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Effect of host and non-host plant volatiles on pheromone- mediated orientation in the beech bark beetle *Taphrorychus bicolor*

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Broadleaf-feeding bark beetles remain far less studied than conifer-infesting species, particularly with respect to their semiochemical orientation and host selection. Here, we investigated the responses of the beech bark beetle *Taphrorychus bicolor* to host- and non-host-derived volatile organic compounds (VOCs) using field trapping experiments and electrophysiological analyses conducted in the Voděradské bučiny National Nature Reserve (Central Bohemia, Czechia). Pheromone-baited traps were supplemented with plant material from the host *Fagus sylvatica* or the non-host species *Picea abies* and *Taxus baccata*, and relative trap catches and male proportions were evaluated using generalized linear mixed-effects models. Traps baited with pheromone alone captured the highest number of *T. bicolor* (122,342 individuals), whereas the addition of *P. abies* branches significantly reduced trap catches and resulted in the lowest proportion of males (14%) among all treatments, suggesting a potential repellent effect of spruce-derived cues. Branches of *F. sylvatica* and *T. baccata* did not significantly affect beetle captures compared with the pheromone-only control, indicating the absence of an attractive effect of host-derived volatiles under the experimental conditions used. VOCs emitted by host beech and non-host spruce were collected using dynamic headspace sampling and analyzed by GC–EAD and GC × GC–TOF–MS. Antennal responses in beech samples were elicited by eucalyptol, γ -terpinene, and terpinolene, whereas in spruce samples two unidentified compounds elicited antennal responses, with host identity explaining 41.2% of the variation in antennal response profiles ($R^2 = 0.412$, $p < 0.001$). No antennal responses were detected to abundant monoterpenes in either VOC blend. This study provides the first evidence of differential antennal responses to host- and non-host-derived VOCs in *T. bicolor*, together with behavioral evidence of a potential repellent effect of non-host volatiles, with implications for mixed forest management strategies aimed at reducing bark beetle pressure on beech stands under ongoing climate change.

KEYWORDS

broadleaf bark beetles, chemical ecology, forest pest management, GC–EAD, host selection, non-host volatiles, scolytinae, semiochemicals

Introduction

European beech (*Fagus sylvatica* L.) is one of the most dominant broadleaved tree species in Central European forests, representing a key component of ecological stability and economic value (Leuschner and Ellenberg, 2017). Historically, it has been regarded as relatively resilient within the climatic conditions of its natural distribution range. However, ongoing climate change is progressively altering these conditions (Vacek et al., 2023). Increasing mean annual temperatures, together with more frequent drought periods and irregular precipitation patterns, are shifting environmental conditions beyond the ecological optimum of European beech (Cavin et al., 2013; Leuschner, 2020; Martinez del Castillo et al., 2022; Schmied et al., 2023; Kašpar et al., 2024), reducing tree vitality and predisposing individuals to attacks by biotic agents (Netherer et al., 2019). In severe cases, climate change-induced drought stress has led to large-scale beech stand mortality across Europe (Eisenbarth et al., 2001; Rondeux et al., 2003; Arend et al., 2006; Steyrer, 2007; Wegler et al., 2026).

Taphrorychus bicolor (Herbst.) has traditionally been regarded as a secondary pest, colonizing mainly thicker branches and thinner parts of trunks of weakened beech trees, as well as freshly broken or fallen woody material (Pfeffer, 1955; Nicolai, 1997; Harz and Topp, 1999; Delb, 2005; Muck, 2008). However, *T. bicolor*, together with *Agrilus viridis* L., played a significant role during the collapse of beech forest stands in Hungary in 2003 and 2004 (Lakatos and Molnár, 2009) and its occurrence following the drought period of 2015–2019 in Central Europe was substantially elevated (Corcobado et al., 2020; Špoula et al., 2024; Galko et al., 2025; Holuša et al., 2025a; Zúmr et al., 2025). Among the biotic agents benefiting from climate change-induced beech decline, the bark beetle *T. bicolor* has emerged as a potential threat to beech in Central Europe (Galko et al., 2025). In the last 20 years, borers on angiosperms have caused tree mortality in Europe exceeding 10.8 million cubic meters, and the affected area has shown a slightly increasing trend during this period (Hlásny et al., 2025). Given the expected large-scale intensification of disturbance regimes across all future climate scenarios (Grünig et al., 2026), a higher incidence of beech forest decline and the associated harmful effects of *T. bicolor* can be anticipated.

The biology and gallery system of *T. bicolor* is well-known (cf. Pfeffer, 1955; Galko et al., 2025). Most galleries have been found on the sun-exposed side of the host material (Kohnle et al., 1987; Kappes and Topp, 2004). *T. bicolor* has also been reported to vector fungal pathogens that reduce the vitality of host trees (Lakatos and Molnár, 2009; Galko et al., 2025). Host colonization is mediated by the male-produced aggregation pheromone bicolorin and acetophenone (Kohnle et al., 1987; Francke et al., 1995), while (E)-conophthorin is another compound produced by males (Dallara et al., 2000). *T. bicolor* is widely distributed throughout Czechia, with the highest abundance at elevations around 600 m and in regions with extensive stands of mature beech (Špoula et al., 2024; Holuša et al., 2025a).

It is well-established that bark beetles are able to perceive a wide range of volatile organic compounds (VOCs) emitted from various sources. Bark beetles use VOCs to navigate within complex semiochemical landscapes, locate suitable host trees, and avoid non-host trees (Webster et al., 2010; Bruce and Pickett, 2011; Bruce, 2015; Webster and Cardé, 2017; Conchou et al., 2019). Pheromones

produced by bark beetles mediate mate finding, aggregation, and interspecific interactions, including the avoidance of already colonized hosts (Tømmerås et al., 1989; Schlyter et al., 1992; Frühbrodt et al., 2024; Ramakrishnan et al., 2025).

