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Research

Maximizing Bark and Ambrosia Beetle (Coleoptera: Curculionidae) Catches in Trapping Surveys for Longhorn and Jewel Beetles

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Abstract

Bark and ambrosia beetles are commonly moved among continents within timber and fresh wood-packaging materials. Routine visual inspections of imported commodities are often complemented with baited traps set up in natural areas surrounding entry points. Given that these activities can be expensive, trapping protocols that attract multiple species simultaneously are needed. Here we investigated whether trapping protocols commonly used to detect longhorn beetles (Coleoptera: Cerambycidae) and jewel beetles (Coleoptera: Buprestidae) can be exploited also for detecting bark and ambrosia beetles. In factorial experiments conducted in 2016 both in Italy (seminatural and reforested forests) and Canada (mixed forest) we tested the effect of trap color (green vs purple), trap height (understory vs canopy), and attractive blend (hardwood-blend developed for broadleaf-associated wood-boring beetles vs ethanol in Italy; hardwood-blend vs softwood-blend developed for conifer-associated wood-boring beetles, in Canada) separately on bark beetles and ambrosia beetles, as well as on individual bark and ambrosia beetle species. Trap color affected catch of ambrosia beetles more so than bark beetles, with purple traps generally more attractive than green traps. Trap height affected both beetle groups, with understory traps generally performing better than canopy traps. Hardwood-blend and ethanol performed almost equally in attracting ambrosia beetles in Italy, whereas hardwood-blend and softwood-blend were more attractive to broadleaf-associated species and conifer-associated species, respectively, in Canada. In general, we showed that trapping variables suitable for generic surveillance of longhorn and jewel beetles may also be exploited for survey of bark and ambrosia beetles, but trapping protocols must be adjusted depending on the forest type.

Key words: multi-lure, surveillance, Scolytinae, trap height, trap color

Ever-increasing national and international trade along with ongoing changes in trade networks is causing an impressive number of forest insect introductions (Brockerhoff and Liebhold 2017, Rassati et al. 2018). This trend is particularly evident for wood-boring Coleoptera, especially bark and ambrosia beetles (Scolytinae), longhorn beetles (Cerambycidae), and jewel beetles (Buprestidae) (Eyre and Haack 2017). These insects may be present in wood-packaging materials, timber, and plants for planting (Meurisse et al. 2019), and are difficult to detect by routine inspections as infested materials may show little or no sign of infestation (Humble 2010). Traps baited with attractive lures placed in and around entry points are commonly used to complement visual inspections and improve chances of intercepting incoming species soon after their arrival (Poland and Rassati 2019). Given that surveillance activities can be expensive and budgets are often limited, the main challenge is to develop trapping protocols that can attract multiple species simultaneously (e.g., Wong et al. 2012, Rassati et al. 2014, Chase et al. 2018). This can be achieved by selecting the trap color, trap height, and attractive lure blend that maximizes detection of target taxa, as recently shown for longhorn and jewel beetles (Rassati et al. 2019). Understanding whether trapping protocols developed for detection of longhorn and jewel beetles can also reliably detect bark and ambrosia beetles requires investigation.

Trap color is a key variable for successfully trapping longhorn beetles and jewel beetles, with many species preferring green traps to purple traps, and some preferring the opposite (Francese et al. 2010, Rhainds et al. 2017, Rassati et al. 2019, Imrei et al. 2020). However, few studies have been published on the effects of trap color on catch of bark and ambrosia beetles. Comparisons of Scolytinae catches among trap colors have produced varied results. Some conifer-infesting bark beetles (e.g., *Dendroctonus* and *Ips* spp.) and ambrosia beetles (e.g., *Trypodendron lineatum* (Olivier)) preferred black-colored traps to white-colored traps (Strom et al. 1999, 2001; Campbell and Borden 2006a,b, 2009), presumably because black traps better resemble the silhouette and color of host tree trunk and bark. Some species preferred dark colors with long wavelengths (e.g., black, brown, red) over light colors such as white and yellow (Dubbel et al. 1985, Strom and Goyer 2001, Chen et al. 2010, Hanula et al. 2011, Werle et al. 2014, Kerr et al. 2017), and other species preferred a specific color, e.g., green by *Hypocryphalus mangiferae* (Stebbing) and *Xylosandrus crassiusculus* (Motschulsky) (Abbasi et al. 2007; Gorzlancyk et al. 2013, 2014), and red by *Hypothenemus hampei* Ferrari (Dufour and Frérot 2008). Thus, further investigation is necessary to understand the effects on Scolytinae detection of trap colors already shown to be suitable for detection of longhorn and jewel beetles, i.e., green, and less so, purple.

Trap height is another key variable affecting trap catches of longhorn (e.g., Graham et al. 2012, Schmeelk et al. 2016, Rassati et al. 2019, Flaherty et al. 2019) and jewel beetles (Imrei et al. 2020). Evidence exists also for Scolytinae, although trends are inconsistent. Several studies reported a higher Scolytinae richness in the understory than in the canopy (Ulyshen and Hanula 2007, Dodds 2014, Hardersen et al. 2014, Flaherty et al. 2019), whereas other studies did not find clear differences among forest strata (Leksono et al. 2005, Wermelinger et al. 2007). In addition, vertical distribution patterns vary between bark beetles and ambrosia beetles: bark beetles are generally more abundant in mid and upper forest strata, whereas ambrosia beetles are generally more abundant in the understory (Sheehan et al. 2019, Ulyshen and Sheehan 2019). However, even the latter patterns are not always consistent, as some ambrosia beetles developing in twigs or branches are more abundant in the canopy and some bark beetles developing in woody debris and stumps are mainly trapped in the understory (Klingeman et al. 2017, Procházka et al. 2018, Miller et al. 2020). Vertical distribution patterns can also change depending on the type, structure, and composition of sampled forest. Procházka et al. (2018) found vertical patterns of ambrosia beetles to vary between lowland and montane forests, and Menocal et al. (2018) found absence of vertical stratification for several ambrosia beetles in avocado orchards. Thus, further investigations are needed to better clarify the effect of trap height on bark and ambrosia beetles.

Among factors affecting catch of wood-boring beetles in traps, semiochemicals are the most studied. Significant progress in our knowledge of longhorn beetle chemical ecology (Hanks and Millar 2016) has led to the development of efficient '*multi-lure*' traps, i.e., single traps baited with multiple longhorn beetle pheromones that attract several longhorn beetle species simultaneously (e.g., Wong et al. 2012, Fan et al. 2019, Rassati et al. 2019). These pheromone blends, which appear to have neutral effect on jewel beetles (Flaherty et al. 2019, Rassati et al. 2019), are often complemented with host volatiles, such as ethanol and α-pinene. The latter volatiles not only synergize longhorn beetle pheromones (Hanks et al. 2012, Miller et al. 2015a, Collignon et al. 2016), but also act as attractants for some jewel beetles (Miller 2006) and bark and ambrosia beetles (Miller and Rabaglia 2009, Ranger et al. 2020). Thus, a blend of pheromones and host volatiles can be potentially used to attract longhorn beetles, jewel beetles, as well as bark and ambrosia beetles simultaneously (Flaherty et al. 2019). The main limitations of this approach are the possible negative interactions that can occur among blend components. For instance, α-pinene can reduce or even interrupt attraction of certain ambrosia beetles to ethanol (Schroeder and Lindelöw 1989, Lindelöw et al. 1993. Miller and Rabaglia 2009, Ranger et al. 2011). Longhorn beetle pheromones can have both positive and negative effects on catch of bark and ambrosia beetles, depending on the species. For example, adding the relatively common cerambycine pheromone, racemic 3-hydroxyoctan-2-one, to ethanol-baited traps significantly reduced catches of *Dryoxylon onoharaensum* (Murayama) (Miller et al. 2015a), *Anisandrus maiche* Kurentsov, *Xyleborinus attenuatus* (Blandford), and *T. lineatum* (Sweeney et al. 2016), but significantly increased catches of *Monarthrum scutellare* (LeConte) (Noseworthy et al. 2012) and *Hypothenemus rotundicollis* Wood & Bright (Miller et al. 2015a). Further studies are thus essential to elucidate how different blends can affect overall detection of bark and ambrosia beetles in traps.

