ECOSYSTEM SERVICES AND DISSERVICES PROVIDED BY PLANT-FEEDING PREDATORY ARTHROPODS

EDITED BY: Maria L. Pappas, George D. Broufas, Alberto Pozzebon, Carlo Duso
and Felix Wäckers
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frontiers Research Topics

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ECOSYSTEM SERVICES AND DISSERVICES PROVIDED BY PLANT-FEEDING PREDATORY ARTHROPODS

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Editorial: Ecosystem Services and Disservices Provided by Plant-Feeding Predatory Arthropods

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Editorial on the Research Topic

Ecosystem Services and Disservices Provided by Plant-Feeding Predatory Arthropods

INTRODUCTION

Omnivorous arthropods are important components of natural and agricultural settings, capable of exploiting both animal and plant food (Coll and Guershon, 2002). Certain omnivorous pests, such as herbivorous thrips, are also capable of consuming prey (Trichilo and Leigh, 1986; Agrawal et al., 1999; van Maanen et al., 2012), whereas diet mixing by zoophytophagous predators such as mirids and generalist phytoseiid mites enables their persistence in the field when prey is scarce (Coll and Guershon, 2002). Plant food exploitation may thus enhance ecosystem services such as biological control these predators provide.

In addition, among omnivorous arthropods, certain zoophytophagous predators (i.e., predators that feed on both prey and plant) have been shown to engage in plant-mediated interactions between microbes and herbivores (e.g., Battaglia et al., 2013; Prieto et al., 2017; Pappas et al., 2018) and to be strongly affected by plant-related factors such as nutritional quality and/or plant defense traits. Despite the importance and wide distribution of omnivorous predators in diverse ecosystems, research so far has mainly focused on their predation potential against key pests of crops.

This Research Topic includes studies that aim to understand and potentially improve ecosystem services provided by omnivorous arthropods. Unexplored ecosystem services as well as disservices are also addressed. Here, we highlight some of the major points arising from these studies.

ALTERNATIVE FOODS TO SUPPORT PLANT-FEEDING PREDATORS

Predatory mites of the family Phytoseiidae play key role in controlling a number of mites and insects that damage crops all over the world. McMurtry (1992) emphasized the role of generalist predatory mites and stressed their capacity to persist on plants when prey is virtually absent by exploiting alternative foods (McMurtry and Croft, 1997; McMurtry et al., 2013). An interesting contribution to this field came from the paper by Sugioka et al.. Since many generalist predatory mites feed on pollen, authors hypothesized that antioxidants in pollen could protect their germ cells from UVB radiation and radiant heat. They compared the effects of pollen or spider mites on the generalist predatory mite *Neoseiulus californicus*. Results showed that protective antioxidant components in pollen improved UVB resistance in *N. californicus*, contributing to their adaptation to solar radiation. In addition, Samaras et al. hypothesized that pollen provisioning results in efficient exploitation of marginally suitable prey species by generalist phytoseiid predators. Cattail pollen was provided as supplementary food source for the phytoseiid mite *Amblydromalus limonicus*, a biological control agent of thrips and whiteflies in greenhouse crops (Knapp et al., 2013), when feeding on a low-quality prey, the two spotted spider mite, *Tetranychus urticae*. Pollen provisioning was shown to result in reduced dispersal of *A. limonicus*, and to favor their predatory performance on spider mites suggesting that plant-based food sources may expand the range of prey species plant-feeding predators can exploit, while also increasing their efficiency in biological control.

Among predatory insects, coccinellids, have also been observed to consume non-prey foods such as nectar and pollen (Hodek et al., 2012). In their study, He and Sigsgaard assessed the effects of aphids species and Mediterranean flour moth eggs, as well as flowers, pollen, and sugar solutions on *Adalia bipunctata* performance. Results suggest that flowering plants can prolong larval survival and adult longevity when prey is absent and that sugar feeding results in adults of high lipid content. These findings highlight the role of non-prey foods in sustaining predator populations and could be useful in managing functional biodiversity in agricultural settings.

ECOSYSTEM DISSERVICES

Potential backslash of promoting zoophytophagous predators is the risk associated with damage inflicted by their phytophagy on crops (Castañé et al., 2011; Dumont et al.). In their systematic review article, Puentes et al. provide a synthesis of publications trends to determine the frequency of plant damage by omnivores and how often their impact on plants is considered or quantified in current literature. Results show that costs to plants are addressed only seldomly and current knowledge on omnivore feeding effects on plants is mainly based on studies on tomato and associated zoophytophagous biocontrol agents. In view of the presented bias, authors stress the need for negative effects on plants to be addressed in studies dealing with effects of zoophytophagous predators. They also highlight the need of studying other plant-predator systems, besides tomato, to generalize conclusions about plant costs of predator phytophagy.

Among zoophytophagous mirids, there are well-known examples where their use in biological control constitutes potential risks (Castañé et al., 2011; Puentes et al.). The work by Sanchez et al., is an attempt to shed light on the impact of *Macrolophus pygmaeus* in the real context of use. Using a complete factorial randomized design, the authors investigated the effect of *M. pygmaeus* on the reduction in the populations of tomato pests and its impact on tomato productivity in different greenhouses in the south of Spain. The results indicated that early establishment of high populations of the mirid, can provide better pest control but can also induce yield losses, and the balance between pros and cons cannot always be in favor of the use of the mirid. According to the authors, a better understanding of the factors that increase the risks associated with *M. pygmaeus* is necessary to ensure the economic viability of its use. In their review article, Dumont et al. proposed the adoption of an evolutionary approach in the optimisation of biological control services provided by plant-feeding predators. In the first part of their review article, trait-specific genetic improvement is proposed as a process to increase "services" (i.e., beneficial zoophagy), and decrease "disservices" (i.e., detrimental phytophagy) provided by zoophytophagous predators. In the second part, potential implications of the selection process on ecological interactions with the host plant, prey and competitors, and potential benefits and challenges of the evolutionary approach in the context of different biological control strategies are discussed.

Finally, Thurman et al. address the range of beneficial and harmful effects that can be generated by generalist predators, focusing on weaver ants. Weaver ants are an excellent model, as they represent the oldest example of an organism being successfully used in biological control, yet they also clearly have negative impacts by guarding honeydew producing pests, attacking other predators and pollinators and using plant shoots to build their tree nests (Way and Khoo, 1992). In this paper, the authors review the literature to assess the net outcome of these variable interactions to agricultural production. They show that the overall effect is almost exclusively positive with broad reaching benefits to crop productivity.

INTERACTIONS IN COMPLEX FOOD WEBS

Knowledge on plant-predator interactions is essential to exploit ecosystem services provided by zoophytophagous predators. Maselou et al. studied the behavioral responses of *M. pygmaeus* to volatiles emitted by host plants, in the presence/absence of prey, or floral resources. They also analyzed plant volatile blends and showed significant differences in volatiles emitted by infested and uninfested plants. These results could be useful to understand ecological interactions among mirid predators and their host plants, and to design strategies to enhance biological control. In addition, Tixier analyzed plant traits and the potential relationships between plants and phytoseiids to identify favorable plants to key predatory mite species. This approach was useful to calculate the probability to detect certain predatory mite species on crops and non-crop plants. The author suggests the involvement of plant experts in future attempts to associate plant traits (or plant phylogeny) and Phytoseiidae diversity using meta-analyses.

Indirect interactions in complex food webs between herbivores, omnivorous pests and natural enemies are the focus of the paper by Vaello et al.. It is shown that the presence of pest thrips that feed on both plants and arthropods reduces the performance of plants and aphids. Interestingly, syrphids, whose larvae are important aphid predators, but may also feed on thrips, were shown to be unaffected by thrips in terms of larval development, yet suffered reduced fecundity as adults. Moreover, adult hoverflies avoided thrips infested plants or thrips aggregation pheromones. These examples show the complex and sometimes idiosyncratic interactions in multitrophic food webs.

Underlining this, Eschweiler et al. studied the interaction in tomato between an endophytic, non-pathogenic strain of

Fusarium oxysporum (Fo162) restricted to roots, the greenhouse whitefly *Trialeurodes vaporariorum* and the zoophytophagous predator *M. pygmaeus*. Adding to recent studies highlighting the ability of beneficial soil microbes to impact the performance and behavior of aboveground zoophytophagous mirid predators via the plant (Battaglia et al., 2013; Prieto et al., 2017; Garantonakis et al., 2018; Pappas et al., 2018), they show that tomato inoculation with Fo162 results in enhanced whitefly control, increased yield and reduced number of fruits with blossom-end rot potentially providing a new preventive biological control strategy against the greenhouse whitefly.

CONCLUSIONS

In summary, this special issue provides an overview of studies dealing with omnivorous arthropods and provided ecosystem services/disservices. An attempt has been made in this special issue to identify gaps and challenges, as well as to highlight future research directions with the aim to reduce provided disservices and identify novel tools in the use of plant-feeding predators in biological pest control.

AUTHOR CONTRIBUTIONS

All authors listed have made a substantial, direct and intellectual contribution to the work, and approved it for publication.

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ORIGINAL RESEARCH
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A Pollen Diet Confers Ultraviolet-B Resistance in Phytoseiid Mites by Providing Antioxidants

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Many plant-dwelling mites including phytophagous spider mites and predacious phytoseiid mites suffer lethal deleterious effects from solar ultraviolet-B (UVB; 280–315 nm wavelength) radiation. Phytoseiid species also often feed on pollen as an alternative food source. As pollen is frequently exposed to solar radiation, it is likely to contain compounds that protect germ cells from UVB radiation and radiant heat. If phytoseiid mites can obtain these protective compounds, pollen feeding may play a role in their adaptation to UVB. In this study, we compared the potential protective effects of tea pollen, peach pollen, and *Tetranychus urticae* mites as food items in *Neoseiulus californicus*. Egg hatchability and adult female survival after UVB irradiation were higher in pollen-fed than mite-fed *N. californicus*. The major protective effects of peach pollen and tea pollen were UVB shielding effects and antioxidant capacity, respectively, and these were derived from distinctive antioxidant components. The major antioxidant in peach pollen was tri-*p*-coumaroylspermidine, although its antioxidant capacity was relatively low; instead, it effectively absorbed UVB radiation. By contrast, the major antioxidants of tea pollen were catechin and epicatechin 3-gallate, which had high antioxidant capacities. Our results indicate that the protective antioxidant components in pollen improved UVB resistance in *N. californicus*, contributing to their adaptation to solar radiation.

Keywords: UV damage, UVB resistance, catechins, tea, peach, *Neoseiulus californicus*, *Tetranychus urticae*, physical control

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INTRODUCTION

Phytophagous spider mites and predacious phytoseiid mites suffer deleterious effects from solar ultraviolet-B (UVB, 280–315 nm wavelength) radiation (Ohtsuka and Osakabe, 2009; Onzo et al., 2010; Sakai and Osakabe, 2010; Sakai et al., 2012; Tachi and Osakabe, 2012, 2014; Koveos et al., 2017). UVB radiation generates DNA lesions such as cyclobutane pyrimidine dimers (CPD) and (6–4) photoproducts (6–4PP; Wang et al., 1974; Sinha and Häder, 2002; Murata and Osakabe, 2017), as well as reactive oxygen species (ROS), such as singlet oxygen, which cause oxidative damage to DNA (Kielbassa et al., 1997; Zhang et al., 1997; Cadet et al., 2015) and lipid peroxidation (Girotti, 1998; Miyamoto et al., 2014; Morita et al., 2016; Atarashi et al., 2017). Therefore, many mites avoid UV damage by residing on the lower side of leaves (Sudo and Osakabe, 2011). Leaves contain compounds that shield against UV radiation to protect their inner organs

(Lavola et al., 1998; Rousseaux et al., 2004; Tegelberg et al., 2004; Izaguirre et al., 2007); therefore, mites below leaves are sheltered from UV (Ohtsuka and Osakabe, 2009; Sakai and Osakabe, 2010).

Spider mite species of the Genus *Panonychus* such as the citrus red mite *Panonychus citri* (McGregor), constitutively produce astaxanthin, which accumulates mainly as esters (Metcalf and Newell, 1962; Atarashi et al., 2017; Bryon et al., 2017). Astaxanthin is the most powerful antioxidant of the carotenoids (Miki, 1991; Camera et al., 2009; Hama et al., 2012). It reduces lipid peroxidation via its antioxidant effects (Atarashi et al., 2017), and thus the eggs of *P. citri* are more tolerant to UVB radiation than the eggs of the two-spotted spider mite *Tetranychus urticae* Koch (Fukaya et al., 2013). Moreover, wild-type *P. citri* females exhibit higher survival rates than albino *P. citri* females, which lack the capacity to produce astaxanthin, under thermal oxidative stress (Atarashi et al., 2017; Bryon et al., 2017), which suggests that intrinsic astaxanthin confers tolerance to UV radiation. Consequently, *Panonychus* species can use upper leaf surfaces (Foott, 1963; Jones and Parrella, 1984; Morimoto et al., 2006; Osakabe et al., 2006; Fukaya et al., 2013).

Upper leaf surfaces may also be predator-free spaces, because predacious phytoseiid mites are more vulnerable to UVB radiation than spider mites (Onzo et al., 2010; Tachi and Osakabe, 2012; Koveos et al., 2017). Nakai et al. (2018) reported that the egg hatchability and survival rate of hatched larvae of the phytoseiid mite *Neoseiulus californicus* (McGregor) after exposure to UVB radiation is higher when parent females feed on *P. citri* than when they feed on *T. urticae*. The eggs likely inherit protective compounds that their mother ingests, and non-enzymatic antioxidants may help phytoseiid mites survive exposure to UVB radiation. Spider mites are potentially reactivated from UV damage through photoenzymatic repair of DNA lesions by CPD photolyase using energy from UVA (315–400 nm wavelength) and visible lights (photoreactivation; Murata and Osakabe, 2014, 2017; Suzuki et al., 2014) though no genes of (6–4) photolyase that repairs 6–4PP are found in *T. urticae* genome (Grbić et al., 2011). Nakai et al. (2018) reported a marked photoreactivation in *N. californicus* (but see Koveos et al., 2017). The enzymes associated with photoreactivation might be protected from oxidative stresses by non-enzymatic antioxidants.

Pollen is a preferred alternative food for many phytoseiid mites, in their natural habitat and in artificial propagation for the production of biological control agents (Castagnoli and Simoni, 1999). Pollen provides nutrients for many phytoseiid mites to develop and reproduce (McMurtry and Croft, 1997; Croft et al., 1998); thus pollen availability (wind-borne pollen in many cases) affects the abundance of phytoseiid mites in the field (Addison et al., 2000; Duso et al., 2004; Villanueva and Childers, 2004). On the other hand, pollen is frequently exposed to solar radiation. Therefore, it likely contains protective compounds that protect germ cells from UVB damage caused by solar radiation (Feng et al., 2000; Koti et al., 2005; Wang et al., 2010; Zhang C. et al., 2014; Žilić et al., 2014). If phytoseiid mites obtain these protective compounds (Stewart et al., 1996), pollen feeding may contribute to their adaptation to solar UVB radiation. Moreover, because spider mites are economically important horticultural pests that have developed serious acaricide resistance, physical control of spider mites using UVB is now under development (Tanaka et al., 2016). Improving UVB resistance in phytoseiid mites is advantageous for the concurrent use of UVB and biological control in greenhouses.

In this study, we first tested a hypothesis that pollen feeding improves UVB resistance of *N. californicus*. For this purpose, we designed experiments to test questions whether pollen diet increased adult survivorship and egg hatchability after UVB irradiation. We also considered the protective effects on photoenzymatic repair system of DNA lesion and the vulnerable age specific effects in eggs. In these experiments, we compared the effects of pollen with those of a prey mite, *T. urticae*. Finally, absorbance spectra and antioxidant capacities of pollen and prey mite extracts were compared and antioxidants in pollen were identified. Consequently, we provide evidence of the importance of pollen as antioxidant source in solar adaptation.

MATERIALS AND METHODS

Mites

Neoseiulus californicus is a widespread Type II phytoseiid mite (McMurtry and Croft, 1997; Luh and Croft, 2001) used for spider mite control in horticultural crops and orchards worldwide. This mite prefers to feed on both *Tetranychus* spider mites and pollen (Castagnoli and Simoni, 1999). Therefore, it can be used to compare the effects of pollen and prey mites (*T. urticae*) on UVB resistance. The *N. californicus* population used in this study was originally established from field population collected from Matsukawa, Nagano Prefecture, Japan (35°36′ N, 137°55′ E; Toyoshima and Hinomoto, 2004) in September 2000. *T. urticae* is a pest of horticultural crops and orchards. Because it has developed resistance to most acaricides, chemical control has been difficult, and alternative management systems are sought. The *T. urticae* population used in this study is a laboratory population cultured on potted kidney bean plants at 25–28°C for more than 9 years. These mites were reared on kidney bean leaves placed on water-soaked cotton in Petri dishes in a chamber at 25°C with a photoperiod of 16:8 (L:D) h (fluorescent lights turned on at 07:00 h and off at 23:00 h). *T. urticae* and pollen were provided as food for *N. californicus*.

Pollen

We used tea (*Camellia sinensis* [L.] Kuntze) and peach (*Amygdalus persica* L.) pollen. Buds were collected from tea trees at the Kitashirakawa Experimental Field of Kyoto University, Kyoto, Japan (35°2′ N, 135°47′ E) and from peach trees of the variety "Akatsuki" from the experimental field of the Nagano Fruit Tree Experiment Station, Suzaka, Japan (36°39′ N, 138°19′ E). Anthers were detached from the buds. After anther dehiscence, tea pollen was separated from the anthers using sieves, whereas peach pollen was used together with the anthers owing to its adherence to anthers. The pollen was stored in a freezer at −20°C until use in bioassays. Pollen from both tea and peach trees was sieved, although peach pollen was adherent, and immediately used for compound extraction.

UVB Irradiation System

UVB irradiation of adult females was performed at 25°C in a laboratory illuminated with fluorescent lamps. Females on leaf disks in Petri dishes were placed on a shelf located at a distance of 0.45 m from an overhead UVB (UVB intensity: 1.43 W m^{-2}, peak weavelength: 312 nm, full width at half maximum: 28) lamp (20 W; YGRFX21701GH; Panasonic Co., Osaka, Japan; **Figure S1A**) affixed to the top of a steel rack (1.9 m high × 0.6 m wide × 0.6 m deep). Petri dishes for untreated controls were placed under UV-opaque film (HB3 polyester film, 25 μm thick; Teijin DuPont Films, Tokyo, Japan), which filtered out >90% of <380 nm wavelength and >99% of <363 nm wavelength (Sakai and Osakabe, 2010).

For experiments on eggs, we used a UVB lamp (6 W; Panasonic Co., Osaka, Japan) affixed to a shelf 0.67 m overhead (UVB intensity: 0.16 W m^{-2}; **Figure S1B**) in a dark growth chamber at 25°C. Two halogen lamps (130 W; JDR110V-85WHM/K7-H; Ushio Lighting Co. Ltd., Tokyo, Japan; **Figure S1C**) affixed to a shelf 67 cm overhead and set at a distance of 22.5 cm from the UVB lamp were used to induce photoreactivation (visible light intensity: 67.7 W m^{-2}).

Effects of Different Foods on UVB Resistance of Phytoseiid Mites

Survival of Adult Females

Five gravid adult females of *N. californicus* within 4 days after their last molt were introduced to 24 kidney bean leaf squares (3.5 × 3.5 cm) on water-soaked cotton in Petri dishes (9 cm in diameter; a leaf square per dish). We prepared three types of food source for phytoseiid mite; 8 of the 24 leaf squares contained *T. urticae* eggs (produced by 10 adult females for 24 h), tea pollen, or peach pollen. The phytoseiid mites had developed on the same food as that prepared on the leaf squares. Four of the 8 leaf squares assigned for a given food type were irradiated with UVB at intensity of 1.43 W m^{-2} (UVB+), while the remaining four leaf squares were covered with UV-opaque film on the same shelf during the UVB-irradiation (UVB-unirradiated control; UVB–). UVB irradiation was performed for 90 min (cumulative irradiance = 7.72 kJ m^{-2}) or for 180 min (15.44 kJ m^{-2}); UVB dose of the former was equivalent to the daily cumulative UVB irradiance in February and early November, and the latter was the similar to that in April and September in Kyoto City, Japan.

After irradiation, phytoseiid mites were individually moved to new leaf squares (1.5 × 1.5 cm), which contained assigned food source, on water-soaked cotton in a rectangular plastic case (10 × 19 × 2 cm). Then the *N. californicus* females were reared in the laboratory (day 0), and survival and behavior were assessed every day until day 5. Damage was determined by stimulating the females with a fine small brush and categorized as four levels: (a) walked normally, (b) walked, but sluggish, (c) did not walk, and (d) died. The prey mites and pollen were properly added during the rearing experiments. This experiment was replicated four times.

We preliminarily confirmed that the individuals that did not walk (c) never recovered and died later; thus, individuals categorized into groups (a) and (b) were grouped as survivors while those in (c) and (d) were considered dead. Prior to statistical analyses, the datasets (numbers of individuals) were combined over the 4 replications. We excluded the data for the phytoseiid mites that escaped from leaf squares from the following data analysis. Consequently, for treatments at 7.72 kJ m^{-2} irradiance, a total of 78, 69, and 78 females were evaluated in the *T. urticae*, tea pollen, and peach pollen treatments, respectively, and 79, 75, and 76 females were evaluated in the untreated control group. For treatments at 15.44 kJ m^{-2} irradiance, the numbers were 78, 77, and 77, and 77, 79, and 74, respectively.

Egg Hatchability

To determine an appropriate UVB dose for evaluating dietary effects, we tentatively tested the effects of doses of 0.174, 0.192, 0.288, and 0.408 kJ m^{-2} on the hatchability of eggs produced by mite- and tea pollen-fed *N. californicus* females. More than 90% of the eggs irradiated at 0.174 kJ m^{-2} hatched, and in contrast, almost all the eggs irradiated at 0.408 kJ m^{-2} died. Eventually, we chose a UVB dose of 0.192 kJ m^{-2} for subsequent experiments because the dietary effects were most clear at this level (**Figure S2**).

Four leaf squares (2 × 2 cm) were placed on water-soaked cotton in 6 Petri dishes. Leaf squares in 2 of the 6 Petri dishes contained *T. urticae* eggs (produced by 10 females for 24 h), tea pollen, or peach pollen. Five gravid adult *N. californicus* females were introduced to each leaf square and reared in the laboratory for egg production. The phytoseiid mites had developed on the same prey or foods as that on the leaf square. Females were removed from Petri dishes after 24 h, 1 of the 2 Petri dishes containing the same food and *N. californicus* eggs was assigned to the UVB irradiation treatment and the other was assigned to the untreated control group. The Petri dish assigned to the UVB irradiation treatment (4 leaf squares) was irradiated with UVB at 0.16 W m^{-2} for 20 min (0.192 kJ m^{-2}) in a dark growth chamber. The Petri dish for untreated controls (4 leaf squares) was put in a cardboard box and placed in a growth chamber during the UVB irradiation treatments. After UVB irradiation, the Petri dish irradiated with UVB was also put in a cardboard box to keep them in the dark and placed in the laboratory (day 0). The number of eggs hatched was counted each day until day 4. The Petri dishes were moved into a transparent plastic box on day 2 to minimize photoreactivation efficiency by the 4 h time lag between UVB irradiation and visible light irradiation of *T. urticae* (Murata and Osakabe, 2014). This experiment was replicated three times. Prior to statistical analyses, the datasets were combined over replications. Consequently, the number of eggs produced by females of *T. urticae*, tea pollen, and peach pollen diets were 100, 89, and 67, respectively, in the UVB irradiation treatment and 109, 89, and 73, respectively, in the untreated control.

Photoreactivation in Eggs

We designed three treatments for *N. californicus* eggs produced by mite-feeding females, tea pollen-feeding females, and peach pollen-feeding females: the eggs were (1) irradiated with UVB but not irradiated with visible light (UVB+/VIS–), (2) irradiated with UVB and then irradiated with visible light (UVB+/VIS+), or (3) never irradiated with either UVB or visible light (UVB−/VIS−). Three Petri dishes containing four leaf squares (2 × 2 cm) were prepared for each treatment. The leaf squares contained the same food as that females had fed on. Five gravid *N. californicus* females were introduced to each leaf square and maintained in the laboratory for 24 h. After females were removed from leaf squares, the Petri dishes assigned to (1) and (2) were irradiated with UVB at 0.16 W m^{-2} for 40 min (0.384 kJ m^{-2}) in a dark growth chamber. The Petri dishes assigned to (3) were kept in the dark in a cardboard box and placed in the growth chamber. Immediately after UVB irradiation, the Petri dishes for (1) were moved inside the cardboard box, and only the Petri dishes for (2) were irradiated with visible light for 90 min (365.58 kJ m^{-2}). Then the Petri dishes for (2) were also put into the cardboard box and placed in the laboratory (day 0). Egg hatchability was observed in the same manner as described in section Egg Hatchability. This experiment was replicated three times. Prior to statistical analyses, the datasets were combined over replications. The number of eggs produced by females of *T. urticae*, tea pollen, and peach pollen diets were 149, 134, and 96, respectively, in (1); 142, 130, and 109, respectively, in (2); and 145, 121, and 87, respectively, in (3).

Age Specific Vulnerability in Eggs

Four Petri dishes containing four leaf squares (2 × 2 cm) were prepared: two Petri dishes were assigned for each type (mite-feeding and tea pollen-feeding) of females, and prey eggs and tea pollen on the leaf squares were prepared as in section Egg Hatchability, but 20 adult *T. urticae* females were introduced to each leaf square for prey egg preparation. One of the two Petri dishes for each type was assigned to the UVB irradiation treatment and the other was the untreated control. Ten adult *N. californicus* females that developed on the same prey or pollen as on the leaf square were introduced to each square. We prepared another four Petri dishes containing six leaf squares (1 × 1 cm) without prey or pollen. Then we moved all *N. californicus* eggs laid on the 4 leaf squares in a Petri dish to one of the six squares in the new Petri dishes every 8 h until 48 h later. After 24 h, to avoid shortages of prey and pollen, the adult *N. californicus* females were moved to newly prepared leaf squares. Immediately after all operations were completed, the eggs in the Petri dishes for UVB irradiation treatment were exposed to UVB radiation at 0.16 W m^{-2} for 20 min (0.192 kJ m^{-2}) in a dark growth chamber. The Petri dishes of untreated controls were put in a cardboard box and placed in the growth chamber during UVB irradiation. Then the UVB-irradiated Petri dishes were also put in the cardboard box and placed in the laboratory (day 0). Using this method, we exposed *N. californicus* eggs categorized into six different age classes to UVB radiation at the same time: 0–8 h, 8–16 h, 16–24 h, 24–32 h, 32–40 h, and 40–48 h. Egg hatchability was observed in the same manner as described in section Egg Hatchability. This experiment was replicated three times. The average number of eggs used for each replication was 91.5 ± 8.0 (SD) and 88.3 ± 6.1 in *T. urticae*-fed UVB irradiated and untreated mites, respectively, and 81.2 ± 9.8 and 80.0 ± 12.4 in tea pollen-fed irradiated and untreated mites, respectively. To evaluate the effects of irradiation time and diet, and the interaction between the two, the hatchability in each replication was transformed as the empirical logit. To evaluate the effects of diet at each irradiation exposure duration, the datasets were combined over replications. The numbers of eggs used for 0–8 h, 8–16 h, 16–24 h, 24–32 h, 32–40 h, and 40–48 h were 81, 95, 89, 91, 105, and 88, respectively, in *T. urticae*-diet and 89, 88, 81, 82, 96, and 94, respectively, in tea pollen-diet.

UVB Shielding Effects and Antioxidant Activities of Pollen Compounds

Preparation of Extracts

Tea pollen (370 mg) and peach pollen (140 mg) from 511 and 315 buds, respectively, were collected and soaked in 20 and 15 mL methanol, respectively, for 3 days under dark conditions in the laboratory at room temperature. The resulting methanol solutions were filtrated using qualitative filter paper (No. 2; Advantec, Co., Ltd., Tokyo, Japan), and concentrated at 45°C *in vacuo* to yield 111 and 51 mg extracts from tea and peach pollen, respectively. Adult *T. urticae* females (1,600 ♀♀, 25 mg) were soaked in 8 mL methanol for 1 day. The methanol solution was centrifuged at 6,000 rpm for 15 min, and the supernatant was concentrated at 45°C *in vacuo* to yield 7.4 mg extract.

UVB Absorbing Capacity

The UVB absorbing capacity was evaluated using two methods. First, the UV spectra (280–315 nm wavelength) of the methanol solutions (10 μg extract mL^{-1}) were measured using a spectrophotometer (UV-1800; Shimadzu Co., Ltd., Kyoto, Japan), and the area under the curve (AUC) was calculated. Second, we analyzed the peak area detected at a wavelength of 300 nm by high-performance liquid chromatography (HPLC; L-7420 UV-Vis detector; Hitachi High-Tech Science Co., Tokyo, Japan) using a reverse-phase column (6 × 100 mm, 5 μm; YMC-Pack ODS-AQ311; YMC Co., Ltd., Kyoto, Japan). UV at 300 nm and shorter wavelengths kill *N. californicus* eggs, whereas UV at 310 nm and longer wavelengths do not (Tachi and Osakabe, 2014). The mobile phase was eluted with a gradient from 0.1% acetic acid/15% methanol to 0.1% acetic acid/70% methanol between 0–40 min, and isocratic 0.1% acetic acid/99.9% methanol between 40–50 min. We calculated the total peak integral values (TPV). Extracts (4 μg) from *T. urticae*, peach pollen, and tea pollen were analyzed with HPLC under the above conditions. The total areas of the peaks detected by an integrator were calculated, and the areas per 4 μg were converted into those per 1 mg fresh weight (FW).

Antioxidant Activity

We evaluated the antioxidant activities of the extracts using 1,1-diphenyl-2-picrylhydrazyl (DPPH) radical scavenging activity. Extracts were resolved with methanol, and 50 μL extract solution and 100 μL DPPH methanol solution (200 μM) were mixed in a well of a 96-well microplate. The extracts were diluted to the concentration appropriate to measure dose-response. The microplate was incubated in the dark at room temperature for 20 min. Then the absorbance of the mixture at 520 nm was measured with a microplate absorbance reader (iMark; Bio-Rad Co., Ltd., Hercules, CA, USA). Radical scavenging activities

(RSAs) were calculated using the following formula:

$$RSA = \frac{A_{control} - A_{sample} - A_{blank}}{A_{control} - A_{blank}} \times 100(\%),$$

where $A_{control}$, A_{sample}, and A_{blank} represent the absorbance at 520 nm of the control that excluded the extract in the reaction mixture, the sample, and the blank (methanol), respectively. Antioxidant activity was evaluated in terms of IC_{50} values (mg FW mL^{-1}) and EC_{50} values (μM).

Isolation and Identification of Antioxidants From Peach Pollen

The methanol extract (434 mg) of peach pollen was dissolved in 60 mL water and partitioned three times with 30 mL ethyl acetate. The aqueous layer was partitioned three times with 30 mL *n*-butanol. The ethyl acetate and *n*-butanol layers were combined and concentrated to yield viscous compounds (189 mg). These compounds were applied to a silica gel (11 g) column and eluted with mixtures of chloroform and methanol. Compounds eluted with 15% and 20% methanol were combined and concentrated to yield viscous compounds (67 mg). The compounds were applied to an ODS (18 g) column and eluted with mixtures of water and methanol. Compounds eluted with 30% methanol solution were concentrated to yield compounds (22 mg). The compounds were subjected to a preparative HPLC (column: YMC-Pack AQ-311 ODS 6 mm i.d. × 100 mm, eluent: 0.1% acetic acid/23% methanol, flow rate: 1.0 mL/min, detection: 254 nm). Compounds eluted at t_R 10.4 and 11.4 min were collected and concentrated to yield compound **2** (1 mg) and compound **3** (0.3 mg), respectively. Concentration of the fraction eluted with 30% methanol from the silica gel column yielded a yellow crystalline compound (compound **1**, 3 mg).

The concentrated methanol extract (33 mg) was dissolved in 30 mL water and partitioned with 15 mL ethyl acetate. The organic layer was concentrated to yield viscous compounds (8 mg). The compounds were subjected to a preparative HPLC (column: YMC-Pack AQ-311 ODS 6 mm i.d. × 100 mm, eluent: 50% methanol aqueous solution containing 0.1 % acetic acid, flow rate: 1.0 mL min^{-1}, detection: 254 nm). The compounds eluted at t_R 7.5, 9.5, 12.3, and 17.6 min were separately collected under darkness, and concentrated to yield compounds **4**, **5**, **6**, and **7,** respectively. For spectral analyses of the substances, we used Nuclear magnetic resonance (NMR; Bruker Avance III 400 [400 M Hz], CD_3OD; Bruker, Billerica, MA, USA) and liquid chromatography coupled with mass spectrometry (LC-MS; Waters Hclass/Xevo G2-S QTof; column: Acquity UPLC BoEH C18; Waters Co., Milford, MA, USA).

Isolation and Identification of Antioxidants From Tea Pollen

The methanol extract (58 mg) from tea pollen was dissolved in 40 mL water and partitioned three times with 15 mL ethyl acetate. Ethyl acetate-soluble compounds (8 mg) were applied to an ODS gel column (4 g, YMC-GEL-ODS-AQ, 12 nm, S-50 μm, YMC, Kyoto, Japan), and eluted with 30 mL each of 0, 10, 20, 30, 50, 70, and 100% methanol in water. Compounds (1 mg) eluted with 30% methanol were purified with an ODS HPLC column (YMC-Pack AQ-311 ODS 6 mm i.d. × 100 mm) by elution with 0.1% acetic acid/40% methanol at 1.0 mL min^{-1}, with the eluate monitored at 254 nm. A compound eluted at t_R 1.7 min was collected and concentrated to yield a trace amount of compound **10** [(+)-catechin]. Compounds (<1 mg) eluted with 50% methanol were purified with an ODS HPLC column under the above conditions. A compound eluted at t_R 2.9 min was collected and concentrated to yield a trace amount of compound **8**. Compounds (1 mg) eluted with 70% methanol were concentrated to yield a mixture (0.8 mg) of compounds **6**, **7**, and **9**. NMR and LC-MS were used for spectral analyses of the substances.

Quantification of Antioxidants

Tea pollen (73, 210, and 136 mg were used for replications) and peach pollen (37, 41, and 62 mg; replications) were newly collected and soaked in 5 mL methanol for 3 days in the dark at room temperature. Consequently, we obtained tea pollen extracts of 15, 51, and 31 mg and peach pollen extracts of 13, 16, and 22 mg. Compounds **7–10** in tea pollen extracts and compounds **1–7** in peach pollen extracts were quantified using HPLC (column: YMC-Pack AQ-311 ODS 6 mm i.d. x 100 mm, flow rate: 1.0 mL min^{-1}). The mobile phases were 0.1% acetic acid/50% methanol (detection at 254 nm) for compounds **7** and **9**, 0.1% acetic acid/35% methanol (detection at 254 nm) for compound **8**, and 0.1% acetic acid/25% methanol (detection at 254 nm) for compound **10**. The mobile phases were 0.1% acetic acid/40% methanol (detection at 272 nm) for compound **1**, 0.1% acetic acid/23% methanol (detection at 254 nm) for compounds **2** and **3**, and 0.1% acetic acid/50% methanol (detection at 254 nm) for compounds **4–7**. Quantification of each compound was performed by comparing integral values of the peak area of the samples to that of the standard compound.

Statistical Analyses

Differences in the survival of adult females, egg hatchability, and photoreactivation efficiency of eggs were evaluated by pairwise comparisons of proportions using Fisher's exact test with less conservative corrections (Benjamini and Hochberg, 1995; [BH]) using "fmsb" package (Nakazawa, 2017) in "R" software (R Core Team, 2014).

The effects of UVB irradiation timing (egg age; 2.4.4) and the diets of parent females on egg hatchability were evaluated using two-way analysis of variance (ANOVA) using the "aov" module followed by Tukey's honestly significant difference (HSD) *post hoc* test ("TukeyHSD" function in R) after conducting a Bartlett's test for homogeneity of variances ("bartlett.test" function in R). Prior to ANOVA, an empirical logit transformation was applied to the dataset (Stevens et al., 2016; Donnelly and Verkuilen, 2017). Data from 40–48 h from the age specific vulnerability in eggs were excluded from the two-way ANOVA and *post-hoc* analyses to ensure equal variance.

AUC and TPV were standardized by subtracting an average value from each raw data point and then dividing the remainder by the standard deviation prior to statistical analyses. The effects of diet and measuring methods on the UVB absorbing capacity were evaluated using a generalized linear regression model

(GLM) with the "glm" module followed by *post hoc* analyses using the Tukey method with the "glht" module of the "multcomp" package in R software.

The RSAs of methanol extracts of the diets were evaluated in the exact same way. Linear regression analyses between dose and RSA in each diet (methanol extract) were performed using "lm" module with the intercept assumed to be equal to 0.

RESULTS

Effects of Different Foods on UVB Resistance in Phytoseiid Mites

Survival of Adult Females

Symptom (b) (walked, but sluggish) appeared soon after irradiation with UVB in *N. californicus* females fed *T. urticae* (**Figures S3, S4**). Consequently, the survival rates were 45.1 and 11.8% at 7.72 and 15.44 kJ m^{-2}, respectively, after 5 days (**Figure 1**). A greater number of *N. californicus* females survived when fed pollen than when fed *T. urticae* for 5 days after UVB irradiation at both 7.72 and 15.44 kJ m^{-2} (**Figure 1**). The number of damaged individuals was higher in females fed tea pollen than in those fed peach pollen at 7.72 kJ m^{-2} (**Figure S3**), and thus the survival rate by day 5 was higher in the latter than in the former, although no statistically significant difference was detected (Fisher's exact test [BH], $P > 0.05$; **Figure 1A**). By contrast, the survival rate of females fed tea pollen was higher than that of those fed peach pollen at 15.44 kJ m^{-2} ($P < 0.05$; **Figure 1B**). Many of the surviving pollen-fed females remained at symptom of (b) (**Figure S4**). Most females (>90%; **Figure 1**) fed pollen survived for 5 days in the control (**Figures S3, S4**), whereas the survival rate of females fed *T. urticae* was lower in both experiments ($P < 0.05$; **Figures 1A,B**).

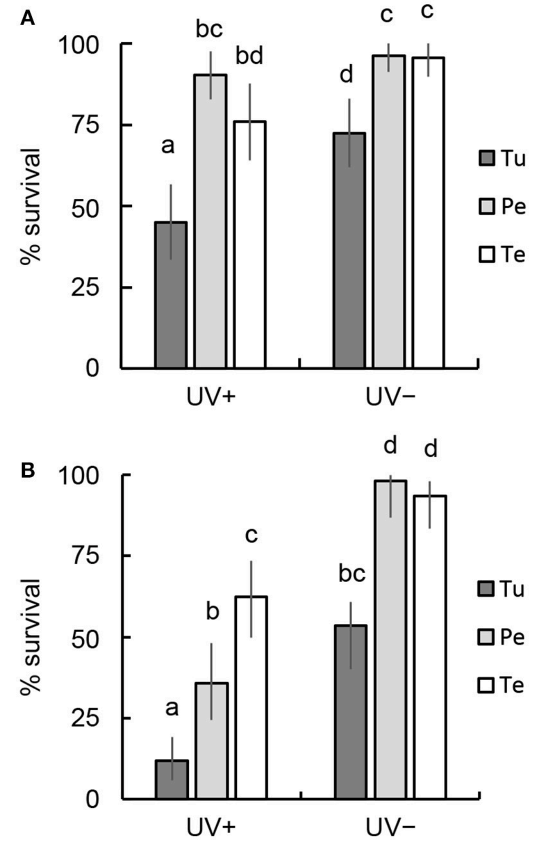

FIGURE 1 | Comparison of the survival rates of adult females fed mites or pollen for 5 days after UVB irradiation. **(A)** 7.72 kJ m^{-2}, **(B)** 15.44 kJ m^{-2}. UV+, irradiated with UVB; UV–, untreated control. Prey and food sources of parental females were *T. urticae* (Tu), peach pollen (Pe), and tea pollen (Te). The vertical lines on each bar show 95% CI. Different letters indicate statistically significant differences based on pairwise comparisons of proportions (Fisher's exact test, $P < 0.05$).

Egg Hatchability

More than 98% of untreated eggs hatched within 4 days, whereas irradiated eggs exhibited decreased hatchability (**Figure 2**). The eggs produced by *T. urticae*-fed females showed the greatest decrease in hatchability after UVB irradiation at 0.192 kJ m^{-2} (50%), whereas the degradation of the hatchability was minimal in eggs produced by tea pollen-fed females (71.9%; Fisher's exact test [BH], $P < 0.05$). The degree of degradation in hatchability was intermediate in the eggs produced by peach pollen-fed females (61.2%).

Photoreactivation in Eggs

Egg hatchability after UVB irradiation at 0.38 kJ m^{-2} without photoreactivation (UV+/VIS–; **Figure 3**) was highest in eggs from peach pollen-fed females and lowest in those from *T. urticae*-fed females (Fisher's exact test [BH], $P < 0.05$). The hatchability was markedly increased by photoreactivation induced by visible light irradiation after UVB irradiation (UV+/VIS+; **Figure 3**), and was highest in eggs from tea pollen-fed females and lowest in those from *T. urticae*-fed females ($P < 0.05$). When the eggs were not irradiated with UVB, hatchability was greater than 98% (UV–/VIS–; **Figure 3**).

Age Specific Vulnerability of Eggs

The vulnerability of eggs to UVB radiation varied by both their age [two-way ANOVA, $F_{(4, 20)} = 40.083$, $P = 2.78 \times 10^{-9}$] and the diet of parent females [$F_{(1, 20)} = 7.434$, $P = 0.013$], whereas the interaction between those factors was not significant [$F_{(4, 20)} = 0.585$, $P = 0.677$; **Figure 4**]. Eggs irradiated within 16 h after oviposition (0–8 h and 8–16 h) were more vulnerable to UVB than those treated more than 16 h after oviposition (Tukey HSD, $P < 0.05$). The effects of female diet on egg vulnerability were obvious in the early vulnerable stages at 0–8 h and 8–16 h.

UVB Shielding Effects and Antioxidant Activities of Pollen Compounds

UVB Absorbing Capacity and Antioxidant Activities of Methanol Extracts of Diets

The AUCs of tea pollen, peach pollen, and *T. urticae* were 2.54, 2.13, and 1.23 per 10 μg extract, respectively (**Figure S5**). The TPVs of tea pollen, peach pollen and *T. urticae* were 1.0×10^6, 1.7×10^6, and 1.1×10^6 per 4 μg extract, respectively

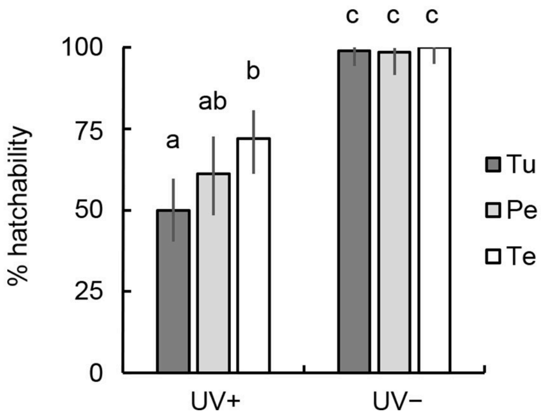

FIGURE 2 | Comparison of the hatchability of *N. californicus* eggs produced by females fed mites or pollen and irradiated with UVB at 0.192 kJ m^{-2}. UV+, irradiated with UVB; UV–, untreated control. Prey and food sources of parental females were *T. urticae* (Tu), peach pollen (Pe), and tea pollen (Te). Vertical lines on bars show 95% CI. Different letters in each bar denote statistically significant differences (Fisher's exact test, $P < 0.05$).

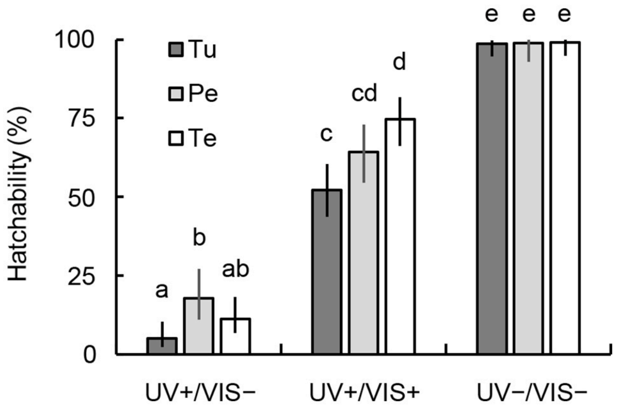

FIGURE 3 | Comparison of the hatchability of *N. californicus* eggs produced by females fed mites or pollen with and without photoreactivation after irradiation with UVB at 0.38 kJ m^{-2}. UV+, irradiated with UVB; UV–, untreated control. Prey and food sources of parental females were *T. urticae* (Tu), peach pollen (Pe), and tea pollen (Te). Vertical lines on bars show 95% CI. Different letters in each bar denote statistically significant differences (Fisher's exact test, $P < 0.05$).

(**Figure S6**). Consequently, the UVB-absorbing capacity per fresh weight (FW) was highest in peach pollen extract (AUC: 739 [mg $FW]^{-1}$, TPV: 15 × 10^7 [mg $FW]^{-1}$), second highest in tea pollen (AUC: 618 [mg $FW]^{-1}$, TPV: 6.1 × 10^7 [mg $FW]^{-1}$), and lowest in *T. urticae* (AUC: 371 [mg $FW]^{-1}$, TPV: 2.6 × 10^7 [mg $FW]^{-1}$) (Tukey method, $P < 0.01$; **Figure 5**). Pollen diets potentially have greater shielding effects against UVB radiation than mite diets.

The RSA of the methanol extracts was highest in tea pollen, followed by peach pollen and *T. urticae* (Tukey method, $P < 0.001$; **Figure 6**). The IC_{50} values per FW were 16, 7, and 1 mg FW mL^{-1} for *T. urticae*, peach pollen, and tea pollen, respectively.

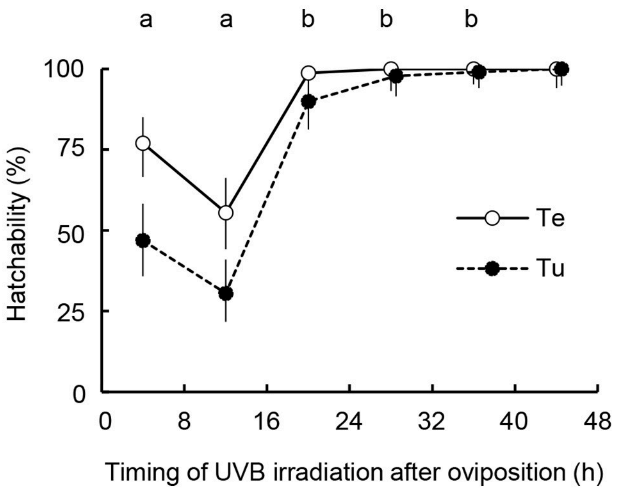

FIGURE 4 | Comparison of age specific vulnerability of *N. californicus* eggs produced by females fed mites or pollen after irradiation with UVB at 0.192 kJ m^{-2}. Prey and food sources of parental females were *T. urticae* (Tu), peach pollen (Pe), and tea pollen (Te). Each plot shows hatchability calculated from combined data over three replications. Vertical lines on bars show 95% CI. Different letters above the plot area indicate statistically significant differences between the timing of UVB irradiation using the Tukey-Kramer method ($P < 0.05$).

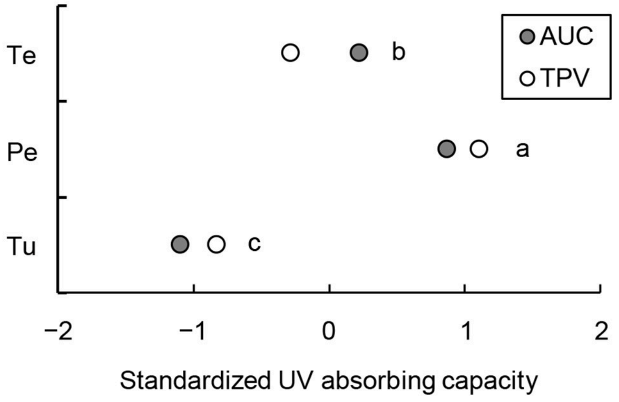

FIGURE 5 | Standardized UVB-absorbing capacity of methanol extracts from *T. urticae* (Tu), peach pollen (Pe), and tea pollen (Te). UVB-absorbing capacity measured as the area under the curve (AUC) of UV spectra at 280–315 nm wavelength by a spectrophotometer and total peak integral values (TPV) by high-pressure liquid chromatography (HPLC) equivalent to fresh weights. Different letters at the right of the plots represent statistically significant differences (Tukey method, $P < 0.01$).

Antioxidants From Peach Pollen

Using HPLC and RSA, compounds **1**–**7** with antioxidant capacity were obtained from the methanol extract of peach pollen. Compounds **1**–**3** were identified as 8-methoxykaempferol 3-*O*-sophoroside (yellow pigment), 1-*O*-feruloyl β-D-glucose, and 1-*O*-(*Z*)-feruloyl β-D-glucose, respectively, by comparing their spectral data (**Figure 7**, **Table S1**) with literature data (Harborne and Corner, 1961;

Stošić et al., 1988). Compounds **4**–**7** were identified as N^1,N^5,N^{10}-tri-*p*-(*Z,Z,Z*)-coumaroylspermidine, a mixture of N^1,N^5,N^{10}-tri-*p*-(*E,Z,Z*)-coumaroylspermidine and N^1,N^5,N^{10}-tri-*p*-(*Z,Z,E*)-coumaroylspermidine, N^1,N^5,N^{10}-(*E,Z,E*)-tri-*p*-coumaroylspermidine, and N^1,N^5,N^{10}-tri-*p*-(*E,E,E*)-coumaroylspermidine, respectively, by comparison of their spectral data (Strack et al., 1990; **Figure 7**, **Table S1**). The purified compounds **4**–**7** were easily isomerized, and gave an equilibrium mixture of **4**, **5**, **6**, and **7** at a ratio of 33:45:20:2. However, the methanol extracts from peach pollen frozen for 2 months contained compound **7** and traces of compounds **4**–**6**, which indicates that compound **7**, with a maximum absorption wavelength of 310 nm (**Figure S7**), is a major isomer in peach pollen.

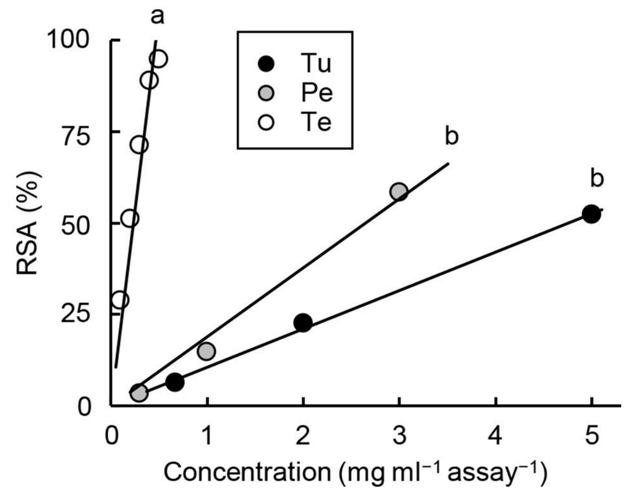

FIGURE 6 | Radical scavenging activities (RSA) of methanol extracts from *T. urticae* (Tu), peach pollen (Pe), and tea pollen (Te). Different letters on the regression line indicate statistical significance (Tukey method, $P < 0.001$). Regression line formulas are Tu: $y = 10.5x$ [SE for slope = 0.2, $r^2 = 0.999$, $F_{(1,\,2)} = 2{,}488$, $P = 0.0004$]; Pe: $y = 18.9x$ [SE for slope = 1.2, $r^2 = 0.989$, $F_{(1,\,2)} = 267.8$, $P = 0.0037$]; and Te: $y = 213.1x$ [SE for slope = 12.2, $r^2 = 0.984$, $F_{(1,\,4)} = 303$, $P = 6.39 \times 10^{-5}$].

The RSAs of compounds **1**–**3** and **7** (containing **4**–**6**) were high (EC_{50} >700 μM; **Table 1**). We tentatively compared the antioxidant activity among compounds **4**–**7** based on RSA only at 400 μM ($n = 3$) because the content of each isomer was insufficient to determine EC_{50} values. The RSA (%) increased as the *Z* isomer of the coumaroyl groups increased: 20.7 ± 1.6 (SE), 15.1 ± 2.7, 9.2 ± 2.3, and 9.2 ± 2.4 in compounds **4**, **5**, **6**, and **7**, respectively. Although its antioxidant activity was low, tri-*p*-coumaroylspermidine was often present in peach pollen, thus its contribution to the total RSA in peach pollen was highest (38%) among the constituents (7% each by **1** and 1-*O*-feruloylglucose [**2**, **3**]; **Table 1**).

Antioxidants From Tea Pollen

Compound **8**, a mixture of compounds **6**, **7**, and **9**, and compound **10** were obtained from the methanol extract of tea pollen as antioxidants, based on their RSAs. Compound **8** was identified as epicatechin 3-gallate by LC-MS and NMR

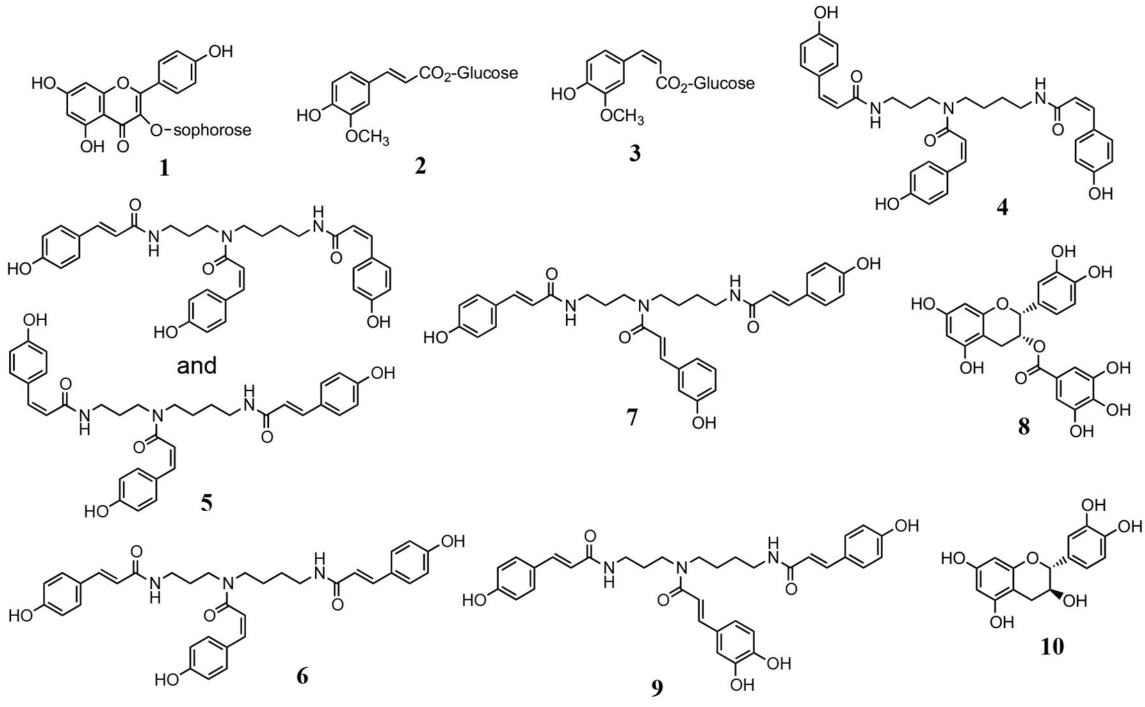

FIGURE 7 | Compounds from peach pollen (**1–7**) and tea pollen (**6–10**).

TABLE 1 | Contents, activities and maximum absorption wavelength of antioxidants in peach and tea pollens.

Compound	Content [mg (g FW)$^{-1}$] ± SD	RSA (EC$_{50}$ ± SE μM)	Maximum absorption wavelength (nm)	Contribution rate (%) for RSA
PEACH POLLEN				
8-Methoxykaempferol 3-*O*-sophoroside (**1**)	38 ± 4	>1,000	272	7
1-*O*-Feruloylglucose (**2**)	4 ± 4	787	297, 327	7
1-*O*-*cis*-Feruloylglucose (**3**)	2 ± 2		298, 328	
tri-*p*-(*EEE*)-Coumaroylspermidine (**7**)^a	34 ± 2	>1,000	299, 310	38
TEA POLLEN				
tri-*p*-(*EEE*)-Coumaroylspermidine (**7**)	2 ± 1	>1,000	299, 310	10^c
di-*p*-Coumaroyl-caffeoylspermidine (**9**)	1 ± 1	169 ± 3	296,311	
di-*p*-Coumaroyl-feruloylspermidine	–	25^b	293, 307	
Epicatechin 3-gallate (**8**)	4 ± 2	33 ± 2	279	12
(+)-Catechin (**10**)	2 ± 1	80 ± 2	–	12
POSITIVE CONTROL FOR RSA				
L-Ascorbic acid		103		

^{a}*Including **4–6**.*
^{b}*Data from Zamble et al. (2006).*
^{c}*By a mixture of tri-p-coumaroylspermidine, **9**, di-p-coumaroyl-feruloylspermidine, tilirosid, isorhamnetin 3-O-β-D-(6-p-coumaroyl) glucoside.*

(Yang et al., 2012; **Figure 7**, **Table S1**). Compounds **6** and **7** were identified as tri-*p*-coumaroylspermidine isomers, similar to the components from peach pollen, and **9** was identified as N^1,N^{10}-di-*p*-(*E,E*)-coumaroyl-N^5-(*E*)-caffeoylspermidine (Bokern et al., 1995; Yang et al., 2012; **Figure 7**, **Table S1**) by NMR and LC-MS analyses. Compound **10** (t_R 5.5 min) was identified as catechin (**Figure 7**, **Table S1**), which would be (+)-catechin, frequently found in tea leaves and flowers (Nanjo et al., 1996; Sano et al., 2001; Yang et al., 2009).

Of the comprehensive antioxidant activity in methanol extract from tea pollen, 12, 12, and 10% of the antioxidant capacity was due to compound **8**, a mixture of compound **10**, and a mixture of compounds **6**, **7**, and **9**, respectively (**Table 1**). In complex spermidines, compound **9** and di-*p*-coumaroyl-feruloylspermidine showed higher antioxidant capacities than compound **7** (**Table 1**). We tentatively confirmed the higher antioxidant capacities of caffeic acid (RSA $EC_{50} = 12\,\mu M$) and ferulic acid (20 μM) compared to *p*-coumaric acid (>1,500 μM), thus the antioxidant capacities of compound **9** and di-*p*-coumaroyl-feruloylspermidine were likely due to caffeoyl- and feruloyl-base, respectively. Catechins **8** and **10** exhibited higher antioxidant capacity and equal to or greater content than complex spermidines (**Table 1**). Therefore, catechins were the major antioxidants, rather than complex spermidines.

DISCUSSION

Interactions between plants and predators have been addressed in evolutionary scenarios of prey–predator relationships between herbivores and predators, such as sequestration of plant-derived toxins by herbivores (Koller et al., 2007; Opitz and Müller, 2009; Suzuki et al., 2011), and exploitation of herbivore-induced plant volatiles by predators (Price et al., 1980; Dicke and Baldwin, 2010; Aartsma et al., 2017). However, little attention has been paid to plant–herbivore–predator tri-trophic interactions or direct plant–predator interactions via protective compounds produced by plants in environmental adaptations of herbivores and predators that affect community development.

Solar UVB radiation has adverse effects on plants (Greenberg et al., 1989; Bothwell et al., 1994), inducing them to accumulate protective compounds in their epidermis that possibly shield against UVB penetration to mesophyll cells (Izaguirre et al., 2007). UVB-absorbing compounds that accumulate in plant leaves include flavonoids and its polymers (tannins), sinapinic acid and its esters, salicylic acid, chlorogenic acid, mycosporine-like amino acids (algae), and others (Dunlap and Shick, 1998; Clé et al., 2008; Dean et al., 2014; Khan et al., 2015; Nascimento et al., 2015; Vidović et al., 2015). Such compounds are frequently induced by UV irradiation (Logemann et al., 2000) and protect plants from oxidative stress not only through their UVB-absorbing capacity but also their antioxidant capacity (Jansen et al., 1998). As pollen is frequently exposed to solar UVB radiation, it is also protected by UVB-absorbing compounds. The content of UVB-absorbing compounds in flower organs such as ovaries is not affected by UVB irradiance, whereas the content of these compounds in pollen is increased by UVB irradiation (Day and Demchik, 1996; Santos et al., 1998; Rozema et al., 2001; Fraser et al., 2014). Moreover, pollen frequently fluoresces under ultraviolet light, whereas the petals and filaments of stamens do not (Berger, 1934; Asbeck, 1955; Pöhlker et al., 2013). Through autofluorescence, pollen may escape part of the energy of UV.

Both UVB-absorbing capacity and DPPH radical-scavenging capacity were higher in methanol extracts from pollen than from spider mites, and the extracts of peach and tea pollen showed distinctive features from each other. Peach pollen had greater UVB absorbance, whereas tea pollen had higher antioxidant capacity. Although no significant differences were detected among UVB-absorbing capacities equivalent to the weight of extracts from diets, the capacities equivalent to the FW of diets was highest in peach pollen, followed by tea pollen and then *T. urticae*, which suggests that the concentration of UVB-absorbing compounds was higher in peach pollen than in tea pollen. In peach pollen, compound **7** was the major antioxidant and presented as an *EEE* isomer, which had the lowest antioxidant capacity among its isomers. However, the absorption wavelength spectrum of compound **7** (peak at 299–310 nm) was consistent with the solar radiation wavelengths causing the largest biological impact (Coohill and Sagripanti, 2009). Peach pollen also contained substances that can shield against UVB: fluorescent substances (**2**, **3**) and a flavonoid glycoside (**1**). Tea pollen also possessed tri-*p*-coumaroylspermidine, but its content was not large compared to that in peach pollen. We found that tea pollen frequently contained catechins (**8**, **10**), as found in tea leaves and flowers (Matsuzaki and Hara, 1985; Sano et al., 2001).

Therefore, the major protective effects of peach pollen and tea pollen were UVB shielding and antioxidant capacity, respectively, and the differences in protective functions were derived from their distinctive antioxidant components. The fact that the protective function of tea pollen was more effective than that of peach pollen suggests the significance of antioxidant capacity for phytoseiid mites. Moreover, the improved hatchability after UVB irradiation of eggs from females fed pollen diets indicates that the females delivered antioxidants to their eggs. Maternal inheritance of an antioxidant essential to diapause induction, β-carotene, has been shown in the eggs of *Tetranychus* spider mites (Veerman and Helle, 1978; Veerman, 1980). In a previous study, egg hatchability and survival rate of hatched larvae after UVB radiation were higher for *N. californicus* females fed *P. citri* than for females fed *T. urticae* (Nakai et al., 2018). *P. citri* possess the strongest antioxidant among carotenoids, astaxanthin (Metcalf and Newell, 1962; Atarashi et al., 2017). Therefore, it is likely that female phytoseiid mites normally (or selectively) deliver antioxidants from food components to their eggs.

Neoseiulus californicus eggs were vulnerable to UVB radiation during the first third of egg development and resistant to UVB at later stages. In a previous study, the same pattern of vulnerability was observed in *T. urticae*: eggs 24–48 h after oviposition were most vulnerable to UVB radiation (Murata and Osakabe, 2014), the vulnerable periods corresponded with periods of embryonic development (Dearden et al., 2002). This suggests that *N. californicus* eggs were commonly vulnerable to UVB radiation at their embryonic development periods, and our findings in this study show that maternal pollen diet mitigated UVB damage during the vulnerable periods of eggs. We also found efficient photoreactivation in *N. californicus*, line with Nakai et al. (2018) (but see Koveos et al., 2017). Interestingly, maternal diet source also affected the photoreactivation efficiency of eggs. When no photoreactivation occurred after UVB irradiation, the peach pollen diet increased egg hatchability. By contrast, when photoreactivation occurred, the tea pollen diet increased hatchability, which suggests an improvement of photoreactivation function with ROS scavenging by antioxidants. The tea pollen diet also significantly increased egg hatchability in the absence of photoreactivation, and the survival of adult females under lower UVB irradiance. Therefore, the ROS scavenging function may be more effective than the shielding function for protecting phytoseiid mites from UVB damage.

Zhang G. H. et al. (2014) showed that antioxidant enzymes of *Neoseiulus cucumeris* (Oudemans) responded to oxidative thermal stress, but the effects were not always sufficient to suppress lipid peroxidation. Other studies have confirmed the responses of antioxidant enzyme systems against oxidative stress, thermal stress and UVB radiation in *P. citri*, but the effects on lipid peroxidation were not clear (Yang et al., 2010; Feng et al., 2015). *P. citri* are frequently exposed to solar UVB radiation and radiant heat owing to their characteristic distribution to the upper surfaces of host plant leaves (Jones and Parrella, 1984; Fukaya et al., 2013). Atarashi et al. (2017) demonstrated that astaxanthin and its esters suppress lipid peroxide accumulation caused by high temperatures and UVB radiation. Spider mites possess carotenoid biosynthetic genes (Altincicek et al., 2012; Bryon et al., 2013, 2017), as they take in plant compounds including carotenoids and transfer them to eggs (Bosse and Veerman, 1996; Kawaguchi et al., 2016). The protective effects of antioxidant compounds from pollen as well as astaxanthin metabolized from β-carotene in spider mites on phytoseiid mites (Veerman, 1970, 1974) provide evidence for a close relationship between the solar adaptations of the predacious mites and the host plants.

The vulnerability of *N. californicus* eggs to UVB radiation evaluated after a single acute UVB irradiation was higher than that of spider mite eggs (Tachi and Osakabe, 2012). Under intermittent UVB irradiation used for spider mite control in strawberry greenhouses (Tanaka et al., 2016), the egg hatchability of *N. californicus* is higher than that of *T. urticae*, whereas the residual effects of UVB irradiation decrease the survival of hatched larvae (Nakai et al., 2018). Our findings show that providing antioxidants improves the robustness of phytoseiid mites for use as spider mite controls, contributing to the development of integrated pest management.

Spider mites are protected from UVB radiation through the shielding effects of UVB-absorbing compounds in plant leaves and antioxidants such as carotenoids that are self-produced or obtained from plants (Sakai and Osakabe, 2010; Atarashi et al., 2017). Phytoseiid mites obtain antioxidants via prey mites (Nakai et al., 2018) and pollen diets. Therefore, the antioxidant network contributes to solar adaptation and survival strategies in plant-dwelling mite communities.

