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The effects of host and habitat preferences in mate location of *Monochamus maculosus*, *Monochamus notatus*, and *Monochamus scutellatus* (Coleoptera: Cerambycidae)

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Abstract

Several *Monochamus* species (Coleoptera: Cerambycidae) use monochamol as an aggregation-sex pheromone, raising questions about how they maintain reproductive isolation. Herbivorous insects use host plant semiochemicals as cues for mate location and, with or without habitat cues, these could confer reproductive isolation among sympatric *Monochamus* spp. To test this hypothesis, host and habitat preferences in mate location were examined for sympatric populations of *Monochamus maculosus*, *Monochamus notatus*, and *Monochamus scutellatus* in the Algoma District, Ontario, Canada. Field experiments were performed to investigate whether differences in host preference, vertical distribution across the forest canopy, spatial distribution within down and standing dead trees, or any combination of these factors could minimise cross-attraction to monochamol. Results showed that more *M. maculosus* were attracted to monochamol combined with jack pine foliage than with balsam fir or white spruce, whereas no differences in host attractivity were observed for the other species. Vertical abundance of *M. maculosus* and *M. scutellatus* was similar across forests. Spatial distribution provided limited evidence for species segregation within hosts. No evidence was found that host or habitat preferences contribute to reproductive isolation in *M. maculosus*, *M. notatus*, or *M. scutellatus*, suggesting that vertical distribution could be driven by resource availability.

Introduction

In most herbivorous insects, host plant location and selection are essential for insect survival and fitness because host plants provide food, shelter, and oviposition sites. Insects depend heavily on olfaction for sensing their surrounding environment (Greenfield 2002) and have developed a complex olfactory system that is extremely sensitive to the detection of behaviourally relevant volatiles

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(Hansson 2002; Wyatt 2014; Dekker and Barrozo 2016). Plant volatile compounds have chemical properties that allow them to travel metres away from the source (Pichersky *et al.* 2006; Baldwin 2010), and the location and selection of host plants at a distance partially result from the detection of plant volatile chemical cues by the insects' well-developed olfactory system. Herbivorous insects may also use habitat odour cues (*e.g.*, general volatile conifer terpenoids, including α -pinene) to facilitate host location (*i.e.*, to locate general areas where hosts are most likely to be found; Webster and Cardé 2017). Differences in the composition and ratios of plant volatile compounds allow insects to discriminate host plants from nonhost plants, to find appropriate host plants within diverse vegetation patches, to determine the nutritional quality of host plants, and to detect the presence of other insects on a host plant (Dicke and Baldwin 2010; Bruce and Pickett 2011).

Insect mate location generally involves the use of species-specific pheromones (Thornhill and Alcock 1983; Greenfield 2002). Increasing evidence suggests that plant volatiles also play an additional, important role in insect mate location because mating in some species occurs on host plants (Anderson and Anton 2014). Herbivorous insects have developed multiple strategies that integrate host plant chemicals and sex pheromones to optimise mating and reproduction (Landolt and Phillips 1997; Reddy and Guerrero 2004; Xu and Turlings 2018). For example, males of many insect orders can use host plant volatiles released during female or larval feeding activity as cues for mate location (Ruther *et al.* 2000; Tooker *et al.* 2002; Estrada and Gilbert 2010). Some species can sequester host plant chemicals during the larval or adult stage to use as sex pheromones or sex pheromone precursors (Hartmann *et al.* 2003, 2004; Fonseca *et al.* 2010; Zarbin *et al.* 2013). In some species of Coleoptera, host plant volatiles have been reported to stimulate the release of pheromones (Jaffé *et al.* 1993; Lextrait *et al.* 1995; Pineda-Ríos *et al.* 2021) or have a synergistic or additive effect in the attractivity of sex pheromones (Ginzel and Hanks 2005; Hanks and Millar 2016; Hanks and Wang 2017).

In the genus *Monochamus* Dejean (Coleoptera: Cerambycidae), the compound monochamol has been reported to be a pheromone or pheromone attractant for at least 14 species (Pajares *et al.* 2010, 2013; Teale *et al.* 2011; Allison *et al.* 2012; Fierke *et al.* 2012; Wickham *et al.* 2014; Lee *et al.* 2017, 2018; Andrade *et al.* 2024). Monochamol is an aggregation-sex pheromone (*sensu* Cardé 2014) produced by males that mediates aggregation of both males and females on larval hosts, where mating usually occurs. Three species of the genus, namely *M. maculosus* (Haldeman) (previously known as *M. mutator* LeConte; Bousquet *et al.* 2017), *M. notatus* (Drury), and *M. scutellatus* (Say), are sympatric and partially synchronic in Ontario, Canada (Bousquet *et al.* 2017), and have been reported to use the same compound as a pheromone or putative pheromone attractant (Fierke *et al.* 2012; Andrade *et al.* 2024). These species have also been reported to use the same tree species in similar physiological conditions (*i.e.*, severely stressed or recently killed trees of the genus *Pinus* Linnaeus, *Picea* Miller, *Abies* Miller, and *Larix* Miller (all Pinaceae)) as mating and oviposition sites (Akbulut and Stamps 2011; Akbulut *et al.* 2017). Although pheromone parsimony in this genus would make sympatric species susceptible to cross-attraction, hybridisation between *M. scutellatus*, *M. maculosus*, and *M. notatus* in the field seems rare.

Host location and acceptance in the Cerambycidae are mediated by chemical cues (Allison *et al.* 2004). Consequently, specific host volatile cues could contribute to the reproductive isolation of *Monochamus* species. In fact, the addition of α -pinene, a volatile emitted by conifer trees, to synthetic monochamol in field trapping experiments has a synergistic or additive effect on the attraction of many *Monochamus* species (Pajares *et al.* 2010; Allison *et al.* 2012; Fierke *et al.* 2012; Macias-Samano *et al.* 2012; Ryall *et al.* 2015; Andrade *et al.* 2024). However, variation in the production of secondary metabolites (*e.g.*, terpenes) between different genera and species of conifers exists (Kopacyk *et al.* 2020). Host species preference for adult feeding and oviposition has been reported in *Monochamus galloprovincialis* (Olivier) (Naves *et al.* 2006a; Koutroumpa *et al.* 2009) and seems to be related to the reproductive potential of female beetles (Akbulut 2009). Females of *M. scutellatus* have been reported to lay more eggs on black spruce, *Picea mariana* (Miller) Britton *et al.* (Pinaceae), than on jack pine, *Pinus banksiana* Lambert (Pinaceae), and

M. scutellatus larvae seem to develop faster on black spruce than on jack pine (Breton *et al.* 2013). In addition, adult body size and mass in some *Monochamus* species seem to vary with host species (Naves *et al.* 2006a, 2006b; Togashi and Appleby 2023), and advantages of size in both adult and larval competition over resources have been reported in the genus (Hughes and Hughes 1987; Victorsson and Wikars 1996; Anbutsu and Togashi 1997a).

Niche partitioning between sympatric species is well documented in bark beetles (Coleoptera: Curculionidae: Scolytinae). The height at which Scolytinae species fly during dispersal seems related with the height of tree structures they attack (Wood 1982; Ulyshen and Hanula 2007), and colonisation of host trees by two or more species seems to affect their spatial distribution in the bole (Paine *et al.* 1981; Safranyik *et al.* 2000; Ayres *et al.* 2001). In this context, pheromones appear to play a role in defining the sequence and patterns of host aggregation and colonisation by more than one Scolytinae species because the presence of species-specific pheromone signals can either enhance or inhibit heterospecific attraction response to specific sections of a tree (Paine *et al.* 1981; Smith *et al.* 1990; Ayres *et al.* 2001). Dodds (2014) hypothesised that niche partitioning in *Monochamus* may occur in a similar way as it does in Scolytinae to minimise competition for mates, for oviposition resources, or for both.

The abundance of sympatric Cerambycidae species has been reported to differ across the vertical strata of the forest canopy, including species of the genus *Monochamus* (Graham *et al.* 2012; Sweeney *et al.* 2020; Vargas-Cardoso *et al.* 2023). Dodds (2014) observed that most of *Monochamus carolinensis* (Oliver) were captured in traps placed in the forest canopy, whereas the majority of *M. scutellatus* were captured in traps placed in the understorey. Hughes and Hughes (1982) reported that female *M. scutellatus* prefer larger-diameter sections of host trees for oviposition, and Ryan *et al.* (2012) found that the distribution of larvae of *M. carolinensis* tends to increase slightly in the upper portions of bole sections. In addition, males of *M. scutellatus* have been reported to engage in aggressive inter- and intra-specific contests to defend portions of hosts that are favoured by females for oviposition (*i.e.*, areas of the trunk with largest circumference) and for access to females (Hughes and Hughes 1982, 1987; Allison and Borden 2001). However, it remains unclear whether differences in flight patterns among Cerambycidae species relate directly to colonisation behaviour in host trees (Dearborn *et al.* 2016).

The main objective of the present study was to investigate host and habitat preferences and their potential contribution to reproductive isolation in sympatric populations of three *Monochamus* spp. – *M. scutellatus*, *M. maculosus*, and *M. notatus* – in the Great Lakes Forest Region of Ontario, Canada. Field experiments were used to test for specific host preferences, vertical distribution across the forest canopy, and spatial distribution within and among lying and standing dead trees. The data were assessed for specific host and habitat preferences that could contribute to their reproductive isolation. It was hypothesised that (1) if the three sympatric *Monochamus* spp. use host volatiles in addition to pheromones to locate mates and have specific host preferences for mating and reproduction, then specific host volatile components minimise the chances of cross-attraction to monochamol and (2) if the three sympatric *Monochamus* spp. segregate as adults at the local spatial forest level, tree level, or both, either during mating or oviposition, specific spatial preferences within and between down and standing dead trees can minimise the chances of cross-attraction between these species.

Materials and methods

Study sites

All field experiments were run in two sites located in the Algoma District, Ontario, Canada. The first field site is a private, unmanaged mixed-wood forest of approximately 30 ha located west of Sault Ste Marie, Ontario, Canada (46° 29' 47.5" N, 84° 29' 09.7" W). The forest is primarily composed of softwood species (~57%), including white spruce, *Picea glauca* (Moench) Voss,

black spruce, *P. mariana*, eastern white pine, *Pinus strobus* Linnaeus, red pine, *Pinus resinosa* Solander ex. Aiton, jack pine, *Pinus banksiana*, balsam fir, *Abies balsamea* (Linnaeus) Miller, tamarack, *Larix laricina* (Du Roi) K. Koch, and eastern hemlock, *Tsuga canadensis* (Linnaeus) Carrière, (all Pinaceae) (Ontario Ministry of Natural Resources and Forestry 2020a). The second field site is a crown softwood pine forest stand of approximately 170 ha located north of Thessalon, Ontario (47° 07' 56.7" N, 83° 08' 31.3" W). This stand is primarily composed of *P. banksiana* (~80%) and is located between softwood pine forest stands that had been clearcut (all trees removed) within two years before the experiments using the short-wood method (Ontario Ministry of Natural Resources and Forestry 2020b).

