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ORIGINAL PAPER

Exploiting trap color to improve surveys of longhorn beetles

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Abstract
Longhorn beetles are commonly moved among continents within wood packaging materials used in trades. Visual inspections carried out at points of entry often fail to detect exotic longhorn beetles as infested materials may have little or no sign of colonization. Black-colored traps baited with pheromones and host volatiles are thus used to improve chances of detection. Here we tested whether existing surveillance protocols for longhorn beetles can be further improved using trap colors different than black. Baited traps of eight different colors (i.e., grey, yellow, green, red, blue, brown, purple and black) were deployed in a randomized complete block design at 16 sites in northern Italy in 2019. A total of 6,001 individuals from 56 longhorn beetle species were trapped. In general, yellow and blue traps caught a significantly higher number of longhorn beetle species than black traps. In addition, trap color significantly affected species richness and abundance at the subfamily and species level, with mixed response mostly linked to the habit of visiting flowers for food. Flower-visiting longhorn beetles mainly exhibited clear preference for flower-related colors, i.e., yellow, green and blue, whereas non-flower-visiting species were more attracted by dark and long-wavelength-dominated colors, like red and brown. Our results clearly indicate that generic surveillance programs should not rely exclusively on black traps and that the use of more trap colors can strongly improve the chance of detecting native and exotic longhorn beetles potentially moved with trades.

Keywords Cerambycidae · Color vision · Early detection · Exotic species · Surveillance

Key message

- Black-colored traps baited with attractive blends are used at ports of entry worldwide to intercept longhorn beetles accidentally introduced via international trade.
- No study thoroughly tested whether colored traps perform better than black traps in detecting longhorn beetles.
- Trap color can strongly increase attractiveness of longhorn beetles to baited traps, especially when targeting flower-visiting species.
- Surveillance programs must include colored traps along with commonly used black traps to improve the likelihood of detecting longhorn beetles potentially moved with trades.

Introduction

World trends of growing national and international trade have led to increased risk of native insect range expansion and exotic insect introductions (Brockerhoff and Liebhold 2017). Among the most frequently intercepted insect groups are wood-boring beetles in the family Cerambycidae (Eyre and Haack 2017). These insects, also known as longhorn beetles, are commonly moved at the larval stage within fresh

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wood packaging materials, round wood and planting material (Wu et al. 2017; Meurisse et al. 2019). Woody materials or live plants containing early instar larvae often have few or no outward signs of infestation (Humble 2010); thus, routine visual inspections carried out at points of entry often fail to detect accidentally introduced species. In addition, exotic longhorn beetles can cause massive economic and ecological damage in the invaded areas (Haack 2017) and eradication campaigns can be extremely costly (Haack et al. 2010; Faccoli and Gatto 2015). A number of phytosanitary regulations have been implemented to reduce the risk of international insect incursions (Allen et al. 2017), but several exotic longhorn beetle species continue to be detected worldwide (Eyre and Haack 2017). Thus, the availability of effective detection tools able to intercept exotic longhorn beetles before they become established in the invaded environment is essential to prevent the damage and reduce overall costs.

A number of innovative tools for early detection of exotic insects have been developed in recent years (Poland and Rassati 2019). Among them, traps baited with blends of pheromones and kairomones and placed in and around entry points represent one of the most efficient and commonly adopted approaches for longhorn beetles (Eyre and Haack 2017). Besides their low cost and ease of use, baited traps benefit from recent advances in longhorn beetle chemical ecology (Hanks and Millar 2016; Millar and Hanks 2017) and our understanding of factors that affect longhorn beetle trapping success (Allison and Redak 2017). Sex and aggregation-sex pheromones have been already identified for more than 300 longhorn beetle species worldwide (Millar and Hanks 2017), and this number is constantly growing. In addition, the effect of trap type (e.g., Graham et al. 2012), trap design (Allison et al. 2014), trap coatings (Graham and Poland 2012) as well as trap position in terms of height above the ground level (e.g., Flaherty et al. 2019; Ulyshen and Sheehan 2019; Miller et al. 2020) and distance from the forest edge (e.g., Allison et al. 2019) have been assessed for several longhorn beetle species. As a result, a wide set of trapping protocols currently exist for both species-specific and generic surveillance programs, allowing phytosanitary inspectors to select from time to time the best trapping protocol according to their needs (Poland and Rassati 2019). There is increasing evidence, however, that the efficacy of baited traps can be further increased by exploiting trap color.

Surveillance programs aimed at intercepting exotic longhorn beetles have so far relied almost exclusively on black traps (Brockerhoff et al. 2006; Bashford 2008; Rassati et al. 2015; Canadian Food Inspection Agency 2017). This practice was supported by a number of studies showing a higher efficacy of black traps compared with white or clear traps in attracting certain longhorn beetle species (De Groot and Nott 2001; Campbell and Borden 2009; Rassati et al. 2012; Kerr et al. 2017). This observation was ascribed to the resemblance of black traps to the silhouette and typical dark colors of host tree bark. Longhorn beetles, however, exploit visual stimuli not only to locate host vs. non-host plants when ovipositing (Campbell and Borden 2009; Lyu et al. 2015), but also to spot mates or feeding substrates (Monnè et al. 2017). The body color, shape and size, for example, are visual cues commonly used by adult longhorn beetles to efficiently locate mates at short-distance range (Wang 2002; Fukaya et al. 2004, 2005; Lu et al. 2007; Johnson et al. 2019). Similarly, pollen- and nectar-feeding longhorn beetles likely exploit flower colors to locate feeding substrates, although such observations exist so far only for a few species (Imrei et al. 2014; Toshova et al. 2016). It is thus reasonable to assume that colored traps might perform better than the commonly used black traps in attracting those longhorn beetle species that exploit colors as visual stimuli during at least a part of their life cycle. Trapping studies carried out so far to test this hypothesis were limited to a low number of colors, including only part of the color spectrum (Braman et al. 2003; Campbell and Hanula 2007; Shipman 2011; Skvarla and Holland 2011; Skvarla and Dowling 2017; Rassati et al. 2019), or a low number of species (Imrei et al. 2014; Toshova et al. 2016; Kerr et al. 2017), and thus, there is a clear need to expand such studies to more colors and a wider range of longhorn beetle species.