Our goal was to investigate whether trapping protocols designed for longhorn beetles and jewel beetles associated either with broadleaf or conifer trees can be exploited also for bark and ambrosia beetles. To this aim, in factorial experiments conducted in Italy and Canada we tested how three key variables commonly exploited for trapping surveys of longhorn and jewel beetles, i.e., trap color, trap height, and attractive blend, can affect species richness and abundance of Scolytinae in traps. These effects were tested separately on bark beetles and ambrosia beetles, as well as on individual species. In addition, in order to test whether the effect of trapping variables change depending on the forest type, these factors were tested both in seminatural forests and reforested forests in Italy. Based on available literature, we predicted that both bark and ambrosia beetles would be preferentially attracted by purple traps than green traps due to a higher resemblance of the former to host tree bark. In addition, we predicted a mixed response to trap height, with higher richness and abundance in the canopy than in the understory for bark beetles and the opposite trend for ambrosia beetles, although we expected this pattern to differ between seminatural and reforested forests. Finally, we predicted that the attractive blend developed for longhorn and jewel beetles associated with broadleaf hosts would reliably attract both bark and ambrosia beetles, whereas the blend developed for conifer-associated species would be more efficient for detecting bark beetles than ambrosia beetles.

Materials and Methods

Study Sites

In 2016, two trapping studies were conducted, one in Italy and one in Canada. The methods, experimental design, and results regarding effects of trap color, trap height, and lure, on detection of Buprestidae and Cerambycidae have already been described (Rassati et al. 2019) but basic methods are described here for the reader's convenience. In Italy, the study was carried out at 17 forest sites (i.e., nine seminatural forests and eight reforested forests) located in the northeast (Supp Table S1 [online only]). By 'seminatural forests' we refer to the remains of old oaks (*Quercus* spp.) and hop-hornbeam (*Ostrya carpinifolia* Scopoli) forests that covered the majority of North-Eastern Italian lowlands after the last ice age and that are today present only in small patches embedded in an agriculture-dominated landscape. By 'reforested forests' we refer to mixed forests recently established (i.e., last 30 yr) to reconvert agricultural fields to woodlands. Both forest types were dominated by oaks, ashes (*Fraxinus* spp.), maples (*Acer* spp.), and hop-hornbeam. Nonetheless, seminatural forests were characterized by taller and more mature trees than reforested forests, as well as by a higher volume of dead wood as a result of different management strategies. In Canada, the study was carried out at Magazine Hill, Halifax, Nova Scotia (Supp Table S1 [online only]), in a mixed broadleaf–coniferous forest dominated by *Acer rubrum* L., *Populus tremuloides* Michx., and *Picea rubens* Sarg., with lesser amounts of *Betula papyrifera* Marsh and *Fagus grandifolia* (Ehrh.), located near an industrial park and container facility that receives goods from overseas.

Trap Type, Trap Color, Trap Height, and Experimental Scheme

In both countries, we used 12-funnel Lindgren traps (Synergy Semiochemicals Corp., Delta, BC, Canada), which were preferred over panel traps as more resistant, simpler and quicker to set up, and thus more suitable to be used in surveillance programs carried out at entry points (Rassati et al. 2014). All traps were coated by the supplier with a 33% solution of Fluon diluted in water to improve trapping efficacy (Allison et al. 2016). In Italy, trap-collecting cups were filled with a 50% solution of ethylene glycol and water, whereas in Canada the cups were filled with a saturated solution of table salt in water, plus a drop of dish detergent to reduce surface tension. We used this technique as traps equipped with wet cups reduce insect escape and help to preserve trapped insects (Allison and Redak 2017). Traps were of two colors: green and purple (known as 'EAB green' and 'EAB purple', respectively; Synergy Semiochemicals Corp.). Half of the traps were set up in the understory and half were set up in the upper one-third of the tree canopy. Understory traps were placed with collecting cups 0.3–1 m above the ground, suspended either from rope tied between two trees or tree branches such as that traps were at least 1 m from the tree bole. Canopy traps were set up following the methodology described by Hughes et al. (2014). Canopy tree stratum ranged from 4–7 m in the youngest reforested forests to 12–15 m in the oldest seminatural forests in Italy, whereas in Canada, it was around 10–15 m.

Traps were deployed in a factorial scheme 2 × 2 × 2 (color × lure × height) both in Italy and Canada. The eight treatments were replicated 17 times in Italy and 6 times in Canada in a randomized complete block design (Supp Fig. S1 [online only]). In Italy, each block was represented by a different site. In Canada, a distance of at least 30 m was kept among blocks and traps. Traps were active from 9 May to 3 August 2016 in Italy, and from 2 May to 22 August 2016 in Canada. Traps were emptied every 3 wk in Italy and every 2 wk in Canada. Collected bark and ambrosia beetles were stored in alcohol or at −10°C until processed, identified to species, and classified as either exotic or native to either Italy or Canada according to the available literature (Bright 1976, Balachowsky 1949, Pfeffer 1995, Bousquet et al. 2013). In Italy, only ambrosia beetles were identified, whereas identification was carried out for both bark beetles and ambrosia beetles in Canada. Voucher specimens of Scolytinae species have been deposited in the insect collections at University of Padua, Padua, Italy and the Atlantic Forestry Center, Fredericton, NB, Canada.

Attractive Lures

In Italy, traps were baited either with UHR (ultra-high release) ethanol or a blend composed by UHR ethanol and five longhorn beetle pheromones, namely racemic 3-hydroxyhexan-2-one (K6), racemic 3-hydroxyoctan-2-one (K8), *syn*-2,3-hexanediols (D6), (*E*/*Z*)-fuscumol, and (*E*/*Z*)-fuscumol acetate (see Supp Table S2 [online only] for information on release devices and rates). The latter blend, hereafter referred to as 'hardwood-blend', was designed mainly for detecting species infesting hardwoods, and attracts a large number of broadleaf-associated longhorn beetles with apparently neutral effect on jewel beetles (Flaherty et al. 2019, Rassati et al. 2019) and Scolytinae (Flaherty et al. 2019). Ethanol enhances attraction of many longhorn beetle species to the above-listed pheromones (Hanks et al. 2012, Miller et al. 2015a, Collignon et al. 2016). Dispenser lures were renewed after 2 mo according to their expected field life.

In Canada, traps were baited either with the same blend used in Italy (i.e., 'hardwood-blend') or a blend composed of UHR ethanol, UHR α-pinene, ipsenol, and 2-undecyloxy-1-ethanol (also known as monochamol) (see Supp Table S2 [online only] for information on release devices and rates). The latter blend, hereafter referred to as 'softwood-blend', was designed mainly for species infesting softwoods (Flaherty et al. 2019). α-Pinene is a common host volatile of conifers and attracts several species of wood-boring beetles (Miller and Rabaglia 2009). Ipsenol is a bark beetle pheromone that often increases catches of wood-boring beetles in traps baited with ethanol and α-pinene (Miller et al. 2015b) and monochamol is an aggregation pheromone produced by mature males of *Monochamus* spp. that is attractive to several species in this genus (Boone et al. 2019). The K6, K8, D6, (*E*/*Z*)-fuscumol, and (*E*/*Z*)-fuscumol acetate lures were replaced after 2 mo; the UHR ethanol, UHR α-pinene, monochamol, and ipsenol lures were not replaced as these lures usually last 16 wk in Eastern Canadian summers.