Host-mediated reproductive isolation

Twelve-unit multifunnel traps (Lindgren 1983) that were coated with Fluon PTFE lubricant to increase the capture rate of attracted beetles (Allison *et al.* 2011, 2016) and were equipped with wet collecting cups containing approximately 200 mL of antifreeze were deployed in linear arrays of eight replicate blocks in a clearcut mixed-wood forest in the second field site (47° 07' 56.7" N, 83° 08' 31.3" W). Each block contained four traps hung at 1.5 m height from iron stands fixed into the ground and spaced 30 m apart ($n = 32$ traps in total). All traps were baited with one bubblecap lure containing synthetic monochamol, and the following treatments were randomly assigned within each replicate block: (1) one mesh bag with no branches or fresh foliage of host trees and one ultra-high release (UHR) α -pinene lure; (2) one mesh bag containing 4.5 kg of branches and fresh foliage of *Abies balsamea*; (3) one mesh bag containing 4.5 kg of branches and fresh foliage of *Pinus banksiana*; and (4) one mesh bag containing 4.5 kg of branches and fresh foliage of *Picea glauca*. Bubblecap lures containing synthetic monochamol (99% purity and release rate of 1.5 mg/day at 30 °C) and UHR α -pinene (98% purity and release rate of 2000 mg/day at 25 °C) were purchased from Synergy Semiochemicals (Delta, British Columbia, Canada). The contents of the mesh bags were prepared one day before their installation on the traps. Branches and foliage of either *A. balsamea*, *P. banksiana*, or *P. glauca* were chopped into small pieces with an electric log splitter (LOGic®, version 120/6; Bell SRL, Reggio Emilia, Italy). Chopped host material (4.5 kg) was placed in a mesh bag and kept at 5 °C until the next morning, when the bags were taken to the field and hung on the traps. All mesh bags containing chopped plant material were replaced weekly.

The traps were inspected weekly during four consecutive weeks from 3 to 27 August 2014. The content of each trap was sieved and placed individually in a Whirl-Pak® bag (710 mL; Whirl-Pak Filtration Group, Pleasant Prairie, Wisconsin, United States of America) containing 95% ethanol, transferred to the laboratory, and kept at 5 °C until processed. Captured beetles of the genus *Monochamus* were sorted and identified to sex and species, using morphological characters (Bousquet *et al.* 2017).

Species abundance across the vertical strata of the forest canopy

Monochamus spp. abundance across vertical strata of the forest canopy was investigated with a field trapping experiment using 12-unit multifunnel traps (Lindgren 1983) that were coated with Fluon PTFE lubricant and were equipped with wet collecting cups containing approximately 200 mL of antifreeze and baited with ultra-high release (UHR) α -pinene and bubblecap lures containing synthetic monochamol (purity and release rates as described above in the section, Host-mediated reproductive isolation) purchased from Synergy Semiochemicals (Delta, British Columbia, Canada). Traps were placed at two different heights in the forest vertical strata at the two field sites: traps were hung at approximately 10 m above ground (hereafter, “canopy traps”) and at 1.5 m above ground (hereafter, “understorey traps”). Canopy and understorey traps were placed in the field following a methodology similar to that in Dodds (2014). To place canopy traps, a Big Shot® launcher (Sherrill Tree, Greensboro, North Carolina, United States of America) was

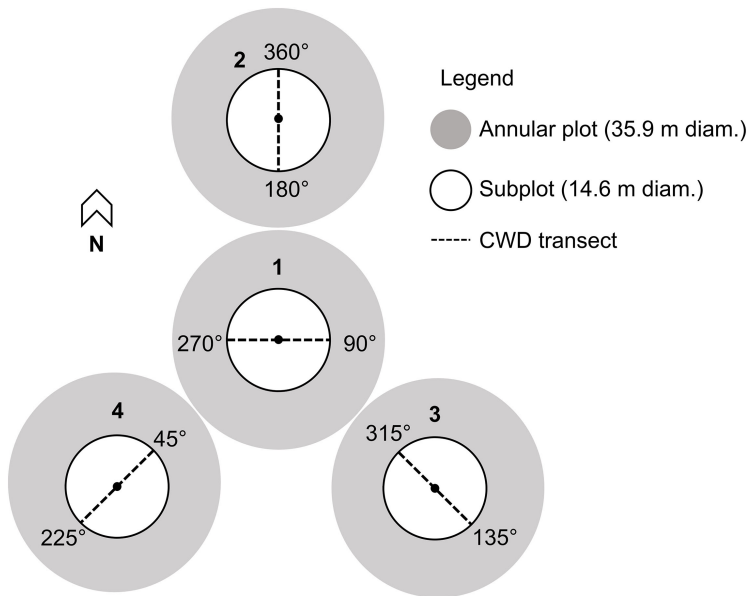


Figure 1. Coarse woody debris (CWD) sampling design for forest inventory and analysis plots implemented in 2022 (adapted from United States Department of Agriculture, Forest Service 2019). The centres of subplots 2, 3, and 4 are 37 m distant from the centre of subplot 1, at azimuths 360° for subplot 2, 120° for subplot 3, and 240° for subplot 4.

used to shoot a weighted bag tied to a throwline through the lower portion of a branch in the canopy of a tree, facilitating the installation of a double-braided nylon rope with single rope pulley attached to its midpoint. The pulley was raised approximately 10 m above ground and positioned at about a 45° angle from vertical, and a second rope looped around the pulley wheel was used to raise the canopy-level trap and secure the position. Understorey level traps were hung from iron stands fixed into the ground under the canopy traps, so that the understorey trap collection cup was approximately 0.5 m above the ground. At the first field site, six pairs of one canopy trap and one understorey trap each were deployed at least 30 m away from one another. At the second field site, 10 pairs of one canopy trap and one understorey trap each were deployed – seven pairs 250 m away from one another, and three pairs of traps 500 m away from one another.

The traps were inspected weekly during eight consecutive weeks from 9 July to 2 September 2021. The contents of each trap were sieved and placed individually in a Whirl-Pak bag (710 mL) containing 95% ethanol, transferred to the laboratory, and kept at 5 °C until processed. Captured beetles of the genus *Monochamus* were sorted and identified to sex and species, using morphological characters (Bousquet *et al.* 2017).

Coarse woody debris assessments

Coarse woody debris assessments were performed in the two field sites. The assessments were performed following the United States Department of Agriculture, Forest Service (2019) line-intersect sampling method for forest inventory and analysis, as illustrated in Fig. 1. In this method, linear transects are established in plots, and individual pieces of coarse woody debris are tallied if the plane of the transect intercepts the central axis of the piece. In June 2022, four plots were established in field site #1, and five plots were established in field site #2. Plots were installed adjacent to the locations where canopy and understorey traps were placed in the two sites (nine plots in total). Plot centres were 150 m apart in the first field site and 800 m apart in the second field site.

Table 1. Classification of the stage of decay for down coarse woody debris pieces (adapted from United States Department of Agriculture, Forest Service 2019)

Decay class	Structural integrity	Texture of rotten portions	Colour of wood	Invading roots	Branches and twigs
1	Sound, freshly fallen, intact logs	Intact, no rot; conks of stem decay absent	Original colour	Absent	If branches are present, fine twigs are still attached and have tight bark
2	Sound	Mostly intact; sapwood partly soft (starting to decay) but cannot be pulled apart by hand	Original colour	Absent	If branches are present, many fine twigs are gone and remaining fine twigs have peeling bark
3	Heartwood sound; piece supports its own weight	Hard, large pieces; sapwood can be pulled apart by hand or sapwood absent	Reddish-brown or original colour	Sapwood only	Branch stubs will not pull out
4	Heartwood rotten; piece does not support its own weight, but maintains its shape	Soft, small blocky pieces; a metal pin can be pushed into heartwood	Reddish-brown or light brown	Throughout	Branch stubs pull out
5	None, piece no longer maintains its shape, it spreads out on ground	Soft; powdery when dry	Reddish-brown to dark brown	Throughout	Branch stubs and pitch pockets have usually rotted down

The species, decay class (Table 1), length (m), and diameters (cm) at the small and large ends and at the intersection with the transect were recorded from each piece of down coarse woody debris along transects that met the conditions described in United States Department of Agriculture, Forest Service (2019). The species, decay class, and diameter at 1.37 m height of dead standing trees along transects were recorded. Pieces of down coarse woody debris in an advanced stage of decay (decay class 5; Table 1) that intersected transects were not sampled due to difficulties in determining the species and delineating the log on the ground to obtain diameter and length measurements.

Spatial distribution within and among lying and standing dead trees

Specific spatial distribution within and among host trees was investigated in the two field sites. Between 19 May and 4 June 2021, 10 healthy trees of *A. balsamea*, *P. banksiana*, and *P. glauca* ($n = 30$ trees total) were selected in the first field site, and 20 healthy trees of *P. banksiana* were selected in the second field site. We then created 15 lying (hereafter, “logs”) and 15 standing (hereafter, “snags”) dead trees of each host species in the first field site (*i.e.*, five logs and five snags of each species). In the second field site, a total of 10 logs and 10 snags of *P. banksiana* were created due to this being the predominant host species in the area. Height and diameter at 1.4 m above ground (breast height) of all trees were recorded. After five months, all snags were felled, and 60-cm sections were removed from the 30% (“lower-bole”), 50% (“middle-bole”), and 70% (“upper-bole”) mark of each snag and log, as measured from the tree base. The diameters of the small and large ends of each bole were recorded, metal identification tags were nailed on individual boles, and all bole sections were subsequently transported to the laboratory. All bole

sections were kept outside until May 2022, after which they were transferred to the laboratory and kept in an upright position at approximately 22 °C under a 16:8-hour light:dark cycle in individual rearing cages made from fibreboard drums (101 cm high × 57.2 cm diameter) capped with rigid opaque polyethylene lids and steel lever-lock ring closures. A circular hole (9 cm diameter) was cut into the centre of each lid to accommodate an inverted opaque plastic cup (475 mL) with a circular exit hole (2.7 cm diameter) cut into its base. A 375-mL transparent cup was placed on top of the larger cup to collect emerged insects, and a 1.5-m-long string was installed in each rearing cage to provide a way for insects to exit the drum. The ends of all bole sections were sealed with paraffin wax before being placed in the rearing cages to reduce desiccation. Boles and rearing cage interiors were sprayed with water until the surfaces were visibly wet every 15 days. All bole sections were inspected weekly for 20 consecutive weeks, from 13 May to 13 October 2022, and all emerged insects were collected. Insects that had not exited the rearing cages were removed manually. The sawdust that accumulated in the bottom of individual drums was collected monthly and inspected for insects. Insects from each rearing cage were stored in a vial containing 95% ethanol. Vials were capped and stored at approximately 5 °C until inspection. Only adult *Monochamus* spp. were sorted, sexed, and identified to species, using morphological characters (Bousquet *et al.* 2017).

In fall 2022, all bole sections were chopped with a hydraulic gas log splitter (Surge Master® 26HVGC-L; Belkin, Playa Vista, California, United States of America), and all larvae were collected. Each larva was placed in a 2-mL micro centrifuge tube (VWR®, VWR International, Radnor, Pennsylvania, United States of America) containing 95% ethanol. Micro centrifuge tubes were capped and stored at approximately 5 °C until inspection. All *Monochamus* larvae were identified to species level, using morphological characters, per Craighead (1923), Chu (1949), and Stehr (1991). *Monochamus* larvae were also compared to identified specimens preserved in the entomological collection of Natural Resources Canada's Great Lakes Forestry Centre (Sault Ste. Marie, Ontario; *Monochamus scutellatus*: reference # S65-1848-01, Vermillion Bay # 18, Red Pine, 23.vi.1965; *Monochamus mutator*: reference # S64-2207-02, Sarnia L. Erie, Red Pine, 29.iv.1964; *Monochamus notatus*: reference # 6386, reg # 42-5-F489, Nipissing Dist., White Pine, 8.vii.1942).