In this study, we investigated whether trap color could be exploited to improve trapping protocols for native and exotic longhorn beetles. In particular, we tested whether longhorn beetle species richness (i.e., number of species) and abundance (i.e., number of individuals) in baited traps would increase using colors different than black. Comparisons among trap colors were made following two main criteria. The first criterion was based on taxonomy (i.e., family, subfamily, and species level). A previous study showed that trap color (green vs. purple) affected longhorn beetles responses differently at the subfamily and species levels (Rassati et al. 2019); thus, we expected to observe a similar pattern in this study. We predicted that Lamiinae, many of which are nocturnal or crepuscular species that do not visit flowers (Monnè et al. 2017), prefer dark and achromatic colors, whereas we expected a clear preference for flower-like colors in diurnally active flower-visiting species such as Lepturinae (Monnè et al. 2017). In addition, we predicted a mixed response for Cerambycinae, given that this subfamily includes species with extremely diverse biological attributes, i.e., from nocturnal species that do not visit flowers to brightly colored diurnal species that commonly visit flowers (Monnè et al. 2017). The second criterion had instead a biological basis and was selected to overcome the heterogeneity that we expected when using the taxonomic criterion. Flower-visiting insects commonly exhibit color preferences (Vuts et al. 2012; Streinzer et al. 2019), and we expected that nectar- and pollen-feeding longhorn beetle species would be more attracted to traps painted with the typical flower colors (e.g., yellow and blue) than to black traps, while longhorn beetle species that do not visit flowers could be efficiently trapped with the commonly used black traps.

Materials and methods

Study area

The study was conducted across 16 sites located in the Euganean Hills area, Veneto Region, northeastern Italy (Table S1; Fig. S1). This area covers about 22,000 ha and is composed of about 100 hills ranging from a few tens of meters to about 600 m a.s.l. in elevation. The landscape is characterized by the presence of fragmented forest patches, interspersed with various types of crop fields and urban areas. The main forest types occurring in the area are: i) chestnut (*Castanea sativa* Miller) forests (ca. 30%); ii) dry forests dominated by *Fraxinus ornus* L. and *Ostrya carpinifolia* Scopoli (ca. 15%); and iii) oak (*Quercus pubescens* Willd.) forests (ca. 10%). In addition, past forest management (i.e., clear cutting) has favored the invasion of black locust (*Robinia pseudoacacia* L.), which now covers around 38% of the total forest area. Finally, some plantations of Austrian pine (*Pinus nigra* Arnold) are present (ca. 2%). Almost all broadleaf forests are coppiced at a small spatial scale (< 0.5 ha) with short rotation cycles (usually < 30 years).

Trap type, trap color and experimental scheme

At each site, we used eight handmade panel traps (see Fig. S2 for details on trap design and dimensions), each painted with one of the following colors: grey, yellow, green, red, blue, brown, purple and black (corresponding to RAL numbers 7034, 1018, 6037, 3020, 5015, 8002, 4008 and 9005, respectively; Fig. S3) (Seven Colors paint factory, Sant'Angelo di Piove di Sacco, Padova, Italy). These colors were chosen because they cover a wide range of the visible spectrum. White was not included due to its low attraction toward longhorn beetles (De Groot and Nott 2001; Campbell and Borden 2009; Kerr et al. 2017). Regarding trap type, we decided to use panel traps because they are generally more effective than multi-funnel traps in trapping longhorn beetles (Allison and Redak 2017). All traps consisted of white corrugated plastic boards that were coated after painting with a 10% solution of Fluon (Insect-A-Stop, Springwood, Queensland, Australia) diluted in water. Fluon was used because it improves trapping efficacy without affecting the relative reflectance of the coated surface (Allison et al. 2016). Trap-collecting cups were half-filled with 50% solution of ethylene glycol to kill and preserve captured beetles, and the solution was replaced at each trap check. The eight treatments (i.e., colors) were replicated 16 times (i.e., sites) in a randomized complete block design, in which each block was represented by a different site (Fig. S1). At each site, traps were deployed in a linear pattern at a distance of 1.5 m apart. Traps were hung on a steel wire strung between two trees at about 5–7 m above the ground (Fig. S1). The latter trees were selected based on position and suitability to hold the weight of the traps, irrespective of the species. This trap height was selected because it is a good compromise to sample both longhorn beetle species active in the canopy and in the understory (Sheehan et al. 2019). In addition, traps were placed along the forest edge at each site. Traps were placed in the field from mid-May to the end of August 2019 and were checked every 3 weeks for a total of 5 times (i.e., 5 June, 26 June, 17 July, 7 August, and 28 August). All trapped longhorn beetles were identified to species using morphological features and keys (Bense 1995). Each species was then classified as either a flower-visiting or non-flower-visiting species using the Titan database (http://titan.gbif.fr/accueil_uk.html), which reports for each longhorn beetle species the scientific name of visited flowers, if any. This list was then validated and adjusted based on other available literature. Voucher specimens were deposited in the insect collection of the Entomology laboratory at the Department of Agronomy, Food, Natural Resources, Animals and Environment (DAFNAE), University of Padua (Italy).