Statistical Analysis

The effects of lure (i.e., hardwood-blend vs ethanol in Italy; hardwood-blend vs softwood-blend in Canada), trap color (purple vs green), trap height (canopy vs understory), and their interactions on ambrosia beetles (both in Canada and Italy) and bark beetles (only in Canada) were tested using either linear mixed-effects models (LMMs) with normal distribution or generalized linear mixed-effects models (GLMMs) with negative binomial distribution (Tables 1 and 2). The total number of species (i.e., species richness) or individuals (i.e., abundance) collected per trap per each lure–height–color combination over the entire trapping period was the response variable. For LMM with normal distribution, abundance was either log- or square root-transformed to satisfy the assumption of normality when necessary. Models included site (for Italy) or block (for Canada) as a random factor to account for spatial dependence in the sampling design. In Italy, the effect of the selected variables on ambrosia beetle catches was tested separately for seminatural forests and reforested forests. LMMs were fitted using the 'lmer' function in the package 'lme4' (Bates et al. 2017) implemented in R (R Core Team 2019), with significance determined by standard *F*-tests. GLMMs were fitted using the 'glmmTMB' function in the package 'glmmTMB' (Magnusson et al. 2017) implemented in R, with significance determined by the Wald chi-square test. Model overdispersion and residual distribution were 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. iNEXT package (Hsieh et al. 2016) for R was used to generate curves showing the mean number of species detected per number of trap samples for each of the eight different trap color–height–lure combinations in both Canada and Italy.

Table 1. Total number of species and individuals of ambrosia beetles caught in Italy in seminatural forests and reforested forests, and results of the statistical models (*P*-value) used to test the effect of attractive lure (ethanol vs hardwood-blend), trap color (green vs purple), trap height (canopy vs understory), and their interactions on ambrosia beetle catches

	Total	Color	Height	Lure	df	Significant interactions	Model	Distribution
Italy								
Seminatural forests								
Species richness	8	0.208	<0.001	0.344	1, 60	–	LMM	Normal
Abundance	78,358	0.013	<0.001	0.330	1, 60	–	LMM	Log-transf.
Ambrosiodmus rubricollis (Eichhoff)*	11	–	–	–	–	–	n.t.	–
Ambrosiophilus atratus (Eichhoff)*	10	–	–	–	–	–	n.t.	–
Anisandrus dispar (Fabricius)	1,163	0.517	<0.001	0.473	1, 59	Color × Height	LMM	Log-transf.
Xyleborinus saxesenii (Ratzeburg)	57,311	0.059	<0.001	0.576	1, 60	–	LMM	Log-transf.
Xyleborus dryographus (Ratzeburg)	21	–	–	–	–	–	n.t.	–
Xyleborus monographus (Fabricius)	313	0.833	0.001	0.741	1, 58	–	GLMM	Neg. bin.
Xylosandrus crassiusculus (Motschulsky)*	154	0.376	0.077	0.136	1, 32	–	LMM	Log-transf.
Xylosandrus germanus (Blandford)*	19,375	<0.001	<0.001	0.004	1, 59	–	LMM	Log-transf.
Reforested forests								
Species richness	7	0.158	0.569	0.840	1, 52	Color × Height	LMM	Normal
Abundance	26,586	0.827	0.234	0.018	1, 51	Color × Height, Height × Lure	LMM	Log-transf.
Ambrosiodmus rubricollis (Eichhoff)*	–	–	–	–	–	–	n.t.	–
Ambrosiophilus atratus (Eichhoff)*	12	–	–	–	–	–	n.t.	–
Anisandrus dispar (Fabricius)	1,519	0.218	0.142	0.782	1, 53	–	LMM	Sqrt-transf.
Xyleborinus saxesenii (Ratzeburg)	22,869	0.250	0.112	0.004	1, 51	Color × Height, Height × Lure	LMM	Log-transf.
Xyleborus dryographus (Ratzeburg)	15	–	–	–	–	–	n.t.	–
Xyleborus monographus (Fabricius)	4	–	–	–	–	–	n.t.	–
Xylosandrus crassiusculus (Motschulsky)*	689	0.177	0.097	0.500	1, 25	–	LMM	Log-transf.
Xylosandrus germanus (Blandford)*	1,478	0.870	0.011	0.858	1, 45	Color × Height	LMM	Log-transf.

Models = LMM: linear mixed-effects model; GLMM: generalized linear mixed-effects model. * = exotic species; n.t. = not tested. Distribution = Log-transf.: normal on log-transformed data; Neg. bin.: negative binomial; Sqrt-transf.: normal on square root-transformed data. df = degrees of freedom in form of numerator, denominator. Degrees of freedoms are reported only once for each species as they were the same for all variables in each model.

Results

General Results

In Italy, a total of 104,944 individuals from eight ambrosia beetle species were caught. Among them, four were exotic species known to be established in Italy (Table 1). Both ambrosia beetle species richness and abundance were higher in seminatural forests than in reforested forests (8 vs 7 species and 78,358 vs 26,586 individuals, respectively) (Table 1). The native *Xyleborinus saxesenii* (Ratzeburg) was the most abundant species in both seminatural and reforested forests (57,311 and 22,869 individuals, respectively), whereas differences among forest types emerged for abundance of the other species collected. In seminatural forests, the exotic *Xylosandrus germanus* (Blandford) was the second most abundant species (19,375 individuals), whereas in reforested forests, its abundance was a 10th of that, and was lower than that of the native *Anisandrus dispar* (Fabricius) (Table 1). In addition, the native *Xyleborus monographus* (Fabricius) was considerably more abundant in seminatural forests than in reforested forests (313 vs 4 individuals), whereas the opposite trend was found for the exotic *X. crassiusculus* (154 vs 689 individuals).

In Canada, a total of 16,492 individuals from 35 scolytine species were caught (Table 2). Among them, seven were exotic species (Table 2). Bark beetles were more species-rich than ambrosia beetles (25 vs 10), whereas the trend was opposite for abundance (13,083 for ambrosia beetles and 3,409 for bark beetles) (Table 2). Among ambrosia beetles, the exotic *X. germanus* was the most abundant species (5,833 individuals), followed by the native *Anisandrus sayi* Hopkins (5,240 individuals) and the exotic *X. attenuatus* (1,606 individuals). Among bark beetles, *Pseudopityophthorus minutissimus* (Zimmermann) was the most abundant species (791 individuals), followed by *Cryphalus ruficollis* Hopkins (672 individuals) and *Pseudopityophthorus asperulus* (LeConte) (626 individuals) (Table 2). These were the first Canadian records for *P. asperulus* and the first Nova Scotia records for the exotic bark beetle, *Hylastes opacus* Erichson (Webster et al. 2020). Two ambrosia beetle species and 10 bark beetle species were represented by less than 10 individuals.

Effect of Trap Color, Trap Height, and Attractive Lure on Bark and Ambrosia Beetles

In Italy, the effects of trap color, height, and lure on ambrosia beetle species richness and abundance differed in seminatural versus reforested forests. In seminatural forests, species richness was significantly affected by trap height ($F = 36.40$) (Table 1), with more species detected in understory traps than canopy traps (Fig. 1A; Supp Table S3 [online only]). In reforested forests, species richness was significantly affected by the interaction between trap color and trap height ($F = 4.96$; $P < 0.030$): purple traps outperformed green traps in the understory but not in the canopy (Fig. 1C; Supp Table S3 [online only]). The species accumulation curves show that in both forest types, purple understory traps baited with ethanol detected the most ambrosia beetle species per trap, whereas green canopy traps baited with the hardwood-blend detected the fewest (Fig. 2A and B).

