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Toward a more effective management of the pine shoot beetle, *Tomicus destruens*, by enhancing the attractant activity of its commercial kairomone: effect of phloem volatiles from fire-injured pines

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Abstract
The pine shoot beetle, *Tomicus destruens* (Woll.) (Coleoptera: Curculionidae: Scolytinae), represents a significant threat in the Mediterranean forests. The beetle attacks weakened or stressed pine trees, thereby increasing the degradation of the forest ecosystem after a drought or wildfires. A commercially available kairomone (CK) composed of α-pinene and ethanol is currently used for monitoring and mass trapping strategies, but its efficacy could be improved. The objective of this study was to compare and identify volatiles present in the phloem of fire-injured *Pinus halepensis*, both before and after being infested by *T. destruens*. Such volatiles, which can either be of new appearance or show an increased abundance when compared with healthy pines, could be evaluated as complements of CK to enhance its attractiveness. The volatiles showing a significantly higher relative abundance in pre- and post-infested fire-injured pines phloem and which are also commercially available were β-myrcene, estragole, p-cymen-8-ol, α-terpineol, p-cymene, and methyl eugenol. An initial field trial showed that the addition of estragole, p-cymene, or methyl eugenol to traps baited with CK significantly increased the number of *T. destruens* captured. Based on these results, a more in-depth study focused on these three compounds was performed in two additional field trials. The enhanced attractant effect of estragole or p-cymene on CK was not validated in the new field trials, but adding high emission rate lures of methyl eugenol to traps baited with CK significantly increased trap catches by 59% and 41% in autumn and spring trials, respectively. To the best of our knowledge, this is the first report of methyl eugenol as a kairomone for *T. destruens*; its potential use in management of this pest is discussed.

Keywords Host selection · Chemical cue · Methyleugenol · *Pinus halepensis* · Coleoptera · Curculionidae

Introduction

Bark beetles play a beneficial role in forest ecosystems, increasing organic matter through wood decomposition (Lieutier et al. 2015). However, it is well known that population dynamics of these insects consist of an "endemic phase" and an "epidemic phase" (Hlásny et al. 2021). During the "endemic phase," beetle populations are lower because trees are under favorable abiotic conditions. These non-stressful conditions allow them to show greater resistance to beetle attacks and result in a sparse distribution of beetle populations, facilitating their natural control and the activity of their natural enemies (Boone et al. 2011; Raffa et al. 2015). Following an abiotic disturbance such as a severe windstorm, prolonged drought and intense heatwave, or a forest fire, the "epidemic phase" may be initiated. During this phase, there is a significant increase in bark beetle populations, a circumstance that enables them to successfully overcome the defenses of healthy trees (Boone et al. 2011). Global warming is accelerating these dynamics, which results in an increase in the appearance of such disturbance episodes and an intensification of the severity of the

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outbreaks (Sommerfeld et al. 2021; Pureswaran et al 2018; Logan et al. 2003).

The Mediterranean pine shoot beetle, *Tomicus destruens* (Woll.) (Coleoptera: Curculionidae, Scolytinae), is one of the main bark beetles that can breed in different pine species such as *Pinus halepensis* Mill., *Pinus pinaster* Ait., *Pinus pinea* L., and exceptionally, *Pinus nigra* Arnold (Pinales: Pinaceae) (Faccoli 2007). *Tomicus destruens* is a monogamous and univoltine species with different overlapping sister generations. The biological cycle presents two differentiated phases throughout the year. In autumn, during the colonization phase, a sexually mature female in collaboration with her male partner bores the maternal gallery in the bark toward the phloem to lay the eggs; in this gallery, both the adult beetles and the immature stages overwinter. In the spring, during the dispersal phase, adults of the new generation emerge from the colonized material and aestivate in the pine shoots. During this period, they feed on the shoots and become sexually mature (Gallego et al. 2008; Peverieri et al. 2008). The parents may also occasionally colonize other trees and establish sister generations (Gallego et al. 2008).

Tomicus destruens can cause significant outbreaks when its hosts are under abiotic stress (Hlávková and Doležal 2022; Lieutier et al. 2015). Traditional methods for mitigating the impact of bark beetle infestations usually rely on the reduction of pest populations through the removal of severely damaged trees, wind or snow-blown branches (Grégoire and Evans 2004) as well as the use of trap trees or bait stations (Holuša et al. 2017; Fettig and Hilszczański 2015). However, these cultural methods are not always effective, which makes it necessary to seek new control options. Semiochemical-mediated control methods stand out as sustainable and ecological control strategies. Semiochemicals are widely used by insects as signals for locating suitable brood hosts (i.e., plant volatiles acting as kairomones), mates (i.e., sex pheromones) and, in many species of bark beetles, for facilitating mass attack of trees to overcome tree defenses and improve colonization success (i.e., aggregation pheromones) (Faccoli et al. 2008; Wood 1982; Raffa 2001); they have several potential applications in bark beetle management (Seybold et al. 2018; Byers 1981).

Mass trapping is a control method based on semiochemicals that may reduce pest populations and, therefore, the impact of bark beetle outbreaks (Schlyter et al. 2001; Faccoli and Stergulc 2008). Among semiochemicals, pheromones provide the highest efficiency in pest control methods due to their high specificity and effectiveness at very low doses (Witzgall et al. 2010). However, in contrast to other species of bark beetles, pheromones do not appear to play a significant role in *T. destruens* attacks (Byers 1995; Vité et al. 1986) and no aggregation pheromone has been identified for this species (Faccoli et al. 2008; Guerrero et al. 1997). Given the lack of known pheromones, identification of kairomones (host volatiles) attractant to *T. destruens* is especially relevant for developing semiochemical-mediated control strategies. Faccoli et al. (2008) found that four monoterpenes (α-pinene, β-myrcene, α-terpinolene, limonene), one sesquiterpene (β-caryophyllene), and one alcohol ((*Z*)-3-hexen-1-ol), released by shoots and bark of stone pine (*P. pinea*) elicited antennal responses in *T. destruens*, independently of their sex but with specific responses according to the degree of sexual maturation (callow and mature individuals). Specifically, α-terpinolene, released only by bark, was active exclusively on mature insects, whereas (*Z*)-3-hexen-1-ol, released only by shoots, was active solely on callow adults.

