Chemoecology (2025) 35:157–166
https://doi.org/10.1007/s00049-025-00425-w

CHEMOECOLOGY

ORIGINAL ARTICLE

No population-level variation in cuticular hydrocarbon profiles of a major agricultural pest, the coffee berry borer, *Hypothenemus hampei*

Ameka Myrie[1] · Eva Schultner[1] · Jan Oettler[1] · Tamara Pokorny[1]

Received: 6 March 2025 / Accepted: 1 July 2025 / Published online: 19 July 2025

Abstract

The Coffee Berry Borer (CBB) *Hypothenemus hampei* (Ferrari) (Coleoptera: Curculionidae: Scolytinae) is an important pest species that has invaded all major coffee-producing areas of the world, causing tremendous economic losses every year. Since its discovery on the island of Jamaica approximately 40 years ago, the beetle has moved from lowland regions with comparably warm and dry climates to higher altitudes with cooler and wetter conditions in the Blue Mountains. Some insects have been shown to react to such environmental variation with changes in their cuticular hydrocarbon (CHC) profiles. To investigate if this is also the case in CBBs, we characterized the CHC profiles of beetles collected from different farms varying in altitude and climate across Jamaica and from one farm in Panama. We found that the CHC profiles of CBBs are mainly composed of straight-chain alkanes and methyl-branched alkanes, and that differences in farm location or rearing conditions (lab or field) may not necessarily result in CHC variation. The coffee berries provide a microclimate which protects the beetles from the conditions outside the coffee berries for the majority of their life cycles, thus potentially buffering this major pest from external environmental selection pressures.

Keywords Chemical communication · Scolytinae · Bark beetles · Invasive species · GC/MS · Climate

Introduction

In insects, cuticular hydrocarbons (CHCs) (straight-chained alkanes, methyl-branched alkanes, and unsaturated alkenes (Stanley-Samuelson and Nelson 1993; Gibbs and Pomonis 1995) are commonly used for protection against desiccation and as signaling molecules in intraspecific communication (Blomquist and Bagnères 2010). Qualitative differences in compounds composition among profiles tend to be used to distinguish species (Soares et al. 2017; Sprenger and Menzel 2020), but may also be found within species (Dembeck et al. 2015). However, most intraspecific variation is quantitative (Sprenger and Menzel 2020).

Both qualitative and quantitative aspects can be (in part) genetically determined (Howard and Blomquist 2005; Martin et al. 2008; Oliveira et al. 2011; Walsh et al. 2020). Nongenetic factors also influence CHCs (Holze et al. 2021) and can include biotic factors like diet, microbiome, parasites, and pathogens, as well as abiotic variables such as humidity and temperature (Sprenger and Menzel 2020). Temperature shifts in particular have been shown to induce changes in the proportion of specific compounds in many insects (Otte et al. 2018; Barnes 2021), including ants (Menzel et al. 2018; Duarte et al. 2019; Sprenger and Menzel 2020; Baumgart et al. 2022; Krapf et al. 2023), beetles (Hadley 1977), and fruit flies (Etges et al. 2017). Environmentally-induced changes to CHC profiles may take place in a matter of hours (Stinziano et al. 2015) or days (Howard et al. 1995) after exposure. These changes can persist over time to eventually become fixed, e.g. in populations of *Drosophila melanogaster* and *Drosophila serrata* from distinct environmental clines (Frentiu and Chenoweth 2010).

Communicated by Günther Raspotnig.

Ameka Myrie
myriemeka@gmail.com

Eva Schultner
eva.schultner@gmail.com

Jan Oettler
joettler@gmail.com

Tamara Pokorny
tamara.pokorny@ur.de

[1] Zoology/Evolutionary Biology, Universität Regensburg, Universitätsstrasse 31, 93053 Regensburg, Germany

The Coffee Berry Borer (CBB, *Hypothenemus hampei*; Coleoptera: Curculionidae, Scolytinae) is originally from Africa (Le Pelley 1973), but has spread to all major coffee-producing regions of the world (Johnson et al. 2020). On the island of Jamaica, CBBs were first discovered in 1978 (Reid 1983) in lowland farms, i.e., low elevation with relatively warm climates (Rhodes and Mansingh 1986), similar to the climate of the CBB's suspected place of origin (Hargreaves 1926; Tutin and Fernandez 1993; Vega et al. 2019; Bush et al. 2020). The CBB has since spread throughout the island to farms in the Highlands and Blue Mountain regions (Rhodes and Mansingh 1986), where the climate is cooler, more humid, and rainy (Myrie et al. 2023).

CBBs spend the majority of their lives within the coffee berry: after a female finds and enters a susceptible berry, she burrows to the endosperm to lay eggs (Baker et al. 1992). The eggs later develop within the berry, and, as adults, engage in sib-mating (Baker 1984; Andreev et al. 1998; Damon 2000). Newly inseminated daughters then leave the natal berry to infest a fresh berry nearby, traveling an average of <40 m, and a maximum distance of 65 m (Gil et al. 2015), assisted by the wind. Limited dispersal, sib-mating and repeated genetic bottlenecks have resulted in low genetic diversity in the CBB (Andreev et al. 1998; Errbii et al. 2024), much like in other invasive species (Tsutsui et al. 2000; Schmid-Hempel et al. 2007; Puillandre et al. 2008; Schmack et al. 2019).

Low genetic variation (Errbii et al. 2024) together with a protected lifestyle inside the coffee berry, and essentially being buffered from environmental perturbations, may limit climatic CHC profile adaptation. Thus, in contrast to many other species, such as ants, where CHC variation is high (Menzel et al. 2018; Buellesbach et al. 2018), intra-specific CHC variation in the CBB may be expected to be low. To test the hypothesis that CBBs show low variation in their CHC profiles, we assessed environmentally induced variability in CHC profiles of beetles collected from three localities in Jamaica, and one locality in Panama, where the CBB was discovered ~ 30 years after it was initially found in Jamaica (Fondo Regional de Tecnología Agropecuaria 2019). For a subset of Jamaican localities, we furthermore analyzed both field and lab-reared beetles to identify potential diet-induced effects (natural coffee beans versus artificial lab diet). Finally, we reviewed the available literature on CHC profiles of the ecologically and economically important Scolytinae beetles.