In seminatural forests, ambrosia beetle abundance was significantly affected by trap color ($F = 6.43$) and trap height ($F = 85.05$) (Table 1); understory traps outperformed canopy traps, and purple traps outperformed green traps (Fig. 1B; Supp Table S3 [online only]). In reforested forests, ambrosia beetle abundance was significantly affected by attractive blend ($F = 5.91$), and the interactions

Table 2. Total number of species and individuals of ambrosia beetles and bark beetles caught in Canada, and results of the statistical models (*P*-value) used to test the effect of attractive lure (softwood-blend vs hardwood-blend), trap color (green vs purple), trap height (canopy vs understory), and their interactions on bark and ambrosia beetle catches

	Total	Color	Height	Lure	df	Significant interactions	Model	Distribution
Canada								
Ambrosia beetles								
Species richness	10	0.752	<0.001	0.529	1, 44	–	LMM	Normal
Abundance	13,083	0.003	<0.001	<0.001	1, 41	Height × Lure	GLMM	Neg. bin.
Anisandrus dispar (Fabricius)*	18	–	–	–	–	–	–	–
Anisandrus sayi Hopkins	5,240	0.820	0.146	<0.001	1, 38	Color × Lure	LMM	Log-transf.
Gnathotrichus materiarius (Fitch)	10	–	–	–	–	–	n.t.	–
Monarthrum mali (Fitch)	2	–	–	–	–	–	n.t.	–
Trypodendron betulae Swaine	1	–	–	–	–	–	n.t.	–
Trypodendron lineatum (Olivier)	230	0.168	<0.001	<0.001	1, 42	–	GLMM	Neg. bin.
Xyleborinus attenuatus (Blandford)*	1,606	0.096	0.458	0.317	1, 44	–	LMM	Normal
Xyleborinus saxesenii (Ratzeburg)*	11	–	–	–	–	–	n.t.	–
Xylosandrus germanus (Blandford)*	5,833	0.334	<0.001	0.504	1, 38	Color × Height	LMM	Log-transf.
Xyloterinus politus (Say)	132	0.002	0.022	0.030	1, 43	Color × Lure	LMM	Normal
Bark beetles								
Species richness	25	0.185	0.396	0.001	1, 43	Height × Lure	LMM	Normal
Abundance	3,409	0.340	0.015	0.580	1, 38	Height × Lure	LMM	Log-transf.
Conophthorus coniperda (Schwarz)	4	–	–	–	–	–	n.t.	–
Cryphalus ruficollis Hopkins	672	0.167	<0.001	<0.001	1, 43	Color × Lure	LMM	Log-transf.
Crypturgus borealis Swaine	86	0.466	0.164	0.626	1, 42	–	GLMM	Neg. bin.
Crypturgus pusillus (Gyllenhal)*	338	0.241	0.138	<0.001	1, 42	–	GLMM	Neg. bin.
Dendroctonus rufipennis (Kirby)	2	–	–	–	–	–	n.t.	–
Dryocoetes affaber (Mannerheim)	34	–	–	–	–	–	n.t.	–
Dryocoetes autographus (Ratzeburg)	53	0.848	<0.001	0.004	1, 42	–	GLMM	Neg. bin.
Hylastes opacus Erichson*	13	–	–	–	–	–	n.t.	–
Hylastinus obscurus (Marsham)*	7	–	–	–	–	–	n.t.	–
Hylesinus aculeatus Say	3	–	–	–	–	–	n.t.	–
Hylurgops pinifex (Fitch)	1	–	–	–	–	–	n.t.	–
Ips grandicollis (Eichhoff)	368	0.982	0.825	<0.001	1, 42	–	GLMM	Neg. bin.
Ips perroti Swaine	1	–	–	–	–	–	n.t.	–
Ips pini (Say)	20	–	–	–	–	–	n.t.	–
Lymantor decipiens (LeConte)	16	–	–	–	–	–	n.t.	–
Orthotomicus caelatus (Eichhoff)	178	0.390	0.001	<0.001	1, 42	–	GLMM	Neg. bin.
Orthotomicus latidens (LeConte)	4	–	–	–	–	–	n.t.	–
Pityogenes hopkinsi Swaine	10	–	–	–	–	–	n.t.	–
Pityokteines sparsus (LeConte)	2	–	–	–	–	–	n.t.	–
Pityophthorus ramiperda Swaine	7	–	–	–	–	–	n.t.	–
Pityophthorus sp.	49	–	–	–	–	–	n.t.	–
Polygraphus rufipennis (Kirby)	121	0.007	0.761	<0.001	1, 42		GLMM	Neg. bin.
Pseudopityophthorus asperulus (LeConte)	626	0.048	<0.001	0.029	1, 44	–	LMM	Log-transf.
Pseudopityophthorus minutissimus (Zimmermann)	791	0.972	0.006	<0.001	1, 42	–	GLMM	Neg. bin.
Scolytus piceae (Swaine)	3	–	–	–	–	–	n.t.	–

Models = LMM: linear mixed-effects model; GLMM: generalized linear mixed-effects model. * = exotic species; n.t. = not tested. Distribution = Log-transf.: normal on log-transformed data; Neg. bin.: negative binomial. df = degrees of freedom in form of numerator, denominator. Degrees of freedoms are reported only once for each species as they were the same for all variables in each model.

between trap color and trap height (F = 8.08; P = 0.006) and trap height and attractive blend (F = 5.77; P = 0.019) (Table 1). Ethanol-baited traps captured more ambrosia beetles than traps baited with the hardwood-blend (Fig. 1D; Supp Table S3 [online only]) and this was more evident in the canopy of reforested forests than in the understory. Purple traps performed better than green traps in the understory of reforested forests but not in the canopy (Fig. 1D).

In Canada, ambrosia beetle species richness was significantly affected only by trap height (F = 16.97) (Table 2), with understory traps outperforming canopy traps (Fig. 1E; Supp Table S4 [online only]). Species accumulation curves showed that green understory traps baited with the softwood-blend detected the most species of ambrosia beetles per trap, whereas the same traps placed in the canopy detected the fewest (Fig. 2C). Ambrosia beetle abundance, instead, was significantly affected by all tested variables (Table 2), plus the interaction between trap height and attractive lure (χ^2 = 28.09; P < 0.001). In general, purple traps, understory traps, and hardwood-baited traps performed better than green traps, canopy traps, and softwood-baited traps, respectively (Fig. 1F; Supp Table S4 [online only]). In addition, the higher attractiveness of hardwood-baited traps than softwood-baited traps was more evident in the canopy than in the understory (Fig. 1F).

Bark beetle species richness was affected by attractive blend (F = 11.71), and marginally by the interaction between trap height and attractive blend (F = 3.54; P = 0.066) (Table 2). Softwood-baited traps outperformed hardwood-baited traps and this trend was more evident in the understory than in the canopy (Fig. 1G; Supp Table S4 [online only]). The species accumulation curves showed that understory traps baited with the softwood-blend detected the most species per trap, with purple and green traps performing almost equally (Fig. 2D). Bark beetle abundance was significantly affected by trap height (F = 6.36) and the interaction between trap height and attractive blend (F = 12.63; P = 0.001) (Table 2). Canopy traps caught more individuals than understory traps (Fig. 1H) and softwood-baited traps performed better than hardwood-baited traps in the understory but not in the canopy (Fig. 1H).