Statistical analyses

Six generalised linear models were used to analyse the effect of host volatiles in the attraction of *M. maculosus*, *M. scutellatus*, and *M. notatus* to monochamol and α -pinene (two generalised linear models per species). For each individual *Monochamus* species, a Poisson and a negative binomial model (hereafter, "NB") were compared to assess for overdispersion in count data. Model selection was performed following the methodology described by Fávero *et al.* (2021). Log-likelihood ratio test and the Akaike's information criterion (AIC) for goodness of fit (Burnham and Anderson 2004; Zuur *et al.* 2009) were used to confirm that the NB regression model presented a better fit to the data in comparison to the Poisson regression model for the three beetle species. Differences in the number of adult *M. maculosus*, *M. scutellatus*, and *M. notatus* collected by traps across different treatments (*i.e.*, host volatiles) were assessed with analyses of deviance with likelihood ratio test (Type II test) based on the NB regression model for each species. *Post hoc* pairwise comparisons with Tukey-adjusted *P*-values were conducted to assess differences in the estimated marginal means (emmeans) for each *Monochamus* species collected between different treatments.

Additionally, eight generalised linear models were used to analyse the effect of trap height (10 m and 1.5 m) on adult captures of *M. maculosus* and *M. scutellatus* in field site #1 and field site #2 (*i.e.*, two generalised linear models per species per field site). For each individual *Monochamus* species from field sites #1 and #2, a Poisson model and a negative binomial regression model were compared to assess for overdispersion in the count data as above. The negative binomial regression model was selected as the most suitable model for the *M. maculosus* and *M. scutellatus*

data from field sites #1 and #2, following the same methodology as above. All statistical analyses were conducted using a significance level of $\alpha = 0.05$.

The volume (m^3), cubic volume per hectare (m^3/ha), density (logs/ha), and percentage of deadwood cover on the ground (*i.e.*, the percentage of ground surface covered by coarse woody debris at the transect level) of individual pieces of down coarse woody debris (“logs”) sampled in the four plots established in field site #1 and the five plots established in field site #2 were calculated following the methodology described in Waddell (2002). The mean volume per hectare was estimated by first summing the cubic volume per hectare of all individual softwood pieces tallied within plots and dividing that sum by the total number of plots established in field site #1 ($n = \text{four plots total}$) and in field site #2 ($n = \text{five plots total}$). The mean density per hectare and mean percentage of deadwood cover on the ground in field site #1 and in field site #2 (per-unit-area value) were estimated using the same methodology to estimate the mean volume per hectare. Descriptive analysis was used to describe differences observed in the mean volume per hectare, mean density per hectare, and mean percentage of deadwood cover on the ground of down coarse woody debris of softwood species between the two field sites. Individual pieces of down coarse woody debris of hardwood species sampled along transects in field site #1 and in field site #2 were excluded from analyses because they would not be used as resources by *Monochamus* species.

Descriptive analyses were conducted to describe the number of adult *Monochamus* spp. that emerged from different bole sections of logs and snags from the two field sites. A generalised linear mixed model with Poisson distribution was performed to analyse the effect of bole section (lower, middle, and upper bole) and tree species (*A. balsamea*, *P. banksiana*, and *P. glauca*) on the number of *M. scutellatus* larvae collected from logs in field site #1. For field site #2, a generalised linear mixed model with Poisson distribution was performed to analyse the effects of bole section on the number of *M. scutellatus* larvae collected from logs. Individual logs were included as a random effect in the two models to account for the dependence structure of the data from different bole section heights at the tree level. Model fit was assessed with diagnostic plots of scaled residuals from the DHARMA package (Hartig 2022) in R, version 4.1.2 (R Core Team 2021). Goodness-of-fit test on the scaled residuals was used to confirm that the observed dispersion was not different than expected with simulation under the fitted model. Two reduced Poisson regression models were fitted for field site #1 data, each including only one fixed-effect predictor (either bole section or tree species), and one null Poisson regression model was fitted for field site #2 data with no fixed-effect predictors. Individual logs were included as a random effect in reduced and null models for both field sites. Full models for field site #1 and for field site #2 were compared with corresponding reduced and null models using the likelihood ratio test to assess the contribution of each fixed-effect predictor to model fit. *Post hoc* pairwise comparisons with Tukey-adjusted *P*-values were performed to determine differences in the estimated marginal mean (emmeans) numbers of larvae between different bole sections averaged over host-tree species from field site #1. All analyses were performed using the software R, version 4.1.2 (R Core Team 2021), using a significance level of $\alpha = 0.05$.

Results

Host-mediated reproductive isolation

A total of 3201 adult *M. maculosus* were captured from 32 traps assigned to the four different treatment groups. The means \pm standard errors of *M. maculosus* collected per week from traps baited with monochamol and α -pinene (control) were 43.0 ± 4.3 , from traps baited with monochamol and *P. banksiana* foliage were 29.1 ± 3.3 , from traps baited with monochamol and *A. balsamea* foliage were 15.2 ± 2.6 , and from traps baited with monochamol and *P. glauca* foliage were 12.8 ± 1.9 . Analysis of deviance with a likelihood ratio test indicated a significant overall effect of trap treatments on the number of adult *M. maculosus* captured (likelihood ratio

Table 2. Paired contrasts of the total number of adult *Monochamus maculosus*, *M. notatus*, and *M. scutellatus* collected per week from multifunnel traps baited with monochamol and either α -pinene (control) or fresh foliage and branches of *Abies balsamea* (Ab treatment), of *Pinus banksiana* (Pb treatment), or of *Picea glauca* (Pg treatment; $n = 4$ dates of collection total; 32 traps used total). Results were obtained using *post hoc* pairwise comparisons of estimated marginal means ($\alpha = 0.05$) from generalised linear models. Clearcut mixed-wood forests in the Algoma Region, Ontario, Canada, were used as collection sites. Results are given on the log (not the response) scale. Asterisks indicate significant differences ($P < 0.05$) between treatment estimated marginal means (emmeans); SE, standard error

Species	Treatment contrast	<i>B</i>	SE	Z ratio	<i>P</i>
<i>M. maculosus</i>	Ab – control	–1.040	0.218	–4.770	< 0.001*
	Ab – Pb	–0.650	0.219	–2.970	0.015*
	Ab – Pg	0.172	0.222	0.777	0.864
	Pb – control	0.390	0.216	1.807	0.269
	Pg – control	1.212	0.219	5.538	< 0.001*
	Pb – Pg	0.823	0.220	3.347	0.001*
<i>M. scutellatus</i>	Ab – control	–0.657	0.246	–2.671	0.037*
	Ab – Pb	–0.434	0.246	–1.761	0.292
	Ab – Pg	–0.338	0.247	–1.371	0.517
	Pb – control	0.223	0.245	0.911	0.798
	Pg – control	0.319	0.245	1.301	0.562
	Pb – Pg	0.095	0.246	0.390	0.979
<i>M. notatus</i>	Ab – control	0.134	0.406	0.329	0.988
	Ab – Pb	0.758	0.442	1.712	0.317
	Ab – Pg	0.134	0.406	0.329	0.988
	Pb – control	0.624	0.447	1.395	0.503
	Pg – control	0.000	0.411	0.000	1.000
	Pb – Pg	–0.624	0.447	–1.395	0.503

$\chi^2 = 40.206$; $df = 3$; $P < 0.001$). *Post hoc* pairwise comparisons (emmeans) indicated that the control treatment resulted in significantly higher *M. maculosus* trap captures than the *A. balsamea* and *P. glauca* treatments did (all $P < 0.001$). The *P. banksiana* treatment resulted in significantly higher *M. maculosus* trap captures than the *A. balsamea* and *P. glauca* treatments did (all $P < 0.05$). No other significant differences in trap captures of *M. maculosus* were observed among treatments (all $P > 0.05$; Table 2; Fig. 2A).

A total of 4336 adult *M. scutellatus* were captured from 32 traps assigned to the four different treatment groups. The means \pm standard errors of *M. scutellatus* collected per week from traps baited with monochamol and α -pinene (control) were 44.5 ± 5.7 , from traps baited with monochamol and *A. balsamea* foliage were 23.1 ± 3.0 , from traps baited with monochamol and *P. banksiana* foliage were 35.6 ± 5.4 , and from traps baited with monochamol and *P. glauca* foliage were 32.3 ± 4.6 . The overall effect of trap treatments on the number of adult *M. scutellatus* captured was not significant (likelihood ratio $\chi^2 = 7.1747$; $df = 3$; $P = 0.066$). However, *post hoc* pairwise comparisons (emmeans) indicated that the control treatment resulted in significantly higher *M. scutellatus* trap captures than the *A. balsamea* treatment did ($P = 0.037$). No other significant differences in trap captures of *M. scutellatus* were observed among treatments (all $P > 0.05$; Table 2; Fig. 2B).

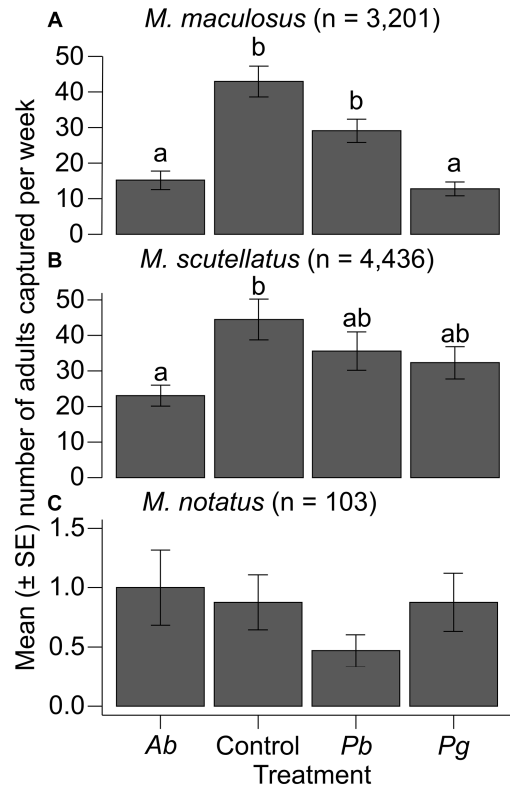


Figure 2. Mean number of adult *Monochamus* spp. caught per week in multifunnel traps baited with monochoamol and α -pinene (control) or monochoamol and fresh branches and foliage of four different host species (Ab, *Abies balsamea*; Pb, *Pinus banksiana*; Pg, *Picea glauca*): **A**, *M. maculosus*; **B**, *M. scutellatus*, and **C**, *M. notatus*. Differences among treatments within *M. maculosus* and *M. scutellatus* were determined with *post hoc* pairwise comparisons of estimated marginal means ($P < 0.05$) from generalised linear models. No significant differences among treatments within *M. notatus* were found with *post hoc* pairwise comparisons of estimated marginal means ($P > 0.05$) from generalised linear models. SE, standard error.

A total of 103 adult *M. notatus* were captured from 32 traps assigned to the four different treatment groups. The means \pm standard errors of *M. notatus* collected per week from traps baited with monochoamol and α -pinene (control) were 0.9 ± 0.2 , from traps baited with monochoamol and *A. balsamea* foliage were 1.0 ± 0.3 , from traps baited with monochoamol and *P. banksiana* foliage were 0.5 ± 0.1 , and from traps baited with monochoamol and *P. glauca* foliage were 0.9 ± 0.2 . The overall effect of trap treatments on the number of adult *M. notatus* captured was not significant (likelihood ratio $\chi^2 = 3.3298$; $df = 3$; $P = 0.343$). *Post hoc* pairwise comparisons (emmeans) indicated that differences in trap captures of *M. notatus* among treatments were not significant (all $P > 0.05$; Table 2; Fig. 2C).