Lures

Each trap was baited with a blend containing the primary pheromone components of the subfamily Cerambycinae and Lamiinae, which is attractive to a wide range of longhorn beetle species (Fan et al. 2019). The blend included: (i) fuscumol (volume amount: 50 mg); (ii) fuscumol acetate (50 mg); (iii) geranyl acetone (25 mg); (iv) 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); (viii) monochamol (50 mg), dissolved in isopropanol as a carrier to a total volume of 1 ml per lure. All compounds were purchased from ChemTica Internacional, S.A. (Heredia, Costa Rica) except prionic acid (Alpha Scents Inc., West Linn, Oregon). One-milliliter aliquots of the blend were filled in glass vials with screw caps and stored at 4 °C until used. Then, at the beginning of the trapping trial and at each trap check (i.e., every three weeks), 1-ml aliquots were poured into a clear polyethylene sachet (Minigrip, 4 × 6 cm × 60μ; Dutscher, Brumath, France) containing a cotton cylinder, which was hung in the center of the trap using a string. The release rate of the blend determined by mass loss under 20 °C conditions is estimated to 0.0263 ± 0.002 g/d (Fan et al. 2019). The pheromone blend was complemented with UHR (ultra-high release rate) ethanol (release rate of about 1.5 g/d at 20 °C; Econex, Spain), which is known to enhance the attraction of many longhorn beetle species to the above-listed pheromones (Miller et al. 2015; Collignon et al. 2016). The ethanol release device was a polylaminated aluminum-foil "blister" that was hung in the center of the trap directly below the sachet containing the pheromone blend. Ethanol was replaced only once during the trapping season based on its expected field life (i.e., 60 days).

Statistical analyses

The effects of trap color (categorical variable) on longhorn beetle species richness and abundance at the family and subfamily taxonomic level were tested using linear mixed-effect models (LMMs). The total number of species (i.e., species richness) and individuals (i.e., abundance) collected per trap color over the entire trapping season were the dependent variables. Abundance was log-transformed to satisfy the assumption of normality. Models included site as random factor to account for spatial dependence in the sampling design and were fitted with the function "lmer" in the package "lme4" (Bates et al. 2017) implemented in R (R Core Team 2019). The same approach as described above was also used to test the effect of trap color on species richness and abundance of flower-visiting vs. non-flower-visiting longhorn beetles. However, the effect of trap color on abundance of individual longhorn beetle species was tested using generalized linear mixed-effect models (GLMMs). The number of individuals collected per trap color over the entire trapping season (negative binomial distribution) was included in the models as a dependent variable and site as a random factor. A negative binomial distribution was used because data were over-dispersed. Only species represented by at least 50 individuals were analyzed. In addition, for each species, only sites where at least 5 individuals were trapped were retained in the analysis. Models were fitted with the function "glmer.nb" in the package "lme4" (Bates et al. 2017). Residual distribution was checked through the "DHARMa" package (Hartig 2017), which uses a simulation-based approach to create readily interpretable scaled residuals from the fitted LMM and GLMM. In all analyses, we used a priori contrasts between black (control) and the other colors instead of a post hoc multiple comparison test between all the color combinations. We planned this analysis a priori considering the number of replicates (no. of sites) according to the power of this analysis. The large number of pairwise comparisons ($n = 28$) would have required a much higher number of replicates that were not technically feasible.

Results

General results

A total of 6001 individuals from 56 longhorn beetle species were caught (Table 1). Cerambycinae was the most represented subfamily in terms of number of species (i.e., species richness) (31 species), followed by Lamiinae (13), Lepturinae (10) and Prioninae (2) (Table 1). The trend was different when considering abundance (i.e., number of individuals) of these subfamilies: Cerambycinae was again the most abundant (4419 individuals), followed by Lepturinae (642 individuals), Prioninae (501 individuals) and Lamiinae (441 individuals) (Table 1). Among Cerambycinae, 80% of individuals belonged to five species, namely the native *Phymatodes testaceus* (L.) (1,218 individuals), *Nathrius brevipennis* (Mulsant) (529 individuals), *Chlorophorus sartor* (Muller) (476 individuals), and *Purpuricenus kaehleri* (L.) (239 individuals), and the exotic *Xylotrechus stebbingi* Gahan (1,084 individuals). By contrast, 13 species were represented by less than 10 individuals each (Table 1). Lepturinae and Prioninae catches were also dominated by only a few species: *Pachytodes erraticus* (Dalman), *Stictoleptura cordigera* (Fuessly), and *Rutpela maculata* (Poda) comprised 90% of the lepturine individuals, whereas *Prionus coriarius* (L.) far exceeded the only other prionine species collected, i.e., *Aegosoma scabricorne* (Scopoli) (476 vs. 25 individuals). A similar pattern was found in the Lamiinae: *Aegomorphus clavipes* (Schrank) and *Leiopus nebulosus* (L.) comprised 90% of lamiine individuals (Table 1). Moreover, 10 out of 13 lamiine species were represented by less than 10 individuals each (Table 1). Regarding the flower-visiting habit, all lepturine and 16 out of 31 cerambycine species were classified as flower-visitors (26 species), whereas both prionine, 15 out of 31 cerambycine, and all lamiine species were classified as non-flower-visitors (30 species).

Effect of trap color at the family, subfamily and species level

At the family level (i.e., Cerambycidae), both longhorn beetle species richness and abundance were significantly affected by trap color (Table S2). For species richness, the mean number of longhorn beetle species was significantly higher in both yellow and blue traps than in black traps, whereas no significant difference was found among black and the other tested colors (Table S3 and Fig. 1a). For abundance, black traps caught a significant higher mean number of individuals than both grey and green traps (Table S3 and Fig. 1b).