Effect of Trap Color, Trap Height, and Attractive Lure on Individual Species

In Italy, tested variables significantly affected abundance of five ambrosia beetle species in seminatural forests and three ambrosia beetle species in reforested forests (Table 1), but with mixed responses. In seminatural forests, understory traps performed significantly better than canopy traps in detecting *A. dispar* (F = 19.11) (Fig. 3A), *X. saxesenii* (F = 43.56) (Fig. 3B), *X. germanus* (F = 131.52) (Fig. 3D), *X. monographus* (χ^2 = 10.43) (Fig. 3E), and marginally *X. crassiusculus* (F = 3.31) (Fig. 3C). In reforested forests, the same pattern was found only for *X. germanus* (F = 6.95) (Fig. 3I) and marginally *X. crassiusculus* (F = 2.97) (Fig. 3H). Trap color significantly affected mean catch of *X. germanus* (F = 20.58) (Fig. 3D) and marginally *X. saxesenii* (F = 3.68) (Fig. 3B) in seminatural forests, with purple traps outperforming green traps, but had no effects on catch of any species in reforested forests (Table 1; Supp Table S3 [online only]). Three species were significantly affected by the interaction between trap color and trap height. In reforested forests, purple traps caught significantly more *X. saxesenii* and *X. germanus* individuals than green traps in the understory but not in the canopy (F = 12.27; P < 0.001 and F = 3.92; P = 0.053, respectively) (Fig. 3G and I; Supp Table S3 [online only]). In seminatural forests, however, green traps caught more *A. dispar* individuals than purple traps in the understory but not in the canopy (F = 2.99; P = 0.088) (Fig. 3A). Finally,

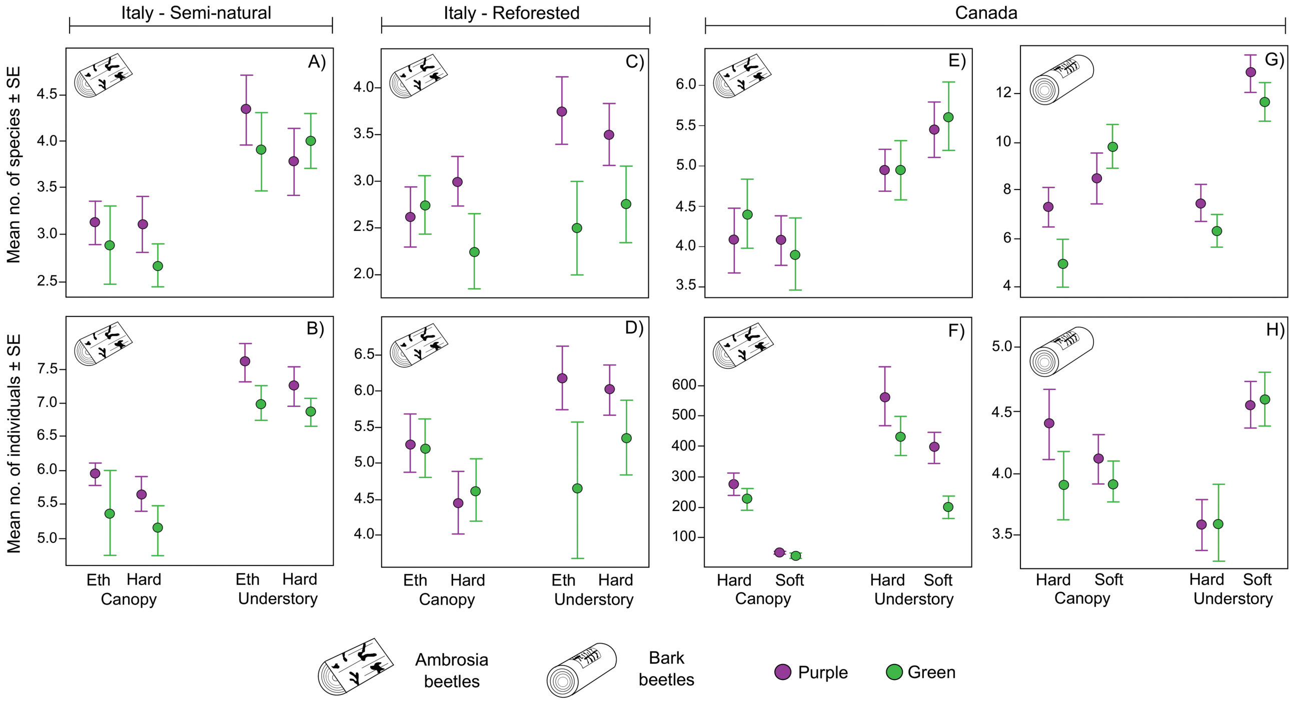

Fig. 1. Effect of trap color, trap height, attractive lures, and their interactions on species richness and abundance of bark and ambrosia beetles caught in Italy (seminatural forests vs reforested forests) and Canada. Abundance of both bark beetles and ambrosia beetles (except for Canada) is log-transformed according to data transformation used in statistical analysis. Eth = ethanol; Hard = hardwood-blend; Soft = softwood-blend.

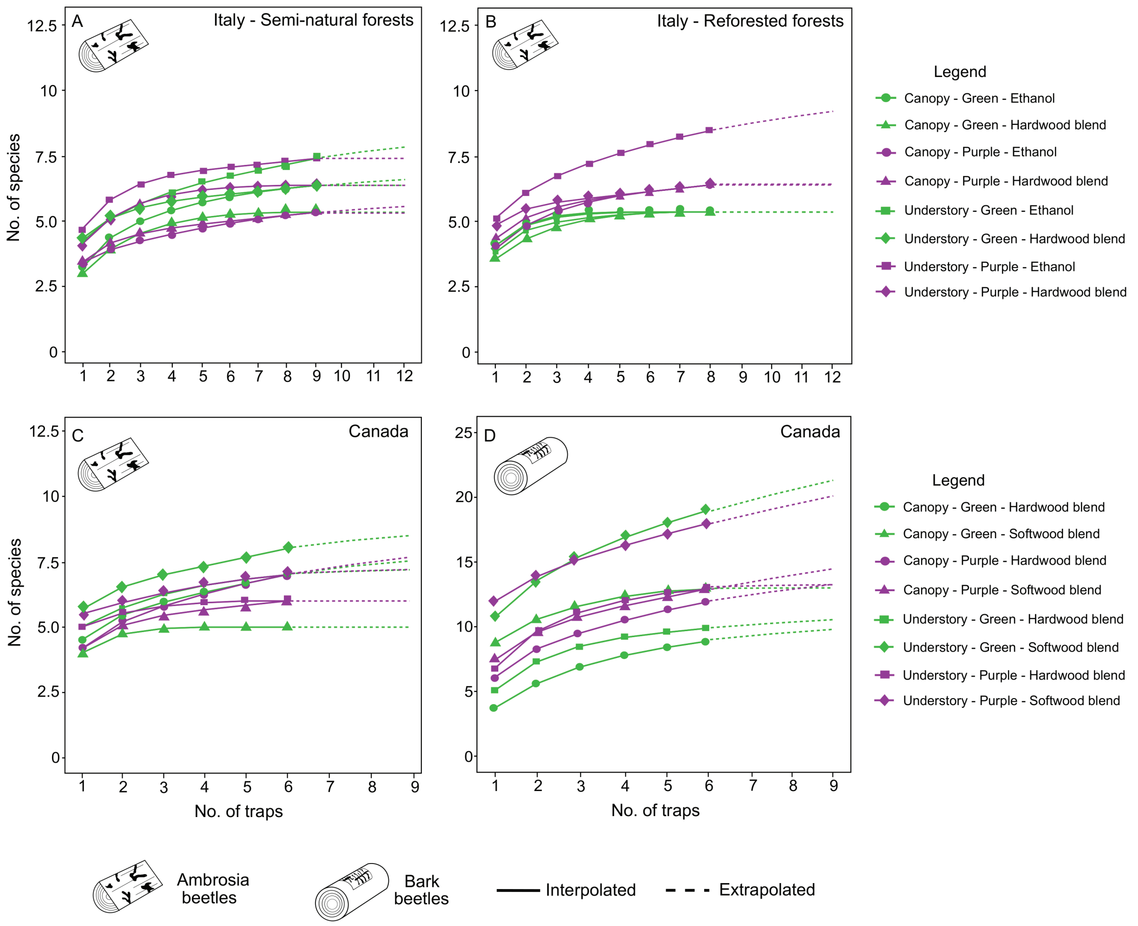

Fig. 2. Interpolation and extrapolation curves showing mean number of ambrosia (A–C) and bark beetle (D) species detected in Italy and Canada per number of trap samples in green versus purple funnel traps placed in the upper canopy versus understory and baited with two different lures. In Italy, the lures were ethanol versus hardwood-blend; in Canada, hardwood-blend versus softwood-blend. See text for details on multi-lure components.

ethanol-baited traps performed better than hardwood-baited traps at detecting *X. germanus* in seminatural forests ($F = 8.83$) (Fig. 3D) and *X. saxesenii* in reforested forests ($F = 8.92$) (Fig. 3G; Supp Table S3 [online only]).

