Host plant scent mediates patterns of attraction/repellence among predatory mites

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Abstract: In mite communities, behavioral and foraging decisions of individuals rely on semiochemicals that they gather from the environment, which contain odors from plants, herbivores, and predators. Because herbivorous mites commonly co-occur with several species of phytoseiid predatory mites, which may engage in intraguild predation (IGP), predator mite decision-making relies on their ability to recognize odors signaling the presence of the herbivore but also that of potential competitors/predators. Here the odor-related foraging decisions of three predatory mites, *Euseius stipulatus* (Athias-Henriot), *Neoseiulus californicus* (McGregor) and *Phytoseiulus persimilis* (Athias-Henriot) (Mesostigmata: Phytoseiidae), which co-occur in citrus, compete for the herbivore *Tetranychus urticae* Koch (Prostigmata: Tetranychidae), and can engage in IGP were investigated. The composition of the volatile blends associated with the three predators was characterized. Moreover, the effect of these odors on the predators foraging decisions was measured. Results revealed that (1) the volatile signature of the three predatory mites is species specific, (2) the predators' foraging behavior is affected by heterospecific predator odors, and (3) predator responses strongly depend on the host plant: mutual attraction and mutual repellence occurred in Cleopatra mandarin and sour orange, respectively. These findings have important consequences for the management of systems where these species occur. The odor blends that make predators that share pest species as prey avoid each other could be used to improve pest control by minimizing undesired negative interactions among predator species, and by locally increasing predation risk on herbivore pest species.

Keywords: Citrus; HIPV; phytoseiidae; IGP; plant defense; predatory mite; *Tetranychus urticae*

1 Introduction

When different species of predators are attracted to patches occupied by their shared herbivore prey, they can engage in intraguild predation (IGP, Polis et al. 1989) and interact through consumptive (predation) and non-consumptive (i.e., competition for food, mutual interference) effects (Rendon et al. 2019). Negative interactions between predators may dampen trophic cascades and reduce control of herbivore populations (Rosenheim et al. 1993; Snyder & Wise, 2001; Finke & Denno 2003; Arim & Marquet 2004; Rendon et al.

2019), jeopardizing a key ecosystem service. In arthropods, predator foraging behaviors that entail a reduction of interference (i.e., avoidance or escape from patches occupied by con- or heterospecific predators) are common (Janssen et al. 1995; 1997; Pallini et al. 1997; Magalhães et al. 2004; Çakmak et al. 2006). These behaviors are often triggered by volatile blends that signal an imminent predation risk (Janssen et al. 1999a; Çakmak et al. 2006). However, IGP is often asymmetric, with one species being more prone to engage in predator-predator interactions (the IG-predator), while the other (the IG-prey) is usually the stronger

competitor at exploiting the shared prey. Because predation is an immediate threat, it is expected that IG-prey will display strong behavioral responses upon perception of presence of other predators than IG-predators would do.

The family Phytoseiidae (Acari: Mesostigmata) comprises more than 2,500 species worldwide including the most common predatory mites in plants (Demite et al. 2017). The two spotted spider mite *Tetranychus urticae* Koch (Acari: Prostigmata) is a polyphagous cosmopolitan agricultural pest (Migeon & Dorkeld 2020) which has been the focus of several biological control programs using phytoseiids since the early 1960s (McMurtry et al. 2015). It is considered a key pest of Spanish citrus, where a phytoseiid complex of around 20 species has been described (Jaques et al. 2015). Phytoseiids have a diversity of lifestyles related to food utilization (McMurtry et al. 2015), ranging from specialized predators of herbivorous spider mites belonging to the genus *Tetranychus* Dufour (i.e., *Phytoseiulus persimilis* (Athias-Henriot)), to pollen feeders that also feed on microarthropods and, importantly, on plant cell-sap (i.e., *Euseius stipulatus* (Athias-Henriot)) (Cruz-Miralles et al. 2021a). Species, such as *Neoseiulus californicus* (McGregor), exhibit intermediate lifestyles feeding on both plant and animal-derived food but not on plant cell-sap (Cruz-Miralles et al. 2021a). *Phytoseiulus persimilis, N. californicus* and *E. stipulatus* can coexist in Spanish citrus orchards and are considered the key predators of *T. urticae* in this agroecosystem (Aguilar-Fenollosa et al. 2011a; 2011b; Pérez-Sayas et al. 2015; Urbaneja-Bernat et al. 2019). Their relative abundance, though, is diverse. *Euseius stipulatus* is the most abundant species in both the canopy and the associated cover crops, irrespective of the species/cultivar and management practices (Aguilar-Fenollosa et al. 2011b). It may represent more than 70% of total phytoseiids in the canopy. The other two species represent from 5 to 15% each. In spite of these contrasting figures, Pérez-Sayas et al. (2015) demonstrated in a field study that only 28.4% of *E. stipulatus* specimens fed on *T. urticae*, whereas this figure boosted to 75.7% for *P. persimilis*. Less abundant but much more efficient *N. californicus* and *P. persimilis* often disappear from the system when continuous availability of pollen in the orchard (i.e., when trees are grown in association with a wild ground cover) enhances the populations of *E. stipulatus,* which out-competes them (Aguilar-Fenollosa et al. 2011a; 2011b; Pina et al. 2012). In this scenario, the biological control of *T. urticae* turns deficient (Aguilar-Fenollosa et al. 2011c). Interestingly, the same study by Pérez-Sayas et al. (2015) revealed the occurrence of IGP, as few individuals of *E. stipulatus* (less than 1.7%) tested positive for either or both *N. californicus* and *P. persimilis*. Asymmetric IG interactions among these species were also pointed out by Abad-Moyano et al. (2010), who identified *E. stipulatus* as the IG-predator in this system. These authors concluded that the IG negative interactions between *E. stipulatus* and *P. persimilis* were of predatory nature, while those between *E. stipulatus* and *N.*

californicus were likely driven by interference. Thus, when these species co-occur in a citrus plant, the two IG-prey, *P. persimilis* and *N. californicus*, likely avoid patches occupied by their IG-predator, *E. stipulatus*, whereas the opposite may not necessary occur.

Recently, Cruz-Miralles et al. (2019) characterized the behavior of *T. urticae* when it was exposed to odors from the three aforementioned phytoseiid species. Likewise, Cabedo-López et al. (2019) characterized that of these predators when they were exposed to odors from *T. urticae*. These authors used a 2-choice olfactometer (i.e., Y-tube) (Bruin et al. 1992), where mites were exposed to the odors of heterospecific mites but also to those of heterospecific mite-infested citrus plants (*T. urticae* was exposed to the odors of the three predators, but not to its own scent). Two *Citrus* species, which exhibit opposite susceptibility responses to *T. urticae*, were used: the highly susceptible *C. reshni* (Cleopatra mandarin) and the highly resistant *C. aurantii* (sour orange) (Bruessow et al. 2010; Agut et al. 2014). As expected, attraction of predators to *T. urticae* odors irrespective of the background (i.e., host-plant) odors was observed. On the contrary, species-specific avoidance response of *T. urticae* to predator odors depended on the background. While herbivore mites were repelled to the sole body odor of the three phytoseiids, and to plants infested with *N. californicus* and *P. persimilis*, they were attracted to *E. stipulatus*-infested plants, regardless of the citrus species (Fig. 1). This result was attributed to the omnivore feeding habits of this species (Cruz-Miralles et al. 2021a). Indeed, plant cell-sap feeding by *E. stipulatus* could make injured plants attractive to the herbivore (Cruz-Miralles et al. 2019).

To date, the behavioral responses of these three phytoseiid species when exposed to odor blends associated with the other two (either body or predator-infested citrus plant odors) have not been characterized. Gaining knowledge on these behavioral responses is important to better understand this system, as it could be used to better manage the systems where these species occur. In the present study, odor-induced behavioral responses were investigated by means of Y-tube olfactometer tests using the *T. urticae* susceptible and resistant citrus genotypes. The hypotheses that odors from the IG-predator (*E. stipulatus*) would repel the two IG-prey (*N. californicus* and *P. persimilis*) independently of the host-plant odors, while the opposite would not occur were challenged. The volatile blends associated with these phytoseiids, which might be responsible of triggering such behavioral responses, were investigated.