For the most intensively studied bark beetle species, *Ips typographus* (L.) (Hlásny et al., 2021), it has been demonstrated that green leaf volatiles (GLVs) emitted by non-host trees exert strong repellent effects (Jakuš et al., 2003; Zhang, 2003; Zhang and Schlyter, 2004; Andersson et al., 2011; Schiebe et al., 2011; Unelius et al., 2014), whereas primary attraction to host-derived VOCs of spruce has not been convincingly confirmed (Lehmanski et al., 2023). However, VOCs emitted by fungi associated with *I. typographus* have been shown to act as attractants, suggesting that microbial symbionts may play an important role in host location (Jirošová et al., 2022b). Examples of repellent compounds for *I. typographus* include (Z)-3-hexen-1-ol, 1-hexanol, 1-octen-3-ol, 3-octanol, and (E)-conophthorin, all of which occur abundantly in the VOC profiles of green leaves (Byers et al., 1998; Zhang, 2003; Zhang and Schlyter, 2004; Unelius et al., 2014; Jakuš et al., 2024).

In contrast, attraction to host-derived VOCs has been demonstrated in several other bark beetle species. In *Ips duplicatus* (Sahlberg, 1836) the monoterpenes α -pinene and limonene emitted in high quantities by the host *Picea abies* (L.) H. Karst., have been shown to be attractive (Duduman, 2014). Similarly, α -pinene, (1S)-(+)-3-carene, (R)-(+)-limonene, and 1-hexanol emitted by host apricot trees were demonstrated to attract the deciduous tree-feeding bark beetle *Scolytus schevyrewi* (Zhu et al., 2020).

Bark beetles perceive odors through the olfactory system, in which the antennae serve as the primary peripheral sensory organ, while the processing and integration occur in the brain (Vosshall, 2001; Schmidt and Benton, 2020). Insect antennae are covered with fine cuticular hairs (sensilla), which typically contain 1–3 olfactory receptor neurons (ORNs) essential for odor detection. Volatile molecules penetrate the cuticular wall into the interior of the sensilla, where they interact with the olfactory neuron receptors (odorant receptors, ORs). Each neuron is capable of responding to a specific range of odors. The interaction between an odor molecule and an OR triggers the excitation of the ORN and the transmission of this signal to the brain. The odor signal is identified (based on a specific combination of activated receptors), integrated with other sensory information, and forms the basis for behavioral responses (Andersson, 2012; Andersson et al., 2015).

To investigate antennal responses of insects to VOCs, gas chromatography coupled to electro-antenographic detection (GC-EAD) is commonly used (Zhu et al., 2020; Schiebe et al., 2019). Comprehensive two-dimensional gas chromatography employing time of flight mass spectrometry (GCxGC-TOF-MS) provides superior sensitivity and resolution, enabling the detection and identification of trace amounts of EAD-active compounds (Adamová et al., 2020; Thakur et al., 2023; Holuša et al., 2025b).

Despite its increasing relevance, little is known about the chemical ecology of *T. bicolor*, particularly with respect to its responses to host- and non-host-derived VOCs. The present study therefore aimed to assess whether non-host VOCs elicit repellent responses in *T. bicolor* and whether host-derived volatiles function as attractants, as has been reported for some coniferophagous bark beetles. In addition, antennal responses to VOCs emitted by *Picea abies* (L.) H. Karst. and *Fagus sylvatica* L. were investigated using GC-EAD and GC $\times$ GC-TOF-MS analyses.

We hypothesize that, similarly to other deciduous tree-feeding bark beetle species (Zhu et al., 2020), host-derived volatiles will promote attraction in *T. bicolor*. Unlike *I. typographus*, for which primary host VOC attraction has not been convincingly demonstrated (Lehmanski et al., 2023), we expect *T. bicolor* to respond positively to beech-derived volatiles given its strict host specialization on *F. sylvatica*. Furthermore, we predict that non-host volatiles will elicit repellent responses in *T. bicolor*, both in field trapping and in antennal recordings, similarly to the well-studied pattern observed in *I. typographus* (Byers et al., 1998; Zhang, 2003; Zhang and Schlyter, 2004; Unelius et al., 2014; Jakuš et al., 2024).

Materials and methods

Field experiment

In the Voděradské bučiny forest near Kostelec nad Černými lesy (Central Bohemia, Czechia) (49.9596906N, 14.7999119E), five experimental plots were established, each with four Ecotrap pheromone traps (see Galko et al., 2016). The traps were placed 50 m apart in a square arrangement. The traps were baited with a beech bark beetle pheromone lure (Alpha Scents, Inc.) combined with branches, leaves, and logs of selected tree species according to the following treatments: pheromone + *F. sylvatica* [*Fagus*]; pheromone + *P. abies* [*Picea*]; pheromone + *Taxus baccata* L. [*Taxus*], and pheromone only [Control]. Plant material was prepared in a single batch for all traps prior to each collection set, using a few branches collected from the same canopy level of one or several individuals. Fresh logs and branches of the respective tree species were prepared for each collection. Beetles were collected daily from traps during spring and summer swarming periods, with plant material rotated among trap position on each sampling day until all treatments had occupied all positions. In total, five complete sampling series were conducted across the 2022 and 2023 seasons.