Alpha-pinene is attractive to *T. destruens* by itself (Peverieri et al. 2004) or in combination with other substances such as β-myrcene, α-terpinolene, or ethanol (Faccoli et al. 2008). Gallego et al. (2008) assessed the attractiveness of (−)-α-pinene and ethanol at different combinations of release rates in a *P. halepensis* forest. Based on those results, a commercial kairomone (CK) composed of α-pinene and ethanol at the optimal release rates is currently being used for trapping of *T. destruens,* but its efficiency could certainly be improved. According to Faccoli et al. (2008), *T. destruens* adults probably follow more specific cues than α-pinene and ethanol, as they can recognize the right host species, its physiological state (healthy and weakened), and specific parts of the host tree (shoots or bark). Thus, our goal was to improve the CK for *T. destruens* by identifying additional host volatiles present in stressed *P. halepensis*, specifically in fire-injured pines, and testing their effects on trap captures in field bioassays.

We focus our study on exploring chemical stimuli involved in the selection by *T. destruens* of moderately fire-injured pines, as wildfires are an important abiotic stressor inducing bark beetle attacks (Santolamazza-Carbone et al. 2011; Hood et al. 2015; Valor et al. 2017). After a fire, insect populations decrease temporarily and increase thereafter because secondary metabolites (terpenes and phenols volatiles) act as kairomones attracting xylophagous insects from outside the fire-damaged area (Lieutier 2004). During a period that may last several years, moderately fire-injured pines invest in secondary metabolism to produce high concentrations of chemical defenses, which protect them from insect attacks, especially bark beetles (Celedon and Bohlmann 2019). However, depending on the extent of fire injury and other factors as tree species, environmental conditions, or beetle population phase, terpene concentrations may decrease or the relative compositions of some volatiles may change (Powell and Raffa 2011; Valor et al. 2017; Kocabıyık et al. 2024). Then, a higher susceptibility of the tree to fire-related insects could

be expected and this might be the proper moment to look for volatiles acting as kairomones, both as attractants for host selection (before colonization) or substances promoting aggregation for massive colonization (after colonization by pioneer beetles).

In this study, we compared the volatiles emitted by phloem samples of healthy *vs.* fire-injured *P. halepensis* trees, both before and after infestation by *T. destruens*, to identify compounds with greater relative abundance in stressed trees. Volatiles identified in the first step that were commercially available (β-myrcene, estragole, p-cymen-8-ol, α-terpineol, p-cymene, and methyl eugenol) were then tested for their effects on trap catches of *T. destruens* when added to traps baited with CK.

Material and methods

Phloem sampling

The phloem utilized for volatile analysis was sampled throughout autumn 2021 and the beginning of 2022 from pines showing non-lethal fire injuries. The pines were located in the perimeter of a forested area that burned in April 2019 in the municipality of Castell de Castells (Alicante, Spain) (38°45′ 24.7″ N 0°11′ 14.4″ W). The control phloem samples were collected from a nearby stand with healthy pines located more than 200 m away (38°45′ 21.0″ N 0°11′ 03.0″ W) from the burnt area. Twenty-two Aleppo pines were selected, of which 16 were located in the perimeter of the fire-damaged area and 6 in the nearby unburnt area. All the pines were 3.5–4.0 m height and about 25 cm diameter at 1.5 m from the ground. When selected, none of the pines showed signs of bark beetle attacks (i.e., reddish boring dust, frass, pitch tubes, and entrance boreholes) during an exhaustive inspection of the trunk surfaces. Furthermore, when selecting fire-damaged sample trees, we included only those with 50–75% of the crown damaged by fire and 30–40% of the bole with visible signs of charring. Under these conditions, survival probability of the fire-injured pine is higher than 70% (Bordón et al. 2012) and it might be expected that its physiological stage can induce *T. destruens* colonizing after an elapsed time of 2 years from the wildfire (Valor et al. 2017). In addition, to favor as much as possible their colonization, all the selected pines were baited with CK (Econex, El Siscar, Spain) at the onset of the experiment, just coinciding with the first phloem sampling on October 4, 2021 (see below). The phloem samples were taken using a Pressler's auger (30 cm length; core diameter 0.5 cm) at a height of 1.5 m from the ground. Each pine was sequentially sampled on three occasions: October 4, 2021 (when no infestation had occurred yet); November 17, 2021 and January 18, 2022, in both cases, when clear signs of attack were already evident. The cylindrical samples obtained were composed, from outside to inside, by bark, phloem, cambium, and a small portion of xylem. The phloem/cambium portion of each sample was separated from the xylem and bark with a scalpel and placed in a 20-mL screw-top headspace vial equipped with silicone-PTFE septa. The vials were immediately placed in a portable fridge containing dry ice and transported to the laboratory where they were stored at −54 ℃ until their analysis.

After the last phloem sampling (January 18, 2022), the sampled pines in the burnt area were cut down and a 2-m-long portion of the trunk from 30 cm to the soil was carefully debarked in the laboratory to obtain the number of boreholes, i.e., the infestation level. Because we wanted to investigate volatiles from trees most attractive to the beetle, we excluded trees with fewer than 30 boreholes. This left us three fire-injured pines with more than 30 (41, 52, and 68) boreholes for phloem volatile analysis (see Section S2 in Supporting Information). We randomly selected three trees from the initial sample of six healthy (control) pines for phloem volatile analysis. The analysis of the volatiles from the first phloem sampling (4 October) allowed us to identify those substances produced exclusively by the effect of fire when compared with the corresponding sampling in the healthy pines. As infestation of the fire-damaged trees had already occurred prior to the collection of phloem samples in November and January, we could not distinguish whether any differences in volatile profiles from healthy pines were due to fire damage, beetle infestation, or both.