Materials and methods

Beetle collection and sample preparation

All beetles used in this study derived from populations in Jamaica and Panama (Table 1). Across the farms, berries infested with CBB, identified by the presence of an entry hole, were collected. In Jamaica, beetles were collected from different localities, i.e., coffee-producing farms categorized by specific environmental conditions (elevation, temperature, humidity, and rainfall). We used beetles from two Jamaican localities - Highlands & Blue Mountains– in this study. Highland farm locations exhibit intermediate conditions with mean temperatures ranging from 18° C to 23° C, humidities between 60% and 80%, and a maximum rainfall of 632 mm per month (Myrie et al. 2023). Blue Mountain farm locations have the lowest temperatures (mean 16° C to 23° C), highest humidity (80-88%), and a maximum monthly rainfall of 339 mm (Myrie et al. 2023). We did not include beetles from the Lowlands, as Lowland coffee production has decreased significantly (Lancashire 1995), making it difficult to collect enough beetles in these regions. In each of the two localities, we collected beetles from 1 to 2 farms from December 2019 to January 2020: Mountain Spring (493 m above sea level (m.a.s.l) in the Highlands, Hopewell and Guava Ridge in the Blue Mountains (>1000 m.a.s.l, approximately 16 km from the Highland locality and 500 m from each other). In Coclé Panama, average yearly temperature was 25° C, with an annual precipitation of 3900 mm (INEC 2017 cited in Fujisawa et al. 2020), even though temperatures oscillate at 21° C (Santos Murgas et al. 2017). There, beetles were collected from one farm

Table 1 Origin of samples used in this study

Locality	Farm	Lab Replicates (*n*)				Field Replicates (*n*)	Coordinates	Country
		Generation						
		F8	F9	F15	F18			
Highlands (493 masl)	Mountain Spring	-	4	2	1	1	18.10905° N, 76.80392° W	Jamaica
Blue Mountains (>1000 masl)	Hopewell	-	2	1	2	2	18.03674° N, 76.67991°W	Jamaica
Blue Mountains (>1000 masl)	Guava Ridge	-	2	2	1	-	18.0325° N, 76.68012° W	Jamaica
Panama (433 masl)	Turega	2	-	-	-	-	8.62155°N, 80.18705°W	Panama

For lab samples, the number of generations that beetles were kept under standardized lab conditions prior to sampling is reported. Each replicate consists of one pool of 50 female beetles in Turega (433 m.a.s.l, Permit: Solicitud No. 0194,0195) in November 2021. Given that the environmental conditions at the Panama farm (Ruane et al. 2013) are different from the conditions at the Jamaican farms, and the fact that it is a mainland country, Panama was treated as a separate "locality" for statistical analyses.

Laboratory populations were established from each of the four farms (Mountain Spring, Hopewell, Guava Ridge, Turega) located in the three localities (Highlands, Blue Mountains, Panama) (Table 1). After collection and dissection of infested beans, beetles were transferred to glass vials containing artificial diet (following Vega et al. (2011), with the addition of formaldehyde (formaldehyde solution min. 37%) as a microbial inhibitor. Beetles were maintained at 27° C throughout the day (for 12 h) and 21° C throughout the night (for 12 h) in a dark climate chamber at the Universität Regensburg, Germany, for 8 to 18 generations before collecting samples for CHC analyses. For two farms from two Jamaican localities (Mountain Spring in the Highlands, Hopewell in the Blue Mountains), we also analyzed CHC profiles of field-reared beetles (Table 1). To this end, one field sample each was collected in Hopewell and Mountain Spring in November 2021; an additional field sample was collected in Hopewell in August 2022. Beetles from field samples were immediately prepared for CHC extraction after being dissected from the coffee berries.

For the field-collected CBBs, coffee berries previously collected from the field were carefully dissected and the live female CBBs extracted. To remove residues of coffee (from field collected beetles) and residues of the artificial diet (from the lab reared beetles), females were placed in an Eppendorf tube filled with Millipore water, and vortexed for 3 s, after which the beetles were placed on a Kim wipe (KIMTECH Science, White Delicate Task Wipes) to remove the remaining water droplets. The beetles were then placed into small chambers (diameter 0.8 cm, depth 0.2 cm) drilled into a glass plate (13 cm x 13 cm, four chambers per plate) to recover from the vortex procedure. Six to seven beetles were placed together into each chamber, and a second glass plate was placed on top, then sealed using adhesive paper labels (Figure S1). The glass plates containing the live beetles were placed in the same beetle-rearing climate chamber with a 12 h:12 h and 27° C:21 °C day: night cycle. After 5 days the beetles were removed from the glass plates, pooled in glass vials in groups of 50, and frozen at -20° C for 90 to 120 min.

Each pool of individuals (50 individuals per pool) was extracted with 750 µl of hexane (≥99%) for 10 min, after which the supernatant was transferred into a fresh vial. To obtain potentially remaining cuticular lipids, a second hexane wash step was conducted for 5 min using 250 µl of hexane, after which both extracts were combined (a total of 1000 µl of hexane from each pooled sample). The solvent of each sample was evaporated to a volume of approximately 200 µl under a stream of nitrogen. Extracts were fractionated before chemical analysis using silica gel columns (Chromabond 100 mg, Macherey-Nagel, Düren, Germany). One column was used per sample and was cleaned successively with 1000 µl of hexane, 1000 µl dichloromethane, 1000 µl methanol, 1000 µl of dichloromethane, and finally 1000 µl of hexane. Then, the column was conditioned using 2 × 500 µl of hexane.

To obtain only the nonpolar extract-fraction, the extract and two 100 µl hexane rinses of the respective vial were added to the column and fractionated using 2 × 500 µl hexane to elute the CHCs. The eluate was captured in a clean vial. Before CHC analysis, the solvent was evaporated entirely under nitrogen and refilled with 50 µl hexane.

Gas chromatography-mass spectrometry and statistical analyses

Chemical analysis was done by gas chromatography with coupled mass spectrometry (GC-MS QP2010 Plus, Shimadzu Corporation, Kyoto, Japan), using a BPX-5 column (length 60.0 m, diameter 0.25 mm, thickness 0.25 µm). Helium was used as carrier gas at a column flow of 1.25 ml per minute. One microlitre of each sample was injected splitless at an injection temperature of 300 °C, with column oven temperature at 150 °C. The oven temperature was raised at 5° per minute to 310° C, where it was held constant for 30 min.

Linear retention indices (LRI) were calculated based on n-alkane calibration runs (C7 - C40). Peaks were manually integrated using GCMS Solution (Postrun Analysis) Version 4.45 (Shimadzu Corporation, Kyoto, Japan). Tentative compound identification was based on LRI and compound mass spectra. Methyl-branch positions were inferred from characteristic fragmentation patterns (corroborated using ChemDraw Professional, PerkinElmer, Buckinghamshire, United Kingdom) and LRI were compared with those reported by Carlson et al. (1998). Overlapping peaks were integrated together and treated as a single peak for further analyses. The proportional area of each CHC peak per sample was calculated by dividing the area of the respective peak by the total area of CHC peaks in the sample. Compounds constituting less than 0.25% were excluded from further analysis. Proportional area for the remaining peaks was recalculated and square-root transformed prior to statistical analysis.

