

A Spatio-Temporally Distinct Chemical Landscape in a Mango Orchard with High *Fopius arisanus* Parasitism

David Arzac

CIRAD, Université de la Réunion, UMR PVBMT

Laura Moquet

CIRAD, Université de la Réunion, UMR PVBMT

Hélène Delatte

CIRAD, Université de la Réunion, UMR PVBMT

Marie-Ludders Moutoussamy

CIRAD, Université de la Réunion, UMR PVBMT

Vincent Jacob

vincent.jacob@cirad.fr

CIRAD, Université de la Réunion, UMR PVBMT

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Abstract

Insects locate suitable oviposition sites by detecting odor cues emitted by their hosts, while navigating a broader field of volatile compounds, an odor landscape that structures their environment. Yet, the influence of background volatiles on insect activity and host searching success remains poorly understood under the complexity of natural conditions. Here, we investigate spatial and seasonal variation in background volatiles which may contribute to parasitoid field activity, together with other biotic and abiotic factors. We combined spatiotemporal parasitism monitoring of parasitism by *Fopius arisanus*, a key biological control agent of the fruit fly *Bactrocera dorsalis*, with VOC profiling of ambient air across mango cultivation sites. Parasitism intensity varied markedly across orchards and seasons and was associated with distinct compound profiles that deviated from the generic mango orchard volatile signature. Higher parasitism was linked to a greater abundance of certain volatiles, such as 3-carene and hexanal, and a lower abundance of others, such as 4-penten-1-ol and methyl salicylate. These compounds reflect underlying plant and habitat conditions and may contribute to either attraction or avoidance by the parasitoid, warranting further experimental validation. Our study highlights how parasitoid activity is embedded within the surrounding odor landscape at the field scale. This perspective expands the view of insect foraging from pairwise interactions to complex environmental odor backgrounds, providing an original framework to guide the discovery of semiochemicals for improved control strategies.

INTRODUCTION

Insects rely on a variety of sensory cues to locate their resources. While visual and mechanical cues contribute to this process (Cornelius et al. 1999; Quilici and Rousse 2012; Kerr et al. 2017), chemical signals, particularly volatile organic compounds (VOCs), are pivotal in guiding insects during the search for food or hosts. Beyond the cues directly associated with the host, the volatile cues associated with the surrounding habitat, referred to here as “background odor”, can significantly influence the insect's host-searching behavior (Webster and Cardé 2017). The presence of background odor has been demonstrated, in some cases, to mask the resource-indicating cues, thereby reducing the response to attractants. In other cases, it has been shown to enhance the insect's response to cues indicating the presence or suitability of resources (Schröder and Hilker 2008). For example, VOCs emitted by plants, either constitutively or in response to herbivory (herbivory-induced plant volatiles), can attract or repel parasitoids (Turlings and Erb 2018). These background odors differ across habitats and seasons, potentially modulating the pressure insects exert on their hosts. Understanding how these environmental factors shape host-searching behavior is crucial for ecological studies and applications such as biological control.

The success of a parasitoid's host-searching behavior depends on its ability to efficiently locate hosts within complex environments (Godfray 1994). This process involves a series of steps, starting with habitat location, followed by host detection, probing, and exploitation (Vinson 1976; Cornelius et al. 1999). VOCs are emitted by various sources, including hosts, host plants, and non-host plants, forming a

complex volatile chemical landscape. The subset of these volatiles that are detected by an insect defines its olfactory landscape. While laboratory studies have identified key compounds influencing the behavior of some parasitoids (Conchou et al. 2019), field-level investigations into olfactory landscapes remain limited. In particular, the contribution of background volatile compounds to the heterogeneity of insect activity under field conditions remains underexplored.

We addressed this question in the model system of *Bactrocera dorsalis* (Hendel, 1912) and its parasitoid *Fopius arisanus* (Sonan, 1932). *Bactrocera dorsalis* is a highly polyphagous pest of major economic importance, reported in 75 countries (Zeng et al. 2019). It was first detected on La Réunion in 2017 (Moquet et al. 2021), where it has become a significant concern for local agriculture. *Fopius arisanus*, a solitary egg-pupal parasitoid, was introduced to La Réunion in 2003 to control *Bactrocera zonata* (Quilici et al. 2005). While the average parasitism rate of *F. arisanus* was only 5% before 2017, it increased to 17% with the arrival of *B. dorsalis* (Moquet et al. 2023). However, this rate remains lower than those observed elsewhere (Van den Bosch and Haramoto 1951; Vargas et al. 2002, 2012). Environmental factors might contribute to this disparity. Examining the interplay between habitat odors and parasitic activity could provide valuable insights into the underlying mechanisms.

The objective of this study was to characterize the specificity of volatile chemical landscapes in mango orchards (*Mangifera indica*) that are favorable to the parasitic activity of *F. arisanus*. To this end, parasitic activity was monitored through a sentinel trap setup, while environmental air was simultaneously sampled across four orchards at different phenological stages using Tenax absorbents analyzed by gas chromatography-mass spectrometry (GC-MS). By exploring the temporal (seasonal and intra-seasonal) and spatial (inter- and intra-orchard) variability of both *F. arisanus* activity and ambient air composition, we aimed to identify volatile compounds potentially associated with parasitoid activity. We prioritized intensive within-orchard sampling to obtain robust and consistent volatile profiles, which limited the number of orchards included and precluded robust site-level statistical correlations. Moreover, parasitic activity at this scale is influenced by multiple confounding factors affecting population dynamics. Nevertheless, this approach provides a set of candidate compounds potentially associated with *F. arisanus* activity and lays the groundwork for future hypothesis-driven investigations.

METHODS AND MATERIALS

Sampling Sites. The experiments were conducted in four orchards, on plots of José mango (a local variety) located in the western part of the Island of La Réunion, specifically in the Grand Fond area of Saint Paul known for its hot and dry climate. In this area, the space dedicated to cultivation is approximately 500 ha, including 150 ha of mango orchards with an average size of 6.1 ha (Vincenot et al. 2009). The area is bounded to the north by a savanna mainly composed of *Heteropogon contortus* and *Leucaena leucocephala* (Robert 2018), to the southwest by a residential zone, to the southeast by a ravine, and to the east by a road. Most of the plots are interspersed with windbreak hedges, and the main wooded areas are primarily composed of *Lantana camara*, *Dichrostachys cinerea*, *L. leucocephala*, *Vachellia farnesiana*, *Ehretia cymosa*, and *Pithecellobium dulce* (Vincenot et al. 2009).