Table 1 Total number of individuals trapped by each trap color

	Black	Brown	Red	Yellow	Green	Blue	Purple	Grey	Total	Flowers
Cerambycinae										
Anaglyptus gibbosus (Fabricius)	10	10	18	14	9	7	10	9	87	Y
Anaglyptus mysticus (Linneaus)	–	3	–	2	–	1	–	1	7	Y
Callimus abdominalis (Olivier)	–	–	–	5	–	–	–	1	6	Y
Cerambyx cerdo (Linneaus)	–	–	–	1	1	1	–	–	3	N
Cerambyx scopolii Fuessly	7	6	3	36	9	10	10	13	94	Y
Cerambyx welensii (Kuster)	2	–	–	1	–	–	–	–	3	N
Chlorophorus figuratus (Scopoli)	–	1	–	17	12	–	–	2	32	Y
Chlorophorus glabromaculatus (Goeze)	23	20	19	33	15	14	15	14	153	N
Chlorophorus sartor (Muller)	1	1	–	395	75	3	–	1	476	Y
Chlorophorus trifasciatus (Fabricius)	–	–	–	1	–	–	–	–	1	Y
Chlorophorus varius (Muller)	–	–	–	–	1	1	–	–	2	Y
Clytus arietis (Linneaus)	2	1	1	5	–	–	1	–	10	Y
Clytus rhamni Germar	–	–	–	18	6	1	1	–	26	Y
Gracilia minuta (Fabricius)	1	1	–	–	–	–	–	1	3	N
Nathrius brevipennis (Mulsant)	51	97	57	29	93	59	77	66	529	N
Neoclytus acuminatus (Fabricius)*	4	4	1	1	–	6	4	5	25	N
Phymatodes testaceus (Linneaus)	292	183	172	65	38	174	197	97	1218	Y
Plagionotus arcuatus (Linneaus)	–	–	1	–	–	–	2	–	3	N
Plagionotus detritus (Linneaus)	3	3	4	6	3	5	12	3	39	N
Poecilium alni (Linneaus)	4	4	5	10	3	8	7	2	43	N
Poecilium fasciatum (Villers)	1	–	–	–	–	–	–	–	1	N
Pseudosphegesthes cinerea (Castelnau & Gory)	1	–	–	2	1	3	–	1	8	N
Purpuricenus kaehleri (Linneaus)	14	25	24	61	48	34	17	16	239	Y
Ropalopus clavipes (Fabricius)	4	3	6	16	11	5	1	4	50	Y
Ropalopus femoratus (Linneaus)	–	–	1	4	1	–	–	1	7	Y
Stenopterus rufus Linneaus	–	–	2	65	7	–	1	–	75	Y
Trichoferus holosericeus (Rossi)	–	–	2	–	–	–	–	1	3	N
Trichoferus pallidus (Olivier)	8	7	7	5	6	17	3	8	61	N
Xylotrechus antilope (Schonherr)	11	18	8	32	18	18	6	15	126	N
Xylotrechus arvicola (Olivier)	–	1	–	1	–	–	2	1	5	Y
Xylotrechus stebbingi Gahan*	220	184	199	87	87	96	120	91	1084	N
Lamiinae										
Aegomorphus clavipes (Schrank)	29	36	52	24	29	53	58	26	307	N
Anaesthetis testacea (Fabricius)	3	3	1	2	1	1	–	–	11	N
Exocentrus adspersus Mulsant	2	–	1	–	–	–	1	–	4	N
Exocentrus lusitanus (Linneaus)	1	1	–	–	2	3	–	1	8	N
Exocentrus punctipennis Mulsant & Guillebeau	–	1	4	–	–	–	–	4	9	N
Leiopus nebulosus (Linneaus)	9	16	10	5	15	11	10	12	88	N
Mesosa curculionoides (Linneaus)	–	–	1	–	1	1	–	–	3	N
Mesosa nebulosa (Fabricius)	–	–	–	–	–	–	–	1	1	N
Monochamus galloprovincialis (Olivier)	–	1	–	–	–	–	–	1	2	N
Oberea linearis (Linneaus)	–	–	–	–	–	–	–	1	1	N
Parmena unifasciata (Rossi)	–	–	1	–	–	–	–	1	2	N
Pogonocherus hispidus (Linneaus)	–	1	1	–	–	–	–	–	2	N
Saperda punctata (Linneaus)	–	–	2	–	–	–	–	1	3	N
Lepturinae										
Anoplodera sexguttata (Fabricius)	–	–	–	–	–	1	–	–	1	Y
Grammoptera ruficornis (Fabricius)	1	–	2	12	–	1	–	–	16	Y
Pachytodes erraticus (Dalman)	2	1	12	106	48	31	–	13	213	Y

Table 1 (continued)

	Black	Brown	Red	Yellow	Green	Blue	Purple	Grey	Total	Flowers
Paracorymbia fulva (De Geer)	–	–	–	–	–	1	–	–	1	Y
Rutpela maculata (Poda)	3	12	15	73	42	8	2	21	176	Y
Stenurella bifasciata (Muller)	–	–	1	3	1	3	–	–	8	Y
Stenurella melanura (Linneaus)	1	–	1	3	–	6	–	3	16	Y
Stenurella septempunctata (Fabricius)	1	1	–	1	1	1	–	–	5	Y
Stictoleptura cordigera (Fuessly)	2	2	4	9	2	161	10	7	197	Y
Stictoleptura scutellata (Fabricius)	2	–	–	–	–	4	1	2	9	Y
Prioninae										
Aegosoma scabricorne (Scopoli)	4	2	4	2	5	4	3	1	25	N
Prionus coriarius (Linneaus)	79	60	154	32	28	38	51	34	476	N

The column "Flowers" indicates whether a given species is known to be a flower-visiting (Y) or non-flower-visiting (N) species. Species are listed alphabetically within each subfamily