Statistical Analyses

All statistical analyses were conducted using R version 4.2.1 (R Core Team 2022). To assess quantitative differences between samples, a principal component analysis (PCA) was run on the transformed proportions of all compounds using the 'prcomp' command of the 'stats' package. To investigate the relationship between CHC profile composition and environmental variables, a linear regression (function lm) was run using principal component 1 (PC1) score as response and "locality" (Highlands, Blue Mountains, Panama) and "rearing condition" (lab or field) as explanatory variables. A second linear regression was run using PC1 score as response and "farm" (Mountain Spring, Hopewell, Guava Ridge, Turega) and "rearing condition" (lab or field) as explanatory variables. Model residuals were tested for normality and dispersion (function testResiduals) using the DHARMa package (DHARMa 0.4.6). Pairwise p-values were calculated and corrected for multiple testing using the emmeans package (function emmeans).

Mean chain length influences the CHC class composition. An increase in chain length will increase lipid melting temperature, which affects the insects' waterproofing abilities (Gibbs and Pomonis 1995). The weighted mean chain length (WMCL) is a parameter that encompasses the overall composition of the CHC profile. It was calculated for each of the 22 samples to identify the average chain length of the compounds using the following formula:

$$\frac{((\text{Retention Index } 100) * \text{Area of Compound})}{(\text{ Area of Compounds})}$$

The WMCLs were compared among farms using a Kruskal Wallis rank sum test (function kruskal.test).

CHC composition in Scolytinae beetles

To assess how CBB profiles compare to those of related beetle species, we conducted two searches of the literature using the phrases "Cuticular Hydrocarbon Scolytinae" and "Cuticular Hydrocarbon Scolytidae", respectively, in Google Scholar to retrieve studies on CHC composition in Scolytinae beetles (formerly considered a family, Scolytidae). In total, these searches identified six studies on the entire CHC profiles of 23 species. For each species, we noted the number of identified compounds and the corresponding compound classes (alkanes, methyl-branched alkanes, alkenes, and alkadienes).

Results

A total of 21 peaks were identified in the CHC profiles of female CBBs (Fig. 1; Table 2). Across all samples, five peaks (Peaks 1, 9, 13, 14, and 18) made up over 70% of the profile (Fig. 1; Table 2).

Principal component analysis revealed no clear separation between samples according to locality (Fig. 2, ANOVA on PC1 scores, factor: locality, $F_{2,22}$=1.818, p=0.191) or farm (Fig. 2, ANOVA, factor: farm, $F_{3,22}$=1.435, p=0.267). There was a slight trend that the two field samples from the Blue Mountain Hopewell farm exhibited higher PC1 scores compared to lab samples (Fig. 2, ANOVA on PC1 scores, factor: rearing condition (field or lab), $F_{1,22}$=4.136, p=0.057).

64% (14/22) of the samples had a weighted mean chain length (WMCL) of ~32, and 36% (8/22) of the samples had

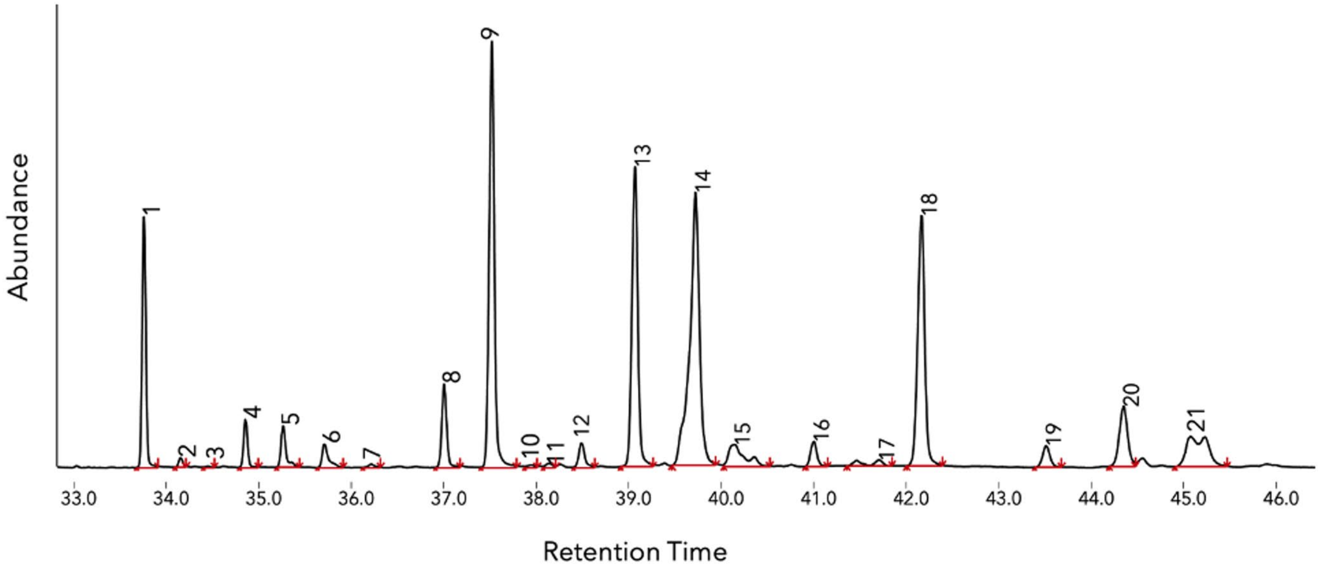

Fig. 1 Cuticular hydrocarbon peaks identified in female Coffee Berry Borers *Hypothenemus hampei*. Numbers above the peaks correspond to the compounds listed in Table 2

a WMCL of ~31 (Figure S2). There was no difference in WMCL based on farm (Figure S2, Kruskal Wallis rank sum test, df=3, $\chi^2=1.797$, $p=0.616$).

The literature search retrieved six studies that reported results of GC/MS analyses of complete CHC profiles of 23 species of Scolytinae beetles from six genera (Table 3). The number of identified CHCs ranged from 9 to 85, with alkanes and methyl-branched alkanes being the most abundant and present in all studied species. 83% (19/23) of species had profiles containing 3 or more compound classes. Alkenes were found in species belonging to the genera *Dendroctonus*, *Conophthorus*, and *Ips* while alkadienes were only found in species belonging to the genera *Conophthorus* and *Ips*. In contrast, the CBB profiles were relatively simple with a comparably low number of compounds from only two compound classes. Only the profiles from species within the Xyleborini tribe were similar in their simplicity to those of the CBB.