The orchards were selected from a group of farmers whose pest management practices were recently characterized (Moquet et al. 2026). None of the selected farmers used pesticides during the fruiting season, although moderate pesticide use may have occurred during other periods of the year. Trapping systems targeting *B. dorsalis* were occasionally used, while fallen fruits were generally removed from the ground, including small immature fruits in some orchards. The first orchard (O1) consists of a large mango plantation (> 30 hectares), the second (O2) consists of a small plantation (3–5 hectares), and the third and fourth orchards (O3 and O4) have medium-size plantations (approximately 10 hectares). A fifth orchard (O5) was selected for the final sampling period to replace the first orchard (O1), which had become unusable due to an accidental fire. O5 was chosen because its size and treatment practices closely matched those of O1.

The experiments were conducted over four periods: the leafing period (June–July) when the trees bore few or no flowers or fruits, the flowering period (August), the early fruiting period (September), and the mature fruit period, corresponding to the beginning of the harvest (November). For each period, parasitism activity and VOCs in environmental air were measured once a week for three consecutive weeks. These measurements were conducted almost simultaneously within each orchard and across the four orchards, though with some temporal offset due to the different durations of the two measurements (4h vs. 24h) and a time delay of less than one hour caused by mobility between sites. During each sampling, a detailed description of the plant composition within a 25-meter radius of each orchard was recorded. The state (absence/presence, height) of the grass vegetation cover of each orchard was recorded at each sampling. At the same time, phenological monitoring, as well as assessments of fruit presence and quantity in the orchards, were carried out at each sampling date. In each orchard, 10 mango trees were randomly selected and monitored throughout the four seasons. During each visit, the phenological stage (leaf development, flowering, small fruits, mature fruits) was recorded. When fruits were present, a score for fruit density ranging from 0 to 4 was assigned to each selected tree. These scores correspond to: 0: no fruit; 1: few fruits; 2: moderately abundant; 3: abundant; 4: very abundant.

Parasitism Activity. For the estimation of parasitic activity, eggs of *B. dorsalis* laid in bananas (*Musa* sp.) were used as sentinel eggs. The bananas were covered with aluminium foil up to about 3 cm from the end, leaving only one part accessible. Then, the fruits were placed for 45 minutes in cages of 30 cm³ containing approximately 500 mature individuals of *B. dorsalis* to allow females to lay their eggs.

On the same day, the infested fruits were placed on different trees at heights between 1 and 2 meters, depending on the size of the tree in the experimental orchards (O1 to O5). Five bananas were placed in each of the selected orchards for 24 hours. The experiments were conducted so that the end of the 24-hour period coincided with the end of the 4-hour long VOC sampling period. Subsequently, bananas were brought back to the lab, and 100 eggs per banana were collected to estimate the percentage of parasitized eggs. This was done by using dechoriation treatment following a modified protocol based on the works of Moretti and Calvitti (2003), and Rousse et al. (2006). Specifically, eggs were rinsed for 2 min with a 2.6% NaClO solution, then rinsed with clear water, and finally observed under a magnifying

glass at 4x magnification in a drop of mineral oil. The first rinsing induced a dechoriation of the eggs, making them translucent and facilitating the observation of potential *F. arisanus* eggs inside. The second rinsing prevented further degradation of the eggs. The percentage of parasitized eggs was calculated as the number of parasitized eggs over the total number of counted eggs x100. The proportion of parasitized bananas was calculated as the number of bananas in which at least one parasitized *B. dorsalis* egg was found divided by the total number of bananas.

For the last sampling season during the mature fruit period, 15 ripe mangoes (on the ground and/or on the tree) were sampled per orchard, when possible, in order to assess *F. arisanus* parasitism rate on mango. The fruits were weighed in the laboratory, then placed in a plastic box containing a sand substrate for pupation ($25^{\circ}\text{C} \pm 2^{\circ}\text{C}$ and $70 \pm 20\%$ humidity). The sand was sifted several times to collect the pupae, and these were kept until emergence and identification as described in Moquet et al. (2023). The parasitism rate was calculated as the number of emerging *Fopius arisanus* divided by the number of emerging individuals (Fruits flies + parasitoids).

Volatile Compound Sampling. Thirty-two samplings of environmental air were collected simultaneously on pre-conditioned Tenax GR tubes (size: 88.9 x 6.35 mm; pre-conditioned one day before the sampling: 250°C for 10 minutes with a helium flow of 100 mL/min), eight per orchard. Two sampling tubes, forming a pair, were connected to a single pump (PAS-500, Spectrex) through a Y-shaped connector and spaced one meter apart. Air flow was calibrated at 175 ml/min per tube. For each orchard, two pairs of tubes were disposed at mid-distance between the trees, 2–3 meters apart depending on the orchard, and were mounted on a rod 1.5 meters above the ground. There was also a distance of 2 to 3 meters between the trees and these pumps. Two other pairs were fixed to the mango tree foliage, one meter above the ground, one to two meters apart, depending on the size of the tree. The sampling lasted four hours, and started between 8 am and 9 am (time-delay due to moving between the orchards). Two additional tubes transported with the 32 other ones, but not connected to any pumps, served as control for residual contaminations.

As a summary, the dataset included 384 samples, which resulted from a combination of 8 samples collected per orchard * 4 orchards * 3 sampling date per period * 4 periods.

Gas Chromatography - Mass Spectrometry. The samples were desorbed using a thermal desorber (Turbomatrix ATD 350 by Perkin Elmer) in splitless mode and analyzed with gas chromatography coupled with mass spectrometry (Clarus SQ 8T by Perkin Elmer). An Elite-5ms column measuring 60m x 0.25mm in diameter was used for compound separation. The program used started at 50°C for 1.5 minutes, then increased from 50°C to 150°C at $4^{\circ}\text{C}/\text{min}$, from 150°C to 250°C at $12^{\circ}\text{C}/\text{min}$, and finally held at 250°C for 8 minutes. Helium was used as the carrier gas, with a continuous flow rate of 2 mL/min in the column, and an injection flow rate of 50 mL/min. The mass spectrometer operated in electron impact (EI) mode at 70 eV. The transfer line temperature was set to 250°C . Spectra were acquired in full-scan mode over a mass range of m/z 50–300, at a scan rate of 2 scans per second, and recorded in

centroid mode. Each sample was briefly inspected to verify signal quality. Some samples showed no detectable signal or obvious oversaturation and were excluded from further analyses.

Data Analysis. Parasitism activity was compared across the four phenological periods and across the four orchards during the mature fruit period using analyses of variance (ANOVA). For significant assays, pairwise analysis was performed with a Tukey's tests. All Data analysis was performed using RStudio (RStudio Team 2023) and R (version 4.3.1).