AUTHOR CONTRIBUTIONS

MO and NH planned the study described herein and wrote manuscript. MO performed the statistical analyses. NS performed bioassay and MK identified components and performed chemical and physical assays. NS and MK wrote the first partial drafts of manuscript. All authors read and approved the final draft for submission.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2018.00133/full#supplementary-material

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Pollen Provisioning Enhances the Performance of *Amblydromalus limonicus* on an Unsuitable Prey

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Amblydromalus limonicus is a polyphagous phytoseiid predator used for the biological control of thrips and whiteflies in greenhouse crops. Besides various prey species, *A. limonicus* can also feed on pollen of different plants. Cattail pollen has been previously shown to be suitable for the development and reproduction of *A. limonicus*. Hence, it could sustain its populations in periods of prey scarcity. In the present study, we hypothesized that pollen provisioning may benefit *A. limonicus* in mixed diets with prey of low quality, such as spider mites and thus, positively impact ecosystem services provided by this predator. For this, the performance and predation efficiency of *A. limonicus* against spider mites was assessed in the presence or absence of pollen. Our results show that pollen significantly shortens the developmental time and increases the survival and oviposition of the predator when mixed with spider mites, although it negatively affects its predation rate. Nevertheless, pollen enhances the maintenance of juvenile predators on the leaf by substantially decreasing their dispersal rate in the mixed diet with spider mites. In addition, the intrinsic rate of population increase (r_m) of *A. limonicus* feeding with spider mites increased with the addition of pollen suggesting an increase in its population. Cattail pollen as supplementary food may thus expand the prey species range that *A. limonicus* could exploit. It can also enhance ecosystem services provided against other pests (thrips and whiteflies) by positively affecting the increase of *A. limonicus* population.

Keywords: phytoseiids, pollen, spider mites, mixed diet, predation, performance

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INTRODUCTION

The success of biological control, an important ecosystem service provided by natural enemies is, in many circumstances, dependent on the availability, or exogenous application of alternative/supplementary foods. Plant-based foods such as nectar and pollen constitute important components of omnivorous diets of many polyphagous predators. They can function as supplemental foods in the presence of prey and as alternative foods when prey is scarce or not available in the crop (Coll and Guershon, 2002; Wäckers, 2005; Messelink et al., 2014). Thus, many omnivorous polyphagous predators rely heavily for population maintenance or build-up on the presence of plant food. These may be already available in the crop or, in the case of augmentative biological control, they are provided intentionally to enhance predator populations.

Among plant-feeding predatory arthropods, generalist predatory mites of the family Phytoseiidae include important biological control agents of key pests of crops of economic importance. Depending on the extent of their reliance of feeding on plant (pollen) and/or animal food, generalist phytoseiids are distinguished in different groups of feeding types [type III and IV according to McMurtry and Croft (1997); McMurtry et al. (2013)]. Among plant foods, the suitability of pollen of different plant species has been tested for their effects on the performance of several phytoseiids (e.g., Broufas and Koveos, 2001; Lorenzon et al., 2012; Goleva and Zebitz, 2013; Samaras et al., 2015). Due to the documented positive effects of many plant pollens, their use as supplementary or alternative foods is considered a promising method for the enhancement of biological control with the use of generalist phytoseiid species. In this context, pollen provisioning mainly aims at the early establishment and population build-up of phytoseiids as a "standing army" of natural enemies in the crop even before the arrival of the pest (Messelink et al., 2014; Pijnakker et al., 2016). Additionally, such tactic could enhance biological control achieved later on during the cropping season, because of the positive effects of the mixed diet (pollen plus prey) on the numerical response of the predators (van Rijn et al., 1999, 2002; Nomikou et al., 2002, 2010; Delisle et al., 2015b; Leman and Messelink, 2015). It can also maintain predator populations in the crop till the end of the cropping season even in the absence of prey and, thus, save growers from the additional costs required for the predator re-introduction. Other benefits of pollen provisioning include the ease of application and relatively limited problems related to its presence on the plants. To date, there is only one commercially available product of narrow-leaved cattail (*Typha angustifolia* L.) pollen (Nurimite$^{\mathrm{TM}}$, Biobest N.V.) used for enhancing phytoseiid populations in several crops (Messelink et al., 2014; Pijnakker et al., 2016).

Main problems related to pollen provisioning include the ability of certain pests to feed on pollen as well as negative effects on the predation rate of phytoseiid mites. For example, thrips (e.g., *Frankliniella occidentalis* or *Thrips tabaci*) which are key pests of several crops can also feed and reproduce on pollen of different plant species (Hulshof et al., 2003). Exogenous application of pollen to a crop with the aim to control thrips may backfire in the case the prey boosts its populations on the applied food. In addition, feeding on a mixed diet of prey and pollen may result in reduced prey consumption because of predator preference for the pollen over prey, or the frequent switching between the two components of the mixed diet (Nomikou et al., 2002, 2004, 2010; van Rijn et al., 2002). Nevertheless, both restrictions seem to be outweighed by the resulting substantial increase in the numerical response of certain predators, most possibly because of the nutritional benefits of mixed diets (Nomikou et al., 2010).

For a given species, the extent pest suppression can be enhanced by the provision of pollen may depend upon the nutritional quality of the components of a mixed diet (pollen and prey) and how this affects predator performance, besides initial predator-prey ratio (Leman and Messelink, 2015). Mixed diets consisting of two or more prey species or a mixture of pollen with prey have been shown to increase the numerical response of phytoseiid predators on prey of both high- (Nomikou et al., 2002, 2010; van Rijn et al., 2002) and low-quality (Messelink et al., 2010). Therefore, in theory, high quality pollen combined with low quality prey would positively affect biological control even in the event of decreased prey consumption per capita on the unsuitable prey (Pappas et al., 2013). On the other hand, variations in the quality of plant food (pollen) may differentially affect the numerical response of the predator on a specific prey (Samaras, 2018) and the same holds for the quality of prey.

Diet mixing is common among generalist predatory arthropods and benefits deriving from this behavior have been mainly attributed to the ability of several species to feed on prey containing different amounts of nutrients and thus actively restores nutritional imbalances in their diets (Mayntz et al., 2005). Studies on phytoseiid predatory mites have documented the positive effects of diet mixing on predator performance (e.g., Nomikou et al., 2002; van Rijn et al., 2002; Messelink et al., 2008; Pappas et al., 2013; Marques et al., 2015; Samaras et al., 2015). These can be roughly divided in two groups, the first assessing mixed diets consisting of different prey species and the second consisting of mixtures of prey with non-prey food. Our study is an addition to the second group differing, however, in that it deals with a prey species of low suitability for the predatory mite.

We hypothesized that the performance of *A. limonicus*, a generalist phytoseiid mite, could be enhanced in a mixed diet of pollen and prey. *Amblydromalus limonicus* is a natural enemy used for the biological control of thrips and whiteflies in greenhouse crops (van Houten et al., 2008; Hoogerbrugge et al., 2011; Knapp et al., 2013). Previous work has documented the high quality of cattail (*T. latifolia* and *T. angustifolia* L.) pollen as alternative food for this predator (Vangansbeke et al., 2014a,b; Samaras et al., 2015). In addition, mixed diets of prey of high quality (thrips larvae) with certain plant pollens have been shown to differentially affect *A. limonicus* population increase (Samaras, 2018). For this study, we assessed the performance of *A. limonicus* when feeding on a mixed diet consisting of cattail pollen (high quality supplementary food) with spider mites. Despite the ability of *A. limonicus* to feed on spider mites, certain species (e.g., *Tetranychus urticae*) produce dense webbing that dramatically hinders *A. limonicus* movement on and inside webs (van Houten et al., 2008). It would thus be important for *A. limonicus* to be able to consume spider mite individuals and increase its populations early enough before the rapid increase in spider mite populations and resulting webs. Moreover, in the absence of other prey, an alternative food of high quality such as cattail pollen could prove advantageous in a mixed diet with a prey of low quality, thus enabling *A. limonicus* to expand its prey range and also exploit spider mites, as was also shown in our previous work for the phytoseiid, *Phytoseius finitimus* (Pappas et al., 2013). We thus assessed the impact of pollen provisioning in a mixed diet with two-spotted spider mite *T. urticae*, a major agricultural pest (Hoy, 2011; Vacante, 2016) on the survival, development, dispersal, and reproduction of *A. limonicus*. In addition, we assessed prey consumption when *A. limonicus* fed on the mixed diet or spider mites alone.

MATERIALS AND METHODS

Predator and Herbivore Rearing

The laboratory rearing of the predatory mite *Amblydromalus limonicus* was established with adults of the commercially available product Limonica® (Koppert B.V. Berkel en Rodenrijs, The Netherlands). The predatory mites were reared on detached French bean leaves (*Phaseolus vulgaris* L.) that were placed with their upper surface on wet cotton wool in plastic cups at 26 ± 1°C and 16:8 (L:D) h. Cattail pollen (*T. latifolia* L.) was provided on the leaves as food for the mites at ∼0.01 mg/cm^2 (Samaras et al., 2015).

Spider mites (*T. urticae*) originated from a population sampled from a tomato field in Alexandria (Northern Greece) and were reared on detached bean leaves on wet cotton wool inside plastic trays. The trays were kept in a climate room at 25 ± 2°C, 16:8 LD and 60–70% RH. Fresh bean leaves were provided every three days and the trays were filled with water to maintain leaf vigor.

Pollen Diet

Cattail (*T. latifolia*) pollen was collected from flowering plants in Northern Greece, as described in Broufas and Koveos (2000). Pollen was air dried for 12 h, sieved (200 mm mesh) and stored at −20°C.

Experimental Set-Up

For the experiments, cucumber (*Cucumis sativus* L., cv Ginga F1, Geostore SA) plants were grown from seed in plastic pots (Ø 12 cm) in a climate room (25 ± 2°C, 16:8 LD, 60–70% RH). The plants were watered every other day and fertilized once a week (N-P-K, 20–20–20). When plants were 4–5 weeks old, leaf discs (3 cm in diameter) were punched out of cucumber leaves and placed with their upper surface individually on wet cotton wool in Petri dishes (5.5 cm in diameter).

Three treatments were included in our experiments: (1) spider mite-infested leaf discs (TUR), (2) pollen on spider mite-infested leaf discs (MIX), and (3) pollen on clean leaf discs (POL). To infest leaf discs with spider mites and create the desired web density simulating the onset of the development of spider mite population, five adult female spider mites were randomly chosen from the stock colony and transferred on each disc. To simulate a spider mite infestation at its early development we allowed spider mites to produce webs in the half of the leaf surface of our experimental arenas. For this purpose, half the surface of each leaf disc was covered with wet filter paper to prevent mites laying eggs and spinning web in that area. This also enabled predatory mites to easily move on the leaf discs and consume prey in all experimental treatments.

After 24 h the filter paper and the mites were removed. The leaf discs were subsequently placed individually to float on water in the cells of multi-well tissue culture plates (Corning®), each consisting of six cells (3.52 cm in diameter). Daily, fresh spider mite larvae ($n = 12$) were offered to each predator on the web-covered half part of the leaf disc after recording the developmental stage, juvenile survival, female oviposition and survival, depending on the experiment (juvenile or adult performance) as well as adult prey consumption i.e., number of dead individuals. For the POL treatment, pollen was placed on the respective half of the leaf disc that was not covered with filter paper during its preparation. Plates of all treatments were maintained in climate boxes at 26 ± 1°C and 16:8 (L:D) h. After hatching, the number of spider mite larvae was set to twelve per leaf disc.

Juvenile Development, Survival, and Dispersal

To assess the effect of pollen provisioning on the development and survival of *A. limonicus* when fed with spider mites, young adult females (3–4 days old) from the stock colony were transferred on bean leaves in plastic cups and allowed to lay eggs for 24 h. Newly hatched larvae of *A. limonicus* were placed individually on the center of the experimental leaf discs prepared as described above. Developmental stage, survival, and dispersal (predators trapped in the wet cotton barrier surrounding the leaf discs were considered as dispersing individuals) were recorded twice daily until mites reached adulthood. For each treatment 48 individuals (predatory mites, each mite on one leaf disc) were used. The effect of diet (treatment) on total developmental time was evaluated with one-way analysis of variance (ANOVA) and means were further compared with Tukey's HSD test ($P < 0.05$). Normality and homoscedasticity were checked by Kolmogorov-Smirnov and Levene's test, respectively, (SPSS, 2011). The percentages of adult emergence (juvenile survival) and cumulative dispersal rate during juvenile development among the different treatments were compared by χ^2 test.

Adult Survival, Egg Production, and Prey Consumption

To assess the effects of pollen provisioning on the performance of *A. limonicus* adults when fed with spider mites, newly molted adults were sexed and placed in pairs (one female plus one male) for 1 day for mating to occur on experimental leaf discs prepared as described above. Afterwards, the male was removed and oviposition, survival, and prey consumption of each female was recorded for the first 2 weeks of each female's life, which is the time period with the highest expected reproduction output. For each treatment, 25 replicates (adult females, each mite on one leaf disc) were used. Data for days 2–10 were only included in the analyses; day 1 data were excluded because of the presence of both males and females on the leaf discs. In addition, data for days 11–14 were excluded because of the low number of surviving individuals in the spider mite diet. To calculate progeny sex ratio, for each treatment, all eggs were collected and transferred to fresh leaf discs as above. Juveniles fed with the same type of food (spider mite larvae, spider mite larvae plus pollen, pollen) as their parents till adult emergence. A generalized linear model with a Poisson error distribution and log link function with time and diet and their interaction as factors was used to evaluate the effects on the mean daily oviposition and prey consumption rates of adult females. In case of significant differences, marginal means were further separated by pairwise comparisons between the levels of the main factor (diet) by Bonferroni test ($P < 0.05$) (SPSS, 2011).

Intrinsic Rates of Population Increase (r_m)

Calculations of the intrinsic rates of increase (r_m) of *A. limonicus* at the different treatments were performed by solving the equation: r_m = (net reproductive rate) x exp[(−$\mathrm{r_m}$) x (egg-to-egg period)] (Sabelis and Janssen, 1994), where net reproductive rate = (peak oviposition rate) x (survival in egg-to-egg period) x (sex ratio) as described in Nomikou et al. (2001).

RESULTS

Effects of Pollen Provisioning in Mixed Diet With Spider Mites on *A. limonicus* Juvenile Development, Survival, and Dispersal

Juvenile survival was significantly affected by treatment (diet) (**Figure 1A**; $\chi^2 = 47.19$, df = 2, $P < 0.001$). Spider mites alone resulted in significantly lower survival percentage compared to pollen alone (**Figure 1A**). However, mixing spider mites with pollen significantly increased juvenile survival to levels comparable to pollen alone (**Figure 1A**). Thus, providing pollen to a diet consisting of spider mites helps in adverting the negative impact of the low quality prey on *A. limonicus* survival.

We further counted the number of live mites found on the leaf discs to assess the rate of predator dispersal in the different treatments (diets). We found a significant effect of diet on the number of dispersing predators (**Figure 1B**; $\chi^2 = 37.50$, df = 2, $P < 0.001$). The highest dispersal was recorded when juveniles fed on spider mites (**Figure 1B**) which, however, decreased with the addition of pollen in a mixed diet with spider mites (**Figure 1B**).

Similarly, juvenile developmental time was significantly affected by diet (**Figure 1C**; $F = 60.17$, df = 2, 89, $P < 0.001$). Mean developmental time was significantly shorter on pollen compared to spider mites (**Figure 1C**). The addition of pollen in a mixed diet with spider mites resulted in a significant decrease in the time needed for *A. limonicus* juveniles to complete development (**Figure 1C**).

Effects of Pollen Provisioning in Mixed Diet With Spider Mites on *A. limonicus* Adult Performance and Predation Efficiency

Adult survival was significantly affected by diet (**Figure 2**, $\chi^2 = 9.15$, df = 2, $P = 0.010$). Feeding on spider mites resulted in a rapid decline in the survival of *A. limonicus* females compared to those feeding on pollen or a mixture of pollen with spider mites (**Figure 2**). No significant difference was recorded in the survival of *A. limonicus* females when these fed on pollen or mixed diet (**Figure 2**).

The numbers of eggs laid by *A. limonicus* from day 2 till day 10 of their adult life were significantly different among diets (**Figure 3A**, $\chi^2 = 69.58$, df = 2, $P < 0.001$) and with time (**Figure 3A**, $\chi^2 = 20.55$, df = 8, $P < 0.05$). On average, females laid a significantly higher number of eggs when feeding on pollen (1.6 ± 0.09 eggs/female/day) compared to those feeding on a mixed diet (1.3 ± 0.08 eggs/female/day) or spider mites (0.009 ± 0.002 eggs/female/day) (**Figure 3A**). However, the females feeding on the mixed diet laid significantly more eggs compared to those feeding on spider mites alone (**Figure 3A**). The interaction between

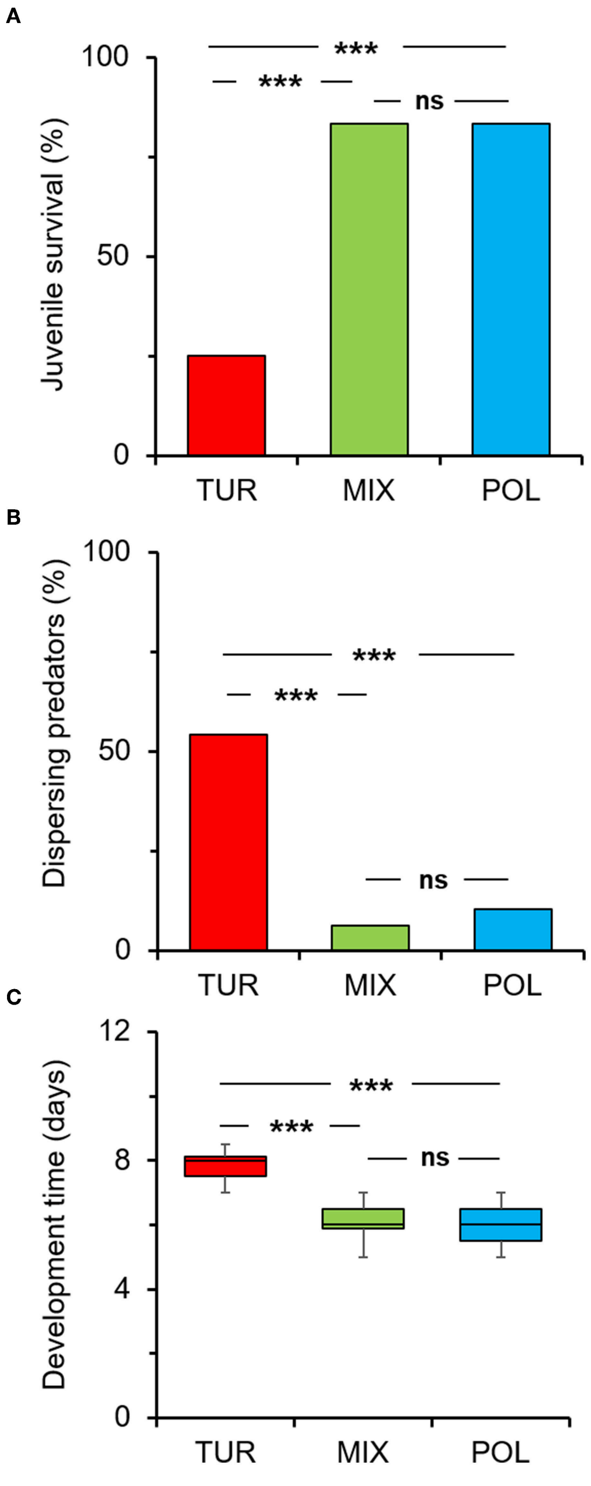

FIGURE 1 | Effects of pollen provisioning in a mixed diet with spider mites on the development and dispersal of *Amblydromalus limonicus* juveniles. Eggs laid by predator females within 24 h were individually transferred on leaf discs where juveniles ($n = 48$ per treatment) had access to either *Typha latifolia* pollen (blue bar, POL), spider mite larvae (red bar, TUR), or a mixed diet consisting of spider mite larvae plus pollen (green bar, MIX) throughout their development to adults. **(A)** Percentage of juvenile survival at reaching

(Continued)

FIGURE 1 | adulthood, **(B)** percentage of dispersing mites per leaf disc, and **(C)** developmental time in the different diets (each box plot horizontal line shows the median, upper and lower box boundaries the quartiles, and whiskers the extreme values within a category). Significant differences between treatments are indicated by asterisks; **A-B**: χ^2-test; **(C)** Tukey-HSD test: $P < 0.001$ (***), ns, not significant.

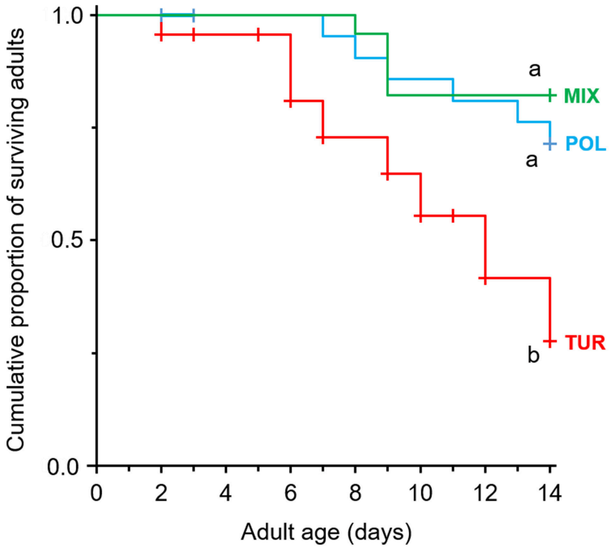

FIGURE 2 | Effects of pollen provisioning in a mixed diet with spider mites on the survival of adult *Amblydromalus limonicus*. Female adults were feeding on either *Typha latifolia* pollen (blue line, POL), spider mite larvae (red line, TUR), or a mixed diet consisting of spider mite larvae plus pollen (green line, MIX) for a period of 2 weeks. Shown are Kaplan-Meier survival curves of adults ($n = 25$ per treatment) feeding on the different diets. Significant differences between treatments are indicated by different letters by Mantel-Cox log-rank tests ($P < 0.05$). Censored observations (dispersing predators) are shown as crosses on the lines.

diet and time was not significant ($\chi^2 = 3.98$, df = 15, $P = 0.998$).

The consumption of prey (spider mites) by *A. limonicus* females was significantly affected by diet (**Figure 3B**, $\chi^2 = 53.35$, df = 1, $P < 0.001$) and not with time (**Figure 3B**, $\chi^2 = 11.27$, df = 8, $P = 0.187$). More spider mites were consumed when *A. limonicus* females had access to spider mites only (2.2 ± 0.13) than when they were also provided with pollen (1.1 ± 0.08) (**Figure 3B**). The interaction between diet and time was not significant ($\chi^2 = 8.43$, df = 8, $P = 0.392$).

Effects of Pollen Provisioning in Mixed Diet With Spider Mites on Intrinsic Rates of Increase (r_m) of *A. limonicus*

The population increase of *A. limonicus* was assessed by calculating intrinsic growth rates (r_m) values on the different diets. The highest r_m value (0.219) was recorded when predators fed on pollen, and the lowest (0.040) on the spider mite diet. Remarkably, this value increased to 0.190 when mixing spider mites with pollen suggesting a higher population increase for *A. limonicus* on the mixed diet.

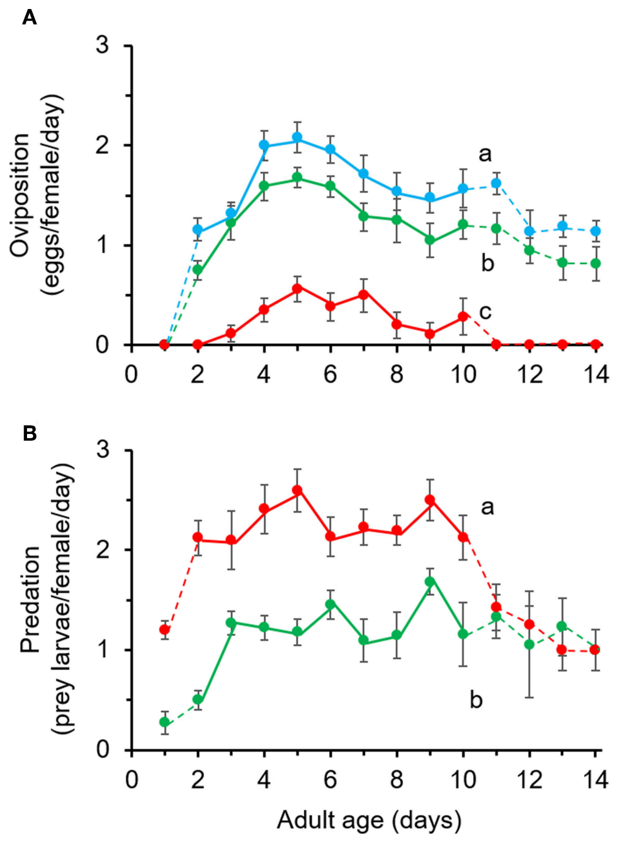

FIGURE 3 | Effects of pollen provisioning in a mixed diet with spider mites on the performance of adult *Amblydromalus limonicus*. Female adults ($n = 25$ per treatment) were feeding on either *Typha latifolia* pollen (blue line, POL), spider mite larvae (red line, TUR), or a mixed diet consisting of spider mite larvae plus pollen (green line, MIX) for a period of 2 weeks. Shown are the mean (± SE) **(A)** number of eggs per female per day and **(B)** number of consumed prey (spider mite larvae) per female per day of young female *A. limonicus* from day 2 to day 10 of their adult life. Only data shown in full lines (day 2–10) were included in statistical analyses. Per panel, lines with different letters are significantly different (GLM followed by Bonferroni test, $P < 0.001$).

DISCUSSION

Generalist phytoseiid predators are capable of exploiting both animal and plant food (McMurtry and Croft, 1997; McMurtry et al., 2013) but to which extent plant food (e.g., pollen) provisioning could affect the performance of phytoseiids that also have access to prey has been scarcely addressed so far (e.g., Nomikou et al., 2002; van Rijn et al., 2002; Messelink et al., 2010; Pappas et al., 2013). Moreover, our limited knowledge on mixed diet effects on phytoseiid performance is restricted to the preferred prey of each particular predator species, and only barely studied in combination with prey species of lower suitability [e.g., spider mites for *P. finitimus* in Pappas et al., 2013]. Our data shows that cattail pollen provisioning could enable *A. limonicus* to better exploit spider mites, a prey of lower quality than its main prey (thrips or whiteflies) via its positive effects on the population increase (r_m) of the predator when feeding on the mixed diet of pollen and spider mites.

The positive impact of pollen provisioning on juveniles and adult life-history traits recorded in our study is in agreement with previous studies with phytoseiids in which the predator performs better on a mixed diet than on the single prey component of the mixed diet. Herein however, the positive effects on *A. limonicus* oviposition were still stronger when feeding on pollen than on the mixed diet. Our study shows the ability of *A. limonicus* to overcome the nutritional limitations imposed by *T. urticae* by also feeding on pollen and does not fall in the group of studies confirming synergistic effects of mixed diet components on predator performance (e.g., Marques et al., 2015).

All life-history traits studied herein did not differ among the pollen and mixed diet treatments with the exception of female egg production which was significantly higher in the pollen diet, suggesting that no synergistic effects were recorded in our study for any of the indexes studied. As we only recorded prey consumption by the adult females, we cannot exclude the possibility that juvenile predators avoided spider mites and mainly relied their feeding on pollen alone during development, although dead spider mite individuals were regularly observed on the experimental leaf discs. On the other hand, adult females were shown to actively prey on spider mite larvae and despite prey consumption being lower in the mixed diet, it did not negatively impact adult survival but the resulting egg production by *A. limonicus* females. Overall, it seems like the overall positive effects of pollen provisioning on *A. limonicus* population increase should be mainly attributed to the enhancement of juvenile development and survival and, to a lesser extent, to increased egg production in the mixed compared to the single prey diet.

Decreased prey consumption can be an important side-effect of prey mixing with pollen that negatively impacts predation efficiency of generalist phytoseiids (van Baalen et al., 2001; Skirvin et al., 2007; Pappas et al., 2013; Leman and Messelink, 2015; Vangansbeke et al., 2016). It may be related to the predator shift exclusively toward pollen grains, which are easier to consume, requiring no energy to forage compared to prey individuals. Moreover, predator shift might also relate to the active foraging of the predator toward a more nutritious food over lower quality prey. Whereas, higher nutritional quality might only explain predator choice of pollen over low quality prey, predator shift to mainly pollen feeding might apply to both low and high quality prey species. On the other hand, active, or random consumption of variable quantities of both pollen and prey by the predator, can result to its satiation and thus, reduced prey consumption compared to predators having access to prey only. In this study, pollen provisioning to *A. limonicus* in a mixed diet with spider mites resulted in reduced spider mite consumption (**Figure 3B**). Similarly, other studies have highlighted the role of pollen in reducing prey consumption. For example, thrips consumption by the phytoseiids *Amblyseius swirskii* or *Neoseiulus cucumeris* decreased by ∼50% when predators were feeding on a mixed diet of pollen and thrips (Skirvin et al., 2007; Delisle et al., 2015a; Leman and Messelink, 2015). We herein recorded a similar percentage (52.7%) in the reduction of prey consumption by *A. limonicus* in the mixed diet compared to spider mites only. Whether this reduction is related to predator satiation or a shift toward pollen cannot be easily inferred from the results of the present study.

Overall effects of pollen provisioning on *A. limonicus* performance derived from the stronger population increase in the mixed diet compared to the diet including only prey. Such an increase suggests that, in the absence of more suitable prey, the population of the predator will still be increasing on the mixed diet but at higher rates than when fed on the low quality prey (spider mites) alone. In the long-term, pollen should increase predator/prey ratios and thus eliminate the low quality effects of the juvenile and adult food (Nomikou et al., 2004). Moreover, our results on *A. limonicus* dispersal in the different diets suggest that pollen provisioning also corroborates the maintenance of juvenile predators in the release area thus, contributing to the population increase of the predator. Similarly, diet mixing of different prey species but no plant food, can result in increased numerical response of the shared predator negatively affecting one or all of the involved prey (also termed "apparent competition") (Holt, 1977; Chaneton and Bonsall, 2000). On the other hand, "apparent mutualism" relates to the satiation of the predator and the subsequent reduction in the consumption of both prey species (Holt, 1977; Holt and Kotler, 1987). Both types of predator-mediated interactions among prey species have been recorded for phytoseiids and, time, seems to be an important determinant of the expression of either type of interaction, with apparent mutualism realized in the short-term whereas apparent competition in the long-term for the predator—prey interaction (Messelink et al., 2008, 2010; van Maanen et al., 2012; Muñoz-Cárdenas et al., 2017). In the present study, we used a mixed diet of spider mites (prey) and pollen (plant food) but the results seem to follow the general trend previously described for mixed diets consisting of prey only. Similar trends in the effects of pollen provisioning as supplementary food on phytoseiid population increase have also been demonstrated in studies (e.g., Nomikou et al., 2002, 2010; van Rijn et al., 2002; Messelink et al., 2010; Pappas et al., 2013) highlighting the importance of pollen in biological pest control.

To conclude, pollen provisioning is shown herein to enable *A. limonicus* population increase in the presence of low quality prey such as spider mites. It is thus expected that, in the long term, this initial build-up of predator population on low quality prey would enable *A. limonicus* to efficiently confront other prey species (e.g., thrips or whiteflies) arriving later in the crop. However, there are a number of restrictions that apply in the extrapolation of our results to real conditions that need to be discussed and further evaluated in future studies. Our experimental set-up was based on the assumption that the predator would have to control a spider mite population at its early development. In this situation, spider mites would produce low webbing and thus, *A. limonicus* would easily move and forage on the leaf surface. This is also particularly important for the juvenile predators, that would consume pollen grains more easily on a relatively free- than on a full-web leaf. Moreover, our set-up included only one prey species which may not be the case in certain time periods during the cropping season. Finally, as we only recorded juvenile development and adult egg production for a limited time period, future studies should include greenhouse experiments to confirm the hypothesis that *A. limonicus* would control spider mites in the long-term via increased population increase. From an applied perspective, *A. limonicus* is an important biological control agent currently used for thrips and whitefly control (van Houten et al., 2008; Hoogerbrugge et al., 2011; Knapp et al., 2013). Previous studies have demonstrated the suitability of several pollens for this predator (Vangansbeke et al., 2014b; Samaras et al., 2015) and pollen provisioning is expected to enhance its ability to control thrips (Samaras, 2018). The results of the present study add on the current literature on the effects of pollen provisioning on the numerical response of phytoseiid predatory mites but also reveal the role of cattail pollen in enhancing the ability of *A. limonicus* to also exploit a prey of low quality and thus, to possibly expand its biological control use to spider mites.

AUTHOR CONTRIBUTIONS

GB and MP conceived and designed the experiments. KS and EF performed the experiments. GB analyzed the data. MP, KS, and GB wrote the manuscript. All authors read, edited and approved the final manuscript.

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A Floral Diet Increases the Longevity of the Coccinellid *Adalia bipunctata* but Does Not Allow Molting or Reproduction

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Adalia bipunctata L. (Coleoptera: Coccinellidae) is a generalist aphidophagous coccinellid and an important natural enemy in many agroecosystems including orchards. Coccinellid species have been observed to consume non-prey food like nectar and pollen, but the value of these foods for *A. bipunctata* is poorly known. The objective of this study was to determine the effect of different prey and non-prey diets on *A. bipunctata* larval development and adult longevity and fecundity. Larval development was studied on three prey diets: The aphids *Dysaphis plantaginea* and *Myzus persicae* and Lepidopteran eggs of *Ephestia kuehniella*; five flower diets: *Matricaria chamomilla, Daucus carota, Fagopyrum esculentum, Anethum graveolens,* and *Sinapis alba*; four pollen diets from three plant species: *Typha angustifolia, Malus pumila* (two varieties) and *A. graveolens;* and 1 M solutions of three sugars: glucose, fructose, and sucrose. Adult longevity and fecundity were tested on one prey diet (*E. kuhniella* eggs), three flower diets (*F. esculentum, A. graveolens,* and *S. alba*); the same four pollen diets and three sugar diets with larvae; and finally a mixed diet of sucrose and *A. graveolens* pollen. A water-only (starvation) control was used for both larval development and adult longevity and fecundity. Adult lipid content was assessed as a measure of how non-prey food affects the ladybeetles' nutritional status. Larvae did not develop beyond the first instar on any of the non-prey diets, but they lived more than twice as long as on *F. esculentum* and sugar diets than on water. Sugar and flower diets improved *A. bipunctata* adult longevity (71–92 days and 10–66 days, respectively) over a pure pollen diet (6–7 days). Fecundity was nil on all non-prey diets, and within a normal range on *E. kuhniella* eggs. The results suggest that pure floral diets do not support *A. bipunctata* molting or reproduction, but flowering plants can prolong *A. bipunctata* larval survival and adults longevity considerably when prey are absent. Adults on sugar diets had high lipid content, indicating that sugar feeding can improve overwintering survival. The findings could be used in agroecosystem design, such as the composition of flower strips for optimal functional diversity.

Keywords: non-prey food, *Adalia bipunctata*, conservation biological control, functional biodiversity, lipid content

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INTRODUCTION

The two-spotted ladybird *Adalia bipunctata* L. (Coleoptera, Coccinellidae) is native to Europe, Central Asia and North America (Majerus, 1994), and one of the most common coccinellids in orchards (Doumbia et al., 1998; Mehrnejad et al., 2011), preferring arboreal habitats, but also found on herbaceous plants in nature (Leather et al., 1999). It is a commercially available species, widely used for aphid control in many countries (Majerus, 1994; Jalali et al., 2010) and for psyllid control (Khan et al., 2016).

Adalia bipunctata is a polyphagous predator with a wide range of prey (Omkar, 2005). *Adalia bipunctata* was observed visiting flowering plants (Free et al., 1975), and pollinivory by *A. bipunctata* in early spring has been detected by gut dissection, especially within the pollen of Rosaceae (Hemptinne and Desprets, 1986). Feeding experiments indicate that pollen represents an alternative food source, enabling females to promptly oviposit at the time of aphid population increase (Hemptinne and Desprets, 1986). Furthermore, Hemptinne and Desprets (1986) reported that *A. bipunctata* larvae completed the development on pollen of Rosaceae alone. In the laboratory, *Harmonia axyridis* (Pallas) can complete development and reproduce on bee pollen alone (Berkvens et al., 2008), whereas *Coleomegilla maculata* (DeGeer) can develop and reproduce on a diet consisting solely of maize pollen (Lundgren and Wiedenmann, 2004). Ladybeetles oviposit in aphid patches (Dixon, 1959; Mills, 1979), but the number of aphids in each patch changes over time, often dramatically, even in the absence of natural enemies (Dixon, 1985). Polyphagy may have served as an evolutionary stepping stone for primarily predaceous groups to adopt new feeding habits (Giorgi et al., 2009), and non-prey foods are probably used by coccinellids to increase survival when prey is scarce (Lundgren, 2009). Thus, the exploitation of non-prey food may expand biological control services by coccinellids.

Plants are sources of pollen and nectar and can provide a habitat for alternative prey and natural enemies too. Flowering plants have been widely used in conservation biological control (Fiedler et al., 2008; Haaland et al., 2011), and can increase natural enemies' longevity, fecundity, and predation or parasitism rates, which in turn can enhance the effectiveness of natural enemies as biocontrol agents (Lee and Heimpel, 2008; Russell, 2015; van Rijn and Wäckers, 2016). The role of pollen and nectar is well studied for hymenopteran parasitoids (e.g., Winkler et al., 2009; Russell, 2015), but increasing attention is being given to the role of non-prey food for predator fitness components such as survival or reproduction, involving studies on coccinellids (Bertolaccini et al., 2008), neuropterans (Resende et al., 2017), predatory mites (Khodayari et al., 2013; Khanamani et al., 2016; Riahi et al., 2017), spiders (Pollard et al., 1995; Nyffeler et al., 2016), and syrphids (van Rijn and Wäckers, 2016). Sugar feeding can improve fitness and performance, as well as nutritional status in coccinellids (Lundgren and Seagraves, 2011; Seagraves et al., 2011).

To contribute to the design of agricultural systems to support *A. bipunctata*, it is important to determine the value of different floral diets and their main sugar constituents for larvae and adults. Five annual flowering plants often used in flower strip mixtures, which represented four different plant families, were tested. Since *A. bipunctata* is an important predator in apple orchard and has a preference for pollen of Rosaceae (Hemptinne and Desprets, 1986), two varieties of apple pollen were included in the study, as well as cattail pollen (*Typha angustifolia*) and *A. graveolens* pollen. The major components of plant nectars are sucrose, fructose and glucose, occurring in different proportions in different plant species (Baker and Baker, 1983), and their value to a given insect species may differ. Therefore, these three sugars were also included in the study. Prey species used were the rosy apple aphid (*Dysaphis plantaginea* L.), a principal apple orchard pest of which *A. bipunctata* is a known major enemy (Wyss et al., 1999), and the peach aphid (*Myzus persicae* L.), occurring in many crops including orchards. Finally, *Ephestia kuhniella* Zeller eggs were tested, as this is a high-value prey often used in mass-rearing. The objective of this study was to determine the effect of whole floral diets, as well as selected pollens and main sugars, on life history parameters related to *A. bipunctata* immature development and adults' survival, reproduction and overwintering. Lipid content was analyzed since it is important for survival and would serve as a measure of how non-prey food affects the ladybeetles' nutritional status.

MATERIALS AND METHODS

Adalia bipunctata Rearing

Insects were taken from a laboratory stock colony at the University of Copenhagen, which started in March 2017 with eggs purchased from EWH BioProduction ApS (Tappernøje, Denmark). In the stock colony, *A. bipunctata* larvae and adults were fed on *D. plantaginea* [leaves of *Plantago lanceolata* L. (Lamiales; Plantaginaceae) infested with *D. plantaginea* were offered]. The colony was maintained in plastic containers, with ventilation holes in the lid screened with fine nylon mesh. A soaked cotton plug fitted into an Eppendorf tube served as a source of water. The stock colony was maintained in a growth chamber at 23 ± 1°C and a 16: 8 h (L: D) photoperiod. For experiments on juvenile development, *A. bipunctata* eggs were collected from the colony and placed in 14-cm Petri dishes in the same growth chamber until hatched, and larvae were isolated after hatching. Newly hatched larvae (<24 h) were used to assess larval development. Larvae were collected from 14-cm Petri dishes and given *E. kuhniella* eggs to feed on. The newly-emerged adults (<24 h) were used for the longevity and fecundity experiment.

Aphid Rearing

Dysaphis plantaginea was reared on its summer host, *P. lanceolata* (Plantain), at 20°C and 16:8 L: D photoperiod. Aphids originated from collections made on Zealand in 2015–2016 in the University of Copenhagen's Pometum and an organic orchard near Køge (Ventegodtgaard, Lille Skensved). The *M. persicae* culture was maintained on pepper plant *Capsicum annuum* var. *grossum* L. (Solanales; Solanaceae). Both *P. lanceolata* and *C. annuum* were grown in the greenhouse under L: D 16:8 conditions at a minimum of 20°C.

TABLE 1 | Information about nectar sugar content and pollen of the five plant species tested.

Species	**Sugars, mM/10 mg dry weight of flower**						**Pollen (protein %)**	**Corolla**		**References**
	Total sugar	**Fructose**	**Glucose**	**Sucrose**	**s/(g+f) ratio**	**g/f ratio**		**Depth mm**	**Width mm**	
Anethum graveolens L.	5.5	1.4	1.7	0.5	–	–	Yes	0	–	Irvin et al., 2007
Fagopyrum esculentum L.	2.5	1.3	0.9	0.2	1.5	1.0	Yes (11.4)	0.5	1.0	Somerville and Nicol, 2006; Vattala et al., 2006; Irvin et al., 2007; van Rijn and Wäckers, 2016;
Sinapis alba L.	–	–	–	–	0.02	1.2	Yes	4.5	4.3	Vattala et al., 2006
Daucus carota L.	27.2*	–	–	–	–	1.0	Yes	0	–	Hicks et al., 2016; Broussard et al., 2017
Matricaria chamomilla L.	–	–	–	–	–	–	Yes	–	–	Lunau and Wacht, 1994; Abd et al., 2007

**(μg/day) per single flower; – data not available.*

Non-prey Food

Plants

Five plant species were selected from four different plant families: Polygonaceae (*Fagopyrum esculentum* L.), Cruciferae (*Sinapis alba* L.), Apiaceae (*Daucus carota* L. and *Anethum graveolens* L.), and Asteraceae (*Matricaria chamomilla* L.) (**Table 1**). These plants are often found in flower strip mixtures. Plants were grown from seed in 13 cm pots in a greenhouse (L: D = 16:8 h, min. 20°C), and were used when flowering. Cohorts of plants were sown once a week from March to July to ensure a steady supply of flowering plants for the duration of the experiment. *D. carota, A. graveolens,* and *M. chamomilla* started flowering in May; while *F. esculentum* and *S. alba* started flowering in June.

Pollen

Four types of pollen were tested. Two varieties of apple pollen (*Malus pumila* L. Rome and *Malus pumila* L. Red Delicious; Firman Pollen Company, WA, United States); cattail pollen (*Typha angustifolia* L.; Biobest NV, Westerlo, Westerlo, Belgium) and *A. graveolens* pollen collected from flowers grown in the greenhouse. Apple pollen is easy to find on apple leaves in orchard during the flowering period (Addison et al., 2000). Cattail pollen has a high value for predatory mites mainly consisting of the family Phytoseiidae (Samaras et al., 2015), and is currently used in greenhouses (Pijnakker et al., 2015). *A. graveolens* produce abundant pollen, which is easily accessible to insects (Irvin et al., 2007). Pollen was sieved with fine mesh (thread diameter = 39 microns) prior to testing, ensuring that only pure pollen powder was used for the experiment.

Sugar Solutions

Sucrose, fructose, and glucose are major components of plant nectars (Baker and Baker, 1983), and their nutritional value to a given insect species varies. Not all mono- and oligo-saccharides are equally suitable for coccinellids (Niijima et al., 1997) therefore, 1 M solutions of two monosaccharides D-(+)-fructose and D-(+)-glucose (Merck KGaA, Darmstadt, Germany) and a disaccharide D-(+)-sucrose (Nordic Sugar, Copenhagen, Denmark) were also tested.

Experimental Design

A. bipunctata Larval Development

Fifteen different diets were tested: flowers of five species (*F. esculentum*, *S. alba*, *D. carota, A. graveolens,* and *M. chamomilla*), four types of pollen (*M. pumila* Rome, *M. pumila* Red Delicious, *T. angustifolia,* and *A. graveolens*), three sugar solutions (1 M glucose, fructose, and sucrose solutions), two species of aphids (*D. plantaginea* and *M. persicae*), and *E. kuehniella* eggs. For each treatment, 17–46 larvae were tested. Water was provided in all treatments and water-only was the starvation treatment. Larvae (<24 h) were selected randomly and placed in individual 30 ml plastic cups with a piece of fine mesh netting held in place by the rim of a lid with a hole in the center, allowing ventilation. A 1 cm layer of agar (15 g/l) in the bottom of the plastic cup provided moisture. Water and sugar solutions were provided by filling a 0.5 ml microcentrifuge tube, sealed with soaked cotton serving as a dispenser. For the aphid treatments, each cup contained a piece of a leaf from *P. lanceolata* infested with *D. plantaginea* or from *C. annuum* infested with *M. persicae*. Pollen diets were placed on a piece of filter paper on the agar layer, and *E. kuehniella* eggs and flower diets were placed on the agar layer directly. The agar served to support flowers and provided a water source, keeping the flowers fresh. Flowers were collected between 10.00 and 12.00 h while blooming in the greenhouse. Only flowers without any insect infestation were chosen. All food types were provided *ad libitum*. Flowers, pollen, aphids and *E. kuehniella* eggs were replaced daily while sugar diets were replaced every other day and water added if necessary. The plastic cups with the agar layer were replaced with new ones when the diets were replaced.

The developmental stage (first, second, third and fourth instar, pupa, and adult) and the survival of *A. bipunctata* larvae were monitored on a daily basis. The day of molting could be determined by observing the cast skins.

A. bipunctata Adult Longevity and Fecundity

Adults (<24 h) were tested with one of the following diets: Three different flowers (*A. graveolens, F. esculentum* and *S. alba*; carrot and chamomile flowers were excluded due to a shortage of flowers), four types of pollen (as above), three types of sugar solutions (1 M glucose, fructose and sucrose solution), *A. graveolens* pedicels (flower removed), and a mixed diet of sucrose solution plus *A. graveolens* pollen. The prey diet of *E. kuehniella* eggs was used as a positive control. Water was provided in all treatments and water-only was the starvation treatment. Rahaman and Aniszewski (2014) reported that *A.bipunctata* can consume young leaves or buds of legume plants when aphids are not available. The pedicel was a plant part available in the flower diet treatments, so *A. graveolens* pedicels were included to test the possible value of the pedicel for *A.bipunctata*, and to serve as an additional negative control. One or two males and one or two females (all <24 h old) were placed together in one container (plastic cup, 6 cm in diameter 7.5 cm height; with a piece of fine mesh netting held in place by the rim of a lid with a hole in the center, as above). A few days after they emerged, adults started to mate. After mating was confirmed by observing first eggs, adults were kept individually in a new 30 ml plastic cup. For each treatment, 25–55 adults were tested, fewer adults (25) were used in the *F. esculentum* flower diet because of a shortage of flowers.

In each container, flowers were provided in a small cylindrical plastic vial with water, plugged with cotton wool to prevent accidental drowning of adults. Flowers were collected between 10.00 and 12.00 h in the greenhouse. Only those without any insect infestation were chosen. Pollen and *E. kuehniella* eggs were placed on the bottom of the container, and sugar solution and water were provided by filling a 0.5 ml microcentrifuge tube, sealed with soaked cotton serving as a dispenser. All food types were provided *ad libitum*. Flowers were replaced daily, *E. kuehniella* eggs, pollen and sugar solution diets were changed every 2–3 days to maintain good quality and avoid the growth of fungi, and water was added if necessary. Containers were replaced with new ones every 2 or 3weeks.

The survival and fecundity of adults were checked daily; Dead individuals were removed and placed in a −20°C freezer for lipid analysis. *Adalia bipunctata* eggs were counted and females moved to new cups. Longevity in the *E. kuehniella* treatment was very long, and after 241 days the remaining adults in that treatment ($n = 20$) were freeze-killed. Lipid content of both dead and freeze-killed adults was determined.

Lipid Analysis

Lipid extraction of *A. bipunctata* adults, who fed on different diets, and newly emerged adults, who fed on *E. kuehniella* eggs at the larval stages, was done in a Soxhlet extractor with petroleum ether (PE) (Williams et al., 2011). Extraction time was 72 h. Prior to extraction, *A. bipunctata* adults were oven-dried at 50°C for 24 h and weighed. After lipid extraction, they were re-weighed to obtain the fat-extracted dry weight. Weighing was done on an XPR Micro and Ultra-Microbalance [readability down to 1 microgram, Mettler-Toledo (HK) MTCN, Hong Kong, China]. The mass of total lipids was calculated as the weight of each individual sample before extraction, minus the weight of the same sample after extraction.

Statistics

The Kaplan-Meier (KM) method was used to fit survival curves of each treatment, using the "surv" and "survfit" function from the "survival" package (Therneau, 2014) in R (R Core Team, 2014) and mean survival time and standard error were extracted from the curves using the "print.survfit" function from the same package. The effect of different diets on the longevity of larvae and adults was tested by Cox proportional hazards model (R function "coxph"). For adults, sex was included in models as well as the interaction effect of sex and diet, with cage as a random effect (using function "cluster") (R Core Team, 2014). Models were reduced by removing higher order non-significant interactions. The "lsmean" function was used to perform pairwise comparisons for each pair of treatments. A General Linear Model (GLM) was used for lipid comparison among treatments and sex, followed by "lsmean" for pairwise comparisons for each pair of treatments. Data are presented as mean values ± standard error (SE).

RESULTS

Larval Development

Larvae did not develop beyond the first instar in any of the non-prey diet treatments, but the survival of larval was significantly affected by diet (Cox PH, $df = 15$, $\chi^2 = 287.1$, $p < < 0.0001$). Larvae lived longer on *F. esculentum* and sugar diets than on other flower and pollen diets (**Table 2**). None of the four pollen diets differed significantly from the starvation treatment (water-only) and were all significantly poorer than all other diets with a significantly shorter survival time. Flowers of *F. esculentum*, *S. alba,* and *A. graveolens* increased the survival of larvae, especially *F. esculentum*, being slightly better than sugar diets. However, the survival of larvae fed on *D. carota* and *M. chamomilla* flowers did not differ from the starvation treatment (**Figure 1**).

Larvae that fed on prey diets completed development in approximately 17 days (**Table 2**). First and second instar stages took from 2 to 3days, third instar developmental time for larvae that fed on *M. persicae* was significantly longer than when the same larvae fed on *D. plantaginea*. The fourth instar took 4–6 days and the pupal stages lasted 4–6 days before emergence. Larvae that fed on *E. kuehniella* eggs developed significantly faster (∼1.3 days) than those on aphid diets (**Table 2**).

Adult Longevity and Fecundity

Adalia bipunctata adults longevity was significantly affected by diet (Cox proportional hazards, $df = 13$, $\chi^2 = 1135.9$, $p < < 0.0001$), however, no significant difference was found between females and males (Cox proportional hazards, $df = 1$, $\chi^2 = 2.1$, $p = 0.15$) and there was no interaction between sex and diet (**Table S1**). Adults survived on average (± *SE*) for 4.93 (±0.19) days in the starvation treatment (water-only). Adults' longevity

TABLE 2 | Developmental time (days) (mean ± SE) of *Adalia bipunctata* larvae fed on different diets.

Treatments	First instar	Second instar	Third instar	Fourth instar	Pupa	Egg-adult
Prey diets						
D. plantaginea	2.33 ± 0.14 (18)ab	1.94 ± 0.06 (18)a	1.94 ± 0.10 (18)b	5.67 ± 0.16 (18)a	5.61 ± 0.12 (18)a	17.50 ± 0.26 (18)a
M. persicae	2.00± 0.16 (20)b	1.90 ± 0.22 (20)a	2.35 ± 0.13 (20)a	5.40 ± 0.23 (20)a	5.40 ± 0.11 (20)a	17.05 ± 0.09 (20)a
E. kuehniella eggs	2.88 ± 0.08 (17)a	1.88 ± 0.12 (17)a	2.18 ± 0.13 (17)ab	4.88 ± 0.08 (17)b	4.41 ± 0.17 (17)b	16.24 ± 0.20 (17)b
Sugar solution						
Fructose	7.05 ± 0.84 (20)ab	–	–	–	–	–
Glucose	7.35 ± 0.68 (20)ab	–	–	–	–	–
Sucrose	6.70 ± 0.85 (20)ab	–	–	–	–	–
Flower diets						
A. graveolens	3.65 ± 0.39 (43)c	–	–	–	–	–
D. carota	2.30 ± 0.11 (40)d	–	–	–	–	–
F. esculentum	9.97 ± 0.67 (38)a	–	–	–	–	–
M. chamomilla	1.65 ± 0.18 (23)e	–	–	–	–	–
S. alba	4.36 ± 0.43 (36)bc	–	–	–	–	–
Pollen diets						
A. graveolens	2.05 ± 0.13 (20)de	–	–	–	–	–
M. pumila Rome	2.10 ± 0.07 (20)de	–	–	–	–	–
M. pumila Red Delicious	2.00 ± 0.10 (20)de	–	–	–	–	–
T. angustifolia	2.10 ± 0.12 (20)de	–	–	–	–	–
Water	2.00 ± 0.07 (20)d	–	–	–	–	–

Different letters within a column indicate significant differences among survival curves ($p < 0.05$). Comparisons for survival of first instar larvae were separated for prey diet and non-prey diet. The number of individuals tested in each treatment is given in parentheses (n).

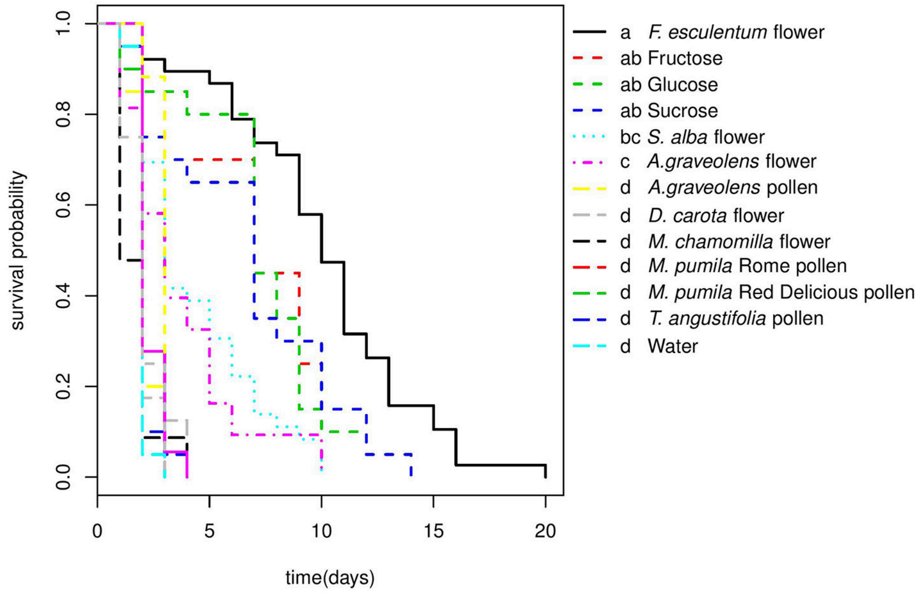

FIGURE 1 | Survival curves of *A.bipunctata* larvae fed on different non-prey diets. Different letters indicate significant differences among treatments after pairwise comparisons of the survival curves ($p < 0.05$).

on *E. kuehniella* eggs was significantly higher than all non-prey diets (**Figure 2**). Among the non-prey diet treatments, highest longevity for both sexes were obtained on sugar diets followed by *A. graveolens* and *F. esculentum* flower diets. In the presence of a 1 M sugar solution, adults survived up to 3 months. For flower diets, adults lived longer on *A. graveolens* (65.97 ± 3.43 days) and *F. esculentum* (56.04 ± 3.72 days) than on *S. alba* (10.11±0.66 days) flowers. Compared to sugar and floral diets, pure pollen diets hardly improved *A. bipunctata* longevity over that of the starvation treatment. Although, for *M. pumila* Red

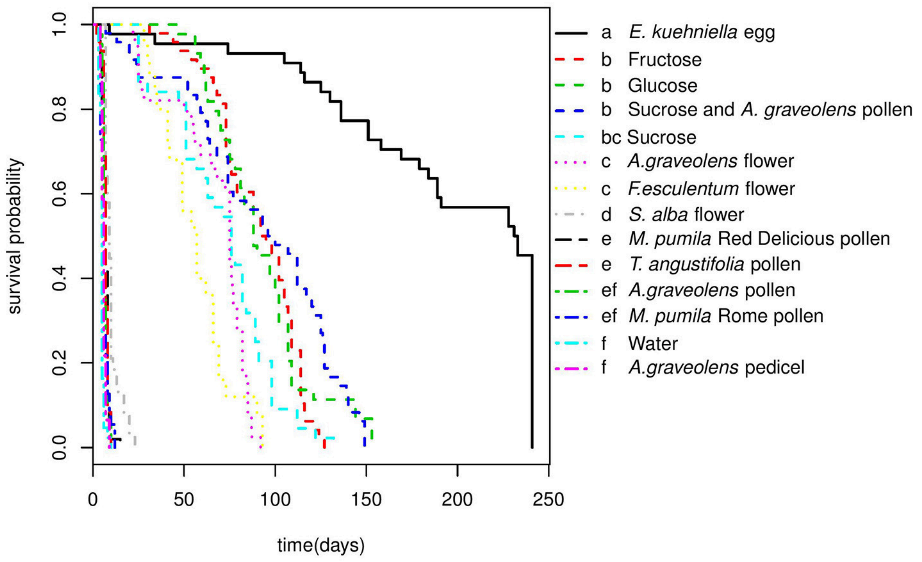

FIGURE 2 | Survival curves of *A.bipunctata* adults (females and males) fed on different diets. Different letters indicate significant differences among treatments after pairwise comparisons of the survival curves ($p < 0.05$).

Delicious and for *T. angustifolia,* the difference was significant ($z = -4.2$, $p = 0.002$; $z = -4.4$, $p = 0.001$) and increased longevity from <5 days on water to around 7 days (an increase of over 40%) (**Table 3**). Despite adults' longevity on pure pollen diets being low, longevity on the mixed diet of *A. graveolens* pollen and sucrose solution was over 40% higher than on the pure sucrose solution diet, which was equivalent to the fructose diet and only surpassed by the *E. kuehniella* diet. There was no significant difference between females and males longevity on different diets, except for the *A. graveolens* pedicel diet, with slightly longer longevity of females ($z = 2.3$, $p = 0.02$; **Table S2**).

Only females that fed on *E. kuhniella* eggs laid eggs, with an average of 699.05 ± 134.00 eggs per female, while none of the females fed on non-prey diets laid eggs (**Table 3**).

Lipid Analysis

Lipid content of adults was affected by diets ($\chi^2 = 197.5$, $p <$ <0.0001), but no significant difference was found between females and males ($\chi^2 = 0.2$, $p = 0.65$). The highest lipid levels were found in individuals fed on sucrose (25%), but it was not statistically different from individuals fed on *E. kuhniella* eggs or newly emerged adults for both females and males ($p = 0.06$ and $p = 0.26$ for females; $p = 0.06$, and $p = 0.26$ for males; **Table 4**). The lipid content of females that fed on sucrose solution was significantly higher than females that fed on fructose or glucose. No significant difference in lipid contents was found in males. Lipid content of adults that fed on sucrose solution alone was much higher than those that fed on the mixed diets of sucrose solution and *A. graveolens* pollen ($z = 9.7$, $p < 0.0001$; **Table 4**). Adults that fed on fructose or glucose solution had the same lipid content as those that fed on *A. graveolens* flowers.

DISCUSSION

In this study, the effect of different non-prey food sources (pollen, sugar solutions, and flowers) and prey diets on longevity and fecundity of *A. bipunctata* adults and survival of *A. bipunctata* larvae were tested. Larvae did not develop beyond the first instar in any of the non-prey diet treatments but could survive up to 10 days on a non-prey diet (**Table 2**). Adults fecundity was nil on all non-prey diets, but non-prey diets increased longevity up to 92 days (**Table 3**). High lipid content was found in adults that fed on sugar solutions (**Table 4**).

None of the four pollen diets differed significantly from the starvation treatment for *A. bipunctata* larval development (**Figure 1**). For adults, *M. pumila* (Red Delicious) and *T. angustifolia* pollen significantly increased longevity by 2 days over water, which was equivalent to a 40% increase in longevity, but still inferior to other non-prey diets (**Table 3**). The larval developmental rate of *A. bipunctata* is mainly dependent on the quality and quantity of food and temperature (Wratten, 1973; Omkar, 2005; Jalali et al., 2010). Hemptinne and Desprets (1986) reported that *A. bipunctata* larvae completed the development on pollen of Rosaceae, although the development time was longer than on a prey diet. Similar results were found for *Harmonia axyridis* (Pallas) provided with a frozen, moist honeybee pollen diet (Berkvens et al., 2008). *Coleomegilla maculata* (DeGeer) can develop and reproduce on a diet consisting solely of maize pollen (Lundgren and Wiedenmann, 2004). On the contrary, in a study conducted by Amala and Yadav (2013), the effects of five different diets on the developmental time of larval *Stethorus rani* (Coleoptera, Coccinellidae) were studied. They found that *S. rani* larvae that fed on a pollen diet had the lowest larval survival percentage compared to other diets and failed to develop to the pupal stage, but those fed on honey and extrafloral nectaries

TABLE 3 | Longevity (days) and fecundity (mean ± SE) of *A. bipunctata* adults fed on different diets.

Treatments	Longevity			Fecundity (eggs/female)
	Females	Males	Females and males	
Sugar solution				
Fructose	95.08 ± 4.25 (24)b	86.17 ± 4.95 (24)bc	90.62 ± 3.32 (48)b	–
Glucose	89.10 ± 4.58 (29)bc	98.60 ± 7.80 (15)b	92.34 ± 4.08 (44)b	–
Sucrose	69.92 ± 5.55 (25)cd	72.58 ± 6.31 (19)bcd	71.07 ± 4.17 (44)bc	–
Flower diets				
A. graveolens	64.17 ± 4.70 (23)d	68.56 ± 4.87 (16)cd	65.97 ± 3.43 (39)c	–
F. esculentum	57.29 ± 5.32 (14)d	54.45 ± 5.04 (11)d	56.04 ± 3.72 (25)c	–
S. alba	10.67 ± 0.88 (24)e	9.14 ± 0.89 (14)e	10.11 ± 0.66 (38)d	–
Pollen diets				
A. graveolens	6.60 ± 0.22 (30)f	6.23 ± 0.40 (13)fg	6.49 ± 0.20 (43)ef	–
M. pumila Rome	6.27 ± 0.41 (33)fg	5.27 ± 0.37 (22)fg	5.87 ± 0.29 (55)ef	–
M. pumila Red Delicious	7.17 ± 0.38 (30)f	6.85 ± 0.31 (20)ef	7.04 ± 0.26 (50)e	–
T. angustifolia	7.09 ± 0.30 (32)f	6.81 ± 0.27 (16)ef	7.00 ± 0.22 (48)e	–
Other diets				
A. graveolens pedicel	6.06 ± 0.23 (31)fg	5.27 ± 0.22 (15)g	5.80 ± 3.43 (39)f	–
E. kuehniella eggs	193.70 ± 13.44 (22)a	191.21 ± 13.42 (22)a	193.48 ± 13.29 (44)a	699.05 ± 134.00 (22)
Sucrose and *A. graveolens* pollen	100.84 ± 8.41 (25)b	83.22 ± 7.53 (23)bcd	92.40 ± 5.82 (48)b	–
Water	4.74 ± 0.19 (31)g	5.42 ± 0.45 (12)efg	4.93 ± 0.19 (43)f	–

*Different letters within a column indicate significant differences among survival curves ($p < 0.05$, **Table S3**). Cox proportional hazard model (R function "coxph") was used. The number of individuals tested in each treatment is given in parentheses (n). No adults fed on non-prey diets lay eggs.*

completed development. *Harmonia axyridis* failed to complete its development or reproduce when fed exclusively on fruit (apple, pear, and raspberries) and fungi, although larval, and adult survival were prolonged when fruit was offered compared with only water (Berkvens et al., 2010). Ladybeetles developed better when offered a mixed diet compared to pollen alone (De Clercq et al., 2005; Berkvens et al., 2008; Bonte et al., 2010; Amala and Yadav, 2013). Possible explanations for the contrasting results in this study and those of Hemptinne and Desprets (1986), may be the different nutritional value of pollen tested. Mixed pollen of Rosaceae was provided in the Hemptinne and Desprets (1986) study, but in the present study, only pollen of one plant species was provided, and the paper does not state if it was bee-pollen or hand-collected pollen. Bee-collected pollen always possesses a higher nutritional value than pollen collected by hand, because it contains larger amounts of sugars from the honey or nectar in the fluid used to cement the grains together (Lunden, 1954; Linskens and Jorde, 1997). Different nutritional requirements of the species tested could also explain inconsistencies in the results. Previous studies indicate that pollen could enable *A. bipunctata* females to promptly oviposit at the time of aphid population increase (Hemptinne and Desprets, 1986). Our results show that pollen diets increased adult longevity by 19–43% compared to starvation (water-only), but not as much as floral and sugar diets, pointing to the need for adults to have access to sugars. However, the value of pollen was also clearly shown by the fact that *A. graveolens* pollen added to a sucrose sugar diet increased adult longevity by over 30% compared to the pure sugar diet.

Sugar solutions prolonged the developmental time of larvae and improved *A. bipunctata* adult longevity (**Tables 2**, **3**). Sugars are easily digestible high-energy foods, and can dramatically increase survival of coccinellids in the absence of prey (Matsuka et al., 1982; Dreyer et al., 1997). In this study, adults that fed on glucose lived longer than those that fed on sucrose. Niijima et al. (1997) mentioned that not all mono- and oligo-saccharides are equally suitable for coccinellids. Sugar-feeding did not support reproduction in this study. A similar result was reported by Smith and Krischik (1999), who found that sugar-feeding seldom supported reproduction in coccinellids on its own. However, sugar consumption can shorten pre-oviposition periods of coccinellids and help females to survive reproductive diapause (Reznik and Vaghina, 2006). The high lipid content of adults that fed on sugars (**Table 4**) supports this finding and also points to the value of sugars in building lipid reserves for survival in periods without prey and for overwintering.