Volatile collection and analysis

The methodology followed for the phloem volatile analysis was based on the protocol described by Morcillo et al. (2019). Phloem volatiles were collected under static conditions by solid-phase microextraction (SPME) with polydimethylsiloxane/divinyl benzene fibers (100 µm PDMS/DVB, Supelco Inc., Bellefonte, PA). Following an incubation period of the sample in a heating block programmed at 50 ℃ during 5 min, the SPME fiber was inserted through the septum and exposed to the vial headspace for 30 min. After volatile collection, SPME fibers were thermally desorbed for 1 min into the injection port of a Clarus 690 GC/MS gas chromatograph coupled to a TSQ single-quadrupole mass spectrometer (Perkin-Elmer Inc., Waltham, MA, USA). The temperature of the injector, which operated in splitless mode, was set at 250 ℃. The GC was equipped with a ZB-5MS (30 m × 250 µm × 0.25 µm)-fused silica capillary column (Phenomenex Inc., Torrance, CA, USA). The oven temperature was held at 40 °C for 1 min, then increased by 5 °C/min up to 250 °C, maintained for 2 min. Helium was employed as the carrier gas at a flow rate of 1.5 mL/min. The MS detection was conducted using

electron ionization (EI, 70 eV) with a mass scan range of *m/z* 35–400. The resulting chromatograms and mass spectra were obtained using the GC–MS Turbomass version 5.4 (PerkinElmer Inc.) software. The identify of compounds was determined by comparing retention times and mass spectra with those of commercial standards, as well as through a search for matches in a mass spectral library (NIST MS Search routine) with a minimum match percentage of 80%.

Following the analysis of phloem volatiles, we identified compounds that were present in significantly higher relative proportions in the fire-injured pines compared to the healthy ones, and those that were commercially available were selected as candidates for testing their effects on capture of *T. destruens* when added to CK-baited traps in field trials.

Field trials

Three field trials were carried out during two consecutive years covering three different periods: autumn 2022 (trial 1), spring 2023 (trial 2), and autumn 2023 (trial 3).

Dispensers of the selected phloem volatiles (β-myrcene, estragole, p-cymen-8-ol, α-terpineol, p-cymene, and methyl eugenol) were designed (Table S3 in Supporting Information) and individually added to traps baited with CK to evaluate their effect on trap captures. The first field trial was carried out from October 13 to December 22, 2022, in a public forest of the municipality of Fontanars dels Alforins (38°45′ 07.4″ N 0°46′ 36.3″ W) (Valencia, Spain), an endemic area for *T. destruens* where no sympatry with the closely related *T. piniperda* occurs (Gallego et al. 2004; Vasconcelos et al. 2006; Horn et al. 2012). The experimental design consisted of seven synthetic host volatile lure treatments (Table 1) replicated five times in randomized blocks. Treatments were spaced about 100 m apart within blocks, and blocks were separated by at least 500 m. We used Crosstraps® (Econex, El Siscar, Spain) equipped with a collecting jar containing 10 mL of a 10% polyethylene glycol aqueous solution. Traps baited with CK only were our controls, and the remaining six treatments consisted of a combination of CK plus one of six selected compounds. At the outset of the experiment, position of the seven treatment traps was randomized within each block. Once per week, traps were checked and rotated clockwise to reduce effects of trap position on catches. Trap catches were transferred to the laboratory, where the *T. destruens* were morphologically identified (Faccoli 2006) and counted. Concurrently to the trap checking, the experimental dispensers were taken from the traps and replaced every week by new ones with the same initial characteristics. The old dispensers were placed in a sealed container with dry ice, transported to the laboratory and stored at −54 °C until they could be weighed. Volatiles emission by experimental dispensers was determined by weight difference, before and after field exposure (gravimetric method), as measured using a precision balance (Mettler-Toledo, Mod. ME204, Mettler-Toledo S.A.E., Barcelona, Spain). The field lifespan of CK dispensers is 60 days according to the manufacturer, so they were not replaced during the field experiments; release rates at 20 °C, also supplied by the manufacturer, were 2 g/day for ethanol and 0.3 g/day for α-pinene.

Table 1 Attractant activity of *Tomicus destruens* commercial kairomone (CK) supplemented with dispensers containing phloem volatiles from fire-injured (pre- and post-infestation) *Pinus halepensis* in trial 1 (Autumn 2022)

Treatment	Emission (mg/day)		*T. destruens* captures (CTD)[c]
	Theoretical[a]	Real[b] (FE)	
Control (CK)			3.68 ± 1.22
CK + β-Myrcene	109	96.72 ± 11.01	3.87 ± 1.36
CK + Estragole	25	55.48 ± 6.43	5.52 ± 2.15*
CK + Methyl eugenol	14	7.33 ± 1.07	5.91 ± 2.10*
CK + p-Cymen-8-ol	7	12.71 ± 2.95	3.78 ± 1.33
CK + α-Terpineol	3	5.48 ± 1.95	3.45 ± 1.52
CK + p-Cymene	3	27.25 ± 2.04	5.04 ± 2.01*

[a]Estimated emission of the volatiles based on both their relative content to α-pinene in the phloem and the field optimal emission of α-pinene (300 mg/day) according to Gallego et al. (2008)

[b]Field emission (FE) of the phloem volatiles obtained by the gravimetric method, shown as mean ± SE (n = 49)

[3]Mean ± SE (n = 7) of *T. destruens* captures per trap and day (CTD). Asterisks indicate significant differences against Control (CK) catches using a GLMM model with a subsequent post hoc test (Dunnett's test at $P < 0.05$)

The second and third trials evaluated only methyl eugenol, p-cymene, and estragole because these were the only compounds that significantly increased trap catches when added to CK-baited traps in the first trial (autumn 2022). These trials included two different release rates of each compound, one that was similar to that experimentally recorded in the autumn 2022 trial (hereafter named "Low") and another one four times higher (hereafter named "High") (see Table 2 in Results and S3 in Supporting Information). Trial 2 was conducted from March 7 to May 3, 2023, and Trial 3 was conducted from October 18 to December 5 2023, in the same experimental area due to the high *T. destruens* population recorded in 2022. Both trials included three experimental blocks with seven traps: One trap baited with CK only and two traps with CK and the two selected emission levels for each product, i.e., two traps for p-cymene (25 and 100 mg/day), two traps for methyl eugenol (10 and 40 mg/day), and finally, two traps more for the estragole (50 and 200 mg/day). Both experiments were conducted following the methods detailed for trial 1.