2   Materials and methods

2.1   Plant material

Three-month-old plants of sour orange and Cleopatra mandarin (10–12 fully developed leaves) were used in the assays. They were grown on vermiculite and peat (1:3;
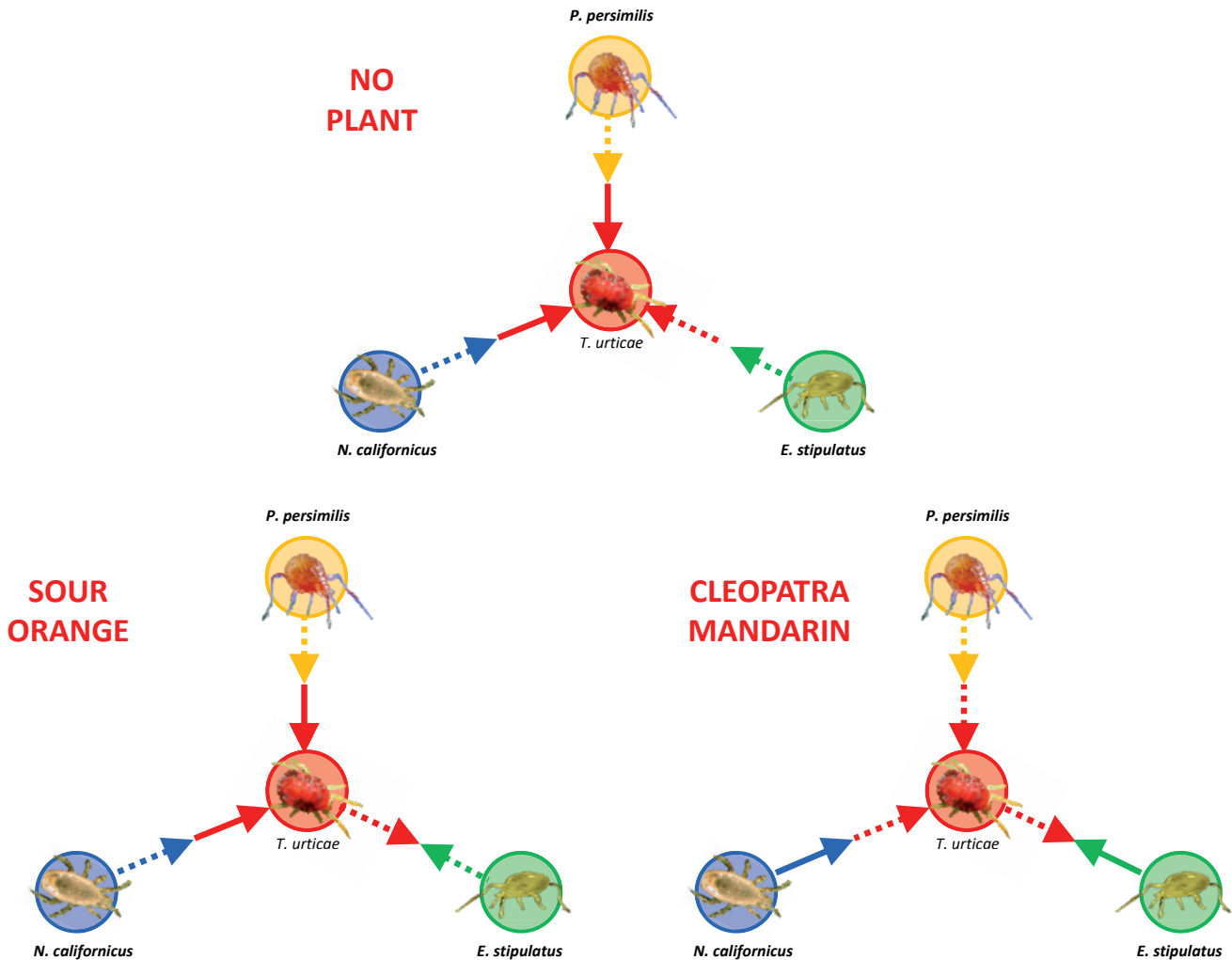
Fig. 1. Interactions observed between *Phytoseiulus persimilis, Neoseiulus californicus, Euseius stipulatus*, and their shared prey, *Tetranychus. urticae*. Arrowheads reflect behavioral responses of *P. persimilis* (orange), *N. californicus* (blue), *E. stipulatus* (green), and *T. urticae* (red) with no background odors and those corresponding to sour orange and Cleopatra mandarin. Arrowheads point at the preferred odor source. The results of these interactions include pursuit (———➤ ———) and mutual attraction (———➤ ◄———). Continuous and dotted lines represent trends at $P \leq 0.05$ and $0.06 > P > 0.05$, respectively. Based on Cabedo-López et al. (2019) and Cruz-Miralles et al. (2019, 2021b).

volume:volume) in 320-ml pots in a climatic chamber. Pesticide-free lemons (*Citrus limon* (L.) Burm f.), bean plants (*Phaseolus vulgaris* L. cv. Buenos Aires Roja), and *Typha* sp. pollen were used to maintain mite stock colonies. Additionally, pesticide-free clementine leaves (*C. clementina* Hort. ex Tan. cv. Clementina de Nules grafted on citrange Carrizo rootstock) were used to rear *E. stipulatus* for the characterization of its body odors.

2.2   Spider mite stock colony

All mite stock colonies and experiments reported below were carried out at controlled environmental conditions of $22 \pm 5°C$; $60 \pm 10\%$ RH and 16:8 h L:D photoperiod with an illuminance of 5,000 lux. *Tetranychus urticae* stock colony was initiated with specimens originally collected in 2001

in clementine orchards close to UJI campus (Castelló de la Plana, Spain). Spider mites were maintained on lemon fruits following Cruz-Miralles et al. (2019). In short, 8-10 lemons were set on top of a wooden structure placed in an open plastic box (40×30×8-cm) half-filled with water. Lemons were replaced weekly.

2.3   Phytoseiidae mites stock colonies

The colonies of *E. stipulatus* and *P. persimilis* were initiated with specimens originally collected in 2012 in commercial clementine orchards close to the UJI campus. Since then, colonies have been maintained on rearing units using standard protocols (Pina et al. 2012). These consist of single bean leaflets placed upside down on a water-saturated sponge in a plastic tray (35×20×7 cm³) filled with water. Strips of wet

tissue were placed on the leaflet along its periphery to ensure a constant water supply to the phytoseiids and to prevent escape. Twice a week, colonies received pollen of *Typha* sp. and a mix of different stages of *T. urticae* as food. For *E. stipulatus*, an additional colony using clementine leaves was established. *Neoseiulus californicus* was regularly obtained from Koppert Biological Systems (SPICAL®).

2.4 Y-tube olfactometer choice assays

A series of olfactometer tests where the three phytoseiid species in Fig. 1 where exposed to heterospecific phytoseiid mite odors and to heterospecific phytoseiid mite-infested sour orange and Cleopatra mandarin plants were carried out. Phytoseiid gravid females were used in these assays. To obtain females devoid of non-body odors, these were first individually moved from the rearing substrate to an arena consisting of a thin black plastic board (9.5 cm diameter) placed on a water-saturated foam cube (3–4 cm thick) in an open plastic box (20×15×4 cm^3) half-filled with water. Females were not fed and were simply cleaned from any debris with a soft paintbrush and immediately further moved depending on their role in the assays (i.e., experimental individual or odor source). When predators were used as experimental individuals, females were further transferred in groups of eight to 50-ml plastic vials containing a water-soaked cotton ball as water supply, where they were starved for 24-h prior to their use in the olfactometer. When females were used as an odor source, 25 specimens were either moved to a mesh bag (10×5 cm) closed with a magnet or deposited on different leaves of a citrus plant. In this case, to prevent ambulatory movement of mites between plants, pots were isolated from each other by singly setting them in 14×14×7-cm trays, placed in another larger tray filled with water. Infested plants remained in a climatic chamber for 48 hours before use in the olfactometer assays. Plants were grouped by species and infestation status and kept separately in different climatic chambers to avoid any exposure to alien plant/phytoseiid volatiles, which could have induced undesired plant defensive responses (Agut et al. 2015).