Adalia bipunctata larval survival and adult longevity on flower diets of different species varied greatly (**Table 3**). The accessibility and quality of the nectar and pollen are important factors that affect the relative preference of natural enemies for specific plant species (Hogg et al., 2011; van Rijn and Wäckers, 2016). The nutritional composition differs among different plant species (**Table 1**). *Adalia graveolens* and *F. esculentum* flowers increased the longevity of adults compared to the starvation treatment, but did not support egg production. The results are in accordance with Togni et al. (2016), who found that when given access to coriander (Coriandrum sativum) flowers increased adult longevity but not reproduction of the coccinellid

TABLE 4 | Lipid content (%) (Mean ± SE) of *Adalia bipunctata* adult fed on different diets.

Treatments	**Lipid content %**		
	Males	**Females**	**Males and females**
Sugar solution			
Fructose	16.94 ± 5.59 (8)abc	14.56 ± 5.17 (8)bc	15.75 ± 3.69 (16)bc
Glucose	13.81 ± 4.36 (8)abcd	7.39 ± 2.04 (8)cd	10.6 ± 2.47 (16)cd
Sucrose	23.92 ± 6.11 (7)a	25.97 ± 4.87 (8)a	25.01 ± 3.72 (15)a
Flower diets			
A. graveolens	10.17 ± 2.44 (8)bcde	7.9 ± 0.98 (8)cd	9.04 ± 1.3 (16)cde
F. esculentum	1.31 ± 0.28 (6)de	5.88 ± 3.68 (8)cd	3.92 ± 2.14 (14)de
S. alba	2.99 ± 2.06 (8)de	1.71 ± 0.5 (7)d	2.39 ± 1.1 (15)de
Pollen diets			
A. graveolens	2.14 ± 0.43 (8)de	1.93 ± 0.47 (8)d	2.04 ± 0.31 (16)e
M. pumila Rome	3.89 ± 2.8 (7)cde	4.17 ± 2.43 (8)cd	4.04 ± 1.78 (15)de
M. pumila Red Delicious	2.23 ± 0.31 (8)de	1.8 ± 0.17 (8)d	2.01 ± 0.18 (16)e
T. angustifolia	4.28 ± 1.74 (8)cde	3.8 ± 1.56 (8)cd	4.04 ± 1.13 (16)de
Other diets			
A. graveolens pedicel	1.86 ± 0.46 (8)de	2.51 ± 0.32 (7)d	2.16 ± 0.29 (15)de
E. kuehniella eggs	19.67 ± 1.52 (8)ab	20.85 ± 0.6 (8)ab	20.26 ± 0.8 (16)ab
Sucrose and *A. graveolens* pollen	0.72 ± 0.05 (8)e	0.66 ± 0.09 (8)d	0.69 ± 0.05 (16)e
Newly emerged adults (larvae were fed on *E. kuhniella* eggs)	21.54 ± 1.28 (6)ab	22.43 ± 1.84 (6)ab	21.99 ± 1.07 (12)ab
Water	3.49 ± 0.39 (8)de	2.6 ± 0.58 (8)d	3.05 ± 0.36 (16)de

Different letters within a column indicate significant differences among treatments ($p < 0.05$). The number of individuals tested in each treatment is given in parentheses (n). General Linear Model (GLM) was used.

Cycloneda sanguinea. The two best-performing flowers in our study, *A. graveolens* and *F. esculentum*, both have well-exposed nectaries, making predator access easy. Sugar content is dominated by fructose and glucose in both *A. graveolens* and *F. esculentum* nectar, and *A. graveolens* has more total sugars than *F. esculentum* (Irvin et al., 2007). While we found no difference between the three sugars for larval survival, adults survived longer on fructose and glucose than on sucrose. These findings suggest that planting flowers such as *A. graveolens* and *F. esculentum* with accessible nectaries and with more fructose and glucose in the nectar would better support *A. bipunctata* than sucrose-dominated flowers.

Some compounds in nectar can be toxic or repellent to flower visitors (Adler, 2000; Wäckers, 2001). For example, glucosinolates (GLS) are present in all parts of Brassicaceae crop species (Merritt, 1996), even in nectar (Bruinsma et al., 2014), inducing deleterious effects on *A. bipunctata* (Francis et al., 2001). This may explain why *A. bipunctata* adults that fed on white mustard flower lived much shorter than those that fed on *A. graveolens* and *F. esculentum*.

Larvae performed poorly on all flower diets except *F. esculentum* (**Table 2**). Although considerable amounts of pollen can be found on the chamomile flower, the nectaries are hidden in a capitulum (Patt et al., 1997), so chamomile may have served as a pure pollen diet, which corresponds with the survival of larvae fed on pollen diets. Restricting the access of predators to nectar can reduce their survival and fitness considerably (Lundgren and Seagraves, 2011; Portillo et al., 2012; van Rijn and Wäckers, 2016). Feeding on *D. carota* flowers can selectively benefit some insects, such as the parasitoid *Cotesia glomerata* (Winkler et al., 2009), while some others such as the lacewing *Chrysoperla carnea* and the herbivore *Pieris rapae* (Lepidoptera: Pieridae) do not benefit (Winkler et al., 2009; Gonzalez et al., 2016). The nectar is accessible and dominated by glucose and fructose (Broussard et al., 2017) but *A. bipunctata* larvae did not benefit from *D. carota* flowers in this study. The reasons for the poor performance of *A. bipunctata* larvae provided with *M. chamomilla* and *D. carota* flower diets, as well as for the poor performance of larvae on pure pollen diets remain speculative but are consistent with the central role of sugars for *A. bipunctata* survival in the absence of prey. While pollen as a pure diet has little value for *A. bipunctata* larvae, and limited value for adults, adult longevity on a sucrose diet supplemented with pollen numerically exceeded the sum of the longevity on sucrose and pollen separately, pointing to a nutritional value of pollen in mixed diets. Evans et al. (1999) and Soares et al. (2004) also reported that ladybeetles benefited from mixed diets.

In this study, lipid content of newly-emerged adults, presumably stored during larval development, was also analyzed. The lipid content of adults that fed on sucrose solution did not differ from that of adults that fed on *E. kuhniella* eggs or newly emerged adults (larvae were fed on *E. kuhniella* eggs) and was significantly higher than of starved individuals (water only). On the contrary, the lipid content of adults fed on pollen diets was significantly lower than that of newly emerged adults but did not differ from that of starved individuals. The lipid reserves in adults fed on water or pollen diets were consumed in a few days, which suggests that sugars contribute to maintain lipid levels, but pollen does not (**Table 4**). In this study, lipid content of adults that fed on sucrose solution was much higher than those that fed on a mixed diet sucrose solution and *A. graveolens* pollen. On the contrary, higher lipid content has been observed in hoverflies that fed on honey and pollen, compared to those that fed on honey alone (Pinheiro et al., 2015). The inconsistency of the results could be due to the different species tested or to *A. bipunctata*'s physiological processes. This should be addressed in future studies.

The results of the present study emphasize the importance of non-prey foods for *A. bipunctata* in agroecosystems such as orchards when prey populations are low. Sugar solutions and flowering plants, especially *F. esculentum* and *A. graveolens*, can prolong *A. bipunctata*longevity, but floral diets did not support adult fecundity. Flowers and sugars could also increase immature survival, though they did not support molting. Whether flowering plants attract or retain *A. bipunctata* in a habitat *per se* is not known, but our results show that longevity of *A. bipunctata* is greatly prolonged by floral diets. In the field, flowering plants may also host alternative prey, which would support both larval development and adult fecundity. Flowering plants can enhance the effectiveness of natural enemies by increasing natural enemies' longevity, fecundity, and predation or parasitism rates (Lee and Heimpel, 2008; Russell, 2015; van Rijn and Wäckers, 2016), and have been widely used in conservation biological control (Fiedler et al., 2008; Haaland et al., 2011). Addison et al. (2000) found pollen to be abundant on apple leaves very soon after the leaves had opened, and predatory mites can use windborne pollen released from cover crops in the field (Warburg et al., 2018). Nectar is also available in apple flowers during flowering in orchards (Toth et al., 2003). However, the effects of floral diets on *A. bipunctata* may decrease in the field due to various abiotic and biotic conditions (Brody, 1997; Adler et al., 2006). Analyses of lipid contents of adults that fed on different diets point to the potential of sugars to contribute toward better winter survival of the adults.

In conclusion, floral diets can prolong *A. bipunctata* longevity, which may expand biological control services by *A. bipunctata*. Further studies on whether prey deprivation might affect the future ability of *A. bipunctata* to provide biocontrol services are needed for conservation biological control. A limitation of this study is that larvae were deprived of prey at the very first instar; however, ladybeetles would lay eggs near an aphid colony and it is rare that the first instar would face the total absence of prey. Further studies on a diet switch (from prey diet to pollen diet on the third/fourth instar) would be especially relevant, since an aphid colony may become extinct before the larvae complete their development (Dixon, 1985). Further studies on prey and non-prey mixed diets are needed in order to obtain a better understanding of the value of non-prey diets in cases where prey is limited in the field. Furthermore, because of various abiotic and biotic conditions, studies on how to provide non-prey foods in cropping systems to improve biological control agents' efficiency are needed for conservation biological control.

DATA ACCESSIBILITY STATEMENT

The dataset supporting this article has been deposited in zenodo at: https://doi.org/10.5281/zenodo.2546385.

AUTHOR CONTRIBUTIONS

XH and LS conceived the study. XH carried out the lab work and wrote the first draft of the manuscript. XH and LS interpreted the results and wrote the manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2019.00006/full#supplementary-material

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A Systematic Review on the Effects of Plant-Feeding by Omnivorous Arthropods: Time to Catch-Up With the Mirid-Tomato Bias?

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Zoophytophagous (omnivorous) predators provide valuable pest control services, and offer an advantage over strict carnivores as plant-feeding enables survival during prey shortage. This putative advantage can potentially be their downside, as plant-feeding may entail damage that negatively affects plant growth/yield (i.e., the cost arising from of omnivore plant-feeding). Yet, benefits conferred by predatory services are usually thought to counterbalance any impact of plant damage. In this systematic review, our goal was to determine how often levels of omnivore damage and its consequences for plants (costs) are considered or quantified. We provide a synthesis of publication trends and findings on omnivore plant-feeding levels, plant injury variables, actual (if quantified) and potential effects on growth/yield, the type of study (lab, greenhouse) and the plants/omnivores most often examined. Our search revealed that measures of omnivore plant-feeding are occasionally reported, but seldom are the direct consequences of such damage also considered. Omnivore plant-feeding were reported in 57% of studies (53 of 93 full-text examined); within these, the majority (>80%) indicated moderate to high levels of plant-feeding. However, only 22% of reports (15 of 69) quantified the effects of omnivore-inflicted damage on plant performance. Of these 15 reports, a greater number found negative consequences for plants compared to those showing no effect (8 vs. 4; 3 with both), with consequences for yield relative to growth being more often evaluated (6 vs. 2). Overall, fruit/leaf injuries relative to stem/flower-feeding were most often examined, and lab/greenhouse experiments predominated. Tomatoes (*Solanum lycopersicum*) and the mirid *Nesidiocoris tenuis* were the most common species studied (34 and 14 reports, respectively). Our results indicate that costs to plants of omnivore-inflicted damage are often neglected. We argue that predatory benefits need to be simultaneously considered with plant-feeding effects to appropriately evaluate pest control services. Publication trends suggest that more studies are evaluating costs to plants, but a paradigm shift is still needed. Furthermore, we found that our understanding of plant-feeding and its effects is disproportionally based on studies examining tomato plants and its omnivorous biocontrol agents. To confirm the generality of findings thus far, other plant omnivore systems should be further considered.

Keywords: biocontrol, omnivore, phytozoophagy, plant indirect defense, plant-feeding, plant injury, tri-trophic interactions, zoophytophagy

INTRODUCTION

Prey and plant-feeding omnivorous arthropods are increasingly being recognized as providers of valuable and effective pest control services (Albajes and Alomar, 1999; Perdikis et al., 2011; Ågren et al., 2012; Zappala et al., 2013; Pérez-Hedo and Urbaneja, 2015; Beitia et al., 2016; van Lenteren et al., 2018a). Several species of omnivorous predators have proven to be key biocontrol agents of economically-important herbivores, for example in tomato, sweet pepper, and willow crops (Dalin et al., 2011; Calvo et al., 2012; Messelink et al., 2015) and show great promise even for potential invading pests (Pérez-Hedo et al., 2017). One of their main advantages as an alternative or complement to other natural enemies, is that plant-feeding enables their establishment and maintenance before pest infestation or during prey shortage. Consequently, the effects associated with the use of plant-food for omnivore performance/preference and prey suppression have received much attention (Naranjo and Gibson, 1996; Coll and Ruberson, 1998; Sanchez et al., 2004; Lundgren, 2009; Stenberg et al., 2011; Maselou et al., 2014; Perdikis and Arvaniti, 2016; Liman et al., 2017). Indeed, plant-feeding has well-documented positive effects on omnivore development, longevity and fecundity (reviewed by Eubanks and Styrsky, 2005), resulting in larger predator populations and stronger herbivore suppression (e.g., Eubanks and Denno, 2000).

On the other hand, direct interaction of omnivorous predators with plants and the consequences of their phytophagy/herbivory for plant performance have received less attention. The predatory services provided by omnivores are often thought to counterbalance any potential plant damage (Coll and Guershon, 2002; Castañé et al., 2011). However, herbivory entails a cost to plants, for example in the form of loss of photosynthetic capacity (Nabity et al., 2008), mobilization/use of resources for damage repair or compensatory responses (e.g., new or larger leaves; Strauss and Agrawal, 1999), or for inducing defenses (chemical, physical etc.; Heil and Baldwin, 2002; Cipollini et al., 2014). In order for the net outcome of omnivore-mediated protection to serve in favor of plants, benefits should outweigh the costs of plant-food use (Heil, 2008). Benefits to plants are those conferred by the decrease in prey numbers resulting from direct predation by omnivores, and the subsequent reduction in pest-inflicted damage. The cost to plants of such predatory services include any direct negative effects arising from omnivore plant-feeding and the damage they inflict. For example, omnivore feeding damage can result in leaf deformations, necrosis and/or fruit abortion, which can in turn affect plant growth and yield (Raman et al., 1984; Castañé et al., 2011; Adar et al., 2015; Bhatt and Patel, 2018). Thus, to evaluate the "net result" (advantageous, neutral or detrimental) of omnivore-mediated plant protection, assessment of both plant benefits and costs is necessary. Yet, predatory benefits are seldom simultaneously considered with the direct consequences of omnivore-inflicted damage to plants (Puentes and Björkman, 2017). Indirect assessment of costs to plants are common and involve descriptions of crop injury, omnivore feeding preferences, or are even dismissed if there are no obvious signs of plant damage (Castañé et al., 2011; Hamdi et al., 2013; Adar et al., 2015). Thus, costs to plants have often been considered of lesser or negligible importance relative to the predatory services provided by omnivorous predators (Dalin et al., 2011; Bhatt and Patel, 2018).

Accounting for the consequences of plant-feeding is critical given that omnivorous predators can exhibit a diversity of habits ranging from zoophytophagous (mostly prey food, occasional plant-feeding) to phytozoophagous (mostly plant food complemented with prey). For instance, for several zoophytophagous biocontrol agents, plant-feeding does not always decrease when prey is abundant; indicating that phytophagy may be obligatory rather than facultative (Gillespie and McGregor, 2000; Castañé et al., 2011; Aubry et al., 2017). Even within conspecific populations can there be considerable genetic variation in diet preference, with some genotypes specializing on plant resources and others relying mostly on prey (Dumont et al., 2017). Other recent studies have also shown that omnivore plant-feeding can result in similar effects as herbivore damage (Puentes and Björkman, 2017) and even induce plant defenses, thus affecting subsequent interactions (Pappas et al., 2015; Naselli et al., 2016; Bouagga et al., 2018a). Therefore, to minimize risks and maximize benefits of services provided by omnivorous predators, a direct evaluation of costs to plants is necessary.

What evidence is there available for evaluating the extent of plant damage caused by omnivorous predators and its consequences for plant performance? To date, only a review by Castañé et al. (2011) has partly addressed this important question. Their review focuses on reported levels and types of damage to vegetable crops caused by four zoophytophagous species of mirid predators. While some studies reporting the consequences of plant-feeding are mentioned, the review is centered on the circumstances (e.g., predator-prey ratios, predator developmental stage, and stylet morphology) resulting in crop damage and its potential economic (yield loss) consequences. We thus, lack a synthesis and evaluation of the evidence that is available for assessing the direct impact on plants of omnivore-inflicted damage.

In this systematic review, our goal was to compile and summarize findings on the levels of plant-feeding by omnivorous predators and the consequences (costs) for plants. We herein refer to plant costs or cost to plants as any direct effect on their performance (growth, reproduction, crop yield) arising from omnivore plant-feeding. Costs can be null if no effect on plant performance is found. More specifically, we addressed how often levels of omnivore damage and costs to plants are considered or quantified, the plant parts consumed or fed upon by omnivores and the accompanying plant damage variables measured, the actual (if quantified) and potential effects on plant performance of such damage, the type of study (lab, greenhouse, field, etc.) and the plant-omnivore combination for which this information is most commonly reported. In addition, we present overall publication trends for papers studying omnivorous predators, and conduct a comparison within this search of the number of studies reporting, or not, measures of plant-feeding or damage by omnivores. Our systematic review, together with an overview of publication trends, will allow us to determine the extent of neglect of plant costs and examine if their assumed minor importance relative to predatory benefits is supported. Note that our review does not aim to evaluate the net result of simultaneously considering omnivore-provided plant protection services and omnivore-inflicted plant damage. Thus, we do not answer whether the overall outcome of biocontrol is positive, negative or neutral for specific plant-omnivore systems. Our systematic review examines the available literature on direct costs of omnivore phytophagy, but we do not quantitatively compare these results to previously known or estimated benefits for specific omnivore species.

METHODS

Literature Search

We performed a systematic literature search, following the steps outlined by Khan et al. (2003), to evaluate the evidence available for determining how much plant damage is usually inflicted by omnivorous predators and its consequences for plant performance. We used Clarivate Analytics' Web of Science platform, and searched in the Web of Science™ core collection using the "field = topic" search field, which searches for terms in the title, abstract or keywords. The document type was limited to Article and Review, all languages, using their Science Citation Index Expanded (SCI-EXPANDED, 1945-present). We were interested in finding publications that examined any form of plant feeding/damage/injury by omnivorous predators, and that potentially examined the consequences of such damage. Thus, the following terms were used in our search:

[("omnivor*" OR "zoophytophag*" OR "phytozoophag" OR "prey- and plant-feed*" OR "plant- and prey-feed*" OR "plant-feeding predator*" OR "plant and prey" OR "prey and plant" OR "plant bug*" OR "omnivor* predator" OR "omnivor* bodyguard" OR "omnivor* arthropod*" OR "omniv* pest*") **AND** ("plant damage" OR "damage to plant*" OR "crop damage*" OR "plant-feeding" OR "plant injur*" OR "injury" OR "damage" OR "phytophagy" OR "plant food" OR "sucking" OR "pierc*" OR "sap-sucking" OR "cost to plant*" OR "plant lesion*" OR "negative effect on plant*" OR "plant performance" OR "plant fitness")].

The search was refined by excluding several Web of Science categories (see "**Supplementary material**") and it was last updated on July 10th, 2018. The process yielded 381 papers to be screened for relevance based on title and abstract (conducted by the author AP). Studies that qualified as relevant were those that indicated that some form of plant-feeding, damage or injury by one or several omnivorous predators had been measured. Studies examining phytophagous/herbivorous insects (even phytophagous plant bugs, e.g., *Lygus* spp.), ant-plant mutualisms, and other non-arthropod species (e.g., wild boars) were excluded. After this process, 76 of the 381 papers remained for full-text scrutiny. While conducting full-text evaluation of these 76 studies (conducted by all authors), we found additional references within these studies that were relevant to our question. A total of 16 additional publications were added to our original search results. During the review process of the paper, a reviewer suggested an additional article for inclusion in the review. Thus, we conducted full-text examination for a total of 93 papers (see Flow diagram; **Figure 1**). After evaluation of full-texts, 40 studies were excluded since these did not actually measure any form of plant-feeding or damage. Many of these studies presented an omnivorous predator perspective, for example examining preferences for certain plant-emitted odors, or comparing performance when fed prey- vs. plant-food (see "**Supplementary material**" for a detailed list of full-text examined studies).

Summary and Classification of Relevant Studies

The remaining 53 studies (**Figure 1**) were organized in a summary table (**Table 1**) that included *Omnivore species* (with Order and Family), *Study type* (Lab, Field, Greenhouse, Growth chamber), *Plant species* (with common name), *Plant damage variable* which was used in the study to evaluate the extent of omnivore plant damage (e.g., leaf or fruit injury), *Plant-feeding level* by the omnivorous predator reported in the study (Zero to High), *Actual (potential) effect on plant* (Actual effect if reported

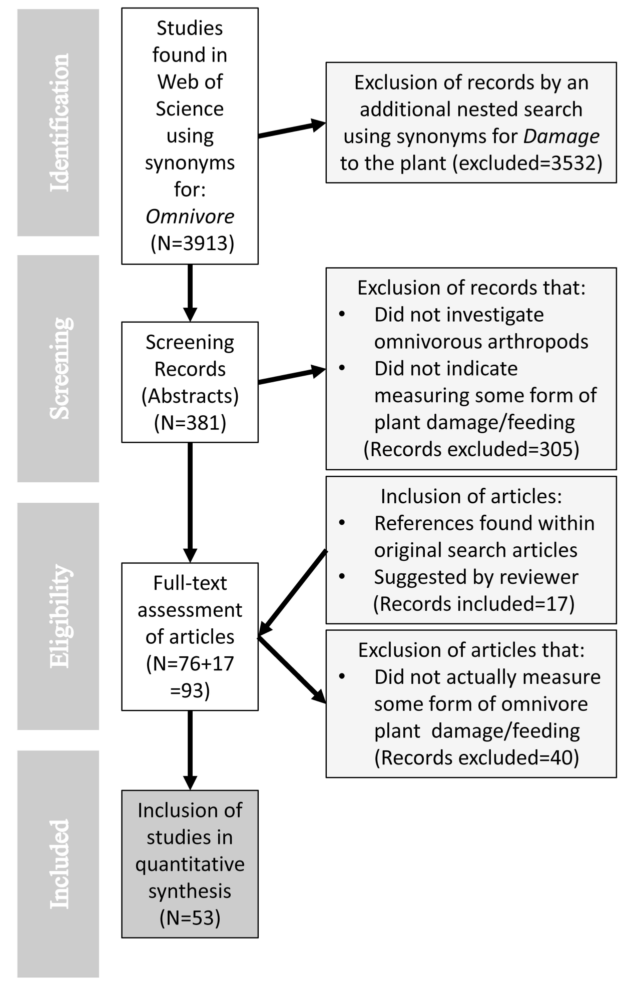

FIGURE 1 | Flow diagram of the selection process used in the systematic review.

TABLE 1 | Summary of results from 53 studies examining the extent of plant-feeding by omnivorous predators and the actual or potential effect of damage on plant performance.

Omnivore species	Study type	Plant species	Plant damage variable	Plant-feeding level*	Actual (potential) effect on plant	References
Brontocoris tabidus (Hemiptera: Pentatomidae)	L	*Gossypium hirsutum* (Cotton)	Leaf injury observations	High	No mechanical damage to cells. (Fluid loss from xylem)	Torres et al., 2010
Campylomma verbasci (Hemiptera: Miridae)	L	*Verbascum thapsus* (Common mullein)	Pollen-feeding frequency	Low to high	(Negative effect on reproduction)	Dumont et al., 2017
Campylomma verbasci	F	*Malus domestica* (Apple)	Fruit injury	Low to high	(Negative effect on yield)	Reding et al., 2001
Campylomma verbasci	L, F	*Malus domestica*	Fruit injury, number, weight, size and abortion. Fruit-puncturing activity, duration	Moderate	**Minor increase in fruit abortion. No effect on fruit size or weight**	Aubry et al., 2017
Campylomma verbasci	L, F	*Malus domestica*	Fruit injury, number and abortion. Fruit-puncturing activity, duration	Low to Moderate	**No effect on fruit abortion**	Aubry et al., 2016
Campyloneuropsis infumatus (Hemiptera: Miridae)	G	*Solanum lycopersicum* (Tomato)	Leaf, fruit injury and abortion	Zero	No observations of fruit abortion, leaf or fruit injury	van Lenteren et al., 2018b
Campyloneuropsis infumatus	GC	*Solanum lycopersicum*	Leaf, stem, petiole and fruit injury	Moderate	**No effect on plant growth**	Silva et al., 2017
Coleomegilla maculata (Coleoptera: Coccinellidae)	L	*Zea mays* (Corn)	Leaf injury and frequency	High	(Negative effect on growth)	Moser et al., 2008
Coleomegilla maculata	L	*Phaseolus vulgaris* (Pinto bean)	Leaf injury	Moderate	(Negative effect on growth)	Lundgren et al., 2010
Dicyphus hesperus (Heteroptera: Miridae)	G	*Solanum lycopersicum*	Fruit injury	Moderate	**No effect on yield quantity, but negative effect on quality**	Shipp and Wang, 2006
Dicyphus hesperus	L	*Solanum lycopersicum*	Leaf injury	Low	(Negative effect on growth)	Vankosky and VanLaerhoven, 2015
Dicyphus hesperus	GC	*Solanum lycopersicum*	Fruit injury, time spent on leaves or fruits	Low to high	(Negative effect on growth, minimal effect on yield)	McGregor et al., 2000
Dicyphus hesperus	L	*Verbascum thapsus*, *Solanum lycopersicum*, *Chrysanthemum coronarium* (Crown daisy)	Fruit injury. Leaf-feeding activity	Low to moderate	(Negative effect on growth, yield)	Gillespie et al., 2012
Dicyphus hesperus	G	*Solanum lycopersicum*	Leaf, flower and fruit injury	Zero to Low	No observations of leaf or flower damage. Very low fruit damage	Calvo et al., 2016
Dicyphus maroccanus (synonym: *D. bolivari*; Heteroptera: Miridae)	G	*Capsicum annuum (Sweet pepper)*	Whole plant injury	Unknown	Omnivore did not establish	Bouagga et al., 2018a
Dicyphus maroccanus	L	*Solanum lycopersicum*	Defensive and phytohormone gene expression, volatile emissions	Not measured	Induced defense (Cost of induction)	Pérez-Hedo et al., 2015a
Dicyphus tamaninii (Heteroptera: Miridae)	GC	*Cucumis sativus* (Cucumber)	Leaf and fruit injury, time spent on leaves or fruits	Low to high	(Negative effect on growth, minimal effect on yield)	Sengonca et al., 2003

(Continued)

TABLE 1 | Continued

Omnivore species	Study type	Plant species	Plant damage variable	Plant-feeding level*	Actual (potential) effect on plant	References
Dicyphus tamaninii	G	*Solanum lycopersicum*	Fruit injury	High	(Negative effect on yield)	Lucas and Alomar, 2002
Dicyphus tamaninii	L	*Cucumis sativus*	Leaf-, stem-feeding activity	Low	(Negative effect on growth)	Montserrat et al., 2004
Dicyphus tamaninii	G	*Curcubita pepo* (Zucchini)	Fruit injury	High	**Negative effect on yield quality/quantity**	Castañé et al., 2003
Dicyphus tamaninii	F, G	*Solanum lycopersicum*	Fruit injury	Low to high	(Negative effect on yield)	Gabarra et al., 1988
Dicyphus tamaninii	F	*Cucumis sativus*	Fruit injury	Zero	No observations of fruit damage	Gabarra et al., 1995
Dicyphus tamaninii	G	*Cucumis sativus*	Fruit injury	Zero	No observations of fruit damage	Castañé et al., 1996
Engytatus varians (Hemiptera: Miridae)	G	*Solanum lycopersicum*	Leaf, fruit injury and abortion	Unknown	Omnivore did not establish	van Lenteren et al., 2018b
Engytatus varians	GC	*Solanum lycopersicum*	Leaf, stem, petiole and fruit injury	Moderate to high	**No effect on plant growth**	Silva et al., 2017
Euseius scutalis (Acari: Phytoseiidae)	GC	*Capsicum annuum*	Leaf injury, plant growth	Not measured	**Negative effect on growth (leaf number, plant height and weight)**	Adar et al., 2015
Frankliniella occidentalis (Thysanoptera: Thripidae)	G	*Cucumis sativus*	Performance/behavior of forthcoming herbivore	Not measured	Induced defense (Cost of induction)	Pappas et al., 2018b
Frankliniella occidentalis	GC	*Gossypium hirsutum*	Leaf injury, peroxidase activity, gossypol gland density	Moderate to high	Induced defense (Cost of induction) (Negative effect on growth)	Spence et al., 2007
Frankliniella occidentalis	L	*Phaseolus vulgaris* (Kidney bean)	Leaf injury	Moderate to high	(Negative effect on growth)	Vangansbeke et al., 2014
Frankliniella occidentalis	L	*Gossypium hirsutum*	Leaf injury	Moderate to high	(Negative effect on growth)	Agrawal et al., 1999
Harmonia axyridis (Coleoptera: Coccinellidae)	L	*Zea mays*	Leaf injury and frequency	Moderate	(Negative effect on growth)	Moser et al., 2008
Macrolophus basicornis (Heteroptera: Miridae)	G	*Solanum lycopersicum*	Leaf, fruit injury and abortion	Zero	No observations of fruit abortion, leaf or fruit injury	van Lenteren et al., 2018b
Macrolophus basicornis	GC	*Solanum lycopersicum*	Leaf, stem, petiole and fruit injury	High	**No effect on plant growth**	Silva et al., 2017
Macrolophus caliginosus (synonym: *M. melanotoma*; Hemiptera: Miridae)	G	*Curcubita pepo*	Fruit injury	High	**Negative effect on yield quality/quantity**	Castañé et al., 2003
Macrolophus caliginosus	F	*Solanum lycopersicum*	Leaf, flower, fruit injury and abortion	High	**Increased flower and fruit abortion, reduced yield quantity/quality. Distorted leaf growth**	Sampson and Jacobson, 1999
Macrolophus caliginosus	G	*Solanum lycopersicum*	Fruit injury	Zero to Low	Minimal fruit damage, not statistically different from controls.	Lucas and Alomar, 2002
Macrolophus caliginosus	L	*Cucumis sativus*	Leaf-, stem-feeding activity	Low to moderate	(Minimal negative effect on growth)	Montserrat et al., 2004

(Continued)

TABLE 1 | Continued

Omnivore species	Study type	Plant species	Plant damage variable	Plant-feeding level*	Actual (potential) effect on plant	References
Macrolophus caliginosus	G	*Cucumis melo* (Galia melon)	Leaf, fruit injury	Zero to Low	Zero to few observations of feeding-punctures (minimal negative effects)	Alomar et al., 2006
Macrolophus pygmaeus (Heteroptera: Miridae)	G	*Solanum lycopersicum*	Fruit injury	High	**Negative effect on yield (distorted fruits, open and visible seeds)**	Moerkens et al., 2016, 2017
Macrolophus pygmaeus	L	*Solanum lycopersicum*	Proteinase inhibitor activity, gene expression, forthcoming herbivore damage	Not measured	Induced defense (Cost of induction)	Pappas et al., 2015, 2016
Macrolophus pygmaeus	L	*Solanum lycopersicum*	Defensive and phytohormone gene expression, volatile emissions	Not measured	Induced defense (Cost of induction)	Pérez-Hedo et al., 2015a, 2018
Macrolophus pygmaeus	L	*Capsicum annuum*	Phytohormone levels	Not measured	Induced defense (Cost of induction)	Zhang et al., 2018
Macrolophus pygmaeus	L	*Nicotiana* spp. (Tobacco plants)	Nitrogen concentrations in predator (from plant-feeding)	Moderate to high	(Negative effect on growth)	Hamdi et al., 2013
Macrolophus pygmaeus	L	*Solanum lycopersicum*	Leaf-feeding frequency	Moderate	(Negative effect on growth)	Han et al., 2015
Macrolophus pygmaeus	G	*Capsicum annuum*	Whole plant injury	Zero	No observations of plant injury	Bouagga et al., 2018a
Macrolophus pygmaeus	GC, L	*Capsicum annuum*	Time spent plant-feeding, phytohormone levels, defensive and phytohormone gene expression, volatile emissions	Low	Induced defense (Cost of induction)	Bouagga et al., 2018c
Nesidiocoris tenuis (Hemiptera: Miridae)	G	*Solanum lycopersicum*	Flower abortion	Moderate to high	**Increased flower abortion**	Sanchez, 2009
Nesidiocoris tenuis	G	*Solanum lycopersicum*	Fruit injury, weight, size and abortion	Moderate	**Increased fruit abortion, but no effect on total yield (fruit weight and number)**	Sánchez and Lacasa, 2008
Nesidiocoris tenuis	L	*Solanum lycopersicum*	Phytohormone levels, defensive and phytohormone gene expression, volatile emissions	Not measured	Induced defense (Cost of induction)	Pérez-Hedo et al., 2015a,b, 2018; Naselli et al., 2016
Nesidiocoris tenuis	L	*Solanum lycopersicum*	Stem injury	Moderate	(Negative effect on growth)	Moreno-Ripoll et al., 2012
Nesidiocoris tenuis	G	*Solanum lycopersicum*	Leaf, stem, flower injury and abortion	Moderate to high	(Negative effect on growth, yield)	Sanchez, 2008
Nesidiocoris tenuis	G	*Solanum lycopersicum*	Leaf, stem, flower injury	Low to Moderate	(Negative effect on growth, minimal effect on yield)	Perdikis et al., 2009
Nesidiocoris tenuis	L	*Solanum lycopersicum*	Leaf, stem, shoot, petiole injury	Moderate to high	(Negative effect on growth)	Biondi et al., 2016
Nesidiocoris tenuis	G	*Solanum lycopersicum*	Leaf injury	High	(Negative effect on growth)	Calvo et al., 2009
Nesidiocoris tenuis	G	*Capsicum annuum*	Whole plant injury	Zero	No observations of plant injury	Bouagga et al., 2018a

(Continued)

TABLE 1 | Continued

Omnivore species	Study type	Plant species	Plant damage variable	Plant-feeding level*	Actual (potential) effect on plant	References
Nesidiocoris tenuis	GC, L	*Capsicum annuum*	Time spent plant-feeding, phytohormone levels, defensive and phytohormone gene expression, volatile emissions	Medium	Induced defense (Cost of induction)	Bouagga et al., 2018c
Nesidiocoris tenuis	G	*Solanum lycopersicum*	Leaf, stem, petiole, flower injury and fruit abortion	High	**Negative effect on growth (plant height, number of leaves) and yield (fewer, smaller fruits)**	Arnó et al., 2010
Orius insidiosus (Heteroptera: Anthocoridae)	L	*Zea mays, Phaseolus lunatus* (Lima bean), *Solanum lycopersicum*	Leaf-probing frequency	Low to moderate	(Negative effect on growth)	Coll et al., 1997
Orius laevigatus (Hemiptera: Anthocoridae)	GC, L	*Capsicum annuum*	Time spent plant-feeding, defensive and phytohormone gene expression, volatile emissions	High	Induced defense (Cost of induction)	Bouagga et al., 2018b
Orius majusculus (Heteroptera: Anthocoridae)	L	*Cucumis sativus*	Time spent leaf-, stem-feeding	Zero to low	(Minimal negative effect on growth)	Montserrat et al., 2004
Orthotylus marginalis (Heteroptera: Miridae)	G	*Salix dasyclados*; *Salix viminalis* (Basket willow)	Plant growth	Not measured directly	**Negative effect on growth**	Puentes and Björkman, 2017
Podisus nigrispinus (Hemiptera: Pentatomidae)	L	*Gossypium hirsutum*	Leaf injury observations	High	No mechanical damage to cells. (Fluid loss from xylem)	Torres et al., 2010
Typhlodromus pyri (Acari: Phytoseiidae)	L	*Malus domestica*	Leaf, fruit injury	Moderate to high	(Negative effect on growth, minimal effect on yield)	Sengonca et al., 2004

Studies were compiled by ***Omnivore species*** *(with order and family),* ***Study type*** *(L, lab; F, field; G, greenhouse; GC, growth chamber),* ***Plant species*** *(with common name),* ***Plant damage variable*** *which was used in the study to describe the extent of omnivore-inflicted damage, and also used by the authors to evaluate levels of plant-feeding by each omnivore (****Plant-feeding level*** ** in table).* ***Actual (potential) effect on plant*** *represents actual effects (in bold) quantified in the study for the omnivore-plant pair in question, while potential effects (in parentheses) are based on the plant-feeding level and the damage variable examined for each omnivore-plant pair (see section Summary and Classification of Relevant Studies in Methods for details on how potential effects were evaluated).* ***Reference*** *(authors, year) includes the studies for which each omnivore-species pair in question was examined. *Plant-feeding levels were assessed based on reports of statistically significant ($P < 0.05$) differences among treatments for the damage variables examined or damage observations conducted by each study (see Section Summary and Classification of Relevant Studies in Methods were evaluated in the Methods for details). Briefly, plant-feeding was classified as follows: Zero, no evidence of plant-feeding; Low, level of plant-feeding differed roughly by <20% among treatments; Moderate, level of plant-feeding differed roughly by about 20–40% among treatments; High, level of plant-feeding differed roughly by more than 40% among treatments. A range of levels indicates that several sub-experiments were conducted, or differences among treatments varied depending on plant damage variable.*

by study; Potential: evaluation conducted by authors of potential effect based on damage variable and extent of omnivore-plant feeding) and *Reference* (authors, year). A more detailed explanation of some of the classification variables follows.

The summary table category *Plant damage variable* comprised any measure of plant-feeding or damage by the omnivore. For example, fruit or leaf injury in the form of number of necrotic rings, punctures, scars, or leaf area damaged. Fruit injury also implied dimples, pits, deformations, open fruits or number of fruits injured. Frequency of leaf or fruit-feeding indicated how often predators probed or fed on plant tissue, or how many individuals engaged in this behavior. Time spent on these activities referred to how much of the omnivore activity budget was dedicated to plant feeding. In **Table 1**, plant damage variables were expressed in a concise form, while in **Table S1** a more detailed description of how damage was measured can be found.

The summary table category *Plant-feeding level* was evaluated by the authors based on actual reports within each study of statistically significant ($P < 0.05$) differences among treatments for the damage variables examined or damage observations conducted. For example, Calvo et al. (2009) examined the cumulative number of necrotic rings on tomato leaves across 15 weeks, and found statistically significant differences among treatments with densities of 0, 1 and 4 *Nesidiocoris tenuis* individuals. Differences in number of necrotic rings among treatments were large (over 40% for all treatment comparisons) with greater densities leading to more rings; thus, omnivore plant-feeding level was expressed as high for this study. Our classification of plant-feeding level was based on the differences in damage reported by each study, and ranged from zero to high using the following criteria: Zero, no evidence of plant-feeding; Low, level of plant-feeding differed roughly by <20% among treatments (e.g., plant-feeding frequency in the presence or absence of prey, time spent feeding on the plant vs. other activities, number of leaf/fruit injuries compared to controls); Moderate: level of plant-feeding differed roughly by about 20–40% among treatments; High, level of plant-feeding differed roughly by more than 40% among treatments. In some instances, several sub-experiments were conducted with different omnivorous species (i.e., more than one specific omnivore-plant species pair per study), or differences in levels of damage among treatments varied depending on plant damage variable (i.e., one omnivore-plant pair can offer multiple reports of an effect on a plant trait); thus, a range of plant-feeding levels are reported were appropriate. It is also important to note that many studies were not directly designed for assessing levels of omnivore plant damage, and our evaluation provides an indication of how much feeding can occur based on the treatments/experimental setting used in each study. We offer suggestions on how to design experiments aimed specifically at examining levels of omnivore plant-feeding and its consequences in section Future prospects.

The summary table category *Actual (potential) effect on plant* is comprised first of any actual effect on plant growth (e.g., reductions in total height, shoot growth, leaf numbers) and yield quality (fruit blemishes) or quantity (fruit numbers or weight) reported by the study. If no actual effect was reported by the study, we conducted an evaluation of potential effects on plant growth or yield based on the damage variable examined and extent of omnivore-plant feeding reported for each case. For example, if an omnivore fed on flowers or fruits at very high levels, there could potentially be negative effects for reproduction or crop yield. Levels of omnivore damage, and whether it was a reproductive or a trait affecting growth, were used to provide a suggestion for potential consequences of such plant-feeding. For studies examining induction of plant defenses following omnivore-plant feeding, a potential effect for the plant was indicated as a "Cost of induction." Inducing defenses can involve resources being diverted or allocated away from other functions such as growth, and instead invested in defense. However, the cost of such resource allocation can range from low to high, and varies depending on the plant trait and species (Heil and Baldwin, 2002; Cipollini et al., 2014; Züst and Agrawal, 2017). Our evaluation of costs are meant as suggestions of potential cost to the plants, and these require further investigation. We also included information on omnivorous predator feeding mode (e.g., pierce-sucking, chewing), and prey species provided in the study, but chose to present a simplified version of the table in the main manuscript. See **Table S1** for a more detailed classification of each study.

Publication Trends

To examine if consideration of plant costs has changed through time, we conducted a comparison of number of publications per year between studies examining omnivorous predators only, and those also considering some form of plant-feeding/damage. From the search described above, we extracted the number of papers per year resulting from the first level search. In other words, those with only synonyms of omnivores (before the AND connector). We then proceeded to run again the nested second level search (after the AND connector, those with synonyms for plant damage) to also extract number of publications per years, and compared results from the two searches. Secondly, we conducted a comparison of publications per year for those studies found to be potentially relevant to our question (93 studies, full-text examined) and those actually included in the systematic review (53 studies). For both comparisons, the number of studies were log transformed in order to illustrate proportional relationships.

RESULTS

Our systematic search yielded 381 publications that included terms associated with "omnivorous predator" and "plant-feeding" or "plant damage." A total of 93 papers were full-text examined and 53 of these remained after this process (**Figure 1**). We used these 53 papers to address how often the extent of plant-feeding by omnivorous predators and its consequences for plants are considered or quantified.

Levels of Omnivore Plant-Feeding, Effects on Plants and Most Common Species

Among the 53 studies examined, some papers presented more than one omnivore-plant relationship (each is considered a report, and hereafter referred to as such) and some examined more than one plant damage variable (hereafter referred to as cases). Thus, sums of reports (69 omnivore-plant reports in total; sum of rows in **Table S1**) and sums of cases (79 cases examining a specific type of plant variable, excluding "Unknown" in *Plant feeding level*; **Table S1**) exceeded the total number of studies. Among the 69 reports, two of the studied omnivore species did not successfully establish (*Plant feeding level*: "Unknown"; **Table 1**). For 13 additional reports, no plant-feeding/damage variable was directly examined (*Plant feeding level*: "Not measured"; **Table 1**), but plants were exposed to omnivores and allowed to inflict damage. Of the remaining 54 reports, 6 recorded no observations of plant damage, while 13 recorded high levels of omnivore plant-feeding (*Plant-feeding level*: "Zero" and "High," respectively; **Table 1**, **Figure 2A**). When considering all levels, the majority (31 out of 54) reported at least moderate levels of plant-feeding (**Table 1**).

Among those reports exposing plants to omnivores and reporting non-zero plant-feeding, only 15 times were the consequences of damage in terms of growth or yield actually measured (Actual effects in bold; **Table 1**). Of these 15 reports, a greater number found negative consequences for plants compared to those reporting a lack of effect (8 and 4 reports, respectively and 3 reports with both; **Table 1**). Of these 8 reporting detrimental effects, 6 found negative effects on yield quantity or quality, while 2 report negative effects on growth (**Table 1**).

In terms of the plant damage variables examined, we found both direct and indirect measures of plant-feeding. Indirect measures included time spent probing or plant-feeding by the omnivore, and frequency of individuals engaging in such behavior (**Table S1**). Direct measures included different forms of plant injury, with feeding punctures and necrotic rings often quantified, while amount of tissue area damaged was rarely estimated (**Table S1**). Overall, the majority of cases evaluated fruit or leaf injuries relative to stem- or flower-feeding (**Table 1**). But among those cases quantifying negative effects on plants (Actual effects in bold; **Table 1**), examination of fruit injuries were most common relative to leaf injuries (**Table 1**).

It is important to note that our search results included several cases that examined the consequences of omnivore plant-feeding for plant defense induction against herbivores. A total of 15 cases examined induction of different defense traits, subsequent performance or preference of herbivores and parasitoid attraction (*Actual effect*: "Induced defense"; **Table 1**; **Figure 2B**). These papers do not directly assess the effects on plant growth or yield, but do show that omnivore feeding induces defenses and this could entail a possible cost to plants (*Potential effect:* "Cost of induction;" **Table 1**). The cost of inducing defenses against herbivores, however, can vary depending on the plant trait induced (chemical, physical, etc.) and the species in question (Heil and Baldwin, 2002; Cipollini et al., 2014; Züst and Agrawal, 2017). The presence or absence of costs following mirid-mediated induction require actual estimation. Plant-damage variables examined in these papers often included volatile emissions and phytohormone profiling/activity (**Table 1**). For the remaining cases that did not directly estimate consequences for plants nor induced defense, we also assessed the potential effects of damage on growth and/or yield (Potential effect in parentheses; **Table 1**). Our evaluation was based on the damage variable examined and extent of omnivore-plant feeding reported for each case (see section Summary and Classification of Relevant Studies), but require actual quantification.

All 69 reports were organized according to whether the study examined traits associated with "Plant growth" (e.g., leaf/stem injuries or feeding, reduced plant height), "Reproduction/yield" (e.g., flower/fruit abortion, fruit distortion, fruit number), or "Induced defense" (e.g., proteinase inhibitor expression, volatile emissions) (*Plant trait examined* column; **Table S1**). Based on this classification, we conducted a comparison of the number of cases reporting an actual lack of effect ("None"; **Figure 2B**), and an actual negative (reported by the study) or potentially negative (evaluated by the authors) on these plant traits ("Negative" and "Potentially negative"; **Figure 2B**). We found that for both Reproduction/yield and Plant growth, more cases show detrimental rather than no effects on such traits (light gray "Negative" bars vs. dark gray "None" bars, **Figure 2B**). Also, a greater number of cases evaluated actual effects for Reproduction/yield traits than for Plant growth traits (comparison of dark gray "None" bars between types of traits, **Figure 2B**). We identified a total of 38 cases with potential negative effects on plant traits (white "Potentially negative" bars, **Figure 2B**; **Table 1**); i.e., those excluding "Zero" in the *Plant-feeding level* column (6 cases; **Table S1**) as well as those that examined "Induced defense" (15 cases; **Table S1**) or "Actual effects" (20 cases; **Table S1**). Among these cases where our evaluation indicated potential negative consequences, plant growth traits were mostly examined relative to reproduction/yield traits (comparison of white "Potentially negative" bars between types of traits, **Figure 2B**).

Furthermore, a total of 17 out 31 reports presented omnivore feeding for damage variables related to plant growth (e.g., stem injury, leaf area damaged), while 8 out 31 reports for variables associated with reproduction/yield (e.g., fruit-feeding punctures), and 6 out of 31 reported on variables affecting both growth and reproduction (**Table 1**).

Tomato plants (*Solanum lycopersicum*) and the omnivorous predator *N. tenuis* were the most common species studied, with 34 and 14 reports (out of 69) examining these species, respectively (**Figures 3A,B**). Cucumber plants (*Cucumis sativus*) and mirids in the genus *Macrolophus* and *Dicyphus* were the next most common species studied (**Figures 3A,B**). Levels of plant-feeding for those omnivore species with more than one occurrence were not consistent among cases, and ranged from zero to high (*Omnivore species* and *Plant-feeding levels*; **Table 1**). Among these omnivore species, plant-feeding was examined on several plant species, except for *N. tenuis* which was almost exclusively examined on tomatoes (*Omnivore* and *Plant species*; **Table 1**). For those studies quantifying the consequences of damage to plants (15 instances, in bold; **Table 1**), *N. tenuis* and *Macrolophus* spp. plant-feeding often resulted in detrimental effects. Plant-feeding by less-represented species, such as *Campylomma verbasci* and *Engytatus varians*, resulted in no negative effects to plants (Actual effects in bold; **Table 1**). Again, tomato plants were over-represented among these 15 cases, with a few instances finding

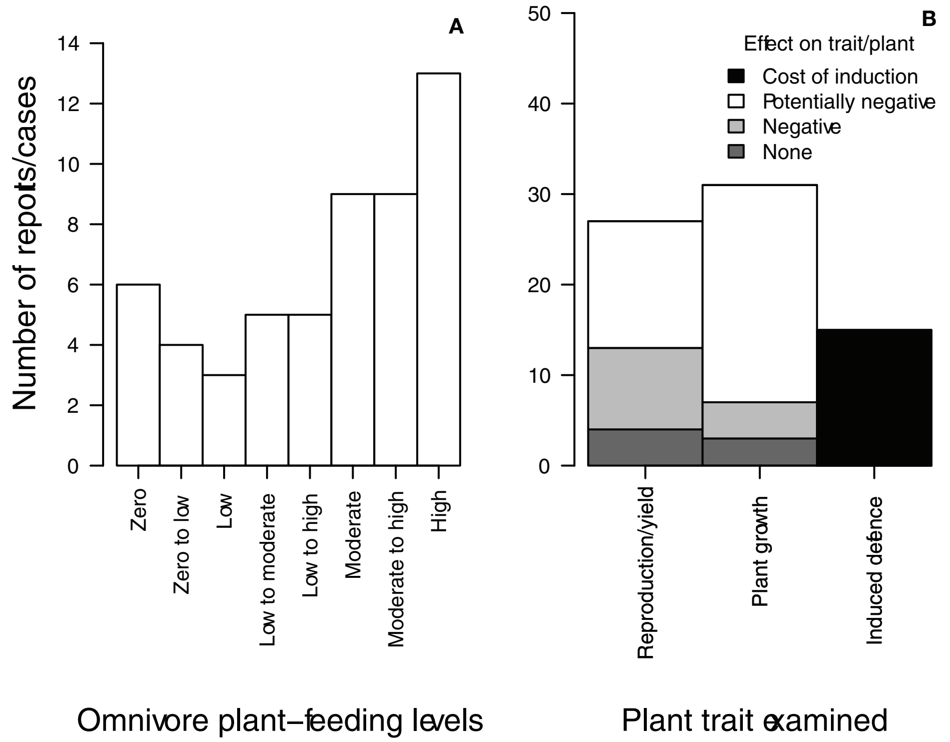

FIGURE 2 | (A) Frequency of reports in 53 studies, which recorded plant-feeding by omnivorous predators ranging in levels from Zero to High (see **Table 1**; "Unknown" and "Not measured" were excluded). **(B)** Frequency of cases in 53 studies for which none, actual or potential effects (*None*, *Negative,* and *Potentially negative* in figure) were recorded or estimated for *Plant growth* and *Reproduction/yield*, and for which a potential *Cost of Induction* for *Induced defense* traits might occur and needs to be quantified (see Methods section Summary and Classification of Relevant Studies and Results section Levels of Omnivore Plant-Feeding, Effects on Plants and Most Common Species for details on the classification of reports). Only cases reporting damage are included (i.e., "Zero" and "Unknown" plant-feeding cases were excluded; **Table 1**).

negative consequences for zucchini and sweet pepper plants (*Plant species* and *Actual effects*; **Table 1**).

For each of the 53 studies examined, one or several experiment types (Greenhouse, Field, Growth chamber, or Lab) with omnivores were reported. Lab and greenhouse experiments predominated with 34 and 25 occurrences respectively across all reports, while field studies were few (6 cases, **Table 1**).

Publication Trends for Studies Considering Plant-Feeding/Damage by Omnivores

Our search on studies examining omnivores without consideration for plant-feeding/damage (See Publication trends in Methods) yielded a total of 3,913 papers between 1945 to present. The number of papers published shows an increasing trend with years (**Figure 4**, green line). Very few records were found before the 1960s, but a steep increase can be observed from those years onward. Our search for studies examining some form of plant-feeding by omnivores (nested in the search above, see section Publication trends), yielded 381 records. A growing number of studies appear to have been considering plant damage by omnivores (**Figure 4A**, red line), but few papers did so before the mid to late 1990s. The smoothers used for the lines indicate that studies considering damage have been increasing proportionally to studies addressing only omnivores (**Figure 4A**).

For those 93 studies that we conducted full-text examination of, the publication years ranged from 1957 to 2018 (**Figure 4B**, green line). Few studies were published before the mid-1990s, and most studies were published in the 2000s. For the 53 studies that we selected, which reported omnivore plant-feeding levels and/or consequences of damage to plants, the range of publication year was 1988–2018 (**Table 1**; **Figure 4B**, red line). Of these 53 studies, only 7 were published before the year 2000 (**Table 1**), indicating that a consideration of omnivore plant damage and its consequence for plants has occurred in more recent years.

DISCUSSION

Summary of Main Findings

Our systematic review addressed how often consequences for plants arising directly from the phytophagy of omnivorous predators, and subsequently affecting plant performance, are considered and/or quantified. We provide a synthesis of the available evidence for assessing plant costs of omnivore-inflicted damage in relation to reductions in plant growth or reproduction/yield. Our search revealed that while some measure

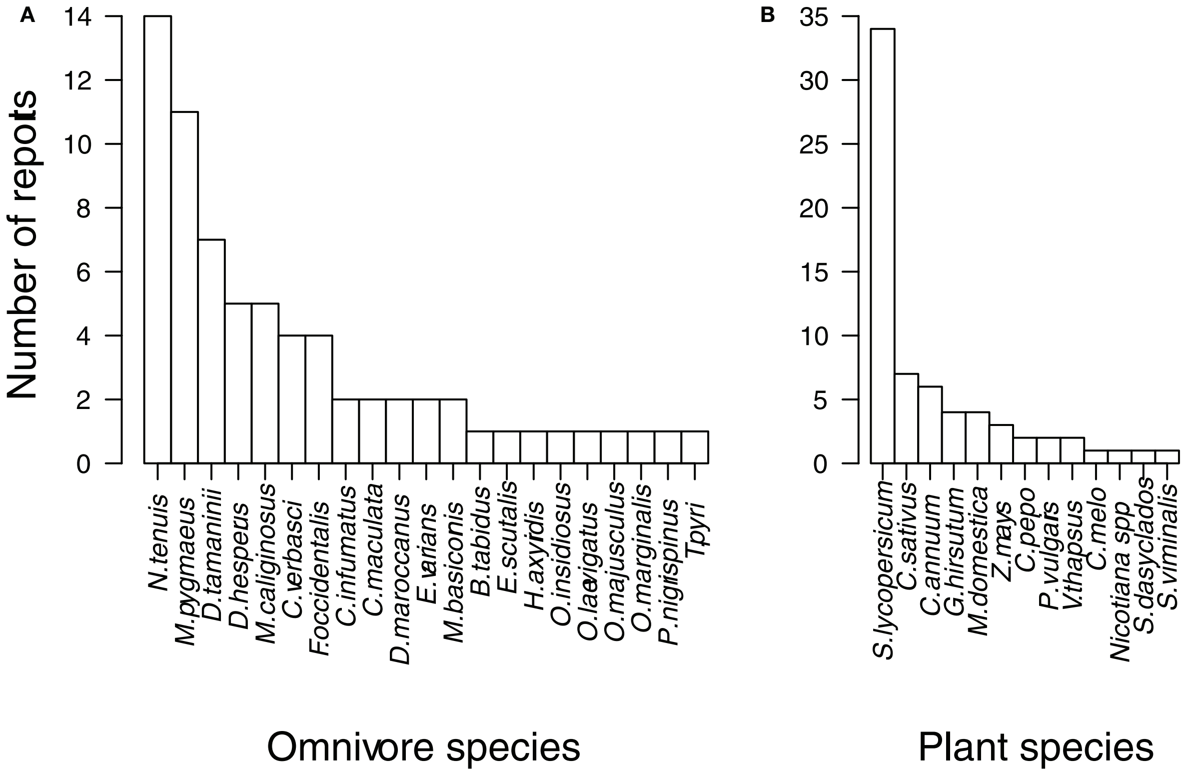

FIGURE 3 | Frequency of reports in 53 studies, which recorded plant-feeding by omnivorous predators, classified according to the **(A)** *Omnivore species* and **(B)** *Plant species* studied. See **Table 1** for full species names.

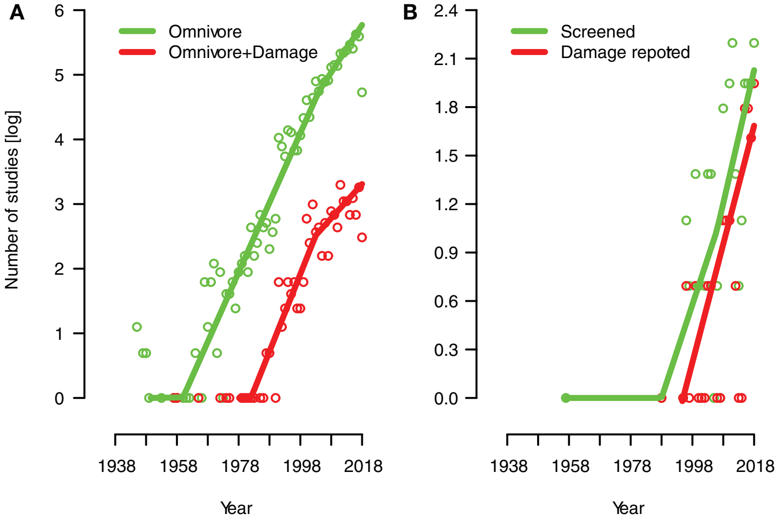

FIGURE 4 | Publication trends (1945-present) for studies examining omnivorous predators without and with consideration for their plant-feeding/damage based on Web of Science systematic searches (see section Publication Trends in Methods). The number of publications per year (log-scale) is presented for **(A)** the 3,913 studies that were found using several search terms synonymous to omnivorous predators (*Omnivore*, green line), and those that additionally included terms for plant-feeding/damage (subset of 381 studies; *Omnivore + Damage*, red line). From these 381 studies, the number of publications per year are presented for **(B)** the 93 studies for which we conducted full-text screening (*Screened*, green line), and the 53 studies that reported damage levels to the plant (subset of studies, *Damage reported,* red line; see **Table 1**). Lines show additive quantile regression smothers and circles are jittered slightly to increase visibility.

of plant-feeding is occasionally reported by studies examining omnivorous predators, it is seldom that the direct consequences of such damage for plants are also considered. Actual measures of plant-feeding levels by omnivores were reported in 57% of studies examined (53 of 93 full-text screened studies). Within these, 24 and 57% of the reports showed high or at least moderate levels of plant-feeding by omnivores, respectively (**Table 1**; **Figure 2A**). However, in only 22% of instances were effects of omnivore-inflicted damage on plant performance quantified (15 out of 69 reports, **Table 1**; **Figure 2B**). Of these 15 reports, a greater number found negative consequences for plants compared to those reporting a lack of effect (8 and 4 reports, respectively and 3 reports with both; **Table 1**), with effects on yield quantity/quality being more often evaluated than effects on growth (**Table 1**; **Figure 2B**). The effects of omnivore plant-feeding described in these cases suggest that dismissal of plant costs without quantification is not warranted.

We also found that the majority of cases evaluated fruit or leaf injuries relative to stem- or flower-feeding, and among those cases quantifying negative effects on plants, assessment of fruit injuries were most common relative to leaf injuries (**Table 1**). Lab and greenhouse experiments predominated across all reports, while field studies were few (**Table 1**). Furthermore, we found a strong bias in the literature toward tomato plants and omnivorous predator species in the mirid family (*Nesidiocoris*, *Macrolophus*, *Dicyphus* spp.) used for biocontrol of tomato pests (**Figures 3A,B**). Hence, the evidence available for evaluating the extent of plant-feeding damage and its effects, lacks representation from a variety of plant-omnivore systems. Our examination of publication trends, however, suggests an increasing awareness of omnivore plant-feeding effects with more recent papers directly addressing this issue. We hope this indicates an ongoing or upcoming paradigm shift, and simultaneous consideration of benefits and costs of omnivorous predatory services becomes standard practice. Below, we discuss our findings in more detail and provide suggestions for future work.

Extent of Plant-Feeding by Omnivorous Predators

Our systematic search results showed that that the degree of plant-feeding by omnivorous predators is reported every so often, with its quantification being done directly or indirectly in different ways. Out of the 93 studies we screened, 57% provided some measure of how much plant-feeding the omnivore in question engaged in. The selected 53 studies (**Table 1**) often had an omnivore perspective, examining feeding preferences based on different plant vs. food-prey availabilities, and its effect on pest control or omnivore performance. Nonetheless, a few studies (∼1/5 of papers) did set out to directly quantify phytophagy or plant damage by the omnivore in question. For example, phytophagy by the mirid *C. verbasci* on apples (e.g., Aubry et al., 2016), damage by *N. tenuis* to tomatoes (e.g., Calvo et al., 2009; Arnó et al., 2010), and damage by the predatory mite *Euseius scutalis* to sweet peppers (Adar et al., 2015). To measure plant-feeding, a range of different variables were reported, but leaf- and fruit-feeding in contrast to stem- or flower-feeding, were most often evaluated (**Table 1**). Indirect measures included time spent probing or plant-feeding, and frequency of individuals engaging in such behavior (e.g., Coll et al., 1997; Montserrat et al., 2004; Han et al., 2015). Direct measures included different forms of plant injury, with feeding punctures and necrotic rings often quantified (**Table S1**), while amount of tissue area damaged/consumed was rarely estimated (e.g., Moser et al., 2008; Lundgren et al., 2010; Vangansbeke et al., 2014; **Table S1**). It, thus, appears as if less effort has been placed on understanding the plant-omnivore interaction, as exemplified by fewer studies examining actual amounts of plant damage relative to crop quality variables. Overall, these results reflect the traditional greater interest in examining consequences of plant-feeding for omnivore performance or predatory services, rather than its effect on plants.

In addition to the damage variables examined, we also evaluated the levels of plant-feeding reported in each study and classified them between zero to high (**Table 1**; **Figure 2A**). Only a small proportion of cases reported zero plant-feeding, relative to the number of studies reporting low to high levels of plant-feeding (**Figure 2A**). Except for one study (van Lenteren et al., 2018b; **Table 1**), those reporting zero observations of damage were evaluating predatory services of the omnivores in question and not specifically examining plant injury. Ideally, observations of "no damage" should be confirmed by studies aimed at evaluating plant-feeding, and corroborated several times before being considered general. Indeed, among those zero-damage papers, two separate studies report the mirid *Dicyphus tamaninii* as inflicting no damage to cucumber plants (**Table 1**). However, when examining all 7 reports of plant-feeding by *D. tamaninii*, we can see that 4 of them actually report high levels (**Table 1**). This inconsistency in the levels of plant-feeding reported is, in fact, observed for all the omnivore species with more than one occurrence in the table (except for *Frankliniella occidentalis*; **Table 1**). Thus, no particular omnivorous predator stands out as frequently inflicting low or high levels of damage.

A lack of consistency in degree of plant-feeding can be explained, in some cases, by the plant species examined. For *D. tamaninii*, high levels of plant damage occur in tomato and zucchinis, yet for other species like *Macrolophus caliginous* reports of damage vary even within the same plant (**Table 1**). Another plausible reason for such variation is differences among studies, not only in terms of experimental conditions, but also in omnivore population origin, prey presence/absence and predator:prey ratios. For instance, it has been shown that even within conspecific populations, omnivorous predators can vary genetically in their zoophytophagous vs. phytozoophagous status (Dumont et al., 2017). Even if the majority of studies were lab/greenhouse experiments, authors do report natural infestations or naturally-collected individuals for lab rearing, thus population origin could be important in explaining study variation across different locations. With regard to prey presence/absence, we do summarize whether or not, and which prey was offered to the omnivorous predator for each case (**Table S1**). However, as our main question addresses the consideration and estimation of plant costs, we were not directly interested in evaluating differences among studies with respect to the prey offered. Castañé et al. (2011) provide an excellent discussion on plant-feeding damage relative to predator:prey ratios at least for *D. tamaninii*, *D. hesperus*, *M. pygmaeus,* and *N. tenuis*.

Effects of Omnivore Plant-Feeding on Plant Performance (Costs to Plants)

In order to determine whether predatory benefits of omnivorous predators counterbalance plant damage, cost to plants arising from the damage inflicted should be known (Heil, 2008). Such costs encompass any negative effects stemming from omnivore plant-feeding, such as decreases in growth, reproduction or yield due for example to leaf deformations, fruit or flower abortion (Castañé et al., 2011). Our results reveal that such costs have been poorly studied, as they are to a large extent neglected when examining plant-feeding by omnivores. Of those reports evaluating plant-feeding/damage, only 22% quantified the actual consequences of damage to plants (**Table 1**). Among the cases within these reports, the majority show detrimental effects relative to no effect for different plant traits (**Figure 2B**). A greater number of these cases evaluated effects on yield quality or quantity, while few examined effects on growth (**Table 1**). As discussed for findings on plant damage variables, this likely reflects a greater focus on examining effects stemming from omnivore prey consumption relative to those effects stemming from the direct plant-omnivore interaction. Of the 15 reports evaluating plant costs, 4 cases reported no effect on yield and/or growth (**Table 1**). A lack of negative effects was found even when omnivore plant-feeding levels were estimated as moderate to high (e.g., Silva et al., 2017; **Table 1**), suggesting that costs cannot be assumed based on plant-feeding levels. However, these cases included species for which our search yielded only one or two instances reporting plant-feeding, such as *E. varians*, *M. basicornis*, and *Campyloneuropsis infumatus*. Thus, it is not possible to determine whether these species often inflict high levels of damage and the generality of non-detrimental effects for plants.

Even though they were few, the studies finding actual negative consequences for plants revealed that yield and growth can be significantly affected by omnivore plant-feeding. Increases in flower or fruit abortion, and reduced height and leaf number were reported in cases examining effects on yield and growth, respectively (**Table 1**). Consequences for growth were little evaluated, but clearly deserve more attention, especially if leaf area/number reductions are common as this can negatively affect the photosynthetic capacity of plants (e.g., Wisdom et al., 1989; Delaney and Higley, 2006). Among these studies reporting costs (i.e., those finding a negative effect on reproduction/growth; excluding those finding no effect), 5 different plant species were represented (sweet pepper, apple, willows, tomato, and zucchini), but 6 out of 11 reports evaluated effects on tomato plants. Likewise, a total of 7 different omnivore species, all in the Miridae except for *E. scutalis* in the Phytoseiidae, were represented. Yet, *N. tenuis* and *Macrolophus* spp., common biocontrol agents of tomato pests, were used in 6 out of 11 reports (**Table 1**). Reports of negative plant effects for *N. tenuis*, and for other mirid species are perhaps not as surprising, given that they have traditionally varied in status as pests or predators (Lu et al., 2010; McColl et al., 2011; Pérez-Hedo and Urbaneja, 2016). However, this bias in the literature makes it difficult to assess generality of results and importance of actual plant costs for other species.