Table 2 Emission rates provided by the dispensers containing phloem volatiles identified from fire-injured (pre- and post-infestation) *Pinus halepensis* during spring and autumn 2023 field trials

Product[a]		Emission rate (mg/day)		
		Theoretical	Real[b]	
			Spring 2023	Autumn 2023
Estragole	Low	50	297.66 ± 103.32	116.98 ± 20.11
	High	200	640.63 ± 196.43	234.97 ± 23.95
p-Cymene	Low	25	37.36 ± 5.9	26.58 ± 1.84
	High	100	260.69 ± 126.8	30.47 ± 5.09
Methyl eugenol	Low	10	14.75 ± 5.23	8.70 ± 1.57
	High	40	48.71 ± 15.16	19.18 ± 7.50

[a]For each product, two emission levels are evaluated: "Low" (emission rate similar to that recorded in the first trial (FE)) and "High" (corresponding to four times the "Low" emission)

[b]Real (recorded) emission rates are shown as mean values ± SE ($n = 35$) and were determined by the gravimetric method

Statistical analysis

The relative percentage composition of each phloem sample was calculated from the GC peak area of each compound with respect to the total integrated chromatogram area. The relative proportion of each compound was compared between healthy- and fire-injured pines using analysis of variance (ANOVA) with a significance level set at $\alpha = 0.05$ in STATGRAPHICS Centurion 19 software, 2023 (Statpoint, Herndon, VA). Previously, the angular transformation (arcsin(sqrt(x/100)) was applied to the percentage values to fulfill the homoscedasticity and normality requirements.

The data from the field trials were analyzed separately. Weekly capture data for each treatment within each experiment were assessed using a generalized linear mixed model (GLMM) implemented in R software version 4.5.1. The GLMM with a Poisson error distribution and log link function was fitted to insect count data using the lme4 package. Weeks with fewer than 10 accumulated captures were excluded from the statistical analysis. Week and treatment were included as fixed effects, and study block was included as a random effect. To specifically test for differences between each treatment and the control (CK alone), post hoc multiple comparisons were made using Dunnett's test, implemented via the emmeans package.

Results

Phloem volatile analysis

The analysis of the phloem volatiles revealed 69 compounds with different relative proportions between fire-injured and healthy pines and throughout the study period (Table S1). The volatile profile of the phloem samples was comprised mostly of terpenoid hydrocarbons, with monoterpenes the most abundant (49.3% of the total number of detected compounds), followed by sesquiterpenes (17.4%) and aromatic compounds (alkylbenzenes and phenolic compounds, 17.4%). Other classes of compounds found in minor proportions were aldehydes (7.0%), esters, acids, and an epoxide (2.0–1.0%).

When comparing fire-injured and healthy pines on each sampling date, there were several compounds that differed significantly in relative percentage of total chromatographic area (% TCA) between fire-injured and healthy pines (Table S1). Compared to healthy pines, fire-injured pines had lower relative percentages of heptanal, benzaldehyde, nonanal, 3-thujene, α-pinene, sabinene, β-pinene, 3-carene, longipinene, and longifolene in at least one of the three sampling periods (Table S1). Conversely, the fire-injured and beetle-infested pines had greater relative proportions of β-myrcene, p-cymene, γ-terpinene, p-cymenene, α-campholenal, trans-verbenol, p-cymen-8-ol, α-terpineol, estragole, verbenone, carveol, carvone, α-cubebene, and methyl eugenol than did healthy pines, mostly in the November sample. The % TCA of methyl eugenol, in particular, was 190-fold greater in the phloem of fire-injured trees to the phloem of healthy pines. If we assume that an increase in the relative proportion is related to an increase in the emission of that substance, and we know that *T. destruens* is attracted to fire-damaged pines, then these compounds may act as attractive kairomones for host-finding. Accordingly, we selected β-myrcene, p-cymene, estragole, p-cymen-8-ol, α-terpineol, and methyl eugenol for evaluation as potential kairomones in field trapping assays due to their ready commercial availability (Fig. 1). Verbenone, although available, was dismissed because of its widely described repellent role against *T. destruens* (Mafra-Neto et al. 2022; Frühbrodt et al. 2024).

