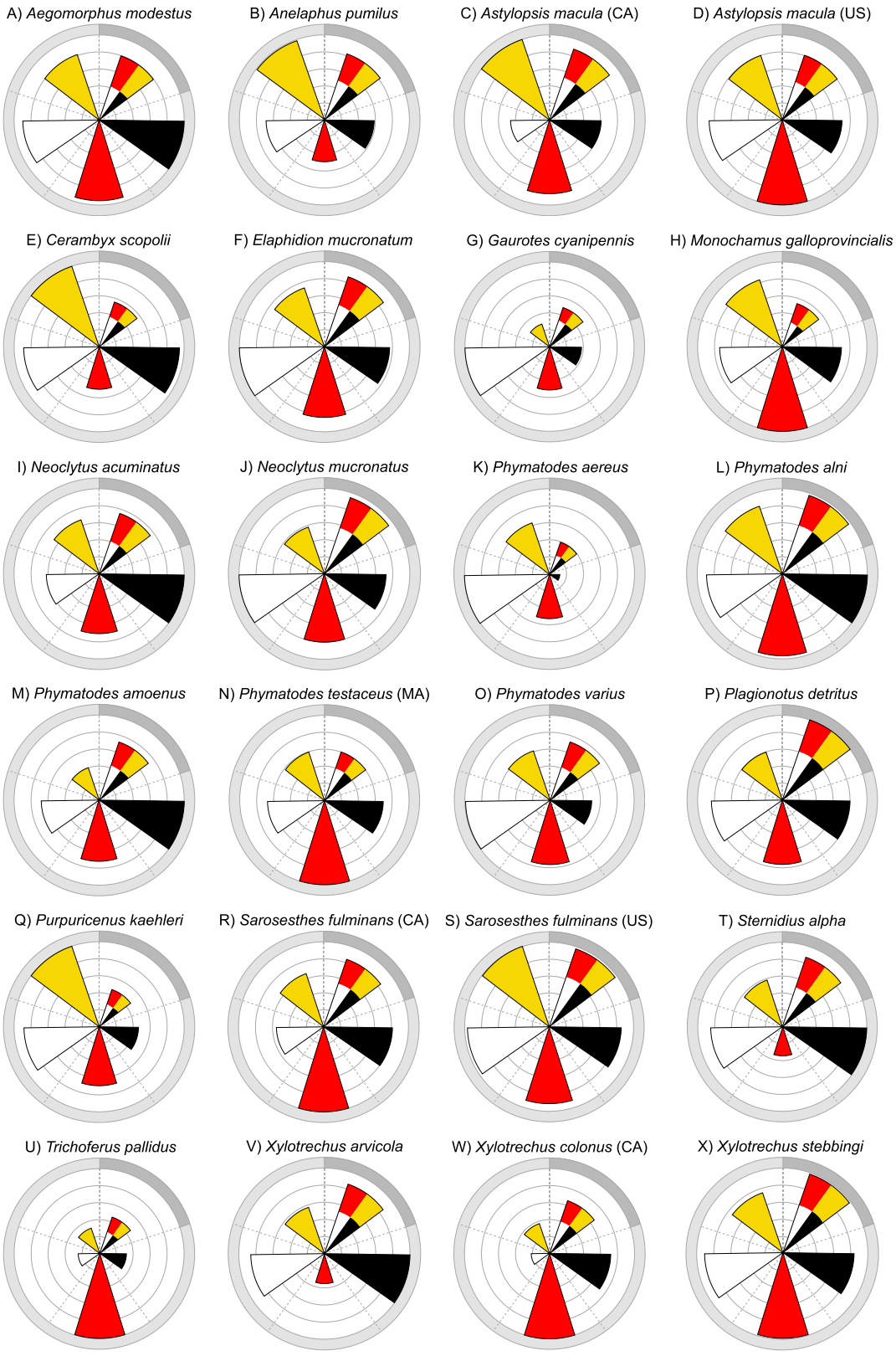

Fig. 7. Number of individuals collected in multi-colored vs. single-colored traps for longhorn beetle species for which multi-colored traps captured a similar number of individuals as all single-colored traps, i.e., no statistically significant difference between multi-colored and single-colored traps (A–X). The length of the cone is proportional to the average number of individuals collected across the season. Standard errors are reported in Table 2. If a species was found in multiple sites where different blends were used, the corresponding site acronyms are indicated (EU = any of the European sites, CA = Canada, MA = Massachusetts, US = Massachusetts + Ohio).