After beetle collection, the samples were preserved in ethanol until laboratory processing. In each sample, the total number of beetles was determined. When the number of individuals was high, the count was estimated based on volume. Beetles were placed into a centrifuge tube (0.6 ml Eppendorf) up to the 0.5 ml mark, gently tapped to compact the material, and then refilled to the same volume. Based on ten test measurements, it was determined that 0.5 ml of beetles contained an average of 272 individuals of *T. bicolor*. From each sample, a subsample of 100 individuals was also examined under a binocular microscope, and sex was determined based on external morphological characteristics (Pfeffer, 1955). Boring activity by attracted males was observed on beech logs suspended near the pheromone traps. During beetle collection, new entrance holes were consistently counted, and their number was added to the total number of males. The total number of *Nemozoma elongatum* L. individuals, which were frequently present in the catches, was also recorded for each sample.

GC–EAD experiment

The beetles used in the GC–EAD experiments were obtained from laboratory-reared colonies. The founder generation originated from beetles captured on a pheromone lures in the Voděradské bučiny forest near Kostelec nad Černými lesy (Central Bohemia, Czechia). The collected beetles were placed onto fresh beech logs and maintained in a climate-controlled chamber at 25°C, 60% relative humidity, and a 12:12 h light–dark photoperiod. When adults of the next generation began to emerge, the logs were debarked, the beetles were collected, and used in laboratory assays.

The dynamic headspace method was used to collect volatile organic compounds (VOC) from *P. abies* and *F. sylvatica*. The terminal portion of a branch (approximately 40 cm in length) from a living tree was enclosed in a baking foil bag and hermetically sealed. A collection cartridge consisting of a glass tube filled with 20 mg of Tenax and fitted with a Teflon septum was installed in the sampling bag. Air was drawn through the collection cartridge at a flow rate 100 ml/min for 24 h by using SKC pocket pumps (SKC, Inc.). Two inlet cartridges were attached to the sampling bag to purify the incoming air. After sampling, the volatiles were eluted from the cartridges with 200 µl of hexane and concentrated by evaporation under ambient conditions to a final volume of 25 µl.

For the GC–EAD experiments, an Agilent 7890B gas chromatograph was used, equipped with an HP-5 capillary column (Agilent Technologies, Inc), 30 m in length, 0.32 mm in diameter, and 0.25 µm film thickness, terminated with a splitter. From the splitter, 5 m of the same column led to the flame ionization detector (FID), and 1 m of the column led to the antenna. The chemical components were mixed with humidified air at a flow rate of 2 l/min at the column outlet and blown onto the prepared antenna. Samples were injected splitless, and the carrier gas for the chromatograph was helium with a constant column flow rate of 3 ml/min. The inlet temperature was set to 250°C, the initial oven temperature was set to 40°C for 1 min, then increased by 10°C/min to 100°C, held for 0.5 min, then increased by 20°C/min to 150°C, and then increased by 40°C/min to a final temperature of 300°C, with 3 min hold. The FID temperature was set to 300°C.

For EAD recordings, the beetle head with antennae was prepared and connected between glass microelectrodes filled with Ringer's solution (NaCl 12.2 g/l, KCl 0.21 g/l, CaCl₂ 0.2 g/l dissolved in distilled water). The reference electrode was connected to the head, and the measuring electrode was connected to the tip of the antennal club. Signals from olfactory receptor neurons (ORNs) were recorded using a Universal probe, amplified (100x), and integrated with IDAC 2; all hardware and the GcEad v. 4.6.1 software were supplied by Ockenfels SYNTech GmbH. A VOC was considered EAD-active if antennal responses were recorded in at least three individuals. The identification of EAD-active compounds was confirmed using synthetic standards at a concentration of 100 ng/µl. Compounds of interest, preselected in GC–EAD records, were identified in the same extracts, using GCxGC-TOF-MS system (Pegasus 4D, LECO, United States) configured as described in Holuša et al. (2025b). Identification and confirmation of detected compounds was performed according to the procedures described in Thakur et al. (2024).

Statistical methods

For a statistical evaluation of the field experiment a generalized linear mixed-effect model (GLMM) was used. The response variable was either the relative trap catches of *T. bicolor* or the male proportion, and the independent variable was trap bait. Relative trap catches were calculated as the ratio of the catch in an individual trap to the total catch recorded on the same sampling date at the locality. This approach allowed us to address the temporal correlation issue because ratios are not affected by the variation in the number of individuals during the swarming period. Moreover, the influence of the collection date on trap catches was tested using the same regression model and was found to be non-significant. To minimize positional effect, baits were rotated among traps throughout the experiment. The locality, in which all four traps were installed and bait rotation was performed, was included as a nested random factor ($n = 5$). Model formulation was carried out in R version 4.4.2 (R Core Team, 2024) using the package glmmTMB, following the procedures described by Brooks et al. (2017). To assess the significance of the independent variable, the drop1 function was employed (Zuur et al., 2009). Estimated marginal means were compared using Tukey-adjusted pairwise contrasts (EMMs; emmeans package in R).

Antennal responses to VOCs detected in GC-EAD recordings were analyzed using a multivariate approach. For each recording, the response amplitude of all detected compounds was treated as a quantitative variable, producing a response matrix in which rows represented individual recordings and columns represented VOC compounds. Prior to analysis, the compound matrix was Hellinger-transformed to reduce the influence of dominant peaks and to make the data suitable for Euclidean-based ordination methods. Differences in antennal response profiles between host species (spruce and beech) were tested using permutational multivariate analysis of variance (PERMANOVA) with Bray-Curtis dissimilarities and 999 permutations. To visualize multivariate differences among recordings, canonical analysis of principal coordinates (CAP) was performed, based on Anderson and Willis (2003) approach. All multivariate analysis of GC-EAD responses were carried out using vegan package (Oksanen et al., 2026).