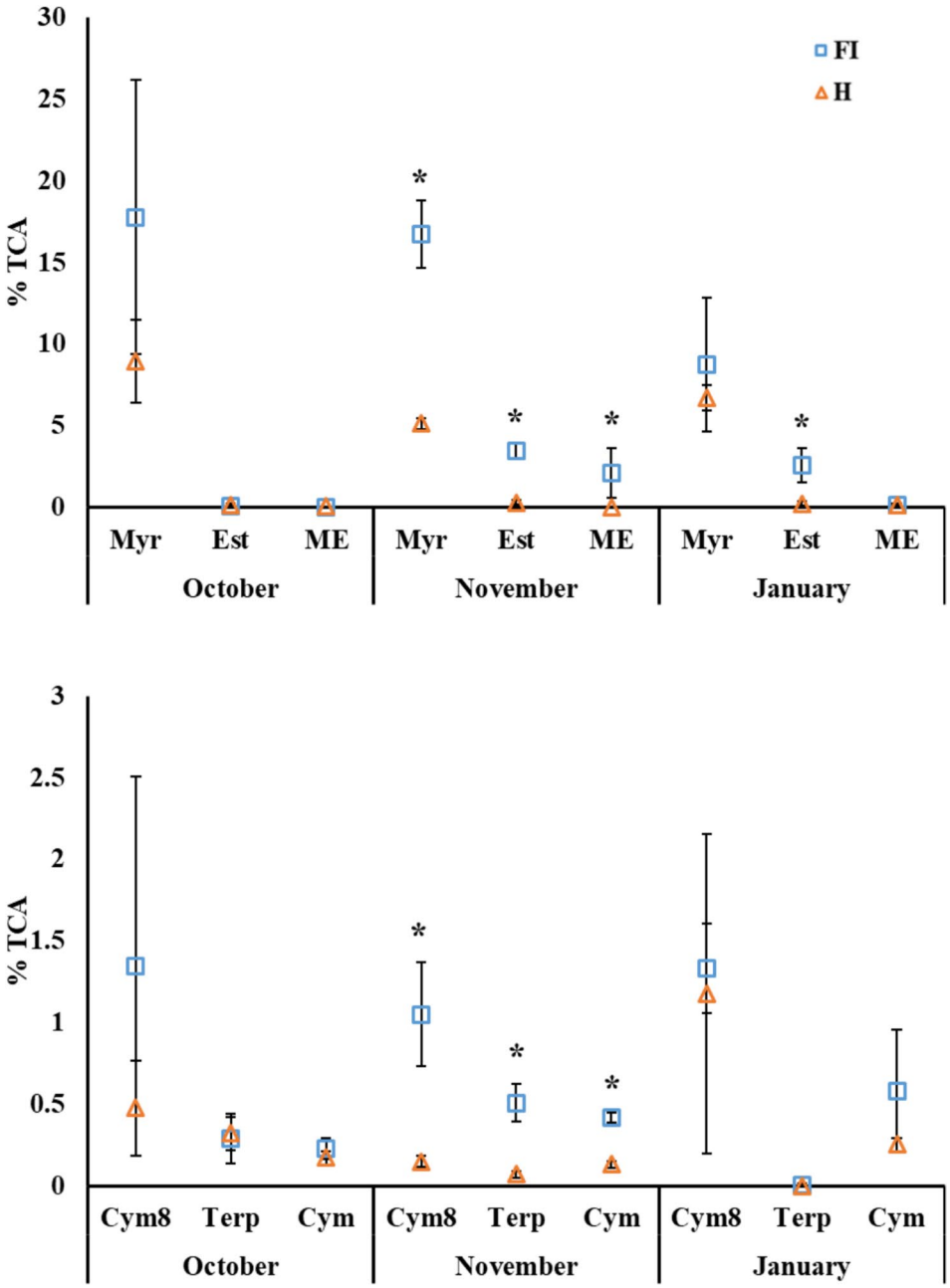


Fig. 1 Relative proportion (percentage of each chromatographic peak regarding the Total Chromatographic Area (% TCA)) of the substances selected to be studied in field assays that exhibited a significant increase in their relative proportions in fire-injured pines (FI) in comparison to healthy pines (H) in the phloem samplings (Myr: β-myrcene, Est: estragole, ME: methyl eugenol, Cym8: p-cymen-8-ol, Terp: α-terpineol, and Cym: p-cymene). Values are shown as mean ± SE ($n = 3$). Within each product, asterisk indicates significant differences between samples (ANOVA followed by the Fisher least significant difference (LSD) test ($P < 0.05$))

Field experiments

Temporal trends of field captures

Tomicus destruens captures during the trial 1 showed an initial decline throughout October, from 7 to 1 CTD at the end of the month. At the end of October the captures increased, reaching a maximum in the first days of December (10 CTD) and decreasing at the end of the experimental period (Fig. 2A).

Population levels were different during the study periods of trials 2 and 3 (Fig. 2B and C), respectively). On the one hand, in trial 2 (Fig. 2B) captures exhibited a decreasing trend, from 4 CTD in the first week of the experiment (mid-March) to less than 1 CTD in mid-April. This trend suggests that the study probably started late in the season. *Tomicus destruens* captures recorded during autumn in trial 3 (Fig. 2C) were higher, reaching a maximum peak of 16 CTD in mid-November.

Trial 1: Autumn 2022

The emission levels of the tested substances provided by the experimental dispensers under field conditions (FE)

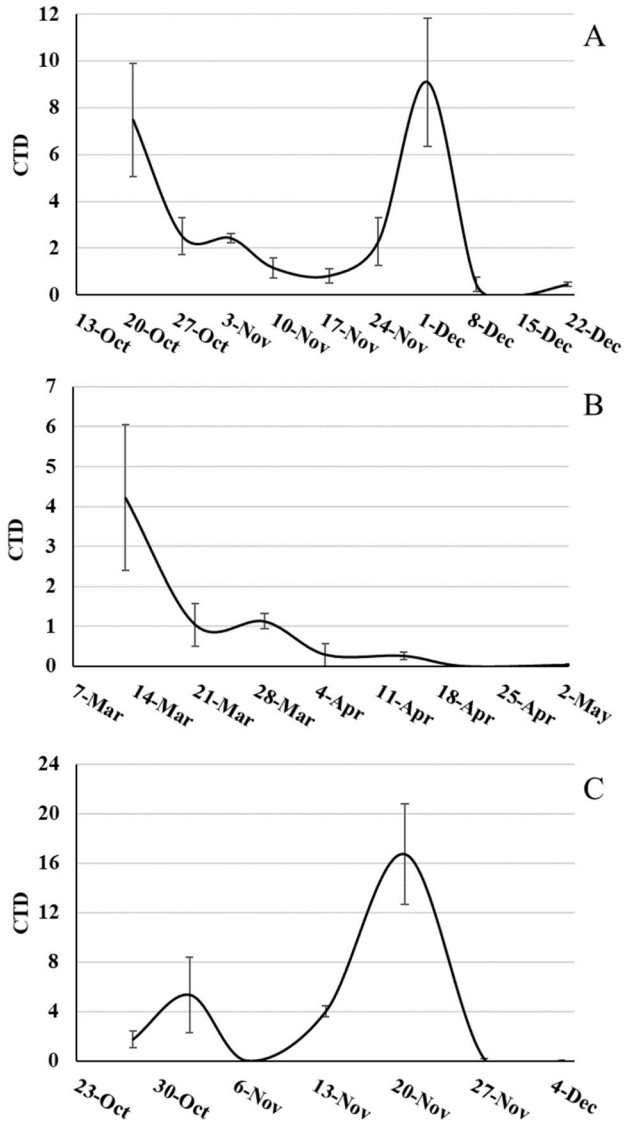


Fig. 2 Mean ± SE of the number of *T. destruens* captured per trap and day (CTD) on control traps (baited only with the commercial kairomone) throughout the study periods: **a** trial 1: autumn 2022; **b** trial 2: spring 2023, and **c** trial 3: autumn 2023

substantially differed, in some cases, from the expected theoretical values. More specifically, for estragole and p-cymen-8-ol the recorded emission doubled the theoretical value, while for methyl eugenol it was half that level (Table 1). However, the maximum deviation was recorded for p-cymene dispensers, which provided a mean emission rate of 27.25 mg/day instead of the expected 3 mg/day.