The olfactory choice assays were conducted using a Y-tube olfactometer (Bruin et al. 1992) consisting of a Y-shaped glass tube (arms 13 cm long and 4 cm diameter) containing a Y-shaped 1-mm diameter metal wire. Two arms were directly connected to the outlets of two identical 5-l glass vessels (Duran, Mainz, Germany) containing different odor sources. Each vessel was connected to an air pump producing a unidirectional airflow of purified air of 1.5 l h^{-1} from those two arms to the base of the remaining arm. Starved phytoseiid females were individually deposited at the beginning of the metal wire in the basal arm and allowed to make a choice. As soon as a mite reached the end of one of the two arms of the wire, the mite was removed and discarded. Mites failing to reach either end of the arms after 10 min were scored as "no choice". Different 2-choice experiments involving phytoseiid-infested and uninfested plants (one plant per vessel), as well as phytoseiids in the mesh bag were performed (see Figs 2–4). To avoid pseudoreplication, each odor combination was evaluated four times at different dates (i.e., four replicates). Each replicate included 10 responding phytoseiids per species. After five females had been tested, the glass vessels were switched. After every 10 females had been tested, the odor sources were replaced and the whole system was rinsed with ethanol (70%), followed by air drying. To exclude any bias from the set-up, before the beginning of the assays, 10 mites were exposed to clean air in both arms. A random choice was expected and confirmed (data not shown). Results were initially subjected to logistic regression to check for the effect of replicate on mite preferences. Similarity between replicates ($P > 0.050$) was a prerequisite to pool the four replicates, which were then subjected to chi-square test to check whether they departed from a 1:1 distribution. IBM SPSS Statistics 23 was used.

2.5 Characterization of phytoseiid associated volatiles

Phytoseiid body odors were characterized following the same approach previously used for *T. urticae* (Cabedo-López et al. 2019). Groups of 400–700 specimens (mixed stages and sexes) per species were placed in 2-ml closed screw-cap gas-chromatography (GC) sterile vials by carefully moving first the specimens to a black plastic board as before and then to the vial. For *E. stipulatus*, separate volatile extractions from specimens obtained from the colonies maintained on bean leaflets and clementine leaves were performed. Moreover, samples of *Typha* sp. pollen, used to feed this species, were also processed. As we were unable to produce the large number of specimens of *P. persimilis* and *N. californicus* required for these analyses, they were obtained from Koppert Biological Systems (SPIDEX® and SPICAL®, respectively). In these cases, additional samples of the carrier material used for the commercialization of these phytoseiids, and the carrier plus the factitious astigmatid prey used, kindly provided by Koppert B.S., were also processed. Three replicates per stock colony (in the case of *E. stipulatus*) or shipment (3 different shipments for *N. californicus* and *P. persimilis*) were considered. Volatiles were collected in static conditions by solid-phase microextraction (SPME) using the same procedure used for collecting *T. urticae* body odors (Cabedo-López et al. 2019). Polidimethylsiloxane/divinylbenzene (PDMS/DVB) SPME fibers (film thickness = 100 μm; Supelco Inc., Bellefonte, PA, USA) were conditioned before volatile sampling in a GC injector at 250°C for 10 min under a 20 ml min^{-1} helium flow rate. Then, fibers were exposed to each sample for 24 h at 23 ± 2°C, under a 16:8 h L:D photoperiod (Alfaro et al., 2011). SPME fibers were thermally desorbed into the GC injection port, set at 250°C for 1 min, and operated in the splitless mode. The extracted volatiles were analyzed by GC coupled to a single quadrupole mass spectrometer (GC-MS) using a Clarus 600 GC-MS (PerkinElmer Inc., Wellesley, MA, USA). The
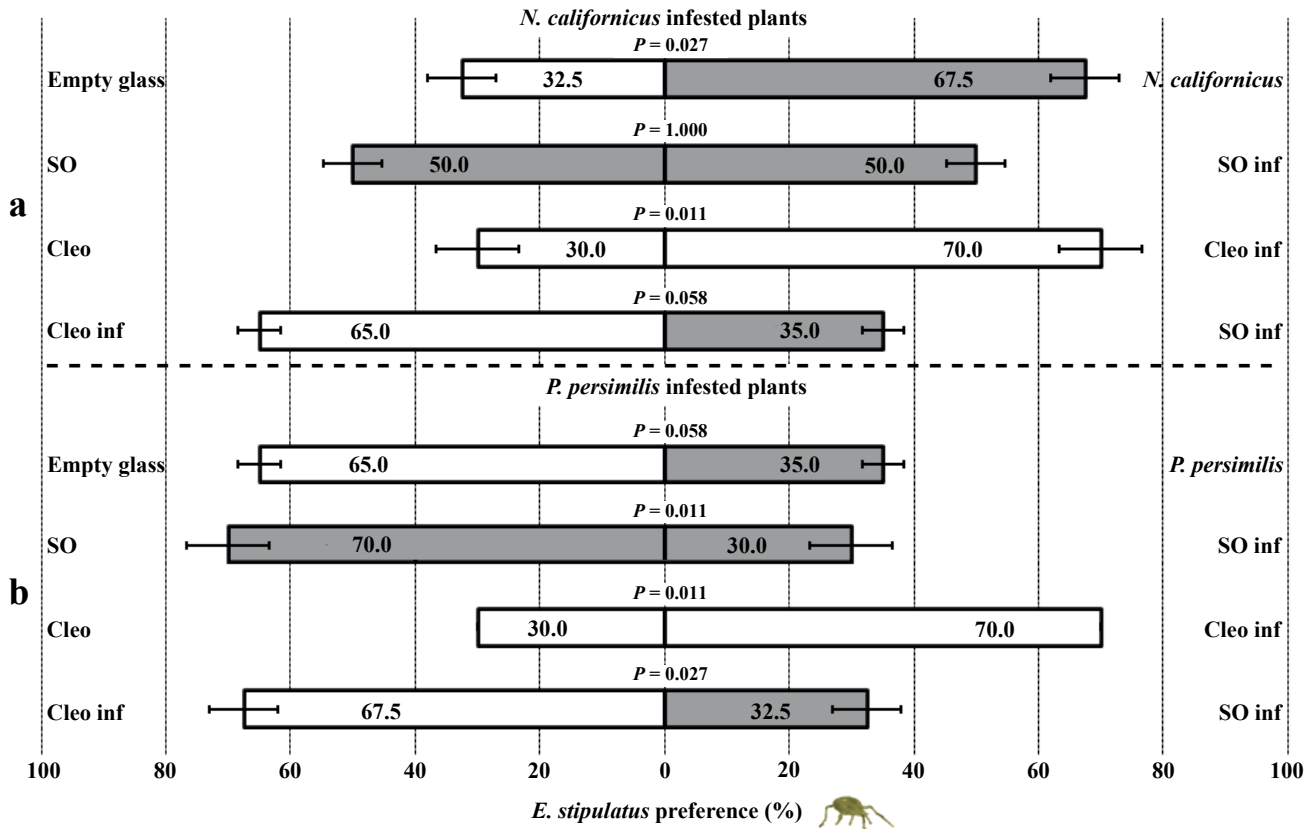
Fig. 2. Olfactory responses (mean ± SE) of *Euseius stipulatus* gravid females to **(a)** *Neoseiulus californicus* and **(b)** *Phytoseiulus persimilis*. For each phytoseiid species combination, *E. stipulatus* had to choose between two odor sources. Four sets of ten females per choice combination were tested. From top to bottom these combinations were: empty glass versus the phytoseiid, sour orange (SO) versus SO-infested plants (SO-inf), Cleopatra mandarin (Cleo) versus Cleo-infested plants (Cleo-inf), and SO-inf versus Cleo-inf. Results of the four replicates per combination were subjected to logistic regression to discard any effect of the replication. Then, data were pooled and subjected to chi-squared test for a 1:1 distribution (chi-squared and P- values for each combination are shown in the figure; df were always 1).

column used was a 30 m × 0.25 mm i.d., 0.25 μm film thickness, ZB-5MS fused silica capillary column (Phenomenex Inc., Torrance, CA, USA). The oven was held at 40°C for 2 min and then programmed at 5°C min^{-1} to 180°C; when reached, temperature was raised to 280°C at 10°C min^{-1} and maintained at 280°C for 1 min (total analysis run of 41 min). Helium was used as the carrier gas with a flow rate of 1.2 ml min^{-1}. Detection was performed in the EI mode (ionization energy, 70 eV; source temperature, 180 °C), and spectra acquisition was done in the scanning mode (mass range m/z 35−400). Chromatograms and spectra were recorded with GC-MS Turbomass software version 5.4 (PerkinElmer Inc.). Volatiles were identified by either comparing their retention times and mass spectra with those of pure standards (Sigma-Aldrich) or by matching to the National Institute of Standards and Technology library (NISTEPANIH Mass Spectral Library, version 2.0, build 4/2005) using match values >80% as a threshold for identification, as described by Wallis et al. (2008). The peak areas in the chromatograms

corresponding to these compounds were calculated and used to estimate their relative abundance.