Table 2 Composition of CHC profiles of female coffee berry borers

Peaks	Compound	Linear Retention Index	Mean Percentage of Area ± SD
1	C29	2900	11.07 ± 3.27
2	15-me C29, 13-me C29	2927	0.59 ± 0.26
3	5-me C29	2947	0.21 ± 0.15
4	3-MeC29	2973	3.67 ± 1.91
5	C30 & 3,7-dime C29, 3,9-dime C29	3000	2.65 ± 0.79
6	15-me C30, 14-me C30, 13-me C30 & 3,x, y-trime C29*	3026	1.63 ± 0.51
7	4-me C30	3055	0.21 ± 0.06
8	C31	3100	3.98 ± 0.83
9	15-me C31, 13-me C31	3126	18.41 ± 2.53
10	5-me C31	3146	0.26 ± 0.09
11	9,17-dime C31*	3156	0.29 ± 0.06
12	3-me C31	3173	1.9 ± 0.7
13	3,17-dime C31, 3,15-dime C31*	3201	14.97 ± 2.19
14	3,11,15-trime C31* & 15-me C32, 13-me C32 & 3,9,15-trime C31*	3228	16.66 ± 3.82
15	3,9,x,17-tetrame C31* (and other tetramethyls)	3244	2.04 ± 0.58
16	3-me C32* & x,14-dime C32*	3281	1.13 ± 0.12
17	C33 & methyl-branched C32*	3300	0.64 ± 0.13
18	17-me C33, 15-me C33	3324	11.12 ± 4.08
19	5,19-dime C33	3371	1.14 ± 0.17
20	3,19-dime C33 & 3,17-dime C33 & 3,15-dime C33*	3399	3.75 ± 0.41
21	3,11,15-trime C33* & 3,9,15-trime C33*	3424	3.68 ± 1.09

Compound abbreviations: alkane with a chain length of n C-atoms: Cn, monomethyl: me, di-/tri-/tetramethyl: dime/trime/tetrame; x, y indicate unknown methyl-branch positions. Asterisks denote uncertain compound identification

Discussion

The composition of CHCs in insects is influenced by various factors including genotype, and the biotic and abiotic environment (Menzel et al. 2017). Saturated compounds such as n-alkanes and mono-methyl alkanes have stronger Van Der Waal forces (Menzel et al. 2017; Maihoff et al. 2023), which should result in better waterproofing abilities than unsaturated compounds such as n-alkenes (Maihoff et al. 2023). If the demand for waterproofing increases, there may also be an increase in the mean chain length of an insect's

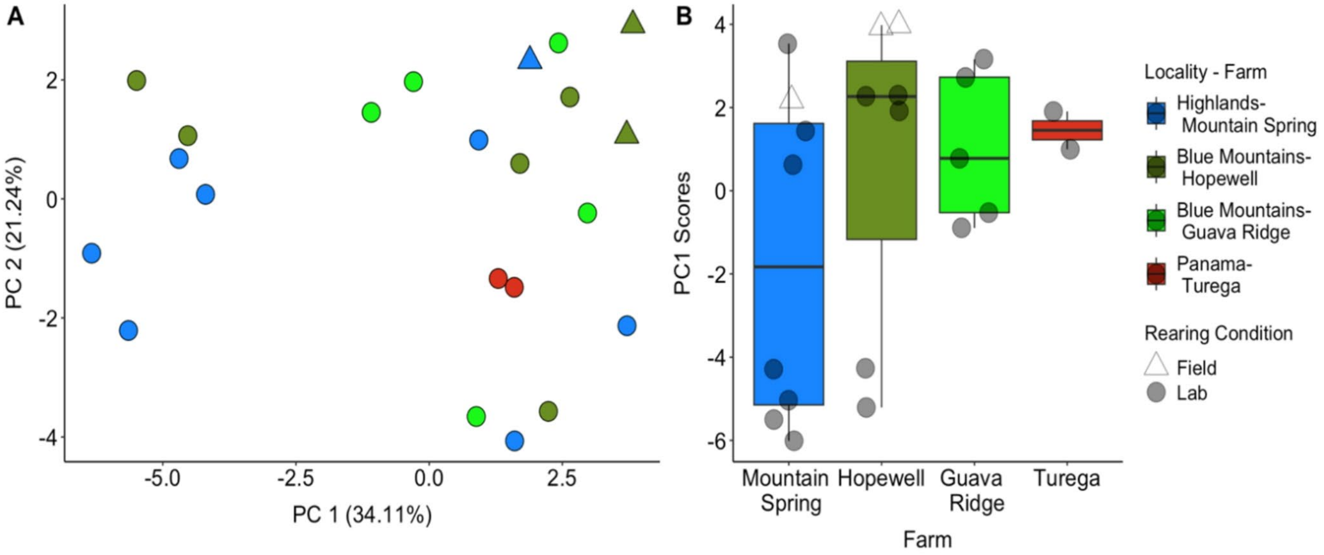

Fig. 2 (A) Principal component plot of square-root transformed proportional peak areas of CHCs extracted from female Coffee Berry Borers. (B) Principal component 1 scores plotted by farm. The blue shade represents the Highland locality, different shades of green represent localities from the Blue Mountains, while the red shade represents the locality from Panama. Triangles represent field samples while circles represent lab samples

Table 3 Cuticular hydrocarbon profile composition in 23 beetle species from six genera in the subfamily scolytinae

Scolytinae Tribe	Scolytinae Species	Number of Peaks	Alkanes	Methyl-Branched Alkanes	Alkenes	Alkadienes	Refs
Xyleborini	*Xyleborinus saxenii*	16	x	x			Melet et al. (2024)
Xyleborini	*Euwallacea fornicatus*	9	x	x			Chen et al. (2017)
Xyleborini	*E. sp.*	25 using 400 females and 16 using 44 females	x	x			Chen et al. (2017)
Cryphalini	*Hypothenemus hampei*	21 (that constitute > 0.25% of the profile)	x	x			This Study
		35–50					Howard and Infante (1996)
Ipini	*Ips grandicollis*	56	x	x	x	x	Page et al. ()1997
Ipini	*I. cribricollis*	51	x	x	x	x	Page et al. (1997)
Ipini	*I. montanus*	85	x	x	x	x	Page et al. (1997)
Ipini	*I. paraconfusus*	84	x	x	x	x	Page et al. (1997)
Ipini	*I. confusus*	82	x	x	x	x	Page et al. (1997)
Ipini	*I. hoppingi*	68	x	x	x	x	Page et al. (1997)
Ipini	*I. lecontei*	76	x	x	x	x	Page et al. (1997)
Hylesinni	*Dendroctonus brevicomis*	41	x	x	x		Page et al. (1990a)
Hylesinni	*D. frontalis*	39	x	x	x		Page et al. (1990a)
Hylesinni	*D. ponderosae*	28	x	x	x		Page et al. (1990a)
Hylesinni	*D. jeffreyi*	26	x	x	x		Page et al.1990a
Scolytini	*Conophthorus conicolens*	40	x	x	x		Page et al. (1990b)
Scolytini	*C. ponderosae*	45	x	x	x	x	Page et al. 1990b
Scolytini	*C. cembroides*	34	x	x	x		Page et al. (1990b)
Scolytini	*C. edulis*	31	x	x	x		Page et al.(1990b)
Scolytini	*C. radiatae*	16	x	x	x		Page et al. (1990b)
Scolytini	*C. coniperda*	20	x	x	x	x	Page et al. (1990b)
Scolytini	*C. resinosae*	17	x	x	x	x	Page et al. 1990b
Scolytini	*C. banksianae*	17	x	x	x	x	Page et al. (1990b)

CHC profile (Menzel et al. 2017; Gibbs and Pomonis 1995; Rouault et al. 2004).