GC-MS data were compiled using MZMine 3.9.0 (Schmid et al. 2023). The ADAP Chromatogram Builder and ADAP Resolver modules (Myers et al. 2017) were used for feature detection. The Hierarchical Clustering method was used for deconvolution and the ADAP Aligner (GC) module based on retention time was employed for list alignment. Finally, the Gap Filling module was used to detect signals that may have been lost during previous processing steps. The separated compounds were tentatively identified based on comparison of both their mass spectra and retention indices (RI) to library databases (NIST 2020 and Wiley 8th Edition). The RIs were calculated from C6 to C20 alkanes eluted under the same conditions as the samples.

For statistical analyses of the GC-MS data, peak heights were divided by the geometric mean within each sample and then Box-Cox transformed. Data were processed using Partial Least Squares Discriminant Analysis (PLS-DA) based on phenological periods and also based on orchards. In parallel, for each PLS-DA analysis, a Permutational Multivariate Analysis of Variance (PERMANOVA) was performed using the "Bray-Curtis" method to assess whether phenological periods and orchards had a significant effect. Additionally, the effects of sampling weeks and sampling configurations were also evaluated. The Variable Importance in Projection scores (VIP scores) were used to assess the importance of each compound in the PLS-DA: either comparing volatile profiles between periods (VIP_{period}) or between orchards during the mature fruit period (VIP_{orchard}).

RESULTS

Parasitism activity and analysis of VOCs in the ambient air within an orchard were studied over four orchards at 12 sampling dates grouped by four periods. The phenology of mango trees, the density of fruits, and the plant composition around each sampling site varied temporally and spatially (Figure S1; Table S1).. The four periods were labeled as "leafing, flowering, small fruit, and mature fruit", in respect with the main phenological state of the mango trees, although low densities of flowers or fruits were observed occasionally in all periods.

Temporal Variability of Field Assessed Parasitism Activity. Sentinel *B. dorsalis* eggs parasitized by wild *F. arisanus* were observed in all four periods tested at different levels (Fig. 1). The percentage of eggs parasitized varied significantly according to phenological period (ANOVA, $F(3,218) = 16.5$, $p < 10^{-8}$), with significantly higher percentage of egg parasitized during the mature fruit period ($10 \pm 2\%$ of eggs parasitized, mean $\pm$ standard error) compared to the other three periods (Tukey, diff = 0.1, $p < 10^{-6}$). No

significant differences were observed among the other three periods corresponding to leafing, flowering, and small fruit phenology of mango trees ($0.2 \pm 0.07\%$ of eggs parasitized, mean $\pm$ standard error). Overall, the proportion of parasitized bananas differed significantly between the periods, with a higher proportion observed during the mature fruit period ($28 \pm 6\%$ of parasitized bananas) than the other three ($8 \pm 27\%$ of parasitized bananas, mean $\pm$ standard error).

Temporal Variability of Environmental VOCs in Mango Orchards. We did not find any difference in the volatile profiles of samples collected on the trees and between the trees (PerMANOVA $F(1,363) = 1.90$, $R^2 = 0.004$, $p > 0.05$), indicating a homogeneous distribution within orchards at a given time. We therefore studied the temporal variability across phenological periods. Some identified VOCs are consistently observed in similar proportions throughout all phenological periods. The most prevalent ones were benzoic acid, nonanal, 4-cyclopentene-1,3-diol, and o-cymene, among others (ANOVA; $p > 0.05$ in all cases). Still, the volatile profiles differed significantly between periods (Fig. 2, PerMANOVA $F(3,363) = 15.21$, $R^2 = 0.100$, $p < 0.001$). The VIP_{period} scores calculated from a PLS-DA revealed the compounds whose abundance differed the most between periods (Fig. 3). The top 20 identified compounds, ranked by decreasing VIP_{period} scores ($VIP_{\text{period}} > 1.27$), are : methyl salicylate, methyl benzoate, 4,6-dimethyldodecane, phthalic anhydride, 2-ethylhexanal, acetophenone, (E)-2-octen-1-ol, benzeneethanol, nonanol, methyl o-anisate, 3-carene, 2-ethyl-1-hexanol, 2-coumaranone, ethylbenzene, ethyl benzoate, decane, 1-decene, hexanal, benzothiazole, and (E)-2-decenol. For instance, an excess of 2-benzofuran-1,3-dione, (E)-2-octen-1-ol, ethyl benzene, benzeothiazole, nonanol and (E)-2-decenol was observed during the leafing period. For the flowering period, methyl salicylate, methyl benzoate, and methyl o-anisate were the most abundant compounds. During the small fruit stage, the compounds in excess were acetophenone, nonanol, and 3-carene. Finally, in the mature fruit stage, certain compounds, such as 3-carene and 2-ethylhexanal, were more abundant than during other periods. In contrast, acetophenone, 2-octen-1-ol, and 4-penten-1-ol, were less abundant during this period than in the others.

We also tested the temporal variability along the three weeks used within each period. There was a significant effect of the sampling week even within the sampling periods (PerMANOVA, leafing period: $F(2,87) = 6.78$, $R^2 = 0.13$, $P < 0.001$; flowering period: $F(2,87) = 7.17$, $R^2 = 0.14$, $P < 0.001$; small fruit period: $F(2,87) = 6.92$, $R^2 = 0.13$, $P < 0.001$; mature fruit period: $F(2,84) = 6.69$, $R^2 = 0.13$, $P < 0.001$). This pattern reflected a gradual transition in the volatile profiles toward those characterizing the subsequent phenological period.

Variability of Field Assessed Parasitism Activity between Orchards with Mature Fruits. During the mature fruit period, the percentage of parasitized eggs observed on bananas differed significantly among orchards (ANOVA, $F(3,56) = 330.96$, $p < 10^{-9}$), with the highest value in orchard O5 (Tukey, $p < 10^{-6}$). However, no significant differences were found among the other three orchards (Fig. 4a). A similar pattern was observed for naturally infested mangoes collected *in situ*. *B. dorsalis* adults emerged from 17 out of 37 fruits collected in orchard O2, 15 out of 33 in orchard O3, 1 out of 15 in orchard O4 and 3 out of 28 in orchard O5. The associated parasitism rate of *F. arisanus* varied between orchards (ANOVA,

$F(3,32) = 12.07$, $p < 10^{-5}$), with higher parasitism rate in orchard O5 (Tukey, $p < 10^{-6}$) and no significant differences between the other three orchards (Fig. 4b).