3   Results

3.1   Host plant scents mediate mutual interference between predators

To challenge the hypothesis that the odors from the IG-predator *E. stipulatus* would repel the two IG-prey but not vice-versa, a series of 2-choice tests were performed. More than 93 % of the phytoseiids used in the olfactometer responded to the odors tested (i.e., mites made a choice) (Fig. 1S, 2S and 3S for results of each choice test). Maximum rates of response were observed for *N. californicus* (94.5 ± 1.1 %; mean ± SE), followed by *E. stipulatus* (94.2 ± 1.1 %) and *P. persimilis* (92.7 ± 1.2 %). Because for each choice test the four replicates showed similar trends (P ≥ 0.262; Table 1S), results of the four replicates per test
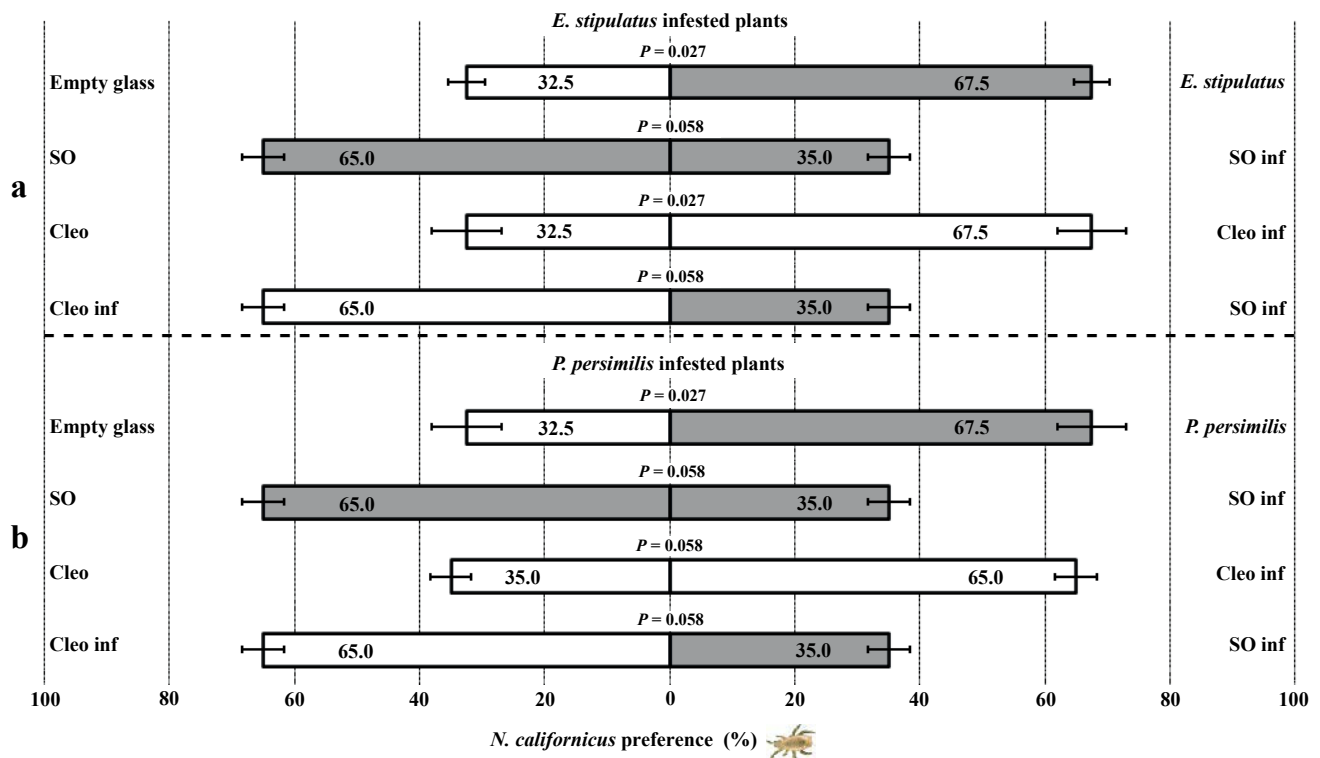
Fig. 3. Olfactory responses (mean ± SE) of *Neoseiulus californicus* gravid females to **(a)** *Euseius stipulatus* and **(b)** *Phytoseiulus persimilis*. For each phytoseiid species combination, *N. californicus* had to choose between two odor sources. Four sets of ten females per choice combination were tested. From top to bottom these combinations were: empty glass versus the phytoseiid, sour orange (SO) versus SO-infested plants (SO-inf), Cleopatra mandarin (Cleo) versus Cleo-infested plants (Cleo-inf), and SO-inf versus Cleo-inf. Results of the four replicates per combination were subjected to logistic regression to discard any effect of the replication. Then, data were pooled and subjected to chi-squared test for a 1:1 distribution (chi-squared and P- values for each combination are shown in the figure; df were always 1).

were pooled and subjected to chi-square analysis. In agreement with our hypothesis, the IG-predator *E. stipulatus* (Fig. 2) was attracted to the IG-prey *N. californicus*' body odors ($P = 0.027$) and to Cleopatra mandarin infested plants, irrespective of the identity of the IG-prey species ($P = 0.011$). However, it mostly avoided *P. persimilis*' body odors ($P = 0.058$). This species became repellent when associated with sour orange odors ($P = 0.011$). When *E. stipulatus* had to choose between the two heterospecific mite-infested citrus species, it mostly preferred Cleopatra mandarin ($P = 0.027$ and 0.058 for *P. persimilis* and *N. californicus*, respectively). Contrary to what was expected, *N. californicus* was highly attracted to the body odors of the other two phytoseiids alone ($P = 0.027$) and also to *E. stipulatus*-infested Cleopatra mandarin plants ($P = 0.027$) (Fig. 3). Same as *E. stipulatus*, *N. californicus* mostly preferred infested Cleopatra mandarin rather than infested sour orange, independently of the infesting heterospecific predator ($P = 0.058$). Finally, *P. persimilis* showed no preference for any of the odor sources tested ($P \geq 0.343$) except for *E. stipulatus* body odors, from which they were mostly repelled ($P = 0.058$) (Fig. 4). These results confirm that plant odors can modulate phytoseiid behavior in a plant-genotype dependent manner (Fig. 5).