Our evaluation of potential plant consequences (Potential effects in parentheses; **Table 1**) following omnivore plant-feeding, points out that detrimental effects could be expected for other important crops (e.g., cotton, corn) and non-mirid species. Furthermore, among these studies, we found that omnivore plant-feeding was mostly reported for plant damage variables potentially affecting plant growth relative to those affecting reproduction/yield ("Potentially negative" white bars, Reproduction/yield vs. Plant growth, **Figure 2B**). This is in contrast to actual reports of negative effects for plants, where reproduction/yield variables were in majority ("Negative" gray bars, Reproduction/yield vs. Plant growth, **Figure 2B**). While these studies do not directly quantify the negative consequences of omnivore plant-feeding, they do provide valuable insight into possible costs based on the range of plant damage variables examined. For instance, some studies provide detailed estimates of omnivore damage in the form of number and size of leaf- and fruit-feeding punctures (Sengonca et al., 2004; Vangansbeke et al., 2014), amount of leaf-tissue damaged (Moser et al., 2008), necrotic rings on stems and flower clusters (Sanchez, 2008), among others (**Table S1**). These studies indicate that there is a large potential for negative effects to occur from omnivore plant-feeding, however, whether or not these are manifested needs to be empirically investigated. We hope that our findings encourage actual quantification of direct plant costs for these cases.

CONCLUSIONS

So, overall, what does the evidence say about the direct effects of omnivore plant-feeding? The evidence, so far, says that the impact of omnivore plant damage can be substantial and the importance of costs to plants relative to predatory benefits should not be neglected. A reduction in herbivore numbers is of course desirable, of interest and should be examined from a biocontrol perspective. However, with the little evidence available on costs to plants we will be unable to appropriately evaluate if omnivore-provided services often serve (or not) in favor of plants. Even if costs are found to be null or low, such knowledge is valuable and necessary, and we argue that costs to plants should be increasingly considered together with the predatory benefits provided by omnivores. Furthermore, not only is available evidence scarce, but it is strongly overrepresented by studies on tomato plants and omnivorous mirid predators. These results likely mirror the large efforts placed in finding pesticide-free pest management strategies in tomatoes, and in understanding the predatory services provided by different mirid species in this system (e.g., Urbaneja et al., 2012; Pérez-Hedo and Urbaneja, 2016). This research has greatly advanced our knowledge on the net outcome of biocontrol services and laid the foundation for work in other systems. Nonetheless, this bias creates a confounding factor when examining literature on effects of omnivore plant-feeding, as search results are largely skewed toward specific species. This should, thus, be considered when interpreting results from our systematic review.

FUTURE PROSPECTS

Despite a generally low consideration of costs to plants in the literature, publications trends did indicate a more recent awareness of omnivore plant-feeding and its consequences for plants. Indeed, we noticed that several recent papers highlighted some of the knowledge gaps documented by our systematic review (e.g., Hamdi et al., 2013; Aubry et al., 2016; Silva et al., 2017; van Lenteren et al., 2018b) and we hope this is indicative of an ongoing paradigm shift. We, thus, make a timely call for future studies to include a more explicit quantification of costs to plants, and to avoid assuming that they are outweighed by benefits.

Our systematic search also yielded several very recent papers examining the effects of omnivore plant-feeding on induction of plant defenses (Pérez-Hedo et al., 2015b, 2018; Bouagga et al., 2018c; Pappas et al., 2018b; Zhang et al., 2018). Results from these studies present new exciting avenues for increasing the value of omnivorous predators as biocontrol agents. It seems they are able to provide more than predatory services, as their previous plant-feeding can reduce subsequent herbivore performance and even attract other natural enemies (Pappas et al., 2015; Pérez-Hedo et al., 2015a,b). Furthermore, they appear to perceive differential volatile emissions from plants colonized vs. non-colonized by beneficial defense-enhancing endophytic fungi; thus, enabling stronger plant protection as both direct and indirect defenses can be utilized (Pappas et al., 2018a). These novel findings, however, have not addressed any potential costs arising from defense induction (**Table 1**). That is, costs in terms of resources being diverted away from other functions (such as growth) and invested in defense following omnivore plant-feeding. Studies examining induced defenses after herbivory have shown that resource allocation costs can range from low to high, and vary depending on plant species and trait (Züst and Agrawal, 2017). We thus, recommend greater consideration of such costs to plants in future studies addressing induced defense.

To study costs to plants associated with omnivore plant-feeding, we suggest that studies include several treatments with or without predators, in the absence and presence of prey, and ideally several plant damage (leaf, stem, flower, fruit injuries) and performance (growth, reproduction) variables should be evaluated. Such treatments could include: (1) Control group with plants receiving no damage; (2) Plants with an omnivorous predator that is allowed to reside but not feed on plants (e.g., impairing stylets/mandibles); (3) Plants with an omnivorous predator allowed to feed on plants. These treatments can be replicated both in the absence and presence of prey (e.g., impaired and unimpaired omnivore alone on plant, or together with insect pest as prey). Examination of additional indirect effects resulting from omnivore feeding, for example on parasitoids, could also be included.

Lastly, future efforts should also be aimed at examining a wider range of omnivore-plant systems. In order to be able to make more general conclusions, we need to broaden the base of knowledge on which our current understanding of costs to plants relies on. Perhaps with the exception of *N. tenuis* on tomato plants, our search results indicate that we cannot conduct complete net effect evaluations (benefits vs. costs) of the pest control services provided by many important omnivorous predators. We strongly believe that it is time to catch-up with the mirid-tomato bias.

AUTHOR CONTRIBUTIONS

AP, JS, and CB conceived and designed the questions addressed in the systematic review, as well as the search strategy employed both for the review and publication trends. AP conducted the systematic searches and selection of studies to be scrutinized. JS and CB also conducted full-text examination and classification of the selected studies. JS analyzed trends. AP wrote the manuscript following discussion of results with JS and CB, which also provided input during revisions.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2018.00218/full#supplementary-material

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How Safe Is It to Rely on *Macrolophus pygmaeus* (Hemiptera: Miridae) as a Biocontrol Agent in Tomato Crops?

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Omnivorous mirids (Hemiptera: Miridae) are unusual as biocontrol agents, as they feed on both plants and pests. Therefore, extensive knowledge of their ecological behavior is required to maximize their predatory side and to minimize crop damage. *Macrolophus pygmaeus* is a known predator of small arthropods, used in European tomato crops for more than 20 years. This mirid is currently considered harmless to tomato, although some controversy remains in relation to the status of the species. The aim of this work was to investigate the benefits that *M. pygmaeus* provides as a predator and the likely damage as a plant feeder. The experiment was carried out in 6 experimental greenhouses in southern Spain. Two treatments, low and high *M. pygmaeus* populations, were assayed in a complete factorial randomized design with three replicates. Low and high *M. pygmaeus* populations were achieved by direct and pre-plant release methods, respectively. Tomato plants with a lower number of *M. pygmaeus* had a significantly higher number of whiteflies and *Tuta absoluta* galleries than those with a higher number of the mirid, and *vice versa*. A significantly higher proportion of aborted flowers and fruits was registered in greenhouses with higher *M. pygmaeus* numbers. Yield was also lower in greenhouses with higher mirid populations. The number of fruits harvested did not differ between treatments, but average fruit weight was significantly lower in the greenhouses with higher mirid numbers. The number of punctures attributed to *M. pygmaeus* on fruits were low in general and slightly higher in the treatment with more mirids. This work shows that *M. pygmaeus* provides both "services," as an efficient biocontrol agent of key pests in tomato crops, and "disservices," as it feeds on the reproductive organs of tomato plants, reducing yield. A deeper understanding of the factors that modulate the zoophytophagous response of this economically important species is needed.

Keywords: omnivorous mirids, biological control, tomato pests, fruit and flower abortion, yield, economical damage

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INTRODUCTION

Omnivorous mirids (Hemiptera: Miridae) do not fit the ideal model of predators from a biological pest control perspective as they feed not only on prey but also on plants, thus providing both services and disservices. Their zoophytophagous and generalist behavior was one of the reasons why the biological pest control community was initially reluctant to include them in Integrated

Pest Management (IPM) programs (Castañé et al., 2011). This point of view has greatly changed in recent decades with several species of mirids being successfully used in the regulation of pest populations, especially on vegetable crops. Several species of omnivorous mirids, such as dicyphines, are key predators in some vegetable crops (e.g., tomato) because of their ability to live on plants with glandular trichomes (Schuh and Slater, 1995; Sanchez and Cassis, 2018). *Dicyphus cerastii* Wagner, *Dicyphus hesperus* Knight, *Dicyphus hyalinipennis* Burmeister, *Dicyphus tamanini* Wagner, *Macrolophus pygmaeus* and *Nesidiocoris tenuis* Reuter (Hemiptera: Miridae) have been reported as effective biocontrol agents of small arthropod pests (Barnadas et al., 1998; Albajes and Alomar, 1999; Ceglarska, 1999; Carvalho and Mexia, 2000; Alomar et al., 2002; Sanchez et al., 2003, 2014; Calvo et al., 2012a,b). Some of these species (i.e., *M. pygmaeus*, *N. tenuis,* and *D. hesperus*) are routinely used in tomato crops for the control of whiteflies and the South American tomato moth *Tuta absoluta* (Meyrick) (Lepidoptera: Gelechiidae) (Gillespie et al., 2007; Castañé et al., 2011; Calvo et al., 2012a,b; Urbaneja et al., 2012; Biondi et al., 2013, 2018). The potential of others, such as *Dicyphus errans* Wolf and *Dicyphus maroccanus* Wagner (Syn. *Dicyphus bolivari* Lindberg) (Hemiptera: Miridae) (Sanchez and Cassis, 2018), has been assayed recently against *Tuta absoluta* on tomato crops (Ingegno et al., 2013, 2017a,b; Abbas et al., 2014). Other species, such as *Engytatus modestus* Distant and *Creontiades pallidus* Rambur (Hemiptera: Miridae), are known to prey on phytophagous arthropods but have a more prominent plant-feeder character and are thus considered as pests (Urbaneja et al., 2001; Ferguson and Shipp, 2002). Nonetheless, the use of omnivorous mirids as predators is not free from controversy and while some species (i.e., *N. tenuis*) are openly considered as beneficial in some parts of the world (e.g., Canary Islands, southern Spain) (Carnero et al., 2000; Calvo and Urbaneja, 2004), they have been reported to cause some troubles in others (e.g., temperate Europe) (Vacante and Tropea-Garzia, 1994; Trottin-Caudal et al., 2006). Besides the likely subjective level of appreciation, it is undeniable that omnivorous mirids are unusual as predators and management strategies are needed that minimize the negative aspects of their phytophagous character while exploiting their predatory side (Albajes and Alomar, 1999; Sanchez, 2009).

Like many other heteropterans, mirids use a lacerate and flush feeding method, in which plant or prey tissues are liquified by digestive enzymes and the mechanical actions of stylets to facilitate their ingestion (Miles, 1972; Cohen, 1995; Wheeler, 2001). As phytophgous insects, they feed on the mesophyll of leaves and the ground tissues of stems, inflorescences, and fruits, which are more balanced in nutrients than phloem or xylem (Wheeler, 2001). Zoophytophagy in mirids is a continuous trait, going from strictly phytophagous species to essentially obligate carnivores (Miles, 1972; Wheeler, 2001; Cassis and Schuh, 2012). In this work, we refer to omnivorous as those species that feed obligatory or facultatively on plants but whose main feeding niche is carnivory. This is the case for some taxa, such as certain *Macrolophus, Dicyphus*, and *Nesidiocoris* species, that are of interest as biological control agents in vegetable crops and feed on both plants and prey, but for whom the contribution of vegetable nutrients to their fitness is generally very low in comparison with animal food (Sanchez et al., 2004; Ingegno et al., 2011). Besides, their perfomance varies greatly with the mirid species, host plant, the availability of alternative host plant, and even the plant part (McGregor et al., 2000; Perdikis and Lykouressis, 2000; Lucas and Alomar, 2001; Wheeler, 2001; Sanchez et al., 2004; Biondi et al., 2016). In the most favorable cases, plant feeding allows the insect to complete its development and reproduce but, generally, the nymphal stage lasts much longer and egg-laying is very limited in comparison to when feeding on prey (Naranjo and Gibson, 1996; Perdikis and Lykouressis, 2000; Sanchez et al., 2004, 2016; Urbaneja et al., 2005; Perdikis et al., 2007; Lykouressis et al., 2008; Ingegno et al., 2011; Mollá et al., 2014). In consequence, omnivorous mirids consume primarily prey when available and phytophagy, as well as plant injury, increases exponentially when animal food is scarce (Sanchez, 2008, 2009; Sanchez and Lacasa, 2008; Calvo et al., 2009; Arnó et al., 2010; Sanchez et al., 2016). Injuries produced by omnivorous mirids vary with the organ affected, and with the plant and mirid species. Mirids produce blemishes, scars, and deformations in tomato and zucchini, and minor injuries in melon fruits (Alomar and Albajes, 1996; Shipp and Wang, 2006; Castañé et al., 2011); feeding on gerbera blossoms may cause deformations and depreciation of flowers (Gillespie et al., 2007). The greatest impact of mirids derives from flower damage and fruit abortion because, rather than having an impact on the cosmetic appearance of the fruit, it materializes in the yield itself (Sanchez and Lacasa, 2008; Sanchez, 2009). This has prompted investigation into the factors that modulate the zoophytophagous response in omnivorous mirids and the development of management strategies to keep populations below critical levels (Alomar and Albajes, 1996; Sanchez and Lacasa, 2008; Sanchez, 2009; Sanchez et al., 2016).

Macrolophus pygmaeus has been marketed and included in programs for the control of pests in European tomato greenhouses for more than 20 years (Malausa and Trottin-Caudal, 1996; Castañé et al., 2011; van Lenteren, 2012). There have been problems with the identification of *Macrolophus* species and in many cases *M. pygmaeus* was identified as *Macrolophus caliginosus* (Martínez-Cascales et al., 2006a,b). In this work, we consider that the citations of *M. caliginosus* on tomato are quite likely misidentifications of *M. pygmaeus* (Castañé et al., 2013). This mirid was originally used for the control of whiteflies but it may potentially prey on other small arthropods - such as thrips, spider mites, leafminers, aphids, and lepidopterans, including the eggs and first instar of *T. absoluta* - (Fauvel et al., 1987; Alvarado et al., 1997; Barnadas et al., 1998; Riudavets and Castañé, 1998; Margaritopoulos et al., 2003; Arnó et al., 2009; Calvo et al., 2009; Urbaneja et al., 2009, 2012; Castañé et al., 2011). *Macrolophus pygmaeus* is currently considered as harmless to tomato crops (Castañé et al., 2011) nonetheless, some controversy still remains in relation to the status of the species. On the one hand, the damage it produces is considered as irrelevant in comparison to the benefits it provides in terms of pest control (Malausa and Trottin-Caudal, 1996; van Lenteren and Tommasini, 2003; Castañé et al., 2011). On the other hand, economic damage has been reported in tomato crops (Sampson, 1996; Sampson and Jacobson, 1999; Moerkens et al., 2016).

The fact is that no conclusive experiments have been carried out to quantify the impact of *M. pygmaeus* in tomato crops, and this issue has not been revised in a long time. The aim of this work was to investigate the trade-off between the benefits that *M. pygmaeus* provides as a pest control agent and the injuries it may cause to tomato crops in greenhouses.

MATERIALS AND METHODS

Crop Setting

The assay was carried out in 6 experimental greenhouses of 5 × 10 m each at the IMIDA experimental station in Dolores de Pacheco, Murcia (Spain), from 14 February to 5 June 2018. Nothing was grown in these greenhouses in the latest 2 years and during this period they were freed of weeds, both inside and the immediate surroundings. The greenhouses were built of polycarbonate, with individual frontal and zenithal meshed openings for ventilation (10 × 14 threads/cm). The temperature was controlled independently in each greenhouse by the Mithra Clima System (Nutricontrol, S.L., Cartagena, Murcia); opening was activated automatically at 20°C and no heating or artificial lighting were provided. The temperature and relative humidity were recorded by the system every minute. There were four rows of 20 tomato plants in each greenhouse; the distance between plants in a row was 0.5 m, with 1 m between rows. Tomato seeds (cv. Optima, Seminis, Murcia) were planted on 1 December 2017 and seedlings 25–30 cm high were transplanted on 14 February 2018. This tomato cultivar is commonly cultivated in the area. The plants were grown in soil, and were watered and fertilized when needed by drip irrigation. Due to the small size of the greenhouses and their good ventilation, no pollinator insects were introduced. No pesticides nor fungicides were applied during the entire period of the assay.

Experimental Design and Sampling

The effect of *M. pygmaeus* on the regulation of the populations of the whitefly *Bemisia tabaci* Gennadius (Hemiptera: Aleyrodidae), as well as other pests (e.g., *T. absoluta*), and its impact on reproductive organs (i.e., flowers and fruits) and yield was quantified. Two release methods for *M. pygmaeus* were assayed, direct and pre-release, in order to achieve low and high population levels of the mirid, respectively. Hereafter, these two treatments will be referred to as "low *M. pygmaeus* population" and "high *M. pygmaeus* population." Each treatment was replicated three times in individual greenhouses, following an experimental randomized block design. *Macrolophus pygmaeus* was provided by Bioline Agroscience (Essex, France). In direct release, 320 adults of *M. pygmaeus* (half females and half males) were released per greenhouse. The adults of *M. pygmaeus* were approximately 7–10 days old. In order to improve the establishment of the mirid, the adults of *M. pygmaeus* to be introduced in each greenhouse were kept during the 24 h prior to their release in three muslin-walled, wooden-framed cages, each with 16 tomato plants (approx. 30–40 cm tall), at 25 ± 2°C, 60–70% RH, and a 16L:8D photoperiod. Twenty-four hours later, the 16 tomato plants of each cage, with the adults of *M. pygmaeus*, were transplanted in their respective greenhouses (four tomato plants per row). In pre-release, the same procedure as in direct release was used but the 320 adults of *M. pygmaeus* were left to multiply for 1 month before their introduction in the greenhouses. The mirids were fed periodically (every 3–4 days) on *Ephestia kuehniella* Zeller (Lepidoptera: Pyralidae); a total of 24 g were provided to each of the three cages during the whole period. The number of *M. pygmaeus* was counted on six plants per cage before they were introduced in the greenhouse, the number of *M. pygmaeus* (nymphs and adults) in the 16 tomato plants introduced in the greenhouse being estimated as 328 ± 18 (mean ± SE) individuals. In both treatments, the tomato plants with the mirids were transplanted in the greenhouses on 27 March 2018; in the 2 weeks following this, the tomato plants were supplemented with 5 g of *E. kuehniella* per greenhouse. *Bemisia tabaci*, provided by Koppert Spain, was introduced twice in all the greenhouses, on 13 March 2018 and 21 March 2018, at 400 adults per greenhouse on each date. *Tuta absoluta* was not introduced because it invariably colonizes tomato greenhouses in southern Spain (Cabello, 2009).

The nymphs and adults of *M. pygmaeus* and the *T. absoluta* galleries and adults were counted *in situ* every 10 days (approx.) on 15 whole tomato plants, selected at random, from the date of the first whitefly release until the end of the experiment. The *B. tabaci* nymphs and adults were counted *in situ* on one leaf from the top, middle, and bottom parts of the plant. The number of *M. pygmaeus* and other arthropods was also recorded on these leaves. To quantify the impact of *M. pygmaeus* on the reproductive organs of tomato plants, the number of flowers and of those aborted was counted in a truss from the apical part of each of the 15 sampled plants on each sampling date, starting 1 week after the release of *M. pygmaeus*. Besides, the number of fruits and of those that did not fructify was counted in the first available truss with no flowers, when inspecting the plants from top to bottom. Fruits were harvested on three occasions: 17 and 28 May, and 4 June 2018. On the three dates, all the fruits in each greenhouse were counted and weighed. Besides, on 28 May, 50 fruits per greenhouse were chosen at random, weighed, and scored individually for *T. absoluta* damage and *M. pygmaeus* punctures. Additionally, on 4 June, fruits were harvested individually from 20 randomly selected plants in each greenhouse and processed individually. They were classified as ripe (completely red), about to ripen (partially green), or green (completely green).

Statistical Analyses

Generalized linear mixed effect models (GLMMs) were used to compare the number of *M. pygmaeus* on plants, the number of *T. absoluta* galleries on plants, and the number of *B. tabaci* (nymphs and adults) on leaves between treatments (low and high *M. pygmaeus* populations). The date of sampling was introduced in the models as a random factor. GLMMs were also used to compare the proportions of aborted flowers and the proportions of aborted fruits on trusses. The data of the abundance of *M. pygmaeus* on plants and the proportion of aborted flowers were normally distributed; thus, the "lmer" function ("lme4" package) was used in the analyses (R-Development-Core-Team, 2017). The data for *T. absoluta* galleries on plants fitted a negative binomial distribution, thus, the "glmmPQL" function ("MASS" package) set to the negative binomial family was used to perform the analyses. The number of *B. tabaci* (nymphs and adults) per leaf and the proportion of aborted fruits fitted log-normal distributions and their analyses were performed using "glmmPQL" ("MASS" package) set to the Gaussian distribution with the link "log." The total yield, number of fruits, and average fruit weight (yield divided by the number of fruits) were compared between treatments using the data obtained for all the fruits of each greenhouse picked on each of the three harvesting dates. Besides, the data from the processing of single tomato fruits at the second and third harvests were used to compare

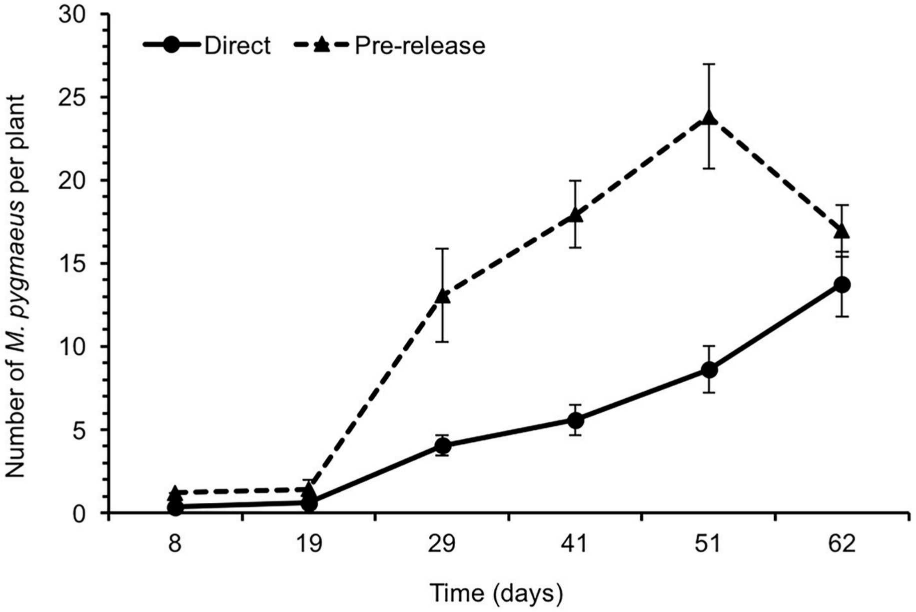

FIGURE 1 | Average number of *Macrolophus pygmaeus* (adults+nymphs) per plant ± SE in tomato greenhouses with direct- and pre-release (see materials and methods). Time since the introduction of *B. tabaci*.

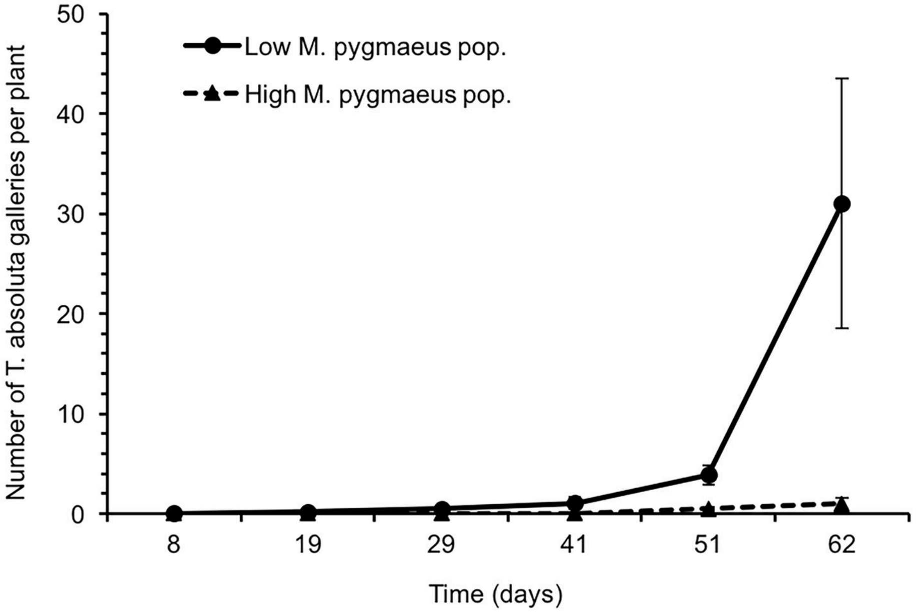

FIGURE 2 | Average number of *Tuta absoluta* galleries ± SE per tomato plant in greenhouses with low and high *M. pygmaeus* populations. Time since the introduction of *Bemisia tabaci*.

the number of *T. absoluta* wounds, the number of *M. pygmaeus* punctures, and the weight of single fruits between the two treatments. In the latter analyses, the state of fruit ripening was introduced in the models as a random factor. In all cases, with the exception of *T. absoluta* damage, the data were normally distributed and the "lmer" function was used to perform the analyses. In the case of *T. absoluta* damage, "glmmPQL" ("MASS" package), set to the Gaussian distribution with the link "log," was used. All the statistical analyses were performed using R software (R-Development-Core-Team, 2017).

RESULTS

Population Dynamics and Impact of *M. pygmaeus* on Pest Insects

Macrolophus pygmaeus reached significantly higher numbers in the greenhouses where populations were built up for 1 month before their introduction (pre-release) than in those where they were released after an acclimation of only 1 day with tomato plants (direct release) [$\chi^2(1) = 26.3$, $P < 0.001$] (**Figure 1**). In the two treatments the *M. pygmaeus* population increased progressively until the end of the experiment (62 days after release), reaching a maximum of 13.8 ± 1.9 and 23.8 ± 3.1 (mean ± SE) individuals per plant in the greenhouses with direct and pre-release, respectively.

Greenhouses with a lower population of *M. pygmaeus* had a significantly higher number of *T. absoluta* galleries than those where the population of the mirid was higher [$\chi^2(1) = 73.9$, $P < 0.001$] (**Figure 2**). The number of *T. absoluta* galleries per plant reached a maximum of 31.0 ± 12.5 and 1.0 ± 0.6 in greenhouses with low and high *M. pygmaeus* populations, respectively. In the same way, the number of *B. tabaci* was significantly higher in greenhouses with lower rather than higher numbers of *M. pygmaeus* [nymphs: $\chi^2(1) = 21.5$, $P < 0.001$; adults: $\chi^2(1) = 36.6$, $P < 0.001$] (**Figure 3**). The whitefly numbers increased progressively in the two treatments, reaching–on day 62–a maximum of 14.8 ± 2.6 and 5.8 ± 0.6 *B. tabaci* nymphs per leaf in the greenhouses with lower and higher mirid density, respectively. The peak of *B. tabaci* adults was registered on day 41 after its introduction, being higher in greenhouses with lower (1.5 ± 0.3 adults of *B. tabaci* per leaf) rather than higher (0.6 ± 0.1 adults of *B. tabaci* per leaf) *M. pygmaeus* populations. No other whitefly species (*T. vaporariorum*), spider mites (*Tetranychus* spp.) or mirid (*N. tenuis*) were registered in samplings. *Frankliniella occidentalis* (Pergande) (Thysanoptera: Thripidae) was observed very occassionally on leaves.

Impact of *M. pygmaeus* on Reproductive Organs of Tomato Plants and Yield

A significantly higher proportion of aborted flowers was registered in greenhouses with higher *M. pygmaeus* numbers [$\chi^2(1) = 15.8$, $P < 0.001$] (**Figure 4**). The proportion of aborted flowers in the greenhouses with lower numbers of mirids was fairly constant and below 1.3%; in contrast, the proportion of aborted flowers reached 12.2 ± 4.1% in the greenhouses with higher mirid numbers (**Figure 4**). In the same way, the proportion of aborted fruits was higher in the greenhouses with higher mirid numbers [$\chi^2(1) = 14.7$, $P < 0.001$] (**Figure 4**). The percentage of aborted fruits was highest at the end of the assay, both at high (46.7 ± 9.1%) and low *M. pygmaeus* populations (27.9 ± 6.1%).

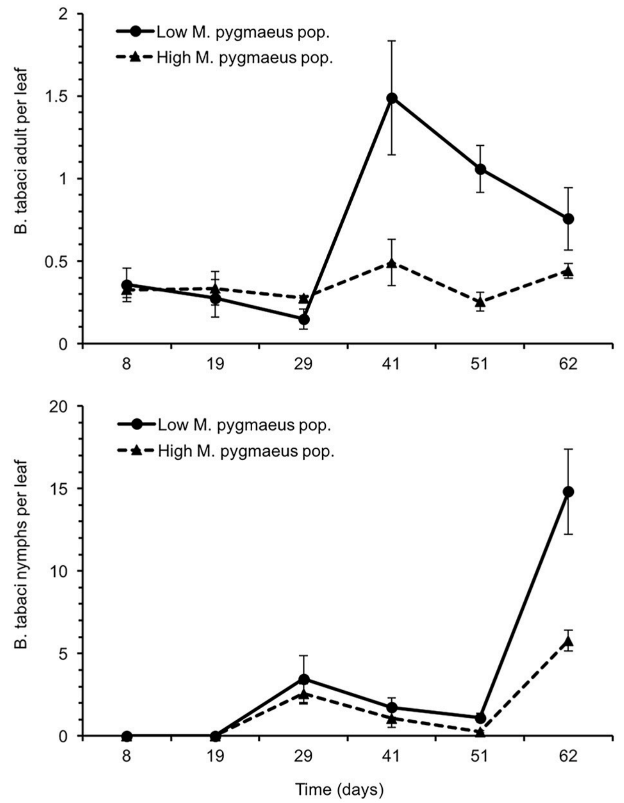

FIGURE 3 | Average number of *Bemisia tabaci* nymphs (lower graph) and adults (upper graph) ± SE per leaf in tomato greenhouses with low and high *M. pygmaeus* populations. Time since the introduction of *Bemisia tabaci*.

Yield was significantly lower in greenhouses with higher numbers of *M. pygmaeus* [$\chi^2(1) = 4.3$, $P < 0.05$] (**Figure 5**). Besides, the average fruit weight (yield/number of fruits) in the greenhouses with higher numbers of *M. pygmaeus* was significantly lower than in those where the mirid was less abundant [$\chi^2(1) = 12.3$, $P < 0.001$] (**Figure 5**). Similar results for fruit weight were obtained from the processing of single fruits at the second and third harvests [$\chi^2(1) = 13.4$, $P < 0.001$] (**Supplementary Material**). In contrast, the number of fruits harvested did not differ between treatments [$\chi^2(1) = 0.114$, $P = 0.736$]. The number of punctures attributed to *M. pygmaeus* was a little higher in the greenhouses with the highest densities of the mirid (mean ± SE: 1.1 ± 0.4 punctures per fruit) than in those with the lowest densities (mean ± SE: 0.8 ± 0.2 punctures per fruit) [$\chi^2(1) = 3.1$, $P = 0.078$] **(Supplementary Material)**. The number of damages due to *T. absoluta* was higher in the greenhouses with the lowest *M. pygmaeus* numbers (0.053 ± 0.055 injuries per fruit) than in those with the highest numbers (0.001 ± 0.003 injuries per fruit), but not significantly so [$\chi^2(1) = 0.153$, $P = 0.696$] **(Supplementary Material)**.

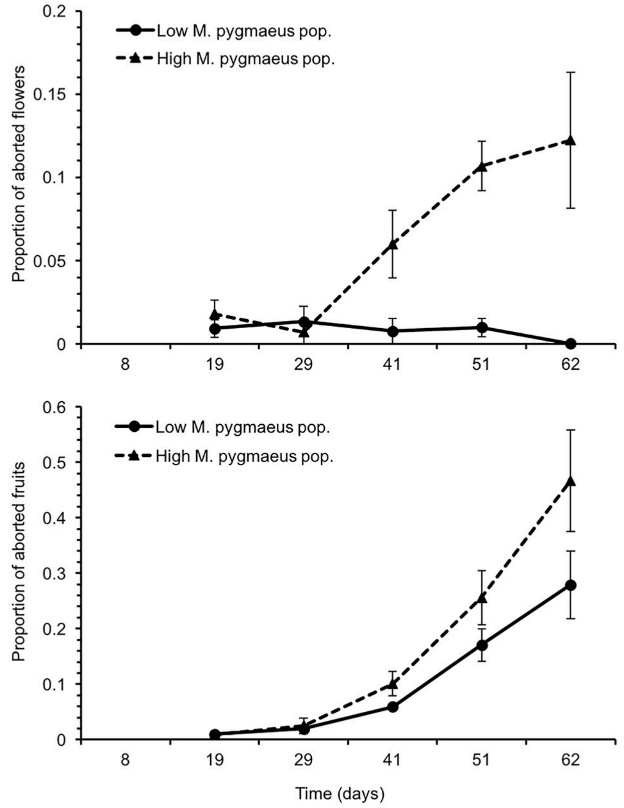

FIGURE 4 | Proportion of aborted flowers (upper graph) and fruits (lower graph) ± SE in tomato greenhouses with low and high *M. pygmaeus* populations. Time since the introduction of *Bemisia tabaci*.

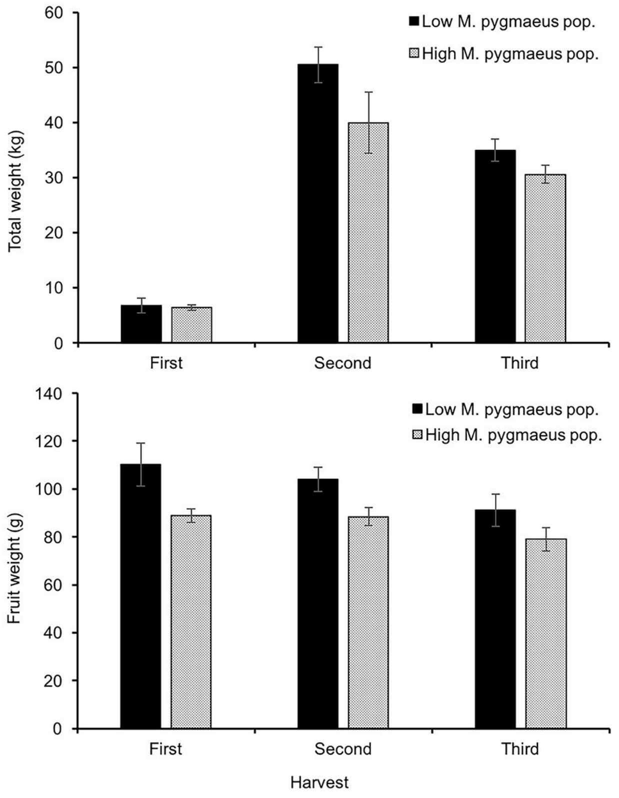

FIGURE 5 | Total yield (upper graph) and fruit weight (lower graph) ± SE in tomato greenhouses with low and high *M. pygmaeus* populations.

DISCUSSION

The two methods of introducing *M. pygmaeus* (pre-release and direct) in the tomato greenhouses differed in the size of the populations of the mirid that they produced. *Macrolophus pygmaeus* was significantly more abundant when the populations had been built up for a month before the introduction than when it was released just after a short period of acclimation (1 day) under controlled conditions. Other authors have reported differences in the establishment and population dynamics of predatory mirids depending on the release method (Lenfant et al., 2000; Calvo et al., 2012a,b; Nannini et al., 2014). In agreement with the results of this work, Nannini et al. (2014) observed that *M. pygmaeus* had a better establishment and reached higher population densities in tomato crops when introduced by pre-planting release, in comparison to conventional release methods.

The differences in the size of the *M. pygmaeus* population had opposite effects on pest control and yield. On the one hand, *M. pygmaeus* provided "services," as greenhouses with higher populations of *M. pygmaeus* had lower incidences of two pests, *T. absoluta* and *B. tabaci*. On the other hand, it provided "disservices," because the greenhouses with higher mirid numbers had higher flower and fruit abortion, and suffered reductions in yield and fruit size. *Macrolophus pygmaeus* is a reputed predator of the whiteflies *B. tabaci* and *Trialeurodes vaporariorum* Westwood (Hemiptera: Aleyrodidae) (Fauvel et al., 1987; Barnadas et al., 1998; Albajes and Alomar, 1999; Perdikis and Lykouressis, 2002; Alomar et al., 2006; Lykouressis et al., 2009; Jaeckel et al., 2011; Sylla et al., 2016). This mirid has also been reported to be one of the main predators of *T. absoluta* in the Mediterranean area and adjacent territories (Arnó et al., 2009; Mollá et al., 2009; Urbaneja et al., 2012; Biondi et al., 2013, 2018; Chailleux et al., 2013; Jaworski et al., 2013; Zappala et al., 2013; Sylla et al., 2016). Efficacy trials in field or semi-field conditions showed that *M. pygmaeus* is able to reduce the incidence and populations of *T. absoluta* in tomato crops (Mollá et al., 2009; Nannini et al., 2014). In the present work *M. pygmaeus* was able to reduce the abundance of both *B. tabaci* and *T. absoluta*; as expected, better control of *T. absoluta* and *B. tabaci* was achieved at the higher abundance of the predator. Other authors have also reported the ability of this mirid to reduce the abundance of these two pests when they were present at the same time (Bompard et al., 2013; Nannini et al., 2014). However, lower predation rates and pest control efficacy were reported for the leafminer in comparison with the whitefly (Jaworski et al., 2013; Nannini et al., 2014).

Omnivorous dicyphines are known to feed on plants, with variations in the kind of injuries they inflict on reproductive and vegetative organs, and their magnitude, depending on the mirid and plant species (Alomar and Albajes, 1996; Calvo and Urbaneja, 2004; Alomar et al., 2006; Sanchez et al., 2006; Shipp and Wang, 2006; Sanchez, 2008, 2009; Sanchez and Lacasa, 2008). *Dicyphus tamaninii* is known to produce small blemishes, scars, and deformation on green tomato fruits, and damage has been reported at times of high mirid abundance and low prey density (Albajes and Alomar, 1999). The feeding marks of *D. hesperus* were characterized as punctures surrounded by yellowish-bleached areas, and severely damaged fruit were downgraded with a 50% decrease in their market value. Shipp and Wang (2006) remarked that this mirid produced significant damage to tomato crops when its abundance was high and the prey density low, with a high proportion of severely damaged fruits when the predator:prey ratio exceeded 1:10 for *D. hesperus*: *F. occidentalis* (Shipp and Wang, 2006). *Nesidiocoris tenuis* is one of the species with the highest intrinsic risk of producing severe damage to tomato crops, because it produces fruit and flower abortion (Sanchez, 2008, 2009; Sanchez and Lacasa, 2008; Calvo et al., 2009), which have never been reported for any of the above mentioned dicyphines. Sanchez and Lacasa (2008) reported percentages of aborted fruits ranging from 8.79 ± 1.64 to 26.31 ± 3.53% (mean ± SE) per truss, in tomato plants exposed for 3 weeks to an average of 0.53 ± 0.26 to 35.2 ± 7.7 *N. tenuis* per plant, respectively. Part of this fruit abortion (10.35 ± 3.68%) was estimated to be due to causes other than *N. tenuis* feeding. Yield loss did not occur for the above reported range of abortion because fruit loss was compensated by an increase in the weight of individual fruit (Sanchez and Lacasa, 2008). *Macrolophus pygmaeus* has always been considered a safe species (Albajes and Alomar, 1999; Lucas and Alomar, 2002; Castañé et al., 2011). The injuries reported for this mirid mainly involve feeding marks on vegetative organs and tomato fruits, but they have not been generally reported in commercial settings (Malausa and Trottin-Caudal, 1996; Castañé et al., 2011). Albajes and Alomar (1999) did not observe any negative effect due to this mirid (identified as *M. caliginosus*) on tomato after several years of its use in conservation IPM programs; currently, it is still considered a non-problematic biocontrol agent in tomato crops (Castañé et al., 2011). Nonetheless, there is controversy in relation to the role of *M. pygmaeus* in tomato crops. Malausa and Trottin-Caudal (1996) found that this mirid (identified as *M. caliginosus*) produced damage at very high densities, even though it was considered harmless to tomato crops. Moerkens et al. (2016) argued that *M. pygmaeus* can cause economic feeding damage on tomato fruits at high population densities, specially when plants are infected with Pepino mosaic virus (PepMV). Sampson (1996) reported an increase in the number of fruits knuckled off in cherry tomato crops with high populations of the mirid (identified as *M. caliginosus*) as the prey ran short. Flower and fruit drop was reported as the most serious kind of damage to tomato crops produced by this mirid in the UK, with economic losses for both cherry and round tomato varieties (Sampson and Jacobson, 1999). The findings of the present work are in agreement with the observations of the latter authors. In the greenhouses with high *M. pygmaeus* populations a maximum of 12.2 ± 0.04% of flower abortion was registered, while flower abortion at low *M. pygmaeus* populations was always below 1.5%. Fruit abortion increased in the two treatments, but it was significantly higher at high than at low *M. pygmaeus* populations, with the maximum difference between treatments (18.8%) reached at the end of the assay. These differences in flower and fruit abortion between low and high *M. pygmaeus* populations indicates a negative impact of the mirid on tomato reproductive organs. The mirid abundance and prey availability may have both accounted for the outcome in flower and fruits abortion rates. The impact of omnivorous mirids on plant reproductive organs is known to be positively and inversely related to mirid and prey abundances, respectively (Sanchez, 2008, 2009; Sanchez and Lacasa, 2008). The much higher fruit abortion, relative to that of flowers, may have been due to intensification of *M. pygmaeus* feeding on young fruit petioles and/or to the effect of environmental factors. Cosmetic damage (e.g., punctures, spots) was very low and did not differ significantly between treatments. In agreement with these results, Lucas and Alomar (2002) did not find significant differences in the number of punctures between fruits exposed to the mirid (identified as *M. caliginosus*) and the controls. *Macrolophus pygmaeus* had a negative impact on production, with lower yields in greenhouses with higher *M. pygmaeus* populations. Surprisingly, the impact on yield was due not to the lower number of fruits at harvest but to the reduction in the weight of single fruits. This is the first time a reduction in fruit weight has been reported for any mirid species. In contrast, an increase in the weight of individual fruits that compensated fruit abortion was reported for *N. tenuis* (Sanchez and Lacasa, 2008; Sanchez, 2009). The reduction in fruit weight may be due to the effect of plant feeding; for instance, limited feeding of the mirid on fruit petioles could interfere with normal development without inducing fruit drop. The differences in the findings of the present work, in relation to what has been reported previously by other authors, may be due to the existence of *M. pygmaeus* subpopulations with different biological attributes. Ecological studies on the structure of *M. pygmaeus* populations using molecular markers showed the existence of several subpopulations in the Mediterranean area (Sanchez et al., 2012; Streito et al., 2017).

Whatever the reasons behind the differences between our findings and what has been reported previously for *M. pygmaeus* by other authors, the results of the present work raise enough concern to revise the status of this mirid. *Macrolophus pygmaeus* is a species of high economic importance that is currently used for pest control in more than 20 European countries and in many others in northern and southern Africa (van Lenteren, 2012). Therefore, the current consideration of this mirid as a "safe" biocontrol agent may have important economic repercussions, worldwide, for tomato crops unless proper management strategies are adopted. Establishment has always been considered a limiting factor for omnivorous mirids and researchers have always looked for strategies to establish high populations prior to pest infestations (Lenfant et al., 2000; Calvo et al., 2012a,b; Backer et al., 2014; Nannini et al., 2014). The results of the present work show that the risk of the early establishment of high populations of omnivorous mirids, *M. pygmaeus* included, should be taken into account. High populations may provide better pest control but that may not compensate for the yield loss derived from the increased plant feeding by the mirid. Molecular tools should be used to identify different subpopulations or strains (Sanchez et al., 2012; Streito et al., 2017), in order to select those with the most desirable biological attributes. These tools may be used also to monitor populations after their release or to detect natural immigration into crops (Sanchez et al., 2012; Streito et al., 2017). The selection of populations or strains and the implementation of appropriate management strategies will help to take advantage of the predatory side of this omnivorous mirid while minimizing the negative impact of its phytophagous side.

AUTHOR CONTRIBUTIONS

JS designed the experiment, sampled in the field, analyzed the data, and wrote the manuscript. EL-G helped in designing the experiment, sampled in the field and digitalised the data. MP-M, LP-F, and MR-S helped with sampling in the field.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2018.00132/full#supplementary-material

Supplementary Data Sheet 1 | Data on the processing of tomato fruits at second and third harvests. Average number of punctures attributed to *Macrolophus pygmaeus*, injuries of *Tuta absoluta* and fruit weight.

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From Evolutionary Aspects of Zoophytophagy to Biological Control

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Zoophytophagy (true omnivory) is a ubiquitous behavior. It allows plant-feeding predators to maximize their development by finding essential nutrients, and to survive when animal resources are scarce. In agroecosystems, some zoophytophagous predators are highly efficient biological control agents. However, when feeding on plants, they can generate crop damage that reduce grower's interest in these predators. Artificial selection on behavioral traits of candidate zoophytophagous predators could improve the ecosystem services they provide. Thus, a zoophytophagous species considered as noxious may become an adequate biocontrol agent, following a selection process. Numerous theoretical and applied aspects should be considered during the selection process for the breeding of desired individuals. This review focuses on the potential of the evolutionary approach to optimize the biological control services provided by plant-feeding predators—or zoophytophagous predators—and discuss some ecological and biological control consequences as well as the limitations of the approach.

Keywords: artificial selection, strain selection, hemiptera, zoophytophagous predators, miridae, ecology of individuals, individual diet specialization, intraguild predation

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INTRODUCTION

Numerous definitions of zoophytophagous organisms have been proposed. In this paper, we consider zoophytophagous organisms (or true omnivores) as the organisms that consume both plant and animal resources during their life cycle. In agroecosystems, these organisms may have the status of pests, equivocal species (sometimes beneficial or sometimes noxious) or useful biological control agents in agroecosystems. True omnivores can be classified along a nutritional gradient from phytozoophagous to zoophytophagous species. We consider biological control as an ecosystem service provided by zoophytophagous predators. Biological control of pest species in crop systems can be achieved using three main strategies (Eilenberg et al., 2001): (1) classical biological control, in which introduced exotic natural enemies can exert a long-term control of a targeted exotic pest; (2) augmentative biological control, where locally occurring natural enemies are reared and released to improve pest controls and (3) conservative biocontrol, in which land-use planning favors the increase of natural enemies. The augmentative strategy can be subdivided in two ways to use biological control, namely inoculative and inundative. The former aims to control pest's population over an extended period (but not permanently), whereas the latter is used to rapidly control the pest's population (over a short-term period). With the inundative strategy, no reproduction by the biological control agent is expected and repeated releases may be necessary (Eilenberg et al., 2001).

Zoophytophagous predators are a solution to the growing need for native natural enemies that efficiently control pests (McGregor et al., 1999; Alomar et al., 2006; Calvo et al., 2009;

Fantinou et al., 2009). The role of these predators is increasingly recognized in perennial or annual cropping agroecosystems (Symondson et al., 2002). Most annual crops have multiple arthropod pest problems, requiring an array of specialists natural enemies for efficient control. These approaches are costly, and ecologically complicated due to the mutual interactions between the biological control agents. Zoophytophagous predators are highly successful because they can consume several pest species avoiding the resurgence of secondary pests (McGregor et al., 1999; Symondson et al., 2002; Alomar et al., 2006; Calvo et al., 2009, 2012; Fantinou et al., 2009; Mollá et al., 2011; Zappala et al., 2013). In addition, zoophytophagous predators have the ability to stay in an environment where prey is scarce by switching from animal resources to plant resources (Lalonde et al., 1999; Castañé et al., 2009; Castañe et al., 2011).

Despite their significant success as generalist predators, the use of zoophytophagous predators as biological control agents remains mitigated by the perceived risk of crop damage entailed by phytophagy. However, phytophagous behavior is beneficial for the predators early establishment and survival when prey is scarce (Gabarra et al., 2004; Castañe et al., 2011). Switching diet contributes to the stabilization of zoophytophagous populations, leading to sustained high predation pressure on prey populations (Diehl and Feißel, 2000). Moreover, phytophagy does not always lead to crop damage and economic loss (Castañe et al., 2011). Therefore, there is currently an increasing recognition of the potential of zoophytophagous predators in biological control (Albajes and Alomar, 1999; Wheeler, 2000; Lucas and Alomar, 2002; Urbaneja-Bernat et al., 2013; Maselou et al., 2014; Beitia et al., 2016; Pérez-Hedo et al., 2018).

The efficacy of zoophytophagous predators is affected by an array of different factors at the individual, the population and the community levels. These factors are intimately linked to plasticity and trade-offs related to the diet of zoophytophagous predators. The degree of the phenotypic plasticity of the zoophytophagous predators could be manipulated by selection processes. Therefore, artificial selection may improve traits related to their efficiency as biological control agents in their specific biotic and abiotic conditions.

We argue that the potential of the zoophytophagous predators as biocontrol agents could be enhanced by artificial selection on various traits including detrimental phytophagy, beneficial zoophagy, and diet specialization. In this review paper, we review artificial selection of biological control agents and propose hypotheses on the ecological and biological control consequences. We focus on the biological control services provided by the zoophytophagous predators at the individual, population, and community levels.

THE COMPLEX ZOOPHYTOPHAGOUS PREDATORS CONTEXT AND THE BIOLOGICAL CONTROL SUCCESS

The ability of zoophytophagous predators to provide effective biocontrol services is determined by an array of biological responses observed at different ecological levels. The value of zoophytophagous predators is not simply linked to their zoophagous abilities as biological control agents (i.e., zoophagy on agricultural pests) (McGregor et al., 1999; Castañé et al., 2009; Calvo et al., 2012; Zappala et al., 2013), but also to their relative detrimental impact as phytophagous organisms (Arnó et al., 2006, 2010; Calvo et al., 2009; Perdikis et al., 2009; Castañe et al., 2011). The classification of true omnivores as zoophytophagous or phytozoophagous is often subjective (Wiedenmann and Wilson, 1996). The term used reflects the perception of the observer (ecologist, agronomist) rather than the actual proportion of resources consumed. For example, several zoophytophagous bugs (plant-feeding predators) (Coll and Guershon, 2002) are successfully used as biological control agents of greenhouse and outdoors pests (Castañé et al., 1996, 2009; McGregor et al., 1999; Alomar et al., 2006; Calvo et al., 2009, 2012; Fantinou et al., 2009; Mollá et al., 2011; Zappala et al., 2013). However, the status of zoophytophagous predators in the agroecosystem is controversial because they may cause crop damage and economic losses. Therefore, to fully exploit the potential of zoophytophagous predators, we have to develop methods that improve the benefit-damage ratio associated with their occurrence on crops (Castañe et al., 2011; Calvo et al., 2012). The optimization of zoophytophagous predators for biological control entails complex interactions between predator's morphological, physiological and behavioral traits and the ecological context.

Since animal and plant diets differ greatly, omnivores display physiological and morphological adaptations that are normally only present in strict zoophagous or strict phytophagous insects (Cooper, 2002; Cooper and Vitt, 2002; Eubanks et al., 2003). For example, zoophytophagous mirids have intermediate stylets between those of strongly toothed zoophagous and those relatively smooth of phytophagous insects (Cobben, 1978; Schaefer and Panizzi, 2000). Roitberg et al. (2005) demonstrated that there may be a cost to be zoophytophagous due to the mandibles being worn out by consuming plants. Stylet wear could reduce predation efficiency, compelling an increase in phytophagy. Omnivorous Heteroptera have also a digestive system and accessory salivary glands that are intermediate to those found in herbivores or predators (Boyd et al., 2002), as well as digestive enzymes from both groups (Schaefer and Panizzi, 2000; Wheeler, 2001). Because of these adaptations, zoophytophagous predators have more detoxifying enzymes, improving the ability to manage secondary toxic compounds. They should therefore be more resistant to certain pesticides than strict predators (Gordon, 1961; Coll et al., 1994; Coll and Guershon, 2002). This resistance may improve their ecosystem services in integrated pest management (IPM) programs.

Behavioral plasticity is mainly responsible for the biological control effect of zoophytophagous predators (Coll and Guershon, 2002). For example, Aubry et al. (2017) demonstrated that *Campylomma verbasci* Meyer-Dür (Hemiptera: Miridae) reduce phytophagy (measured as plant feeding punctures) in presence of prey (aphids or spider mites). In this species, most of the damage on apple fruits is caused by the overwintering population during bloom (Aubry et al., 2016). However, adults tend to leave apple trees once the prey population is depleted. The mullein bug is no longer noxious after bloom as plant-feeding does not induce fruit damage (for fruits > 13 mm) and its status becomes beneficial (Aubry et al., 2016). This shift is also observed in other mirids species in open field and greenhouse conditions (Gabarra et al., 2004; Montserrat et al., 2004; Sanchez, 2008), and successfully used to develop management decision charts for *Dicyphus tamaninii* Wagner (Hemiptera: Miridae) in tomato crops (Alomar and Albajes, 1996) or *C. verbasci* in apple orchards (Coll, 1996).

The potential impact of omnivores on prey (noxious or beneficial status) depends not only on their ability to persist during prey scarcity, but also on their response when the consumption of alternative plant and animal resources decreases their prey consumption (Cottrell and Yeargan, 1998; Eubanks and Denno, 2000b). For example, nutrition on high quality plant resources can result in relatively large and persistent populations of omnivores (Eubanks and Styrsky, 2005). By contrast, strict predators will either starve or migrate when their prey is scarce, allowing prey to escape predation at low densities and populations to rebound (Eubanks and Styrsky, 2005).

At the community level, plant-feeding and prey-feeding decisions have important implications for predator-prey dynamics, for energy flows within food webs (Lalonde et al., 1999; Coll and Guershon, 2002) and, consequently, for the noxious/beneficial status of the zoophytophagous predators. Omnivory disperses the direct effects of consumption throughout the trophic web, rather than concentrating them at a specific trophic level (Eubanks, 2005) which favors larger, persistent and often less variable populations. When prey populations decline, omnivores can move to relatively profitable plants providing a mechanism that promotes the stability of the communities (Gillespie et al., 2012). Thus, phytophagy from zoophytophagous predators should promote bottom-up control and increase the likelihood of trophic cascades (Eubanks and Denno, 1999, 2000b; Denno and Fagan, 2003) which will ultimately benefit the plant (Eubanks, 2005).

Intraguild predation (IGP) is defined as predation between species sharing a similar resource (Lucas, 2012) and can also alter the feeding behavior, the development, and the biological control services of zoophytophagous species (Rosenheim et al., 1993; Rosenheim and Harmon, 2006; Vance-Chalcraft et al., 2007). An increase in extraguild prey density should reduce IGP by providing alternative prey options, regardless of intraguild predator density (Lucas and Rosenheim, 2011; Lucas, 2012). Aubry et al. (2017) showed that the presence of extraguild prey reduces phytophagous behavior in the mullein bug *C. verbasci* even in the presence of some intraguild predators. Aubry et al. (2017) suggested that the reduction in feeding punctures might have been caused either by predation on mullein bugs or by a change in behavior of the mullein bug (e.g., escaping, hiding). Concerning the zoophagous impact on the prey population, Lucas and Alomar (2002) showed that the presence of an IGP predation delayed the development of the zoophytophagous *Macrolophus caliginosus* Wagner (Hemiptera: Miridae). The guild context can greatly change the propension to attack plants or prey and the status of a zoophytophagous predator.

TOWARD ARTIFICIAL SELECTION

The last two decades have been marked by a significant increase in knowledge in ecology of individuals (Bolnick et al., 2002; Dall et al., 2004, 2012; Dingemanse et al., 2010; Réale et al., 2010a,b; Ellner, 2013). The ecology of individuals aims to integrate intraspecific phenotypic variation in ecological models (Judson, 1994; Grimm, 1999; Łomnicki, 1999; Clutton-Brock and Sheldon, 2010; Bolnick et al., 2011; Wolf and Weissing, 2012). The later models focus on the mainstream response of the focal population while discarding individual variations. These models are often based on the premise that individuals are interchangeable or have the capacity to adapt optimally to all situations (Sih et al., 2004). However, it has been demonstrated in several taxonomic groups that behavioral differences among individuals have considerable ecological consequences (Sih et al., 2004, 2012; Réale et al., 2007; Araújo et al., 2011; Bolnick et al., 2011). Recently, some studies have demonstrated that native biological control agents can be improved by exploiting intraspecific behavioral differences in various traits related to their efficiency (Lommen et al., 2008, 2013; Tabone et al., 2010; Nakayama et al., 2013: Seko et al., 2014; Dumont et al., 2016, 2017a). Therefore, some authors (Hoy, 1986; Rosenheim and Hoy, 1988; Hopper et al., 1993; Nachappa et al., 2010, 2011; Lommen et al., 2013, 2017; Dumont et al., 2016, 2017a; Kruitwagen et al., 2018) suggested that genetic improvement of biocontrol agents could rely on intraspecific behavioral differences.

The first successful examples of genetic improvement of biocontrol agents were intended to increase their pesticide resistance (Hoy and Knop, 1981; Hoy, 1985, 1986, 1990; Rosenheim and Hoy, 1988; Havron et al., 1991). More recently, intraspecific behavioral variations are of interest to researchers especially in nematodes (Segal and Glazer, 2000; Shapiro-Ilan et al., 2003), mites (Pels and Sabelis, 1999; Jia et al., 2002; Maeda and Liu, 2006; Nachappa et al., 2010, 2011), coccinelids (Tourniaire et al., 2000; Lommen et al., 2008; Seko and Miura, 2009; Adachi-Hagimori et al., 2011) and parasitoid wasps (Baya et al., 2007; Kruitwagen et al., 2018). The performance (as biological control agent) of native predators and parasitoids has been improved in the control of their natural or exotic prey (Kraaijeveld et al., 2001; Rouchet and Vorburger, 2014). Recently, the concept of genetic improvement applied to zoophytophagous predators arouses a growing interest. Dumont et al. (2016, 2017a) used this approach on the mullein bug, but this species is not commercialized as biological control agent. It is even considered as a pest species by some authors (Thistlewood et al., 1989; McBrien et al., 1997).

A biocontrol strategy that relies on zoophytophagous predators should aim to increase their effectiveness while minimizing their detrimental behavior. The emerging field of genetic improvement on biocontrol agents offers a promising avenue for achieving these goals (Dumont et al., 2016, 2017a;). Dumont et al. (2016, 2017a) reported genetic variations in zoophagy and individuals' diet specialization in mullein bug. Thus, these authors suggested that zoophytophagous populations are in fact composed of a mix of individuals specialized, to some degree, on animal or plant diet. Therefore, it is possible to manipulate the composition of zoophytophagous predator's population by artificial selection by favoring prey-specialized individuals over more plant-specialized ones (Dumont et al., 2017a; Kruitwagen et al., 2018). Hence, it could increase these predators' efficiency as biocontrol agents and/or reducing the risk of damage.

TRAITS TO TARGET WITH SELECTION IN ZOOPHYTOPHAGOUS BUGS

The genetic improvement process can target several traits (i.e., morphology, physiology, behavior and life history traits) of biological control agents to optimize their effectiveness (Hoy, 1976; Rosenheim and Hoy, 1988; Lommen et al., 2017). In zoophytophagous predators, we propose that selection should target feeding behaviors, such as zoophagy and phytophagy. The feeding behavior of zoophytophagous predators is motivated among others by the need of water, nutrient complementarity, response to resource availability and quality and risks of predation (Gillespie and McGregor, 2000; Coll and Guershon, 2002; Lemos et al., 2009; Portillo et al., 2012). Hence, the selection process can target many traits related to feeding behavior. Heritable genetic variation in targeted traits is required to operate selection. The phenotype (i.e., behavior or life-history traits) results from the interaction between the genotype and the environment. The selective breeding in zoophytophagous predators should occur in condition representative of the field and under which the targeted trait is beneficial/detrimental.

Zoophytophagous predators have the ability to adjust their level of zoophagy and phytophagy according to the environmental conditions and the quality and availability of food resources (Calvo et al., 2009; Aubry et al., 2016, 2017). The premise underlying genetic improvement in these predators is that phenotypic plasticity may be limited, expensive (in term of fitness), often requires a trade-off and has a genetic basis (DeWitt et al., 1998; Scheiner and Berrigan, 1998; Agrawal et al., 2002). The behavioral type of individuals (also called "animal personality" or "behavioral syndrome") is described as interindividual differences maintained over context and time (Réale et al., 2007; Sih et al., 2012; Toscano et al., 2016). Individuals respond to environmental conditions (exhibiting phenotypic plasticity), but individual differences in this response demonstrate that phenotypic plasticity is not infinite (Dingemanse et al., 2010; Dingemanse and Wolf, 2013). Thus, the selection we propose would not transform a population of zoophytophagous predators into a strict predator. Selected individuals will always have the ability to exploit animal and plant resources and adjust to changing conditions. The proposed selection focuses on genetic differences in behavioral plasticity.

Decreasing Detrimental Phytophagy

Zoophytophagous bugs feed on plants to meet different needs, namely water, nutrients and proteins (Gillespie and McGregor, 2000; Lemos et al., 2009; Portillo et al., 2012; Urbaneja-Bernat et al., 2013). While damage can be caused by plant feeding, phytophagy is not always detrimental (Castañe et al., 2011). The specific plant structure providing the required resources is highly determining the level of damage resulting from phytophagy (Castañe et al., 2011). For example, the consumption of pollen, a food source rich in protein, can fill a need in the absence of prey without necessarily causing an increase in damage. In addition, crop damage may depend on the phenological stage of the plant or cultivar (Aubry et al., 2016). Therefore, damage results from a complex interaction among the biological agent's traits, plant species and environment (Castañe et al., 2011). For an effective selection on phytophagy, it is necessary to understand these interactions that lead to the consumption of certain plant parts (those that generate crop damage) (Castañe et al., 2011). Castañe et al. (2011) report that stylet morphology or saliva composition does not generate differences in damage caused by four different species of mirids [*D. tamaninii*, *Dicyphus Hesperus* Knight (Hemiptera: Miridae), *Macrolophus pygmaeus* (Rambur) (Hemiptera: Miridae), and *Nesidiocoris tenuis* (Reuter) (Hemiptera: Miridae)]. Therefore, differences in damage could rather be caused by bugs behavior, resource preferences and response to conditions (Castañe et al., 2011). Hence, the first step of a genetic improvement program would be to identify the conditions that lead to crop damage and, then, target the predator's phytophagous traits that modulate the response to these conditions.

Increasing Beneficial Zoophagy

An increase in zoophagy without increasing detrimental phytophagy would enhance the benefit-damage ratio in zoophytophagous predators. Dumont et al. (2016) observed significant genetic variation in zoophagy in mullein bugs. Mullein bug's lines that were highly zoophagous on spider mites were also more zoophagous on aphids (Dumont et al., 2016). However, extraoral digestion requires a substantial amount of water for the considerable amount of digestive enzymes injected into zoophytophagous predator's prey and also to maintain their physiological status (Sinia et al., 2004; Castañe et al., 2011). Hence, there is always a level of phytophagy with predation (Aubry et al., 2017). An increase in zoophagy can be positively correlated with phytophagy (Sinia et al., 2004). Sinia et al. (2004) observed that *D. hesperus* individuals provided with prey (eggs of *Ephestia kuehniella* Zeller; Lepidoptera: Pyralidae) fed more frequently on plants than individuals deprived of animal resources. Nevertheless, several studies demonstrated that the phytophagy tends to be constant and not related to the level of zoophagy (Salamero et al., 1987; Gillespie and McGregor, 2000; Sanchez, 2008; Aubry et al., 2017). Thus, phytophagy should probably be considered essential rather than facultative (Castañe et al., 2011; Aubry et al., 2017). However, the relationship between zoophagy and water requirement may not be linear and could be modulated by the type of resource consumed (e.g., size of the prey, water content in the prey, etc.). This relationship would have to be understood to improve zoophytophagous bug's level of zoophagy.

Zoophagy is the result of a series of behaviors that lead to the consumption of prey. The predator must find and identify its prey, capture it, kill it and consume it. A change in efficiency in any of these components of predation would generate an increase or a decrease in zoophagy. A selection on components of predation behavior did increase the benefits provided by the specialist mite predator *Phytoseiulus persimilis* Athias-Henriot (Acari: Phytoseiidae) (Nachappa et al., 2010, 2011). Nachappa et al. (2011) demonstrated that selected lines of *P. persimilis* with high levels of prey consumption, conversion efficiency or olfactory response were more efficient in controlling spider mites in the field compared to a commercial population. Applying similar selection on zoophytophagous predators could lead to significantly different results, especially on their stability over a long-term period. Even after selection for higher zoophagy, zoophytophagous predators would still be able/need to feed on plant tissue. The response of highly-zoophagous strains to conditions of prey scarcity would have to be determined to ensure that the benefit-damage ratio is in fact enhanced.

Aggressiveness influences predator-prey interactions (Riechert and Hedrick, 1993). The more aggressive the predators, the more zoophagous they will be (Riechert and Hedrick, 1993). Hedrick and Riechert (1989) observed that aggressive desert spiders *Agelenopsis aperta* Gertsch (Araneae: Agelenidae) (measured as attack latency) exhibited a higher frequency of attack than non-aggressive individuals toward several prey. Aggressiveness in *A. aperta* spiders is genetically determined (Hedrick and Riechert, 1989). Moreover, high level of aggressiveness leads to wasteful killing (Maupin and Riechert, 2001). Increasing aggressiveness in zoophytophagous predators could result in more zoophagy (both in frequency of attacks and range of prey attacked) and wasteful killing. Dumont et al. (2016) reported some degree of wasteful killing in *C. verbasci* belonging to highly zoophagous lines. In zoophytophagous predators, wasteful killing is interesting to increase the benefit-damage ratio. Bugs may not invest as much extra oral digestive enzymes in unconsumed prey (wasted prey) as in fully consumed prey. Therefore, the relationship between the number of prey killed (zoophagy) and water requirement could be modulated by selection on aggressiveness.