We hypothesized that CHC profiles in the Coffee Berry Borer show comparably low levels of variation based on their lifestyle and genetic background. In support, we did not find consistent variation among profiles of beetles from different localities or farms. We also did not detect major differences between profiles of laboratory- and field-reared beetles, though field sample size was very small, and this result would need to be verified.

Given that the coffee berry protects CBBs from external conditions for most of its life, there may be little selective pressure on CHC profiles to adjust to different macro-climatic conditions. Therefore, the most parsimonious explanation as to why there were no differences in the CHC composition of CBBs based on locality is the sheltered life inside the coffee berry (Dias et al. 2008). A berry provides a constant microclimate that may protect the beetles effectively, preventing exposure to environmental fluctuations. CBBs can remain and reproduce inside the same coffee berry on the coffee plant for up to 5 months, only emerging to infest new berries or when the current berry (usually fallen berries) becomes waterlogged (Constantino et al. 2021). The CBBs can also use fallen coffee berries as a post-harvest reservoir (Aristizábal et al. 2016) for up to 140 days when there are no susceptible berries left (Constantino et al. 2021). Even though CBBs can fly for up to three hours (Baker 1984), CBBs located on productive farms have no requirement to cover extensive flight distances due to the proximity of shrubs (Gil et al. 2015), which means that the beetles are not exposed to the environmental conditions outside the berry for extended periods of time. Additionally, female beetles might leave the natal berries preferentially when outside conditions are favorable, which would further reduce the impact of climatic factors. Though our samples were collected on a relatively small geographical scale, the lack of discernible variation in weighted mean chain lengths provides additional support for the idea that there may be little to no environmental selection pressure on CHC profiles in the CBB.

Our results align with a study on the bark beetle *Conophthorus ponderosae*, which showed that beetles from different host trees and different localities had similar CHC profiles (Page et al. 1990). In contrast, *Xyleborinus saxenii* bark beetles sampled in their native range exhibited differences in CHC profiles according to sample site (Melet et al. 2024). Other beetles protected from the external environment throughout their lifecycle include bruchid beetles such as *Bruchidius uberatus* (Ernst et al. 1990), weevils (Chapman 1983), and cerambycids, which emerge as adults from the trunks and branches of trees (Haack 2006; Geib et al. 2008; Haack et al. 2010). Cerambycids exhibit CHC differences between sexes (Zhang et al. 2003; Kerr et al. 2024) but not between conspecifics from the same population; sex differences have also been found in CBBs (Howard and Infante 1996).

Overall, very little work has been done on CHCs in Scolytinae beetles, illustrated by our literature search, which recovered data from a mere 23 species belonging to six genera. This represents less than 1% of Scolytinae species (23 out of 6000 species; Hulcr et al. 2015) and only a tiny fraction of overall beetle species (>400,000 species; McKenna et al. 2019). The CHCs of the CBB were previously investigated by Howard and Infante (1996), who reported a total of 35–50 compounds for female beetles. Of these, 22 constituted on average more than 0.25% of the total profile (Howard and Infante 1996; Table 4), which is similar to the results obtained here (21 peaks). Additionally, the five peaks with the highest relative abundances are the same across both studies (based on tentative compound identifications). Qualitatively, while profiles of most other studied Scolytinae beetles also included unsaturated compounds, the profile of the CBB consists exclusively of saturated CHCs. Profiles lacking alkenes and alkadienes were otherwise reported only from *Xyleborinus saxenii* and *Euwallacea spp*. While the presence or absence of unsaturated CHCs was consistent within genera, more studies are needed to evaluate the pattern of CHC composition across the Scolytinae phylogeny and its ecological relevance.

Though the available data are very limited, our comparative approach allows some conclusions about Scolytinae CHCs. First, profiles of most species contain alkanes and methyl-branched alkanes, typically thought to be the compounds most involved in waterproofing (Gibbs and Pomonis 1995; Wagner et al. 2001; Gibbs and Rajpurohit 2010). Second, profiles vary qualitatively between species and can be as complex as those of other insect orders.

To better understand the extent of CHC variability in this major pest, future studies should compare profiles from different continents and from its native range in Africa. Further, CHC biosynthesis is impacted by what an organism eats (Otte et al. 2015), and diet has been shown to commonly impact profile composition in insects (Steiger et al. 2007; Geiselhardt et al. 2012; Kühbandner et al. 2012; Fedina et al. 2012; Otte et al. 2018). The CBB infests and feeds on the commercial coffee species *Coffea arabica* and *Coffea canephora* (Baker 1984; Navarro-Escalante et al. 2021); it remains to be shown whether differences in the two *Coffea* species (host plants) are a natural cause of variation in CHC profiles of CBBs.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00049-025-00425-w.

Acknowledgements We extend our gratitude to JACRA (Jamaica Agricultural Commodities Regulatory Authority) and Ms. Shevanne Staniger for their support in gaining access to coffee farms in Jamaica. Our appreciation also goes to Alonso Santos Murgas and Hermogenes Fernandez for their assistance with permits for Panama. Thanks to Orville Simms, Yulian, and Jose Pascual for their help in the field. Lastly, we would like to thank Joachim Ruther for his assistance with the equipment used in this project.

Author contributions A.M., E.S., J.O., and TP conceived of the study; A.M., E.S., and TP designed the experiments, A.M and TP analysed the data, A.M visualised the data; A.M, E.S, and TP wrote the manuscript with comments from J.O. All authors read and commented on the final version of the manuscript.

Funding Open Access funding enabled and organized by Projekt DEAL. A.M. was supported by the Deutscher Akademischer Austauschdienst (DAAD). Grant number: 91727749.

Data availability The raw data tables used to generate all the figures and statistics included in the manuscript are available upon request from the corresponding authors.

Declarations

Conflict of interest All authors declare that there is no conflict of interest related to the research presented in this study.