Results

Field experiment

The number of captured *T. bicolor* individuals was highest during the spring swarming period and gradually declined thereafter. However, the proportional distribution of beetles among bait treatments within the same phase of the vegetation season did not differ significantly ($df = 12$, $p = 0.65$). The highest total number of *T. bicolor* individuals was captured in traps baited with pheromone only (122,342), followed by traps containing pheromone combined with beech logs and branches (87,389), pheromone with yew branches (69,852), whereas the lowest number of beetles was recorded in traps with added spruce branches (36,723). Details of trap catches are given in the Supplementary Table 1.

Differences in relative trap catches of *T. bicolor* among bait types were statistically significant ($df = 3$, $p < 0.001$; Figure 1). Traps containing pheromone only (control) showed significantly higher catches compared with all other treatments (Table 1), although the difference between the control and the beech treatment (*Fagus*) was at the threshold of statistical significance (contrast t -test, $df = 394$, $p = 0.047$; Table 1). Nevertheless, the presence of fresh beech material did not increase trap catches relative to the control.

Traps baited with beech material captured more individuals than the remaining two treatments; however, this difference was significant only in comparison with the spruce treatment (contrast t -test, $df = 394$, $p < 0.001$; Table 1). The effect of yew branches (*Taxus*) did not differ significantly from that of beech branches (contrast t -test, $df = 394$, $p = 0.499$; Table 1). A comparison of the two coniferous tree species (*Picea* and *Taxus*) revealed a surprisingly higher capture of *T. bicolor* in traps baited with yew (contrast t -test, $df = 394$, $p < 0.001$; Table 1).

The absolute number of captured male *T. bicolor* followed the trend observed for the total number of beetles captured in traps. However, with respect to the proportion of males captured across the compared bait treatments, a different pattern emerged. Significant differences in male proportion were detected among traps ($df = 3$, $p < 0.001$; Figure 2).

The lowest proportion of males was recorded in traps baited with spruce (*Picea*) (14%), and this value differed significantly from all other treatments (Table 2). The highest proportion of captured males was observed in traps baited with beech (*Fagus*) (25%), followed by the control treatment (21%) and yew (*Taxus*) (20.6%). Differences among these three treatments were not statistically significant (Table 2).

GC-EAD experiment

A total of 40 GC-EAD recordings were measured for VOC samples from *F. sylvatica* and *P. abies*. In the *F. sylvatica* samples, the compounds, identified by GC $\times$ GC-TOF-MS analysis as *trans*-2-hexenal, eucalyptol, γ -terpinene, and terpinolene were antennally active for *T. bicolor*. The EAD-active compounds in the *P. abies* samples were *trans*-2-hexenal and two unidentified components (Figure 3). Trace concentration of the pheromone component bicolorin was also detected in both samples, which elicited a strong antennal response (Supplementary Figure 1). *Trans*-2-hexenal occurred in the spruce samples only in trace amounts, in contrast to its higher abundance in beech samples. Both samples contained high concentrations of monoterpenes such as α -pinene, β -pinene, 3-carene, camphene, and limonene; however, none of these compounds elicited antennal responses.

Discussion

Field experiments revealed that the highest number of *T. bicolor* were captured in traps baited with pheromone alone, without the addition of plant material. Traps supplemented with leaves, branches, and logs of *F. sylvatica* or *T. baccata* yielded slightly lower catches than the control treatment, approaching but not reaching statistical significance. In contrast, traps supplemented

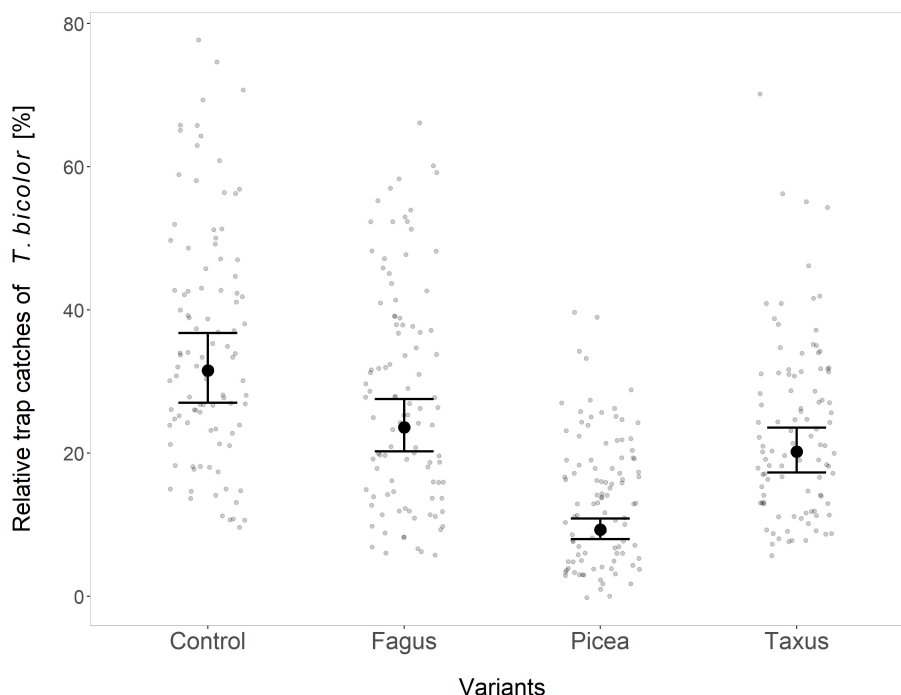


FIGURE 1

Relative trap catches of *Taphrorychus bicolor* (%). The black dot represents the fitted value and whiskers 95% confidence intervals of the GLMM model $\log(\text{Proportion}) \sim \text{Variant} + (1 | \text{Plot})$, (Gaussian family). The smaller dots in the background are original values.

TABLE 1 Pairwise contrast comparison of variants in the generalized linear mixed-effect model (GLMM) $\log(\text{Proportion}) \sim \text{Variant} + (1 | \text{Plot})$, (Gaussian family), using Tukey-Kramer HSD controlling error.