Optimizing Zoophytophagous Predators Through Diet Specialization

Individual differences in morphological, physiological, and behavioral traits can generate diet specialization (i.e., when individuals use only a subset of the resources consumed by the whole population) (Bolnick et al., 2002; Toscano et al., 2016). This diet specialization occurs when individuals respond differently to ecological and environmental factors (e.g., predation risk and intraspecific competition) or when individuals differ in their efficiency in exploiting available resources (Svanbäck and Bolnick, 2005; Araújo et al., 2011; Toscano et al., 2016). Sokolowski (2001) argues that the link between genotype and foraging behavior is complex and depends on the effect of several genes. This complexity can generate considerable inter-individual differences in the resource consumption choice. The resource choice of the individuals reflects their ability to deal with these resources (Bolnick et al., 2002). Therefore, different phenotypes in the population would perform better in the exploitation of some resources. These differences would constitute a form of individual specialization in ecological niches (Bolnick et al., 2002). Such differences in specialization would be maintained in populations by different factors, including heterogeneous spatial and/or temporal abundance, availability and quality of resources (Jaenike and Grimaldi, 1983; Wilson and Yoshimura, 1994; Svanbäck and Bolnick, 2005; Araújo et al., 2011. The variations could be exploited as part of a zoophytophagous predator improvement program (Dumont et al., 2016, 2017a).

In zoophytophagous predators, diet specialization can be expressed in different ways depending on the availability of resources. For example, Dumont et al. (2017a) have observed that when prey (spider mites) and pollen (a major source of plant protein) are simultaneously available, some strains of mullein bugs feed mainly on prey while others have a diet exclusively composed of pollen, expressing their food specialization. In the absence of pollen, the strain specialized on this resource generally had a lower zoophagy level than the strain specialized on animal resources (Dumont et al., 2017a). However, the food specialization observed by Dumont et al. (2017a) does not necessarily point out a benefit-damage gradient on which their strains could be classified. Pollen consumption does not generate crop damage (Torres et al., 2010; Aubry et al., 2016).

In zoophytophagous predators, the diversity of food resources requires an ability to cope with many complex information that may exceed their cognitive abilities (Bernays, 1996). Such a diversity of information to process is likely to lead to food and host specialization (Bernays and Wcislo, 1994). The processing of complex information would be costly for zoophytophagous predators in terms of decision time, assessment of food quality and oviposition site selection (Bernays and Wcislo, 1994; Bernays and Bright, 2001). Bernays et al. (2004) find that generalist (phytophagous) species spend more time dispersing and assessing resources and have shorter feeding bouts compared to specialists. The food specialization resulting from information management could be genetic (Dumont et al., 2017a) and/or be the result of previous experience (Lins et al., 2014; Rim et al., 2017; Lima-Espindola et al., 2018). An alternative strategy to complex information management for omnivorous predators would be to be less selective and more opportunistic. Opportunistic predators would be more likely to attack prey regardless of their quality (Eubanks and Denno, 2000a). The genetic improvement of zoophytophagous predators for biological control could be through selection on a specialization in the management of relevant information (e.g., specific prey detection) or predator responsiveness to prey.

SELECTION CONSEQUENCES ON ECOLOGICAL INTERACTIONS

The feeding behavior of zoophytophagous predators is modulated by their interaction with the host plants (Sanchez et al., 2004; Aubry et al., 2016; Biondi et al., 2016), prey (Biondi et al., 2016; Aubry et al., 2017) and/or intraguild predators/competitors (Lucas and Alomar, 2001, 2002; Perdikis et al., 2014; Aubry et al., 2017). Thus, the zoophytophagous predators responses to biotic conditions will influence the predator population mean value. However, individual behavioral differences cause variation around this mean depending on individual's characteristics and population composition (Sih et al., 2012). The individuals' functional role at the population and community levels may differ according to their behavioral type and diet (Sih et al., 2004, 2012; Hughes et al., 2008; Araújo et al., 2011; Bolnick et al., 2011; Pruitt and Ferrari, 2011). The inherent ecological variation caused by selection would in turn influence their application to biological control.

Interactions With Host Plants

Host plants play a central role in the success of zoophytophagous predators, as they provide both food resources (e.g., water, carbohydrates, proteins), habitat for their prey and substrate for egg laying (Sanchez et al., 2004). A selection on the feeding behavior (i.e., phytophagy, zoophagy, diet specialization) of zoophytophagous predators will modulate host preference for nutrition and oviposition. These predators use various cues related to plant quality and prey availability to discriminate and select their host (Coll, 1996; Eubanks and Denno, 2000a,b; Grosman et al., 2005; Lins et al., 2014; Ingegno et al., 2016). For instance, zoophytophagous predators are attracted to volatiles from prey-infested plants (herbivore-induced plant volatiles; HIPVs) (Lins et al., 2014; De Backer et al., 2015; Silva et al., 2018). Lins et al. (2014) observed that both *M. pygmaeus* and *N. tenuis* responded positively to plants infested by their prey [whitefly *Bemisia tabaci* Gennadius (Hemiptera: Aleyrodidae) and the tomato borer *Tuta absoluta* Meyrick (Lepidoptera: Gelechiidae)]. Moreover, experienced predators are more reactive to plant volatiles than naïve individuals (Lins et al., 2014; Rim et al., 2017; Lima-Espindola et al., 2018). Hence, prey-specialized or highly-zoophagous individuals could be more reactive to HIPVs than their plant-specialized or lowly-zoophagous counterpart due to 1) increased experience with hosts infested with prey and/or 2) genetic correlation between zoophagy and olfactory response to HIPVs (Nachappa et al., 2010). In contrast, plant-specialized bugs could rather rely on cues related to plant quality to choose their host. The same cues could be used by ovipositing females to find sites to lay their eggs (Sanchez et al., 2004). Females tend to select oviposition sites to optimize their offspring survivorship and performance (Coll, 1996; Seagraves and Lundgren, 2010). The result would be a spatial distribution of zoophytophagous predators that reflects their food specialization. In the agricultural environment, the plants infested by pests could be least interesting for the plant-specialized bugs due to plant's depletion or plant's defensive mechanisms, whereas they would be the most interesting for the prey-specialized ones.

Phytophagy in zoophytophagous predators can trigger plant defensive responses, such as the emission of HIPVs or the expression of defense-related genes (Pappas et al., 2015, 2016; Pérez-Hedo et al., 2015a, 2018; Naselli et al., 2016; Bouagga et al., 2018a). Zoophytophagous predator's prey or competitors (i.e., parasitoid wasps) can be responsive to these HIPVs (Bouagga et al., 2018a). These interactions vary, however, depending on the species involved (Perez-Hedo et al., 2015b). For instance, plant feeding by the zoophytophagous bug *N. tenuis* activated both abscisic and jasmonic acids in tomato plants, which repel both *B. tabaci* and *T. absoluta* (Pérez-Hedo et al., 2015a). However, *B. tabaci* is not repelled by plant where *M. pygmaeus* and *Dicyphus maroccanus* Wagner (Hemiptera: Miridae) had been feeding (Perez-Hedo et al., 2015b). The tomato borer *T. absoluta* is even attracted by the plant on which *M. pygmaeus* and *D. maroccanus* fed (Perez-Hedo et al., 2015b). Moreover, the whitefly parasitoid *Encarsia formosa* Gahan (Hymenoptera: Aphelinidae) is attracted to plant volatiles emitted in response to zoophytophagous bugs phytophagy (Pérez-Hedo et al., 2015a; Bouagga et al., 2018a). Therefore, phytophagy by zoophytophagous predators can enhance plant protection against main pests (Bouagga et al., 2018b). Selection to favor lowly-phytophagous strains would thus reduce this advantage provided by zoophytophagous predators. However, even a low level of phytophagy or non-detrimental phytophagy could induce HIPVs from host plants (Pérez-Hedo et al., 2015a, 2018).

Phytophagy by zoophytophagous predators can induce direct plant defense responses against herbivores (Pappas et al., 2015). Pappas et al. (2015) observed that phytophagy by the zoophytophagous predator *M. pygmaeus* triggers a defensive response in tomato that is effective against a subsequent infestation of the two-spotted spider mite *Tetranychus urticae* Koch (Acari: Tetranychidae). This defensive mechanism was, however, ineffective against greenhouse whitefly *Trialeurodes vaporariorum* Westwood (Hemiptera: Trialeurodes) (Pappas et al., 2015, 2016). Zoophytophagous predators may therefore have indirect biological control effect over certain prey. A selection that reduces phytophagy in a zoophytophagous predator will result in minimizing this path by which the predator can affect their prey. In addition, plants defensive responses can be induced by an endophytic fungus, and reduce damage from both zoophytophagous predators (Garantonakis et al., 2018) and pests (Pappas et al., 2018). Garantonakis et al. (2018) observed less damage from the zoophytophagous predator *N. tenuis* on tomato plants inoculated with the fungal endophyte *Fusarium solani* strain K than on uninoculated plants. The authors have not determined whether the symbiosis between the plant and the fungal endophyte confers on the plant the ability to repair damage or repel *N. tenuis* (reduction of phytophagy). In the first case, more zoophagous (but not necessarily less phytophagous) lines would be very useful in biological control. These strains would increase the level of benefits by consuming more prey without proportionally increasing damage. In the second case (the plant-fungus symbiosis repelling the zoophytophagous predator), strains specialized in prey resources may be less sensitive to this plant defense mechanism than more phytophagous strains. Inoculation of the plants with beneficial soil microorganims may be a method of control compatible with the release of prey-specialized zoophytophagous predator strains.

Phytophagy is not necessarily detrimental depending on the plant material consumed and the plant and omnivore phenology (Castañe et al., 2011; Aubry et al., 2015, 2016). In many omnivores, the combined effect of consuming two types of resources can improve their diet nutritional quality of the diet. This synergistic effect (trophic facilitation) can strongly affect their selective value (Waldbauer and Friedman, 1991; Singer and

Bernays, 2003) and consequently their use as biocontrol agents. For example, the spring generation of *C. verbasci*'s nymphs hatching on apple trees can feed on apple fruit supplemented by pollen or prey to reach adulthood (Aubry et al., 2015). Plant resources can also have a synergistic effect on prey consumption (Eubanks, 2005). Predaceous Hemipteran need a substantial amount of water for predation which can be provided by plant tissue (Gillespie and McGregor, 2000; Han et al., 2015). Indeed, a certain level of phytophagy by *C. verbasci* is always observed even in the presence of prey (Aubry et al., 2017).

Interactions With Prey

At the population level, several models predict that omnivores may have a greater suppressive effect on prey populations than strict predators (Polis, 1991; Holt and Lawton, 1994; Holt and Polis, 1997). Unlike strict predators, omnivorous predators compete with their prey for the shared plant resource (Diehl and Feißel, 2000) and are unlikely to starve or migrate when prey is rare because they feed at more than one trophic levels (Eubanks and Denno, 1999). In fact, the shared plant contributes to the maintenance of a greater predation pressure on the herbivorous prey by favoring a larger and more stable omnivore population density (Diehl and Feißel, 2000). The competition between prey and individuals from selected strains (highly zoophagous or prey-specialized strains) for plant resources should be negligible. In the presence of prey, the predator should feed on it rather than alternative plant resources. Phytophagy by the predator would not be intensive enough to generate high level of competition with its prey. The omnivorous predator will maintain its advantage over strict predators despite selection on zoophagy and food specialization since it will always be able to supplement their diet with plant resources. These resources would only be a smaller proportion of their diet.

An increase in prey consumption in zoophytophagous predators would translate into an increase in predations risk for the prey. High prey consumption and diet specialization on prey can result from a high level of activity (Toscano et al., 2016; Start and Gilbert, 2017). Thus, the rate of encounters with the prey and the rate of attacks against them would increase with the level of activity of the predator. In response to this increase in predation risk, prey can adopt costly strategies to avoid predators (Preisser et al., 2005). Preisser et al. (2005) estimated that prey demography was as impacted by intimidation (indirect effect of predation) as direct consumption. Prey could avoid predation by selecting host plants less favorable for their zoophytophagous predators (Bernays and Graham, 1988). However, this strategy may be less effective against zoophytophagous predator strains specialized in animal resources. The success of such strains would depend less on their host plants than strains that include more plant resources in their diet.

Interactions With Competitors and Intraguild Predation

Intra- and interspecific competition among natural enemies could be altered by selection on diet specialization, high zoophagy and aggressiveness. In the first place, all these traits can be correlated to individual levels of competitiveness. More aggressive individuals are usually better competitors and can use a higher proportion of resources or prevent other individuals to exploit them (Bolnick et al., 2002, 2011; Svanbäck and Bolnick, 2005, 2007; Pruitt and Ferrari, 2011; Pruitt and Riechert, 2012; Sih et al., 2012). In the case of zoophytophagous predators, since more aggressive individuals are expected to be more zoophagous, highly-zoophagous strains could be more competitive on prey resources than phytophagous strains. Therefore, highly-zoophagous strains would have potential strong impact on interspecific competitors. In various crop systems, different zoophytophagous species naturally colonize the plants (Albajes and Alomar, 1999; Montserrat et al., 2000; Alomar et al., 2002). For instance, *Dicyphus maroccanus* and *N. tenuis* are both present on tomato plants in eastern Spain (Salas Gervassio et al., 2017). However, *N. tenuis* tends to displace *D. maroccanus* from plants because of higher competitive abilities. A selection to increase *N. tenuis* level of zoophagy would only exacerbate this situation, whereas such selection on *D. maroccanus* could allow a better equilibrium between both species. Similarly, highly-zoophagous strains would increase intraspecific competition resulting in a potential diet switch in less competitive individuals (Robinson and Wilson, 1998; Bolnick, 2001; Araújo et al., 2009).

Zoophytophagous predators are often found in systems with other biological control agents. Most commonly with other zoophytophagous predators (Lucas and Alomar, 2001, 2002; Perdikis et al., 2014) or parasitoid wasps (McGregor and Gillespie, 2005). For instance, *D. hesperus* bugs and parasitoid wasps can be used simultaneously in a greenhouse to increase the impact on whitefly populations (McGregor and Gillespie, 2005). Together, biological control agents lead to larger decrease in pest populations (Bennett et al., 2009). However, *D. hesperus* bugs reduce both the density of whitefly populations and extend a more scattered distribution or prey (Bennett et al., 2009). Under these conditions, the parasitoid wasp *E. formosa* is less effective (Bennett et al., 2009). The level of the predator's zoophagy has an impact on the distribution or prey. More zoophagous strains tend to eliminate all prey from one patch before searching for and exploiting another patch (Nachappa et al., 2011). The result is a prey distribution that included less patch but with denser prey densities in these. A selection to increase the zoophagy level of the predator. *D. hesperus* could modulate the distribution of prey so as to favor the cohabitation between *D. hesperus* and *E. formosa*.

Increased zoophagy could be associated with an increase in the level of predation risk. The highly-zoophagous individuals should spend more time on parts of the plants where prey is numerous (e.g., leaves). These prey would attract other predators, which can in turn be intraguild predators of zoophytophagous predators (Lucas et al., 1998; Lucas and Alomar, 2001; Fréchette et al., 2007). Therefore, the choice of resources for zoophytophagous predators should affect the level of risk and the rate of encounter with predators. Moreover, zoophagy and aggressiveness is positively correlated with boldness (the level of risk taken in presence of predators) (Riechert and Hall, 2000; Sih et al., 2012). However, intraguild predators among zoophytophagous predators may be limited (Perdikis et al., 2014).

In some situations, zoophytophagous predators are intraguild predators in IGP interactions (Snyder and Ives, 2003; Bennett et al., 2009). For instance, *D. hesperus* kills the parasitoid wasps *E. formosa* pupae when feeding on parasited whiteflies (Bennett et al., 2009). Highly-zoophagous or prey-specialized *D. hesperus* strains could have a stronger impact on a parasitoid wasp's population than strains that rely more on plant food resources. The consequences would be that genetic improvement of zoophytophagous predators for a higher level of zoophagy is not consistent with a biological control program involving several types of predators. However, the negative impact of predation on intraguild prey may not always disrupt biological control (Snyder and Ives, 2003). Snyder and Ives (2003) observed that generalist bugs *Nabis* sp. (Hemiptera: Nabidae) and *Orius* sp. (Hemiptera: Anthocoridae) decrease populations of parasitoid wasps by about 50% but the impact of these biological agents on aphid's populations was additive.

IMPACT ON BIOLOGICAL CONTROL: BENEFITS AND CHALLENGES

Genetic improvement of biocontrol agents can be adapted to different biological control strategies. The strategy will depend on the crop (e.g., perennial or annual), the targeted pests, the environment (e.g., field or greenhouse) and the biological control agents. Different strains of the same biological control agent could meet different needs or be better adapted to different conditions. Thus, genetic improvement can serve all types of biological control approaches (i.e., inoculative, inundative and conservation). However, understanding the impact of zoophytophagous predators at the population and community levels is needed to predict the effects of selection on their efficiency as biological control agents on the long term.

Inundative Strategy

Improving biocontrol agents would be more suitable for the inundative strategy (Lommen et al., 2017). Highly-zoophagous or prey-specialized strains could provide rapid and strong impact sought after by the inundative biocontrol strategy (Nachappa et al., 2011). For instance, high level of conversion efficiency and dispersal in the specialist predatory mite *P. persimilis* were associated with better spatio-temporal correlation between the predator and the prey (Nachappa et al., 2011). The authors suggested that all three selected lines achieve biological control objectives by using different paths. However, these paths may not be all stable over a long period (Nachappa et al., 2011). The study by Nachappa et al. (2011) suggests that different strains could be developed to fit different biological control needs. For instance, highly-zoophagous strains could provide rapid and intense decrease in pest populations, but at the cost of lower stability on the long run. In the case of zoophytophagous predators, obtaining a strong, rapid and localized impact on pest's population resulting from the use of highly zoophagous strains would allow to achieve these objectives while releasing fewer individuals than with a generic population (Dumont et al., 2016). As the risks of damage increase when the density of predators and their prey is high, fewer individuals would mean less risk during periods of low prey level. Thus, once predators have significantly reduced pest populations, there will be fewer zoophytophagous predators to cause damage. Moreover, the response of the selected strains to the various conditions is important in determining their value as biological control agents. Under conditions of prey scarcity, zoophytophagous predators will either turn to plant resources, cannibalism or disperse elsewhere to find their prey. In the case of a prey-specialized strain, the last two options are more likely. However, both options will have the effect of reducing zoophytophagous predator populations on crops, while the former option maintains (within certain limits) populations of predators in the absence of pests.

The genetic improvement approach could help promote effective zoophytophagous predators that cause significant level of damage when prey is scarce. For instance, the bug *N. tenuis* is a proven efficient biocontrol agent of major pest species in tomato greenhouses (Sanchez et al., 2004, 2014; Calvo et al., 2009; Urbaneja et al., 2009; Desneux et al., 2011; Bompard et al., 2013; Jaworski et al., 2013; Zappala et al., 2013). The release of *N. tenuis* decreased *B. tabaci* populations by about 90% (Calvo et al., 2009, 2012) and regulated populations of *T. absoluta* (Mollá et al., 2011). However, the benefit provided by *N. tenuis* on crop comes at a high cost. Once *N. tenuis* has successfully reduced the pest population, it increasingly feeds on the tip of the tomato plant and flowers, which cause important damage (Sanchez, 2008; Sánchez and Lacasa, 2008; Calvo et al., 2009; Arnó et al., 2010; Castañe et al., 2011). Artificial selection to decrease the level of detrimental phytophagy in *N. tenuis* would considerably increase its benefit-damage ratio. It would make it possible to use this effective predator on a larger scale without incurring the current risks. A selection on the food specialization of this predator would have a similar effect while maintaining the level of zoophagy that makes it successful as biological control agent.

Introduced biological control agents are not always adapted to local conditions, but individuals in the natural population can be (Hopper et al., 1993; Hufbauer and Roderick, 2005). In biological control, it is generally suggested to introduce genetically diversified populations, which will allow adaptation to new conditions (Hopper et al., 1993). However, artificial selection is reducing genetic diversity (Falconer and Mackay, 1996). Thus, biological control agent release could be effective in a specific condition or to achieve specific goals, but their long-term effects could be mitigated (Nachappa et al., 2011). Repeated introductions may be necessary in this context. Thus, the genetic improvement of biological control agents would better fit in an inundative strategy, rather than in a classical biological control strategy (Lommen et al., 2017).

Inoculative Strategy

The inoculative strategy consists in an intentional release of biological control agents aiming to favor the establishment of predators in the agroecosystem so that it acts for an extended period on target pest populations (Eilenberg et al., 2001). This strategy differs from the inundative strategy by the expectation that the biological control agent will control the pest after the agent's reproduction. Therefore, it is necessary that the biological control agent reproduces in the agricultural environment. The stability of the predator-prey cycle is therefore a foundation of this approach. For the same biocontrol agent, selection on different traits will have consequences on predator-prey dynamics (Nachappa et al., 2011). For instance, Nachappa et al. (2011) noted that the selection for high voracity in *P. persimilis* is more in line with inundative biocontrol objectives, while selection for high olfactory response and high conversion rate meet the needs of inoculative control. In the case of zoophytophagous predators, a specialization on animal resources could be positively correlated with a strong olfactory response to HIPVs or increased fertility. Whether these correlations are genetic or not, they would improve the performance of zoophytophagous predators in the context of an inoculative strategy.

The stability of the trait-selected populations on the long-term is also a key issue in preserving the biological control services quality of the selected strains. The ability of the selected strains to adapt to their new environment can be compromised by the limited genetic variation arising from the selection process (Hopper et al., 1993; Fauvergue et al., 2012; Roderick et al., 2012). The establishment of the released individuals in the agroecosystem is needed to meet the requirements of the inoculative biological strategy. Hence, genetic improvement of biological control agents may in fact, have a negative impact on this important aspect (Hopper et al., 1993). Moreover, the release of zoophytophagous predators from the selected population will introduce their genes into the genetic pool of local populations. These genes could be conserved or not by natural selection (Hufbauer and Roderick, 2005). Thus, the effect of the selection may decrease over time without repeated introductions of the selected strains. In addition, the introduction of new genes in local populations could have consequences for the evolution of local populations (Thrall et al., 2011; Richardson et al., 2014).

Conservation Strategy

In agroecosystems, agricultural practices can act as a selective force on arthropods, ultimately modifying local populations (Thrall et al., 2011). The evolution in agroecosystems can occur at an ecological time scale (Lankau, 2011; Palkovacs et al., 2011; Sih et al., 2011; Sih, 2013). This evolution, which often is very rapid under the influence of anthropogenic action, should no longer be neglected in pest management programs (Ashley et al., 2003; Stockwell et al., 2003; Lankau, 2011; Sih et al., 2011; Sih, 2013). Evolutionary processes can be concretely utilized using approaches that influence, genetic variability, selection, connectivity and gene flow (Lankau, 2011). For example, growers use pesticides alterations to prevent the development of resistance (Thrall et al., 2011). Such approaches maintain adequate genetic variability in populations and varying sources of selection (Hendry et al., 2011). However, even in alternation, pesticides may not prevent all types of selection (Thrall et al., 2011). Zoophytophagous predators may be threatened by chemical treatments either by direct effects on their survival and reproduction (Moser and Obrycki, 2009; Torres et al., 2010) or indirectly by a reduction in the prey's abundance (Kinkorová and Kocourek, 2000).

Agricultural practices (e.g., pesticide use, landscape management) could select for traits other than resistance. For instance, in the mullein bug's case, the spring generation females lay their eggs either on a herbaceous host (e.g., mullein plants) or on apple trees (McMullen and Jong, 1970). Host plant selection could be motivated by diet specialization (i.e., females preferably select sites that provide the optimal diet for their offspring), but it should consider host plants and prey phenology. Prey-specialized strains may remain on apple trees if prey populations are high, whereas plant-specialized strains are expected to move to herbaceous hosts to feed mainly on pollen (e.g., mullein plant). Consequently, nymphs emerging on apple trees in July (prey-specialized strains) may be negatively affected by insecticide use targeting pest species, as opposed to the nymphs that emerge on the herbaceous hosts outside the orchards (plant-specialized strains). Therefore, chemical treatments will become more threatening to beneficial individuals (from prey-specialized strains), rather than detrimental ones. This uncontrolled selection's process could quickly lead to undesirable changes in mullein bugs natural populations considering the high heritability of the diet specialization in this species (Dumont et al., 2016, 2017a). Ultimately, such changes in the populations' composition could lead to variations in benefits and risks associated with local mullein bug populations. This means that any type of management strategy, or conservative biocontrol program should be evaluated first in terms of "Would this action constitute a selective force? And, will the consequences improve or negatively affect the genetic pool of the resident zoophytophagous populations?."

OTHER RELATED LIMITS AND CHALLENGES

There will always be some degree of crop damage risks associated with zoophytophagous predators. Environmental conditions modulate the benefits and risks associated with such predators. The objective of selection for zoophytophagous predators is to improve the benefit-damage ratio in the circumstances where these predators have an economic impact (positive or negative). Thus, the improvement of benefit-damage ratio must be significant to worth the costs of selecting and maintaining selected lines under breeding conditions.

Keeping selected strains in long-term breeding for the purpose of releasing in crop systems entails some challenges, such as maintaining the desired traits in rearing units over a long period. Artificial breeding conditions could favor undesirable changes in the reared populations and increase inbreeding. The process of selections should be repeated at certain intervals to introduce new genes in mass-reared populations. Furthermore, increased zoophagy may entail increased aggressiveness and cannibalistic behaviors (Dumont et al., 2017b). In turn, such a trait could complicate the massive production of biological control agents. Therefore, the production protocols should be adapted to take such kinds of changes into account.

CONCLUSIONS

It appears that the status of zoophytophagous biocontrol agents is highly variable according to the ecological context (Gillespie and McGregor, 2000; Arnó et al., 2006; Perdikis et al., 2009; Calvo et al., 2012; Biondi et al., 2016). In turn, this status may change rapidly. The exploitation of plant and animal resources implies a variation in the behavioral, physiological and morphological traits of zoophytophagous species (Coll and Guershon, 2002). The abundant source of individual genetic variation in zoophytophagous predators offers a unique opportunity to modify populations by selecting traits and individuals more adequate for biological control purposes (Dumont et al., 2016, 2017a). Selected lines of biological control agents would improve their impact on pest populations by being more voracious, having more or less dispersal, higher levels of wasting prey (i.e., killed prey left unconsumed), and a stronger numerical response. The benefits of an omnivorous predator over a strict predator should not be lost. Furthermore, agricultural practices could generate evolution/selection of local populations (Thrall et al., 2011). As a result these practices may influence the ecosystem services and disservices associated with zoophytophagous predators.

AUTHOR CONTRIBUTIONS

All authors contributed equally to the writing and editing of the text. The example on mullein bug was drawn by OA and FD in their PhD thesis, which was supervised by EL.

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REVIEW
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Weaver Ants Provide Ecosystem Services to Tropical Tree Crops

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Generalist predators bring a complex mix of beneficial and harmful effects to agroecosystems. When these predators feed on herbivorous pests, biological control is improved with the potential to increase crop yield. However, generalists often feed on predators, pollinators, and plants, which might worsen pest outbreaks and reduce fruit set. For example, weaver ants (*Oecophylla smaragdina*) are major predators of several key, economically-damaging pest insects of tropical fruit and nut crops. Yet the ants also attack other predatory arthropods and important pollinators, while tending trophobiont honeydew producers like mealybugs (Pseudococcidae) that are themselves pests. Finally, ants will supplement their diet with sugars from floral and extrafloral nectaries, a form of plant feeding that presumably carries a physiological cost to the plant. Here, across previously-published experimental studies that compared treatments where ants were present vs. excluded, we summarize the effects of weaver ants on beneficial and pest insects and tree-crop productivity. Our quantitative review revealed nearly ubiquitous benefits of *Oecophylla* ants for tropical agriculture. Treatments with ants present generally showed lower pest densities and damage from pest insects in the families Coreidae, Miridae, Pentatomidae, and Tephritidae. Pest reduction was seen on cacao (*Theobroma cacao*), cashew (*Anacardium occidentale*), and mango (*Mangifera indica*) trees. The single exception to these pest reductions occurred when ants facilitated the population growth of mealybugs and other honeydew producers. In general, we found that *Oecophylla* ants provided the valuable ecosystem service of natural pest control to a diversity of tropical tree crops. Despite the potential for the ants to harm other predators or pollinators, evidence for these ecosystem disservices was rare and other beneficial insects co-exist well with this group of ants. Our findings bolster the general finding that ant species that tend herbivores who are not themselves pests can provide broad-reaching benefits to plant productivity. More generally, our findings are consistent with the many cases where non-pest prey bolster densities of polyphagous predators with benefits for biological control despite some degree of plant feeding by the predators.

Keywords: ***Oecophylla*, biocontrol, yield, generalists, predators, agroecosystems, ants**

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INTRODUCTION

Biological control agents can be broadly divided into specialists and generalists. Specialists have long been used as successful biological control agents, with part of their effectiveness lying in an ability to quickly reproduce and outnumber the relatively few prey/host species on which they feed (Snyder and Ives, 2001). The disadvantage of these predators' specificity, however, is that they provide little protection against the emergence of pest species other than the relatively narrow range of hosts/prey species that they attack (Symondson et al., 2002). In contrast, generalist predators can combat a suite of pests and this polyphagy allows them to remain in a field as various prey species become more or less common (Offenberg, 2015; Thurman et al., 2017). However, the same diverse feeding habits can lead to harmful attacks on predators and parasitoids (Snyder and Ives, 2001, 2003; Mathews et al., 2011; Ramesh et al., 2016) weakening biological control, or on pollinators (Dukas, 2005; Rodriguez-Girones et al., 2013; Yamasaki et al., 2016), decreasing fruit set (Abdulla et al., 2015, 2017; Anato et al., 2015, 2017). Furthermore, some broadly polyphagous generalists feed on the host plant in addition to arthropod prey (Eubanks and Denno, 1999; Bluthgen and Fiedler, 2002, 2004; Ingegno et al., 2011), and we must consider the potential direct crop damage caused by their plant-feeding.

Arboreal ants (Formicidae) present one class of generalist predators that supplements its diet with plant material. This can occur either when ants feed directly on host plant nectar, or indirectly while tending herbivorous insects that release sugars or other nutrients on which the ants feed (i.e., a trophobiotic relationship is in place) (Hölldobler and Wilson, 1990; Bluthgen and Fiedler, 2002; Bluthgen et al., 2004). An example of this trophobiosis is when aphids (Aphididae) produce a sugary honeydew secretion while feeding on a plant, which the ants can then consume. Stable food resources provided by the plant and/or trophobionts can then support relatively large ant colonies able to effectively antagonize and kill herbivore species that otherwise might damage the plant (Bluthgen and Fiedler, 2002; Davidson et al., 2003). Weaver ants (*Oecophylla* spp.) are recorded to harvest nectar from their host plant, while also "farming" trophobionts like soft scales (Coccidae) and mealybugs (Pseudococcidae) (Bluthgen and Fiedler, 2002). This is thought to make the ants highly territorial with large resident colonies unlikely to leave a site, and thus likely to heavily impact any herbivores attempting to colonize the host plant (Peng et al., 2002; Offenberg, 2015). In fact, weaver ants are the oldest documented form of biological control with records of *Oecophylla smaragdina* being conserved for natural pest control in 304 AD China (Way and Khoo, 1992).

Weaver ants have the potential to control agricultural pests across many tropical countries, as *Oecophylla smaragdina* (Fabricius) is found in Australia, India, and South-East Asia, and *Oecophylla longinoda* (Latrielle) in Sub-Saharan Africa (Vayssieres et al., 2015; Wetterer, 2017). *Oecophylla smaragdina* has been recorded to control over 50 pest species in eight different horticultural crops (Peng and Christian, 2004; Offenberg et al., 2013), while in sub-Saharan Africa its congener *O. longinoda* was observed consuming 48 arthropod species comprising 78.7% of all mango pests (Vayssieres et al., 2015). Previous reviews of *Oecophylla* spp. as biological control agents suggest that these ants successfully manage pests in some situations (Way and Khoo, 1992; Van Mele, 2008; Offenberg, 2015), with the potential to improve yields, although individual cases suggest harmful effects of the ants on other beneficial arthropods that could counterbalance these benefits (e.g., Delabie, 2001; Bluthgen et al., 2006). In order to determine when ant presence is generally improving crop production in the tropics, we need to carefully consider the relative strengths of these ant's helpful vs. harmful effects.

Here, we conduct a quantitative literature review of the potential for the weaver ants *Oecophylla smaragdina* and *O. longinoda* to control a diversity of pests and improve yields across a wide range of tropical tree fruit and nut crops. We first quantify the impact of *Oecophylla* spp. on crop yield, pest density and damage. We then supplement this analysis with case studies on how *Oecophylla* spp. feed on their host plant, harvest honeydew producers, and deter some predators, parasitoids and pollinators. Together, this generates a holistic assessment of the costs and benefits of using these ants as biocontrol agents. Insights from the case studies presented here help define the conditions when weaver ants provide ecosystem services vs. disservices. We also seek to provide a blueprint for when other ant species, and generalist biological control agents more broadly, might be expected to improve biological control based on their relationship to their host plant and resident harmful and beneficial arthropods.

MATERIALS AND METHODS

We began with a comprehensive literature search using Web of Science and "*Oecophylla*" as the search term. A total of 356 papers resulted from this search (last conducted March 2018), and all abstracts from these papers were reviewed to find 97 that considered the effects of *Oecophylla* spp. in agriculture. After reviewing the methods and data of these 97 articles, we identified 34 that (1) experimentally compared ant treatments that included either *O. smaragdina* or *O. longinoda* to a no-ant control treatment, and/or (2) reported changes in crop yield (11 of the 34 studies), pest numbers (8 of the 34 studies), and/or pest damage (15 of the 34 studies) under +ant and − ant treatments. These studies came from a range of crop systems with fourteen studies in mango, eight in cashew, four in mahogany, three in cacao, three in citrus, two in coconut palm, only one study each for palm oil and pongamia crops. We had hoped to find data reporting how ant manipulation impacted beneficial insects like predators and pollinators in agroecosystems, but these data were too sparsely studied for analysis. After extracting data from the studies, we then analyzed the pooled results of these papers according to their response variables (crop yield, pest density, or pest damage) by performing sign tests on how frequently ant treatments (ants and no ants) were shown to increase or decrease the aforementioned response variables.

Additional studies located in the original literature search were then reviewed for case studies that investigated how weaver

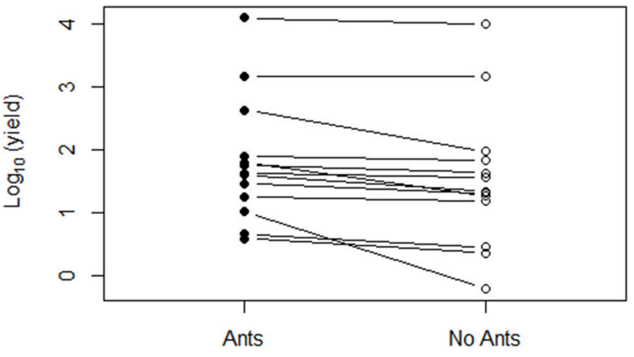

FIGURE 1 | Measurements of the influence of *Oecophylla* spp. as biological control agents on crop yields (log-transformed) for cacao, cashew, citrus, coconut palm, and mango trees were compiled from 11 studies. Lines compare treatments for each study, indicating how yields increased under ant treatments compared to yields from trees without ants (Vanderplank, 1960; Sporleder and Rapp, 1998; Peng et al., 1999; Ayenor et al., 2007; Dwomoh et al., 2009; Bharti and Silla, 2011; Abdulla et al., 2015, 2017; Anato et al., 2015, 2017; Bisseleua et al., 2017).

ants interact with their host tree and arthropod community to provide possible mechanistic underpinnings for the patterns seen in the quantitative literature review.

RESULTS

Our quantitative literature review found that the weaver ants *O. smaragdina* and *O. longinoda* generally reduced pest density and damage when summed across crop and pest types (**Figures 1**, **2**). Overall, ant presence in trees resulted in higher yields than were seen in trees where ants were experimentally excluded (sign test: 12/13, $p < 0.005$; **Figure 1**). There were lower pest densities in 13 out of 16 case studies (sign test: 13/16, $p < 0.05$; average = −13.94% pests; **Figure 2A**) and less pest damage in 18 out of 19 case studies (sign test: 18/19, $p < 0.0001$; average = −10.92%) (**Figure 2B**). Ants presence correlated with higher yields across five crop types, with average increases of 7.96% in cacao (*Theobroma cacao*), 55.75% in cashew (*Anacardium occidentale*), 16.47% in citrus, 49.51% in coconut palm (*Cocos nucifera*), and 30.37% in mango (*Mangifera indica*) orchards (**Figure 3**). Ants reduced pest density and/or damage for herbivores in seven insect families (Chrysomelidae, Coreidae, Curculionidae, Miridae, Pentatomidae, Tephritidae, and Thripidae) (**Figures 4A,C**). Reductions in pest damage and/or densities were seen in trees with ants compared to those without ants, across all crops for which these data were sufficient to be statistically analyzed, in cacao (*Theobroma cacao*), cashew (*Anacardium occidentale*), mango (*Mangifera indica*), and mahogany (*Khaya senegalensis*) (**Figures 4B,D**). These results were also consistent across the two ant species (**Supplementary Figure 1**).

In particular studies, the presence of ants significantly reduced pest densities of leaf-footed bugs (Coreidae; Peng et al., 1999; Dwomoh et al., 2009), mirid bugs (Miridae; Peng et al., 1999; Ayenor et al., 2007; Dwomoh et al., 2009; Forbes and Northfield, 2017a), stink bugs (Pentatomidae; Peng et al., 1999; Hosetti and Rudresh, 2012) and fruit flies (Tephritidae; Van Mele et al., 2007; Adandonon et al., 2009; Migani et al., 2017) (**Figure 4A**). Particular studies reported reduced pest damage from weevils (Curculionidae; (Peng and Christian, 2007; Peng et al., 2014; Abdulla et al., 2016)), fruit flies (Peng and Christian, 2006; Diame et al., 2015; Abdulla et al., 2017), and mirid bugs (Peng et al., 1995, 2014; Peng and Christian, 2008; Olotu et al., 2013; Abdulla et al., 2015) in the presence of ants (**Figure 4C**). Most studies focused on heteropteran, weevil, or fruit fly pests, with single studies focusing on density of leaf beetles (Chrysomelidae; average = −46.1%; Forbes and Northfield, 2017a) and thrips (Thripidae; average = −80.74%; Peng and Christian, 2004), and damage by snout moths (Pyralidae; average = −94.86%; Peng et al., 2011, 2014). Interestingly, damage from thrips increased by 68.75% under ant treatments compared to the no ant control treatment in one cashew orchard study (Anato et al., 2015), which contrasts with other cases of reduced thrips density (Peng and Christian, 2004) and damage (Abdulla et al., 2015) by ants in mango and cashew orchards, respectively. In the case where thrips damage increased, overall crop yield increased by as much as 150% under ant treatments compared to the control (Anato et al., 2015), suggesting that increases in pest damage by thrips was still outweighed by overall benefits from *Oecophylla* spp. being present.

DISCUSSION

Weaver ants, like many other generalist arthropod predators, fill complex ecological roles in agroecosystems (e.g., Peng et al., 1999, 2014; Van Mele and Cuc, 2000; Peng and Christian, 2004; Pierre and Idris, 2013; Abdulla et al., 2015, 2017; Anato et al., 2017; Forbes and Northfield, 2017a). The ants have the potential to contribute beneficial ecosystem services by feeding on pest insects, but also could provide disservices when they shelter other herbivores with which they form trophobiotic relationships (Offenberg et al., 2013; Forbes and Northfield, 2017a), and/or when the ants prey upon beneficial arthropod predators and pollinators (Gonzalvez et al., 2013; Rodriguez-Girones et al., 2013; **Figures 5A,C**). Thus, it was perhaps surprising that our quantitative review for studies across studies from Africa, Australia, and Southeast Asia, from a diversity of pest complexes, and a range of tree crop species (**Supplementary Table 1**) yielded such consistently beneficial effects of *Oecyphylla* ants (**Figures 1–4**). These benefits were robust across several pest families and species, the species of tree upon which ants were experimentally manipulated, and which of the two key *Oecyphylla* species was being considered (**Figures 1–4**; **Supplementary Figure 1**). Thus, any concerns about weaver ants sufficiently degrading biological control or pollination to harm crop yields (e.g., Tsuji et al., 2004; Offenberg et al., 2013) appear to be largely rare and unwarranted. Indeed, it appears that any harm weaver ants cause to crops from harvesting homopterans, or deterring predators, parasitoids, and pollinators is outweighed by their benefits in pest reduction and increased yields (**Figure 5B**). Several lines of evidence suggest

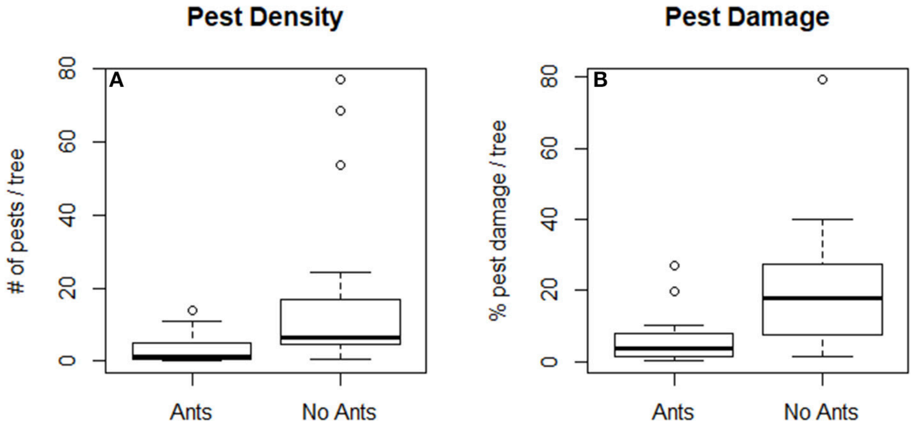

FIGURE 2 | Percentage of pest density **(A)** and pest damage **(B)** per tree for several tropical crops for trees with and without *Oecophylla* spp. ants. Ant treatments had significantly fewer pests and less pest damage than treatments without ants. Outliers are shown as white dots, while the solid black line indicates the median and the box shows the distribution of the dataset compiled from 25 studies (Peng et al., 1995, 1999, 2011, 2012, 2013, 2014; Sporleder and Rapp, 1998; Peng and Christian, 2004, 2005b, 2006, 2007, 2008; Ayenor et al., 2007; Van Mele et al., 2007; Adandonon et al., 2009; Dwomoh et al., 2009; Hosetti and Rudresh, 2012; Olotu et al., 2013; Pierre and Idris, 2013; Abdulla et al., 2015, 2016, 2017; Anato et al., 2015; Diame et al., 2015; Forbes and Northfield, 2017a).

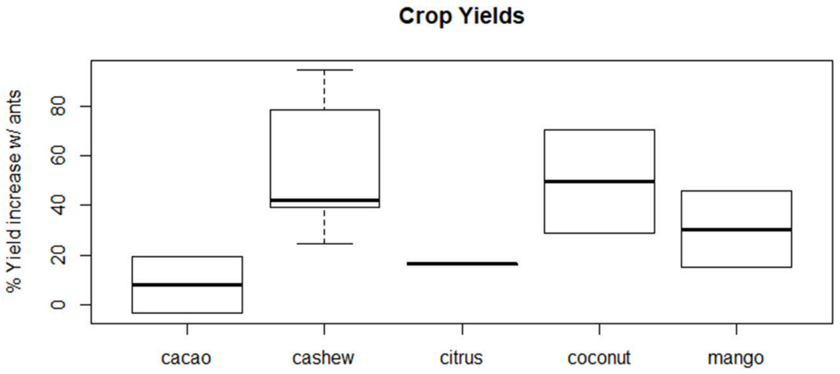

FIGURE 3 | Crop yields were higher when ants (*Oecophylla* spp.) were present, compared to when they were absent in cacao (*Theobroma cacao*, average increase = 7.96%; Ayenor et al., 2007; Bisseleua et al., 2017), cashew (*Anacardium occidentale*, average increase= 55.75%; Dwomoh et al., 2009; Abdulla et al., 2015; Anato et al., 2015, 2017), citrus (average increase = 16.47%; Bharti and Silla, 2011), coconut palm [*Cocos nucifera*, average increase = 49.51%; (Vanderplank, 1960; Sporleder and Rapp, 1998)], and mango [*Mangifera indica*, average increase = 30.37%; (Bharti and Silla, 2011; Abdulla et al., 2017)] orchards.

that suppression of pests by ants can be as effective as insecticide applications for controlling pests (**Figure 5B**) (e.g., Peng and Christian, 2005b, 2007, 2008; Dwomoh et al., 2009; Abdulla et al., 2016, 2017), although ants might be most usefully deployed as one aspect of integrated pest management schemes that incorporate a range of tactics (Peng and Christian, 2005a).

The sole exception to the broader trend of *Oecophylla* spp. increasing crop yields was found when no profits were gained for a Thai mango orchard after a leafhopper pest, *Idioscopus clypealis* (Cicadellidae), wiped out the crop (Offenberg et al., 2013). In this study, the weaver ant *O. smaragdina* was observed protecting and harvesting honeydew from the leafhopper, in effect facilitating the pest's destruction of mango flowers (Offenberg et al., 2013). Additionally, a single study recorded an >150% increase in mealybug (Pseudococcidae) density in an Australian cacao orchard when weaver ants were present (Forbes and Northfield, 2017a). In this case, mealybugs were not considered major cacao pests and their outbreak with ants present was not considered an ecosystem disservice (Forbes and Northfield, 2017a); however, crop yields were not measured and ant-mediated disservices cannot be entirely excluded in this case study. While our quantitative review revealed general benefits for crop yields despite concomitant benefits to some herbivores that the ants tend for honeydew, some caveats are needed. Some honeydew producers can be vectors for plant viruses or other pathogens (e.g., Parrella et al., 2003; Dzahini-Obiatey et al., 2006; Tsai et al., 2010), with the potential to yield infections that harm plants. Because weaver ants tend a wide diversity of potential pathogen vectors this indirect facilitation of plant diseases could be widespread if overlooked; for example, a survey of *O. smaragdina* in tropical northern Australia revealed that ants were engaged in tropobiotic relationships

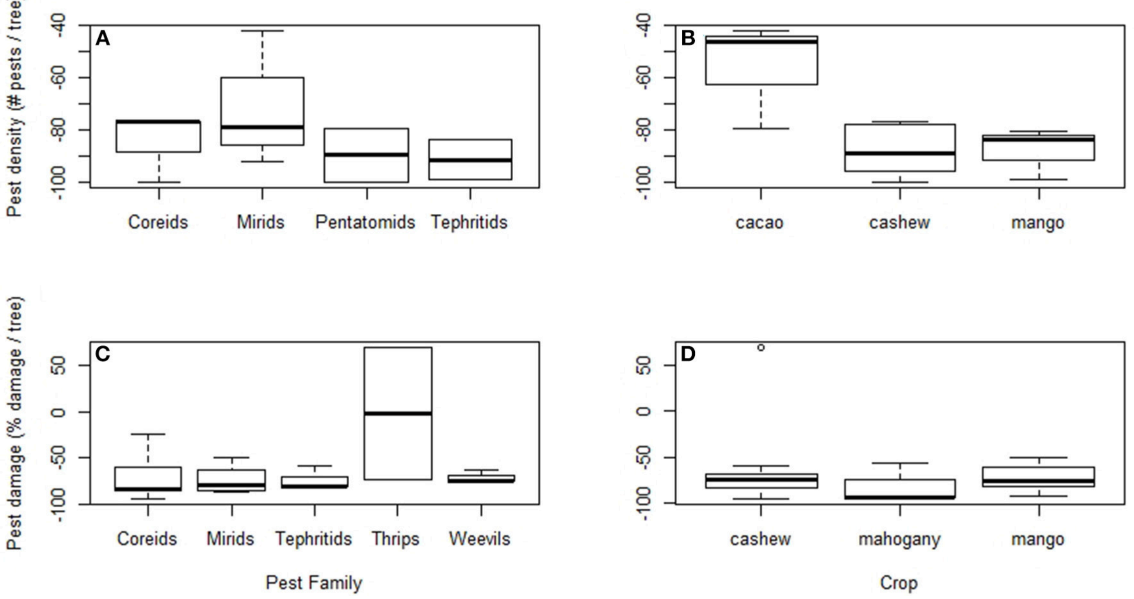

FIGURE 4 | When compared to a control, pest density under ant treatments (*Oecophylla* spp.) was significantly lower across pest insect families **(A)** and crop types **(B)**. Similarly, pest damage was significantly reduced under ant treatments across pestiferous insect families **(C)** and three different crops **(D)**. Reduction in pest damage and density was calculated as a percentage of pest density or damage in ant treatments compared to the control [((Ant-No Ant)/No Ant)*100] (Peng et al., 1995, 2011, 2012, 2014; Sporleder and Rapp, 1998; Peng and Christian, 2006, 2007, 2008; Ayenor et al., 2007; Van Mele et al., 2007; Adandonon et al., 2009; Dwomoh et al., 2009; Abdulla et al., 2015, 2016, 2017; Anato et al., 2015; Diame et al., 2015).

not only with homopterans such as scale insects (Coccidae, Psuedococcidae, and Margarodidae) and aphids (Aphidae), but also treehoppers (Membracidae), leafhoppers (Cicadellidae), and caterpillars (Lepidoptera: Lycaenidae) (Bluthgen and Fiedler, 2002). Surveys of potential honeydew producers and the diseases they may vector must therefore be closely monitored in weaver ant biocontrol programs.

The literature also includes many instances of weaver ants feeding on predatory insects (e.g., Vayssieres et al., 2015), including deterring predatory mantids (Ramesh et al., 2016), other beneficial ants (Philpott and Armbrecht, 2006), and parasitoid wasps (Mathews et al., 2011; Appiah et al., 2014; **Figure 5A**). Weaver ants have also been observed deterring and capturing several pollinator species (Tsuji et al., 2004; Gonzalvez et al., 2013; Rodriguez-Girones et al., 2013; **Figure 5C**). Thus it is perhaps surprising that net ant impacts were overwhelmingly positive for crop yields (**Figure 3**), rather than ants disrupting biological control through intense intraguild predation (e.g., Snyder and Ives, 2001) or weakening fruit set by deterring pollinators (Tsuji et al., 2004; see also, Huey and Nieh, 2017). Unfortunately, our literature search yielded only a few cases where other predators or pollinators (e.g., Vayssieres et al., 2015) were counted following weaver ant exclusion, preventing us from making a meaningful quantitative analysis of how the ants interact with other arthropod groups. Nonetheless, a careful reading of the literature presents several possible resolutions to this apparent conundrum. First, beneficial insects may represent a relatively small proportion of all prey taken by the ants. For example, in a mango orchard only five of 241 prey species captured by *O. longinoda* were predators or pollinators (Vayssieres et al., 2015). Second, weaver ants often co-exist with a suite of predators adapted to forage among ants such as the ant-mimicking mantis *Euantissa pulchra* (Ramesh et al., 2016), jumping spider ant-mimics such as *Cosmophasis bitaeniata* (Allan and Elgar, 2001), *Myrmarachne* sp. (Ceccarelli, 2009) and *Phintella piatensis* (Nelson and Jackson, 2009) and a suite of web-spinning spiders that co-exist with the ants (Forbes and Northfield, 2017b; **Figure 5A**). A similar situation has been reported for ant-pollinator interactions, where weaver ants were observed capturing and deterring stingless bees (*Nomia* sp.) on the shrub *Melastoma malabathricum* but not larger carpenter bees (*Xylocopa* sp.); because the carpenter bees were the most effective pollinators ants yielded no overall change in pollination efficiency (Gonzalvez et al., 2013; **Figure 5C**).Altogether then, the apparent potential for widespread negative interactions between ants and beneficial insects may rarely be realized in real world agroecosystems. A few instances have been recorded, however, as parasitism rates of the mealybug *Rastrococus iceryoides* (Pseudococcidae) decreased 35% (from 86.6 to 51.4%) in the presence vs. absence of tending weaver ants (Tanga et al., 2016). So, it remains possible that there are some cases of severe interference between weaver ants and beneficial insects that remain to be recognized.

While *Oecophylla* spp. has been observed feeding on floral and extra floral nectaries on their host trees (Rickson and Rickson, 1998; Bluthgen and Fiedler, 2002), along with other plant materials like seeds (Vayssieres et al., 2015), plant resources

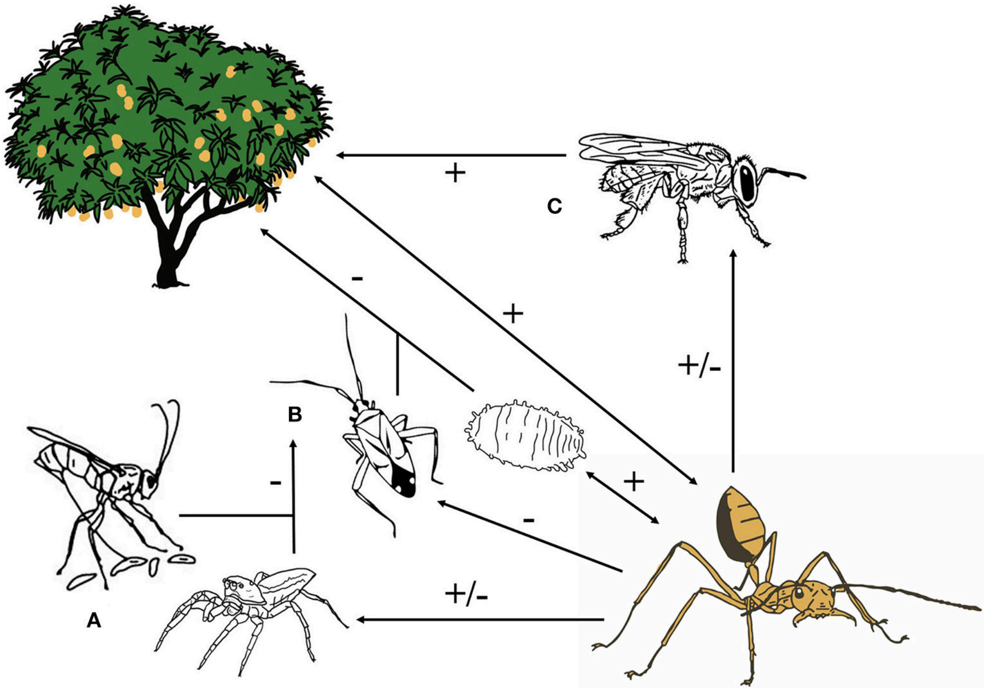

FIGURE 5 | Weaver ants (*Oecophylla* spp.) interact with predators and parasitoids **(A)**, pests **(B)**, pollinators **(C)**, and a host tree. Overall impacts of *Oecophylla* spp. on these groups of arthropods and their host tree can be positive, negative, or both where certain groups of predators, parasitoids or pollinators benefit from ant presence, while others are deterred. Information on these interactions was gathered from a global meta-analysis on both *O. smaragdina* and *O. longinoda* as biological control agents in mango, cashew, and other tropical crops.

have never been experimentally manipulated to measure impacts on weaver ant densities and impacts. Nutrient flow from the ants back to their host plant was inferred when Asian weaver ants (*O. smaragdina*) were fed ^{15}N-labeled glycine and the ant's fecal droplets were absorbed on coffee leaves (*Coffea arabica*). This in turn led to increased levels of total nitrogen and ^{15}N compared on leaves with than without ants (Pinkalski et al., 2018; see also Pinkalski et al., 2016; Vidkjaer et al., 2016). These direct nutrient exchanges from ants to their host plant are suspected to play a role in improving plant health (Pinkalski et al., 2018). This foliar uptake of ant-provided nutrients has only recently been recorded, but sheds light on the extent of possible mechanisms for nutrient exchange which may support a mutualistic relationship between *Oecophylla* spp. and a broad range of host trees. In general, there is a need for more work specifically documenting benefits of plant feeding for weaver ants, and vice versa.

In general, ants are abundant, cooperative and polyphagous, two characteristics which emphasize their potential to control pests in agroecosystems around the world (Philpott and Armbrecht, 2006). Red imported fire ants (*Solenopsis invicta*) were previously recorded to have variable effects on arthropod communities in agroecosystems. However, a study on the relationship between fire ants and the cotton aphid (*Aphis gossypii*) explained some of this variation as the ants were more likely to forage and deter pests from cotton plants with aphids (Kaplan and Eubanks, 2005). In effect, this ant-homopteran trophobiotic relationship facilitated ant impact on the cotton arthropod community where roughly 27% of herbivore and 54% of predator taxa were adversely effected (Kaplan and Eubanks, 2005). Similarly, *Azteca* ants harvest scale insects and the ants' presence in coffee plantations has a negative relationship with potential herbivores (Vandermeer et al., 2002). These trophobiotic relationships between ants and honeydew-producing insects may facilitate biological pest suppression (Styrsky and Eubanks, 2007). In a review of ants harvesting trophobionts, this relationship was found to indirectly benefit host plants in the majority of cases as the density of more antagonistic herbivores were reduced (Styrsky and Eubanks, 2007). Interference in pollination from ant-guards also seems relatively rare as plants and their ant guards have evolved different mechanisms to promote plant-ant health. For instance, ant-guards (such as *Crematogaster* spp.) on *Acacia* trees are deterred from early flower dehiscence to allow pollinator access (Willmer and Stone, 1997). Additionally, ant guards (*Crematogaster* spp.) of the myrmecophytic plant *Macaranga winkleri* are prevented from interfering with pollination as the primary pollinators, thrips (*Dolichothrips fialae*), produce an ant-repelling acid from their anuses (Yamasaki et al., 2016). Overall, we see ant-plant (Yamasaki et al., 2016) and ant-trophobiont (Kaplan and Eubanks, 2005) nutrient exchanges facilitating ant-defense of plants with novel strategies to avoid conflicts of interest like decreased pollination.

Previous reviews of generalist predators have found that generalists can significantly reduce pest species in agroecosystems (Symondson et al., 2002; Offenberg, 2015). Symondson et al. (2002) found that approximately 75% of case studies showed that pest species were significantly reduced under generalist predator treatments. In order to be successful in biological control programs, generalist predators must maintain a high population density when pest populations decline, be opportunistic in feeding habits in order to maintain that population abundance, and exploit attacks by resurgent pests (Symondson et al., 2002). These characteristics can be found in generalist predators which supplement their diet by feeding on their host plant (Eubanks and Denno, 1999). Big-eyed bugs, *Geocoris punctipes* (Geocoridae) are omnivorous predators which supplement their predatory diet by feeding on lima bean pods (Eubanks and Denno, 1999). When prey density is low or of poor quality, these predators can be sustained based on the quality of their host plant (Eubanks and Denno, 1999). Overall, host-plant feeding, appears to sustain generalist predators through prey scarcity and improve biological pest suppression.

Ecosystem services are the products of complex interactions and we emphasize the importance of crop, pest, pollinator, and predator context for when these services may be reaped. We also suggest that host-plant feeding, whether directly or indirectly through trophobionts, may be a predictive variable for when generalist predators provide ecosystem services. The classification of host-plant feeding as an ecosystem disservice is also largely context specific as no instances of direct crop damage from generalist predators was found in this review and indirect damage cause by predators via their trophobionts primarily occurs when certain diseases are present (Forbes and Northfield, 2017a). Weaver ants (*Oecophylla* spp.) have been shown to effectively reduce pest damage and density from a suite of arthropods and increase crop yields around the world. The case-dependency of when their trophobiotic relationships become antagonistic, however, must be further investigated. Further research on the dynamics of nutrient exchanges between ants, trophobionts, and plants, particularly when this nutrient exchange may be critical to pest suppression, remains to be investigated. Additionally, the interactions that *Oecophylla* spp. have with other beneficial arthropod taxa should be explored for agroecosystems to record the impact of ants on pollination, predation, and parasitism. These insights may then shed light on the context-dependent cases for when ecosystem services from ants and other plant-feeding generalist predators may be most reliably achieved.

AUTHOR CONTRIBUTIONS

JT developed the paper, conducted the quantitative literature review, wrote and revised the body of the text, performed statistical analyses, and created all figures in R and original illustrations using Photoshop. TN helped develop the paper, revised drafts of the manuscript, conducted statistical analyses, and assisted in creating figures in R. WS helped develop the paper and revised drafts of figures and the manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2019.00120/full#supplementary-material

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The Role of Host Plants, Alternative Food Resources and Herbivore Induced Volatiles in Choice Behavior of an Omnivorous Predator

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Macrolophus pygmaeus, Rambur (Heteroptera, Miridae) is a generalist predator found on various plant species and has also the ability to feed both on animal and plant tissue. Foraging behavior of *M. pygmaeus* and ultimately its efficacy as a biological control agent, is known to be affected by olfactory stimuli. Here, we elaborate on the response of this omnivore predator to volatiles produced by host plants by conducting olfactometric bioassays under laboratory conditions. In particular, we explored: (i) the relationship between previous experience and plant choice of *M. pygmaeus* nymphs by comparing its attractiveness to pepper and aubergine plants and (ii) how the presence of an aphid prey, *Myzus persicae* (Sulzer), or floral resources may influence choices made by *M. pygmaeus*. When the two host plants were provided, aubergine plants were found to be more attractive than pepper plants, regardless the previous experience of *M. pygmaeus*. Furthermore, the presence of *M. persicae* made aubergine plants more attractive to *M. pygmaeus* nymphs than uninfested aubergine plants. The gas chromatography-mass spectrometry analysis showed that plants infested with *M. persicae* emitted additional compounds as compared to the volatiles emitted from uninfested plants. In particular, four compounds, (*E*)-β-farnesene, (*E,E*)-TMTT, 2-methylbutanal oxime and dodecanal were found present only in the headspace of aubergine plants with aphids. However, *M. pygmaeus* did not show preference for the floral resources. Our results indicate that the response of *M. pygmaeus* is tuned toward the various stimuli in its habitat.

Keywords: ***Macrolophus pygmaeus*, aubergine, pepper plant, Y-tube olfactometer, volatiles**

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INTRODUCTION

The generalist predator *Macrolophus pygmaeus,* Rambur (Hemiptera: Miridae), is a widely used biological control agent for several pests such as aphids, whiteflies, mites as well as the serious invasive pest *Tuta absoluta* (Meyrick) (Lepidoptera: Gelechiidae) on tomato crops (Perdikis et al., 2011; Calvo et al., 2012; Urbaneja et al., 2012; Zappala et al., 2013; Moreno-Ripoll et al., 2014). In particular, in Greece, *M. pygmaeus* is recorded to act as an efficient natural enemy (through natural colonization) in the control of aphids in field tomato crops (Lykouressis et al., 1999–2000). In addition, this mirid is also characterized for its omnivorous behavior, feeding on both plant and prey, which in some cases, depending on the suitability of the plant, allows development and reproduction in the absence of prey (Perdikis and Lykouressis, 1997, 1999, 2000). Unlike other omnivores, *M. pygmaeus* is considered as harmless and has been widely used in biological control programs (Castañé et al., 2011). However, Moerkens et al. (2016) reported that *M. pygmaeus*, can cause economic damage in tomato crops regardless the presence or absence of prey. In addition, Sanchez et al. (2018), reported that high populations of this mirid may lead to a yield reduction due to increased plant feeding. Yet, further research is necessary regarding other species of host plants. Recently, Zhang et al. (2018), have reported that *M. pygmaeus* can induce plant defenses in pepper plants. Similar results have been presented in previous studies concerning *M. pygmaeus* and other mirid species (Pappas et al., 2015, 2016; Pérez-Hedo et al., 2015a,b). In general, further consideration is required prior of using omnivores in biological control, since their ability to feed on both plant tissue and prey may have positive (survival of omnivores) and negative (preference for plant resources rather than prey) effects (Eubanks and Denno, 1999; Perdikis and Lykouressis, 1999; Maselou et al., 2014).

In order to switch between more than one trophic level, omnivores are equipped with morphological and physiological as well as phylogenetic and behavioral traits (Coll and Guershon, 2002). The behavioral characteristics for collection of information and action by a predator, has drawn a lot of attention by researchers in the recent years especially for predator species which can be used effectively in biological control (Ingegno et al., 2011, 2013, 2016; Lins et al., 2014; De Backer et al., 2015). Predator's orientation and the ability to detect and explore available patches with prey is related to various stimuli such as chemicals, visual and acoustic signals or even variation in temperature and humidity (Greany and Hagen, 1981; Letourneau, 1998).

It is well documented that olfactory stimuli are used by natural enemies for host or prey location and enhance efficacy by reducing searching time and increasing attack rates on prey (Dicke and Sabelis, 1988; Vet and Dicke, 1992; Dicke and Vet, 1999). These odors can derive from the prey or the host plant but can also be induced in plants in response to herbivore feeding (Greany and Hagen, 1981; Dicke et al., 1990; Vet and Dicke, 1992; Dicke and Vet, 1999; Hilker and Meiners, 2002). Environmental abiotic conditions and developmental stage of the plant are known to influence the blend of emitted volatiles (Boege and Marquis, 2005; Koricheva and Barton, 2012). The induction of volatiles are known to differ among herbivore species, or in the presence of more than one pests, but it has also been reported that different plant species infested by the same herbivorous species, emit different compounds of volatiles (Dicke and Sabelis, 1988; Turlings et al., 1990; Vet and Dicke, 1992; Tumlinson et al., 1993; Dicke, 1994, 1999; Sabelis et al., 1999; Bruce and Pickett, 2007; Ingegno et al., 2011; Cai et al., 2014). Moreover, plant feeding by omnivores may also affect the reproduction and development of herbivores through induced plant defenses (Pappas et al., 2015; Zhang et al., 2018).

Omnivores have been reported to utilize volatiles from host plants and herbivore-induced plant volatiles (HIPVs) to detect their host plant and prey (Lins et al., 2014; Rim et al., 2015, 2017). This response to HIPVs may be either inherited or acquired through experience (Vet and Dicke, 1992; Steidle and van Loon, 2003; de Boer and Dicke, 2006). Therefore, the effect of these volatiles to an omnivore's performance as biological control agent and their possible use as attractants, is of high importance during the implementation of a biological control strategy.

It has been reported that *M. pygmaeus* responds to volatiles from plants with prey, but not to volatiles emitted directly by the prey (Ingegno et al., 2011; Lins et al., 2014). Lins et al. (2014) found that *M. pygmaeus* exhibits a learning ability (experience) toward prey which may result in more efficient foraging. *M. pygmaeus* was able to discriminate a tomato plant infested by *T. absoluta* from a non-infested plant using olfactory cues (De Backer et al., 2015) as well as spider mite infested tomato plants over clean air (Pappas et al., 2018). However, little information is available regarding its response to volatiles produced from alternative plant food resources such as flowers. A previous study has shown that the presence of flowers on aubergine or pepper plants reduces *M. pygmaeus* predation on the aphid *Myzus persicae*, Sulzer (Heteroptera, Aphididae) (Maselou et al., 2014).