Species abundance across the vertical strata of the forest canopy

A total of 335 adult *M. maculosus* were collected from 12 traps at field site #1 and 4450 were collected from 20 traps at field site #2. Adult *M. maculosus* captures were significantly affected by trap height in the two field sites, but the species' abundance across the vertical strata of the forest canopy differed between the two sites. At field site #1, the mean \pm standard error of adults collected per week from canopy traps (4.8 ± 0.6) was significantly higher than that from understorey traps (2.2 ± 0.4 ; GLM $\beta_{\text{understorey}} = -0.7841$; standard error = 0.1985; $Z = -3.95$; $P < 0.001$). At field site #2, the mean \pm standard error of adults collected per week from canopy traps (15.9 ± 1.1) was significantly lower than that collected each week from understorey traps (39.7 ± 3.0 ; GLM $\beta_{\text{understorey}} = 0.9123$; standard error = 0.1007; $Z = 9.05$; $P < 0.001$; Fig. 3A).

A total of 824 adult *M. scutellatus* were collected from 12 traps at field site #1 and 3616 were collected from 20 traps at field site #2. At field site #1, the mean \pm standard error of adults collected per week from canopy and understorey traps was 10.5 ± 1.9 and 6.6 ± 1.1 , respectively.

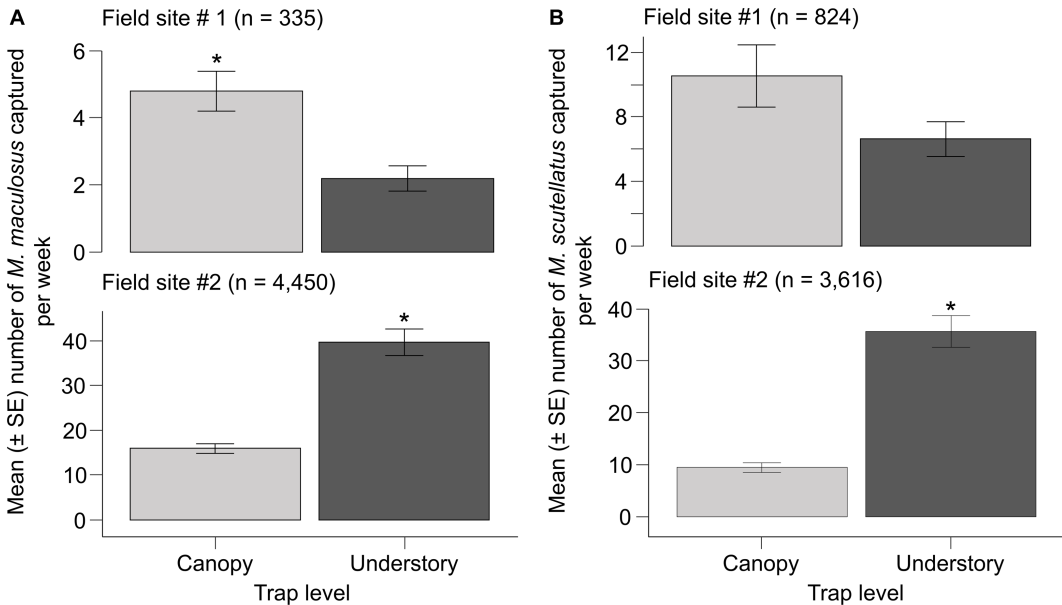


Figure 3. Mean number of adult *Monochamus* spp. captured per week in canopy (hung at ~10 m height) and understorey multifunnel traps (hung at 1.5 m height) baited with α -pinene and monochamol placed in field sites #1 and #2: **A**, *M. maculosus* and **B**, *Monochamus scutellatus*. Differences between trap levels within individual species were determined with generalised linear models ($P < 0.05$). SE, standard error.

Trap height did not have a significant impact on the number of *M. scutellatus* captured at field site #1 (GLM $\beta_{\text{understorey}} = -0.4645$; standard error = 0.2438; $Z = -1.90$; $P = 0.056$). However, trap height had a significant impact on the number of *M. scutellatus* captured at field site #2 with a lower mean \pm standard error of adults collected per week from canopy traps (9.5 ± 0.9) than from understorey traps (35.7 ± 3.1 ; GLM $\beta_{\text{understorey}} = 1.3289$; standard error = 0.1410; $Z = 9.42$; $P < 0.001$; Fig. 3B).

Nineteen adult *M. notatus* were collected from 12 traps at field site #1. Of these, a mean \pm standard error of 0.2 ± 0.1 individuals were collected per week from canopy traps, and 0.2 ± 0.1 individuals were collected from understorey traps. In addition, one adult *M. marmorator* was collected from a canopy trap at field site #1. At field site #2, a total of four adult *M. notatus* were collected from 20 traps. All adult *M. notatus* at field site #2 were collected from understorey traps, and no adults were collected from canopy traps. Collections of *M. notatus* at field sites #1 and #2 and of *M. marmorator* at field site #1 were excluded from analyses due to the low numbers of individuals captured.

Coarse woody debris assessments

A total of eight down coarse woody debris pieces were recorded in the four plots established in field site #1, and a total of 52 down coarse woody debris pieces were recorded in the five plots established in field site #2 (Supplementary material, Table S1). The mean \pm standard error length and diameter across the small and large ends of down coarse woody debris pieces were 7.9 ± 1.5 m and 12.5 ± 1.5 cm, respectively, in field site #1 and 6.1 ± 0.5 m and 10.6 ± 0.3 cm, respectively, in field site #2. The mean volume of down coarse woody debris of softwood per hectare was $7.0 \text{ m}^3/\text{ha}$ in field site #1 and $27.2 \text{ m}^3/\text{ha}$ in field site #2. Field site #1 had a mean density of 94 logs/ha (softwood), with a mean percent of deadwood cover on ground of 0.67 %, whereas field site #2 had a

Table 3. Total number of adult *Monochamus* spp. that emerged from 45 bole sections removed from lying dead trees from field site #1 ($n = 5$ bole sections per tree species and bole section level) and from 30 bole sections removed from lying dead trees from field site #2 ($n = 10$ bole sections per level) and their corresponding origin in terms of tree species and bole section level (60-cm-long sections removed from the 30% – “lower”, 50% – “middle”, and 70% – “upper” levels of each experimental tree height, as measured from the tree base)

Field site	Tree species	Bole section level	<i>Monochamus</i> species	Total number of adults	
1	<i>Abies balsamea</i>	Lower	<i>M. scutellatus</i>	2	
		Middle	<i>M. scutellatus</i>	2	
		Upper	<i>M. scutellatus</i>	2	
	<i>Pinus banksiana</i>	Lower		<i>M. maculosus</i>	2
				<i>M. scutellatus</i>	2
		Middle		<i>M. maculosus</i>	4
				<i>M. scutellatus</i>	3
		Upper		<i>M. maculosus</i>	6
				<i>M. scutellatus</i>	3
	<i>Picea glauca</i>	Lower		n/a	0
				n/a	0
		Middle		<i>M. scutellatus</i>	2
Upper					
2	<i>Pinus banksiana</i>	Lower	n/a	0	
		Middle	<i>M. scutellatus</i>	1	
		Upper	n/a	0	

mean density of 628 logs/ha (softwood), with a mean percent of deadwood cover on ground of 2.97%. Dead standing trees were observed only in field site #2; all were *P. banksiana* ($n = 6$ dead standing trees total). Of these six dead standing trees, three were from decay class 1, two from decay class 2, and one from decay class 4. The mean \pm standard error diameter of dead standing trees at 1.4 m height was 4.0 ± 0.5 cm.

Spatial distribution within and among lying and standing dead trees

A total of 27 adult *Monochamus* spp. emerged from 75 bole sections removed from logs at the two field sites (Table 3). No adults emerged from bole sections removed from snags at the two field sites ($n = 75$ bole sections from snags; 150 bole sections in total). The number of adult *Monochamus* spp. that emerged from bole sections was too low for statistical analyses.

A total of 307 larvae were collected from the 150 bole sections from the two field sites: 203 larvae were collected from 90 bole sections from field site #1; 104 larvae were collected from 60 bole sections from field site #2. Of these, 300 larvae were identified (Supplementary material, Table S2). Seven larvae were not identifiable because they had been destroyed during the log splitting process (field site #1: $n = 2$; field site #2: $n = 2$; four larvae total) or because morphological identification was not possible (field site #1: $n = 2$; field site #2: $n = 1$; three larvae total). Out of the 300 larvae identified, 292 were identified to the genus *Monochamus*; of the 292, 265 were identified as *M. scutellatus*. Twenty-seven *Monochamus* larvae could not be identified to species because they had been damaged during the log splitting process (field site #1: $n = 7$; field site #2: $n = 4$; 11 larvae total) or because their morphological identification to species was not possible (field site #1: $n = 7$; field site #2: $n = 9$; 16 larvae total). Only *M. scutellatus* larvae were considered for analyses because approximately 90% of all *Monochamus* larvae collected from the

150 bole sections were *M. scutellatus* (field site #1: $n = 177$ of 191; field site #2: $n = 88$ of 101, tentatively identified as *M. scutellatus*). A few *M. notatus* larvae may have been identified as *M. scutellatus*. The two species' morphology is very similar, and the differences are hard to distinguish; that is, compared to matured *M. scutellatus* larvae, matured *M. notatus* larvae tend to be more robust, have coarser hair, and present a more continuous band of hair across the anterior area of the pronotum; Craighead 1923). Trapping experiments during the same period show that only 0.3% of all 8948 adult *Monochamus* individuals collected at the two field sites were *M. notatus* (see the section, Species abundance across vertical strata of the forest canopy, in Results). Morphological differences between *M. scutellatus* and *M. maculosus* larvae are visible under the microscope, making distinguishing the two species possible: that is, the tubercles on the ventral ampullae of matured *M. maculosus* are glabrous, whereas matured *M. scutellatus* larvae have the tubercles on the ventral ampullae covered with thin asperites (Craighead 1923; Supplementary material, Fig. S1).

A total of 177 *M. scutellatus* larvae were collected from 90 bole sections at field site #1. The means \pm standard errors of *M. scutellatus* larvae collected per bole in field site #1 were 3.8 ± 0.5 for sections removed from logs and 0.1 ± 0.1 for sections removed from snags. Collections of *M. scutellatus* larvae from snag sections in field site #1 were excluded from analyses because few such individuals were collected. Including bole section height significantly improved the model fit for field site #1 compared to a reduced model containing only host tree species as a fixed effect (likelihood ratio $\chi^2 = 10.008$, $df = 2$, $P = 0.006$), indicating that bole section height is an important predictor of the number of *M. scutellatus* larvae collected from logs. The mean number \pm standard error of larvae collected per bole from middle sections (4.7 ± 0.9) was significantly higher than that from upper sections (2.6 ± 0.7 ; emmean $B = 0.599$, standard error = 0.199, Z ratio = 3.006, $P = 0.007$). No significant differences were observed in the means \pm standard errors of *M. scutellatus* larvae collected per bole between lower-bole (4.1 ± 0.9) and either middle-bole (emmean $B = -0.136$, standard error = 0.174, Z ratio = -0.780 , $P = 0.715$) or upper-bole sections (emmean $B = 0.464$, standard error = 0.204, Z ratio = 2.268, $P = 0.060$). No significant improvement in the model fit for field site #1 was observed when host tree species was added to a model with bole section as a fixed effect (likelihood ratio $\chi^2 = 2.758$, $df = 2$, $P = 0.251$), suggesting no significant effect of host tree species in the *M. scutellatus* larval abundance in logs (Fig. 4A).