Contrast	Estimate	SE	df	t ratio	P-value
Control– <i>Fagus</i>	0.29	0.111	394	2.604	0.0469
Control– <i>Picea</i>	1.219	0.111	394	10.967	<0.0001
Control– <i>Taxus</i>	0.445	0.111	394	4.005	0.0004
<i>Fagus</i> – <i>Picea</i>	0.93	0.111	394	8.363	<0.0001
<i>Fagus</i> – <i>Taxus</i>	0.156	0.111	394	1.401	0.4996
<i>Picea</i> – <i>Taxus</i>	–0.774	0.111	394	–6.962	<0.0001

with the non-host *P. abies* captured significantly fewer beetles, which may indicate a potential repellent effect of spruce-derived cues. The lowest proportion of males was recorded in traps baited with *P. abies* (14%), whereas the highest male proportion was observed in traps baited with *F. sylvatica* (25%). Male proportions in traps baited with *F. sylvatica*, *T. baccata*, and the pheromone alone were very similar, and differences among these treatments were not statistically significant.

These findings support the assumption that *T. bicolor*, similar to coniferophagous bark beetles, is able to distinguish between host and non-host trees already during flight, prior to landing (Zhang and Schlyter, 2004; Huber et al., 2021; Lehmannski et al., 2023). For example, *I. typographus* has been shown to discriminate among odor sources separated by only several tens of centimeters, thereby avoiding non-host trees even in the immediate proximity of a host (Andersson et al., 2011).

Notably, *T. bicolor* did not exhibit increased attraction to traps with its primary host, *F. sylvatica*. Fresh beech leaves, branches, and logs likely emitted cues indicating the tree's robust defense ability.

In particular, leaves could release volatiles (C_6 -alcohols), serving as a remote signal of habitat unsuitability for colonization (Schlyter and Birgersson, 1999) consistent with the saproxylic character of *T. bicolor*.

As plant material used in the field experiments, a small log section (approximately 10 cm in diameter) and several fresh branches with leaves/needles were always employed. The plant material originated from mature trees and was, for each trap, randomly pooled from several individuals to increase VOC variability, because VOC profiles are known to differ substantially among individual trees (Van Meeningen et al., 2016). Prior to each replication, fresh material was prepared, meaning that the plant material used during the experiment was between 1 and 4 days old. Nevertheless, changes in VOC profiles may have occurred even within this short period, particularly during the summer replications. Terpenoid compounds contained in woody tissues are known to oxidize gradually after cutting (Schiebe et al., 2019). Although efforts were made to minimize this effect by reducing the exposure time, it could not be entirely avoided.

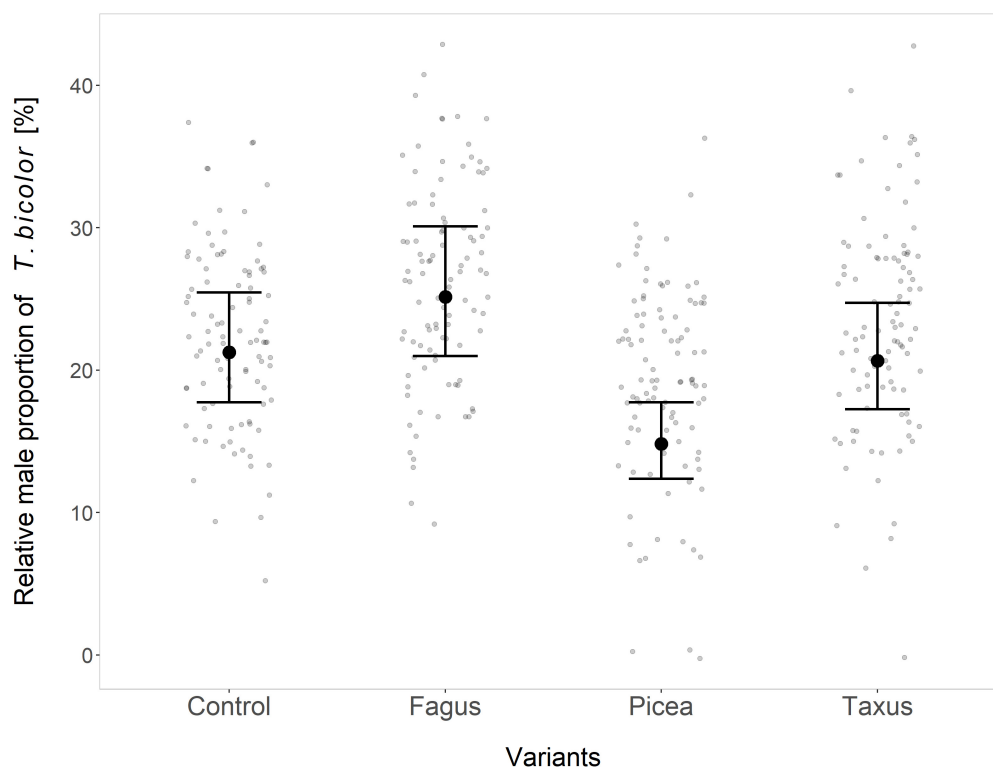


FIGURE 2

Relative male proportion of *Taphrorychus bicolor* (%). The black dot represents the fitted value and whiskers 95% confidence intervals of the GLMM model $\log(\text{Male_proportion}) \sim \text{Variant} + (1 | \text{Plot})$, (Gaussian family). The smaller dots in the background are original values.

TABLE 2 Pairwise contrast comparison of variants in the generalized linear mixed-effect model (GLMM) $\log(\text{Male_proportion}) \sim \text{Variant} + (1 | \text{Plot})$, (Gaussian family), using Tukey-Kramer HSD controlling error.