Based on the results of Maselou et al. (2014, 2015) and considering the importance of *M. pygmaeus* as a biological control agent and the rather limited knowledge of the role of volatiles stimuli to its behavior, we set out to elucidate the behavioral response of the predator toward plant resources using olfactometric bioassays. We specifically addressed the following hypotheses: (i) if plant choice in *M. pygmaeus* is influenced by previous experience, predators reared on plant species of different suitability (aubergine plants vs. pepper plants), would show different host plant selection behavior, (ii) the presence of alternative food resources (flower) or prey (aphid-infested plants) alter the volatile blend and considering that they are a feeding source for *M. pygmaeus*, their volatiles would be more attractive for the omnivore than the volatiles emitted from uninfested and non-flowering plants. We also assessed the predator preference for flowering plants vs. non-flowering plants with prey.

MATERIALS AND METHODS

Plant Cultivation and Insect Rearing

Aubergine (cv. Bonika F1) and pepper plants (cv. Vidi) were grown from March to October in a greenhouse in the Agricultural University of Athens at temperature 22.5 ± 2.5°C (mean ± SD), under natural light. The plants used in all experiments were approximately of the same age, 20–25 cm tall with 5–6 true leaves. *M. pygmaeus* rearing was initiated by releasing adults and nymphs collected from a tomato field in central Greece (Co. Boeotia). The predators were reared separately on potted sweet pepper (cv. Vidi) and aubergine (cv. Bonika F1). Each week new non-flowering aubergine or pepper plants were provided to maintain the rearings. The two colonies of *M. pygmaeus* were maintained for at least 15 generations on each plant species provided *ad libitum* with *Ephestia kuehniella* Zeller (Lepidoptera: Pyralidae) eggs as a food supply. Eggs of the *E. kuehniella* were obtained from Koppert BV (Entofood, Berkel en Rodenrijs, The Netherlands). *M. persicae* rearing was established on aubergine plants by releasing adults and nymphs collected from aubergines in the premises of Agricultural

University of Athens. All cultures were kept in wood-framed cages (80 cm length × 80cm width × 70 cm height) in a greenhouse under the same conditions (22.5 ± 2.5°C, natural light).

OLFACTOMETER BIOASSAYS

The olfactory bioassays were conducted at 25 ± 1°C, 65 ± 5% RH under constant light. For each objective we tested the volatile sources presented in **Table 1**. In total eleven comparisons were carried out, six referring to our first objective, (effects of omnivore's experience on plant choice) and five to the response of t *M. pygmaeus* nymphs toward the presence of floral resources and prey. Responses of predator nymphs to volatiles were observed in a two-choice Y-tube glass olfactometer (2.5 cm and 3.0 cm inside diameter at the entry and in the two side arms, respectively) formed by an entry arm (12 cm in length) and two side arms (15 cm in length, 70° angle). The tube was positioned horizontally, and the two side arms were each connected to a glass container (3.5 L or 0.5 L in volume for the assays with plants or individual flowers, respectively). The airflow was produced by an air pump adjusted at the end of the olfactometer with a flow meter to 250 mL min^{-1} and passed through an activated charcoal filter. The glass containers with volatile sources were kept behind a white panel, preventing insects from visually detecting the plants. When plants were used for the bioassays, pots were covered with aluminum foil to restrict the emission of volatiles from soil or plastic. All procedures were carried out wearing gloves. The flowers were cut just before the experiment and maintained in contact with water until use in the experiments. Fifth instar *M. pygmaeus* predators were used in the experiments after being deprived from prey for 24 hours to exclude the influence of variable hunger levels. These were obtained from nymphs of 1st or 2nd instar that were transferred from the rearing cages to potted caged aubergine or pepper plants with eggs of *E. kuehniella* in a temperature controlled room in 25°C, 65 ± 5% R. H. and a photoperiod of 16:8 (L:D) h and left to develop to the 5th instar. Approximately 1 h before trials were initiated, the predators were placed into individual tubes. Each nymph was individually introduced at the downwind end of the entry arm and observed until covering more than 10 cm inside each chosen arm. The experiments took place from 12:00 p.m. to 17:00 p.m. since *M. pygmaeus* has been previously reported to be more active during the afternoon (Perdikis et al., 2004). Nymphs not making a choice for a side arm within 10 min were considered as having made no choice and were excluded from data analysis. Each predator was tested only once and then discarded. The final number of *M. pygmaeus* nymphs that had made a choice for each pair of volatiles was 40. After testing a batch of five nymphs, the volatile sources were switched between left and right sides of the arms to minimize positional bias. After testing ten nymphs, the Y-tube and glass containers were washed with neutral soap and alcohol (70%) and autoclaved at 120°C for 20 min. Approximately, 8–10 insects were tested daily and plants or flowers were replaced daily, therefore 5–6 plants or 10–15 flowers were used per treatment.

Headspace Collection and Analysis of Plant Volatiles

Volatile collection was performed from uninfested, flowering and aphid infested aubergine plants as described by Anastasaki et al. (2018) with slight modifications. A glass container (3.5 L) as described above was used for volatile collection. Single-potted plants were placed in each glass container, with pot and soil wrapped with aluminum foil. Purified air, through an activated charcoal filter, passed through the glass containers. Plant volatiles were drawn by vacuum pump (Dymax 5, Charles Austen Pumps Ltd, UK) with a rate of 360mL/min onto a Teflon made trap (5 cm length × 3mm id) containing 30 mg Porapak Q (80/100 mesh, Supelco, Bellefonte, USA) tapped with a 2 mm glass wool and 3mmTeflon tubes in each end. Prior to the analysis, traps were sequentially washed with 1 mL methanol, diethyl ether, and n-pentane (Fisher Chemicals, Bishop, UK) and blown dry with N_2. Collection of headspace volatiles was performed continuously for 6 h. Three replicates per treatment were carried out. The collection of volatiles was carried out at the same experimental conditions and time period as for the olfactometer bioassays (12:00–18:00). After volatile collection,

TABLE 1 | Olfactometer bioassays involving *M. pygmaeus* nymphs originating either from pepper or aubergine plants (see details in the Materials and Methods).

Objective	*M. pygmaeus* host plant origin	Odor source 1		Odor source 2
I	Pepper	Pepper plant	vs.	Air
		Aubergine plant	vs.	Air
		Pepper plant	vs.	Aubergine plant
	Aubergine	Aubergine plant	vs.	Air
		Pepper plant	vs.	Air
		Pubergine plant	vs.	Pepper plant
II	Pepper	Flower from pepper plant	vs.	Air
	Aubergine	Flower from aubergine plant	vs.	Air
	Aubergine	Aphid-infested aubergine plant	vs.	Uninfested aubergine plant
		Flowering aubergine plant	vs.	Uninfested aubergine plant
		Flowering aubergine plant	vs.	Aphid-infested aubergine plant

traps were extracted immediately with 0.5 mL n-pentane. Sample volumes were reduced to 150 µL and stored in a freezer (at −20°C) in a sealed GC vial with conical inserter until use.

The identification of the chemical compounds was performed with gas chromatography-mass spectrometry (GC-MS). One microliter of the extract was injected in a Varian CP-3800 GC, with a 1079 injector coupled with a 1200L quadrupole mass spectrometer. Separation of the analytes was performed with a Varian VF5ms capillary column (30 m, 0.25 mm i.d, 0.25 µm film thickness). Splitless mode was set to 0.75 min. Then, the injector split ratio was set at 80:1. At 5 min, the split ratio was set to 70:1. The flow rate of the carrier gas helium was 1 mL min^{-1}. The column temperature was maintained at 40°C for 1 min, increased with a rate of 1.2°C min^{-1} to 65°C and with a rate at 3°C min^{-1} to 180°C. The column was heated with a rate of 15°C min^{-1} to the final temperature of 250°C. Mass spectrometer was operated in Electron ionization mode (EI) with ion energy of −70 eV, filament current 50 µA and source temperature 200°C. Data acquisition was performed in full scan (MS) with scanning range 40–300 amu. Compounds were identified by comparing their retention time and mass spectra with that of commercial standards whenever possible or tentatively by comparing their elution order, mass spectra and RI values from Adams (2007); NIST, 2005; Wiley 275 mass spectra libraries and literature data (Adams, 2007; Anastasaki

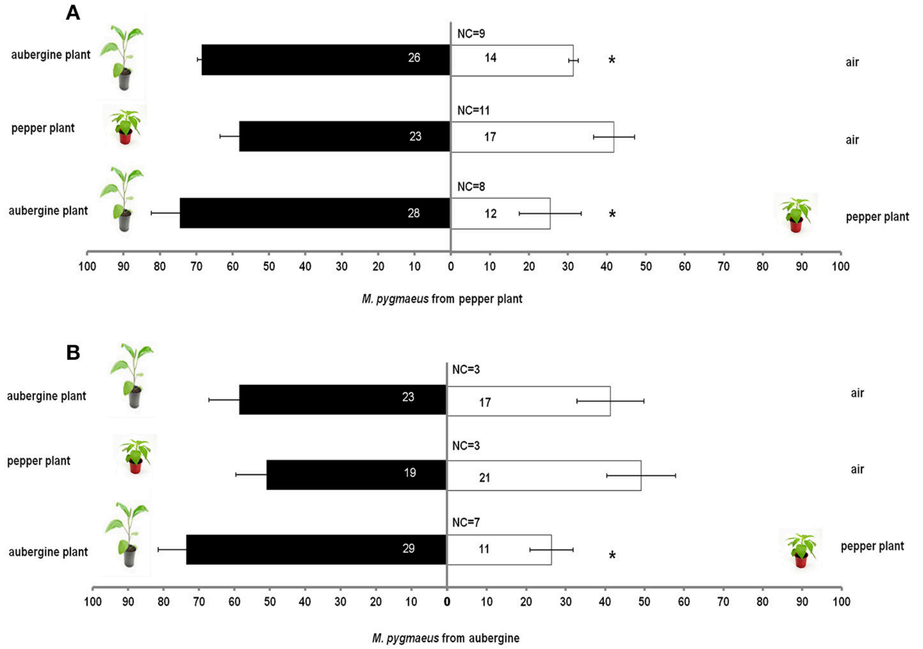

FIGURE 1 | Response of *M. pygmaeus* nymphs originating from pepper **(A)** or aubergine **(B)** plants in a Y-tube olfactometer to the odors of pepper plant, aubergine and clean air for each compared pair. Number in bars represent individuals that moved toward the odor source. *t* test ($^*P < 0.05$; *df*: 1) (NC, number of individuals that did not make a choice).

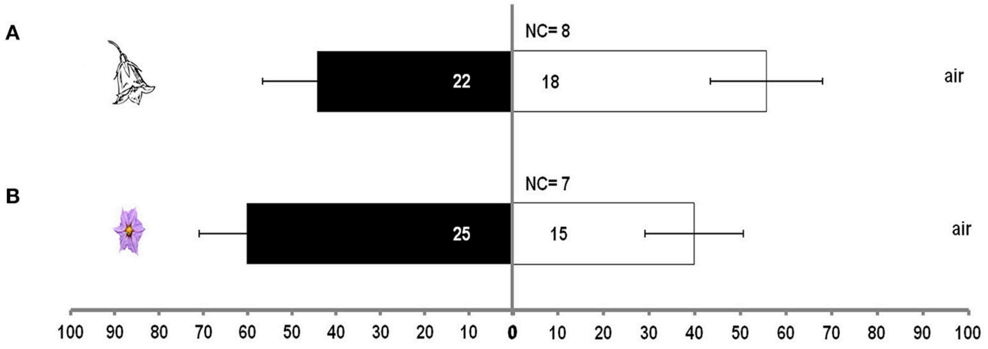

FIGURE 2 | Response of *M. pygmaeus* nymphs originating from pepper or aubergine plants in a Y-tube olfactometer to the odors of one pepper flower or one aubergine flower over clean air. Numbers in bars represent individuals that moved toward the odor source. *t* test ($P < 0.05$; *df*: 1) (NC, number of individuals that did not make a choice). **(A)** Flower from pepper plant. **(B)** Flower from aubergine plant.

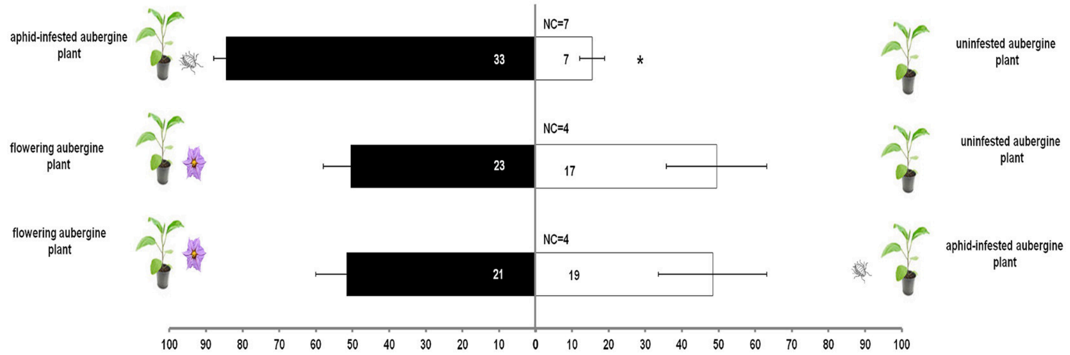

FIGURE 3 | Response of *M. pygmaeus* nymphs originating from aubergine plants in a Y-tube olfactometer to the odors of an aphid-infested aubergine over an uninfested aubergine, a flowering aubergine over an uninfested aubergine and a flowering aubergine over an aphid-infested aubergine plant. Number in bars represents individuals that moved toward the odor source. *t* test (*$P < 0.05$; *df:* 1) (NC, number of individuals that did not make a choice).

et al., 2018). We also used retention indices (RI) of a series of n-alkane (C_8-C_{20}).

Statistical Analysis

In the olfactometer bioassays, the responses of *M. pygmaeus* nymphs were analyzed by a logistic regression to investigate the influence of predator host plant origin. Each bioassay with one pair of plants (or plant vs. air) served as a replicate. Predator host plant origin and plant treatment (pepper or aubergine) were used as fixed factors. Non-significant interactions were removed from the final model (Agresti, 2013). In comparisons of plants vs. air the number of *M. pygmaeus* choosing plants (aubergine or pepper) out of the total individuals responding was used as the response variable. In comparison of aubergine plants vs. pepper plants, the number of individuals choosing aubergine plants out of total individuals responding was used as the response variable. Logistic regression was also used to investigate the influence of flowers on *M. pygmaeus* behavioral choices. In this case, the number of individuals moving toward the flower odor chamber out of total responding was the response variable. The effect of plant treatment (i.e., flowering plant or aphid infested plant) was analyzed by logistic regression and the number of individuals choosing flowering or aphid infested plants out of total responding was used as the response variable. To determine whether there was a preference for an odor source within a treatment combination, we used one sample *t*-test on the proportion of *M. pygmaeus* preferring the response variable in each replicate. Data were arcsine-transformed and tested against arcsine (0.5), i.e., no preference for either odor source. Nymphs that did not make a choice were excluded from the statistical analysis. All analyses were performed using SPSS version 19.0 (SPSS, Chicago, IL)[1].

The total ion chromatogram peak areas of identified compounds were calculated by Varian MS Workstation software (version 6.9). The effect of treatment on the relative peak area of each volatile identified was determined with analysis of variance and comparisons among means were performed using the LSD test. Volatile data were also log-transformed and subjected to multivariate analysis with SIMCA 14.1 software (Umetrics, Umeå, Sweden). Specifically, projections to latent structures-discriminant analysis (PLS-DA) were performed with Pareto scaling.

RESULTS

Olfactometer Bioassays

Host plant origin (aubergine or pepper) of *M. pygmaeus* nymphs had a significant effect on the response of nymphs toward aubergine or pepper plants in comparison with air ($\chi^2 = 34.9$, $df = 15$, $P = 0.002$). When *M. pygmaeus* originated from pepper plants, the nymphs were attracted to aubergine plants in comparison with air ($t = 14.4$, $df = 4$, $P < 0.001$). No other significant differences were observed between aubergine or pepper plants in comparison with air (Pepper plant vs. clean air $t_{\text{pepper}} = 1.6$, $df = 4$, $P = 0.185$; $t_{\text{aubergine}} = 0.2$, $df = 4$, $P = 0.835$; Aubergine plant vs. clean air: $t_{\text{aubergine}} = 1.1$, $df = 4$, $P = 0.332$, **Figure 1**).

There was no significant effect of *M. pygmaeus* nymph origin in comparisons of aubergines over pepper plants ($\chi^2 = 11.1$, $df = 8$, $P = 0.197$). *M. pygmaeus* nymphs were more attracted to aubergine than to pepper plants ($t_{\text{pepper}} = 2.55$, $df = 5$, $P = 0.05$; $t_{\text{aubergine}} = 4.03$, $df = 5$, $P = 0.01$, **Figure 1**).

Treatment had no significant effect in the case of single aubergine or pepper flower over clean air ($\chi^2 = 13.8$, $df = 8$, $P = 0.08$). *M. pygmaeus* nymphs did not discriminate between clean air and volatiles from an aubergine ($t = 1.1$, $df = 4$, $P = 0.337$) or a pepper flower ($t = 0.36$, $df = 4$, $P = 0.738$) (**Figure 2**).

M. pygmaeus nymphs did not discriminate between flowering and unifensted or aphid-infested aubergine plants ($\chi^2 = 26.4$, $df = 18$, $P = 0.092$, **Figure 3**). Predator nymphs were more attracted to aphid-infested aubergine plants than to uninfested ones ($t = 7.9$, $df = 3$, $P = 0.004$, **Figure 3**).

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[1] SPSS v. 19.0.0., 2010. SPSS Inc., Chicago

TABLE 2 | Volatile composition of headspace of uninfested (CON), flowering (FLO), and aphid infested aubergine plants (APH) expressed as total peak area (102 ± SE, *n* = 3).

ID	RI[a]	Compounds	CON	FLO	APH	*F*[b]	*P*[c]
1	800	Octane	3.08 ± 1.02a[d]	0.00b	3.48 ± 1.28a	14.48	**0.005***
2	802	Hexanal	0.00b	3.85 ± 0.92a	0.00b	17.77	**0.003***
3	811	Butyl acetate	0.00b	0.06 ± 0.04b	0.61 ± 0.16a	13.08	**0.006***
4	835	2-methylbutanal oxime	0.00b	0.00b	1.00 ± 0.45a	4.92	**0.054***
5	856	m-xylene	4.39 ± 1.52a	0.00b	4.29 ± 1.55ab	4.00	0.079
6	864	o-xylene	3.91 ± 0.42a	6.02 ± 1.87a	8.29 ± 1.47a	2.47	0.165
7	887	p-xylene	1.79 ± 0.21a	2.42 ± 0.11a	3.54 ± 1.15a	1.71	0.259
8	900	Nonane	1.04 ± 0.15b	2.92 ± 0.79a	0.84 ± 0.19b	5.79	**0.040***
9	906	Heptanal	0.26 ± 0.26b	0.76 ± 0.16ab	1.87 ± 0.75a	3.22	0.112
10	927	α-pinene	5.02 ± 0.29a	5.28 ± 0.01a	3.99 ± 0.88a	1.62	0.273
11	938	β-citronellene	0.00b	3.78 ± 0.95a	0.00b	15.90	**0.004***
12	978	m-menth-1-ene	1.60 ± 0.23a	1.90 ± 0.17a	0.84 ± 0.16b	8.47	**0.018***
13	972	β-pinene	1.33 ± 0.27a	1.02 ± 0.08a	2.02 ± 0.47a	2.58	0.156
14	976	p-menthane	1.15 ± 0.46a	1.75 ± 0.48a	1.27 ± 0.66a	0.34	0.726
15	985	Hydrocarbon 1	3.81 ± 1.12a	3.90 ± 0.19a	5.17 ± 1.10a	0.69	0.540
16	993	Butyl butanoate	0.97 ± 0.35ab	0.00b	1.81 ± 0.28a	8.31	**0.026***
17	1000	Decane	7.89 ± 1.34a	7.78 ± 2.23a	1.59 ± 0.61b	5.45	**0.045***
18	1005	3-δ-carene	3.81 ± 0.65a	2.54 ± 0.29a	3.06 ± 0.25a	2.13	0.201
19	1016	Hydrocarbon 2	3.91 ± 0.88a	1.35 ± 0.78a	1.67 ± 0.96a	2.55	0.158
20	1021	p-cymene	1.54 ± 0.42a	0.56 ± 0.32a	1.20 ± 0.07a	2.62	0.152
21	1025	Limonene	3.89 ± 0.21a	4.54 ± 0.23a	6.16 ± 1.20a	2.63	0.152
22	1028	Eucalyptol	1.12 ± 0.27b	2.29 ± 0.08a	0.56 ± 0.14b	23.76	**0.001***
23	1030	Ethylhexanol	3.40 ± 1.25a	2.53 ± 0.01a	3.08 ± 0.60a	0.30	0.753
24	1032	Benzyl alcohol	0.13 ± 0.13a	0.00a	0.00a	1.00	0.422
25	1034	Unknown 1	0.36 ± 0.14a	0.43 ± 0.25a	0.00a	1.95	0.222
26	1044	Hydrocarbon 3	0.54 ± 0.26a	0.62 ± 0.21a	0.69 ± 0.53a	0.05	0.956
27	1055	Hydrocarbon 4	1.87 ± 0.51a	1.52 ± 0.59a	0.38 ± 0.31a	2.59	0.155
28	1061	Hydrocarbon 5	1.82 ± 0.23a	1.38 ± 0.35a	1.17 ± 0.15a	1.69	0.262
29	1063	Hydrocarbon 6	1.23 ± 0.49a	0.99 ± 0.24ab	0.00b	4.35	0.068
30	1076	Dihydromyrcenol	2.78 ± 0.14a	3.44 ± 0.67a	2.30 ± 0.33a	1.73	0.255
31	1100	Undecane	5.90 ± 0.52a	0.31 ± 0.12b	1.21 ± 0.35b	66.89	**0.000***
32	1101	Linalool	0.90 ± 0.19b	4.81 ± 0.32a	3.03 ± 0.97a	10.76	**0.010***
33	1109	Nonanal	5.11 ± 0.46a	3.72 ± 0.53a	5.30 ± 0.41a	3.16	0.116
34	1114	(*E*)4,8-dimethyl-1,3,7-nonatriene	0.14 ± 0.03b	0.21 ± 0.03b	0.61 ± 0.12a	16.69	**0.004***
35	1115	Hydrocarbon 7	0.43 ± 0.01a	0.42 ± 0.07a	0.17 ± 0.01b	11.20	**0.009***
36	1146	Camphor	0.69 ± 0.19a	1.38 ± 0.38a	0.89 ± 0.22a	1.65	0.269
37	1148	Menthone	0.44 ± 0.07ab	0.76 ± 0.09a	0.25 ± 0.13b	6.62	**0.030***
38	1165	2-(*Z*)-nonenal	0.83 ± 0.15a	0.63 ± 0.15a	0.66 ± 0.06a	0.75	0.511
39	1166	Benzyl acetate	0.54 ± 0.27a	0.80 ± 0.17a	0.79 ± 0.17a	0.49	0.638
40	1168	Isoborneol	0.00b	0.45 ± 0.07a	0.36 ± 0.06a	18.89	**0.003***
41	1191	Phenyl ethyl acetate	0.29 ± 0.08a	0.53 ± 0.11a	0.52 ± 0.02a	2.88	0.133
42	1194	α-terpineol	0.56 ± 0.09a	0.64 ± 0.15a	0.66 ± 0.04a	0.28	0.769
43	1200	Dodecane	1.83 ± 0.12a	2.43 ± 0.06a	1.97 ± 0.33a	2.32	0.180
44	1204	Verbenone	0.13 ± 0.04a	0.11 ± 0.07a	0.19 ± 0.10a	0.32	0.737
45	1207	Decanal	3.05 ± 0.19a	2.61 ± 0.51a	3.00 ± 0.45a	0.31	0.748
46	1232	Citronellol	0.00b	0.23 ± 0.03a	0.22 ± 0.07a	8.63	**0.017***
47	1253	Linalyl acetate	0.36 ± 0.08a	0.57 ± 0.01a	0.41 ± 0.15a	1.37	0.323
48	1274	Unknown 2	0.56 ± 0.17a	0.00a	0.55 ± 0.26a	3.19	0.114
49	1281	Unknown 3	0.14 ± 0.07a	0.38 ± 0.22a	0.21 ± 0.08a	0.76	0.510
50	1286	Isobornyl acetate	0.57 ± 0.13a	1.01 ± 0.07a	0.58 ± 0.22a	2.65	0.150

(Continued)

TABLE 2 | Continued

ID	RI[a]	Compounds	CON	FLO	APH	*F*[b]	*P*[c]
51	1300	Tridecane	0.83 ± 0.16a	0.84 ± 0.07a	1.02 ± 0.20a	0.48	0.639
52	1311	Undecanal	0.33 ± 0.07a	0.30 ± 0.01a	0.27 ± 0.05a	0.32	0.736
53	1322	Hydrocarbon 8	1.02 ± 0.53a	0.55 ± 0.32a	0.55 ± 0.36a	0.44	0.662
54	1344	Unknown 4	0.83 ± 0.15a	0.00a	0.82 ± 0.82a	0.61	0.578
55	1371	Unknown 5	3.88 ± 0.37b	5.52 ± 0.17a	3.25 ± 0.60b	7.73	**0.022***
56	1400	Tetradecane	1.39 ± 0.32a	1.30 ± 0.01a	2.07 ± 0.69a	0.93	0.444
57	1405	Longifolene	0.30 ± 0.05a	0.31 ± 0.03a	0.32 ± 0.06a	0.02	0.977
58	1412	Dodecanal	0.00a	0.00a	0.16 ± 0.08a	4.00	0.079
59	1431	(*Z*)-α-bermamotene	0.38 ± 0.4b	0.52 ± 0.10b	1.79 ± 0.06a	54.87	**0.000***
60	1452	Geranyl acetone	0.83 ± 0.29a	0.73 ± 0.30a	0.00a	3.53	0.097
61	1453	(*E*)-β-farnesene	0.00b	0.00b	1.23 ± 0.10a	15.79	**0.004***
62	1500	Pentadecane	1.00 ± 0.30a	0.91 ± 0.11a	1.35 ± 0.60a	0.36	0.709
63	1523	Lilal	0.43 ± 0.08a	0.37 ± 0.06a	0.35 ± 0.18a	0.14	0.869
64	1529	Unknown 6	0.80 ± 0.31a	0.44 ± 0.26a	0.46 ± 0.18a	0.64	0.558
65	1570	Unknown 7	0.25 ± 0.07a	0.90 ± 0.52a	0.00a	2.361	0.175
66	1575	(*E.E*)-4,8,12-trimethyl-1,3,7,11-tridecatetraene	0.00a	0.00a	0.20 ± 0.05b	15.79	**0.004**
67	1583	Unknown 8	1.68 ± 0.09b	0.84 ± 0.26c	3.34 ± 0.29a	29.92	**0.001***
68	1600	Hexadecane	0.91 ± 0.22a	0.82 ± 0.09a	0.54 ± 0.16a	1.62	0.274

[a] *Retention Index relative to C8-20 n-alkanes on a VF5ms column. Calculated Retention Index relative to C8-C20 n-alkanes. Identification achieved by comparing mass spectra and RI with authentic standard (s) or tentative (t) with mass spectra libraries and literature data (Adams, 2007; Anastasaki et al., 2018).*

[b] *F values, df = 2.*

[c] *Probability values for each F-test. Significant values ($P < 0.05$) are denoted in bold and marked with an asterisk for each compound.*

[d] *Mean values followed by different letters are significantly different ($P < 0.05$).*

Headspace Collection and Analysis of Plant Volatiles

In total 68 compounds were isolated from the headspace of aubergine plants (**Table 2**). Among them, 49 were found in all three plant categories. We confirmed that differences exist in volatile emissions of uninfested, flowering and aphid-infested plants. Dodecanal, (*E*)-β-farnesene, 2-methylbutanal oxime and (*E,E*)-4,8,12-trimethyl-1,3,7,11-tridecatetraene –[(*E,E*)-TMTT] were found only in the volatile blend of aphid-infested aubergines. Furthermore, hexanal and β-citronellene were found only in the headspace of flowering aubergines, while benzyl alchool was isolated only in the headspace of non-infested ones. Additionally, unknown compounds 1 and 7, hydrocarbon 6 and geranyl acetone were emitted from uninfested and flowering aubergines but not from aphid-infested plants. Terpenoids, including monoterpenes and sesquiterpenes, was the most abundant class of compounds. The main monoterpenes identified on all plant treatments were α- and β-pinene, limonene and 3-δ-carene. Significant emissions of esters, aromatic hydrocarbons and hydrocarbons ($F_{\text{est}} = 14.260$, $df = 2$, $P = 0.005$; $F_{\text{ahyd}} = 6.940$, $df = 2$, $P = 0.027$; $F_{\text{hyd}} = 46.538$, $df = 2$, $P < 0.001$) were observed in the volatile blend of all plants. The total relative peak area of terpenoids aldehydes and alchools did not differ significantly between treatments ($F_{\text{terp}} = 1.752$, $df = 2$, $P = 0.252$; $F_{\text{ald}} = 1.741$, $df = 2$, $P = 0.253$; $F_{\text{alc}} = 1.919$, $df = 2$, $P = 0.227$) (**Figure 4**). Plants infested with *M. persicae* had significantly higher emissions of butyl acetate, 2-methylbutanal oxime, heptanal, (*E*)-4,8-dimethyl-1,3,7-nonatriene [(*E*)-DMNT], citronellol, (*Z*)-α-bermamotene, (*E*)-β-farnesene, (*E,E*)-TMTT and unknown 8 compared to uninfested plants (**Table 2**).

Projection to latent structures discriminant analysis (PLS-DA) of all treatments together presented three major clusters of samples, where the aphid-infested and the flowering plants were separated from the uninfested aubergine plants and from each other (**Figure 5A**). The PLS-DA analysis identified 24 compounds with a VIP value higher than 1 (**Table 3**). **Figure 5B** shows the contribution of emitted volatile compounds to the two principal components, which explained 36.3 and 23.3% of the variance, respectively.

DISCUSSION

In the present study, the response of *M. pygmaeus* nymphs toward plant resources was evaluated. Our first hypothesis that predator's plant experience affects the preference of nymphs was partly supported by our findings. Aubergine plants were more attractive to *M. pygmaeus* nymphs over air originating from pepper plants. However, our olfactory trials revealed that regardless the host plant origin of the predator pepper or aubergine plants), *M. pygmaeus* was more attracted to aubergine than to pepper plants. Previous studies have focused on adult behavior. Ingegno et al. (2011) have studied the effect of different host plants species in comparison with tomato plants on the response of *M. pygmaeus* adults. However, the influence of rearing plant on the choice behavior of *M. pygmaeus* nymphs has

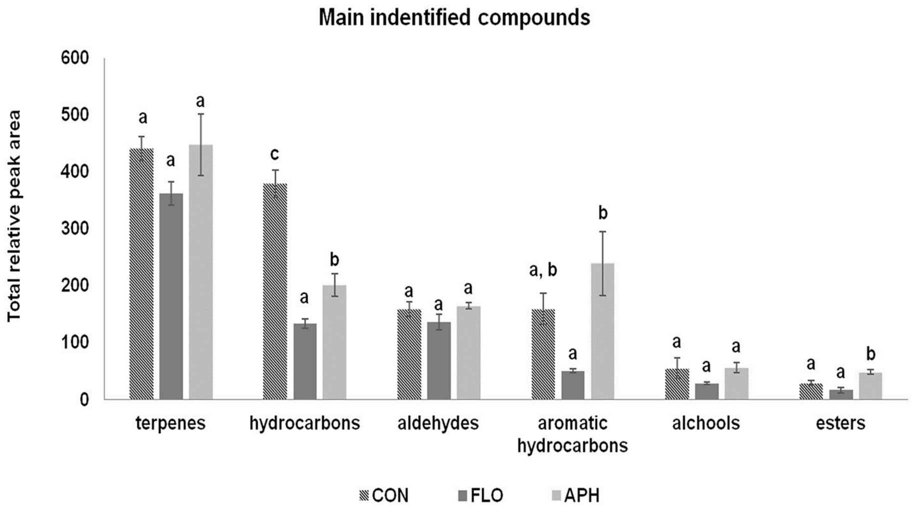

FIGURE 4 | Volatile composition of aubergine plants expressed as total peak area (±SE, $n = 3$) according to volatile chemical classes emitted by uninfested (CON), flowering (FLO) and aphid-infested aubergine plants. Treatments followed by a different letter are significantly different (ANOVA, $P < 0.05$).

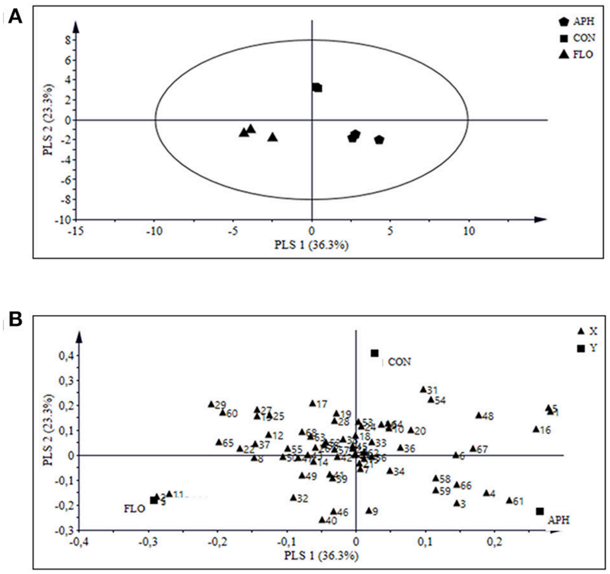

FIGURE 5 | Projection to Latent Structures Discriminant Analysis (PLS-DA) of volatile compounds produced by aphid-infested aubergine plants ($n = 3$, APH), flowering aubergine plants ($n = 3$, FLO) or uninfested plants ($n = 3$, CON). The score plot **(A)** visualizes the structure of the samples according to the first two PLS components with explained variance in brackets. The ellipse defines Hotelling's T^2 confidence region (95%). The loading plot **(B)** defines the orientation of the PLS panels with the original variables in the X (volatile variables) and Y space (class variables: APH, FLO, and CON). For number interpretation of the volatiles please refer to **Table 2**.

not been studied previously. In the present study we tested two host-plant species, pepper and aubergine plants, which according to Perdikis and Lykouressis (2000, 2004a,b) have shown different suitability for the development and survival of *M. pygmaeus* and have been characterized among a wide range of host plants as the least and most suitable plant, respectively. Other mirid species, such as *Dicyphus hesperus* Knight (Hemiptera:Miridae), both adults and nymphs, exhibit a similar behavior by choosing host plants on which nymph survival without prey was substantial (Sanchez et al., 2004).

Our second hypothesis that the volatiles emitted by a flower or prey would affect the response of *M. pygmaeus* nymphs was supported in the case of prey only. Predator nymphs were attracted to aphid-infested aubergines over uninfested ones. Previous studies have shown that *M. pygmaeus* adults do not respond in the presence of prey without the plant (Ingegno et al., 2011; Lins et al., 2014). Following the outcomes of Maselou et al. (2014), we carried out olfactometer bioassays in a plant scale using aubergine plants since they were found to be more attractive to *M. pygmaeus* nymphs. Likewise, there was a tendency for attraction toward flowering aubergine over non-flowering plants though not statistically significant. Given that *M. pygmaeus* nymphs can also feed on plant pollen (Perdikis and Lykouressis, 2000; Vandekerkhove and De Clercq, 2010), we expected that flowering plants would be more attractive than non-flowering plants. The fact that *M. pygmaeus* nymphs did not show a clear preference for the flowering plants suggests that these floral resources may be exploited after the establishment of the species on the plant. On the contrary, *M. pygmaeus* nymphs showed a clear preference for aphid-infested over uninfested aubergine plants. Similar outcomes on adults of *M. pygmaeus* (Ingegno et al., 2011; Lins et al., 2014), *D. errans* (Ingegno et al., 2013) and *N. tenuis* (Rim et al., 2015) were reported in Y-tube olfactometer studies. However, when we compared a flowering aubergine with an aphid-infested one, we recorded equal attraction, suggesting that floral resources may affect *M. pygmaeus* nymphs behavior. Previous studies showed that *M. pygmaeus* nymphs consumed less prey on flowering aubergine or pepper plants. This reduction was higher in aubergine than pepper plants (Maselou et al., 2014). Landis et al. (2000) showed

TABLE 3 | Variable importance to the projection (VIP) of volatiles for the corresponding PLS-DA plots, with value more than 1.0, which can be chosen as the characteristic volatile compounds for the differentiation between treatments.

No	Compound	VIP value
1	Hexanal	1.92
2	m-xylene	1.92
3	Octane	1.90
4	β-citronellene	1.81
5	Hydrocarbon 6	1.70
6	(*E*)-β-farnesene	1.69
7	Undecane	1.63
8	Butyl butanoate	1.60
9	Isoborneol	1.56
10	Geranyl acetone	1.50
11	2-methylbutanal oxime	1.44
12	Butyl acetate	1.43
13	Unknown 4	1.43
14	Citronellol	1.37
15	Unknown 2	1.37
16	Hydrocarbon 3	1.35
17	Heptanal	1.34
18	Decane	1.26
19	β-pinene	1.22
20	Unknown 8	1.18
21	Unknown 1	1.18
22	Linalool	1.14
23	(*E-E*)-TMTT	1.11
24	(*Z*)-α-bermamotene	1.08

that the presence of flowering plants in agroecosystems is a conceptually simple mean to increase densities of predators and parasitoids, since several natural enemies use pollen and/or nectar as alternative food. However, increased abundance of predators and parasitoids to be of benefit for biological control, should translate into increased predation (Stephan et al., 2016). Studies on mirids have shown that habitat management could lead to higher predator abundance and as a result to higher prey consumption (Perdikis et al., 2011; Ingegno et al., 2017).

In our study, a higher number of volatile compounds were detected in the headspace of aubergine plants compared to other studies (MacLeod and Gonzales de Treconis, 1983; Van Den Boom et al., 2004; Rim et al., 2015; Darshanee et al., 2017). Terpenoids were the most abundant volatiles in all plant treatments in agreement with previous studies for different host plants (Ingegno et al., 2016; Anastasaki et al., 2018). *M. pygmaeus* females responded positively to compounds emitted by *T. absoluta* infested tomato plants and also to spider mite infested plants (De Backer et al., 2017; Pappas et al., 2018). In both of the above studies a different profile of induced volatiles was identified compared to our study.

The volatile blend emitted by uninfested, flowering and aphid-infested aubergine plants differed both qualitative and quantitatively. The PLS-DA analysis revealed a separation between different treatments, indicating an alteration of volatile blend on aubergine plants after aphid infestation as well as in flowering aubergine compared to uninfested aubergine plants. The loading plot shows that hexanal and β-citronellene were responsible for the differentiation of flowering aubergine plants, while the terpenoids *E*-(β)-farnesene and (*E,E*)-TMTT as well as the nitrogen compound 2-methylbutanal oxime for the differentiation of aphid-infested aubergines plants. These compounds isolated only in aphid-infested aubergine plants, had also a VIP value greater than 1. The terpenoid (*E*)-β-farnesene isolated only from aphid-infested aubergine plants, is known to play important role as a foraging cue for aphid natural enemies (Du et al., 1998; Verheggen et al., 2007; Hegde et al., 2011). (*E*)-β-farnesene is a well-known alarm pheromone released from aphids to warn individuals of the same species (Pickett and Griffiths, 1980), and has also been found to act as a kairomone for several aphid predators (Verheggen et al., 2008). Plants may also emit (*E*)-β-farnesene either constitutively (Gibson and Pickett, 1983) or inductively (Schnee et al., 2006). In our study, aphids were not exposed to any predator, which may suggest that the emission of (*E*)-β-farnesene was emitted by the plant itself and not by aphids, though, we cannot exclude the possibility that other kind of irritation might have occurred. In addition, we did not isolate (*E*)-β-farnesene from uninfested aubergine plants which further suggests that its emission was induced by aphid feeding. (*E,E*)-TMTT is related to herbivory attack (Paré and Tumlinson, 1999; Tholl et al., 2011). It has been found to be emitted by cotton (Hegde et al., 2011) and pepper plants (Moayeri et al., 2007) after aphids' infestation. In a recent study, (*E,E*)-TMTT emitted from *T. absoluta*-infested tomato plants was shown to provoke antennal responses of *M. pygmaeus* in a gas chromatography coupled with mass spectrometer and electroantennographic detectors (GC-MS-EAD) (De Backer et al., 2017). Another compound found only in aphid-infested aubergine plants was 2-methylbutanal oxime. This nitrogen containing compound was recorded from aubergine plants infested by *Spodoptera litura* larvae (Rim et al., 2015) and *Tetranychus urticae* (Van Den Boom et al., 2004; Rim et al., 2015). Also it, was found to elicit an olfactory response and attraction of natural enemies of *Lymantria dispar* (McCormick et al., 2014).

In this study we demonstrated that aphid infestation induces a change in the volatile emissions of aubergine plants that influences the foraging behavior of *M. pygmaeus* nymphs. Although aubergines at their flowering stage had a distinct volatile profile both from the uninfested and aphid-infested aubergine plants, *M. pygmaeus* nymphs did not discriminate between them. These observations are in agreement with the hypothesis that insects respond to a ratio of volatiles for host recognition rather than to individual compounds (Bruce, 2015). In addition, small qualitative differences are usually more important than obvious quantitative differences in volatiles that affect insect behavior (Bruce et al., 2010). Studies on electroantennogram (EAGs) responses of *M. pygmaeus* adults exposed to volatile compounds emitted either by host or non-host plants showed significant EAGs records in plants with very different volatile profiles and the maximum deflection values in the EAGs correlated with the concentrations of sesquiterpenes and alcohols (Ingegno et al., 2016). In other experiments, *M. pygmaeus* adults perceived better the entire volatile blend of *Tuta absoluta*-infested tomato plants than individual compounds and synthetic blends (De Backer et al., 2017).

In conclusion, our results show that *M. pygmaeus* nymphs prefer aubergine over pepper irrespectively of their host plant origin. They were also shown to prefer aphid-infested over uninfested aubergine plants. Flowering plants were shown to be equally attractive to *M. pygmaeus* nymphs compared to aphid-infested plants.. The results of our experiments may have practical implications for the application of *M. pygmaeus* in biological control programs. For example, in order to determine the appropriate time for the introduction of this mirid in the crop as a biological control agent. However, a more detailed knowledge of the role of HIPVs is desirable to better understand the behavior of *M. pygmaeus*.

AUTHOR CONTRIBUTIONS

DM, PM: Conceived and designed the experiments; DM, EA: Performed the experiments; DM, EA, PM: Analyzed the data and wrote the paper; PM: Contributed reagents, materials, analysis tools; DM, EA, PM: contributed to revisions.

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Predatory Mites (Acari: Phytoseiidae) in Agro-Ecosystems and Conservation Biological Control: A Review and Explorative Approach for Forecasting Plant-Predatory Mite Interactions and Mite Dispersal

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Phytoseiidae mites are efficient predators, able to control pest mites and small arthropods in crops all over the world, using three biological control strategies: (i) augmentation, (ii) classical, and (iii) conservation. This paper focuses on the latter strategy. Most of those predatory mite species are generalist predators; they are naturally present in agro-ecosystems both on crops and adjacent natural vegetation. Because of such characteristics, their occurrence is usually associated with the use of fewer pesticides, providing relief to ecosystem services. As a first baseline for managing their occurrence in agro-ecosystems, a review of the present knowledge of plants and predatory mite interactions and predator dispersal ability is proposed. In addition, based on the author's own occurrence database, the study aims at analyzing (i) plant traits and the potential co-evolutionary relationships between plants and predatory mite species and (ii) how this can be used to forecast favorable plants to key predatory mites. For this, some examples were taken, i.e., vine and citrus crops, and three species, *Kampimodromus aberrans*, *Euseius stipulates,* and *Typhlodromus* (*Typhlodromus*) *pyri*. The main conclusion is that the occurrence database can help in determining the probability of finding predatory mite species on crops and non-crop plants. However, because some elements are lacking, especially predatory mite density, plant traits and the true overall distribution, it is currently, difficult to associate plant traits and plant phylogeny to Phytoseiidae diversity. Additional meta-analyses in collaboration with plant specialists would be required. Finally, the paper presents some examples of agroecosystem management at different scales (intercropping, agroforestry, borders management, landscape).

Keywords: biological control, natural enemies, agroecosystem management, mites, agro-environmental management

INTRODUCTION

Current agricultural practices are increasingly questioned and face two major worldwide challenges to (i) increase crop yields for feeding more humans on the planet, (ii) provide more quality food to address health concerns and (iii) avoid pollution for resource sustainability. In this context, crop protection, especially pesticide use, is an increasing threatening practice. However, crop protection is still necessary to ensure food quality and sufficiently high yield (Oerke, 2006). Several measures have been taken in several countries to limit the use of pesticides. For instance, the European Directive 2009/128/EC (https://eur-lex.europa.eu/eli/dir/2009/128/2009-11-25) aims at achieving the sustainable use of pesticides, reducing health risks and promoting the use of integrated pest management and other alternative plant protection strategies. National plans should be implemented to cope with such objectives (i.e., training of professionals, requirements for the sale of pesticides, pesticide application equipment). In France, the Ecophyto plan aims to halve the application of pesticides by 2025.

Biological control is considered a key solution to control arthropods (Altieri, 1999; Power, 2010). This paper exclusively focuses on predatory mites belonging to the Phytoseiidae family and the term predatory mites is used throughout the text to refer to mites of this family. These predators are used to control mite pests as well as small insects (McMurtry and Croft, 1997; Gerson et al., 2003). The Phytoseiidae family contains more than 2,400 species worldwide (Demite et al., 2018), used in the three biological control strategies. First, the classical biological control aims at controlling invasive pests, introducing natural enemies in the targeted area, from the pest origin zone. These measures are usually expensive and are funded by the government. One example is the successful introduction of *Typhlodromalus aripo* De Leon, to control *Mononychellus tanajoa* (Bondar) in Africa (Yaninek et al., 1989). The second strategy, augmentative biological control, consists of a mass release of natural enemies (exotic or endemic) in crops. The natural enemies are usually commercialized by private companies, and producers have to buy them for releasing. These natural enemies are usually specific to their prey and this strategy is essentially applied in greenhouses. One example is the mass-releases of *Phytoseiulus persimilis* Athias-Henriot in greenhouses, with a world market corresponding to 12% of the total natural enemy market (Van Lenteren, 2006). Finally, the third strategy, conservation biological control, consists of enhancing the occurrence of natural enemies in the agro-ecosystem, through its management (Letourneau et al., 2011; Ratnadass et al., 2012). This biological control strategy applies mainly to controlling endemic pests, essentially in open fields and perennial crops. These studies are usually funded by governmental measures as no economic benefits are expected for private companies. I will focus on this latter biological control strategy, as it is the most promising in the context of agro-environmental management. Furthermore, most predatory mites are food-generalists (able to feed on several prey and also on plant exudates, pollen, and fungi) and they are naturally present in agro-ecosystems, both on crops and adjacent natural vegetation. Such characteristics make them good candidates for providing ecosystem services as natural enemies of pest species, resulting in the reduction of pesticide applications (Prischmann et al., 2006; McMurtry et al., 2015).

For conservation biological control implementation, an integrated knowledge of predatory mite biodiversity is required to determine factors affecting the presence of these natural enemies in reservoir zones and their dispersal between those reservoirs and crops. First, the available knowledge on plant and predatory mite interactions and their dispersal abilities was reviewed. Then, based on the present occurrence knowledge, new approaches to forecast predator occurrence on plants are proposed, assuming that this occurrence is related to plant traits and potential co-evolutionary relationships between plants and mites. Finally, examples of the impact of agro-ecosystem management on predatory mite occurrence are provided for several scales (i) within the crops, (ii) in the near borders of the crops and (iii) at a landscape scale.

PLANTS AS RESERVOIR ZONES FOR PREDATORY MITES

Most predatory mites of the Phytoseiidae family are not dependent on a given prey species as they are food-generalists (McMurtry et al., 2013, 2015). However, they are greatly affected by plant characteristics, especially the phylloplan structure (Karban et al., 1995). Some authors reported that the phylloplan (phenotypic characteristics of the leaf surface) features impacted predatory mite densities more than prey availability (Duso, 1992; Karban et al., 1995; Duso et al., 2004b). McMurtry et al. (2013) divided the Phytoseiidae family into four main categories depending on feeding habits: (i) specialized, (ii) selective, (iii) generalists, and (iv) pollen feeders.

Domatia and leaf hairiness are the most documented plant features affecting mite behavior and biology. Schmidt (2014) provided an excellent review of these relationships. The hypotheses proposed to explain such relations are: (i) escape from cannibalism and predation, (ii) maintaining favorable conditions of humidity, especially for egg survival and (iii) pollen retention and alternative food presence in domatia. However, some structures are not favorable to predatory mites, i.e., glandular trichomes of Solanaceae reportedly trap the predators and hinder their movement. The structures affecting predatory mites are not totally characterized. A few studies focused for instance on vein height, presence of nectaries, types of trichomes and domatia. Prischmann et al. (2005a) hypothesized that old galls of Eriophyid mites could serve as refugia for predatory mites. Some authors demonstrated that extrafloral nectaries positively impacted the development of predatory mites (Walter, 1996; van Rijn and Tanigoshi, 1999). Weber et al. (2016) showed that the artificial addition of sugar (imitation of nectaries) on *Vitis riparia* and *Vitis munsoniana* enhanced the densities of fungivorous mites (some Phytoseiidae and many Tydeiidae), with an associated negative impact on powdery mildew.

Pollen can also affect predatory mite densities. Some of them even develop better on pollen than on prey

(Flechtman and McMutry, 1992). However, a few studies focused on the relationship between predatory mites and the pollen of the plants on which these predators occur. Such a relationship was suggested for citrus (Kennett et al., 1979; Grout and Richards, 1992), avocado (McMurtry and Johnson, 1965; Maoz et al., 2008; Gonzalez-Fernandez et al., 2009) and grapevine (Duso and Vettorazzo, 1999). Daud (2003) studied the effect of pollen of *Mabea fistulifera* Mart. (Euphorbiaceae) on *Euseius citrifolius* Denmark and Muma, the main species found on this plant. He showed that *M. fistulifera* pollen was particularly suitable for *E. citrifolius*. However, a direct link between predatory mite species and pollen produced by the plants, where these species occur, is not totally evident. The pollen of birch is suitable for the development of *Kampimodromus aberrans* (Oudemans), whereas this species was never recorded on this plant (Kasap, 2005). The pollen of *Typha* sp. is currently used for rearing various predatory mites and is sometimes spread in crops to increase the densities of those predators. However, only few species were recorded on *Typha* sp. and the species known to feed on this pollen, were not reported on this plant (i.e., *Amblyseius swirskii* Athias-Henriot, *Euseius stipulatus* (Athias-Henriot) (Maoz et al., 2014; Beltrà et al., 2017). Predatory mite densities in vineyards in Italy, were correlated with the amount of Poaceae pollen found on vine leaves. This correlation was attributed to the great quantity of Poaceae in cover crops (Duso et al., 2009). Karban et al. (1995) assumed to find higher predatory mite densities on male than on female plants because of pollen production. However, such a correlation was not observed.

Several studies also showed that plants with hairy leaves could trap pollen better than those with smooth leaves (i.e., Kreiter et al., 2002; Roda et al., 2003; Duso et al., 2004b). Roda et al. (2003) demonstrated that the hairier the apple leaves are, the higher the densities of *Typhlodromus* (*Typhlodromus*) *pyri* Scheuten are, because of a greater pollen and fungal spore quantity.

Some authors also reported that some predatory mite species could feed on plants. This was observed for several species, as *T.* (*T.*) *pyri*, *Typhlodromus* (*Anthoseius*) *rhenanus* (Oudemans), *Euseius finlandicus* (Oudemans), *K. aberrans*, *T. aripo*, *Euseius scutalis* (Athias-Henriot), and *Euseius hibisci* (Chant) (Chant, 1959; Porres et al., 1975; Kreiter et al., 2002; Magalhães and Bakker, 2002; Nomikou et al., 2003; Sengonca et al., 2004; Adar et al., 2012). For this latter species, evidence of plant feeding behavior was observed on avocado but not on citrus leaves, suggesting that plant characteristics affect plant-feeding behavior. Plant tissue might constitute an alternative food and a source of water but does not allow egg production because of its low nutritional value (Nomikou et al., 2003). Thus, it is not clear if those predators would feed on plants when other food sources exist.

The impact of plant compounds on the relationship between plants and predatory mites is not well-documented, except for the impact of VOC (volatile organic compounds) on specialist feeding predators, that are attracted by the compounds emitted by plants once attacked by pests (i.e., Van den Boom et al., 2002). Onzo et al. (2012) showed that cassava cultivars with pubescent leaves were more attractive to *T. aripo* than glabrous leaves. Ferrero et al. (2014) showed that *Phytoseiulus longipes* Evans was more attracted to clean tomatoes than clean beans, suggesting that plant volatile compounds could affect *P. longipes* behavior.

Relationships between plant and predatory mites are complex; all factors affecting their occurrence on plants are not known. There are more than 374,000 plant species (Christenhusz and Byng, 2016) and 2,400 predatory mite species (Demite et al., 2018). This huge number of partners clearly suggests complex and numerous interactions. In a framework of conservation biological control, knowing which plants are favorable to which predatory mites is a key step.

HOW TO DETERMINE THE FAVORABLE PLANTS FOR THE TARGETED PREDATORY MITE SPECIES?

Information on the occurrence of the predatory mite species on plants is available from several publications related to faunistic surveys. The challenge is to retrieve, compile and analyse this information to determine (i) which predator species are present in crops and (ii) the probability of finding these species on non-crop plants.

Tixier et al. (data not publicly available) compiled this information from 1,959 publications, in a database containing 30,684 reports worldwide, of the 2,400 Phytoseiidae species, on 4,900 plant species in 228 countries. This database allows determining the predatory mite species reported for each plant and locality. As an example of the information extracted from the database, **Table 1** shows the predatory mite species encountered all over the world on *Convolvulus arvensis* L., a common weed species. Twenty-five species belonging to 11 genera were recorded. Among them, 16 were reported once. The two species most frequently observed were *P. persimilis* and *Typhlodromus* (*Typhlodromus*) *athiasae* Porath and Swirski.

The objectives here are to use the information contained in this database to determine/forecast the probability of occurrence of predatory mite species in crops and in non-crop plants. Three approaches are proposed.

First, information will be analyzed to determine how the present predatory mite distribution could help to determine the species most likely to be found on two crops (vine and citrus) in different areas of the world. Then, for the most frequent predatory mite species, the non-crop plants more likely to host them will be investigated.

Second, because plant traits affect predatory mite diversity, an analysis of their occurrence in relation to some plant traits will be provided to determine how plant features can be indicators of the presence of some key predatory mite species.

Finally, because relationships between plants and predatory mites might have an evolutionary basis, an analysis of phylogenetic relationships of plants and associated predatory mite diversity will be provided to determine how plant family or genera could be used to forecast the predator species occurrence.

The common limit for these three approaches is that the densities of predatory mites are not always recorded in publications. Furthermore, the sampling methods and the way

TABLE 1 | Species of predatory mites (Acari: Phytoseiidae) and number of reports on *Convolvulus arvensis* L. around the world.

Genus	Species	Number of reports
Amblyseius	*andersoni*	1
	largoensis	2
	meridionalis	1
	swirskii	1
Euseius	*stipulatus*	3
Galendromimus (Nothoseius)	*borinquensis*	1
Galendromus (Galendromus)	*occidentalis*	1
Phytoseiulus	*macropilis*	1
	persimilis	6
Neoseiulus	*californicus*	2
	comitatus	1
	conterminus	1
	fallacis	1
	herbarius	1
	longilaterus	1
	umbraticus	1
	setulus	1
Phytoseius	*plumifer*	3
Proprioseiopsis	*messor*	2
	rotundus	1
Typhlodromips	*sessor*	1
Typhlodromus (Anthoseius)	*recki*	3
	kerkirare	1
Typhlodromus (Typhlodromus)	*athiasae*	4
	pyri	2

Data are issued from the own author database: occurrence of predatory mite species and their associated number of records all over the world (unpublished data).

to report the results differ. We thus have to assume that the most frequently recorded species are also those found in the highest densities (which is not always the case, see below). The objective here is to propose new ways to investigate the relationships between plants and predatory mite species with an applied objective of conservation biological control: how to manage the plant biodiversity within the agro-ecosystems? This paper thus aims to propose the first baseline for further and deeper analyses. For this, I focused on two crops, vine and citrus (two perennial crops where augmentative biological control is poorly applied) and on generalist predators (Types III and IV) because they might be the most adapted to such a biological control strategy (perennial presence in agro-ecosystems and difficulty to rear the predatory mites for mass-releasing).

Assessing Predatory Mite Diversity Based on Recorded Fauna

Predatory Mites in Crops

Using the database cited before, the examples of two crops, *Citrus* sp. and *Vitis vinifera*, were studied.

Citrus Trees

Two hundred and ninety-seven predatory mite species belonging to 38 genera were found in 78 countries (1,231 records in total). On hundred and thirty-five species were recorded once and could be assumed to not play a key role in biological control. The same applies for 134 additional species reported between 2 and 9 times. Thus, among the 297 species, only 28 were found more than 10 times, corresponding to 594 reports in 57 countries (**Table 2**). The two most frequent species were *E. stipulatus* and *Amblyseius largoensis* (Muma). *E. stipulatus* prevailed in the Palearctic region along with *Iphiseius degenerans* (Berlese), *T.* (*T.*) *athiasae*, *A. swirskii,* and *E. scutalis*. In the Neotropical region, the two most frequent species were *Euseius concordis* (Chant) and *Iphiseiodes zuluagai* Denmark & Muma, whereas *Amblydromalus limonicus* (Garman & McGregor) and *Typhlodromalus peregrinus* (Muma) were prevalent in the Nearctic citrus fauna region. In the Oriental region, *A. largoensis* prevailed (20 reports) followed by *Neoseiulus californicus* (McGregor) and *Chanteius contiguus* (Chant). General conclusions for the Ethiopian and Australasian regions cannot be drawn because of the low number of records on citrus in these two regions. The analysis of this database therefore provides the probability to find predatory mite species in some world regions. As a consequence, because of the high probability to find *E. stipulatus* in Europe, crop management would aim to favor this species. More accurate information can also be extracted for countries or for more limited areas, depending on the number of existing reports (to ensure correct forecasting).

Vineyards

One hundred and sixty-seven predatory mite species belonging to 31 genera were found in 40 countries all around the world (558 records in total). Eighty-eight species were recorded once and could be assumed to not play a key role in biological control. The same applies for 69 additional species retrieved <10 times **(Table 2)**. Among the 167 predatory mites, only ten were reported more than 10 times. The four most frequent species were *T.* (*T.*) *pyri*, *E. finlandicus*, *Amblyseius andersoni* (Chant), and *K. aberrans*. These ten species essentially occurred in the Palearctic region, certainly because this region was the most sampled. In the other regions, because of a low number of surveys, it is difficult to forecast predatory mite species occurrence. Furthermore, the present analysis focused on large geographical zones. Yet, fauna diversity depends on the country and more limited geographic zones (Prischmann et al., 2002). In European vineyards, Tixier et al. (2013) showed that only five species were frequently observed (*K. aberrans*, *T.* (*T.*) *pyri*, *T.* (*T.*) *exhilaratus*, *E. finlandicus,* and *Phytoseius finitimus* Ribaga) and that their occurrence differed depending on countries and agricultural practices. For instance, the main species occurring in vineyards in the South of France was *K. aberrans* whereas *T. (T.) pyri* prevailed in vineyards in the North of France (Kreiter et al., 2000).

Predatory Mites on Non-crop Plants

The database can help in determining which of the non-crop plants reported the most frequent predatory mite species. Considering the previous examples and focusing mainly on the Palearctic region, the predatory species to be favored would be *E. stipulatus* in citrus orchards and *K. aberrans* and *T.* (*T.*) *pyri* in vineyards.

TABLE 2 | The 28 and 10 most frequently reported predatory mite species on *Citrus* sp. and *Vitis vinifera,* respectively, and their number of reports in the six biogeographic regions.

	Australasian	Ethiopian	Nearctic	Oriental	Palearctic	Neotropical	Total
***Citrus* sp.**							
Amblydromalus limonicus	1		21			1	23
Amblyseiella setosa			12				12
Amblyseius aerialis			8			9	17
Amblyseius andersoni					21		21
Amblyseius herbicolus	1	2	5	5		7	20
Amblyseius largoensis	2	2	8	20		10	42
Amblyseius swirskii					22		22
Amblyseius tamatavensis	2	5		4			11
Chanteius contiguus				10			10
Euseius concordis					1	23	24
Euseius hibisci			9	1		2	12
Euseius scutalis					22		22
Euseius stipulatus					88		88
Iphiseius degenerans		6			28		34
Iphiseiodes quadripilis		1	10			5	16
Iphiseiodes zuluagai						15	15
Galendromus floridanus			11	1		2	14
Neoseiulus barkeri		1	1	2	9	1	14
Neoseiulus californicus				10	13	1	24
Paraseiulus talbii					18		18
Phytoseiulus persimilis		1			20		21
Phytoseiulus macropilis			5		1	5	11
Typhlodromalus peregrinus		1	14				15
Typhlodromus (Anthoseius) cryptus					15		15
Typhlodromus (Anthoseius) rhenanoides					13		13
Typhlodromus (Anthoseius) transvaalensis	2	2	2	2	1	2	11
Typhlodromus (Typhlodromus) athiasae					31		31
Typhlodromus (Typhlodromus) phialatus					18		18
Vitis vinifera							
Amblyseius andersoni					24		24
Euseius finlandicus				1	29		30
Euseius stipulatus					11		11
Kampimodromus aberrans					21		21
Neoseiulus californicus				1	5	12	18
Paraseiulus talbii					10		10
Phytoseius finitimus					15		15
Typhlodromus (Anthoseius) recki					13		13
Typhlodromus (Typhlodromus) exhilaratus					15		15
Typhlodromus (Typhlodromus) pyri	2		2	1	53		58

Data are issued from the own author database: occurrence of predatory mite species and their associated number of records all over the world (unpublished data).

Euseius Stipulatus

Euseius stipulatus was reported on 131 plant species belonging to 102 genera and 54 families (339 reports). Among the 131 plant species, 35 are crops (171 records, 17 genera and 12 families). This species was reported 96 times on non-crop plants belonging to 83 genera and 47 families. The number of reports by plant species was usually low. The highest number of reports was observed on *Ficus carica* L. (8) and to a lesser extent on species of the genera *Rubus*, *Clematis*, *Malva, Crataegus*, *Eriobotrya*, *Prunus*, *Quercus*, *Rosa,* and *Urtica* (**Table 3**).

Kampimodromus Aberrans

Kampimodromus aberrans was reported on 166 plant species belonging to 109 genera and 52 families (289 reports). Among the 166 plant species, 35 were crops (200 records, 19 genera, and 12 families). *K. aberrans* was reported 133 times on non-crop plants

TABLE 3 | Number of reports (and occurrence frequency in %) of *Euseius stipulatus*, *Typhlodromus* (*Typhlodromus*) *pyri* and *Kampimodromus aberrans* on genera and families of non-crop plants, wordwide.