Variability of Environmental VOCs between Orchards with Mature Fruits. During the mature fruit period, we did not find any difference in the volatile profiles of samples collected on the trees and between the trees (PerMANOVA $F(1,84) = 1.15$, $R^2 = 0.01$, $p > 0.05$). However, the VOC composition significantly differed between the orchards (Fig. 5a, PerMANOVA $F(3,84) = 1.99$, $R^2 = 0.06$, $p < 0.001$). The VIP_{orchard} scores calculated from a PLS-DA revealed the compounds that differed the most between orchards in the mature fruit period (Fig. 5b, Figure S2). We observed a discontinuity in the distribution of these scores, with a gap separating a group of highly contributive compounds ($VIP_{\text{orchard}} > 1.27$, a threshold also used in the VIP_{period} analysis to highlight the top 20 identified compounds) from a cluster of lower-scoring compounds. In decreasing order of VIP_{orchard} , these high-contributing compounds include: Hexanal, 4-penten-1-ol, 3-carene, methyl salicylate, 5-pentyl-dihydro-2(3H)-furanone, 2,4-dimethyl-3-pentanol, 1-chlorohexane, ethylbenzene, *p*-xylene, undecanal, α -pinene, cyclohexanol, 1-ethyl-2-methylbenzene, decanal, 2-ethyl-1-hexanol, benzeneethanol, benzeneacetaldehyde, benzoic acid, phenol, nonane, and 5-ethyl-2(5H)-furanone. For instance, an excess of hexanal and 3-carene was observed in O5. In contrast, 4-penten-1-ol and methyl salicylate were less abundant in O5 compared to the other orchards.

Finally, comparison of VIP_{period} and VIP_{orchard} scores revealed that some compounds differed both among orchards and across phenological periods. However, a substantial proportion of the inter-orchard variation in volatile profiles was not associated with seasonal variation (figure S3).

DISCUSSION

In this study, we examined the temporal and spatial variation in *F. arisanus* activity and ambient VOC profiles across mango orchards. Our results show that both *F. arisanus* activity and VOC profiles vary across periods and among orchards. In particular, *F. arisanus* was more frequently observed in one orchard than in the others, and this orchard also differed from the others in the abundance of several volatile compounds. Thus, our study adds substance to the hypothesis that olfactory landscape modulates the efficiency of *F. arisanus*, a key parasitoid for the biological control of fruit fly pests, by identifying potential drivers of its activity. These observations call for further investigation to determine whether and which of these compounds influence *F. arisanus* behavior and activity, and how they do so.

Our methodological choices proved appropriate for addressing our research question for two main reasons. On the one hand, assessing parasitism activity using a sentinel system, banana fruits artificially infested with *B. dorsalis* eggs and available all year round, enabled consistent monitoring across seasons, independently of host availability. Although banana emit different volatile compounds than mangoes, the parasitism rates observed on them closely matched those observed on naturally infested mangoes, as assessed when the latter were available within the orchards. This suggests that our measure serves as a reliable proxy of local parasitic pressure, regardless of host-specific volatile emissions. On the other hand, in addition to inter-orchard variability, a significant intra-orchard sampling

effort was also carried out. The variability in volatile chemical profiles between samples collected within the same orchard, whether on or between the trees, was low compared to the variability between orchards and sampling weeks. This lack of obvious spatial structure within orchards suggests that the four-hour air sampling protocol effectively filtered out spatio-temporal heterogeneity in compound distribution (Celani et al. 2014; Jacob et al. 2017), allowing us to capture a specific feature: the average chemical composition at the orchard scale.

The observed variability of parasitoid activity can be explained by multiple factors. Measured parasitism peaked during the mature fruit period of mango trees, which coincided with the warm season. Through an effect on developmental time (Groth et al. 2017; Nanga Nanga et al. 2021), temperature plays a crucial role in the population dynamics of both Tephritidae and *F. arisanus* (Rousse et al. 2009). In addition, population dynamics is coupled with the dynamic of resource availability. Previous studies have shown that fruit phenological stage and maturation significantly influence oviposition preferences, infestation rates, and the development of Tephritidae (Messina and Jones 1990; Diatta et al. 2013; Bisognin et al. 2015). Consequently, the mature fruit period likely provides increased host availability for *F. arisanus*, thereby promoting population growth and, in turn, increasing parasitoid activity.

During the mature fruit period, we observed notable differences in parasitic activity between orchards in close proximity (located just a few hundred meters away). *Bactrocera dorsalis* infestation was confirmed in all four orchards, indicating that host presence was not limiting during the sampling period. More specifically, the parasitic activity of *F. arisanus* was significantly higher in one of the studied orchards than in others. Although the use of insecticides or fungicides may alter the local abundance and efficacy of predatory insects and parasitoids (Farah et al. 2020; Cai et al. 2020; Mohapatra et al. 2020; Quandahor et al. 2024; Wan et al. 2025), such effects are considered unlikely in the present study, given the moderate phytosanitary management of selected orchards. In addition, plant protection products are prohibited during mature fruit season in La Réunion (Deguine et al. 2018). More likely, the observed differences reflect local conditions favoring the persistence and reproduction of *F. arisanus* populations (Messina and Jones 1990; Diatta et al. 2013; Bisognin et al. 2015). The orchard exhibiting the highest parasitism rate was at a more advanced stage of fruit maturation and showed a higher density of mango fruits than the other orchards, likely supporting higher local reproduction of both Tephritidae and, consequently *F. arisanus*. However, sustaining high parasitoid activity also requires that individuals remain within suitable orchards despite potential movement across the landscape. Although the dispersal capacities of *F. arisanus* have not been specifically quantified, hymenopteran parasitoids generally exhibit substantial dispersal abilities (Boivin 2001), often guided by habitat- and host-associated cues (Tentelier 2006; Lopes 2007). *Fopius arisanus* itself has been shown to efficiently locate its host (Quilici and Rousse 2012), suggesting an ability to track spatial and temporal changes in host distribution within orchard mosaics. Thus, despite asynchronous phenological fruit maturation across orchards, we conducted synchronous sampling to obtain a temporal snapshot of VOCs diversity likely to act as key chemical cues involved in *F. arisanus* habitat and host location, including VOCs directly emitted by fruits. An alternative protocol involving sampling orchards at a fixed phenological stage would not have been appropriate, as late-blooming orchards are also more heavily infested by

Tephritidae due to recruitment from early-blooming orchards. Under the hypothesis that VOCs support *F. arisanus* populations within orchards, the chemical specificity of the most highly parasitized orchard may reflect a volatile profile enhancing host-searching behavior at the landscape scale, through both attractive and deterrent effects on parasitoid activity.