In Canada, tested variables significantly affected five ambrosia beetle species and seven bark beetle species (Table 2). Among ambrosia beetles, *A. sayi* ($F = 252.26$), *T. lineatum* ($\chi^2 = 56.07$), and *Xyloterinus politus* (Say) ($F = 5.02$) were significantly affected by the attractive blend (Table 2); hardwood-baited traps caught more *A. sayi* (Fig. 4A) and *X. politus* (Fig. 4E) individuals than did softwood-baited traps (Supp Table S4 [online only]), whereas the opposite trend was found for *T. lineatum* (Fig. 4B; Supp Table S4 [online only]). Trap height affected abundance of *T. lineatum* ($\chi^2 = 41.16$), *X. germanus* ($F = 132.50$), and *X. politus* ($F = 5.57$): in all cases, understory traps outperformed canopy traps (Fig. 4B, D, and E; Supp Table S4 [online only]). Purple traps caught more individuals than green traps only for *X. politus* ($F = 10.55$) (Fig. 4E) and marginally *X. attenuatus* ($F = 2.87$) (Fig. 4C). The latter pattern was found in the understory but not in the canopy for *X. germanus* ($F = 5.32$; $P = 0.026$) (Fig. 4D), and in softwood-baited traps but not in hardwood-baited traps for *A. sayi* ($F = 4.83$; $P = 0.034$) (Fig. 4A).

Among bark beetles, seven species were significantly affected by attractive blend, although with mixed patterns (Table 2). Softwood-baited traps performed better than hardwood-baited traps for *C. ruficollis* ($F = 20.05$) (Fig. 4F; Supp Table S4 [online only]), *Crypturgus pusillus* (Gyllenhal) ($\chi^2 = 48.70$) (Fig. 4G), *Dryocoetes autographus* (Ratzeburg) ($\chi^2 = 8.13$) (Fig. 4H), *Ips grandicollis* (Eichhoff) ($\chi^2 = 87.74$) (Fig. 4I), *Orthotomicus caelatus* (Eichhoff) ($\chi^2 = 24.03$) (Fig. 4J), and *Polygraphus rufipennis* (Kirby) ($\chi^2 = 12.75$) (Fig. 4K), whereas hardwood-baited traps performed better than softwood-baited traps for *P. asperulus* ($F = 5.03$) (Fig. 4L) and *P. minutissimus* ($\chi^2 = 38.32$) (Fig. 4M). Trap height affected abundance of five bark beetle species (Table 2), but again with mixed responses. Understory traps performed better than canopy traps for *C. ruficollis* ($F = 27.49$) (Fig. 4F), *D. autographus* ($\chi^2 = 20.67$) (Fig. 4H), and *O. caelatus* ($\chi^2 = 10.50$) (Fig. 4J), whereas the opposite trend was found for *P. asperulus* ($F = 14.64$) (Fig. 4L) and *P. minutissimus* ($\chi^2 = 7.29$) (Fig. 4M). Lastly, purple traps performed better than green traps in detecting *P. rufipennis* ($\chi^2 = 7.04$) (Fig. 4K) and *P. asperulus* ($F = 4.13$) (Fig. 4L).

Discussion

Traps baited with attractive lures are set up in or around international points of entry to improve the chance of intercepting incoming wood-boring beetles and complement visual inspections of imported commodities (Poland and Rassati 2019). Trapping protocols that simultaneously detect longhorn beetles and jewel beetles have been recently developed for both broadleaf- and conifer-associated species (Flaherty et al. 2019, Rassati et al. 2019), but

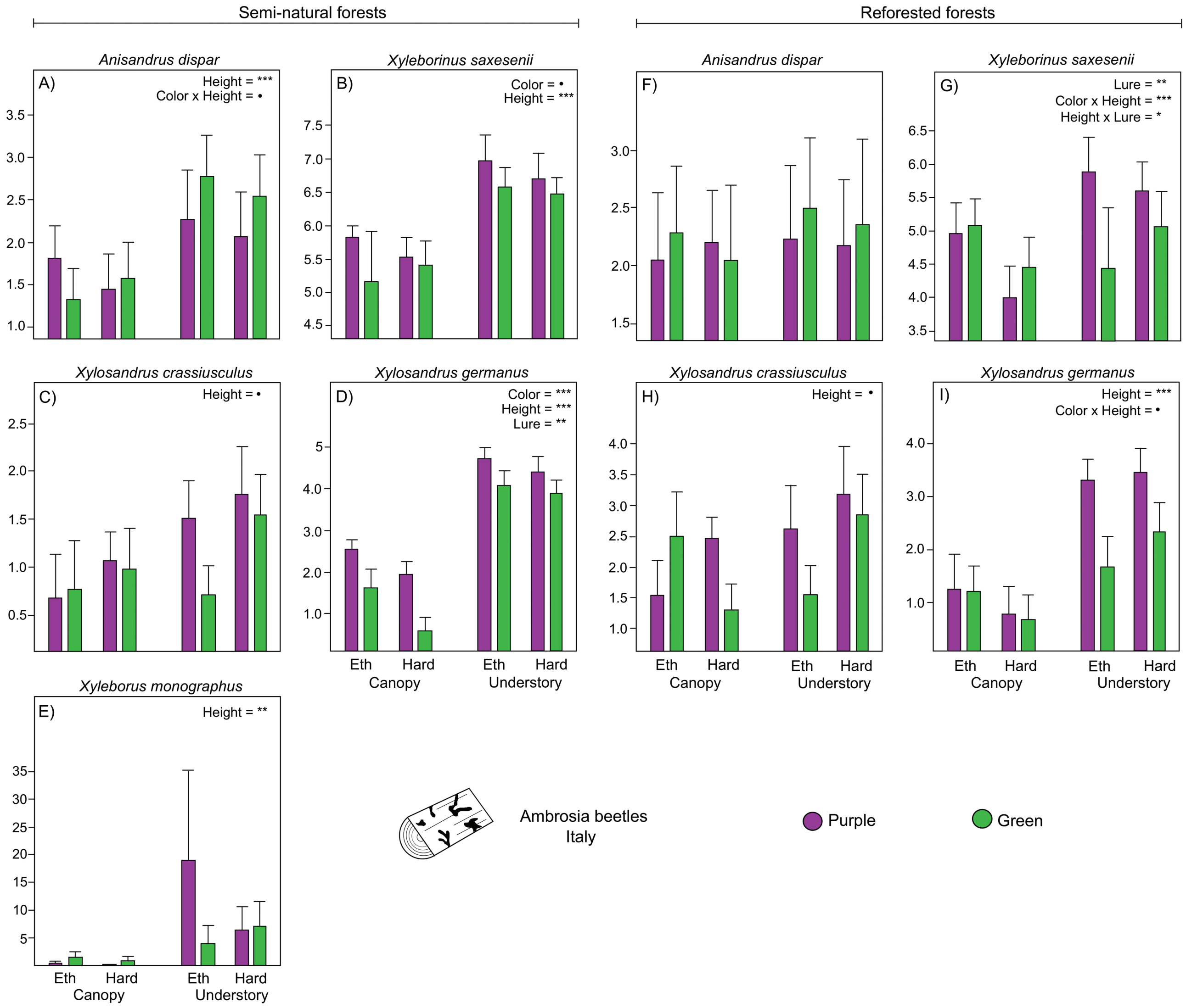

Fig. 3. Effect of trap color, trap height, attractive lures, and their interactions on ambrosia beetle species caught in Italy in seminatural forests and reforested forests. Significant explanatory variables and/or interactions are displayed within each box with black asterisk/s or black circle depending on the *P*-value: ****P* < 0.001; ***P* < 0.01; **P* < 0.05; •*P* < 0.1. Except for *X. monographus*, abundance is transformed according to data transformation used in statistical analysis (A, B, C, D, G, H, I = log-transformed; F = square root-transformed). Eth = ethanol; Hard = hardwood-blend.