		E. stipulatus	***T. (T.) pyri***	***K. aberrans***
Plant family	**Plant genus**	**Number of reports**	**Number of reports**	**Number of reports**
Pinaceae	*Abies*		3 (0.86)	
Euphorbiaceae	*Acalypha*	2 (1.20)		
Sapindaceae	*Acer*	1 (0.60)	11 (3.17)	10 (5.00)
Compositae	*Achillea*		1 (0.29)	
Campanulaceae	*Adenaphora*			1 (0.50)
Apiaceae	*Aegopodium*		1 (0.29)	
Sapindaceae	*Aesculus*		5 (1.44)	1 (0.50)
Rosaceae	*Agrimonia*		4 (1.15)	2 (1.00)
Amaranthaceae	*Amaranthus*	3 (1.80)		
Leguminosae	*Amorpho* 1			1 (0.50)
Betutaceae	*Alnus*		5 (1.44)	
Malvaceae	*Althaea*		1 (0.29)	
Apiaceae	*Anthriscus*		1 (0.29)	
Apiaceae	*Apium*			1 (0.50)
Araliaceae	*Aralia*			1 (0.50)
Araucariaceae	*Araucario*			1 (0.50)
Ericaceae	*Arbutus*	2 (1.20)		
Composilae	*Artemisia*		2 (0.58)	
Poaceae	*Arundo*	2 (1.20)		
Asparagaceae	*Asparagus*	2 (1.20)		1 (0.50)
Betulaceae	*Betula*		1 (0.29)	
Compositae	*Bidens*	1 (0.60)		
Boraginaceae	*Baraga*	2 (1.20)	2 (0.58)	1 (0.50)
Nyctaginaceae	*Bougainvillea*	1 (0.60)		
Boraginaceae	*Bourreria*	1 (0.60)		1(0.50)
Cucurbitaceae	*Bryonia*	2 (1.20)	2 (0.58)	1(0.50)
Buxaceae	*Buxus*		4 (1.15)	1(0.50)
Lamiaceae	*Calamintha*			1(0.50)
Theaceae	*Camellia*			1(0.50)
Betulaceae	*Carpinus*		5 (1.44)	1(0.50)
Compositae	*Carthamus*	1 (0.60)		
Fagaceae	*Castanea*	1 (0.60)	1 (0.29)	2 (1.00)
Bignoniaceae	*Catalpa*			1 (0.50)
Cannabaceae	*Celtis*		3 (0.86)	7(3.50)
Leguminosae	*Ceratonio*			1(0.50)
Cupressaceae	*Chamaecyparis*		2 (0.58)	
Amaranthaceae	*Chenopodium*	1 (0.60)		
Compositae	*Chrysanthemum*	1 (0.60)		
Compositae	*Cichorium*	1 (0.60)		
Compositae	*Cirsium*	1 (0.60)		
Cistaceae	Cistus		5 (1.44)	5 (2.50)
Verbenaceae	*Citharexylum*	1 (0.60)		
Ranunculaceae	*Clematis*	7 (4.20)	8 (2.31)	3 (1.50)
lamiaceae	*Clinopodium*		1 (0.29)	
Convolvulaceae	*Convolvulus*	3 (1.80)	2 (0.58)	
Compositae	*Conyzo*	1 (0.60)	2 (0.58)	1 (0.50)
Coriariaceae	*Coriaria*			1(0.50)
Cornaceae	*Comus*	3 (1.80)	9 (2.59)	5 (2.50)
Betulaceae	*Cary/us*	2 (1.20)	14 (4.03)	20 (10.00)
Rosaceae	*Crataegus*	4	4(1.15)	2 (1.00)
Compositae	*Crepis*		1 (0.29)	
Taxodiaceae	*Cryptomerio*		2 (0.58)	
Cupressaceae	Cupressus	2 (1.20)		1(0.50)
Leguminosae	*Cytisus*	2 (1.20)	2 (0.58)	
Poaceae	*Dactylis*			1(0.50)
Compositae	*Dahlia*			1(0.50)
Thymelaeaceae	*Daphne*	2 (1.20)	2 (0.58)	
Solanaceae	*Datura*	1 (0.60)		
Sterculiaceae	*Dombeya*	1 (0.60)		
Boraginaceae	*Echium*	2 (1.20)	4 (1.15)	1(0.50)
Ericaceae	*Erica*		1 (0.29)	1(0.50)
Rosaceae	*Eriobotrya*	4 (2.40)		3 (1.50)
Myrtaceae	*Eucalyptus*	2 (1.20)		
Compositae	*Eupotorio*		1 (0.29)	
Euphorbiaceae	*Euphorbia*		4 (1.15)	2 (1.00)
Celastraceae	*Evonymus*	1 (0.60)		
Fagaceae	*Fagus*		4 (1.15)	
Moraceae	*Ficus*	8 (4.80)	3 (0.86)	5 (2.50)
Apiaceae	*Foeniculum*		1 (0.29)	
Oleaceae	*Fraxinus*	3 (1.80)	6 (1.73)	5 (2.50)
Araliaceae	*Hedera*	1 (0.60)		
Rubiaceae	*Galium*		2 (0.58)	
Leguminosae	*Genista*		1 (0.29)	
Geraniaceae	*Geranium*		2 (0.58)	1 (0.50)
Compositae	*Gerbera*			1 (0.50)
Iridaceae	*Gladiolus*			1 (0.50)
Araliaceae	*Hedera*		3 (0.86)	1 (0.50)
Apiaceae	*Heracleum*		1 (0.29)	
Malvaceae	*Hibiscus*	1 (0.60)		
Poaceae	*Hole us*	1 (0.60)	1 (0.29)	
Rosaceae	*Holodiscus*			1 (0.50)
Poaceae	*Hordeum*	1 (0.60)		
Cannabaceae	*Humulus*		5 (1.44)	1(0.50)
Hypericaceae	*Hypericum*	2 (1.20)	2 (0.58)	
Compositae	*Inula*			1 (0.50)
Oleaceae	*Jasminum*	1 (0.60)		
Juglandaceae	*Juglans*		6 (1.73)	4 (2.00)
Cupressaceae	*Juniperus*		6(1.73)	1 (0.50)
Pinaceae	*Larix*		1 (0.29)	
Lauraceae	*Laurus*	1 (0.60)		
Magnoliaceae	*Liriodendron*		1 (0.29)	
Caprifoliaceae	*Lonicera*	2 (1.20)	6 (1.73)	2 (1.00)
Leguminosae	*Lotus*		2 (0.58)	
Brassicaceae	*Lunaria*		1 (0.29)	
Caryophyllidae	*Lychnis*	2 (1.20)	2 (0.58)	
Malvaceae	*Malva*	6 (3.59)		1 (0.50)

(Continued)

TABLE 3 | Continued

Plant family	Plant genus	*E. stipulatus*	*T. (T.) pyri*	*K. aberrans*
		Number of reports	Number of reports	Number of reports
leguminosae	*Medicago*		1 (0.29)	
Meliaceae	*Melia*			1 (0.50)
Leguminosae	*Melilotus*		2 (0.58)	
Lamiaceae	*Mentha*		1 (0.29)	1 (0.50)
Euphorbiaceae	*Mercurialis*	2 (1.20)		
Rosaceae	*Mespilus*		1 (0.29)	1 (0.50)
Leguminosae	*Mimosa*	2 (1.20)		
Moraceae	*Morus*	1 (0.60)		1 (0.50)
Boraginaceae	*Myosoti*		1 (0.29)	
Myrtaceae	*Myrtus*	2 (1.20)		
Apocynaceae	*Nerium*	1 (0.60)		
Santalaceae	*Osyris*			1 (0.50)
Apiaceae	*Pastinaca*		1 (0.29)	
Lauraceae	*Persea*		1 (0.29)	
Arecaceae	*Phoenix*	2 (1.20)		
Pinaceae	*Picea*		7 (2.02)	
Compositae	*Picris*	1 (0.60)	1 (0.29)	1 (0.50)
Pinaceae	*Pinus*	1 (0.60)	6(1.73)	
Anacardiaceae	*Pistacia*	2 (1.20)	3 (0.86)	1 (0.50)
Pittosporaceae	*Pittosporum*	1 (0.60)		
Plantaginaceae	*Plantago*	1 (0.60)		
Platanaceae	*Platanus*			6 (3.00)
Lamiaceae	*Phlomis*			1 (0.50)
Dryopleridaceae	*Polystichum*		1 (0.29)	
Salicaceae	*Populus*		1 (0.29)	3 (1.50)
Lamiaceae	*Prunella*			1 (1.50)
Rosaceae	*Prunus*	4 (2.40)		4 (2.00)
Rosaceae	*Pseudocydonia*			1 (0.50)
Pinaceae	*Pseudotsuga*		2 (0.58)	
Pteridaceae	*Pteris*		1 (0.29)	
Boraginaceae	*Pulmonaria*			1 (0.50)
Rosaceae	*Pyrocantho*		2 (0.58)	
Fagaceae	*Quercus*	4(2.40)	19 (5.48)	17 (8.50)
Ranunculacea	*Ranunculus*			1 (0.50)
Rhamnaceae	*Rhamnus*		3 (0.86)	
Anacardiaceae	*Rhus*			2 (1.00)
Grossulariaceae	*Ribes*		10(2.88)	1 (0.50)
Euphorbiaceae	*Ricinus*	3 (1.80)	3 (0.86)	
Rosaceae	*Rosa*	4(2.40)	2 (0.58)	1 (0.50)
Rubiaceae	*Rubia*	2 (1.20)	2 (0.58)	1 (0.50)
Rosaceae	*Rubus*	7(4.19)	22 (6.34)	7 (3.50)
Polygonaceae	*Rumex*	1 (0.60)		
Asparagaceae	*Ruscus*	1 (0.60)		1 (0.50)
Salicaceae	*Salix*	3 (1.80)	6(1.73)	1 (0.50)
Lamiaceae	*Salvi*			1 (0.50)
Adoxaceae	*Sambucus*	3 (1.80)	2 (0.58)	3 (1.50)
Scrophulariaceae	*Scrophularia*	1 (0.60)	1 (0.29)	
Asparagaceae	*Semele*	1 (0.60)		
Caryophyllaceae	*Silene*		1 (0.29)	1 (0.50)
Caprifoliaceae	*Sixolix*		1 (0.29)	
Smilacaceae	*Smilax*	2 (1.20)		
Solanaceae	*Solanum*	3 (1.80)	1 (0.29)	
Compositae	*Sonchus*	1 (0.60)	1 (0.29)	
Leguminosae	*Sophora*	1 (0.60)		
Rosaceae	*Serbus*		9 (2.59)	3 (1.50)
Asparagaceae	*Spathodea*	1 (0.60)		
Oleaceae	*Syringa*		2 (0.58)	
Compositae	*Taraxacum*	1 (0.60)		
Taxodiaceae	*Taxodium*		1 (0.29)	
Taxaceae	*Taxus*		4 (1.15)	1 (0.50)
Lamiaceae	*Teucrium*		1 (0.29)	1 (0.50)
Cupressaceae	*Thuja*		4 (1.15)	1 (0.50)
Malvaceae	*Tilia*		10 (2.88)	5 (2.50)
Apiaceae	*Tori/is*	2 (1.20)		
leguminosae	*Trifolium*	1 (0.60)	1 (0.29)	
Poaceae	*Triticum*	1 (0.60)		
Pinaceae	*Tsugo*		4(1.15)	1 (1.50)
Ulmaceae	*Ulmus*	2 (1.20)	15 (4.32)	8 (4.00)
Compositae	*Urospermum*			1 (0.50)
Urticaceae	*Urtica*	4 (2.40)		
Ericaceae	*Vaccinium*		4 (1.15)	
Scrophulariaceae	*Verboscum*		2 (0.58)	
Adoxaceae	*Viburnum*		2 (0.58)	
Apocynaceae	*Vincetoxicurr*	3 (1.80)	8(2.31)	5 (2.50)
Caprifoliaceae	*Weigela*	2 (1.20)	1 (0.29)	
Leguminosae	*Wisteria*		1 (0.29)	1 (0.50)
Compositae	*Xanthium*	1 (0.60)		1 (0.50)

Data are issued from the own author database: occurrence of predatory mite species and their associated number of records all over the world (unpublished data).

belonging to 86 genera and 45 families. The highest number of reports were observed on *Corylus avellana* L. (14 reports) and on plants of the genera *Quercus*, *Acer*, *Celtis*, *Rubus* and *Ulmus* (**Table 3**).

Typhlodromus (Typhlodromus) pyri

Typhlodromus (*Typhlodromus*) *pyri* was reported on 197 plant species belonging to 112 genera and 53 families (532 reports). Among the 197 plant species, 28 were crops (347 records, 12 genera, and 7 families). This species was recorded 168 times on non-crop plants (100 genera and 50 families). The highest number of reports was observed on plants of the genera *Rubus*, *Quercus,* and to a lesser extent *Acer*, *Corylus*, *Ribes*, *Tilia,* and *Ulmus* (**Table 3**).

Plants favorable to *E. stipulatus* are different to those favorable to *K. aberrans* and *T.* (*T.*) *pyri*, whereas plants, where these two latter species are the most often recorded, are quite similar (i.e., *Ulmus* sp., *Acer* sp., *Rubus* sp., *Quercus* sp., *Corylus* sp.). In an applied point of view, these data indicate that a similar/close agro-ecosystem management can favor both *K. aberrans* and *T.* (*T.*) *pyri*.

The use of the database allows forecasting some trends on the biodiversity assembling on crops and non-crop plants. However, some limits exist. Predatory mite biodiversity, even if greatly affected by plant characteristics, can also depend on other factors, especially agricultural practices. For instance, surveys carried out in apple orchards in France in 2012 showed that (i) three species prevailed [*A. andersoni*, *T.* (*T.*) *pyri,* and *K. aberrans*] and (i) fauna modification occurred as the main species reported 10 years ago, *N. californicus,* was hardly found in 2012 (Tixier et al., 2014). Fauna in crops can thus change over time, depending on cultural practices, especially pesticide application (Prischmann et al., 2005c). Another factor affecting predatory mite diversity is local climatic conditions. One such illustration is the different fauna on trees of *Celtis australis* L. planted 1 km apart, on dry soil or near a river (Tixier et al., 2005a, 2007). The main species found in the former condition was *T.* (*T.*) *phialatus* whereas the main species found in the latter condition was *K. aberrans*. Another limit is that the approach proposed herein is based on the frequency of predatory mite species but not on their abundance. The same weight is given to species found in high densities as to those found in low quantities. As stated before, information on abundance is not always provided in publications and sampling techniques differ depending on the surveys; thus this information is difficult to retrieve and compare. Finally, for forecasting approaches, the number of reports should be high enough. The examples studied before on the distribution of *E. stipulatus*, *K. aberrans,* and *T.* (*T.*) *pyri*, showed that it was impossible to provide the probability of occurrence in some areas because of the low number of reports. Clearly, information on predatory mite distribution is lacking, which makes the determination of an occurrence probability difficult.

A modeling approach, to determine *a priori* favorable plants, based on (i) plant traits, (ii) predatory mite traits, or (iii) taxa, will be therefore proposed in the following paragraphs.

Relationships Between Predatory Mites and Plant Traits for Forecasting Predator Distribution

This approach consists of determining how predatory mite occurrence can be explained by morphological plant and predator traits. For instance, the number of trichomes on leaves (>217 vs. <217 trichomes/cm^2) and the domatia structure (close vs. open) were a key feature discriminating between favorable and unfavorable plants to *K. aberrans* (Kreiter et al., 2002). Additionally, the main factors explaining high densities of *K. aberrans* on 11 trees were domatia numbers of the primary axil, domatia structure on the first and secondary veins and trichome densities on the primary vein (Tixier et al., 2005b). Similarly, there was a positive relationship between *Typhlodromus* (*Anthoseius*) *caudiglans* Schuster densities and vine leaf characteristics (density of vein hairs, bristles in leaf axils, and presence of leaf domatia) (Karban et al., 1995). Kreiter et al. (2002) proposed a correlation between trichome densities and predatory mite size.

The examples studied previously on citrus and vineyards showed that predatory mite species encountered on these two crops differ. As some authors (Kreiter et al., 2002) showed that phylloplan hairiness "select" predatory mite species based on their size (smaller predators on plants on hairy leaves and bigger predators on plants with glabrous leaves), we herein investigated how the species found on citrus and *V. vinifera* differ in body length. The female body length of the 297 and 167 species found on citrus and vine, respectively, was retrieved from original description and/or re-descriptions (data used by Tixier et al., 2012). The weighted mean of the body length of species recorded on citrus was 347.59 μm whereas that of species recorded on vine was 334.69 μm. The same trend was observed when only the main species found on these two crops were considered (28 species on citrus, 10 on vine). The weighted mean of the body length of the 28 predatory mite species reported on citrus was 342.6 μm whereas that of the 10 species mainly retrieved on vine was 322.15 μm. The relation between the frequency of the number of species and records according to body length range, also showed that species found on vine are usually smaller than those observed on citrus (**Figures 1A,B**). These trends can be associated to phylloplan hairiness, with a smooth surface being more favorable to bigger mites (Kreiter et al., 2002). For a prediction approach, species with a body length <330 μm might be more frequent on *V. vinifera* and those with a body length more than 330 μm might be more abundant on citrus. However, this result is only a trend, abundance of each species would certainly improve this forecasting.

E. stipulatus, *K. aberrans,* and *T.* (*T.*) *pyri* were not reported on the same plant species. To determine how this distribution is associated to plant features, the non-crop plants where these species were reported were classified as follows: (i) low plants (herbaceous plants), (ii) medium high plant (shrubs) and high plants (trees). *E. stipulatus* was mainly recorded on herbaceous plants (41.9%) whereas *T.* (*T.*) *pyri* and *K. aberrans* were mainly reported on trees (36.8 and 56%, respectively) (**Figure 2**). These are only trends and clearly, information on densities would certainly allow for a more accurate determination of the non-crop plants favorable to *K. aberrans*, *T.* (*T.*) *pyri,* or *E. stipulatus*. However, based on these first trends, it seems that arboreal plants would be favorable to *T.* (*T.*) *pyri* and *K. aberrans* whereas grass would rather favor *E. stipulatus*. This information can be used for agro-ecosystem management: weed management might more affect the occurrence of *E. stipulatus* than that of the two other species.

To further expand the study of the interaction between plant and predatory mite traits, more information is clearly needed. Collaboration with botanists and plant ecologists would allow more plant traits to be included, as public databases on plant characteristics are rare. Weber et al. (2015) published a database containing the number of species and genera with extrafloral nectaries (EFNs) for each plant family. These structures positively affect predatory mite in providing alternative food (Walter, 1996; van Rijn and Tanigoshi, 1999; Mayuko and Yano, 2008). From my own database, the number of predatory mite species and the number of their reports per plant family were compiled, to investigate a potential link between EFNs

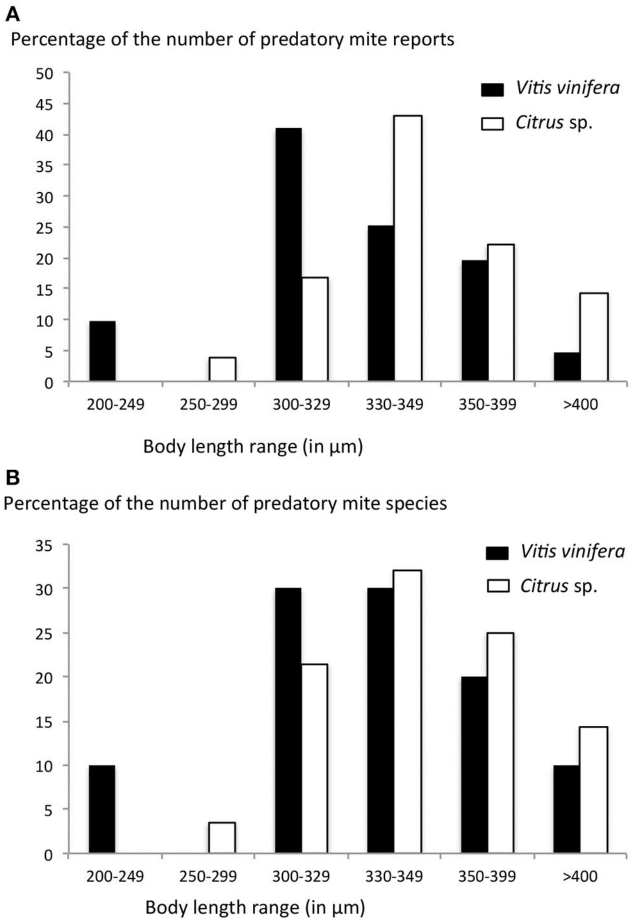

FIGURE 1 | (A) Percentage of the numbers of reports of predatory mites and **(B)** percentage of the number of species of predatory mites reported on *Citrus* sp. and *Vitis vinifera* according to the their body length (range in µm). Data are issued from two own author databases: (i) occurrence of predatory mite species and their associated number of records all over the world (unpublished data), (ii) body lengths of the predatory mite species are issued from original descriptions and the data were those used in Tixier et al. (2012).

and predator occurrence. Few plant species were reported to harbor EFNs (4,017 plant species in 119 families) (http://www.extrafloralnectaries.org/the-list.html). The number of predatory mite reports on these 119 families is 17,899. No correlation was observed between the number of plants with EFNs in each plant family and the number of predatory mite species, nor with the number of predatory mite reports (**Tables 4**, **5**). The correlation tests between the number of plant genera with EFNs, the % of species and genera with EFNs in each plant family and the number of predatory mite reports and species, were not significant either (**Table 4**). All the plants of a family where predatory mites were reported do not harbor EFNs, which can explain why these simple and global correlations were not significant (information compared was not sufficiently accurate). Furthermore, the biology of predatory mites differ according to species and genera considered. Additional studies considering the predatory mite species associated to plants with EFNs could thus be interesting. Finally, Weber et al. (2012, 2015) stated that the number of unreported cases of plants with EFNs might be as high as the number of species already reported, suggesting an incomplete knowledge of these plant traits. The correlations between the number of plant genera with EFNs and the number of plant genera hosting predatory mites, was also tested. The R^2-value (0.35) seems to show that there is a relationship between the plants where predatory mites were reported and EFNs' occurrence. However, the correlation coefficient between the number of genera where predatory mites were found and the total number of genera per plant family was much higher ($R^2 = 0.64$), suggesting that the more genera a family contains (diverse at genus level) the higher the probability to find predatory mite species is (**Table 4**). To more accurately determine how predatory mite occurrence is associated to EFNs' presence, I focused on the Adoxaceae family where two genera among four, contain EFNs: *Sambucus* and *Viburnum* (**Table 6**). Predatory mites were only reported on these two genera. On the seven *Sambucus* species where predatory mites were observed, four harbored EFNs (37 predatory mite records, 21 species). On the three *Sambucus* species without EFN, only a few numbers of records and predatory mite species were observed (3 reports, 3 species). Finally, on six *Sambucus* species with EFNs, no predatory mite was reported. On the 12 *Viburnum* species where predatory mites were observed, four harbor EFNs (17 records, 16 species). On the 8 *Viburnum* species without EFN, much more reports and predatory mite species were recorded (35 reports, 22 species). On 14 *Viburnum* species with EFNs, no predatory mite was reported. As noted in the previous global analyses, no clear association between EFNs and predatory mite occurrence was observed. However, some cues can be noted (i) EFNs were only present on the genera *Sambucus* and *Viburnum* within the family Adoxaceae, and predatory mites were only reported on these two genera as well, (ii) for the genus *Sambucus* more predatory mite species and reports were observed on plant species with EFNs. As no direct association between EFNs and predatory mite was observed, this seems to show that even if EFNs are favorable to predatory mites, other factors might explain their abundance and diversity on plants. Finally, I analyzed the occurrence of the three species previously studied [*E. stipulatus*, *K. aberrans,* and *T.* (*T.*) *pyri*] on the families with EFNs. On the 54 families where *E. stipulatus* was reported (339 records), 29 families contained plants with EFNs (136 records). On the 53 families where *T.* (*T.*) *pyri* was recorded (532 records), 18 families contained plants with EFNs (201 records). Finally, on the 52 families where *K. aberrans* was reported (289 records), 25 families contained plants with EFNs (126 records). Again, no clear association with these species and plants with or without EFNs was observed. Incomplete records of predatory mites, as well as lack of accurate information on plants traits can explain such results.

Evolutionary Relationships Between Plants and Predatory Mites

The hypotheses are that (i) plants and predatory mites have a common evolutionary history and (ii) a relationship between plant and predatory mite phylogeny exists. This hypothesis, assuming that plant traits affecting predatory mites are not

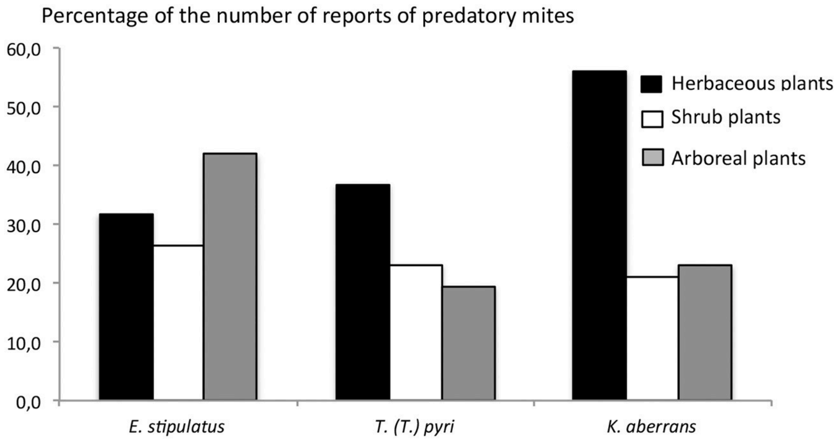

FIGURE 2 | Percentage of the number of reports of *Euseius stipulatus*, *Kampimodromus aberrans,* and *Typhlodromus* (*Typhlodromus*) *pyri* recorded on herbaceous, shrubs and arboreal plants. Data are issued from the own author database: occurrence of predatory mite species and their associated number of records all over the world (unpublished data).

TABLE 4 | Correlation coefficients between several variables concerning (i) the plants with extrafloral nectaries (EFNs) (number and percentage of plant species per family with EFNs, number and percentage of plant genera per family with EFNs, total number of plant genera per family, total number of plant genera per family with EFNs, number of plant genera per family where predatory mites were reported) and (ii) the number of predatory mite species (Phytoseiidae) and reports per plant family.

Variables compared	R^2
Number of plant species/family with EFNs vs. Number of Phytoseiidae reports/plant family	0.023
Number of plant species/family with EFNs vs. Number of Phytoseiidae species/plant family	0.033
Number of plant genera/family with EFNs vs. Number of Phytoseiidae reports/plant family	0.046
Number of plant genera/family with EFNs vs. Number of Phytoseiidae species/plant family	0.06
Percentage of species with EFNs/family vs. Number of Phytoseiidae reports/plant family	0.009
Percentage of genera with EFNs/family vs. Number of Phytoseiidae reports/plant family	0.034
Number of plant genera/family with EFNs vs. Number of plant genera/family with Phytoseiidae records	0.35
Total number of plant genera/family vs. Number of plant genera/family with Phytoseiidae records	0.65

Data are issued from two databases: (i) the own author database on the occurrence of predatory mite species and their associated number of records per plant all over the world (unpublished data) and (ii) a world public database including the list of plant species with EFNs (http://www.extrafloralnectaries.org/the-list.html).

convergent characters, has not been totally tested yet. Karban et al. (1995) showed no effect of phylogenetic relationships of grape species on predatory mite densities. This latter study focused on densities and not on predatory mite diversity. No study to my knowledge investigated the relationship between plant phylogeny and predatory mite taxa. Weber et al. (2016) showed that 61% of the 87 plant families containing species with domatia were also reported to have species with EFNs, and that the two traits occurred non-randomly in the same clades across Eudicots. Weber et al. (2012), focusing on the genus *Viburnum*, revealed an EFNs and mite domatia co-occurrence and that these two traits were evolutionarily correlated. One can thus wonder how this plant evolution (and relationships) can affect the predatory mite diversity. Weber et al. (2012) showed an additive effect of habitat (domatia) and food (EFNs) on mite abundance (especially tydeid mites but also to a lesser extent Phytoseiidae). Accessing the database used by plant evolution/ecology specialists and cross-checking data on predatory mite occurrence, might provide elements to assess the relationship between plant and predatory mites.

As a first step of such a large future study, and considering only *E. stipulatus*, *K. aberrans,* and *T.* (*T.*) *pyri*, I investigated the evolutionary relationships between the plant genera/family where these three predatory mite species were mainly observed. *Euseius sipulatus* was the main species reported from *Citrus* sp. (family Rutaceae, superior taxa: Sapindales). Concerning non-crop plants, *E. stipulatus* was mainly reported on six plant families (Rosaceae, Moraceae, Urticaceae, Malvaceae, Ranunculaceae, Fagaceae) belonging to four superior taxa (Rosales, Malvales, Papaverales, Fagales) (**Figure 3A**). No taxonomic relationship was noted between Rutaceae and the other families where this species was mainly found. This can be explained by the fact that agricultural practices affect predatory mite occurrence more than the phylogenetic relations between plants and predators (i.e., Prischmann et al., 2005b). Considering non-crop plants, no clear phylogenetic relationship was observed between the different families and superior taxa when this species

TABLE 5 | Four categories of plant families with EFNs established according to the number of reports of predatory mites (Phytoseiidae) recorded on them.

Number of Phytoseiidae reports/family	Number of plant families with EFN	Families	Min–Max of the number of Phytoseiidae species/family	Number of plant with EFN per family: mean (min–max)	% plant species with EFN per family (min–max)
Plant family with more than 1000 Phytoseidae reports	6	Asteraceae, Euphorbiaceae, Poaceae, Rosaceae, Rutaceae, Solanaceae	233–335	90 (16–369)	0.2–6.4%
Plant family with between 500 and 1,000 Phytoseidae reports.	3	Fagaceae, Malvaceae, Vitaceae	204–346	106 (2–308)	0.3–7.9%
Plant family with between 100 and 500 Phytoseidae reports	22	Adoxaceae, Amaranthaceae, Anacardiaceae, Annonaceae, Apocynaceae, Bignoniaceae Boraginaceae, Combretaceae, Concolvulaceae, Cucurbitaceae, Ericaceae, Lamiaceae, Meliaceae, Moraceae, Musaceae, Myrtaceae, Oleaceae, Rhamnaceae, Rubiaceae, Salicaceae, Sapindaceae, Verbenacaeae	59–217	31 (1–267)	0.00–33.4%
Plant family with less than 100 records	87	see **Supplementary File 1**	0–62	28 (1–920)	0–100%

Categories of plant families with EFNs	Number of Phytoseiidae reports/family	Min–Max of the number of Phytoseiidae species/family	Number of plant species with EFNs per family: mean (min–max)	% plant species with EFNs per plant family (min–max)
Six families: Asteraceae, Euphorbiaceae, Poaceae, Rosaceae, Rutaceae, Solanaceae	More than 1,000	233–335	90 (16–369)	0.2–6.4%
Three families: Fagaceae, Malvaceae, Vita	Between 500 and 1,000	204–346	106 (2–308)	0.3–7.9%
22 families: Adoxaceae, Amaranthaceae, Anacardiaceae, Annonaceae, Apocynaceae, Bignoniaceae Boraginaceae, Combretaceae, Concolvulaceae, Cucurbitaceae, Ericaceae, Lamiaceae, Meliaceae, Moraceae, Musaceae, Myrtaceae, Oleaceae, Rhamnaceae, Rubiaceae, Salicaceae, Sapindaceae, Verbenacaeae	Between 100 and 500	59–217	31 (1–267)	0.00–33.4%
87 families: see **Supplementary File1**	<100	0–62	28 (1–920)	0–100%

The table also reports the minimal and maximal number of predatory mite species per family and the mean number (min-max) and percentage (min-max) of plant species with extrafloral nectaries (EFNs) for each family. Data are issued from two databases: (i) the own author database on the occurrence of predatory mite species and their associated number of records per plant all over the world (unpublished data) and (ii) a world public database including the list of plant species with EFNs (http://www.extrafloralnectaries.org/the-list.html).

was mainly reported. Rosales and Fagales belong to Eurosids I, Malvales belong to Eurosids II whereas Ranunculales does not belong to Eu-Rosids. *K. aberrans* and *T.* (*T.*) *pyri* were the main species reported on *V. vinifera* in Europe (family Vitaceae, superior taxa: Vitales). No direct phylogenetic relationship between Vitales and the other plant taxa where these two species were reported were observed (**Figures 3B,C**). The same conclusions can thus be drawn: agricultural practices mostly affect predatory mite distribution comparing to evolutionary relationships between plants and predatory mites. Considering non-crop plants, *K. aberrans* mainly occurred on Rosales and Fagales. These taxa are included in the same clade; however, *K. aberrans* was also reported on Proteales and Sapindales and these two taxa belong to different lineages. The same conclusions can also be drawn for *T.* (*T.*) *pyri,* mainly reported from Rosales and Fagales on one hand and from two close taxa Malvales and Sapindales on the other hand. Finally, these results show that the three predatory mite species were mainly reported on Rosales and then on Fagales for *K. aberrans* and *T.* (*T.*) *pyri* and on Papaverales for *E. stipulatus*. As these three predatory mite species belong to different genera and sub-families, no clear phylogenetic relationships between plant and predatory mite evolution can be concluded.

Focusing on the 15 species included in the genus *Kampimodromus*, I investigated if species of a same genus are reported on phylogenetically related plant taxa. **Table 7**

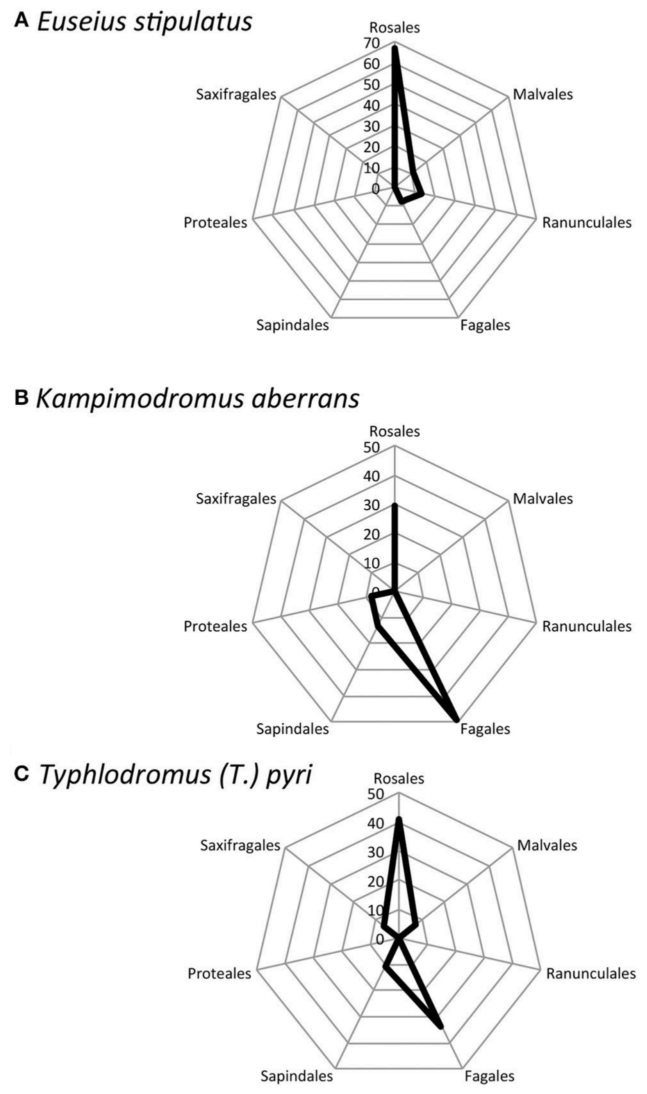

FIGURE 3 | Percentage of the number of reports of **(A)** *Euseius stipulatus*, **(B)** *Kampimodromus aberrans,* and **(C)** *Typhlodromus* (*Typhlodromus*) *pyri* recorded on superior plant taxa. Data are issued from the own author database: occurrence of predatory mite species and their associated number of records all over the world (unpublished data). The "Plants database" (https://plants.usda.gov/classification.html) was used to associate the plant families, where predatory mites were found, to the plant orders.

TABLE 6 | Number of reports and number of species of predatory mites reported on plant species of the genera *Sambucus* and *Viburnum* (Adoxaceae) with and without extrafloral nectaries (EFNs).

	Number of reports	**Number of species**
***Sambucus* Genus**		
*Sambucus canadensis**	1	1
*Sambucus javonica**	1	1
*Sambuscus nigra**	28	14
*Sambuscus nigra**	7	7
Sambuscus sibirica	1	1
Sambuscus sieboldiana	1	1
Sambuscus simpsonii	1	1
Total number of reports/species of predatory mites on plants with EFNs	37	21
Total number of reports/species of predatory mites on plants without EFNs	3	3
***Viburnum* Genus**		
Viburnum carlesii	1	1
*Viburnum dilatatum**	3	3
Viburnum lantana	13	9
Viburnum lanthanum	1	1
Viburnum laurestinus	1	1
Viburnum odoratissimum	3	3
*Viburnum opulus**	8	12
Viburnum rigidum	2	2
*Viburnum sargentii**	2	2
Viburnum suspensum	2	2
Viburnum tinus	12	6
*Viburnum wrightii**	4	5
Total number of reports/species of predatory mites on plants with EFNs	17	16
Total number of reports/species of predatory mites on plants without EFNs	35	22

**Corresponds to plant species with EFNs. Data are issued from two databases: (i) the own author database on the occurrence of predatory mite species and their associated number of records per plant all over the world (unpublished data) and (ii) a world public database including the list of plant species with EFNs (http://www.extrafloralnectaries.org/the-list.html).*

shows the number of reports, the number of species found on plant families and superior taxa, as well as the number of plant genera where the 15 *Kampimodromus* species were observed. The highest number of reports and the highest number of *Kampimodromus* species and plant genera occupied, were observed on Rosales and Fagales. Rosales and Fabales belong to the clade EuRosids I and are evolutionary related. Then, *Kampimodromus* species are reported in two other plant groups neither phylogenetically related to each other, nor with Eu-Rosids I: Sapindales (EuRosids II) and Lamiales (Eu-Asterids I) (The Angiosperm Phylogeny Group, 2003). No clear relationship between phylogeny of Phytoseiidae and plant phylogeny was thus noted. However, all the biodiversity and distribution of predatory mites is not known; the phylogeny of the family Phytoseiidae is not stabilized. Furthermore, additional studies on other predatory mite genera could provide different results. At that state and focusing on the examples herein studied, it does not seem appropriate to use phylogenetic relations between plant and predatory mites to forecast their distribution on plants.

Predatory Mite Dispersal Abilities

The Mode of Dispersal and Factors Affecting Predatory Mite Movement

Predatory mites are wingless organisms. Dispersal ability depends on the species considered, abiotic (temperature, humidity, practical practices) and biotic conditions (i.e., food

TABLE 7 | Superior plant taxa where species of the genus *Kampimodromus* were recorded (associated number of reports and number of species) and the number of plant genera hosting *Kampimodromus* species within those superior plant taxa.

Plant taxa	Number of reports	Number of *Kampimodromus* species	Number of plant genera occupied by *Kampimodromus* species
Abetiales	1	1	1
Asterales	1	1	1
Boraginales	2	2	2
Buxales	1	1	1
Cornales	1	1	1
Dipsacales	2	2	2
Fabales	1	1	1
Fagales	21	8	5
Lamiales	10	4	6
Laurales	1	1	1
Malpighiale	1	1	1
Malvales	2	1	1
Myrtales	1	1	1
Poales	1	1	1
Proteales	2	2	2
Rosales	20	7	10
Santales	1	1	1
Sapindales	16	4	1

Data are issued from the own author database: occurrence of Kampimodromus species and their associated number of records all over the world (unpublished data). The "Plants database" (https://plants.usda.gov/classification.html) was used to associate the plant families, where of Kampimodromus species were found, to the plant orders.

availability) (Sabelis and Dicke, 1985). In a framework of conservation biological control, it is important to assess why dispersal occurs, for enhancing movements between agro-ecosystem components. Most studies dealing with dispersal were based on the use of traps in field conditions (i.e., Tixier et al., 1998, 2000, 2006; Mailloux et al., 2010; Aguilar-Fenollosa et al., 2011a,b, 2012; Liguori et al., 2011; Sahraoui et al., 2012, 2016), or on the assessment of dispersal behavior (i.e., distance traveled from a release point) in lab conditions. Only one genetic population study was carried out on the dispersal of *Neoseiulus womersleyi* (Schicha) between tea orchards and between this crop and the non-crop plant, *Tithonia rotundifolia* Torch, in Japan (Hinomoto et al., 2011) (see below).

Predatory mites can move via ambulatory dispersal. This dispersal applies to low distances, usually from plant to plant, within crops. Ambulatory dispersal of *N. californicus* and *Neoseiulus fallacis* (Garman) was observed from cover crops to apple trees (Johnson and Croft, 1976, 1979, 1981; Berry and Holtzer, 1990; Fauvel and Gendrier, 1992; Pratt et al., 1998; Auger et al., 1999; Jung and Croft, 2001a). Berry and Holtzer (1990) reported different walking behaviors of *N. fallacis,* depending on the densities of prey. An edge-walking behavior seemed to be adopted when prey was scarce. Jung and Croft (2001a) reported that ambulatory dispersal was essentially used by females, and that larvae were the less dispersive stage. However, Sahraoui et al. (2016) showed no difference in sex-ratio and the immature/adult ratio of mites dispersing along citrus trunks. Jung and Croft (2001a) reported a walking speed ranging from 0.1 to 0.4 mm/s for *N. fallacis* (2.7 h to move through 1 m). Raworth et al. (1994) indicated than *N. californicus* would be able to walk 10 m within 1 h at 25°C. Lopez et al. (2017) studied the dispersal of *A. swirskii* to determine how it moved from bank plants to crops. They showed that canopy connectedness increased the dispersal of *A. swirskii* to the crops, whereas no impact of the prey *Polyphagotarsonemus latus* Banks was observed. Similarly, Buithenuis et al. (2010) showed a limited dispersal of *Neoseiulus cucumeris* (Oudemans) in non-continuous plant canopies. Auger et al. (1999) studied the dispersal of *N. californicus* between infested and non-infested dwarf alfalfa under different abiotic conditions. They showed that the main factors affecting the dispersal of this species were food deprivation and high temperatures (35°C). They also stressed that high light intensities (40,000 lux) and drought-stressed alfalfa increased dispersal. Some studies focused on the impact of agricultural practices on predatory mite dispersal. Sahraoui et al. (2016) showed that plowed plots favored *E. stipulatus* dispersal from weeds to trees.

Predatory mites can also disperse aerially *via* the wind (Tuovinen, 1994; Tixier et al., 1998). This dispersal seems to be the main colonization means of *Galendromus* (*Galendromus*) *occidentalis* (Nesbitt) and *K. aberrans* in orchards in the USA and vineyards in France, respectively (Johnson and Croft, 1979; Whalon and Croft, 1986; Dunley and Croft, 1990; Tixier et al., 1998, 2000; Jung and Croft, 2001a). Aerial dispersal ability seems to depend on the species considered. In aerial traps located under citrus trees canopy, *E. stipulatus* was not captured (Sahraoui et al., 2016). Tixier et al. (1998, 2000) showed that males, females, and immature stages of *K. aberrans* dispersed in the same way, whereas Jung and Croft (2001a) reported that the female was the main dispersal stage for *N. fallacis*. The dispersal rate was correlated to wind speed and starvation for food-specialist species (*P. persimilis*) (Jung and Croft, 2001b). These authors showed that starved individuals dispersed on a higher distance than well-fed ones. Several studies demonstrated a take-off behavior (Johnson and Croft, 1976, 1981; Sabelis and Afman, 1994). This behavior seems to be more frequent for starved mites (Jung and Croft, 2001b). Some authors reported that wind speed affected dispersal and especially the take-off behavior (2 m/s). The highest dispersal activity of *P. persimilis* was observed for a wind speed ranging between 4 and 8 m/s (Sabelis and Afman, 1994). Dispersal on a distance higher than 100 m via air currents was demonstrated (Johnson and Croft, 1981; Hoy et al., 1985; Dunley and Croft, 1990); Hoy et al. (1985) documented aerial dispersal of *G.* (*G.*) *occidentalis* for at least 200 m. In the genetic population study carried out in tea orchards in Japan, Hinomoto et al. (2011) showed a dispersal of max. One hundred meters of *N. womersleyi* between orchards and non-crop plants.

Phoretic dispersal is more assumed than really tested. *K. aberrans* females were observed on female aphids of *Myzocallis coryli* (Goeze) (Krantz, 1973). Fain and Krantz (1990) noted the association of *Asperoseius* species on the body of Diptera.

Dispersal and Predatory Mite Traits

Very few studies focus on the relationship between predatory mite traits and their dispersal ability. The dispersal ability of the majority of the predatory mite species is unknown. Jung and Croft (2001b) demonstrated that in general, specialist species had more walking and aerial dispersal rates than generalist species. These authors studied the "landing process and control" after aerial dispersal for 13 predatory mite species. They showed (i) a positive correlation between the mite body weight and the fallen speed and (ii) a negative correlation between the mite body weight and the distance of dispersal. They also demonstrated that the "landing control" could be affected by mite movement and to a lesser extent by dorsal chaetotaxy. Active mites had a slower falling speed than inactive (anesthetized) mites. Finally, no direct correlation was observed between the fallen speed and morphological features; even if a higher length of the dorsal setae *Z5* increased the fallen speed, whereas a smaller length of the setae *s4* negatively impacted this parameter (Jung and Croft, 2001b).

Few studies focus on the impact of host plant characteristics (especially hairiness) on predatory mite dispersal. The few existing studies generally deal with ambulatory dispersal and foraging behavior. Sarwar (2014) showed, studying three plant species (*Phaseolus lunatus* L., *Lablab purpureus* [L.] and *Phaseolus vulgaris*), that leaf area, thickness and hairiness significantly affected the abundance of *N. womersleyi* and its searching behavior. Rezaie et al. (2016) noted different predation rates of *N. californicus,* in different strawberry cultivars. They explained a higher predation rate by lower trichome densities on leaves, as trichome would protect prey from predation. Koveos and Broufas (2000) reported that due to the dense trichomes covering the lower surface of apple leaves compared to peach leaves, *E. finlandicus* movement decreased on apple leaves compared to peach leaves, resulting in an increase of prey handling time.

Predatory mite morphological features and taxonomic attributes, cannot be clearly associated since there are very few studies based on the dispersal ability of the species. No prediction of predatory mite dispersal, based on their traits can thus presently be proposed, to improve agro-ecosystem management.

The Agro-Ecosystem Management

In this section, we will present the knowledge that could be used to manage the agro-ecosystem, i.e., which plants should be associated to crops for favoring predatory mite occurrence and biological control, at different scales within the plots (through cover crops and agroforestry management) and out of the plots (through natural neighboring vegetation and landscape management). The objective is not to provide an exhaustive review of the studies carried out on this topic, but to propose, through some examples, elements for answering the following key questions: (i) what plants and what kind of management will favor the predatory mite species desired? (ii) what management will favor dispersal from non-crop plants to trees? It is difficult to address these questions in a single publication, as no general rule exists. However, compiling all elements and evidence discussed, could provide some answers.

Cover Crops/Ground Cover

Many studies showed that cover crops or weeds constitute a reservoir for predatory mites (i.e., Liang and Huang, 1994; Aucejo et al., 2003; Pereira et al., 2006; Mailloux et al., 2010). Cover crops can provide food for predatory mites, especially pollen and prey. They can also provide habitats, and depending on the leaf features of the cover crop plants, the predatory mite abundance and diversity can differ. Finally, cover crops might modify microclimate conditions in the crops, affecting predatory mite development. However, the direct impact of ground cover on the densities and diversity of those predators on the associated crops, is not easy to show. Furthermore, contradictory results exist in literature, depending on cover crop management, the predatory mite species considered and prey densities on crops.

(Markó et al., 2012) showed that densities and diversity of predatory mites in apple orchards increased with flowering ground cover plants in spring and autumn. They attributed this result to the pollen provided by the cover crop plants. They also noted that *T.* (*T.*) *pyri* gradually displaced *A. andersoni* in the presence of flowers. Similarly, Grafton-Cardwell et al. (1999) tested the effects of pollen of different plants on *Euseius tularensis* Congdon, in lab conditions and showed that in field conditions, a mixture of these plants (as cover crops) had a positive effect on the densities of *E. tularensis* in young citrus orchards. Funayama and Sonoda (2014) suggested that conservation of *Plantago asiatica* L. in apple orchards favored *Amblyseius tsugawai* Ehara populations, because of the suitable pollen produced by this plant.

Aguilar-Fenollosa et al. (2011a) studied the impact of different soil management on *T. urticae* and predatory mites on citrus trees. They observed a better regulation when *Festuca arundinacea* L. was used as cover crop, compared to bare soil or wild cover. Their hypothesis was that this plant, because favorable to *T. urticae*, hosted specialist predatory mite species (*P. persimilis*, *N. californicus*) more efficient for controlling citrus pests than the most species found currently, *E. stipulatus*. They thus proposed (i) to plant *F. arundinacea* for favoring *P. persimilis* and *N. californicus* and (ii) to avoid flowers in the orchards for disfavouring *E. stipulatus*. On the opposite end, Alston (1994) indicated the necessity to have floor vegetation plants in apple orchards, that do not harbor spider mites. Aucejo et al. (2003) studied the predatory mite fauna of cover plants in citrus orchards in Spain. They recommended avoiding plants hosting great densities of *T. urticae* (*Equisetum palustre* L., *C. arvensis* L., *Tribulus terrestris* L., *Parietaria officinalis* L.) and proposed a list of plants with a benefit ratio for predatory mites. De Villiers and Pringle (2011) studied the occurrence of *T. urticae* and predatory mites on vines and plant cover in South Africa. They reported an association between predatory mite dynamics on weeds and vineyards depending on the amount of prey present on the cover plants. They concluded that vineyard management could be associated with plants favoring *T. urticae*. However, they also noted the importance to manage the ratio of *T. urticae*/predatory mites on cover plants, to avoid *T. urticae* infestation in vineyards.

Sahraoui et al. (2016) showed that some plant species within citrus orchards are an important reservoir for *E. stipulatus* (*Amarantus retroflexus* L., *Chenopodium murale* L.) the main predatory mite found on the trees. They attributed the presence of *I. phiseius degenerans* (Berlese) in one part of an orchard on citrus trees to the occurrence of this species, in great densities, on *Solanum nigrum* L. Even though no global impact of ground cover management was observed on predatory mite diversity and densities on trees, they noted the lowest densities on trees when weeds were chemically controlled. The detrimental impact of herbicides reported in other studies (Liang and Huang, 1994; Pereira et al., 2006) could be due to: (i) the direct lethal effect of glyphosate (Kreiter and Le Menn, 1993) and/or (ii) the indirect herbicide effects through habitat destruction (Gauvrit, 1996).

Cover crops can also be used for winter habitats (Fadamiro et al., 2008). Croft and McGroarty (1977) reported that *N. fallacis* wintered in the grass under the apple trees and then migrated to the trees in summer, when prey was scarce in the ground cover. Because *A. andersoni* winters in litter, Szabo and Penzes (2013) proposed a new method to release *A. andersoni* in apple orchards by bringing litter into a new orchard. Higher densities of this species were observed in the plots where the litter was introduced.

The presence of predatory mites in the cover crop is not sufficient to ensure efficient biological control, as the predators have to disperse to the crops. Very few studies deal with the dispersal of predatory mites from the ground cover to crops. In some cases, no effect of ground cover management was stressed especially for *N. fallacis* in apple orchards in the USA (i.e., Stanyard et al., 1997), suggesting no movement between these two compartments. Nyrop et al. (1994) showed for instance that the application of pyrethroids on the cover crop did not impact *N. fallacis* on trees, suggesting limited dispersal from weeds to apple trees. Johnson and Croft (1981) reported that the dispersal of *N. fallacis* from weeds to apple trees was related to the densities of prey [*Panonychus ulmi* (Koch)] on apple trees (no dispersal when prey was scarce on trees). Sahraoui et al. (2016) noted that even if *E. stipulatus* was not the main species dispersing from weeds to citrus, it was the prevailing species on trees. The authors therefore discussed the competition abilities of *E. stipulatus* on citrus with regards to the other species present on weeds and dispersing along the trunk. They also noted that the densities of predatory mites moving from the ground cover to the citrus canopy along the tree trunk, were higher when the ground was plowed, suggesting that physical weed destruction enhanced predatory mite movement.

Effects other than the reservoir role can also exist. Burgio et al. (2016) studied predatory mite communities in vineyards managed with several cover crops. They observed higher predatory mite densities on vines managed with ground cover. However, no effect of the different ground cover treatments (sweet alyssum, phacelia, buckwheat, faba bean, vetch and oat) was observed on predatory mite densities on vines, where the main species were *T. (T.) pyri* and *K. aberrans*. As stated before, these species are mainly found on trees and not on herbaceous plants. Experiments carried out in the South of France, showed that predatory mites were present on herbaceous cover plants; however the main species encountered were not those occurring on vines (Tixier et al., 2015). As in (Burgio et al., 2016), the densities of predatory mites were usually higher in vineyards with cover crop than in vineyards without cover crops. Another hypotheses than simple reservoir effects can thus be drawn: (i) effect of cover crop pollen deposited on the vine leaves, (ii) effect of micro-climate conditions in vineyards managed with cover crops and/or (iii) effect of cover crop on vine physiology. No study was carried out to test the two latter hypotheses, whereas the former is well-documented (Madinelli et al., 2002). Liang and Huang (1994) found high densities of predatory mites in citrus orchards associated with *Ageratum conyzoides*. They also showed that the presence of such cover crops modified the orchard microclimate, reducing the temperature (−5°C) and increasing relative humidity (+5%). Cover crops could thus create abiotic favorable conditions for the development of predatory mites in orchards.

Agroforestry Management

Few studies were carried out on the impact of agrofrestry management (i.e., plantations of trees within crops) on predatory mite communities. The most documented study was carried out in the South of France, where vines were co-planted with *Sorbus domestica* L. or *Pinus pinea* L. (Barbar et al., 2005, 2006, 2009; Liguori et al., 2011; Tixier et al., 2015). A 10-year survey showed that agroforestry management did not increase biodiversity within the plot. Vine cultivar characteristics mostly affected predatory mite densities comparing to agroforestry management. Furthermore, the agroforestry effect was different according to the vine cultivar. On Grenache cv., lower densities were observed on co-planted vines than in monoculture plots, with higher densities in vines co-planted with *S. domestica* than with *P. pinea*. On Syrah cv., predatory mite densities in co-planted vines with *S. domestica* and in the control plot were similar, and much lower than those on vines co-planted with *P. pinea*. Several hypotheses were proposed: (i) different quality and quantity of pollen produced by the two co-planted trees (*P. pinea*, anemophilic pollination; *S. domestica*, entomophilous pollination), (ii) different abilities of Grenache and Syrah cultivars to capture pollen because of their different leaf hairiness and (iii) the impact on predatory mite habitats due to differences in tolerance to drought stress, according to the co-planted trees. After a 10 year-study, no clear conclusion could be drawn on a positive effect of agroforestry management considering the co-planted trees: *P. pinea* and *S. domestica*. Complex interactions between plant physiology (stress) and predatory mites might exist. Furthermore, the impact varied according to the co-planted trees and we can assume that other reservoir trees would be more interesting especially in favoring *K. aberrans* (such as *C. australis* L. or *F. carica* L.).

Borders of the Plots

Many studies showed the presence of predatory mites on non-crop plants in vineyard and orchard borders (i.e., Boller et al., 1988; Tuovinen and Rokx, 1991; Coli et al., 1994; Prischmann and James, 2003; Duso et al., 2004a; Demite et al., 2015). For instance, several surveys were carried out in France on the natural vegetation surrounding vineyards (i.e., Tixier et al., 1998, 2000, 2006; Barbar et al., 2005). Those studies often showed great densities of predatory mites (and especially of the most efficient species in vineyards, *K. aberrans*) on non-crop plants

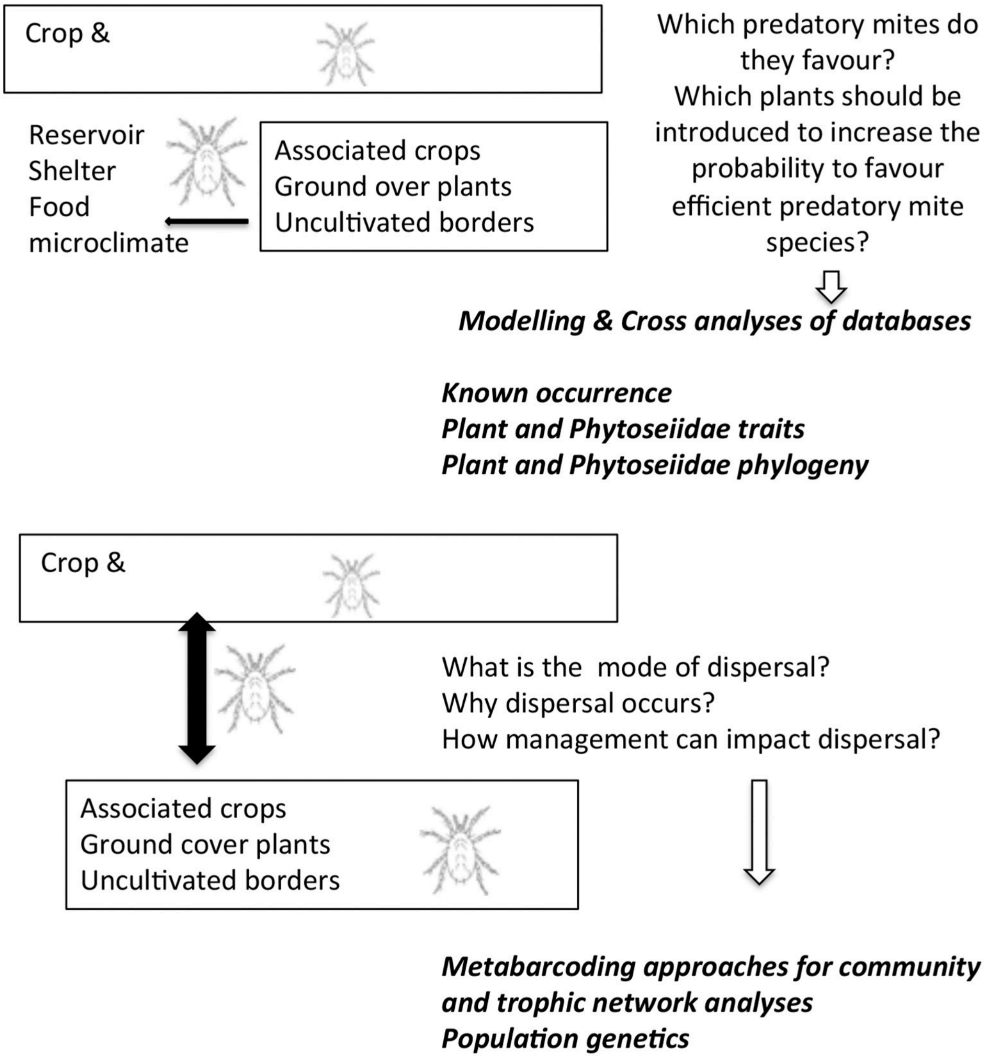

FIGURE 4 | Synthesis of the key questions and further future approaches (in bold and italics) for agro-environmental management of predatory mites in agro-ecosystems.

such as *C. australis*, *F. carica*, *Quercus pubescens* Wild. and *Cornus sanguinea* L. High densities of *K. aberrans* dispersing via the wind into the vine plots were observed. However, a population genetic study suggested a low gene flow between vines and non-crop habitats (Tixier et al., 2002). The "bridge" between crops and neighboring non-crop plants is therefore not well-understood or documented. Todokoro and Isobe (2010) noted that *T. rotundifolia* (Mill.) was favorable to *N. womersleyi* because it hosted great densities of *T. urticae*. They therefore proposed to use this plant within tea orchards, as *T. urticae* is not harmful to this crop and *N. womersleyi* can control *Tetranychus kanzawai* Kishida, the main pest found on tea orchards. Through a genetic population study, Hinomoto et al. (2011) suggested that *T. rotundifolia* and tea trees should be planted each 100 m. Genetic population studies would probably bring new elements to better characterize dispersal ability and factors explaining movement from the neighboring natural vegetation. Metabarcoding approaches, are used more frequently to compare predatory mite communities according to different management modalities (i.e., Mollot et al., 2014) also providing elements on factors affecting trophic networks within agro-ecosystems.

Landscape Effects

Landscape effect on predatory mite densities is poorly investigated. A study was recently carried out in France (Sentenac et al., 2018). As previously demonstrated, a clear relationship between the density of pollen and predatory mite densities on vine leaves was observed. The preliminary results showed no landscape effect. The densities of *T.* (*T.*) *pyri* in Burgundy were not related with the proportion of non-crop areas (semi-natural habitats: SNH) for buffers at 100 and 1,000 m. Some meta-analyses noted that densities of generalist predators were related to the proportion of SNH for buffers included between 0 and 6 kms (Chaplin-Kramer et al., 2011; Veres et al., 2013; Landis, 2017). However, predatory mites are wingless organisms and their dispersal is not efficient at high distances. Furthermore, the % SNH can also be a too global indicator, as *K. aberrans* and *T.* (*T.*) *pyri* usually occur on deciduous trees and SNH includes both trees and grasses. Clearly, the landscape approach needs to be developed for assessing effects at different distances.

CONCLUSIONS

Numerous studies focused on the agro-ecosystem management for biological control purposes and associated ecosystem services (less pesticides, well-being, human and animal health, fewer exotic natural enemies . . .). Many surveys were and are still being carried out to characterize the predatory mite species occurring on non-crop plants and the relationships between this fauna and that found on crops. Even if not complete, a huge amount of information exists on the occurrence of predatory mite species on plants. However, little is known on the parameters that explain this occurrence. The first modeling attempts carried out herein, showed that a prediction could be made to some extent, based on the known distribution. However, because predatory mite occurrence is not well-known, new approaches to forecast plant and predatory mite associations are needed. In the present study, we proposed and illustrated two approaches based on (i) plant traits and (ii) plant phylogeny. The preliminary results obtained are not completely satisfactory especially because of the scarce information on plant traits and the taxonomic levels investigated (too global analyses). The present work therefore constitutes a preliminary baseline for further studies, investigating more accurate taxonomic levels (i.e., species levels) and/or functional traits (i.e., feeding types of Phytoseiidae). For this, more data on plant characteristics (i.e., types of EFNs, domatia, trichomes) should be compiled in collaboration with plant specialists and cross-analyzed with predatory mite diversity and occurrence. Development in automatized plant phenotyping, as well as meta-analyses of data and modeling approaches, would certainly help to develop such studies. Considering the dispersal of predatory mites within agro-ecosystems, progress has been made but factors affecting this dispersal are not clearly understood and studies on predatory mite traits associated with dispersal ability, might be a research track for future applications in biological control. In addition, development of genetic studies for determining the population structures of predatory mites, both in and outside of the crops, would provide answers on agro-ecosystem management impact. Finally, agro-ecosystem management can act as a reservoir for predatory mites (e.g., providing alternative food) but can also impact microclimate conditions. Interactions are thus complex and the presence of predatory mites on non-crop plants does not necessary imply efficient biological control on the adjacent crops. The scale of agro-ecosystem management is therefore also important, and certainly differs depending on the predatory mite species, their habitats (trees vs. herbaceous vegetation) and their feeding habits. Recent development in metabarcoding approaches, for studying communities and trophic networks, might certainly help in deciphering interactions within an agro-ecosystem and the potential impacts of agro-ecosystem management (i.e., cover crops, border management) on these interactions and trophic networks.

Clearly, new methodological (i.e., metabarcoding, population genetics) and analytical (cross-analyses of database) developments as well as interdisciplinary approaches (e.g., botany, plant and mite ecology, agronomy, plant ecophysiology, genetics, etc. . .) constitute a future outlook, for managing agro-ecosystems better and enhancing biological positive interactions (**Figure 4**).

AUTHOR CONTRIBUTIONS

M-ST wrote alone the manuscript, based on an analysis of literature and compilation and analysis of databases on Phytoseiidae mites and plants.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2018.00192/full#supplementary-material

Supplementary File 1 | Data on the plant families with extrafloral nectaries (EFNs) and the number of predatory mite reports on these families.

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Role of Thrips Omnivory and Their Aggregation Pheromone on Multitrophic Interactions Between Sweet Pepper Plants, Aphids, and Hoverflies

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In complex food webs, plants are commonly attacked by multiple herbivorous species, affecting the preference and performance of other herbivores and natural enemies. The role of omnivorous insects in ecosystems may be more complex because of the consumption of both plant and animal organisms. However, the effect of omnivorous insects on herbivores and natural enemies, has received little attention so far. The main goal of this study was to investigate whether the dual herbivore interaction between aphids and thrips, an omnivorous pest, on a sweet pepper system, may affect different trophic levels, from plant and aphid performance until the third trophic level, i.e., preference and performance of the predatory hoverfly *Sphaerophoria rueppellii*. Additionally, we tested whether the aggregation pheromone of the thrips *Frankliniella occidentalis*, could disturb the oviposition behavior of the predatory hoverfly. Our results show that the presence of thrips decreases host plant and aphid performance. Furthermore, despite not affecting syrphid larval performance, thrips presence reduces fecundity of the adults that emerge from those larvae. Additionally, we observed that syrphids avoid ovipositing on plants with either thrips or thrips aggregation pheromone. The present study reveals how the presence of thrips or a semiochemical compound related to thrips, can impact the behavior and performance of an aphidophagous predator.

Keywords: dual attack, *Frankliniella occidentalis*, *Myzus persicae*, *Sphaerophoria rueppellii*, omnivore-herbivore interaction, pheromone

INTRODUCTION

In nature, plants are commonly attacked by multiple herbivorous species. Plant responses to feeding by single herbivores can impact the preference and performance of other herbivores (Stam et al., 2014; Pineda et al., 2017; Vaello et al., 2018), affecting the attractiveness and performance of natural enemies (Shiojiri et al., 2002; Ponzio et al., 2014; Stam et al., 2017). Many of multi-attack interactions include omnivorous arthropods which are capable of exploiting both plant and prey resources, ensuring their survival in the absence of one resource (Coll and Guershon, 2002). Thus, in dual attack situations, herbivores that co-exist with omnivores on the same plant compete for plant food but also have a potential risk of omnivore predation. For example, negative performance and preference where observed in the herbivore whitefly *Trialeurodes vaporariorum* (Westwood 1856) (Hemiptera: Aleyrodidae) in co-occurring system with the omnivorous thrips *Frankliniella occidentalis* Pergande 1895 (Thysanoptera; Thripidae) (Pappas et al., 2018). Moreover, these omnivore-herbivore interactions may cascade up to other trophic levels. For example, thrips control by *Amblyseius swirskii* (Athias-Henriot 1962) (Acari: Phytoseiidae) was delayed in the presence of the whitefly *T. vaporariorum*, whereas the control of this whitefly was improved in the presence of thrips (Messelink and Janssen, 2008; Messelink et al., 2010).

Most of the studies about the responses of predators to dual herbivory are mainly focused on the behavior of predatory mites (De Boer et al., 2008; Zhang et al., 2009; Lima et al., 2017) or predatory bugs (Moayeri et al., 2007), whereas predator performance, and effects of omnivorous arthropods, have received little attention so far. Predatory hoverflies (Diptera: Syrphidae) are important aphid natural enemies, which are often studied in the context of biological control (Brewer and Elliott, 2004; Pineda and Marcos-García, 2008; Almohamad et al., 2009; Amorós-Jiménez et al., 2014, 2015; Amiri-Jami et al., 2017), being commercially used as biological control agents in greenhouse crops. Gravid syrphid females, searching for plants on which they lay eggs, are able to detect and avoid potential intra- or interspecific competition (Hindayana et al., 2001; Fréchette et al., 2007; Pineda et al., 2007; Amorós-Jiménez et al., 2015). Thus, oviposition behavior is the first step in a successful biological control program, especially for natural enemies with larval stages much less mobile than the adult stage, such as the case of hoverflies. Although a previous study demonstrated syrphid's vulnerability to predation by other generalist predators (Fréchette et al., 2007), to our knowledge no information is available about syrphid behavior, under dual herbivore attack.

In sweet pepper crops, but also in many other crops worldwide, the phloem feeder aphid *Myzus persicae* (Sulzer 1776) (Hemiptera: Aphididae) and the thrips *F. occidentalis* often co-occur on a same plant (Messelink et al., 2013). Thrips usually feed on leaf tissue or plant pollen, but may also feed from eggs of predatory mites (Faraji et al., 2002; Janssen et al., 2003), eggs of spider mites (Agrawal and Klein, 2000) or crawlers of the whitefly *Trialeurodes vaporariorum* (Westwood 1856) (Hemiptera: Aleyrodidae) (van Maanen et al., 2012). Nowadays, aphids are a major problem in biological control programs on sweet pepper (Bloemhard and Ramakers, 2008), and thrips have been described to disturb and even prey on aphid predators and other natural enemies (Magalhães et al., 2005; Messelink et al., 2013). The predatory hoverfly *Sphaerophoria rueppellii* (Wiedemann 1830) (Diptera: Syrphidae) is commonly released in greenhouse crops to control, among other aphid species, the green peach aphid *M. persicae* (Amorós-Jiménez et al., 2012, 2015), however the potential disruption of syrphids through thrips presence is not known.