previous studies (e.g., Cavaletto et al., 2021), on multi-colored traps does not appear to reduce their overall attractiveness, further supporting the utility of multi-colored traps even when Lamiinae are the target taxa. Finally, for Lepturinae, multi-colored traps were generally significantly more effective than black or red traps, but significantly less effective than white traps at some sites. To date, a few Lepturinae pheromones have been identified (reviewed in Hanks and Millar, 2016), but none were included in the multi-lure blend used in this study (Fan et al., 2019). Lepturinae males and females typically encounter one another on flowers, where they feed and mate (Monné et al., 2017). As such, their behavior may be greatly influenced by the search for visual cues resembling flowers, such as those provided by yellow and white traps (Toshova et al., 2016; Cavaletto et al., 2021; Besana et al., 2025), and by a general avoidance of colors that deviate from these cues, such as black and red (Cavaletto et al., 2021; Besana et al., 2025). Although white traps in our study may have functioned as supernormal mimics of commonly visited floral hosts (e.g., white Apiaceae and Asteraceae) (Prokopy and Owens, 1983; Arnold et al., 2010), the significantly lower efficacy of multi-colored traps compared to white traps may be explained by two non-mutually exclusive mechanisms. First, the reduced proportion of white surface area on multi-colored traps likely decreases their overall visibility, particularly at greater distances (Giurfa et al., 1996). Second, the inclusion of colors such as black or red may diminish the attractiveness of the white portions, thereby reducing overall trap efficacy.

At the species level, four main behavioral groups can be identified based on each species' response to the tested traps. The first group includes species for which the multi-colored trap captured more individuals than any of the single-colored traps. This pattern could partly be explained by the simultaneous influence of flower-seeking and host-seeking behaviors. The two species in this group (i.e., *C. verrucosus* and *M. minor*) are anthophilous and may be attracted to floral colors for both feeding and mating purposes (Gosling, 1984; McDowell, 2011; Walczak et al., 2014). In the case of females, darker colors resembling tree bark may also serve as cues for oviposition sites. Sex-specific attraction to colors has been documented in longhorn beetles (Sukovata et al., 2022) and other beetle taxa (e.g., Poland et al., 2019); however, this remains speculative in our study, as the sex of individuals was not determined. The second group includes species that preferred one or two single-colored traps over the multi-colored ones. All species in this group are diurnal and, except for the two *Monochamus* spp., are known flower visitors (Sláma, 1998; Walczak et al., 2014; Skabeikis et al., 2016; Kim et al., 2021). *Monochamus sartor* is likely more attracted to the prominent black silhouette of the black traps, which may resemble the bark of its conifer host trees. For *Monochamus scutellatus*, two different responses were observed: in Canada, significantly more individuals were collected in red traps compared to multi-colored ones, whereas in Massachusetts, catches in white and yellow traps were significantly lower than in multi-colored traps. A general preference of *Monochamus* spp. for darker colors is not surprising and it was reported in other *Monochamus* species (de Groot and Nott, 2001; Campbell and Borden, 2009; Huh et al., 2025; Huh and Park, 2025). The differing responses instead may be attributed either to variations in the lure blend used or to specific characteristics of the study sites. The cerambycine *A. gibbosus* and the lepturines *P. erraticus* and *R. maculata* were significantly more attracted to the typical floral colors (i.e., white or yellow), consistent with findings from previous studies (Cavaletto et al., 2021; Besana et al., 2025). As stated above, this result suggests two non-mutually exclusive possibilities: the size of the visual stimulus (i.e., the dominance of a single color) enhances trap attractiveness, and/or the presence of multiple colors diminishes the appeal of the preferred color(s). The third group includes species for which one or more single-colored traps captured fewer individuals than the multi-colored trap. This pattern may be attributed to the low attractiveness, or even repellence, of certain colors to specific species. For example, some species appeared to avoid black and/or red (e.g., *Eburia quadrigeminata* (Say), *Lepturges angulatus* (LeConte)), while others avoided white and/or yellow (e.g., *P. testaceus*, *P. coriarius*, *Pyrrhidium sanguineum* (Linnaeus), and *Rhagium mordax* (De Geer)). General avoidance or low attractiveness of specific colors has also been reported in previous studies (Imrei et al., 2014; Cavaletto et al., 2021; Sukovata et al., 2022; Besana et al., 2025), albeit the underlying mechanisms remain poorly understood. Finally, species in the fourth group did not exhibit any significant difference in capture rates between the multi-colored traps and the single-colored traps (e.g., *Aegomorphus modestus* (Gyllenhal), *Elaphidion mucronatum* (Say), *Xylotrechus stebbingi* Gahan). In addition, although we did not perform multiple comparisons between single-colored traps, some species seem to be more attracted by some colors over others, despite not showing any difference with the multi-colored trap (e.g., *Gaurotes cyanipennis* (Say), *Phymatodes aereus* (Newman)). It is also worth noting that a few species, such as *Xylotrechus antilope* (Schönherr) and *Cerambyx scopolii* Fuessly, that were previously reported to be highly attracted to yellow traps (Cavaletto et al., 2021; Besana et al., 2025) did not exhibit the same preference in this study. This discrepancy may be attributed to differences in the specific shade of yellow used across studies or local variation. In the abovementioned studies, the yellow on the trap surface was brighter and slightly shifted towards a green hue, though in the present study the yellow was markedly lower in brightness and had a more red-shifted hue. These findings underscore that nuanced differences in color can change the attractiveness to a given longhorn beetle species. Therefore, identifying and standardizing the optimal color shade becomes essential for maximizing trap efficacy for specific target species (Santer and Allen, 2024).