their efficacy in detecting bark and ambrosia beetles is less known, particularly the effects of trap color and longhorn beetle pheromones. Here we show the effects of trap color, trap height, and attractive lure blend on catches of bark and ambrosia beetles, and propose two trapping protocols for generic surveillance of longhorn beetles, jewel beetles, and bark and ambrosia beetles at risk of arriving and establishing in broadleaf or mixed forests close to entry points.

Trap color generally affected abundance of ambrosia beetles in traps but not species richness, and had almost no effect on catch of bark beetles. Previous studies reported that bark and ambrosia beetle abundance was greater in dark-colored traps (resembling bark of host trees) than in light-colored traps (Dubbel et al. 1985, Chen et al. 2010, Hanula et al. 2011, Allison and Redak 2017) and that yellow and white traps were avoided (Strom and Goyer 2001, Werle et al. 2014, Kerr et al. 2017). Here we confirmed the lack of response to color by most bark beetles, and showed that ambrosia beetles were generally detected more often in purple traps than in green traps. The latter result was largely due to an apparent preference for purple traps by the dominant ambrosia beetle species, i.e., *X. saxesenii* and *X. germanus* in Italy, and *X. germanus*, *A. sayi*, and *X. attenuatus* in Canada. However, two species (the ambrosia beetle *A. dispar* and the bark beetle *C. ruficollis*) preferred green traps to purple traps, similar to trends reported for some other bark and ambrosia beetles (Abbasi et al. 2007; Gorzlancyk et al. 2013, 2014). Why certain bark and ambrosia beetle species displayed an apparent color preference while other species did not might be explained by differences in their daily flight activity pattern. For instance, diurnal species of hawk moths are known to perceive colors differently than crepuscular or nocturnal species (Balkenius et al. 2006). Nonetheless, understanding whether this is valid also for bark and ambrosia beetles requires further investigation, as daily flight activity pattern is known for only a limited number of species (Mendel 1991, Seo et al. 2017, Menocal et al. 2018). Our results also showed that the effect of trap color differed depending on the forest type. This was evident in Italy for *X. germanus* and *X. saxesenii*: these two species preferred purple traps to green traps both in the understory and the

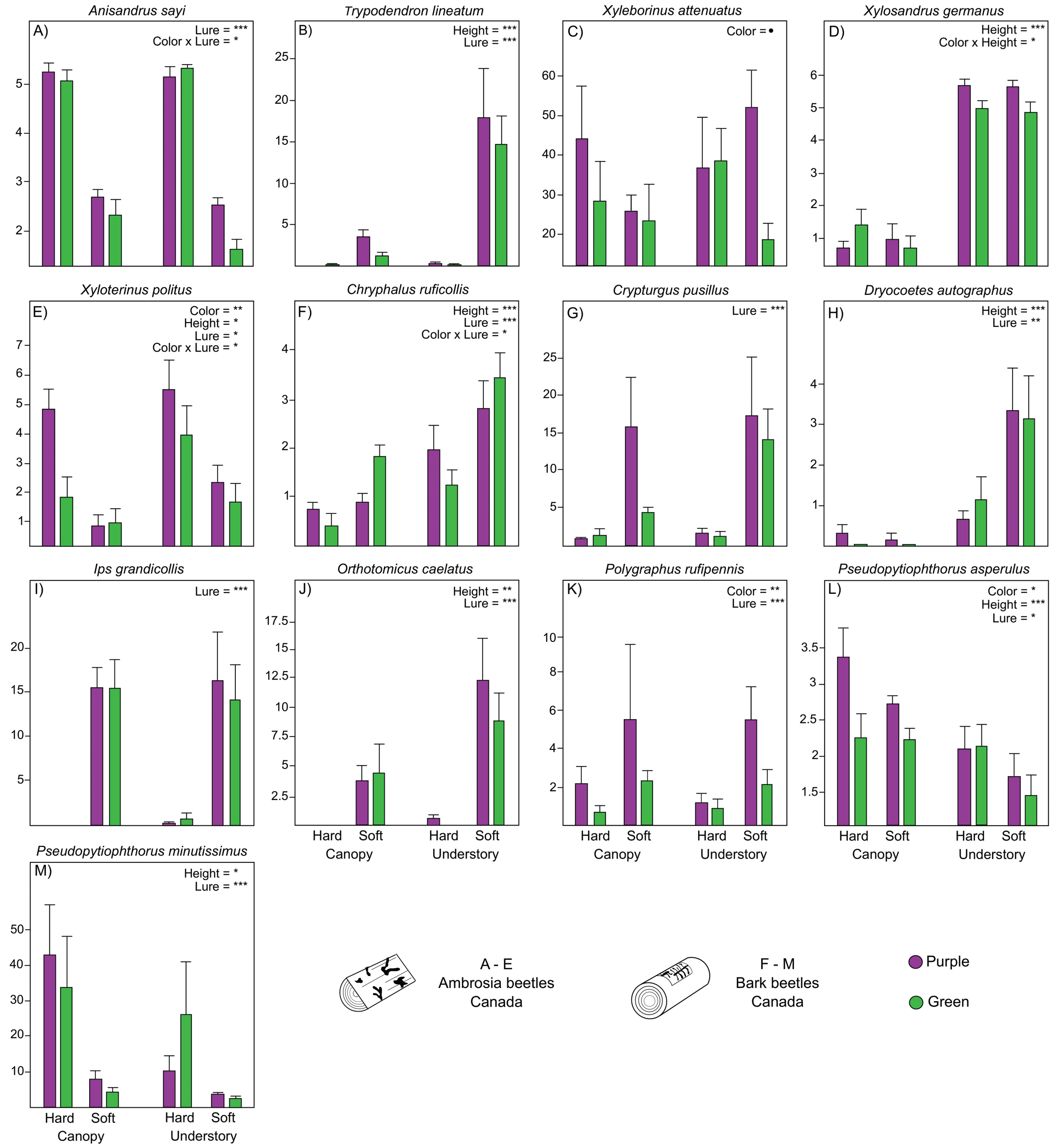

Fig. 4. Effect of trap color, trap height, attractive lures, and their interactions on ambrosia beetles (A–E) ambrosia beetles and bark beetles (F–M) caught in Canada. Significant explanatory variables and/or interactions are displayed within each box with black asterisk/s or black circle depending on the *P*-value: ****P* < 0.001; ***P* < 0.01; **P* < 0.05; •*P* < 0.1. Abundance of *A. sayi*, *X. germanus*, *C. ruficollis*, and *P. asperulus* is log-transformed according to data transformation used in statistical analysis. Hard = hardwood-blend; Soft = softwood-blend.

canopy of seminatural forests, whereas this preference was evident only in the understory of reforested forests. Our results support those of Niemeyer (1985) who found that beetle response to trap color was affected by the environment in which the traps were located. Seminatural forests had taller and more mature trees than reforested forests, and this may have affected light levels and relative reflectance of traps in the understory and canopy, which may have, in turn, induced a different response of beetles to trap colors. Unfortunately, we did not measure light levels or reflectance from traps in our plots, so this is purely speculative.