Contrast	Estimate	SE	df	t ratio	P-value
Control– <i>Fagus</i>	–0.168	0.115	394	–1.464	0.4603
Control– <i>Picea</i>	0.361	0.115	394	3.147	0.0096
Control– <i>Taxus</i>	0.029	0.115	394	0.253	0.9943
<i>Fagus</i> – <i>Picea</i>	0.529	0.115	394	4.611	<0.0001
<i>Fagus</i> – <i>Taxus</i>	0.197	0.115	394	1.717	0.316
<i>Picea</i> – <i>Taxus</i>	–0.332	0.115	394	–2.894	0.0209

Another potential source of VOC profile variation was plant compounds induced by insect activity and volatiles produced by the insects themselves. Branches placed in close proximity to the pheromone lures attracted *T. bicolor* to land and attempt gallery initiation. This behavior was observed predominantly on beech, where additional emission of beetle-derived pheromones may have occurred, although attempts at boring were also recorded on non-host spruce and yew. In spruce, occasional boring activity by *Pityogenes chalcographus* (L.) was additionally observed, potentially contributing to the blend of emitted volatiles. On the other hand, these compounds represent volatiles commonly present in the environment in which the field experiment was set. Therefore, we consider it likely that the VOCs produced by our baits were far more influential than any potential additional sources of contamination. Consequently, it cannot be excluded that some of the VOCs detected in our samples were herbivore-induced rather

than constitutive, representing a limitation inherent to field-based experimental designs of this kind.

The tree species *T. baccata* is an interesting case, as its wood is known to be toxic and it is not infested by any bark beetles (Thomas and Polwart, 2003). Therefore, it was selected for the behavioral experiments as a non-host species for *T. bicolor*. However, no statistically significant effect of *T. baccata* in combination with pheromone on *T. bicolor* attraction was detected in the field experiments, and thus it was not included in the subsequent analyses. The similar trap catches recorded for the *T. baccata* and *F. sylvatica* treatments suggest that *T. bicolor* did not exhibit differential behavioral responses to the volatiles of these two tree species. This is noteworthy given that the VOC profiles of *T. baccata* and *F. sylvatica* are known to differ considerably (Roberts et al., 2019; Soudek et al., 2025), implying that *T. bicolor* may lack the sensory or behavioral mechanisms necessary to discriminate between these species based on their volatile emissions alone.

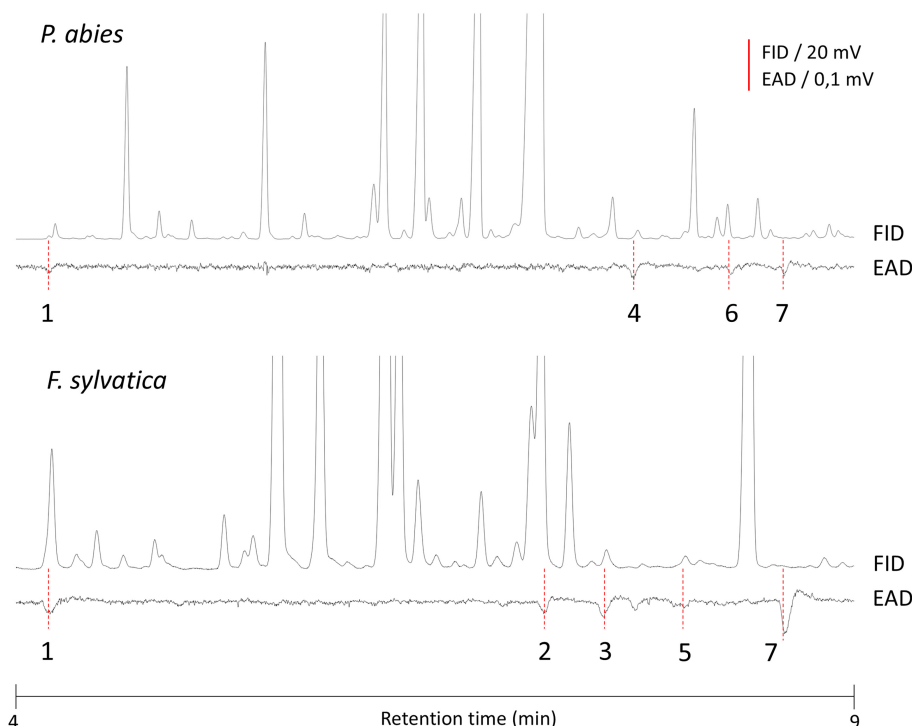


FIGURE 3

Gas chromatography coupled to electro-antenographic detection (GC-EAD) responses of *Taphrorychus bicolor* to volatiles emitted from *P. abies* and *F. sylvatica*. Red dotted lines connect the antennal responses and the relevant compounds in the FID chromatogram. The active compounds were: 1, *trans*-2-hexenal; 2, eucalyptol; 3, γ -terpinene; 4, unknown; 5, terpinolene; 6, unknown; 7, bicolorin. Canonical analysis of principal coordinates (CAP) ordination showed a clear separation between responses obtained from spruce and beech along the first canonical axis (Figure 4). Several volatile compounds were associated with spruce, as indicated by vectors oriented toward the spruce cluster, whereas other compounds were associated with beech recordings. The dispersion of individual responses within each host group suggests moderate variability in antennal activity. The PERMANOVA analysis revealed a significant difference in antennal response profiles between host species ($df = 1$; $p < 0.001$). Host species explained 41.2% of the variation in the multivariate antennal response matrix ($R^2 = 0.412$), indicating that a substantial proportion of variation in antennal responses to volatile compounds was associated with host identity. The significant host effect detected by PERMANOVA was consistent with the CAP ordination, which showed separation of GC-EAD recordings according to host species.