*Indicate species exotic to Italy

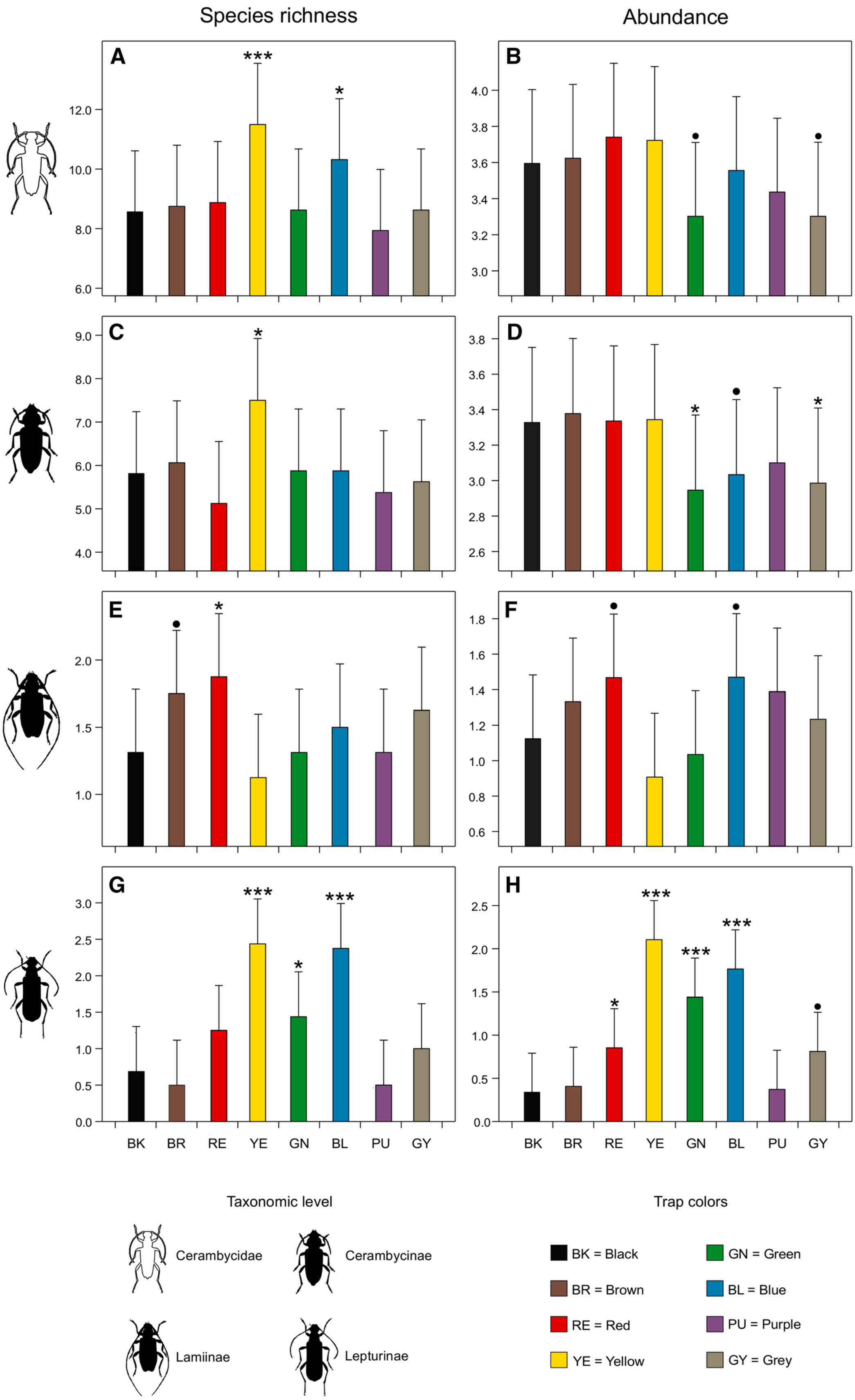
At the subfamily level, trap color affected species richness of Cerambycinae, Lamiinae and Lepturinae (Table S2). The subfamily Prioninae was not analyzed because it was represented by only two species. For Cerambycinae, yellow traps caught significantly more species than black traps, but no difference was found between black and the other tested colors (Table S3 and Fig. 1c). For Lamiinae, both brown and red traps caught significantly more species than black traps (Table S3 and Fig. 1e). For Lepturinae, three colors attracted significantly more species than black, which were yellow, blue and green (Table S3 and Fig. 1g). Trap color also significantly affected the abundance of the three subfamilies analyzed (Table S2). For Cerambycinae, the mean number of individuals was significantly higher in black than in green, grey and blue traps (Table S3 and Fig. 1d). For Lamiinae, the mean number of individuals was higher in both red and blue traps compared with black traps (Table S3 and Fig. 1f). For Lepturinae, yellow, green, blue, red and grey traps caught significantly higher number of individuals than black traps (Table S3 and Fig. 1h).

At the lowest taxonomic level tested (i.e., individual species), 18 longhorn beetle species were represented by at least 50 individuals and thus were retained for analysis. Trap color significantly affected 13 of these species (Table S2). Five out of the eight analyzed cerambycine species were collected in significantly higher number by trap colors different than black. *Cerambyx scopolii* Fuessly, *C. sartor*, *Stenopterus rufus* L. and *Xylotrechus antilope* (Schonherr) showed a preference for yellow traps, although other colors also appeared to be more efficient than black (e.g., green for *C. sartor* and *S. rufus*) (Table S4 and Fig. 2). *N. brevipennis* showed instead a preference for brown and green traps. Black was more efficient than other colors for the native *P. testaceus* and the exotic *X. stebbingi* (Table S4 and Fig. 2). Also, the Lamiinae *A. clavipes* was caught in higher numbers by trap colors different than black, that are red, blue and purple. Among Lepturinae, *P. erraticus* and *R. maculata* were mainly caught in yellow and green traps, although other trap colors were also more efficient than black traps, whereas *S. cordigera* showed a preference for blue traps (Table S4 and Fig. 2). Finally, among Prioninae, *P. coriarius* was efficiently trapped with black traps, which showed a higher efficiency than green, yellow, blue and grey traps (Table S4 and Fig. 2).

Effect of trap color on flower-visiting versus non-flower-visiting longhorn beetles

Trap color affected species richness of both flower-visiting (χ^2=88.33; $P < 0.001$) and non-flower-visiting longhorn beetles ($\chi^2 = 14.27$; $P = 0.046$), but the effect was different between these two groups. For flower-visiting longhorn beetles, the number of species was significantly higher in yellow, blue and green traps than in black traps (Table S5 and Fig. 3a), whereas yellow traps and green traps were significantly less efficient than black traps for non-flower-visiting species (Table S5 and Fig. 3c). Trap color also affected the abundance of both groups ($\chi^2 = 47.78$ and $P < 0.001$ for flower-visiting; $\chi^2 = 44.61$ and $P < 0.001$

Fig. 1 Effect of trap color on longhorn beetle species richness and abundance at the family (A-B) and subfamily levels (C–H). Within each panel, colors that attracted a significantly different mean number of species or individuals than black traps are indicated with black asterisk/s or black circle depending on the P value: *** = $P < 0.001$; ** = $P < 0.01$; * $P < 0.05$; filled circle = $P < 0.1$. Abundance at the family and subfamily level are log-transformed. Error bars indicate the 95% confidence intervals for the mean ▶