The mean captures per day obtained for each treatment at those emission levels are included in Table 1. The GLMM analyses revealed that both fixed effects, week ($\chi^2 = 6280.1$, $df = 6$, $P < 0.001$) and treatment ($\chi^2 = 275.14$, $df = 6$, $P < 0.001$), had significant effects on the mean captures registered. Statistical differences of the mean captures throughout the weeks were expected due to the natural population dynamics of the pest.

Regarding treatments, statistical analysis revealed that CK in combination with methyl eugenol, estragole, or p-cymene achieved the highest number of captures, significantly differing from the control treatment ($P < 0.001$). Specifically, *T. destruens* captures increased by 60.44%, 49.86%, and 36.80%, when adding methyl eugenol, estragole, or p-cymene, respectively, to CK. Captures obtained with CK alone or in combination with α-terpineol, β-myrcene, or p-cymen-8-ol did not statistically differ ($P > 0.05$). These results allowed us to select methyl eugenol, estragole and p-cymene for an in-depth study in the second-year field trials.

Trials 2 and 3: spring and autumn 2023

After the first-year study, the three compounds that were potentially able to increase significantly the captures in combination with the kairomone were studied using two different emission rates, as shown in Table 2. Despite laboratory adjustments to the different dispenser configurations (see Table S2), achieving the theoretical emission rates was not always possible (Table 2). Moreover, seasonal variations were observed with higher emissions for all compounds during spring. We expected the high emission to be fourfold the low one by the theoretical predictions, and this proportion was maintained during spring for methyl eugenol and p-cymene. However, in the case of estragole, the high emission was twice higher than the low one and both emission rates exceeded the theoretical value. Conversely, in autumn period, and despite temperatures being higher than in spring (AEMET 2023), most experimental dispensers provided lower, more controlled, emissions for the three compounds because of the dispensers' adjustments (see Table S2). Accordingly, no difference was observed between the high and low emission rates for p-cymene, while the high emission of methyl eugenol was lower than expected. Finally, the emission rates of estragole, although lower than in spring, maintained the proportion, with the high emission rate being double than that of the low one.

The mean captures per day obtained for each treatment at the two different emission levels in both seasons of 2023 are included in Table 3. The GLMM analyses revealed that the two fixed factors (week and treatment) showed significant effects on the mean captures registered in both seasons ($\chi^2 = 973.7$, $df = 4$, $P < 0.001$ for week in spring 2023 and $\chi^2 = 1773.1$, $df = 3$, $P < 0.001$ in autumn 2023; as well as, $\chi^2 = 74.436$, $df = 6$, $P < 0.001$ for treatment in spring 2023 and $\chi^2 = 331.22$, $df = 6$, $P < 0.001$ for autumn 2023).

Adding estragole to CK-baited traps had no effect of trap catch of *T. destruens* in spring or fall of 2023, at either high or low release rates (Table 3). Adding p-cymene to

Table 3 Mean (±) numbers of *Tomicus destruens* captured in traps baited with commercial kairomone (CK) alone vs. CK plus dispensers containing phloem volatiles identified from fire-injured (pre-and post-infestation) *Pinus halepensis* in trials 2 (spring 2023) and 3 (autumn 2023)

Treatment[a]		*Tomicus destruens* captures[b]	
		Spring 2023	Autumn 2023
Control (CK)	Emission	1.66 ± 0.87	6.94 ± 3.34
CK + Estragole	High	1.29 ± 0.78	7.72 ± 5.29
	Low	1.25 ± 0.77	7.41 ± 2.25
CK + p-Cymene	High	1.36 ± 0.79	4.86 ± 2.65*
	Low	1.31 ± 0.71	4.02 ± 2.18*
CK + Methyl eugenol	High	2.65 ± 1.46*	9.78 ± 4.83*
	Low	1.96 ± 1.19	6.50 ± 2.17

[a]For each product, two treatments were performed: "Low" emission (similar emission rate to that recorded in the first trial and "High" emission corresponding to four times the Low emission; the theoretical emission level, in mg/day, of each treatment is shown in Table 2

[b]Values represent captures/trap and day (CTD) and are shown as mean ± SE ($n = 5$). Within a column, asterisks indicate significant differences against Control (CK) catches using a GLMM model with a subsequent post hoc test (Dunnett's test at $P < 0.05$)

CK-baited traps had no effect on catches of *T. destruens* in spring 2023 but significantly reduced catches in autumn 2023, at both the high and low release rate (Table 3). Traps baited with CK + methyl eugenol at the high release rate captured significantly more *T. destruens* in both seasons than did CK-baited traps (59% more in spring and 41% more in fall), but this effect was not observed at the lower release rate.

Discussion

Climate change is likely to lead to increased severity of the *T. destruens* outbreaks due to the intensification of the pest epidemic phases and the rise in extreme climatic episodes caused by global warming (Hlásny et al. 2021; Sommerfeld et al. 2021). Therefore, the development of more effective control methods is becoming crucial. Semiochemical-based control approaches are among those being currently outlined as preferred methods due to their efficacy, sustainability, and ecofriendliness (Faccoli et al. 2008; Gitau et al. 2013). With this aim in mind, identifying additional kairomonal compounds to implement a more efficient monitoring and control of *T. destruens* in forests is required. A potential source of these new kairomones is constituted by an array of chemicals (inducible defenses) whose biosynthesis is triggered when trees are subjected to biotic stressors, such as insect or pathogen invasions, as well as abiotic stressors, including droughts, flooding, windstorms, and wildfires (Mageroy et al. 2023; Davi et al. 2020; Krokene 2015; Ferrenberg et al. 2014). These inducible substances include terpenes and phenolic compounds that, among other uses, are intended to deter the establishment of bark beetles in conifers (Celedon and Bohlmann 2019). However, under certain circumstances, pests have evolved strategies to recognize some of these compounds, or even their relative proportions, to identify the emitter as a suitable host (Kocabıyık et al. 2024; Wood 1982).