Our investigations revealed a shared baseline in VOC composition across all studied orchards and periods. Compounds consistently detected in all the orchards and periods, such as benzoic acid, octanal, 4-cyclopentene-1,3-diol, and o-cymene, may contribute to the olfactory signature of mango orchards. In parallel, we observed the presence of *F. arisanus* in mango orchards in all seasons. This observation is consistent with other studies on fruit fly parasitoids, which report year-round presence with seasonal peaks (Schliserman et al. 2016). It could suggest that even if the period is not ideal for *F. arisanus*, the orchards remain somewhat attractive. This may imply that the chemical profile common to all seasons constitutes a host habitat permissive to wasp activity. Notably, the local mango cultivar 'José' is known for its multiple flowering cycles, as has also been reported for other varieties (Ramírez and Kallarackal 2015). Fruits, although few in number, were occasionally present on some trees outside the main fruiting season, potentially offering an alternative resource for both parasitoids and Tephritidae (Figure S1).

Despite this shared baseline, we observed significant differences in the abundance of some compounds between periods. For example, the mature fruit stage was characterized by high abundance of 3-carene and low abundance of acetophenone, 2-octen-1-ol, and 4-penten-1-ol. These compounds were already detected in emissions of some species of fruits (Guedes et al. 2004; Güler and Şekerli 2013). Especially, 3-carene has been reported in the emissions of different mango varieties (Xie et al. 2023; Miano et al. 2024). For the flowering period, methyl salicylate, methyl benzoate, and methyl o-anisate were the most abundant compounds. Methyl anisate, a derivative of methyl benzoate, and methyl o-anisate have been reported in various plants and is commonly associated with floral odor (Dudareva et al. 2000). Methyl salicylate has been reported in various studies on plant-emitted VOCs and plays an essential role in plant-to-plant communication and predator recruitment (Shulaev et al. 1997; James and Price 2004; Zhu and Park 2005; Leppik et al. 2014; Xu et al. 2024). It is typically emitted by plants under stress, particularly when damage is caused by herbivorous insects (Ament et al. 2010; Blande et al. 2010). The elevated levels of methyl salicylate observed during the flowering period might reflect seasonal biotic stress, potentially induced by insects that feed on plants outside the mature fruit period, such as Miridae or gall midges (Cecidomyiidae), which are known to attack mango flowers (Amouroux et al. 2014; Atiama et al. 2017).

Seasonal differences in VOC composition of environmental air could be also explained by abiotic factors. Environmental parameters such as light, humidity, and temperature play a significant role in biogenic compound emissions (Kalogridis et al. 2016; Madmony et al. 2018). For example, certain VOC groups, such as monoterpenes and isoprenes, are synthesized at increased rates under high temperatures to maintain photosynthetic processes (Guenther et al. 1995). Kalogridis et al. (2016) demonstrated seasonal variations in ambient isoprene emissions from white oak forests, and Madmony et al. (2018) showed that water stress could also trigger monoterpene emissions on *Picea abies*. Our

study identified several monoterpenes, including 3-carene, limonene, *p*-cymene, *o*-cymene, and α -pinene, which may also be responses to abiotic stress factors.

Moreover, each orchard exhibited a distinct chemical signature at the time of sampling, although only one was associated with high parasitoid activity. Multiple levels of stress combined with other biotic factors such as phenological stage and species composition can influence VOC emissions by plants (Bracho-Nunez et al. 2011). Phenological stages differed between orchards, and it can influence VOC emissions (Bracho-Nunez et al. 2011). Mango density also differed between orchards, which may affect the load of fruit-derived chemicals in the chemical landscape. Differences in the surrounding plant community (Table S1), may also have contributed to orchard-specific VOC profiles. These variations in VOC composition can be important cues for *F. arisanus* to recognize the most favorable periods for the hosts in specific habitat and can contribute to the higher abundance of the parasitoid in the studied orchards during the fruiting season.

Some compounds were more abundant in the orchard with high parasitic activity than in others. For example, hexanal and its derivatives are often associated with Green Leaf Volatiles (GLVs), which are emitted by plants in response to stress, including damage, pathogen infections, or herbivory (Engelberth and Engelberth 2020). Given its advanced state, the highly parasitized orchard may have been more susceptible to such stresses, particularly due to the presence of mature fruits, the high fruit density potentially attracting pests such as fruit flies, and damage from harvesting. The compound 3-carene, as previously mentioned, has been detected and identified as a VOC emitted by various mango varieties (Miano et al. 2024), so its abundance in this orchard could be due to the high mango density. In turn, it would increase the parasitism of banana, even though this fruit does not emit 3-carene (Facundo et al. 2013). Moreover, this high fruit density and the strong odor potentially associated with host fruits may make the area more attractive to fruit flies and its parasitoids (Aluja and Prokopy, 1993, Othim et al., 2019). Given the ability of *F. arisanus* to locate and track its host (Quilici and Rousse 2012), and considering the link between host and parasitoid population dynamics, our results appear consistent.

Conversely, some compounds appeared to be less abundant in the orchard with the highest parasitism rate compared to the others. One example is 4-penten-1-ol, which, along with some of its derivatives, has been reported in plants of the Brassicaceae family (Gruber et al. 2009; Lukić et al. 2023). Another example, methyl salicylate, is a case in itself, since our observation contrasts with previous studies suggesting that this compound attracts natural enemies of herbivores (Shulaev et al. 1997; James and Price 2004; Zhu and Park 2005; Leppik et al. 2014; Xu et al. 2024). However, the effect may not be universal, as shown in *Diadegma semiclausum* (Hellén) (Hymenoptera: Ichneumonidae) (Snoeren et al. 2010) and in some insect predators in strawberry crops (Lee 2010). In the case of the tri-trophic interaction among plants/Tephritid/*F. arisanus*, an attraction of the parasitoid to methyl salicylate may not have been selected since the pest has limited impact on the plant fitness (Clarke 2017) and the subsequent fruit degradation does not seem to induce the emission of stress-related volatile compounds (Niinemets et al. 2013; Miano et al. 2024).

To conclude, multiple interacting factors including VOC emissions, the presence of host tephritids and host fruits, microclimatic conditions, and agricultural practices- must be considered when interpreting the spatial and temporal patterns of *F. arisanus* activity observed in this study. Nevertheless, the emission of specific VOCs, such as 3-carene and GLVs, which increased during mango fruiting, may contribute to shaping a favorable olfactory landscape for *F. arisanus*. If these compounds coincide with high *B. dorsalis* abundance, they could participate in the attraction and retention of the parasitoid. Further research is needed to clarify the extent to which such VOCs mediate parasitoid recruitment in orchard ecosystems.

Declarations

Competing Interests -

The authors have no relevant financial or non-financial interests to disclose.