References

Andreev D, Breilid H, Kirkendall L et al (1998) Lack of nucleotide variability in a beetle pest with extreme inbreeding. Insect Mol Biol 7:197–200. https://doi.org/10.1046/j.1365-2583.1998.72064.x

Aristizábal LF, Bustillo AE, Arthurs SP (2016) Integrated pest management of coffee berry borer: strategies from Latin America that could be useful for coffee farmers in Hawaii. Insects 7:6. https://doi.org/10.3390/insects7010006

Baker P (1984) Some aspects of the behavior of the coffee berry borer in relation to its control in Southern Mexico (Coleoptera, Scolytidae). Folia Entomológica Mexicana (México) 61:9–24

Baker PS, Barrera JF, Rivas A (1992) Life-History studies of the coffee berry borer (*Hypothenemus hampei*, Scolytidae) on coffee trees in Southern Mexico. J Appl Ecol 29:656–662. https://doi.org/10.2307/2404473

Barnes L (2021) Insect developmental plasticity: the role in a changing environment. https://doi.org/10.18297/tce/vol1/iss1/28. The Cardinal Edge 1:

Baumgart L, Wittke M, Morsbach S et al (2022) Why do ants differ in acclimatory ability?? Biophysical mechanisms behind cuticular hydrocarbon acclimation across species. J Exp Biol 225:jeb243847. https://doi.org/10.1242/jeb.243847

Blomquist GJ, Bagnères A-G (eds) (2010) Insect hydrocarbons: biology, biochemistry, and chemical ecology. Cambridge University Press, Cambridge

Buellesbach J, Whyte BA, Cash E et al (2018) Desiccation resistance and Micro-Climate adaptation: cuticular hydrocarbon signatures of different Argentine ant supercolonies across California. J Chem Ecol 44:1101–1114. https://doi.org/10.1007/s10886-018-1029-y

Bush ER, Jeffery K, Bunnefeld N et al (2020) Rare ground data confirm significant warming and drying in Western wquatorial Africa. PeerJ 8:e8732. https://doi.org/10.7717/peerj.8732

Campuzano-Duque LF, Herrera JC, Ged C, Blair MW (2021) Bases for the establishment of robusta coffee (*Coffea canephora*) as a new crop for Colombia. Agronomy 11:2550. https://doi.org/10.3390/agronomy11122550

Carlson DA, Bernier UR, Sutton BD (1998) Elution patterns from capillary GC for Methyl-Branched alkanes. J Chem Ecol 24:1845–1865. https://doi.org/10.1023/A:1022311701355

Chapman PJ (1983) The Plum Curculio as an Apple pest, vol 684. New York State Agricultural Experiment Station No

Chen Y, Dallara PL, Nelson LJ et al (2017) Comparative Morphometric and Chemical Analyses of Phenotypes of Two Invasive Ambrosia Beetles (*Euwallacea spp.*) in the United States. Insect Sci 24:647–662. https://doi.org/10.1111/1744-7917.12329

Computing R Foundation for Statistical Computing, Vienna, Austria. https://cran.r-project.org/mirrors.html

Constantino LM, Gil ZN, Montoya EC, Benavides P (2021) Coffee berry borer (*Hypothenemus hampei)* emergence from ground fruits across varying altitudes and climate cycles, and the effect on coffee tree infestation. Neotrop Entomol 50:374–387. https://doi.org/10.1007/s13744-021-00863-5

R Core Team (2022) R: A Language and Environment for Statistical

Damon A (2000) A review of the biology and control of the coffee berry borer, *Hypothenemus hampei* (Coleoptera: Scolytidae. Bull Entomol Res 90:453–465. https://doi.org/10.1017/S0007485300000584

de Oliveira CC, Manfrin MH, de Sene F M, et al (2011) Variations on a theme: diversification of cuticular hydrocarbons in a clade of cactophilic *Drosophila*. BMC Evol Biol 11:179. https://doi.org/10.1186/1471-2148-11-179

Dembeck LM, Böröczky K, Huang W et al (2015) Genetic architecture of natural variation in cuticular hydrocarbon composition in *Drosophila melanogaster*. Elife 4:e09861. https://doi.org/10.7554/eLife.09861

Dias BA, Neves PMOJ, Furlaneto-Maia L, Furlaneto MC (2008) Cuticle-Degrading proteases produced by the entomopathogenic fungus *Beauveria Bassiana* in the presence of coffee berry borer cuticle. Brazilian J Microbiol 39:301–306. https://doi.org/10.1590/S1517-838220080002000019

Duarte BF, Michelutti KB, Antonialli-Junior WF, Cardoso CAL (2019) Effect of temperature on survival and cuticular composition of three different ant species. J Therm Biol 80:178–189. https://doi.org/10.1016/j.jtherbio.2019.02.005

Ernst WHO, Decelle JE, Tolsma DJ, Verweij RA (1990) Lifecycle of the bruchid beetle *Bruchidius Uberatus* and its predation of *Acacia nilotica* seeds in a tree savanna in Botswana. Entomol Exp Appl 57:177–190. https://doi.org/10.1111/j.1570-7458.1990.tb01429.x

Errbii M, Myrie A, Robinson D, Schultner E, Schrader L, Oettler J (2024) Genetic

Etges WJ, de Oliveira CC, Rajpurohit S, Gibbs AG (2017) Effects of temperature on transcriptome and cuticular hydrocarbon expression in ecologically differentiated populations of desert *Drosophila*. Ecol Evol 7:619–637. https://doi.org/10.1002/ece3.2653

Fang J-X, Chen D-F, Shi X et al (2023) Solid-phase Microextraction and Cuticular

Fedina TY, Kuo T-H, Dreisewerd K et al (2012) Dietary effects on cuticular hydrocarbons and sexual attractiveness in *Drosophila*. PLoS ONE 7:e49799. https://doi.org/10.1371/journal.pone.0049799

Fondo Regional de Tecnología Agropecuaria (2019) Management and Control of Coffee Berry Borer in Robusta Coffee in Central America. In: FONTAGRO. https://www.fontagro.org/en/blog/control-y-manejo-de-la-broca-en-cafe-robusta-en-centroamerica/. Accessed 18 Sep 2023

Frentiu FD, Chenoweth SF (2010) Clines in cuticular hydrocarbons in two *Drosophila* species with independent population histories: cuticular hydrocarbon clines in two *Drosophila* species. Evolution 64:1784–1794. https://doi.org/10.1111/j.1558-5646.2009.00936.x

Geib SM, Filley TR, Hatcher PG et al (2008) Lignin degradation in Wood-Feeding insects. Proc Natl Acad Sci United States Am 105:12932–12937. https://doi.org/10.1073/pnas.0805257105

Geiselhardt S, Otte T, Hilker M (2012) Looking for a similar partner: host plants shape mating preferences of herbivorous insects by altering their contact pheromones. Ecol Lett 15:971–977. https://doi.org/10.1111/j.1461-0248.2012.01816.x

Gibbs A, JG Pomonis P (1995) Physical properties of insect cuticular hydrocarbons: the effects of chain length, Methyl-Branching and unsaturation. https://doi.org/10.1016/0305-0491(95)00081-X