3.2   Green Leaf Volatiles are widely present in phytoseiid scents

A total of 27 (Table 1), seven (Table 2), and 29 (Table 3) different volatiles were identified in the different samples (phytoseiid, pollen, carrier, carrier+prey) considered for *E. stipulatus, N. californicus* and *P. persimilis*, respectively. In the case of *E. stipulatus*, only ten volatiles were identified in their body odors, from which three were also found in the pollen used to feed them. Remarkably, the same corporal volatiles were observed irrespective of the feeding substrate (bean leaflet or clementine leaf) used for the rearing. The body odors of *N. californicus* contained four volatiles and one of them (geranyl fomate) was also found in the sample containing the carrier and the factitious prey used for its commercialization. Finally, the most complex body odor corresponded to *P. persimilis*, as 20 volatiles, mostly monoterpenes, were retrieved from this phytoseiid. Most of them were found in the woody carrier used for its commercialization as well. 2-hexanol was the only volatile found in the body odors of *P. persimilis* but not in its carrier. Three different isomers of this Green Leaf Volatile (GLV, Tanaka et al. 2018), namely 1-, 2-, and 3-hexanol, constituted the only volatile consistently found in the body odors of the
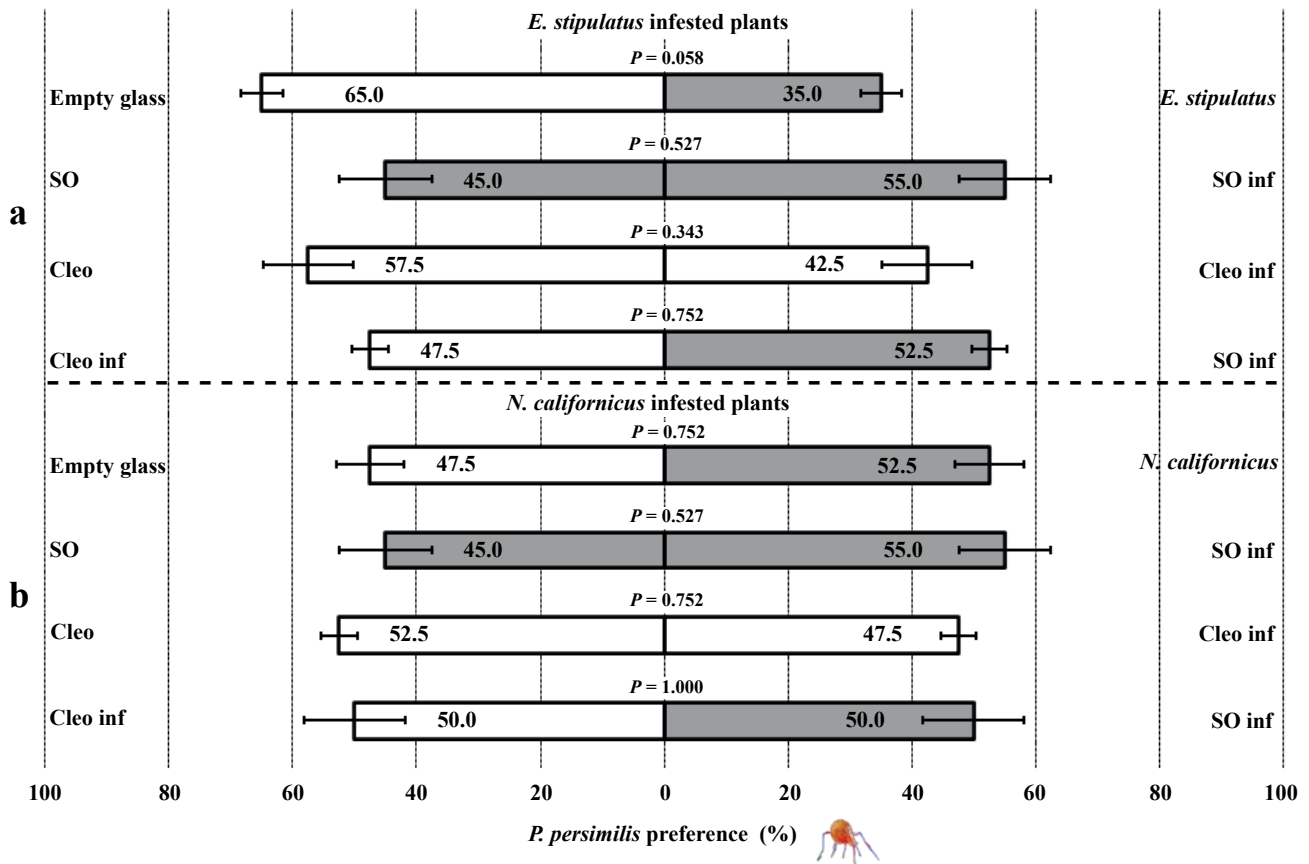
Fig. 4. Olfactory responses (mean ± SE) of *Phytoseiulus persimilis* gravid females to **(a)** *Euseius stipulatus* and **(b)** *Neoseiulus californicus*. For each phytoseiid species combination, *P. persimilis* had to choose between two odor sources. Four sets of ten females per choice combination were tested. From top to bottom these combinations were: empty glass versus the phytoseiid, sour orange (SO) versus SO-infested plants (SO-inf), Cleopatra mandarin (Cleo) versus Cleo-infested plants (Cleo-inf), and SO-inf versus Cleo-inf. Results of the four replicates per combination were subjected to logistic regression to discard any effect of the replication. Then, data were pooled and subjected to chi-squared test for a 1:1 distribution (chi-squared and P- values for each combination are shown in the figure; df were always 1).

three phytoseiid species studied here (i.e., *E. stipulatus, N. californicus* and *P. persimilis*). Another GLV, 2-hexanone, was present in the body blends associated with *N. californicus* and *P. persimilis*. Interestingly this volatile was also found in the carrier of *P. persimilis* but was not in that of *N. californicus*, which suggests species-specific sequestration of substrate odors by these phytoseiids. Most of the remaining volatiles were found only in one species. However, limonene was found in the body odors of *E. stipulatus* and *P. persimilis* and also in *Typha* spp. pollen and in the carrier of *P. persimilis*.

4   Discussion

Results show that the volatile signature of the three predatory mites included in this study is species-specific. As expected, these odors affected predators' foraging behaviors.

Importantly, behavioral changes were affected by host-plant odors. Indeed, the host plants tested here clearly mediated the probability of encounter between predators. This may have important consequences on the patterns of local coexistence of IG-predators and IG-prey and, consequently, on the predation risk of the shared prey, which is also plant-geno-type dependent. These changes may ultimately affect higher organizational levels including the community.

4.1   Plants and mite volatile blends

Plant secondary metabolites have been identified in the body odors of arthropods (Beran et al. 2019). Their sequestration by arthropods, either directly by herbivory or indirectly through their prey, for their own defense and communication is well documented (Opitz & Müller, 2009). However, none of the volatiles identified in the present study was found in the scents produced by the shared prey, *T. urticae*, or the host plants (Agut et al. 2014; Cabedo-López et al. 2019). One
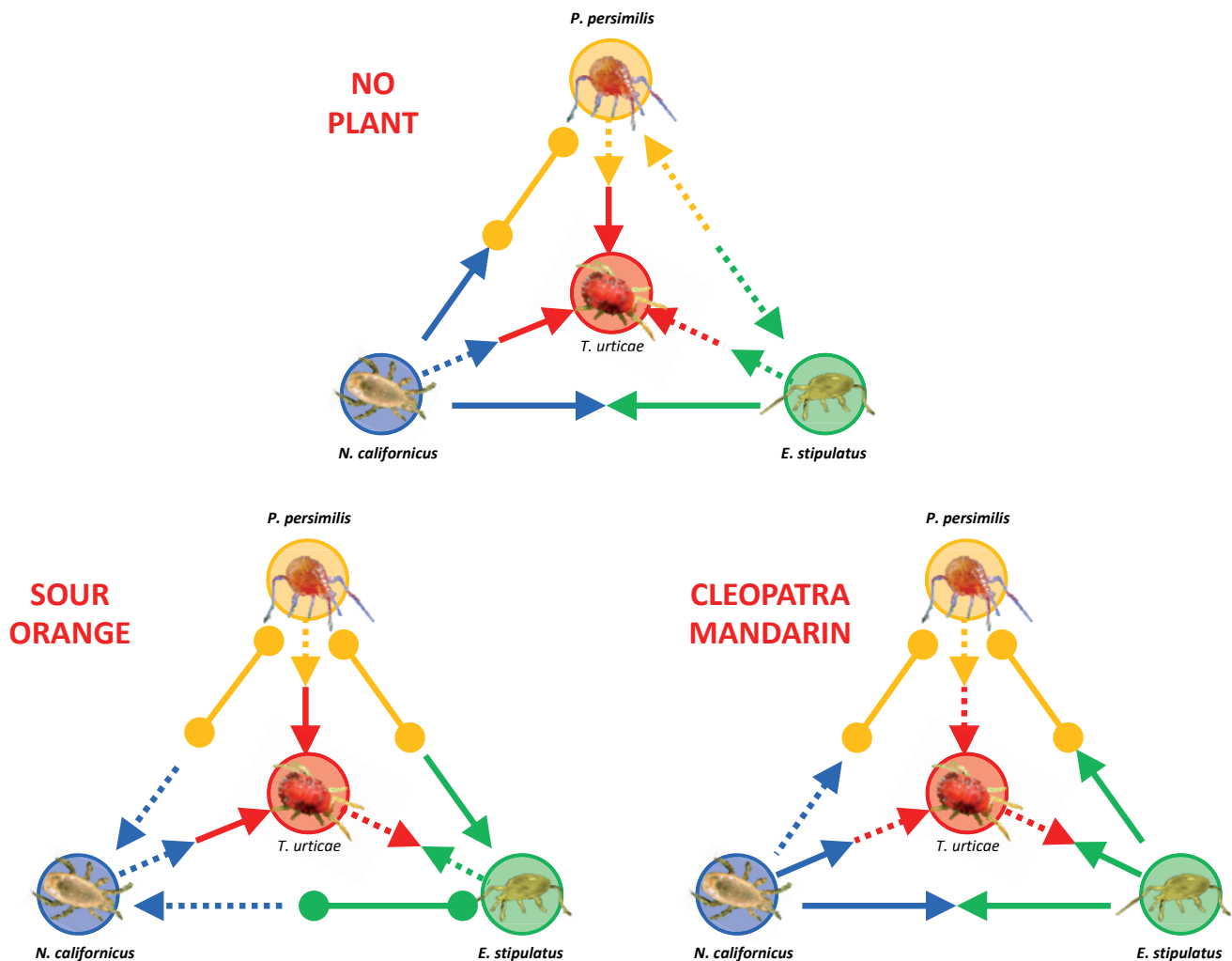
Fig. 5. Interactions observed between *Phytoseiulus persimilis, Neoseiulus californicus, Euseius stipulatus*, and their shared prey, *T. urticae*. Arrowheads reflect behavioral responses of *P. persimilis* (orange), *N. californicus* (blue), *E. stipulatus* (green), and *T. urticae* (red) with no background odors and those corresponding to sour orange and Cleopatra mandarin. Arrowheads point at the preferred odor source. The results of these interactions include pursuit (⟶   ⟶), mutual attraction (⟶ ⟵), mutual avoidance (⟵   ⟶), avoidance (⟵● ●⟶), and attraction (⟶● ●⟶). Continuous and dotted lines represent trends at $P \leq 0.05$ and $0.06 > P > 0.05$, respectively. Interactions including *T. urticae* were presented in Fig. 1.