As a starting point in this research, inducible defenses among the phloem volatiles in fire-injured pines were sought. The study focused on phloem volatiles from fire-injured (weakened) and fire and beetle-injured (colonized) pines, as pines being affected by a wildfire exhibit a very high susceptibility to *T. destruens* attacks (Santolamazza-Carbone et al. 2011). Similar studies were previously conducted by Kelsey et al. (2014), who analyzed the phloem chemical composition of drought-stressed and healthy Aleppo pines (*Pinus halepensis* Mill.) and concluded that stressed pines showed differences in monoterpene composition and rates; in addition, they produced 2.1 times more ethanol than healthy pines. This latter finding is in accordance with previous work which reports that ethanol is a product of the anaerobic fermentation of phloematic sugars in weakened and drying trees (Kimmerer and Kozlowski 1982). In a subsequent study, Morcillo et al. (2019) attributed the variation in phloem terpene composition observed in previously debilitated pines by *Candidatus Phytoplasma pini* to bark beetle attacks. The volatile profile analyses of our phloem samples revealed that the chemical composition between fire-injured, both pre- and post-infestation, and healthy Aleppo pines was similar, but the relative proportions of certain compounds were significantly altered. From the six differential compounds selected to be subsequently assessed, two of them, β-myrcene and p-cymen-8-ol, were considered fire-induced defenses, as elevated proportions relative to those observed in healthy pines prior to infestation (sampling of 4th October) were exhibited, albeit not significantly (Table S1). The remaining products (estragole, α-terpineol, p-cymene, and methyl eugenol) were not detected in significantly higher proportions until the sampling carried out in November, which suggested the possibility of them being chemical defenses induced by the subsequent attack of *T. destruens*. Independently of their origin, any of these six chemical defenses might be playing a key role in the host–insect chemical communication.

The second part of this research was conducted to evaluate, in field conditions, the effect of the selected compounds when added to traps baited with the commercial lure for *T. destruens,* i.e., α-pinene plus ethanol. As a first step, to assess the activity of the products in the field, we designed experimental dispensers that provided different emission levels for each candidate compound under

laboratory conditions. However, their release rates under field conditions differed from the theoretical calculation in some cases, probably because of the basic approach of their design, highly dependent on climatic conditions. Considering these limitations, the research findings suggest interesting insights into the potential roles that these substances might perform during borer colonization.

A key finding in our study was the identification, for the first time, of the behavioral effect of methyl eugenol on a bark beetle under field conditions. Adding a high release rate lure of methyl eugenol to traps baited with the commercial lure consistently increased the number of *T. destruens* captured. Some insect species have adapted to using methyl eugenol as a stimulant or attractant cue to locate host plants as well as a source for pharmacophagy, defined as the action of acquiring defensive chemicals by feeding on non-nutritive food (Tan and Nishida 2012). Methyl eugenol acts as a strong attractant for the oriental fruit fly, *Bactrocera dorsalis* (Hendel) (Diptera: Tephritidae) (Tan and Nishida 2012; Kido et al. 1996), major pest of tree fruits. Furthermore, two carabid pest species, *Cetonia aurata* (Linneo) and *Potosia cuprea* (Fabricius) (Coleoptera: Scarabaeidae), as well as larvae of the rice stem borer, *Chilo suppressalis* Walker (Lepidoptera: Pyralidae) are attracted to traps baited with blends containing methyl eugenol (Vuts et al. 2010; Tan and Nishida 2012). Nevertheless, to the best of our knowledge, no prior studies have investigated the role of methyl eugenol in bark beetle chemical communication.

Methyl eugenol is a phenylpropanoid chemical that can be found in a wide variety of plant species. However, until this study, it had only been described in one pine species, *Pinus ponderosa* Douglas ex C. Lawson, as a component of the needles essential oil (Krauze-Baranowska et al. 2002). In our phloem volatiles analysis, methyl eugenol was 190-fold more abundant in fire-injured pines than in healthy pines when evaluated in November. In addition, the relative proportion of methyl eugenol in the phloem was positively related to the intensity of *T. destruens* attack, as indicated by the number of pitch tubes or boreholes in the bark. Our most severely attacked pine, with 68 boreholes, 29 *T. destruens* adults and a multitude of larvae had up to 714-fold the relative proportion of methyl eugenol found in healthy pines. One month and a half earlier (4 October sampling), when the insect flight had just started and *T. destruens* colonization had not yet begun, the relative proportions of methyl eugenol detected were almost negligible in both fire-injured and healthy pines (Table S1). These results would suggest the role of methyl eugenol as a host defense induced by *T. destruens* attacks. Furthermore, it could be even hypothesized that the product could act as an aggregative cue. However, this requires further research.

The predominant strategy of bark beetle species to overcome tree defenses is based on pheromone-mediated cooperative behavior (Raffa et al. 2015). However, there is no evidence of the existence of an aggregation pheromone for *T. destruens* (Lieutier et al. 2015). Instead, trunk colonization by pine shoot beetles proceeds from repeated tree interceptions by pioneer beetles through random flights and by the subsequent increase in attraction to new colonizers due to increased host volatile (e.g., α-pinene and ethanol) emission stimulated by the pioneer attacks (Byers 1992; Faccoli et al. 2008; Lieutier et al. 2015). Our findings for *T. destruens* seem to support this model, as methyl eugenol emission was not only increased in beetle-attacked trees but increased catches when added to traps baited with CK, as discussed below.

Our results also demonstrate that methyl eugenol enhanced *T. destruens* attraction, under different seasons and population levels, with emission rates exceeding 20 mg/day. These data could have important practical consequences, given that high emission rates of methyl eugenol combined with CK allow for the more efficient detection of low population densities. This enhanced monitoring would help to detect more quickly incipient epidemic outbreaks, and therefore, earlier pest control measures, such as mass trapping, could be implemented. In this regard, an extensive study to optimize and adjust the proportion of methyl eugenol in the kairomone blend will be necessary.