In field site #2, 88 *M. scutellatus* larvae were collected from 60 bole sections. All *M. scutellatus* larvae in field site #2 were collected from bole sections removed from logs (mean \pm standard error: 2.9 ± 0.3 larvae collected per bole), and no larvae were collected from bole sections removed from snags. The means \pm standard errors of *M. scutellatus* larvae collected per bole from lower, middle, and upper sections of logs were 3.0 ± 0.6 , 3.3 ± 0.5 , and 2.5 ± 0.7 , respectively. No significant improvement in the model fit for field site #2 was observed when bole section height was included as a fixed effect compared to the null model (likelihood ratio $\chi^2 = 1.1296$, $df = 2$, $P = 0.568$), suggesting that bole section height does not significantly explain the variation observed in the number of *M. scutellatus* larvae collected from logs (Fig. 4B).

Discussion

Pheromones are widely used among insects to mediate mate location and recognition and are often observed to differ qualitatively, quantitatively, or both among species (Symonds and Elgar 2008; Wyatt 2014; Allison and Cardé 2016). Research on the pheromone biology of the genus *Monochamus* has revealed a general pattern of pheromone parsimony, with several species using monochamol as their aggregation-sex pheromone or putative pheromone attractant, including the sympatric *M. maculosus*, *M. notatus*, and *M. scutellatus* in eastern Canada (Hanks and Millar 2016; Millar and Hanks 2017; Andrade *et al.* 2024). Hybridisation among *Monochamus*

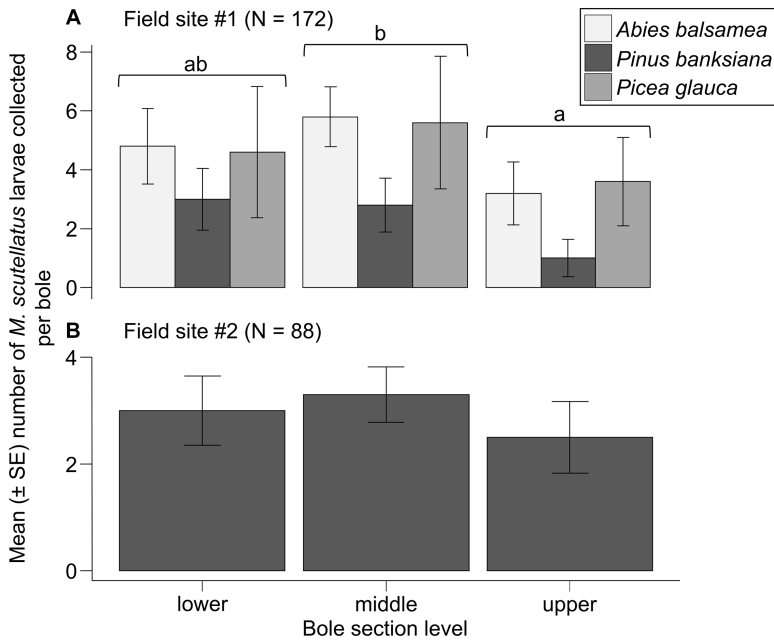


Figure 4. Mean number of *Monochamus scutellatus* larvae collected per bole from sections removed at 30% (lower), 50% (middle), and 70% (upper) height measured from the base of lying dead trees (logs) of **A**, *Abies balsamea*, *Pinus banksiana*, and *Picea glauca* in field site #1, and of **B**, *Pinus banksiana* in field site #2. Differences among bole section levels averaged over host tree species in field site #1 were determined with *post hoc* pairwise comparisons of estimated marginal means ($P < 0.05$) from a generalised linear mixed model. SE, standard error.

species in the field seems rare despite this pheromone parsimony, suggesting that additional mechanisms facilitate reproductive isolation among the three species, including differences in host and habitat preferences (Dodds 2014; Togashi and Appleby 2023). Although the present study found no evidence of specific host and habitat preferences of sympatric *M. scutellatus*, *M. maculosus*, and *M. notatus* that confer reproductive isolation, our results suggest that vertical abundance across the forest canopy in *M. maculosus* and *M. scutellatus* could be driven by resource availability, and that *M. scutellatus* seems to prefer softwood material lying on the forest floor over standing dead trees for oviposition.

Vertical stratification in wood-boring Cerambycid beetles in temperate North American forests is likely driven by resource availability, with species abundance across vertical strata positively correlating with the abundance of larval resources. Cerambycid species captured in higher numbers in traps near the ground than in traps in the canopy have been observed to develop in fallen logs, and species captured in lower numbers in traps near the ground than in traps in the canopy have been observed to develop in twigs and cones located in the canopy (Vance *et al.* 2003; Ulyshen and Hanula 2007). The vertical abundance of *M. maculosus* in forests may be driven by the availability of oviposition resources. Traps deployed in a forest stand managed for harvesting that had a high volume and density of coarse woody debris lying on the floor (field site #2) showed greater beetle abundance in the understorey than in the canopy. Conversely, *M. maculosus* trapping collections conducted in a private, unmanaged forest stand that was observed to have a low volume and density of down, coarse woody softwood debris (field site #1) presented greater beetle abundance in the canopy than in the understorey.

The vertical abundance of *M. scutellatus* in forests may also be driven by the availability of oviposition resources: as with our *M. maculosus* data, trapping collections of *M. scutellatus* in field site #2 during the present study showed greater beetle abundance in the understorey than in the

canopy, but we observed no differences in *M. scutellatus* abundance between understorey and canopy trap collections in field site #1.

Studies have shown that forest canopies usually have a lower amount of deadwood compared to the forest floor (see Nordén *et al.* 2004), but much of the dead wood in forests begins in the canopy in the form of standing dead trees, dead branches and twigs, and rotting heartwood (Fonte and Schowalter 2004). Although the present study found no evidence of host or habitat partitioning between *M. maculosus*, *M. notatus*, and *M. scutellatus* that could explain their reproductive isolation, our results suggest that *M. scutellatus* prefer ovipositing on down coarse conifer logs to ovipositing on standing dead conifers. This oviposition habitat preference in *M. scutellatus* could be related to differences in the physiological conditions of dead wood position for larval development: suspended and standing dead wood generally is drier and decays more slowly than does dead wood that is in contact with the ground (Hjältén *et al.* 2007; Jomura *et al.* 2008). Boulanger *et al.* (2013) observed that higher wood moisture content estimates from wood discs positively affected the larval occurrence of *M. scutellatus* on fire-killed black spruce, *P. mariana*, trees. Dyer and Seabrook (1978) reported that *M. notatus* and *M. scutellatus* females lay eggs only on logs with water content ranging between 10% and 60% of total dry weight. Although adult insects should select hosts that will optimise larval survival and development (Jaenike 1978), oviposition preferences and larval suitability are not necessarily related. Although some species make optimal oviposition choices to assure the highest offspring fitness (Pöykkö 2006), others choose to oviposit on plants on which their larvae have poor development or fitness (Courtney 1981; Haavik *et al.* 2017) to, perhaps, avoid competitors and natural enemies (Price *et al.* 1980; Thompson 1988). Larval cannibalism is common in the genus *Monochamus* (Victorsson and Wikars 1996; Anbutsu and Togashi 1997a; Dodds *et al.* 2001), and females seem to avoid ovipositing on host material already occupied by conspecific eggs or larvae (Anbutsu and Togashi 1997b, 2000; Peddle *et al.* 2002).

Markovic *et al.* (2014), Kopaczyk *et al.* (2020), and Pinto-Zevallos *et al.* (2020) showed that insect behavioural responses can be affected by variation in plant secondary metabolites induced by a variety of biotic and abiotic stresses. In the present study, chopping host plant material into small pieces to bait traps in the field may have altered the chemical composition of the wood's volatiles or the dynamics of host volatile release, affecting *Monochamus* spp. responses in different ways than natural host material does. The differences we observed in the numbers of adult *M. scutellatus* and *M. maculosus* captured in canopy and understorey traps between the two field site locations in the present study indicate that oviposition resource availability may be an important factor driving the vertical distribution of these species across the forest canopy; however, additional spatial and temporal replications (*i.e.*, field collections using understorey and canopy traps in sites presenting different resource availability scenarios during multiple years) are needed to confirm or refute this hypothesis. *Monochamus* adults are known to require maturation feeding on twig bark and needles of healthy host trees for a period of 7–12 days (Akbulut and Stamps 2011), and adult *Monochamus* continue to feed while being reproductively active (Akbulut *et al.* 2017). Maturation feeding and oviposition may occur at different vertical strata of the forest (*e.g.*, feeding or maturation may occur in the canopy of healthy trees, and oviposition may occur in freshly dead host material on the forest floor). Canopy structure and tree density can influence the dispersion and structure of pheromone plumes (Murlis *et al.* 2000; Peterson *et al.* 2010; Cardé 2021). The differences we observed in the vertical distribution of *M. maculosus* and *M. scutellatus* between an unmanaged, mixed-wood forest stand (field site #1) and a managed, pine-dominated stand (field site #2) may be related to how differences in the structure and species composition between the two sites affected the dispersion and structure of pheromone plumes. These differences in tree species composition, management practices, and forest structure may also contribute to microclimatic variation, potentially influencing physical aspects of trees, such as bark thickness, that are relevant to *Monochamus* colonisation (Naves *et al.* 2006a; Han *et al.* 2016).

Although the present study found no evidence of specific host and habitat preferences that could prevent cross-attraction between *M. maculosus*, *M. notatus*, and *M. scutellatus*, other factors may account for their reproductive isolation. Differences in phenological and diel patterns of flight behaviour between *M. scutellatus* and *M. maculosus* or *M. notatus* may contribute to their reproductive isolation (Andrade *et al.* 2025). However, the broad overlap in phenological and diel flight activity patterns of *M. maculosus* and *M. notatus* (Andrade *et al.* 2025) suggests the existence of other isolating mechanisms. Evidence shows that close range or contact pheromones play an important role in the mate-recognition systems of male Cerambycidae (Ginzel 2010; Millar and Hanks 2017), and differences in cuticular hydrocarbons of females may contribute to the reproductive isolation of closely related species (Ginzel *et al.* 2003, 2006; Silk *et al.* 2011). Differences in the relative proportions of cuticular hydrocarbons related to sex have been observed in *M. scutellatus* (Brodie *et al.* 2012) and *M. galloprovincialis* (Ibeas *et al.* 2009), but contact pheromone compounds have not yet been identified in the genus. Future investigations into whether differences in cuticular compounds prevent interspecific mating between *Monochamus* species are needed. In addition, Pershing and Linit (1986) and Wallin *et al.* (2013) have noted morphological differences in male genitalia among *Monochamus* species: whether these differences contribute to reproductive isolation requires study. The present study's results suggest that resource availability and suitability may drive the vertical abundance of *M. scutellatus* and *M. maculosus* across the forest canopy. These findings suggest that the chances of finding a mate in *Monochamus* may be improved if, in addition to using an aggregation-sex pheromone, males and females aggregate on larval host plants that are in a particular physiological condition (freshly cut logs of conifers lying on the forest floor).

Supplementary material. The supplementary material for this article can be found at <https://doi.org/10.4039/tce.2025.10042>.

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Competing interests. The authors declare that they have no competing interests.

References

- Akbulut, S. 2009. Comparison of the reproductive potential of *Monochamus galloprovincialis* on two pine species under laboratory conditions. *Phytoparasitica*, **37**: 125–135. <https://doi.org/10.1007/s12600-008-0019-y>.
- Akbulut, S. and Stamps, W.T. 2011. Insect vectors of the pinewood nematode: a review of the biology and ecology of *Monochamus* species. *Forest Pathology*, **42**: 89–99. <https://doi.org/10.1111/j.1439-0329.2011.00733.x>.