possible explanation for the poor correspondence between plant and phytoseiid odors is that the amounts produced by mites are orders of magnitude below those produced by plants and, therefore, below detection limits of procedures used to characterize plant volatiles, which differ from those used for mites (Cabedo-López et al. 2019). One additional explanation in the cases of *N. californicus* and *P. persimilis* could be the rearing substrate/carrier used by Koppert B.S. Indeed, the monoterpenes associated with *P. persimilis* also appeared in its woody carrier. Likewise, geranyl formate was found in *N. californicus* and in its factitious prey. However, this was not the case in *E. stipulatus*, which had been reared on two different plant substrates. This suggests a selective sequestration of plant secondary metabolites by *E. stipulatus* regardless of the host plant. This is also supported by the

fact that hexanoic acid was found in *Typha* sp. pollen and *P. persimilis* carrier but was not in either *E. stipulatus* or *P. persimilis*. Further studies with *N. californicus* and *P. persimilis* from different mass rearing systems would be instrumental to check whether this selective sequestration is not restricted to *E. stipulatus*.

4.2   Plant-scents and food web interactions

Janssen et al. (1999a) suggested that 'a logical first step in determining the occurrence and strength of arthropod food web interactions is to study responses of the species in the food web to odours associated with the presence of food, predators (intraguild) and competitors'. However, until now, the effect of host plant odors on these interactions has been mostly restricted to the study of the volatiles emitted by plants

Table 1. Compounds detected in the volatile collections of *Euseius stipulatus* reared on bean leaflets and clementine leaves, as well as the *Typha* sp. pollen supplied for feeding (relative mean ± standard error percentage considering the total chromatogram area of the detected compounds).

Name	id.[2]	rt (min)	*E. stipulatus*[1]				pollen	
			Bean		Clementine			
			mean	se	mean	se	mean	se
hexanal	C	6.97	0	–	0	–	6.70	1.40
1-hexanol	C	9.47	4.29	0.34	0.76	0.01	0	–
heptanal	C	10.61	0	–	0	–	0.71	0.19
sabinene	T	13.15	0	–	0	–	0.11	0.04
β-pinene	C	13.35	0	–	0	–	0.37	0.17
1-octen-3-ol	C	13.53	52.51	0.39	54.20	5.66	0	–
3-octanone	T	13.64	36.44	2.14	31.49	2.49	0	–
myrcene	C	13.72	0	–	0	–	0.19	0.15
ethyl hexanoate	C	14.05	0	–	0	–	2.50	1.28
3-octanol	T	14.08	1.21	0.17	0.36	0.22	0	–
hexanoic acid	C	14.38	0	–	0	–	0.61	0.15
1,3,8-p-menthatriene	T	15.04	0	–	0	–	0.32	0.28
limonene	C	15.19	0.04	0.01	1.28	0.54	8.59	4.38
γ-terpinene	T	16.2	0	–	0	–	0.58	0.40
2-octen-1-ol	T	16.82	0.29	0.11	1.03	0.15	0	–
ethyl heptanoate	T	17.44	0	–	0	–	2.21	1.51
nonanal	C	17.81	0.66	0.15	12.21	2.65	31.68	31.16
3-nonen-1-ol	T	19.58	3.19	0.70	0.29	0.23	0	–
2-nonenal	C	19.7	0	–	0	–	0.90	0.02
1-nonanol	C	20.08	1.33	0.65	0.29	0.23	0	–
ethyl octanoate	T	20.64	0	–	0	–	0.64	0.59
decanal	C	21.04	0.04	0.01	0.29	0.23	0.60	0.36
methyl nonanoate	T	21.5	0	–	0	–	0.70	0.62
ethyl nonanoate	T	23.67	0	–	0	–	40.03	22.81
ethyl decanoate	T	26.44	0	–	0	–	0.49	0.25
β-gurjunene	T	29.38	0	–	0	–	2.00	1.46
ethyl laurate	C	31.5	0	–	0	–	0.07	0.04

[1] Means of three replicates of individuals collected in two different stock colonies maintained in the laboratory, three on clementine leaves and the other three on bean leaflets. The compounds highlighted in grey are detected only in the phytoseiid samples and those in a box are found in the phytoseiid and the pollen samples.
[2] Identification of the compound: C, confirmed with commercial standard; T, tentative with spectra and high probability matches (> 80%) according to NIST mass spectral database (Wallis et al. 2008).

in response to herbivory in the recruitment of natural enemies of herbivores (Rowen & Kaplan 2016). The results of the present study prove that plant scents can additionally modify the IG relationships among predators. The expectations of the experiments reported here were that the IG-predator would trigger repellence in IG-prey but not vice-versa and that this would be independent of plant scents. However, none of the three phytoseiids triggered the expected unidirectional avoidance (Fig. 5). *Phytoseiulus persimilis* was the only phytoseiid whose choices were independent of the pres-

ence of heterospecific predators on the plant. Moreover, *P. persimilis* presence on sour orange repelled both heterospecifics, which means that they perceived *P. persimilis* odors as high risk cues. The presence of *P. persimilis*, though, became attractive in Cleopatra mandarin, which highlights the importance of the background plant volatile blend in these choices. Janssen et al. (1997; 1999b) also observed contrasting behaviors in commercial strains of *P. persimilis* and *N. californicus* on *T. urticae*-infested cucumber and bean plants. This result was attributed to lack of co-evolution between

Table 2. Compounds detected in the volatile collections of *Neoseiulus californicus*, the carrier only and the carrier+prey employed for shipment (relative mean ± standard error percentage considering the total chromatogram area of the detected compounds).

Name	id.[2]	rt (min)	*N. californicus*[1]		carrier	carrier + prey	
			mean	se		mean	se
3-methyl-1-butanol	C	5.31	0	–	0	26.90	11.20
2-hexanone	C	6.55	21.83	4.50	0	0	–
3-hexanol	C	6.91	4.57	0.98	0	0	–
2-hexanol	C	7.02	48.28	7.31	0	0	–
2,3-butanediol	C	7.23	0	0.00	0	46.12	12.10
2-heptanone	C	10.3	0	0.00	0	21.66	10.61
geranyl formate	T	23.19	25.33	8.90	0	5.32	2.27

[1] Means of nine replicates of individuals and three of carrier only and carrier+prey samples. The compounds highlighted in grey are detected only in the phytoseiid samples and those in a box both in the phytoseiid and the carrier+prey samples.
[2] Identification of the compound: C, confirmed with commercial standard; T, tentative with spectra and high probability matches (> 80%) according to NIST mass spectral database (Wallis et al. 2008).

Table 3. Compounds detected in the volatile collections of *Phytoseiulus persimilis* and the carrier employed for shipment (relative mean ± standard error percentage considering the total chromatogram area of the detected compounds).

Name	id.[2]	rt (min)	*P. persimilis*[1]		carrier	
			mean	se	mean	se
1-pentanol	C	6.05	0	–	0.82	0.61
2-hexanone	C	6.55	11.32	3.47	0.31	0.31
2-hexanol	C	7.14	5.33	1.31	0	–
1-hexanol	C	9.45	0	–	5.23	0.02
2-heptanone	C	10.06	0	–	3.25	0.59
3-thujene	T	11.69	0.19	0.05	0.39	0.38
1-isopropyl-4-methylenebicyclo[3.1.0]hex-2-ene	T	12.47	0.43	0.10	0.84	0.08
benzaldehyde	C	12.94	0	–	2.26	0.14
β-pinene	C	13.36	0.14	0.05	0.59	0.58
2-octanone	T	13.92	0	–	6.18	2.08
β-terpinene	T	14.35	0.09	0.04	0.41	0.12
hexanoic acid	C	15.16	0	–	1.13	1.12
limonene	C	15.2	0.32	0.18	0.23	0.11
2-octenal	T	16.21	0	–	1.01	1.00
1-nonanol	C	16.64	0	–	3.47	1.06
fenchone	T	17.31	1.35	0.23	1.42	0.24
nonanal	C	17.66	0	–	1.02	0.90
pinocarveol	T	19.19	0.89	0.14	1.34	0.22
camphor	C	19.35	1.58	0.31	2.37	0.35
linalool	T	19.64	0.44	0.06	0.80	0.45
pinocamphone	T	19.75	0.34	0.10	0.73	0.07
pinocarvone	T	19.73	0.14	0.05	1.03	0.27
borneol	T	20.19	3.45	0.27	2.22	0.02
4-terpinenol	T	20.41	10.93	1.53	6.91	0.30
terpineol isomer	T	20.66	7.05	3.04	6.90	0.66
terpineol isomer	T	20.89	52.50	2.54	43.20	1.33
myrtenol	T	21.05	2.56	0.73	0.53	0.00
verbenone	C	21.26	0.92	0.39	4.74	0.92
carvone	C	22.45	0.08	0.02	0.67	0.01