Trap height significantly affected species richness and abundance of ambrosia beetles, but only abundance of bark beetles. For ambrosia beetles, understory traps outperformed canopy traps in most cases, whereas for bark beetles we observed a less clear pattern. A higher species richness and abundance in understory traps was expected for ambrosia beetles, which are known to be more active in the lower forest strata (Flaherty et al. 2019, Sheehan et al. 2019, Ulyshen and Sheehan 2019), whereas the lack of a clear response was less expected for bark beetles, which have been reported to be more active in the upper forest strata (Sheehan et al. 2019, Ulyshen and Sheehan 2019). Nonetheless, there is increasing evidence that vertical stratification is mostly species-specific (Procházka et al. 2018, Miller et al. 2020). Preference for a given forest stratum is mainly linked to the main ecological habit of a species, and this should be taken into account when planning a species-specific surveillance program. The bark beetles *P. asperulus* and *P. minutissimus*, for example, typically colonize small branches and twigs (Ambourn et al. 2006), and this may explain why we caught more in canopy traps than in understory traps. The ambrosia beetles, *X. germanus* and *T. lineatum*, usually attack the lower part of stressed or dying trees (Foit et al. 2010, Ranger et al. 2020), and this may explain why they were caught more in understory traps than in canopy traps. Trap catch of other ambrosia beetles, such as *A. sayi* and *X. attenuatus*, and bark beetles, such as *I. grandicollis*, did not differ between canopy and understory traps, confirming that for some species trap height is not an important variable (Klingeman et al. 2017, Miller et al. 2020). Our results also confirmed that vertical distribution patterns can differ depending on forest type and structure (Ulyshen 2011, Procházka et al. 2018). This was particularly evident for *A. dispar*, for which trap catches were affected by trap height in seminatural forests but not in reforested forests. This pattern might be explained by the greater height of both trees and canopy traps in seminatural forests than in reforested forests; tree height is in fact considered one of the key variables affecting arthropod vertical stratification in deciduous temperate forests (Ulyshen 2011).

In Italy, ambrosia beetle catches were similar in traps baited with either ethanol or the hardwood-blend, suggesting that the longhorn beetle pheromones in the hardwood-blend had little effect on species of ambrosia beetles present in our sites. Nonetheless, total ambrosia beetle abundance and abundance of *X. saxesenii* in reforested forests, as well as abundance of *X. germanus* in seminatural forests, were higher in ethanol-baited traps than hardwood-blend-baited traps. Negative effects of racemic 3-hydroxyoctan-2-one (K8) on certain ambrosia beetle species, including *X. attenuatus*, congeneric of *X. saxesenii*, have been observed in previous studies (Noseworthy et al. 2012, Miller et al. 2015a, Sweeney et al. 2016), and its presence in the hardwood-blend may account for our results. Why these effects were evident in one forest type and not the other, depending on the species, is unknown. However, differences among sites in the effects of lure on trap catches have been previously observed for longhorn beetles (Rassati et al. 2020) and other saproxylic beetles (Bouget et al. 2009). We speculate that two mechanisms may be involved. First, forest structure may affect the microclimate near traps, in particular temperature, which, in turn, affects release rates of lures and, potentially, the attraction of certain ambrosia beetle species. Release rates of ethanol and α-pinene have had both positive (Ranger et al. 2011) and negative effects (Bakke 1983, Montgomery and Wardo 1983, Salom and McLean 1990) on trap catches of ambrosia beetles, depending on the species. Second, the amount of dead or dying trees was higher in seminatural forests than in reforested forests, and dead or dying trees can act as source of ethanol and host volatiles that could potentially compete with baited traps.

In Canada, traps baited with the hardwood-blend generally detected more ambrosia beetle individuals than traps baited with the softwood-blend, whereas the softwood-blend was generally more attractive to bark beetles than the hardwood-blend. This was not surprising and can be explained mainly by host associations. Most of the ambrosia beetles we captured are polyphagous on broadleaf trees, whereas 18 of 25 bark beetles we captured are associated with conifers. Differences from this pattern were exhibited by some species and can be also explained by host association. For example, catches of the ambrosia beetles *A. sayi* and *X. politus*, associated mainly with broadleaf trees (https://www.barkbeetles.info/index.php), were significantly lower in traps baited with the softwood-blend than the hardwood-blend. This was likely due to the high release rate of α-pinene in the softwood-blend that is presumably perceived as a nonhost signal by these species (Miller and Rabaglia 2009, Ranger et al. 2011, Flaherty et al. 2019). By the same token, catch of the conifer-associated ambrosia beetle, *T. lineatum*, was greater in traps baited with the softwood-blend than the hardwood-blend. Similarly, conifer-associated bark beetle species, such as *C. pusillus*, *C. ruficollis*, *I. grandicollis*, *O. caelatus*, and *P. rufipennis*, preferred the more conifer-like softwood-blend, whereas broadleaf-associated species (e.g., *P. asperulus* and *P. minutissimus*) preferred the hardwood-blend. However, catches of some species known to be associated with broadleaf trees (e.g., *X. attenuatus* and *X. germanus*) were not affected by lure blend, as previously observed by Flaherty et al. (2019).

In conclusion, we showed that the same trapping variables exploited for detection of longhorn beetles and jewel beetles (Flaherty et al. 2019, Rassati et al. 2019) can also be used to detect bark and ambrosia beetles, but the trapping protocol should be adjusted depending on the forest targeted nearby entry points. In a broadleaf forest, managers should consider baiting multi-funnel traps with the hardwood-blend lures with green traps in the canopy and purple traps in the understory. The green canopy traps can reliably detect longhorn beetles and jewel beetles (Rassati et al. 2019), as well as bark beetles living in the upper forest strata that are not affected by trap color. The purple understory traps can reliably attract longhorn beetles living in the lowest forest strata (Flaherty et al. 2019, Rassati et al. 2019) as well as ambrosia beetles, which mostly forage near the ground, tend to prefer dark colors, and are not affected by longhorn beetle pheromones present in the hardwood-blend. In a mixed forest, managers should instead complement the abovementioned protocol with understory and canopy purple traps baited with the softwood-blend, which can increase chances of detecting wood-boring beetles associated with conifer trees (Flaherty et al. 2019), including bark and ambrosia beetles. It is important to point out that both in Canada and Italy ambrosia beetle communities were largely dominated by a few species, and it is thus necessary to understand if the proposed trapping protocols can be considered efficient also for ambrosia beetle species having different ecological habits. Furthermore, it is important to underline that these trapping protocols are valid for generic surveillance programs aimed at trapping as many species as possible (Poland and Rassati 2019), whereas species-specific surveillance programs have to be adjusted depending on the biological and ecological habits of the target species. Further studies should also investigate whether multi-lure blends developed to simultaneously attract both conifer- and broadleaf-associated longhorn beetles (Fan et al. 2019) are also suitable for detecting jewel beetles and bark and ambrosia beetles. Similarly, future studies should investigate the differential efficacy of purple and green traps versus the commonly used black traps (Brockerhoff et al. 2006; Rassati et al. 2015a,b; Rabaglia et al. 2019). This is an important aspect as the adoption of colored traps for surveillance of wood-boring beetles requires specific data to justify the additional costs. In addition, the potential efficacy of multicolored traps (e.g., half-green/half-purple multi-funnel traps) is worth investigating, as this could decrease the number of traps needed and the overall costs of the surveillance program. Lastly, given that this study mainly targeted natural areas embedded in a urban-dominated landscape, it would be interesting to understand performance of the proposed protocols in forest-dominated areas.

Supplementary Data

Supplementary data are available at *Journal of Economic Entomology* online.

Acknowledgments

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