- Akbulut, S., Togashi, K., and Linit, M.J. 2017. Cerambycids as plant disease vectors with special reference to pine wilt. In *Cerambycidae of the World: Biology and Pest Management*. Edited by Q. Wang. CRC Press, Boca Raton, Florida, United States of America. Pp. 223–266.
- Allison, J.D. and Borden, J.H. 2001. Observations on the behaviour of *Monochamus scutellatus* (Coleoptera: Cerambycidae) in northern British Columbia. *Journal of the Entomological Society of British Columbia*, **98**: 195–200. Available from <https://journal.entsocbc.ca/index.php/journal/article/view/564> [accessed 4 July 2025].
- Allison, J., Borden, J., and Seybold, S. 2004. A review of the chemical ecology of the Cerambycidae (Coleoptera). *Chemoecology*, **14**: 123–150. <https://doi.org/10.1007/s00049-004-0277-1>.
- Allison, J.D. and Cardé, R.T. 2016. Pheromones: reproductive isolation and evolution in moths. In *Pheromone Communication in Moths: Evolution, Behavior and Application*. Edited by J.D. Allison and R.T. Cardé. University of California Press, Oakland, California, United States of America. Pp. 11–24.
- Allison, J.D., Graham, E.E., Poland, T.M., and Strom, B.L. 2016. Dilution of fluon before trap surface treatment has no effect on longhorned beetle (Coleoptera: Cerambycidae) captures. *Journal of Economic Entomology*, **109**: 1215–1219. <https://doi.org/10.1093/jee/tow081>.
- Allison, J.D., McKenney, J.L., Millar, J.G., McElfresh, J.S., Mitchell, R.F., and Hanks, L.M. 2012. Response of the woodborers *Monochamus carolinensis* and *Monochamus titillator* (Coleoptera: Cerambycidae) to known cerambycid pheromones in the presence and absence of the host plant volatile α -pinene. *Environmental Entomology*, **41**: 1587–1596. <https://doi.org/10.1603/EN12185>.
- Allison, J.D., Wood Johnson, C., Meeker, J.R., Strom, B.L., and Butler, S.M. 2011. Effect of aerosol surface lubricants on the abundance and richness of selected forest insects captured in multiple-funnel and panel traps. *Journal of Economic Entomology*, **104**: 1258–1264. <https://doi.org/10.1603/EC11044>.
- Anbutsu, H. and Togashi, K. 1997a. Effects of spatio-temporal intervals between newly hatched larvae on larval survival and development in *Monochamus alternatus* (Coleoptera: Cerambycidae). *Researches on Population Ecology*, **39**: 181–189. <https://doi.org/10.1007/BF02765264>.
- Anbutsu, H. and Togashi, K. 1997b. Oviposition behavior and response to the oviposition scars occupied by eggs in *Monochamus saltuarius* (Coleoptera: Cerambycidae). *Applied Entomology and Zoology*, **32**: 541–549. <https://doi.org/10.1303/aez.32.541>.
- Anbutsu, H. and Togashi, K. 2000. Deterred oviposition response of *Monochamus alternatus* (Coleoptera: Cerambycidae) to oviposition scars occupied by eggs. *Agricultural and Forest Entomology*, **2**: 217–223. <https://doi.org/10.1046/j.1461-9563.2000.00061.x>.
- Anderson, P. and Anton, S. 2014. Experience-based modulation of behavioural responses to plant volatiles and other sensory cues in insect herbivores. *Plant, Cell and Environment*, **37**: 1826–1835. <https://doi.org/10.1111/pce.12342>.
- Andrade, S.M.M., Guignard, Q., Smith, S.M., and Allison, J.D. 2024. Confirmation that monochamol is a male-produced aggregation-sex pheromone for *Monochamus maculosus* Haldeman (Coleoptera: Cerambycidae). *Journal of Chemical Ecology*, **50**: 409–418. <https://doi.org/10.1007/s10886-024-01530-w>.
- Andrade, S.M.M., McTavish, M.J., Smith, S.M., and Allison, J.D. 2025. The role of pheromone and temporal mechanisms in the reproductive isolation of *Monochamus maculosus*, *Monochamus notatus*, and *Monochamus scutellatus* (Coleoptera: Cerambycidae). *Environmental Entomology*, **54**: 1–10. <https://doi.org/10.1093/ee/nvaf017>.
- Ayres, B.D., Ayres, M.P., Abrahamson, M.D., and Teale, S.A. 2001. Resource partitioning and overlap in three sympatric species of *Ips* bark beetles (Coleoptera: Scolytidae). *Oecologia*, **128**: 443–453. <https://doi.org/10.1007/s004420100665>.
- Baldwin, I.T. 2010. Plant volatiles. *Current Biology*, **20**: R392–R397. <https://doi.org/10.1016/j.cub.2010.02.052>.

- Boulanger, Y., Sirois, L., and Hébert, C. 2013. Distribution patterns of three long-horned beetles (Coleoptera: Cerambycidae) shortly after fire in boreal forest: adults colonizing stands *versus* progeny emerging from trees. *Environmental Entomology*, **42**: 17–28. <https://doi.org/10.1603/EN12003>.
- Bousquet, Y., Laplante, S., Hammond, H.E.J., and Langor, W. 2017. Cerambycidae (Coleoptera) of Canada and Alaska: Identification Guide with Nomenclatural, Taxonomic, Distributional, Host-plant, and Ecological Data. Nakladatelství Jan Farkač, Prague, Czech Republic.
- Breton, Y., Hébert, C., Ibarzabal, J., Berthiaume, R., and Bauce, É. 2013. Host tree species and burn treatment as determinants of preference and suitability for *Monochamus scutellatus scutellatus* (Coleoptera: Cerambycidae). *Environmental Entomology*, **42**: 270–276. <https://doi.org/10.1603/EN12201>.
- Brodie, B.S., Wickham, J.D., and Teale, S.A. 2012. The effect of sex and maturation on cuticular semiochemicals in *Monochamus scutellatus* (Coleoptera: Cerambycidae). *The Canadian Entomologist*, **144**: 801–808. <https://doi.org/10.4039/tce.2012.82>.
- Bruce, T.J. and Pickett, J.A. 2011. Perception of plant volatile blends by herbivorous insects: finding the right mix. *Phytochemistry*, **72**: 1605–1611. <https://doi.org/10.1016/j.phytochem.2011.04.011>.
- Burnham, K.P. and Anderson, D.R. 2004. Multimodel inference: understanding AIC and BIC in model selection. *Sociological Methods & Research*, **33**: 261–304. <https://doi.org/10.1177/0049124104268644>.
- Cardé, R.T. 2014. Defining attraction and aggregation pheromones: teleological *versus* functional perspectives. *Journal of Chemical Ecology*, **40**: 519–520. <https://doi.org/10.1007/s10886-014-0465-6>.
- Cardé, R.T. 2021. Navigation along windborne plumes of pheromone and resource-linked odors. *Annual Review of Entomology*, **66**: 317–336. <https://doi.org/10.1146/annurev-ento-011019-024932>.
- Chu, H.F. 1949. How to Know the Immature Insects. An Illustrated Key for Identifying the Orders and Families of Many of the Immature Insects with Suggestions for Collecting, Rearing and Studying them. William C. Brown Publishing Company, Dubuque, Iowa, United States of America.
- Courtney, S.P. 1981. Coevolution of pierid butterflies and their cruciferous foodplants: III. *Anthocharis cardamines* (L.) survival, development and oviposition on different hostplants. *Oecologia*, **51**: 91–96. <https://doi.org/10.1007/BF00344658>.
- Craighead, F.C. 1923. North American Cerambycid Larvae. A Classification and the Biology of North American Cerambycid Larvae. Technical Bulletin No. 27. Department of Agriculture, Ottawa, Ontario, Canada.
- Dearborn, K.W., Heard, S.B., Sweeney, J., and Pureswaran, D.S. 2016. Displacement of *Tetropium cinnamopterum* (Coleoptera: Cerambycidae) by its invasive congener *Tetropium fuscum*. *Environmental Entomology*, **45**: 848–854. <https://doi.org/10.1093/ee/nvw045>.
- Dekker, T. and Barrozo, R.B. 2016. Contextual modulation of moth pheromone perception by plant odors. In *Pheromone Communication in Moths: Evolution, Behavior and Application*. Edited by J.D. Allison and R.T. Cardé. University of California Press, Oakland, California, United States of America. Pp. 101–112.
- Dicke, M. and Baldwin, I.T. 2010. The evolutionary context for herbivore-induced plant volatiles: beyond the ‘cry for help’. *Trends in Plant Science*, **15**: 167–175. <https://doi.org/10.1016/j.tplants.2009.12.002>.
- Dodds, K.J. 2014. Effects of trap height on captures of arboreal insects in pine stands of northeastern United States of America. *The Canadian Entomologist*, **146**: 80–89. <https://doi.org/10.4039/tce.2013.57>.

- Dodds, K.J., Graber, C., and Stephen, F.M. 2001. Facultative intraguild predation by larval Cerambycidae (Coleoptera) on bark beetle larvae (Coleoptera: Scolytidae). *Environmental Entomology*, **30**: 17–22. <https://doi.org/10.1603/0046-225X-30.1.17>.
- Dyer, L.J. and Seabrook, W.D. 1978. Some aspects of oviposition site selection in *Monochamus notatus* and *M. scutellatus* (Coleoptera: Cerambycidae). *Journal of Chemical Ecology*, **4**: 199–210. <https://doi.org/10.1007/BF00988055>.
- Estrada, C. and Gilbert, L.E. 2010. Host plants and immatures as mate-searching cues in *Heliconius* butterflies. *Animal Behaviour*, **80**: 231–239. <https://doi.org/10.1016/j.anbehav.2010.04.023>.
- Fávero, L.P., Souza, R.D.F., Belfiore, P., Corrêa, H.L., and Haddad, M.F. 2021. Count data regression analysis: concepts, overdispersion detection, zero-inflation identification, and applications with R. *Practical Assessment, Research & Evaluation*, **26**: 13. <https://doi.org/10.7275/44nn-cj68>.
- Fierke, M.K., Skabeikis, D.D., Millar, J.G., Teale, S.A., McElfresh, J.S., and Hanks, L.M. 2012. Identification of a male-produced aggregation pheromone for *Monochamus scutellatus* and an attractant for the congener *Monochamus notatus* (Coleoptera: Cerambycidae). *Journal of Economic Entomology*, **105**: 2029–2034. <https://doi.org/10.1603/EC12101>.
- Fonseca, M.G., Vidal, D.M., and Zarbin, P.H. 2010. Male-produced sex pheromone of the cerambycid beetle *Hedypathes betulinus*: chemical identification and biological activity. *Journal of Chemical Ecology*, **36**: 1132–1139. <https://doi.org/10.1007/s10886-010-9850-y>.
- Fonte, S.J. and Schowalter, T.D. 2004. Decomposition in forest canopies. In *Forest Canopies*. Second edition. Edited by M.D. Lowman and H.B. Rinker. Elsevier Academic Press, Burlington, Massachusetts, United States of America. Pp. 413–422.
- Ginzel, M.D. 2010. Hydrocarbons as contact pheromones of longhorned beetles (Coleoptera: Cerambycidae). In *Insect Hydrocarbons: Biology, Biochemistry and Chemical Ecology*. Edited by G.J. Blomquist and A.G. Bagnères. Cambridge University Press, New York, New York, United States of America. Pp. 375–389.
- Ginzel, M.D. and Hanks, L.M. 2005. Role of host plant volatiles in mate location for three species of longhorned beetles. *Journal of Chemical Ecology*, **31**: 213–217. <https://doi.org/10.1007/s10886-005-6735-6>.
- Ginzel, M.D., Millar, J.G., and Hanks, L.M. 2003. (Z)-9-pentacosene: contact sex pheromone of the locust borer, *Megacyllene robiniae*. *Chemoecology*, **13**: 135–141. <https://doi.org/10.1007/s00049-003-0239-z>.
- Ginzel, M.D., Moreira, J.A., Ray, A.M., Millar, J.G., and Hanks, L.M. 2006. (Z)-9-nonacosene: major component of the contact sex pheromone of the beetle *Megacyllene caryae*. *Journal of Chemical Ecology*, **32**: 435–451. <https://doi.org/10.1007/s10886-005-9010-y>.
- Graham, E.E., Poland, T.M., McCullough, D.G., and Millar, J.G. 2012. A comparison of trap type and height for capturing cerambycid beetles (Coleoptera). *Journal of Economic Entomology*, **105**: 837–846. <https://doi.org/10.1603/EC12053>.
- Greenfield, M.D. 2002. Chemical signaling and the olfactory channel. In *Signalers and Receivers: Mechanisms and Evolution of Arthropod Communication*. Edited by M.D. Greenfield. Oxford University Press, New York, New York, United States of America. Pp. 22–111.
- Haavik, L.J., Dodds, K.J., and Allison, J.D. 2017. Suitability of eastern pines for oviposition and survival of *Sirex noctilio* F. *PLOS One*, **12**: e0174532. <https://doi.org/10.1371/journal.pone.0174532>.
- Han, J.H., Kim, H.K., Kang, W.J., and Kim, G.H. 2016. Feeding and oviposition preference of the Sakhalin pine sawyer, *Monochamus saltuarius* (Coleoptera: Cerambycidae), for various tree species. *Entomological Research*, **46**: 331–336. <https://doi.org/10.1111/1748-5967.12182>.