[1] Means of nine replicates of individuals and three of carrier samples. The compounds highlighted in grey are detected only in the phytoseiid samples and those in a box only in the carrier.
[2] Identification of the compound: C, confirmed with commercial standard; T, tentative with spectra and high probability matches (> 80%) according to NIST mass spectral database (Wallis et al. 2008).

these species in new highly artificial protected cultivation systems (Janssen et al. 1999b). However, *P. persimilis* and *E. stipulatus* specimens used in the olfactometer were originally collected in longtime established citrus orchards in the same area. Although *N. californicus* was purchased, this species also co-occurs with the former two in *Citrus* spp. (Aguilar-Fenollosa et al. 2011b). Interestingly, avoidance amongst the three predator species was the rule in sour orange. This behavior would likely promote local spatial segregation and thus, should favor coexistence of these IG predators in sour orange by reducing the encounter rates among them. Moreover, because the behavioral responses between *T. urticae* and each of the three predators were similar in both citrus species (Fig. 1), the predation risk of the herbivore would likely be higher in sour orange than in Cleopatra mandarin due to predator interference occurring less frequently in the former citrus species.

5 Conclusions

Sour orange is at present extensively cultivated worldwide. In the past it used to be the most commonly used rootstock for citrus in the Mediterranean and the Americas. This was due to its high adaptability and induction of excellent fruit quality. However, it had to be massively replaced after establishment of the citrus quick decline disease, a deadly disease for cultivars grafted on this rootstock, which killed almost 100 million citrus trees worldwide (Moreno et al. 2008). Bruessow et al. (2010) pointed at this replacement as a trigger for *T. urticae* to become a key pest of citrus during the second half of the XX century (Jaques et al. 2015). This change was attributed to bottom-up mechanisms, as sour orange displays higher basal and earlier inducible defenses against this herbivore than other citrus rootstocks, notably Cleopatra mandarin, which are systemically transferred from the roots to the canopy (Agut et al. 2014; 2015; 2016). IG predator avoidance in sour orange could provide a complementary plausible explanation for the increasing prevalence of *T. urticae* in citrus orchards. This finding, which is most probably not restricted to *Citrus* spp., should be further explored and exploited to facilitate coexistence of IG predators in important agro-ecosystems with the ultimate goal of increasing the predation risk of the shared prey and therefore, its suppression. Only a thorough understanding of these interactions will enhance the ability to predict and manage these complex systems in a more sustainable way (Gish et al. 2015). The present situation where chemical control is no longer the preferred pest management practice is triggering the development of alternative more sustainable pest management methods. In the case of citrus, the use of sour orange not as a rootstock but as a companion plant or in intercropping systems should be further evaluated as a means of promoting conservation biological control and

to increase the resilience of the crop. Furthermore, identifying and synthetizing odor blends that make predators that share pest species as prey to avoid each other, could improve pest control by minimizing undesired negative interactions among predator species, and by locally increasing predation risk on herbivore pest species.

References

Abad-Moyano, R., Urbaneja, A., Hoffmann, D., & Schausberger, P. (2010). Effects of *Euseius stipulatus* on establishment and efficacy in spider mite suppression of *Neoseiulus californicus* and *Phytoseiulus persimilis* in clementine. *Experimental & Applied Acarology, 50*(4), 329–341. https://doi.org/10.1007/s10493-009-9320-9

Aguilar-Fenollosa, E., Ibáñez-Gual, M. V., Pascual-Ruiz, S., Hurtado, M., & Jacas, J. A. (2011a). Effect of ground-cover management on spider mites and their phytoseiid natural enemies in clementine mandarin orchards (I): Bottom-up regulation mechanisms. *Biological Control, 59*(2), 158–170. https://doi.org/10.1016/j.biocontrol.2011.06.013

Aguilar-Fenollosa, E., Ibáñez-Gual, M. V., Pascual-Ruiz, S., Hurtado, M., & Jacas, J. A. (2011b). Effect of Ground-Cover Management on Spider Mites and their Phytoseiid Natural Enemies in Clementine Mandarin Orchards (II): Phytoseiid Mite Dynamics. *Biological Control, 59*, 171–179. https://doi.org/10.1016/j.biocontrol.2011.06.012

Aguilar-Fenollosa, E., Pascual-Ruiz, S., Hurtado, M., & Jacas, J. A. (2011c). Efficacy and economics of ground cover management as a conservation biological control strategy against *Tetranychus urticae* in clementine mandarin orchards. *Crop Protection (Guildford, Surrey), 30*(10), 1328–1333. https://doi.org/10.1016/j.cropro.2011.05.011

Agut, B., Gamir, J., Jacas, J. A., Hurtado, M., & Flors, V. (2014). Different metabolic and genetic responses in citrus may explain relative susceptibility to *Tetranychus urticae. Pest Management Science, 70*(11), 1728–1741. https://doi.org/10.1002/ps.3718

Agut, B., Gamir, J., Jaques, J. A., & Flors, V. (2015). *Tetranychus urticae* -triggered responses promote genotype-dependent conspecific repellence or attractiveness in citrus. *The New Phytologist, 207*(3), 790–804. https://doi.org/10.1111/nph.13357

Agut, B., Gamir, J., Jaques, J. A., & Flors, V. (2016). Systemic resistance in citrus to *Tetranychus urticae* induced by conspecifics is transmitted by grafting and mediated by mobile amino acids. *Journal of Experimental Botany, 67*(19), 5711–5723. https://doi.org/10.1093/jxb/erw335

Alfaro, C., Vacas, S., Zarzo, M., Navarro-Llopis, V., & Primo, J. (2011). Solid phase microextraction of volatile emissions of

Ceratitis capitata (Wiedemann) (Diptera: Tephritidae): influence of fly sex, age, and mating status. *Journal of Agricultural and Food Chemistry, 59*(1), 298–306. https://doi.org/10.1021/jf104183c

Arim, M., & Marquet, P. A. (2004). Intraguild predation: A widespread interaction related to species biology. *Ecology Letters, 7*(7), 557–564. https://doi.org/10.1111/j.1461-0248.2004.00613.x

Beran, F., Köllner, T. G., Gershenzon, J., & Tholl, D. (2019). Chemical convergence between plants and insects: Biosynthetic origins and functions of common secondary metabolites. *The New Phytologist, 223*(1), 52–67. https://doi.org/10.1111/nph.15718

Bruessow, F., Asins, M. J., Jacas, J. A., & Urbaneja, A. (2010). Replacement of CTV-susceptible sour orange rootstock by CTV-tolerant ones may have triggered outbreaks of *Tetranychus urticae* in Spanish citrus. *Agriculture, Ecosystems & Environment, 137*(1-2), 93–98. https://doi.org/10.1016/j.agee.2010.01.005

Bruin, J., Dicke, M., & Sabelis, M. W. (1992). Plants are better protected against spider-mites after exposure to volatiles from infested conspecifics. *Experientia, 48*(5), 525–529. https://doi.org/10.1007/BF01928181

Çakmak, I., Janssen, A., & Sabelis, M. W. (2006). Intraguild interactions between the predatory mites *Neoseiulus californicus* and *Phytoseiulus persimilis. Experimental & Applied Acarology, 38*(1), 33–46. https://doi.org/10.1007/s10493-005-6247-7

Cabedo-López, M., Cruz-Miralles, J., Vacas, S., Navarro-Llopis, V., Pérez-Hedo, M., Flors, V., & Jaques, J. A. (2019). The olfactive responses of *Tetranychus urticae* natural enemies in citrus depend on plant genotype, prey presence, and their diet specialization. *Journal of Pest Science, 92*(3), 1165–1177. https://doi.org/10.1007/s10340-019-01107-7

Cruz-Miralles, J., Cabedo-López, M., Pérez-Hedo, M., Flors, V., & Jaques, J. A. (2019). Zoophytophagous mites can trigger plant-genotype specific defensive responses affecting potential prey beyond predation: The case of *Euseius stipulatus* and *Tetranychus urticae* in citrus. *Pest Management Science, 75*(7), 1962–1970. https://doi.org/10.1002/ps.5309