Species richness
Abundance
A
***
*
12.0
10.0
8.0
6.0
B
4.0
3.8
3.6
3.4
3.2
3.0
●
●
C
*
9.0
8.0
7.0
6.0
5.0
4.0
D
3.8
3.6
3.4
3.2
3.0
2.8
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BK
BR
RE
YE
GN
BL
PU
GY
BK
BR
RE
YE
GN
BL
PU
GY
Taxonomic level
Cerambycidae
Cerambycinae
Lamiinae
Lepturinae
Trap colors
BK = Black
GN = Green
BR = Brown
BL = Blue
RE = Red
PU = Purple
YE = Yellow
GY = Grey

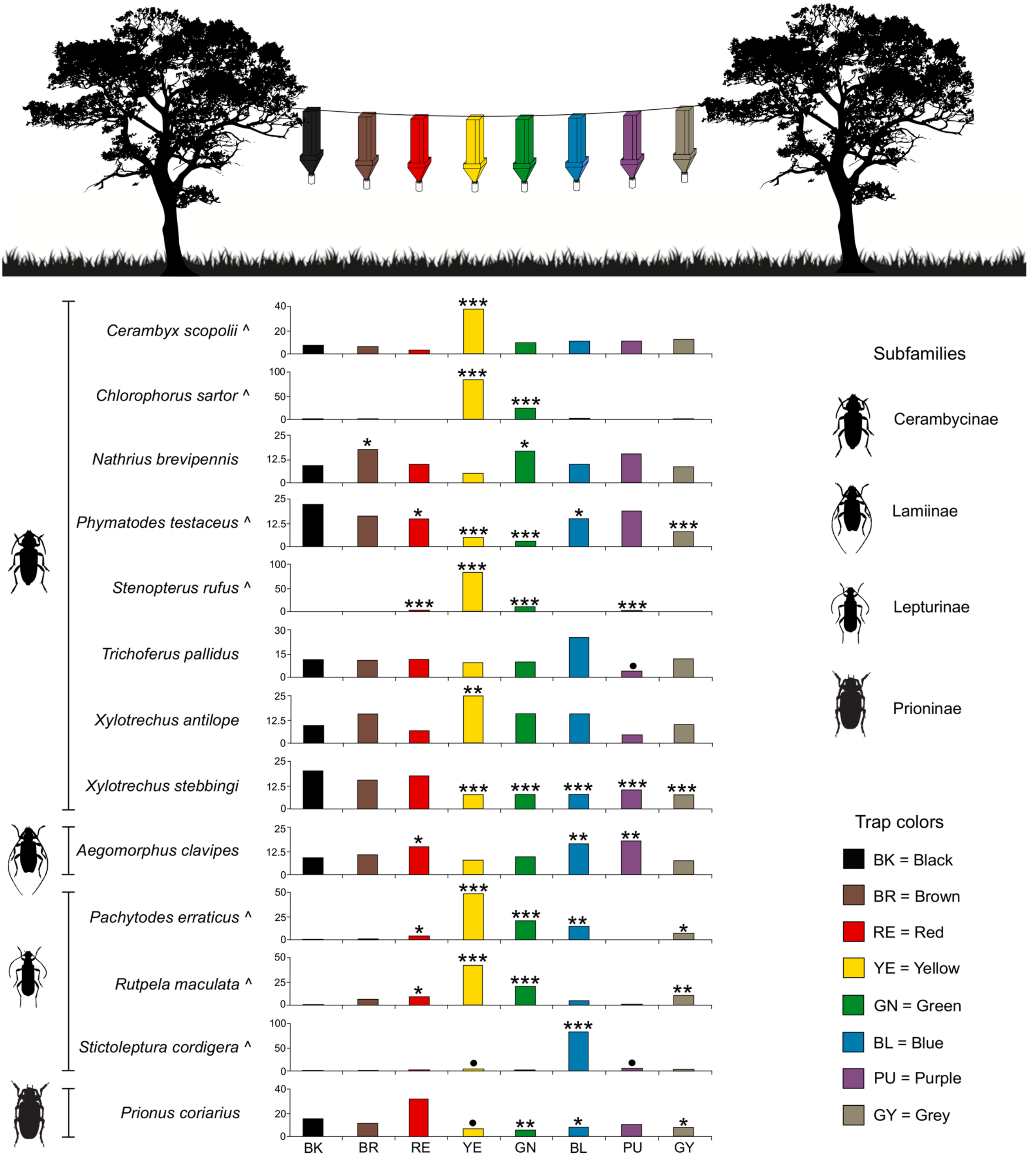

Fig. 2 Proportion of individuals collected in traps painted with the eight tested colors. Data are shown only for longhorn beetle species that were significantly affected by trap color (Table S4) and are presented in alphabetical order within each subfamily. An ^ after a species name indicates flower-visiting species. Within each bar plot, colors that attracted a significantly different mean number of individuals than black traps are indicated with black asterisk/s or black circle depending on the P value: *** = $P < 0.001$; ** = $P < 0.01$; * $P < 0.05$; filled circle = $P < 0.1$