An important aspect that warrants further investigation is the impact of multi-colored traps on non-target taxa. If multi-colored traps result in reduced bycatch of beneficial insects compared to single-colored traps, this could provide an additional justification for their use in monitoring or early-detection programs. In addition, it would be valuable to investigate whether additional colors could be incorporated into a single trap, or whether some of the colors used in this study could be replaced with others known to be attractive to different beetle taxa. For example, the specific green shade commonly used in monitoring *Agrilus* jewel beetles (Francese et al., 2010; Santoiemma et al., 2024b) may be a suitable alternative. Incorporating such colors could lead to the development of traps effective for multiple taxa simultaneously. Among the colors tested in this study, red appears to be the best candidate for replacement. Although red has previously been shown to be more attractive than black for some longhorn beetles and was found to be more effective than multi-colored trap in some cases, it is likely that longhorn beetles might be only weakly sensitive towards longer wavelengths, as is the case for most beetle families (van der Kooi et al., 2021; Belušič et al., 2025). This implies that red surfaces may be perceived as nearly achromatic and therefore are less visually salient to these beetles.

Another visual element to consider in future studies on trap design is surface gloss, which can be found in signaling structures of many animal and plant species. Recent behavioral experiments with bumblebees showed that surface gloss enhances object long-distance visibility, and that its importance at short distances depends on the object's color (Dietz et al., 2025). The importance of surface gloss for visual signaling and its interactive effect with object color (Dietz et al., 2025) yields opportunities to manufacture traps using this additional visual effect, which is independent from pigment.

5. Conclusions

Although we cannot exclude the possibility that some of the observed trends were influenced by the fact that all traps were to some extent multi-colored, with a black upper cap and bottom funnel, and a white collector cup, this study demonstrates that monitoring and surveillance programs targeting longhorn beetles can be improved by employing multi-lure baited multi-colored traps. These traps can capture a greater number of species and individuals compared to standard black traps,

likely by appealing to a wider range of ecological and behavioral preferences. Additionally, multi-colored traps may reduce the need for deploying multiple single-colored traps to cover the full spectrum of species present in a given area. However, single-colored traps may still be preferable in specific cases, particularly when monitoring efforts focus on the subfamily Lepturinae or on target species that have demonstrated a specific color preference over several studies.

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CRediT authorship contribution statement

L. Besana: Writing – original draft, Writing – review & editing, Visualization, Methodology, Investigation, Conceptualization. **G. Santoiemma:** Writing – original draft, Writing – review & editing, Investigation, Formal analysis. **A. Biondi:** Writing – review & editing, Supervision, Funding acquisition. **E.G. Booth:** Investigation. **G. Cavaletto:** Methodology, Investigation, Conceptualization. **V. Caruso:** Investigation. **S.M. Devine:** Investigation. **J.A. Francese:** Writing – review & editing, Investigation, Supervision, Funding acquisition. **E. Franzen:** Investigation. **A. Gugliuzzo:** Writing – review & editing, Investigation. **J.M. Gutowski:** Writing – review & editing, Investigation. **R. Johns:** Writing – review & editing, Investigation, Funding acquisition. **E. Owens:** Investigation. **R. Plewa:** Writing – review & editing, Investigation. **A.M. Ray:** Writing – review & editing, Supervision, Funding acquisition. **A. Roques:** Writing – review & editing, Methodology, Investigation, Supervision. **K. Sućko:** Writing – review & editing, Investigation. **C.J. van der Kooi:** Writing – review & editing, Methodology, Investigation, Funding acquisition. **D. Rassati:** Writing – original draft, Writing – review & editing, Methodology, Conceptualization, Supervision, Funding acquisition.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2025.123365.

Data availability

Data will be made available on request.

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