Cruz-Miralles, J. Cabedo-López, Guzzo, M., Ibáñez-Gual, M.V., Flors, V., & Jaques, J.A. (2021a). Plant-feeding may explain why the generalist predator *Euseius stipulatus* does better on less defended citrus plants but *Tetranychus* sp.-specialists *Neoseiulus californicus* and *Phytoseiulus persimilis* do not. *Experimental & Applied Acarology, 83*, 167–182. https://doi.org/10.1007/s10493-020-00588-x

Cruz-Miralles, J., Cabedo-López, M., Guzzo, M., Pérez-Hedo, M., Flors, V., & Jaques, J. A. (2021b). Plant defense responses triggered by phytoseiid predatory mites (Mesostigmata: Phytoseiidae) are species-specific, depend on plant genotype and may not be related to direct plant feeding. *BioControl, 66*(3), 381–394. https://doi.org/10.1007/s10526-021-10077-8

Demite, P.R., Moraes, G.J. de, McMurtry, J.A., Denmark, H.A., & Castilho, R.C. (2017). Phytoseiidae Database. http://www.lea.esalq.usp.br/phytoseiidae. Accessed on 13 May 2020

Finke, D. L., & Denno, R. F. (2003). Intra-guild predation relaxes natural enemy impacts on herbivore populations. *Ecological Entomology, 28*(1), 67–73. https://doi.org/10.1046/j.1365-2311.2003.00475.x

Gish, M., De Moraes, C., & Mescher, M. C. (2015). Herbivore-induced plant volatiles in natural and agricultural ecosystems: Open questions and future prospects. *Current Opinion in Insect Science, 9*, 1–6. https://doi.org/10.1016/j.cois.2015.04.001

Janssen, A., van Alphen, J. J. M., Sabelis, M. W., & Bakker, K. (1995). Odour-mediated avoidance of competition in *Drosophila* parasitoids: The ghost of competition. *Oikos, 73*(3), 356–366. https://doi.org/10.2307/3545959

Janssen, A., Bruin, J., Jacobs, G., Schraag, R., & Sabelis, M. W. (1997). Predators use volatiles to avoid prey patches with conspecifics. *Journal of Animal Ecology, 66*(2), 223–232. https://doi.org/10.2307/6024

Janssen, A., Pallini, A., Venzon, M., & Sabelis, M. W. (1999a). Behaviour and indirect interactions in food webs of plant-inhabiting arthropods. In J. Bruin, L. P. S. van der Geest, & M. W. Sabelis (Eds.), *Ecology and Evolution of the Acari. Series Entomologica* (Vol. 55, pp. 231–249). Dordrecht: Springer; https://doi.org/10.1007/978-94-017-1343-6_16

Janssen, A., Pallini, A., Venzon, M., & Sabelis, M. W. (1999b). Absence of odour-mediated avoidance of heterospecific competitors by the predatory mite *Phytoseiulus persimilis. Entomologia Experimentalis et Applicata, 92*(1), 73–82. https://doi.org/10.1046/j.1570-7458.1999.00526.x

Jaques, J. A., Aguilar-Fenollosa, E., Hurtado-Ruiz, M. A., & Pina, T. (2015). Food web engineering to enhance biological control of *Tetranychus urticae* by Phytoseiid mites (Tetranychidae: Phytoseiidae) in citrus. In D. Carrillo, G. J. de Moraes, & J. E. Peña (Eds.), *Prospects for biological control of plant feeding mites and other harmful organisms, Progress in Biological Control 19* (pp. 251–269). Heidelberg: Springer; https://doi.org/10.1007/978-3-319-15042-0_10

Magalhaes, S., Tudorache, C., Montserrat, M., van Maanen, R., Sabelis, M. W., & Janssen, A. (2004). Diet of intraguild predators affects antipredator behavior in intraguild prey. *Behavioral Ecology, 16*(2), 364–370. https://doi.org/10.1093/beheco/arh171

McMurtry, J. A., Sourassou, N. F., & Demite, P. R. (2015). The Phytoseiidae (Acari: Mesostigmata) as biological control agents. In D. Carrillo, G. J. de Moraes, & J. E. Peña (Eds.), *Prospects for biological control of plant feeding mites and other harmful organisms, Progress in Biological Control 19* (pp. 133–149). Heidelberg: Springer; https://doi.org/10.1007/978-3-319-15042-0_5

Migeon, A., & Dorkeld, F. (2020). Spider Mites Web: a comprehensive database for the Tetranychidae. http://www.montpellier.inra.fr/CBGP/spmweb. Accessed on 13 May 2020

Moreno, P., Ambrós, S., Albiach-Martí, M. R., Guerri, J., & Peña, L. (2008). Citrus tristeza virus: A pathogen that changed the course of the citrus industry. *Molecular Plant Pathology, 9*(2), 251–268. https://doi.org/10.1111/j.1364-3703.2007.00455.x

Opitz, S. E. W., & Müller, C. (2009). Plant chemistry and insect sequestration. *Chemoecology, 19*(3), 117–154. https://doi.org/10.1007/s00049-009-0018-6

Pallini, A., Janssen, A., & Sabelis, M. W. (1998). Predators induce interspecific herbivore competition for food in refuge space. *Ecology Letters, 1*(3), 171–177. https://doi.org/10.1046/j.1461-0248.1998.00019.x

Pérez-Sayas, C., Pina, T., Gómez-Martínez, M. A., Camañes, G., Ibáñez-Gual, M. V., Jaques, J. A., & Hurtado, M. A. (2015). Disentangling mite predator-prey relationships by multiplex PCR. *Molecular Ecology Resources, 15*(6), 1330–1345. https://doi.org/10.1111/1755-0998.12409

Pina, T., Sá Argolo, P., Urbaneja, A., & Jacas, J. A. (2012). Effect of pollen quality on the efficacy of two different life-style predatory mites against *Tetranychus urticae* in citrus. *Biological Control, 61*(2), 176–183. https://doi.org/10.1016/j.biocontrol.2012.02.003

Polis, G. A., Myers, C. A., & Holt, R. D. (1989). The ecology and evolution of intraguild predation: Potential competitors that eat each other. *Annual Review of Ecology and Systematics, 20*(1), 297–330. https://doi.org/10.1146/annurev.es.20.110189.001501

Rendon, D., Taylor, P. W., & Whitehouse, M. E. S. (2019). Multiple intraguild predators reduce mortality risk of a mutual agricultural pest prey in simple, but not in complex, experimental settings. *Austral Ecology, 44*(6), 1065–1075. https://doi.org/10.1111/aec.12773

Rosenheim, J. A., Wilhoit, L. R., & Armer, C. A. (1993). Influence of intraguild predation among generalist insect predators on the suppression of herbivore population. *Oecologia, 96*(3), 439–449. https://doi.org/10.1007/BF00317517

Rowen, E., & Kaplan, I. (2016). Eco-evolutionary factors drive induced plant volatiles: A meta-analysis. *The New Phytologist, 210*(1), 284–294. https://doi.org/10.1111/nph.13804

Snyder, W. E., & Wise, D. H. (2001). Contrasting trophic cascades generated by a community of generalist predators. *Ecology, 82*(6), 1571–1583. https://doi.org/10.1890/0012-9658(2001)082[1571:CTCGBA]2.0.CO;2

Tanaka, T., Ikeda, A., Shiojiri, K., Ozawa, R., Shiki, K., Nagai-Kunihiro, N., … Matsui, K. (2018). Identification of a Hexenal Reductase That Modulates the Composition of Green Leaf Volatiles. *Plant Physiology, 178*(2), 552–564. https://doi.org/10.1104/pp.18.00632

Urbaneja-Bernat, P., Ibáñez-Gual, V., Montserrat, M., Aguilar-Fenollosa, E., & Jaques, J. A. (2019). Can interactions among predators alter the natural regulation of an herbivore in a climate change scenario? The case of *Tetranychus urticae* and its predators in citrus. *Journal of Pest Science, 92*(3), 1149–1164. https://doi.org/10.1007/s10340-019-01114-8

Wallis, C., Eyles, A., Chorbadjian, R., McSpadden Gardener, B., Hansen, R., Cipollini, D., … Bonello, P. (2008). Systemic induction of phloem secondary metabolism and its relationship to resistance to a canker pathogen in Austrian pine. *The New Phytologist, 177*(3), 767–778. https://doi.org/10.1111/j.1469-8137.2007.02307.x

The pdf version (Adobe JavaScript must be enabled) of this paper includes an electronic supplement: **Supplement Table S1, Fig. S1, S2, S3**