Gibbs AG, Rajpurohit S (2010) Cuticular lipids and water balance. In: Bagnères A-G, Blomquist GJ (eds) Insect hydrocarbons: biology, biochemistry, and chemical ecology. Cambridge University Press, Cambridge, pp 100–120

Gil ZN, Benavides P, De Souza O et al (2015) Molecular markers as A method to evaluate the movement of *Hypothenemus hampei* (Ferrari). J Insect Sci 15:72. https://doi.org/10.1093/jisesa/iev058

Haack RA (2006) Exotic bark- and wood-boring Coleoptera in the united states: recent establishments and interceptions. Can J for Res 36:269–28836. https://doi.org/10.1139/x05-249

Haack RA, Hérard F, Sun J, Turgeon JJ (2010) Managing invasive populations of Asian longhorned beetle and Citrus longhorned beetle: A worldwide perspective. Ann Rev Entomol 55:521–546. https://doi.org/10.1146/annurev-ento-112408-085427

Hadley NF (1977) Epicuticular lipids of the desert tenebrionid beetle, *Eleodes armata*: seasonal and acclimatory effects on composition. Insect Biochem 7:277–283. https://doi.org/10.1016/0020-1790(77)90025-7

Hargreaves H (1926) Notes on the coffee Berry-Borer (*Stephanoderes hampei*, Ferr.) in Uganda. Bull Entomol Res 16:347–354. https://doi.org/10.1017/S0007485300028637

Holze H, Schrader L, Buellesbach J (2021) Advances in Deciphering the genetic basis of insect cuticular hydrocarbon biosynthesis and variation. Heredity 126:219–234. https://doi.org/10.1038/s41437-020-00380-y

Howard RW, Blomquist GJ (2005) Ecological, behavioral, and biochemical aspects of insect hydrocarbons. Ann Rev Entomol 50:371–393. https://doi.org/10.1146/annurev.ento.50.071803.130359

Howard RW, Infante F (1996) Cuticular hydrocarbons of the host-Specific ectoparasitoid *Cephalonomia Stephanoderis* (Hymenoptera: Bethylidae) and its host the coffee berry borer (Coleoptera: Scolytidae). Ann Entomol Soc Am 89:700–709. https://doi.org/10.1093/aesa/89.5.700

Howard RW, Howard CD, Colquhoun S (1995) Ontogenetic and environmentally induced changes in cuticular hydrocarbons of *Oryzaephilus surinamensis* (Coleoptera: Cucujidae). Ann Entomol Soc Am 88:485–495. https://doi.org/10.1093/aesa/88.4.485

Hulcr J, Atkinson T, Cognato A et al (2015) Morphology, Taxonomy and Phylogenetics of Bark Beetles. pp 41–84

"Hydrocarbon Differences Related to Reproductive Activity in Juniper bark borer *Semanotus bifasciatus* Motschulsky. J Syst Evol 61:498–505. https://doi.org/10.1111/jse.12947

Johnson MA, Ruiz-Diaz CP, Manoukis NC, Verle Rodrigues JC (2020) Coffee berry borer (*Hypothenemus hampei*), a global pest of coffee: perspectives from historical and recent invasions, and future priorities. Insects 11:882. https://doi.org/10.3390/insects11120882

Kerr J, Romo C, O'Connor B et al (2024) Exploring the nature of *Arhopalus ferus* (Coleoptera: cerambycidae: Spondylidinae) pheromone attraction. J Chem Ecol. https://doi.org/10.1007/s10886-024-01508-8

Krapf P, Arthofer W, Ayasse M et al (2023) Global change May make Hostile - Higher ambient temperature and nitrogen availability increase ant aggression. Sci Total Environ 861:160443. https://doi.org/10.1016/j.scitotenv.2022.160443

Kühbandner S, Hacker K, Niedermayer S et al (2012) Composition of cuticular lipids in the pteromalid Wasp *Lariophagus distinguendus* is host dependent. Bull Entomol Res 102:610–617. https://doi.org/10.1017/S000748531200017X

Lancashire RJ (1995) Jamaican Coffee - The Finest In The World! http://wwwchem.uwimona.edu.jm/lectures/coffee.html. Accessed 13 Dec 2023

Le Pelley RH (1973) Coffee insects. Ann Rev Entomol 18:121–142. https://doi.org/10.1146/annurev.en.18.010173.001005

Maihoff F, Sahler S, Schoger S et al (2023) Cuticular hydrocarbons of alpine bumble bees (Hymenoptera: *Bombus*) are Species-Specific, but show little evidence of Elevation-Related climate adaptation. Front Ecol Evol 11

Martin SJ, Helanterä H, Drijfhout FP (2008) Evolution of Species-Specific cuticular hydrocarbon patterns in Formica ants: evolution of ant cuticular hydrocarbons. Biol J Linn Soc 95:131–140. https://doi.org/10.1111/j.1095-8312.2008.01038.x

McKenna DD, Shin S, Ahrens D et al (2019) The Evolution and Genomic Basis of Beetle Diversity. Proceedings of the National Academy of Sciences 116:24729–24737. https://doi.org/10.1073/pnas.1909655116

Melet A, Leibold V, Schmitt T, Biedermann PHW (2024) Highly diverse cuticular hydrocarbon profiles but no evidence for aggression towards Non-Kin in the Ambrosia beetle *Xyleborinus saxesenii*. Ecol Evol 14:e11274. https://doi.org/10.1002/ece3.11274

Menzel F, Blaimer BB, Schmitt T (2017) How Do Cuticular Hydrocarbons Evolve? Physiological Constraints and Climatic and Biotic Selection Pressures Act On A Complex Functional Trait. Proceedings of the Royal Society B: Biological Sciences 284:20161727. https://doi.org/10.1098/rspb.2016.1727

Menzel F, Zumbusch M, Feldmeyer B (2018) How ants acclimate: impact of Climatic conditions on the cuticular hydrocarbon profile. Funct Ecol 32:657–666. https://doi.org/10.1111/1365-2435.13008

Myrie A, Hall T, Luke D et al (2023) Coffee berry borer, *Hypothenemus hampei* (Ferrari) (Coleoptera: Curculionidae): Activity and Infestation in the High Mountain and Blue Mountain Regions of Jamaica. Insects 14:694. https://doi.org/10.3390/insects14080694

Navarro-Escalante L, Hernandez-Hernandez EM, Nuñez J et al (2021) A coffee berry borer (*Hypothenemus hampei*) genome assembly reveals a reduced chemosensory receptor gene repertoire and Male-Specific genome sequences. Sci Rep 11:4900. https://doi.org/10.1038/s41598-021-84068-1

Otte T, Hilker M, Geiselhardt S (2015) The effect of dietary fatty acids on the cuticular hydrocarbon phenotype of an herbivorous insect and consequences for mate recognition. J Chem Ecol 41:32–43. https://doi.org/10.1007/s10886-014-0535-9