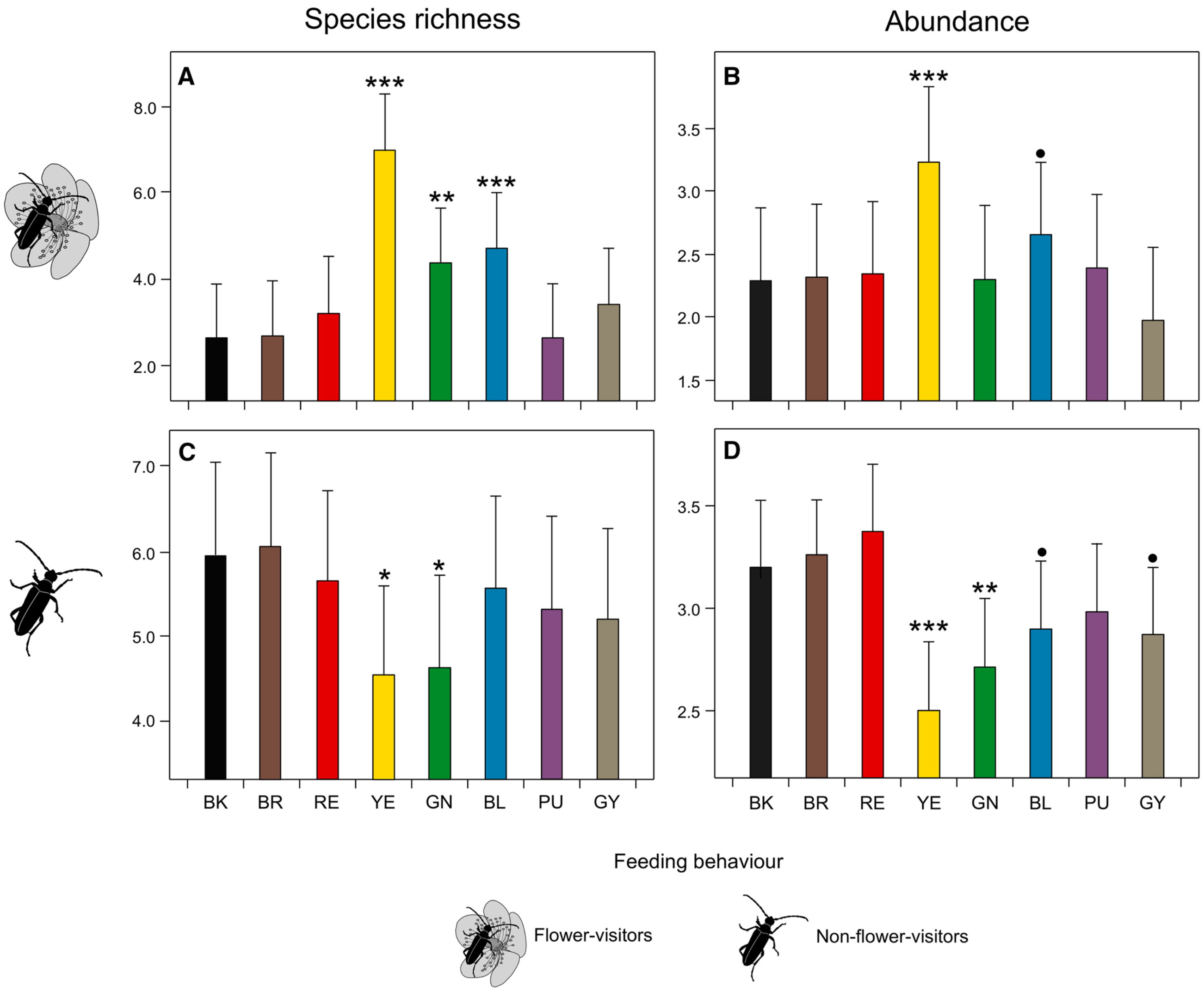

Fig. 3 Effect of trap color on species richness and abundance of flower-visiting (A, B) vs. non-flower-visiting (C, D) longhorn beetles. Only significant results are shown. Within each panel, colors that attracted a significantly different mean number of species or individuals than black traps are indicated with black asterisk/s or black circle depending on the P value: ***=$P<0.001$; **=$P<0.01$; * $P<0.05$; filled circle =$P<0.1$. Abundance of both flower-visitors and non-flower-visitors are log-transformed. Error bars indicate the 95% confidence intervals for the mean

for non-flower-visiting). The mean number of individuals of flower-visiting species was significantly higher in yellow traps and blue traps than in black traps (Table S5 and Fig. 3b), whereas the opposite trend occurred for non-flower-visiting species, with yellow traps, along with green, blue and grey traps, catching significantly lower numbers of individuals than black traps (Table S5 and Fig. 3d).

Discussion

Surveillance programs for longhorn beetles commonly exploit traps baited with pheromones and host volatiles placed in and around entry points. However, most of these programs rely almost exclusively on black-colored traps. Here, we showed that trap color can strongly affect longhorn beetle species richness and abundance in traps, with mixed responses at subfamily and species level. In addition, we showed that the response of longhorn beetles to trap color appears to be linked to their ecology, especially the habit of visiting flowers for food. Our results provide evidence that trap color should be considered an important variable when planning surveillance programs for longhorn beetles and that the use of colored traps can strongly improve the likelihood of intercepting native and exotic species moved with national and international trade.

Trap color significantly affected longhorn beetle species richness at the family level. Yellow and blue traps caught a significantly higher number of species than black traps, clearly indicating that generic surveillance programs should not rely exclusively on black traps. The use of black traps is based on studies showing that black or dark colors are more effective than white, transparent or clear traps in attracting longhorn beetles (De Groot and Nott 2001; Campbell and Borden 2009; Rassati et al. 2012; Kerr et al. 2017). However, most of these studies targeted individual species, and the higher efficacy of black vs. clear traps was not supported by analyses carried out at the family level (Bouget et al. 2008; Allison and Redak 2017). The option of using colored traps was rarely considered in the past, likely because indications that colors different than black can efficiently attract longhorn beetles were controversial and based on comparisons among a limited number of colors (Shipman 2011; Skvarla and Holland 2011; Skvarla and Dowling 2017; Rassati et al. 2019). Thus, our results provide the first evidence that colored traps can strongly increase the overall attractiveness of longhorn beetles to baited traps. This pattern was not valid for abundance, probably due to a high variation of preferences among species that leveled out at family level.