However, this interpretation cannot be fully confirmed without dedicated electrophysiological analyses of *T. baccata* volatiles.

Instead, the results indicate a potential repellent effect of the non-host *P. abies*. This pattern mirrors well-established findings for *I. typographus*, for which primary host attraction has not been conclusively demonstrated, whereas a wide range of effective non-host repellents has been identified (Lehmanski et al., 2023). For instance, Byers et al. (1998) described (Z)-3-hexen-1-ol and 1-hexanol, compounds occurring in birch leaves, as repellents to *I. typographus*. Zhang (2003) reported that C₆–C₈ alcohols and *trans*-conophthorin exert stronger repellent effects when applied in combination. While individual compounds only moderately reduce attraction, their mixtures markedly suppress pheromone-mediated attraction. Unelius et al. (2014) indicated a combination of (–)-verbenone, 1-hexanol, and technical *trans*-conophthorin as the most effective repellent blend. More recently (+)-*trans*-4-thujanol was shown to act as a strong repellent for *I. typographus*, particularly affecting females, in contrast to other repellents that tend to repel males more strongly (Blažytė-Čereškienė et al., 2016; Jirošová et al., 2022a).

Based on the repellent effects of non-host volatiles, a push-pull management strategy was developed for *I. typographus* combining repellent non-host volatiles with pheromone-baited traps to protect valuable stands (Jakuš et al., 2003, 2024).

However, Lindmark et al. (2022) questioned the effectiveness of this approach, reporting continued attacks within treated stands. These authors therefore advocated a shift toward close-to-nature forest management, including mixed-species stands and the promotion of resistant tree species.

A similar principle of repellence by non-host volatiles may apply to the broadleaf-feeding bark beetle *T. bicolor*. However, given the lower economic importance of beech compared with spruce, the development and application of synthetic repellent-based management strategies is unlikely to be economically justified. Instead, increasing forest resilience through the establishment of mixed beech stands—particularly at sites corresponding to natural beech–spruce forest types—represents a more sustainable approach. In mixed forests, herbivore damage generally decreases with increasing tree-species diversity, a phenomenon attributed to associative resistance, driven by reduced resource concentration and increased semiochemical complexity, making it more challenging for herbivores to locate suitable host plants and mates (Jactel and Brockerhoff, 2007; Guyot et al., 2016; Klapwijk and Björkman, 2018).

Establishing mixed forests by promoting the natural regeneration of beech is an important objective of contemporary forest management. One practical approach is to release individual beech trees growing within or adjacent to spruce monocultures by

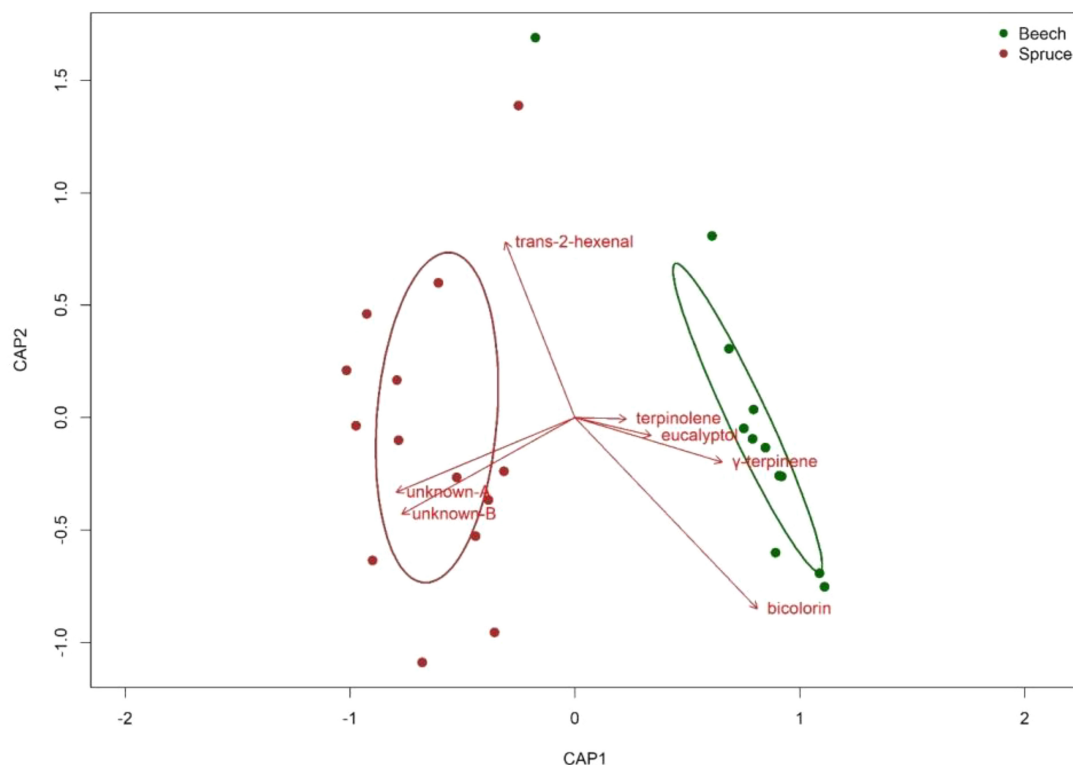


FIGURE 4

Gas chromatography coupled to electro-antennographic detection (GC–EAD) responses to volatiles emitted from *P. abies* and *F. sylvatica*. Canonical analysis of principal coordinates (CAP) showing variation in antennal responses of *T. bicolor* to volatile compounds across GC–EAD recordings. Points represent individual recordings colored by host species (spruce, red; beech, green), and ellipses indicate group dispersion. Red arrows represent volatile compounds contributing to variation in antennal responses.

removing surrounding spruce. However, trees that have developed under closed canopy conditions may experience stress upon sudden exposure, particularly in the case of beech (Leuschner, 2020). Such stressed trees may become susceptible to *T. bicolor* attack. To mitigate this risk, felling could be carried out in spring, with spruce branches left to accumulate in the newly opened space. In accordance with our results, the volatile compounds emitted by spruce branches may reduce the incidence of *T. bicolor* by acting as potential repellent cues.