- Hanks, L.M. and Millar, J.G. 2016. Sex and aggregation-sex pheromones of cerambycid beetles: basic science and practical applications. *Journal of Chemical Ecology*, **42**: 631–654. <https://doi.org/10.1007/s10886-016-0733-8>.
- Hanks, L.M. and Wang, Q. 2017. Reproductive biology of cerambycids. *In* *Cerambycidae of the World: Biology and Pest Management*. Edited by Q. Wang. CRC Press, Boca Raton, Florida, United States of America. Pp. 133–160.
- Hansson, B.S. 2002. A bug's smell: research into insect olfaction. *Trends in Neurosciences*, **25**: 270–274. [https://doi.org/10.1016/S0166-2236\(02\)02140-9](https://doi.org/10.1016/S0166-2236(02)02140-9).
- Hartig, F. 2022. DHARMa: Residual Diagnostics for Hierarchical (Multi-level/Mixed) Regression Models. Available from <https://cran.r-project.org/web/packages/DHARMa/vignettes/DHARMa.html> [accessed 16 October 2025].
- Hartmann, T., Theuring, C., and Bernays, E.A. 2003. Are insect-synthesized retronecine esters (creatonotines) the precursors of the male courtship pheromone in the arctiid moth, *Estigmene acrea*? *Journal of Chemical Ecology*, **29**: 2603–2608. <https://doi.org/10.1023/A:1026361628676>.
- Hartmann, T., Theuring, C., Beuerle, T., and Bernays, E.A. 2004. Phenological fate of plant-acquired pyrrolizidine alkaloids in the polyphagous arctiid, *Estigmene acrea*. *Chemoecology*, **14**: 207–216. <https://doi.org/10.1007/s00049-004-0276-2>.
- Hjältén, J., Johansson, T., Alinvi, O., Danell, K., Ball, J.P., Pettersson, R., *et al.* 2007. The importance of substrate type, shading and scorching for the attractiveness of dead wood to saproxylic beetles. *Basic and Applied Ecology*, **8**: 364–376. <https://doi.org/10.1016/j.baae.2006.08.003>.
- Hughes, A.L. and Hughes, M.K. 1982. Male size, mating success, and breeding habitat partitioning in the white spotted sawyer, *Monochamus scutellatus* (Say) (Coleoptera: Cerambycidae). *Oecologia*, **55**: 258–263. <https://doi.org/10.1007/BF00384497>.
- Hughes, A.L. and Hughes, M.K. 1987. Asymmetric contests among sawyer beetles (Cerambycidae: *Monochamus notatus* and *Monochamus scutellatus*). *Canadian Journal of Zoology*, **65**: 823–827. <https://doi.org/10.1139/z87-130>.
- Ibeas, F., Gemeno, C., Díez, J.J., and Pajares, J.A. 2009. Female recognition and sexual dimorphism of cuticular hydrocarbons in *Monochamus galloprovincialis* (Coleoptera: Cerambycidae). *Annals of the Entomological Society of America*, **102**: 317–325. <https://doi.org/10.1603/008.102.0214>.
- Jaenike, J. 1978. On optimal oviposition behavior in phytophagous insects. *Theoretical Population Biology*, **14**: 350–356. [https://doi.org/10.1016/0040-5809\(78\)90012-6](https://doi.org/10.1016/0040-5809(78)90012-6).
- Jaffé, K., Sánchez, P., Cerda, H., Hernández, J.V., Jaffé, R., Urdaneta, N., *et al.* 1993. Chemical ecology of the palm weevil, *Rhynchophorus palmarum* (L.) (Coleoptera: Curculionidae): attraction to host plants and to a male-produced aggregation pheromone. *Journal of Chemical Ecology*, **19**: 1703–1720. <https://doi.org/10.1007/BF00982302>.
- Jomura, M., Kominami, Y., Dannoura, M., and Kanazawa, Y. 2008. Spatial variation in respiration from coarse woody debris in a temperate secondary broad-leaved forest in Japan. *Forest Ecology and Management*, **255**: 149–155. <https://doi.org/10.1016/j.foreco.2007.09.002>.
- Kopaczyk, J.M., Warguła, J., and Jelonek, T. 2020. The variability of terpenes in conifers under developmental and environmental stimuli. *Environmental and Experimental Botany*, **180**: 104–197. <https://doi.org/10.1016/j.envexpbot.2020.104197>.
- Koutroumpa, F.A., Sallé, A., Lieutier, F., and Roux-Morabito, G. 2009. Feeding and oviposition preferences of *Monochamus galloprovincialis* on its main hosts *Pinus sylvestris* and *Pinus pinaster*. *Entomologia Hellenica*, **18**: 35–46. <https://doi.org/10.12681/eh.11606>.
- Landolt, P.J. and Phillips, T.W. 1997. Host plant influences on sex pheromone behavior of phytophagous insects. *Annual Review of Entomology*, **42**: 371–391. <https://doi.org/10.1146/annurev.ento.42.1.371>.

- Lee, H.R., Lee, S.C., Lee, D.H., Choi, W.S., Jung, C.S., Jeon, J.H., *et al.* 2017. Identification of the aggregation-sex pheromone produced by male *Monochamus saltuarius*, a major insect vector of the pinewood nematode. *Journal of Chemical Ecology*, **43**: 670–678. <https://doi.org/10.1007/s10886-017-0864-6>.
- Lee, H.R., Lee, S.C., Lee, D.H., Jung, M., Kwon, J.H., Huh, M.J., *et al.* 2018. Identification of aggregation-sex pheromone of the Korean *Monochamus alternatus* (Coleoptera: Cerambycidae) population, the main vector of pinewood nematode. *Journal of Economic Entomology*, **111**: 1768–1774. <https://doi.org/10.1093/jee/toy137>.
- Lextrait, P., Biémont, J.C., and Pouzat, J. 1995. Pheromone release by the two forms of *Callosobruchus maculatus* females: effects of age, temperature and host plant. *Physiological Entomology*, **20**: 309–317. <https://doi.org/10.1111/j.1365-3032.1995.tb00820.x>.
- Lindgren, B.S. 1983. A multiple funnel trap for scolytid beetles (Coleoptera). *The Canadian Entomologist*, **115**: 299–302. <https://doi.org/10.4039/Ent115299-3>.
- Macias-Samano, J.E., Wakarchuk, D., Millar, J.G., and Hanks, L.M. 2012. 2-Undecyloxy-1-ethanol in combination with other semiochemicals attracts three *Monochamus* species (Coleoptera: Cerambycidae) in British Columbia, Canada. *The Canadian Entomologist*, **144**: 764–768. <https://doi.org/10.4039/tce.2012.77>.
- Markovic, D., Glinwood, R., Olsson, U., and Ninkovic, V. 2014. Plant response to touch affects the behaviour of aphids and ladybirds. *Arthropod–Plant Interactions*, **8**: 171–181. <https://doi.org/10.1007/s11829-014-9303-6>.
- Millar, J.G. and Hanks, L.M. 2017. Chemical ecology of cerambycids. *In* *Cerambycidae of the World: Biology and Pest Management*. Edited by Q. Wang. CRC Press, Boca Raton, Florida, United States of America. Pp. 161–209.
- Murlis, J., Willis, M.A., and Cardé, R.T. 2000. Spatial and temporal structures of pheromone plumes in fields and forests. *Physiological Entomology*, **25**: 211–222. <https://doi.org/10.1046/j.1365-3032.2000.00176.x>.
- Naves, P.M., De Sousa, E.M., and Quartau, J.A. 2006a. Feeding and oviposition preferences of *Monochamus galloprovincialis* for certain conifers under laboratory conditions. *Entomologia Experimentalis et Applicata*, **120**: 99–104. <https://doi.org/10.1111/j.1570-7458.2006.00430.x>.
- Naves, P., De Sousa, E., and Quartau, J.A. 2006b. Reproductive traits of *Monochamus galloprovincialis* (Coleoptera: Cerambycidae) under laboratory conditions. *Bulletin of Entomological Research*, **96**: 289–294. <https://doi.org/10.1079/BER2006422>.
- Nordén, B., Götmark, F., Tönnerberg, M., and Ryberg, M. 2004. Dead wood in semi-natural temperate broadleaved woodland: contribution of coarse and fine dead wood, attached dead wood and stumps. *Forest Ecology and Management*, **194**: 235–248. <https://doi.org/10.1016/j.foreco.2004.02.043>.
- Ontario Ministry of Natural Resources and Forestry. 2020a. 2020–2030 Algoma Forest Management Plan, plan text. P. 356. Available from https://nrnp.mnr.gov.on.ca/s/published-submission?language=en_US&recordId=a0z3g000000CdqjAAC [accessed 4 July 2025].
- Ontario Ministry of Natural Resources and Forestry. 2020b. Northshore Forest 2020–2030 Forest Management Plan, plan text. P. 312. Available from https://nrnp.mnr.gov.on.ca/s/published-submission?language=en_US&recordId=a0z3g000000CdVPAA0 [accessed 4 July 2025].
- Paine, T.D., Birch, M.C., and Švihra, P. 1981. Niche breadth and resource partitioning by four sympatric species of bark beetles (Coleoptera: Scolytidae). *Oecologia*, **48**: 1–6. <https://doi.org/10.1007/BF00346980>.
- Pajares, J.A., Álvarez, G., Hall, D.R., Douglas, P., Centeno, F., Ibarra, N., *et al.* 2013. 2-(Undecyloxy)-ethanol is a major component of the male-produced aggregation pheromone of *Monochamus sutor*. *Entomologia Experimentalis et Applicata*, **149**: 118–127. <https://doi.org/10.1111/eea.12113>.