Trap color significantly affected longhorn beetle species richness and abundance also at the subfamily level, but the effect differed between subfamilies. A previous study showed that Cerambycinae and Lamiinae were differentially attracted by purple and green traps (Rassati et al. 2019), a trend that was attributed to the different flight activity patterns (nocturnal vs. diurnal) of the main representatives of the two subfamilies. Our results confirmed that the biological attributes shared by most longhorn beetle species within a given subfamily affect their response to trap colors. Lepturinae, most of which are diurnally active and flower-visitors (Monnè et al. 2017), exhibited clear preference for flower-related colors, i.e., yellow, green and blue, over black. In contrast, Lamiinae, of which many are nocturnal or crepuscular species and do not visit flowers (Monnè et al. 2017), were more attracted by dark and long-wavelength-dominated colors, like red and brown. Cerambycinae, which include both diurnal flower-visiting species and nocturnal non-flower-visiting species (Monnè et al. 2017), showed a less clear pattern, with large discrepancies between trends for species richness (i.e., yellow traps more efficient than black traps) and abundance (i.e., black traps more efficient than green and grey traps).

At the species level, 13 longhorn beetle species were significantly affected by trap color. Nonetheless, patterns among these species were found to be quite heterogeneous and only partially generalizable using taxonomical or biological criteria. Within the subfamily Cerambycinae, for example, the exotic *X. stebbingi* showed a clear preference for black over other colors, similar to what was found by Skvarla and Dowling (2017) for *Xylotrechus colonus* (Fabricius), indicating that choice behavior was largely guided by achromatic vision. *Xylotrechus antilope*, instead, showed a different pattern, with a strong preference for yellow traps over black traps, despite the fact that both of these *Xylotrechus* species are non-flower-visitors. Within the flower-visitors, *R. maculata* and *S. cordigera* showed clear preferences for yellow/green and blue over black, respectively. The difference in color preference might be linked either to the colors of the most commonly visited flowers or to differences in the (visual guided) mate-finding behavior. *X. stebbingi* and *X. colonus*, for example, are mainly crepuscular or nocturnal species (Rassati et al. 2020), whereas *X. antilope* is mainly diurnal, with maximal activity in the late morning to early afternoon (Molander et al. 2019). This difference is also reflected in their body coloration: *X. antilope* is black with yellow stripes and likely mimic vespid wasps (Mitchell et al. 2017), *X. stebbingi* and *X. colonus* are reddish-grayish, which likely allow them to camouflage when moving on tree bark. It is thus likely that these longhorn beetle species exploit different visual channels (i.e., acromatic in *X. stebbingi* and *X. colonus* and chromatic in *X. antilope*), representing an adaptation to their diel activity pattern. The preference of *X. antilope* for yellow may be linked to an innate preference for the yellow color present on their body and thus a mechanism involved in mate location. *R. maculata* and *S. cordigera* are both flower-visitors, but the range of visited flowers varies between them. Flower color is one of the most important features used by flower-visiting insects to locate flowers and discriminate between plant species (Gumbert 2000; Streinzer et al. 2019), and it is likely that *R. maculata* and *S. cordigera* have innate preference for colors that correspond to those of the most commonly visited flowers. Further studies are, however, needed to elucidate these mechanisms.

Both species richness and abundance of flower-visiting and non-flower-visiting longhorn beetles were affected by trap color, but with opposite patterns. Colors that attracted a higher number of flower-visiting species and individuals than black traps (i.e., yellow, green and blue) resulted in being less efficient than black traps for non-flower-visiting longhorn beetles and vice versa. The ability to discriminate among different colors and an innate preference for blue or yellow is well documented in flower-visiting insects (e.g., Giurfa et al. 1995; Gumbert 2000; Schaefer et al. 2004;

Balamurali et al. 2019), but only a few observations have been reported so far in longhorn beetles (Imrei et al. 2014; Toshova et al. 2016), despite the presence of several spectrally different photoreceptor types found in Coleoptera (Sharkey et al. 2017). Our results provide evidence that flower-visiting longhorn beetles are able to distinguish color, guided by a chromatic visual channel, and indicate that color is exploited to locate feeding substrates in addition to locating potential mate (Johnson et al. 2019). Most non-flower-visiting longhorn beetles feed on twig bark or tree foliage, or do not feed at all (Monnè et al. 2017), and it is thus not surprising that such beetles are not attracted by typical flower colors. For the latter longhorn beetles, choosing the darkest colors (in our case black, brown and red) might be a proper mechanism to distinguish dark objects (e.g., the tree trunk) against bright background (sky), as well as between bark of host vs. non-host tree species (Campbell and Borden 2005).

In conclusion, we showed that trap color is a key visual cue that can be exploited to develop efficient trapping protocols for longhorn beetles. Different cerambycid subfamilies may require different trap colors; thus, the use of different colored traps can strongly increase the efficiency of the overall surveillance program. Currently, multi-funnel traps or panel traps used for trapping longhorn beetles can be found on the market only in a few colors, i.e., black, green and purple, but our results clearly indicate that more options are needed. In addition, showing that visual stimuli are used by both flower-visiting and non-flower-visiting longhorn beetles, our study opens up a new perspective in this field of research. As recently shown for horseflies (Megli č et al. 2019), a detailed investigation of vision and color perception mechanisms can lead to important improvements in trapping techniques for a given taxon. For longhorn beetles, such an approach could result in benefits for surveillance strategies of exotic and native species moved in trade (Poland and Rassati 2019), management of native and exotic species damaging urban or forest trees (Pawson and Watt 2009; Pawson et al. 2009), and also monitoring strategies for endangered species (Larsson 2016). Future studies should try to investigate to what extent color vision is involved in longhorn beetle mate location, as well as to explore whether males and females show different preferences. In addition, it would be important to test whether trap color can affect other wood-boring beetles, such as bark and ambrosia beetles or jewel beetles. This would allow to develop a trapping protocol that can attract several wood-boring beetle species simultaneously, saving resources and improving the overall efficacy of generic surveillance programs.

Author's contribution

DR, GC, LM and JS conceived the study; DR and GC wrote the manuscript; GC and SM conducted field experiments; DR, GC and LM analyzed the data; MF provided funds; FG identified beetles. All authors contributed to and approved the manuscript.

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Availability of data and materials Raw data are available in the Supplementary Materials.

Code availability Not applicable.

Compliance with ethical standards

Conflicts of interest Authors declare that they have no conflict of interests.

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

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