From the branches of *P. abies* that had the most pronounced effect on the *T. bicolor* behavior in the field experiments, a sample of volatiles was collected using the dynamic headspace method and analyzed by GC–EAD. A control sample from the host tree *F. sylvatica* was collected and analyzed in the same manner. Together with the PERMANOVA results, the CAP ordination indicates that antennal responses to volatile compounds differ between host species, and that specific compounds contribute to this differentiation. *T. bicolor* antennae responded to eucalyptol, γ -terpinene, and terpinolene in beech samples, and to two unidentified compounds in spruce samples. This represents a novel finding, as olfactory responses to host- and non-host-related VOCs have not previously been investigated in *T. bicolor*. Distinct sets of compounds elicited antennal responses in beech and spruce samples, reflecting the differences in VOC composition between the two tree species. *T. bicolor* did not respond antennally to the dominant monoterpenes detected in either VOC blend, including α -pinene, β -pinene, 3-carene, camphene, limonene, and sabinene,

despite their high abundance. The occurrence of monoterpenes in the VOC profile of beech has also been reported previously (Tollsten and Müller, 1996; Holzke et al., 2006). This sensory pattern clearly distinguishes *T. bicolor* from conifer-infesting bark beetles such as *I. typographus*, which are known to perceive these compounds (Toommeras, 1985; Andersson et al., 2009; Andersson, 2012; Kalinová et al., 2014; Schiebe et al., 2015, 2019; Raffa et al., 2016). Future studies should therefore address the behavioral relevance of individual EAD-active compounds to further elucidate the mechanisms underlying host selection in *T. bicolor*.

This study provides the first evidence of antennally active volatiles from both host and non-host trees for *T. bicolor*, suggesting that these compounds influence its host-finding behavior. For other broadleaf-feeding bark beetle species, only a limited number of studies addressing the effects of host and non-host volatiles are available, making the present work one of the first contributions to this research area. For example, Zhu et al. (2020) investigated host volatiles from apricot trees in relation to the bark beetle *S. schevyrewi*, identifying 21 antennally active compounds, including monoterpenes such as camphene, α -pinene, (1S)-(+)-3-carene, and (R)-(+)-limonene. In contrast to *T. bicolor*, these monoterpenes were behaviorally attractive to *S. schevyrewi*. Ranger et al. (2010) reported that ethanol was attractive and methanol was slightly attractive to *Xylosandrus germanus*. Ranger et al. (2021) showed that verbenol inhibits ethanol-mediated attraction. Martini et al. (2015) reported that the ambrosia beetle *Xyleborus glabratus*,

which is unusual among ambrosia beetles in attacking healthy trees, is attracted to host-derived sesquiterpenes.

Conclusion

Taphrorychus bicolor, as a representative of broadleaf-feeding bark beetles, was shown to perceive host and non-host volatiles, similarly to coniferophagous bark beetles. Traps equipped with a pheromone lure supplemented with branches of the non-host *P. abies* captured the lowest number of *T. bicolor* individuals, as well as the lowest proportion of males, among all treatments, suggesting a potential repellent effect of spruce-derived volatiles. The second non-host species tested, *T. baccata*, did not significantly affect trap catches relative to the pheromone-only control, nor did the addition of host *F. sylvatica* material increase catches, indicating the absence of an attractive effect of beech-derived volatiles under the experimental conditions used.

Gas chromatography coupled to electro-antenographic detection analyses revealed antennal responses of *T. bicolor* to eucalyptol, γ -terpinene, and terpinolene in beech VOC samples, and to two unidentified compounds in spruce VOC samples. PERMANOVA confirmed a significant difference in antennal response profiles between the two host species, with host identity explaining 41.2% of the variation in the multivariate antennal response matrix. The sets of EAD-active compounds differed between the two tree species. Notably, no antennal responses were recorded to the most abundant monoterpenes present in either sample, including α -pinene, β -pinene, 3-carene, camphene, and limonene, further distinguishing *T. bicolor* from coniferophagous bark beetles, which commonly perceive and respond to these compounds.

This study provides the first evidence of differential antennal responses to host- and non-host-derived VOCs in *T. bicolor*, together with behavioral evidence of a potential repellent effect of non-host volatiles, and represents one of the first contributions addressing the chemical ecology of broadleaf-feeding bark beetles. The findings suggest that mixed forest management strategies incorporating non-host tree species may contribute to reducing *T. bicolor* pressure on beech stands, particularly in the context of ongoing climate change-induced beech decline.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Ethics statement

Ethical approval was not required for the study involving animals in accordance with the local legislation and institutional requirements because it was a pest insect species which is not under the ethical law.

Author contributions

JB: Writing – review & editing, Investigation, Methodology, Data curation, Writing – original draft, Conceptualization, Visualization. MN: Writing – original draft, Data curation, Writing – review & editing, Investigation. JH: Software, Writing – original draft, Writing – review & editing, Investigation, Supervision, Data curation, Methodology. BK: Writing – review & editing, Conceptualization, Supervision, Writing – original draft. RM: Methodology, Writing – original draft, Data curation, Supervision, Conceptualization, Visualization, Software, Resources, Writing – review & editing.

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Conflict of interest

The author(s) declared that this work was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/ffgc.2026.1802499/full#supplementary-material>

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