- Pajares, J.A., Álvarez, G., Ibeas, F., Gallego, D., Hall, D.R., and Farman, D.I. 2010. Identification and field activity of a male-produced aggregation pheromone in the pine sawyer beetle, *Monochamus galloprovincialis*. *Journal of Chemical Ecology*, **36**: 570–583. <https://doi.org/10.1007/s10886-010-9791-5>.
- Peddle, S., De Groot, P., and Smith, S. 2002. Oviposition behaviour and response of *Monochamus scutellatus* (Coleoptera: Cerambycidae) to conspecific eggs and larvae. *Agricultural and Forest Entomology*, **4**: 217–222. <https://doi.org/10.1046/j.1461-9563.2002.00145.x>.
- Pershing, J.C. and Linit, M.J. 1986. Biology of *Monochamus carolinensis* (Coleoptera: Cerambycidae) on Scotch pine in Missouri. *Journal of the Kansas Entomological Society*, **59**: 706–711.
- Peterson, H., Thistle, H., Lamb, B., Allwine, G., Edburg, S., and Strom, B. 2010. Plume dispersion in four pine thinning scenarios: development of a simple pheromone dispersion model. *Intermountain Journal of Sciences*, **16**: 73–86.
- Pichersky, E., Noel, J.P., and Dudareva, N. 2006. Biosynthesis of plant volatiles: nature's diversity and ingenuity. *Science*, **311**: 808–811. <https://doi.org/10.1126/science.1118510>.
- Pineda-Ríos, J.M., Cibrián-Tovar, J., Hernández-Fuentes, L.M., López-Romero, R.M., Soto-Rojas, L., Romero-Nápoles, J., *et al.* 2021. α -Terpineol: an aggregation pheromone in *Optatus palmaris* (Coleoptera: Curculionidae) (Pascoe, 1889) enhanced by its host-plant volatiles. *Molecules*, **26**: 2861. <https://doi.org/10.3390/molecules26102861>.
- Pinto-Zevallos, D.M., Martins, C.B., Andrade, S.M.M., Zawadneak, M.A., and Zarbin, P.H.G. 2020. Plant volatiles induced by *Duponchelia fovealis* (Lepidoptera: Crambidae) in two cultivars of strawberry and its attraction to the predator *Podisus nigrispinus* (Hemiptera: Pentatomidae). *Arthropod–Plant Interactions*, **14**: 685–693. <https://doi.org/10.1007/s11829-020-09790-5>.
- Pöykkö, H. 2006. Females and larvae of a geometrid moth, *Cleorodes lichenaria*, prefer a lichen host that assures shortest larval period. *Environmental Entomology*, **35**: 1669–1676. <https://doi.org/10.1093/ee/35.6.1669>.
- Price, P.W., Bouton, C.E., Gross, P., McPherson, B.A., Thompson, J.N., and Weis, A.E. 1980. Interactions among three trophic levels: influence of plants on interactions between insect herbivores and natural enemies. *Annual Review of Ecology and Systematics*, **11**: 41–65. Available from <https://www.jstor.org/stable/2096902> [accessed 4 July 2025].
- R Core Team. 2021. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. Available from <https://www.R-project.org/> [accessed 28 November 2021].
- Reddy, G.V. and Guerrero, A. 2004. Interactions of insect pheromones and plant semiochemicals. *Trends in Plant Science*, **9**: 253–261. <https://doi.org/10.1016/j.tplants.2004.03.009>.
- Ruther, J., Reinecke, A., Thiemann, K., Tolasch, T., Francke, W., and Hilker, M. 2000. Mate finding in the forest cockchafer, *Melolontha hippocastani*, mediated by volatiles from plants and females. *Physiological Entomology*, **25**: 172–179. <https://doi.org/10.1046/j.1365-3032.2000.00183.x>.
- Ryall, K., Silk, P., Webster, R.P., Gutowski, J.M., Meng, Q., Li, Y., *et al.* 2015. Further evidence that monoammonol is attractive to *Monochamus* (Coleoptera: Cerambycidae) species, with attraction synergised by host plant volatiles and bark beetle (Coleoptera: Curculionidae) pheromones. *The Canadian Entomologist*, **147**: 564–579. <https://doi.org/10.4039/tce.2014.67>.
- Ryan, K., de Groot, P., and Smith, S.M. 2012. Evidence of interaction between *Sirex noctilio* and other species inhabiting the bole of *Pinus*. *Agricultural and Forest Entomology*, **14**: 187–195. <https://doi.org/10.1111/j.1461-9563.2011.00558.x>.
- Safranyik, L., Linton, D.A., and Shore, T.L. 2000. Temporal and vertical distribution of bark beetles (Coleoptera: Scolytidae) captured in barrier traps at baited and unbaited lodgepole pines the year following attack by the mountain pine beetle. *The Canadian Entomologist*, **132**: 799–810. <https://doi.org/10.4039/Ent132799-6>.

- Silk, P.J., Sweeney, J., Wu, J., Sopow, S., Mayo, P.D., and Magee, D. 2011. Contact sex pheromones identified for two species of longhorned beetles (Coleoptera: Cerambycidae), *Tetropium fuscum* and *T. cinnamopterum*, in the subfamily Spondylidinae. *Environmental Entomology*, **40**: 714–726. <https://doi.org/10.1603/EN10213>.
- Smith, M.T., Payne, T.L., and Birch, M.C. 1990. Olfactory-based behavioral interactions among five species in the southern pine bark beetle group. *Journal of Chemical Ecology*, **16**: 3317–3331. <https://doi.org/10.1007/BF00982101>.
- Stehr, F.W. 1991. *Immature Insects*. Volume 2. Kendall/Hunt Publishing Company, Dubuque, Iowa, United States of America.
- Sweeney, J., Hughes, C., Webster, V., Kostanowicz, C., Webster, R., Mayo, P., and Allison, J.D. 2020. Impact of horizontal edge–interior and vertical canopy–understorey gradients on the abundance and diversity of bark and woodboring beetles in survey traps. *Insects*, **11**: 573. <https://doi.org/10.3390/insects11090573>.
- Symonds, M.R. and Elgar, M.A. 2008. The evolution of pheromone diversity. *Trends in Ecology and Evolution*, **23**: 220–228. <https://doi.org/10.1016/j.tree.2007.11.009>.
- Teale, S.A., Wickham, J.D., Zhang, F., Su, J., Chen, Y., Xiao, W., *et al.* 2011. A male-produced aggregation pheromone of *Monochamus alternatus* (Coleoptera: Cerambycidae), a major vector of pinewood nematode. *Journal of Economic Entomology*, **104**: 1592–1598. <https://doi.org/10.1603/EC11076>.
- Thompson, J.N. 1988. Evolutionary ecology of the relationship between oviposition preference and performance of offspring in phytophagous insects. *Entomologia Experimentalis et Applicata*, **47**: 3–14. <https://doi.org/10.1111/j.1570-7458.1988.tb02275.x>.
- Thornhill, R. and Alcock, J. 1983. Motivation to copulate. *In The Evolution of Insect Mating Systems*. Edited by R. Thornhill and J. Alcock. Harvard University Press, Cambridge, Massachusetts, United States of America. Pp. 119–143.
- Togashi, K. and Appleby, J.E. 2023. Influence of host pine species on the adult body mass and emergence date of *Monochamus carolinensis*, *M. notatus*, *M. scutellatus* and *M. titillator* (Coleoptera: Cerambycidae). *Journal of Forestry Research*. **28**: 145–151. <https://doi.org/10.1080/13416979.2022.2138094>.
- Tooker, J.F., Koenig, W.A., and Hanks, L.M. 2002. Altered host plant volatiles are proxies for sex pheromones in the gall wasp, *Antistrophus rufus*. *The Proceedings of the National Academy of Sciences*, **99**: 15486–15491. <https://doi.org/10.1073/pnas.252626799>.
- Ulyshen, M.D. and Hanula, J.L. 2007. A comparison of the beetle (Coleoptera) fauna captured at two heights above the ground in a North American temperate deciduous forest. *The American Midland Naturalist*, **158**: 260–278. [https://doi.org/10.1674/0003-0031\(2007\)158\[260:ACOTBC\]2.0.CO;2](https://doi.org/10.1674/0003-0031(2007)158[260:ACOTBC]2.0.CO;2).
- United States Department of Agriculture, Forest Service. 2019. *Forest Inventory and Analysis National Core Field Guide*. Volume I: Field Data Collection Procedures for Phase 2 Plots. Version 9.0. Department of Agriculture, Forest Service, Washington, District of Columbia, United States of America.
- Vance, C.C., Kirby, K.R., Malcolm, J.R., and Smith, S.M. 2003. Community composition of longhorned beetles (Coleoptera: Cerambycidae) in the canopy and understorey of sugar maple and white pine stands in south–central Ontario. *Environmental Entomology*, **32**: 1066–1074. <https://doi.org/10.1603/0046-225X-32.5.1066>.
- Vargas-Cardoso, O.R., Toledo-Hernández, V.H., Corona-López, A.M., Corona-López, A.M., Flores-Palacios, A., Figueroa-Brito, R., *et al.* 2023. Host plant selection by Cerambycidae in two different strata in association with seasonality and physical wood characteristics in a tropical dry forest. *Ecological Entomology*, **48**: 610–621. <https://doi.org/10.1111/een.13259>.
- Victorsson, J. and Wikars, L.O. 1996. Sound production and cannibalism in larvae of the pine-sawyer beetle, *Monochamus sutor* L. (Coleoptera: Cerambycidae). *Entomologisk Tidskrift*, **117**: 29–33.

- Waddell, K.L. 2002. Sampling coarse woody debris for multiple attributes in extensive resource inventories. *Ecological Indicators*, **1**: 139–153. [https://doi.org/10.1016/S1470-160X\(01\)00012-7](https://doi.org/10.1016/S1470-160X(01)00012-7).
- Wallin, H., Schroeder, M., and Kvamme, T. 2013. A review of the European species of *Monochamus* Dejean, 1821 (Coleoptera, Cerambycidae), with a description of the genitalia characters. *Norwegian Journal of Entomology*, **60**: 11–38.
- Webster, B. and Cardé, R.T. 2017. Use of habitat odour by host-seeking insects. *Biological Reviews*, **92**: 1241–1249. <https://doi.org/10.1111/brv.12281>
- Wickham, J.D., Harrison, R.D., Lu, W., Guo, Z., Millar, J.G., Hanks, L.M., and Chien, Y. 2014. Generic lures attract cerambycid beetles in a tropical montane rain forest in southern China. *Journal of Economic Entomology*, **107**: 259–267. <https://doi.org/10.1603/EC13333>.
- Wood, D.L. 1982. The role of pheromones, kairomones, and allomones in the host selection and colonization behavior of bark beetles. *Annual Review of Entomology*, **27**: 411–446. <https://doi.org/10.1146/annurev.en.27.010182.002211>.
- Wyatt, T.D. 2014. Perception and response to chemical communication: from chemosensory receptors to brains, behaviour, and development. *In* *Pheromones and Animal Behavior: Chemical Signals and Signature Mixtures*. Second edition. *Edited by* T.D. Wyatt. Cambridge University Press, New York, New York, United States of America. Pp. 173–223.
- Xu, H. and Turlings, T.C. 2018. Plant volatiles as mate-finding cues for insects. *Trends in Plant Science*, **23**: 100–111. <https://doi.org/10.1016/j.tplants.2017.11.004>.
- Zarbin, P.H., Fonseca, M.G., Szczerbowski, D., and Oliveira, A.R. 2013. Biosynthesis and site of production of sex pheromone components of the cerambycid beetle, *Hedypathes betulinus*. *Journal of Chemical Ecology*, **39**: 358–363. <https://doi.org/10.1007/s10886-013-0252-9>.
- Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A., and Smith, G.M. 2009. *Mixed Effects Models and Extensions in Ecology with R*. Springer Science+Business Media LLC, New York, New York, United States of America.