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Author Contribution

Author contributions - David Arzac: Investigation, Formal analysis, Writing – Original Draft. Laura Moquet, Hélène Delatte and Vincent Jacob: Conceptualization, Methodology, Supervision. Marie-Ludders Moutoussamy: Investigation. All authors: Writing - Review & Editing.

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Data Availability

Data availability - Data have been deposited in a long term repository and will be available upon publication

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Figures

Figure 1

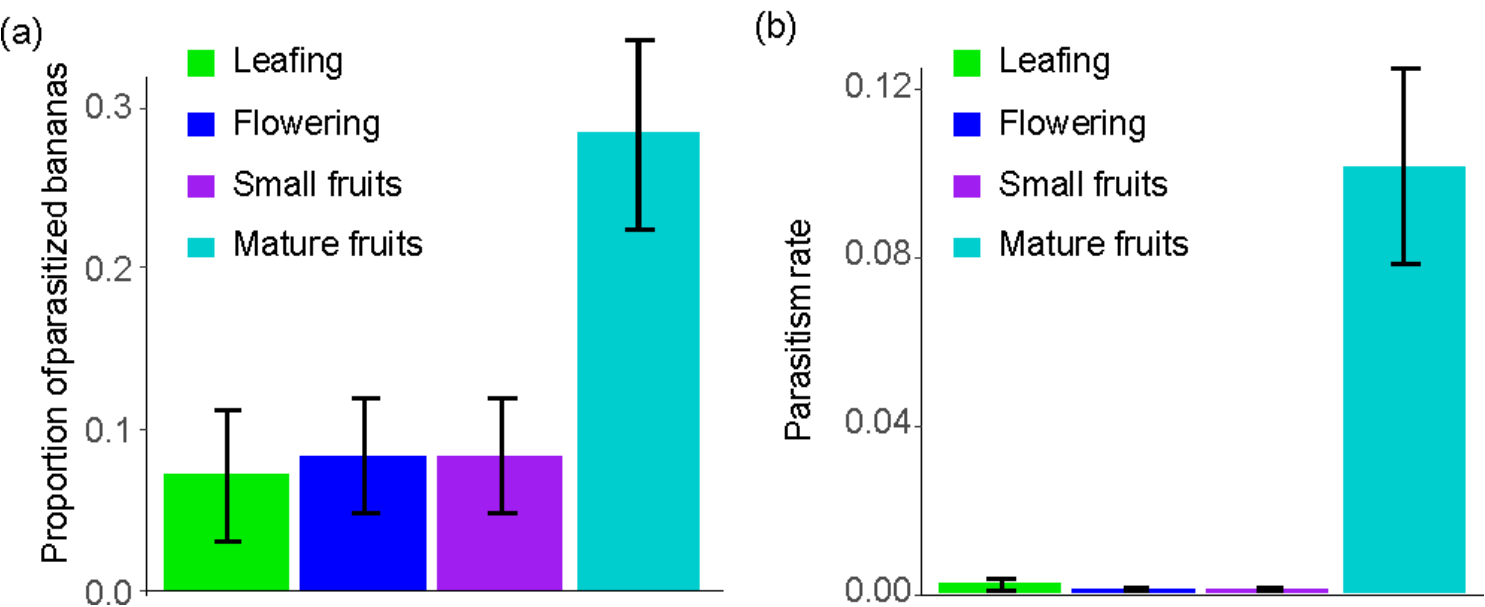


Figure 1

Assessment of *F. arisanus* parasitic activity across phenological periods. (a) Proportion of parasitized bananas across the four phenological periods. Each bar represents the mean and error bars the standard error, calculated across orchards and over three weekly sampling sessions (n= 60 bananas per period). (b) Percentage of parasitized eggs per banana; same conventions as in (a).