Adding estragole to CK-baited traps increased mean beetle captures in autumn 2022, when its mean emission rate was 55.5 mg/day, but not in spring and autumn 2023 when emission rates were 2–12X higher. Similarly, Munro et al (2020) found that adding estragole at similar release rates (48 mg/day) to traps baited with aggregation pheromones increased mean catches of *Dendroctonus frontalis* (Zimmermann) and *D. terebrans* (Olivier) (Coleoptera: Curculionidae: Scolytinae). However, previous results had showed that estragole was an attraction inhibitor of *D. frontalis* when using high release rates (160 mg/day) (Hayes et al. 1994). Moreover, estragole has reduced trap catches of *Ips typographus* (L.) (Coleoptera: Curculionidae: Scolytinae) (Moliterno et al. 2023) and *Tomicus piniperda* (Coleoptera: Curculionidae: Scolytinae) (Haack et al. 2004), the latter being a species closely related to *T. destruens*. Due to these contrasting results showing estragole either as an attractant or inhibitor of attraction, it has been proposed as a "multifunctional"-type semiochemical that enhances attraction at low release rates but inhibits attraction at high rates (Munro et al. 2020).

The effects of adding p-cymene to CK-baited traps on catch of *T. destruens* varied among field trials and were inconclusive. Similar emission rates of p-cymene increased catches in autumn 2022, decreased catches in autumn 2023, and had no effect on catches in spring 2023. p-Cymene was cited in relation to the construction of the maternal galleries in the case of *Scolytus intricatus* Ratz (Coleoptera:

Curculionidae: Scolytinae) in oak (Vrkočová et al. 2000) and was reported as a quantitatively induced monoterpene in the phloem of *Pinus brutia* (Ten.) following attacks of *T. destruens* (Kocabıyık et al. 2024).

The relative proportions of α-terpineol and β-myrcene in phloem volatiles were greater in fire-injured/beetle-infested pines than healthy pines, but neither compound affected mean catch of *T. destruens* when added to CK-baited traps at release rates of 5.48 mg/day and 96.7 mg/day, respectively. α-Terpineol is cited in numerous studies as a semiochemical cue related to bark beetle infestations. Viklund et al. (2019) described α-terpineol as repellent to the spruce bark beetle *Polygraphus poligraphus* (L.) (Coleoptera: Curculionidae: Scolytinae), despite its possible attractant effect when combined with (−)-terpinen-4-ol. This latter effect, in addition, could be conditioned by the release rates or ratio of the two compounds. β-Myrcene, instead, was described in past studies as a precursor of ipsenol and ipsdienol, aggregation pheromones of *Ips paraconfusus* Lanier (Byers 1981), and synergistically increasing attraction of the mountain pine beetle, *Dendroctonus ponderosae* Hopkins, to its aggregation pheromones (Erbilgin et al. 2017; Borden et al. 2008). Similarly, Erbilgin et al. (2017) found lower amounts of β-myrcene and terpinolene in lodgepole pines (*Pinus contorta* Douglas) that were resistant to mountain pine beetle. More remarkably, β-myrcene has been proposed as a compound that would modulate host location in *T. destruens* (Faccoli et al. 2008). Although we found that phloem volatiles of fire-damaged pines had a higher relative proportion of β-myrcene than healthy pines, the variability among samples was very high and the difference was not significant in trees sampled prior to *T. destruens* infestation. The lack of significance may be due, in part, to our low sample size ($n = 3$), but the lack of positive effects on trap catch of *T. destruens* suggests that β-myrcene may not act as a reliable volatile signal of host susceptibility to *T. destruens.* However, further research should be carried out before ruling out this product as a *T. destruens* chemical cue.

The last compound selected and assayed in the field was p-cymen-8-ol. Known as a typical component of the essential oils of many plant species (Camilotti et al. 2015; Ogunwande et al. 2012; Slavkovska et al. 2001), this substance did not increase *T. destruens* captures under our experimental conditions. Scarce information is available about this compound; specifically, and regarding insect borers, Higgs and Evans (1978) detected p-cymen-8-ol in the larval frass of *Hylotrupes bajulus* (L.) (Coleoptera: Cerambycidae) and associated it, in conjunction with (−)-verbenone, to the egg-laying behavior of females.

Finally, there were several compounds with higher occurrence in the phloem of fire-injured pines that could not be assayed. Most of these compounds were not commercially available, although this was not the case regarding verbenone. This compound was dismissed due to its extensive description as one of the most prominent bark beetle aggregation inhibitors (Mafra-Neto et al. 2022; Frühbrodt et al. 2024), including some *Tomicus* species (Wu et al. 2019; Poland et al. 2004). Its high presence in the fire-injured pines phloem should be related to the fact that this substance is profusely produced in highly degraded tissues (Bracalini et al. 2024), such as those being affected by a fire. Moreover, verbenone has been usually associated with advanced bark beetle attacks, which greatly affect wood decomposition, providing an adequate environment for colonization of later saproxylic insects.

A key issue to highlight about this research is that the attractant effect of the fire-injured (pre- and post-infestation) host volatiles studied has only been performed by combining them, individually, at two emission rates with the commercial kairomone. Thus, under our conditions, the lack of efficacy of any of the products tested may be a consequence of using inadequate emission rates or non-optimal blends, that is, mixtures of these same products or the combination with other compounds also emitted by the tree before or after the infestation. Furthermore, the ratio of each product in the blend may be also crucial for proving activity (Kocabıyık et al. 2024). Therefore, a more in-depth study of the compounds is necessary to ascertain whether they are actually involved in the chemical communication of *T. destruens*. Thus, as already mentioned, additional blends containing α-pinene, ethanol, and methyl eugenol, at different ratios, should be further evaluated. Moreover, studies intended to examine the effect of including other host volatiles in the previous blend are also necessary; these would be the subject of future work.

Author contributions

P.M.and S.V. conceived and designed research. P.M., S.V., I.A., and A.G. conducted the experiments. P.M., A.G., and S.V. analyzed the data and wrote the manuscript. A.G., S.V., I.A., and P.M. revised the manuscript, and all authors read and approved the manuscript giving explicit consent to submit.

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Data availability All data supporting the findings of this study that are not available within the manuscript or supplementary information files can be requested from the corresponding authors, subject to the restrictions imposed by the project's funding agency.

Declarations

Competing interests The authors declare no competing interests.

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