Otte T, Hilker M, Geiselhardt S (2018) Phenotypic plasticity of cuticular hydrocarbon profiles in insects. J Chem Ecol 44:235–247. https://doi.org/10.1007/s10886-018-0934-4

Page M, Nelson LJ, Haverty MI, Blomquist GJ (1990a) Cuticular hydrocarbons as chemotaxonomic characters for bark beetles: Dendroctonus ponderosae, D. jeffreyi, D. brevicomis, and D. frontalis (Coleoptera: Scolytidae). Ann Entomol Soc Am 83:892–901. https://doi.org/10.1093/aesa/83.5.892

Page M, Nelson LJ, Haverty MI, Blomquist GJ (1990b) Cuticular hydrocarbons of eight species of North American cone beetles, *Conophthorus Hopkins*. J Chem Ecol 16:1173–1198. https://doi.org/10.1007/BF01021018

Page M, Nelson LJ, Blomquist GJ, Seybold SJ (1997) Cuticular hydrocarbons as chemotaxonomic characters of pine engraver beetles (*Ips spp.*) in the grandicollis subgeneric group. J Chem Ecol 23:1053–1099. https://doi.org/10.1023/B:JOEC.0000006388.92425.ec

Puillandre N, Dupas S, Dangles O et al (2008) Genetic bottleneck in invasive species: the potato tuber moth adds to the list. Biol Invasions 10:319–333. https://doi.org/10.1007/s10530-007-9132-y

Reid JC (1983) Distribution of the coffee berry borer *(Hypothenemus hampei)* within jamaica, following its discovery in 1978. Trop Pest Manage 29:224–230. https://doi.org/10.1080/09670878309370806

Rhodes LF, Mansingh A (1986) Distribution of the coffee berry borer *Hypothenemus hampei* ferr. In jamaica, and an assessment of the chemical control programme (1979–1982). Int J Trop Insect Sci 7:505–510. https://doi.org/10.1017/S1742758400009735

Rouault J-D, Marican C, Wicker-Thomas C, Jallon J-M (2004) Relations between cuticular hydrocarbon (HC) polymorphism, resistance against desiccation and breeding temperature; A model for HC evolution in *D. melanogaster* and *D. simulans*. Genetica 120:195–212. https://doi.org/10.1023/b:gene.0000017641.75820.49

Ruane AC, Cecil LD, Horton RM et al (2013) Climate change impact uncertainties for maize in panama: farm information, climate projections, and yield sensitivities. Agric for Meteorol 170:132–145. https://doi.org/10.1016/j.agrformet.2011.10.015

Santos Murgas A, Añino Ramos YJ, Gómez De Huertas IY (2017) Primer Registro de *Celidophylla Albimacula* Saussure y Pictet, 1898 (Orthoptera: Tettigoniidae) en Panamá. Insecta Mundi 1–4

Schmack JM, Brenton-Rule EC, Veldtman R et al (2019) Lack of genetic structuring, low effective population sizes and major bottlenecks characterise common and German wasps in new Zealand. Biol Invasions 21:3185–3201. https://doi.org/10.1007/s10530-019-02039-0

Schmid-Hempel P, Schmid-Hempel R, Brunner PC et al (2007) Invasion success of the bumblebee, *Bombus terrestris*, despite a drastic genetic bottleneck. Heredity 99:414–422. https://doi.org/10.1038/sj.hdy.6801017

Soares ERP, Batista NR, Souza R da S, et al (2017) Variation of cuticular chemical compounds in three species of *Mischocyttarus*

(Hymenoptera: Vespidae) eusocial wasps. Revista Brasileira De Entomol 61:224–231. https://doi.org/10.1016/j.rbe.2017.05.001

Sprenger PP, Menzel F (2020) Cuticular hydrocarbons in ants (Hymenoptera: Formicidae) and other insects: how and why they differ among individuals, colonies, and species. Mymecological News 30:1–26. https://doi.org/10.25849/MYRMECOL.NEWS_030:001

Stanley-Samuelson D, Nelson D (1993) Insect Lipids: Chemistry, Biochemistry, and Biology

Steiger S, Peschke K, Francke W, Müller JK (2007) The Smell of Parents: Breeding Status Influences Cuticular Hydrocarbon Pattern in the Burying Beetle *Nicrophorus vespilloides*. Proceedings. Biological Sciences 274:2211–2220. https://doi.org/10.1098/rspb.2007.0656

Stinziano JR, Sové RJ, Rundle HD, Sinclair BJ (2015) Rapid desiccation hardening changes the cuticular hydrocarbon profile of *Drosophila melanogaster*. Comparative biochemistry and physiology. Part A. Mol Integr Physiol 180:38–42. https://doi.org/10.1016/j.cbpa.2014.11.004

Tsutsui ND, Suarez AV, Holway DA, Case TJ (2000) Reduced Genetic Variation and the Success of an Invasive Species. Proceedings of the National Academy of Sciences 97:5948–5953. https://doi.org/10.1073/pnas.100110397

Tutin CEG, Fernandez M (1993) Relationships between minimum temperature and fruit production in some tropical forest trees in Gabon. J Trop Ecol 9:241–248. https://doi.org/10.1017/S0266467400007239

Variation in Jamaican Populations of the Coffee Berry Borer Hypothenemus hampei. Genome Biol Evol 16:evae217. https://doi.org/10.1093/gbe/evae217

Vega FE, Kramer M, Jaramillo J (2011) Increasing coffee berry borer (Coleoptera: curculionidae: Scolytinae) female density in artificial diet decreases fecundity. J Econ Entomol 104:87–93. https://doi.org/10.1603/ec10353

Vega FE, Smith LT, Davies NMJ et al (2019) Elucidation of hosts, native distribution, and habitat of the coffee berry borer (*Hypothenemus hampei*) using herbaria and other museum collections. Front Plant Sci 10:1188. https://doi.org/10.3389/fpls.2019.01188

Wagner D, Tissot M, Gordon D (2001) Task-Related environment alters the cuticular hydrocarbon composition of harvester ants. J Chem Ecol 27:1805–1819. https://doi.org/10.1023/A:1010408725464

Walsh J, Pontieri L, d'Ettorre P, Linksvayer TA (2020) Ant cuticular hydrocarbons are heritable and associated with variation in colony productivity. Proc Royal Soc B: Biol Sci 287:20201029. https://doi.org/10.1098/rspb.2020.1029

Zhang A, Oliver J, Chauhan K et al (2003) Evidence for contact sex recognition pheromone of the Asian longhorned beetle, *Anoplophora glabripennis* (Coleoptera: Cerambycidae). Z Für Didaktik Der Naturwissenschaften 90:410–413