Figure 2

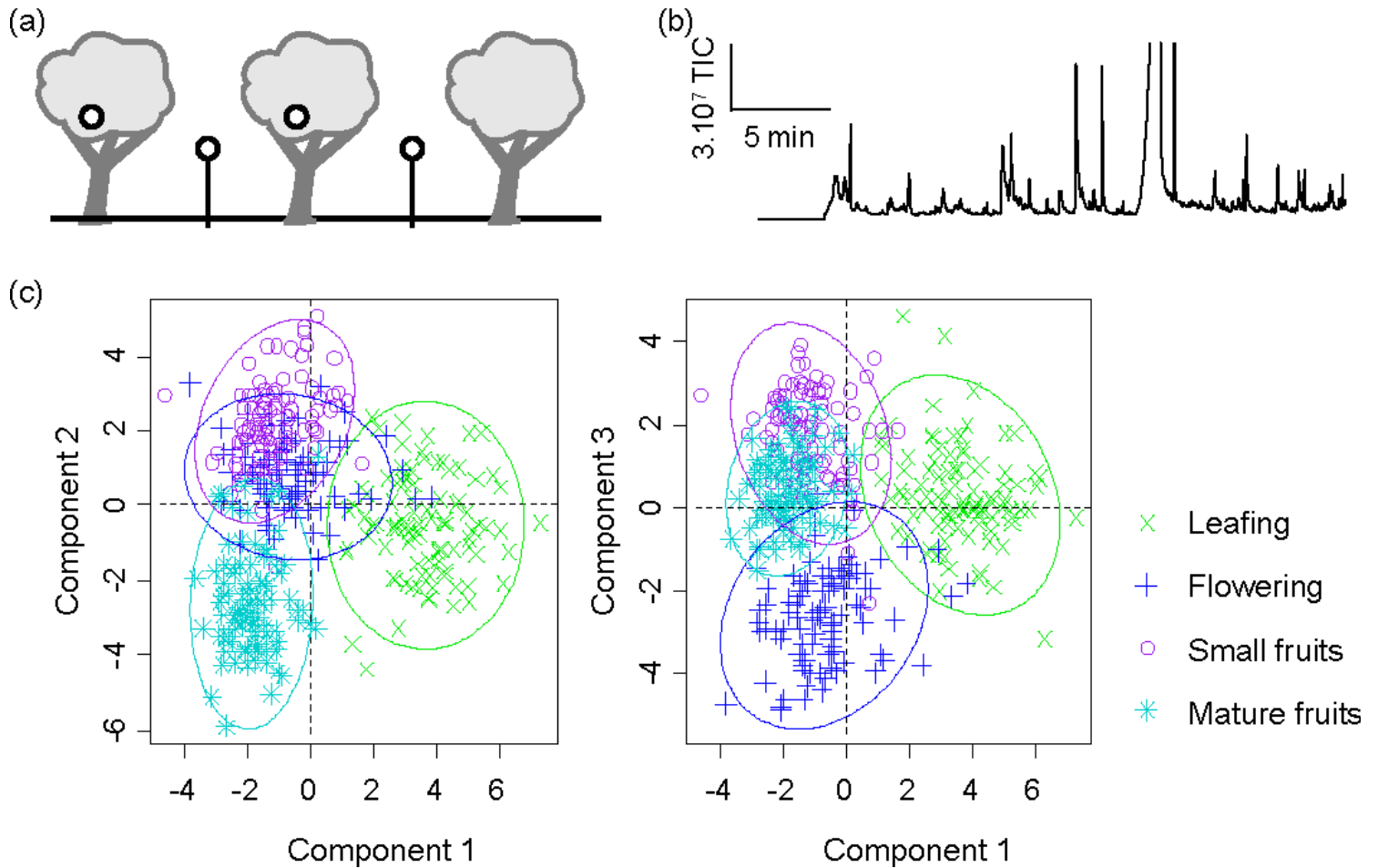


Figure 2

Chemical variability of environmental air across phenological periods. (a) Schematic drawing of the air sampling on tenax cartridges (circles) mounted on a rod in between the trees or directly on the trees. (b) Example gas chromatogram of an air sample. TIC: total ion current of the mass spectrometer. The trace begins at the GC injection time. (c) Visualization of samples chemical composition through a PLS-DA grouped by phenological periods. Projection of all VOC samples ($n=8$ per each 4 orchard and per time point, 3 time points per period) on components 1 to 3. Each point represents an orchard sampled at one point in time. Ellipses represent the 95% confidence region for the distribution of samples within each phenological period.

Figure 3

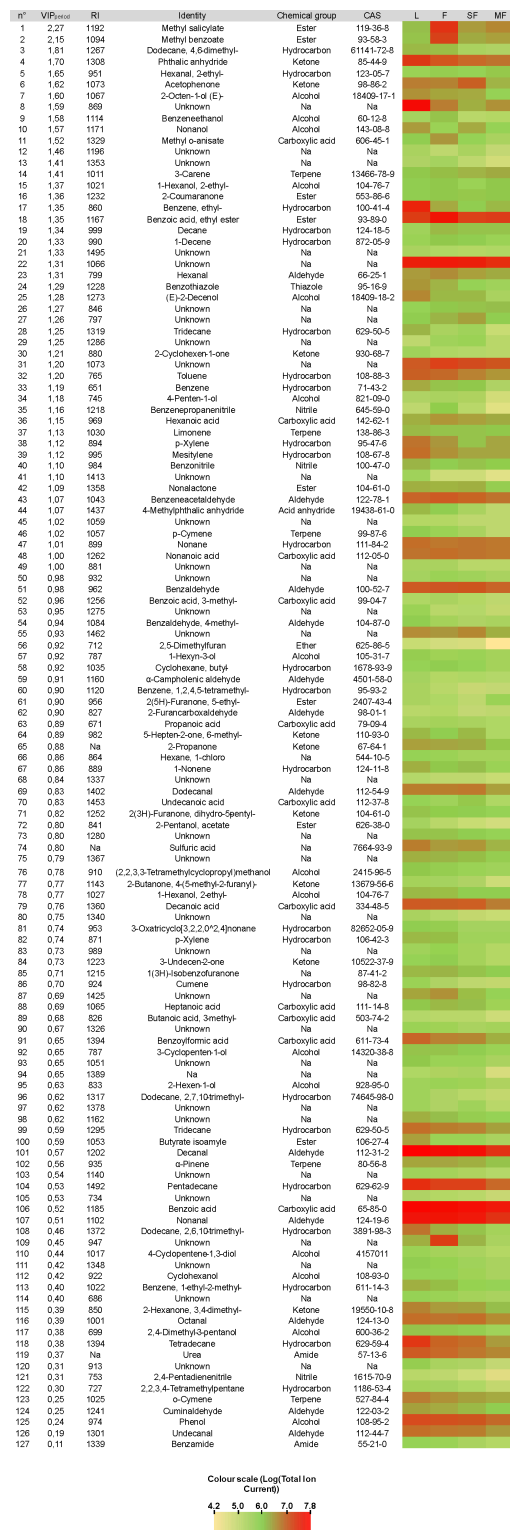


Figure 3

List of the 127 putatively identified compounds, ranked by decreasing importance in distinguishing phenological periods. This ranking is ordered by decreasing value of VIP_{period} , based on the PLS-DA performed across phenological periods (Figure 2). For each compound, the putative identification chemical group and CAS number are indicated (Na: not attributed). For the construction of the heatmap, the mean peak value of each compound was calculated for each period. A $\log_{10}$ transformation was then

applied to each of the resulting mean values. (L: Leafing period; F: Flowering period; SM: Small fruit period; MF: Mature fruit period). Note that only the mean is represented but not the variability, which may explain why some compounds with low VIP_{period} value appear to differ across periods.