Thus, in this study, we investigated how the interaction between aphids and omnivorous thrips may affect different trophic levels, from plant and aphid performance to the third trophic level, assessing preference and performance of a predatory hoverfly. Previous studies have shown that dual herbivory by insects belonging to different feeding guilds can affect plant performance (Ponzio et al., 2016), and how through plant-mediated interactions, the performance of future herbivores feeding on those plants can be decreased (Erb et al., 2011; Pappas et al., 2018). Based on those studies, we hypothesize that in presence of *F. occidentalis* (omnivorous and plant cell-content feeder), sweet pepper growth and aphid (plant phloem feeder) performance will be negatively affected. Regarding the effects of thrips presence on syrphids, we expect a reduced number of eggs oviposited on plants with dual herbivory compared with only aphids presence, and associated to this, a negative syrphid performance. This hypothesis is based on previous studies where *F. occidentalis* preyed on eggs from its natural enemy *Iphiseius degenerans* (Berlese 1889) (Acari: Phytoseiidae) (Faraji et al., 2002; Janssen et al., 2003) and also where non-prey insects such as ants were able to reduce the performance and oviposition of the hoverfly *Episyrphus balteatus* (de Geer 1776) (Diptera: Syrphidae) (Amiri-Jami et al., 2017). Moreover, we expected that the aggregation pheromone of *F. occidentalis* [(R)-lavandulyl acetate: neryl (S)-2-methylbutanoate], could be used by *S. rueppellii* to discriminate between plants with or without thrips. This hypothesis is based on our previous results showing that the thrips aggregation pheromone was attractive to a thrips natural enemy, the predatory bug *Orius laevigatus* (Fieber 1860) (Hemiptera: Anthocoridae) (Vaello et al., 2017).

MATERIALS AND METHODS

Plants and Insects

The study system consisted of sweet pepper (*Capsicum annuum* L., var. California wonder), a cultivar commonly used in greenhouse crops, the aphid *M. persicae*, the omnivorous thrips *F. occidentalis,* and the hoverfly *S. rueppellii*. Sweet pepper plants were grown from seeds in plastic pots (5.5 cm in diameter, 7 cm in height) with a mix of soil and vermiculite 1:1, in a climatic chamber at 24°C, 60% relative humidity (RH) and a 16 h light and 8 h dark photo regime. Insects were reared at the CIBIO, University of Alicante, Spain. *M. persicae* was reared on *C. annuum* plants for multiple generations and *F. occidentalis* was reared on fresh green beans *Phaseolus vulgaris* L. (Fabaceae) as described by Espinosa et al. (2002), under the same conditions as above. The predator *S. rueppellii* was provided by BioNostrum Pest Control S.L. (Alicante, Spain) in three different life stages: eggs, pupae and adults (10 ± 1 day old). *S. rueppellii* was maintained as described by (Amorós-Jiménez et al., 2012).

Performance of Sweet Pepper and *Myzus persicae*

Aphid population growth was measured in the presence of single or dual herbivory. We established two treatments: (i) single herbivory: 20 sweet pepper plants (5 weeks old) were infested with 10 individuals of *M. persicae* adults (8 ± 1 days old) on the second fully expanded leaf of each plant, during 3 days (ii) dual herbivory: 20 sweet pepper plants were arranged as for the treatment of single herbivory, but 3 days before each plant was infested with 10 *F. occidentalis* larvae (2 days old) on the second fully expanded leaf of each plant, allowing the colonization and feeding on the plant. All the plants were individually enclosed in plastic cages with two windows with anti-thrips gauze to prevent the escape of insects and ensure ventilation. Twice a week, the location of the cages with plants was randomized, to minimize positional effects. After 7 days of infestation, the total number of *M. persicae* individuals was counted in both treatments. Plant height was measured before and after infestation, and above and belowground biomass was collected at the end of the experiment and oven dried (40Â°C during 5 days) before measuring dry weight.

Performance of *Sphaerophoria rueppellii*

To assess the performance of *S. rueppellii*, we used the same treatments as explained above in a new experiment. After 3 days of aphid infestation in single herbivory and dual herbivory (and after 6 days of thrips infestation in dual herbivory treatment), three *S. rueppellii* larvae (2 days old since eggs hatched) were transferred to each of the infested plants with a fine paint brush. In total 120 larvae were used (20 plants × 2 treatments × 3 larvae per plant). Larval development was monitored daily, and larval mass was recorded on the second instar (L2), third instar (L3), and pupal stage. Newly emerged adults were kept in a net cage (60 × 60 × 30 cm) separately for each treatment. Adults were provided with water, sucrose, multi-flower bee pollen, and an aphid-infested pepper plant as oviposition stimulus to allow ovaries maturation. Then 9 days old *S. rueppellii* females were allowed to lay eggs individually for 48 h in cages (60 × 60 × 30 cm) with an aphid-infested sweet pepper plant (infested with 10 individuals of *M. persicae* adults (8 ± 1 days old) on the second expanded leaf, during 3 days). The number of females used were: 21 for the treatment with aphids and 17 for the treatment with aphids and thrips. Fertility was measured by counting the number of eggs laid by females 24 and 48 h after release. A new aphid-infested plant was offered after 24 h. Fecundity was measured counting the hatched first instar (L1) larvae 2 days after syrphid oviposition. After the oviposition assay, wing length was determined for males and females separately as a surrogate for total body size in syrphids and as a good indicator for adult fitness (Stubbs and Falck, 1983; Kingsolver and Huey, 2008; Amorós-Jiménez et al., 2014). Morphological measurements were always done using the left wing, to avoid any effect due to asymmetry. We used an Image Analyzer LEIKA (M205C/DFC425, Cambridge, United Kingdom) for wing length measurements. All the bioassays were performed in climate chamber at 24°C, 60% relative humidity (RH) and a 16 h light and 8 h dark photo regime.

Oviposition Preference of *S. rueppellii*

Oviposition preference was determined in a two-choice experiment. An insect-proof cage (30 × 30 × 60 cm) was placed inside a climatic chamber. Two sweet pepper plants (5 weeks old) were placed in two different corners of the cage to test the oviposition preference for plants infested with single (aphids) or dual herbivory (aphids and thrips). Plant position was randomized for every new replicate. To study the oviposition response, a total number of 60 individuals of syrphid females (9 days old), obtained from pupae from BioNostrum Pest Control S.L., were tested. The number of eggs after 2 and 24 h were recorded individually per female syrphid. The oviposition preference bioassay was performed in climate chamber at 24°C, 60% relative humidity (RH) and a 16 h light and 8 h dark photo regime.

In a new experiment we tested the syrphid oviposition response to single herbivore (aphids) vs. a component of *F. occidentalis* aggregation pheromone (R)-lavandulyl acetate:neryl (S)-2-methylbutanoate [RLA:NMB] (Hamilton et al., 2005). RLA and NMB were synthesized according to Hamilton et al. (2005) and Zada and Harel (2004), respectively. The purity of the compounds was analyzed by gas chromatography–mass spectrometry (GC-MS) integration, and the optical purity was estimated from the corresponding specifications of the starting materials (RLA 99.2% purity, 98.7% enantiomeric excess (ee) and NMB 91.5% purity, 98.0% ee). In order to prepare the odor source, tested compounds were individually diluted (1:1, v/v) in paraffin oil (Sigma-Aldrich, USA). The ratio used in this experiment was selected according to previous results testing the attraction of the natural enemy *O. laevigatus* to *F. occidentalis* aggregation pheromone (Vaello et al., 2017). Parafilm oil (2 μl) (used as control) and 1RLA:2.3NMB blend (2 μl) were applied on a piece of filter paper (1 × 1 cm) that was placed on the second expanded leaf of the sweet pepper plant. After 15 min, the female adults were released (the filter paper was kept in the plant during all the oviposition experiment). The treatments used in this case were: (i) Aphid treatment: 10 *M. persicae* (8 ± 1 days old) were placed on the second fully expanded leaf from each sweet pepper plant, and after 3 days we added 2 μl of paraffin oil on the plant, as described above, (ii) Aphid-pheromone treatment: 10 *M. persicae* (8 ± 1 days old) were placed on the second fully expanded leaf from each sweet pepper plant, and after 3 days we added to the plant 2 μl of 1 RLA: 2.3NMB ratio from *F. occidentalis* aggregation pheromone. The oviposition cage consisted of an insect-proof cage (30 × 30 × 60 cm) which was placed in a climatic chamber. A total number of 84 syrphid female individuals (9 days old obtained from BioNostrum Pest Control S.L.) were tested in this experiment. The parameters used to study ovipositional response were: number of eggs laid at 2 and 24 h after syrphid release. The oviposition preference bioassay was performed at 24°C, 60% relative humidity (RH) and a 16 h light and 8 h dark photo regime.

Thrips Predation

To assess how herbivores can affect predator performance, potential predation on syrphid eggs by omnivore thrips was recorded in two experiments. In the first experiment we observed the predation and/or damaged eggs with a Petri dish bioassay of two treatments: (i) Aphid treatment: 10 aphids (8 ± 1 days old) were placed in a sweet pepper leaf with 10–15 syrphid eggs in a Petri dish and (ii) Aphid and thrips treatment: 10 aphids (8 ± 1 days old) and 10 second instar thrips larvae (3 ± 1 days old) were placed on a sweet pepper leaf with 10–15 syrphid eggs in a Petri dish. Syrphid eggs were obtained by confining 15–20 mature females in an insect-proof cage (30 × 30 × 60 cm) with aphid

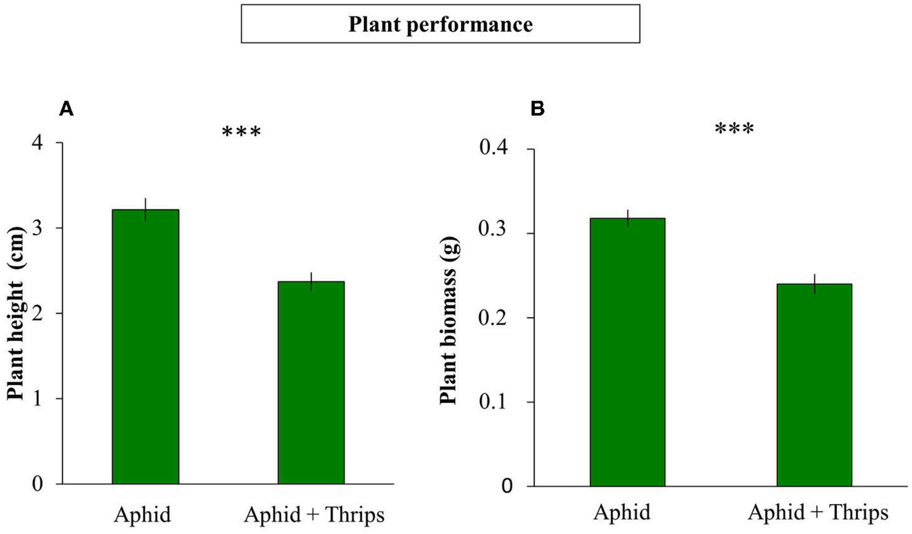

FIGURE 1 | Plant performance of 6-week-old sweet pepper after 1 week of herbivory: **(A)** plant height difference (before and after infestation with aphid vs. aphid + thrips); **(B)** total plant biomass. Bars represent means ± SE ($n = 20$ replicates). Asterisks indicate significant differences between infestation treatments: $^{***}P < 0.001$ (*t*-test).

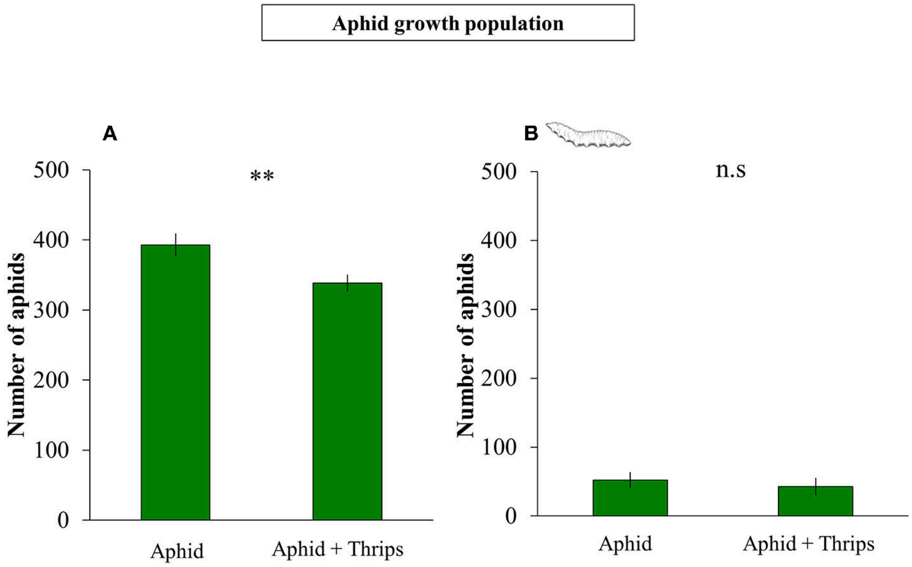

FIGURE 2 | Number of aphids on plants infested with aphid vs. aphid + thrips after: **(A)** 1 week of herbivore infestation; **(B)** development of *S. rueppellii* larvae feeding on infested plants until pupal stage. Bars represent means ± SE ($n = 20$ replicates). Asterisks indicate significant differences between infestation treatments: $^{**}P < 0.01$, n.s not significantly different ($P > 0.05$, GLM Poisson).

infested sweet pepper plants as stimulus; after 2 h we selected leaves with syrphid eggs for the experiment and aphids were removed carefully with a paint brush. After 24 h of introducing aphids and thrips in the Petri dish, eggs were observed under a binocular microscope, to record egg damage, and after 48 h, survival rate was followed in time to observe egg hatching.

A second experiment was conducted with entire sweet pepper plants (5 weeks old). Each treatment included 20 sweet pepper plants that were infested with 10 individuals of *M. persicae* adults (8 ± 1 days old) on the second fully expanded leaf of each plant for 3 days. All the plants were individually enclosed in plastic cages with two windows with anti-thrips gauze to prevent the escape of insects and ensure ventilation. Afterwards, one adult female of *S. rueppellii* was allowed to oviposit for 24 h on each plant. Eggs were counted and we left on the plant a number of 10–15 eggs (to standardize the numbers of eggs per plant).

From the results of the Petri dish experiment, we selected two treatments with different thrips life stages, with the aim to assess the effect of thrips life stage on predation behavior: (i) Larval treatment: 10 second instar thrips were transferred on the plant with a fine paint brush. (ii) Adult treatment: 10 adults (15 ± 1 days old) were released on the plant with a fine paint brush. Egg damage, hatching and larval survival at 48 h were observed. Both experiments were performed in a climate chamber at 24°C, 60% relative humidity (RH) and a 16 h light and 8 h dark photo regime.

Statistical Analyses

Plant performance (plant height and plant biomass) was analyzed with a *t*-test. Aphid density was analyzed with Generalized Linear Models (GLM) with Poisson distribution and dispersion parameter estimated. Regarding data on syrphid performance; weight and wing length measures were analyzed with *t*-test, fecundity was analyzed using a GLM with Poisson distribution and fertility with a GLM with binomial distribution. Results from the oviposition experiment were analyzed with the Wilcoxon test. All statistical tests were performed using SPSS 15.0.; SPSS Inc., Chicago, IL, USA.

RESULTS

Thrips Presence Decreases Plant Performance and Aphid Population

Plant height was measured before and after infestation, and the height between these two time points was reduced when thrips were present in the system compared to only aphids ($F_{(1,38)} = 1.325$; $P < 0.001$; **Figure 1A**). Similarly, plant biomass was lower when thrips and aphids were together on the same plant compared to aphids alone ($F_{(1,38)} = 0.312$; $P < 0.001$; **Figure 1B**). After 7 days of herbivore infestation, the population of aphids was higher in plants without thrips ($F_{(1,38)} = 7.261$; $P = 0.007$; **Figure 2A**). We also measured plant performance when *S. rueppellii* was present. The difference in plant height between single or dual herbivory in the presence of syrphid larvae was not significant ($F_{(1,38)} = 0.999$; $P = 0.166$), whereas plants had lower biomass when thrips were also present ($F_{(1,38)} = 0.346$; $P = 0.046$). The population of aphids when syrphids were present after 7 day-infestation, did not show differences between single or dual herbivory ($F_{(1,38)} = 0.339$; $P = 0.561$; **Figure 2B**).

Thrips Presence Decreases Fecundity but Not Fertility of *S. rueppellii*

S. rueppellii larval development, was not affected by the presence of thrips in our study system. Parameters such as larval and pupal biomass, adult survival and wing length were not significantly affected by single or dual herbivory (**Table 1**). However, in the adults that developed from larvae feeding on an aphid colony with thrips presence, fecundity was negatively affected by thrips, with a lower number of eggs laid by female adults, both at 24 h ($F_{(1,36)} = 11.648$; $P = 0.001$) and 48 h ($F_{(1,36)} = 15.057$; $P < 0.001$; **Figure 3A**) after female adults release. In contrast, fertility was not affected by the presence of thrips, with similar egg hatching ($F_{(1,28)} = 1.435$; $P = 0.231$; **Figure 3B**), nor was the mortality of the emerging first instar larvae (L1) ($F_{(1,28)} = 0.360$; $P = 0.549$).

TABLE 1 | Morphological traits of *S. rueppellii* when fed on *M. persicae* with and without the presence of *F. occidentalis*.

Measure	Thrips absent	Thrips present
L2 weight (mg)	1.342 ± 0.081	1.417 ± 0.160
L3 weight (mg)	11.834 ± 0.454	11.738 ± 0.303
Pupa weight (mg)	9.595 ± 0.141	10.728 ± 1.980
Wing length males (mm)	3.619 ± 0.024	3.656 ± 0.034
Wing length females (mm)	3.881 ± 0.024	3.843 ± 0.041

Measures represent means ± SE. Data here presented were not significantly different between the two treatments (t-test analyses).

Syrphid Females Avoid Ovipositing on Plants With Thrips or Their Aggregation Pheromone

The presence of *F. occidentalis* in an aphid colony did not affect the decision of *S. rueppellii* to lay their eggs in the first 2 h after syrphid release ($Z = -1.550$; $P = 0.121$). However, after 24 h, the number of eggs recorded on plants infested with aphids and thrips was less than on plants without thrips ($Z = -3.178$; $P = 0.001$; **Figure 4A**). In the second experiment where we tested the oviposition behavior in the presence of a synthetic infochemical of the thrips aggregation pheromone, we observed similar results. Females did not show significant differences selecting an oviposition place between plants with aphids vs. plants with aphids and thrips aggregation pheromone on the first 2 h ($Z = -1.299$; $P = 0.194$). However, after 24 h, the number of eggs on plants with aphids and thrips aggregation pheromone was lower than in plants with only aphids ($Z = -2.992$; $P = 0.003$; **Figure 4B**).

Thrips-Predator Interaction Does Not Affect Final Syrphid Survival

In a first Petri dish assay we tested whether thrips would damage hoverfly eggs. We observed that *F. occidentalis* second instar larvae damage syrphid eggs, causing loss of turgor on its surface ($F_{(1,58)} = 15.661$; $P < 0.001$; **Figures 5A**, **6**), although no effect on survival rate was recorded ($F_{(1,58)} = 1.964$; $P = 0.161$; **Figure 5B**). In a second experiment, we tested if the developmental stage of thrips affects differently egg damaging in an experiment with whole plants. The results showed that adult thrips caused lower syrphid egg damage than second instar thrips larvae ($F_{(1,38)} = 6.843$; $P = 0.009$; **Figure 5C**), and for the Petri dish experiment, this damage did not affect syrphid survival ($F_{(1,38)} = 0.285$; $P = 0.594$; **Figure 5D**).

DISCUSSION

The present study demonstrated that the effects of the omnivorous insect *F. occidentalis*, in dual herbivore interaction with aphids, could scale up to the third trophic level. Thrips

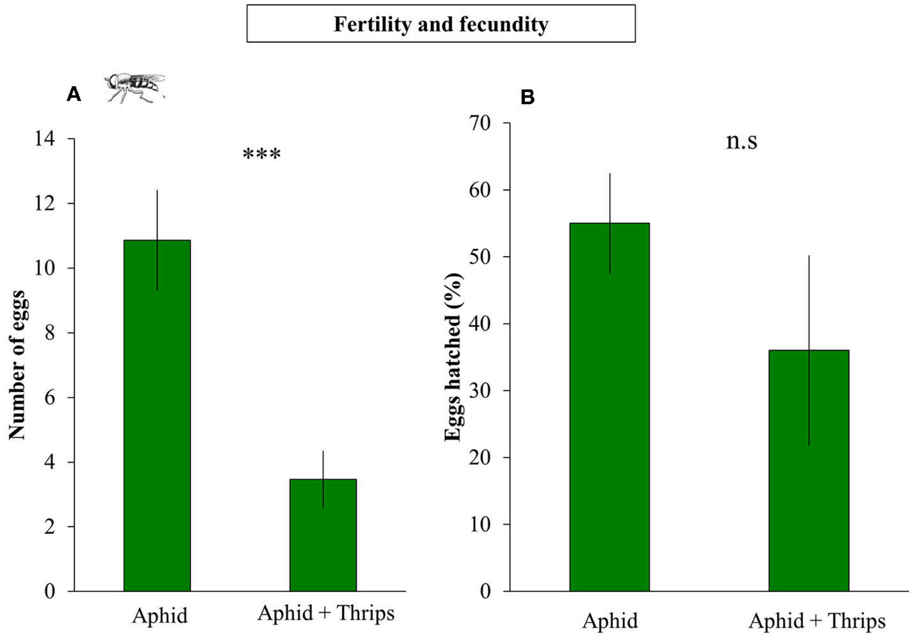

FIGURE 3 | Fecundity and fertility of *S. rueppellii* female adults after completing their life cicle feeding on aphid-infested plants ($n = 21$ replicates) and on aphid + thrips-infested plants ($n = 17$ replicates). **(A)** Number of syrphid's eggs laid (Fecundity) and **(B)** number of viable eggs hatching (Fertility). Bars represent means ± SE. Asterisks indicate significant differences between infestation treatments: $^{***}P < 0.001$, n.s not significantly different $P > 0.05$ (GLM).

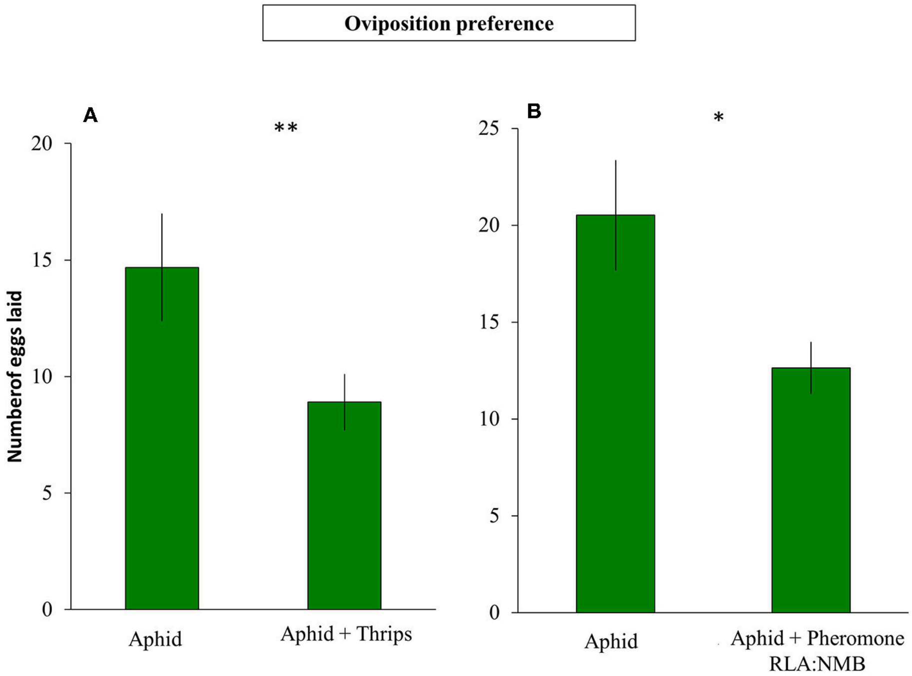

FIGURE 4 | Oviposition of *S. rueppellii* on sweet pepper plants after 24 h **(A)** Number of syrphid eggs laid on aphid vs. aphid+thrips-infested plants ($n = 60$ replicates) and **(B)** number of syrphid eggs laid on aphid-infested plants vs. aphid-infested plants plus 2 μl of 1 RLA: 2.3NMB *F. occidentalis* aggregation pheromone ($n = 42$ replicates). Bars represent means ± SE. Asterisks indicate significant differences between infestation treatments: $^{**}P \leq 0.001$, $^{*}P < 0.05$ (Wilcoxon test).

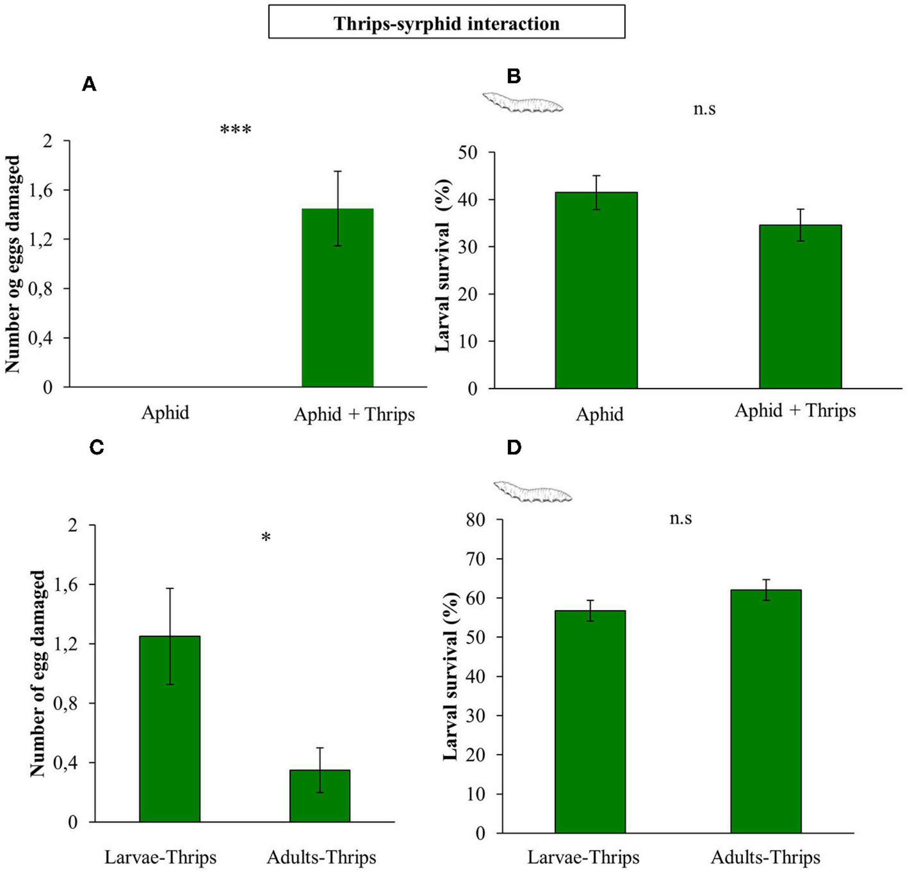

FIGURE 5 | Direct effects of the presence of thrips on syrphid performance. **(A)** *S. rueppellii* eggs damaged by prey in a Petri dish experiment; **(B)** *S. rueppellii* larval survival after prey presence in a Petri dish experiment; **(C)** *S. rueppellii* eggs damaged by larvae vs. adults thrips on entire plants and **(D)** *S. rueppellii* larval survival in the presence of second instar larvae and adults thrips on entire plants. Bars represent means ± SE ($n = 20$ replicates). Asterisks indicate significant differences between infestation treatments:$^{***}P < 0.001$, $^{*}P < 0.05$ and n.s not significant differences ($P > 0.05$, GLM).

FIGURE 6 | Egg of *S. rueppellii* damaged by a *F. occidentalis* second instar larva.

affected plant growth as well as aphid population growth but also the ovipositional preference and performance of the aphidophagous hoverfly *S. rueppellii*. We also provide the first evidence of thrips predation on syrphid eggs, although without affecting syrphid juvenile survival in our study. Moreover, we showed how specific chemical cues from the aggregation pheromone of *F. occidentalis* could disrupt syrphid ovipositional behavior.

Thrips can affect plant-mediated interactions with arthropods such as spider mites or whiteflies (Pallini et al., 1998; Agrawal et al., 1999; Pappas et al., 2018). However, although the simultaneous presence of thrips and aphids is common in many agricultural crops, few studies have focused on their interactions. Despite that in our study the number of thrips was much lower than the number of aphids (10 thrips vs. more than 300 aphids per plant), thrips presence reduced the growth of sweet pepper plants, as it has been shown for a range of vegetable crops (Welter et al., 1990; Shipp et al., 1998).This reduction in plant performance is probably due to the induction of plant defenses by thrips in early stages of plant development (5 weeks old), producing an energetic cost associated with plant defense (Agrawal, 1998). In a previous study, we showed that the performance of *F. occidentalis* on *M. persicae* pre-infested plants was enhanced (Vaello et al., 2018). In this study, we observed the opposite direction of this interaction showing a negative effect of thrips on aphids. Hence, our results show both direct effects of thrips herbivory in sweet pepper growth (with reduced host-plant quality) and indirect effects on aphid performance (with lower aphid population).

Due to these effects on aphids, we hypothesized that the performance of the predator *S. rueppellii* could be negatively influenced by thrips presence indirectly via the reduced population of prey (aphids) in the presence of thrips. Our results show that the fecundity of *S. rueppellii* was reduced, although larval development was not affected by thrips presence. This type of effects has been shown for the hoverfly *E. balteatus,* whose larval survival was not different when feeding on aphids on two different plant species, in contrast to its fecundity (Amiri-Jami et al., 2017). Similar results were found between thrips and predatory mites, where the net reproduction of *Neoseiulus californicus* (McGregor 1954) (Acari: Phytoseiidae) was reduced in the presence of thrips (Choh et al., 2017). However, the fact that in the presence of *S. rueppellii,* aphid population was not affected by the presence of thrips indicates that thrips do not interfere with the hoverfly success as biological control agent.

Moreover, in this study we also demonstrate that thrips presence can have direct effects on predators. We observed that thrips larvae could damage the surface of the chorion of syrphid eggs (**Figure 6**), without however affecting juvenile survival. The lack of effect on survival rate may be explained by the fact that the hatching rate of *S. rueppellii*'s eggs was <60 %, and probably the effect of egg damage by thrips was diluted, although we still observed a trend. Probably in natural conditions with plants experiencing higher infestation of thrips, the survival rate of syrphids would be lower. Regarding the opposite direction, although thrips are a rare prey for syrphids, a previous study already reported *Sphaerophoria quadrituberculata* Bezzi, 1915 (Diptera: Syrphidae) feeding on thrips *Cercothrips afer* Priesner, 1925 (Thysanoptera: Phlaeothripidae) (Callan, 1955). In previous assays we observed that <10% of *S. rueppellii* larvae were able to feed and complete their life cycle until adulthood, feeding exclusively on thrips (Marcos-García, pers. comm.). These findings suggest that syrphids developing in co-occurrence conditions predate preferably on aphids but they could occasionally also consume non-preferred prey such as thrips (**Figure 7**). Feeding on a non-optimal prey may decrease predator performance, as occurred with the predator *N. californicus* in the presence of thrips (Choh et al., 2017). One possibility is therefore that syrphid larvae feed with thrips to protect themselves, but this behavior needs to be further tested.

FIGURE 7 | First instar of *S. rueppellii* larva feeding on *F. occidentalis* second instar larva.

Moreover, we suggest that another direct effect of thrips on hoverflies could be related to causing stress on their larvae with a later effect on fecundity. In a recent study, the presence of ants in aphid colonies reduced the performance and oviposition of *E. balteatus* through disturbing syrphid predation or with ants preying on syrphid larvae (Amiri-Jami et al., 2017). In a similar way, here we observed reduced oviposition in aphid-infested plants with thrips presence, and a reduced performance associated to that behavior. Hoverflies show an oviposition preference for plant-aphid species combinations that maximize their performance, either avoiding heterospecific competitors (Almohamad et al., 2009), intraguild interactions (Pineda et al., 2007), or a risk to their offspring (Almohamad et al., 2009). The "intimidation" by omnivorous herbivores to predators may induce the ecology of fear (Clinchy et al., 2013), triggering stress to predators, decreasing the number of eggs laid and preventing optimal oviposition searching.

Syrphids exploit various chemical blends from plants and insects when searching for oviposition sites, such as the semiochemical (E)-β-farnesene (EβF), the main component of the alarm pheromone of most aphid species (Francis et al., 2005; Verheggen et al., 2008). However, limited information exists about syrphids response to semiochemicals from non-preferred prey. Our results show that the aggregation pheromone of *F. occidentalis* leads to oviposition avoidance by *S. rueppellii*, indicating that predators are able not only to rely on semiochemicals from a non-preferred prey, but also using it to distinguish unsuitable oviposition places. Although not evaluated in the current study, one possibility is that syrphid females retain their eggs in the absence of suitable oviposition sites, as occurred for *Eupeodes corollae* (Fabricius. 1794) (Diptera: Syrphidae) in the absence of aphids (Almohamad et al., 2009). In contrast, the predatory bug *O. laevigatus*, a natural enemy of *F. occidentalis,* responded positively to the aggregation pheromone of its prey (Vaello et al., 2017). Thus, the aggregation pheromone RLA:NMB seems to act both as an attractant for a thrips predator such as *O. laevigatus* and as repellent for *S. rueppellii*. Moreover, the fact that *S. rueppellii* prefers to oviposit on plants without thrips, could be due to the detection of fewer aphids in colonies with thrips presence as we observed. Further possibilities to be tested are whether *S. rueppellii* avoids competition or intraguild predation with other predators with this behavior (such as *O. laevigatus*), or how the presence of thrips may alter the volatile blend produced by plants infested with aphids, affecting in the end the oviposition behavior of syrphids.

In conclusion, this study shows that although the presence of omnivorous insects can affect three trophic levels, the efficiency of the biological control may not be compromised, as was shown for *S. rueppellii* that controlled the aphid population in both the presence and the absence of thrips. This study also raised awareness about how an aggregation insect pheromone may act as a repellent for natural enemies. Hence, in a biological control context, it is crucial to analyse the effect of co-occurring pest species interactions to predict the effectiveness of natural enemies, especially for oviposition site selection and subsequent predator performance.

AUTHOR CONTRIBUTIONS

TV, AP, and MÁM-G conceived and designed the research. TV conducted the experiments. TV and AP analyzed the data. TV, AP, and MÁM-G interpreted the results and wrote the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Tomato Inoculation With a Non-pathogenic Strain of *Fusarium oxysporum* Enhances Pest Control by Changing the Feeding Preference of an Omnivorous Predator

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Mirid predators, a special group of plant-feeding omnivorous predators, have become important biological control agents for pest control in greenhouse cropping systems. Their efficacy and behavior may potentially be affected by microorganisms that induce plant defenses or change plant quality. Here we studied the interaction between a root restricted endophytic non-pathogenic strain of *Fusarium oxysporum* (Fo162) in tomato plants, the greenhouse whitefly *Trialeurodes vaporariorum* (Westwood) and the plant-feeding mirid predator *Macrolophus pygmaeus* (Rambur). In the absence of prey, inoculation of tomato plants with the Fo162 endophyte significantly reduced the reproduction of *M. pygmaeus* compared to plants without the endophyte. In contrast, the population growth of *M. pygmaeus* was not affected by the Fo162 endophyte in the presence of whiteflies. Moreover, the combination of the predator and endophyte resulted in lower whitefly densities than the predator alone. Whitefly population development was not different between endophyte-inoculated and untreated plants. Thus, endophyte inoculation of tomato plants seems to shift the feeding preference of this omnivorous predator from plant consumption toward relatively more prey consumption, resulting in enhanced suppression of the herbivore. Moreover, the negative effect of the endophyte on *M. pygmaeus* reproduction could easily be eliminated by providing decapsulated cysts of *Artemia franciscana* Kellogg as a supplemental food source. Together, this suggests an overall net positive effect of the Fo162 endophyte on a preventive biological control strategy in tomato using *M. pygmaeus*. Besides the enhanced whitefly control, endophyte-inoculation of tomato plants both with or without the predator also resulted in a higher yield and a reduced number of fruits with blossom-end rot, a disorder caused by limitations in uptake and transport of calcium to the fruits. This suggests that the Fo162 endophyte is also involved in the acquisition of essential nutrients for the benefit for the plant. Since both the Fo162 endophyte and the predator *M. pygmaeus* can

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induce plant defense, further studies need to elucidate the exact mechanisms that occur when both organisms are present. Our findings confirm the importance of studying endophytes and induced plant responses in a multi-trophic context with herbivores and their natural enemies.

Keywords: biological control, endophytic fungi, multitrophic interactions, *Macrolophus pygmaeus*, *Trialeurodes vaporariorum*

INTRODUCTION

Plant-feeding generalist predators, a specific group of true omnivores, have become important biological control agents in various cropping systems (Coll and Guershon, 2002; Dumont et al., 2018) and particularly in greenhouse crops (Messelink et al., 2012). Plant-feeding generalist predators of the family Miridae, also called zoophytophagous predators, are among the most important predatory bugs used for biocontrol. This family includes well-known species such as *Macrolophus pygmaeus* (Rambur), *Nesidiocoris tenuis* (Reuter), *Dicyphus errans*, and *Dicyphus hesperus* (Sanchez and Cassis, 2018). They perform well on plants with high trichome densities like tomato and eggplant and have become very successful for two reasons. The first reason is their ability to predate on several important pest species such as whiteflies (Montserrat et al., 2000), aphids (Alvarado et al., 1997), spider mites (Hansen et al., 1999), leaf miners (Arnó et al., 2003) and Lepidopterans, including the important South American moth *Tuta absoluta* (Urbaneja et al., 2009; Ingegno et al., 2013, 2019). The second reason is their capacity to persist in crops prior to pest invasions by feeding on alternative food and plant resources (Perdikis et al., 2011; Messelink et al., 2014). Preventive releases or "crop inoculations" with generalist omnivorous predators have proven to be very effective for controlling pests that infest crops later in the growing season (Calvo et al., 2012; Messelink et al., 2015). Interestingly, the plant-feeding behavior of mirid predators can also induce plant defense responses by activating the jasmonic acid (JA) signaling pathways (Pappas et al., 2015; Perez-Hedo et al., 2015; Zhang et al., 2018b). Previous exposure of tomato plants to *M. pygmaeus* caused an increase in mortality and decrease of egg production of the two-spotted spider mite *Tetranychus urticae* Koch (Pappas et al., 2015). Similarly, in sweet pepper plants, previous feeding by these mirid bugs reduced the reproduction of both western flower thrips *Frankliniella occidentalis* (Pergande) and *T. urticae* (Zhang et al., 2018b). Moreover, activation of the JA pathway by mirid predators has been shown to attract the whitefly parasitoid *Encarsia formosa* (Gahan) and repel some pest species in tomato and sweet pepper plants (Perez-Hedo et al., 2015; Bouagga et al., 2017; Zhang et al., 2018a).

Induced plant responses or plant quality can also influence the feeding behavior of omnivores themselves. Induced plant responses caused a shift in the feeding preferences of the omnivorous thrips *F. occidentalis* from plant feeding to prey feeding (spider mite eggs) (Agrawal et al., 1999). Studies with host plants from different quality confirmed that low host plant quality increases prey consumption of this omnivore (Magalhães et al., 2005).

A perhaps largely overlooked factor by which plant-feeding predators can be influenced is the effect of microorganisms proliferating inside plants on induced plant defenses and plant quality (Schouten, 2016; Van Overbeek and Saikkonen, 2016). Fungal and bacterial species that are capable of colonizing the root cortex and/or other plant tissues without provoking visual disease symptoms are generally referred to as endophytes (Wilson, 1995). Such endophytes often have beneficial effects on plant performance (Clay and Schardl, 2002; Waller et al., 2005; Rodriguez et al., 2009; Schouten, 2016). Besides increasing nutrient uptake, endophytes may enhance resistance against plant pathogens and herbivores through changes in defensive chemistry (Alabouvette et al., 1993; Vidal, 1996; Backman and Sikora, 2008; Vega et al., 2009; Schouten, 2016). However, these endophyte-generated effects on herbivores can be versatile, depending on plant species, endophytic strain, and the feeding-mode and degree of specialism of the herbivore (Hartley and Gange, 2009).

Besides the herbivores themselves also their natural enemies can be affected by endophytes, and this has been reported for both parasitoids and predators (Omacini et al., 2001; Bultman et al., 2009; Hartley and Gange, 2009; Saari et al., 2014; Garantonakis et al., 2018; Pappas et al., 2018). Plant-mediated effects of endophytes on natural enemies may increase in complexity when the natural enemies are plant-feeding. To date, it is not known if and how endophytes can affect such multitrophic food-web interactions between plants, herbivores and plant-feeding natural enemies. Here we studied how the presence of a root-restricted non-pathogenic endophytic strain of *Fusarium oxysporum* in tomato plants affects the performance of the greenhouse whitefly *Trialeurodes vaporariorum* (Westwood) and its control by the plant-feeding mirid predator *M. pygmaeus*. When inducing plant defense responses or altering plant quality, the endophyte may directly affect the survival and/or reproduction of whiteflies and mirid predators. Moreover, the endophyte may indirectly affect whitefly densities by changing the feeding behavior of the plant-feeding predator. The results of our study may be interesting for both understanding endophyte-mediated multitrophic interactions and for further developing biological pest control strategies.

MATERIALS AND METHODS

Plants, Insects, and Endophyte

All tomato plants (*Lycopersicum esculentum* L. cv. Capricia, Rijk Zwaan, The Netherlands) for the greenhouse trials were grown in rockwool blocks in a greenhouse compartment with an average temperature of 20°C and a relative humidity of

70%. The predator *M. pygmaeus* was obtained from Koppert Biological Systems (Berkel & Rodenrijs, The Netherlands) and reared for one generation on tomato plants (cv. Capricia) supplemented with frozen eggs of the flour moth *Ephestia kuehniella* Zeller. The greenhouse whitefly, *T. vaporariorum* was reared on tomato plants (cv. Capricia) in small greenhouse compartments. The fungal endophyte used in this study was the non-pathogenic strain Fo162 of *Fusarium oxysporum*, which was isolated from the cortical tissue of surface-sterilized tomato roots from Kenya (Hallmann and Sikora, 1994). This strain is known to induce plant defense responses in tomato (Bogner et al., 2017) and previous studies have shown effects on phloem feeding insects (Martinuz et al., 2012; Menjivar et al., 2012). Endophyte inoculum was produced on solid potato dextrose agar (PDA) in petri dishes.

Population Dynamics and Tomato Yield

The effect of the endophyte Fo162 on greenhouse whitefly population dynamics was tested both in the presence and in the absence of the predator *M. pygmaeus* in a greenhouse trial on tomato plants. The four treatment combinations [(1) untreated, (2) the endophyte, (3) the predator, and (4) the endophyte + predator] were organized in a randomized complete block design with 5 replicates: Twenty plants of 6 weeks old were placed individually in cylindrical insect cages (1.6 m diameter, 3 m high) made of fine insect gauze (mesh size 0.22 × 0.31 mm) in a greenhouse compartment of 98 m^2 at the Institute of Wageningen University & Research, BU Greenhouse Horticulture in Bleiswijk, the Netherlands. Each plant was placed on a 1 m rockwool slab and supplied with nutrients through drip irrigation without recirculation in order to prevent contamination with endophyte spores among treatments. The nutrient solution was specifically developed for tomato (Sonneveld and Voogt, 2009), which was composed by the following recipe: macronutrient (mM): [Ca(NO3)2.4H2O.0.2NH4NO3] (5.4); KNO3 (6.0) KH2PO4.2H2O (1.5); K2SO4 (2.0); MgSO4.7H2O (2.4); CaCl2.2H2O (1.5); and micronutrients (μM): H3BO3 (25); MnSO4.4H2O (15); ZnSO4.7H2O (5); CuSO4.5H2O (1.5); NaMoO4.2H2O (1.5); and FeDTPA (30). Plants were grown according to standard cultivation methods: each plant was allowed to grow up along a rope attached to the top of the cage (3 m high), which was extended as soon as the plants reached the top of the rope. The plants were subsequently rotated when this stage was reached and the lower leaves were picked to fit the plant in the cage. Picked leaves were left in the cages to allow the remaining predators and whiteflies to move back to the plant. Half of the treatments were inoculated with the endophyte by pipetting 10^6 spores (harvested from a culture on PDA and solved in 3 ml of water) near the roots in the rockwool blocks right after planting the tomato plants. This procedure was repeated after one week. Five days after the second endophyte application, 6 female and 6 male predatory bugs were introduced per cage in 2 of the 4 treatments. Two weeks after the second endophyte inoculation twenty female whiteflies of mixed age were released per cage in all treatments. Densities of whitefly eggs, larvae and pupae were assessed at 2, 5, 8, and 11 weeks, and predators at 3, 6, 9, and 12 weeks, after their release respectively. Cages were entered through a zip opening and closed again before assessing the plants. Numbers of predators (nymphs and adults) were counted on the whole plant while carefully turning leaves and disturbing the predators as less as possible. The densities of whitefly juveniles were assessed by picking each time 6 terminal leaflets per plant: 3 from the bottom and 3 from the top, and counting all eggs, larvae and pupae under a binocular microscope. Prior to removing the leaves from the cage, adult whiteflies, as well as all *M. pygmaeus* nymphs and adults, were shaken from the leaves. Tomato fruits were harvested when they were ripe and the number of fruits were counted each time after harvesting. The first tomatoes were ripening 9 weeks after planting. Fruit weight was not measured, but the harvested tomatoes were in general similar sized which makes it plausible to use the number of tomatoes as approximation for the yield. Some of the fruits showed dark rotting spots at the bottom, also referred to as blossom-end rot, which is a physiological disorder caused by a calcium imbalance within the plant (Ho et al., 1993). The number of tomatoes affected by blossom-end rot were counted separately from “healthy” tomatoes. Temperature and relative humidity were registered every 5 min throughout the experiment with a climate recorder (Hoogendoorn Growth Management) inside one of the cages. The experiment was conducted in March-June, and during that period the average daily temperature and relative humidity in the cages was 20.0°C (range 18.2–21.7°C) and 62% (range 47–77%), respectively. Plants were grown under natural light conditions.

Predator Survival and Reproduction

A separate greenhouse experiment was set-up to assess effects of the endophyte Fo162 on the survival and reproduction of *M. pygmaeus* on plants in the absence of prey. Moreover, it was tested whether potential negative effects of the endophyte can be compensated with supplemental food consisting of decapsulated cysts of *Artemia franciscana* Kellogg (obtained from Smulders wholesale, Artemia quick HS aqua, Ulestraten, The Netherlands). These decapsulated cysts are known to be a good alternative food source for *M. pygmaeus* (Vandekerkhove et al., 2009). All four combinations of endophyte and alternative food were tested in a two-factorial randomized complete block design containing 5 replicates. Five-week old tomato plants (cv. Capricia) were placed individually in insect cages (60*60*90 cm, mesh size 0.5 mm) in a greenhouse compartment similar to the one used in the previous experiment. Nutrients were supplied through drip irrigation without recirculation in order to prevent contamination with endophyte spores among treatments. Fertilization was similar to the previous experiment. Also endophyte inoculation was performed in the same way as in the population dynamic experiment. One week after the second endophyte inoculation, twelve couples of 1-week-old *M. pygmaeus* males and females were introduced in each cage. The supplemental food was added weekly by dusting 0.5 g of *A. franciscana* cysts with a brush over the entire plant. Twenty-five days after their release, all juvenile and adult predators present on each plant were collected with an aspirator, counted and stored in 70% ethanol. Subsequently, the number of nymphs were counted separately per stage in the laboratory under a binocular microscope (40x) after putting the individuals on a white filter paper. Temperature and relative humidity in the greenhouse compartment were recorded every 5 min throughout the experiment with the same climate recorder as the one used in the population dynamic experiment. The experiment was conducted in September-October and the average daily temperature and relative humidity in the greenhouse during the presence of the predators was 19.4°C (range 18.5–21.2°C) and 74% (range 69–79%), respectively. Natural light was supplemented with 9000 lux artificial light for 2 hours per day during the last 4 weeks of the trial. Artificial lights were also switched on during the day when the natural light intensity was below 300 Watt.

Statistical Analyses

All whitefly and predator density data in the population dynamic trial were log (+1) transformed to adjust the data for homogeneity of variance and normality, followed by a repeated measures ANOVA, with predator and endophyte presence as factors. Differences among treatments were analyzed by Fisher's Least Significant Difference (LSD) *post hoc* tests ($p < 0.05$). Differences among treatments in the total number of produced tomato fruits per plant and the percentage of tomato fruit with blossom-end rot was analyzed with a two-way ANOVA with predator and endophyte as factors. Fruit numbers were log (+1) transformed and fractions of fruit with blossom-end rot arcsine transformed prior to this analyses to meet the requirements for a normal distribution of the data, followed by Fisher's LSD *post hoc* tests ($p < 0.05$). A two-way ANOVA was also used to analyse the data of the predator survival and reproduction trial, with endophyte and supplemental food application as the two factors. Because a faster juvenile development would result in a larger proportion of the older nymphal stages, we also looked at differences in the proportion of third nymphal stages among treatments (the oldest nymphal stage found after 25 days). The proportion of surviving adults and third nymphal stages were arcsin transformed and the total number of offspring were log transformed to get a normal distribution of the data prior the ANOVA analyses, followed by Fisher's LSD *post hoc* tests ($p < 0.05$). All statistical analyses were performed using the statistical package GenStat, Release 19.1.

RESULTS

Population Dynamics and Tomato Yield

We found a significant interaction effect between the endophyte and the *M. pygmaeus* treatment on the number of whiteflies over time [$F_{(1,16)} = 4.68$, $p = 0.046$]. The factor predator alone was statistically significant [$F_{(1,16)} = 182.49$, $p < 0.001$], whereas the factor endophyte alone was not significant [$F_{(1,16)} = 1.4$, $p = 0.255$]. The endophyte treatments had no significant effect on whitefly population development, but combining the two factors enhanced control of whiteflies significantly compared to the treatment with predators alone (**Figure 1A**). In other words, the endophyte showed an effect on whiteflies only in the presence of predators. Overall predator densities were not significantly different on plants inoculated with the endophyte compared to untreated plants [$F_{(1,8)} = 1.29$, $p = 0.289$, **Figure 1B**]. The factor predator did not have a significant effect on both the total number of produced tomato fruits per plant [$F_{(1,16)} = 1.19$, $p = 0.292$] and the number of fruits with blossom-end rot [$F_{(1,16)} = 0.05$ $p = 0.825$], neither was the interaction with the endophyte factor significant. After removing the predator factor from the model, the factor endophyte did show a significant effect on both the total number of produced tomato fruits per plant [$F_{(1,18)} = 4.95$, $p = 0.039$] and the number of fruits with blossom-end rot [$F_{(1,18)} = 4.54$, $p = 0.047$]. There were no differences among treatments in the appearance of the first ripe fruits, so this was not further analyzed. Plants treated with the Fo162 endophyte gave a significant higher yield (numbers of fruit) and the tomato fruits were less affected by blossom-end rot (**Figures 2A,B**).

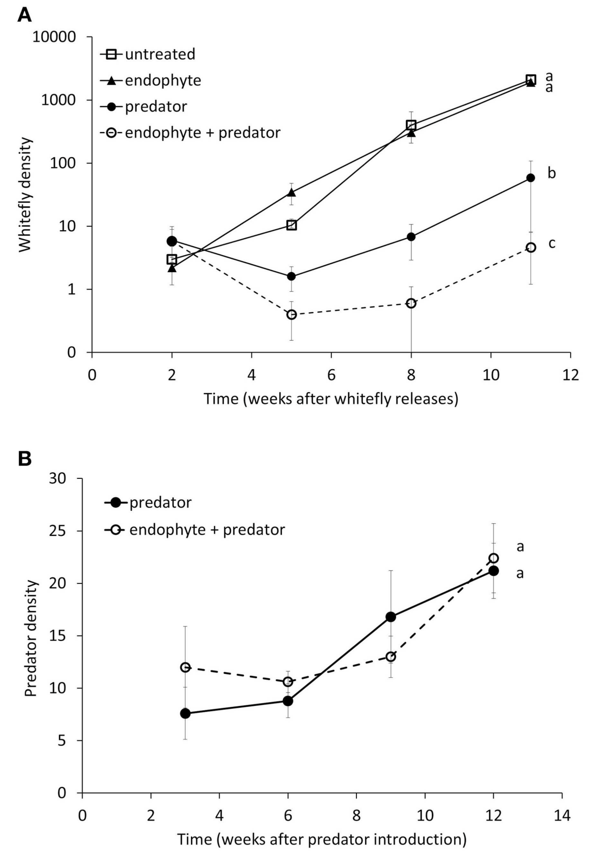

FIGURE 1 | Population dynamics of **(A)** the greenhouse whitefly *Trialeurodes vaporariorum* and **(B)** the predator *Macrolophus pygmaeus* on tomato plants treated with the endophyte Fo162, the predator *M. pygmaeus*, both, or none of them (untreated). Predators were added 1 week and the endophyte inoculations were done 2 and 3 weeks prior to the whitefly release, respectively. Data shown are the mean (± SE) (Log) densities of juvenile whiteflies per 6 leaflets and predator densities per plant. Different letters next to the curves indicate overall significant differences among treatments (Fisher's LSD-tests, $p < 0.05$).

Predator Survival and Reproduction

The survival of *M. pygmaeus* adults 25 days after their release on plants was not significantly affected by the factor

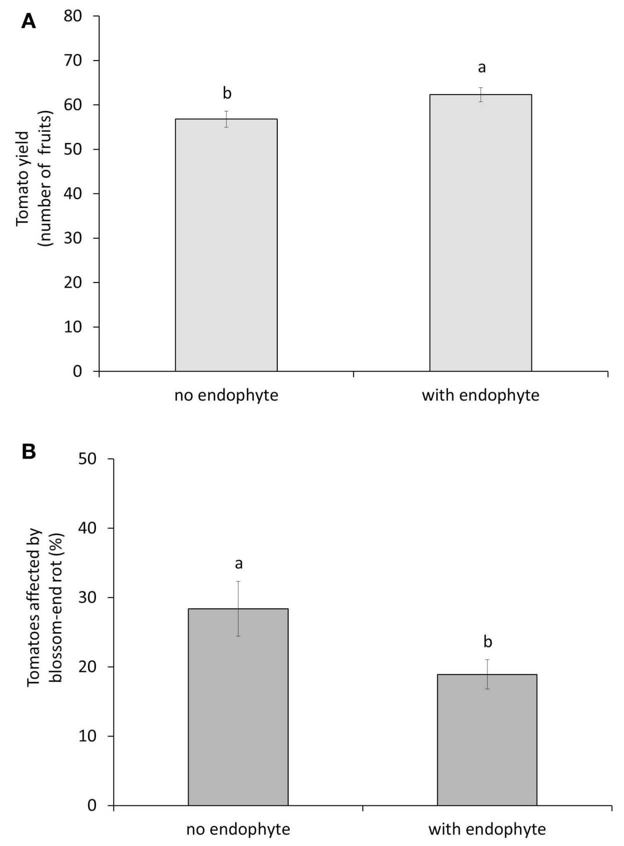

FIGURE 2 | Total number (±SE) of fruits **(A)** and the percentage (±SE) of these fruits with blossom-end rot **(B)** from tomato plants without or with inoculation of the endophyte Fo162. Different letters above bars indicate significant differences between treatments (ANOVA, $p < 0.05$).

endophyte [$F_{(1,16)} = 0.3$, $p = 0.593$], nor was the interaction between supplemental food application and endophyte treatment significant [$F_{(1,16)} = 3.15$, $p = 0.095$]. In contrast, the application of supplemental food increased survival significantly [$F_{(1,16)} = 26.11$, $p < 0.001$, **Figure 3A**]. The total number of offspring was significantly affected by the interaction of the factors endophyte and supplemental food [$F_{(1,16)} = 10.08$, $p = 0.006$]. In the absence of supplemental food, the endophyte reduced the predator's offspring, but this negative effect of the endophyte completely disappeared when Artemia was provided as supplemental food source (**Figure 3B**). The juvenile stages present at the day of assessment all belonged to the first, second and third nymphal stage (**Figure 3B**). The application of supplemental food also enhanced juvenile developmental time, since a significantly larger proportion of third nymphal stages were present in these treatments than in the treatments without food [$F_{(1,16)} = 9.71$, $p = 0.007$]. Juvenile developmental time, reflected by the proportion of third nymphal stages, was not affected by the factor endophyte [$F_{(1,16)} = 2.2$, $p = 0.157$], nor was the interaction between the factors endophyte and food significant [$F_{(1,16)} = 0$, $p = 0.974$].

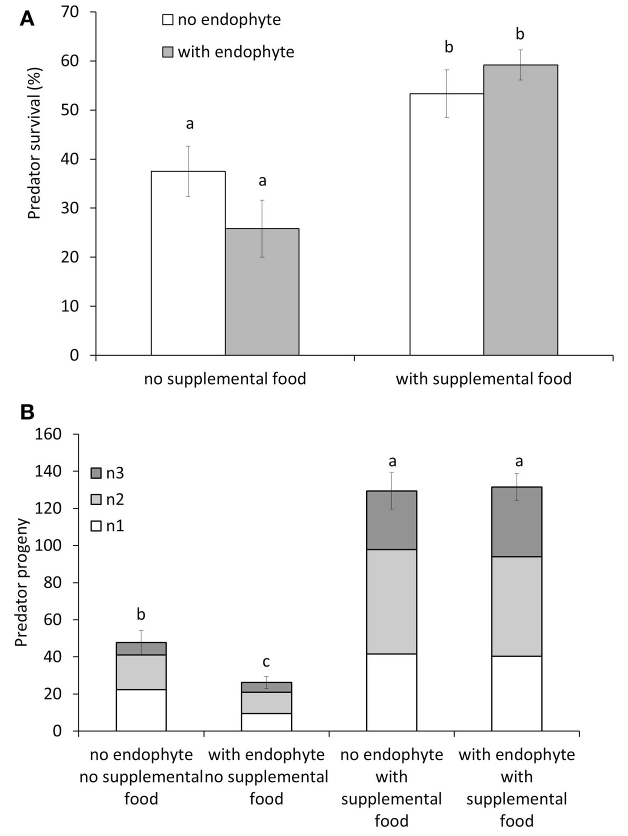

FIGURE 3 | Survival **(A)** and reproduction **(B)** of the predator *Macrolophus pygmaeus* on tomato plants treated with the endophyte Fo162, the supplemental food source *Artemia franciscana* or a combination of both compared to untreated plants. Shown is the mean (±SE) percentage of survival of 24 released adult predators 2 weeks after their introduction **(A)** and the mean (±SE) total number of first, second and third nymphal stages (n1, n2, n3) produced **(B)**. Different letters above bars indicate significant differences among treatments (Fisher's LSD-tests, $p < 0.05$).

DISCUSSION

Here we show for the first time that plants inoculated with a root-associated endophyte can shift the feeding preference of an omnivorous predator from plant feeding toward relatively more prey consumption, resulting in enhanced suppression of the herbivore. The presence of the endophyte Fo162 can thus further improve the whitefly control efficacy of the already rather effective predation by *M. pygmaeus*. This enhanced control is remarkable, because reproduction of the predator was significantly reduced on endophyte treated plants without prey or supplemental food, and we also observed a clear trend (although statistically not significant) of lower adult survival on endophyte-treated plants compared to untreated plants. Thus, this negative effect of the endophyte on predator reproduction shifted to a positive effect in terms of pest control, because of the predator's flexible feeding behavior. In the presence of whiteflies, the predator population remained unaffected by the endophyte. Providing Artemia cysts as a supplemental food source also eliminated the negative effect of the endophyte on predator survival and reproduction. Hence, providing these supplemental food sources could be used to increase predator populations in the absence of pests on endophyte inoculated plants. Plant feeding by *M. pygmaeus* was probably not completely abandoned on endophyte-treated plants because of the considerable amount of water they need for their extra-oral digestion when feeding on prey (Casta et al., 2011). Moreover, the predator *M. pygmaeus* is known to develop and reproduce on plants even without prey (Lykouressis et al., 2008), suggesting that plant nutrients form an important part of their diet (Portillo et al., 2012). It has been shown before that reduced host plant quality can induce a feeding shift of omnivores (Agrawal et al., 1999; Magalhães et al., 2005), but that such a shift from plant to prey feeding can be mediated by an endophyte was unknown.

An unexpected additional positive effect of the endophyte in this study was the reduction we observed in the number of fruits with blossom–end rot in endophyte-treated plants compared to plants without endophyte inoculation. Blossom-end rot is a disorder caused by limitations in uptake and transport of calcium to the fruits (Ho et al., 1993). The endophyte Fo162 apparently enhanced the uptake of essential nutrients, including calcium, which reduced the number of fruits with disorders. Moreover, the endophyte also increased the total number of produced fruits during the experimental time. This all indicates that the Fo162 *F. oxysporum* strain can be beneficial for the tomato plants in several ways, similar to what was observed for the Fo162-Arabidopsis interaction (Martinuz et al., 2015). It is generally accepted that, although many strains of *F. oxysporum* are notorious for being pathogenic (Gordon and Martyn, 1997), non-pathogenic *F. oxysporum* strains can be beneficial for plants by suppressing Fusarium wilt disease (Ogawa and Komada, 1985; Postma and Rattink, 1992) and nematode infestations (Martinuz et al., 2013; Schouten, 2016). Overall, Fo162 not only positively affected the whitefly control by a plant-feeding predator, but also reduced blossom-end rot and increased yield.

As omnivorous predators also use plant nutrients for their development (Portillo et al., 2012), it may have seemed logical to expect a positive effect of endophyte-facilitated nutrient acquisition on the survival and reproduction of *M. pygmaeus* due to the expected better nutritional value of the plants. In fact, this has also been shown for studies with other root-colonizing fungi: tomato plants colonized by *Trichoderma longibrachiatum* promoted population growth of *M. pygmaeus* and were more attractive for these predators (Battaglia et al., 2013) and similar results were found for the arbuscular mycorrhizal fungus *Rhizophagus irregularis* (Prieto et al., 2017). Yet, in our study we found a negative effect of the endophyte on the reproduction of *M. pygmaeus*, and a positive effect on fruit quality and yield, indicating that other mechanisms than changes in nutritional value of the plant are involved as well. Other studies with the Fo162 endophyte showed this fungus may both induce plant defense responses and release various secondary metabolites by itself (Bogner et al., 2017), including indole acetic acid and 4-hydroxybenzoic acid, which may directly or indirectly have affected the survival, reproduction and feeding behavior of *M. pygmaeus*, similar to what was found for sedetary plant parasitic nematodes (Martinuz et al., 2013; Le et al., 2016).

In this study, we were not able to detect any effect of the endophyte on the whitefly population growth, whereas Menjivar et al. (2012) showed that the Fo162 endophyte negatively affected the feeding preferences of greenhouse whiteflies. This endophyte may be able to induce plant volatiles that influence the plant preference of whiteflies, but this study shows that it does not affect reproduction of whiteflies in a situation where the whiteflies were forced to feed on endophyte treated plants. These results suggest that due to being an obligate herbivore, whitefly may have adapted to certain levels of plant defenses in the course of co-evolution, e.g., by tolerating or degrading toxic secondary plant metabolites. Since *M. pygmaeus* is a zoophytophagus predatory bug, such selection pressure might be less pronounced or even absent in this species. At the same time, however, specialist natural enemies, like aphid parasitoids, can also experience a negative effect of endophytes through their host (Omacini et al., 2001). In general it has been observed that pests can adapt to plant defense responses, whereas their natural enemies still encounter negative effects (Ode, 2006). Another possible reason for the difference in endophyte effects on whiteflies and plant-feeding predators is their completely different mode of plant feeding. Whiteflies rarely damage mesophyll cells in their search for phloem sieve elements, thus remaining unaffected by defensive secondary metabolites stored in mesophyll cells (Walling, 2008). Omnivorous predatory bugs, however, use their stylets to lacerate the mesophyll cells, solubilizing cell contents and consuming the cellular slurry (Wheeler, 2001), and are therefore probably more exposed to the endophyte-induced plant defensive compounds. In addition to the endophyte induced plant defenses, the omnivorous predator may also induce defenses (Pappas et al., 2015). However, previous studies showed that the JA-signaling pathway induced by *M. pygmaeus* did not affect whitefly and aphid phloem feeders (Pappas et al., 2015; Zhang et al., 2018b). Thus, a synergistic effect of the predator induced and endophyte-induced plant defenses on whiteflies is not likely. However, how those two defense inducers interact is not known and deserves further studies.

Plant feeding by mirid predators can not only induce plant defenses, but in some cases also cause considerable plant damage (Casta et al., 2011; Puentes et al., 2018). Although *M. pygmaeus* is in general considered as a safe predator, it can cause serious plant damage at high predator levels and low prey densities (Sanchez et al., 2018). Greenhouse observations indicate this damage may even increase when plant are infected by the Pepino Mosaic Virus (Moerkens et al., 2016). More serious plant damage can be caused by the related omnivorous predator *N. tenuis* (Arnó et al., 2010), making this predator a controversial biological control agent (Pérez-Hedo and Urbaneja, 2016). The results of our study suggest that plant feeding by omnivorous predators can be reduced by endophytes, which may potentially also reduce crop damage caused by the predator's plant feeding. Indeed, another non-pathogenic Fusarium strain [*Fusarium solani* strain K (FsK)] was shown to reduce feeding damage by *N. tenuis* in young tomato plants (Garantonakis et al., 2018). Hence, this reduction of plant feeding damage by omnivorous predators might be another benefit of inoculating plants with fungal endophytes. In addition, a recent study by Pappas et al. (2018) showed increased attraction of *M. pygmaeus* to tomato plants that were colonized by this same endophyte (FsK), even in the absence of prey. This attraction to pest-free plants that are colonized by endophytes might result in an additional negative effect on *M. pygmaeus* reproduction. However, any negative effects of endophytes on population growth of omnivorous predators can probably be eliminated rather easily by providing supplemental food sources, as was shown in our study.

Overall, this work shows that the trophic level, on which an omnivorous predator operates can be influenced by a fungal endophyte. Our findings confirm the importance of studying endophytes and induced plant responses in a multi-trophic context with herbivores and their natural enemies, as unexpected interactions may occur (Bezemer et al., 2005; Kaplan and Thaler, 2011). Moreover, it confirms the importance of studying the impact of below-aboveground interactions on predator-pest interactions (Hooper et al., 2000; Van Der Putten et al., 2001, 2009; Wardle et al., 2004), even in simplified ecosystems as described by us. Changing plant quality by endophytes may also be a useful tool for enhancing biological pest control with omnivorous predators and reducing plant damage caused by omnivorous plant feeding.

DATA AVAILABILITY

The datasets generated for this study are available on request to the corresponding author.

AUTHOR CONTRIBUTIONS

GM, JE, and AS designed the study. GM, JE, and RvH-S conducted the greenhouse trials. GM and HK analyzed the data. JE, HK, AS, and GM wrote the paper.

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