Figure 4

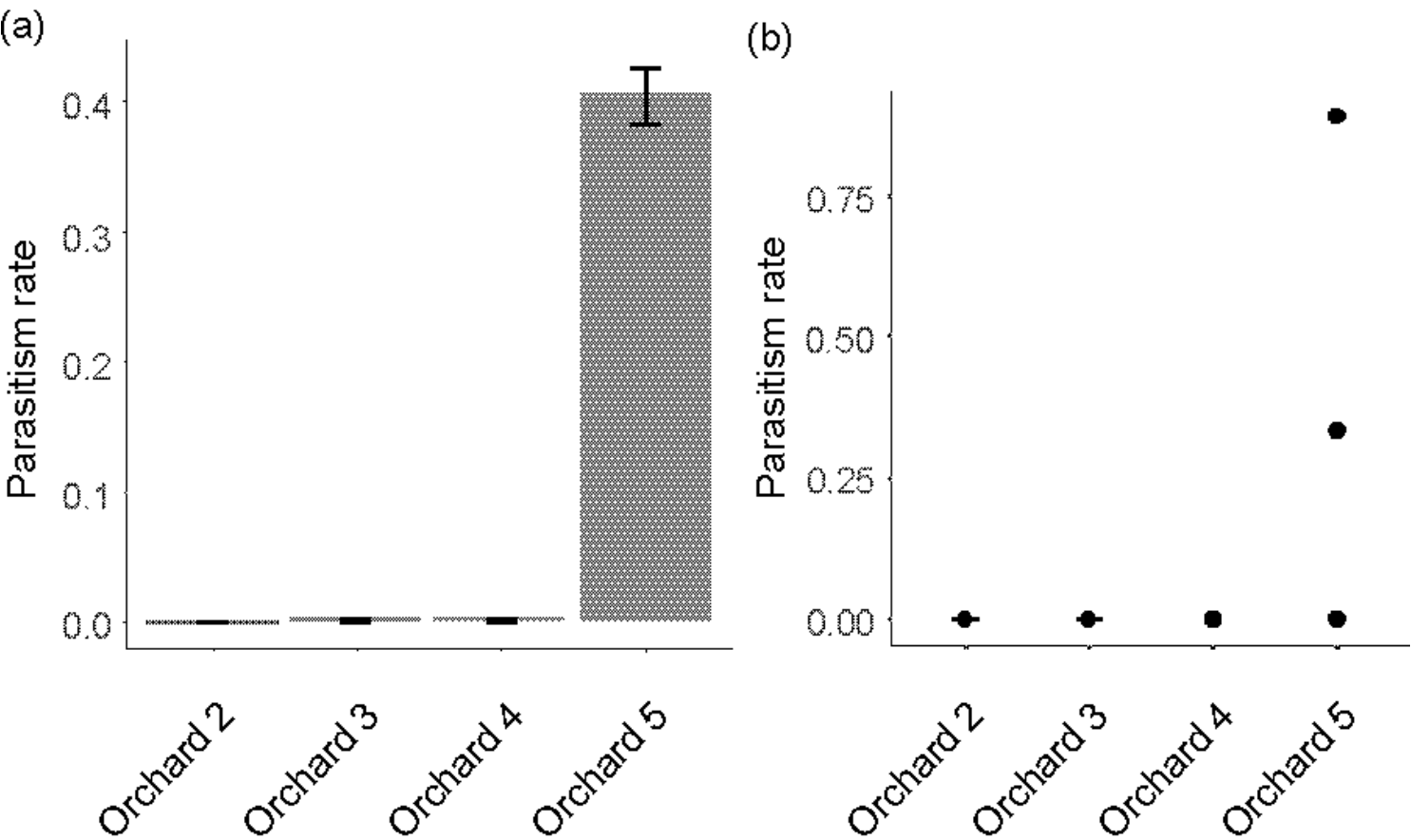
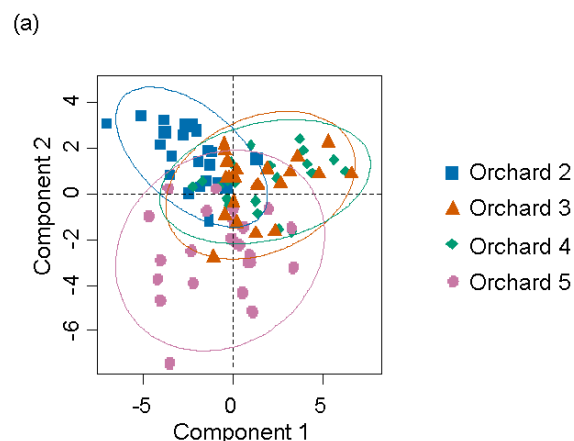


Figure 4

Parasitism of *Fopius arisanus* on bananas and mangoes across orchards during mature fruit period. (a) Evaluation of the percentage of eggs parasitized by *Fopius arisanus* on bananas ($n=15$ per orchard) and (b) parasitism rate on mangoes ($n_{orchard\ 2}=17$, all at 0; $n_{orchard\ 3}=15$, all at 0; $n_{orchard\ 4}=1$; $n_{orchard\ 5}=3$, the last two numbers are low because few fruits with tephritid eggs were available in these orchards) across orchards during the mature fruit period (mean $\pm$ standard error) including individual sample points.

Figure 5



(b)

n°	VIP _{orchard}	RI	Identity	Chemical group	CAS	O2	O3	O4	O5
23	3,04	799	Hexanal	Aldehyde	66-25-1				
34	2,16	745	4-Penten-1-ol	Alcohol	821-09-0				
14	2,16	1011	3-Carene	Terpene	13466-78-9				
8	2,03	869	Unknown	Na	Na				
1	1,96	1192	Methyl salicylate	Ester	119-36-8				
71	1,86	1252	2(3H)-Furanone, dihydro-5-pentyl-	Ketone	104-61-0				
117	1,75	699	2,4-Dimethyl-3-pentanol	Alcohol	600-36-2				
66	1,73	864	Hexane, 1-chloro	Na	544-10-5				
17	1,72	860	Benzene, ethyl-	Hydrocarbon	100-41-4				
38	1,66	894	o-Xylene	Hydrocarbon	95-47-6				
126	1,66	1301	Undecanal	Aldehyde	112-44-7				
102	1,64	935	α -Pinene	Terpene	80-56-8				
112	1,63	922	Cyclohexanol	Alcohol	108-93-0				
113	1,57	1022	Benzene, 1-ethyl-2-methyl-	Hydrocarbon	611-14-3				
101	1,54	1202	Decanal	Aldehyde	112-31-2				
26	1,54	846	Unknown	Na	Na				
97	1,49	1378	Unknown	Na	Na				
78	1,49	1027	1-Hexanol, 2-ethyl-	Alcohol	104-76-7				
9	1,45	1114	Benzeneethanol	Alcohol	60-12-8				
43	1,41	1043	Benzeneacetaldehyde	Aldehyde	122-78-1				
106	1,37	1185	Benzoic acid	Carboxylic acid	65-85-0				
125	1,35	974	Phenol	Alcohol	108-95-2				
47	1,34	899	Nonane	Hydrocarbon	111-84-2				
61	1,29	956	2(5H)-Furanone, 5-ethyl-	Ester	2407-43-4				
41	1,27	1413	Unknown	Na	Na				

Colour scale (Relative intensity per compound)

0.3 1.0 1.5 2.0 2.6

Figure 5

Chemical variability of environmental air across orchards during mature fruit period. Visualization of PLS-DA results grouped by orchards during the mature fruit period and the ranking of the compounds used in that contributed to this analysis. (a) Projection all VOC samples collected during the mature fruit period on axes 1 and 2 of the PLS-DA grouped by orchards (n=8 per each 4 orchard and per 3 time point during the mature fruit period). Ellipses represent the 95% confidence region for the distribution of

samples within each orchard. (b) The top 25 compounds (out of 127, Figure S1) ranked by decreasing value of VIP_{orchard} , based on the PLS-DA performed across orchards during the mature fruits period (Figure 5a). For each compound, the putative identification chemical group and CAS number are indicated (Na: not attributed). For the construction of the heatmap, the mean peak value of each compound was calculated for each orchard. Then, each of these values was normalized by the mean value of that compound across the four orchards. (O2: Orchard 2; O3: Orchard 3; O4: Orchard 4; O5: Orchard 5).

Supplementary Files

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